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Environmental determinants of woody and herb plant species richness patterns in Great Britain[1]

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Abstract: There is evidence that broad-scale species richness patterns of woody plants correlate with contemporary gradients of environmental energy inputs and water availability. However, climate–richness relationships for herbaceous species are less well known. Here we analyze the seed-bearing flora of Great Britain, quantifying the relationships between total, herb, and woody plant species richness and 14 environmental predictors measuring levels of energy, water, or combined energy and water. PCAs of the environmental variables identified the primary trends of environmental variation across Great Britain related to mean annual temperature and annual precipitation. OLS multiple regression and partial regression analyses identified mean annual temperature as the strongest driver of richness for all species groups. Similarly, reparameterized versions of published energy–water models for woody plant species richness and for angiosperm family richness gradients also identified energy variables as the primary predictors of the richness of all, woody, and herb species.

Keywords: AIC, herbaceous plant richness, latitudinal biodiversity gradient, seed-bearing plants, water–energy dynamics, woody plant richness.

Résumé : Il y a des évidences indiquant que les patrons à grande échelle de la richesse en espèces des plantes ligneuses sont corrélés avec les gradients environnementaux actuels de l'apport en énergie et de la disponibilité en eau. Cependant, pour les plantes herbacées, les relations entre le climat et la richesse en espèces sont moins bien connues. Nous analysons ici la flore des plantes à graines de la Grande-Bretagne en quantifiant les relations entre la richesse totale en espèces, celles des herbes et des plantes ligneuses et quatorze variables environnementales explicatives mesurant les niveaux d'énergie, d'eau, ou une combinaison de l'énergie et de l'eau. Des analyses en composantes principales des variables environnementales ont identifié la température moyenne annuelle et les précipitations annuelles comme facteurs explicatifs des principales tendances de la variabilité environnementale à travers la Grande-Bretagne. Des analyses de régression multiple MCO (moindres carrés ordinaires) et de régression partielle ont identifié la température moyenne annuelle comme le principal facteur d'influence de la richesse pour tous les groupes d'espèces. Des versions reparamétrisées de modèles énergie-eau publiés dans la littérature pour la richesse en espèces des plantes ligneuses et pour les gradients de richesse de la famille des angiospermes ont également identifié des variables énergétiques comme principaux facteurs explicatifs de la richesse de toutes les espèces, ligneuses et herbacées.

Mots-clés : critère d'information d'Akaike (AIC), dynamique énergie-eau, gradient latitudinal de biodiversité, plantes à graines, richesse des plantes herbacées, richesse des plantes ligneuses.

Introduction

A number of hypotheses have been proposed to explain the spatial distribution of plant species richness at broad scales (Wright, 1983; Currie & Paquin, 1987; Adams & Woodward, 1989; O'Brien, 1993; 1998; Francis & Currie, 2003; Hawkins *et al.*, 2003; Whittaker, Nogués-Bravo & Araújo, 2007). In general, it is widely accepted that contemporary climate (Currie, 1991; O'Brien, 1993; 1998; Francis & Currie, 2003) and regional and historical factors (Montoya *et al.*, 2007; Svenning & Skov, 2007; Qian, 2009) strongly influence patterns of plant species richness over broad geographic extents. Because all (photosynthetic) plants require sunlight and water for survival, energy and water availability are considered to be the major environmental determinants of plant richness variation at large scales.

There have been various attempts to build general models explaining plant richness variation based on climate. Francis and Currie (2003) developed a model comprising water deficit and potential evapotranspiration (PET) that explained up to 84% of the global pattern of richness of angiosperm families. Using a different approach, O'Brien (1993; 1998) developed a conceptual framework to define the biological basis of the observed strong co-variation between woody plant species richness and rainfall

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and energy, which she termed the "biological relativity to water–energy dynamics" hypothesis (O'Brien, 2006) (for brevity, we use the expression "water–energy dynamics"). Although this modelling approach was developed using woody plant richness data from Africa, the author suggested that tree diversity gradients in cold climates would be reasonably modelled by rainfall alone since this variable reflects conditions when there is sufficient energy for woody plants to be active (O'Brien, 1998). This prediction was verified by Hawkins *et al.* (2007) for tree richness patterns in Europe and North America, providing further evidence that the water–energy dynamics hypothesis might be a sensible explanation for observed climate richness relationships.

However, tests of these ideas have focused on woody species (*e.g.*, Field, O'Brien & Whittaker, 2005; Field, O'Brien & Lavers, 2007; Hawkins *et al.*, 2007), whereas analyses involving herbaceous plants have been conducted at smaller spatial scales (*e.g.*, Bhattarai & Vetaas, 2003). Thus, the ability of the water–energy dynamics hypothesis to explain richness gradients of all plant forms awaits confirmation. This is a basic issue for understanding the geographic distribution of biodiversity and predicting how plant species richness patterns may shift as a response to future climate changes.

Here, we explore these issues for Great Britain using plant species distribution maps (atlas data) available at a resolution of 10 km (Preston, Pearman & Dines, 2002). Our main goals were to identify the primary environmental drivers of plant species richness in Great Britain and to determine whether these drivers differ between herbaceous and woody plants. We also tested the ability of the Francis and Currie (2003) and O'Brien (2006) climate models to account for the observed variation in species richness of woody and herbaceous plants in this region.

Methods

DISTRIBUTION DATA

Distribution maps of the terrestrial seed-bearing flora of Great Britain (Preston, Pearman & Dines, 2002) were digitized and processed in Arc GIS 9.3 to generate cell richness values for herbs (1305 species), woody plants (147 species), and for all species combined.

ENVIRONMENTAL VARIABLES

Potential explanatory variables were selected on the supposition that climatic gradients are the main factors determining broad-scale species richness variation (O´Brien, 1993; 1998; Hawkins *et al.*, 2003; Rodríguez, Belmontes & Hawkins, 2005; Whittaker, Nogués-Bravo & Araújo, 2007). Most studies have used measures of energy availability (Schall & Pianka, 1978), water availability (O'Brien, Field & Whittaker, 2000), or combined water–energy variables (Currie, 1991; Francis & Currie, 2003) as predictors of species richness. Accordingly, we included a set of 14 variables, grouped into 4 main categories:

i. Energy: Annual potential evapotranspiration (PET), minimum monthly potential evapotranspiration (Min PET), and maximum monthly potential evapotranspiration (Max PET), mean annual temperature, mean January temperature, annual range of temperature, insolation (hours of sunshine), number of frost days, and growing season length. These variables were selected as alternative measures of ambient energy (Hawkins *et al.*, 2003; Rodríguez, Belmontes & Hawkins, 2005). Gridded data sets were obtained from Met Office Weather and Climate Change Forecasts for the UK and worldwide (Perry & Hollis, 2005). We calculated PET using the Thornthwaite formula (Thornthwaite, 1948).

ii. Water: Annual precipitation, annual rainfall, and water deficit (WD). Following Francis and Currie (2003), rainfall was estimated as the total precipitation in months with mean temperatures above 0 ºC, and WD as PET minus annual actual evapotranspiration (see below). Precipitation data were obtained from the Met Office (Perry & Hollis, 2005).

iii. Combined water–energy: Annual actual evapotranspiration (AET). This variable was generated by combining values of temperature and precipitation through Turc's formula (Turc, 1954).

iv. Topography: Elevation range was included as a measure of mesoscale climatic variation (O'Brien, Field & Whittaker, 2000) and calculated as the difference between maximum and minimum elevations in each grid cell. Elevation data were obtained from GTOPO30, a global digital elevation model developed by the US Geological Survey at EROS Data Center regional scale (available at http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html).

STATISTICAL ANALYSES

Relationships between environmental predictors and richness were investigated by generating 2 sets of OLS (Ordinary Least Squares) multiple regression models (see below). Firstly, a set of models (hereafter *ad hoc* models) was generated based on the empirical relationships found in our environmental data. Initially, Pearson's correlations were used to relate plant species richness variables with the environmental predictors. Then, we carried out a principal component analysis (PCA), using a "broken stick" stopping criterion (Jackson, 1993), in order to reduce data dimensionality. However, all water, energy, and topography variables exhibited their highest loadings ($> |0.70|$) in the first PCA factor. This indicated strong covariation of water and energy gradients across Great Britain, and also that a PCA-based data reduction was not appropriate to evaluate potential separate effects of these gradients on our plant richness variables. Thus, we adopted a modified strategy based on generating a Varimax-rotated PCA. This rotation maximizes the variance of the loadings across the PCA factors, thus making their interpretation easier and more reliable (*i.e.*, easier to replicate with different data samples) (*e.g.*, see Cattell, 1978). In other words, this procedure allows a clearer identification of major environmental gradients, as well as of the predictors that best represent them (*i.e.*, those showing higher loadings in the main rotated PCA factors). The highest factor loadings (> |0.90|) for the first factor corresponded to 4 energy predictors (mean annual temperature, mean January temperature, min PET, and growing season length) (Table I), of which mean annual temperature was the strongest correlate of richness variables in all cases (Pearson *r*'s ranging from 0.60 to 0.69) (Appendix I), whereas the highest factor loadings (> |0.86|) for the second factor corresponded to 2 water variables (annual precipitation and annual rainfall), with annual precipitation being the strongest correlate of richness variables in all cases (Pearson *r*'s ranging from –0.41 to –0.48) (Table II). Thus, we selected mean annual temperature and precipitation for our *ad hoc* models. Additionally, since multicollinearity among model predictors is not reduced by this procedure, we complemented it with partial regression analysis, which we used to partition the variance explained by the variables included in the *ad hoc* models into independent and covarying components (*e.g.*, see Hawkins, Porter & Diniz-Filho, 2003).

As a complement to this modelling exercise, we conducted a set of analyses aimed at exploring potential influences of spatial autocorrelation on *ad hoc* models. On the one hand, we built Moran's *I* correlograms for each plant group using 22 distance classes to quantify how well temperature and precipitation removed spatial autocorrelation in model residuals. On the other hand, we used simultaneous autoregressive (SAR) models (*e.g.*, Kissling & Carl, 2008) and spatial eigenvector mapping (SEVM) (Borcard & Legendre, 2002) to generate spatial versions of our *ad hoc* models and check for overall consistency of their standardized regression coefficients (Bini *et al.*, 2009).

Secondly, following Montoya *et al.* (2007), another set of models consisted of reparameterized versions of published climatic models that have shown strong statistical explanatory power of large-scale richness patterns of vegetation. Specifically, we analyzed the water deficit and PET model of Francis and Currie (2003) (hereafter F&C)

TABLE I. Loadings (expressed as correlations) of the environmental predictors in the 2 first factors of the Varimax-rotated principal component analyses (PCA) performed. Correlations higher than |0.85| are highlighted in bold and indicate that, in all cases, Factor 1 is mainly associated with energy inputs to the environment and Factor 2 reflects water availability. The cumulative percentage of variance described by these factors is also given.

	PCA factors	
Environmental predictor	Factor 1	Factor 2
Energy variables		
Mean annual temp.	**0.90**	–0.31
Mean January temp.	**0.98**	–0.04
Annual temp. range	0.26	–0.53
PET	**0.87**	–0.41
Min PET	**0.90**	–0.03
Max PET	0.45	–0.80
Insolation	0.76	–0.46
Number of frost days	**–0.88**	0.11
Growing season length	**0.93**	–0.13
Water variables		
Annual precipitation	–0.31	**0.86**
Annual rainfall	–0.31	**0.86**
Water deficit	0.10	**–0.91**
Energy and water		
AET	0.51	0.78
Topography		
Elevation range	–0.41	0.48
Cumulative variance (%)	50.44	79.56

TABLE II. OLS models for total, herb, and woody plant richness. For each richness variable and grain, models are ranked from best to worst fits (according to increasing AIC), with the ΔAIC values indicating the difference between each model and the best model in AIC units. Adjusted R^2s, standardized regression coefficients (in parenthesis), and the AIC weights (W_i) are also given.

Model type	Predictors[1] in model and their standardized regression coefficients				AIC	ΔAIC	W_i	R^2
Total richness								
ad hoc	Mean Ann Temp (0.59)	Ann Precip (–0.18)			25746	0	1.00	0.49
F&C	WD (–0.10)	PET (–2.05)	PET^2 (2.76)		25921	175	0.00	0.45
RWEM4	Rain (–0.31)	MinPET (0.18)	MinPET^2 (0.22)	ln(ER) (–0.08)	26201	455	0.00	0.38
RWEM2	Rain (–0.35)	MinPET (0.19)	MinPET^2 (0.22)		26218	472	0.00	0.37
RWEM1	Rain (–0.11)	MaxPET (–0.05)	MaxPET^2 (0.53)		26380	634	0.00	0.32
RWEM3	Rain (–0.11)	MaxPET (–0.06)	MaxPET^2 (0.54)	ln(ER) (0.01)	26382	636	0.00	0.33
Herb richness								
ad hoc	Mean Ann Temp (0.59)	Ann Precip (–0.19)			25307	0	1.00	0.50
F&C	WD (–0.10)	PET (–2.12)	PET^2 (2.84)		25456	149	0.00	0.46
RWEM4	Rain (–0.31)	MinPET (0.16)	MinPET^2 (0.25)	ln(ER) (–0.08)	25727	420	0.00	0.39
RWEM2	Rain (–0.35)	MinPET (0.17)	MinPET^2 (0.25)		25746	439	0.00	0.38
RWEM3	Rain (–0.12)	MaxPET (–0.12)	MaxPET^2 (0.59)	ln(ER) (0.03)	25957	650	0.00	0.33
RWEM1	Rain (–0.12)	MaxPET (–0.11)	MaxPET^2 (0.59)		25995	688	0.00	0.33
Woody richness								
ad hoc	Mean Ann Temp (0.53)	Ann Precip (–0.13)			15866	0	1.00	0.38
F&C	WD (–0.02)	PET (–1.19)	PET^2 (1.76)		16147	281	0.00	0.30
RWEM3	Rain (–0.02)	MaxPET (–0.44)	MaxPET^2 (0.13)	ln(ER) (0.10)	16200	334	0.00	0.28
RWEM1	Rain (–0.02)	MaxPET (–0.49)	MaxPET^2 (0.02)		16214	348	0.00	0.28
RWEM4	Rain (–0.29)	MinPET (0.31)	MinPET^2 (–0.05)	ln(ER) (–0.05)	16371	505	0.00	0.23
RWEM2	Rain (–0.30)	MinPET (0.31)	MinPET^2 (–0.05)		16374	508	0.00	0.22

[1] Predictors: Mean Ann Temp = Mean annual temperature; Ann Precip = Annual precipitation; WD = Water deficit; Rain = Rainfall, total precipitation in months when mean temperature > 0 ºC; PET = annual potential evapotranspiration (Thornthwaite's formula); MaxPET = maximum monthly potential evapotranspiration (Thornthwaite's formula); MinPET = minimum monthly potential evapotranspiration (Thornthwaite's formula); ER = elevation range (O'Brien, 1993; 1998; Field, O'Brien & Whittaker, 2005); F&C = the water–energy model of Francis and Currie (2003). RWEM (1, 4) = regional water–energy models (O'Brien, 1998; Field, O'Brien & Whittaker, 2005).

in which PET is modelled including a linear and a quadratic term, and 4 versions of O'Brien's water–energy models (hereafter regional water–energy models; RWEM); namely, 2 models including rainfall and linear and quadratic terms of either MaxPET or MinPET (RWEM1 and RWEM2 models) and 2 models that also include topography measured as log-transformed range in elevation (RWEM3 and RWEM4 models) (see O'Brien, 1998 and Field, O'Brien & Whittaker, 2005 for a discussion of the theoretical bases of these models).

Finally, we generated 3 Information Theory–derived indexes (AIC, ΔAIC, and the Akaike weights W_i) to identify the model best supported by the data across all models (see Burnham & Anderson 2002; Johnson & Omland, 2004). All statistical analyses were performed in R (R Development Core Team, 2009) including its packages "vegan" (Oksanen *et al.*, 2009) and SAM (Rangel, Diniz-Filho & Bini, 2010).

Results

Overall, the geographic pattern of total, herb, and woody plant species richness in Great Britain was similar for all species groups, with species richness generally increasing southwards, although with some high richness areas also occurring in central England (see Figure 1). Consistent with the observed patterns of distribution of species richness variables across Great Britain, richness values for all, herb, and woody plant species were spatially autocorrelated, reflecting patterns characteristic of clines, with higher positive spatial autocorrelation occurring at shorter distances and gradually becoming negative at larger distances (Figure 2).

Because richness patterns are similar, the relationships between plant species richness and most environmental predictors are also similar in herb and woody plants. Energy-related variables were generally the strongest

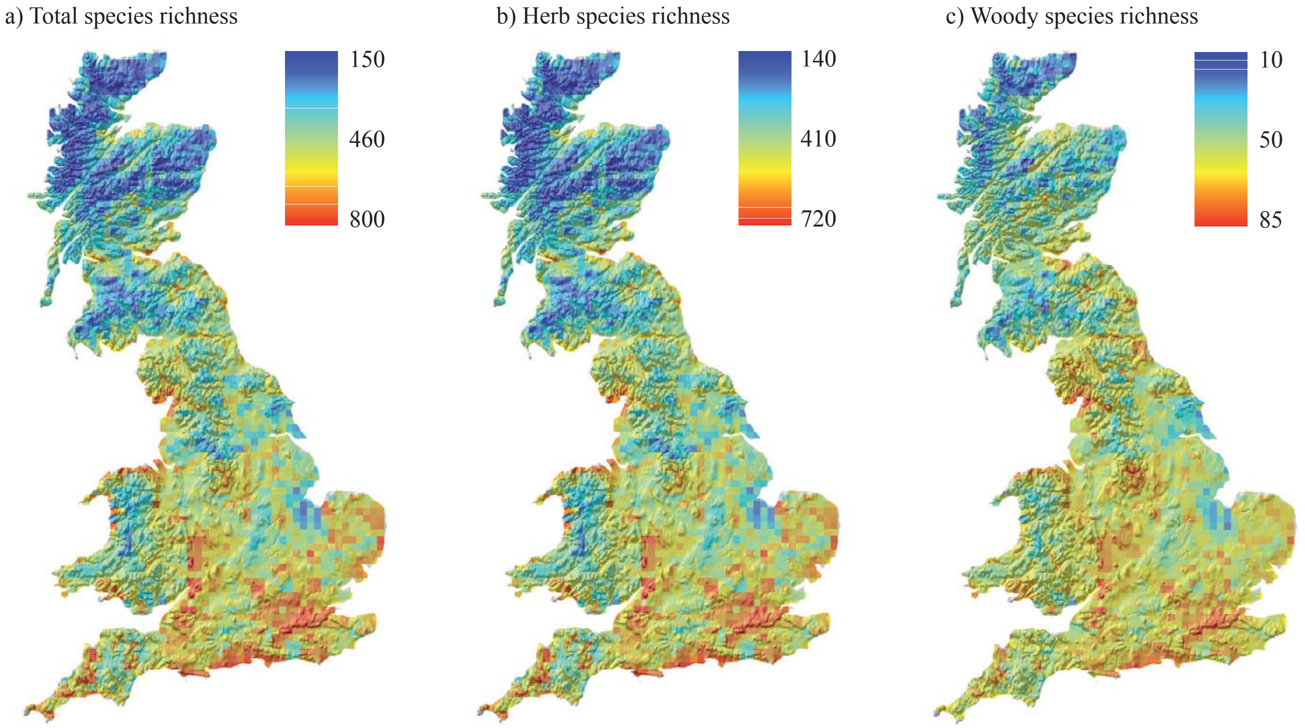

FIGURE 1. Geographical patterns of total (a), herb (b), and woody (c) plant species richness in Great Britain.

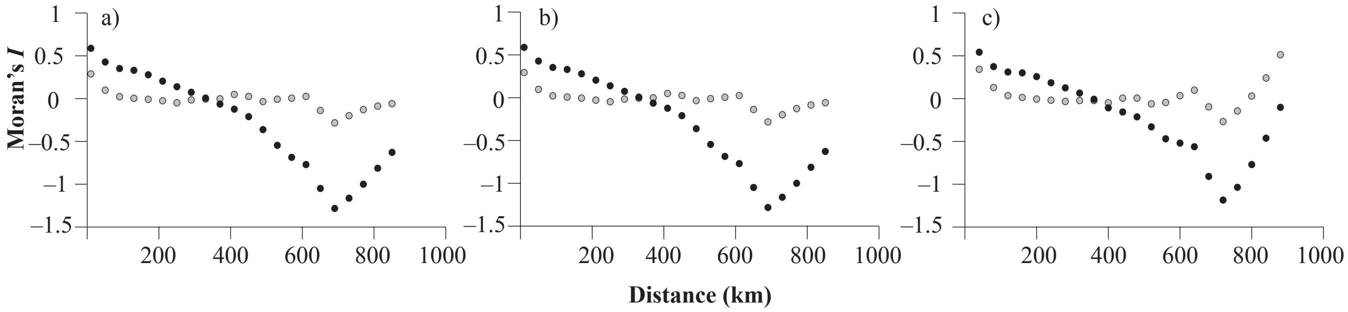

FIGURE 2. Moran's *I* correlograms for OLS multiple regression (*ad hoc*) models including mean annual temperature and annual precipitation fitted to the richness of total (a), herb (b), and woody (c) plants (black circles) and for residuals (grey circles).

positive correlates of plant species richness, with mean annual temperature and insolation showing the highest correlation in all cases (Appendix I). Correlations with water variables were more moderate, but surprisingly, negative (Appendix I).

According to their coefficients of determination and the Information Theory–derived indexes, the *ad hoc* models provided the best description of richness patterns in all plant groups (Table II). As is commonly the case in grid-based analyses, these models also accounted for most of the spatial autocorrelation in the data except for the shorter distance classes (Figure 2). Still, SAR and SEVM versions of the *ad hoc* models suggested that this residual autocorrelation did not affect standardized regression coefficients, as their sign and rank were similar in all instances (Table III).

Across all models, energy-related variables were generally more important for plant species richness variation than water variables (Figure 3), as indicated by the absolute values of the standardized regression coefficients of the predictors in the models. This was not true, however, for RWEM models that included MinPET (*i.e.*, RWEM2 and RWEM4), but these models showed poorer fits than *ad hoc* and F&C models (Table II).

We also found that the variance explained by the models was higher for herbs and total plant richness than for woody plants (*e.g.*, R^2 = 0.50, R^2 = 0.49, and R^2 = 0.38, respectively for the *ad hoc* models). Partial regression analyses of the relationships described by the best model (*i.e.*, *ad hoc* models) indicated substantial covariance between energy (*i.e.*, mean annual temperature) and water availability (annual precipitation) (Figure 4). However, the independent effects of temperature on richness were far greater than those of precipitation in all cases. This suggests that broad-scale patterns of total, herb, and woody plant species richness across Great Britain are primarily driven by energy gradients.

Discussion

Our data indicate that plant species richness patterns in Great Britain are largely associated with current climatic gradients, consistent with previous analyses of woody plant gradients in different parts of the world (Currie & Paquin, 1987; Currie, 1991; O' Brien, 1993; 1998; Hawkins *et al.*, 2007; Montoya *et al.*, 2007), with global plant family richness gradients (Francis & Currie, 2003), and also with results found for all vascular plant richness in the Austrian Alps (Moser *et al.*, 2005). Given the overwhelming evidence that plants respond to contemporary climate (see Hawkins *et al.*, 2003 for a review involving numerous plant and animal groups), this aspect of our results was expected. The paucity of distributional data for herbaceous plants has limited most tests of the O'Brien (1993; 1998; 2006) water–energy dynamics hypothesis to woody plant species. In a recent compilation of the literature on the relationship between contemporary climate and broad-scale biogeographic patterns of species richness (Hawkins *et al.*, 2003), only 2 of a total of 22 studies for plants were for herbaceous species (Schulze *et al.*, 1996) or grasses (Meserve & Glanz, 1978). Even so, our results for total, herb, and woody plant

Table III. Standardized regression coefficients and coefficients of determination (R^2) of multiple regressions for total, herb, and woody plant species richness, according to ordinary least-squares (OLS), simultaneous autoregressive models (SAR), and spatial eigenvector mapping (SEVM). All coefficient estimates were significant. Predictors: Mean Ann Temp = Mean annual temperature; Ann Precip = Annual precipitation. Moran's *I* residual autocorrelation and the Akaike information criterion (AIC) values are also given.

Richness variable	Predictors in the model				
	Mean Ann Temp	Ann Precip	AIC	Moran's *I*	R^2
Total					
OLS	0.59	–0.19	25476	0.305	0.49
SAR	0.19	–0.06	25335	0.210	0.58
SEVM	0.40	–0.20	24829	0.158	0.66
Herb					
OLS	0.59	–0.19	25307	0.294	0.50
SAR	0.19	–0.06	24918	0.212	0.57
SEVM	0.39	–0.20	24413	0.152	0.66
Woody					
OLS	0.53	–0.14	15866	0.342	0.38
SAR	0.08	–0.02	15513	0.214	0.52
SEVM	0.38	–0.12	14486	0.139	0.66

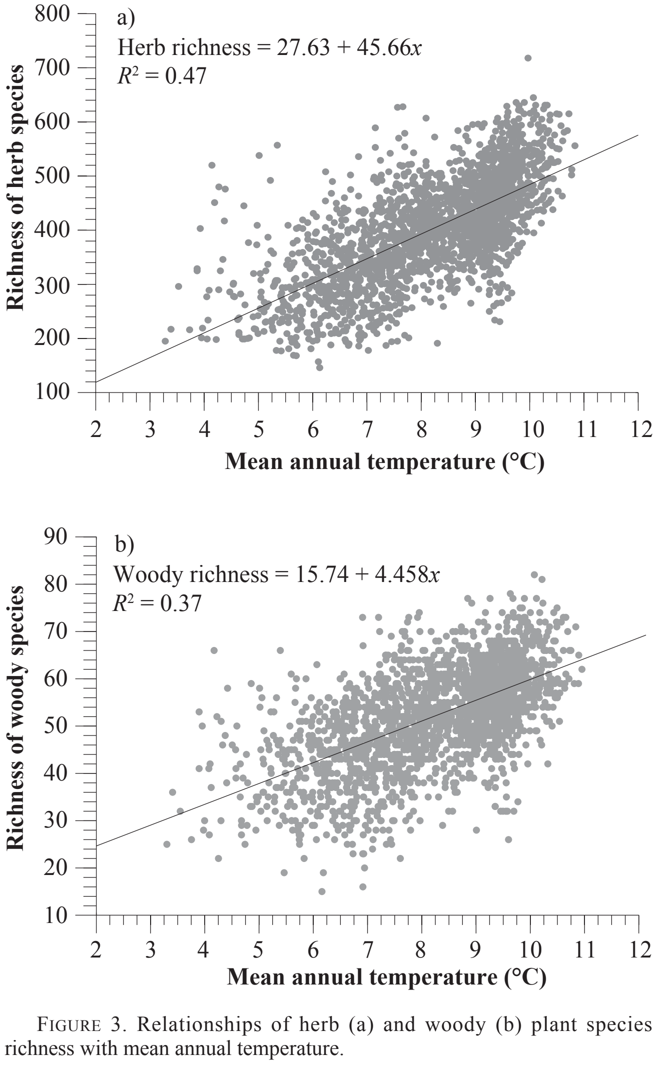

Figure 3. Relationships of herb (a) and woody (b) plant species richness with mean annual temperature.

species do not identify the reparameterized versions of O'Brien's water–energy models (see O'Brien, 1998; Field, O'Brien & Whittaker, 2005) as the strongest empirical predictors of plant richness. OLS, SAR, and SEVM models and partial regression analyses suggest that the richness of British plants is far more strongly associated with temperature than with precipitation or rainfall. This is inconsistent with the proposition derived from the water–energy dynamics hypothesis that plant diversity gradients in cold climates can be reasonably modelled by rainfall alone (see O'Brien, 1998).

A strong influence of energy in climate models in Great Britain also contrasts with the results of Hawkins *et al.* (2007), who found that woody plant richness gradients in both North America and Europe were better explained by rainfall than by temperature. This discrepancy may be partially due to differences in the scale of analysis and the geographical area covered by both studies, but it is likely that it also reflects that the macroclimate of Great Britain is generally humid (see the updated Köppen–Geiger climate classification developed by Kottek *et al.*, 2006), so water availability limits plant richness in few or no parts of the island.

An alternative theoretical framework in which to place our results is the conjecture of Hawkins *et al.* (2003), which ascribes a major role to energy in cold macroclimates and to water availability in warm macroclimates. The strong associations of energy variables with richness patterns of both herbaceous and woody plants are similar irrespective of the modeling approach. So far, water has been found to be the strongest correlate of woody species richness in the Neotropics (Gentry, 1992; Clinebell *et al.*, 1995), of tree species in South America (Kay *et al.*, 1997) and Madagascar (Ganzhorn *et al.*, 1997), of herb and shrub richness in Chile (Meserve & Glanz, 1978), and of grass richness in Namibia (Schulze *et al.*, 1996). In contrast, in temperate regions of the Northern Hemisphere, woody plant richness measurements have generally appeared strongly associated with the combined variation of water and energy, as measured by actual evapotranspiration (Currie & Paquin, 1987; Currie, 1991), or by a variable estimating net primary production based on water and energy relationships (Adams & Woodward, 1989). Consistent with these results, the Hawkins *et al.* (2003) conjecture, and with the temperate macroclimate of Great Britain, we found that, for all plant species groups, species richness gradients were primarily determined by energy inputs to the environment. This has implications for initiatives aimed at conserving local plant biodiversity (*e.g.*, see Prendergast *et al.*, 1993), but it still does not change the fact that similar richness gradients and associations with environmental predictors were observed in all plant groups.

Unexpectedly, we found that our climatic models better explain richness patterns in herbs than in woody plants (best models [*ad hoc*]: $R^2 = 0.50$ *versus* $R^2 = 0.38$). Although our study was not designed to explore the causes of such differences between herb and woody richness patterns, they may be associated with evolutionary processes and dispersal. Herbs and wood species show differences in their respective generation times (time from seed germination to the first flower) (Eriksson & Bremer, 1991; Smith & Donoghue, 2008), and these differences can impose limits to climate tolerance evolution (Smith & Beaulieu, 2009). In contrast to the short generation times and high rates of molecular evolution displayed by herbaceous species (Smith & Donoghue, 2008; Smith & Beaulieu, 2009), woody plant species are constrained by long generation times and slow rates of molecular evolution. This limits their divergence from ancestral climate tolerances before they migrate to available space, thus reducing the area they can potentially colonize. In addition, there is evidence to suggest that occasional events of long-distance dispersal dominated the Holocene colonization of northern temperate forests by woodland herbs (Cain, Damman & Muir, 1998), which also contrasts with the lags in colonization documented for woody plant species in the same period (Svenning & Skov, 2007). This means that climate space as explored by woody species is often smaller when compared to herbaceous taxa (Smith & Beaulieu, 2009) and that, in a context of environmental change, herbaceous species may be able to better track the new emerging environmental conditions. Thus, the differences in generation times and dispersal events between herbs and woody plant species likely play a role in the spatial patterns of these 2 groups across Great Britain.

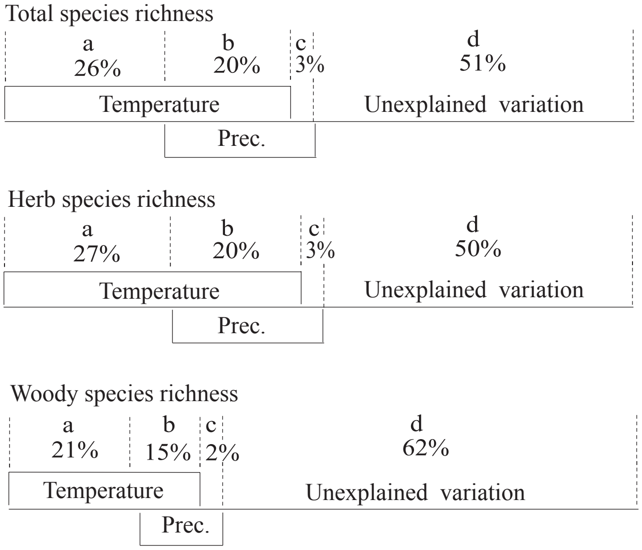

FIGURE 4. Results of partial regression analyses using mean annual temperature (Temperature) and annual precipitation (Prec.) as predictors of total (a), herb (b), and woody (c) plant species richness patterns in Great Britain. The unexplained variation (d) is $1 - R^2$ of an OLS model including both temperature and precipitation (*i.e.*, the R^2 of this model equals the portion a + b + c). The overlap between temperature and precipitation (b) is equal to (a + b) + (b + c) – (a + b + c), where (a + b) is the R^2 of a regression using temperature and (b + c) is the R^2 of a regression using precipitation. Variation explained by temperature only is given by (a) and by precipitation only by (c).

In summary, consistent with previous analyses of plant species gradients worldwide, plant species richness patterns in Great Britain (both herbs and woody plant species) are largely associated with current climatic gradients, with energy variables being most relevant (according to Hawkins *et al.*'s conjecture). The climate–richness models developed here show that herbaceous species have clearer relationships in their richness patterns with current climate when compared to woody plants. Attributes such as short generation times and long-distance dispersal events could make herbaceous species more able to respond to environmental changes and less sensitive to the actions of non-climatic factors that might be able to disrupt the signal left by climate on richness gradients, such as those caused by human impacts. The long history of human occupation in Britain (Ingrouille, 1995) is consistent with this interpretation, and suggests a future avenue of investigation into the drivers of plant richness gradients in highly populated regions.

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Appendix I

APPENDIX I, TABLE 1. Correlations of total, herb, and woody plant species richness with 14 environmental predictors in Great Britain.

	Species richness		
Environmental predictor	Total	Herb	Woody
Energy variables			
Mean annual temp.	0.69	0.69	0.60
Mean January temp.	0.65	0.64	0.50
Annual temp. range	0.30	0.31	0.37
PET	0.67	0.66	0.54
Min PET	0.53	0.52	0.38
Max PET	0.57	0.57	0.53
Insolation	0.73	0.72	0.60
Number of frost days	0.60	0.58	0.41
Growing season length	–0.60	–0.58	–0.41
Water variables			
Annual precipitation	–0.48	–0.48	–0.41
Annual rainfall	–0.48	–0.48	–0.41
Water deficit	0.33	0.33	0.26
Energy and water			
AET	0.10	0.10	0.09
Topography			
Elevation range	–0.42	–0.42	–0.37