Glacial refugia of temperate trees in Europe: insights from species distribution modelling

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Summary

1. The Pleistocene is an important period for assessing the impact of climate change on biodiversity. During the Last Glacial Maximum (LGM; 21 000 years ago), large glaciers and permafrost reached far south in Europe. Trees are traditionally thought to have survived only in scattered Mediterranean refugia (southern refugia hypothesis), but a recent proposal suggests that trees may have been much more widely and northerly distributed (northern refugia hypothesis).

2. In this study, the southern vs. northern refugia hypotheses were investigated by estimating the potential LGM distributions of 7 boreal and 15 nemoral widespread European tree species using species distribution modelling. The models were calibrated using data for modern species distributions and climate and projected onto two LGM climate simulations for Europe. Five modelling variants were implemented.

3. Models with moderate to good predictive ability for current species range limits and species richness patterns were developed.

4. Broadly consistent results were obtained irrespective of the climate simulation and modelling variant used. Our results indicate that LGM climatic conditions suitable for boreal species existed across Central and Eastern Europe and into the Russian Plain. In contrast, suitable climatic conditions for nemoral tree species were largely restricted to the Mediterranean and Black Sea regions. Large proportions of these northern and southern regions would have been suitable for a number of boreal or boreal plus nemoral tree species, respectively.

5. These findings are consistent with recent palaeoecological and phylogeographic data regarding LGM distributions of trees and other boreal and nemoral taxa.

6. Synthesis. It is clear that the view of the LGM landscape in Europe as largely treeless, especially north of the Alps, needs to be revised. Trees were probably much more widespread during the LGM than hitherto thought, although patchily distributed at low densities due to low atmospheric CO2 concentrations and high wind-speeds. The findings presented here help explain the occurrence of mammal assemblages with mixtures of forest, tundra and steppe species at many localities in southern Central and Eastern Europe during the LGM, as well as the phylogeographic evidence for the extra-Mediterranean persistence of many boreal species.

Key-words: climate change, cryptic refugia, hind-casting, ice age refugia, Last Glacial Maximum, maximum entropy species distribution modelling, Pleistocene, pleniglacial vegetation, range dynamics, tree species distributions

Introduction

A key issue in ecology and conservation biology is to understand how climate change affects biodiversity. The Pleistocene (2.6 million to 11 500 years ago) is an important period for assessing the impact of climate change due to its multiple oscillations between warm interglacial conditions and cold glacial conditions. The Pleistocene ice ages caused massive losses from the European tree flora (Watts 1988; Mai 1995), leaving Europe with relatively cold- and drought-tolerant taxa (Svenning 2003). Most extinctions occurred in the early part of this period (Watts 1988; Lang 1994). During the latter part of the Pleistocene, the main response of the European tree flora to the dramatic climate changes was migration.
but is also receiving support from phylogeographic studies of mainly based on evidence from pollen and plant macrofossils, et al (Bennett et al. 1991; Taberlet & Cheddadi 2002). Due to a dry LGM climate in the Mediterranean lowlands, mid-altitude locations were the key refuge locations for temperate trees (Bennett et al. 1991; Willis 1994; Tzedakis et al. 2002). However, a recent controversial proposal, the northern refugia hypothesis, suggests that trees were distributed much more widely in Europe during the LGM. According to this hypothesis, trees occurred not only across Southern Europe, but also in the southern parts of Central Europe (Willis et al. 2000; Stewart & Lister 2001; Willis & van Andel 2004). This proposal is mainly based on evidence from pollen and plant macrofossils, but is also receiving support from phylogeographic studies of certain species (e.g. Betula pendula Roth, B pubescens Ehr., Populus tremula L., and Salix caprea L.; Palmé et al. 2003; Petit et al. 2003; Maliouchenko et al. 2007). These species all have wide boreal distributions. The phylogeographic evidence for nemoral tree species appears to be more consistent with the southern refugia hypothesis (e.g. Petit et al. 2003), and similar conclusions have been reached for animals (Schmitt 2007). However, even for the non-boreal tree Fagus sylvatica L., survival as far north as the Carpathians has been suggested (Magri et al. 2006).

The present study complements the previous palaeoecological and phylogeographic studies and investigates the two contrasting (southern and northern) refugia hypotheses by estimating the potential LGM distributions of 22 boreal and nemoral European tree species using species distribution modelling (Guisan & Zimmerman 2000; Elith et al. 2006) based on the current distributions of the species, in combination with LGM climate simulations. This ‘hindcasting’ approach is valid given the evidence for climatic niche conservatism; the response of European trees to the Quaternary climate changes was mainly migration or extinction, not evolution (e.g. Huntley & Webb III 1989; Lang 1994). Furthermore, there is a great deal of consistency in the general response of individual tree species to the different episodes of climate change (Lang 1994).

There have been a few previous hindcasting studies: two studies modelled the potential range of 31 mammal species and 8 pollen-type taxa in North America during the LGM, and the present based on their distributions during the other period, concluding that the species had had highly conservative climatic niches and tracked the changing climate by migration (Martinez-Meyer et al. 2004; Martinez-Meyer & Peterson 2006). In Europe, vegetation simulations have been used to estimate the potential LGM range of the boreal tree Pinus sylvestris (Cheddadi et al. 2006). Another study used general estimates of the climatic requirements of cool- and warm-temperate trees as functional groups to estimate their potential refugia (Leroy & Arpe 2007). The former study provided evidence in favour of the northern refugia hypothesis, while the latter was consistent with the southern refugia hypothesis. The goals of the present study are to determine: (i) whether predictive models linked to estimates of LGM climate indicate that nemoral and/or boreal tree species could have found suitable climatic conditions north of the Mediterranean region during the LGM; (ii) whether northern regions would have been suitable for a few or for many tree species; and (iii) whether trees would have been concentrated in only a few limited northern regions or if they could have occurred widely, but in diffuse populations.

Methods

STUDY SPECIES

We focused on the species at the centre of the refugia debate, namely boreal and nemoral tree species. Trees were defined as woody plants reaching ≥ 20 m in height (Svenning & Skov 2005). A key assumption of bioclimatic species distribution modelling is that the ranges of the modelled species are, to a large extent, in equilibrium with climate. For European tree species, there is evidence that this is only true for widespread, northern species (Svenning & Skov 2004). Thus, only species with wide northern distributions were included in the present study. These are also the species which are most likely to have had northern refugia and have been most discussed in the refugia debate (Willis et al. 2000; Willis & van Andel 2004; Cheddadi et al. 2006; Leroy & Arpe 2007). The boreal tree species were Alnus incana (L.) Moench, Betula pendula, B pubescens, Picea abies (L.) Karsten, Pinus sylvestris L., Populus tremula and Salix caprea. The nemoral tree species were A. glutinosa (L.) Gaertner, Carpinus betulus L., Fagus sylvatica, P. alba L., P nigra L., Quercus petraea (Mattuschka) Liebl., Q. robur L., S alba L., S fragilis L., Taxus baccata L., Tilia cordata Mill., T. platyphyllos Sco., Ulmus glabrae Hudson, U. laevis Pallas and U. minor Miller.

SPECIES DISTRIBUTION DATA

For 20 of the 22 species, data on their distributions came from Atlas Florae Europaeae (AFE: Jalas & Suominen 1972–1994), which uses an equal-area mapping unit of c. 50 × 50 km based on the Universal Transverse Mercator projection and the Military Grid Reference System (hereafter, the AFE grid). Data on the distribution of T. cordata and T. platyphyllos came from an outline map from the European Forest Genetic Resources Programme (EUFORGEN: http://www.bioversityinternational.org/networks/euforgen/). These maps were georeferenced and digitized as presence-absence in each AFE grid cell, recording presence whenever the distribution outline overlapped with at least 50% of an AFE grid cell. For T. cordata, distribution data were also available from a grid map in Pigott (1991); however, using these data produced very similar results to those based on the EUFORGEN data (not shown).

CLIMATE DATA

Data on current climate (monthly temperature and precipitation) were obtained from the CRU CL 2.0 data set (New et al. 2002, http://www.cru.uea.ac.uk/cru/data/hrg.htm) at a 10° resolution. To assess modelling uncertainty due to uncertainty in the LGM climate data,
two LGM climate simulations were used: (i) the Stage 3 Project (S3P) simulation (c. 60-km resolution), which reconstructed the LGM climate in Europe using a nested high-resolution mesoscale model during the phase 4 of the Oxygen Isotope Stage 3 Project (S3P home page: http://www.esc.cam.ac.uk/index.php/component/content/article/274 (Pollard & Barron 2003); and (ii) the Laboratoire de Météorologie Dynamique's LMDZHR simulation, which reconstructed the LGM climate using a general circulation model with a stretched grid over Europe (c. 60-km resolution) (Jost et al. 2005). Estimates of the present climate as simulated by the two climate models were also available and were used to compute the anomalies between modelled present and LGM conditions for monthly temperature and precipitation. To improve the representation of small-scale climatic variation caused by topography, high-resolution LGM climate estimates were obtained by interpolating the anomalies to 10° resolution and subtracting them from the CRU present climate data set (cf. Hijmans & Graham (2006) for a similar approach). During the LGM, sea level was lowered by 110 m (Ruddiman 2001). The LGM coastline was estimated by lowering the sea level of the Earth Topography-5 (http://www.ngdc.noaa.gov/mgg/lliers93mmg01.html) elevation-bathymetry raster by 110 m and interpolating the CRU data to the now inundated areas.

From the monthly mean temperature and precipitation values in each climate data set, we computed 12 climatic variables of potential importance as determinants of plant distributions (Table 1; e.g. Walter & Breckle 1986; Prentice et al. 1992; Sykes et al. 1996; Skov & Svenning 2004) for use in the species distribution modelling.

### Table 1. The climatic predictor variables used in this study, their acronyms, units and present-day ranges at 10° resolution in Europe (31.3°W to 68.7°E latitude and 27.6°–82.9°N longitude)

<table>
<thead>
<tr>
<th>Climatic variable</th>
<th>Unit</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean summer temperature</td>
<td>°C</td>
<td>−3.3 to 30.6</td>
</tr>
<tr>
<td>Temperature seasonality</td>
<td>°C</td>
<td>2.4–14.1</td>
</tr>
<tr>
<td>Absolute minimum temperature</td>
<td>°C</td>
<td>−55.8 to 1.1</td>
</tr>
<tr>
<td>Growing degree days</td>
<td>gdd</td>
<td>0–5357</td>
</tr>
<tr>
<td>Annual precipitation</td>
<td>pann</td>
<td>95–3300</td>
</tr>
<tr>
<td>Mean summer precipitation</td>
<td>psun</td>
<td>0–219</td>
</tr>
<tr>
<td>Winter precipitation</td>
<td>pwin</td>
<td>0–907</td>
</tr>
<tr>
<td>Precipitation seasonality</td>
<td>psea</td>
<td>2–99</td>
</tr>
<tr>
<td>Water balance</td>
<td>wbal</td>
<td>−1060 to 2983</td>
</tr>
<tr>
<td>Summer water balance</td>
<td>wb_sum</td>
<td>−149 to 161</td>
</tr>
<tr>
<td>Minimum monthly precipitation</td>
<td>pmin</td>
<td>0–162</td>
</tr>
<tr>
<td>Water balance seasonality</td>
<td>wb_sea</td>
<td>4–111</td>
</tr>
</tbody>
</table>

*Mean for June, July and August. ^Standard deviation of monthly mean values. 1Estimated following Prentice et al. (1992). 2Computed following Zimmermann & Kienast (1999) using a 5°C base temperature. 3Summed precipitation over the year. 4Computed as the yearly sum of the monthly differences between precipitation and potential evapotranspiration following Skov & Svenning (2004). 5Mean summer water balance, computed for June, July and August. 6Minimum monthly value.

### SPECIES DISTRIBUTION MODELLING

The southern vs. northern refuge hypotheses were investigated for the 22 tree species using species distribution modelling to estimate their climatic niches and hindcast their potential distributions during the LGM, that is, the geographic distribution of suitable climate conditions for these species during that period. The general modelling approach was to calibrate the distribution models using the data for current species distributions and climate, evaluate their predictive ability in terms of the modern distribution, and then project the models onto the LGM climate data. The refuge hypotheses were evaluated by considering the LGM predictions for the individual study species as well as, more synthetically, the predicted LGM tree species richness, computed as the sum of the predicted presences of the 22 study species per AFE cell as well as for the 7 boreal and 15 nemoral tree species separately.

Many algorithms exist for species distribution modelling (e.g. Guisan & Zimmermann 2000). Given that the AFE data are clearly not complete for eastern Europe, a crucial region in the present study given its cold winters, we based our modelling on two algorithms that only use the species’ presence (presence-only data) (Elith et al. 2006; Pearce & Boyce 2006): (i) maximum entropy species distribution (Maxent) modelling (Phillips et al. 2006), and (ii) a standard rectilinear climatic envelope (Bioclim) model (Guisan & Zimmermann 2000). Maxent is well-suited for species distribution modelling theoretically (Phillips et al. 2006) and has been shown to perform well compared to other methods (Elith et al. 2006; Hijmans & Graham 2006; Phillips et al. 2006). However, it can sometimes overfit species–climate relationships, limiting transferability (Peterson et al. 2007). Bioclim is much less prone to overfitting due to its simplicity, and in previous modelling algorithm comparisons it gave results that were among the most divergent from Maxent (Elith et al. 2006). In addition, Hijmans & Graham (2006) concluded that Bioclim was little prone to overprediction and could be used as a conservative approach. Therefore, Bioclim was used as a supplementary alternative.

The Maxent modelling was performed with all background points available in the study area (n = 4878) and the recommended default values for convergence threshold (10−4), maximum number of iterations (500) and regularization multiplier (1) (Phillips et al. 2006). The logistic output format ranges from low (minimum: 0) to high (maximum: 1) probability of presence. Two alternative approaches were used to select the threshold for converting the continuous logistic probability scale to a binary prediction of potential presence (suitable climate) or absence (unsuitable climate). First, for each species, the threshold was selected that produced the best match to its range limit in the north-eastern part of the study area (northern Russia, according to AFE) and further east (based on outline maps available from EUFORGEN and Hultén & Fries (1986)), that is, under climatic conditions most similar to those thought to limit tree species distributions northward in Europe during the LGM. This approach is referred to as the north-eastern limit (nelim) criterion. As the nelim criterion involves a certain degree of subjectivity, the threshold was also selected using Maxent’s maximum training sensitivity plus specificity threshold (mst + s) criterion, which has recently been shown to produce highly accurate predictions (Jiménez-Valverde & Lobo 2007).

The Maxent modelling was implemented with two sets of predictor variables: (i) a simple set consisting of three variables (gdd, tmin and wbal) generally thought to be of key importance for plant distributions (Sykes et al. 1996; Skov & Svenning 2004), and (ii) a set of all 12 climatic variables. It can be argued that the former provides a more parsimonious and, therefore, more robust description of the climatic niche space. Hence, species distribution modelling (see below) based on the 3-variable set will be less prone to overfitting of the species–climate relationships and, probably have greater
transferability to other spatiotemporal domains (Peterson et al. 2007). The 12-variable set, conversely, allows for greater complexity in species-climate relationships. In total, three different implementations were used: the 3-variable set with nelim and mts+s thresholds and the 12-variable set with the mts+s threshold.

Bioclim was parameterized in two ways: using (i) the 10th and 90th percentiles, and (ii) the outlier-corrected (Skov & Svenning 2004) minimum and maximum observed values for each climatic predictor variable across a species’ present-day range. When all climatic variables in the predictor set fell within the inner range defined by these values, a species’ potential presence was predicted. The 10th and 90th percentile range was used as a highly conservative estimate of a species’ tolerance with respect to each climatic factor. Only the 3-variable climatic predictor set was used for the Bioclim-modelling, as the 12-variable set would produce overly conservative climatic niche estimates.

The models were calibrated using species occurrences across the AFE grid (n = 4878 grid cells), using grid cell means for the climatic variables, but projected onto the modern and LGM climate data at 10° resolution to allow a more fine-scale indication of the potential LGM distributions. Modelling was done for a study area ranging from 31.3 to 68.7°E latitude and 27.6 to 82.9°N longitude for the present day. A slightly smaller study area (10.9–50.0°E latitude and 33.9–74.7°N longitude) was used for the LGM projections, reflecting the geographic coverage of the LGM simulations.

Evaluation of the models’ predictive abilities was done using three approaches: The first method was visual evaluation of the models’ abilities to predict the species’ present distribution across Europe, emphasizing the north-eastern part of the study area. In the second approach, the Receiver Operating Characteristics Area-Under-the-Curve (AUC) was computed for the Maxent models using Maxent’s internal validation procedure, which randomly partitions the data. The AUC is the current standard statistical measure of the accuracy of predictive distribution models (Fielding & Bell 1997), and was used. AUC was primarily used to assess the relative accuracy of different models for the same species. In the third approach, as a synthetic measure of the models’ predictive abilities, the observed species richness (sum of the observed presence of the 22 study species per AFE cell) was regressed against the predicted tree species richness (sum of the predicted presence of the 22 study species per AFE cell) for each modelling implementation. For this analysis, the easternmost part of the study area was excluded (leaving 2255 AFE cells) because this region is incompletely inventoried in AFE.

All species distribution and climate variable maps were computed and used in the Lambert Azimuthal Equal Area projection. All GIS modelling was performed using ArcGIS 9.2 (ESRI, Redlands, CA). Species distribution modelling was done using Maxent version 3.0.6 (http://www.cs.princeton.edu/~schapire/maxent/) and Bioclim modelling, implemented in ArcGIS 9.2 using Python 2.4 (http://www.python.org/).

**Results**

**PREDICTION OF CURRENT TREE DISTRIBUTIONS**

Visual evaluation of the models’ predictions of the species’ present distribution indicated that the Maxent model, using the 3-variable data set and the manually adjusted nelim criterion, gave the best results, providing reasonable estimates of the species’ northern and north-eastern range limits (Fig. 1). The Maxent models based on the automated mts+s criterion often failed to predict large proportions of the northern and north-eastern range (Figs S1 and S2 in Supporting Information). The Bioclim minimum–maximum model provided predictions that to a greater extent encompassed these parts of the species ranges. However, it provided overly conservative estimates of the north-easternmost range of many of the study species (e.g. *A. incana*, Betula spp., *Picea abies*, *P. sylvestris*, *P. tremula* and *S. caprea*) and predicted range limits too far to the north for other species (e.g. *Q. robur* and *U. glabra*) (Fig. S3). As expected, the Bioclim 10th–90th percentile model correctly placed the core of each species’ range, but was too conservative with respect to the range limits (see Fig. S4).

The AUC values for the random-30% test data sets using the Maxent models were similar for the two predictor variable sets; the mean (± standard deviation) was 0.751 ± 0.056 for the 3-predictor set and 0.767 ± 0.060 for the 12-variable set. The regressions between the observed tree species richness and the predicted tree species showed that all modelling methods predicted overall tree species richness well (Table 2). The richness predicted using the Maxent models based on all 12 climatic predictors and the mts+s criterion bore the closest relationship to the observed richness, having both the highest $r^2$ and the slope closest to one (Table 2). However, the best model according to visual evaluation (Maxent with the 3-variable predictor set and the nelim criterion) also produced a fairly high $r^2$ and a slope close to one (Table 2).

**POTENTIAL TREE DISTRIBUTIONS DURING THE LGM**

Qualitatively similar results were obtained for all LGM climate simulations and species distribution modelling methods, although the clearly unrealistic Maxent models based on the mst + t criterion (see above) indicated a more fragmented

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**Table 2.** Linear regressions between the observed and predicted tree species richness for each species distribution modelling implementation ($n = 2255$ AFE cells)

<table>
<thead>
<tr>
<th>Modelling method</th>
<th>Predictors†</th>
<th>$F$</th>
<th>Intercept</th>
<th>Slope</th>
<th>$r^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxent(3-pred)</td>
<td>3</td>
<td>2872****</td>
<td>0.418</td>
<td>0.734</td>
<td>0.560</td>
</tr>
<tr>
<td>Maxent(nelim)</td>
<td>3</td>
<td>3043****</td>
<td>1.674</td>
<td>0.698</td>
<td>0.575</td>
</tr>
<tr>
<td>Maxent(nelim)</td>
<td>12</td>
<td>6412****</td>
<td>0.744</td>
<td>0.781</td>
<td>0.740</td>
</tr>
<tr>
<td>Bioclim(min-max)</td>
<td>3</td>
<td>2229****</td>
<td>1.739</td>
<td>0.625</td>
<td>0.498</td>
</tr>
<tr>
<td>Bioclim(10p-90p)</td>
<td>3</td>
<td>2120****</td>
<td>6.663</td>
<td>0.521</td>
<td>0.485</td>
</tr>
</tbody>
</table>

* $P < 0.05$; ** $P < 0.01$. *** $P < 0.001$. **** $P < 0.0001$.
† 3 and 12 indicate whether the 3- or the 12-variable predictor set was used.

AFE: north-eastern limit threshold.
mts+s: maximum training sensitivity plus specificity threshold.
min-max: Corrected minimum–maximum range.
10p-90p: 10th to 90th percentile range.
Fig. 1. Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees in Europe. Modelling was performed using Maxent with three predictor variables (gdd, tmin, wbal) and the presence threshold set using the north-eastern limit criterion.
In all cases, a LGM climate favourable to a potentially high number of nemoral tree species was largely restricted to the Mediterranean region and around the Black Sea (Fig. 2). To a variable extent, southwest France, northern parts of the Balkans and the southern Russian Plain were also modelled as being climatically suitable for many nemoral tree species (Fig. 2). A few nemoral species may have experienced a suitable climate further north (Fig. 2). The nemoral species finding suitable LGM conditions relatively far north were especially *A. glutinosa, Q. robur, T. cordata, U. glabra* and *U. laevis* (only to the east; Fig. 3).

In contrast to the nemoral species, the results indicate that many boreal tree species would have found suitable climatic conditions during the LGM across Central and Eastern Europe and into the Russian Plain (Fig. 2). *Betula pubescens, Picea abies* and *P. sylvestris* would have potentially ranged farthest north and east (Fig. 3). The boreal tree species would also have been able to thrive in much of the Mediterranean region (Figs 2 and 3).

**Fig. 2.** Potential diversity of boreal (*n* = 7, columns 1 and 2) and nemoral (*n* = 15, columns 3 and 4) tree species during the LGM using different LGM climate simulations (LMDZHR and S3P) and species distribution modelling methods: (a) Maxent with three predictor variables (gdd, tmin, whal) and the presence threshold set using the north-eastern limit criterion, (b) Maxent with all 12 climatic predictor variables and maximum training sensitivity plus specificity threshold, (c) Bioclim with outlier-corrected minimum–maximum limits, and (d) Bioclim with 10th and 90th percentile limits.
Fig. 3. Modelled potential distributions of 22 nemoral and boreal (underlined) trees in Europe during the LGM (LMDZHR simulation) using Maxent with three predictor variables (gdd, tmin, wbal) and the presence threshold set using the north-eastern limit criterion.

Discussion

There is no doubt that the dramatic climate changes during the Quaternary have had strong impacts on the range dynamics of European tree species. However, a key point of contention is whether trees were restricted to the Mediterranean peninsulas and other southern areas during the LGM (the southern refugia hypothesis), or also survived further north (the northern refugia hypothesis). In this study, it was estimated that suitable LGM climatic conditions existed across Central and Eastern Europe and into the Russian Plain for boreal tree species, but were largely restricted to the Mediterranean and Black Sea regions for nemoral tree species. The modelling also indicated that large proportions of these northern and southern regions would have been suitable for a number of boreal or boreal plus nemoral tree species, respectively.

Hindcasting Uncertainties

The conclusions reached in this study rely on how well the climate simulations estimate the LGM climate in Europe, and on the accuracy of the species distribution modelling methodology. It can reasonably be concluded that the LMDZHR and S3P climate simulations (Pollard & Barron 2003; Jost et al. 2005) provide an adequate basis for the analyses reported here. Both simulations were consistent with previous coarse-scale simulations (Pollard & Barron 2003; Jost et al. 2005; Leroy & Arpe 2007). Earlier studies suggested that these simulations underestimate the LGM cooling inferred from the pollen data, especially in south-western Europe in winter (Kageyama et al. 2001; Pollard & Barron 2003; Jost et al. 2005). However, new and improved pollen-based temperature reconstructions show that this discrepancy was largely caused by overestimation of the LGM cooling in the earlier reconstructions. This error was caused by not accounting for the low atmospheric CO₂ concentration during the LGM and the impact on vegetation (Ramstein et al. 2007; Wu et al. 2007). The revised pollen-based temperature estimates are consistent with the climate simulation estimates, although the latter fall in the warmer part of the confidence intervals for the pollen-based estimates (Ramstein et al. 2007; Wu et al. 2007). There is, however, still uncertainty in the LGM climate reconstructions, as is clear from the differences between the LMDZHR and S3P climate simulations. Notably, the S3P simulation differed from the LMDZHR simulation by being generally colder in the Mediterranean peninsula, but warmer closer to the ice sheet in Central Europe (Pollard & Barron 2003; Jost et al. 2005) (Fig. 2). Nevertheless, the LGM potential range projections in this study did not differ substantially between climate simulations, indicating that our findings were robust with respect to the existing uncertainty in the climate data.

Predictive modelling of species distributions and the impact of climate change has attracted much interest in recent years due to its relevance to science and society (e.g. Fischlin et al. 2007). The theoretical basis and the performance of different species distribution modelling algorithms have received thorough treatment, and the methodology is well developed (e.g. Guisan & Zimmermann 2000; Pearson & Dawson 2003; Guisan & Thuiller 2005; Phillips et al. 2006; Elith et al. 2006). There are, however, still uncertainties and concerns about how to implement and interpret species distribution modelling (e.g. Araújo & Guisan 2006; Dormann 2007; Peterson et al. 2007). Hence, this type of modelling should always be applied and interpreted cautiously (e.g. Guisan & Thuiller 2005; Dormann 2007). A key premise of species distribution modelling is that species distributions are largely controlled by the factors represented by the predictor variable (the equilibrium postulate) (Guisan & Thuiller 2005). Previous studies indicate that many tree species have ranges that are currently not in equilibrium with the climate in Europe (Svenning & Skov 2004, 2005, 2007a,b). This potential problem was handled by only including species with wide northern distributions, as there is evidence that widespread northern species fill their climatic potential range more than other European tree species (Svenning & Skov 2004). Other important issues are related to the algorithms and predictor variables used. Different species distribution algorithms often produce quite different results (Elith et al. 2006); hence, it is dangerous to generalize from results based on a single algorithm. This issue was handled by implementing two methods, Maxent and Bioclim, which have behaved very differently in previous modelling comparisons (Elith et al. 2006). Selection of predictor variables is also crucial (Dormann 2007); models are likely to provide greater transferability across space and time when based on factors causally involved in determining a species’ range. Therefore, a set of three key bioclimatic variables was emphasized (gdd, tmin and wbal). These are generally thought to be highly important for predicting plant distributions (Sakai & Weiser 1973; Woodward 1988; Sykes et al. 1996; Skov & Svenning 2004). A set of 12 climatic predictor variables was also used to allow for more complex species–climate relationships. Our results demonstrate that care is needed to avoid generating unrealistic estimates of the species’ climatic niches. For example, according to the regression analysis of observed vs. predicted current species richness, the Maxent model with the 12-variable predictor set and the mts + s criterion yielded the best prediction of current species richness. However, the climatic niche estimates produced by Maxent modelling with the mts + s criterion were clearly misleading (Figs S1 and S2). Hence, the superior prediction of the current richness patterns probably reflected overfitting of the climatic relationships and the presence threshold (Peterson et al. 2007). The assumption of niche conservatism is another issue when using species distribution modelling for hind- or forecasting of species’ range responses to climatic change (Martínez-Meyer et al. 2004; Martínez-Meyer & Peterson 2006). Although species may evolve to adapt to a changing climate (Davis et al. 2005), the primary responses of European trees to the Quaternary climate changes were migration or extinction, not evolution (e.g. Huntley & Webb III 1989; Lang 1994; Svenning 2003). Furthermore, previous research using species distribution modelling to study range dynamics between the LGM and the present have concluded in favour of strong climatic niche conservatism (Martínez-Meyer et al. 2004).
Glacial refugia of European trees

There is also increasing palaeoecological evidence of boreal trees such as *Picea, Pinus* (notably *P. sylvestris* and *P. cembra* L.), *Larix* and *Betula* in Central and Eastern Europe (Willis *et al.* 2000; Willis & van Andel 2004; Cheddadi *et al.* 2006). In contrast, there is at best little direct palaeoecological evidence of nemoral trees in these areas during the LGM itself (Willis *et al.* 2000; Willis & van Andel 2004). An exception is a reported LGM find of *Taxus baccata* from Slovakia (Stewart & Lister 2001). These findings are repeated further east, where a recent synthetic palynological study provides evidence that boreal trees (especially *Pinus* and *Betula*) occurred widely on the Russian Plain during the LGM (Simakov 2006). That study reconstructed patches of forest tundra occurring north of 56°N; forest steppe was present between 53°N and 56°N, and dominant between 49°N and 53°N. Forest refugia, including both boreal and nemoral trees, were scattered across the steppe further south (Simakov 2006).

Phylogeographic studies provide similar evidence. Nemoral trees and shrubs have genetically divergent populations in the different Mediterranean peninsulas, as well as additional patterns of genetic diversity that are consistent with LGM survival in the traditional Mediterranean refugia (e.g. Petit *et al.* 2003). Boreal tree species such as *B. pendula*, *B. pubescens*, *P. tremula* and *S. caprea* exhibit phylogeographic patterns that are consistent with more northern and coherent LGM distributions (Palmé *et al.* 2003; Petit *et al.* 2003, Maliouchenko *et al.* 2007). Phylogeographic evidence for such northern LGM ranges is also found in other species with wide boreal or continental distributions (Schmitt 2007). A wide, but probably diffuse occurrence of trees during the LGM is furthermore consistent with the occurrence of non-analogue mammal assemblages in much of southern Central and Eastern Europe during the LGM, with forest species co-occurring with tundra and steppe species at many localities (Sommer & Nadachowski 2006).

Conclusion

The results of this study help to qualify the northern vs. southern refugia debate. The results indicate that nemoral trees were probably largely confined to the traditional southern refugia, but with many species being potentially widespread within this region. Many boreal tree species may have been widespread not only in these southern areas, but also in Central and Eastern Europe, including the Russian Plain. These findings, based on hindcasting using species distribution models, agree well with recent palaeoecological and phylogeographic evidence. It is clear that the view of LGM vegetation in Europe as largely treeless, especially north of the Alps, needs to be revised. Trees were probably much more widespread than previously believed, but at low densities and more or less restricted to moist microsites due to the low atmospheric CO₂ concentration. High wind speeds may have caused further patchiness. These findings help explain the occurrence of mammal assemblages with mixtures of forest, tundra and steppe species at many LGM localities in southern Central and Eastern Europe during the LGM.
The results also explain the phylogeographic evidence for the persistence of many boreal species north of the Mediterranean.

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References


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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1 Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Maxent with the 3-variable predictor set (gdd, tmin, wbal) and the maximum training sensitivity plus specificity presence threshold.

Figure S2 Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Maxent with the 12-variable predictor set and the maximum training sensitivity plus specificity presence threshold.

Figure S3 Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Bioclim with the 3-variable predictor set (gdd, tmin, wbal) and presence determined using the corrected minimum-maximum range.

Figure S4 Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Bioclim with the 3-variable predictor set (gdd, tmin, wbal) and presence determined using the 10- to 90-percentile range.

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Figure S1  Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Maxent with the 3-variable predictor set (gdd, tmin, wbal) and the maximum training sensitivity plus specificity presence threshold.
Betula pubescens

Carpinus betulus

Fagus sylvatica

Picea abies

Pinus sylvestris

Populus alba

Populus nigra

Populus tremula

Quercus petraea

Quercus robur

Salix alba

Salix caprea

Salix fragilis

Taxus baccata

Tilia cordata

Tilia platyphyllos

Ulmus glabra

Ulmus laevis

Ulmus minor
Figure S2  Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Maxent with the 12-variable predictor set and the maximum training sensitivity plus specificity presence threshold.
Figure S3  Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Bioclim with the 3-variable predictor set (gdd, tmin, wbal) and presence determined using the corrected minimum-maximum range
Figure S4  Present observed and modelled potential distributions of 22 nemoral and boreal (underlined) trees using Bioclim with the 3-variable predictor set (gdd, tmin, wbal) and presence determined using the 10- to 90-percentile range.
As my Editor’s Choice article from this issue I have selected a paper by Helen Alexander et al. (2009) entitled “Detection, survival rates, and dynamics of a cryptic plant, Asclepias meadii: applications of mark-recapture models to long-term monitoring studies”. This study addresses the difficulties in predicting population trajectories caused by imperfect censuses in demographic studies. It follows on from several recent papers in Journal of Ecology (Kéry & Gregg 2003, 2004; Lesica & Crone 2007; Shefferson & Simms 2007; Shefferson & Tali 2007) that have addressed the fact that, although plants stand still and wait to be counted, as John Harper noted, ensuring that all of them are accounted for in a census poses a challenge. The three main problems are (i) that many plant species can become dormant for one or more years, and then re-emerge, (ii) that emergent herbaceous perennial plants can be very hard to find in a given year if they suffer heavy herbivory, and (iii) even without these complications, detection rates can be poor. For example, flowering plants are likely to be more conspicuous than vegetative plants. Problems such as these might present little difficulty for estimating changes in the size of a population if detection probability remained constant between years, or was equal for plants of different ages, sizes and status, but this is not the case.

Mead’s milkweed (Asclepias meadii) is a very rare, long-lived perennial species of prairies and glades with low annual reproductive output. Many years can pass before newly recruited plants achieve flowering status. Unless plants have been recorded and marked on previous occasions, non-flowering and grazed plants are very difficult to find, especially in years in which tallgrass prairie habitats are not burnt. Alexander et al. used 15 years of data and mark-recapture methods to estimate the size of a population of Mead’s milkweed, and to predict its future trajectory. They also carried out repeat surveys within one year of the study to determine the proportion of plants marked in a first survey that became almost undetectable later in the flowering season as a result of herbivory, and the likelihood of surveys made on different occasions failing to record plants that were not subject to herbivory.

Mead’s milkweed is a federally-threatened species. Accurate counts of plants are vital to assess the success of different management regimes for conserving its remaining populations. However, Alexander et al. report low detection probabilities, especially for plants that had not been marked in previous years, and great variation in recorded population size and in the proportion of plants flowering between years. Their analyses allowed them to infer that the actual population size was much higher each year than the population size they recorded, and that, despite strong variation in the estimated population size, there was slow population growth that could not be appreciated from the year by year counts.

Alexander et al. make important recommendations for ecologists to consider before embarking on demographic surveys of plants. Their proposals are likely to be especially pertinent for programmes of work that involve monitoring and management of rare species.
They suggest that, when detection probability is low, sampling protocols should aim to maximise searching efficiency per unit area, even if this means surveying somewhat smaller areas and fewer plants. Although dormancy is usually the explanation offered for periodic absences of individual plants during a lengthy observation period, herbivory and detection failure were also important causes. It is advised that if surveys are carried out early in a species’ growing season, plants may be missed because they emerge too late to be observed. Alexander et al. recommend that, at the start of any monitoring programme set to last for several years, repeat blind surveys should be carried out within the same year to determine whether plant detectability is a problem for these or other reasons. Finally, the authors recommend the development of improved sampling and analytical methods to overcome the problems in understanding current population behaviour and predicting future population trends when the ability to detect plants in monitoring exercises is imperfect.

In the same issue of Journal of Ecology there is also a Future Directions article by Maestre et al. on the stress gradient hypothesis for competition and facilitation in plant communities. This paper develops interesting and important new hypotheses that could be tested experimentally to lay the foundation for reconciliation of differences between the results of previous studies in this field. This paper is timely in view of the forthcoming British Ecological Society Symposium on Facilitation in Plant Communities, which will be organised by Rob Brooker and Ragan Callaway, and held at the University of Aberdeen from 20-22 April this year. Details of the meeting, and registration, are available at:

http://www.britishecologicalsociety.org/meetings/index.php

The list of speakers and topics promises an excellent meeting, and attendance is recommended for all with an interest in this field. Accommodation is limited, however, so that early registration is advisable. If you are unable to attend, however, all is not lost, because Journal of Ecology will be publishing the best papers from this meeting as a Special Feature, late in 2009.

Mike Hutchings
Executive Editor, Journal of Ecology

References


