

An explanation for conflicting records of Triassic–Jurassic plant diversity

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Macrofossils (mostly leaves) and sporomorphs (pollen and spores) preserve conflicting records of plant biodiversity during the end-Permian (P-Tr), Triassic–Jurassic (Tr-J), and end-Cretaceous (K-T) mass extinctions. Estimates of diversity loss based on macrofossils are typically much higher than estimates of diversity loss based on sporomorphs. Macrofossils from the Tr-J of East Greenland indicate that standing species richness declined by as much as 85% in the Late Triassic, whereas sporomorph records from the same region, and from elsewhere in Europe, reveal little evidence of such catastrophic diversity loss. To understand this major discrepancy, we have used a new high-resolution dataset of sporomorph assemblages from Astartekløft, East Greenland, to directly compare the macrofossil and sporomorph records of Tr-J plant biodiversity. Our results show that sporomorph assemblages from the Tr-J boundary interval are 10–12% less taxonomically diverse than sporomorph assemblages from the Late Triassic, and that vegetation composition changed rapidly in the boundary interval as a result of emigration and/or extirpation of taxa rather than immigration and/or origination of taxa. An analysis of the representation of different plant groups in the macrofossil and sporomorph records at Astartekløft reveals that reproductively specialized plants, including cycads, bennettites and the seed-fern *Lepidopteris* are almost absent from the sporomorph record. These results provide a means of reconciling the macrofossil and sporomorph records of Tr-J vegetation change, and may help to understand vegetation change during the P-Tr and K-T mass extinctions and around the Paleocene–Eocene Thermal Maximum.

extinction | palaeobotany | palynology | taphonomy | Triassic–Jurassic

Compilations of stratigraphic ranges of land plants through geological time do not show abrupt declines in taxonomic diversity (1–3). This contrasts sharply with the history of animal life, which is marked by five geologically rapid decreases in global taxonomic diversity, known as mass extinctions (4, 5). This fundamental difference between the evolutionary histories of plants and animals may be due to the persistence of higher plant taxa, and has led to the suggestion that plants are more resistant to mass extinction than animals (1, 6–9). Despite this, studies of fossil plants during times of faunal mass extinction have revealed extensive ecological disruption and decreased plant genus/species diversity on local and regional scales (8, 9), suggesting that plants are not immune to the myriad environmental changes accompanying mass extinctions.

However, plant fossils preserve conflicting records of diversity loss during these critical intervals in Earth history. Estimates of diversity loss based on macrofossils (mostly leaves) are typically much higher than estimates of diversity loss based on sporomorphs (pollen and spores). The end-Permian mass extinction [P-Tr; ~251 million years ago (Ma)] in Australia saw a 97% regional diversity loss of macrofossils but a 19% loss of sporomorph diversity (8, 10), and the end-Cretaceous mass extinction (K-T; ~65 Ma) in North America resulted in a 70–90% diversity loss of macrofossils but a 25–30% loss of sporomorph diversity (11, 12). These discrepancies present a barrier to understanding floral change during episodes of faunal mass extinction. This hampers

efforts to decipher the causes of mass extinctions and also questions the extent to which plants are more persistent than animals in the face of global change. Additionally, these observations raise doubts about the potential of the fossil record to provide accurate and consistent data on the response of terrestrial vegetation to episodes of major environmental change, which raises doubts about the utility of the fossil record as a source of information from which we can augment our understanding and management of the current climate and biodiversity crises. To explore this issue, we have investigated the macrofossil and sporomorph records of vegetation change during the Triassic–Jurassic mass extinction (Tr-J; ~200 Ma).

The Tr-J coincided with massive volcanism associated with the opening of the Atlantic Ocean (13–15), which led to a four-fold increase in atmospheric CO₂ levels (16) and a consequent rise in global temperatures of between 3 and 6 °C (16–18). Compilations of stratigraphic ranges of animal taxa indicate that 23% of marine families (5), 63% of marine invertebrate genera (19), and 22% of terrestrial families suffered extinction at this time (5). In contrast, family-level compilations of plant diversity indicate that only the Peltaspermaeae, a clade of seed-ferns, was lost from the Earth's biota at the Tr-J (e.g., ref. 9). Investigations of macrofossils in Jameson Land, East Greenland, have shown a genus-level extinction rate of ~17% and have revealed that standing species richness across the region declined by ~85% at the Tr-J (20, 21). Plants with specialized reproductive biology (insect pollinated) were among those taxa at greatest risk of extinction or extirpation (21), and relative abundance distributions of macrofossil genera have shown that the pace of biodiversity loss in this region was abrupt rather than gradual (22). The Tr-J in the Newark Basin, North America, records a regional sporomorph diversity loss of ~60% (23), but existing sporomorph records spanning the Tr-J in East Greenland, although qualitative, provide little evidence of such catastrophic diversity loss (24, 25). There is also little evidence for abrupt biodiversity loss in sporomorph records from nearby sections in Europe (e.g., ref. 26), where the Tr-J is characterized by compositional change (e.g., refs. 26 and 27).

Using a new high-resolution dataset of sporomorph assemblages from a Tr-J section at Astartekløft, East Greenland, we present a case study that offers broad insights into the taphonomic processes causing discrepancies between the macrofossil and sporomorph records of plants. Specifically, this study aims to provide (i) quantitative estimates of Tr-J terrestrial plant diversity at within- and among-sample scales; (ii) an assessment of the nature and timing of compositional change in the source vegetation; and (iii) an analysis of the agreement between the macrofossil and sporomorph records of the source vegetation. Our results show that the sporomorph record does not preserve an

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abrupt loss of terrestrial plant biodiversity across the Tr-J in East Greenland, and that the vegetation changed composition rapidly in the boundary interval. Reproductively specialized plants, which include cycads (28), bennettites (29, 30), and the seed-fern *Lepidopteris* (21), are underrepresented in the sporomorph fossil record, and this provides one explanation for the discrepancy between macrofossil and sporomorph records of Tr-J vegetation change.

Results

The macrofossils and sporomorphs analyzed here were collected from eight horizons rich in plant macrofossils at Astartekløft in Jameson Land, East Greenland (Fig. 1 and ref. 21). The Tr-J boundary at Astartekløft is approximated by the first occurrence of the pollen morphospecies *Cerebropollenites thiergartii* in plant bed 5 (following recommendations in ref. 32). Accordingly, plant beds 1–4 are of Late Triassic (Rhaetian) age, plant bed 5 represents the topmost upper Rhaetian and plant beds 6 and 7 are of Early Jurassic (Hettangian) age (Fig. 1). A total of 2,898 macrofossils were recorded in situ from plant beds 1–7 (SI Text, Dataset S1). Rock samples for sporomorph analysis were taken at 10 cm intervals within each plant bed and a total of 14,579 sporomorphs were recorded from 40 productive samples (Table 1 and Dataset S2).

Floral Diversity and Composition. Within-sample richness and Simpson’s diversity index values (D) fluctuate through the section (Fig. 1). Median richness declines through the Triassic from plant bed 1 to plant bed 5 (Fig. 1). Plant bed 6 (earliest Jurassic) records the lowest median richness in the section and plant bed 7 records the highest median richness in the entire section (Fig. 1). Median D is lowest in plant bed 6 and highest in plant bed 7 (Fig. 1). The lowest D values are recorded in samples from plant bed 1 (Fig. 1). The interquartile ranges of within-sample richness and D are large, demonstrating considerable variation within-samples from each plant bed. Using a Kruskal–Wallis test, there is no statistically significant difference in median within-sample richness (KW = 12.319_{6,1,4,7,6,9,3,4} $p = 0.0905$) or median D

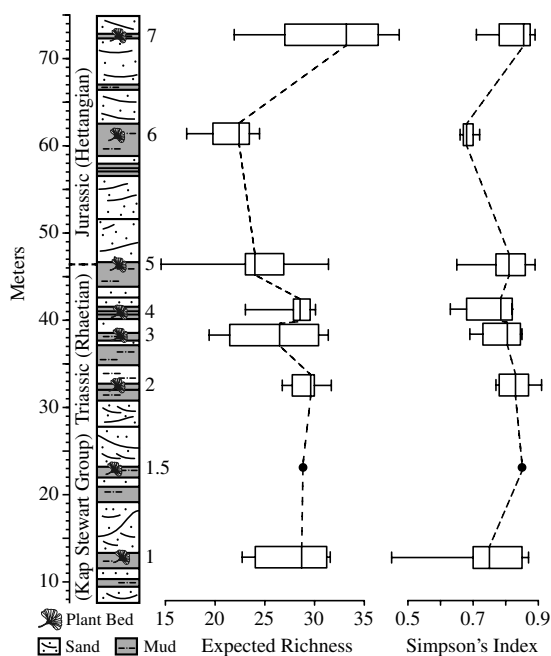


Fig. 1. Schematic sedimentary log of the Astartekløft section (adapted from ref. 31). Box and whisker plot of rarefied within-sample sporomorph richness at 301 counted sporomorphs, and Simpson’s diversity index. Boxes show median and interquartile range. Whiskers represent maximum and minimum.

Table 1. Diversity of Tr-J sporomorph and macrofossil assemblages at Astartekløft

| Plant bed | Sporomorphs | | | | | | | Macrofossils | | | | | | | |
|-------------------------------|-------------|------|------|------|------|------|------|--------------|------|------|------|------|------|-------|------|
| | 1 | 1.5 | 2 | 3 | 4 | 6 | 7 | 1 | 1.5 | 2 | 3 | 4 | 5 | 6 | 7 |
| No. samples | 6 | 1 | 7 | 4 | 6 | 3 | 4 | 4 | 2 | 4 | 4 | 3 | 4 | 1 | 4 |
| No. individuals | 2379 | 361 | 2528 | 1475 | 2139 | 1083 | 1408 | 153 | 55 | 248 | 556 | 547 | 361 | 126 | 821 |
| S_{obs} | 44 | 30 | 45 | 41 | 46 | 35 | 47 | 11 | 7 | 11 | 9 | 11 | 15 | 11 | 8 |
| Chao2 _(max) | 48 | — | 50 | 43 | 51 | 39 | 52 | — | — | — | — | — | — | — | — |
| Jackknife2 _(max) | 53 | — | 54 | 48 | 56 | 46 | 58 | — | — | — | — | — | — | — | — |
| Coleman _(n=3) | 40 | — | 40 | 40 | 42 | 37 | 45 | — | — | — | — | — | — | — | — |
| Coleman _(n=4) | 42 | — | 42 | 41 | 44 | 39 | 47 | — | — | — | — | — | — | — | — |
| Mean S_{alpha} | 29 | 30 | 31 | 27 | 29 | 25 | 33 | 7.78 | 6.27 | 6.73 | 4.84 | 8.18 | 7.99 | 11.00 | 5.51 |
| S_{beta} | 15 | 0 | 14 | 14 | 17 | 12 | 14 | 3.22 | 6.73 | 4.27 | 4.16 | 2.82 | 7.01 | 0.00 | 2.49 |
| Proportion S_{alpha} | 0.67 | 1.00 | 0.68 | 0.66 | 0.63 | 0.60 | 0.70 | 0.71 | 0.90 | 0.61 | 0.54 | 0.74 | 0.53 | 1.00 | 0.69 |
| Proportion S_{beta} | 0.33 | 0.00 | 0.32 | 0.34 | 0.37 | 0.40 | 0.30 | 0.29 | 0.10 | 0.39 | 0.46 | 0.26 | 0.47 | 0.00 | 0.31 |
| D_{total} | 0.73 | 0.85 | 0.85 | 0.88 | 0.81 | 0.84 | 0.70 | 0.83 | 0.76 | 0.81 | 0.81 | 0.81 | 0.66 | 0.74 | 0.64 |
| Mean D_{alpha} | 0.70 | 0.85 | 0.83 | 0.79 | 0.75 | 0.80 | 0.69 | 0.77 | 0.73 | 0.74 | 0.74 | 0.65 | 0.60 | 0.74 | 0.60 |
| D_{beta} | 0.03 | 0.00 | 0.02 | 0.09 | 0.05 | 0.04 | 0.01 | 0.05 | 0.03 | 0.07 | 0.00 | 0.02 | 0.02 | 0.00 | 0.04 |
| Proportion D_{alpha} | 0.96 | 1.00 | 0.98 | 0.89 | 0.94 | 0.95 | 0.98 | 0.99 | 0.93 | 0.96 | 0.91 | 0.98 | 0.97 | 1.00 | 0.94 |
| Proportion D_{beta} | 0.04 | 0.00 | 0.02 | 0.11 | 0.06 | 0.05 | 0.02 | 0.01 | 0.07 | 0.04 | 0.09 | 0.02 | 0.03 | 0.00 | 0.06 |

S_{obs} , number of taxa in all samples; S_{alpha} , number of taxa within samples; S_{beta} , among-sample diversity; D_{total} , Simpson’s diversity index for all samples; D_{alpha} , Simpson’s diversity index within samples; D_{beta} , among-sample Simpson’s diversity index.

values ($KW = 10.32_{6,1,4,7,6,9,3,4}$ $p = 0.1712$) between plant beds (Fig. 1).

Estimates of among-sample sporomorph richness using the Chao2 and Jackknife2 metrics indicate that plant bed 5 is the least taxonomically rich plant bed of Triassic age, and that plant bed 7 is the most taxonomically rich plant bed at Astartekløft (Fig. 2). The Chao2 and Jackknife2 metrics estimate total species richness (33), and the trends in sporomorph species richness using these metrics are largely confirmed by Coleman rarefaction, which estimates species richness for a subsample of the pooled total species richness (33). This lends support to the trends in expected among-sample sporomorph richness through the section. The Jackknife2 estimator presents the only discrepancy, calculating the same estimate of maximum richness for plant beds 5 and 6 (Fig. 2 and Table 1).

Ordination of “Wisconsin” standardized (34, 35) sporomorph data using nonmetric multidimensional scaling (NMDS) shows that samples from plant beds 1 to 4 overlap in empirical space, indicating that there are no discernable differences in the composition of samples from these horizons (Fig. 3). Samples from plant beds 5, 6, and 7 form discrete groups in the ordination space, demonstrating that they are compositionally distinct both from samples of Triassic age, and from each other (Fig. 3). The differences in median NMDS Coordinate 1 and Coordinate 2 sample scores for these four sample groups are statistically significant. Wisconsin standardized data: NMDS Coordinate 1 ($KW = 23.03_{24,9,3,4}$ $p < 0.0001$); NMDS Coordinate 2 ($KW = 26.59_{24,9,3,4}$ $p < 0.0001$). These compositional differences are also evident in relative abundance data (SI Text and Fig. S1).

Comparison of Macrofossil and Sporomorph Records. Plant macrofossils and sporomorphs are both used to track past vegetation change, but the degree to which the two groups of fossils give the same picture of the vegetation is often unclear (36). We have investigated this issue at Astartekløft by using scatter diagrams and mean-difference plots (37) to compare the relative representation of three plant groups in the macrofossil and sporomorph

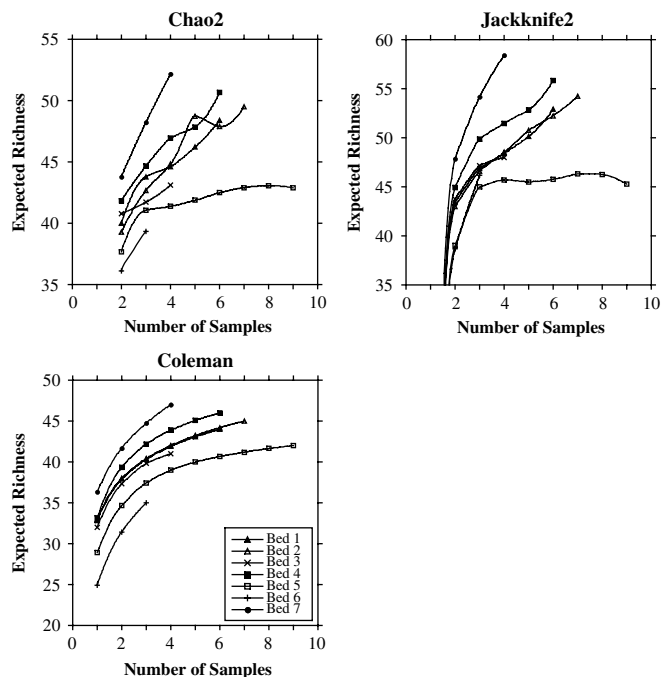


Fig. 2. Chao2 and Jackknife2 richness estimates and Coleman rarefaction curves for plant beds 1–7 (excluding plant bed 1.5). Curves show mean number of expected taxa (y-axis) for a given number of pooled samples (x-axis).

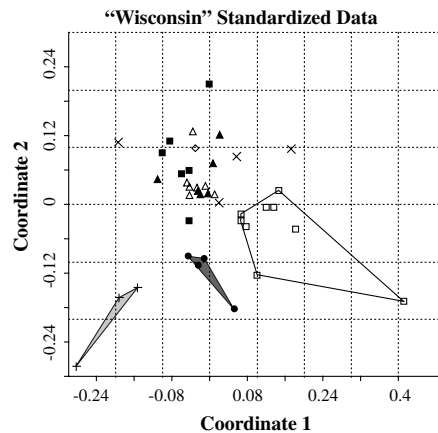


Fig. 3. Nonmetric multidimensional scaling plot of Wisconsin standardized data. Samples from plant bed 5 represented by open squares and enclosed within an unshaded envelope. Samples from plant bed 6 represented by vertical crosses and enclosed within a pale gray envelope, and samples from plant bed 7 represented by closed circles and enclosed within a dark gray envelope.

records. These groups are as follows: Ferns (1); Conifers and Corystosperms (2); Monosulcate Producers (comprising cycads, bennettites, ginkgos and the seed-fern *Lepidopteris*) (Fig. 4). See SI Text and Tables S1, S2, and S3 for details of all plant groups at Astartekløft).

Ferns. The scatter diagram indicates that this group of plants is generally a greater component of the sporomorph record than the macrofossil record and the mean difference between the macrofossil and sporomorph records of this plant group is -22.33% (Fig. 4). The difference between fossil groups does not tend to get larger or smaller as the mean increases (Fig. 4).

Conifers and Corystosperms. The scatter diagram indicates that this plant group generally constitutes less than $\sim 25\%$ of the total plant assemblage in both the macrofossil and sporomorph records (Fig. 4). There is evidence of a major disagreement between the two fossil groups in plant beds 3 and 5, where the relative abundance of this plant group increases dramatically in the macrofossil record, but not in the sporomorph record (Fig. 4). The mean difference between the macrofossil and sporomorph records of this plant group is 11.69% (Fig. 4). The agreement between the two fossil groups improves as mean values approach $\sim 25\%$, but then worsens as the mean increases further (Fig. 4). The disagreement in plant bed 3 is caused by high abundance of the broad-leaved conifer *Podozamites* and in plant bed 5 by high abundances of *Podozamites* and the “swamp conifer” *Stachyotaxus* (see Dataset 1).

Monosulcate Producers. The scatter diagram indicates that this group of plants is almost entirely absent from the sporomorph record at Astartekløft, but is a major component of the macrofossil record (Fig. 4). The mean difference between the macrofossil and sporomorph records of this plant group is 49.25% (Fig. 4). The difference between the macrofossil and sporomorph records of this plant group increases as the mean increases and that there is reasonable agreement between the two fossil groups only when relative abundance is very low ($<10\%$). These data indicate that reproductively specialized plants such as cycads (28), bennettites (29, 30), and *Lepidopteris* (21) are effectively silent in the sporomorph record at Astartekløft.

Taphonomic Selection and Taxonomic Resolution. Macrofossils and sporomorphs record different parts of the source vegetation at Astartekløft. Macrofossil assemblages are weighted toward

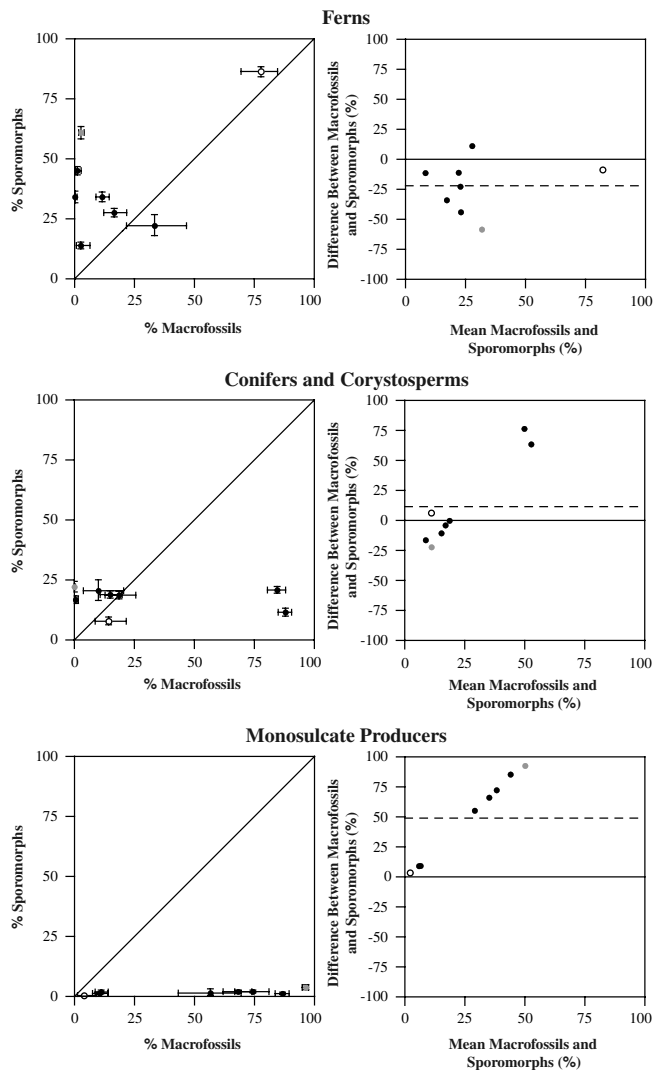


Fig. 4. Scatter diagrams and mean-difference plots illustrating the agreement between the macrofossil and sporomorph records of the Astartekløft vegetation. Each plant bed represented by a single data point ($n = 8$). Closed black circles = plant beds 1–5 (overbank deposits), open circle = plant bed 6 (poorly developed coal swamp) and closed grey circle = plant bed 7 (abandoned channel). Scatter diagrams: solid diagonal line of equality, error bars represent 95% binomial confidence intervals. Mean-difference plots: solid horizontal line of equality, dashed horizontal line showing mean difference between macrofossil and sporomorph records.

woody taxa such as conifers, cycads, bennettites and ginkgos, whereas sporomorph assemblages are weighted to ferns and other spore-producing plants such as lycopods (Fig. 4 and Table S1). This pattern is consistent with the observation that woody plants are dominant in leaf litter and fossil leaf accumulations (38–40), and is congruent with the notion that fern spores have high preservation potential in fluvial/deltaic systems (41). The sporomorph morphotypes at Astartekløft are likely to have been produced by a number of different parent plants. This imposes taxonomic smoothing onto the sporomorph record and this effect is distributed unevenly across plant clades. For example, the monosulcate pollen grain *Cycadopites* was produced by at least four orders of plants in three classes (Table S3), whereas the trilete spore *Baculatisporites* was produced by ferns of the Osmundaceae family (42). Both macrofossils and sporomorphs fail to accurately census certain plant groups at Astartekløft, and therefore likely underestimate the diversity of the source vegetation.

Discussion

A Catastrophic Diversity Decline? Our results indicate that sporomorph diversity within-samples, as measured by species richness and D , did not decline catastrophically across the Tr-J at Astartekløft. Sporomorph richness among-samples is slightly lower in plant bed 5 according to both richness estimators and Coleman rarefaction (Fig. 2). Depending on the estimator, expected richness in plant bed 5 is 10% (Chao2) or 12% (Jackknife2) lower than mean richness from a preboundary bin comprising plant beds 1–4 (Table 1), and we interpret this as a result of detrimental environmental change at the Tr-J. This richness decline is less pronounced than that recorded in the Newark Basin, North America (~60%) (23) and agrees with previous work on Tr-J sporomorph records in East Greenland (24, 25) and elsewhere in Europe (26), which also provide little evidence of catastrophic richness loss.

The shapes of the expected richness curves indicate that plant bed 5 is fully sampled whereas all other plant beds are under-sampled (Fig. 2 and ref. 43). In the case of undersampling “a rising Chao estimator can [be] regarded as a valid estimator of minimum richness, given the available data” (p. 692 in ref. 44). Consequently, differences in maximum estimated richness between plant bed 5 and plant beds with higher richness (Table 1) should be viewed as minimum differences. Plant bed 5 saturates more quickly than other plant beds of Triassic age because it is less rich taxonomically and because of the distribution of species within the sample set. Both Chao2 and Jackknife2 provide increasingly high richness estimates as the number of taxa that occur in only one sample and exactly two samples increases (45). This indicates that there are more such rare taxa in plant beds 1–4, and fewer in plant bed 5 (43, 46), in agreement with the trend in macrofossil relative abundance distributions at Astartekløft, which increase in slope up-section as a result of the loss of rare taxa (22).

Vegetation Heterogeneity. We have examined Tr-J vegetation heterogeneity at Astartekløft through additive partitioning of species richness and D values into alpha (within-sample) and beta (among-sample) components of diversity (47, 48). Beta diversity is thought to increase in heterogeneous landscapes with patchy vegetation where few species are shared by samples, and will decrease in homogeneous landscapes where the species composition of each sampling unit is identical (45). Neither the beta component of richness, nor the beta component of D , show a sharp increase or decrease in any plant bed, and nowhere does beta diversity exceed alpha diversity (Table 1). This pattern is consistent in both the macrofossil and sporomorph records, and supports the idea that vegetation heterogeneity did not change dramatically across the Tr-J at Astartekløft (21). These results also suggest that vegetation heterogeneity was similar in the three depositional environments present at Astartekløft (Table 1). It should be noted, however, that sporomorph samples were collected vertically within each plant bed and therefore do not contain an explicitly spatial component, whereas macrofossils were collected from small quarries spaced laterally along each plant bed (ref. 21 and SI Text) and therefore do contain a spatial component.

Compositional Change. Ten sporomorph taxa are absent from every sample in bed 5 but present in samples from plant beds 1–4 (*Lycopodiumsporites semimuris*, *Cingulizonates rhaeticus*, *Concavisporites* A, *Triancoraesporites ancora*, *Nevesisporites limatulus*, *Alisporites* sp., *Classopollis ?zwolinskai*, *Eucommiidites troedssonii*, *Ovalipollis ovalis*, and *O. breviformis*), whereas just three sporomorph taxa have their first appearance in plant bed 5 (*Trachysporites asper*, *Lycopodiacites rugulatus*, and *Cerebropollenites thiergartii*) (Fig. S2). This suggests that local emigration and/or extirpation of plants played a greater role in changing the com-

position of the standing vegetation in plant bed 5 than immigration and/or origination (Fig. 3, cf. ref. 49). A similar pattern is recorded in the macrofossil record, where recovery of the vegetation in the Jurassic was achieved by recruitment of new dominant plants from within the Jameson Land region, rather than by origination or significant immigration of exotic taxa (21). The discreet groups formed by samples from beds 6 and 7 in the ordination space indicate that the vegetation did not return to a Triassic composition once it had changed in plant bed 5 (Fig. 3). Because plant beds 6 and 7 represent environments that were not present during the Triassic at Astartekløft (21) this may reflect the influence of depositional environment on sample composition. Nevertheless, this observation strongly suggests permanent compositional change in the East Greenland vegetation across the Tr-J, in common with the macrofossil record (21).

Macrofossil and Sporomorph Records of Tr-J Plant Diversity in East Greenland. The macrofossil record indicates a complete regional turnover of dominant taxa and an 85% decline in species richness at the Tr-J in East Greenland (20, 21). A midcanopy habit was also eliminated at the Tr-J in this region (21). At Astartekløft, a ~35% loss in macrofossil generic richness is recorded prior to the Tr-J boundary in plant beds 3 and 4 (21), and a decline in evenness is recorded in plant beds 3, 4, and 5 (ref. 12; see also *D* values in Table 1). None of these aspects of Tr-J vegetation change are clearly expressed in the sporomorph record at Astartekløft.

The analysis of the agreement between the macrofossil and sporomorph records at Astartekløft may help to explain this discrepancy (Fig. 4). Changes in the relative abundance of bennettites and cycads are a major factor in Tr-J vegetation change in East Greenland (21). For example, among bennettites *Pterophyllum* declines from 20% in the Triassic to 1.3% in the Jurassic and *Anomozamites* declines from 17% to 0.1% (12), and among cycads four form genera (*Doratophyllum*, *Ctenis*, *Pseudoctenis*, and *Nilssonia*) are present in Triassic rocks at Astartekløft, but are absent from Jurassic strata (21). It is clear that the sporomorph record fails to adequately sample the group of plants containing these taxa at Astartekløft (Fig. 4) and consequently, changes in their relative abundance in the source flora will be masked in the sporomorph record. Additionally, the only family level extinction among plants during the Tr-J, that of the Peltaspermaeae (9), is also obscured in the sporomorph record because the pollen grains produced by this family (*Cycadopites*, ref. 50) were also produced by several other plant groups (Table S3).

Reworking of sporomorphs at Astartekløft may also obscure changes in vegetation diversity and ecology that are expressed in the macrofossil record. The presence of channelized sandstone bodies laid down from river channels several meters deep (21, 51) suggest that reworking is possible. Although previous work at Astartekløft did not highlight pervasive reworking (24), certain sporomorph taxa occur in very low abundance in strata younger than their accepted stratigraphic range. Sporomorphs that are likely to have been reworked include single specimens of *Rhaetipollis germanicus* in plant bed 6 and 7, one specimen of *Limbosporites lundbladii* in a single sample from plant bed 7, and two specimens of *Lunatisporites* sp. and three specimens of *Ovalipollis ovalis* in a single sample from plant bed 7 (Dataset 2 and Fig. S2). Macrofossils with discontinuous stratigraphic ranges may be associated with sporomorphs with continuous ranges. One example is the macrofossil *Cladophlebis*, a fern of the Osmundaceae family, and the spore *Baculatisporites comaumensis* (ref. 42 and Fig. S2). Whether this is due to reworking or other factors remains unclear, and further work is required to understand the impact of reworking on the reconstruction of vegetation diversity and ecology using sporomorphs.

Conclusions

Quantitative analyses of sporomorph diversity do not support a catastrophic decline of terrestrial plant biodiversity in East Greenland. The Tr-J boundary interval is characterized by a modest decline in richness among-samples (Fig. 2) and rapid compositional change that was apparently driven by emigration and/or extirpation rather than immigration and/or origination of taxa (Fig. 3). This is in contrast to the macrofossil record of Tr-J vegetation in the same area, which preserves evidence of abrupt biodiversity loss and changes in forest structure (21, 22). This discrepancy may be explained by the poor representation of certain plant groups in the sporomorph record (Fig. 4). The clearest example is the effective absence of reproductively specialized plants that produced monosulcate pollen grains of the *Monosulcites/Cycadopites* and *Chasmatosporites* morphotypes [cycads (28), bennettites (29, 30) and *Lepidopteris* (21)] in the sporomorph record at Astartekløft (Fig. 4). This pattern apparently extends to Mesozoic sediments worldwide (52), and if Late Triassic diversity loss among reproductively specialized plants is characteristic of the Tr-J in a wider geographic area, this may explain why sporomorph records across the Tr-J in Europe also preserve little evidence of diversity loss (e.g., refs. 26, 27).

This Tr-J case study provides broader insights into the nature of the fossil plant record as it raises the possibility that the floral composition of a biome may affect the quality of its representation in the sporomorph record. Using the relationships shown in Fig. 4, biomes apparently rich in cycads, bennettites and ginkgos, such as the warm temperate biome (Fig. S3 and refs. 53 and 54), may be poorly reflected in Tr-J sporomorph assemblages. Those biomes with a lower proportion of these plants, and perhaps a higher proportion of conifers, which have the smallest mean difference between the macrofossil and sporomorph records at Astartekløft (Fig. 4), may be more accurately reflected in sporomorph assemblages. One example might be the summerwet tropical biome in which cycads were rare and ginkgos were absent (Fig. S3 and refs. 53 and 54). This suggestion may factor in to an explanation of the high regional extinction rates among sporomorphs in the Newark Basin (14), which was situated between 16–25° North during the Tr-J (55) and close to, or within, the summerwet tropical biome (53, 54).

The P-Tr, Tr-J, and K-T faunal mass extinctions were accompanied by diversity losses, ecological changes, and extinctions among plants that were locally/regionally severe and also selective (8, 9). Our results demonstrate that these local/regional patterns will be strongly influenced by the choice of fossil group used to study the vegetation. Our results provide a means of reconciling the contradictory macrofossil and sporomorph records of Tr-J vegetation change in East Greenland, and highlight a mechanism by which similar discrepancies at the P-Tr and K-T mass extinctions may be understood. Additionally, by demonstrating that changes in the diversity and ecology of reproductively specialized plants are not recorded faithfully by sporomorphs at the Tr-J, our results provide support for the idea that the ~20% extinction among sporomorphs following the Paleocene–Eocene Thermal Maximum (PETM) in the paratropical Gulf Coast of North America is likely to be a considerable underestimate, and therefore may represent a major Cenozoic plant extinction event (43). The magnitude of regional sporomorph diversity loss following the PETM, which is not recognized as an episode of faunal mass extinction (4, 5), was apparently greater than sporomorph diversity loss at the Tr-J in East Greenland (e.g., Fig. 2).

Materials and Methods

Lithology and Palynological Processing. Samples from plant bed 6 consist of coaly mudstone. Samples from all other plant beds consist of dark gray mudstone and siltstone. 15–20 g of each sample was washed and crushed, then dried for 24 h at 60 °C. Each sample was treated twice alternately with cold HCl (30%) and cold HF (38%). Residues were then sieved with 250 μm and 15 μm mesh. Organic and inorganic residues were separated using ZnCl₂.

At least 350 sporomorphs were counted per slide, but where one morpho-type dominated the assemblage, counts were increased until at least 150 sporomorphs of the nondominant type were recorded.

Floral Diversity and Composition. Within-sample richness was estimated using individual-based rarefaction using the program PAST (56). These analyses calculate expected richness at lower sample sizes, allowing richness in samples of different sizes to be compared. Simpson's diversity index (D) calculations were performed using the R package Stratigraph (57, 58). D is weighted toward the most abundant species in a sample and is thus responsive to dominance (45). Among-sample richness was estimated using the Chao2 and Jackknife2 metrics (randomized 10,000 times), and Coleman rarefaction (without sample replacement) was used to compensate for differences in sampling intensity between plant beds (43, 45). These analyses were undertaken using the program EstimateS Version 8.2 (33). Additive diversity partitioning analyses were performed using the R package Stratigraph (results

weighted by total number of individuals) (57, 58). NMDS ordination was performed in PAST (56). Wisconsin standardization scales the abundance of each taxon to its maximum value, and represents the abundance of each taxon by its proportion in the sample, which equalizes the effects of rare and abundant taxa and removes the influence of sample size on the analysis (34, 35). Ordination on Wisconsin standardized data is likely to be sensitive to the disappearance and appearance of individual taxa. Singletons (taxa that occurred in only one sample) were removed for the ordination. Kruskal-Wallis tests were performed in R (57).

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