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Geographical gradients of species richness: a test of the water-energy conjecture of Hawkins *et al.* (2003) using European data for five taxa

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ABSTRACT

Aims We present an analysis of grid-based species-richness data for European plants, mammals, birds, amphibians and reptiles, designed to test the proposition of Hawkins *et al.* (2003a) that the single best factor describing richness variation switches from the water regime to the energy regime in the mid-latitudes and that the 'breakpoint' is related to the physiological character of the taxa. We go on to develop subregional models showing the extent to which regional model fits vary as a function of the extent of the study system, and compare the relative performance of 'water', 'energy' and 'water–energy' models of richness for southern, northern and pan-European models.

Location Western Europe.

Methods We use atlas data comprising species range data for 187 species of mammals, 445 species of breeding birds, 58 amphibians, 91 reptiles and 2362 plant species, inserted into a c. 50 × 50 km grid cell system. We used 11 modelled climate variables, averaged for the period 1961–90. Statistical analyses were carried out using generalized additive models (GAMs), with splines simplified to a maximum of four degrees of freedom, and we tested for spatial autocorrelation using Moran's *I* values obtained at 10 different distance intervals. We selected favoured models on the grounds of deviance explained combined with a simple parsimony criterion, such that we selected either: (1) the best two-variable energy, water or water–energy model, or (2) a four-variable water–energy model, where the latter improved on the best two-variable model by a minimum of 5% deviance explained.

Results Threshold energy values, at which richness shows a transition from an increasing to a decreasing function of annual solar radiation, were identified for all taxa apart from reptiles. We found conditional support for the switch from dominance of water variables (southern models) to energy variables (northern models). Our favoured models switched between 'water' and 'energy' for mammals, and between 'energy' and 'water–energy' for birds, depending on whether we used data of pan-European extent, southern or northern subsets. Deviance explained in our favoured models varied from 15% (birds, southern Europe) to 72% (amphibians, northern Europe), i.e. ranging from very poor to good fits with the data. Comparison with previous work indicates that our models are generally consistent with (if sometimes weaker than) previous findings.

Main conclusions Our models are incomplete representations of factors influencing macro-scale richness patterns across Europe, taking no explicit account of, for example, topographic variation, human influences or long-term climatic variation. However, with the exception of birds, for which only the northern model attains over one-third deviance explained, the models show that climate can account for meaningful proportions of the deviance. We find general support for considering water and energy regimes together in modelling species richness, and for the proposition that water is more limiting in southern Europe and energy in the north. Our analyses

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demonstrate the sensitivity of model outcomes to the geographical location and extent of the study system, illustrating that simple curve-fitting exercises like these, particularly if based on regions with the complex history and geography characteristic of Europe, are unlikely to provide the basis for global, predictive models. However, such exercises may be of value in detecting which aspects of water and energy regimes may be of most importance in refining independently generated global models for regional application.

Keywords

Amphibians, birds, climate models, Europe, GAM, mammals, plants, species richness gradients, water–energy dynamics.

INTRODUCTION

Geographical gradients in the diversity of plant and animal species have long fascinated biogeographers and ecologists (Lomolino *et al.*, 2004). Recent years have seen considerable advances in our knowledge and understanding of these patterns. Correlations between the distribution of diversity and contemporary environmental properties (e.g. climate, topographic relief) and known historical variations in these properties (e.g. glaciations, tectonic uplift, sea-level change) are gradually becoming understood (e.g. O'Brien, 1993, 1998; McGlone, 1996; Kerr & Packer, 1997; O'Brien *et al.*, 2000; Francis & Currie, 2003; Hawkins *et al.*, 2003a,b) and there are signs that we may at last be developing a synthetic, consilient body of theory to understand these phenomena (Whittaker *et al.*, 2001; Hawkins *et al.*, 2003a; Currie *et al.*, 2004; Field *et al.*, 2005; O'Brien, 2006). Within this body of theory, it is important to distinguish different phenomena under the general heading of diversity gradients, in particular, the metric of diversity that is under examination (e.g. inventory or differentiation metrics), and the true scale (grain or focal scale) and extent (geographical limits) of the study system (Whittaker *et al.*, 2001, 2003; Rahbek, 2005).

In the present paper we are concerned with geographical gradients in species richness across Europe using species range data transposed into a c. 50 × 50 km grid cell system. Europe is not the ideal region of the world from which to develop species-richness models of *global* applicability, for a number of reasons. First, the contemporary climate has a strong maritime (Gulf Stream)–continental gradient, meaning that maritime grid cells have water–energy regimes atypical of continental interiors. Secondly, the configuration of the continent and British Isles involves many such grid cells. Thirdly, the region has experienced pronounced climatic change during the Quaternary, with very extensive ice sheets. Fourthly, because of the distribution of mountain massifs within southern and eastern Europe, the impacts of these oscillations in climate on European diversity are thought to have been particularly significant (e.g. Hewitt, 2000; Araújo & Pearson, 2005). Fifthly, on a coarse scale, it is likely that the spatial signal of climate history is to some degree correlated with spatial variation in contemporary climate (Hawkins *et al.*, 2003b). Finally, humans have been influencing species distributions in Europe from prehistoric times in ways that are only partially understood (cf. Pyšek *et al.*, 2004; Willis & van Andel, 2004; Willis *et al.*, 2004).

For these reasons, species-richness models calibrated with European data are unlikely to travel as well as the products of European viticulture. However, analyses of European data can contribute to our understanding of diversity patterns in a number of ways. For example, on the one hand, palaeoecological and phylogeographical analyses are contributing to insights into the role of refugia, and the ability of particular species and taxa to respond (migration, phenotypic change) to climate change (e.g. Hewitt, 2000; Schmitt & Hewitt, 2004; Schmitt & Krauss, 2004; Willis & van Andel, 2004; Araújo & Pearson, 2005; Hampe & Petit, 2005; Svenning & Skov, 2004). On the other hand, Europe can provide a test region for species-richness models developed elsewhere, whereby geographical variation in model fit, and the distribution of residuals, may be used to validate/falsify theoretical expectations (O'Brien *et al.*, 1998, 2000; Whittaker & Field, 2000; Rodríguez *et al.*, 2005). Indeed, for the same reasons that we would not choose to use Europe as the basis for developing global models, we can regard the region as a tough test-bed for macro-scale climate-based models or richness: if they work here, we must be on to something.

An important starting premise of this paper, grounded on numerous recent studies (although by no means universally accepted), is that the geographical gradients in species richness are essentially climatic gradients (Hawkins *et al.*, 2003a,b), explicable in relation to climatic variables and how climate has varied through time. Underpinning these climatic gradients is the dynamic relationship between energy and water regimes (water–energy dynamics *sensu* O'Brien, 1998, 2006). In an important recent synthesis of the empirical literature, Hawkins *et al.* (2003a, p. 3105) wrote ... 'We conclude that the interaction between water and energy, either directly or indirectly (via plant productivity), provides a strong explanation for globally extensive plant and animal diversity gradients, but for animals there is also a latitudinal shift in the relative importance of ambient energy vs. water moving from the poles to the equator ...' Specifically, they argue from an examination of some 38 published studies that animal richness is constrained by the interaction of energy and water, but that in high latitudes energy represents the limiting component of the interaction, while in lower latitudes, water is the key limiting component.

For birds and butterflies, Hawkins *et al.* (2003a) went further in presenting in map form a hypothesis pertaining to the

geographical (essentially latitudinal) 'breakpoint' at which the transition from dominance of the water regime gives way to dominance of the energy regime. Their map reflects the geographical location of the energy optimum and indicates that butterflies (solar ectotherms) have a more southerly breakpoint than birds (endotherms). In Europe, the bird breakpoint is shown running through the English Channel, along the eastern border of the Netherlands, up to the northern coast of Poland and then inland along a consistent line of latitude. The butterfly breakpoint runs through the Pyrenees, along the northern Mediterranean coast through Marseille and Genova, and thereafter roughly along the parallel to Odessa on the Black Sea.

An important implication of the Hawkins *et al.* (2003a) analysis is that the extent of the study system (and thus the range of climatic variation encompassed) will significantly influence the form of model fits between climate and species richness. The present paper presents an analysis of 50 × 50 km grid-based European species-richness data for five taxa, specifically plants, mammals, birds, amphibians and reptiles, the goals of which are as follows: (1) to test the conjecture, based on Hawkins *et al.* (2003a), that the single best factor describing species-richness variation switches from water to energy in the mid-latitudes; (2) and that, in so far as such switches occur, the breakpoint for animal taxa occurs further north for more endothermic taxa; (3) having determined a breakpoint in relation to the energy regime, we go on to develop separate models for northern and southern Europe, thus testing the extent to which regional model fits may vary as a function of study system extent; (4) finally, we compare the relative performance of 'water', 'energy' and 'water-energy' models and discuss these findings in relation to previous work on climate-species-richness gradients.

Model fitting is undertaken using generalized additive models (GAMs) (Hastie & Tibshirani, 1990). We emphasize that the empirical approach adopted for model fitting in this study is not mechanistically or theoretically grounded, and is not intended to produce globally applicable models (cf. O'Brien, 1998; Field *et al.*, 2005). However, it may nonetheless produce insights into how regionally derived models may be apparently at variance with one another, and yet be consistent with simple global models, and how global models might be fine-tuned to improve fits in higher-latitude regions.

MATERIALS AND METHODS

Species data

The species-range data used to compile the (native) species-richness data used herein are derived from published atlases and comprise 187 species of mammals (Mitchell-Jones *et al.*, 1999), 445 breeding bird (Hagemeijer & Blair, 1997), 58 amphibian, 91 reptile (Gasc *et al.*, 1997) and 2362 plant species (Jalas & Suominen, 1972–96). The data vary with regard to taxonomic coverage as follows. Terrestrial vertebrates comprise all known species, whereas plants comprise only approximately 20% of the European flora, as documented in the *Atlas Flora Europaeae* (Jalas & Suominen, 1972–96; Lahti & Lampinen, 1999). Plant species include all

pteridophytes, all gymnosperm families and a subset of angiosperms (Salicales, Myricales, Junglandales, Fagales, Urticales, Proteales, Santales, Aristolochiales, Balanophorales, Polygonales, Centrospermae and Ranales). It is important to bear in mind that plant data have a bias towards well-represented groups in western and central Europe, while important families in the Mediterranean region are missing (Araújo, 2003). Examples of missing taxa include Asteraceae, Caprifoliaceae, Cistaceae, Ericaceae, Gramineae, Labiatae, Leguminosae, Oleaceae and Rhamnaceae.

The grid used is based on the Common European Chorological Grid Reference System (CGRS). The chorological data were inserted into a c. 50 × 50 km grid map based on the Universal Transverse Mercator (UTM) projection and the Military Grid Reference System (MGRS). In this study the mapped area included western, northern and southern Europe, but excluded most of the eastern European countries (except for the Baltic states), where recording effort was both less uniform and less intensive. For more details on data properties and conversion see Williams *et al.* (2000). In a companion paper based on the same data set, Nogués-Bravo & Araújo (2006) demonstrate that variable selection in species-richness models is remarkably robust to variation in the effective area of the grid cells caused by topographic variation, projection errors and overlap with the sea. Nonetheless, in the present paper we excluded all grid cells of less than 50% land area, such that for all models 1983 grid cells were used (see Fig. S1 in Supplementary Material for a representation of the cells).

Climate data

Climate data included 11 variables developed for Europe in the context of the EC-funded ATEAM project (<http://www.pik-potsdam.de/ateam/>), based on data for the period 1961–90. Variables used in our analyses were: mean annual temperature (°C) (TANN), mean temperature of the coldest month per year (°C) (MTC), mean temperature of the warmest month per year (°C) (MTW), annual solar long-wave radiation (W m^{-2}) (ASR), mean annual precipitation (mm) (PANN), mean winter precipitation (mm) (PWIN), mean summer precipitation (mm) (PSUM), mean spring precipitation (mm) (PSPR), mean autumn precipitation (mm) (PAUT), mean annual growing degree days ($> 5^\circ\text{C}$) (GDD), and the moisture index (MI) calculated as the ratio of mean annual actual evapotranspiration over mean annual potential evapotranspiration (as Shafer *et al.*, 2001). These climate variables are often seen as controlling factors of the physiological processes limiting the spatial distribution of species, particularly among plants (e.g. Woodward & Williams, 1987; Prentice *et al.*, 1992; Sykes *et al.*, 1996; Sitch *et al.*, 2003).

The climatic variables used are not necessarily the optimal variables for developing the simplest possible global models of richness variation for particular taxa. For instance, E.M. O'Brien and colleagues have developed interim general models (IGMs) predicting the capacity for richness of woody plants globally based on the following three variables: annual rainfall (water), Thornthwaite's minimum mean monthly potential evapotranspiration

(energy), and a log function of topographic range of a grid cell ($\log(\text{Topog})$) {as so: $\text{richness} = a + b(\text{water}) + [c(\text{energy}) - d(\text{energy}^2)] + e(\log(\text{Topog}))$, where a to e are constants} (for details see O'Brien, 1998; Field *et al.*, 2005). However, our chosen variables are appropriate variables for representing energy and water regimes across Europe and have been used successfully in other recent studies of species richness (e.g. Nogués-Bravo & Araújo, 2006), the distribution of individual species in relation to climate (e.g. Araújo *et al.*, 2005a,b; Thuiller *et al.*, 2005) and dynamic vegetation modelling (e.g. Prentice *et al.*, 1992; Sykes *et al.*, 1996; Sitch *et al.*, 2003).

Temperature variables and solar radiation were selected as energy variables while precipitation variables and MI were regarded as water-availability proxies. MI is really a composite variable reflecting both energy and water regimes, as follows. AET is likely to be more indicative of water availability in Mediterranean Europe and of the energy regime in northern Europe. AET cannot exceed PET, so that in northern Europe the ratio (i.e. MI) is likely to approach 1, whereas in southern Europe PET may considerably exceed AET, thus revealing an increasing water deficit corresponding to lower values of MI. Hence, the use of MI as a water variable should be viewed with some circumspection.

Statistical analyses

Statistical analyses were carried out using GAMs (Hastie & Tibshirani, 1990), which are non-parametric extensions of generalized linear models that apply non-parametric smoothers to each predictor and additively calculate the component response. Being a non-parametric and completely data-driven approach, GAMs avoid making untested assumptions on the relationship between climate and species richness. A GAM is expressed by:

$$g(E(Y)) = \alpha + s_1(X_{1i}) + s_2(X_{2i}) + \dots + s_p(X_{pi}) \quad (1)$$

where g is the link function that relates the linear predictor with the expected value of the response variable Y , X_{pi} is a predictor variable and s_p is a smoothing function. A Poisson distribution was selected, using a log link function. This is recommended (Crawley, 1993) as species richness is often considered as a form of count data. Explained deviance and chi-square tests were calculated to summarize the ability of selected variables to explain the spatial pattern of species richness and to provide estimates of statistical significance. The splines used to relate each climate variable to species richness were simplified to a maximum of four degrees of freedom (see Wood & Augustin, 2002, for an extensive mathematical explanation of penalized splines). The objective of limiting the number of splines to four is to prevent overfitting and consequent difficulty in interpreting the resulting functions in ecological terms.

The development of the GAMs for each taxon followed the following protocol. First, the species richness of each group (amphibians, reptiles, mammals, birds and plants) was regressed separately against each of the climate variables in order to explore the ability of each variable to account for the species-richness patterns. Secondly, we derived two-variable energy models by

selecting the two variables accounting for the highest explained deviance from among the available energy variables. Thirdly, we then repeated this procedure using the two best water variables. This approach allows us to capture complementary aspects of the energy (or water) regime such as seasonality of temperature (precipitation) regimes. Fourthly, we combined the best energy and best water variable to provide a two-variable water–energy model of equivalent complexity to the other two-variable models. Finally, we combined the two selected water variables and two selected energy variables as input for a four-variable combined water–energy GAM for each taxon. Chi-square tests for statistical significance were used to retain or to drop a variable in the model.

Our aim in allowing only two water and two energy variables into the models was to develop comparatively simple and interpretable models in which collinearity and noise were reduced. We compared the two-variable and four-variable models using a general cross-validation procedure (UBRE score; see Wood & Augustin, 2002), which aims to maximize the trade-off between model fit and the overall smoothness. In all cases, the four-variable models were shown to be improvements over the best two-variable model. However, on grounds of parsimony, we adopt the more stringent but arbitrary approach of choosing as our 'favoured' model the best two-variable model unless the four-variable model accounted for a minimum of 5% more of the deviance than the best two-variable model.

As a further step in the analysis, we tested for spatial autocorrelation using Moran's I values obtained at 10 different distance classes to create correlograms of the residuals of the four-variable species-richness models using SAM software (Rangel *et al.*, 2006). The statistical significance of Moran's I ($P < 0.05$) is based on distances by randomization (using a Monte Carlo procedure; 200 permutations). Spatial autocorrelation, where present, can inflate estimates of statistical significance, and may influence the order in which variables are selected: evidence of spatial autocorrelation in the residuals after model fitting indicates the existence of missing variables or of systematic spatial patterns in data quality (e.g. Diniz-Filho *et al.*, 2003; Segurado *et al.*, 2006).

Having first developed a pan-European model using this approach, we then used annual solar radiation (ASR) to split the data set for each taxon into a southern and northern set, based on the inflexion point (optimum) in the ASR–richness fitted GAM, i.e. the point at which the trend in richness switches from positive to negative with increasing ASR. We used ASR as it was the energy variable showing the highest explanatory power for each taxon. We then developed separate models for northern and southern regions following the above approach. The exception to this was the reptile data set, in which a continuous positive relationship was detected with solar radiation, and so in this case we present only a pan-European model. Unless otherwise indicated, all analyses were carried out using the MGCv package (Wood & Augustin, 2002) implemented in R software (Ihaka & Gentleman, 1996).

RESULTS

The first step in our analysis was to fit an energy model (using ASR) and, where a clear optimal relationship was obtained, to

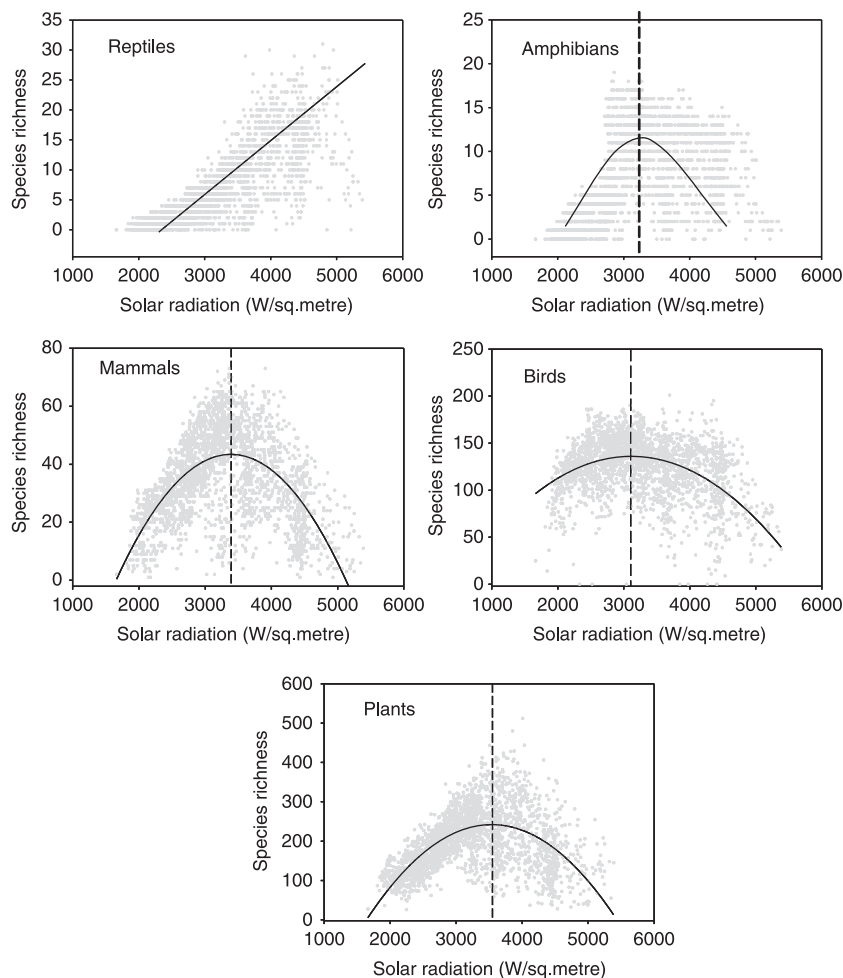


Figure 1 Relationships between annual solar radiation (ASR) and species richness using the GAM procedures described in the text. The threshold ASR values, where species richness changes from a positive to a negative trend (using GAM), were used to select breakpoints to split the data sets for development of separate southern and northern models (except for reptiles). Explained deviance by ASR in pan-European models: reptiles 63.2%, amphibians 46.7%, mammals 40.9%, birds 25%, plants 38.9%.

identify the energy optima as a basis for splitting the data to develop separate northern European and southern European models. Examination of Fig. 1(a)–(e) suggests, to varying degrees, a strong constraint of energy on richness up to values of annual solar radiation receipt of *c.* 3100 W/m² for birds, *c.* 3200 W/m² for amphibians, *c.* 3400 W/m² for mammals and 3600 W/m² for plants. There was no evidence of a ‘threshold’ in the reptile data. The univariate ASR models account for varying amounts of the deviance in the data (reptiles 63.2%, birds 17%, amphibians 46.7%, mammals 40.9% and plants 38.9%), whilst the location of the breakpoints is shown by the dashed vertical lines in Fig. 1, and their geographical location by the isopleths of ASR mapped in Fig. 2. Beyond the optimum energy regime, in all cases apart from the reptiles (where no threshold occurs), there is evidence of declining richness with increasing energy.

There appears, from visual examination, to be a fairly clearly delimited maximum richness for a given solar radiation value, particularly in the lower-energy rising limb, but this is much less evident at higher energy values, and in the declining limbs of the graphs. This is indicative that other variables, in particular aspects of the water regime, assume a greater significance in higher-energy regions (below).

The percentage deviance explained by the various GAMs was variable: from 10.3% (water) to 18% (four-variable water–

energy) for the southern Europe bird data, contrasting with a range from 33.8% (water) to 72.5% (four-variable water–energy) for the northern Europe amphibian data (Table 1). In general, the explanatory power of the energy models exceeded that of the water models (Fig. 3). The two-variable water–energy models outperformed the equivalent energy and water models for six of the 13 species-richness data sets, although only in two cases by more than 2% deviance (Table 1). The improvement in model performance of the four-variable water–energy models over the best two-variable energy or water models varied from just 2.2% for the northern mammal model to 9.4% for the pan-European bird data. Were we concerned simply with developing the most elegant and simple models within this analysis, for some taxa we could stop the analysis with a single variable, hence, the pan-European reptiles’ GAM based on W m^{−2} accounted for 63.2% deviance, which is only marginally improved upon in the two- and four-variable solutions (the latter accounts for 66.7% of the deviance). Moreover, we might choose to build upon such a start point with the inclusion of non-climatic variables, but we stress that our goal here is to explore the relative roles of the water regime and the energy regime rather than to find the most complete geographical/environmental model.

In Table 1, we have also highlighted our preferred model based on an arbitrary parsimony criterion, i.e. selecting the best

Table 1 Explained deviance (%) accounted for by water, energy and water–energy generalized additive models (GAMs). Models were developed after splitting data into northern and southern sets based on the energy optimum (Fig. 1), except for reptiles, for which there was no internal optimum. The inherent complexity of all two-variable models is the same, being based on the best two variables in each category, and being limited to four splines for each variable. The four-variable water–energy is based on the best two water variables and the best two energy variables. Our favoured model is based on the following criteria: (1) we chose the two-variable model explaining the most deviance, or (2) we selected the four-variable water–energy model in cases where this model outperformed the best two-variable water or energy GAM by at least 5% deviance. The favoured models highlighted in bold are those explaining > 50% of the deviance

Taxon	Data set	Water	Energy	Two-variable water–energy	Four-variable water–energy	Favoured model
Number of variables		2	2	2	4	
Reptiles	All	42.9	64.4	65.7	66.7	Two-variable water–energy
Amphibians	All	21.8	52.7	53.1	56.5	Two-variable water–energy
	North	33.8	66.7	72.2	72.5	Two-variable water–energy
	South	11.8	19.3	16.9	28.4	Four-variable water–energy
Birds	All	17.8	20.9	21.2	30.3	Four-variable water–energy
	North	29.7	52.4	39.8	54.7	Energy
	South	10.3	14.6	15.0	18.0	Two-variable water–energy
Mammals	All	21.3	43.6	36.6	47.7	Energy
	North	20.7	56.1	49.0	58.3	Energy
	South	39.1	38.0	36.1	42.4	Water
Plants	All	38.3	43.4	46.8	49.3	Two-variable water–energy
	North	46.4	57.1	47.7	63.6	Four-variable water–energy
	South	42.6	41.1	33.7	51.1	Four-variable water–energy



Figure 2 Cut-off lines marking the switch from a positive species-richness–energy relationship to a negative species-richness–energy relationship, according to a GAM fitted to data for annual solar radiation (ASR). The threshold values thus selected were as follows: birds 3100 W/m², amphibians 3200 W/m², mammals 3400 W/m² and plants 3600 W/m² (Figure 1). The reptile species-richness model had no energy threshold and so only a single model was developed for the whole region. The extent of the study area is mapped in grey.

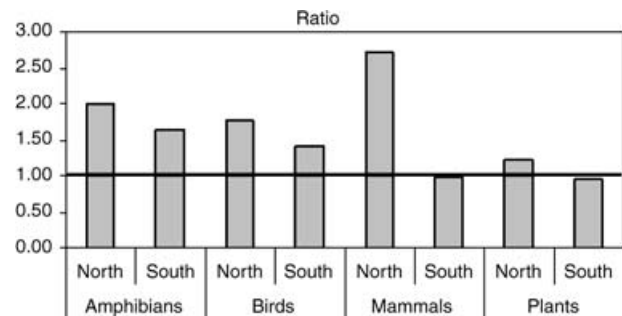


Figure 3 Ratio (explained deviance of 'energy' / explained deviance of 'water availability') of the two-variable energy and two-variable water availability models (from Table 1). Values above 1 indicate that the energy variables have a higher explanatory power than water and vice versa.

two-variable model unless the four-variable model outperforms it by at least 5%. On this crude basis, we find for a mix of energy, water and water–energy models, with seven out of 13 of our favoured models accounting for > 50% deviance in the species data. In all cases, the favoured northern Europe model is clearly superior to the favoured southern Europe model, indicating clearer (or at least simpler) climatic gradients in richness in the north than the south (Table 1). The general higher explanatory power of energy variables is particularly evident in the northern

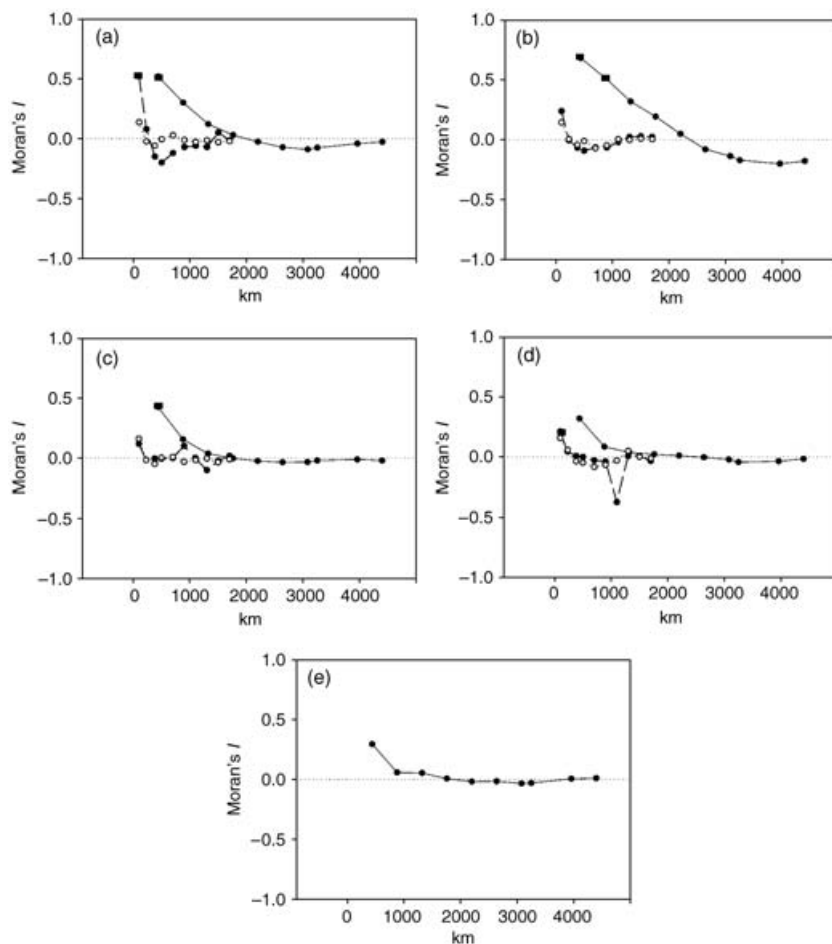


Figure 4 Moran's I correlograms of residuals after fitting favoured models for (a) amphibians, (b) mammals, (c) birds, (d) plants, and (e) reptiles. Solid lines (filled symbols), pan-European models; dashed lines (filled symbols), northern models; dotted lines (open circles), southern models; except for the reptiles (panel e), where only a single, pan-European model was developed. Significant Moran's I values ($P < 0.05$) are shown as squares. Circles are non-significant values.

models, with this north–south contrast declining from mammals to amphibians, to birds, to plants. This is consistent with the interpretation of the patterns in Fig. 1 offered above, i.e. that energy limitation in the northern low-energy sector is more pronounced than in the south, and that this indicates in turn a greater importance of water regime in the south.

Moran's I values show significant spatial autocorrelation, at the finest scale of analysis, in the residuals of the favoured pan-European model for mammals, birds and amphibians and in the favoured northern model for amphibians (Fig. 4). This is indicative of the relatively high levels of unexplained deviance left over having fitted what amount to fairly simple climate-based models across a region of considerable environmental complexity (and see Supplementary Fig. S1). Interestingly, the residuals from the favoured southern models are not significantly autocorrelated, despite these models generally (plants being the exception) having lower explanatory power than both northern and pan-European models.

Given the nature of the data-fitting procedures involved in GAM, the interpretation of the models depends in large part on the shape of the response functions involved. We therefore illustrate these functions in Fig. 5 (and see also Fig. S2 in Supplementary Material), by means of a selection of single-variable model fits, focusing on the best single water and energy variables for each taxon for northern and southern European data sets (or, in the case of reptiles, the pan-European data set).

DISCUSSION

Our first goal was to test the proposition that the key factor controlling species-richness variation switches (for animals more than for plants) from water (low-latitude driver) to energy (high-latitude driver) in the mid-latitudes. Hawkins *et al.* (2003a) suggested this pattern from an extensive review of recent species-richness–climate models. We assessed this proposition by the simple approach of developing separate models guided by the empirically determined 'threshold' point (optimum) in the humped relationship between species richness and energy for amphibians, birds, mammal and plants. For reptiles, there was no evidence of such a threshold within the range sampled, and our preferred pan-European model was an energy model. Among the other taxa, the location of the apparent energy optimum can be ordered from south to north as follows: plants, mammals, amphibians, and finally birds. For birds, the line (Fig. 2) described by the optimum (Fig. 1d) runs roughly parallel to but south of the threshold proposed by Hawkins *et al.* (2003a; their Fig. 3), beyond which the positive relationship between bird species richness and potential evapotranspiration (energy) breaks down.

If Hawkins *et al.*'s (2003a) conjecture on the respective roles of water and energy regimes is robust, we would expect to find that by developing separate models for northern and southern

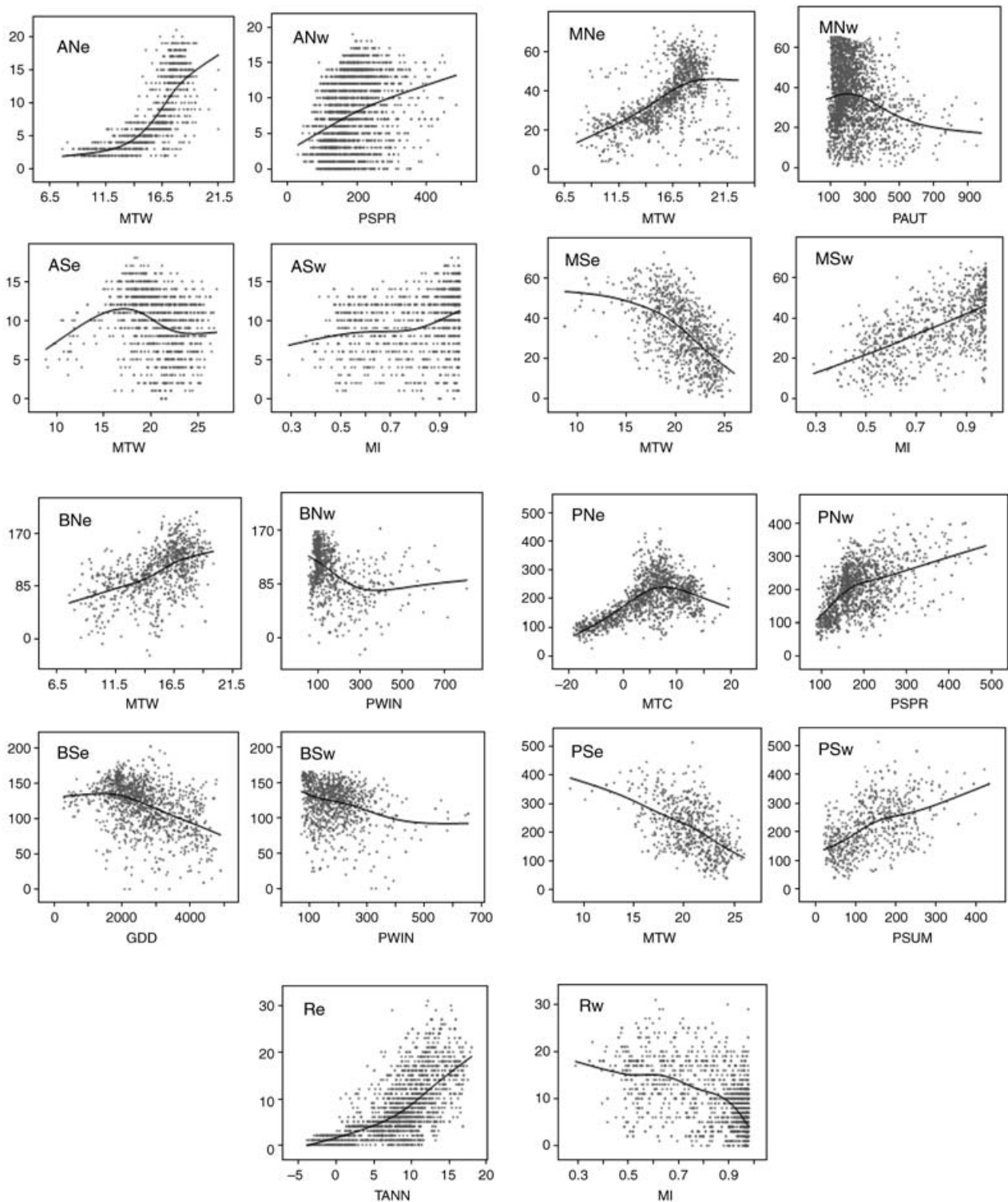


Figure 5 The relationships between the best single energy variable and species richness, and between the best single water variable (in terms of explained deviance) and species richness, using the GAM procedures described in the text. (Note: when solar radiation is the best variable, the second best variable is plotted instead, since ASR–species-richness plots are given in Fig. 1) Panel labels are as follows: A, amphibians; M, mammals; B, birds; P, plants; R, reptiles; N, northern data set, S, southern data set; e, energy variable; w, water variable (e.g. ANe = amphibians, northern data set, best energy variable). For reptiles the fits are for pan-European data.

regions, models featuring energy variables should emerge first for the northern data sets, and water variables should emerge for the southern data sets. Support for this tendency comes from the shift in the ratio of explained deviance towards energy rather than water in northern vs. southern models (Fig. 3). However, taking our 'favoured models' as the standard, only the mammal results fit this expectation unambiguously (energy, north; water, south). The bird results are similar, with energy emerging for the northern data set, and a (poorly fitting) water–energy model in the south. For amphibians and plants, on the other hand, the favoured models are in each case water–energy models (Table 1). We thus find (only) conditional support for the geographical switch from water to energy proposed by Hawkins *et al.* (2003a).

The second goal was to establish if the transition in response to energy for animals occurs further north for more endothermic taxa, in which case, for example, mammals should show the highest-latitude threshold. In practice, the simple analysis reported in Fig. 1 shows an inconsistent pattern in relation to ectothermic/endothermic character. The most northerly limit is for birds, next comes amphibians, and then mammals (and finally, plants), with no evidence of a breakpoint for reptiles within the study area.

One weak point of our analysis as a test of this hypothesis is the poor explanatory power of the ASR model for birds (Fig. 1d) on which basis the breakpoint was selected. The energy peak is far less pronounced than that for mammals, amphibians and plants, suggesting that it may not be as robust an indicator of an energy optimum. Indeed, visual analysis of a plot of the best water and energy variables (winter rainfall and ASR, respectively), indicates a more complex relationship with climatic conditions (Supplementary Fig. S2; perhaps, in turn, indicating a more powerful role for nonclimatic factors, cf. Blondel *et al.* (1988) and Newton (2003)). Whilst we have used the energy variable that emerged in our analyses as explaining the most deviance, it is conceivable that it is not the best choice for checking this particular hypothesis. It is, however, at least a common standard applied across each of our data sets.

Our third goal was concerned with the sensitivity of model fits to the geographical extent of the study system. Numerous papers (as referenced herein) have been published over the last 20 years analysing species-richness gradients in relation to possible climatic drivers of those gradients. They have varied in the form and quality of the species data, the focal scale of the analyses, the methods of analysis and the extent of the study system. The present analysis is not free from issues of data quality (see Materials and Methods, and Supplementary Fig. S1), but does standardize focal scale and methods, allowing examination of the implications of varying the extent of the study system. The differences in explanatory power of the 'best' two- and four-variable models arising from our analysis are noteworthy, with the favoured models switching amongst 'water', 'energy' and 'water–energy' for birds and mammals depending on whether we used data of pan-European extent, southern or northern subsets, and the explanatory power shifting between water and energy from south to north (as above). This illustrates that analyses based on limited geographical regions, which do not capture a sufficient range of environmental conditions, are unlikely to provide a

sound basis for developing global models of richness. If general models are to be developed from analyses of limited geographical regions, the study area must be well chosen, and protocols for analysis carefully selected and justified (as O'Brien, 1993, 1998; Field *et al.*, 2005; and see also Nogués-Bravo & Araújo, 2006; Hawkins *et al.*, in press).

Fourthly, we asked whether our models, which in practice are of very variable explanatory power, hold value and can be interpreted in the light of previous work. Particular caution is needed in interpreting those of our models that have low explanatory power (Table 1) and that show significant spatial autocorrelation in the residuals (Fig. 4).

For reptiles, the favoured model is a two-variable water–energy model (66% deviance, no significant spatial autocorrelation of residuals). Species-richness values are greatest in the dry areas of southern Europe (for a coincident analysis of individual species' niches see Araújo *et al.*, 2006). Thus, the energy variables show a direct relationship (more energy, more species) with reptile species richness (as, e.g. Currie, 1991; Hawkins *et al.*, 2003a) and an inverse relationship (more water availability, fewer species) with water availability (Figs 1 and 5). Among the water variables, MI (mean ratio of annual actual evapotranspiration over annual potential evapotranspiration) accounts for the highest amount of deviance. These results concur with those of Meliadou & Troumbis (1997) and of Rodríguez *et al.* (2005). The latter authors used a larger array of environmental variables in modelling species richness of reptiles (and amphibians) for Europe using quadrats of 2.5° latitude by 2.5–5.0° longitude, and reported a positive linear relationship between richness and potential evapotranspiration (energy) accounting for 71% of the variance.

The coarse-scale pan-European analyses of amphibian species richness by Rodríguez *et al.* (2005) were of similar explanatory power to our pan-European model, with two alternative models accounting for c. 60% of the variance in their data. These were, first, actual evapotranspiration and second, an estimate of plant biomass, indicating that a combination of water–energy balance and productivity best explains the pattern. They speculated that one or other of two mechanisms might link amphibian species richness to plants: (1) food chains based on plant productivity set energetic limits or (2) plant cover might dictate habitat suitability for amphibians.

In our much finer-scale analyses, the energy variables explain the greatest proportion of deviance in all models, with the clearest and strongest fit being for the north, with a positive monotonic relationship between species richness and MTW (Fig. 5). The parabolic relationship between energy and species richness evident for the pan-European model (Fig. 1) remains weakly evident in the southern Europe model. Bringing in the water variables improves the model fit most strongly in the south, but here the overall deviance explained is only 28.4%. Moreover, whereas species richness shows a general trend of increasing with spring rainfall in northern Europe, there is only a slight increase in richness with water (MI) in southern Europe (Fig. 5).

Considering both the form and limited power of climate variables for the southern amphibian subset, it seems that our ability to capture the relationships governing species richness at the macro-scale is much diminished compared to the north. This

may be because the availability of surface water and associated microhabitat characteristics crucial to amphibians are themselves dictated by topographic and hydrological conditions not well related to general climatic indices of the water regime at this scale of analysis (e.g. Nogués-Bravo & Martínez-Rica, 2004). Also, the high percentages of explained deviance attributed to present climate variables for pan-European reptile and amphibian data sets could in some measure be a statistical artefact, as may be indicated by significant Moran's *I* values for the latter (Fig. 4). Historical climate shifts in Europe also show a north–south pattern of intensity of climate change over glacial cycles, and the signal of history could be embedded in the present pattern of species richness of these groups (and see the map of residuals in Supplementary Fig. S1). In illustration, Araújo & Pearson (2005) found low levels of equilibrium between current climate conditions and species distributions of reptile and amphibian species in Europe, and they showed that their distribution patterns are linked to three major ice age refugia: Iberia, Italy and the Balkans (see also, e.g. Babik *et al.*, 2005).

For mammal species richness, relationships with energy are positive in the northern model and negative in the southern, consistent with the pan-European pattern (Figs 1c & 5). Relationships between mammal species richness and water availability, in the form of summer rainfall and MI (32.1% and 33.1% explained deviance), in the southern model shows a reduction in richness in the driest areas. Hence, for mammals, we see a switch from an energy model (positive effect) in the north to a water (limitation) model in the hotter parts of the south. This is consistent with the varying emphasis of regional models from across the world reported by Hawkins *et al.* (2003a) and by Hawkins & Pausas' (2004) analyses for north-east Spain. The marked north–south difference in the form of the relationship between mammal species richness and climate is reflected in the significant autocorrelation evident in the residuals from the pan-European model (Figs 4 & S1). Once more, we should note that historical processes relating to climate change and how it may have impacted differentially within Europe have also been invoked in explaining patterns of species richness and genetic diversity in European mammals (e.g. Taberlet *et al.*, 1998; Baquero & Tellería, 2001). These patterns have also undoubtedly been affected by humans over many millennia (e.g. Blondel & Aronson, 1999). Both forms of historical process are likely to have influenced species-richness patterns, and may be responsible for some of the residual variation in our models (see Supplementary Fig. S1 for a map of the residuals from the pan-European model).

The bird models follow similar tendencies to those for mammals, but the fit is considerably poorer, especially in the south, and again the pan-European model shows significant spatial autocorrelation in the residuals at the finest scale of analysis (Figs 4 & S1). Only the northern European model exceeds one-third of the deviance explained. Here, again, we see a comparatively straightforward positive trend of species richness with increased ambient energy in the north (cf. Lennon *et al.*, 2000), contrasting with a collapse in the explanatory power of energy in the hotter south. But, unlike some other warm-region studies (Hawkins *et al.*, 2003a,b), the deviance explained by water regime

variables in the southern Europe model remains stubbornly low. Interestingly, for the pan-European bird data set, inclusion of both water and energy variables produced a marked improvement in model fit, consistent with Hawkins *et al.*'s (2003a) finding that AET (related to net primary productivity/water balance) can account for 72% variation in bird species richness in global analyses of richness variation across continents, and with Kalmar & Currie's (2006) global model of bird species richness on islands, which includes both temperature and precipitation variables.

Finally, the favoured plant models were all water–energy models, with the data supporting the existence of a positive monotonic increase in richness with increasing rainfall (Fig. 5), and a parabolic relationship with energy regime (Fig. 1). The latter is evident in both the pan-European and northern models, with the southern data representing the declining limb of the curve as represented by MTW (Fig. 5). Comparing our southern and northern plant data sets, we find a switch in relation to seasonality, which may be important for developing more complete models for plants (cf. Field *et al.*, 2005). For the northern subset, spring precipitation accounts for 34.1% of the deviance and summer precipitation just 4%, whereas the corresponding figures for the southern subset are 23.4% and 29.4%, i.e. empirically, spring precipitation appears key in the north, and summer precipitation in the south. Similarly, there is a switch between north and south in the deviance accounted for by mean temperature of the coldest month and the warmest month (north, MTC 48.4% deviance, MTW 31.3%; south, MTC 17.9% and MTW 26.0%). This indicates that excessive cold temperatures tend to be limiting to species richness in the north, whereas excessive hot temperatures are crucial in constraining richness in the south. This trend is not evident in the variables selected for the animal taxa, as MTW accounts for more deviance than MTC for mammals and amphibians in both the north and south, whilst for birds they are of equivalent explanatory power (not illustrated). These differences may be explicable in relation to the underlying physiological constraints on different life forms (cf. Hawkins *et al.*, 2003a; Rodríguez *et al.*, 2005; O'Brien, 2006).

We thus find that our results support the proposition that water–energy dynamics (*sensu* O'Brien, 1993, 1998, 2006) determine the capacity for richness in plants globally, whilst indicating that incorporating different aspects of seasonality (of water or energy regimes) may help improve regional model fits. Interestingly, Hawkins *et al.* (in press) find that for tree richness, the decline in species richness at higher latitudes can be modelled effectively based merely on summer rainfall (as suggested by O'Brien, 1998; Field *et al.*, 2005). The difference between our findings and those of Hawkins *et al.* (in press) and Field *et al.* (2005) may be explicable in the inclusion of all growth forms of plants in the present study, instead of just trees. This is because we can anticipate that richness in other plant growth forms must in some respects be determined both by direct responses to water–energy regimes and indirectly in relation to competition with tree forms (cf. Bhattarai & Vetaas, 2003). With the average modular size of trees being orders of magnitude larger than for herbaceous and small shrub taxa, transitions from forest to non-forest ecosystems may give rise to increased plant density and

thus contribute to contrasting spatial patterns in tree and total plant species richness. Our results may also be biased by the taxonomic limitations of the source data (above).

In conclusion, our analyses of species-richness patterns of five European taxa at a scale of 50×50 km (grain) provide some interesting insights into how emergent relationships between richness and climate vary depending on the extent of the system and the focal taxon. Our approach in the present paper, whilst assuming that climate provides a first-order explanation for richness variation at the macro-scale, has been *atheoretical* in the sense that we have used an extremely flexible GAM approach to model fitting. Despite this flexibility, in cases where energy accounts for meaningful proportions of deviance, and with the exception of reptiles (extreme solar ectotherms), we can see that the general form of the relationship is consistent with the existence globally of a parabolic species-richness–energy relationship, with the extent of the study system determining whether positive, negative or parabolic forms are returned (Figs 1 & 5). Species-richness relationships with the water variables also vary with system extent and with taxon choice (see Fig. 5).

Overall, our results support the proposition that, for the taxa considered, there is greater evidence for energy limitation (i.e. cool climates limit richness) in northern Europe, whereas water variables assume relatively greater prominence in southern Europe (water availability limits species richness in hotter climates), while emphasizing the importance of water and energy regimes in combination to an understanding of plant species richness (see O'Brien, 2006). Our attempt to identify a geographical line marking the threshold between energy and water (cf. Hawkins *et al.*, 2003a) produced a pattern inconsistent with the idea that more endothermic taxa evidence a more northerly breakpoint. But the relatively poor model fits for the bird data, and the differences in the details of the models between taxa, render this 'test' inconclusive. Moreover, it is important to note that our analyses are at a finer spatial scale (c. 50×50 km cells) than those on which Hawkins *et al.* (2003a) based their division (c. 220×220 km cells), which may also influence the outcome (Lennon *et al.*, 2001; Rahbek & Graves, 2001; Whittaker *et al.*, 2001; B. A. Hawkins, pers. comm.). Additionally, differences in the derivation of the species-range data and grid resolution (or grain) between the two studies may also have influenced the patterns recovered in the two analyses. Notwithstanding, the comparison of southern, northern and pan-European models produces insights generally consistent with previous modelling work, and in addition helps to identify which aspects of water and energy regimes may be of most importance in refining regional model fits.

Finally, we stress that our models were always going to be incomplete, even as macro-scale analyses, as we have made no attempt to incorporate topographic heterogeneity and we have no proxy measure by which to incorporate 'history' within our analyses. Repeated climatic oscillations over the last few million years (especially within the Quaternary) have left strong imprints on the structure of biological diversity in and across Europe (e.g. Hewitt, 2000; Willis & Whittaker, 2000; Schmitt & Hewitt, 2004; Willis *et al.*, 2004; Habel *et al.*, 2005; Robledo-Arnuncio *et al.*,

2005; Svenning & Skov, 2005; and many other papers). The interaction of climate change with the complex topography of the continent and the general pattern of more extreme climate change impacts in the north of Europe means that Europe is a region in which disentangling the roles of present climate from past climate change will always be a substantial challenge. Moreover, the role of humans in altering the biogeography, especially of the Mediterranean region (see, e.g. Blondel & Aronson, 1999), may further confound attempts to capture climate–species-richness relationships (see also Araújo, 2003; Gaston & Evans, 2004). Thus, we caution that some portion of the deviance accounted for in our models may incorporate the signal of history, and that historical effects are doubtless bound up in the variance not accounted for in our models (Supplementary Fig. S1; and see, e.g. O'Brien *et al.*, 1998; Hawkins & Porter, 2003; Field *et al.*, 2005; Svenning & Skov, 2005).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article online at www.blackwell-synergy.com/loi/geb

Figure S1 Maps of the residuals for each grid cell after fitting the favoured pan-European model (as specified in Table 1) for each taxon

Figure S2 The species richness of each taxon across an environmental space defined by the best energy variable (*x*-axis) and the best water variable (*y*-axis), using a smoothing function based on running averages of the original data

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