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The latitudinal gradient of diversity through the Holocene as recorded by fossil pollen in Europe

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ABSTRACT

To assess the impacts of Pleistocene glaciation on the latitudinal diversity gradient, I examined plant family diversity during the last interglacial at 24 sites in Europe between 39° and 71°N latitude. Familial richness and turnover were calculated for 1000-year intervals for each site. Although familial turnover varied from 6 to 59% per 1000 years, familial richness remained essentially constant at 16 (67%) of the sites. For the remaining sites, the rates of change of richness were very low (2–3 families per 1000 years) and were not associated with latitude. These results do not support 'historical' hypotheses for the latitudinal diversity gradient, because neither local species richness nor the slope of the gradient have changed meaningfully in the last 10,000 years. Instead, they support hypotheses that invoke contemporary mechanisms to explain the inverse relationship between latitude and diversity. Additionally, the lack of change both in richness at individual sites and in the latitudinal diversity gradient through time suggest that the ecological and evolutionary processes that regulate diversity within local communities operate in a systematic fashion across large spatial and temporal scales. Future hypotheses for the latitudinal gradient of diversity should include universal rules that determine how resources are divided among species at local and global scales without regard to the identify of particular species.

Keywords: community ecology, fossil pollen, latitude, plants, regulation, richness.

INTRODUCTION

In recent years, questions about biological diversity have stimulated much social and political activity, while the fundamental mechanisms responsible for the creation and maintenance of diversity have remained among the greatest mysteries in ecology (e.g. Hutchinson, 1959; Brown, 1981; Wilson, 1988; Ricklefs and Schluter, 1993). Through the last century of empirical ecology, it has become clear that a small number of patterns, such as the latitudinal gradient of diversity, species–area relationships and rank-abundance distributions, leave distinctive signatures in ecological communities (Ricklefs and Schluter, 1993; Brown, 1995; Rosenzweig, 1995). Although it is unlikely that any one of

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these pervasive ecological patterns will be explained easily, it is important to seek general mechanisms that regulate diversity.

The latitudinal gradient of species richness is one of the most robust patterns in nature, and it may provide insights into the mechanisms that control diversity at local and global scales (Pianka, 1966; Stevens, 1989; Lidgard and Crane, 1990; Rohde, 1992; Brown, 1995; Rosenzweig, 1995; Brown and Lomolino, 1998). In spite of its ubiquity, the relationship of increasing species diversity with decreasing latitude has eluded explanation and remains one of the most challenging questions in ecology. In 1966, Pianka presented a summary of six hypotheses for the cause of the latitudinal gradient (Table 1). Since that time, several new hypotheses have been proposed. In 1992, Rohde presented an updated summary that included 28 hypotheses. Conspicuously, while some have received less attention in recent times, none have been removed from the growing list (Price, 1991). Some of these hypotheses are new ideas and some represent subdivisions of existing hypotheses. The most promising explanations combine subsets of pre-existing hypotheses (e.g. MacArthur and MacArthur, 1961; MacArthur, 1972; Kaufman, 1995; Rosenzweig, 1995; Brown and Lomolino, 1998).

There are two general types of hypotheses for the latitudinal diversity gradient: 'historical' hypotheses invoke the legacy of past events, whereas 'ecological' hypotheses emphasize the effects of current environmental conditions. These two classes of hypotheses make different predictions about patterns of diversity since the last glacial maximum. The 'historical' hypotheses, as defined by Pianka (1966), 'assume(s) that all communities tend to diversify in time and therefore older communities have more species than younger ones'. These hypotheses predict that species richness in northern latitudes should increase in the aftermath of Pleistocene glaciation as the result of colonization, speciation or some combination of the two. Simpson (1964) observed that the gradient of species diversity should be steepest in most recently glaciated communities. Therefore, the historical hypotheses predict that (1) species richness at high latitude sites increases over time (Fig. 1a) and (2) the steepness of the diversity gradient decreases over a sufficiently long period (Fig. 1b).

The 'ecological' hypotheses, on the other hand, attribute the latitudinal diversity gradient to contemporary processes and environmental variables that covary with latitude, such as climatic stability and productivity. Importantly, they predict that the contemporary latitudinal gradient should remain consistent as long as the regulating mechanisms

Table 1. Hypothesized causes of the latitudinal diversity gradient summarized by Pianka (1966)

Theory	Explanation
Time	Communities diversify through time; therefore, older communities have more species than younger ones
Spatial heterogeneity	Physical environments become more complex and diverse in the tropics
Competition	Natural selection is primarily driven by physical factors in temperate regions, whereas biological interactions are more important in the tropics
Predation	More predators in the tropics prevent competitive exclusion
Climatic stability	Regions with stable climates allow increasingly fine divisions of resources, resulting in smaller niches
Productivity	Greater productivity results in greater diversity

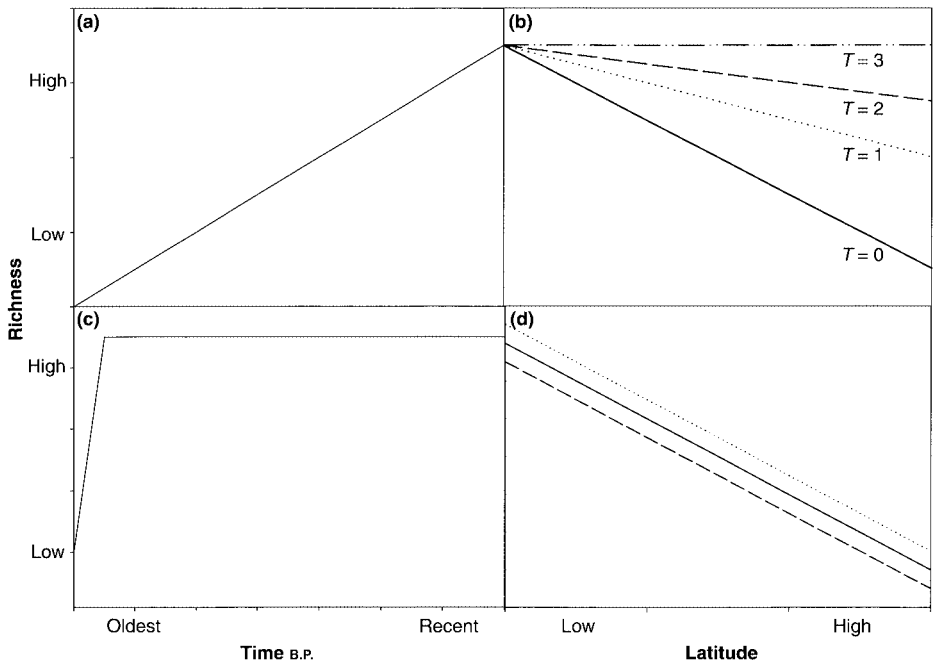

Fig. 1. (a, b) Models of the predictions of the 'historical' hypotheses: (a) the gradual increase of diversity at an individual site through time after the retreat of the glaciers; (b) the gradual decrease in the slope of the latitudinal diversity gradient through time after the retreat of the glaciers. (c, d) Models of the predictions of 'ecological' hypotheses: (c) the rapid increase of diversity following the retreat of the glaciers and the maintenance of richness in the ensuing period of relatively small environmental change; (d) the conservation of the slope of the latitudinal diversity gradient through time.

and their relationship to latitude remain consistent. If latitudinal variation in climate and other important variables has been relatively constant during the last 10,000 years, the 'ecological' hypotheses predict that the latitudinal diversity gradient should be established rapidly following glacial retreat and then remain almost constant (Fig. 1c). If increasing global temperature and productivity have allowed local sites to support more species, the 'ecological' hypotheses predict that these changes would lead to increased diversity at all latitudes (Fig. 1d).

Fossil pollen data provide a unique opportunity to test some of these predictions. Primarily collected to reconstruct historical climate and vegetation patterns, the fossil pollen data provide a unique sample of the composition of many temperate plant communities for about the last 10,000 years (Huntley and Birks, 1983). I have used richness estimates obtained from fossil pollen to quantify the latitudinal diversity gradient and to test the predictions of the two types of hypotheses. Specifically, if 'historical' processes are primarily responsible for the latitudinal diversity gradient, we should see a decrease in the slope of the latitudinal gradient due to progressive accumulation of species at high latitude sites. On the other hand, if 'ecological' processes determine the nature and magnitude of the latitudinal diversity gradient, then we should see no change in the slope of the gradient and little or no change in richness at individual sites.

In conducting these analyses, I have made a number of assumptions, upon which the strength of the conclusions depend:

1. *Palynological richness is correlated with species richness.* Different reproductive strategies dictate that there is not a one-to-one relationship between the richness and abundance of pollen in a lakebed and species on a landscape. Some species are under-represented and others are over-represented in any individual sample. However, diversity of pollen types is clearly a function of plant species diversity and there is a long tradition of estimating geographic range, plant community composition and climate from pollen data (Odgaard, 1999).
2. *Plant family richness is correlated with plant species diversity.* Pollen at each site was identified to different taxonomic levels, from species to order, by the original investigators. To standardize the data, all identifications were converted to families. Several studies have shown that increased species diversity is correlated with increased diversity at higher taxonomic levels, and that latitudinal patterns are consistent at various taxonomic levels (Gentry, 1988; Williams *et al.*, 1994; Kaufman, 1995; B.J. Enquist *et al.*, unpublished data). Furthermore, the hierarchical taxonomic scheme assures that turnover in family composition cannot happen more rapidly than turnover in genera or species. Therefore, family turnover is a conservative estimate of species turnover.
3. *There is no systematic trend in the geographic area that is sampled by individual lakebeds, through time or across latitude.* Although the area represented by any fossil sample is imprecisely known and may change through time (Odgaard, 1999), I assume that the fossil pollen deposited in a lakebed over a 1000-year period provides an unbiased estimate of the plants in the surrounding area.
4. *Failure to meet precisely assumptions 1–3 will contribute to residual variation both in the estimate of diversity at a site through time and in the estimate of the slope of the latitudinal gradient.* This residual variation should increase scatter that might weaken or obscure patterns of diversity, but not create patterns where none exist. The probability of arriving at a false conclusion due to biases in the pollen data is further reduced by the fact that I am comparing 24 locations both across time and across 40° of latitude.
5. *Correction factors will not add information and may introduce additional, unnecessary complexity and uncertainty into a coarse but robust analysis*. The appropriateness of various correction factors, such as those for production and loading rates, taxonomic precision and geographic extent, is debated and is not likely to have a significant impact on this analysis (Odgaard, 1999).
6. *Any study of ecological communities, especially for taxonomically and morphologically diverse taxa such as plants, relies on the estimation of species composition*. Both contemporary and palaeographic studies are influenced by spatial and temporal averaging, incomplete detection and inaccurate identification. The magnitude of these impacts varies between studies at different spatial and temporal scales (Enquist *et al.*, 2000). This study avoids any biases that may be introduced by comparing fossil pollen records with extant plant communities by using only pollen from the same cores.

In summary, these six assumptions are unlikely to lead to biased answers to the questions asked by this paper: (1) Was there a directional change in the summed family richness for 1000-year intervals at a single site through time? (2) Has the latitudinal gradient of plant family diversity changed during the Holocene?

METHODS

Pollen data were obtained from the European Pollen Database (EPD) hosted on the World Wide Web by the National Atmospheric and Oceanic Administration (http://www.ngdc.noaa.gov.). The EPD was chosen for its quality, extent and availability.

A subset of localities within the EPD was chosen for examination using Siteseer, a program created by John Keltner of the Illinois State Museum, available as freeware from the NOAA website. A large group of candidate sites was initially selected, based on latitude, longitude, altitude, number of radiocarbon dates and number of samples. After a stringent quality and quantity control that included screening for specific details of sample number, sampling consistency and dating, a subset of 24 sites was chosen for analysis (Table 2; Fig. 2). Sites were located between 2° and 29°E longitude and 39° and 71°N latitude. Six sites were chosen in each of four discrete, latitudinal bands at approximately 10° intervals. Pollen data were collected, analysed and reported by the original investigators; data for each site were presented for multiple strata, the age of which has been estimated from radiocarbon dating.

Pollen at each site was identified to different taxonomic levels, from species to order, by the original investigators. To standardize the data, all identifications were converted to families. In two cases, the original identification was only made to order. For this analysis,

Table 2. List of sites and locations

Site name	Latitude (°N)	Longitude (°W)	Contributor
Bruvatnet	70.1	28.3	H. Hyärinen
Trollvatnet	69.5	23.3	H. Hyärinen
Suovalampi	69.4	28.5	H. Hyärinen
Rattuvarri	69.2	20.2	H. Hyärinen
Akuvaara	69.1	27.4	H. Hyärinen
Mukkavaara	68.6	21.0	H. Hyärinen
Mäyrälampi	62.2	26.1	Y. Vasari
Aholami	61.5	25.1	A. Vasari
Syrjalansuo	61.1	28.1	I. Vuorela
Lake Maardu	59.3	25.0	L. Saarse
Åntu Sinijarv	59.1	26.2	L. Saarse
Kirikumae	57.4	27.2	L. Saarse
Lake Skvzetuszewskie	52.3	17.2	K. Tobolski
Slopiec	50.5	20.5	K. Szczepanek
Szymbark	49.4	21.1	K. Szczepanek
Puscizna Rekowianska	49.3	19.5	A. Obidowicz
Hozelec SK-5-A	49.0	28.2	V. Jankovska
Ampoix	48.1	2.6	J.L. De Beaulieu
Lago di Martignano	42.1	12.2	B. Huntley
Kupena	41.6	24.2	A. Huttunen
Edessa	40.5	21.6	S. Bottema
Khimaditis Ib	40.4	21.4	S. Bottema
Ioannina I	39.5	20.4	S. Bottema
Lake Xinias	39.0	22.2	S. Bottema

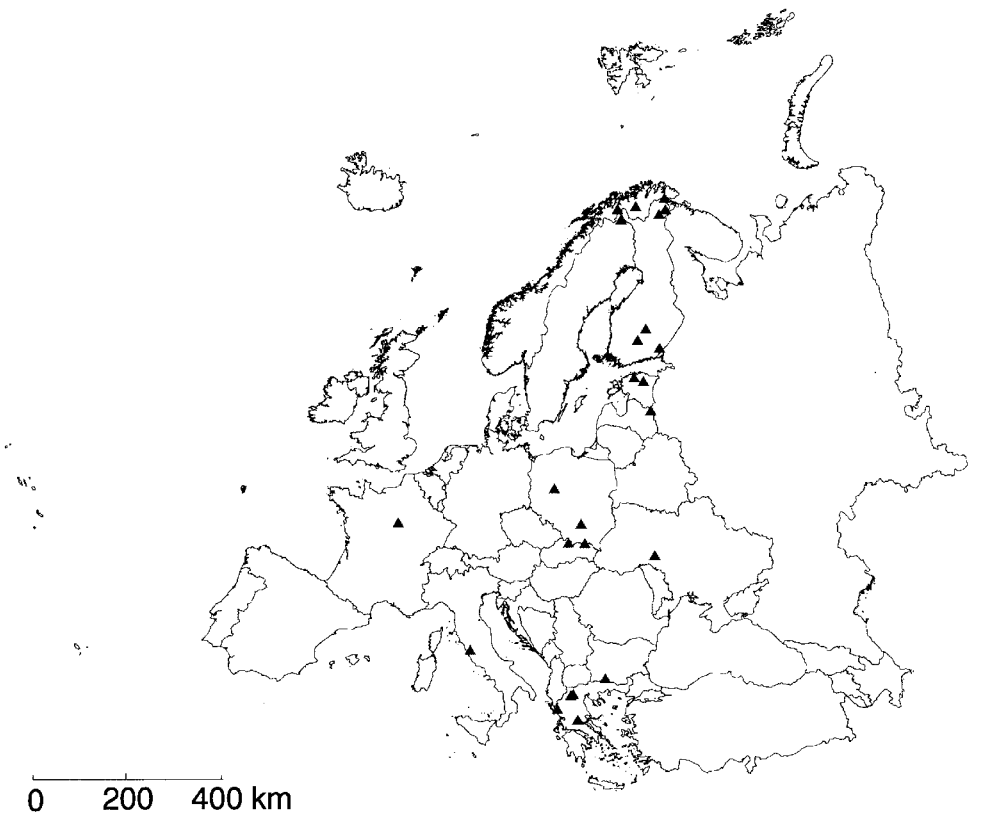

Fig. 2. A map of Europe with locations of sites indicated by triangles.

I assumed that each of these orders represented only one family. Most taxonomic designations were made with the assistance of the W^{3}Tropicos database, hosted on the Missouri Botanical Garden website (http://www.mobot.org), and the Integrated Taxanomic Information System, available through the World Wide Web from the US Government (http://www.itis.usda.gov). Additional assignments were made from Walters and Keil (1977).

Familial data were chosen as the most consistent estimate of diversity. Other authors have demonstrated that spatial patterns of richness hold at different taxonomic levels. These studies concluded that the increase in richness along the latitudinal gradient was primarily due to the addition of higher taxonomic groups, such as families and orders (Gentry, 1988; Kaufman, 1995). The choice of family data represents a compromise between consistency and completeness. Although some resolution is lost by lumping identified species and genera into families, comparisons between intervals are facilitated by consistency of units. Unfortunately, pollen data are limited by preservation and identification. Examination of the data indicates that the trends are similar, but accompanied by varying degrees of noise, at different taxonomic levels (family, genus, species or morphotype). A subset of the data was analysed using the finest level of taxonomic resolution reported by the original authors, and the results are qualitatively identical to those reported here.

Pollen abundance data were converted to presence or absence in each stratum to estimate richness. Because deposition rates and, consequently, the amount of time represented by each stratum, varied within and between sites and time periods, the presence/absence data were summed for 1000-year intervals to avoid sampling biases caused by unequal periods of accumulation and to facilitate comparisons of time intervals with unequal numbers of identified strata. Any family present in at least one strata within a 1000-year interval was recorded as present. To determine the effects of sampling, richness was plotted against the number of strata within a 1000-year interval; no relationship was found.

Rates of richness change at individual sites were calculated as the slope of the linear regression of family richness against time in 1000-year intervals. In this analysis, a slope statistically different from 0 is consistent with a change in diversity, while the r^2 values provide an estimate of the magnitude of variation in diversity between time steps. Because I was interested in the overall direction of diversity change and not the sample-to-sample variation, r^2 values were noted, but not used for analysis.

To further elucidate community dynamics, family turnover rates were calculated at 1000-year intervals and between the first and last sample for each site. Turnover was calculated as a proportion of dissimilarity, or one minus the Jaccard Similarity Index (Brown and Lomolino, 1998):

$$1 - (C/A + B - C)$$

where A is the number of families present in the first sample, B is the number present in the second sample and C is the number of families common to both samples.

Two analyses were performed to quantify change in the latitudinal gradient of diversity through time. First, richness was plotted as a function of sample age and latitude at each site for only the oldest and most recent samples. The slope of the regressions through the samples of each age estimates the decrease in familial richness with increasing latitude. Differences in the slopes of the two regressions quantify change in the gradient over the approximately 10,000-year study period. Linear regressions appeared to provide a reasonable fit to the data, and have often been used to describe the latitudinal diversity gradient outside of the tropics. Although several investigators have determined that the latitudinal gradient of diversity is not linear, the most important inflection occurs at the tropical boundary and, in most taxa, diversity outside the tropics appears to decrease steadily towards the poles (Kaufman, 1995).

Finally, the change of the slope of the latitudinal gradient over time was also analysed using all time intervals in a linear regression model in Minitab. Starting with the most general linear model:

$$\text{Richness} = \hat{a}_0 + \hat{a}_1\text{*(time)} + \hat{a}_2\text{*(latitude)} + \hat{a}_3\text{*(time*latitude)}$$

where $\hat{a}_0$ is the y-intercept, and the remaining terms represent the influence on the slope of time, latitude, and both time and latitude. The results were then categorized into one of three possible outcomes:

1. If none of the terms equalled zero, then the model suggested that the latitudinal diversity gradient had a different slope and y-intercept for each time interval and no reduced model could be used to characterize the latitudinal diversity gradient over time.

2. If $\hat{a}_3 = 0$, then the slopes of each time period were the same and only the y-intercepts varied between time periods.
3. If $\hat{a}_3$ and $\hat{a}_1 = 0$, then I concluded that the slopes and y-intercepts for all time periods were the same.

The model was used with all slopes of richness from individual sites, including non-significant values. The statistical significance for individual sites partially relies on the assumption of linearity in the individual site data, which was clearly violated ($P < 0.001$; Fig. 4). However, the objective was to compare total change at many sites over a broad latitudinal range. Although fitted polynomial regressions portrayed the changes at an individual site well, they were inappropriate for between-site comparisons of overall trends.

RESULTS

Most of the individual sites showed no significant change in familial richness over the last 10,000 years. Statistics for the rate of change of richness for all 24 sites are presented in Table 3. In Fig. 3, the oldest periods are plotted nearest the origin, so that positive slopes

Table 3. List of slopes and *P*-values for all sites

Site	n^a	Time interval (years B.P.)	r^2	Slope	*P*
Bruvatnet	12	12,000–1000	0.02	–0.000944	0.6719
Trollvatnet	9	11,000–3000	0.50	–0.000517	0.0330*
Suovalampi	8	10,000–3000	0.18	0.000464	0.2979
Rattuvarri	8	11,000–4000	0.06	0.000167	0.5593
Akuvaara	9	9000–1000	0.13	0.000250	0.3409
Mukkavaara	10	10,000–1000	0.06	0.000133	0.0573
Mäyrälampi	8	8000–1000	0.37	0.001810	0.1095
Aholami	9	10,000–2000	0.47	0.000940	0.0625
Syrjalansuo	12	11,000–1000	0.17	0.000336	0.1809
Lake Maardu	9	10.000–2000	0.89	0.000667	0.0001**
Åntu Sinijarv	11	13,000–3000	0.55	0.000473	0.0090**
Kirikumae	12	13,000–2000	0.35	0.000297	0.0433*
Lake Skvzetuszewskie	10	10,000–1000	0.56	0.002697	0.0127*
Slopiec	11	11,000–1000	0.35	0.001373	0.0573
Szymbark	6	9000–3000	0.30	0.000964	0.2060
Puscizna Rekowianska	10	9000–1000	0.17	0.00037	0.2386
Hozelec SK-5-A	9	12,000–4000	0.36	–0.0008	0.0864
Ampoix	10	11,000–2000	0.05	0.000364	0.5348
Lago di Martignano	12	12,000–1000	0.18	–0.000424	0.1465
Kupena	12	13,000–2000	0.56	–0.001538	0.0053**
Edessa	11	11,000–1000	0.76	0.003036	0.0005**
Khimaditis Ib	11	11,000–1000	0.62	0.002336	0.0042**
Ioannina I	11	12,000–2000	0.20	0.000745	0.1697
Lake Xinias	11	14,000–2000	0.0007	0.000027	0.9404

[a] The number of 1000-year intervals used to calculate slopes and *P*-values. Statistical significance: * $P < 0.05$; ** $P < 0.01$.

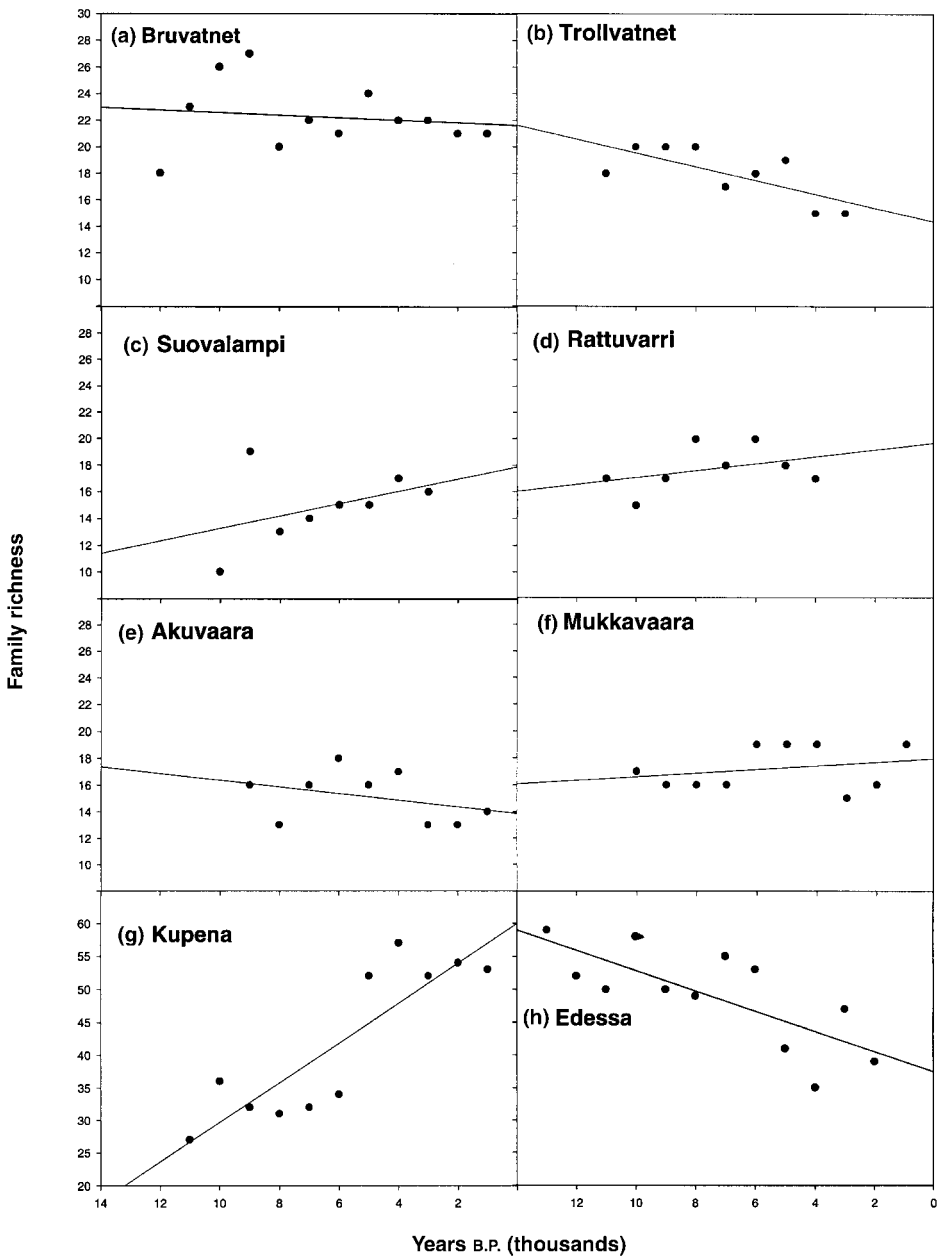

Fig. 3. (a–f) Family richness through time at the highest latitude sites. (g, h) Sites with the largest increase and decrease, respectively (note that the y-axis scale changes for g and h). Slopes, *P*-values and r^2-values are listed in Table 3.

indicate increasing diversity and negative slopes decreasing diversity through time. Sixteen (67%) of the 24 sites had slopes that were not statistically different from zero ($P > 0.05$). Of the statistically significant slopes ($P < 0.05$), two were negative and six were positive. These

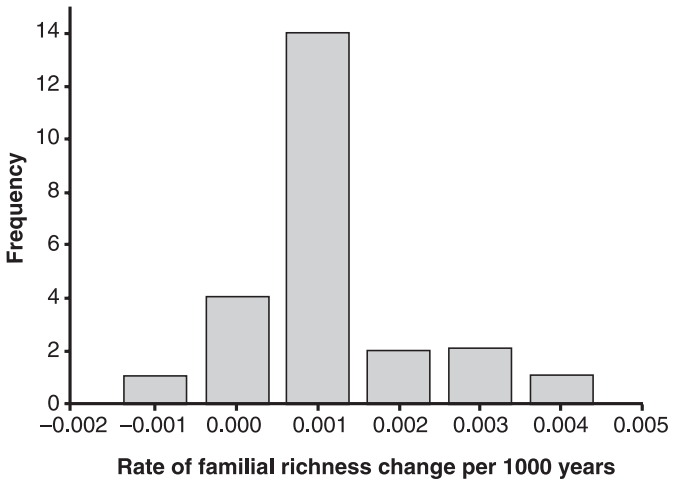

Fig. 4. Frequency-distribution of all slopes, including non-significant values ($n = 24$).

slopes ranged from −1.538 to 3.036 families per 1000 years. A frequency distribution of all slopes gave a unimodal distribution with a peak near zero (Fig. 4). The frequency distribution was not significantly different from a normal distribution ($W' = 0.946729$; $P < 0.01$) according to the sample correlation determined by Minitab (Christensen, 1996). The mean (0.00055) and 95% confidence interval (0.00009, 0.00102) of the slopes show that the mean is very close to zero.

Of particular interest is the pattern shown by the six sites at highest latitude (Fig. 3a–f). At approximately 79°N, glaciation would certainly have had a much more dramatic impact on these plant communities than in more southerly locations (Peltier, 1994). Of these six sites, only one, Trollvatnet, had a slope different from zero and, interestingly enough, the slope was positive, suggesting that diversity decreased in the last 9000 years (Fig. 3b).

Although richness did not appear to change through time, there was substantial family turnover. When calculated for 1000-year intervals, familial turnover for the 24 sites ranged from $23.7 \pm 0.133\%$ to $32.2 \pm 0.087\%$ (mean ± standard deviation; Fig. 5a). The values for 1000-year intervals were not much less than total long-term turnover, calculated using only the first and last samples from each site. Long-term turnover ranged from $39.2 \pm 0.074\%$ to $41.5 \pm 0.112\%$ (Fig. 5b).

In accordance with the pattern at individual sites, there was no change in the latitudinal gradient of familial diversity over time (Fig. 6). The permanence and constant steepness of the latitudinal diversity gradient was indicated by the slopes of the regressions of familial richness against latitude: –0.784 families per °N latitude for the oldest samples and –0.711 families per °N for the most recent samples. These slopes were not statistically different from each other ($P > 0.05$), although the y-intercept was slightly higher for the most recent samples ($P < 0.05$).

The linear regression model, which included all values of slope from each time interval, also showed no change in the slope of the latitudinal diversity gradient over time. The results of the full model,

$$\text{Richness} = 77.5 - 1.33*(\text{time}) - 0.828*(\text{latitude}) + 0.0105*(\text{time}*\text{latitude})$$

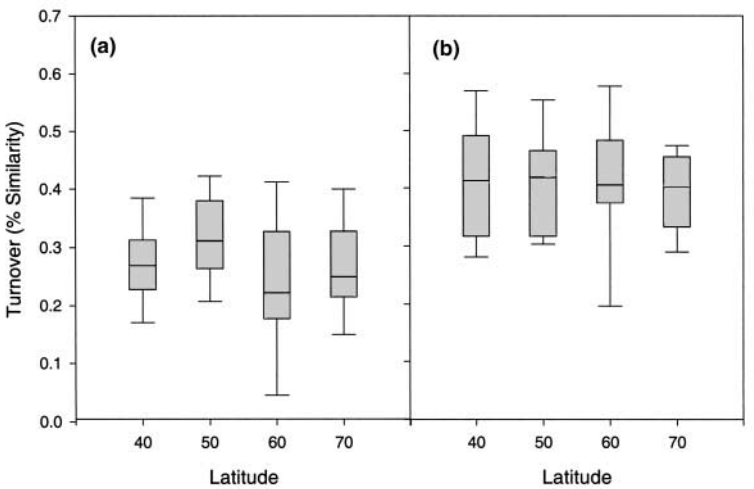

Fig. 5. (a) Short-term turnover (1000-year intervals). (b) Long-term turnover (oldest to most recent). Boxes enclose 25th and 75th percentiles and median value. Outliers are 10th and 90th percentiles.

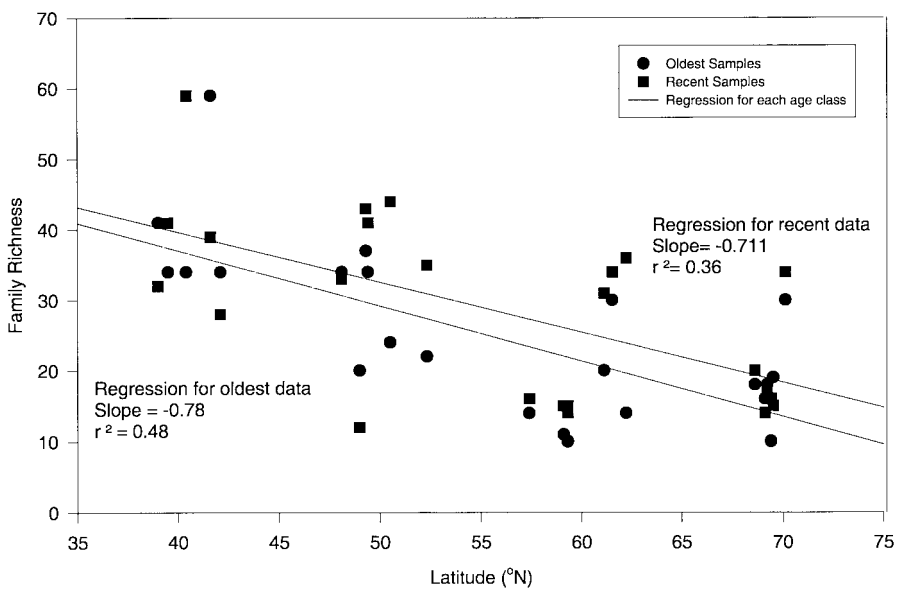

Fig. 6. The change in the latitudinal gradient of plant family diversity in Europe as recorded by pollen deposition. The upper and lower regressions are produced by the youngest and oldest samples respectively. The two slopes are not significantly different from each other ($P < 0.05$).

could not reject the hypothesis that $\beta_3 = 0$ ($P = 0.524$); therefore, the slope of the latitudinal gradient was not statistically different between time steps. As a result, the reduced model was applied to test for significant differences in the y-intercept. The results,

$$\text{Richness} = 73.9 - 0.774*(\text{time}) - 0.760*(\text{latitude})$$

rejected the hypothesis that $\beta_1 = 0$ ($P < 0.001$, $r^2 = 0.49$). Therefore, the data are consistent with the supposition that the y-intercept varied significantly throughout the period of study. Taken together, these results provide significant evidence that the slope of the latitudinal diversity gradient remained constant, while its height changed throughout the period of study (as in Fig. 1d).

DISCUSSION

This paper documents four patterns in the fossil record of European plant communities from the last 10,000 years: (1) large changes in the composition at each location, (2) a lack of a directional trend in diversity at individual locations, (3) a lack of a change in the slope of the latitudinal gradient of diversity and (4) a significant gradient of diversity across 40° of latitude. Taken together, these four patterns provide some insights into the mechanisms that control diversity at local and continental scales.

Maintenance of diversity at individual sites

Familial richness at individual sites was remarkably consistent over long ecological time scales: there was no overwhelming directional trend in diversity at all 24 sites. The rates of change of familial richness at the 24 sites fail to show long-term increases in diversity that would change the nature of the latitudinal gradient (Table 3). A close inspection of Fig. 6 shows that about one-third of the points above the pair of regression lines are from the oldest samples, whereas about one-third of the points below the regressions are from the most recent samples. The observed constant diversity concurs with reports of other authors that are often overlooked or not emphasized (e.g. Rosenzweig, 1975, 1995; Parody *et al*., in press; see Brown *et al.*, in press, for a complete discussion). Wilson (1985), for example, observed constant species richness in the ant fauna of the West Indies since the Miocene, despite, or possibly as the result of, high turnover in species composition. Evidence from ants preserved in amber, benthic invertebrates and many other taxa suggest that species richness can remain relatively constant for long periods of time.

But these communities are not static: despite consistent richness, community composition, as reflected by pollen deposition, varied by as much as 50% between samples. Plant communities are highly plastic assemblages that reflect the individualistic responses of species to abiotic and biotic environmental conditions (Gleason, 1926; Whittaker, 1956). However, the maintenance of richness within a community during species turnover suggests that describing community composition solely as the result of 'coincidence', as has been done by Gleason (1926) and reiterated by Stone *et al.* (1996), is incomplete. Equally inaccurate is Clements' (1936) assertion that communities behave as super-organisms with their own ontogeny. These results suggest that there is a complex interaction between local community composition and regional diversity (Rosenzweig, 1975, 1995; Wilson, 1985; Brezonik *et al.*, 1993; Frost *et al.*, 1998; Ernest and Brown, in press; see Brown *et al.*, in press, for a complete review). Although a community does not experience ontogenic or evolutionary processes, there appear to be deterministic ecological properties of a site that regulate the composition and especially the richness of its flora. Surprisingly, at intermediate time scales – tens to thousands of years – the deterministic processes that regulate

richness often appear to be robust to historical ecological events, such as glaciation and some human disturbances, that have profound effects on the species composition of the community.

Of course, there are also circumstances when diversity in continental systems changes as the result of environmental or evolutionary processes. Global plant diversity, for example, has increased over geological time and local community diversity, particularly in arid habitats, has increased as new forms have evolved to fill new niches (Niklas, 1997). Similarly, Wilf and Labandeira (1999) have shown that herbivorous insect diversity of southwestern Wyoming changed predictably over geological time in response to climate change. These contrasting results provide an opportunity to identify the extent of environmental and evolutionary changes that are required to significantly change diversity within communities (Brown *et al.*, in press).

The latitudinal diversity gradient

As reflected in the fossil pollen record, the pattern of decreasing plant family diversity with increasing latitude does not appear to have changed meaningfully over the last 10,000 years. With indistinguishable slopes, samples from any time period yielded the same rate of decreasing familial richness with increasing latitude. Apparently, richness at the most northern sites increased too rapidly to be detected in 1000-year samples immediately following the retreat of the ice sheets and then remained approximately constant throughout the Holocene. The consistent slope of the gradient through the substantial climatic fluctuations that have taken place during the last 10,000 years (Davis, 1986) clearly contradicts the predictions of the 'historical' hypotheses and those authors who have concluded that the latitudinal diversity gradient is largely the result of historical events, such as differential extinction rates during periods of significant climate change (e.g. Latham and Ricklefs, 1993; Strayer and Reid, 1999).

The consistent slope of the diversity gradient through time suggests that the causal mechanisms of the latitudinal gradient have operated in a relatively constant manner for the last 10,000 years. Furthermore, a gradient of decreasing plant richness with increasing latitude has been documented since the radiation of the angiosperms in the Early Cretaceous (Lidgard and Crane, 1990). The slope of the gradient from the tropics to the poles has been negative for at least 150 million years, suggesting that the fundamental deterninants of the gradient have been qualitatively similar for a period that includes enormous climatological, evolutionary and physical changes. Throughout this time, there have been a small number of things that have remained constant, including a gradient of decreasing available energy and increasing seasonality from the tropics to the poles. Combined, the evidence appears to contradict the assertions that the contemporary patterns of global diversity are the result of historical events.

CONCLUSION

Although ecology still lacks a mechanistic explanation for the latitudinal diversity gradient, the present results suggest the operation of deterministic processes that apparently regulate local diversity regardless of species composition over intermediate time scales, leading to conserved species richness during periods of extreme change in composition. However, these same processes regulate diversity change predictably across 40° of latitude. The

strength of the regulating mechanism can be inferred by the extent to which diversity is constant through time or space. It is apparent from the conservation of both the latitudinal gradient across 10,000 years and the maintenance of diversity at an individual site that many of the factors that regulate diversity do not operate independently of each other across spatial and temporal scales and are robust to comparatively short-term environmental changes within a certain range of magnitude (but see Latham and Ricklefs, 1993).

The results of this study, which included all plant habits, are qualitatively different from those of Silvertown (1985), who only studied tree diversity in Europe over roughly the same time period. Silvertown found that tree richness increased until about 6000 years ago and then remained relatively constant. The disparity between the results suggests the impact of natural history on community composition and the effect of taxonomic breadth (as opposed to resolution) in investigations of spatial and temporal diversity dynamics. The differences between these two studies may be due to different colonization abilities of different taxa and important biological differences between temperate and tropical communities in the abundance of various plant habits. Among other differences, temperate communities appear to have a much larger percentage of herbaceous plant species, while tropical and low latitude temperate sites are often dominated by woody vegetation (Gentry, 1991). Taxonomic scale can alter the results of latitudinal gradient studies for a number of taxa, including plants, insects, birds and mammals (e.g. Price, 1991).

Since the pattern of decreasing richness with increasing latitude has not changed in the last 10,000 years and major perturbations such as glaciation have not had a dramatic, long-lasting influence on familial or species richness of plants at northern latitudes, hypotheses for the latitudinal gradient of plant diversity that invoke historical processes to explain the current pattern of decreasing diversity with increasing latitude are cast into doubt. The fossil pollen data show that while community composition changed dramatically through time, familial richness in temperate plant communities often has not shown a directional trend over the 10,000 years of the Holocene. Although this is not a long time relative to rates of plant speciation or tectonic processes, it is a long ecological time. The robust nature of diversity patterns through such a long period suggests the continuous operation of fundamental processes, such as latitudinal variation in resource availability and the mechanisms that govern how these resources are apportioned among species. The pattern observed here matches the predictions of the 'ecological' hypotheses: contemporary ecological processes are controlling latitudinal patterns of diversity.

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