Plio-Pleistocene climate change and geographic heterogeneity in plant diversity–environment relationships

Jens-Christian Svenning, Signe Normand and Flemming Skov

Plio-Pleistocene climate change may have induced geographic heterogeneity in plant species richness–environment relationships in Europe due to greater in situ species survival and speciation rates in southern Europe. We formulate distinct hypotheses on how Plio-Pleistocene climate change may have affected richness–topographic heterogeneity and richness–water-energy availability relationships, causing steeper relationships in southern Europe. We investigated these hypotheses using data from Atlas Florae Europaeae on the distribution of 3069 species and geographically weighted regression (GWR). Our analyses showed that plant species richness generally increased with topographic heterogeneity (ln-transformed altitudinal range) and actual evapotranspiration (AET). We also found evidence for strong geographic heterogeneity in the species richness–environment relationship, with a greater increase in species richness with increasing topographic heterogeneity in southern Europe (mean standardized local slope 0.610 ± 0.245 SD in southern Europe, but only 0.270 ± 0.175 SD in northern Europe). However, the local AET slopes were, at most, weakly different between the two regions, and their pattern did not conform to predictions, as there was a band of high local slopes across southern-central northern Europe. This band broadly matches the transition between the temperate and boreal zones and may simply reflect the fact that few species tolerate the boreal climate. We discuss the potential explanations for the contrasting findings for the two richness–environment relationships. In conclusion, we find support for the idea that Plio-Pleistocene climate change may sometimes affect current species richness–environment relationships via its effects on regional species pools. However, further studies integrating information on species ages and clade differentiation rates will be needed to substantiate this interpretation. On a general level, our results indicate that although strong richness–environment relationships are often found in macroecological studies, these can be contingent upon the historical constraints on the species pool.

Understanding what determines species diversity is a key challenge for 21st century science (Pennisi 2005). A strong tradition attempts to understand large-scale variation in species richness as a function of current environment and its capacity for species coexistence, its control on species distributions, or its effects on speciation rates (Currie et al. 2004). At large spatial scales, current climate has been singled out by many studies as the primary determinant of species richness (Hawkins et al. 2003), with topographic heterogeneity playing an important supplementary role (Simpson 1964, Kerr and Packer 1997, O’Brien et al. 2000). However, with the increasing availability of phylogenetic and paleoclimatic data, there is increasing focus on the impact of past evolutionary and geologic history on species richness (Wiens and Donoghue 2004, Hawkins et al. 2006, Araújo et al. 2008). This issue has received considerable attention in Europe, which was particularly strongly affected by the Plio-Pleistocene ice ages. Notably, the European flora suffered massive diversity losses from these climate changes (Mai 1995) through strong climatic sorting, where warmth- and moisture-demanding taxa were lost (Svenning 2003). These losses appear to have left strong legacies in the current flora. The overall diversity, at least in terms of trees, is lower than in climatically comparable areas of East Asia and North America (Latham and Ricklefs 1993, Ricklefs and Latham 1999; but cf. Francis and Currie 1998). Furthermore, there are strong indications that many species have distributions that are not in equilibrium with the current climate, in large part due to limited postglacial migration (Svenning and Skov 2004, 2007a, Svenning et al. 2008a), with potentially strong contingent effects on geographic diversity patterns (Svenning and Skov 2005). Notably, richness of range-restricted tree species is concentrated in areas with the warmest climate during the Last Glacial Maximum (LGM) (Svenning and Skov 2007b), and closeness to the general source refuge area for postglacial recolonization is a strong predictor of tree species richness in central and northern Europe (Svenning and Skov 2007a).

Although explanations of species richness primarily evoke the current environment of the area, historical effects
are often raised as alternative possibilities. However, there is increasing realization that the two may interact (Zobel 1997, Wiens and Donoghue 2004, Pärtel et al. 2007). Reflecting the latter idea, we propose two derived hypotheses for how richness–environmental relationships in Europe should vary according to the Plio-Pleistocene climate change impacts on the regional species pools (cf. Pärtel et al. 2007).

The first hypothesis considers the relationship of species richness to topography. Topographic heterogeneity may increase species richness via several mechanisms: 1) increased possibilities for species to coexist due to greater habitat diversity and effective surface area (Simpson 1964, Kerr and Packer 1997, O’Brien et al. 2000, Turner 2004, Turner and Hawkins 2004); 2) increased speciation due to greater historical possibilities for allopatric and parapatric speciation (Simpson 1964, Jetz and Rahbek 2002, Turner 2004); and 3) decreased extinction due to greater possibilities for tracking climatic changes with small-scale altitudinal range shifts (Bennett et al. 1991, Turner 2004). While the first mechanism is ahistorical and will act in all regions, the second and third mechanisms will be strongest in the regions experiencing the smallest amplitude of Plio-Pleistocene climate oscillations (Turner 2004; cf. Dynesius and Jansson 2000, Jansson and Dynesius 2002). During glacial maxima like the Last Glacial Maximum (LGM) 21 000 yr ago, the vast majority of the European plant species only survived in southern and, to some extent, southern central Europe. Notably, much of northern Europe was completely glaciated, allowing little or no in situ survival. Subsequently, a proportion of the flora recolonized northern Europe during the late- and postglacial periods, but there is evidence that many species experienced strong dispersal limitation and are still more or less restricted to the southern refuge region (Svenning and Skov 2004, 2007a, b). As a consequence, effects of topographic heterogeneity on speciation and extinction rates will only be of major relevance in southern Europe with its high degree of in situ survival (cf. Paun et al. 2005 for an example), and only its effects on habitat diversity will be relevant in northern Europe, where the flora predominantly reflect postglacial recolonization. Therefore, we expect species richness to increase most strongly with topographic heterogeneity in southern Europe.

The second hypothesis concerns the relationship of species richness to climate. Current climate may drive species richness patterns in two ways (Currie et al. 2004): 1) the climate sets a fixed upper limit for how many species can coexist in a given area and 2) alternatively, the climate affects richness via its effects on the size of the available species pool (notably, the speciation rate) and/or its effect on the distribution of individual species (see also Pärtel et al. 2007). By considering the climatic and biogeographic history of Europe during the last few million years, it is possible to formulate more specific predictions regarding the historical impacts on the species richness–climate relationship. Before the shift to a summer-dry climate in the Mediterranean and the onset of the strong northern hemisphere glaciations 2–4 million yr ago (Suc 1984, Ruddiman 2001), Europe was characterized by a warmer and wetter climate (Willis and McElwain 2002, Salzmann et al. 2008). Hence, the pre-ice age species pool in Europe would have been strongly biased towards species adapted to mild and moist conditions. As noted above, the subsequent climatic changes caused a strong ecological sorting of the species pool, with extinctions concentrated among the warmth- and moisture-demanding species (Svenning 2003). Within Europe, such losses were much stronger in the north than in the south, where many Tertiary relicts can still be found (Mai 1995, Svenning and Skov 2007b). Due to the greater survival of warmth- and moisture loving species in this region and the at least partial failure of many of these species to expand northwards by tracking the late- and postglacial climate changes, we expect to find a greater proportion of warmth- and moisture-loving species in the regional species pool and, consequently, steeper increases in richness with increasing water-energy availability in southern Europe. A caveat to these predictions is that at the same time, clades able to adapt to cold and dry climates would also have experienced some diversification (Paun et al. 2005), but also primarily in southern Europe (cf. Dynesius and Jansson 2000, Jansson and Dynesius 2002). Such diversification would counteract the tendency for a greater proportion of warmth- and moisture-loving species in the southern European species pool and weaken or remove the expected geographic heterogeneity in the richness–climate relationship. However, it would still contribute to geographic heterogeneity in the richness–topography relationship.

Summarizing the above considerations, we expect that Plio-Pleistocene climate change may have induced geographic heterogeneity in the plant species richness–topography and –climate relationships in Europe, causing steeper relationships in the region least impacted by the Pleistocene ice ages (including neighboring areas), i.e. south of 50° latitude (hereafter, southern Europe). However, although all related to Plio-Pleistocene climate change, the mechanisms invoked are not identical for the two relationships.

Materials and methods

Species richness

Species data came from Atlas Florae Europaeae (AFE; Vol. 1–13), which covers ca 20% of the European flora and maps species distributions on an equal-area grid with cells of ca 50 × 50 km (AFE cells; 1972–1994) and <www.fmnh.helsinki.fi/english/botany/afe/>). The study area (n = 2312 AFE cells) included most of Europe within 34°N–71°N and 11°W–32°E, excluding the former Soviet Union, where the sampling effort has been relatively low and variable. Species richness across Europe was computed from the distribution of 3069 plant species as the total number of species per AFE cell. Only species-level information was used, i.e. subspecies and varieties were merged.

Predictors of species richness

The interaction between water and energy is often seen as a key driver of large-scale gradients in plant species richness (Currie and Paquin 1987, O’Brien 1998, O’Brien et al. 2000, Hawkins et al. 2003). Therefore, we represented current
climate by two predictor variables of clear biological importance for plants (Stephenson 1998): actual evapotranspiration (AET, mm yr$^{-1}$), which indicates the amount of simultaneously available, biologically useful energy and water at a site, and water deficits (WD, mm yr$^{-1}$), which is computed as the difference between potential evapotranspiration (PET, mm yr$^{-1}$) and AET and estimates the degree of drought at a site. In addition, we considered including several additional climatic variables in the analyses: PET and annual mean temperature (AMT, °C) to represent energy and heat availability without mixing in water availability, growing-degree-days (GDD; 5° base), and absolute minimum temperature (TMIN). However, only AMT was included as an additional predictor, as PET was highly correlated with WD (r = 0.873), while GDD and TMIN both had very high correlations with AMT (r = 0.945 and 0.932, respectively). The correlation between AET and WD was just r = 0.264, while the correlations between AMT and AET or WD were r = 0.690 and 0.695, respectively. Topographic heterogeneity was represented by ln-transformed altitudinal range (lnAR), following O’Brien et al. (2000). The correlations of lnAR with the three climatic predictor variables were low (r = 0.091–0.298). Data for AET and PET, came from the 30’-resolution United Nations Environment Programme (UNEP, 2018) data set (<www.grid.unep.ch>), which covers the approximate time period of 1920–1980 (Ahn and Tateishi 1994a, b). Data for AMT, GDD, and TMIN were obtained from the 10’-resolution climate grid CRU CL 2.0 (New et al. 2002; <www.cru.uea.ac.uk/cru/data/hrg.htm>), while the altitude data came from the 30’-resolution Worldclim grid (Hijmans et al. 2005; <www.worldclim.org/>). The climatic and topographic variables were recomputed as means (or range, in the case of topography) for each AFE cell.

### Statistical analyses

We first used ordinary-least-squares (OLS) linear regression modeling to assess the global richness–environment relationships and select the best set of climatic and topographic predictor variables (AET, AMT, WD, lnAR). The latter was done using information-theoretic model selection based on the Akaike information criterion (using its small-sample unbiased version, AIC$_c$; Burnham and Anderson 2002), as well as by considering the explanatory power of the predictor variables: the best model according to AIC$_c$ was pruned of predictor variables that could be removed without reducing R$_{adj}^2$ by more than 1%. As species richness represents counts of species, richness was always square-root transformed to ensure variance homogeneity. Inspection of residual plots indicated approximate linearity of the relationship between richness and all four predictor variables, at least after accounting for the other predictors and spatial filtering (see below). Hence, the four predictors were modeled primarily as linear terms. However, to allow for the possibility of minor nonlinearity in the relationships, we also fitted models by expanding the best model with one or more quadratic terms of its environmental predictor variables, and included these in the model selection. We used eigenvector-based spatial filtering (Diniz-Filho and Bini 2005, Griffith and Peres-Neto 2006) in the OLS modeling to ensure that the model selection was not biased by spatial autocorrelation (Diniz-Filho et al. 2008). Preliminary analyses indicated spatial autocorrelation in the residuals of non-filtered models. Spatial filters were generated as the eigenvectors of principal coordinate analysis of a pairwise matrix of geographic distances between all AFE cells, following the approach of Diniz-Filho and Bini (2005), originally developed by Borcard and Legendre (2002). Geographic distances were truncated at 1000 km (Diniz-Filho and Bini 2005). The spatial filters were added to the OLS regression models, controlling for spatial autocorrelation, and thereby allowing us to get unbiased estimates of regression coefficients and their significance levels (Diniz-Filho et al. 2003, Diniz-Filho and Bini 2005). To avoid excessive numbers of explanatory variables and overcorrection for spatial autocorrelation, we obtained a reduced set of spatial filters using the following procedure (Diniz-Filho and Bini 2005): the filters were successively added to the multiple regression as explanatory variables with P-to-enter < 0.05 until spatial autocorrelation in the residuals of an OLS multiple regression of species richness was reduced to negligible levels. After selecting 15 filters (no. 1–6, 8–9, 11, 13–14, 16, 18–20) this way, the maximum Moran’s I for the residuals was 0.06 (for the default 22 distance classes). Adding additional filters (up to no. 40) did not further reduce this value.

The present study investigates whether there is spatial heterogeneity (spatial non-stationarity sensu Fotheringham et al. 2002)) in the relationships between species richness and key potential environmental drivers, i.e. climate and topography. We did this by comparing the best OLS linear regression models to geographically weighted regression (GWR) models, again using information-theoretic model selection based on AIC$_c$ (Fotheringham et al. 2002). Most regression techniques assume that relationships between variables are constant over space. In contrast, GWR is a spatially local technique, which is based on the premise that such relationships may not be constant over space and allows explicit estimation and mapping of spatial variation in the relationships to be estimated, e.g. in terms of regression coefficients (Fotheringham et al. 2002). In GWR, a separate set of regression parameters is obtained for each locality through weighted regression, where the contribution of each observation to the analysis for a specific locality depends on its geographical distance from that locality, with a weighting that declines with distance. The weighting is implemented by a spatial kernel function, the bandwidth (b) of which defines the steepness of the distance-decay in the weighting function and the scale of the analysis. We used a bi-squared kernel function, where the weight of locality j for the local regression analysis for locality i is w$_{ij}$ = (1 – (d$_{ij}$/b)$^2$)$^2$, if d$_{ij}$ < b, and w$_{ij}$ = 0 otherwise, where d$_{ij}$ is the distance between localities i and j. With a fixed bandwidth, the sample size underlying the results of the GWR at a given location will vary, causing problems if it sometimes becomes low (Brunsdon et al. 2001). To avoid this problem, we used an adaptive spatial kernel (Fotheringham et al. 2002), here implemented so it always uses a given percentage of cells, selected as the nearest neighbors, for calibrating the local models. As GWR is sensitive to bandwidth, the percentage used was optimized by searching between 10 and 30% of all cells with The Golden Section Search to minimize AIC$_c$. 
The 30% upper limit was chosen to ensure that the modeling was clearly localized, while the 10% lower limit was chosen to ensure that the local models were based on a large sample size and spanned a sufficiently large region to include much variability in the environmental variables. As GWR is particularly sensitive to multicollinearity (Wheeler and Tiefelsdorf 2005), we only included linear terms of the predictor variables in the GWR analyses.

We found spatial heterogeneity in the richness–environment relationships, and therefore analyzed the GWR results to test whether richness increased more steeply with topographic heterogeneity and water-energy availability (and/or temperature) in southern Europe than in northern Europe. As the GWR procedure inevitably introduces strong spatial autocorrelation in the estimated local parameters, we used correlation to assess the influence of region (represented by an indicator variable: southern (1) or northern Europe (0)) on the GWR slopes with one-tailed tests of significance using Dutilleul’s method for estimating the geographically effective number of degrees of freedom (Rangel et al. 2006). In addition, we used standard analysis of covariance (ANCOVA) to assess how much of the variation in the GWR coefficients that can be ascribed to regional differences (categorical variable: northern or southern Europe) and/or non-linearity in the global relationships (i.e. when the GWR coefficients for a given predictor vary with that predictor). Since the GWR coefficients for a given predictor cannot be considered independent from that predictor, and since the GWR procedure inevitably introduces strong spatial autocorrelation in the estimated local parameters, we only give p-values for the ANCOVAs for standard reference.

Regression analyses and spatial filter computations were performed using SAM 3.0 (Rangel et al. 2006), while ANCOVAs were done in JMP 6 (SAS Inst.).

### Results

The best global model included all four environmental predictors (Table 1). However, this model only had negligibly higher explanatory power (0.2%) than the best two-predictors model, AET+lnAR (square-root (total richness) = 3.74 ± 0.00846 AET + 1.23 lnAR+the 15 filters and their coefficients, F ratio = 166.8, p < 0.0001; Table 1). Therefore, we focus on the AET+lnAR model from here on. The geographic patterns in lnAR and AET are shown in Fig. 1. There was some indication of minor nonlinearity in the relationships for lnAR: adding lnAR$^2$ to the AET+lnAR model reduced AIC$_c$ by 123.9, but only increased $R^2_{adj}$ to 0.573. Adding AET$^2$ did not change AIC$_c$ or $R^2_{adj}$ while adding both quadratic terms reduced AIC$_c$ by 121.9 and also increased $R^2_{adj}$ to 0.573. The regression coefficient for lnAR$^2$ indicated a slightly accelerated increase in richness with lnAR.

The GWR model was clearly superior to the corresponding global models in terms of both model fit ($R^2_{adj}$), AIC$_c$, and spatial autocorrelation in the residuals, providing strong evidence for spatial heterogeneity in the relationship plant species richness to climate (AET) and topography (Table 2). Maps of key GWR results are given in Fig. 1. As is clear from the map of the GWR residuals, the GWR model for lnAR and AET was able to account for much of the spatial structure in species richness (Fig. 1). The local GWR coefficients for both lnAR and AET were highly variable (lnAR: mean 0.449 ± 0.274 SD; AET: mean 0.357 ± 0.481 SD; values for the standardized coefficients), but were mainly positive (lnAR, 96%; AET, 79%; Fig. 1).

As hypothesized, the increase in plant species richness with topographic heterogeneity was much stronger in southern Europe (standardized local lnAR coefficient, mean 0.610 ± 0.245 SD) than in northern Europe (0.270 ± 0.175; correlation, r = 0.620 ($r^2$ = 0.384), geographically effective DF = 7.1, one-tailed p = 0.032; Fig. 2). In contrast, the increase in richness with AET tended to be lower in southern Europe (standardized local AET coefficient, mean 0.256 ± 0.517 SD relative to northern Europe (0.468 ± 0.411), but the relationship was weak and not significant (r = −0.22 ($r^2$ = 0.048), geographically effective DF = 42.6, both one- and two-tailed p > 0.1, Fig. 2). The ANCOVAs additionally showed that the local lnAR coefficients were strongly controlled by region and only moderately influenced by lnAR and the lnAR×region interaction, while variation in the local AET coefficients were largely unexplained by region, AET, and AET×region (Table 3, Fig. 2). Hence, the steeper richness–lnAR relationships in southern Europe, to a large extent, reflect a truly regional effect rather than nonlinearity in the global richness–lnAR relationship. Interestingly, the moderate nonlinearity indicated again implies an accelerating increase in richness with lnAR (Fig. 2).

### Discussion

Our analyses showed that plant species richness in Europe increased with topographic heterogeneity and AET (i.e. water-energy availability), but, in agreement with previous analyses, they also suggested that there were additional important geographic patterns beyond those explainable by current climate. Compatible with the outlined Plio-Pleistocene climate change impacts on regional species pools and

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Table 1. Model selection for the 15 global OLS multiple linear regression models for total plant species richness in Europe (lnAR, ln-transformed altitudinal range; AET, mean actual evapotranspiration; AMT, annual mean temperature; WD, water deficit). All models include the 15 spatial filters. The explanatory power ($R^2_{adj}$), number of explanatory variables (k), and the delta AIC$_c$ value are provided for the five best models in terms of AIC$_c$, as well as the single environmental predictor variable models. n = 2312 AFE cells.

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>$R^2_{adj}$</th>
<th>ΔAIC$_c^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>lnAR+ AET + WD + AMT</td>
<td>19</td>
<td>0.552</td>
<td>0$^1$</td>
</tr>
<tr>
<td>lnAR+ AET + WD</td>
<td>18</td>
<td>0.550</td>
<td>9.3$^2$</td>
</tr>
<tr>
<td>lnAR+ AET + AMT</td>
<td>18</td>
<td>0.550</td>
<td>10.8$^3$</td>
</tr>
<tr>
<td>lnAR + AET</td>
<td>17</td>
<td>0.550</td>
<td>11.8$^4$</td>
</tr>
<tr>
<td>lnAR + WD</td>
<td>17</td>
<td>0.533</td>
<td>97.3$^5$</td>
</tr>
<tr>
<td>lnAR</td>
<td>16</td>
<td>0.532</td>
<td>98.0$^6$</td>
</tr>
<tr>
<td>AMT</td>
<td>16</td>
<td>0.472</td>
<td>377.9$^{11}$</td>
</tr>
<tr>
<td>AET</td>
<td>16</td>
<td>0.444</td>
<td>498.5$^{14}$</td>
</tr>
<tr>
<td>WD</td>
<td>16</td>
<td>0.443</td>
<td>503.3$^{15}$</td>
</tr>
</tbody>
</table>

$^a$ $R^2_{adj}$ = 0.438 for a model with just the 15 spatial filters and no environmental variables.

$^b$ Superscript indicates model rank according to ΔAIC$_c$, e.g. 3 means the 3rd best model.
the hypothesized contingent effects on richness–environment relationships, we found evidence for strong geographic heterogeneity in the species richness–environment relationship in general, as well as a greater increase in species richness with increasing topographic heterogeneity in southern Europe, than in northern Europe. However, contrary to expectation, species richness did not increase more strongly with AET in southern Europe. Furthermore, all models had relatively moderate explanatory power, suggesting that factors and relationships beyond those modeled are involved in generating the European plant species richness pattern (e.g. exact refuge locations, postglacial migration patterns, ...)

The GWR analysis showed that species richness increased much more strongly with topographic heterogeneity in southern Europe (Fig. 1, 2), exactly as predicted given that the positive effects of topographic heterogeneity on speciation and species survival would only be relevant in this region due to the limited glacial maximum in situ survival of plant species in northern Europe. The effect was especially strong where topographic heterogeneity is high, i.e. in high-mountain areas (Fig. 2). Although there is increasing discussion of relatively high-latitude survival of temperate species during the LGM (Willis et al. 2000, Svenning et al. 2008b), the Scandinavian mountains were fully glaciated during this period (Ruddiman 2001), prohibiting any significant in situ plant species survival. Historically, there has been much discussion of potential LGM survival of arctic-alpine species on nunataks in Scandinavia, but this idea has not received much support for South American birds, and Turner and Hawkins (2004) for Ne- and Palearctic birds (also cf. Ruggiero and Hawkins 2008). As the Plio-Pleistocene climate oscillations had the strongest impacts at high latitudes, survival and speciation rates are expected to have been higher at lower latitudes (Dynesius and Jansson 2000) and, as consequence, a stronger increase in richness with topographic heterogeneity at low latitudes in general is predicted. Notably, in the North American study, topographic heterogeneity is found to be the dominant predictor relative to potential evapotranspiration (PET) in regions with PET >1000 mm yr$^{-1}$ (Kerr and Packer 1997). Most of the PET <1000 mm yr$^{-1}$ region (roughly corresponding to Canada) was covered by the massive Laurentide ice sheet during the LGM (Ruddiman 2001), while the unglaciated regions south thereof experienced high in situ survival rates (Rowe et al. 2004, McLachlan et al. 2005).

Although the topography-related patterns here, and in previous studies, agree well with the predictions based on Plio-Pleistocene climate change impacts on regional species pools, it is important to consider that a latitudinal gradient in the current environment may also be involved: at high latitudes, more of the increased habitat diversity due to increasing topographic heterogeneity is likely to be comprised of species-poor habitats or uninhabitable glaciated areas (Turner 2004, Turner and Hawkins 2004). On the other hand, north-south slope habitat differentiation will be greater at higher latitudes (Turner 2004). Further macroecological studies, integrating additional information, notably on species ages and clade differentiation rates, will be needed to differentiate between these possibilities or, more likely, assess their relative importance.

The geographic pattern in the local AET slopes did not conform to our prediction for the richness–climate relationship, based on Plio-Pleistocene climate change impacts on the regional species pools. Although slopes were in fact high in southern Europe, contrary to expectation, there was also.

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Table 2. Global and local models of plant species richness (square-root transformed) in Europe: comparison of global AET + lnAR ordinary least-squares regression models with and without the 15 spatial filters to the corresponding geographically weighted regression (GWR) model. GWR was implemented using the bi-squared kernel function with an adaptive spatial kernel (10% closest cells), optimized using The Golden Section Search to minimize AICc, searching from the 10 to the 30% closest cells. n = 2312 AFE cells. Whole model p always < 0.001.

<table>
<thead>
<tr>
<th>Predictors$^a$</th>
<th>Global OLS (no filters)</th>
<th>Global OLS (15 filters)</th>
<th>Global OLS (15 filters)</th>
<th>GWR</th>
</tr>
</thead>
<tbody>
<tr>
<td>Effective no. of parameters</td>
<td>Linear</td>
<td>3</td>
<td>18</td>
<td>+Quadratic</td>
</tr>
<tr>
<td>F</td>
<td>609</td>
<td>167</td>
<td>173</td>
<td>69.5</td>
</tr>
<tr>
<td>$R^2_{adj}$</td>
<td>0.345</td>
<td>0.550</td>
<td>0.574</td>
<td>0.646</td>
</tr>
<tr>
<td>$\Delta AIC_c$</td>
<td>1346</td>
<td>496</td>
<td>372</td>
<td>0</td>
</tr>
<tr>
<td>Moran’s $I^b$</td>
<td>0.275</td>
<td>0.063</td>
<td>0.065</td>
<td>−0.014</td>
</tr>
</tbody>
</table>

$^a$ Just the linear terms for lnAR and AET or also the quadratic term for lnAR ($lnA R^2$).

$^b$ Maximum absolute value of model residual Moran’s $I$ for 22 equal-frequency distance classes (for the OLS models always the first class, 0–185 km).
a band of high local slopes across southern-central northern Europe (Fig. 1). Interestingly, this band broadly matches the transition between the temperate (nemoral) and boreal zones. Hence, it may reflect a general contrast between the low-AET and species-poor boreal zone (roughly north of $60^\circ$N) and the higher-AET and more species-rich temperate zone (south of $60^\circ$N; Fig. 2). This may therefore simply reflect that fewer species tolerate the boreal climate, causing a sharp drop in diversity, i.e. a direct effect of the current climate on species distributions (cf. Currie et al. 2004).

Several studies have shown that richness/climate patterns largely reflect the diversity patterns of the more widespread

Figure 2. Local standardized regression coefficients for ln-transformed altitudinal range (lnAR) and actual evapotranspiration (AET) from the GWR analysis (Table 2) in relation to region (northern versus southern Europe) and lnAR or AET, respectively. The ANCOVA analyses in Table 3 are illustrated by linear OLS fits for each region, separately.

Table 3. ANCOVA of standardized local GWR coefficients by region (northern vs southern Europe) and the environmental predictor variable (lnAR, ln-transformed altitudinal range; or, AET, mean actual evapotranspiration). ***, p < 0.001; ****, p < 0.0001.

<table>
<thead>
<tr>
<th>lnAR AET</th>
<th>lnAR AET</th>
</tr>
</thead>
<tbody>
<tr>
<td>$R^2_{adj}$</td>
<td>0.484</td>
</tr>
<tr>
<td>F ratio</td>
<td>725****</td>
</tr>
<tr>
<td>$\text{Sum of squares}$</td>
<td>$\text{Sum of squares}$</td>
</tr>
<tr>
<td>Region</td>
<td>30.0****</td>
</tr>
<tr>
<td>AET or lnAR</td>
<td>15.8****</td>
</tr>
<tr>
<td>Interaction</td>
<td>1.3****</td>
</tr>
<tr>
<td>AET</td>
<td>70.4****</td>
</tr>
<tr>
<td>lnAR</td>
<td>4.4****</td>
</tr>
<tr>
<td>lnAR AET</td>
<td>2.4***</td>
</tr>
<tr>
<td>lnAR AET</td>
<td>18.9****</td>
</tr>
</tbody>
</table>

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species (Jetz and Rahbek 2002, Svenning and Skov 2007b). In Europe, widespread species must all have experienced broad-scale postglacial range expansions, and their ranges are likely to be more closely in equilibrium with the present climate (although not completely so: Svenning et al. 2008a) than the ranges of less widespread species (cf. Svenning and Skov 2007b). Although this effect will be reduced in the localized GWR approach, historical control of the richness–climate relationship is still likely to be less strong than of the richness–topography relationship, which is mainly driven by less widespread species (see also Jetz and Rahbek 2002). We have already mentioned an additional mechanism that could weaken or remove geographic heterogeneity in the richness–climate relationship resulting from greater survival of warmth- and moisture-loving taxa in southern Europe: clades able to adapt to the cold and/or dry ice age climate also experienced diversification (Paun et al. 2005), but this would also primarily have been in southern Europe (cf. Dynesius and Jansson 2000, Jansson and Dynesius 2002). Although local AET slopes are actually high in southern Europe such a mechanism may explain why they were not higher than at the temperate-boreal transition. Geographic variation in diversification of taxa with contrasting climatic requirements could also offer an explanation for the high variation in not just the strength, but even the sign of the richness–AET relationship in southern Europe (Fig. 2).

In conclusion, we find partial support for the idea that Plio-Pleistocene climate change affects current species richness–environment relationships via its effects on regional species pools (cf. Pärtel et al. 2007). As hypothesized, there was strong geographic heterogeneity in the species richness–environment relationships, and the increase in richness with topographic heterogeneity was much stronger in southern Europe, where the less severe glaciation impacts have allowed for increased survival and speciation in topographically variable areas. However, further studies, integrating information on species ages and clade differentiation rates will be needed to substantiate this interpretation. In contrast, although geographically variable, the richness–climate relationship did not vary as predicted, perhaps because this pattern is more dominated by wide-ranging species with ranges more closely in equilibrium with the current environment. On a general level our results indicate that, although strong richness–environment relationships are often found in macroecological studies (Hawkins et al. 2003), these can be highly historically contingent due to historical constraints on the species pool (Wiens and Donoghue 2004, Pärtel et al. 2007). Furthermore, our results highlight the importance of considering not only the average richness–environment relationships, but also their geographic heterogeneity, if we wish to progress in our understanding of what determines species diversity.

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