Quaternary climate changes explain diversity among reptiles and amphibians

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It is widely believed that contemporary climate determines large-scale patterns of species richness. An alternative view proposes that species richness reflects biotic responses to historic climate changes. These competing "contemporary climate" vs "historic climate" hypotheses have been vigorously debated without reaching consensus. Here, we test the proposition that European species richness of reptiles and amphibians is driven by climate changes in the Quaternary. We find that climate stability between the Last Glacial Maximum (LGM) and the present day is a better predictor of species richness than contemporary climate; and that the 0°C isotherm of the LGM delimits the distributions of narrow-ranging species, whereas the current 0°C isotherm limits the distributions of wide-ranging species. Our analyses contradict previous studies of large-scale species richness patterns and support the view that "historic climate" can contribute to current species richness independently of and at least as much as contemporary climate.

The question of why certain areas contain more species than others has fascinated biogeographers and ecologists for over more than two centuries (Forster 1778, von Humboldt 1807). However, in spite of the abundance of hypotheses to explain gradients of species richness, testable predictions capable of differentiating between them have only rarely been presented (Rohde 1992, Willig et al. 2003). Two hypotheses that have generated considerable interest over the past 20 yr are the "species richness energy" (Wright 1983, Turner et al. 1988, Currie 1991) and "water-energy" (O'Brien 1998, Francis and Currie 2003, Hawkins et al. 2003). In essence, these "contemporary climate" hypotheses propose that the amount of resources available for conversion into food affects the numbers of individuals in regions and accordingly the numbers of species that can co-exist. In contrast, the "historic climate" stability hypothesis proposes that species are differentially excluded from areas that experience the most severe climate changes, whereas persistence and speciation are favored by climate stability over time (McGlone 1996, Dynesius and Jansson 2000, Wiens and Donoghue 2004, Ricklefs 2006, Jablonski et al. 2006). Proponents of the contemporary climate hypotheses do not dismiss the existence of a historical climate signature on current patterns of species richness, but take the view that species distributions, hence species richness, are close to equilibrium with contemporary climate; it follows that if species adjust quickly to changing climate conditions, factors associated with contemporary climate should take precedence in explaining diversity patterns, while historical climate factors could be considered to affect residual variation (Currie 1991, O'Brien 1998, Kerr and Currie 1999, Whittaker and Field 2000, Francis and Currie 2003, Hawkins et al. 2003).

Despite attempts to merge the two hypotheses into a single framework (Ricklefs 2004, Hawkins et al. 2005, 2006, Whittaker et al. 2007), comparative testing of the "contemporary" and "historic" climate hypotheses has been hampered by the difficulties in generating quantitative estimates of historical climate events with which to undertake analyses. Developments in climate change modeling have now enabled the production of high-resolution paleoclimate simulations that allow improved testing of the historical climate mechanisms underlying species richness patterns. Here, we use climate simulations for the Last Glacial Maximum (LGM, ca 21 thousand years ago (kya)) and contemporary climate to test the hypothesis that

gradients of richness among complete lineages (reptiles and amphibians) and across wide areas (Europe) can be elucidated by past climate changes. A previous analysis has shown that contemporary climate can explain a high proportion of the variance in the geographical patterns species richness among European reptiles and amphibians (Whittaker et al. 2007), but the question is whether the consideration of an appropriate alternative "historical climate" hypothesis contributes to a statistical explanation of the contemporary species richness pattern beyond (or instead of) that provided by measures of current climate. Europe is a particularly suitable region for the study of the role of past climates on large-scale patterns of species richness, due to the pronounced climate changes that occurred during the Pleistocene, and because isolation from Africa by the Mediterranean sea and from warm areas to the east by mountain ranges and seas, prevented colonization from enriched faunas in the south thus helping to maintain the signature of past climate changes (Holman 1998).

Discrimination of the impacts of historical climate versus contemporary climate on current patterns of species richness is further challenged, since areas that have been climatically stable over time are often characterized by high levels of contemporary energy and water-energy (Fjeldsa and Lovett 1997, Hawkins and Porter 2003). However, if "historic climate" contributes to current species richness independently of and at least as much as contemporary climate, we predict that appropriate measurements of historic climate changes (here, the anomaly between LGM and current climate) should be at least as effective as contemporary climate (both the "energy" or "water-energy" variants) in statistically explaining the contemporary gradients of species richness. While high correlations do not necessarily imply causation, weak correlations can be used to support the conditional dismissal of a causal relationship.

Nevertheless, teasing apart the contributions of different factors to species richness gradients would require that specific predictions capable of differentiating between them are made. Here, we make one additional prediction that is specific to historical climate explanations of species richness. Studies have shown that contemporary climate is a poor predictor of species richness among narrow ranging species (Rahbek and Graves 2001, Jetz et al. 2004, Rahbek et al. 2007). Several factors might cause narrow ranging species to be poorly predicted by contemporary climate variables, but if climate history had a strong impact on the distributions of narrow ranging species we would expect these species to occur preferentially in areas that remained favorable during the last glacial period, i.e. in the case of amphibians and reptiles, areas that maintained mean annual temperatures above freezing. This prediction implies that limited colonization ability has precluded the occupation of new areas by narrow ranging species during interglacial periods. In contrast, we would expect contemporary mean annual freezing conditions to be a better predictor of richness among wide-ranging species, assuming such species were more successful post-glacial colonizers.

Material and methods

Species richness

Species data comprised all European amphibian and reptile species (Gasc et al. 1997), projected on a UTM (Universal Transverse Mercator) 50 km European grid. Three measurements of species richness were used: total number of species per grid cell; number of species per grid cell among the top 50% narrower-ranging species (ranging from 1 to 69 occurrence records for amphibians and 1 to 72 records for reptiles) and number of species among the 25% wider-ranging species (ranging from 599 to 2087 occurrence records for amphibians and 206 to 1996 records for reptiles). The 50% threshold for narrow ranging species was selected because of the highly skewed frequency distribution of range sizes (i.e. most species having narrow range sizes and very few having wide range sizes). Had the 25% threshold been selected, only 62 and 130 European grid cells (out of 2187) would have been selected for amphibian and reptile species, respectively.

Predictors of species richness

Correlates of species richness were examined using two contemporary climate variables (annual mean temperature and annual total precipitation sum) (New et al. 2000), and two variables reflecting long term climate stability (the anomaly between mean annual temperatures and annual total precipitation sum in the LGM and at present). Mean annual temperatures and annual precipitation sum for the LGM were calculated using a General Circulation Model (GCM). The GCM used in this study is the HadAM3 version of the UK Meteorological Office's Unified Model (Wood et al. 1999). It has a horizontal grid resolution of $2.5° \times 3.75°$ in latitude and longitude with 19 levels in the vertical, and a time step of 30 min. The model incorporates prognostic cloud, water and ice, has a mass-flux convection scheme with stability closure and uses mean orography. The model was integrated for the LGM over 20 simulated years and climatological means were compiled for the final 14 yr. Time-series analysis of various climate variables for the entire 20 yr simulation shows that disregarding the first 6 yr allows the climatology model to reach full equilibrium.

The HadAM3 model was initialised with monthly sea surface temperatures derived from the Climate Long-Range Investigations, Mapping and Prediction data set (CLIMAP Project Members 1981). The distribution of surface ice and water cover for the LGM was derived from the ICE-4G model (Peltier 1994). The atmospheric concentration of CO_2 was specified at 200 ppm in agreement with measured values in ice core records (Petit et al. 1999). All other trace gas concentrations were specified at modern levels. The experimental design conforms to recommendations outlined by the Palaeoclimate Modelling Intercomparison Project, PMIP (Joussaume and Taylor 1999). An analysis of climate outputs from an ensemble of models, all initialised with

PMIP boundary conditions for the LGM, indicates that the HadAM3 General Circulation Model's predictions for the European region are in accordance with predictions generated by other models (Kageyama et al. 1999).

Statistical analyses

Spatial autocorrelation exaggerates Type I errors in regression and correlation analysis. In order to determine p values after the contribution of spatial autocorrelation is removed we undertook the following analyses. Firstly, a spatially explicit simultaneous autoregressive (SAR) model was used to assess spatially corrected p values for the association between species richness and individual contemporary and historic climate variables (Table 1). Second, partial regressions using simple ordinary least square (OLS) regression and SAR (Table 2) were used to partition the variance explained by contemporary (mean annual temperatures, and total annual precipitation sum) versus historic climate (mean annual temperature and total annual precipitation sum stability between the LGM and the present day). In all analyses, precipitation was modelled as a linear effect. Performance of partial regressions was estimated using Akaike information criterion (AIC) (Burnham and Anderson 2002). Diagnosis of spatial autocorrelation in the original data and in the residuals of OLS model was also performed using Moran's I coefficients estimated for 20 distance classes. All analyses were implemented using the statistical package for spatial analysis in macroecology; SAM (Rangel et al. 2006). For more details see Appendix.

Table 1. Standardized regression slopes (B) and associated t-values for the full spatially explicit simultaneous autoregressive (SAR) model including all predictors, for reptiles and amphibians. The R^2_{FULL} coefficients are the full SAR coefficients of determination, which includes both the effects of predictor as well as spatial error structure, while the "partial" coefficient of determination, R^2_{ENV} shows only the "semi-local" effect of environmental predictors, taking into account broad-scale spatial structure.

Predictor	B	t	R^2_{ENV}	R^2_{FULL}
Reptiles				
Temperature	0.274	3.967**	0.066	0.468
Temperature^2	0.071	1.121		
Precipitation	0.041	2.003*	0.001	0.357
Temperature stability	0.495	5.236**	0.090	0.544
Temperature stability^2	0.062	0.630		
Precipitation stability	−0.059	3.125**	0.002	0.356
Amphibians				
Temperature	0.970	11.186**	0.045	0.558
Temperature^2	−0.798	10.330**		
Precipitation	−0.009	0.337	0.001	0.423
Temperature stability	−0.408	3.407**	0.056	0.534
Temperature stability^2	−0.712	5.816**		
Precipitation stability	0.065	2.600**	0.004	0.445

*$p < 0.05$; **$p < 0.01$.

Results and discussion

Both mean contemporary annual temperatures and historic temperature stability between the LGM and the present significantly predict species richness of reptiles and amphibians in Europe ($p < 0.01$; see spatially explicit simultaneous autoregressive (SAR) analysis, Table 1). Species richness among reptiles is also significantly correlated with

Table 2. Coefficients from partial regression analyses based on ordinary least square regression (OLS) and the simultaneous autoregressive model (SAR) used to separate the contribution of the contemporary and historic climate hypotheses, respectively. The historic climate stability hypothesis (H_1) proposes that species richness is best predicted by temperature and precipitation stability between the Last Glacial Maximum (LGM) and present, while contemporary temperature and precipitation values are allowed to act as controls. Tests of the contemporary climate hypotheses included two variants. The contemporary energy hypothesis (H_2) proposes that species richness is best predicted by current temperature values, while the contemporary water-energy hypothesis (H_3) proposes that species richness is best predicted by contemporary temperature and precipitation values. For both hypotheses historic temperature and precipitation stability are allowed to act as controls. Values in (a) indicate the variation explained by the main predictor(s); values in (b) indicate the variation explained by the controlling factors.

	Total a	Total b	Total a+b	Only a	Only b	Shared
OLS model						
H_1 Historic climate stability						
Reptiles	0.509	0.439	0.577	0.118	0.048	0.391
Amphibians	0.404	0.261	0.453	0.192	0.049	0.212
H_2 Contemporary climate (energy)						
Reptiles	0.435	0.509	0.556	0.047	0.121	0.388
Amphibians	0.264	0.404	0.452	0.048	0.188	0.216
H_3 Contemporary climate (water-energy)						
Reptiles	0.439	0.509	0.557	0.048	0.118	0.391
Amphibians	0.261	0.404	0.453	0.049	0.192	0.212
SAR model						
H_1 Historic climate stability						
Reptiles	0.094	0.070	0.121	0.051	0.027	0.043
Amphibians	0.059	0.046	0.090	0.044	0.031	0.015
H_2 Contemporary climate (energy)						
Reptiles	0.066	0.094	0.121	0.027	0.055	0.039
Amphibians	0.045	0.059	0.081	0.022	0.036	0.023
H_3 Contemporary climate (water-energy)						
Reptiles	0.07	0.094	0.12	0.026	0.05	0.044
Amphibians	0.046	0.059	0.09	0.031	0.044	0.015

contemporary precipitation (p <0.05), whereas species richness among both reptiles and amphibians is significantly related to "historic" precipitation stability (p <0.01). Because contemporary temperature values are highly correlated with historic temperature stability (r =0.74, Fig. 1), partial regression analysis was used to partition the effects of contemporary climate (both the energy and water-energy variants) and historic climatic stability. Variation due to historic climate stability was seen to be greater than variation explained due to factors associated with contemporary climate, despite important shared variance between the two components (Table 2). This was true both for partial regressions using coefficients derived from ordinary least square (OLS) regression as well as the more conservative SAR model (Table 2). These results are consistent with our first prediction that historic climate changes can take precedence over contemporary climate in explaining current gradients of species richness.

Reptiles and amphibians rely on external warmth to raise their body temperature and become active. Their ability to cope with lower temperatures is limited, and many species find it difficult survive in regions where mean annual temperatures are below freezing. However, despite evidence that contemporary temperature and precipitation exert strong effects on the richness (Whittaker et al. 2007) and distributions of individual species of reptiles and amphibians in Europe (Araújo et al. 2006), we find, in concurrence with our second prediction, that the distribution of narrow ranging species is markedly constrained by the mean annual freezing conditions in the LGM, whereas widespread species are more constrained by current mean annual freezing conditions (Fig. 2). These results support the prediction that a large number of widespread species are likely to have large range sizes because they have been able to largely adjust to current climate conditions by means of colonization, while narrow-ranging species are at least partly restricted because of their poor ability to track climate

changes (Jansson 2003). There are certainly other factors causing rarity among species, but if colonization ability was not limiting the post glacial distribution of species, we would expect that several endemics of southern European alpine and temperate environments would now extend their ranges into central and northern Europe. Given that there are generally more narrow ranging species than there are wide ranging species (Gaston 1996) and that narrow ranging species are less likely to be at equilibrium with current climate conditions (Webb and Gaston 2000), it is likely that the impact of historic climates on current species richness is a more widespread phenomenon than previously acknowledged by proponents of contemporary climate hypotheses. However, we also predict that the historic signature on contemporary richness gradients is likely to be reduced among organisms with greater colonization abilities, such as birds and some plants (Araújo and Pearson 2005). This prediction is supported by two recent studies that analyzed the impact of contemporary LGM climates on the richness of a selected sample of northeastern Australian endemic fauna (Graham et al. 2006) and European flora (Svenning and Skov 2007); these studies demonstrated that historic climate was the single best explanatory variable of richness among narrow-ranging low dispersing endemic animals in Australian rainforest as well as narrow-ranging plant species in Europe, whereas contemporary climate was best at explaining richness among wide-ranging and good-disperser species.

Previous studies investigating the combined effects of contemporary and historic climate on species richness have often used coarse estimates of historic climates to undertake analyses. These have included the presence of glaciated vs non-glaciated areas (Currie 1991) and the time since the retreat of ice (Hawkins et al. 2003). However, the assessment of relationships between a high-resolution quantitative response variable (species richness) and high-resolution quantitative (contemporary climate) predictor
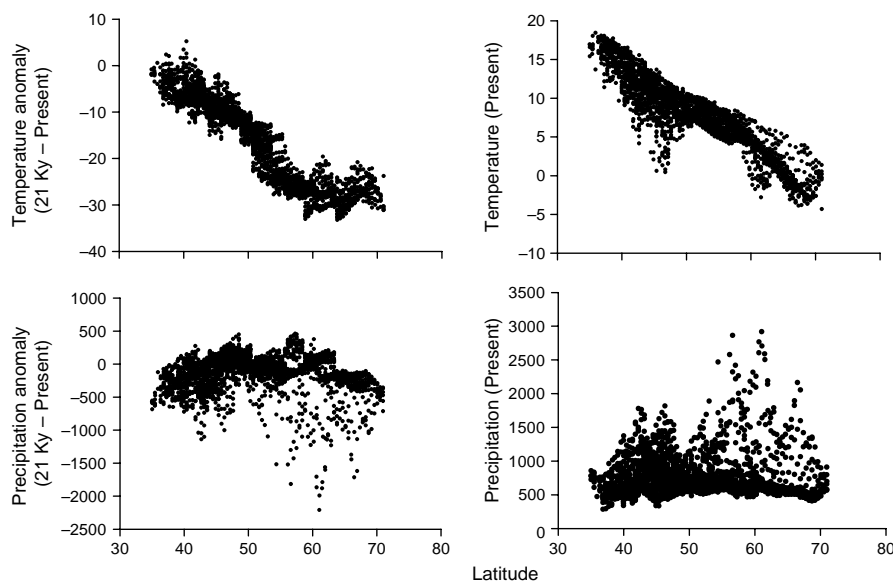

Fig. 1. Contemporary temperature and precipitation values (1969–1990) and stability in the temperature and precipitation values between the Last Glacial Maximum (LGM; 21 kya) and present day, plotted against latitude. The paleoclimate simulation used here is based on the HadAM3 General Circulation Model.
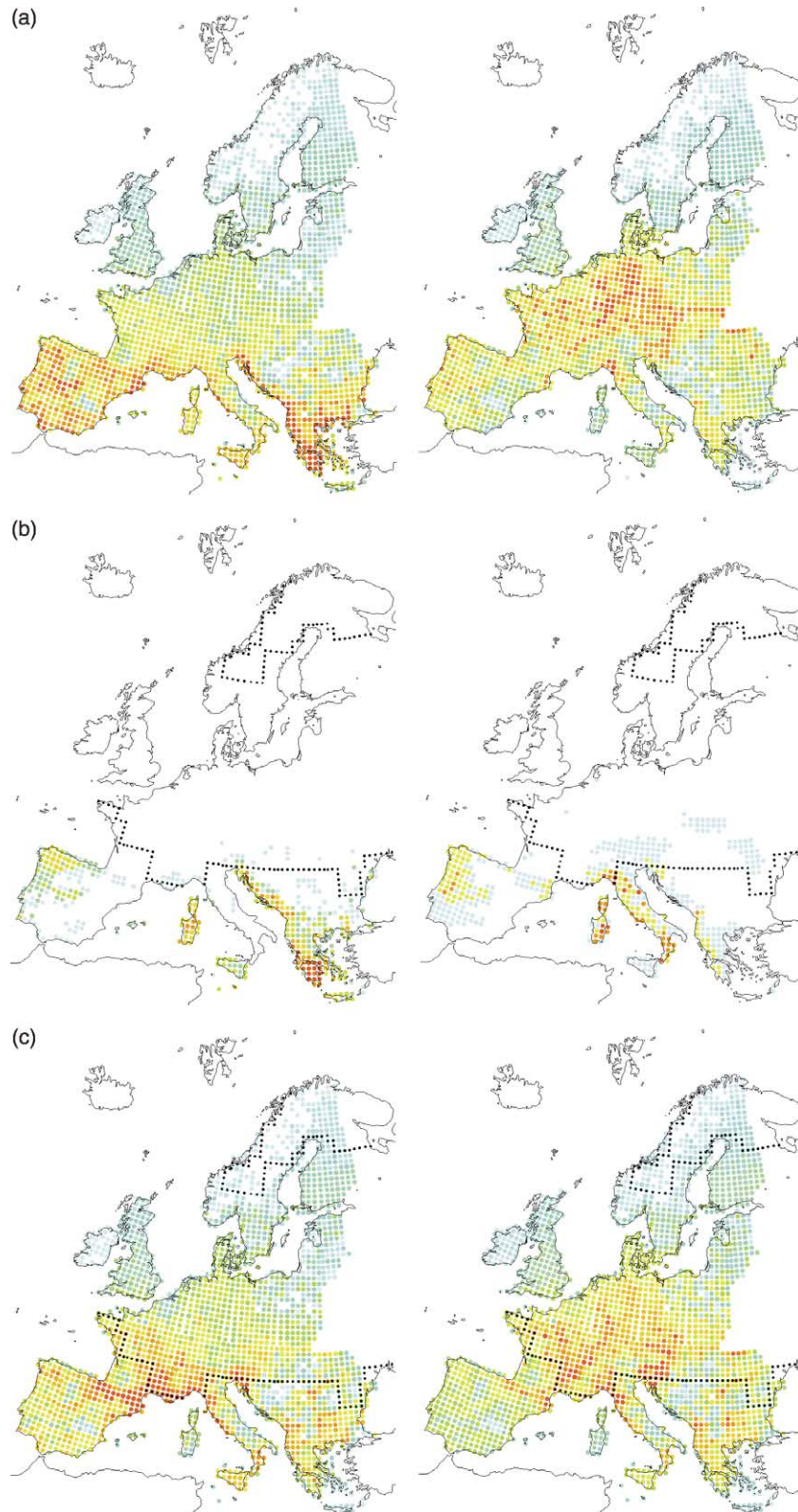
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Fig. 2. Species richness among all (a) European reptile (left) and amphibian (right) species; (b) the top 50% narrow-ranging; and (c) the top 25% wide-ranging species. Species richness scores in each map are divided into thirty three equal-frequency color classes, such that maximum scores are shown in red and minimum scores are shown in blue. The horizontal line through the south of Europe represents the 0°C isotherm during the Last Glacial Maximum (LGM; 21 kya), whereas the line through the north represents the current 0°C isotherm. The paleoclimate simulation used to draw the 0°C isotherm in the LGM is based on the HadAM3 General Circulation Model.

variables is bound to produce higher estimates of correlation than assessments comparing the same response variable with low-resolution quantitative or qualitative (historic climate) predictor variables, especially if predictor variables are collinear. This results in a bias in the statistical analyses that inevitably leads to favoring contemporary explanations of species richness. Thus, before drawing conclusions regarding the precedence of contemporary climate in shaping current species richness gradients it is important to exercise caution and factor in the best estimates of paleoclimate variation which, according to our results, are likely to have had a major impact on current gradients of species richness among European reptiles and amphibians. There may be cases, however, where highly mobile species have adjusted their distributions to contemporary climate thus showing smaller concordance with historical climate. In such cases, the signature of past climates on species richness might be more pronounced among species with narrow range sizes (Rahbek and Graves 2001, Jetz et al. 2004, Graham et al. 2006, Svenning and Skov 2007, Rahbek et al. 2007).

Differentiating between contemporary and historical climate hypotheses is important not only for theoretical reasons, but also because an understanding of the mechanisms that generate and maintain species richness gradients provides valuable insights for predicting the impacts of future climate changes on biodiversity. If it is the contemporary climate that drives species richness patterns, then current climate variables can be used to accurately predict the effects of climate change on biodiversity; if, as shown here, the mechanisms underlying contemporary patterns of species richness are strongly influenced by the history of climate, then these predictions may be misleading and alternative approaches should be developed.

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Appendix

European species richness of reptiles and amphibians exhibited a strong level of spatial autocorrelation (Fig. S1). Over short distances, the species richness of both amphibians and reptiles exhibited coincident patterns (positive autocorrelation), and these patterns tended to decrease with geographic distance. For reptiles, a steady decrease in spatial autocorrelation is observed, and Moran's I autocorrelation coefficients decrease until a high negative spatial autocorrelation for the largest distance classes was observed. Amphibian species richness displayed a more irregular spatial structure, and Moran's I autocorrelation coefficients stabilised around zero after a geographic distance of ca 1500 km (Fig. S1).

Part of this spatial autocorrelation within the data – especially the long distance spatial autocorrelation – was due to the environmental predictors ("contemporary" and "historic" climate) since the residuals of OLS regression (used to separate the contribution of the contemporary and historic climate predictors) only accounted for short distance spatial autocorrelation (i.e. up to 400 km), which was greater for amphibians than for reptiles (Fig. S1). To quantify the effect of short distance spatial autocorrelation

in the estimation of p values in regression analyses, we used a SAR model. Spatial covariance among sampling units was incorporated into model residuals using the inverse of the geographic distances (d) between them, expressed as $1/d^2$ for reptiles, and $1/d^3$ (the value best matching the irregular spatial structure of amphibian species richness).

In the SAR model, including all predictors, partial standardized regression coefficients were significant for contemporary temperature as well as temperature and precipitation stability during the LGM (Table 1). Effectively, these results indicate that "historic climate" contributes to species richness patterns independently of and at least as effectively as contemporary climate. For both reptiles and amphibians, partial slopes of historic temperature stability were steeper than partial slopes for contemporary temperature. Contemporary precipitation was also seen to be a significant predictor of reptile species richness,
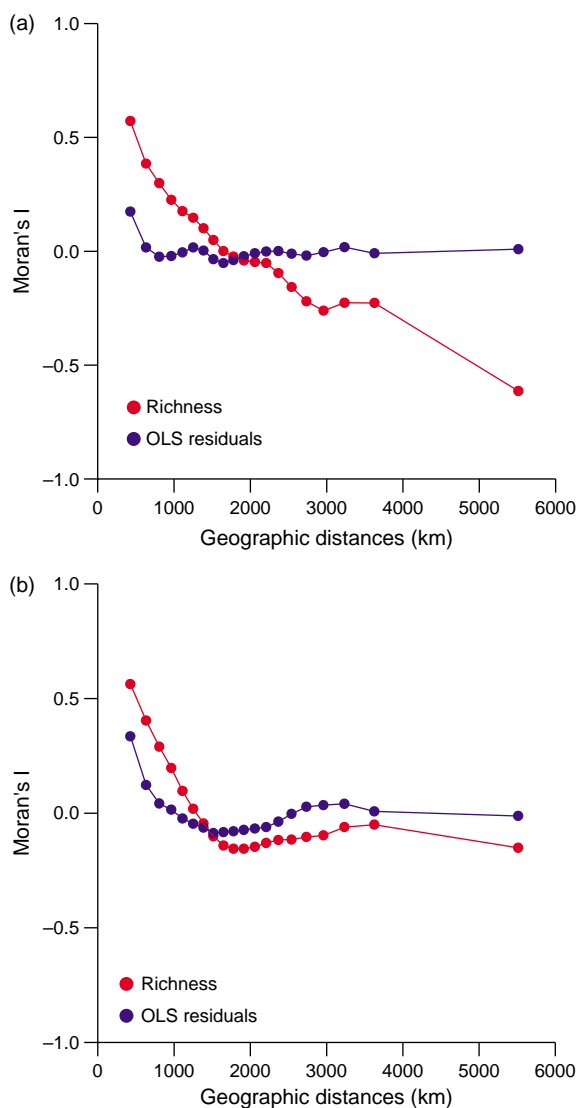
Fig. S1. Spatial correlograms based on Moran's I autocorrelation coefficients for original richness (red) and ordinary least squares (OLS) regression residuals from a full model including all environmental predictors (blue), for reptiles (a) and amphibians (b).

whereas precipitation stability was significant as a predictor of both reptile and amphibian species richness.

Partial regression coefficients, required to separate the unique effects of contemporary climate and historic climatic stability, were obtained with algebraic manipulations of OLS and SAR regression coefficients of determination, i.e. Nagelkerke's R^2 (Table 1) (Legendre and Legendre 1998). The R^2 coefficients of determination for SAR were obtained either from the full model including the effect of predictors and spatial structure of the error term (R^2_{FULL}); or from a model expressing only the relative effect of the environmental predictors after taking broad-scale spatial structures into account (R^2_{ENV}). The R^2_{ENV} is the pseudo-R^2 obtained by correlating observed and expected values of spatial regression. Because the expected values were obtained without taking into account the confounding effects of spatial autocorrelation in parameter estimates (Hawkins et al. 2007), they are usually smaller than R^2_{FULL}. The R^2 values for the full model are similar (although slightly higher) to those obtained for the OLS (Table 1) (for discussion of these R values and their interpretation see Haining 2003, Rangel et al. 2006). This is because spatial autocorrelation in the OLS was relatively small (at least for reptiles) and concentrated in the first distance classes. In contrast, partial regression coefficients capturing the effects of predictors variables alone are much smaller, because they remove the effects of broad-scale spatial structures and can

therefore be interpreted as "semi-local" coefficients (Fotheringham et al. 2000). Nevertheless, they support the qualitative statements that can be made based on the OLS regression coefficients, as they reveal that the unique effects of temperature stability between the LGM and the present day are both independent to, and greater than the effects of current climate. It is worth noting that the shared effect of contemporary and "historical climate", which is very high in OLS partial regressions, is low for partial regressions based on SAR (Table 2). This is because the common effect is mainly caused by a broad-scale latitudinal trend – covariance – that was taken into account in the SAR model.

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