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Contemporary richness of holarctic trees and the historical pattern of glacial retreat

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The length of time land has been available for colonization by plants and other organisms could provide a partial explanation of the contemporary richness gradients of trees. According to this hypothesis, increasing times of land availability entail higher chances of recolonization, which eventually have positive effects on tree richness. To test this, we generated a dataset of the Holarctic trees and evaluated the influence of cell age, a measure of the time since an area became free of ice, on the observed tree richness gradients. We found that cell age is associated with richness in both Europe and North America, after controlling for contemporary climate patterns, suggesting that the historical pattern of glacial retreat in response to post-Pleistocene global warming has left a signal still detectable after at least 14 000 yr. The results were consistent using a range of modelling approaches or whether Europe and North America were analyzed separately or in concert. We conclude that, although secondary to contemporary climate, the post-glacial recolonization hypothesis is broadly supported at temperate latitudes.

The extent to which past events drive broad-scale gradients in species richness forms the basis of hypotheses focused on a range of historical factors (Qian and Ricklefs 1999, Ricklefs and Latham 1999, Svenning and Skov 2005). One such hypothesis argues that the length of time since an area has become suitable for species establishment, termed “environmental age” (Begon et al. 1996), “patch age” (Hastings 2003) or simply “age” (Hawkins and Porter 2003, Rodríguez et al. 2006), can be an important determinant of species richness. This is well established in the context of island biogeography (MacArthur and Wilson 1967), but has also been applied to areas that became habitable after the retreat of Pleistocene ice sheets (Currie 1991). The prediction in the latter case is that species richness in areas that remained uncovered by ice during the last glacial period (between 20 000 and 10 000 yr BP) will be greater than in areas covered by ice. Recent support for this post-glacial recolonization hypothesis has been reported for northern North American mammals and birds, although the effects were secondary compared to those of current climate (Hawkins and Porter 2003). In contrast, earlier studies focused on trees found no evidence of effects of recent glacial history on the richness gradients of North America (Currie and Paquin 1987, Adams and Woodward 1989) and Eurasia (Adams and Woodward 1989). This discrepancy is intriguing, since animals, especially vertebrates, are on average probably much more dispersive than plants, and it seems unlikely that vertebrates have been affected by glaciation whereas trees have not.

A fundamental issue when testing hypotheses of richness gradients at broad scales is that experiments are impossible, so we have to rely on the strength of correlations of richness patterns with explanatory variables linked with the hypotheses of interest, many of which may be collinear. The rationale is that if a particular variable accounts for very little independent variance in richness, then the hypothesis to which the variable is related is probably not a good proximate explanation (Currie 1991, Hawkins et al. 2003). The choice of variables to include in analyses also becomes critical and can obviously influence conclusions, and this may be especially important when testing historical hypothesis. For example, Currie and Paquin (1987) estimated glacial effects by differentiating only between glaciated and non glaciated areas. This does not take into account the pace at which the ice sheets retreated nor the spatial pattern of retreat. Adams and Woodward (1989), on the other hand, concluded that recent glacial history had no effect on tree richness based entirely on indirect evidence; that is, by claiming that models including contemporary factors explained so much of the variance in tree richness that there was no need to invoke historical explanations. This overlooks the fact that strong associations between richness and current conditions do not exclude a possible secondary role of recent glacial history (Whittaker and Field 2000, Hawkins and Porter 2003).

Here we revisit the question of whether recent glacial history has influenced the tree richness gradient of the Holarctic using an age variable that reflects the spatio-temporal pattern of glacial retreat, measured by the time previously glaciated areas became free of ice coverage (Turner et al. 1988, Hawkins and Porter 2003, Rodríguez et al. 2006). Our rationale resembles that proposed by Whittaker and Field (2000) to asses the impact of historical legacies in determining gradients of tree richness (Hawkins and Porter 2003). However, whereas these authors suggested building climate models for richness in regions not impacted by a certain historical factor, and then examine residuals over regions expected to be impacted by that factor, we directly generate contemporary climate models for areas that are previously thought to be affected by cell age and determine if adding this factor to the models improves their explanatory power. We also evaluate the effects of glacial history by adding age to reparameterized versions of published models generated to explain global biogeographic patterns of woody plant species richness (O'Brien 1998, Field et al. 2005), or to explain global gradients of angiosperm family richness (Francis and Currie 2003). Our goals are to determine 1) whether a historical signal of the last glaciation exists in northern temperate regions, and 2) the relative role this signal plays in explaining the contemporary diversity patterns of temperate trees.

Material and methods

Tree richness

We constructed a GIS database containing all tree species (defined as any woody plant growing to ≥ 4 m anywhere in its range) present in North America (676 species) and Europe (187 species). Complete range maps were found in the literature for all North American and most European (84.5%) tree species. For the remaining European species, partial distribution maps (5%) or no maps were available (11%). In such cases, maps were drawn based on written descriptions of the distribution of each species (see Appendix 1 for details and references to build the database). For both continents, maps were digitized in ArcGis 9.1 and rasterized at two grains (27.5×27.5 km for mapping and 110×110 km for statistical analysis). The larger grain generated 1830 cells: 1444 cells for North America and 386 cells for Europe). All islands except Great Britain as well as all coastal cells covering $<50\%$ of inland cells were excluded from the analysis.

Environmental and historical predictors

Selection of environmental predictor variables was based on previous studies of broad-scale plant richness gradients (Currie and Paquin 1987, Adams and Woodward 1989, Currie 1991, Francis and Currie 2003, Hawkins et al. 2003, Field et al. 2005). To explore all previous approaches used to model richness, 11 non-historical environmental variables were generated. Mean annual temperature (MeanTemp), annual temperature range (TempRange, the difference between mean maximum and minimum monthly temperature) and mean January temperature (JanTemp, Currie and Paquin 1987, Adams and Woodward 1989) were obtained at <http://www.grid.unep.ch/data/summary.php?dataid=GNV15> and annual potential evapotranspiration (PET_{PT}, calculated using the Priestley-Taylor formula) and annual actual evapotranspiration (AET) at <http://www.grid.unep.ch/data/summary.php?dataid=GNV183>. Water deficit (WD) was estimated as the difference between PET and AET (Francis and Currie 2003). Annual precipitation (AnnPrecip) is available at <http://www.grid.unep.ch/data/grid/gnv174.php>. Rainfall, a measure of the availability of liquid water, was estimated as the total monthly precipitation for all months with a mean temperature above 0°C (O'Brien 1998, Field et al. 2005, Hawkins et al. in press). We also calculated minimum monthly potential evapotranspiration (hereafter $minPET_{Th}$) using Thornwaite's formula (Thornwaite 1948) for use when generating models based on O'Brien's (1998) water-energy dynamics framework. O'Brien (1998) recommended that when $minPET < 14$ or > 45 mm and rainfall < 1000 mm, the maximum monthly PET ($maxPET_{Th}$) should be used rather than the minimum monthly PET. Since 95.2% of the cells in the Holarctic have $minPET < 14$ or > 45 mm, and 90.5% have $rainfall < 1000$ mm, we also estimated $maxPET_{Th}$. Range in elevation (ER) was used as an estimate of mesoscale vertical climatic variation within cells, calculated as the difference between maximum and minimum elevation within a grid cell and ln-transformed (O'Brien 1998, Field et al. 2005). DEM data are available at <http://www.ngdc.noaa.gov/seg/cdroms/ged_iia/datasets/a13/fnoc.htm>. Insolation/solar radiation data (Rad) (Currie and Paquin 1987, Adams and Woodward 1989), defined as the monthly averaged insolation incident on a horizontal surface for a given month, were obtained from <http://eosweb.larc.nasa.gov/cgi-bin/sse/global.cgi>, and estimated as the yearly total solar radiation incident on each cell. Growing season length/potential growing season (PGS) was calculated as the number of months with mean temperature $>0°C$ (O'Brien 1993, 1998). No productivity measure was included in the analysis for two reasons. First, climate strongly influences plant productivity at large extents, so including both climatic and productivity variables does not test alternative hypotheses, but only adds an intermediate link in the presumed causal chain leading from climate to tree richness. Second, when working with trees, climatic-richness relationships should focus on more direct estimators of climate rather than indirect or non-independent variables such as productivity, which depend on biological activity (Whittaker and Field 2000).

Finally, we calculated cell age to reflect the time a cell has been available for colonization by trees and other organisms as Pleistocene ice sheets retreated. Cell age was estimated for Europe using changes in ice cover at 1 Kyr intervals from Peltier (1993). For North America, we used the temporal series of maps developed by Dykes and Prest (1987). Cells not completely covered by ice during the last glacial maximum were assigned an age of 20 000 yr (Rodríguez et al. 2006).

Analytical protocols

The relationships between predictor variables and tree richness were tested using standard regression and model selection techniques based on Information theory (Burnham and Anderson 2002, Johnson and Omland 2004). Candidate models were ranked based on the Akaike information criterion (AIC), which measures the information lost when approximating reality by a model, so the model with the lowest value was considered the best given the data. For each model, AIC was computed as $AIC = n\log(\varepsilon^2) + 2K$, where n represents the sample size, ε^2 is the variance of the residuals of each regression model, and K is the number of parameters in the model.

Regression models based on gridded richness data often contain small-scale spatial autocorrelation in the residuals, which leads to a violation of independence (Diniz-Filho et al. 2003) and, consequently, underestimation of variances in the residuals and inflated degrees of freedom. This can influence AIC since it is calculated using the model residuals. To resolve this potential problem, we corrected the residual variances of all models by recalculating geographically effective sample sizes (n^*), as $n^* = n/[(1+p)/(1-p)]$, where p is the first-order autoregressive parameter of the residuals, approximated by the standardized Moran's I at the first distance class (Cressie 1993, Haining 2003), estimated for each model. The corrected AIC (AIC_c) thus allows models to be ranked and weighted after correcting for the presence of small-scale residual autocorrelation, thereby providing a quantitative measure of relative support for each competing model. Model's performance was addressed using ΔAIC_c, which is a measure of each model relative to the best model, and is given by the difference between AIC_c of each model and the minimum AIC_c found (the best model having $\Delta AIC_c = 0$). The level of support to choose among competing models was fixed at $\Delta AIC_c \leq 2$ (Burnham and Anderson 2002). Thus, values of $\Delta AIC_c \leq 2$ (independent of AIC scale) suggest the models are equally likely, whereas $\Delta AIC_c > 10$ indicates poor fit relative to the best model, and the model is very unlikely. All statistical analyses were performed using STATISTICA (StatSoft 2003) and Spatial Analyses in Macroecology [SAM] (Rangel et al. 2005).

We note that the analysis might be considered "biased" by the inclusion of many contemporary variables but only one historical variable. We took this conservative approach because historical effects are more controversial than modern climate. Also, we are not examining all possible historical effects, but a specific effect related to a single event (the most recent Ice Age). The selection of environmental variables was not random but was based on previous analyses connecting broad-scale richness patterns of these regions to contemporary climate (see above). The main goal of the analysis was not to test associations between contemporary climate and tree richness patterns, which are already well documented; rather, we focused on the statistical contribution of glacial history to richness patterns. Our initial approach was to identify the best regression models describing richness patterns of temperate trees of Europe and North America considered together based on contemporary climatic variables, and then adding cell age and test for improved model fit. Climatic models were based on modelling frameworks that have shown strong statistical explanatory power of broad-scale richness patterns of vegetation: two versions of O'Brien's water-energy models (hereafter regional water-energy models [RWEM]; O'Brien 1998, Field et al. 2005) and the water deficit model of Francis and Currie (2003) (hereafter F&C). The widely reported parabolic relationship between energy and richness may fail to be detected at temperate latitudes because studies restricted to this latitudinal range represent a portion of the theoretical energy-richness curve, and a positive, monotonic relationship between richness and climatic energy can be expected at high latitudes (Whittaker and Field 2000). Following this argument and because AIC penalizes for the addition of variables into the models, linear and non-linear versions of the RWEM and F&C models were also compared and tested with AIC_c. In addition, we also used an ad hoc approach to generate models different from the former ones and that potentially included all climatic variables which have been shown to correlate with tree richness. Multicollinearity was minimized both by using energy and water variables that were not strongly correlated with each other ($r < 0.6$), and by restricting the ad hoc models to one energy variable and one water variable. Because effects of glacial retreat would be expected to be strongest where the land was covered by ice, we first analyzed only glaciated cells. However, to test if the historical signal was detectable at the continental scale, we also generated models for the entire continents. We then generated multiple regression models for the glaciated parts of Europe and North America separately to determine if the results across both regions were consistent within each geographic region.

Finally, past and present climates are spatially correlated across Europe and North America, and therefore collinearity between cell age and climatic variables can complicate interpretation of the regression models, even if independent effects are detected in the multiple regressions. To explore this we used partial regression to partition the variance explained by contemporary (environmental effects) and historical (glaciation) effects into independent and covarying components (Legendre and Legendre 1998). The coefficients of determination for the current environmental variables and cell age were obtained separately from simple regression, while for climate and age combined were generated from multiple regressions. Once we obtained the three coefficients of determination (climate, age, climate+age), we proceeded to partition the independent effects of climate and age, as well as the combined effect of overlapping climate and age. Because of broad consistency in the results across Europe and North America, partial regressions were performed on the combined data only.

Results

Tree richness

The spatial distribution of tree species richness in Europe presents a clear latitudinal pattern, with more species in the southern mountainous areas and the Mediterranean regions (Mediterranean basin hotspot, Myers et al. 2000) (Fig. 1a). There is also a west-to-east gradient of increasing richness, which combined with the latitudinal gradient results in the highest richness in the Balkans and the eastern coast of the Adriatic Sea. Maximum richness in North America is in the coastal southeast (Fig. 1b), further to the south than reported in an earlier tree analysis (Currie and Paquin 1987). Western North America has lower richness than the east, but with relatively high diversity in the California floristic province (Myers et al. 2000). Similar patterns are found at both 27.5 × 25.7 km and 110 × 110 km grains (110 × 110 km maps are provided in Appendix 3).

Glaciated areas

If cell age influences the pattern of recolonization following glacial retreat, it should be most obvious in the region historically covered by ice (Rodríguez et al. 2006). Even so, in this part of the world, as expected, most of the variation in temperate tree richness can be accounted using variables describing present climatic conditions (Tables 1A, B and Appendix 2). On the other hand, the addition of cell age substantially increased the explanatory power of regression models using all four modelling approaches, as indicated by ΔAIC_c (Tables 1A, B). Clearly, the strongest models combine contemporary and historical climatic patterns irrespective of the combination of specific predictor variables in the models.

In terms of model fit, coefficients of determination of climate models are moderate to high (Table 1), and adding cell age to the models contributes substantial independent explanatory power, especially to models containing fewer predictor variables. The weakest contribution of history occurs in our best ad hoc model (Table 1A), a clear indication of collinearity among cell age and the additional climatic predictors in this more complex model. Indeed, partial regressions show that most of the "effects" of post-Pleistocene global warming are collinear with contemporary climate (Fig. 2). However, it remains that, after accounting for climate, cell age explained an additional 6.1 and 15.8% of the variance in tree richness with respect to the best published models (F&C and quadratic RWEM2, respectively), and 3.4% relative to the best model generated in our ad hoc approach. These results are consistent with a secondary influence of glacial history on the contemporary richness patterns of trees in the far north.

Regression models generated for Europe and North America separately sometimes differed from the bi-regional models in the particular predictor variables included, but the inclusion of cell age significantly reduced the AIC_c in all eight cases (Table 2A, B). Thus, any independent historical effects operating in the Nearctic and Palearctic do not alter the finding that cell age contributes explanatory power to environmental models across the Holarctic.

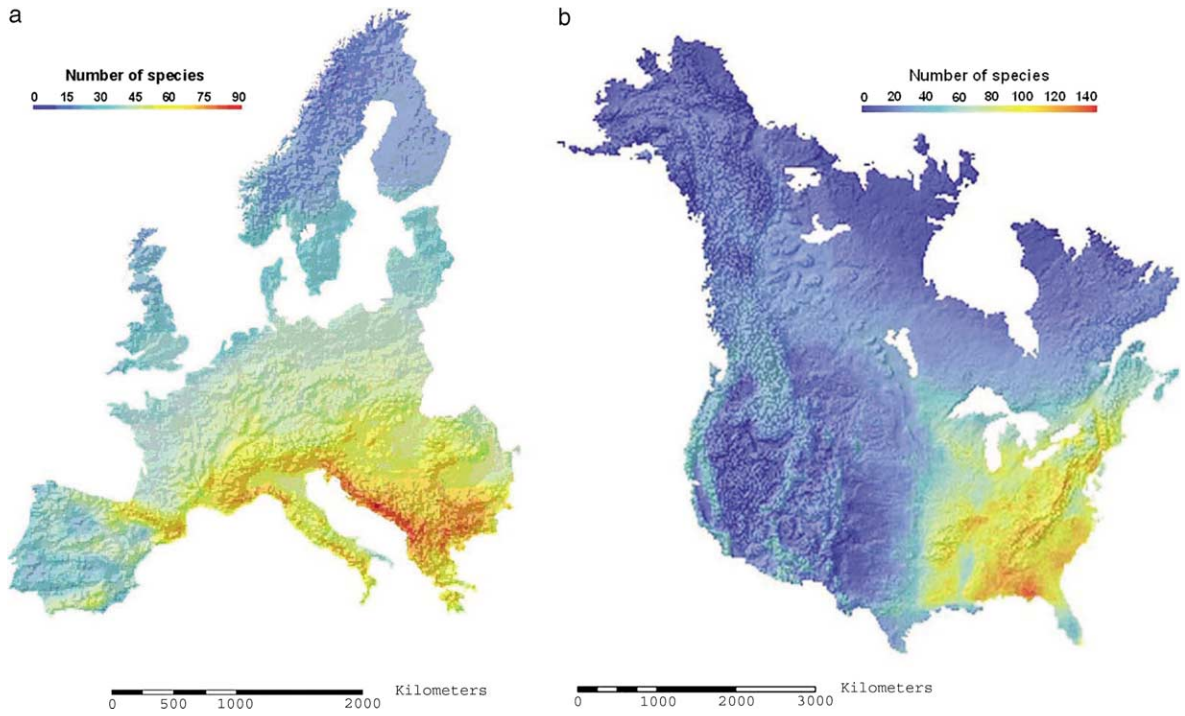

Fig. 1. Tree richness distribution for Europe and North America at 27.5 km^2 grain.

Table 1. Summary of regression models for tree richness using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age. For each region, the ΔAIC_c compares the best model ($\Delta AIC_c = 0$) with the best models generated under each of the other three modelling frameworks. R^2 of each model is also given.

Model type	Predictors in model						AIC_c	ΔAIC_c	R^2
A) Glaciated regions									
RWEM1	Rainfall	$minPET_{Th}$	$minPET^2_{Th}$				2649.4		0.430
	Rainfall	$minPET_{Th}$	$minPET^2_{Th}$	Age			2479.0	332.4	0.592
RWEM2	Rainfall	$minPET_{Th}$	$minPET^2_{Th}$	Ln(ER)			2637.4		0.434
	Rainfall	$minPET_{Th}$	$minPET^2_{Th}$	Ln(ER)	Age		2477.6	331.0	0.593
F&C	WD	PET_{PT}	PET^2_{PT}				2300.3		0.730
	WD	PET_{PT}	PET^2_{PT}	Age			2146.6	0	0.792
ad hoc	Rainfall	PET_{PT}	PET^2_{PT}	Ln(ER)	PGS		2275.1		0.694
	Rainfall	PET_{PT}	PET^2_{PT}	Ln(ER)	PGS	Age	2241.8	95.2	0.727
B) Entire regions									
RWEM1	Rainfall	$maxPET_{Th}$	$maxPET^2_{Th}$				5670.8		0.648
	Rainfall	$maxPET_{Th}$	$maxPET^2_{Th}$	Age			5649.3	78.7	0.683
RWEM2	Rainfall	$maxPET_{Th}$	$maxPET^2_{Th}$	Ln(ER)			5592.7	22.1	0.661
	Rainfall	$maxPET_{Th}$	$maxPET^2_{Th}$	Ln(ER)	Age		5613.0		0.689
F&C	WD	PET_{PT}	PET^2_{PT}				6070.1		0.725
	WD	PET_{PT}	PET^2_{PT}	Age			6031.0	460.4	0.739
ad hoc	Rainfall	PET_{PT}	PET^2_{PT}				5570.6	0	0.738
	Rainfall	PET_{PT}	PET^2_{PT}	Age			5596.3		0.740

Predictors: rainfall=total precipitation in months when mean temperature >0°C; $maxPET_{Th}$=maximum monthly potential evapotranspiration (Thornwaite's formula); $minPET_{Th}$=minimum monthly potential evapotranspiration (Thornwaite's formula); ER=elevation range (O'Brien 1993, 1998, Field et al. 2005); PET_{PT}=annual potential evapotranspiration (Presley-Taylor formula); WD=water deficit (Francis and Currie 2003); PGS=potential growing season (O'Brien 1993, 1998); TempRange=annual temperature range (Currie and Paquin 1987, Adams and Woodward 1989); Age=number of years cell exposed after glacial retreat; RWEM1=regional water-energy models (O'Brien 1998, Field et al. 2005); F&C=the water-energy model of Francis and Currie (2003).

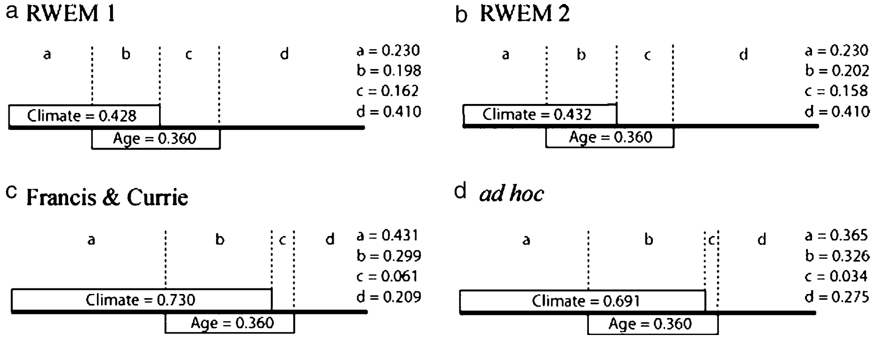

Fig. 2. Partial regression analyses for the best models describing tree richness in the glaciated regions of North America and Europe combined, partitioning the independent contributions of climate (a) and cell age (c), and the covariance between climate and cell age (b). (d) Represents the proportion of variation in richness not explained by either factor.

Entire regions

Even when including parts of North America and Europe that were not glaciated during the most recent glacial cycle, cell age generated better fitting models than when it was excluded in three of our four best models (Table 1B). Exceptionally in our best ad hoc model, including age did not increase the predictive power of the model. Also, even in the three other models, where age improves the predictions, increases in model R^2's were substantially lower (1–4%) than when modelling richness in the parts of the Holarctic that were covered by ice.

Discussion

We find that incorporating a variable that quantifies the spatial pattern of glacial retreat increases the statistical explanatory power of regression models of tree richness, irrespective of the particular model approach used or whether considering Europe and

Table 2. Summary of regression models for tree richness in the glaciated parts of Europe and North America, using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age. For each region, the ΔAIC_c compares the best model ($\Delta AIC_c = 0$) with the best models generated under each of the other three modelling frameworks. Adjusted R^2 of each model is also given.

Model type	Predictors in model							AIC_c	ΔAIC_c	R^2
A) Glaciated Europe										
RWEM1	Rainfall	maxPET$_{Th}$						325.1		0.522
	Rainfall	maxPET$_{Th}$	Age					250.7	21.6	0.713
RWEM2	Rainfall	maxPET$_{Th}$	maxPET$^2_{Th}$	Ln(ER)				261.9		0.707
	Rainfall	maxPET$_{Th}$	maxPET$^2_{Th}$	Ln(ER)	Age			242.4	13.3	0.765
F&C	WD	PET$_{PT}$	PET$^2_{PT}$					266.8		0.691
	WD	PET$_{PT}$	PET$^2_{PT}$	Age				248.2	19.1	0.763
ad hoc	Rainfall	TempRange	PET$_{PT}$					233.8		0.755
	Rainfall	TempRange	PET$_{PT}$	Age				229.1	0	0.784
B) Glaciated North America										
RWEM1	Rainfall	minPET$_{Th}$						2272.6		0.466
	Rainfall	minPET$_{Th}$	Age					2033.1	184.5	0.667
RWEM2	Rainfall	minPET$_{Th}$	Ln(ER)					2266.6		0.469
	Rainfall	minPET$_{Th}$	Ln(ER)	Age				2025.3	176.7	0.672
F&C	WD	PET$_{PT}$	PET$^2_{PT}$					1982.2		0.766
	WD	PET$_{PT}$	PET$^2_{PT}$	Age				1884.8	36.1	0.806
ad hoc	Rainfall	PET$_{PT}$	PET$^2_{PT}$	WD	Ln(ER)	PGS		1924.8		0.784
	Rainfall	PET$_{PT}$	PET$^2_{PT}$	WD	Ln(ER)	PGS	Age	1848.6	0	0.815

Predictors: rainfall=total precipitation in months when mean temperature >0°C; maxPET$_{Th}$=maximum monthly potential evapotranspiration (Thornwaite's formula); minPET$_{Th}$=minimum monthly potential evapotranspiration (Thornwaite's formula); ER=elevation range (O'Brien 1993, 1998, Field et al. 2005); PET$_{PT}$=annual potential evapotranspiration (Presley-Taylor formula); WD=water deficit (Francis and Currie 2003); PGS=potential growing season (O'Brien 1993, 1998); TempRange=annual temperature range (Currie and Paquin 1987, Adams and Woodward 1989); Age=number of years cell exposed after glacial retreat; RWEM1=regional water-energy models (O'Brien 1998, Field et al. 2005); F&C=the water-energy model of Francis and Currie (2003).

North America separately or in concert. These results are similar to those reported by Hawkins and Porter (2003) for northern North American birds and mammals and are consistent with the hypothesis that the length of time an area has been deglaciated has left a detectable legacy on the contemporary richness gradient of trees. Araújo and Pearson (2005), using bioclimatic envelope modeling of European plants, reptiles and amphibians, similarly concluded that current species distributions are not at equilibrium with the contemporary climate, due to lagged recolonization of northern latitudes following Holocene warming. In addition, Svenning and Skov (in press) have shown that the governing climatic conditions of the Last Glacial Maximum strongly control tree richness of species with restricted geographical ranges over the unglaciated European regions, which might be reflecting the historical glacial refugia of these trees.

Although Europe and North America have experienced different glacial histories (Elenga et al. 2000, Prentice et al. 2000, Tarasov et al. 2000, Williams et al. 2000), the effects derived from glacial retreat on contemporary tree richness display a global and consistent historical signal. Given that late-Pleistocene glaciers were restricted to the far northern latitudes and glaciation was not extensive in Asia and the Southern Hemisphere (Hewitt 2000), the historical signal we detect synthesizes the emergence of nearly all of the new colonisable territories after post-Pleistocene global warming and its effects on tree richness. This suggests that historical factors widely shape currently observed diversity patterns, and first approaches to explore their influence may follow a top-down analysis from general signals to more specific and regionally-dependent historical effects.

In all tests of historical vs contemporary influences on diversity gradients, it is difficult to be certain what variables measure, as many elements of climate are collinear. Past and present climatic gradients are especially strongly correlated at large extents, making it difficult to partition their effects on richness patterns (Hawkins et al. 2006, and Fig. 2). Thus, it remains possible that cell age covaries with some unknown element of contemporary climate, and this is what generates the observed relationships, or vice versa. We cannot exclude this possibility, but because we investigated a large number of climate variables, it reduces the probability that we have missed something. Second, we used a range of modelling approaches, and all lead to the same conclusion (although the strength of the historical signal is clearly influenced by the structure of the specific regression model). Finally, the collinearity problem exists for all environmental predictors, present or past, and it has even been argued that it is the correlations with current conditions that are artifactual and historical conditions actually drive tree diversity (McGlone 1996). We are unable to resolve this fundamental issue, but it remains that our historical variable contributes to statistical models of tree richness under almost all approaches, while at the same it is not the best predictor by itself. A reasonable conclusion is that both past and current climates drive the richness pattern, not one or the other in isolation.

It is not surprising that partial coefficients of determination for cell age are stronger in models restricted to glaciated areas of Europe and North America than in models for the entire continents. Glaciation effects would be expected to be weaker when non-glaciated areas are included, as trees were not excluded from southern Europe (Bennett et al. 1991) or even from the non-glaciated parts of extreme northwestern North America (Brubaker et al. 2005). Further, although we can date the exposure of land within glaciated areas using maps of ice coverage, we assigned a single arbitrary age on non-glaciated cells, irrespective of the presence of absence of forest during the glacial maximum. The lack of temporal resolution for cells in these areas is very likely to weaken any models using regression.

The quantitative contribution of cell age varies substantially depending on the climatic modelling approach we use. The strongest apparent relationship of richness and history is found when using O'Brien's water-energy models (RWEM1 and RWEM2) in the glaciated regions, whether regions are modelled combined or separately. In these models, the differences between predicted and residual richness are substantial. For North America, the observed richness for recently exposed cells (<7000 yr BP) averages 7.2 species, whereas the RWEM2 predicts 20.0, suggesting that less than half of the species that should exist in northeastern Canada are actually present. Even using the ad hoc climate model, in which the contribution of age is much less (Table 2B), predicted richness is still 11.2 species. Thus, both models suggest a substantial lag in recolonization in the far northeast. In contrast, observed richness in the youngest European cells (exposed <10 000 yr BP) averages 16 species, whereas the RWEM2 predicts 17.2 species, and the ad hoc model predicts 15.6. That Europe should show weaker effects of glacial retreat than North America is expected (Hawkins and Porter 2003), since the area covered by ice was much smaller in Europe (advancing forest species had less distance to move), and the ice melted earlier (there has been more time for species to reach exposed areas). This is despite the fact that the overall response of trees to glacial history suggests stronger effects in European tree patterns, as previous phylogeographical and paleoecological studies have shown (Elenga et al. 2000, Prentice et al. 2000, Tarasov et al. 2000, Williams et al. 2000).

The analysis raises an obvious paradox. We found a clear effect of time since glaciation on species richness despite the evidence from the pollen record that boreal forests rapidly advanced behind the retreating ice sheets (Strong and Hills 2005), and that postglacial migration of trees northward was completed thousands of years ago (Kullman 2002). Although some of these studies are controversial, and other studies claim that migration lags after ice melting might be involved (Fang and Lechowicz [2006] for the distribution of *Fagus sylvatica* in northern Britain, and Svenning and Skov 2004), it has been suggested that the effects of glacial retreat are not due to delayed recolonization, but to an increased rate of global extinction following ineffective migration (Turner 2004). Provided the larger amplitude of climatic change at higher latitudes, it is likely that ice extension-contraction processes have selectively extirpated species and clades more strongly at higher latitudes, which would explain the largely depressed tree richness observed in these regions.

It is important to bear in mind that our test of “historical” effects is focused on a relatively short time period, and somewhat crudely measures “history” in contrast to contemporary climate. Any patterns we observe have been derived from the most recent historical period of climatic change, and thus do not explicitly include long-term differential rates of diversification and speciation within the Holarctic during the glacial-interglacial cycles. Since colonization may occur relatively rapidly (average rates of spread of 100–1000 m yr^{-1} for trees that have successfully recolonized the far north; McLachlan et al. 2005), the historical signal estimated by cell age is primarily a consequence of the spatial rearrangement of species already existing in the Pleistocene. Other potential effects of history based on speciation and extinction cycles on current tree richness remain unquantified, and might well be hidden in the variance that was not explained by our models, or possibly embedded in the structure of the explained variance (Bennett et al. 1991, Qian and Ricklefs 1999), generating the complex signal we detect. For example, there is evidence that cold climates in northern and central regions and dry conditions in southern peninsulas have strongly shaped the tree species pool in Europe (Bennet et al. 1991, Willis 1996, Svenning 2003, Willis and van Andel 2004), and polar desert conditions near the ice-sheets and in recently deglaciated areas may have contributed to lagged recolonization by trees (migration lags) and delays in ecological communities establishment over newly available territories (Hewitt 1999, Svenning and Skov 2004, 2005). These conditions extended further south in Europe and North America (Hewitt 2000) and may have been crucial for diversity patterns of sessile organisms, likely generating non-linear responses of trees to global warming. Also, cell age implicitly makes the unlikely assumption that recolonizable land and non-glaciated regions (cell age = 20 000 yr) are physically homogeneous, and ignores geographical barriers to migration and different dispersal capabilities of species. These potential effects cannot be directly evaluated with our data, which makes our analysis conservative with respect to modern climate. However, given that the older the effects are the more difficult they are to detect, and that cell age directly tracks the spatio-temporal pattern of ice retreat following the most recent glacial episode, it seems reasonable to consider cell age as an indicator that primarily describes the effects associated with glacial retreat, even though it might also include additional correlated effects. Consideration of different historical influences on diversity patterns of species represents an important line for future research.

In sum, following many authors we find that the main driver of the broad scale variation of tree richness in Europe and North America is the current climate, but unlike previous studies, we also find that the shrinking of ice sheets at the end of the Pleistocene has apparently left a detectable signal in the tree richness gradient, at least in the northern half of the Holarctic. Thus, a full understanding of contemporary species richness gradients requires an understanding of spatial patterns of climate change as well as static climatic patterns estimated at any point in time. Given the rapid rate as which climates are currently changing, this message seems particularly timely.

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Ecography

E4873
Montoya, D., Rodríguez, M. A., Zavala, M. A. and Hawkins, B. A. 2007. Contemporary richness of holarctic trees and the historical pattern of glacial retreat. – Ecography 30: 173–182.

Appendix 1. Source references to build tree richness maps for North America (1) and Europe (2).

1. North America

The database comprises 676 North American tree species (defined as any woody plant growing to ≥4 m anywhere in its range). Range maps were available for every species and were taken primarily from Little (1971), supplemented with Elias (1980) and Hosie (1990).

North American refrences:

Elias, T. S. 1980. The complete trees of North America. – Reinhold, New York.
Little, E. J. Jr 1971. Atlas of United States trees Vols 1–5. – US Govt. Printing Office, Washington, DC.
Hosie, R. C. 1990. Native trees of Canada. – Fitzhenry and Whiteside, Markham, Notario.

2. Europe

Plant families and their 187 tree species native to western Europe were included. For each species, the "source type" code indicates whether its range map was established by digitizing published maps ("m"), through written descriptions of its distribution ("d"), or by combining both methods ("m/d") when published maps only covered its range partially (see references included in the last column and below the Table). Complete and partial range maps were used for 158 (84.5%), and 9 (5%) species, respectively; and written descriptions of range distributions for 20 (11%) species. The latter were converted into maps following a three step process. First, we checked the digital version of Flora Europaea (ref. 28) to know the countries in which each species was present. Second, we searched national and regional floras, as well as the electronic database EUNIS (ref. 8) for written descriptions of the presence of each species in specific areas and localities. And third, we reconstructed the range distribution map of the species by taking into account these informations. For one species (*Arbutus andrachne*) it was necessary to take into account its habitats combined with the CORINE Land Cover database (ref. 9) to attain a finer picture of its distribution.

Family	Genus	Species	Source type	References
Aceraceae	*Acer*	*campestre*	m	10
Aceraceae	*Acer*	*granatense*	m	10
Aceraceae	*Acer*	*heldreichii*	m	11, 28
Aceraceae	*Acer*	*hyrcanum*	m	11, 28
Aceraceae	*Acer*	*lobelii*	m	10
Aceraceae	*Acer*	*monspessulanum*	m	10
Aceraceae	*Acer*	*obtusatum*	m	10
Aceraceae	*Acer*	*opalus*	m	10
Aceraceae	*Acer*	*platanoides*	m	10
Aceraceae	*Acer*	*pseudoplatanus*	m	10
Aceraceae	*Acer*	*tataricum*	m/d	11, 13, 28
Anacardiaceae	*Pistacia*	*atlantica*	m	11, 28
Anacardiaceae	*Pistacia*	*lentiscus*	m	10
Anacardiaceae	*Pistacia*	*terebinthus*	m	10
Anacardiaceae	*Rhus*	*coriaria*	m	10
Apocynaceae	*Nerium*	*oleander*	d	5, 21, 22, 23, 24, 26, 28
Aquifoliaceae	*Ilex*	*aquifolium*	m	10
Betulaceae	*Alnus*	*cordata*	m	10, 17
Betulaceae	*Alnus*	*glutinosa*	m	10, 17
Betulaceae	*Alnus*	*incana*	m	10, 17
Betulaceae	*Betula*	*pendula*	m	10, 17
Betulaceae	*Betula*	*pubescens*	m	10, 17

Buxaceae	*Buxus*	*balearica*	m	4, 28
Buxaceae	*Buxus*	*sempervirens*	m	10
Caprifoliaceae	*Sambucus*	*nigra*	m	10
Celastraceae	*Euonymus*	*europaeus*	m	10
Celastraceae	*Euonymus*	*latifolius*	m	10
Cornaceae	*Cornus*	*mas*	m	10
Corylaceae	*Carpinus*	*betulus*	m	10, 17
Corylaceae	*Carpinus*	*orientalis*	m	17
Corylaceae	*Corylus*	*colurna*	m	10, 17
Corylaceae	*Corylus*	*maxima*	m	10, 17
Corylaceae	*Ostrya*	*carpinifolia*	m	10, 17
Cupressaceae	*Cupressus*	*sempervirens*	m	10, 17
Cupressaceae	*Juniperus*	*communis*	m	10, 17
Cupressaceae	*Juniperus*	*drupacea*	m	18
Cupressaceae	*Juniperus*	*excelsa*	m	10, 17
Cupressaceae	*Juniperus*	*foetidissima*	m	10, 17
Cupressaceae	*Juniperus*	*navicularis*	d	6, 28
Cupressaceae	*Juniperus*	*oxycedrus*	m	10, 17
Cupressaceae	*Juniperus*	*phoenicea*	m	10, 17
Cupressaceae	*Juniperus*	*thurifera*	m	10, 17
Cupressaceae	*Tetraclinis*	*articulata*	m	10, 17
Elaeagnaceae	*Hippophae*	*rhamnoides*	m	10
Ericaceae	*Arbutus*	*andrachne*	d	8, 9, 12, 21, 28
Ericaceae	*Arbutus*	*unedo*	m	10
Ericaceae	*Erica*	*arborea*	m	10
Ericaceae	*Vaccinium*	*arctostaphylos*	d	8, 28
Fagaceae	*Castanea*	*sativa*	m	10, 17
Fagaceae	*Fagus*	*sylvatica* + subsp. *orientalis*	m	10, 17
Fagaceae	*Quercus*	*canariensis*	m	10, 17
Fagaceae	*Quercus*	*cerris*	m	10, 17
Fagaceae	*Quercus*	*coccifera*	m	10, 17
Fagaceae	*Quercus*	*congesta*	m	10, 17
Fagaceae	*Quercus*	*dalechampii*	m	10
Fagaceae	*Quercus*	*faginea*	m	10, 17
Fagaceae	*Quercus*	*frainetto*	m	10, 17
Fagaceae	*Quercus*	*hartwissiana*	m	17
Fagaceae	*Quercus*	*ilex*	m	10, 17
Fagaceae	*Quercus*	*macrolepis*	m	10, 17
Fagaceae	*Quercus*	*mas*	m	19
Fagaceae	*Quercus*	*pedunculiflora*	m	10, 17
Fagaceae	*Quercus*	*petraea*	m	10, 17
Fagaceae	*Quercus*	*polycarpa*	m	10
Fagaceae	*Quercus*	*pubescens*	m	10, 17
Fagaceae	*Quercus*	*pyrenaica*	m	10, 17
Fagaceae	*Quercus*	*robur*	m	10, 17
Fagaceae	*Quercus*	*suber*	m	10, 17
Fagaceae	*Quercus*	*trojana*	m	10, 17
Hippocastanaceae	*Aesculus*	*hippocastanum*	m	10
Juglandaceae	*Juglans*	*regia*	m	10, 17
Lauraceae	*Laurus*	*nobilis*	m	10, 17
Leguminosae	*Ceratonia*	*siliqua*	m	10
Leguminosae	*Cercis*	*siliquastrum*	m	10
Leguminosae	*Laburnum*	*alpinum*	m	10
Leguminosae	*Laburnum*	*anagyroides*	m	10
Moraceae	*Ficus*	*carica*	m	10, 17
Oleaceae	*Fraxinus*	*angustifolia*	m	10
Oleaceae	*Fraxinus*	*excelsior*	m	10
Oleaceae	*Fraxinus*	*ornus*	m	10
Oleaceae	*Fraxinus*	*pallisiae*	m	11, 28
Oleaceae	*Olea*	*europaea*	m	10
Oleaceae	*Phillyrea*	*latifolia*	m	10
Oleaceae	*Syringa*	*josikaea*	d	2, 28
Oleaceae	*Syringa*	*vulgaris*	m	10

Pinaceae	*Abies*	*alba*	m	10, 17
Pinaceae	*Abies*	*cephalonica*	m	10, 17
Pinaceae	*Abies*	*pinsapo*	m	10, 17
Pinaceae	*Abies*	*sibirica*	m	10, 17
Pinaceae	*Larix*	*decidua*	m	10, 17
Pinaceae	*Larix*	*sibirica*	m	10, 17
Pinaceae	*Picea*	*abies*	m	10, 17
Pinaceae	*Picea*	*omorika*	m	10, 17
Pinaceae	*Pinus*	*cembra*	m	10, 17
Pinaceae	*Pinus*	*halepensis*	m	10, 17
Pinaceae	*Pinus*	*heldreichii* + var. *leucodermis*	m	10, 17
Pinaceae	*Pinus*	*nigra*	m	10, 17
Pinaceae	*Pinus*	*peuce*	m	10, 17
Pinaceae	*Pinus*	*pinaster*	m	10, 17
Pinaceae	*Pinus*	*pinea*	m	10, 17
Pinaceae	*Pinus*	*sylvestris*	m	10, 17
Pinaceae	*Pinus*	*uncinata*	m	10, 17
Platanaceae	*Platanus*	*orientalis*	m	20
Rhamnaceae	*Frangula*	*alnus*	m	10
Rhamnaceae	*Rhamnus*	*catharticus*	m	10
Rosaceae	*Cotoneaster*	*granatensis*	d	6, 28
Rosaceae	*Crataegus*	*calycina*	m	16, 28
Rosaceae	*Crataegus*	*laciniata*	d	1, 6, 8, 12, 27, 28
Rosaceae	*Crataegus*	*monogyna*	m	10
Rosaceae	*Crataegus*	*nigra*	d	1, 3, 7, 14, 25, 26, 28
Rosaceae	*Crataegus*	*pentagyna*	d	1, 2, 7, 14, 26, 28
Rosaceae	*Malus*	*dasyphylla*	d	1, 2, 7, 12, 25, 26, 27, 28
Rosaceae	*Malus*	*florentina*	m/d	13, 22, 28
Rosaceae	*Malus*	*sylvestris*	m	10
Rosaceae	*Mespilus*	*germanica*	m	10
Rosaceae	*Prunus*	*avium*	m	10
Rosaceae	*Prunus*	*brigantina*	m/d	5, 22, 28
Rosaceae	*Prunus*	*cerasifera*	m	10
Rosaceae	*Prunus*	*cocomilia*	m/d	8, 22, 28
Rosaceae	*Prunus*	*domestica*	m	11, 28
Rosaceae	*Prunus*	*laurocerasus*	m/d	11, 13, 28
Rosaceae	*Prunus*	*lusitanica*	m	10
Rosaceae	*Prunus*	*mahaleb*	m	10
Rosaceae	*Prunus*	*padus*	m	10
Rosaceae	*Prunus*	*webbii*	m	22, 28
Rosaceae	*Pyrus*	*amygdaliformis*	m	10
Rosaceae	*Pyrus*	*austriaca*	d	14, 15, 28
Rosaceae	*Pyrus*	*bourgaeana*	m/d	6, 11, 28
Rosaceae	*Pyrus*	*cordata*	m	10
Rosaceae	*Pyrus*	*elaeagrifolia*	m	11, 28
Rosaceae	*Pyrus*	*magyarica*	d	26, 28
Rosaceae	*Pyrus*	*nivalis*	m/d	1, 3, 13, 15, 22, 23, 25, 26, 28
Rosaceae	*Pyrus*	*pyraster*	m	13, 28
Rosaceae	*Sorbus*	*aria*	m	10
Rosaceae	*Sorbus*	*aucuparia*	m	10
Rosaceae	*Sorbus*	*austriaca*	d	13, 28
Rosaceae	*Sorbus*	*dacica*	d	2, 28
Rosaceae	*Sorbus*	*domestica*	m	10
Rosaceae	*Sorbus*	*graeca*	d	1, 2, 3, 12, 13, 15, 25, 27, 28
Rosaceae	*Sorbus*	*hybrida*	m	16, 28
Rosaceae	*Sorbus*	*intermedia*	m	10
Rosaceae	*Sorbus*	*latifolia*	d	1, 6, 13, 23, 28
Rosaceae	*Sorbus*	*meinichii*	m	16, 28
Rosaceae	*Sorbus*	*mougeotii*	m/d	11, 13, 28
Rosaceae	*Sorbus*	*torminalis*	m	10
Rosaceae	*Sorbus*	*umbellata*	m	11, 28
Salicaceae	*Populus*	*alba*	m	10, 17
Salicaceae	*Populus*	*canescens*	m	10, 17

Salicaceae	*Populus*	*nigra*	m	10, 17
Salicaceae	*Populus*	*tremula*	m	10, 17
Salicaceae	*Salix*	*acutifolia*	m	10, 17
Salicaceae	*Salix*	*aegyptiaca*	m	10, 17
Salicaceae	*Salix*	*alba*	m	10, 17
Salicaceae	*Salix*	*appendiculata*	m	10, 17
Salicaceae	*Salix*	*atrocinerea*	m	10, 17
Salicaceae	*Salix*	*borealis*	m	10
Salicaceae	*Salix*	*caprea*	m	10, 17
Salicaceae	*Salix*	*daphnoides*	m	10, 17
Salicaceae	*Salix*	*fragilis*	m	10, 17
Salicaceae	*Salix*	*pedicellata*	m	10, 17
Salicaceae	*Salix*	*pentandra*	m	10, 17
Salicaceae	*Salix*	*pyrolifolia*	m	10, 17
Salicaceae	*Salix*	*salviifolia*	m	10, 17
Salicaceae	*Salix*	*triandra*	m	10, 17
Salicaceae	*Salix*	*viminalis*	m	17
Salicaceae	*Salix*	*xerophila*	m	10, 17
Styracaceae	*Styrax*	*officinalis*	m	11, 28
Tamaricaceae	*Tamarix*	*africana*	m	10
Tamaricaceae	*Tamarix*	*boveana*	m	10
Tamaricaceae	*Tamarix*	*canariensis*	m	10
Tamaricaceae	*Tamarix*	*dalmatica*	m/d	8, 22, 28
Tamaricaceae	*Tamarix*	*gallica*	m	10
Tamaricaceae	*Tamarix*	*hampeana*	d	8, 12, 28
Tamaricaceae	*Tamarix*	*parviflora*	d	12, 28
Tamaricaceae	*Tamarix*	*smyrnensis*	d	2, 8, 12, 28
Tamaricaceae	*Tamarix*	*tetrandra*	d	8, 12, 28
Taxaceae	*Taxus*	*baccata*	m	10, 17
Tiliaceae	*Tilia*	*cordata*	m	10
Tiliaceae	*Tilia*	*platyphyllos*	m	10
Tiliaceae	*Tilia*	*rubra*	m	11, 28
Tiliaceae	*Tilia*	*tomentosa*	m	11, 28
Ulmaceae	*Celtis*	*australis*	m	10, 17
Ulmaceae	*Celtis*	*caucasica*	m	10, 17
Ulmaceae	*Celtis*	*tournefortii*	m	10, 17
Ulmaceae	*Ulmus*	*glabra*	m	10, 17
Ulmaceae	*Ulmus*	*laevis*	m	10, 17
Ulmaceae	*Ulmus*	*minor* + subsp. *canescens* + *procera*	m	10, 17

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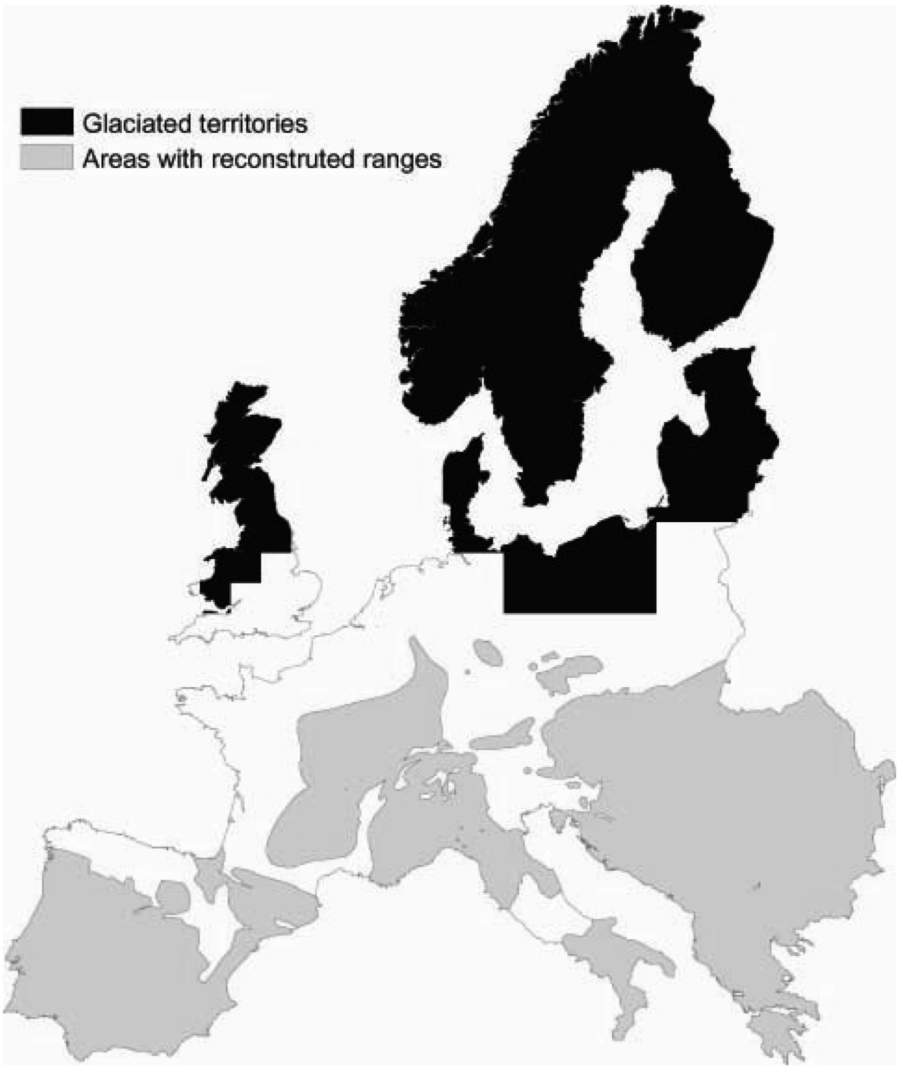

Fig. 1. European territories covered by ice during the last Pleistocene glaciation and areas including tree species for which only partial range maps (*Acer tataricum, Malus florentina, Prunus brigantina, P. cocomilia, P. laurocerasus, Pyrus bourgaeana, P. nivalis, Sorbus mougeotii, Tamarix dalmatica*), or no maps were found (*Arbutus andrachne, Cotoneaster granatensis, Crataegus laciniata, C. nigra, C. pentagyna, Juniperus navicularis, Malus dasyphylla, Nerium oleander, Pyrus austriaca, P. magyarica, Sorbus austriaca, S. dacica, S. graeca, S. latifolia, Syringa josikaea, Tamarix hampeana, T. parviflora, T. smyrnensis, T. tetrandra, Vaccinium arctostaphylos*). The range maps of these species were drawn by taking into account published descriptions of their areas of distribution. This was not necessary for any of the tree species present in the glaciated territories, as for all of them a complete range map was found in the literature.

Appendix 2. Coefficients of regression models.

Table 1. Summary of regression models for tree richness using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age.

Model type	Predictors in model					
A) Glaciated regions						
RWEM1	0.724*Rainfall	–0.740*minPET$_{\mathrm{Th}}$	0.486*minPET$_{\mathrm{Th}}^{2}$			
	0.548*Rainfall	–0.590*minPET$_{\mathrm{Th}}$	0.295*minPET$_{\mathrm{Th}}^{2}$	0.445*Age		
RWEM2	0.731*Rainfall	–0.740*minPET$_{\mathrm{Th}}$	0.482*minPET$^{2}_{\mathrm{Th}}$	0.064*Ln(ER)		
	0.551*Rainfall	–0.590*minPET$_{\mathrm{Th}}$	0.295*minPET$^{2}_{\mathrm{Th}}$	0.024*Ln(ER)	0.443*Age	
F&C	–0.530*WD	0.518*PET$_{\mathrm{PT}}$	0.600*PET$^{2}_{\mathrm{PT}}$			
	–0.480*WD	0.386*PET$_{\mathrm{PT}}$	0.578*PET$^{2}_{\mathrm{PT}}$	0.278*Age		
ad hoc	0.229*Rainfall	0.443*PET$_{\mathrm{PT}}$	0.133*PET$^{2}_{\mathrm{PT}}$	0.089*Ln(ER)	0.207*PGS	
	0.238*Rainfall	0.422*PET$_{\mathrm{PT}}$	0.110*PET$^{2}_{\mathrm{PT}}$	0.039*Ln(ER)	0.067*PGS	0.238*Age
B) Entire regions						
RWEM1	0.791*Rainfall	0.204*maxPET$_{\mathrm{Th}}$	–0.130*maxPET$^{2}_{\mathrm{Th}}$			
	0.710*Rainfall	0.234*maxPET$_{\mathrm{Th}}$	–0.180*maxPET$^{2}_{\mathrm{Th}}$	0.207*Age		
RWEM2	0.820*Rainfall	0.293*maxPET$_{\mathrm{Th}}$	–0.210*maxPET$^{2}_{\mathrm{Th}}$	0.122*Ln(ER)		
	0.736*Rainfall	0.289*maxPET$_{\mathrm{Th}}$	–0.230*maxPET$^{2}_{\mathrm{Th}}$	0.079*Ln(ER)	0.188*Age	
F&C	–0.730*WD	1.510*PET$_{\mathrm{PT}}$	–0.350*PET$^{2}_{\mathrm{PT}}$			
	–0.730*WD	1.340*PET$_{\mathrm{PT}}$	–0.250*PET$^{2}_{\mathrm{PT}}$	0.145*Age		
ad hoc	0.650*Rainfall	0.781*PET$_{\mathrm{PT}}$	–0.450*PET$^{2}_{\mathrm{PT}}$			
	0.612*Rainfall	0.715*PET$_{\mathrm{PT}}$	–0.420*PET$^{2}_{\mathrm{PT}}$	0.060*Age		

Table 2. Summary of regression models for tree richness in the glaciated parts of Europe and North America, using four modelling frameworks. The best model under each framework not including cell age is given, coupled with the equivalent model after adding cell age.

Model type	Predictors in model						
A) Glaciated Europe							
RWEM1	–0.350*Rainfall	–0.950*maxPET$_{\mathrm{Th}}$					
	–0.400*Rainfall	–0.650*maxPET$_{\mathrm{Th}}$	0.553*Age				
RWEM2	–0.440*Rainfall	–4.200*maxPET$_{\mathrm{Th}}$	3.200*maxPET$^{2}_{\mathrm{Th}}$		–0.470*Ln(ER)		
	–0.400*Rainfall	–2.300*maxPET$_{\mathrm{Th}}$	1.500*maxPET$^{2}_{\mathrm{Th}}$		–0.290*Ln(ER)	0.368*Age	
F&C	0.086*WD	0.036*PET$_{\mathrm{PT}}$	0.757*PET$^{2}_{\mathrm{PT}}$				
	0.022*WD	0.284*PET$_{\mathrm{PT}}$	0.296*PET$^{2}_{\mathrm{PT}}$	0.369*Age			
ad hoc	–0.200*Rainfall	–0.450*TempRange	0.755*PET$_{\mathrm{PT}}$				
	–0.180*Rainfall	–0.300*TempRange	0.615*PET$_{\mathrm{PT}}$	0.273*Age			
B) Glaciated North America							
RWEM1	0.703*Rainfall	–0.130*minPET$_{\mathrm{Th}}$					
	0.534*Rainfall	–0.120*minPET$_{\mathrm{Th}}$	0.478*Age				
RWEM2	0.706*Rainfall	–0.130*minPET$_{\mathrm{Th}}$	0.056*Ln(ER)				
	0.520*Rainfall	–0.120*minPET$_{\mathrm{Th}}$	–0.080*Ln(ER)	0.501*Age			
F&C	–0.520*WD	0.625*PET$_{\mathrm{PT}}$	0.492*PET$^{2}_{\mathrm{PT}}$				
	–0.480*WD	0.433*PET$_{\mathrm{PT}}$	0.524*PET$^{2}_{\mathrm{PT}}$	0.246*Age			
ad hoc	0.093*Rainfall	0.386*PET$_{\mathrm{PT}}$	0.551*PET$^{2}_{\mathrm{PT}}$	–0.430*WD	0.095*Ln(ER)	0.109*PGS	
	0.132*Rainfall	0.356PET$_{\mathrm{PT}}$	0.480*PET$^{2}_{\mathrm{PT}}$	–0.410*WD	0.021*Ln(ER)	0.003*PGS	0.243*Age

Table 1, 2. Legend and model coefficients.
Predictors: rainfall = total precipitation in months when mean temperature >0°C; maxPET$_{\mathrm{Th}}$ = maximum monthly potential evapotranspiration (Thornwaite's formula); minPET$_{\mathrm{Th}}$ = minimum monthly potential evapotranspiration (Thornwaite's formula); ER = Elevation Range (O'Brien 1993, 1998; Field et al. 2005); PET$_{\mathrm{PT}}$ = annual potential evapotranspiration (Presley-Taylor formula); WD = Water deficit (Francis and Currie 2003); PGS = Potential growing season (O'Brien 1993, 1998); TempRange = Annual Temperature Range (Currie and Paquin 1987, Adams and Woodward 1989); Age = number of years cell exposed after glacial retreat; RWEM1 = Regional Water-Energy Models (O'Brien 1998, Field et al. 2005); F&C = The water-energy model of Francis and Currie (Francis and Currie 2003).

Essentially, the relationship between tree richness and water and energy is positive across Europe and North America (Table 1B), with higher energy-water inputs increasing richness levels: highest richness is found in hot and wet areas. Water deficit is negatively related to tree richness, indicating that water stress constraints the number of species. Elevation range, a measure of the mesoscale vertical climatic variation, is positively associated to richness, given that highly heterogeneous regions encompass more species. For glaciated regions together and glaciated North America (Tables 1A, 2B), these relationships hold except for minPET$_{Th}$, which has negative coefficients. We believe this is because minPET$_{Th}$ represents the energy of the coldest month and above a certain line of latitude its value drops to zero. This is the likely reason why RWEMs generally perform worst in our study areas. PGS reflects favourable conditions for trees to grow and reproduce and is positively associated to tree richness in the models. Glaciated Europe (Table 2A) shows some intriguing coefficients which differ from the general pattern. Rainfall is negatively associated with richness. That tree richness at higher latitudes is not restricted by water but energy is commonly argued, but North America indeed has positive rainfall coefficients. One possible explanation is that different climatic patterns between the continents result in trees growing in glaciated Europe more stressed by excessive water and flooded soils. This is supported by the WD coefficients: richness increases with WD, in contrast to glaciated North America. Also, historical factors might be driving richness in glaciated Europe more strongly than in glaciated North America, as paleoecological studies have shown. MaxPET$_{Th}$ also has negative coefficients. We believe maxPET$_{Th}$ is not a good energy measure (it measures energy in the warmest month); in fact, a positive relationship between energy and tree richness is shown in F&C model, which uses PET$_{PT}$ instead of maxPET$_{Th}$, and the F&C model globally performs better than RWEMs in temperate regions. Elevation range is negatively associated with tree richness. In northern regions, high altitudes represent cold conditions unfavourable to tree's growth, and elevation range consequently relates negatively to richness. Although ln(ER) has positive coefficients in glaciated North America (Table 2B) and across both glaciated regions (Table 1A), its coefficients are very low, even shifting to negative values (RWEM2 + Age, Table 2B). Range in elevation may have more influence on tree richness at more local scales. Age is positively associated with tree richness in every model and region analyzed (Tables 1, 2), indicating that longer times of land availability for trees (free of ice) are associated with higher richness.

Appendix 3. Tree richness distribution for Europe and North America at 110 km^2 grain. Scale is provided.