

REPORT

Deterministic Plio-Pleistocene extinctions in the European cool-temperate tree flora

Jens-Christian Svenning
Department of Systematic
Botany, University of Aarhus,
Nordlandsvej 68, DK-8240
Risskov, Denmark
E-mail: svenning@biology.au.dk

Abstract

Extinctions have been important in the shaping of modern phylogeographic patterns. A classic example is the heavy Plio-Pleistocene losses that have caused Europe to have a depauperate temperate tree flora compared to eastern North America and eastern Asia. To investigate the mechanisms involved in this extinction event, I test the hypothesis that the present European status (extinct, relictual, or widespread) of cool-temperate tree genera found in Pliocene Europe is predictable from their modern climatic requirements. As a prerequisite for this analysis, I test for genus-level conservatism in climatic requirements by comparing congeneric values across Europe, eastern Asia and North America, and find strong evidence hereof. I find a high degree of ecological determinism in the fate of European Pliocene tree genera, still widespread taxa being more tolerant of cold growing season and winter temperatures than extinct and relictual taxa, and relictual taxa being more drought tolerant than extinct taxa.

Keywords

Climatic change, cold tolerance, diversity loss, drought tolerance, evolutionary stasis, extinction pattern, forest refugia, macroecology, Neogene, temperate trees.

Ecology Letters (2003) 6: 646–653

INTRODUCTION

Regional-scale extinctions have strongly shaped modern floras and global phylogeographic patterns (Mai 1995; Wen 1999; Morley 2000; Willis & McElwain 2002). A well-known example is the Neogene development of the European tree flora (e.g. Tallis 1991; Mai 1995). Tree diversity varies markedly among the major north-hemispheric moist-temperate forest regions at both regional and local scales, eastern Asia and to a lesser extent eastern North America being the richest and Europe and western North America the poorest (Campbell 1982; Grubb 1987; Latham & Ricklefs 1993a,b; but cf. Huntley 1993). The diversity differences cannot be explained by modern climate (Latham & Ricklefs 1993b; Ricklefs & Latham 1999), but reflect differential rates of extinction, speciation and immigration (Latham & Ricklefs 1993a,b; Ricklefs & Latham 1999; Wen 1999; Qian & Ricklefs 2000). Regional extinctions constitute a strong causal factor for the present low tree diversity in Europe (e.g. Tallis 1991; Latham & Ricklefs 1993a; Mai 1995). Whereas the subtropical–tropical components of the European Tertiary flora began declining in diversity already by the Eocene–Oligocene transition (33.7 Myr), temperate tree diversity remained high in Europe into the Pliocene

(Mai 1995). Subsequently, severe step-wise reductions in temperate tree generic diversity began with the first strong glaciation in Europe in the Late Pliocene (2.4 Myr) and continued into the Middle Pleistocene, with only few later extinctions (Van der Hammen *et al.* 1971; Watts 1988; Tallis 1991; Lang 1994). The classical explanation for the severe Plio-Pleistocene extinctions in Europe is that the east–west orientation of European mountain ranges and the Mediterranean Sea prevented temperate trees from migrating south during cold stages, while migration in North America and East Asia was not similarly curtailed (Reid 1935; summarized by Huntley 1993). Recent paleoclimatological research, however, suggests that the climatic conditions in the southern refugial areas were of greater importance for the differential extinction rates (Grubb 1987; Huntley 1993). In eastern Asia and eastern North America, large areas harboured temperate forest even during the last glacial maximum (Takahara *et al.* 2000; Williams *et al.* 2000; Yu *et al.* 2000). The Mediterranean region, in contrast, experienced a shift from moist warm-temperate climate to the current summer-dry climate in the middle Pliocene 3.2 Myr, resulting in the loss of moist forest from its coastal lowlands (Suc 1984). From 2.3 Myr onwards the Mediterranean experienced even greater dryness in glacial periods

(Suc 1984), during the more severe parts of which European temperate trees as a consequence became restricted to localized refuges in mountains and moist valley-bottoms in southern Europe (Tallis 1991; Birks & Line 1993; Tzedakis 1993; Willis 1996) and very small refuges further north (Willis *et al.* 2000; Stewart & Lister 2001). A large proportion of the temperate tree genera present in Europe in the Pliocene did not survive there to the present, the majority having disappeared already by the close of the Early Pleistocene (Van der Hammen *et al.* 1971; Watts 1988; Tallis 1991; Martinetto 2001). Here, a macroecological analysis (*sensu* Brown 1995) of this important extinction event is provided. Europe's moist broadleaved forests are currently largely restricted to areas with mean annual temperature (MAT) <12.0°C (cf. Fig. 26 in Breckle 2002; Schönwiese & Rapp 1997, p. 59). Therefore, this analysis is restricted to cool-temperate tree genera, i.e., those whose natural modern global distribution includes areas with MAT < 12.0 °C. The loss of warm-temperate moist forest genera can be attributed to a trivial lack of habitat in Europe (cf. Michaux *et al.* 1979; Suc 1984). The question remains, however, whether extinction among cool-temperate genera was a random process reflecting small population sizes in refuges (cf. Birks & Line 1993), or caused by deterministic ecological sorting. It is well accepted that climatic conditions are among the most important determinants of plant species ranges and global vegetation patterns, the three most important factors being maximum cold, growing season heat, and drought (e.g. Sakai & Weiser 1973; Woodward 1988; Sykes *et al.* 1996; Chuine & Beaubien 2001; Breckle 2002). Given the strong oscillations in temperature and dryness during the Plio-Pleistocene (e.g. Suc 1984; Tallis 1991; Utescher *et al.* 2000) plant requirements with respect to these factors seem likely to have been important for survival of cool-temperate genera through this period. Indeed, Watts (1988) suggested frost tolerance to be an important factor in Plio-Pleistocene tree extinctions in Europe (also cf. Latham & Ricklefs 1993b). Here, the ecological sorting hypothesis is tested by comparing to what extent extinct and surviving tree genera differ in these climatic requirements (see Campbell 1982 for an early discussion of Neogene cool-temperate tree extinctions in Europe through ecological sorting by edaphic requirements and migration ability). The European Plio-Pleistocene climatic requirements of the tree genera are inferred from their modern requirements in extra-European regions. To avoid circularity, climatic parameters estimated from modern European distributions of the genera still extant in the region were not used. It has been suggested that temperate trees exhibit a high degree of evolutionary plasticity in climatic and other ecological requirements (Ricklefs & Latham 1992; but cf. Latham & Ricklefs 1993b). If this argument is true, it may not be possible to use the

current ecology of tree taxa to represent their ecological demands in the past. Consequently, before analysing the extinction pattern conservatism in climatic requirements is tested (or climatic adaptability) among temperate tree genera by comparing congeneric values between North America and Europe or East Asia.

MATERIALS AND METHODS

Assembly of the data set

A list of the cool-temperate tree genera of Pliocene Europe was compiled by including all such genera with European Pliocene pollen or macrofossil records as well as all contemporary native cool-temperate tree genera known from pre-Pliocene deposits. In this study, the main source of information on the Tertiary tree flora of Europe was Mai's (1995) monograph (see Supplementary Materials for the full reference list). Tree genera were defined as those containing at least some contemporary tree species, as defined in Latham & Ricklefs (1993a), i.e. self-standing woody perennials reaching ≥ 8 m in height (for sources of size information, cf. Supplementary Materials). Contemporary European genera that include tree species, but not in Europe were omitted. Europe was defined to the exclusion of Caucasus, Asia Minor, Macaronesia and Mediterranean islands. From the total list of Pliocene European tree genera, only those with cool-temperate extra-European representatives today were included in the present study. That is, those with minimum MAT < 12.0 °C based on the combined extra-European data (see below). Furthermore, to ensure the exclusion of all non-cool temperate genera, any genera that are not hardy outdoors anywhere in Europe according to the European Garden Flora (The European Garden Flora Editorial Committee 1986–2000) were excluded. Among the few genera for which data on minimum MAT could not be found, most were clearly not cool-temperate. However, *Pyrus* was included in the final list of cool-temperate Pliocene European tree genera because it clearly contains cool-temperate species in both Europe and Asia (cf. The Flora Europaea Editorial Committee 1964–1993; Krössmann 1968; The European Garden Flora Editorial Committee 1986–2000). For each cool-temperate tree genus of Pliocene Europe, its present status in Europe was scored as (based on The Flora Europaea Editorial Committee 1964–1993; Krössmann 1968) as (1) extinct (in Europe, but not globally), (2) relictual, occurring only in Southern Europe, or (3) widespread, also north of the Alps (cf. Campbell 1982).

Extra-European climatic data were compiled for each genus using the data provided for North American tree species in Thompson *et al.* (1999–2000) (these data will be referred to as the USGS data), supplementing with data

for non-North American genera from the Palaeoflora Database (Utescher & Mosbrugger 2001). The climatic parameters used were derived by comparing spatial climate data to distribution maps for the taxa concerned (please refer to the source publications for more detailed descriptions of the methods). In the case of the USGS data, the genus parameters were computed after excluding all non-tree species with the exception that large shrub (3–7 m height) species were included for those few genera with tree species in Eurasia, but only shrub representatives in North America (i.e. *Corylus*, *Lindera* and *Stewartia*). For the Palaeoflora dataset, a similar attempt was made to exclude shrub species from tree genera with tree representatives also listed. Apart from shrubs, other growth forms were always excluded from both data sets. Finally, all European species and all collective taxa possibly including European species from the Palaeoflora data were excluded.

For each genus, the following climatic parameters were selected to describe its climatic requirements (winter cold tolerance, summer heat requirement and drought tolerance): mean temperature of the coldest month (MTC), mean annual temperature (MAT) and mean annual precipitation (MAP). Attention was focused on these simple parameters because they were included in both data sets (Thompson *et al.* 1999–2000; Utescher & Mosbrugger 2001). For summer heat requirements and drought tolerance, growing degree days (GDD) and the moisture index actual evapotranspiration/potential evapotranspiration (AE/PE) are thought to control plant distributions more directly (Thompson *et al.* 1999–2000). These parameters were also used in the analyses, but were only available in the USGS data set. For each climatic parameter, its minimum across the minima for the taxa in a genus was used to represent the genus-level minimum tolerated value for that parameter. The extra-European climatic data for each genus were combined giving preference to the USGS data and only using the Palaeoflora Database data for genera without USGS data due to the more heterogeneous quality of the Palaeoflora data (Utescher & Mosbrugger 2001).

When available, the following additional data on the climatic requirements of each genus were also compiled: (1) hardiness as estimated in The European Garden Flora Editorial Committee (1986–2000) and converted to an ordinal hardiness scale (HD) ranging from 1 (H1) to 7 (G2); (2) ecophysiological data on freezing tolerance (FT, i.e. lowest temperature tolerated; e.g. Sakai & Weiser 1973; cf. Supplementary Materials for the full reference list); (3) distribution across major Chinese forest zones (based on Wang 1961), converted to an ordinal latitudinal scale [CFZ; rain forest = 0, evergreen forest = 1, mixed mesophytic forest (including montane coniferous forest restricted

to this zone) = 2, temperate deciduous forest with oak = 3, northern hardwoods = 4, boreal forest = 5]; and (4) minimum GDD based on its present-day European distribution (Sykes *et al.* 1996). Each genus was assigned the maximum HD and CFZ and minimum FT (each taxon being represented by its least tolerant organ: twigs, buds, or leaves) and GDD values across its taxa. Non-tree species were excluded as for the USGS and Palaeoflora data.

Note that parameter acronyms from this point onwards always refer to the genus-level extreme value, as described in this section. Climatic parameter calculated for a single region (North America, Europe or East Asia) have acronyms with subscripts as in Table 1. If no subscripts are given, the parameters are based on the combined extra-European information. The complete data set is given in Supplementary Materials.

Table 1 Spearman rank correlation coefficients of climatic limit parameters for cool-temperate tree genera between North America (NA) and Europe (EU) or East Asia (AS)

	HD _{AS}	HD _{EU}	CFZ _{AS}	GDD _{EU}	FT _{AS}
MAT_{NA}					
r_s	0.71	0.70	-0.73	0.74	0.62
P	<0.0001	<0.0001	<0.0001	0.0008	0.0001
n	46	34	47	17	33
GDD_{NA}					
r_s	0.65	0.67	-0.69	0.65	0.58
P	<0.0001	<0.0001	<0.0001	0.0046	0.0005
n	46	34	47	17	33
MTC_{NA}					
r_s	0.72	0.78	-0.78	0.74	0.70
P	<0.0001	<0.0001	<0.0001	0.0007	<0.0001
n	46	34	47	17	33
MAP_{NA}					
r_s	0.56	0.25	-0.70	0.41	0.56
P	<0.0001	n.s.	<0.0001	n.s.	0.0007
n	46	34	47	17	33
AE/PE_{NA}					
r_s	0.51	0.16	-0.69	0.43	0.53
P	0.0003	n.s.	<0.0001	n.s.	0.0016
n	46	34	47	17	33
HD_{NA}					
r_s	0.73	0.76	-0.67	0.28	0.65
P	<0.0001	<0.0001	<0.0001	n.s.	<0.0001
n	45	31	43	15	32
FT_{NA}					
r_s	0.76	0.68	-0.77	0.78	0.66
P	<0.0001	0.0028	<0.0001	0.0076	0.0011
n	21	17	22	10	21

MAT, mean annual temperature; GDD, growing-degree-days; MTC, mean temperature of the coldest month; MAP, mean annual precipitation; AE/PE, actual evapotranspiration/potential evapotranspiration; HD, hardiness; FT, freezing tolerance; CFZ, Chinese forest zones (see text for definitions).

Analyses

To examine evolutionary conservatism in climatic requirements, the genus-level climatic parameters were computed separately for North America, Europe and East Asia (excluding species reaching into Europe) and tested for correlations among genus-level values for the climatic parameters for North America and Europe or East Asia. The design of the Palaeoflora Database precluded its use in this analysis (cf. Utescher & Mosbrugger 2001). Subsequently, ecological determinism was tested in the Plio-Pleistocene extinctions among European tree genera by comparing the climatic requirements (as estimated from their present extra-European distributions) of the extinct, relictual and still widespread genera. To check if the major findings were robust if phylogenetic autocorrelation in species traits at the familial and higher levels was controlled for, the sister taxa pairwise comparative method of Møller & Birkhead (1992) was applied by selecting genera within families that differ in their present European status (randomly selecting one, if several had identical status) to test (1) that widespread taxa have lower MAT and MTC than their extinct sister taxa; and (2) that relictual taxa have lower MAP than their extinct sister taxa. In the present study, the term sister taxa simply refers to confamilial genera. Family circumscriptions followed Mabberley (2000), but were checked for monophyly following Judd *et al.* (1999) before use in the sister taxa comparisons. Consequently, *Alangium* was treated as included in Cornaceae, while *Celtis* was excluded from Ulmaceae with respect to these analyses.

RESULTS

Evolutionary conservatism in climatic requirements

A high degree of correspondence was found in the temperature requirements (MAT, GDD, MTC, HD, FT and CFZ) of cool-temperate tree genera when comparing North America and Eurasia (Table 1). A similar pattern is indirectly implied for their moisture requirements (MAP, AE/PE) through the correlation of moisture and temperature parameters (MAP and MAP, Spearman $r_s = 0.53$, $P < 0.0001$, $n = 73$; MAP and MTC, $r_s = 0.56$, $P < 0.0001$, $n = 73$; AE/PE and GDD, $r_s = 0.55$, $P < 0.0001$, $n = 56$).

A principal component analysis (PCA) on MAT, MTC and MAP revealed that the strong primary gradient in climatic requirements of the cool-temperate genera was a temperature-dominated gradient equally related to MAT and MTC, but also with a strong relationship to MAP (Table 2). The second principal component corresponded to a pure precipitation gradient (Table 2). The correlations of the 'improved' climatic parameters GDD and AE/PE as well as

Table 2 Principal components analysis on the correlation matrix of the main climatic limit parameters (combined extra-European values) for the cool-temperate tree genera

	Principal components		
	PC-1	PC-2	PC-3*
Eigenvalue	2.36	0.58	0.06
% variance	78.8	19.2	2.0
Pearson r with			
MAT	0.94	-0.28	0.17
MTC	0.95	-0.24	-0.18
MAP	0.75	0.66	0.01

*Using the 90% criterion (Quinn & Keough 2002) only the first two components were used for further analyses.

MAT, mean annual temperature; MTC, mean temperature of the coldest month; MAP, mean annual precipitation.

Table 3 Spearman rank correlations of the principal components (PC) from the PCA reported in Table 2 with independent climatic limit parameters (see text for definitions)

r_s	n	PC-1	PC-2
GDD _{NA}	56	0.90 (<0.0001)	-0.13 (n.s.)
AE/PE _{NA}	56	0.74 (<0.0001)	0.55 (<0.0001)
HD	71	0.57 (<0.0001)	-0.12 (n.s.)
FT	46	0.78 (<0.0001)	-0.01 (n.s.)

GDD, growing-degree-days; AE/PE, moisture index; HD, hardness; FT, freezing tolerance. Spearman rank correlations were used due to ordinal nature of HD and a certain lack of normality in GDD and FT. Subscripts refer to region-specific parameters: North America (NA).

the horticultural and ecophysiological measures of cold tolerance to the two principal components from the climatic PCA support the above interpretation (Table 3).

Ecological determinism in the Plio-Pleistocene extinctions

The fate of European Pliocene tree genera was strongly determined by their climatic requirements, as represented by the requirements of their present-day representatives in North America and Asia (Fig. 1; Table 4). Inspection of Fig. 1 shows that widespread and extinct genera occur in distinct regions of the MAT–MAP space with the exception of a few outliers and with the relictual genera being nested within the lowermost part of the 'extinct' region (likewise in Fig. 2). Overall, genera with MAT < 0.0 °C have had a high probability of glacial survival through the Plio-Pleistocene and postglacial range expansion, while those with MAT > 2.5 °C largely have become extinct or relictual. Among the latter two groups, the relictual genera are strongly concentrated at MAP < 270 mm year⁻¹, i.e. among the

most drought tolerant, although a similar number of extinct genera also have $\text{MAP} < 270 \text{ mm year}^{-1}$. Given the high correlation of summer heat requirements and winter cold tolerance across genera it is not possible to point one out as

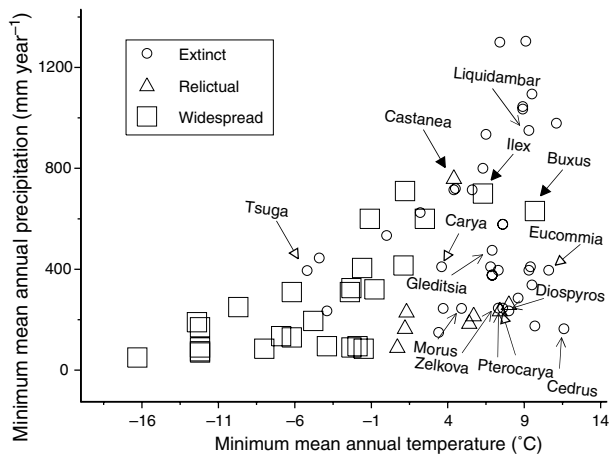


Figure 1 Current European status of cool-temperate tree genera present in Pliocene Europe as a function of the climatic requirements (minimum mean annual temperature, MAT and minimum mean precipitation, MAP) of their present-day extra-European representatives. Filled arrows indicate the only widespread broadleaved evergreen cool-temperate tree genera in Europe (*Ilex* and *Buxus*) and the only relictual genus that appear to be little tolerant of drought (*Castanea*). Empty arrows indicate those regionally extinct genera that occurred at least until the late Early Pleistocene in Central and Western Europe (Lang 1994). Open-headed arrows indicate regionally extinct genera surviving in West Asia, North Africa and/or Mediterranean islands.

the most important (Tables 1–3). While the relictual genera are nearly as thermophilic as the extinct ones, they are more drought tolerant (Table 4). The supposedly superior bioclimatic parameters GDD and AE/PE provide no improved distinction between the groups of genera compared to MAT and MAP (Table 4; Fig. 2).

For the pairwise comparison of sister taxa, six pairs (*Cornus* and *Alangium*; *Juniperus* and *Thuja*; *Fagus* and

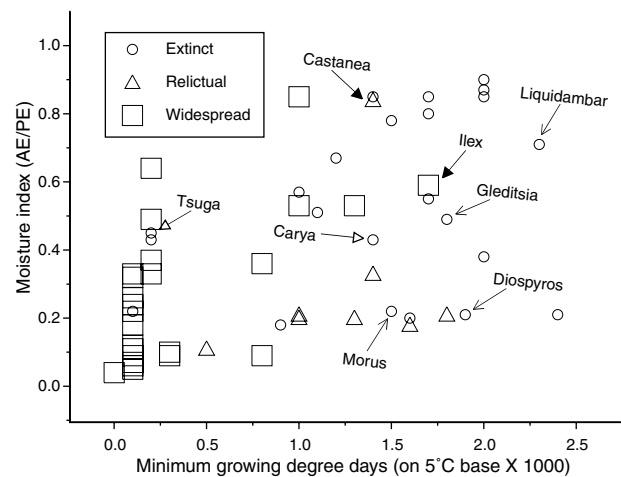


Figure 2 Current European status of cool-temperate tree genera present in Pliocene Europe as a function of the climatic requirements [minimum growing-degree-days, GDD_{NA} and minimum moisture index (actual evapotranspiration/potential evapotranspiration), AE/PE_{NA}] of their present-day North American representatives. Arrows indicate genera of special interest as in Fig. 1.

Table 4 Comparisons of climatic requirements of cool-temperate tree genera grouped according to their Neogene fate in Europe, analysed by one-way ANOVA (Kruskal–Wallis test gives very similar, significant results)

Parameter	Extinct (mean \pm SD)	Southern (mean \pm SD)	Widespread (mean \pm SD)	ANOVA			
				r^2	F	d.f.	P
n	39	8	26				
MAT ($^{\circ}\text{C}$)	$6.26 \pm 4.00\text{a}$	$4.26 \pm 2.88\text{a}$	$-4.47 \pm 2.28\text{b}$	0.53	29.1*	2	<0.0001
MTC ($^{\circ}\text{C}$)	$-7.98 \pm 6.39\text{a}$	$-12.0 \pm 5.76\text{a}$	$-23.4 \pm 9.14\text{b}$	0.49	34.0	2	<0.0001
MAP (mm year^{-1})	$547 \pm 322\text{a}$	$273 \pm 206\text{b}$	$274 \pm 215\text{b}$	0.20	9.07* [†]	2	0.0013
PC-1	$0.917 \pm 0.973\text{a}$	$0.0645 \pm 0.742\text{b}$	$-1.40 \pm 1.37\text{c}$	0.49	33.8	2	<0.0001
PC-2	$-0.0365 \pm 0.899\text{ab}$	$-0.589 \pm 0.582\text{a}$	$0.236 \pm 0.409\text{b}$	0.10	7.25*	2	0.0044
n	23	8	25				
GDD_{NA}	$1.46 \pm 0.640\text{a}$	$1.25 \pm 0.407\text{a}$	$0.368 \pm 0.453\text{b}$	0.50	26.6 [†]	2	<0.0001
AE/PE_{NA}	$0.536 \pm 0.255\text{a}$	$0.285 \pm 0.232\text{b}$	$0.282 \pm 0.219\text{b}$	0.23	7.77	2	0.0011

*Welch ANOVA due to lack of variance homogeneity (Levene's test, $P < 0.05$).

[†]MAP has skewness = 1.1, GDD_{NA} has kurtosis = -1.4.

Different letters indicate Tukey–Kramer's HSD test with $P < 0.05$ (Wilcoxon two-sample test gives identical results). The climatic limit parameters are: MAT, mean annual temperature; MTC, mean temperature of the coldest month; MAP, mean annual precipitation; PC-1 and PC-2, first and second principal components from the PCA in Table 2; GDD, growing-degree-days; AE/PE, moisture index. Subscripts refer to regions-specific parameters: North America (NA).

Lithocarpus, *Picea* and *Tsuga*; *Taxus* and *Torreya*; *Ulmus* and *Zelkova*) were available to test the first hypothesis and all deviated in MAT and MTC in the expected direction (one-tailed sign test, $P < 0.05$, in both cases). Only four pairs (*Castanea* and *Lithocarpus*; *Cercis* and *Robinia*; *Cupressus* and *Chamaecyparis*; *Juglans* and *Platycarya*) were available to test the second hypothesis, with just the latter two deviating in the expected direction (one-tailed sign test, $P = 0.69$). If *Gleditsia* had been chosen as a contrast to *Cercis* instead of *Robinia*, then three of four contrasts would have deviated in the expected direction (one-tailed sign test, $P = 0.31$). The other three contrasts had no alternatives or were insensitive to the choice of genera.

DISCUSSION

Evolutionary conservatism in climatic requirements

North American and Eurasian populations of most temperate forest tree genera appear to have been genetically isolated for 2–33 Myr with most divergences dating to the Miocene 5.3–23.8 Myr (Ricklefs & Latham 1992; Wen 1999; Manos & Stanford 2001), reflecting the Neogene disruption of the early to mid-Tertiary continuous Eurasian–North American temperate forest biome (Tallis 1991; Willis & McElwain 2002). The analyses done here indicate strong evolutionary conservatism in climatic requirements among cold-temperate tree genera. This finding is contrary to the suggestion of Ricklefs & Latham (1992) that temperate trees exhibit much evolutionary plasticity in their climatic and other ecological requirements, but in agreement with other reports of ecological conservatism among temperate tree genera (Kornas 1972; Huntley *et al.* 1989; also cf. Latham & Ricklefs 1993b). Based on a study of the climatic control of the distribution of *Fagus* in North America and Europe, Huntley *et al.* (1989, p. 559) conclude that “North American and European *Fagus* populations have nevertheless retained closely similar climatic responses since their separation between 25 and 10 My ago, suggesting that these climatic responses are linked to fundamental physiological limitations that have been unable to change through evolution on this time scale”. Furthermore, the successful use of fossil floras, interpreted using the climatic requirements of the nearest living relatives, in Tertiary paleoclimatic reconstructions in Europe as far back as the Oligocene (e.g. Utescher *et al.* 2000) also imply a high degree of evolutionary stasis in climatic requirements.

Ecological determinism in the Plio-Pleistocene extinctions

The results of the present study suggest that the modern European cool-temperate tree flora developed from a much

more diverse Pliocene tree flora through a highly deterministic ecological sorting process. Genera that are currently widespread in Europe differ from extinct and relictual genera by their greater tolerance of cold growing season and winter temperatures (i.e. in agreement with Watts 1988), while relictual genera are more tolerant of drought than extinct genera. The sister-taxa pairwise comparisons showed that the greater cold tolerance of widespread genera compared to extinct genera was robust to phylogenetic autocorrelation in species traits at the family level and above. The sister-taxa pairwise comparisons were inconclusive with respect to the greater drought tolerance of relictual genera relative to extinct genera, in large part due to the low sample size. The patterns found are consistent with the existence of two types of glacial temperate tree refugia in southern Europe: (1) relatively frequent cool, moist mid-altitude mountain refuges; and (2) warmer, but rarer and probably more drought-prone low-altitude valley-bottom refugia (Birks & Line 1993; Willis 1996). Genera that are still widespread were sufficiently cold-tolerant to survive in cool mountain refuges whereas relictual genera were more thermophilic but sufficiently drought-tolerant to survive in lowland refuges. The relictual genera are much less well separated from the extinct genera than the widespread genera are (Figs 1 and 2). A possible explanation is that the scarcity of warm lowland refugia relative to cool montane refugia resulted in greater stochasticity in the survivorship of the thermophilic, but drought-tolerant taxa compared to cold-tolerant taxa. Certainly, many of the extinct genera occurring at the bottom of Fig. 1 interspersed with the relictual genera have had a greater survival ability than most other extinct genera: *Zelkova* and *Pterocarya* were the last tree genera to go extinct in continental Europe, surviving into the last glaciation (Follieri *et al.* 1986; Lang 1994) and together with *Cedrus*, *Diospyros* and *Morus* they have relictual occurrences on Mediterranean islands, Western Asia and/or North Africa (The Flora Europaea Editorial Committee 1964–1993; Krössmann 1968). Among all the less drought-tolerant extinct genera only *Liquidambar* and *Gleditsia* also survive in these areas (Figs 1 and 2). It is also noteworthy that the four regionally extinct genera (*Tsuga*, *Eucommia*, *Carya* and *Pterocarya*) that were periodically widespread in Europe as late as the late Early Pleistocene or even the Middle Pleistocene (e.g. Lang 1994) appear more tolerant of dry climate than many other extinct genera, but less so than most relictual genera (Figs 1 and 2). While the widespread, relictual and extinct genera, as groups, differ in climatic requirements, a small number of genera do not fit the general pattern well, notably the only widespread broad-leaved evergreen cool-temperate tree genera in Europe, *Ilex* and *Buxus* (see Figs 1 and 2). Several explanations are possible: (1) The present-day extra-European climatic parameters are not representative of the past climatic

requirements of these genera in Europe for methodological or evolutionary reasons. In their climatic analyses of European Tertiary floras, Utescher *et al.* (2000) found that a few taxa were consistently climatic outliers, apparently having different climatic requirements in the European Tertiary as compared to their modern day requirements. An instructive example is *Castanea*, which appears to be much less drought tolerant than the other relict taxa (see Figs 1 and 2). However, this genus has its optimum on dry soils in both North America and Europe (Campbell 1982), perhaps indicating a greater degree of drought tolerance than inferred from its modern large-scale distributions. (2) Alternatively, stochasticity or ecological factors other than cold or drought (cf. Campbell 1982) might have had some role, albeit minor, in the Plio-Pleistocene fate of the cool-temperate tree genera in Europe.

CONCLUSION

The different fates of European cool-temperate tree genera during the Plio-Pleistocene appear to largely reflect a deterministic ecological sorting process determined by evolutionarily conservative limits to the tolerance of cold and drought. Trees often show adaptation to local environmental conditions and such adaptation has probably been of importance during past range expansions (e.g. Davis & Shaw 2001). However, an important lesson from the findings reported here is to expect fairly limited evolutionary adaptability of temperate tree genera in the face of rapid and strong future climatic changes. Consequently, it will be important to focus conservation actions on climatically stable areas (Taberlet & Cheddadi 2002) and potential migration routes.

ACKNOWLEDGEMENTS

I am grateful to Henrik Balslev for many helpful comments and Torsten Utescher for help in accessing the Palaeoflora Database data. I thank the Danish Natural Science Research Council for financial support through grant 21-01-0415.

SUPPLEMENTARY MATERIAL

Supplementary material for this paper is available from <http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE477/ELE477sm.htm>

REFERENCES

- Birks, H.J.B. & Line, J.M. (1993). Glacial refugia of European trees – a matter of chance? *Diss. Bot.*, 196, 283–291.
- Breckle, S.-W. (2002). *Walter's Vegetation of the Earth*. Springer-Verlag, Berlin.
- Brown, J.H. (1995). *Macroecology*. University of Chicago Press, Chicago.
- Campbell, J.J.N. (1982). Pears and persimmons: a comparison of temperate forests in Europe and eastern North America. *Vegetatio*, 49, 85–101.
- Chuine, I. & Beaubien, E.G. (2001). Phenology is a major determinant of tree species range. *Ecol. Lett.*, 4, 500–510.
- Davis, M.B. & Shaw, R.G. (2001). Range shifts and adaptive responses to Quaternary climate change. *Science*, 292, 673–679.
- Follieri, M., Magri, D. & Sadori, L. (1986). Late Pleistocene *Zelkova* extinction in central Italy. *New Phytol.*, 103, 269–273.
- Grubb, P.J. (1987). Global trends in species-richness in terrestrial vegetation: a view from the Northern Hemisphere. In: *Organization of Communities Past and Present: the 27th Symposium of the British Ecological Society, Aberystwyth 1986* (eds Gee, J.H.R. & Giller, P.S.). Blackwell Scientific Publications, Oxford, pp. 99–118.
- Huntley, B. (1993). Species-richness in north-temperate zone forests. *J. Biogeogr.*, 20, 163–180.
- Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989). Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *J. Biogeogr.*, 16, 551–560.
- Judd, W.S., Campbell, C.S., Kellogg, E.A. & Stevens, P.F. (1999). *Plant Systematics: a Phylogenetic Approach*. Sinauer Associates, Sunderland, USA.
- Kornas, J. (1972). Corresponding taxa and their ecological background in the forests of temperate Eurasia and North America. In: *Taxonomy, Phytogeography and Evolution* (ed. Valentine, D.H.). Academic Press, London, pp. 37–59.
- Krössmann, G. (1968). *Die Bäume Europas*. Verlag Paul Parey, Berlin.
- Lang, G. (1994). *Quartäre Vegetationsgeschichte Europas: Methoden und Ergebnisse*. Gustav Fischer Verlag, Jena.
- Latham, R.E. & Ricklefs, R.E. (1993a). Continental comparison of temperate-zone tree species richness. In: *Species Diversity in Ecological Communities: Historical and Geographical Perspectives* (eds Ricklefs, R.E. & Schluter, D.). The University of Chicago Press, Chicago, pp. 294–314.
- Latham, R.E. & Ricklefs, R.E. (1993b). Global patterns of tree species richness in moist forests: energy-diversity theory does not account for variation in species richness. *OIKOS*, 67, 325–333.
- Mabberley, D.Y. (2000). *The plant-book: a portable dictionary of the vascular plants*. Cambridge University press, Cambridge.
- Mai, D.H. (1995). *Tertiäre Vegetationsgeschichte Europas – Methoden und Ergebnisse*. Gustav Fischer Verlag, Jena.
- Manos, P.S. & Stanford, A.M. (2001). The historical biogeography of Fagaceae: tracking the Tertiary history of temperate and subtropical forest of the Northern Hemisphere. *Int. J. Plant Sci.*, 162, 77–S93.
- Martinetto, E. (2001). The role of central Italy as a centre of refuge for thermophilous plants in the late Cenozoic. *Acta Palaeobot.*, 41, 299–319.
- Michaux, J., Suc, J.-P. & Vernet, J.-L. (1979). Climatic inference from the history of the Taxodiaceae during the Pliocene and the Early Pleistocene in Western Europe. *Rev. Palaeobot. Palynol.*, 27, 185–191.
- Morley, R.J. (2000). *Origin and Evolution of Tropical Rain Forests*. John Wiley & Sons, Chichester.

- Møller, A.P. & Birkhead, T.R. (1992). A pairwise comparative method as illustrated by copulation frequency in birds. *Am. Nat.*, 139, 644–656.
- Qian, H. & Ricklefs, R.E. (2000). Large-scale processes and the Asian bias in species diversity of temperate plants. *Nature*, 407, 180–182.
- Quinn, G.P. & Keough, M.J. (2002). *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Reid, E.M. (1935). British floras antecedent to the Great Ice Age. *Proc. R. Soc. Lond. B*, 118, 197–202.
- Ricklefs, R.E. & Latham, R.E. (1992). Intercontinental correlation of geographical ranges suggests stasis in ecological traits of relict genera of temperate perennial herbs. *Am. Nat.*, 139, 1305–1321.
- Ricklefs, R.E. & Latham, R.E. (1999). Global patterns of tree species richness in moist forests: distinguishing ecological influences and historical contingency. *OIKOS*, 86, 369–373.
- Sakai, A. & Weiser, C.J. (1973). Freezing resistance of trees in North America with reference to tree regions. *Ecology*, 54, 118–126.
- Schönwiese, C.-D. & Rapp, J. (1997). *Climate Trend Atlas of Europe Based on Observations 1891–1990*. Kluwer Academic Publishers, Dordrecht.
- Stewart, J.R. & Lister, A.M. (2001). Cryptic northern refugia and the origins of the modern biota. *Trends Ecol. Evol.*, 16, 608–613.
- Suc, J.P. (1984). Origin and evolution of the Mediterranean vegetation and climate in Europe. *Nature*, 307, 429–432.
- Sykes, M.T., Prentice, I.C. & Cramer, W. (1996). A bioclimatic model for the potential distributions of north European tree species under present and future climates. *J. Biogeogr.*, 23, 203–233.
- Taberlet, P. & Cheddadi, R. (2002). Quaternary refugia and persistence of biodiversity. *Science*, 297, 2009–2010.
- Takahara, H., Sugita, S., Harrison, S.P., Miyoshi, N., Morita, Y. & Uchiyama, T. (2000). Pollen-based reconstructions of Japanese biomes at 0, 6000 and 18,000 ¹⁴C yr cBP. *J. Biogeogr.*, 27, 665–683.
- Tallis, J.H. (1991). *Plant Community History – Long-term Changes in Plant Distribution and Diversity*. Chapman and Hall, London.
- The European Garden Flora Editorial Committee (1986–2000). *The European Garden Flora. A Manual for the Identification of Plants Cultivated in Europe, Both Out-of-doors and Under Glass*, vols I–VI. Cambridge University Press, Cambridge.
- The Flora Europaea Editorial Committee (eds) (1964–1993). *Flora Europaea*, vols 1–5. Cambridge University Press, Cambridge.
- Thompson, R.S., Anderson, K.H. & Bartlein, P.J. (1999–2000). *Atlas of Relations between Climatic Parameters and Distributions of Important Trees and Shrubs in North America*. US Geological Survey Professional Papers 1650-A,-B,-C. US Department of Interior, US Geological Survey, Reston, VA.
- Tzedakis, P.C. (1993). Long-term tree populations in northwest Greece through multiple Quaternary climatic cycles. *Nature*, 364, 437–440.
- Utescher, T. & Mosbrugger, V. (2001). *Palaeoflora Database* (WWW document). URL <http://www.geologie.uni-bonn.de/Palaeoflora/>
- Utescher, T., Mosbrugger, V. & Ashraf, A.R. (2000). Terrestrial climate evolution in northwest Germany over the last 25 million years. *Palaios*, 15, 430–449.
- Van der Hammen, T., Wijmstra, T.A. & Zagwijn, W.H. (1971). The floral record of the Late Cenozoic of Europe. In: *The Late Cenozoic Glacial Ages* (ed. Turekian, K.K.). Yale University Press, New Haven, CT, pp. 391–424.
- Wang, C.-W. (1961). *The Forests of China with a Survey of Grassland and Desert Vegetation*. Harvard University, Cambridge, MA.
- Watts, W.A. (1988). Europe. In: *Vegetation History* (eds Huntley, B. & Webb, T. III). Kluwer Academic Publishers, Dordrecht, pp. 155–192.
- Wen, J. (1999). Evolution of eastern Asian and eastern North American disjunct distributions in flowering plants. *Ann. Rev. Ecol. Syst.*, 30, 421–455.
- Williams, J.W., Webb, T., III, Richard, P.H. & Newby, P. (2000). Late Quaternary biomes of Canada and the eastern United States. *J. Biogeogr.*, 27, 585–607.
- Willis, K.J. (1996). Where did all the flowers go? The fate of the temperate European flora during glacial periods. *Endeavour*, 20, 110–114.
- Willis, K.J. & McElwain, J.C. (2002). *The Evolution of Plants*. Oxford University Press, Oxford.
- Willis, K.J., Rudner, E. & Sömegi, P. (2000). The full-glacial forests of central and southeastern Europe. *Quatern. Res.*, 53, 203–213.
- Woodward, F.I. (1988). *Climate and Plant Distribution*. Cambridge University Press, Cambridge.
- Yu, G., Chen, X., Ni, J., Cheddadi, R., Guiot, J., Han, H. *et al.* (2000). Palaeovegetation of China: a pollen data-based synthesis for the mid-Holocene and last glacial maximum. *J. Biogeogr.*, 27, 635–664.

Editor, I. F. Woodward

Manuscript received 28 February 2003

First decision made 11 April 2003

Manuscript accepted 22 April 2003