

History of a latitudinal diversity gradient: woody plants in Europe 13,000–1000 years B.P.

JONATHAN SILVERTOWN Biology Department, Open University, Milton Keynes MK7 6AA

ABSTRACT. A pollen atlas of Europe is used to estimate the taxonomic diversity (taxon richness) of woody plants between 40°N and 70°N between 13,000 and 1000 years before the present (Y.B.P.). A gradient of decreasing taxonomic diversity with increasing latitude has existed for woody plants in Europe since 13,000 Y.B.P. The slope of this diversity gradient increased through the Holocene and was half as steep 13,000 years ago as it was 1000 Y.B.P. The slope of the diversity gradient increased with time after the retreat of the ice sheet because the colonization rate for new woody taxa was higher in southern Europe than in northern Europe. An equilibrium pattern of taxon richness may have been reached 6000 Y.B.P.

These results support the hypothesis that modern differences in the diversity of woody plants between higher and lower latitudes in Europe are mostly a consequence of contemporary climatic limits rather than of differences in the time available for colonization since the retreat of the ice sheet.

Introduction

Latitudinal gradients in taxonomic diversity (taxon richness) have been recorded for many groups of animals and plants, particularly in North America (Fischer, 1960; Simpson, 1964; Cook, 1969; Kiester, 1971; Glenn-Lewin, 1976). Pianka (1966) remains the most comprehensive review of latitudinal diversity gradients and the hypotheses which have been advanced to explain them. These hypotheses divide into two groups: (1) Those depending upon community structure (e.g. species packing or size or number of niches at different latitudes); and (2) Those depending upon history (either in ecological or in evolutionary time).

The authors of earlier studies (who were mostly zoologists) strongly favoured structural hypotheses, though Baker (1970), considering the problem from a botanical viewpoint believed the importance of history to have been underemphasized.

Structural and historical hypotheses tend

to address the problem of latitudinal differences in diversity from two different perspectives. Structural hypotheses have sought to account for the stable coexistence of large numbers of species in tropical habitats in terms of the niche structure of communities, leading to the question 'Why are there so many tropical trees?' (Janzen, 1970; Leigh, 1982) echoing Hutchinson's (1959) famous paper 'Homage to Santa Rosalia – or Why are there so many kinds of animals?' Ultimately this perspective supposes that tree diversity in the temperate zone is limited by competition and that temperate communities with low species densities are (or are nearly) saturated with species. This conclusion is at odds with the fact that very high species densities can be found in some temperate communities such as among plants of calcareous grassland (Silvertown, 1979). Historical hypotheses, on the other hand, are not concerned with the issue of competition and coexistence, but explain low temperate diversity as a consequence of recent climatic changes in the temperate zone. From

this perspective the important question is rephrased as 'Why are there so few temperate trees?'

There are a number of possible theoretical solutions to the question of how high densities of species can coexist (e.g. Grubb, 1977; Connell, 1978; Huston, 1979; Weiner & Conte, 1981; Pickett, 1980; Tilman, 1982; Leigh, 1982) and it is timely to re-examine geographical diversity patterns from an historical perspective.

Studies published in the last decade have shown that latitudinal gradients in taxonomic diversity are not as common on other continents as they are in North America (e.g. Barbour & Brown, 1974; Schall & Pianka, 1978). This and the confirmation of some reverse gradients and more complex patterns of diversity (e.g. Janzen, 1981; Richardson & Lum, 1980) has led to historical and climatic hypotheses becoming more prominent in the literature of the subject. However, there are still very few instances where the history of a diversity gradient is known. In a few cases the fossil record shows that diversity gradients of some marine taxa are ancient and stable (e.g. Stehli *et al.*, 1969; but see Van Valen, 1969, for a contrary view) but the dynamic history of modern terrestrial diversity gradients has never been explored.

In this paper I use the palynological maps of plant distribution compiled by Huntley & Birks (1983) to investigate the history of

taxonomic diversity in woody plants in Europe between 13,000 and 1000 years B.P.

Methods

Huntley & Birks (1983) present maps of pollen distribution for woody and non-woody plants between 13,000 and 0 years before present (Y.B.P.) compiled from cores taken throughout Europe. The pollen record places constraints upon the use and the interpretation of these maps for the present purpose:

(1) Pollen grain types often cannot be identified to species and so maps of the distribution of two plant taxa may represent two groups of different taxonomic rank, according to the distinctiveness of pollen morphology. As a result we cannot measure species diversity *per se* but we can estimate taxonomic diversity from the number of pollen types represented at a site.

(2) The record is incomplete or sporadic for some taxa. This is especially so for herbs which were therefore omitted from this study.

(3) The later record is more extensive than the earlier record which is represented by fewer sampling sites.

(4) Europe is not uniformly sampled with cores. This is particularly so for the period earlier than 10,000 Y.B.P. when most cores are south of 55°N. This difficulty and (3) above

TABLE 1. Linear regression and correlation statistics for mean taxon number on latitude ($n = 6$), 1000 Y.B.P. to 13,000 Y.B.P. a = intercept, b = slope of the regression, r = correlation coefficient, P = significance level of r .

Regression (10° Y.B.P.)	a	b	r	P
1	14.96	-1.97	-0.96	< 0.01
2	17.55	-2.28	-0.98	< 0.01
3	14.40	-1.73	-0.96	< 0.01
4	15.91	-1.91	-0.95	< 0.01
5	14.81	-1.89	-0.98	< 0.01
6	14.19	-1.63	-0.95	< 0.01
7	12.83	-1.53	-0.95	< 0.01
8	13.64	-1.77	-0.95	< 0.01
9	10.83	-1.46	-0.99	< 0.01
10	11.03	-1.36	-0.93	< 0.01
11	5.74	-0.73	-0.85	< 0.05
12	5.25	-0.42	-0.97	< 0.01
13	7.18	-1.07	-0.93	< 0.01

are considered again in the results section of this paper.

(5) Long-distance transport of pollen means that its presence in a core cannot automatically be interpreted as evidence that the plants themselves are present. Huntley & Birks (1983) offer interpretations of their maps which take this into account.

(6) The relationship between the abun-

dance of pollen in a core and the true historical abundance of the plant is different for different taxa since, for example, a wind pollinated tree sheds much more pollen than does an insect pollinated one. This is not a problem in the present study which uses only qualitative (presence/absence) data for taxa using the individual criteria for presence of each taxon given by Huntley & Birks in their atlas. It is

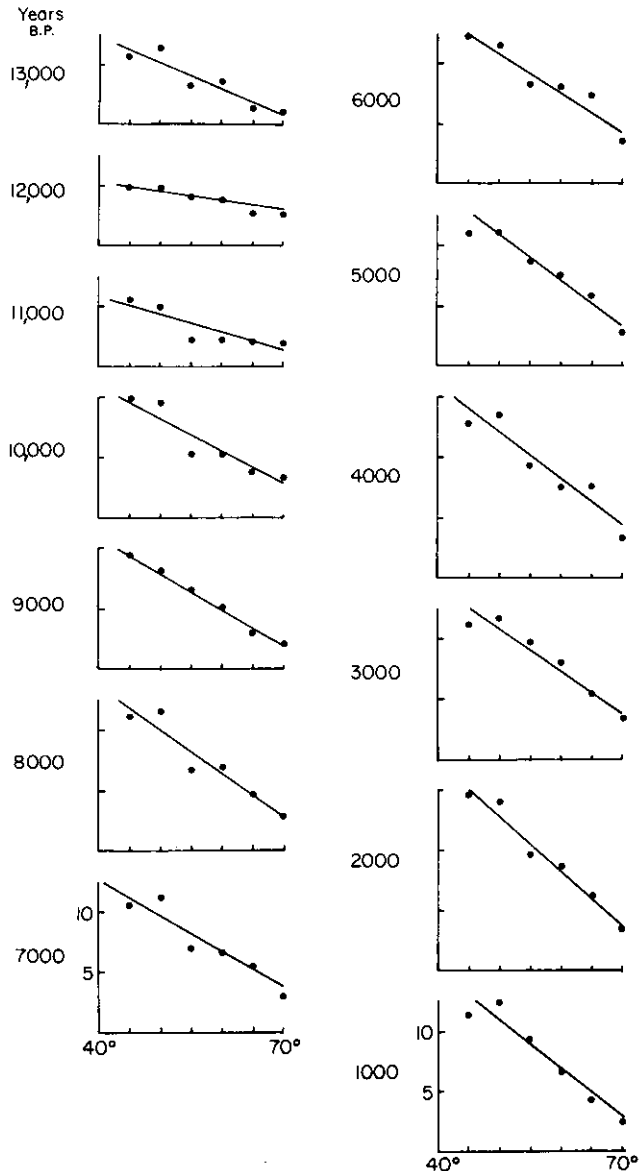


FIG. 1. The latitudinal gradient in woody plant diversity in Europe, 13,000–1,000 Y.B.P.

conceivable that some rare entomophilous woody plants are entirely missing from the record.

Maps of pollen distribution for thirty woody taxa were used in this study. The thirty taxa and the probable number of species each contains are listed in Appendix 1. Ideally the distribution of each taxon would be mapped at every 1000 year interval between 13,000 and 1000 years B.P. but in practice few taxa have an uninterrupted series of thirteen maps. Where an n -thousand-and-five-hundred-year map was given, this was used in place of the missing data. Huntley & Birk's maps were transformed into grid maps recording the presence/absence of each taxon in squares 5° latitude \times 5° longitude between 40° N and 70° N, 10° W and 45° E at each 1000 year time interval. The number of taxa present in each square of this grid at each time interval was obtained by addition of the maps for the thirty individual taxa. Mean taxonomic diversities were calculated for each of the six 5° latitudinal bands between 40° N and 70° N, ignoring squares in each band where no species occurred at a particular date. As an alternative measure of taxonomic richness the total numbers of taxa per 5° latitudinal band were also calculated. The two measures lead to the same conclusions in each of the tests described below. To avoid duplication only results from tests using mean taxonomic diversity are given here.

The following regressions and correlations were computed:

(1) Mean number of taxa per 5° latitude band against latitude at each time interval. The slopes of these thirteen linear regressions measure the slope and direction of the diversity gradient each 1000 years.

(2) Slope of the diversity gradient at each time interval against time. The slope of this regression measures how the slope and direction of the latitudinal diversity gradient changed with time.

(3) Mean taxon number against time for each of the 5° bands of latitude. The slopes of these six regressions measure the rate of colonization which occurred in each of the six latitude bands during 12,000 years.

Results

The latitudinal diversity gradient 13,000–1000 years B.P.

A gradient of decreasing taxonomic diversity with increasing latitude has existed for woody plants from 13,000 Y.B.P. through to 1000 Y.B.P. between latitudes 40° N and 70° N (Table 1, Fig. 1).

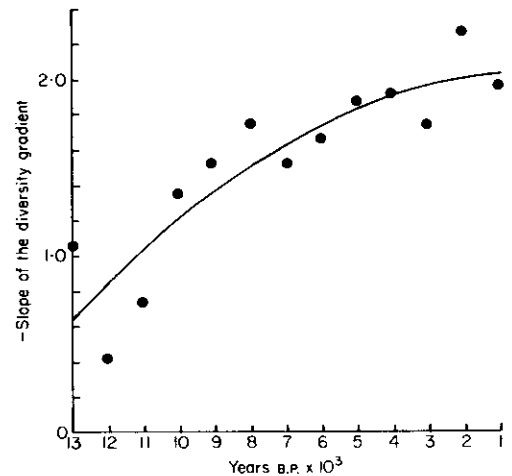


FIG. 2. The change in the slope of the latitudinal diversity gradient of woody plant diversity with time. $\chi^2 = 2.036 - 0.008Y$, $r = -0.87$, $P < 0.001$.

TABLE 2. Linear regressions of taxon number on time ($n = 13$) for six 5° latitude bands. Symbols as in Table 1.

Band	Latitude	a	b	r	P
1	$40-45^\circ$ N	14.9	-0.69	-0.87	< 0.01
2	$45-50^\circ$ N	15.4	-0.74	-0.89	< 0.01
3	$50-55^\circ$ N	11.5	-0.64	-0.95	< 0.01
4	$55-60^\circ$ N	9.4	-0.45	-0.86	< 0.01
5	$60-65^\circ$ N	7.4	-0.38	-0.74	< 0.01
6	$65-70^\circ$ N	3.8	-0.13	-0.68	< 0.05

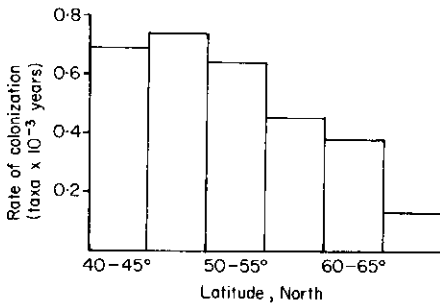


FIG. 3. Rate of colonization by new taxa in the six 5° bands of latitude from 40°N to 70°N between 13,000 and 1000 Y.B.P.

The slope of the diversity gradient became steeper with time (Fig. 2), increasing most rapidly around 10,000 Y.B.P. and less rapidly after 6000 Y.B.P. This relationship is best fitted by a curvilinear regression ($x^2 = 2.036 - 0.008y$, $r = -0.882$, $P < 0.001$). Neither problem 3 nor 4 (Methods, above) affects this result since the diversity trend is quite clear for the period 1000–10,000 years B.P. when records are good.

The taxonomic diversity of woody plants increases significantly with time in all six 5° bands of latitude (Table 2). The rate of colonization decreases with latitude (Fig. 3).

Discussion

A clear latitudinal gradient in the taxonomic diversity of woody plants has existed in Europe since 13,000 years B.P. This gradient was more shallow 13,000 years ago, when the ice sheet still covered much of northern Europe, than it was 1000 years ago long after its retreat. These changes in the gradient with time emphasize the importance of history in determining diversity patterns.

The increasing slope of the gradient through time sheds interesting light on the causes of diversity differences between higher and lower latitudes in Europe. Two alternative situations may be envisaged. On the one hand, higher latitudes may be impoverished by comparison with lower latitudes because less time has elapsed since these latitudes were freed from the influence of the ice sheet and because tree migration rates are slow and

colonization is still occurring (e.g. Davis, 1981). On the other hand, the paucity of species at higher latitudes may be a contemporary effect of climate which acts as an active barrier to migration of new taxa from the south.

Though this dichotomy between the effects of time and the effects of climate is a little arbitrary since both influence colonization rates, the evidence presented here clearly suggests that climate rather than time is the more important limitation on woody plant diversity in Northern Europe. If time were the major limitation we might expect the latitudinal diversity gradient to become less steep as we approach the present day and as higher latitudes 'fill up' again with species. The fact that the gradient actually becomes more steep is explained by higher colonization rates in lower as compared with higher latitudes (Fig. 3). The difference in these rates must be related to climate, though it is not necessary to suppose that geographical distribution limits are set by physiological tolerance of climate *per se* (Carter & Prince, 1981).

Differences in rates of colonization between southern and northern Europe might also be related to the existence of more refugia in the south than in the north. Such refugia would allow a rapid increase in mean taxon diversity as plants spread within bands of latitude as the climate ameliorated. This process of spread within low latitude bands might be an important one in shaping the changes in the diversity gradient with time observed in this study. If so, we might expect *total* species numbers per latitude band to change little in the south during the Holocene, since the presence of plants in refugia there would raise taxon number to a high starting level at the beginning of the period. In consequence a latitudinal diversity gradient computed in *total* species numbers would be steep at around 13,000 Y.B.P. and get shallower in more recent time. In fact the gradient computed this way (Silvertown, unpublished) behaves like that described here (Figs. 1 and 2) and becomes steeper with time. This means that southern refugia are not detectable at the map resolution used here. Of course it does not mean that such refugia did not actually exist, merely that they were small and perhaps few.

The distribution of woody plants in Europe in the last 1000 years is heavily influenced, if not dominated, by human activities. However, Fig. 2 suggests that, at least in its gross features, the diversity of woody plants in Europe had achieved equilibrium well before this time perhaps as early as 6000 Y.B.P.

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Appendix 1. Taxa used in the estimation of woody plant diversity in Europe from pollen maps (Huntley & Birks, 1983).

Taxon	No. of native European species in taxon		No. of maps in period 13,000–1000 Y.B.P.
	All species	Widespread spp.	
<i>Abies</i>	6	1	13
<i>Acer</i>	13	3	10
<i>Alnus</i>	4	2	12
<i>Betula</i>	4	2	13
<i>Carpinus betulus</i>	1	1	10
<i>Castanea sativa</i>	1	1	4
<i>Corylus</i> -type	4	1	12
<i>Ephedra</i>	3	0	4
<i>Fagus</i>	2	1	11
<i>Fraxinus excelsior</i> -type	3	1	11
<i>Fraxinus ornus</i>	1	0	5
<i>Hippophae rhamnoides</i>	1	0	2
<i>Juglans regia</i>	1	1	3
<i>Juniperus</i> -type	> 8	1	8
<i>Larix</i>	2	0	8
<i>Olea europaea</i>	1	0	4
<i>Ostrya</i> -type	2	0	7
<i>Phillyrea</i>	2	0	4
<i>Picea</i>	2	1	13
<i>Pinus</i> (Diploxyton)	10	1	13
<i>Pinus</i> (Haploxyton)	3	0	5
<i>Pistacia</i>	3	0	5
<i>Populus</i>	4	1	6
<i>Quercus</i> (Deciduous-type)	22	4	13
<i>Quercus</i> (Evergreen)	3	0	10
<i>Salix</i>	69	c. 7	6
<i>Tilia</i>	4	2	12
<i>Ulmus</i>	5	1	12
<i>Empetrum</i>	2	0	6
Ericaceae	40	3	6