Insect Conservation and Diversity (2008) **1**, 142–150

Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata)

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Abstract. 1. Environmental correlates of broad-scale patterns of Odonata species richness were studied in Europe and part of northern Africa using 220 × 220-km gridded data. Relationships with 11 environmental variables were tested using multiple regression.

2. Two models were constructed: (i) for the entire data set covering both Europe and northern Africa, and (ii) only for Europe.

3. Across both regions, actual evapotranspiration had the strongest relationship with richness, followed by weaker associations of potential evapotranspiration (a concave polynomial) and summer vegetation index (a positive linear relationship). Within Europe the strongest predictor was a concave polynomial of potential evapotranspiration, followed by vascular plant species richness (a positive relationship) and annual precipitation (a concave polynomial).

4. A test of metabolic theory identified strong non-linearity in the temperature-richness relationship, and geographically weighted regression indicated consistency with the theory in a very limited part of Europe.

5. The results are most consistent with the hypothesis that broad-scale species richness patterns are primarily determined by water–energy balance, similar to many fully terrestrial insect groups.

Key words. Autocorrelation, Europe, metabolic theory, northern Africa, Odonata, species richness, species-energy hypothesis.

Introduction

In the past 15 years, large numbers of studies have addressed the question of what drives broad-scale patterns of species richness (Kerr *et al*., 2001; Hawkins *et al*., 2003b; Currie *et al*., 2004, and references therein). A major focus of this research has been to identify the strongest environmental correlates of species richness data extracted from secondary data sources such as distribution atlases. Among the many hypotheses that have been proposed to explain diversity gradients, three have recently attracted much attention. These are:

H1: *The energy-richness hypothesis* or the *more individuals hypothesis* (Wright, 1983; Clarke & Gaston, 2006). This hypothesis states that patterns of species richness are determined by the input of productive energy available to primary producers. With increasing available energy, population densities increase, making populations less extinction-prone (Evans *et al*., 2005). The amount of productive energy in the system is determined by the amount of photosyntetically active radiation and water availability (Clarke & Gaston, 2006). Under this hypothesis, species richness should be primarily influenced by water–energy balance (which drives plant production), for example by actual evapotranspiration or a combination of potential evapotranspiration and precipitation (Hawkins *et al*., 2003b).

H2: *Metabolic theory* or *temperature-dependent evolutionary rate* (Rohde, 1992; Allen *et al*., 2002, 2007). Higher diversity is expected in warmer areas because of increased physiological processes, higher mutation rates, shorter generation times, and therefore higher speciation rates. All of these are believed to be positively correlated with temperature. Under this hypothesis,

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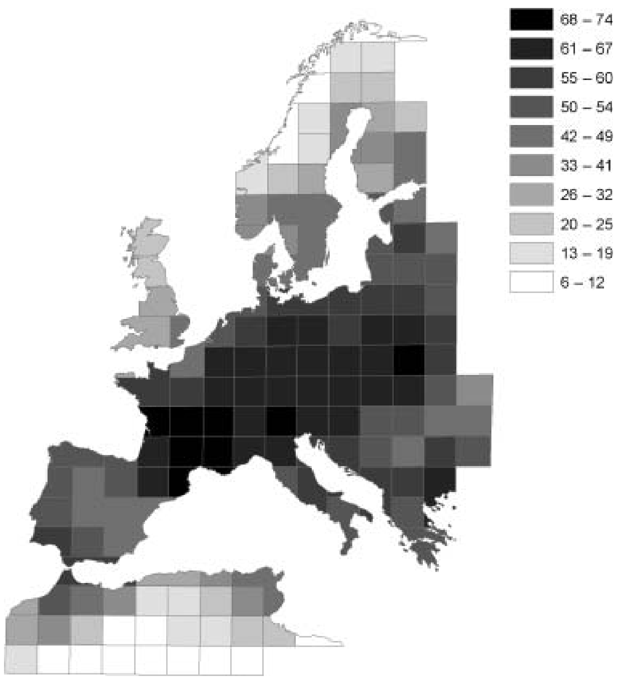

Fig. 1. Geographical pattern of Odonata species richness in Europe and northern Africa.

the diversity of ectotherms should be set primarily by temperature, with a linear relationship defined by a specific slope (see Hawkins *et al*., 2007a).

H3: *Habitat heterogeneity* (Kerr & Packer, 1997; Kerr *et al*., 2001). Because most animal species have habitat preferences, a greater diversity of habitats in an area should generate higher richness (this is essentially tautological with respect to plants, since habitats are often defined by the presence of key plant groups). Thus, we can predict that remotely sensed habitat heterogeneity or proxies of habitat heterogeneity (topography, species richness of plants) should be strong predictors of species richness.

The strongest empirical support for these hypotheses seems to be for climate (in particular H1; Hawkins *et al*., 2003b; Currie, 2007). However, the underlying mechanism is not clear (Currie *et al*., 2004). This may partly be caused by the lack of knowledge from local scales (most studies have used atlas-derived data), or perhaps because the hypotheses have been tested mainly on vertebrates and large vascular plants (see Hawkins *et al*., 2003b for review). Broad-scale analyses of diversity determinants in invertebrates are rather few, mostly restricted to families of large beetles (Kerr & Currie, 1999; Lobo *et al*., 2002), butterflies (Kerr *et al*., 2001; Hawkins & Porter, 2003), termites (Eggleton *et al*., 1994) or ants (Kaspari *et al*., 2000). Therefore, additional studies of new taxa, particularly the under-studied insects, potentially provide valuable pieces to the biodiversity riddle. Curiously, there is one group – the dragonflies – which has rarely been in the subject of broad-scale studies (but see Hof *et al*., 2006) although there is reliable information about their geographical distributions (Askew, 2004; Dijkstra & Lewington, 2006), and they are of great conservation interest (IUCN, 2004).

The goal of this study is to examine the three general hypotheses described above with respect to broad-scale variation of species richness of dragonflies (Odonata) in Europe and northern Africa. However, because of the geographical context of the study and the specific life history of dragonflies, two additional hypotheses are also considered to be relevant to western Palearctic Odonata species richness patterns:

H4: *Glaciation history*. This hypothesis obviously may apply to Europe, whose biota was strongly displaced by the Pleistocene ice movements. Therefore, species richness should be lower in areas most recently exposed by the retreat of the ice sheet during the most recent ice age (Montoya *et al*., 2007; Svenning & Skov, 2007).

H5: *The extent of water bodies.* All dragonflies are restricted to water as nymphs. Therefore, the amount of free-standing water (wetlands, ponds, rivers) may be the limit to population sizes and consequently influence both extinction and colonisation rates, which will result in impoverished species richness in areas with few bodies of water.

Materials and methods

Species richness patterns of Odonata in Europe and northwestern Africa (Fig. 1) were studied. The area was divided into 147 grid cells. Each cell was 220 km × 220 km, except for coastal cells in which cases neighbouring cells were merged to reduce differences in area. The grid was derived from the grid used by Hawkins and Porter (2003), although 15 cells from the eastern edge of the original grid were discarded because no distributional data were available for them.

The grid was overlaid on the range maps in Dijkstra and Lewington (2006), and the presence of each species was recorded. Recorded were only the species which had their main area of distribution in the grid cell (the dark purple in Dijkstra and Lewington, 2006) or where the species was reported to be uncommon/scattered but not declining (blue on the range maps). As is always the case, the range maps in Dijkstra and Lewington (2006) are estimates of true ranges which may limit the power of our analyses. On the other hand, it has been recently shown that this problem can be circumvented by using a sufficiently large grid resolution (Hurlbert & Jetz, 2007), and high quality range maps can capture richness gradients quite well (La Sorte & Hawkins, 2007). Even so, the distributional data from northern Africa may suffer from lack of knowledge and could be influenced by geographical isolation and specific climatic conditions. Therefore, two analyses were performed: (i) European and African data together (147 grid cells) and (ii) only European data (112 grid cells). Furthermore, data for water surface area were available only for Europe (Table 1), so this hypothesis could be tested only for this subset of data.

To assess the strength of evidence for the various hypotheses explaining Odonata species richness, 11 environmental variables were tested and are summarised in Table 1. For detailed descriptions and sources of those variables see Hawkins and Porter (2003). Each of the two data sets (Europe vs. Europe + northern Africa)

Table 1. Overview of variables used in regression analyses of Odonata species richness in Europe and northern Africa. For detailed description and data sources see Hawkins and Porter (2003).

	Details and (units)	Related hypothesis (see Introduction)	Mean		Median		Range	
			Eur + Afr	Eur	Eur + Afr	Eur	Eur + Afr	Eur
Odonata species richness			42.8	49.4	49	53	1–74	1–74
PET	Potential evapotranspiration (mm × day^{-1}) – a measure of the ability of the atmosphere to remove water from the surface through the processes of evaporation and transpiration assuming no control on water supply. It is a frequently used measure of energy input of an area.	H1	630.9	497	578.5	482	71–1350	71–1007
AET	Actual evapotranspiration (mm × day^{-1}) – the quantity of water that is actually removed from a surface due to the processes of evaporation and transpiration. It is a measure of water-energy balance.	H1	377.1	426.4	414	436	34–616	143–616
AGVI	Annual global vegetation index – an estimate of plant productivity within an area.	H1	74.6	80.44	77	80	42–110	49–110
SGVI	Summer global vegetation index – an estimate of plant productivity within an area.	H1	102.9	118.6	116.5	123	39–158	68–158
T_{annual}	Mean annual temperature (°C)	H1, H2	9.45	6.6	8.8	7.3	(–5.8)–24.2	(–5.8)–16.8
Elevation span	Highest minus lowest altitude (m) – a measure of intra-cell climatic gradients and a surrogate for habitat heterogeneity. We used the $\log_{10}$ form in all analyses.	H3	1264.7	1261	881	876	56–4657	56–4657
Land cover	Number of land cover types	H3	5.15	5.5	5	6	1–9	2–9
Plant species richness	Number of species of vascular plants	H3	1161	1236	1323	1363	150–2100	225–2100
Age	Thousands of years since the last glaciation (never glaciated cells were assigned 20)	H4	18	17.47	20	20	85–20	8.5–20
Precipitation	Mean annual precipitation (mm)	H1	574.5	689	582.5	619	19–2042	234–2042
Water surface area†	Not available for northern Africa. Dominant annual average soil water regime class of the soil profile. The variable consists of semi-quantitative units on a 1–4 scale.	H5	NA	1.49	NA	1.39	NA	0–3.4

†Available at http://eusoils.jrc.it/ESDB_Archive/ESDBv2/fr_intro.htm

was analyzed using ordinary least square (OLS) multiple regression in R (R Development Core Team, 2007). The best regression models containing one, two and three terms were constructed, starting with a full model (all possible terms) and removing the redundant terms using function 'step' in R [the function successively removes the terms with highest value of Akaike information criterion (AIC)]. The resulting models were trimmed manually (AIC as the selection criterion) so that we obtained the specified number of predictors. The reverse procedure was then employed – stepwise forward addition of terms (function 'add1' in R) which started with the null model (no terms at all) and one term was successively added in each step. The effect of every term in every step was assessed both as a linear effect and as a second-order polynomial, and the form providing the better AIC score was selected. Models from both procedures were compared and the model with the lowest AIC was selected as our best model. In case two values of AIC were indistinguishable (i.e. $\Delta\text{AIC} < 2$), the model with fewer number of terms was selected.

Inspection of the residuals in our two best OLS models revealed significant residual autocorrelation in the first distance class, indicating either the presence of a spatially structured process not accounted for by the variables in the model or that adjacent cells were more similar than expected due to the use of range map data. To examine the potential influence of residual spatial autocorrelation, an autocorrelation term was added into residuals of the best model using simultaneous autoregressive models (SAR; Fortin & Dale, 2005) and resulting standardised SAR coefficients were compared with the OLS coefficients. The SAR was performed in SAM 2.0 package (Rangel *et al.*, 2006). Although raw regression coefficients are unbiased by the presence of residual spatial autocorrelation, standardised coefficients may be unstable, and spatial modelling can be used to identify this instability (Hawkins *et al.*, 2007b).

Table 2. Alternative multiple regression models for species richness of Odonata. Models are ranked by the number of predictors in the model. Values of coefficients of determination (R^2) and the Akaike information criterion (AIC) are provided. The integers (1–4) under each term indicate the rank of the term in the multiple regression model according to its partial coefficient of determination. Models with similar values of AIC are considered to be statistically indistinguishable. Text in bold indicates the best model (see also Figs 1, 2). For abbreviations of model terms, see Table 1.

			Model terms				
	R^2	AIC	AET	PET	SGVI	Plants	Precipitation
Europe + Africa							
no term	0	879.2					
1 variable	0.758	653	1				
2 variables	0.8	619.5	1	2†			
3 variables	**0.81**	**610**	**1**	**2†**	**3**		
Europe only							
no term	0	620					
1 variable	0.76	466.2		1†			
1 variable	0.75	466.3	1†				
2 variables	0.77	457.9		1†		2	
2 variables	0.77	457.7	1†		2		
3 variables	**0.79**	**454.7**		**1†**		**2**	**3†**

†predictor entered the model as second order polynomial.

The metabolic theory was tested by comparing the slope(s) of a richness–temperature scatterplot against the value predicted by the version of the theory presented in Brown *et al.* (2004; b = –0.65). However, it was obvious from the scatterplot that the relationship was non-linear and it was inappropiate to estimate a single slope across the entire region. Therefore, the procedure of Da Silva Cassemiro *et al.* (2007) was followed by performing a geographically weighted regression (GWR) to estimate locally weighted slopes in different parts of the region. These slopes were then mapped to identify where slopes were closest to that predicted by the theory. The GWR was performed in Spatial Analysis in Macroecology (SAM, Rangel *et al.*, 2006).

Results

The dragonfly richness gradient is what would be expected for an insect with an aquatic nymphal stage and terrestrial adults, with richness being greatest in mesic Central Europe and lowest in both Scandinavia (cold) and northern Africa (dry) (Fig. 1). Thus, in the complete data set (Europe and northern Africa), the strongest term entering in all models was a positive linear coefficient of actual evapotranspiration (AET) (Table 2). Secondary variables appeared respectively in the

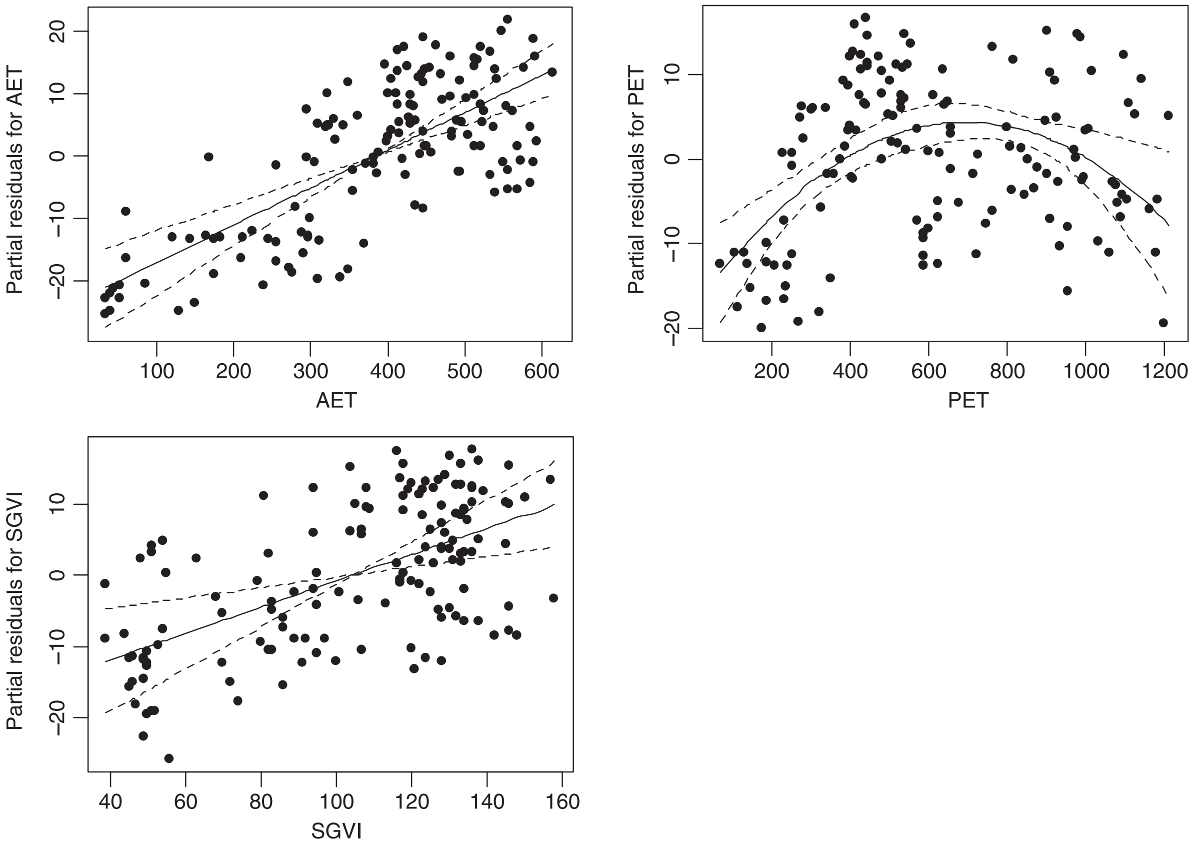

Fig. 2. Partial effects of predictor variables in the best OLS multiple regression model of Odonata species richness. Partial residuals are residuals remaining after fitting all model terms on the species richness except for the term of interest. Data are from Europe and northern Africa. Solid lines are regression lines, dashed lines are standard errors.

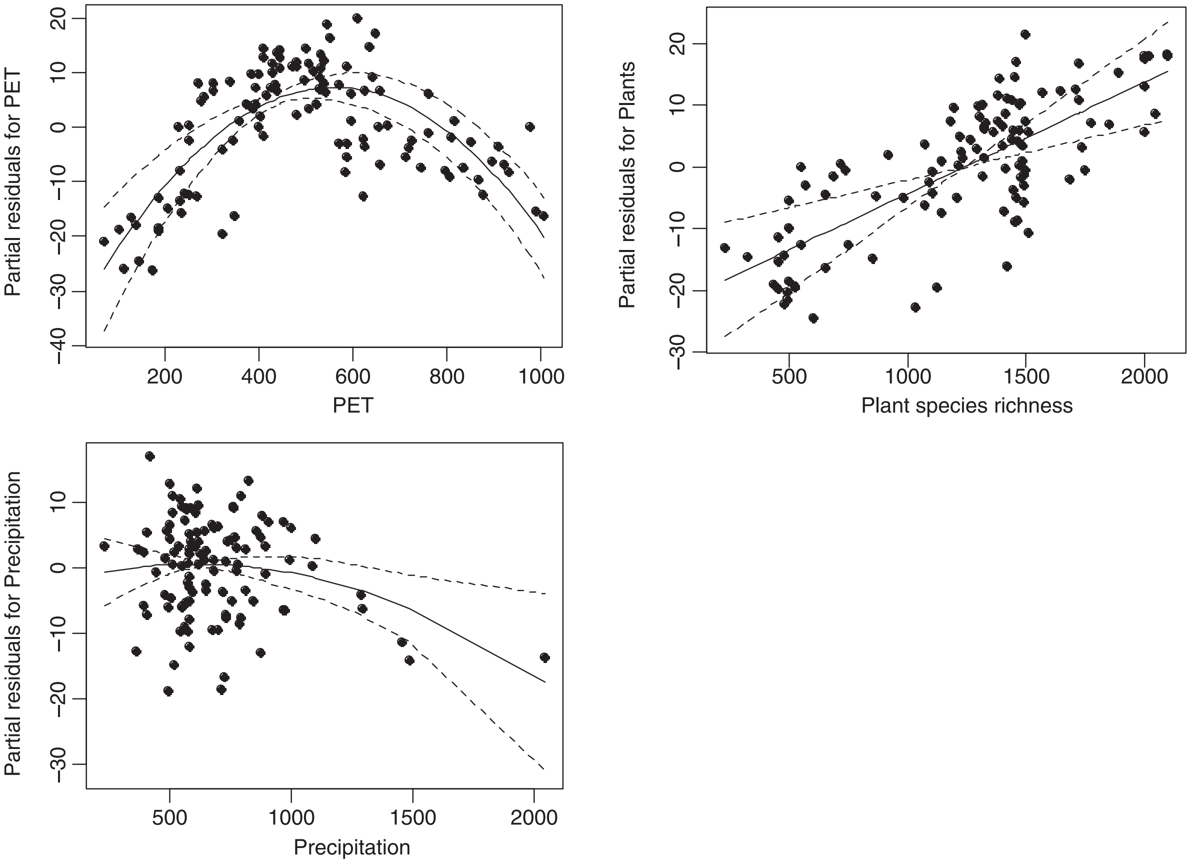

Fig. 3. Partial effects of predictor variables in the best OLS multiple regression model of European Odonata species richness. Partial residuals are residuals remaining after fitting of all model terms on the species richness except for the term of interest. Solid lines are regression lines, dashed lines are standard errors.

Table 3. Standardised coefficients (slopes) of individual predictors in the best multiple regression models (see Table 2 – models in bold letters). Here, we show that the incorporation of spatial structure into the best models using SAR did not change the coefficients of the most important predictors.

Predictor	OLS	*P*	SAR	*P*
Europe + Africa				
AET	0.47	< 0.001	0.47	< 0.001
PET	1.01	< 0.001	0.65	0.08
PET^2	–0.98	< 0.001	–0.5	0.15
SGVI	0.32	0.001	0.32	0.012
Europe only				
PET	2.17	< 0.001	1.7	< 0.001
PET^2	–2.18	< 0.001	–1.4	< 0.001
Plant species richness	0.52	< 0.001	0.39	0.01
Precipitation	0.16	0.32	0.11	0.38
Precipitation^2	–0.27	0.1	–0.18	0.16

model as it grew more complex: a concave polynomial of potential evapotranspiration (PET) and a linear positive coefficient of the summer global vegetation index (SGVI) (Table 2). The model with the lowest AIC was the three-variable model [AET + (PET + PET^2) + SGVI] (Fig. 2, Table 2). The model explained 81% of the variance in species richness.

Within Europe, the single best predictor of species richness was the concave polynomial of PET (Table 2). However, it was not distinguishable from the concave polynomial of AET

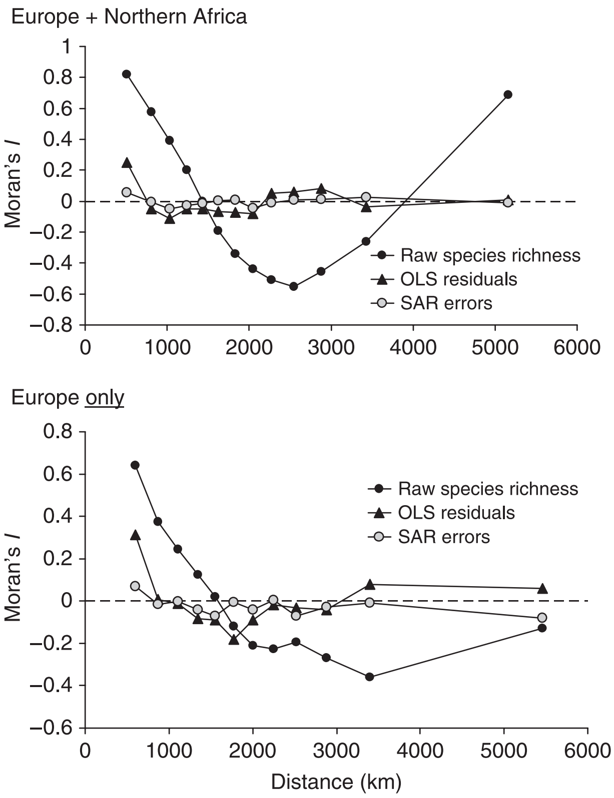

Fig. 4. Correlograms for (i) raw species richness data, (ii) residuals after fitting the best OLS model and (iii) errors of the SAR model. Moran's *I* is the measure of spatial autocorrelation between the value of at an average grid cell and the surrounding cells. The spatial autocorrelation was very strong in the raw species richness data. The best OLS models accounted for considerable part of it, but there still remained significant autocorrelation at first distance class that was incorporated in the SAR model.

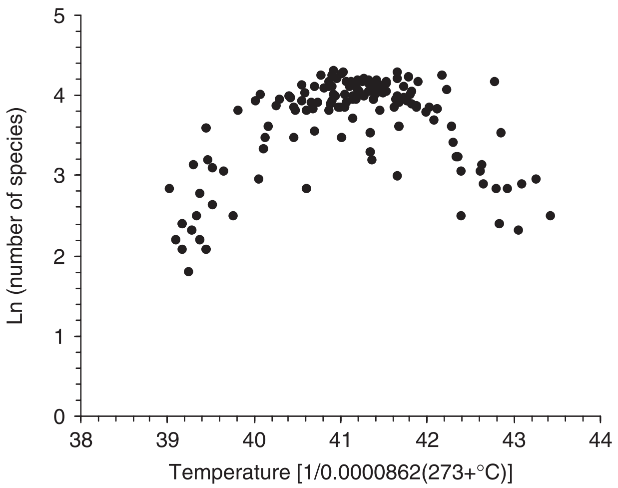

Fig. 5. Scatterplot of richness (ln transformed) and temperature rescaled to compare against predictions of metabolic theory [$1/T_k$ where *T* is temperature in Kelvines and k is the Boltzman's constant (0.0000862)]. Warmer cells are to the left of the plot and cooler cells are to the right.

(Table 2). We found two indistinguishable models in the two-variable model sets [(AET + AET^2) + SGVI and (PET + PET^2) + plant species richness]. Even though the shape of the AET relationship was concave, the curvature was so slight that the effect could be described as positive along the whole extent of the variable rather than strictly hump shaped. The best AIC was found for a single three-variable model [(PET + PET^2) + plant species richness + (precipitation + precipitation^2)] (Fig. 3, Table 2), which explained 79% of the variance in species richness.

After incorporation of spatial structure (SAR) into our best models, the standardised coefficients of the most important variables (AET, PET) did not change qualitatively (Table 3). This indicates that the OLS regression models are robust. Correlograms for OLS residuals and SAR errors are in Fig. 4.

Following the transformations of species richness and temperature necessary to test the metabolic theory, the relationship was strongly non-linear, with richness decreasing with increasing temperature in the hottest cells (recalling that temperature is measured as an inverse) (Fig. 4), no relationship at intermediate temperatures, and decreasing richness with decreasing temperature in the coldest cells (Fig. 5). Not surprisingly, geographically weighted regressions indicated that richness is depressed by increasing temperatures in northern Africa and much of southern and Central Europe, whereas it increases with increasing temperatures in northern Europe and scattered locations in Iberia, France and Bulgaria (Fig. 6). However, even when the relationship is in the same direction as predicted by temperature-based hypotheses, slopes close to those predicted by metabolic theory were found only when the regressions were anchored in just several cells in northern Europe (Fig. 6). Thus, we find no support for hypotheses that propose that temperature is the primary environmental driver of richness gradients, or for the specific patterns predicted by metabolic theory.

Discussion

The most important factor determining Odonata species richness was actual evapotranspiration or potential evapotranspiration – both measures of energy available to the primary producers in an area. This is most consistent with H1 (the species-energy hypothesis), although water–energy balance is not a direct measure of productivity or numbers of individuals. Given that AET or PET alone were able to explain over three-quarters of species richness variability in both data sets supports the notion argued by Currie (2007) that climate is a strong constraint to species richness, with the rest of the environmental complexity adding little. The proportion of variability explained by our environmental model across Europe and northern Africa is strikingly similar to the values reported by Hawkins and Porter (2003) and Hawkins *et al.* (2003a) who also found AET to be the strongest predictor of species richness of European butterflies ($R^2 = 0.8$) and European birds ($R^2 = 0.85$). Although it may seem surprising to

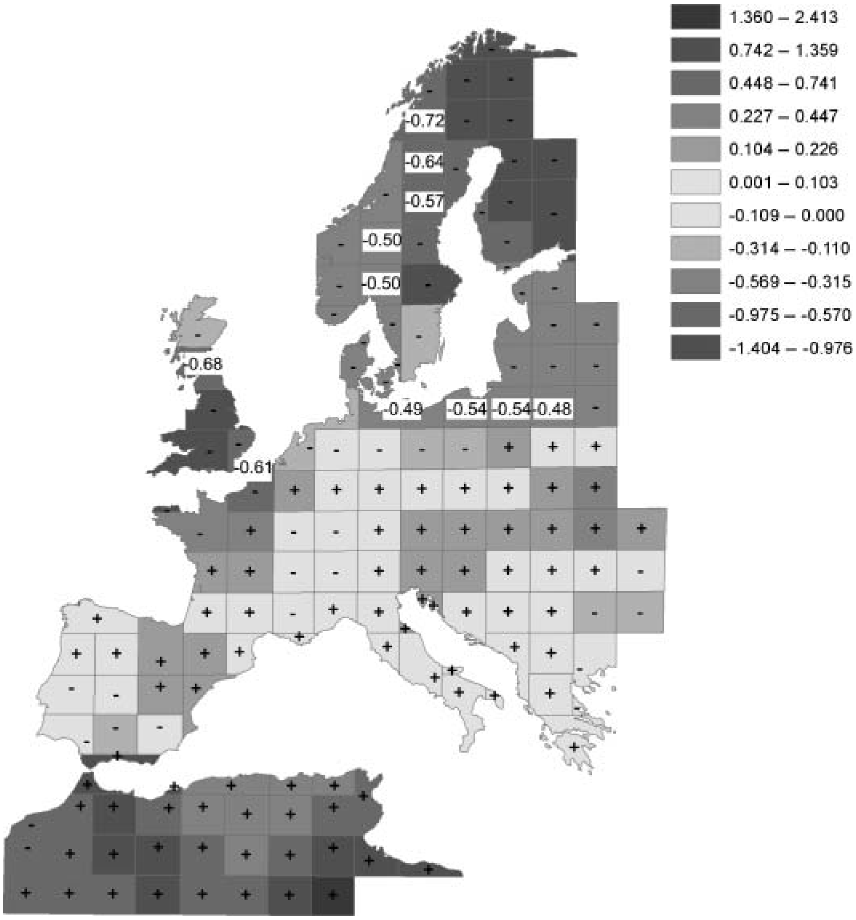

Fig. 6. Spatial variation in the slopes of geographically weighted regressions of ln richness against $1/T_k$. Shading classifies magnitudes of slopes, and +/– indicates if the relationship when the regression is anchored in each cell is positive (richness decreases with increasing temperature) or negative (richness increases with increasing temperature). The grid cells with values close to –0.65 (± 0.2) are highlighted.

find that similar trends in animal groups with quite distinct life strategies (aquatic dragonflies vs. terrestrial butterflies), it is consistent with the view that at large geographical scales general patterns may emerge across very different taxonomic groups (Lawton, 1999). However, as evapotranspiration is only an indirect measure of productive potential, it obviously did not explain all of the variation attributable to productivity. The remaining fraction of this variation remained to be explained by the vegetation index which mirrors the actual vegetation and site conditions rather than the potential ones. We interpret these results to be in concordance with the species-energy hypothesis, although they do not address the historical influences that may drive speciation and extinction rates (see e.g. Hawkins *et al.* 2007c).

A result that further supports the notion of the importance of available productive energy is the differences in the primary explanatory variables in the two data sets: the species richness is governed mainly by *potential* evapotranspiration in Europe but when the North African data were added the strongest variable was *actual* evapotranspiration. This supports the water-energy conjecture (Hawkins *et al.*, 2003b; Whittaker *et al.*, 2007) that in the north where water is broadly available, the limiting factor is the energy input whereas in the arid south (northern Africa) species richness is limited by water. This generates the hump-shaped response of species richness to potential evapotranspiration (a measure which ignores water availability) and the positive linear response to actual evapotranspiration (see also O'Brien, 2006).

There was a weak (yet significant) positive relationship of odonate richness with plant species richness in the models restricted to only European data. Although the positive association of plant species richness with animal species richness has been widely reported on local scale (Siemann *et al.*, 1998), the relationship has rarely been observed on large spatial scales (Hawkins & Porter, 2003; Hawkins & Pausas, 2004). This study shows that dragonflies may be one of the cases of such relationship. However, plant species richness explained only very small fraction of species richness variability – in fact so small, that such result would have been interpreted as being unimportant in similar studies (Hawkins & Porter, 2003). Furthermore, since all dragonflies and damselflies are predatory in both nymphal and adult stage, any relationship between their richness and that of plants cannot be directly causal and must reflect either indirect effects via prey availability or be spurious. We also found no support for the *glaciation history* or the *extent of water bodies* hypotheses, as neither relevant variable entered our regression models. We cannot conclude that such effects do not exist, but they have no independent predictive value beyond that provided by the variables in our environmental models.

Several studies investigating species richness patterns of other insect taxa have been carried out in comparable latitudes and spatial scales. The work which is most inconsistent with our findings is Kerr *et al.* (2001), who found habitat heterogeneity to be the most important factor shaping species richness patterns in Canada. However, Kerr *et al.*'s result is inconsistent with most other recent works. The primary explanatory variable for North American tiger beetles (Kerr & Currie, 1999), *Epicauta* (Kerr & Packer, 1997) and butterflies (Hawkins *et al.*, 2003b) was potential evapotranspiration. European butterflies (Hawkins & Porter, 2003) were associated with actual evapotranspiration and southwestern North American ants (Davidson, 1977) were influenced by a combination of precipitation and temperature. Our results are consistent with those studies, adding additional evidence that both water and energy are key for shaping species richness patterns of insects whether terrestrial or aquatic.

Acknowledgements

We are grateful to J.A.F. Diniz-Filho for help with the GWR analysis. The research was supported by the Grant Agency of Charles University (GAUK 106108) and by the Grant Agency of the Academy of Sciences of the CR (IAA601970801). P.K. was partly supported by doctoral grant 206/08/H049.

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Accepted 13 May 2008