Fossil Plant Relative Abundances Indicate Sudden Loss of Late Triassic Biodiversity in East Greenland

Jennifer C. McElwain,1* Peter J. Wagner,2 Stephen P. Hesselbo3

The pace of Late Triassic (LT) biodiversity loss is uncertain, yet it could help to decipher causal mechanisms of mass extinction. We investigated relative abundance distributions (RADs) of six LT plant assemblages from the Kap Stewart Group, East Greenland, to determine the pace of collapse of LT primary productivity. RADs displayed not simply decreases in the number of taxa, but decreases in the number of common taxa. Likelihood tests rejected a hypothesis of continuously declining diversity. Instead, the RAD shift occurred over the upper two-to-four fossil plant assemblages and most likely over the last three (final 13 meters), coinciding with increased atmospheric carbon dioxide concentration and global warming. Thus, although the LT event did not induce mass extinction of plant families, it accompanied major and abrupt change in their ecology and diversity.

Ecological theory shows that relative abundance distributions (RADs) provide important information on the ecological assembly rules for communities in both the present (1, 2) and past (3). The general ecological rules that underpin community assembly are also independent of species composition, thus providing a metric of past diversity that is applicable to communities of disparate composition, phylogenetic history, and age (1, 2). Differences among RADs reflect differences in dominance and rarity as well as richness. RADs describe dominance and rarity more exactly than does evenness (i.e., uniformity of abundances) alone (4). Hypotheses of ecological deterioration make predictions about changes in RADs over time without necessarily predicting extinction (5, 6). Therefore, if prolonged ecological deterioration precedes a mass extinction, then RADs could reveal ecological deterioration better than richness or evenness alone.

We use RADs to examine the pace of diversity loss leading to the Triassic-Jurassic boundary (TJB). The TJB extinction is one of the five greatest in Earth history (7), but the pace of biodiversity loss remains uncertain (8–12). This hampers our ability to distinguish between competing hypotheses on the causal mechanisms of the TJB mass extinction. Gradual extinction patterns have been reported. RADs offer an opportunity to re-examine the pace of LT biodiversity change in greater detail than provided by either changes in richness or evenness.

We assessed trends in RADs over six taphonomically similar Rhaetian-aged fossil plant beds from Astartekløft, East Greenland (10). First, we determined the most likely RAD model for each bed based on the expected number of taxa with x specimens given the observed sample size (3). We considered four RAD models: geometric and the zero-sum multinomial, which are governed largely by ecological succession (1, 2); and lognormal and Zipf, which are governed by increasing ecospace due to facilitation or niche construction (1). Because the different RADs do not represent special cases of each other, we use Akaike’s modified information criterion to choose the best model (3, 13).

Second, we assessed a series of increasingly complicated temporal models of LT plant diversity change. We did this by assessing the likelihood of a range of models, and thus the joint likelihood that 2+ assemblages shared the same RAD. Because not all beds fit the same RAD model, we labeled each model with a more general aspect of diversity: the hypothesized number of genera (S) with frequency greater than 10−6 (S > 10−6). In order of increasing complexity, we considered (i) uniform diversity over the whole Rhaetian-aged portion of the Astartekløft section (ΔSf = 0); (ii) linear diversity decrease over the same interval (ΔSf > 0); (iii) static diversity followed by linear decrease in the later Rhaetian portion of the section; (iv) static diversity followed by curvilinear decrease in the later Rhaetian portion of the section.

The simpler temporal models are special cases of the more complicated temporal models. Thus, we can use log-likelihood ratios to test whether a more complicated temporal model is significantly better than a simpler one (14). We tested hypothesized RAD shifts by how well those hypotheses predict observed abundances given the best general RAD model and the hypothesized shift in Sf+1, not by how well they predict the best exact model. Second, we reach identical conclusions using Sf+1 or Sf+1.

Table 1. Modified Akaike’s information criteria (AICc) for best examples of each general RAD model. AICc = −2ln[L(data)]/n/n − (k–3), where H is the best hypothesis from each model, n is the number of species, and k is the number of parameters (k = 1 for geometric; otherwise k = 2). The lowest AICc value (bold) gives the best fit (13).

<table>
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<th>AICc</th>
<th>k</th>
<th>n</th>
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**Fig. 1.** Trends in Late Triassic plant community relative abundance distributions (RADs) and diversity for Astartekløft, East Greenland. (A) Best-fit RAD hypotheses for each bed. (B) Most likely richness of genera with \( f > 10^{-6} \) for each bed \( S_{f>10^{-6}} \). Bars give 1-unit support (i.e., \( \ln L \leq 1 \) less than maximum); bar width decreases both with increasing sample size and increased fit of general model to the data \((14)\). Lines give predicted diversity given the best hypothesis from three different models of diversity change over meters of sediment. \( m \) in the equations gives meters beyond 13 m and 37 m (the heights of apparent shifts). The final hypothesis has one more parameter, as \( S_f \) is static until bed 3.

**Table 2.** Hypotheses of changing diversity going up-section, given here as the changing numbers of taxa \( S \) with relative abundance \( >10^{-6} \). \( k \) gives the number of varying parameters for each hypothesis. \( \ln L \) gives the log-probability of all observed abundances given the hypothesis and the best model from Table 1. \( P \) gives the probability of the difference in log-likelihoods if the simpler hypothesis is correct. Because simple hypotheses are special cases of the complex hypotheses, we assess \( P \) using log-likelihood ratio tests. The best \( 3k \) hypothesis, linear decrease in diversity over the last 13 m, is omitted as it is worse than the best \( 2k \) hypothesis.

<table>
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<th>Hypothesis</th>
<th>( k )</th>
<th>( \ln L )</th>
<th>( P )</th>
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<td>( S_{f&gt;10^{-6}} = 19.9 )</td>
<td>1</td>
<td>-232.7</td>
<td>—</td>
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<tr>
<td>( S_{f&gt;10^{-6}} = 40.4-15.1 )</td>
<td>2</td>
<td>-224.8</td>
<td>7.0 \times 10^{-5}</td>
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<tr>
<td>( S_{f&gt;10^{-6}} = 34.1-15.1 )</td>
<td>4</td>
<td>-220.7</td>
<td>0.018</td>
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in last 13 m

Like confidence-interval studies \([15]\), RADs account for unsampled taxa, with lower sample sizes leading to best-fit RADs positing greater numbers of unsampled taxa \( (3) \). Although samples from the same RAD over time will show gradual last occurrences of taxa [the Signor-Lipps effect \((16)\)], our likelihood tests will show indistinguishable RADs and thus suggest constant diversity \((17)\). Thus, the Signor-Lipps effect cannot create trends in RADs, even if sampling decreases up-section. The RAD approach has the two additional advantages of implying changes in rarity among (unspecified) unsampled taxa and requiring fewer fossiliferous horizons, as the statistical power comes from the number of sampled fossils rather than the number of occurrences.

We analyze genera rather than species. Because 95% of fossil plant genera in Kap Stewart Group strata have monospecific occurrences within plant beds \((10)\), species-level patterns cannot differ too greatly from genus-level patterns. Moreover, most species determinations for the Kap Stewart flora reflect leaf surface micromorphological traits \((18)\), which might not be taxonomically reliable \((10)\). Genera also add a conservative bias, as the greater taxon numbers provided by species would increase our ability to recognize different RADs.

Taphonomic studies demonstrate that despite some general biases \([10]\) for further discussion], leaf litter from temperate and relatively low diversity subtidal floodplain forests provides a relatively accurate indication of both the richness and the dominance-diversity relationship of the live forest community \((19)\). We assume that similar processes affected leaf litter on and preservation from LT floodplain forests of East Greenland \((10)\). RADs of census-collected fossil leaf collections from Greenland should therefore elucidate patterns of changes in LT plant community assembly and diversity for this region. All six LT fossil plants beds at Astartekløft [with the exception of bed 5 \((17)\)] likely represent a geologically instantaneous sample of the standing plant community preserved during river flooding on one or several occasions. RADs from these beds are therefore unlikely to be subjected to any significant time averaging, which can result in lognormal RADs by mixing of different exponential distributions \((3)\).

All beds except bed 3 best fit geometric RADs; bed 3 best fits a lognormal RAD (Table 1 and Fig. 1A). This suggests that LT plant communities were predominantly assembled by simple niche-partitioning rather than more complex assembly rules \((3)\). More important, the best RADs for each bed show a distinct trend toward increasing slope moving up-section and thus decreasing diversity through time (Fig. 1A), especially above 35 m (Fig. 1B). The best hypothesis of continuously decreasing plant diversity (where \( S_{f>10^{-6}} \) declines by 0.777 per meter; Fig. 1B) is significantly more likely than
is the best hypothesis of static diversity (Table 2). The likelihood improves significantly more given a hypothesis of an identical geometric RAD for the first three beds (the first 24 m) and decreasing diversity decreasing markedly over the last three beds [the final 13 m (17)]. Variations on the final model show that we cannot reject the idea that the plant diversity shift is concentrated in the upper 9 m of the Rhaetian aged Astartekløft, sedimentary rocks (beds 3 to 5A; Fig. 2), although we can reject the idea that the shift was distributed over the upper 23 m (beds 1.5 to 5A) or the upper 6 m (beds 4 and 5A). Regardless of the exact timing, a hypothesis of continuous, gradual plant diversity loss suggested by richness decrease alone (10) is not tenable (20).

Environmental degradation on ecologic time scales causes community diversity and complexity and increases RAD slopes (5, 6). We see the same pattern here, but on an evolutionary time scale. If sedimentation for the section was fairly constant and if the Rhaetian is completely represented, then the shift in RADs most likely begins approximately 300,000 to 500,000 years before the TJB. Extraordinarily high sedimentation rates would be required for beds 3 to 5 to represent a snapshot of ecologic time-scale processes. Conversely, large decreases in sedimentation rates over beds 3 to 5 relative to beds 1 to 2 are required to salvage the hypothesis that diversity decreased continuously through the section. There is no sedimentological or taphonomic support for either proposition.

Within uncertainties, the abrupt diversity loss coincides with a moderate +0.95‰ positive excursion in organic matter carbon-isotope composition (Fig. 2) just before the onset of the main TJB negative carbon isotopic excursion (9). These results suggest that the decline in plant diversity at Astartekløft coincided with a major transition between different states in the global carbon cycle from predominantly 13C-sink to 13C-source processes. Available low-resolution CO2 records indicate that the diversity loss occurred between minimum CO2 values reported for the interval [480 ± 160 parts per million by volume (ppmv)] at 32 m and maximum values (1240 ± 400 ppmv) at 47 m (8) and coincided with a major sea level fall across Europe (11, 21). Concurrently, the inferred global mean surface temperature difference from present (ΔGMS) changed from 2 ± 1.0°C to 7 ± 1.0°C ΔGMS (8). Interpolating between available CO2 estimates indicates that the sudden diversity drop between 33 and 37 m coincided with a mere ≈100 to −350 ppmv rise in CO2 concentration. This was followed by a more protracted diversity decline with a lessening slope approaching the TJB, as atmospheric CO2 (8) and estimated ΔGMS increased to their respective maximum values (21). Therefore, although CO2-induced global warming was likely an important contributory factor to plant species turnover at the TJB (46 m), an alternative or additional triggering mechanism for the abrupt loss of plant diversity between 33 and 37 m at Astartekløft may be possible.

We cannot extrapolate the vegetation responses from one locality globally. However, global hypotheses for the end-Triassic extinctions must predict local patterns; thus, hypotheses failing to predict the Kap Stewart patterns are unlikely as global explanations. Moreover, the most parsimonious explanation for the trends we observe is that they represent regional responses to global environmental change. This argument is supported by the observation that the highest occurrences of plant species at Astartekløft at ~46 m are contemporaneous with those from 12 other Kap Stewart Group localities (18) and that high turnover of fossil plant taxa within the TJB interval has been recorded in North America (22), UK (21), Sweden (18), Spain (23), Austria (24), and Italy (25). Correlation of the stable carbon isotope profiles from across the globe (9, 21, 24, 25) suggests that the abrupt loss in plant diversity at Astartekløft began at the onset, not the zenith, of the main global carbon isotopic excursion and before turnover of 90% of macrofossil plant species in the Jameson Land region (10, 18). Palynology further supports this temporal correlation as the first appearance of the morphospecies Cerebropollenites thiergarti coincides with the turn to more negative 813C values in TJB sections at Astartekløft (26), St Audries Bay (UK), and Tiefengraben (Austria) (24). The abrupt loss in Astartekløft plant diversity also coincides with several patterns indicating severe environmental disturbance to the marine environment, including turnover (27) and extinction of shallow marine shelly invertebrates (23), a shallow-water carbonate production crisis (21), and at least local proliferation of green algal phytoplankton (21, 24).

The abrupt plant diversity loss between 33 and 37 m is consistent with expected plant responses to a catastrophically rapid rather than gradual environmental change and argues against the currently favored extinction mechanisms invoking gradual CO2-induced global warming due to slow release of CO2 from the mantle associated with extrusion of basalt over an area of >10 million km2 (CAMP; Central Atlantic Magmatic Province) (9, 10). Proposed mechanisms of rapid environmental change include a meteorite impact (12), exhalation of thermogenic methane or other gases generated by intrusion of CAMP sill magma (11), sulfur dioxide aerosol release during CAMP eruptions (28), or biogenic methane release from gas hydrates (29). An alternative explanation for the abrupt diversity loss is that it represents a threshold response of LT vegetation to relatively minor increases in CO2 concentration and/or global temperature. High-resolution proxy CO2 and SO2 records, coupled with controlled environment experiments, are required to test further the primary drivers of abrupt LT biodiversity loss.

References and Notes
17. Supporting materials are available on Science Online.
18. T. M. Harris, Medd. Gronl. 112, 82 (1917).
30. J.C. collected plant paleoecological data, S.P.H collected isotopic and stratigraphic data, and P.J.W. undertook data analyses. J.C.M. and P.J.W. cowrote the paper, and all authors contributed equally to interpretation. We gratefully acknowledge funding from a Marie Curie Excellence Grant (MEXT-CT- 2006-042531) to J.C.M. and NSF-EAR-0207874 to P.J.W. This is Paleobiology Database contribution 95.

Supporting Online Material
www.sciencemag.org/cgi/content/full/324/5934/1554/DC1

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Figs. S1 to S3
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Methods

Assessing whether two assemblages share the same diversity.

We assess the likelihoods of particular RAD hypotheses using established protocol that both contrast different RAD models and accommodate sample size (S1). Of course, in addition to the most likely RAD for any one bed, there exist a range of other hypotheses that cannot be rejected (S2, 3). For example, the best-fit RADs for beds 1 and 2 are well within the range of RADs within 1-unit support of the best hypothesis for bed 1.5 (see, e.g., Fig. S1).

If all the beds had fit the same RAD model, then we could simply have examined hypotheses of static vs. shifting parameters. However, Bed 3 fits a lognormal significantly better than it fits a geometric whereas all of the other beds fit the geometric model best (Table 1). We therefore assessed one aspect of diversity: i.e., the richness (number) of taxa of some minimum abundance (here, $S_{f>10^{-6}}$; note that the same results are achieved with other values of $f$). We modified the test to find RADs with $S_{f>10^{-6}}$ in increments of 0.1 and assessed the likelihood of each for each bed. We restricted this to the model producing the most-likely RAD. In the case of beds best fitting geometric RADs, only the slope needs to be varied, and a particular set of slopes could be used for all beds. However, for Bed 3, two variables (the true richness and an “evenness” parameter of the log-normal) needed to be assessed. For any combination of richness and evenness, there was a different number of taxa with $S_{f>10^{-6}}$. Therefore, for each $S_{f>10^{-6}}$, we used the lognormal parameters maximizing the likelihood of that $S_{f>10^{-6}}$ given Bed 3’s data.

We then examined the likelihood of the predicted $S_{f>10^{-6}}$ for each hypothesis of changing diversity given the distribution of each bed. We could use log-likelihood ratio tests because the simpler
hypotheses all are special cases of the more complicated ones. The null hypothesis, a single
diversity, is the special case of decreasing diversity over time in which the slope of decrease is 0.
The continuously decreasing diversity hypothesis is a special case of the 4-parameter hypothesis in
which the exponential component of decrease is invariant and at 0 (thus making it linear) and in
which the onset of decrease is invariant and always in the first bed.
Note that the Signor-Lipps effect (S4) cannot affect inferences made using this approach. The
Signor-Lipps effect is important only when using “range-through” inferences of richness: that is,
counting taxa not found in a bed but assumed to be present because they are observed in lower
(earlier) and higher (later) beds. Here, such taxa are ignored in the analyses. The analyses infer
some number of unsampled-but-present taxa, which no doubt includes some unspecified range-
through taxa. However, the range-through taxa might be locally extinct at this time; conversely, the
unsampled-but-inferred taxa might also include taxa with last appearances preceding the bed or first
appearances after the bed.

*Testing whether two portions of the same bed represent the same fauna.*

Bed 5, at 46 meters in the section, marks the TJB in East Greenland (S5, 6). There is a marked shift
in generic composition within that bed itself (Fig S2), with an apparent “turnover” around 46.6
meters. We modify the techniques used above with existing techniques (e.g., S2) to assess whether
the floral composition of the first 30 cm (Bed 5A) is appreciably different from that of the last 30
cm (Bed 5B).

Although the “lumped” assemblage of Bed 5 best fits a Zero Sum RAD, the Zero Sum does a poor
job of predicting either Bed 5A or Bed 5B: in fact, that model can be rejected for both 5A and 5B
individually (Table S1). Moreover, whereas a geometric RAD fits Bed 5A significantly better than
any other RAD, both the Zipf and Lognormal fit bed 5B significantly better than does the
geometric. Thus, we can reject the hypothesis that Beds 5A and 5B reflect the same constructional rules. In the absence of any compelling evidence of taphonomic changes (each part of Beds 5A and 5B contains taxa that are sampled elsewhere in Bed 5), this suggests a marked ecologic turnover.

Of additional potential interest is the fact that the implied diversity of Bed 5B is appreciably greater than that of Bed 5A (Fig. S3). This is consistent with an idea of rapid ecological rebound, with the rebound supporting a much larger number of relatively rare \(10^2 > f > 10^3\) genera. It also is consistent with the idea that the community assemblage rules were more complicated in the rebound than afterwards. Alternatively, because mixing of exponential distributions also creates lognormal distributions, it is possible that the assembly rules were inconsistent and that Bed 5B essentially mixes communities. However, as this is based on only 44 specimens, this inference is very tentative.
Fig. S1. Best model RADs for beds 1, 1.5 and 2, plus RADs within one unit support of the ML RAD for bed 1.5. We clearly cannot reject the idea that all three beds had the same RAD and that the differences in best model RADs are simply due to sampling error.
Fig. S2. Bed 5, divided into 10 cm units. Widths represent generic abundance, with narrowest lines representing one specimen. Bed 5A = 4630–4660 cm; Bed 5B = 4660–4690 cm.
Fig. S3. Best RADs (geometric and Zipf, respectively) for Beds 5A and 5B. See Table S1.
Table S1. Modified Akaike’s Information Criteria (AICc) for best examples of each general RAD model. AICc = -2*lnL[H | data] * n/(n-k-1) where n is the number of specimens and k is the number of parameters (k=1 for geometric, k=2 for others.)

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