

Paratropical floral extinction in the Late Palaeocene–Early Eocene

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Abstract: The Palaeocene–Eocene Thermal Maximum (PETM) at *c.* 55.8 Ma marks a transient (*c.* 100 ka duration) interval of rapid greenhouse warming that had profound effects on marine and terrestrial biota. Plant communities responded rapidly with major compositional turnover. The long-term effects on tropical vegetation communities that stem from the brief period of global warming are unclear. We present pollen data from the paratropical US Gulf Coast (eastern Mississippi, western Alabama and Georgia), which had background Palaeocene mean annual temperatures of 26–27 °C. Sporomorph data (pollen and spores) demonstrate that taxonomic diversity increases over *c.* 1 Ma in the Late Palaeocene but this trend is replaced, with the first occurrences of taxa that mark the Early Eocene, by a pronounced extinction into the Early Eocene (*c.* 20% of the palynoflora). Taxonomic diversity also decreases by up to 38% in the Early Eocene. The timing of the extinction is not clearly resolved but may be restricted to the earliest part of the Early Eocene. Two richness estimators (Chao 2 and Jackknife 2) both demonstrate that Late Palaeocene samples contain significantly more taxa than those in the Early Eocene. Extinction on the US Gulf Coast proves that ancient tropical ecosystems were highly susceptible to changes in diversity mediated directly or indirectly by environmental change even during equable greenhouse climates in the early Palaeocene.

The impacts of rapid climate warming and changes in atmospheric carbon dioxide on modern tropical plant communities are the subjects of intense study (Bazzaz 1998; Clark 2004; Cowling *et al.* 2004; Körner 2004). Research interest centres on the role that tropical forests play in the carbon cycle because tropical forests are both significant sources and sinks of CO₂ (Bazzaz 1998; Mahli & Grace 2000). Changes in tropical forest structure, composition and biodiversity caused by factors such as deforestation or autogenic community responses may have significant negative feedbacks on the atmospheric carbon cycle (Bazzaz 1998; Bush *et al.* 2004; Clark 2004; Cowling *et al.* 2004; Wright 2005). In the future, extinction of selected plant species and changes in the geographical range of many other plants are expected (Bazzaz 1998; Bush *et al.* 2004; Cowling *et al.* 2004). However, the long-term impact of warming is unknown and wholly speculative (Hughes 2000; Woodruff 2001; Clark 2004). The geological record preserves intervals of past rapid climate warming in which the response of plant communities can be studied in detail and on different time scales. Specifically, predictions on geographical range changes and diversity dynamics as a result of rapid warming can be explored using the fossil record of plant organs such as pollen.

The Palaeocene–Eocene Thermal Maximum (PETM) is foremost among these warming events (Zachos *et al.* 2001, 2003; Nunes & Norris 2006) and marks the beginning of the Eocene Epoch at 55.8 Ma (Gradstein *et al.* 2004; Zachos *et al.* 2005). During the PETM global land and sea surface temperatures increased by 5–10 °C (Kennett & Stott 1991; Fricke *et al.* 1999; Zachos *et al.* 2001; Fricke & Wing 2004) over *c.* 10–20 ka before returning to warm background levels again over the succeeding *c.* 100 ka (Röhl *et al.* 2000; Bowen *et al.* 2001; Farley & Eltgroth 2003; Zachos *et al.* 2003, 2005). Climate modelling predicts that >4500 Gt of light carbon was released into the atmosphere and oceans during the initial stages of the PETM (Zachos *et al.*

2005). Major transient floral and faunal composition changes are recorded at high latitude (Clyde & Gingerich 1998; Wing *et al.* 2005) as a result of the ensuing warming. Despite a paucity of floral localities from within the brief PETM interval (e.g. Wing 1998; Jaramillo 2002; Harrington 2003*a, b*; Wing *et al.* 2005), several regions globally have excellent plant records both immediately before and after the PETM. For example, in North America, plant and pollen records are documented from different vegetation types from the warm-temperate Bighorn Basin in Wyoming (43°N, 107°W), which had a mean annual background temperature of *c.* 16–17 °C (Wing 1998; Wing & Harrington 2001), to the paratropical eastern US Gulf Coast (32°N, 87°W) (Frederiksen 1994, 1995; Harrington 2003*a*; Harrington *et al.* 2004), which had a Late Palaeocene–Early Eocene background mean annual temperature of *c.* 26–27 °C (Wolfe & Dilcher 2000; Ivany *et al.* 2004). The changes of the US Gulf Coast floras provide an example of the responses of a warm-adapted, taxonomically diverse vegetation type to the impact of rapid climate warming. Hence, we use pollen records from the eastern US Gulf Coast to explore whether there are significant diversity changes in paratropical vegetation types during the Late Palaeocene–Early Eocene. A previous investigation (Harrington *et al.* 2004) focused on the changes in composition that resulted from immigration of Eocene taxa but lacked sufficient sampling coverage to thoroughly tackle questions on changes in diversity. Thus, we present sporomorph (pollen and spore) data from an expanded series of sections over an extended time period (>1.5 Ma) from the eastern US Gulf Coast, which are used to analyse changes in taxonomic diversity and composition.

Diversity changes

Previous studies from high latitudes such as the Bighorn Basin, Wyoming have documented a decline in taxonomic diversity

across a 2.5 Ma period that is centred on the Palaeocene–Eocene boundary (Wing *et al.* 1995; Wing 1998). The influence of the PETM as well as the geographical extent of this decrease in taxonomic diversity is unclear. So far, the only report of a long-term decrease in richness is from the Bighorn Basin (Wing *et al.* 1995; Wing 1998), although pioneering work from the eastern US Gulf Coast suggests a sharp decrease in taxonomic diversity that is present in the latest Palaeocene or earliest Eocene (Frederiksen 1994, 1998). Frederiksen (1994) coined the phrase the ‘Late Paleocene Extinction Event’ for this diversity decline. A previous study on the taxonomic diversity dynamics of the eastern US Gulf Coast failed to detect any long-term (e.g. >1 Ma) decrease in taxonomic diversity that paralleled the records from the Bighorn Basin (Frederiksen 1994, 1998). Pollen records from tropical South America are compromised by poor temporal correlation potential with North America but show some decrease in taxonomic diversity in the latest Palaeocene (Rull 1999; Jaramillo & Dilcher 2000; Jaramillo 2002; Jaramillo *et al.* 2006). There are limited data from other geographical areas. Hence, the only robust record of change is from the warm-temperate or subtropical Bighorn Basin. The paratropical US Gulf Coast record requires reappraisal to test the veracity of the initial findings by Frederiksen (1994) on diversity changes in the Late Palaeocene–Early Eocene.

Stratigraphy of the eastern US Gulf Coast

We chose the US Gulf Coast as a suitable paratropical region for palynological investigation because it contains sediments conducive for palynological research (Elsik 1974; Frederiksen 1980, 1988, 1994, 1998; Harrington 2001, 2003a, Harrington *et al.* 2004). The stratigraphy of the eastern US Gulf Coast (Fig. 1) is also well known through multidisciplinary study of pollen, dinoflagellate cysts (Edwards & Guex 1996), planktonic Foraminifera (Mancini 1981; Mancini & Oliver 1981; Berggren *et al.* 1985), calcareous nannoplankton (Gibson *et al.* 1982; Gibson & Bybell 1994), magnetostratigraphy (Rhodes 1995; Rhodes *et al.*

1999) and sequence stratigraphy (Mancini & Tew 1995). The exact position of the PETM is still unknown, although Harrington *et al.* (2004) have suggested that it lies in the upper Tusahoma Formation in Mississippi, based on the presence in the Harrell Core of typical ‘Eocene’ palynomorphs such as *Interpollis microsuplicingensis* and *Brosipollis* spp. (see Tschudy 1973; Elsik 1974; Frederiksen 1980; Harrington 2003b). The Early Eocene is present at the Red Hot Truck Stop in Meridian, Mississippi (Harrington 2003a) because diagnostic early Wasatchian mammal teeth are present in uppermost strata in the Tusahoma Formation (Beard & Dawson 2001). Sediments above the mammal lag at the Red Hot Truck Stop in the Bashi and Hatchetigbee formations contain Early Eocene calcareous nannoplankton and planktonic Foraminifera (Gibson & Bybell 1994), although a short unconformity separates the Tusahoma Formation from the Bashi and Hatchetigbee formations (Frederiksen *et al.* 1982; Ingram 1991; Mancini & Tew 1995; Frederiksen 1998).

The general depositional environments on the eastern US Gulf Coast are muddy strand-line, very shallow marine settings that periodically became emergent and formed swamps that are now preserved as lignites in the upper Tusahoma and Hatchetigbee formations (Mancini 1981; Gibson *et al.* 1982; Mancini & Tew 1995). An attempt to identify the PETM through stable carbon isotopes of some of these lignites in the upper Tusahoma Formation (Harrington *et al.* 2004) failed to find the characteristic -2% to -3% negative $\delta^{13}\text{C}$ excursion (e.g. Kennett & Stott 1991; Bowen *et al.* 2001; Koch *et al.* 2003). In this paper, we use the first occurrence of sporomorphs characteristic of the Early Eocene in North America (Frederiksen 1995, 1998; Harrington 2003b), as a proxy for the Palaeocene–Eocene boundary and accept that this is a probable, rather than unequivocal indication of the boundary. The Eocene sporomorph suite includes the following sporomorph taxa: *Granulatisporites luteticus*, *Nuxpollenites* spp., *Celtis tschudyii*, *Interpollis microsuplicingensis*, *Thomsonipollis sabinetownensis*, *Brosipollis* spp., and *Platycarya* spp. (Tschudy 1973; Elsik 1974; Frederiksen 1980, 1998; Harrington 2001, 2003a, b; Harrington *et al.* 2004).

Materials and methods

Study sections

Seven sections (Fig. 1) from eastern Mississippi (eight samples from Ackerman Mine; 69 samples from Knight Core number 1; 82 samples from Harrell Core number 1; 14 samples from Red Hot Truck Stop), western Alabama (19 samples from Bear Creek; 20 samples from Hatchetigbee Bluff) and western Georgia (five samples from Fort Gaines) preserve Late Palaeocene or Early Eocene pollen assemblages that can be dated with varying degrees of precision. The stratigraphic context and composition of the Harrell, Red Hot Truck Stop, Bear Creek and Hatchetigbee sections have been discussed previously (Harrington 2001, 2003a, Harrington & Kemp 2001; Harrington *et al.* 2004). Ackerman Mine and Fort Gaines may be age equivalent and span the boundary between the Nanafalia–Tusahoma formations (Fig. 1). However, the distance between them is great (>500 km) and the degree of diachroneity at the base of the Tusahoma Formation is unknown on any precise time scale. We include these sections only because they provide valuable information on the diversity and composition of the upper Nanafalia Formation. The majority of samples are from the Tusahoma Formation from Lauderdale County, Mississippi, which spans the final c. 1 Ma of the Palaeocene (Berggren *et al.* 1985; Frederiksen 1998). All the samples represent deposition in a strand-line or estuarine setting, with the exception of Ackerman Mine, which represents a swamp environment. The sections are depositionally similar to one another to minimize taphonomic bias, although Bear Creek and Fort Gaines may represent relatively more distal facies because they contain some dinoflagellate

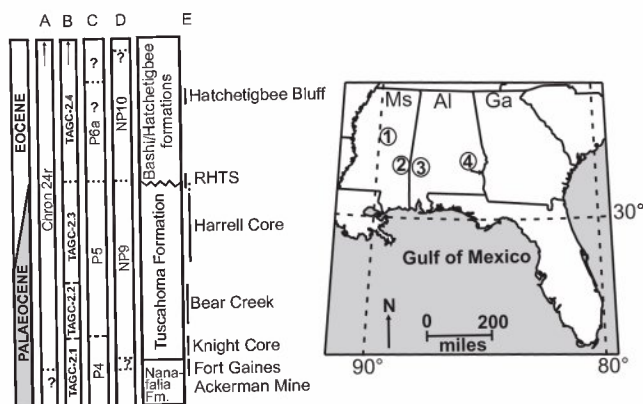


Fig. 1. Stratigraphy of the eastern US Gulf Coast presented against (a) magnetostratigraphic time scale (Rhodes 1995; Rhodes *et al.* 1999), (b) sequence stratigraphy (Mancini & Tew 1995), (c) planktonic foraminiferal zones (Mancini & Oliver 1981; Berggren *et al.* 1985), (d) nannoplankton zones (Gibson & Bybell 1994), and (e) stratigraphic position of sections together with a map showing the location of sampled sections. RHTS, Red Hot Truck Stop. 1, Ackerman Mine; 2, Knight Core; Harrell Core and Red Hot Truck Stop; 3, Bear Creek and Hatchetigbee Bluff; 4, Fort Gaines.

cysts (Harrington 2001; Harrington & Kemp 2001) and Ackerman Mine is predominantly lignites and represents very shallow coastal environments. The Knight Core is taken from Lauderdale County, Mississippi near Meridian (Section 20, Township 6N, Range 20E) and represents sediments deposited in the uppermost part of sequence cycle TAGC 2.1 (Fig. 1) in the 20 m below the Greggs Landing Marl in the lower Tuscahoma Formation. The chronological order of sections is determined by their position relative to marl members within the Tuscahoma Formation and to the sequence cycle in which they belong. The position of the PETM is not known exactly on the US Gulf Coast but it falls in the upper Tuscahoma Formation in the upper part of cycle TAGC 2.3 (Harrington *et al.* 2004). Pollen assemblages from the Red Hot Truck Stop are earliest Eocene and may lie within part of the PETM or immediately above it (Harrington 2003a) because Early Eocene mammals are found in some lag deposits here (Beard & Dawson 2001). The first occurrence of 'Eocene' pollen occurs within the Harrell Core; this may overlap partially with strata within the Red Hot Truck Stop, which contain a fuller suite of these immigrant taxa (Harrington 2003a).

Sporomorph analysis

A combined total of 225 samples were taken for palynological analysis from the seven sections. Sample preparation followed a basic procedure of maceration with mortar and pestle, chemical digestion of carbonates (HCl) and silicates (30% HF) followed by light oxidation to remove excess amorphous organic material (2 min in 70% HNO₃). Residues were stained with safranin and aliquots were mounted evenly onto two coverslips. Between most stages, residues were sieved with a 10 µm mesh. More than 400 spore and pollen grains were counted for most samples, although some samples proved less productive. Smaller sample sizes (e.g. 170–200 grains) reflect this disparity in yield.

Statistical methods

Both composition and diversity are of interest in this paper, and a variety of techniques were used to explore these components of the sporomorph assemblages. Detrended correspondence analysis (DCA) was used on presence-absence (= incidence) data to graphically represent compositional differences in co-occurrence patterns of taxa between different sections over time. The MVSP program (Kovach 1998) computed the DCA. A 2D space is created by plotting axis 1 sample scores against axis 2 sample scores within which samples are located depending on their composition. If samples are clustered close together, this demonstrates that they have strong compositional similarities.

To assess changes in taxonomic diversity, several methods were employed. The number of taxa present in each sample was calculated using standard range-through assumptions to provide an estimate of standing richness, as follows. Taxa were recorded as present in a sample if they are known from strata both above and below even if they are not actually present within a sample. All singleton taxa were removed because these are subject to factors such as sampling intensity (Wing 1998). Standing richness is robust to sampling intensity and immune to lithofacies changes. To decrease edge effects, ranges of taxa from the sections at the base and top of the sequence were taken from published sources (Tschudy 1973; Elsik 1974; Frederiksen 1980, 1994, 1998). The variable sedimentation rates and questionable completeness of the sedimentary record on the Gulf Coast means that confidence intervals such as those advocated by Holland (2003) are not suitable for application to estimate stratigraphic ranges of the sporomorph taxa.

A separate set of statistical analyses were undertaken on the samples from within selected sections that represent the same or similar depositional environments to compare between-sample diversity. These sections are the Knight Core, the Harrell Core, the Red Hot Truck Stop and Hatchetigbee Bluff (Fig. 2). The relative stratigraphic order of these four sections is confidently known. The Harrell Core is split further into a lower part, which represents all samples that are unequivocally Palaeocene because they lack diagnostic Eocene taxa, and an upper part, which is characterized by the first occurrences of taxa that identify the Eocene on the US Gulf Coast (Harrington *et al.* 2004). Hence, there are five sections with multiple samples that have been statistically examined to

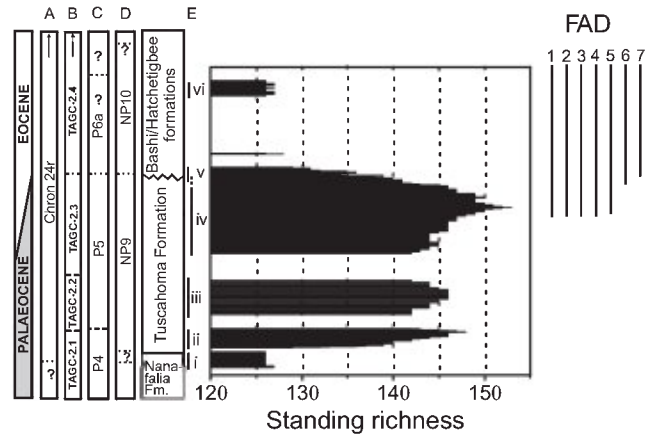


Fig. 2. Sedimentary logs of the Knight Core, Harrell Core, Red Hot Truck Stop and Hatchetigbee Bluff showing sampling positions.

estimate taxonomic diversity. These sections are referred to as bins and are examined by richness estimators commonly used by ecologists (Colwell & Coddington 1994; Coddington *et al.* 1996; Magurran 2004). We used Chao 2 and Jackknife 2. These techniques were originally devised to study sampling units that invariably refer to area (e.g. quadrats, kilometre squared areas) and their performance is well modelled (Magurran 2004). But time can be substituted for space and these techniques can be used to estimate time-series data (Colwell & Coddington 1994) such as the pollen data presented here. The choice of metric follows recommendations by Colwell & Coddington (1994), Coddington *et al.* (1996) and Magurran (2004).

Both Chao 2 and Jackknife 2 extrapolate, rather than interpolate, the number of species that any given bin may contain. Extrapolation is useful because diverse datasets, such as the US Gulf Coast pollen record (Harrington 2001; Harrington *et al.* 2004), can have many taxa that are rare and not present consistently in every sample. Such rare taxa are often more important for estimating taxonomic diversity than common taxa (Colwell & Coddington 1994; Magurran 2004). Chao 2 (Chao 1987; Colwell & Coddington 1994) is sensitive to high-diversity datasets but can predict richness at low numbers of samples. Chao 2 requires statistical reiteration and knowledge on the number of species found in only one sample (uniques) and the number of species found in just two samples. It reaches its maximum estimates when all taxa except one are uniques and considers the collection complete when all taxa occur in at least two samples (Coddington *et al.* 1996). The jackknife family of metrics has also been positively reviewed (Brose *et al.* 2003), especially the second-order jackknife, or Jackknife 2 (Colwell & Coddington 1994; Magurran 2004). Jackknife 2 also requires incidence data and reaches its maximum values when all species are uniques. It takes the number of taxa present in one sample only and in exactly two samples into account. Jackknife 2 is identical to Chao 2 in considering an inventory complete when all taxa are known from at least two samples (Coddington *et al.* 1996). In this study, we have randomized all statistical metrics 1000 times, which has allowed us additionally to calculate one standard deviation around the mean for the pooled samples. The success of both methods depends on whether the curve saturates quickly and stops estimating taxa by the time the collection is complete, and both methods can be used to study richness with a small number of samples that is less than the number of samples within a complete inventory.

In ecological area studies, the expected number of taxa is a function of the properties of the area under investigation and the factors that affect this. These can include the size of the area, the heterogeneity of habitat, local climate, soils, disturbance regimes, differences in evenness of the community, and patchiness. There are important caveats that need to be established when using these techniques with palaeontological data. In palaeontological studies the time series could be affected by how much time a bin contains, the range of lithofacies, variations in climate,

immigration, and temporary extirpation, extinction and speciation events. Most of these influences are analogous to ecological factors, but immigration, speciation and extinction (see Foote 2000) are important exceptions that may play a significant role in inflating richness estimates if a bin contains a significant period of time with a gradual turnover in community membership.

To test the effectiveness of the estimators, we used rarefaction to examine empirical within-bin diversity as a function of numbers of taxa at any given number of pooled samples. Rarefaction was required because all the bins have different numbers of samples within them. If rarefied estimates are plotted on the x -axis as increasing sample sizes against expected numbers of taxa on the y -axis, the shape of the cumulative rarefaction curves provides information on how evenly distributed the taxa are within samples (Olszewski 2004) and how many taxa can be expected if the sampling effort was reduced (Miller & Foote 1996). The Coleman rarefaction method (without sample replacement) allows the standardization of all bins through interpolation to the same number of samples within any given bin (Foote 1992; Miller & Foote 1996). EstimateS version 7.5 (Colwell 2005) was used to calculate rarefaction curves and variance around the mean as well as the richness estimators. We also used rarefaction to examine within-sample diversity. In these separate analyses, we compared all samples within each bin at the same number of counted specimens (171 sporomorph grains per sample). The program BioDiversity Pro (McAleese *et al.* 1997) was used to compute these within-sample statistics. The statistical distribution of the pollen data is difficult to determine even after statistical manipulation. Hence, we use the non-parametric Mann–Whitney U-test and Kruskal–Wallis one-way ANOVA (Sokal & Rohlf 1980) to test statistical

significance of variables such as DCA sample scores and within-sample rarefied richness.

Results

Diversity

Standing richness estimates (Fig. 3) provide some approximation of the taxonomic diversity dynamics on the US Gulf Coast. A number of trends are apparent. The flora shows a strong increase in taxonomic richness at the Nanafalia–Tuscahoma Formation boundary *c.* 1 Ma before the Palaeocene–Eocene boundary (also observed by Frederiksen 1998). There are some fluctuations in taxonomic diversity in the Late Palaeocene but diversity remains consistently high if average range-through values are considered in the Knight Core and both lower and upper Harrell Cores (Table 1). A rapid increase in diversity is recorded immediately prior to the first occurrence of taxa that we consider typical of Eocene assemblages (Fig. 3). A significant decrease in taxonomic diversity that reaches a nadir in the lowermost Bashi–Hatchetigbee Formation follows the spike in peak diversity in the upper Tuscahoma Formation. Samples from Hatchetigbee Bluff show no recovery from this diversity decline but rather a stable level of taxonomic diversity comparable with the upper Nanafalia Formation. Samples from the upper part of the Red Hot Truck Stop have lost *c.* 20% of the taxa ($n = 37$) that are present in the

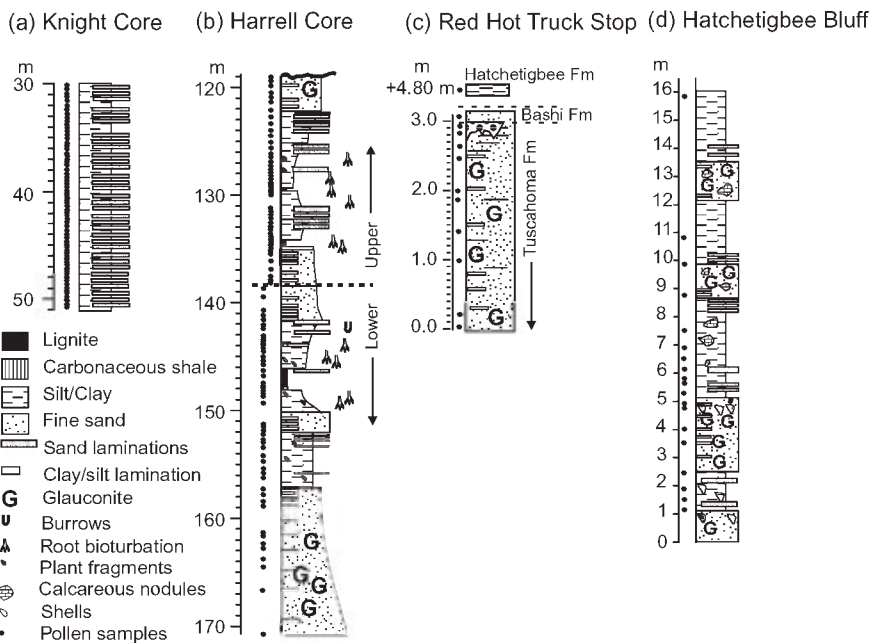


Fig. 3. Standing richness (range-through taxonomic diversity) on the eastern US Gulf Coast presented against the same stratigraphy as shown in Figure 1. (i) Ackerman Mine and Fort Gaines; (ii) Bear Creek; (iii) Knight number 1 Core; (iv) Harrell Core; (v) Red Hot Truck Stop; (vi) Hatchetigbee Bluff. First appearance data (FAD) for: 1, *Granulatisporites luteicus*; 2, *Nuxpollenites* spp.; 3, *Celtis tschudyii*; 4, *Interpollis microsupplingensis*; 5, *Thomsonipollis sabinetownensis*; 6, *Brosipollis* spp.; 7, *Platycarya* spp.

Table 1. Maximum estimates of richness using Chao 2 and Jackknife 2 for the sampled sections from the eastern US Gulf Coast

Estimator	Knight Core	Lower Harrell Core	Upper Harrell Core	Red Hot Truck Stop	Hatchetigbee Bluff
Number of samples	69	53	38	14	20
S_{obs}	136	155	152	112	102
Range-through	143	146	147	131.5	126
Chao 2	147	173	172	138	110
Jackknife 2	159	186	186	150	118
$E_{S(n=14)}$	101	122	127	110	98

S_{obs} , actual number of taxa within each bin; $E_{S(n=14)}$, Coleman rarefaction for 14 samples.

most diverse part of the upper Harrell Core in the upper Tuscaloosa Formation. These 37 taxa are not observed higher in the stratigraphic record and are not recorded in any other palynological investigations of the Early Eocene (e.g. Tschudy 1973; Elsik 1974; Frederiksen 1980, 1998). These taxa represent regional extinctions in the Late Palaeocene–Early Eocene. However, there is a substantial edge effect that affects the standing richness estimates. Low richness at the beginning and end of the time interval under review could be an artefact of the range-through estimation method.

Results from richness estimators confirm the broad pattern of results derived from standing richness. Each bin contains a different number of actually observed species (S_{obs}) (Table 1). Chao 2 and Jackknife 2 agree with one another on the number of taxa expected within each bin (Table 1; Fig. 4). Jackknife 2 estimates are consistently greater than those of Chao 2 but both metrics agree that there is an increase in richness throughout the Tuscaloosa Formation (Harrell Core) in the Late Palaeocene, followed by a decrease in the earliest Eocene (Red Hot Truck Stop) that carries forward into the Early Eocene (Table 1, Fig. 4). Depending on the estimator, one would expect between 147 and 159 taxa in the Knight Core, rising to 173–186 taxa in the lower Harrell Core. This represents an increase in taxonomic richness of 17–23% throughout the Late Palaeocene (Table 1). About the same number of taxa are expected in the upper Harrell Core but this is post-dated in the Red Hot Truck Stop by a drop to 138–150 expected taxa. A further decrease in expected richness is observed in Hatchetigbee Bluff, to 109–118 taxa. These results are independent of the number of samples within each bin (Table 1). These trends are confirmed by rarefaction, which compensates for the differences in sampling intensity (Table 1).

An important consideration for evaluating richness estimators, in addition to the maximum estimate of species richness expected if all samples are pooled within a bin, is the shape of the expected richness curve with increasing sampling intensity (Fig. 4). Chao 2 (Fig. 4) shows the same rankings of bins as Jackknife 2, with the richest bins stabilizing and predicting the number of taxa after *c.* 18 samples have been pooled. However, the Hatchetigbee Bluff section saturates after about 14 samples

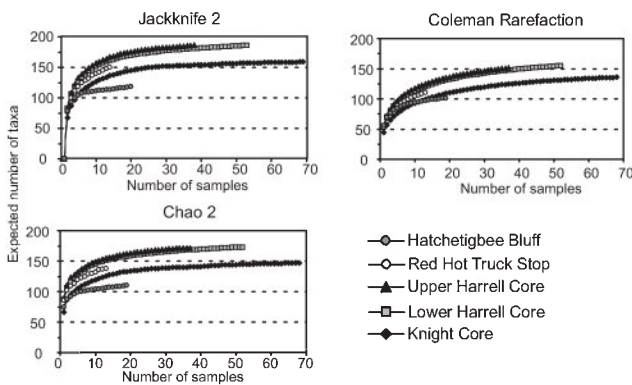


Fig. 4. Estimates of taxonomic richness using Jackknife 2, Chao 2 and Coleman rarefaction estimates from five sections on the eastern US Gulf Coast. Estimates are plotted as increasing numbers of pooled samples along the *x*-axis against expected number of species on the *y*-axis. To aid visual inspection of the estimates, 95% error bars are not plotted. The first estimate using one sample only is not plotted for Chao 2 because this estimate is extremely large and distorts the *y*-axis scale.

because it is taxonomically less rich. The Red Hot Truck Stop is under-sampled but has an estimation curve identical to that of the Knight Core, lower Harrell Core and upper Harrell Core bins. The Coleman rarefaction data (Fig. 4), which show the expected number of taxa through interpolation, confirm the results of the richness estimators. Rarefaction also demonstrates that there are differences in evenness between some of the bins because the rarefaction curve for Hatchetigbee Bluff saturates at a much lower number of pooled samples than the Knight Core (Fig. 4). This means that the taxa within the Hatchetigbee Bluff bin are relatively more evenly distributed compared with the Knight Core, which has a rarefaction curve that climbs slowly and saturates at higher levels of sampling intensity. The Hatchetigbee Bluff section is more even both between and within samples (Fig. 5). All the bins have different average numbers of taxa within samples (Fig. 5) and are significantly different from one another, as demonstrated by a Kruskal–Wallis one-way ANOVA on the five bins ($KW = 62.53$, $P < 0.0001$). However, there are clear distinctions between the Knight Core and both lower and upper Harrell Cores compared with the other two younger bins (Fig. 5). Whereas the Hatchetigbee Bluff bin is significantly more diverse within samples than the Knight Core ($U = 84$, $P < 0.0001$), the lower Harrell Core ($U = 215$, $P < 0.0001$) or upper Harrell Core ($U = 124$, $P < 0.0001$), there is no statistically significant difference between Hatchetigbee Bluff and the Red Hot Truck Stop ($U = 133$, $P = 0.6128$). Whereas Tuscaloosa samples (Knight Core and both parts of the Harrell Core) have an average of 29 taxa if 171 grains are counted, the Bashi–Hatchetigbee Formation samples have an average of 35 taxa if 171 grains are counted. This result is statistically significant ($U = 4007$, $P < 0.0001$). Hence, although the Eocene samples tend to have more taxa within samples, this does not lead to greater taxonomic diversity between samples. Eocene samples

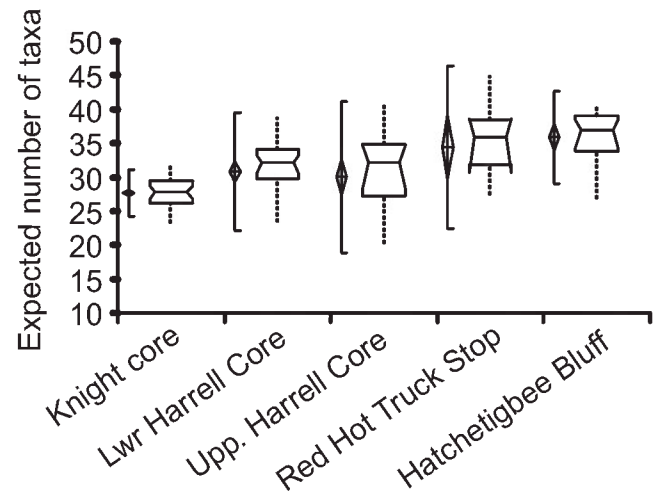


Fig. 5. Box and whisker plot of rarefied within-sample richness at 171 counted grains from the Knight Core, lower and upper Harrell Cores, Red Hot Truck Stop and Hatchetigbee Bluff. The open diamond represents the mean and 95% confidence interval around the mean. The bracket within which the diamond is centred on is the 95% parametric percentile range. The box represents the median (central horizontal line), the 95% confidence interval around the median (the sloped part of the box either side of the median), and the interquartile range (the top and bottom horizontal lines of the box).

therefore have higher alpha diversity, but beta diversity is lower, leading to more homogeneous floras with low turnover rate.

One essential problem with the estimators, and the rarefaction analysis, is the duration of the bins. There is no method to correct for this. However, we have split the upper 12 m of the Harrell Core, which should be compositionally similar and taphonomically comparable with the Red Hot Truck Stop, into four 3 m bins and re-ran Coleman rarefaction, Jackknife 2 and Chao 2 analyses. These estimates (Fig. 6) correct, to some degree, the disparity in bin duration that we assume is present. They show that in the same thickness of stratigraphic section the Red Hot Truck Stop contains similar, but still lower, numbers of taxa compared with the upper Harrell Core. The richness estimators continue to show that the Harrell Core samples probably contain more taxa than the Red Hot Truck Stop. Assemblages in the Harrell Core have more taxa that are present as rare, singleton occurrences.

Composition

The early Palaeogene palynofloras on the eastern US Gulf Coast contain an unusual admixture of plant families with modern predominantly temperate affinities, such as Juglandaceae (walnut family), Betulaceae–Myricaceae (birches, sweet gales), and Ulmaceae (elms) together with many families of mainly subtropical to tropical affinity (Harrington *et al.* 2004) including Anacardiaceae (mangoes–cashews), Annonaceae (sweetsop), Apocynaceae (oleanders), Bombacaceae (balsa), Burseraceae (frankincense) Palmae (palms) and Symplocaceae (tea family). The flora of the Gulf Coast is distinctly different from that of any other region within North America during the Late Palaeocene and Early Eocene (Frederiksen 1980, 1998; Harrington 2003b, 2004). There are very few similarities with South America during the Palaeocene; previous estimates from literature reviews indicate that *c.* 0.7% of South American taxa are

shared with the US Gulf Coast (Jaramillo & Dilcher 2001). We tested this result with primary data from our slides of palynomorphs from North and South America that represent the Late Palaeocene and Early Eocene and found some family level correlations; for instance, for Annonaceae, Bombacaceae and Palmae, which are present on both continents, although only a handful of morphospecies are shared. These include annonaceous *Proxapertites magnus* (= *Matanomadhiasulcites maximus* of Frederiksen 1998), the Araceae *Proxapertites psilatus*, a systematically unknown periporate taxon *Multiporopollenites pauciporatus* (Jaramillo & Dilcher 2001), and a single occurrence of the monolet fern *Cicatricosporites* sp. All other taxa on the US Gulf Coast are either shared with other areas of North America or are unique (Frederiksen 1980; Harrington 2004).

DCA on presence–absence data from all seven sections demonstrates (Figure 7) that there is a clear compositional difference between Late Palaeocene and Early Eocene samples. If samples are split by region, Palaeocene samples from Mississippi belong to a different population from samples that are Eocene in composition. In this case, we drop 35 equivocal Eocene samples from the top of the Harrell Core that contain Eocene indicators but include the 13 samples from the Red Hot Truck Stop that are more arguably Eocene (Harrington 2003a). This temporal split is statistically significant for both axis 1 sample scores ($U_{(133,13)} = 1725$, $P < 0.0001$) and axis 2 sample scores ($U_{(133,13)} = 1710.5$, $P < 0.0001$). The secular divisions in composition are repeated for the Alabama–Georgia samples, which are also significantly different between the Palaeocene and Eocene for both axis 1 sample scores ($U_{(24,20)} = 470$, $P < 0.0001$) and axis 2 scores ($U_{(24,20)} = 475$, $P < 0.0001$). The composition shifts illustrated by DCA reflect changes in the co-occurrence patterns of taxa because the input data are presence–absence.

Discussion

The US Gulf Coast pollen data show two interesting results: the first is an increase of *c.* 15% in taxonomic richness within the Late Palaeocene associated with a shift in composition, and the second is a pronounced *c.* 35% decrease in diversity in the Early Eocene that is accompanied by associated changes in the co-occurrence

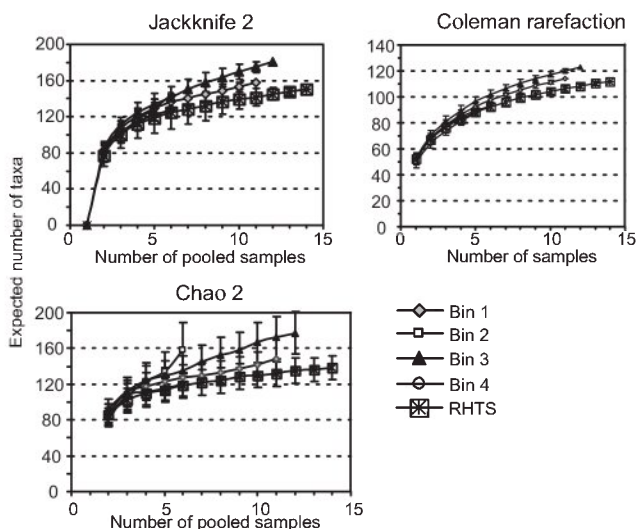


Fig. 6. Estimates of taxonomic richness using Jackknife 2, Chao 2 and rarefaction estimates from four 3 m bins from the top 12 m of the Harrell Core sections and from the Red Hot Truck Stop (RHTS). Estimates are plotted as increasing numbers of pooled samples along the x-axis and expected number of species on the y-axis. Estimates based on one sample are not plotted for the Chao 2.

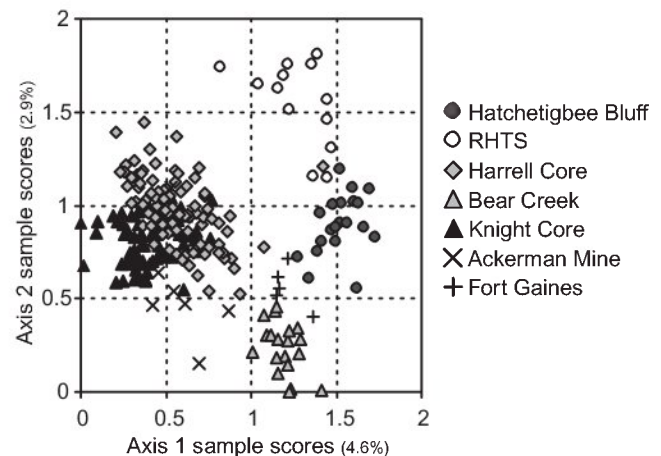


Fig. 7. Detrended correspondence analysis on incidence data from Ackerman Mine, Fort Gaines, Bear Creek, the Knight Core, the Harrell Core, the Red Hot Truck Stop (RHTS) and Hatchetigbee Bluff. Axis 1 sample scores are plotted against axis 2 sample scores.

patterns of range-through taxa. The Eocene diversity decrease and composition change is mediated in part by a *c.* 20% regional extinction in sporomorphs. These results confirm previous work by Frederiksen (1998) and suggest that even though the number of samples in our study is an order of magnitude greater than Frederiksen's the same result is observed. The increase in taxonomic richness may be a result of climate warming throughout the last 1 Ma of the Late Palaeocene that is evident from US continental interior leaf margin analysis (Wing 1998; Wing *et al.* 2000), and terrestrial and globally averaged deep-water stable oxygen isotope records from various proxies (Fricke *et al.* 1999; Zachos *et al.* 2001; Koch *et al.* 2003; Fricke & Wing 2004). The apparent increase in standing richness between the Nanafalia–Tusahoma formations *c.* 1 Ma before the P–E boundary may correlate with similar patterns observed in Wyoming across the Tiffanian–Clarkforkian land mammal age boundary (Wing *et al.* 1995; Wing 1998; Wilf 2000), which also is around 1–1.2 Ma before the PETM (Gingerich 2003), and in northern South America (Jaramillo *et al.* 2006).

The epithet 'Terminal Paleocene Extinction Event' (Frederiksen 1994) is wholly appropriate for the taxonomic decrease in the upper Tusahoma or lower Bashi–Hatchetigbee formations. If 20% is a realistic estimate of palynomorph extinction across the Late Palaeocene–Early Eocene interval, which has also been estimated by Frederiksen (1998), then it qualifies as a major Cenozoic plant extinction event. To put this figure in perspective, Wilf & Johnson (2005) reassessed the plant extinction rate at the K–T (Cretaceous–Palaeocene) boundary in North Dakota (USA) and found that 57% of the megafloora became extinct at the K–T boundary. In comparison, 30% of the palynoflora (Johnson *et al.* 1989; Nichols 2002) became extinct at the K–T boundary from the same sections. Assuming that the palynoflora truly underestimates extinction by a factor of *c.* 50% relative to the megafloora at the K–T boundary, this could equate to an extinction rate of *c.* 40% of plants on the US Gulf Coast in the Early Eocene. The majority of angiosperm plants on the US Gulf Coast were probably animal pollinated in the same way that modern tropical forests are dominated overwhelmingly by animal-pollinated plants (Bush 1995; Bush & Rivera 1998). Animal-pollinated plants tend to produce pollen in low abundance that tends also not to transport easily into depositional settings where pollen may be readily encountered (Bush 1995; Bush & Rivera 1998). Hence, the pollen record will underestimate the true picture of plant diversity changes throughout the Late Palaeocene–Early Eocene interval on the US Gulf Coast.

Statistical artefacts?

An important consideration is whether the results represent a statistical artefact and reflect the vagaries of the sedimentary record on the US Gulf Coast, the sampling protocol and the metrics used to estimate taxonomic diversity more than primary change in plant diversity. A lack of samples in the lower Bashi–Hatchetigbee formations will bunch the last occurrence of extinction taxa into the upper Tusahoma Formation even though they may go extinct some time in the Early, but not necessarily earliest, Eocene. This will result in a sharp decrease in standing richness in the upper Tusahoma Formation. Although we observe such a result, this does not dispute our finding that extinction does occur. It merely confounds attempts to delimit the timing of extinction. A conservative estimate therefore places the extinction interval anywhere from the first introduction of immigrants in the upper Harrell Core but before deposition of the Hatchetigbee Bluff section. The obvious candidate causing

such a decline in standing richness is cooling in the Early Eocene that occurs after the PETM but before the Early Eocene Climatic Optimum *c.* 2 Ma after the PETM (Wing *et al.* 2000). This cool period correlates with the lowest standing richness of plants in the Bighorn Basin (Wing 1998; Wing *et al.* 2000). Standing richness estimates do not permit us to dismiss this possibility.

Under-sampling of the basal Bashi–Hatchetigbee formations will have no impact on the performance of the richness estimators on binned data. In addition, the bins should not be affected by the cool interval unless it is actually contained partially or wholly within a bin. We are confident that the Eocene bins do not contain the cool period; the Red Hot Truck Stop section contains early Eocene mammals that belong to the early Graybullian subdivision of the Wasatchian land mammal age (Beard & Dawson 2001), and is thus too old to contain this cool interval, which occurs in the late Graybullian subdivision (Wing *et al.* 2000). Stable oxygen isotopic data from *Venericardia* spp. shells in the central part of the Hatchetigbee Bluff section show clearly that Hatchetigbee Bluff was hot with a mean annual temperature of 26–27 °C and low seasonality of temperature at about 1 °C (Ivany *et al.* 2004). Furthermore, the composition of these palynofloras is similar to those from the Red Hot Truck Stop. Hence, the Eocene bins probably do not record a significant cooling signal.

The duration of time within each bin will affect the resulting richness estimate. This bias was identified by Wing (1998), who managed to scale estimates of bootstrapped diversity to the size of each bin he reviewed in the Bighorn Basin. This procedure is possible only if there is a robust and continuous chronostratigraphic model with no breaks in sedimentation. The US Gulf Coast lacks such temporal precision and it is not possible to estimate time within bins. It is unlikely that an individual bin exceeds more than a few 100 ka. For example, the Tusahoma Formation has a duration of *c.* 1 Ma and represents at most *c.* 107 m of section in Mississippi (Gibson & Bybell 1994; Mancini & Tew 1995) but no bin exceeds 25 m in stratigraphic section in the Tusahoma Formation. With increasing time the probability increases that extrinsic factors, such as climate change, and intrinsic factors, such as competition, immigration and speciation, will lead to community change. However, the estimator will predict maximum diversity, which assumes that all taxa coexist at the same time. We have demonstrated that the Red Hot Truck Stop would still contain fewer taxa than the rest of the upper Tusahoma Formation if the same number of samples were studied regardless that the Red Hot Truck Stop, as a whole, is undersampled. This provides support for placing an Eocene decrease in diversity early in the Early Eocene. The decrease in taxonomic diversity is real and not totally a statistical artefact.

Mechanisms

The causes for the extinction and diversity decline on the US Gulf Coast are unknown. If cooling is discounted, then some direct or indirect impact from the PETM is probable. Our data are not sufficiently resolved to tackle the cause but several triggers can be hypothesized, although few can be tested with empirical palaeontological data. These include: (1) possible continental-scale drying during part of the PETM, which has so far been postulated only for parts of the Bighorn Basin (Wing *et al.* 2005); (2) negative feedbacks on plant communities from increased atmospheric CO₂ fertilization; this assumes that there is an increase in CO₂ during the PETM (see Gingerich 2003; Zachos *et al.* 2005); (3) changes in animal trophic structure, which are proved from other parts of North America with the

appearance of Eocene mammals (Clyde & Gingerich 1998) that also occur on the US Gulf Coast (Beard & Dawson 2001) and which may detrimentally change animal–plant interactions for herbivory (Terborgh *et al.* 2006), seed dispersal and/or pollination; (4) climate warming that is too fast for plants to change geographical range. This last theory is probably discountable because tropical plants can respond extremely rapidly to warming (Bush *et al.* 2004; Huguen *et al.* 2004) and Palaeogene plants could change geographical ranges rapidly too (Wing *et al.* 2005). However, our data do offer an explanation for the suppressed levels of diversity in the Early Eocene. The flora of the US Gulf Coast is unique and geographically constrained (Harrington 2004). Tropical plants did not interchange between North and South America with ease. Hence, the only major routes into the US Gulf Coast are through high latitudes, which were cooler than the Gulf Coast during the early Palaeogene (Greenwood & Wing 1995; Fricke & Wing 2004) and unlikely to support plants ideally suited to the warmth of the US Gulf Coast. Essentially, the eastern US Gulf Coast was like an island that took time to either evolve new species or recruit them from immigration after an Early Eocene cull. Frederiksen (1980, 1988) has shown that taxonomic diversity was not replenished until the Early Eocene Climatic Optimum, which demonstrates a considerable recovery time of *c.* 2 Ma.

Conclusions

The Late Palaeocene–Early Eocene pollen floras of the eastern US Gulf Coast were diverse and responsive to environmental changes. The flora shows a notable increase in taxonomic diversity across the Nanafalia–Tusahoma Formation boundary *c.* 1 Ma before the Palaeocene–Eocene boundary. There is an increase of 15% in taxonomic diversity from the lower to upper Tusahoma Formation that probably represents a response to the well-documented climate warming throughout the latest Late Palaeocene. Contrary to previous reports (Harrington *et al.* 2004), diversity decreases with the first occurrence of typical Eocene taxa and there is a sharp decrease in taxonomic diversity in the upper Tusahoma Formation that cannot be explained solely by taphonomic or statistical artefacts. Results from the combined Early Eocene sections demonstrate extinction across the Palaeocene–Eocene boundary of *c.* 20% of sporomorph taxa and a diversity decline of up to 37% between the most diverse Palaeocene bin and the least diverse Eocene bin. Techniques for estimating taxonomic diversity such as classic standing richness can be combined with richness estimators such as Chao 2 and Jackknife 2 to provide more informed estimates of taxonomic diversity. Differences in evenness between Palaeocene and Eocene assemblages affect the estimates but still show the Eocene as significantly less rich than the Palaeocene. Our results show that even ancient tropical ecosystems in equable greenhouse climates, such as those climates present in much of the early Palaeogene, were highly susceptible either directly or indirectly to perturbations in climate and changes in environment.

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