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Structure of the North American vegetation gradient during the late Paleocene/early Eocene warm climate

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ABSTRACT

Late Paleocene/early Eocene pollen and spore data taken from the US Gulf Coast (paleolatitude 32°N), western interior basins (Wyoming, North Dakota; paleolatitude 44–47°N) and Canadian Arctic (paleolatitude > 68°N) represent a vegetation proxy for ancient paratropical, subtropical and temperate biomes. These data provide information on the latitudinal diversity gradient of plants during an ancient greenhouse climate with non-freezing winters at polar latitudes. Comparing pollen data from the early Paleogene with a pollen data set compiled at the same latitudes from the late Holocene (3000 years B.P. to present) reveals that the diversity gradient between middle to high latitudes was steeper than today at the same sampling intensity. The gradient is a step-like decrease of about 50% in taxonomic diversity with increasing latitude between regions. The diversity gradient is formed by the 'spillover' of paratropical taxa into other regions of North America, which reflects the modern pattern of plant ranges. Taxa present in the Arctic, therefore, have great geographic ranges with endemism greatest in the paratropical biome. Paleogene diversity gradients show that decreasing diversity with increasing latitude is ancient and not dependent upon freezing temperatures.

Keywords: Eocene, latitudinal diversity gradient, North America, Paleocene, palynology, vegetation.

INTRODUCTION

The late Paleocene/early Eocene is characterized by a greenhouse climate with low equator to polar temperature gradients (Zachos *et al.*, 1994, 2001). Vegetation flourished at all latitudes in this equable climate from the poles (Hickey *et al.*, 1983; McIntyre, 1994; McIver and Basinger, 1999; Frederiksen *et al.*, 2002) to the equator (Jaramillo and Dilcher, 2001). However, the latitudinal gradient of vegetation diversity is poorly documented in past greenhouse climates and any knowledge of the gradient during such warm intervals is

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particularly desirable. In this paper, I present an initial attempt to reconstruct the latitudinal diversity gradient of ancient vegetation during the late Paleocene/early Eocene from North America using pollen data.

North America is an excellent continent with which to focus on latitudinal diversity patterns because modern plant diversity is known from the Canadian Arctic through to the Florida everglades and at different sampling scales (e.g. Currie and Paquin, 1987; Gentry, 1988; Qian, 1998; Fine, 2001; Pither, 2003). The underlying processes that control the modern latitudinal distribution of vascular plants are manifold (Currie and Paquin, 1987; O'Brien, 1993; Rosenzweig, 1995; Rosenzweig and Sandlin, 1997; Francis and Currie, 1998, 2003; Huston, 1999; Gaston, 2000; Fine, 2001; Pither, 2003) but a key criterion is climate and specifically energy availability (O'Brien, 1993; Francis and Currie, 1998, 2003). In North America, prolonged freezing during winter is a critical aspect of climate control that modulates the diversity gradient with increasing latitude (Fine, 2001; Pither, 2003). In contrast, freezing temperatures were not a feature of the early Paleogene in North America, even at polar latitudes where mean annual temperatures are estimated from fossil floras (Greenwood and Wing, 1995), stable oxygen isotopes (Tripati *et al.*, 2001) and computer climate modelling (Shellito *et al.*, 2003).

Unfortunately, the coupling of modern pollen assemblage diversity with parent plant diversity is inadequately modelled at large, biome scales, although changes in pollen assemblage composition are interpretable in a latitudinal context (e.g. Fauquette *et al.*, 1999; Haberle and Bennett, 2001). Studies on Holocene pollen data can identify factors that effect the censual capabilities of pollen floras. Hence, in this paper, the pollen data from the late Holocene establish the current *pollen* floral diversity gradient in eastern North America in addition to providing an 'icehouse' counterpoint to the late Paleocene/early Eocene gradient.

Fossil pollen and spores (sporomorphs) are present in sediments from the eastern US Gulf Coast at paleolatitude *c.* 32°N (Harrington, 2001), through the continental western interior at paleolatitude *c.* 44–47°N (Wing and Harrington, 2001; Wing *et al.*, 2003), and into the Canadian Arctic at paleolatitude > 70°N (Doerenkamp *et al.*, 1976; McIntyre, 1989, 1991; Kalgutkar and McIntyre, 1990; Kalkreuth *et al.*, 1996; Frederiksen *et al.*, 2002). All these areas (Fig. 1) represent different vegetation types and can be time-constrained to the late Paleocene/early Eocene (Harrington, 2003a). The US Gulf Coast was paratropical in the late Paleocene/early Eocene and had a mean annual temperature of about 27°C and mean annual range of temperature of about 2°C (Wolfe and Dilcher, 2000). There are no modern analogues for this flora, although it contained plants that have current tropical affinities such as Annonaceae, Bombacaceae, Burseraceae, Myrtaceae, Sapotaceae and Sterculiaceae (Harrington, 2003b). Northern Wyoming and North Dakota had a mean annual temperature of about 11–18°C and represented a warm-temperate/subtropical vegetation type (Hickey, 1977; Wing, 1998). Water stress was lacking in the western interior during the early Paleogene and the precipitation mean was probably similar to modern Pennsylvania (Hickey, 1977; Wilf *et al.*, 1998). The nearest analogue to this vegetation type is today found in Japan, south-east China and the eastern USA (Hickey, 1977). The Arctic floras were temperate (McIver and Basinger, 1999), although the coldest months were <5°C but above freezing (Greenwood and Wing, 1995; Tripati *et al.*, 2001).

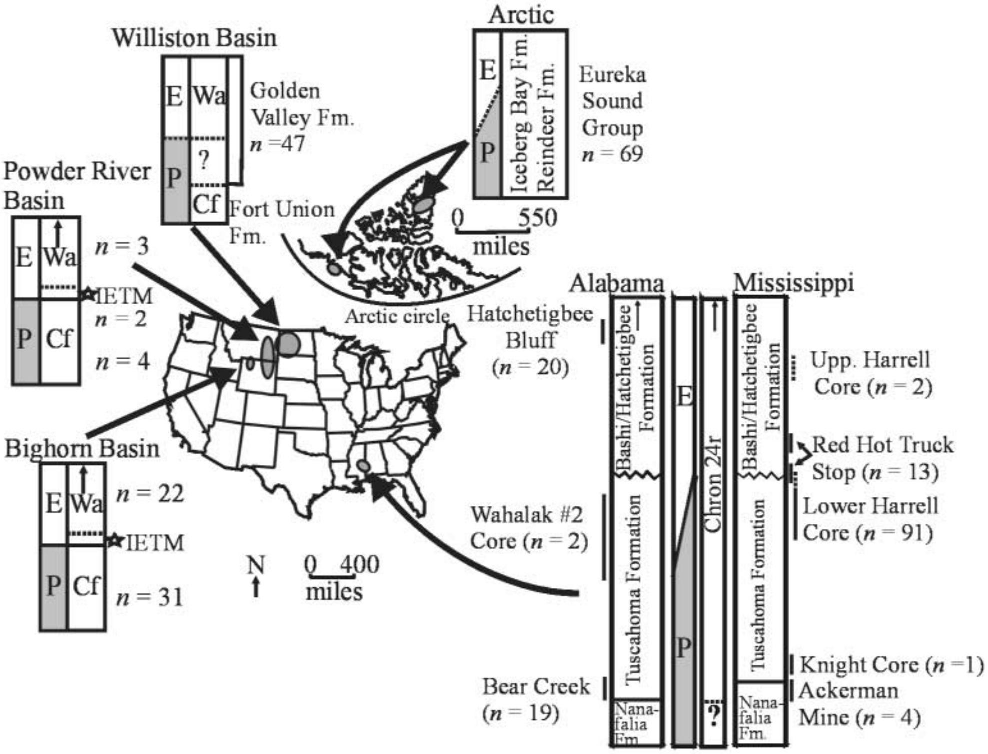

Fig. 1. Location and basic stratigraphy of late Paleocene/early Eocene sampling sites around North America. Numbers (*n* =) refer to the number of samples within each section. P = Paleocene, E = Eocene, IETM = Initial Eocene Thermal Maximum, Cf = Clarkforkian NALMA, Wa = Wasatchian NALMA. The Paleocene/Eocene boundary is not known with certainty in the Arctic but is picked at the first occurrence of *Tilia*-type pollen (Harrington, 2003a).

METHODS AND SECTIONS

Quaternary data

North American pollen data from 53 localities were selected from the Global Pollen Database (www.ngdc.noaa.gov) and are listed in electronic Appendix 1 together with the original contributor references. Localities were chosen that met certain, basic criteria: (1) all localities are below 600 m elevation; (2) they are on the eastern coastal plain and are not water-stressed; (3) they represent infilled lakes; and (4) they have six or more samples that are dated robustly to within the past 3000 years. The transect along eastern North America represents the best comparison to the Paleogene data because the present western interior is at considerable altitude (> 1000 m) with limiting precipitation; interior floras, therefore, are less diverse than lowland coastal regions at comparable latitude in North America (e.g. Currie and Paquin, 1987; Fine, 2001). In most cases, the pollen records from the individual localities from the Canadian Arctic (latitude 73.08°N) through to the Florida everglades (latitude 26.16°N) represent regional pollen floras. Therefore, all aquatic pollen were removed from the data matrix because these represent the extra-local flora and do not provide information on the diversity of the regional flora. The data from all the localities were combined into one matrix and the floral lists were standardized to one another by grouping some species into genera. This is necessary because, in some collections in the Global Pollen Database, pollen types are recognized to genus level only. Hence, some information on species level composition is lost but 192 taxa were recorded in total that represent mainly familial and generic composition.

Paleogene data

Early Paleogene data come from the eastern US Gulf Coast, the western interior and the Canadian Arctic (Fig. 1). The pollen assemblages are from a variety of different depositional environments, which can be split into two basic types: swamps (bogs, wet soils, reduced floodplains, infilled channels) and marginal marine sediments (including estuarine deposits and brackish water strand lines). Swamp samples are provided on the US Gulf Coast by the Ackerman Mine ($n = 4$), Knight Core ($n = 1$), lower Harrell Core ($n = 9$), Wahalak #2 Core ($n = 2$), Red Hot Truck Stop ($n = 2$) and upper Harrell Core ($n = 2$). All these sections are located in eastern Mississippi and western Alabama and occur in the Tuscahoma and Hatchetigbee formations (Fig. 1), which represent the late Paleocene and early Eocene (Gibson *et al.*, 2000). The catchment area for pollen and spores in these samples is local to the swamp and considered para-autochthonous. Samples representing estuarine and marginal marine sediments are present on the US Gulf Coast and come from Bear Creek ($n = 19$), the lower Harrell Core ($n = 74$), the Red Hot Truck Stop ($n = 11$) and Hatchetigbee Bluff ($n = 20$). Each sample represents a much larger catchment area than the swamp samples and potentially includes pollen and spores washed onto the coastal plain from the entire Gulf Coast region. The Bear Creek section is the oldest and lies in Chron 24r (Rhodes, 1995). In the Paleocene, Chron 24r occurs within the Clarkforkian North American land mammal age (NALMA) (Butler *et al.*, 1981), which represents the last 1 million years of the Paleocene. The lower Harrell Core contains part of the upper Tuscahoma Formation and is either late Paleocene or early Eocene. Samples from both the Red Hot Truck Stop (Beard *et al.*, 1995; Harrington, 2003b) and Hatchetigbee Bluff localities are early Eocene (Harrington, 2001). The exact stratigraphic position of the Paleocene/Eocene boundary 54.9 million years ago, as determined by the Initial Eocene Thermal Maximum, is unknown but it lies in the upper Tuscahoma Formation (Harrington, 2001).

Unlike the US Gulf Coast, only swamp samples are available for analysis in the western interior. Samples from the western interior are broadly time correlative with the US Gulf Coast samples and come from the Bighorn Basin ($n = 53$; Wing and Harrington, 2001), Powder River Basin ($n = 9$; Wing *et al.*, 2003) and Williston Basin ($n = 46$; G.J. Harrington, unpublished data). If samples are aggregated from the different basins (Fig. 1), they allow analysis of regional diversity patterns so that comparisons can be sought between the US Gulf Coast and the western interior. Sporomorph assemblages are from the Clarkforkian to early Wasatchian NALMAs and can be dated relative to the Paleocene/Eocene boundary in each basin (Hickey, 1977; Wing and Harrington, 2001; Wing *et al.*, 2003). Chronology in the Williston Basin is less precise than in the Bighorn or Powder River basins, but pollen samples span the uppermost Fort Union Formation and lower Golden Valley Formation that lie in the Clarkforkian to early Wasatchian NALMAs (Hickey, 1977).

Published sources provide information on palynofloras from the Canadian Arctic (Doerenkamp *et al.*, 1976; McIntyre, 1989, 1991; Kalgutkar and McIntyre, 1990; Kalkreuth *et al.*, 1996). All these publications contain photographs of fossil pollen and spores so that sporomorph taxonomy can be standardized with primary collected data from the US Gulf Coast and western interior. These sediments cannot be dated as accurately relative to the Paleocene/Eocene boundary as the other regions, but 69 samples can be dated by some means (mammal remains or dinoflagellate cysts) to the late Paleocene/early Eocene (reviewed in Harrington, 2003a). These samples represent a mix of swamp and marginal marine pollen floras that reflect the regional vegetation type at paleolatitude > 68°N.

Data analysis

A variety of techniques were used to determine whether significant differences existed in floral composition and diversity in different regions within North America. Testing differences in taxonomic diversity here involved analysis of both within individual pollen samples and among collections of pollen samples. In all diversity analyses, from both Holocene and Paleogene sporomorph assemblages, sample count data were used. Rarefaction analysis was used to study within-sample swamp diversity patterns in the Paleogene data using the BioDiversity Pro program (McAleece *et al.*, 1997). Rarefaction analysis allows an assessment of within-sample diversity at the same count size (Birks and Line, 1992) and was necessary because the Paleogene swamp samples have greatly differing count totals. In this case, within-sample diversity was studied at 291 grains because all samples contain at least that number of counted specimens. Unfortunately, data are not available from the Arctic for studying within-sample analysis at polar latitudes because published data are in the form of stratigraphic range charts or floral lists.

Non-parametric bootstrap analysis allows the study of among-sample diversity at the same sampling intensity (Colwell and Coddington, 1994). In both Holocene and Paleogene data sets, samples were permutated 100 times. Holocene sections were grouped into subtropical (< 36°N), temperate (36–46°N), boreal (46–56°N) and tundra (>56°N) biomes using the latitudinal limits of Rosenzweig (1995) (see electronic Appendix 1). Individual localities were also bootstrapped so that among-sample diversity could be compared if six samples were pooled from every locality. Regional estimates of Paleogene diversity used marginal marine and swamp samples from the US Gulf Coast and the combined pollen data from the Bighorn, Powder River and Williston basins. Paleogene samples from all major regions were time-averaged into either late Paleocene, early Eocene, or Paleocene + Eocene bins because sediments around North America are not precisely correlated in the early Paleogene. The effects of time-averaging on diversity estimates are discussed below. In the Canadian Arctic, 44 distinct taxa in 69 samples were identified from the late Paleocene/early Eocene (see electronic Appendix 2). Hence, in the western interior basins and on the US Gulf Coast, pollen samples were bootstrapped to allow estimation of between-regional diversity if 69 samples were pooled from all regions. As a counterpoint to the Paleogene data, samples were bootstrapped from some late Holocene localities at comparable latitudes to the Paleogene data at 30–34°N and 44–47°N. The EstimateS program (Colwell, 1997) computed all bootstrap estimates.

Detrended correspondence analysis (DCA) displays compositional information between samples on major vectors through the data on multiple axes (Hill, 1973). Ordination on the Holocene data compares changes in composition over latitude with changes in diversity.

Samples from the US Gulf Coast and from the western interior were ordinated using swamp samples only. The count data used in diversity analyses were converted to presence/absence data for the ordinations because the co-occurrences of taxa are of greater interest than the changes in relative abundance of dominant taxa which would control ordination based on relative abundance data.

RESULTS

Do Holocene pollen records demonstrate diversity and composition gradients?

Late Holocene pollen records show a regional diversity gradient from the Arctic through to the Florida everglades (Fig. 2a) with a break at about 55°N marking the transition from tundra to boreal biomes. There is an increase in taxonomic diversity through to about 44°N, but below this latitude the pattern of increasing diversity degenerates into noise (Fig. 2a). Pollen assemblages in latitudes greater than 55°N have a mean diversity of 25 taxa if six samples are pooled in each locality, but below 44°N localities have a mean of 43 taxa. This is statistically significant using a Mann-Whitney *U*-test ($U = 11$, $P < 0.0001$). Changes in regional diversity along the latitudinal gradient are associated with changes in composition (Fig. 2b). The DCA axis 1 sample scores are negatively correlated with regional diversity ($r_s = -0.61$, $P < 0.0001$) and show a continuum of change in the co-occurrence of plant taxa from the boreal through to the subtropical biomes. The DCA axis 1 scores capture only 10% of the variance, but this is still twice the statistical variance of axis 2, which accounts for 5%. If within-biome composition is compared between biomes, a Kruskal-Wallis one-way analysis of variance between all DCA axis 1 sample scores indicates that the pollen floras in each biome belong to different populations (Kruskal-Wallis statistic = 43.52, $P < 0.0001$). The exceptions are boreal and tundra vegetation that share significant similarities in composition (Fig. 2b) and could come from the same population ($U = 69$, $P = 0.1519$). However, if average diversity within biomes is compared between different biomes (Fig. 3a), boreal and tundra populations are distinct but subtropical and temperate populations are not ($U = 119$, $P = 0.5623$).

Different sets of factors influence pollen assemblages in the tundra and boreal biomes. These records contain pollen that are transported considerable distances from other biomes. In open habitats above the tree limit, these include many tree and shrub genera such as *Alnus*, *Betula*, *Corylus*, *Quercus*, *Picea* and *Pinus* as well as herbs (Lamb, 1985; Eisner *et al.*, 1995; Gajewski, 1995). In total, long-distance transport can contribute up to 20–50% of the pollen flora at polar latitudes and is more prevalent with increasing latitude (Gajewski, 1995). This may explain why some individual tundra localities have diversity comparable with localities in the temperate biome (Fig. 2a).

Between-biome diversity estimates conform better with expectations that diversity decreases with increasing latitude (Fig. 3b). The subtropical bootstrap curve does not saturate fully even after 200 samples have been pooled, although most of the diversity is captured if 100 samples are pooled. In contrast, the temperate, boreal and tundra diversity curves show significant saturation even if 50 samples are pooled. The discrepancy between within- and between-biome taxonomic diversity (Fig. 3a,b) is influenced by two factors. First, subtropical vegetation overall has significantly greater taxonomic diversity than temperate vegetation at all sampling scales (Gentry, 1988; Qian, 1998; Fine, 2001). Hence,

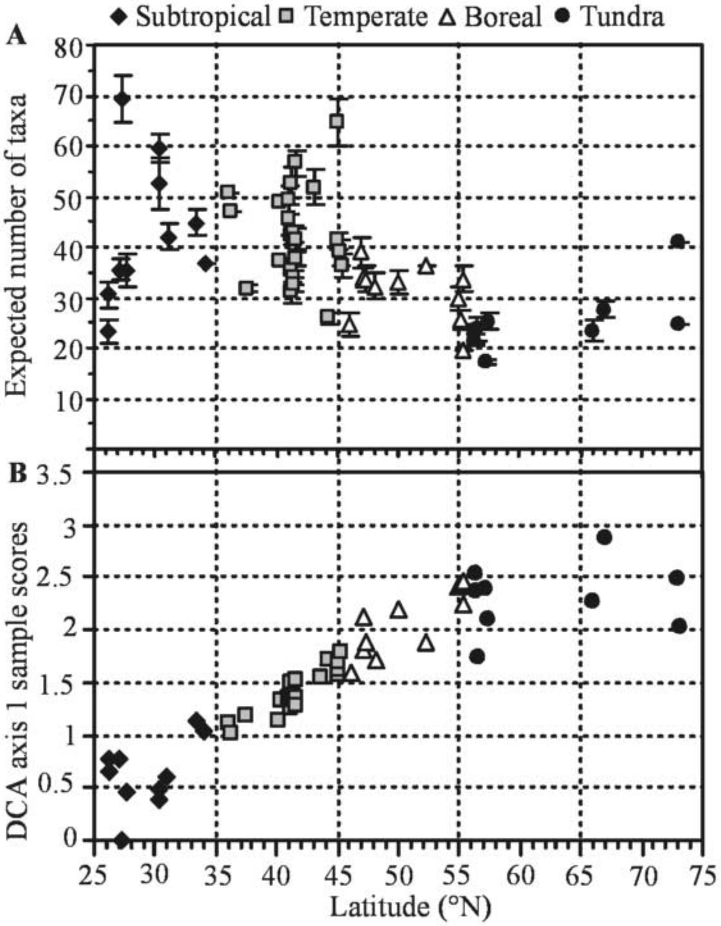

Fig. 2. (A) Bootstrapped regional diversity of 53 Holocene lake records from lowland, eastern North America plotted against latitude. Six samples are pooled in each locality. Error bars represent one standard deviation and data were randomly re-sampled 100 times. (B) Detrended correspondence analysis axis 1 sample scores of the same 53 time-averaged Holocene samples. The first axis explains 10% of the variance.

more samples are needed for pollen floras to faithfully census the parent flora in subtropical vegetation types; six samples within any individual locality are simply not enough to capture the potential diversity. Second, a greater proportion of plants is pollinated by animals in the subtropics (Regal, 1982; Whitehead, 1983). Zoophilous plants are under-represented in pollen assemblages because they generally produce pollen in lower abundance than anemophilous plants (Proctor *et al.*, 1996) and pollen that require animals for dispersal are not usually carried effectively by the wind either (Whitehead, 1983). Therefore, pollen from zoophilous plants are under-represented in the pollen record and are recorded inconsistently because they are present in very low abundance. This effect is dampened, as Fig. 3b demonstrates, by pooling large numbers of samples.

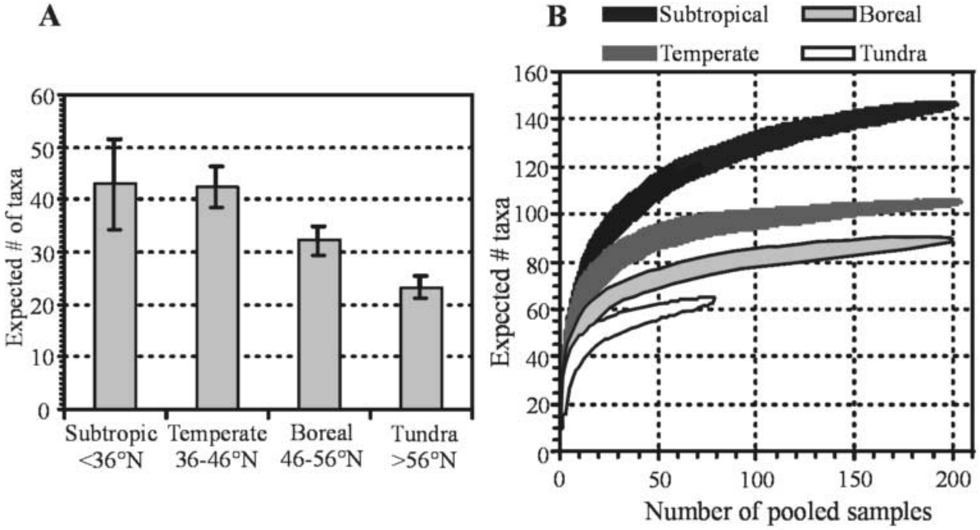

Fig. 3. Holocene pollen diversity estimates by biome. (A) Mean regional diversity at six pooled samples in every sampled locality within a biome. Error bars represent 95% confidence intervals. (B) Biome bootstrapped diversity curves. All curves include one standard deviation error bars and were randomly re-sampled 100 times. Localities used in this analysis are noted in electronic Appendix 1.

Are there differences in Paleogene composition and diversity within middle latitudes?

In total, 235 taxa are identified from the late Paleocene/early Eocene from North America (see electronic Appendix 2), but they are not evenly distributed across the continent because the pollen floras on the US Gulf Coast are completely different compositionally from those in the western interior (Fig. 4). There is no overlap in the position that Gulf Coast samples occupy in the DCA ordination with those from any sub-region within the western interior. The floras are dissimilar despite the western interior sharing 73% of its flora with the US Gulf Coast (Fig. 5a; see electronic Appendix 2). Sporomorph lists spanning the late Paleocene/early Eocene (see electronic Appendix 2) further indicate that the Gulf Coast had a high proportion (45%) of endemic taxa that are not found anywhere else in North America (Fig. 5a). This level of endemism is very similar to modern floras in North America, which show the greatest endemism in the subtropical biome (Fig. 5b).

Within-sample diversity of swamps on the US Gulf Coast average 24 taxa (standard deviation = 8) if 291 grains are counted versus 18 taxa (standard deviation = 4) in the western interior. This trend is statistically significant ($U = 1363$, $P = 0.005$). If among-sample diversity is considered from the regions as a whole, the Gulf Coast is taxonomically twice as diverse at identical sampling intensities as the western interior in both the Paleocene and the Eocene (Fig. 6). Time-averaging of about 2 million years does not alter the regional diversity gradient between the two regions (Fig. 6) despite some turnover and immigration across the Paleocene/Eocene boundary (Harrington, 2001, 2003a; Wing and Harrington, 2001). Bootstrapping provides empirical support for the analyses based on floral lists (e.g. Fig. 5a; see electronic Appendix 2) that are prone to bias due to unequal sampling between regions. The greater difference between the regions in among- rather than within-sample diversity probably reflects the same processes that influence the Holocene

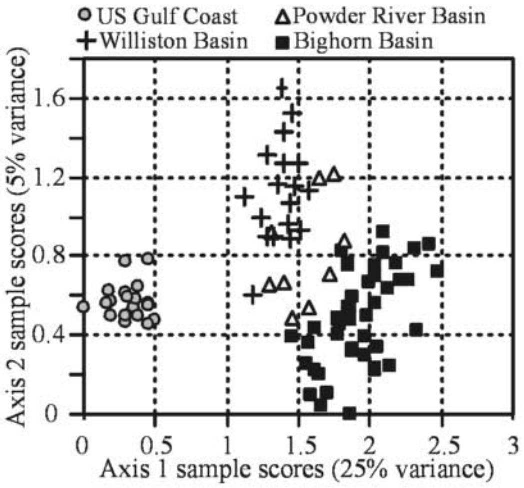

Fig. 4. Detrended correspondence analysis on early Paleogene swamp floras from the US Gulf Coast, Bighorn, Powder River and Williston basins.

data at comparable latitudes (Fig. 3a,b). Comparisons of late Holocene versus binned Paleocene + Eocene data (Fig. 7a) indicate that pollen floral diversity is not significantly greater at high middle latitudes (the western interior basins) under the late Paleocene/early Eocene warm climate. However, lower-middle latitude vegetation (US Gulf Coast) is significantly more diverse than in the late Holocene even if estimates from the Paleogene are taken from just swamps (Fig. 7b). Data demonstrate a much steeper diversity gradient within middle latitudes in the Paleogene greenhouse than in the present day. This pattern probably reflects climate because models of early Paleogene temperature indicate that the tropical climate belt extended from the equator to about 30°N (e.g. Greenwood and Wing, 1995; Shellito *et al.*, 2003).

Continental scale composition and diversity gradient in the late Paleocene/early Eocene

Comparisons across North America show a striking diversity gradient at the same sampling intensity in all regions (Fig. 8). When 69 samples are pooled from the pollen records on the US Gulf Coast ($n = 188$ taxa) and in the western interior ($n = 90$ taxa), data show a decrease in taxonomic richness of about 50% between all regions with increasing latitude. The Paleogene diversity gradient is essentially controlled by the geographic ranges of paratropical Gulf Coast plants (Fig. 5a). For example, the western interior and Arctic share, respectively, 73% and 86% of their taxa with the Gulf Coast but few taxa are endemic to either region (Fig. 5a). If polar latitudes required special plant adaptations in the Paleogene, this should be reflected in a significantly higher proportion of endemic taxa than the western interior. This is not observed (Fig. 5a). Instead, the opposite is documented, with decreasing proportions of endemic taxa with increasing latitude; the proportional increases in abundance of taxa shared with other regions, relative to endemic taxa, are significant by contingency table analysis ($\chi^2 = 24.98$, $P < 0.0001$). Hence, taxa in the Arctic tend to have much greater geographic ranges than those in lower latitudes. The modern floral diversity

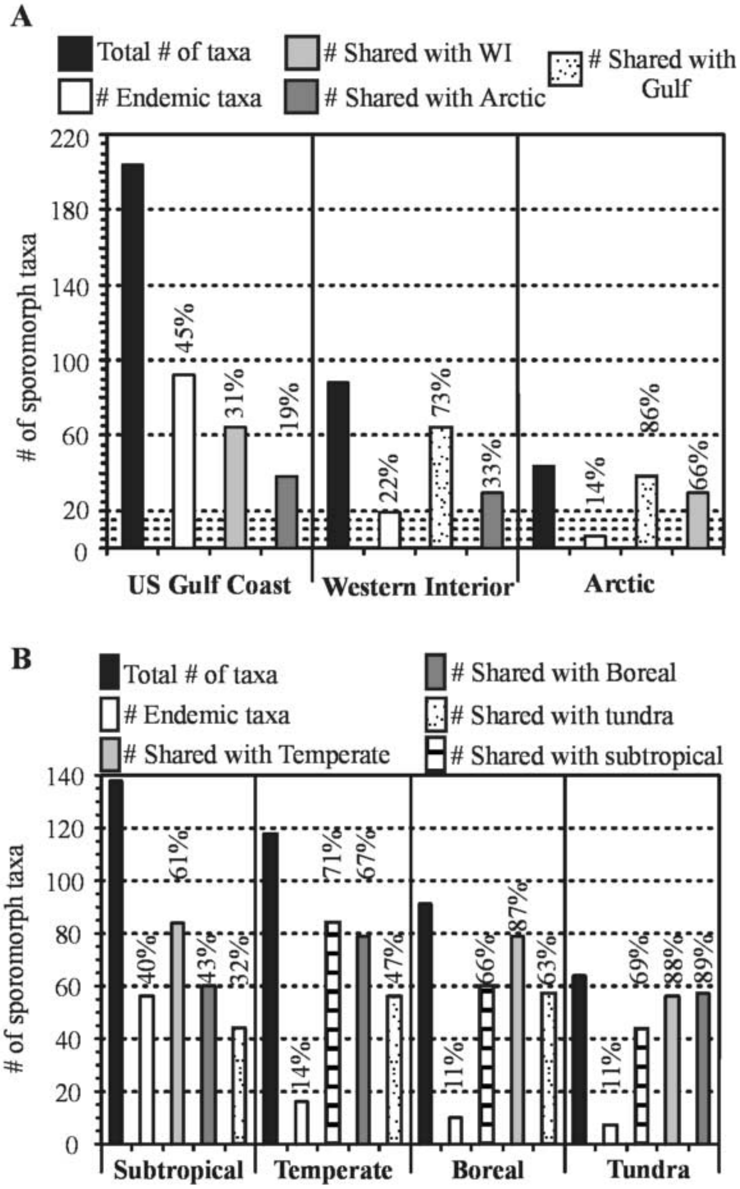

Fig. 5. (A) Total number of Paleogene taxa in each region and the number of taxa shared with the other regions around North America. Data compiled from primary collection data and from publications (see electronic Appendix 2). Percentage figures above the columns indicate the proportion of the flora shared with another region or that are endemic to a given region. (B) Total number of Holocene taxa in each biome and the number shared with other biomes in eastern North America. Percentage figures above the columns indicate the proportion of the flora shared with another region or that are endemic to a given region.

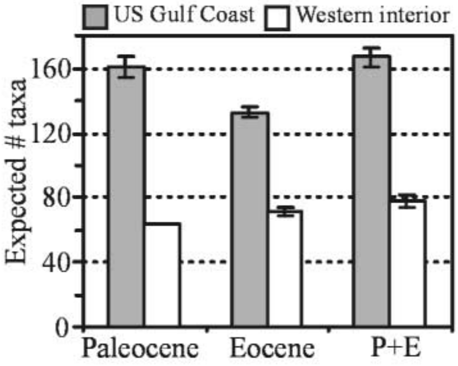

Fig. 6. Bootstrapped diversity estimates of Paleocene, Eocene and combined Paleocene and Eocene (P + E) regional floras from the US Gulf Coast (Bear Creek, lower and upper Harrell Core, Red Hot Truck Stop and Hatchetigbee Bluff sections) and western interior (Bighorn, Powder River and Williston basins) if 27 samples were randomly pooled. Twenty-seven represents the number of available Paleocene samples in the western interior. Paleocene and Eocene bins exclude the Williston Basin data because the exact position of the Paleocene/Eocene boundary is unknown here. However, the time-averaged Paleocene/Eocene bin includes all three western interior basins. Error bars represent one standard deviation and data were randomly re-sampled 100 times.

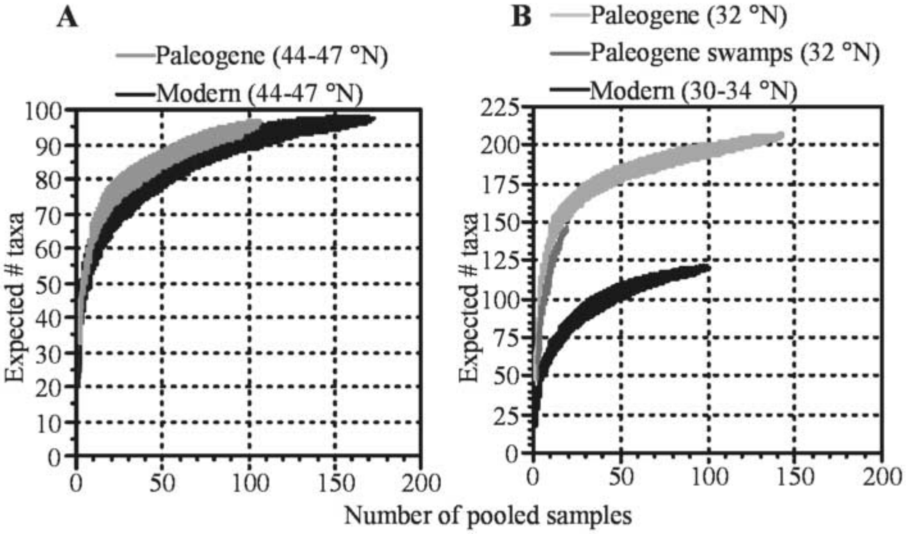

Fig. 7. Bootstrapped diversity curves of Paleogene data compared with Holocene data from the same latitudes. All curves include one standard deviation error bars and were randomly re-sampled 100 times. (A) High-middle latitude combined Paleocene and Eocene samples from the Bighorn, Powder River and Williston basins plotted with Holocene pollen data. (B) Low-middle latitude combined Paleocene and Eocene samples from Bear Creek, lower and upper Harrell Core, Red Hot Truck Stop and Hatchetigbee Bluff with Holocene data.

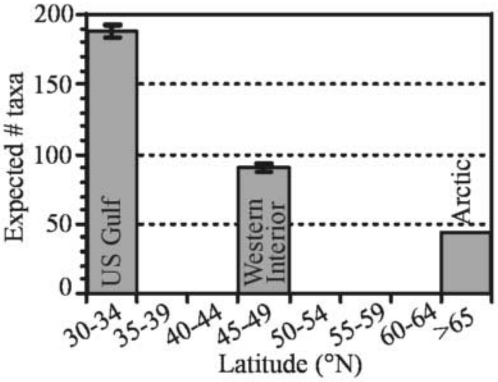

Fig. 8. (A) Bootstrapped diversity estimates of regional, time-averaged Paleocene/Eocene floras from the US Gulf Coast and western interior (WI) compared with the Canadian Arctic if 69 pooled samples were sampled at random. Sixty-nine represents the number of available samples in the Arctic for comparison with the other regions. Error bars on the US Gulf Coast and western interior data represent one standard deviation. Data were randomly re-sampled 100 times.

gradient is similarly influenced by the spillover of 'tropical' plants into cooler regions (Rosenzweig and Sandlin, 1997; Fine, 2001) and this is reflected in the Holocene pollen floras (Fig. 5b). Holocene pollen data also show that biomes tend to share greater floristic similarities with immediately neighbouring biomes rather than with just the subtropical biome (Fig. 5b). The geographic ranges of plant taxa, therefore, appear to bleed into one another. However, it is puzzling that many plants were excluded from polar or even high-middle latitudes during the frost-free late Paleocene/early Eocene. At very high latitudes, polar light regimes would exert considerable stress on plants and favour deciduous habits. This interpretation is supported by paleobotanical data from the high Arctic (Hickey *et al.*, 1983; McIver and Basinger, 1999). But this was not a factor affecting the western interior basins that are only half as taxonomically diverse as the US Gulf Coast. Unfortunately, geological data are not refined enough to allow estimates of energy variables, such as annual potential evapotransition, that may be significant for explaining diversity gradients (e.g. Currie and Paquin, 1987; O'Brien, 1993; Francis and Currie, 2003).

Historical factors such as different evolutionary histories within biomes (e.g. Latham and Ricklefs, 1993) are probably insignificant for explaining the ancient diversity gradient for two reasons. First, the gradient is predominantly controlled by plants with geographic ranges that extend from the paratropics, and most plants are not biome-specific at higher latitudes. Second, no major climate barriers are known that may have hindered the expansion of plant ranges throughout North America; plants evolving in one biome had theoretically unlimited opportunities to disperse and dilute the composition of other biomes in a frost-free world. Clearly, aspects of local climate must play a key role in controlling the geographic ranges of ancient plants. But frost, specifically, was not an important factor in dictating plant geographic ranges in the late Paleocene/early Eocene.

CONCLUSIONS

North American Holocene pollen assemblages are affected by taphonomic problems relating to sampling intensity, long-distance pollen transport and pollinator mode in the different biomes. But pollen data still reflect successfully both composition and diversity changes between biomes. Specifically, Holocene pollen data confirm findings that floras are less diverse, certainly at biome scales, with increasing latitude and that most taxa 'spill over' into other biomes. Hence, there are few endemics in any one region with the exception of the subtropical biome that is considerably more diverse than the temperate, boreal and tundra biomes. Comparisons with pollen data also from North America during an interval of greenhouse climate in the late Paleocene/early Eocene show striking differences in the floral diversity and composition gradient. Early Paleogene palynofloras show that the vegetation diversity gradient between three regions at paleolatitudes 32°N, 44–47°N and > 70°N was steeper within middle latitudes and between middle to high latitudes than in the recent at the same sampling intensity. If 69 samples are taken from each region, the gradient manifests as an approximate 50% decrease in taxonomic diversity from the US Gulf Coast ($n = 188$ taxa) to the western interior ($n = 90$), and again an approximate 50% decrease in taxonomic diversity from the western interior to the Canadian Arctic ($n = 44$). The Paleogene vegetation gradient is also composed of 'spillover' taxa from the paratropical Gulf Coast that range northward, but this effect appears more pronounced in the early Paleogene than in the Holocene. Climatic data are lacking to explain why plant taxa are excluded with increasing latitude but freezing temperatures were not a significant climatic variable in the late Paleocene/early Eocene. Data demonstrate that decreasing taxonomic diversity with increasing latitude is an ancient phenomenon even in equable, greenhouse climates.

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