



Original article

Assessing the influence of environmental and human factors on native and exotic species richness

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ABSTRACT

Understanding the ecological determinants of biological invasions is a key issue for predicting the spread of exotic species over broad geographical extents. The goal of this study was to investigate independent and combined effects of climatic and human-related factors on native and exotic plant species richness in Great Britain. We used multiple and partial regression techniques and spatial methods to investigate the effect of these variables on species richness. The highest plant richness was found in southeastern Great Britain and the lowest in the North for both native and exotic species. We found that energy input was the best predictor of either native or exotic plant richness, followed by water availability. Richness increased linearly with energy input for native plants, but exponentially for exotics. This is probably due to the lower chances of exotic species to succeed in low-energy sites, and/or to the lower species saturation of more productive ecosystems. The low portion of richness variance explained by human footprint was probably due to the study scale and to the overlapping between climatic and human factors. We conclude that the environment–human models are robust to enhance our understanding of the factors controlling the distribution of exotic species. Models containing water–energy measures can be a key component for explaining the broad-scale patterns of exotic species.

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1. Introduction

Understanding the ecological determinants of biological invasions is a key issue for predicting the spread of exotic species – i.e. species that have been transported from one region across a major geographical barrier (Richardson et al., 2000) – over broad geographical extents. The invasion and expansion of exotic plants have been postulated to be the result of both biotic (e.g. competition, facilitation, human-related factors) and abiotic factors (e.g. environmental factors) (Callicott et al., 1999; Stohlgren et al., 2003; Davis et al., 2005; Richardson et al., 2005; Thuiller et al., 2006). Most of the studies on the spatial distribution of exotic species show that biotic factors are important predictors of the exotic species distribution at local (Huston, 1999; Whittaker et al., 2001) and global scales (Gaston, 2003). Additionally, some abiotic factors have been successfully used to describe the geographical distribution of exotic species over a broad-scale extent (Stohlgren et al.,

2003; Davis et al., 2005; Richardson et al., 2005; Thuiller et al., 2006). Among these, climatic variables and human-related factors have been proposed as the most plausible explanations of exotic plant distribution.

To date, most research on the geographical distribution of vascular plants has postulated that plant richness is largely determined by climatic factors, assuming that this distribution is generally driven by the amounts of energy and water that are available in the environment (Currie, 1991; O'Brien, 1993; Hawkins et al., 2003, 2007; Francis and Currie, 2003). However, most of these studies have made no distinction between native and exotic species. Human-related factors are also relevant determinants of susceptibility to exotic invasion. Human activity is often linked to the distribution of exotic plants (Taylor and Irwin, 2004). Thuiller et al. (2006) demonstrated that human-related factors strongly influence the spatial patterns of plant invasions, after accounting for climatic factors. However, the degree to which native and exotic plants respond to similar climatic and human-related driving forces remains unclear.

Another important issue regarding the spatial distribution of exotic species is the relationship between native and exotic plant richness. The literature shows contrasting hypotheses. On the one hand, some studies report a negative relationship between native

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and exotic species richness (Espinosa-García et al., 2004), thus supporting the biodiversity–invasibility hypothesis; i.e. that more diverse communities are more resistant to invasion than species-poor communities (Elton, 1958). This hypothesis is based on the idea that resources are limited, so that a high richness community leaves fewer resources available for newly arrived exotic species (Hierro et al., 2005). On the other hand, broad-scale studies have described a positive relationship between native and exotic species (D'Antonio and Vitousek, 1992; Levine and D'Antonio, 1999; Stohlgren et al., 2003), suggesting that the same environmental factors that allow high native diversity also allow high exotic diversity (Hierro et al., 2005). Yet, it is important to assess to what extent climatic and human-related factors and/or the richness of native community are responsible for explaining the biogeographical distribution of exotic species.

In the present study, we assess the relationship between native and exotic plant richness, and how climatic and human-related factors affect their geographical distribution in Great Britain. This area is appropriate for identifying the relative effect of different factors on exotic flora because of its insularity and the high quality and quantity of information on species distribution. To address these issues, we initially described the geographical pattern of native and exotic species richness. Then, we assessed the relationship between native and exotic species richness. Finally, we investigated the independent and joint effects of climate and human-related factors on the geographical distribution of native and exotic species richness by means of partial regression analyses. By analyzing the complex determinants of exotic species richness, including abiotic and biotic processes, this study provides a better insight into how to address the conservation problems derived from exotic plant species invasions.

2. Methods

2.1. Species richness data

Vascular plant species richness values for Great Britain were generated by processing the maps of the New Atlas of British and Irish flora (Preston et al., 2002), which compiles data on plant species occurrences in 10×10 km UTM grid cells. Specifically, this atlas comprises over 3354 plant species distribution maps obtained from 9,058,358 records. After excluding all hybrids from the analysis, we digitalized and processed in Arc GIS 9.1 a total of 3054 maps at the original resolution of 10×10 km, encompassing 1462 native and 1592 exotic species. We analyzed a final subset of 2252 cells of this grid that resulted after the exclusion of all islands and coastal cells covered by less than 50% of land mass.

2.2. Environmental and human data

We used the same grid to generate a battery of 15 explanatory variables quantifying energy, water, and combined water–energy amounts, as well as the footprint left by humans on ecosystems.

1. 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 (the number of 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 et al., 2005). Gridded data sets were obtained from Met Office Weather and Climate Change Forecasts for the UK and worldwide (Perry and Hollis, 2005).

We calculated PET using the Thornthwaite formula (Thornthwaite, 1948).

2. Water: Precipitation and rainfall. Following Francis and Currie (2003), rainfall was estimated as the total precipitation in months with mean temperatures above 0°C . Annual precipitation data were obtained from the Met Office (Perry and Hollis, 2005).
3. Combined water–energy: Annual actual evapotranspiration (AET) and water deficit (WD). Annual AET was generated by combining values of temperature and precipitation through the Turc's formula (Turc, 1954) and WD was calculated as PET minus AET, following Francis and Currie (2003).
4. Topography: Elevation range was included as a measure of mesoscale climatic variation (O'Brien et al., 2000) and calculated as the difference between maximum and minimum elevations in each grid cell. Elevation data were obtained from Clark (1992).
5. Human footprint: This variable consisted of cell averages of the biome-normalized footprint values generated by Sanderson et al. (2002) at 1-km resolution by combining global records of population density, land use, transport access (roads, rivers, etc.), and electrical power infrastructure (data available at: http://www.ciesin.columbia.edu/wild_areas/).

2.3. Data analysis

Initially, Pearson's correlations were used to relate native and exotic plant species richness. Then, environmental and human footprint effects on species richness variables were investigated through ordinary least squares (OLS) multiple regressions combined with partial regression analysis techniques (see below). However, given the high number of climate-related variables (i.e. 14) and the potential multicollinearity problems that this might cause on multiple regression models, we first established the main trends of variation of climate across Great Britain through a Varimax-rotated principal component analysis (VrPCA), a procedure that permits a clear identification of the major trends in the data, as well as to pinpoint the variables that best represent them (i.e. those showing higher loadings in the main rotated factors) (e.g. see Cattell, 1978) (Table 1). According to the 'broken stick' stopping criterion (Jackson, 1993), these major trends were captured by the two first factors of the VrPCA, which jointly described 79.6% of the variance in climate. The highest factor loadings ($>|0.90|$) for the first factor corresponded to four energy predictors (namely, mean annual temperature, mean January temperature, min PET, and growing season length). On the other hand, the highest factor loadings ($>|0.86|$) for the second factor corresponded to the three water variables (i.e. annual precipitation, annual rainfall and WD).

Human footprint was not included in the PCA because this variable is weakly collinear with climate variables ($r \geq |0.36|$ in all cases) and, specially, because we wanted to investigate human influences on richness explicitly.

Taking this into account, for each species richness variable, we generated an OLS multiple regression model including the first two PCA axes, representing energy and water inputs to the environment, and human footprint, which we called *ad hoc* model (see below). In order to quantify the amount of variation in richness that can be explained exclusively or in concert by climate and human footprint, we complemented these analyses with partial regressions (Legendre and Legendre, 1998; Lobo et al., 2002; Peres-Neto et al., 2006). Also, in order to assess how well our OLS regression models accounted for the patterns in native and exotic richness, we generated a Moran's *I* correlogram using 20 distance classes for each plant group, testing for significance in the autocorrelation of

Table 1

Principal Component Analysis (PCA) of the database of 14 climate variables in Great Britain. The loadings of the variables in the first two axes, or factors are provided as simple correlations. Higher loadings ($>|0.85|$) are highlighted in bold, and show that Factor I reflects energy related trends, and Factor II water availability.

Environmental predictor	PCA factors	
	Factor I (energy)	Factor II (water)
Energy		
Mean annual temperature	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	0.79
Insolation	0.76	0.46
No-frost days	-0.88	-0.11
Growing season length	0.93	0.13
Energy and water		
AET	0.51	-0.78
Water deficit	0.10	0.91
Water		
Annual precipitation	-0.31	-0.86
Annual rainfall	-0.31	-0.86
Topography (mesoclimate)		
Elevation range	-0.41	-0.48
Cumulative variance (%)	50.44	79.56

model residuals using the code in R for “Plotting/calculating spatial autocorrelation” developed by Dormann et al. (2007). Complementarily, Following Bini's et al. (2009) recommendations, we generated simultaneous autoregressive (SAR) versions of all the models in order to compare OLS results with those obtained when spatial autocorrelation is explicitly included in the regressions (see also Dormann et al., 2007; Kissling and Carl, 2008).

Finally, following Montoya et al. (2007), we compared the OLS *ad hoc* models with a battery of published water–energy models that we reparameterized with our data. These were the water deficit and

PET model of Francis and Currie (2003) (hereafter F&C) in which PET is modeled including a linear and a quadratic term, and four versions of O'Brien's water–energy models (hereafter regional water–energy models; RWEM); namely, two models including rainfall and linear and quadratic terms of either MaxPET or minPET (RWEM1 and RWEM2 models); and two models that also include topography measured as log-transformed range in elevation (RWEM3 and RWEM4 models) (see O'Brien, 1998; Field et al., 2005 for a discussion on the theoretical bases of these models). Model comparisons were based on two Information Theory derived indexes, AIC and DAIC (see Montoya et al., 2007 for technical details).

All statistical analyses were performed in Statistica (StatSoft Inc., 2003), Spatial Analysis in Macroecology (SAM: Rangel et al., 2006), and R (R Development Core Team., 2009) including its packages ‘vegan’ (Oksanen et al., 2009) and ‘spdep’ (Bivand et al., 2009).

3. Results

3.1. Species richness patterns

For both groups of plants the highest species richness occurred in southeastern England and the lowest in the Scottish Highlands. Native richness followed a north-to-south gradient, whereas exotic richness was much patchier with high values around London and, secondarily, in different sites as far north as southern Scotland (Fig. 1).

Overall, there was a strong correlation between native and exotic richness, following a positive exponential function, indicating that areas with little native richness sustained very little exotic richness, whereas areas with high native richness sustain almost the same richness of exotics (Fig. 2).

3.2. Effects of climatic and human variables on native and exotic species richness

As indicated by the rank ordering provided by increasing AIC values as well as by the model's coefficients of determination (R^2 s),

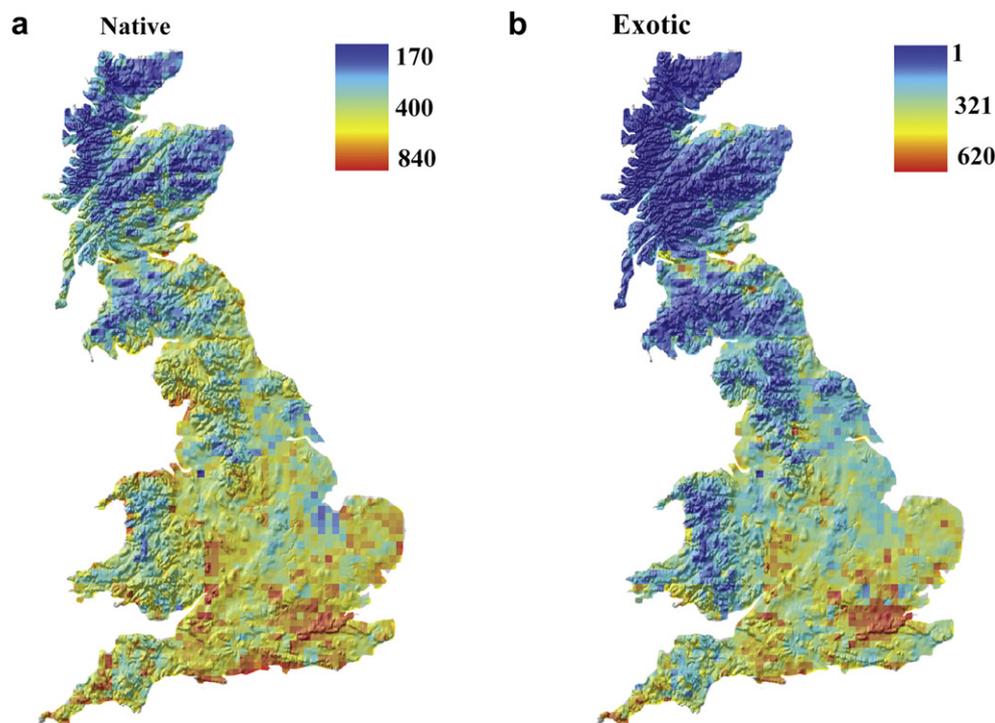


Fig. 1. Biogeographical distribution of the richness of native (a) and exotic (b) plant species in Great Britain.

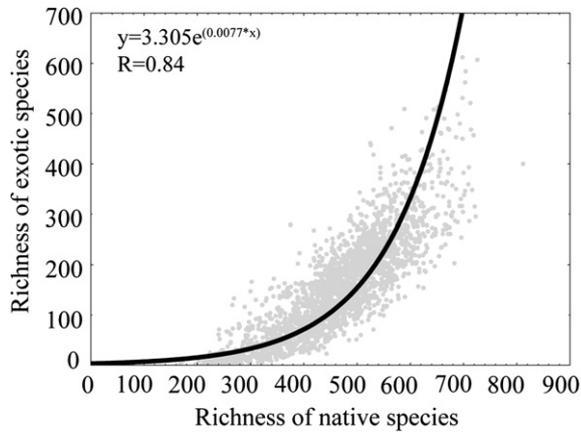


Fig. 2. Exponential regression between native and exotic plant species richness in Great Britain.

our *ad hoc* models (i.e. those generated to include human footprint and two PCA factors reflecting gradients of energy and water) provided clearly better descriptions of native and exotic plant richness patterns than the reparameterized versions of published models we generated (see A.1 for details). Consequently, our subsequent analyses and interpretations were restricted to the *ad hoc* models, which explained 52% and 63% of native and exotic richness variation, respectively (Table 2). The standardized regression coefficients of these models indicated that energy (PCA factor I) contributed the most to explain the variation of species richness in both species groups ($\beta = 0.600$ for natives and $\beta = 0.574$ for exotics). This was also illustrated by partial regressions, where the energy component *per se* (i.e. the “pure effect” obtained after excluding the variance co-explained with water and human footprint) explained 31 and 29% of native and exotic richness, respectively, whereas the water component *per se* (i.e. after controlling for the other variables) only explained 1 and 2% (Fig. 3). The regression coefficients of these models also showed that human footprint was positively and significantly associated with native and exotic richness ($\beta = 0.110$ and 0.154 , respectively) (Table 2, Fig. 3). However, partial regression indicated that the “pure effect” of human footprint (i.e. after controlling for climate) was insignificant for both species groups ($\leq 2\%$) (Fig. 3). Additionally, single-variable regressions of richness on energy suggested that native and exotic species respond differently to this factor. Native richness showed a linear response, whereas a positive exponential response was found for exotic richness (Fig. 4).

Residual spatial autocorrelation in the native and exotic richness gradients after fitting the OLS *ad hoc* models was low at all distance classes, but still statistically significant at the shortest ones (Fig. 5).

Table 2

Standardized regression coefficients and coefficients of determination (R^2) of multiple regressions for native and exotic plant species richness in Great Britain, according to ordinary least squares (OLS) and simultaneous autoregressive models (SAR). Significant values are highlighted in bold. SAR models were performed with SAM (Rangel et al., 2006).

Richness variable		Predictors in model			
		PCA factor I (energy)	PCA factor II (water)	Human footprint	R^2
Natives	OLS	0.600	0.300	0.110	0.52
	SAR	0.554	0.274	0.091	0.55
Exotics	OLS	0.574	0.440	0.154	0.63
	SAR	0.526	0.408	0.125	0.77

Thus, following Bini's et al. (2009) recommendations, we compared these models with SAR models that incorporated spatial autocorrelation explicitly. We found that the relative importance and the significance of the standardized coefficients did not change; that is, energy (PCA factor 1) remained the main predictor of native and exotic plant richness, followed by water availability (PCA factor 2) and human footprint (Table 2). This reinforced that the OLS *ad hoc* models, albeit being simpler than the SAR models, are also robust descriptions of the richness patterns of Great Britain's native and exotic plants.

4. Discussion

4.1. Comparison of richness patterns between natives and exotics

The richness of exotic plant species was positively correlated with the richness of native species across Great Britain (cf. Wright, 1983; Pino et al., 2005; Davies et al., 2006), which suggests that native ecosystems are not species saturated in this island, and agrees with the prediction of “the richer gets richer” principle (Stohlgren et al., 2003), i.e. areas with high native richness are invaded by a larger number of species than areas with low native richness. Negative correlations between native and exotic species richness have been found in studies using finer scales and interpreted as a sign of the biological resistance exerted by the native community to the establishment of exotics (Knops et al., 1997; Tilman, 1999). We find no evidence of this in our data, although we cannot discard it at the scale of local communities in the study area.

We also found that the positive relationship between native and exotic plant richness is not linear, but exponential, i.e. natives-poor areas supported very little exotic species, while natives-rich areas were proportionally more heavily invaded by exotics. On the basis that low-richness sites correspond with those receiving less energy (Table 2) and then less productive, two non-exclusive hypotheses might explain the exponential relationship between native and exotic richness: 1) Among the pool of exotic species reaching Great Britain, a smaller proportion are pre-adapted to be successful in poor sites than in richer sites. 2) Resource-rich areas of Great Britain (those receiving more energy and supporting higher native richness) are less saturated in species than resource-poor ones.

4.2. Predictors for native and exotic species richness distribution

Our results indicated that climate exerts a strong influence on the distribution of native and exotic species richness, whereas human-related factors had little influence. For both groups of species, the best predictor of richness was energy, which is consistent with previous findings (Currie, 1991; Qian, 1998; Moser et al., 2005). Therefore, native and exotic richness responded to the same environmental controls at the island scale, which indicates that areas with favorable conditions for native species also favor exotic species (Levine and D'Antonio, 1999; Pino et al., 2005). However, the shape of richness response to energy differed between groups, being almost linear for natives and exponential for exotics (Fig. 4). This agrees with the above discussed exponential correlation between the richness of both groups, and highlights the higher vulnerability of high-energy sites to invasions.

Regarding the role of human footprint on exotic plant richness, many studies reported that human-mediated disturbances increase the chances for exotic plant establishment (Almasi, 2000; Pyšek et al., 2002; Lake and Leishman, 2004; Von Holle and Motzkin, 2007). Hulme (2008) found that exotic species in Great Britain were strongly overrepresented in anthropogenic habitats. Therefore, we expected higher exotic plant richness as human influence

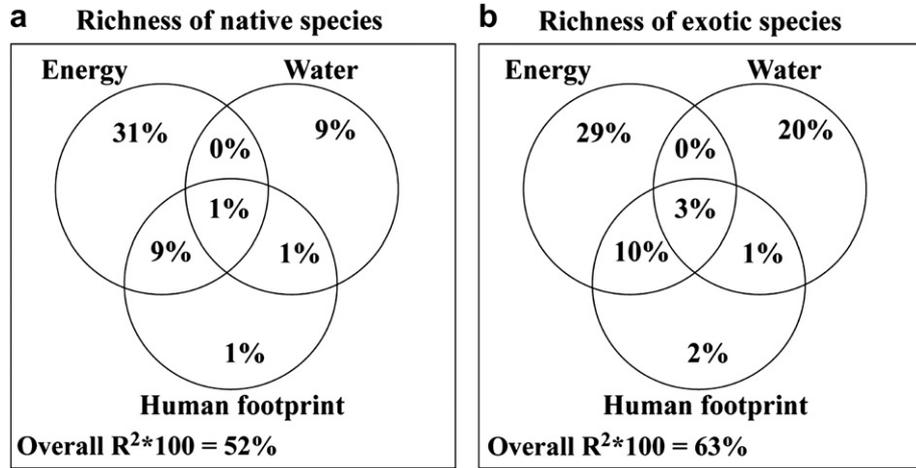


Fig. 3. Proportion of native (a) and exotic (b) richness variance explained by energy inputs (PCA axis I), water availability (PCA axis II) and human footprint, separating the variance co-explained by two or three variables.

increases. However, although positive, the effect of human footprint on the richness of exotic plants in Great Britain was found to be weak. This result is probably due to the scale of the study, where human influence might be masked by the strong control of climate over species richness. In addition, human influences may co-vary with environmental areas receiving more energy inputs (Moreno-Rueda and Pizarro, 2007). This explains the reduction for the human impact relevance in explaining richness when climatic

factors were accounted for (Fig. 3). Therefore, we expect human influence to become more important at finer scales, with lower variation of macroclimatic traits.

Herein we provide a general framework of native and exotic species richness determinants. Our results emphasize that the same model, containing water and energy predictors, successfully explains the richness distribution of both exotic and native plants over broad scales. Human pressure was less effective for explaining exotic richness at the present study scale, possibly because human pressure is also determined by climatic factors. Native species richness linearly increased at increasing energy input (PET, temperature, insolation), while exotic species richness did it exponentially. This may reflect either the lower chances for exotics to succeed in low-energy sites, or/and a lower species saturation of higher energy ecosystems. Our findings highlight that energy input is the best predictor for susceptibility to exotic plant invasions at a broad scale in temperate ecosystems.

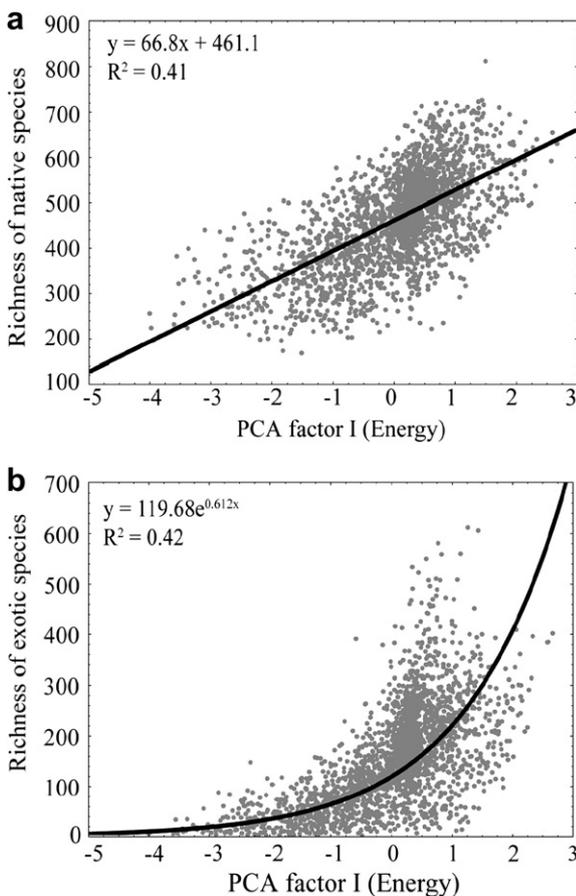


Fig. 4. Linear and exponential regression of native (a) and exotic (b) plant species richness, respectively, with PCA factor I (energy).

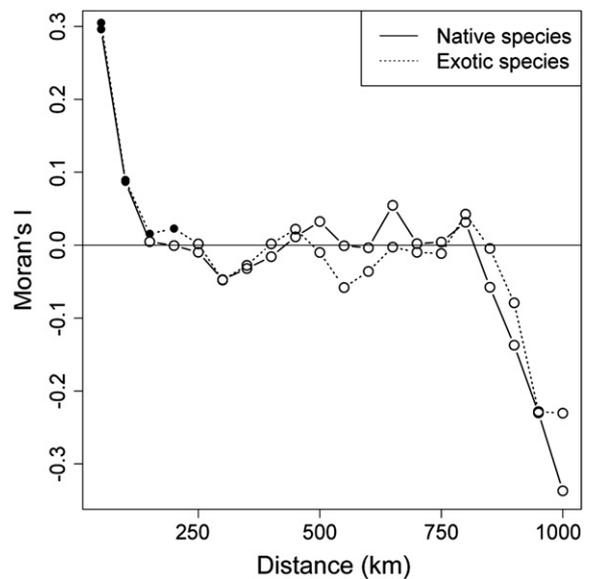


Fig. 5. Moran's *I* correlograms for the residuals of OLS multiple regression models including human footprint and climate (energy and water) fitted to the richness of native and exotic plants in Great Britain. Black symbols indicate significant spatial autocorrelations ($p < 0.001$).

Appendix

Table A.1

OLS regression models for native and exotic plant richness. For each richness variable, models are ranked from best to worst fits (i.e. according to increasing AIC), with the Δ AIC values indicating the difference in AIC units between each model and the best model (the one with the lowest AIC). Adjusted R^2 s and standardized regression coefficients (in parenthesis) are also given.

Model	Predictors in model and their standardized regression coefficients				AIC	Δ AIC	Adjusted R^2
Native							
<i>ad hoc</i>	Factor 1 (0.60)	Factor 2 (0.30)	H.footprint (0.11)		25702.9	0.0	0.52
F&C	WD (−0.12)	PET (−4.05)	PET ² (4.68)		25888.1	185.2	0.47
RWEM4	Rain (−0.31)	minPET (0.14)	minPET ² (0.20)		26121.1	418.2	0.41
RWEM2	Rain (−0.33)	minPET (0.15)	minPET ² (0.20)		26125.3	422.3	0.41
RWEM3	Rain (−0.17)	MaxPET (−2.72)	MaxPET ² (3.12)		26281.5	578.6	0.37
RWEM1	Rain (−0.16)	MaxPET (−2.21)	MaxPET ² (2.08)		26285.7	582.8	0.37
Exotic							
<i>ad hoc</i>	Factor 1 (0.57)	Factor 2 (0.44)	H.footprint (0.14)		24943.1	0.0	0.62
F&C	WD (−0.15)	PET (−5.91)	PET ² (6.63)		25199.8	256.8	0.58
RWEM3	Rain (−0.14)	MaxPET (−6.50)	MaxPET ² (7.04)		25227.3	284.2	0.58
RWEM1	Rain (−0.14)	MaxPET (−6.25)	MaxPET ² (6.80)		25227.9	284.8	0.58
RWEM4	Rain (−0.37)	minPET (0.12)	minPET ² (0.16)		25553.4	610.3	0.51
RWEM2	Rain (−0.44)	minPET (0.14)	minPET ² (0.16)		25630.5	687.4	0.49

Predictors: WD = /Water deficit; Rain = Rainfall, total precipitation in months when mean temperature >0 °C; PET = /annual potential evapotranspiration (Thornthwaite's formula); MaxPET = /maximum PET; minPET = /minimum PET; ER = /elevation range (O'Brien, 1993, 1998; Field et al., 2005); H.footprint = Human footprint (Sanderson et al., 2002). *ad hoc* = Our OLS models (see Methods). F&C = the water–energy model of Francis and Currie (2003). RWEM (1, 4) = /regional water–energy models (O'Brien, 1998; Field et al., 2005).

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