Ice age legacies in the geographical distribution of tree species richness in Europe

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ABSTRACT

Aim This study uses a high-resolution simulation of the Last Glacial Maximum (LGM) climate to assess: (1) whether LGM climate still affects the geographical species richness patterns in the European tree flora and (2) the relative importance of modern and LGM climate as controls of tree species richness in Europe.

Location The parts of Europe that were unglaciated during the LGM.

Methods Atlas data on the distributions of 55 tree species were linked with data on modern and LGM climate and climatic heterogeneity in a geographical information system with a 60-km grid. Four measures of species richness were computed: total richness, and richness of the 18 most restricted species, 19 species of medium incidence (intermediate species) and 18 most widespread species. We used ordinary least-squares regression and spatial autoregressive modelling to test and estimate the richness–climate relationships.

Results LGM climate constituted the best single set of explanatory variables for richness of restricted species, while modern climate and climatic heterogeneity was best for total and widespread species richness and richness of intermediate species, respectively. The autoregressive model with all climatic predictors was supported for all richness measures using an information-theoretic approach, albeit only weakly so for total species richness. Among the strongest relationships were increases in total and intermediate richness with climatic heterogeneity and in restricted richness with LGM growing-degree-days. Partial regression showed that climatic heterogeneity accounted for the largest unique variation fraction for intermediate richness, while LGM climate was particularly important for restricted richness.

Main conclusions LGM climate appears to still affect geographical patterns of tree species richness in Europe, albeit the relative importance of modern and LGM climate depends on range size. Notably, LGM climate is a strong richness control for species with a restricted range, which appear to still be associated with their glacial refugia.

Keywords

Climate change, diversity gradients, endemism, energy, history, Pleistocene ice ages, Quaternary, range size, spatial autoregressive modelling, species pool.

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INTRODUCTION

Species richness exhibits marked large-scale geographical gradients across the Earth. The proposal that modern climate controls species richness has generated much support over the last few decades (Currie, 1991; Currie *et al.*, 2004; Hawkins *et al.*, 2004; Turner, 2004). Modern climate may drive richness through its control of productivity, because speciation rates are climatically determined, or richness may simply vary as a function of the distribution of climatic tolerances of the individual species in the regional species pool (Currie *et al.*, 2004). Spatial heterogeneity in climate may promote species richness by facilitating resource partitioning (Kerr & Packer, 1997). A long-standing, yet controversial, alternative is that species richness is controlled by history,

notably past climate (McGlone, 1996; Ricklefs, 2004). The climatic changes of the last few million years have caused strong range transformations (Webb & Bartlein, 1992) and severe regional extinctions (e.g. van der Hammen *et al.*, 1971; Jordan, 1997), with persistent global diversity anomalies as a likely result (Latham & Ricklefs, 1993). To the extent that modern ranges are still constrained by post-glacial recolonization (Svenning & Skov, 2004), species richness will be concentrated in areas where glacial climate was least stressful or steep topographic relief permitted short-distance climate tracking (McGlone, 1996; Jetz *et al.*, 2004; Turner, 2004). Globally, areas with high endemic species richness generally experienced little Quaternary climate change (Jansson, 2003).

It is well known that the European tree flora was strongly affected by the late Neogene–Quaternary climate changes, experiencing dramatic range transformations (Huntley & Birks, 1983; Bennett *et al.*, 1991; Cheddadi *et al.*, 2005) and heavy losses (van der Hammen *et al.*, 1971; Mai, 1995). The predominant view in recent decades has been that forests and trees were restricted to localized refugia in southern Europe during the Last Glacial Maximum (LGM; Bennett *et al.*, 1991; Brewer *et al.*, 2002; also cf. Hewitt, 2000). However, recent palaeobotanical studies have reported much wider LGM distributions of boreal and alpine trees in Central and Eastern Europe, with some nemoral species persisting in northern refugia, too (Willis *et al.*, 2000; Stewart & Lister, 2001; Willis & van Andel, 2004). A wider LGM distribution of trees is also supported by studies of mammalian palaeofaunas (Stewart & Lister, 2001; Hernández Fernández, 2006) and phylogeographical studies of boreal trees (Willis & van Andel, 2004; Aguinagalde *et al.*, 2005) and forest-dependent animals (e.g. Deffontaine *et al.*, 2005). For eastern North America it is generally accepted that forest or parkland covered much of the region during the LGM (Jackson *et al.*, 2000), and there is increasing evidence for the survival of nemoral trees close to the ice margin (e.g. McLachlan *et al.*, 2005).

From the above, it is clear that post-glacial range expansions in European tree species may have occurred via two different mechanisms (Pearson, 2006): (1) rapid migration from southern refugia mediated by efficient long-distance dispersal (Clark *et al.*, 1998), which also allowed tracking the variable Holocene climate with negligible time lag (Webb, 1986; Huntley & Webb, 1989; Huntley *et al.*, 1989; Pitelka & Plant Migration Workshop Group, 1997; Tinner & Lotter, 2006), and (2) slow migration from widespread refugia, some of which were located close to the modern range limits (Kullman, 2002; also cf. Yansa, 2006). Small modern ranges reflect narrow or unusual environmental requirements in the former case (cf. Gaston, 2003), or surviving the LGM in just a few, marginal refugia in the latter case. Providing support for the slow migration hypothesis, many tree species appear to have failed to recolonize large parts of their climatically suitable potential ranges in Europe (Svenning & Skov, 2004). Furthermore, geographical variation in tree species composition and richness across Europe includes non-environmental broadscale patterns that are likely to be historical legacies (Svenning & Skov, 2005).

In this paper, we use a recently available high-resolution simulation of European LGM climate to assess directly, for the first time, whether Quaternary climate change still affects the geographical richness patterns in the European tree flora. In continuation of this we also assess the relative importance of modern and LGM climate as richness controls. Applying Marquet *et al.*'s (2004) deconstruction approach, we investigate these questions for different range size categories too. We expect the importance of LGM climate as a richness control to be greater for species with small ranges than for widespread species (cf. Jetz & Rahbek, 2002; Jetz *et al.*, 2004). In the light of our results we also discuss the likely mechanism of post-glacial range expansion (rapid or slow migration), and whether LGM climate may indirectly contribute to the observed richness–modern climate relationships via its impact on the regional species pool (McGlone, 1996).

MATERIALS AND METHODS

Study area and data sets

The study area includes those parts of Europe that were unglaciated during the LGM, thereby avoiding confounding the effects of glacial climate with the physical impact by glaciers. The exact margins of the study area and its spatial resolution were determined by the geographical coverage and resolution of the data sets used: (1) tree species richness was computed from species distribution grid maps in *Atlas Florae Europaeae* (AFE; Jalas & Suominen, 1972–94), which uses an equal-area mapping unit of *c.* 50×50 km based on the Universal Transverse Mercator (UTM) projection and the Military Grid Reference System (MGRS); (2) modern climatic variables were derived from monthly values of mean temperature and precipitation obtained for the period 1961–90 from the Hadley Centre for Climate Prediction and Research (http://www.metoffice.com/research/hadleycentre/) in a $10' \times 10'$ resolution; and (3) palaeoclimatic variables were derived from the 60×60 km grid simulation of the LGM climate (21,000 year BP) in Europe produced by the phase 4 of the Oxygen Isotope Stage 3 Project (Barron & Pollard, 2002; http://www.esc.cam.ac.uk/oistage3/Details/Homepage.html). All GIS operations were computed using ARCVIEW 9.1 (Environmental Science Research Institute, Redlands, CA, USA). Using standard routines (ZonalStatistics) the data sets were combined in a grid that matched the coarsest data set, i.e. with 60-km grid cell size. Cells containing < 16 terrestrial $10'$ cells were eliminated, leaving a total of 879 grid cells. The resulting study area roughly covered the nemoral and Mediterranean biomes (see Fig. 1).

The study species were the 55 tree species in AFE that occur in the study area (Table 1; for further explanation see Svenning & Skov, 2005). In addition to total species richness, we computed richness of the 18 most restricted species, 19 species of medium incidence (intermediate species) and 18 most widespread species for each grid cell. The widespread species include primarily nemoral and boreal species, while the intermediate and restricted species include mainly Mediterranean, southern nemoral and alpine species (Table 1). Range sizes were based on their native distributions across all of Europe (i.e. the 1283 60-km grid cells, which were covered by AFE and included ≥ 16 terrestrial $10'$ cells
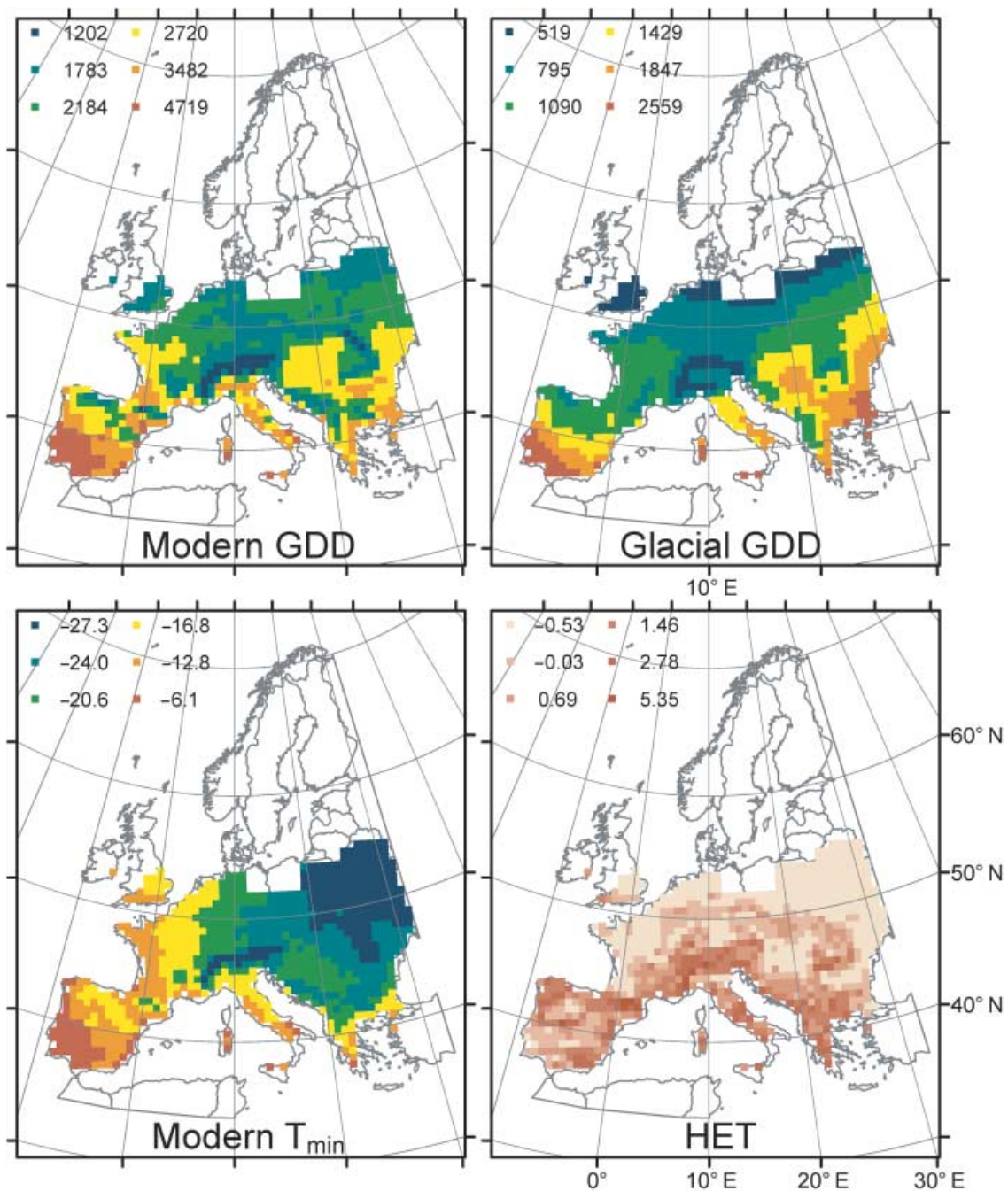
Figure 1 Modern and Last Glacial Maximum growing-degree-days [GDD_{now} and GDD_{lgm} (°)], modern minimum temperature [$TMIN_{now}$ (°)] and climatic heterogeneity (HET) per 60×60 km grid cell ($n = 879$) in the unglaciated parts of Europe. The legend indicates the maximum value for each colour category. HET is unitless, and GDD is a degree sum, computed with a 5 °C base (see Materials and Methods).

in the current climate data set) to better reflect the extent of their post-glacial range expansion (Table 1).

We tested the importance of modern and LGM climate as richness determinants using three climatic variables of well-known importance for temperate tree species distributions, namely growing-degree-days (GDD), absolute minimum temperature (TMIN) and water balance (WAT) (Sykes *et al.*, 1996; Svenning & Skov, 2004). Using the modern and LGM climate data, growing-degree-days was computed following Prentice *et al.* (1992) using

a 5 °C base, minimum temperature was estimated from the mean temperature of the coldest month as in Prentice *et al.* (1992), and water balance was computed as the yearly sum of the monthly differences between precipitation and potential evapotranspiration following Lugo *et al.* (1999). The glacial climate variables (GDD_{lgm}, $TMIN_{lgm}$, WAT_{lgm}) were computed directly for the 60-km cell grid, while the modern climate variables (GDD_{now}, $TMIN_{now}$, WAT_{now}) were derived as means for each 60-km cell of the values at the original 10′ resolution (Fig. 1).

Table 1 The 55 tree species studied and, in parentheses, their range sizes across all of Europe (number of occupied 60-km grid cells, see Materials and Methods), organized according to range size categories. Nomenclature follows the *Atlas Florae Europaeae* (Jalas & Suominen, 1972–94). Only species growing to at least 20 m were included. Bold face indicates species endemic to Europe *sensu Atlas Florae Europaeae*

Widespread	Intermediate	Restricted
Alnus glutinosa (1185)	*Quercus pubescens* (518)*	*Corulus colurna* (105)
Populus tremula (1165)	***Abies alba*** (459)	***Pinus cembra*** (105)
Betula pendula (1104)	*Picea abies* (420)	*Quercus pedunculiflora* (88)
Betula pubescens (1057)	*Quercus cerris* (282)	*Juglans regia* (57)
Ulmus glabra (1039)	*Celtis australis* (279)	*Laurus nobilis* (56)
Quercus robur (988)	*Pinus nigra* (219)	***Pinus heldreichii*** (52)
Pinus sylvestris (976)	*Quercus ilex* (219)	***Pinus peuce*** (39)
Salix alba (953)	*Ostrya carpinifolia* (199)	***Abies borisii-regis*** (36)
Salix fragilis (896)	*Quercus pyrenaica* (180)	*Fagus orientalis* (35)
Ulmus minor (872)	*Castanea sativa* (178)	*Juniperus excelsa* (31)
Alnus incana (843)*	***Larix decidua*** (175)	*Quercus canariensis* (25)
Quercus petraea (836)	*Quercus frainetto* (174)	***Abies cephalonica*** (12)
Fagus sylvatica (755)	*Pinus pinaster* (156)	***Picea omorika*** (12)
Populus nigra (744)	*Quercus suber* (154)	***Alnus cordata*** (9)
Taxus baccata (728)	*Quercus rotundifolia* (140)	*Pinus brutia* (9)
Carpinus betulus (698)	*Quercus faginea* (136)	***Abies pinsapo*** (5)
Ulmus laevis (654)	*Pinus halepensis* (127)	***Quercus sicula*** (2)
Populus alba (627)	*Pinus pinea* (121)	*Juniperus drupacea* (1)
	Pinus uncinata (111)	

*These two species would have switched categories if the data set with 879 grid cells had been used for the ranking.

Furthermore, standard deviations of modern GDD, TMIN and WAT were computed for each 60-km cell as measures of climatic heterogeneity. A synthetic descriptor of climatic heterogeneity (HET) was then computed as the mean of the three standard deviation variables, after standardizing each (Fig. 1). We note that climatic heterogeneity is strongly controlled by topography and may not be only a descriptor of the modern environment but also an indicator of historical opportunities for enhanced climate tracking by short-distance altitudinal migration (McGlone, 1996; Lobo *et al.*, 2001; Jetz *et al.*, 2004; Turner, 2004). Hence, we did not classify HET with the modern or glacial climate variables, but let it constitute its own category in the analyses.

Analyses

We used a three-pronged strategy based on multiple linear regression to test for the effect of LGM climate and evaluate the relative importance of the climatic controls: (1) we assessed the relative support for models with or without each set of climate variables using an information-theoretic approach; (2) we compared the size of the standardized regression coefficients for the modern and glacial climatic variables in multiple regressions with the full set of climatic variables included; and (3) we used partial linear regression to assess the amount of variation in species richness that can uniquely be attributed to modern or LGM climate or climatic heterogeneity.

The species richness measures were square-root transformed to reduce skewness. After transformation, total and intermediate species richness had low skewness (−0.20 and −0.47, respectively), while richness of widespread and restricted species remained somewhat left-skewed (skewness = −1.69) or right-skewed (skewness = 1.49), respectively. After being rescaled to a non-negative minimum by subtracting the original minimum value from all values, HET and WAT_{lgm} were square-root transformed so that all seven original explanatory variables had skewness $< |\pm 1|$. The square of the standardized GDD_{now}, $TMIN_{now}$ and WAT_{now} were also included as predictors to allow for nonlinear relationships with modern climate (skewness 2.3–4.0). All variables were standardized before analysis to allow comparison of the regression coefficients.

Multicollinearity is likely to be a problem when variables are highly correlated, with $r \geq 0.90$ and tolerance < 0.10 (Tabachnick & Fidell, 2001; Quinn & Keough, 2002). Glacial and modern TMIN were highly correlated ($r = 0.92$, $P < 0.0001$), and both had tolerances < 0.10. As a consequence we excluded $TMIN_{lgm}$ from the set of predictors, causing tolerances to be 0.10 (GDD_{now}) and 0.23–0.52 (the other eight variables). Furthermore, residual scatter plots were examined to check the assumptions of normality, linearity and homoscedasticity (Tabachnick & Fidell, 2001).

We fitted two kinds of multiple regressions, namely ordinary least squares (OLS) multiple regression models and conditional autoregressive (CAR) models that accounted for spatial autocorrelation (Lichstein *et al.*, 2002). We fitted both kinds of models, since their ecological interpretability is a contested issue (Lennon, 2000; Diniz-Filho *et al.*, 2003). In CAR models the estimated value of the response is a function of both the explanatory variables and the values of the response variable at neighbouring sites, adjusted for the values of the explanatory variables at those sites (Lichstein *et al.*, 2002). A 100-km neighbourhood distance with neighbour weights $w_{ij} = 1$ was used for the CAR models. Preliminary analyses showed that these neighbourhood specifications removed spatial autocorrelation from the residuals to a similar or greater extent than 100-km or 1000-km neighbourhood distances with neighbour weights $1/d_{ij}$

or $1/d_{ij}^2$, where d_{ij} is the distance between the focal cell and a neighbouring cell. We used standardized variograms to assess the degree of spatial autocorrelation in the residuals of the OLS and CAR models (Rossi *et al.*, 1992; Legendre & Legendre, 1998).

We used an information-theoretic approach to assess the degree of support for two sets of candidate models for each measure of species richness (Burnham & Anderson, 2002; Johnson & Omland, 2004). The first set of models consisted of four OLS models, namely: (1) the linear modern climate (MOD) model with GDD_{now}, $TMIN_{now}$ and WAT_{now}, (2) the nonlinear modern climate (MOD^2) model that also includes GDD_{now}^2, $TMIN_{now}^2$ and WAT_{now}^2, (3) the climatic hetereogeneity (HET) model with HET, and (4) the Last Glacial Maximum climate (LGM) model with GDD_{lgm} and WAT_{lgm}. The second set of models included the 11 OLS that can be fit using all possible combinations of the four sets of climate variables described above (MOD, MOD^2, HET and LGM) and the 11 corresponding CAR models. The two sets of models were used to assess the overall strength of modern and LGM climate and HET as richness predictors ignoring or accounting for the other explanatory variables and spatial autocorrelation, respectively. Since the number of parameters estimated in any model was $\ll n/40 \approx 22$ ($n = 879$ grid cells), we used the original Akaike information criterion (AIC) rather than its small-sample unbiased derivative (Burnham & Anderson, 2002). As AIC values contain arbitrary constants, the AIC of each model was rescaled by subtracting the minimum AIC value in the model set, i.e. the best model has a rescaled AIC, ΔAIC = 0 (Burnham & Anderson, 2002). Models with ΔAIC = 2 have substantial support, while models with ΔAIC > 10 have essentially no support (Burnham & Anderson, 2002). Akaike weights were used to measure the probability that a given model was the best model for the observed data within the set of candidate models (Burnham & Anderson, 2002). Different routines scale likelihoods differently, so to obtain comparable likelihood estimates we computed the OLS likelihood estimates from CAR models with a null neighbourhood (Lichstein *et al.*, 2002).

Model fit was represented by Nagelkerke's R^2, which yields identical values to the traditional R^2 when computed for OLS models (Nagelkerke, 1991). We used partial regression analysis to assess the amount of variation in species richness that can uniquely be attributed to modern or LGM climate or climatic heterogeneity, i.e. once the effect of the other explanatory variable sets has been taken into account (Legendre & Legendre, 1998). The partial R^2 for a given set of climate variables was computed by subtracting the R^2 for the model with the two other sets of climate variables from the R^2 for the model with all nine climate variables (Legendre & Legendre, 1998).

OLS regressions were computed in JMP 6.0 (SAS Institute, Cary, NC, USA), while model likelihoods, autoregressive models and variograms were computed in S-PLUS 7.0 including the S+ SpatialStats module (Insightful Corporation, Seattle, WA, USA).

RESULTS

Total species richness is concentrated in a southern band of mountainous regions (Fig. 2). The geographical pattern in richness of intermediate species is similar, albeit with a stronger southern bias, while richness of widespread species is concentrated in Central Europe, and richness of restricted species is strongly associated with the southern Balkans (Fig. 2).

Considered separately and ignoring spatial autocorrelation, modern climate (including the nonlinear terms) was clearly the superior explanatory factor for total and widespread tree species richness in terms of relative model support and model fit (Table 2). In contrast, climatic heterogeneity was the strongest explanatory factor for intermediate tree species richness, while LGM climate received strong support as the best single explanatory factor for restricted tree species richness (Table 2). In the latter case model fit was only marginally higher than for modern climate, but was achieved using half the number of free parameters. When the whole suite of the 22 climate models was considered, the CAR model with all nine climatic predictors was always superior (Table 3). The CAR approach provided much superior model fits than the OLS approach (Table 3) and strongly reduced the spatial autocorrelation in the model residuals compared with the OLS residuals (Fig. 3). According to its Akaike weight the probability that the CAR model with all nine predictors was the best model was 100% for richness of widespread, intermediate and restricted species, while it was only marginally more strongly supported ($W = 53\%$) for total species richness than the CAR model with just the modern climate variables and HET ($W = 47\%$; Table 3).

Considering the size of the regression coefficients, modern climate and climatic heterogeneity were particularly important for widespread and intermediate tree species richness, respectively, while LGM climate had its strongest influence on richness of restricted species (Table 3). However, the CAR results also indicated that all richness measures increased sharply with GDD_{now}, had unimodal relationships with $TMIN_{now}$, had increasing or unimodal relationships with WAT_{now}, and increased with HET (Table 3). With respect to glacial climate, GDD_{lgm} and WAT_{lgm} had very small regression coefficients for total richness (Table 3). Restricted and, to a lesser extent, intermediate species richness increased with GDD_{lgm}, while richness of widespread species exhibited an unexpected decrease with GDD_{lgm} (Table 3). Similar but weaker patterns were observed for WAT_{lgm} (Table 3). The CAR results were generally consistent with the bivariate relationships (Fig. 4), except that the bivariate richness–GDD_{now} relationships were negative or bimodal (Fig. 4). The OLS and CAR model residuals did not indicate problems with lack of normality, nonlinearity or heteroscedasticity, except for a tendency of the restricted species richness residuals to show increasing variance at larger predicted values. This pattern reflected the large proportion of grid cells with 0 (67%) or 1 restricted species (20%). To check that this did not compromise the results, we refitted the OLS and CAR models for the restricted species after randomly subsampling the grid cells with 0 or 1 restricted species each to the number of cells with two restricted species (Table 3). The residuals were now homoscedastic, while the results remained qualitatively unchanged, albeit the GDD_{lgm} relationship was actually strengthened (Table 3).
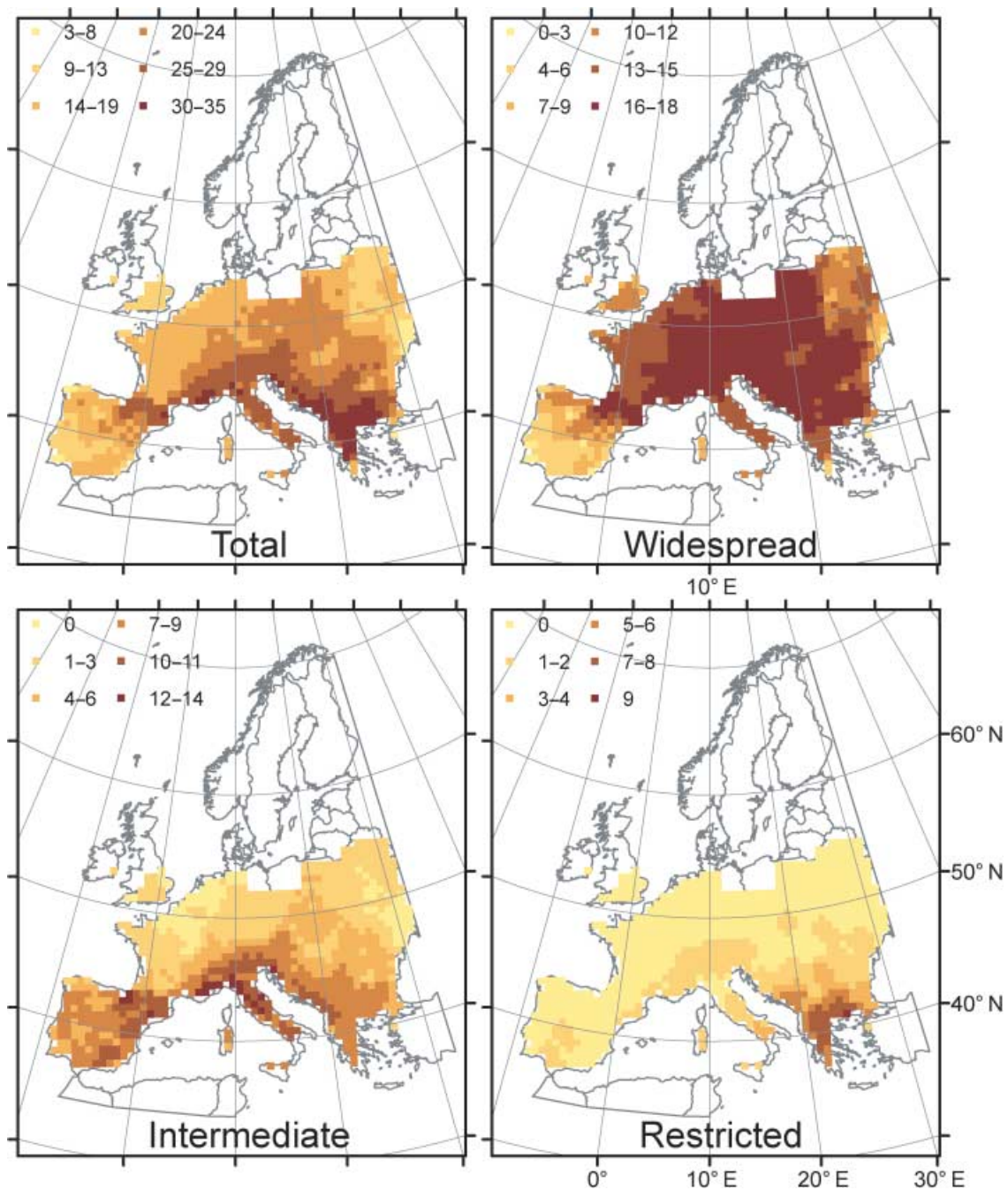
Figure 2 Total tree species richness and richness of widespread, intermediate and restricted tree species per 60 × 60 km grid cell (*n* = 879) in the unglaciated parts of Europe. The legend indicates the number of species per grid cell of a given colour.

The OLS partial regression analyses showed that total species richness had a large variation fraction uniquely attributable to modern climate and a smaller, but still considerable, fraction uniquely attributable to climatic heterogeneity (Fig. 5). Only modern climate accounted for a large unique variation fraction for richness of widespread species, while only climatic heterogeneity did so for richness of intermediate species (Fig. 5). Glacial climate only accounted for a considerable unique variation fraction for richness of restricted species (Fig. 5). The CAR

partial regression analyses produced small partial R^2 values for the three climate variable sets, just 0.1–4.8% of the total variation explained, but did not change the relative importance of modern and LGM climate and HET (results not shown).

DISCUSSION

The main aim of the present study was to assess whether glacial climate still asserts direct control on the geographical variation in

Table 2 Comparison of linear modern climate (MOD), nonlinear modern climate (MOD^2), climatic heterogeneity (HET) or Last Glacial Maximum climate (LGM) OLS models showing their model log likelihoods (*LL*), number of free parameters (*k*), rescaled Akaike information criterion (ΔAIC), Akaike weights (*W*, probability that a given model is the best out of the four models in the set) and model fit (Nagelkerke's R^2)

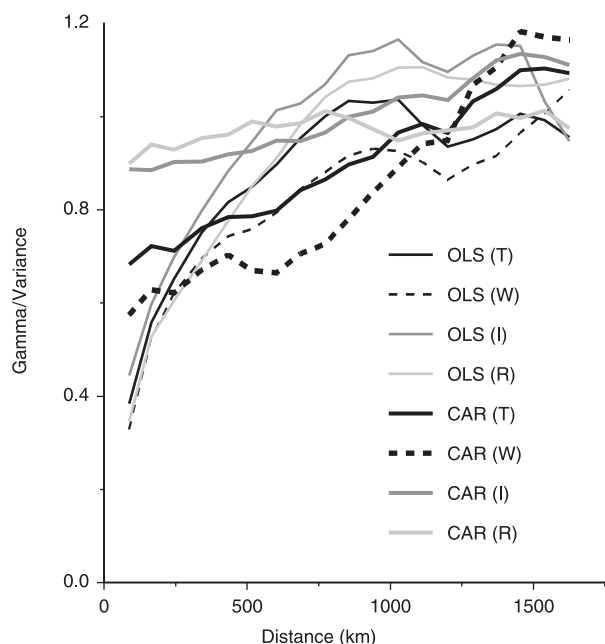| Richness	Model	*LL*	*k*	ΔAIC	*W* (%)	R^2
All	MOD	−2901	5	378	0	0.161
	MOD^2	−2709	8	0	100	0.458
	HET	−2814	3	200	0	0.312
	LGM	−2916	4	406	0	0.132
Widespread	MOD	−2761	5	457	0	0.391
	MOD^2	−2530	8	0	100	0.640
	HET	−2978	3	886	0	0.002
	LGM	−2870	4	673	0	0.219
Intermediate	MOD	−2849	5	346	0	0.255
	MOD^2	−2793	8	240	0	0.344
	HET	−2678	3	0	100	0.495
	LGM	−2879	4	403	0	0.204
Restricted	MOD	−2912	5	195	0	0.140
	MOD^2	−2829	8	36	0	0.288
	HET	−2881	3	130	0	0.199
	LGM	−2816	4	0	100	0.310

Figure 3 Standardized variograms of the residuals for total (T), widespread (W), intermediate (I) and restricted (R) species richness from OLS and CAR models with the nine climatic variables as predictors.

tree species richness in Europe: We found only weak support for LGM climate as a control of total tree species richness (Table 3). In contrast, the simple regression models (Table 2), the size of the autoregressive model coefficients (Table 3) and the partial R^2s

(Fig. 5) all provide support for the importance of modern climate and, to a lesser extent, climatic heterogeneity. The importance of modern climate is consistent with the known influence of climate on the population dynamics and range
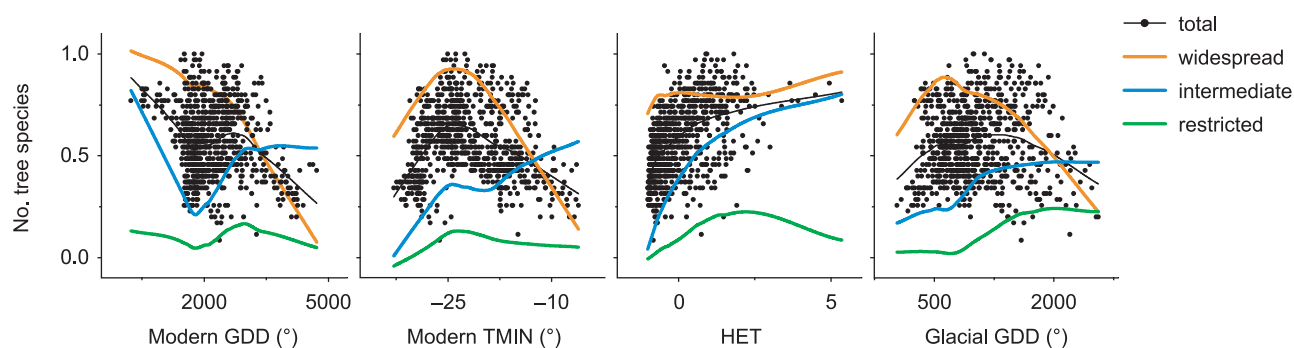
Table 3 Autoregressive models for tree species richness as a function of modern and glacial growing-degree-days (GDD$_{now}$ and GDD$_{lgm}$) and water balance (WAT$_{now}$ and WAT$_{lgm}$), modern minimum temperature (TMIN$_{now}$) and climatic heterogeneity (HET) (n = 879 grid cells). The model fit (Nagelkerke's R^2; with R^2 for the corresponding OLS model in parentheses), model log likelihood (*LL*), number of free parameters (*k*), the rescaled Akaike information criterion (ΔAIC) and the Akaike weight [*W*, probability (in percentage) that this model is the best out of the 22 models in the set, see Materials and Methods] are given

Terms	All	Widespread	Intermediate	Restricted	
Intercept	−0.149**	−0.337****	−0.089	0.329****	(−0.372****)
GDD$_{now}$	**0.529****	**0.371****	**0.410****	**0.305****	**(0.337**)**
GDD$^2_{now}$	**0.315****	0.183***	0.162***	0.203***	(0.140)
TMIN$_{now}$	**−0.351****	**−0.317****	−0.183**	−0.234***	(−0.240**)
TMIN$^2_{now}$	**−0.549****	**−0.430****	−0.187****	**−0.383****	(−0.245**)
WAT$_{now}$	0.269****	0.185***	0.205****	0.170**	**(0.305***)**
WAT$^2_{nov}$	−0.079*	−0.085**	−0.008	−0.006	(−0.032)
HET	**0.309****	0.121****	**0.307****	0.150****	(0.206****)
GDD$_{lgm}$	−0.038	**−0.381****	0.180****	**0.393****	**(0.601****)**
WAT$_{lgm}$	0.028	−0.061**	0.072***	0.099***	(0.198****)
R^2	0.813 (0.629)	0.836 (0.654)	0.849 (0.624)	0.806 (0.498)	
LL (*k*)	−2242 (12)	−2185 (12)	−2147 (12)	−2257 (12)	
ΔAIC (*W*)	0.0 (52.7)†	0.0 (100.0)	0.0 (100.0)	0.0 (100.0)	

Regression results are shown for all AFE tree species and the 18 common, 19 intermediate or 18 restricted species, separately. The table gives the regression coefficients and the model fit (Nagelkerke's R^2; also given in parentheses for the corresponding OLS model). For restricted richness, regression coefficients are also given, in parentheses, for a data set where the numbers of grid cells with 0 or 1 restricted species were reduced by random subsampling to 33 cells each (= number of cells with two restricted species), i.e. n = 185 cells. Bold type indicates coefficients > | ±0.30 |. The corresponding effect test and whole-model test *P*-values are also given (*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$).
†The CAR model with just the six modern climate variables and HET had ΔAIC = 0.2 and W = 47.3% (*LL* = −2244, *k* = 10).

Figure 4 Tree species richness for the four species groups (given in proportion of their respective maximum values) as a function of modern growing-degree-days (GDD_{now}) and minimum temperature ($TMIN_{now}$), climatic heterogeneity (HET) and Last Glacial Maximum growing-degree-days (GDD_{lgm}). Curves are locally weighted OLS regression fits with a span of 0.5. HET is unitless, and GDD is a degree sum, computed with a 5 °C base (see Materials and Methods).
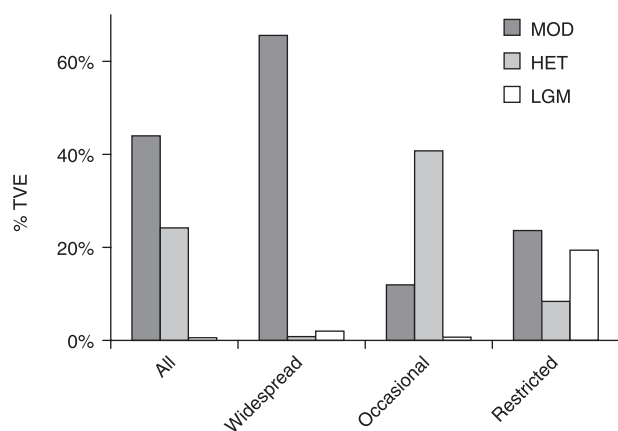

Figure 5 Partial OLS regression results: The variation fraction uniquely attributable to modern climate (MOD; including all six linear and nonlinear variables), climatic heterogeneity (HET) or Last Glacial Maximum climate (LGM) is shown for each richness measure (in percentage of the total variation explained, TVE).

limits of temperate and boreal tree species (e.g. Brubaker, 1986; also cf. Cheddadi *et al.*, 2005). It also appears consistent with interpretations of the European and North American pollen record to support that tree species distributions and diversity have been in equilibrium with climate throughout most of the Holocene (Silvertown, 1985; Webb, 1986; Huntley & Webb, 1989; Huntley *et al.*, 1989; Tinner & Lotter, 2006). However, considering the strong spatial autocorrelation remaining in the species richness patterns after accounting for the influence of climate (Fig. 3; also compare the R^2 for the OLS and CAR models in Table 3) we believe that it is more plausible that species ranges and richness are only partially in equilibrium with modern climate (cf. Svenning & Skov, 2004, 2005).

An additional important aim of the present study was to estimate the relative importance of modern and LGM climate as controls of tree species richness in Europe. Deconstructing tree species richness according to range size categories showed that the relative importance of modern and LGM climate and climatic heterogeneity depended on range size (Tables 2 and 3; Fig. 5).

The geographical species richness peaks for the intermediate and restricted species (Fig. 2) coincide well with the main known glacial refugia for non-boreal trees in Europe, while this was not the case for the widespread species (Huntley & Birks, 1983; Bennett *et al.*, 1991). Correspondingly, variation partitioning showed that richness of widespread species was largely controlled by modern climate, while LGM climate and climatic heterogeneity were codominant with modern climate as controls of richness of restricted and intermediate species, respectively (Fig. 5; also cf. Table 2). Nevertheless, models including modern climate together with LGM climate and climatic heterogeneity as predictors were strongly supported for all three range size categories (Table 3). However, for widespread species LGM climate–richness relationships in the CAR model were not meaningful, e.g. the strong negative relationship between richness and GDD_{lgm} (Table 3). Even if these species had more widespread LGM distributions in Europe than traditionally thought (Willis *et al.*, 2000; Stewart & Lister, 2001; Willis & van Andel, 2004), it is implausible that their LGM distributions were biased towards particularly cold areas. We suspect that this relationship simply reflects the strong northern post-LGM range expansions of these species. The strong increase in restricted, and to a lesser extent intermediate, species richness with GDD_{lgm} and their weaker, but also positive, relationships with WAT_{lgm} show that species with relatively small ranges are most numerous where LGM climate was least cold and arid (Table 3), in particular in the Balkans (Figs 1 and 2). While the generally high GDD_{lgm} values in much of the Balkans coincide with the main concentration of restricted tree species in Europe, southern Iberia with equally high GDD_{lgm} values contains only few restricted species (Figs 1 and 2). This difference can be explained by the drier glacial and modern climate in the latter region (cf. Bennett *et al.*, 1991). Grid cells with $GDD_{lgm} \geq 1500°$ had median $WAT_{lgm} = 123$ mm and $WAT_{now} = -100$ mm in the Balkans ($n = 61$) and median $WAT_{lgm} = -35$ mm and $WAT_{now} = -325$ mm in Iberia ($n = 45$). These results are consistent with the traditional importance for the glacial survival of European tree species assigned to the Balkans in the palaeobotanical literature (Huntley & Birks, 1983; Bennett *et al.*, 1991; Willis, 1994; Tzedakis *et al.*, 2002), albeit the Iberian Peninsula has clearly also constituted an important

refuge area (Carrión *et al.*, 2003; González-Sampériz *et al.*, 2005). The positive species richness–HET relationships found for all richness measures (Table 3; Fig. 4) may partly reflect greater present-day habitat diversity (cf. Currie & Paquin, 1987; Kerr & Packer, 1997). However, greater historical opportunities for climate tracking in areas with high spatial climatic heterogeneity, i.e. by short-distance altitudinal migration, probably also contribute (e.g. McGlone, 1996; Lobo *et al.*, 2001; Tzedakis *et al.*, 2002). The patterns found here for European trees fit the general pattern that restricted-range plant and animal species throughout the world are generally concentrated in topographically complex or climatically stable areas that have offered unusually good opportunities for long-term species survival and speciation during the Quaternary (Jetz & Rahbek, 2002; Jansson, 2003; Jetz *et al.*, 2004).

Our results allow consideration of the likely mechanism of the post-glacial tree species range expansions in Europe. If the traditional estimates of post-LGM migration rates of up to 1–2 km year^{-1} (Huntley & Birks, 1983) have been typical of European tree species, one would expect both individual ranges and species richness to have continuously tracked the variable climatic conditions since the LGM and consequently be in equilibrium with current climate (Webb, 1986; Huntley & Webb, 1989; Huntley *et al.*, 1989; Pitelka & Plant Migration Workshop Group, 1997). In contrast, we have found that the richness patterns for the less widespread species appear to still be constrained by LGM refugia locations and, more generally, only partially in equilibrium with modern climate. This is expected under the slow migration hypothesis, where the range expansions of the intermediate and restricted species have been strongly dispersal limited as a result of few or marginal refugia. The widespread species may have achieved their large and often fast post-LGM range expansions by slow migration from more widely occurring and northern refugia (Kullman, 2002; McLachlan *et al.*, 2005; Pearson, 2006). As already mentioned there is increasing evidence for much wider LGM distributions of trees and other forest species in Central and Eastern Europe than hitherto thought (Willis *et al.*, 2000; Stewart & Lister, 2001; Willis & van Andel, 2004; Hernández Fernández, 2006). Along this line of thinking, Bennett and Willis (1995) proposed that tree species distributions in Europe are controlled not only by modern climate, but also by their ability to spread and historical factors, notably the size and location of their LGM populations (see also Cheddadi *et al.*, 2005). Furthermore, evidence exists that the ranges of many European tree species are strongly dispersal limited, notably low filling of their potential ranges as estimated by bioclimatic envelope modelling, strong non-environmental broadscale patterns in tree species richness and composition, and extensive naturalization of many tree species beyond their native ranges (Svenning & Skov, 2004, 2005). Other authors have also suggested that the post-LGM recolonization of Europe and North America has been at least transiently dispersal limited for some species (e.g. Davis, 1976; Johnstone & Chapin, 2003).

The unimodal relationships between richness and $TMIN_{now}$ and WAT_{now} (Table 3, Fig. 4) are contrary to general expectations (Currie *et al.*, 2004; Hawkins *et al.*, 2004; Turner, 2004). However,

these relationship may reflect historical sorting of climate tolerances in the regional species pool (McGlone, 1996; Currie *et al.*, 2004). McGlone (1996) argued that the observed relationships between climate and tree species richness result mainly from the impact of Quaternary climatic cycles on regional species pools via reduced speciation and survival in the most affected areas. In the case of European tree diversity, the negative relationship with $TMIN_{now}$ at high values of $TMIN_{now}$ (Fig. 4) follows logically from the impact of Plio-Pleistocene climatic changes on the regional species pool. During this period a large proportion of the European tree flora was lost due the onset of the summer-dry Mediterranean climate and the repeated glaciations (van der Hammen *et al.*, 1971; Mai, 1995). The scarcity of warm, moist glacial refugia caused extinctions, which particularly affected frost- and drought-sensitive taxa (Svenning, 2003). The extinctions included numerous tree genera that form an important and diverse component of modern warm-temperate vegetation in East Asia and North America (Mai, 1995). As evidence exists that at least some of the surviving cold-tolerant tree species do not thrive under mild climatic conditions (Sykes *et al.*, 1996), a negative or unimodal richness–$TMIN_{now}$ relationship is expected as a consequence of this historical sorting process. The positive relationship between tree species richness and GDD_{now} in the autoregressive models (Table 3) is consistent with the diversity–energy relationship generally observed for trees and other organisms (Currie & Paquin, 1987; Currie, 1991; Hawkins *et al.*, 2004). However, the relatively low tolerance for GDD_{now} and the negative or bimodal bivariate richness-GDD_{now} relationships (Fig. 4) raise concern regarding the robustness of this finding.

In conclusion, our findings suggest that LGM climatic conditions after 21,000 years continue to be an important control of the geographical patterns of tree species richness in Europe. However, the relative importance of modern and LGM climate depends on species range sizes. Notably, LGM climate appears primarily to be an important richness determinant for the restricted species, which appear to still be concentrated in their glacial refugia. Climatic heterogeneity is an important diversity control, particularly for richness of intermediate species, and may to some extent also reflect glacial survival opportunities. Our findings add to the growing evidence that post-LGM range expansions of many tree species in Europe and North America have been slower (McLachlan *et al.*, 2005; Pearson, 2006; Yansa, 2006) than generally thought (Webb, 1986; Huntley *et al.*, 1989; Pitelka & Plant Migration Workshop Group, 1997) and limited by dispersal (Davis, 1976; Johnstone & Chapin, 2003; Svenning & Skov, 2004, 2005). Our results imply that to conserve European tree diversity under future global warming, areas that are climatically heterogeneous or expected to experience the least changing climate will be of crucial importance, in particular for the many species with small ranges.

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