

Relationships of climate, residence time, and biogeographical origin with the range sizes and species richness patterns of exotic plants in Great Britain

Fábio Suzart de Albuquerque ·
Pilar Castro-Díez · Marta Rueda ·
Bradford A. Hawkins · Miguel Á. Rodríguez

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Abstract Based on atlas data with a 10-km cell resolution for 1,406 exotic plant species inhabiting Great Britain, we investigate the extent to which arrival time (residence time) and biogeographical origin (climate suitability) are associated with range sizes of exotic plants and how exotic plant richness is related to current climate and the human footprint. We grouped species according to four arrival periods (archaeophytes and three classes of neophytes), and three broad biogeographical origins, each reflecting a different macroclimate similarity with the study region (northern Holarctic > Mediterranean > and tropical–subtropical). While we found that mean range sizes increased with residence time, no strong effect of the region of origin on range size was detected. Also, across all groups, species richness was primarily and positively associated with temperature,

whereas relationships with human footprint were much weaker, albeit also positive in all cases. The proportion of variance explained by environmental models of richness increased from groups comprising recently arrived species to those that arrived earlier, and from tropical–subtropical species to exotics coming from the Holarctic. Our data also illustrate how these trends translate into richness patterns and their association with climate, which become more similar to native richness patterns as residence time and macroclimatic matching increase. In contrast, broad-scale human alteration of ecosystems appeared to be less important for variation in exotic richness than climate, although we did not evaluate anthropogenic effects at finer scales.

Keywords Biodiversity · Climate suitability · Exotic species · Human footprint · Latitudinal diversity gradient · Residence time · Species richness

F. S. de Albuquerque (✉)
Centro Andaluz de Medio Ambiente (CEAMA),
Department of Ecology, Faculty of Biology,
University of Granada, Av del Mediterráneo S/N,
18007 Granada, Spain
e-mail: fsuzart@ugr.es

P. Castro-Díez · M. Rueda · M. Á. Rodríguez
Department of Ecology, Faculty of Biology,
University of Alcalá, 28871Alcalá de Henares,
Madrid, Spain

B. A. Hawkins
Department of Ecology & Evolutionary Biology,
University of California, Irvine 92697, CA, USA

Introduction

Although hypotheses to explain the spread of exotic species were proposed long ago (De Candolle 1883; Elton 1958), biological invasions have attracted increasing attention in the past 25 years (Baker 1986; Rejmánek 1995; Pyšek et al. 2004; Cadotte et al. 2006; Richardson and Pyšek 2006), coinciding with the increase in habitat degradation, climate change, biodiversity loss, overexploitation, and

spread of invasive species (Vitousek et al. 1997; Sala et al. 2000). Understanding the factors that determine the spatial distribution of exotic species is a primary objective of invasion ecology.

In the last decade, studies at broad spatial scales have attempted to explain exotic plant spread highlighting the importance of the time lag since introduction. These ideas are encapsulated by the residence time hypothesis, which states that the longer an exotic species has been in its introduced area, the greater its probability to be widespread (Hamilton et al. 2005; Rejmánek et al. 2005; Wilson et al. 2007; Lambdon et al. 2008; Kuster et al. 2008). Residence time integrates propagule pressure (i.e., the quantity, frequency, and timing of reproductive material reaching a new area and disseminating within it) and aspects of evolutionary adjustment. A longer residence time generates higher propagule pressure, either by a larger number of introductions or by the development of a larger propagule bank in the invaded region (Kolar and Lodge 2001; Sakai et al. 2001; Pyšek and Richardson 2007). In addition, evolutionary adjustments can enhance the chances of invasion success through time (Lee 2002; Hänfling and Kollmann 2002; Maron et al. 2004; Ghalambor et al. 2007) via hybridization and/or adaptation to the novel environment (Sakai et al. 2001; Bossordorf et al. 2005). Although interest in the residence time hypothesis is relatively recent, it has received consistent empirical support (e.g., Rejmánek 2000; Castro et al. 2005; Pyšek and Jarošík 2005; Pyšek et al. 2009; Williamson et al. 2009), thus has emerged as one of the basic tenets of invasion ecology (e.g., see reviews by Cadotte et al. 2006; Richardson and Pyšek 2006; Pyšek and Richardson 2007).

Another potential determinant of the establishment of exotic species is the degree of climate matching between the target region and the species' native region, as climate is expected to be a strong abiotic filter (Scott and Panetta 1993; Widrlechner and Iles 2002; Thuiller et al. 2006). Accordingly, introduced species should have a greater chance of establishment if they come from areas with a climate that matches climate conditions in the introduced region (Duncan et al. 2001).

Human activities have also been considered to favor the establishment of exotic species, particularly, because by transforming natural habitats, humans can make available to the aliens resources

previously capitalized by local species (Rejmánek 1996; Almasi 2000; Lake and Leishman 2004). For this reason, variables associated with human actions should affect the distribution of exotic plant species. However, human pressure and climate may not influence the distribution of all exotics equally. Firstly, species with longer residence times in the invaded region should be better adjusted to climatic conditions, whereas more recently arrived species are expected to depend more on human disturbances. Secondly, climate may better explain the spatial richness pattern of exotic species coming from the same biogeographical region than that of species with more dissimilar origin due to the formers' exposure to more similar environments over evolutionary time.

In this study, we assess (1) the relationships of distribution size ranges of exotic plant species with their biogeographical origins and with the time since their first-recorded presence or minimum residence time (MRT) (Castro et al. 2005); (2) the role of climate and human activities in determining patterns of richness of exotic species; and (3) whether the richness of exotic species grouped by geographical origin and MRT have similar distribution patterns. The three questions are examined using the exotic flora of Great Britain. This area was selected because of the high quality and quantity of species distribution information. Specifically, we test the following predictions: exotics introduced earlier are more widespread in Great Britain, as they have longer to adjust their distributions to the British climate; exotic species coming from the biogeographic region to which Great Britain belongs (i.e., the northern Holarctic) are more widespread than those of Mediterranean and tropical–subtropical origin; by combining the former two predictions and the expected effects of human influences, the climate best explains the spatial richness patterns of Holarctic species with longer MRT, whereas human activities are key for the patterns of recently arrived species with Mediterranean or subtropical/tropical origins.

Materials and methods

Plant species data

Distribution maps were extracted from the New Atlas of the British and Irish Flora (Preston et al. 2002).

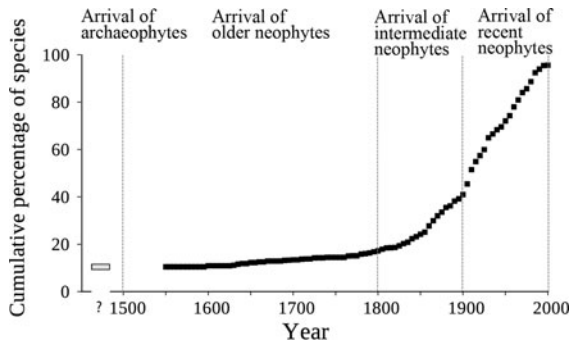


Fig. 1 Pattern of accumulation of exotic plant species in Great Britain between <500 and 2,000. *Dashed lines* divide the curve into four time periods used to differentiate four species groups: i.e., <1,500, the introduction of the earliest exotics (archaeophytes; no arrival dates exist for these species); 1,500–1,800, a long period of gradual colonization (older neophytes); >1,880–1,900, a first acceleration of the pace of arrivals (intermediate neophytes); and >1,900, a second acceleration (recent neophytes) that represents the appearance of about two-thirds of the exotics currently inhabiting the island

After excluding ferns and aquatic species, we digitized and processed in ArcGIS 1,406 exotic species at the original resolution of 10×10 km (UTM grid cells). We analyzed a database comprising 2,252 cells that resulted after excluding islands and coastal cells covering less than 50% of land mass. The range size of each species in Great Britain was calculated as the number of occupied grid cells (NOGC).

Published first records in the wild for exotic species in Great Britain (see Preston et al. 2002; Williamson et al. 2003) show a pattern of species accumulation over time (Fig. 1). Based on the temporal differences in the numbers of introductions, we distinguish four periods: the first includes 153 exotics that are known to have reached the island before 1500, but for which exact arrival times are unknown (Preston et al. 2002; Williamson et al. 2003); the second extends from 1550 until ca. 1800 (including 100 species) and is characterized by a slow increase in the number of exotics, followed by two periods representing a first (until ca. 1900; 341 species) and a second (until the present; 812 species) acceleration of the numbers of introductions. Hereafter, we refer to these groups as archaeophytes (MRT > 500 year), older neophytes (MRT = 200–500 year), intermediate neophytes (MRT = 100–200 year), and recent neophytes (MRT < 100 year).

Preston et al. (2002) also provided information about the biogeographical origin of neophyte species (this was not available for all exotic species), and we

classified neophytes into three groups: (1) northern Holarctic neophytes, comprising those species whose centers of origin are in extra-Mediterranean Europe, in extra-tropical Asia, or in North America (398 species); (2) Mediterranean neophytes, which originated either in southern Europe, northern Africa, or the Middle East (358 species); and (3) tropical–subtropical neophytes, which originated in the Neotropics, Afrotropics, or Indo-Pacific region (330 species).

Explanatory variables

We initially generated 15 potential explanatory variables of species richness gradients, which we grouped into the following five categories:

- (1) **Energy:** Mean annual temperature, mean January temperature, annual range of temperature, insolation (hours of sunshine), number of frost days, growing season length, and Thornwaite's (1948) annual potential evapotranspiration (PET), minimum monthly potential evapotranspiration (min PET) and maximum monthly potential evapotranspiration (Max PET). These variables were selected as alternative measures of ambient energy (O'Brien 1998; Hawkins et al. 2003a; 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).
- (2) **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°C and WD as PET minus annual actual evapotranspiration. Precipitation data were obtained from the Met Office (Perry and Hollis 2005).
- (3) **Combined water–energy:** Annual actual evapotranspiration (AET). This variable was generated by combining the values of temperature and precipitation through the Turc's formula (Turc 1954).
- (4) **Topography:** Elevation range was included as a measure of mesoscale climatic variation (e.g., Rodríguez et al. 2008) and was 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 US geographical Survey at EROS Data center regional scale—and is available at <http://www1.gsi.go.jp/geowww/globalmap-gsi/gtopo30/gtopo30.html> (Accessed 29 July 2011).

- (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/) (Accessed 29 July 2011).

Data analysis

To investigate the relationships between residence time and exotic species range expansion, we used one-way ANOVA combined with the Tukey's unequal-N-HSD test to compare (1) mean numbers of occupied grid cells (NOGCs) by archaeophytes and the three groups of neophytes and also (2) mean values of MRT among these neophyte groups. We also used one-way ANCOVA to evaluate whether differences in terms of biogeographical origin may influence mean range expansions (i.e., NOGCs) among neophytes, using MRT as a covariable to control for its potential effects. On the other hand, we are aware that *P* values derived from these cross-species analyses may be biased by phylogenetic autocorrelation among species. However, there are no well-resolved phylogenies for plants that would encompass the species included in our database. Thus, all probability tests associated with cross-species comparisons are potentially too liberal, and only the strongest results are considered to be “significant.”

Potential effects of climate and the human footprint on the species richness of each of the groups differentiated previously were investigated through OLS multiple regressions combined with partial regression. However, given the large number of climate-related variables and the multicollinearity among them, we first established the main trends of variation in climate across Great Britain through a Varimax-rotated principal component analysis

(VrPCA), a procedure that permits a clear identification of the major environmental trends in the data, as well as to identify the variables that best describe them (i.e., those with higher loadings in the main rotated factors) (e.g., see Cattell 1978). According to the “broken stick” stopping criterion (Jackson 1993), these 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 (mean annual temperature, mean January temperature, min PET, and growing season length), of which mean annual temperature was the strongest correlate of richness for all species groups (Pearson *r*'s ranging from 0.57 to 0.82). We thus selected mean annual temperature for the multiple regression models. The highest factor loadings (> 0.86) for the second factor corresponded to the three water variables (i.e., annual precipitation, annual rainfall, and WD), with annual precipitation being the strongest correlate of richness in all cases (Pearson *r*'s ranging from −0.36 to −0.69). Thus, we also selected annual precipitation for further modeling.

For each species richness variable, we generated an OLS multiple regression model including mean annual temperature, annual precipitation, and the human footprint as predictors and used their standardized regression coefficients to rank their relative influences on richness. Although it is well known that spatial autocorrelation does not bias OLS regression coefficients (Cressie 1993; Fortin and Dale 2005; Schabenberg and Gotway 2005) and that autocorrelation is not an issue for OLS regression unless when using inferential statistics (i.e., *P* values), which we avoid in the spatial context, we also acknowledge that spatial autocorrelation is a matter of concern to some workers. Consequently, we evaluated the robustness of the standardized regression coefficients of our OLS models by comparing them with those of spatial models generated with spatial eigenvector mapping (SEVM) techniques (Borcard and Legendre 2002) implemented with a forward method of eigenvector selection that focuses on minimizing residual autocorrelation (Griffith and Peres-Neto 2006). Additionally, we conducted partial regressions to partition the variation explained by climate (i.e., mean annual temperature + annual precipitation) and the human footprint into independent and covarying components

(e.g., see Hawkins et al. 2003b). Analyses were performed using R (R Development Core Team 2009) including the Package “vegan” (Oksanen et al. 2009), STATISTICA 8.0 (StatSoft, Tulsa, OK, 2007) and Spatial Analyses in Macroecology (SAM, Rangel et al. 2010).

Results

Minimum residence time (MRT), region of origin, and range size

As expected, neophyte range sizes are significantly correlated with the minimum length of time exotics have been in Great Britain (log–log scale $r = 0.559$, archaeophytes excluded) (Fig. 2). Archaeophytes also have larger ranges than neophytes, and within neophytes, range sizes decrease from older to intermediate to recent neophytes (Table 1). These results identify MRT as a key determinant of exotic range expansion in Great Britain. Also, comparison of MRTs between neophyte groups defined by regions of origin found differences among them (one-way ANOVA $F = 49.9$, $P \ll 0.0001$), with mean MRT being higher for northern Holarctic and Mediterranean neophytes (113.4 ± 3.4 SE and 109.4 ± 3.6 SE, respectively) and lower for tropical–subtropical neophytes (66.8 ± 3.8 SE), as indicated by the Tukey’s unequal-N-HSD test. Coupled with the

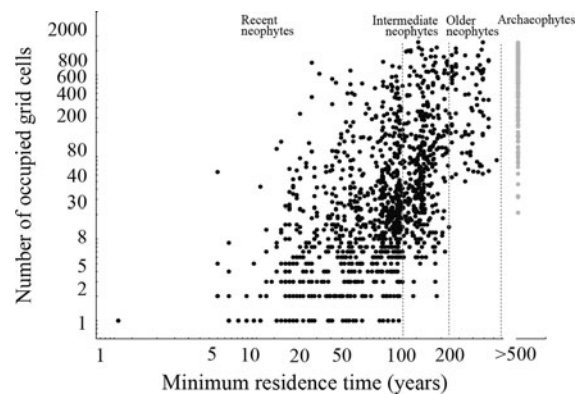


Fig. 2 Relationship between exotic plant species’ range sizes (expressed as numbers of occupied grid cells [NOGCs]) and minimum residence time (MRT, in years) in Great Britain. Dashed lines separate the points into four time periods and species groups (see Fig. 1). All archaeophytes were assigned a MRT of 500 years

Table 1 Mean number of occupied grid cells (NOGCs) by archaeophytes and three groups of neophytes differing in terms of mean residence time (MRT)

MRT species group	Mean NOGC (± 1 SE)	N
Archaeophytes (MRT > 500 years)	997.2 (± 54.7)	153
Older neophytes (MRT = 200–500 years)	637.8 (± 60.3)	100
Intermediate neophytes (MRT = 100–200 years)	253.5 (± 24.2)	341
Recent neophytes (MRT < 100 years)	72.7 (± 6.2)	812

NOGCs were compared with one-way ANOVA ($R^2 = 0.40$), followed by the Tukey’s unequal-N-HSD test, and all means were different at $P < 0.001$, although the significance tests may be biased by uncontrolled phylogenetic autocorrelation (see “Materials and methods”). The number of species (N) of each group is also given

Table 2 Mean number of occupied grid cells (NOGCs) for all neophytes with different regional origins

Region of origin	Mean NOGC (± 1 SE)	N
Northern holarctic neophytes	232.2 (± 21.2)	398
Mediterranean neophytes	165.7 (± 19.0)	358
Tropical–subtropical neophytes	89.2 (± 13.1)	330

Mean NOGCs were compared with one-way ANCOVA including minimum residence time (MRT) as a covariate and were marginally non-significant assuming some overestimation of the degrees of freedom due to phylogenetic autocorrelation ($F = 3.19$; $P = 0.041$). Relationships with MRT were substantially stronger ($F = 239.6$; $P \ll 0.0001$). The number of species (N) of each plant group of is also given

observed strong influence of MRT on neophyte distributions, these results indicate that relationships between neophyte range size and region of origin need to be investigated after controlling for MRT. We did this with ANCOVA including MRT as covariable. The relationship between neophyte range size and MRT was once again evident in this analysis, but that with region of origin was marginally non-significant assuming that significance levels might have been inflated to some extent by the presence of phylogenetic autocorrelation in the data (Table 2). Also, MRT alone accounted for almost the same variance ($r^2 = 0.197$) as the linear model including this variable as well as region of origin ($R^2 = 0.203$), thus indicating that, if any, the role of species’ native region in determining neophyte range expansion across Great Britain has been very weak and comparatively much lower than that played by MRT.

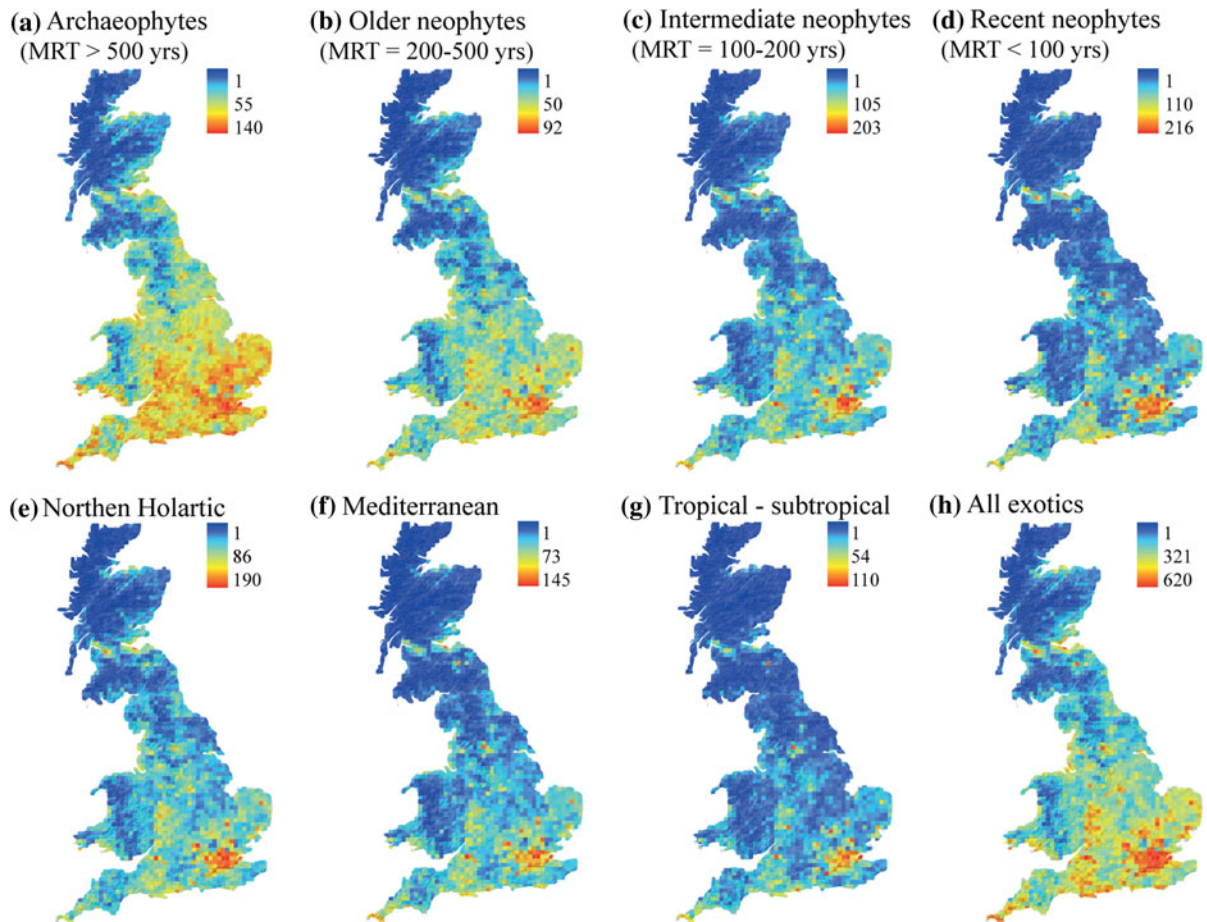


Fig. 3 Species richness maps at a 10×10 km grain for exotic plant groups differing in terms of minimum residence time (**a–d**), for neophytes differentiated according to their region of origin (**e–g**), and all species combined (**h**)

Exotic species richness patterns

In general, the richness of all groups of exotics increases to the south, with the fewest species in the Scottish Highlands and the most in London and neighboring shires (Fig. 3). However, the spatial details of the gradients vary with MRT, being gradual and “smooth” for the archaeophytes (Fig. 3a) and increasingly more abrupt and localized with decreasing MRT (Fig. 3b,c). The group of most recently arrived species is characterized by a southeastern richness hotspot with very few species over most of the island (Fig. 3d). Similarly, although with less obvious differences, the “smoothness” of the richness gradient also varies among neophyte groups defined by biogeographical origin, being smoother for northern Holarctic and Mediterranean species and more localized for tropical–subtropical species

(Fig. 3e–g). The richness map for all species integrates all these trends and shows a north-to-south gradient of increasing richness (Fig. 3h).

Percentages of variance explained by the OLS multiple regression models including mean annual temperature, annual precipitation, and human footprint varied among plant groups (Table 3). For the groups generated according to MRTs, there was a clear trend of decreasing model performance from the Archaeophytes to the recent neophytes. Similarly, for the groups of neophytes distinguished by biogeographical origin, the models explained more variance for northern Holarctic and Mediterranean species than for tropical–subtropical species.

In all regression models, the sign and rank of the standardized regression coefficients of the variables were similar in OLS and spatial regression models (see Table 3). Temperature had the strongest

Table 3 Multiple regression results for models including two climate variables (mean annual temperature [Temp.] and annual precipitation [Prec.]) and the human footprint (HF) as

predictors of the species richness of all exotic seed-bearing plants inhabiting Great Britain and of groups of exotic species defined by minimum residence time and by region of origin

Species richness variable	Standardized regression coefficients			R^2
	Temp.	Prec.	HF	
All exotics	0.55 (0.43)	−0.28 (−0.26)	0.15 (0.10)	0.62
Minimum residence time (MRT)				
Archaeophytes (>500 years)	0.58 (0.54)	−0.40 (−0.37)	0.08 (0.08)	0.77
Older neophytes (=200–500 years)	0.57 (0.49)	−0.30 (−0.28)	0.13 (0.10)	0.66
Intermediate neophytes (=100–200 years)	0.50 (0.26)	−0.23 (−0.13)	0.16 (0.09)	0.51
Recent neophytes (<100 years)	0.45 (0.18)	−0.09 (−0.06)	0.18 (0.07)	0.34
Region of origin				
Northern Holarctic neophytes	0.50 (0.22)	−0.23 (−0.14)	0.17 (0.08)	0.51
Mediterranean neophytes	0.51 (0.37)	−0.22 (−0.24)	0.16 (0.09)	0.51
Tropical–subtropical neophytes	0.50 (0.23)	−0.08 (−0.07)	0.16 (0.08)	0.39

The standardized regression coefficients of the three predictors are provided for the OLS models and (in parentheses) for spatial models generated with spatial eigenvector mapping (SEVM) techniques (see “Materials and methods”). Coefficients of determination (R^2) of the OLS regressions are also included

standardized coefficient, suggesting that exotic richness patterns were mainly driven by environmental energy gradients. Positive partial coefficients were also found for the regression coefficients of the human footprint, but they were always substantially lower than those of temperature (Table 3). Coefficients for precipitation were variable in magnitude but were negative in all models (Table 3), suggesting that exotic richness is lower in wetter areas. Partial regression analyses found that most of the variation explained by the models is attributable to independent “effects” of climate and that the variation explained by the human footprint (ranging between 13 and 15% across exotic richness variables) overlaps with climate to a large extent, with little or no independent “effect” ($\leq 3\%$) (Fig. 4).

Discussion

As expected, there is clear tendency for alien species’ range sizes to increase with minimum residence time in Great Britain, which identifies MRT as a pivotal factor in the current distribution of exotic species in this region. One of the most robust emerging generalizations in invasion biology is that the probability of invasion increases with the time since the introduction (Rejmánek 2000; Castro et al. 2005; Wilson et al. 2007). Even so, although in our study,

archaeophytes have larger mean geographical ranges than older neophytes (with MRT > 200–500 years), the magnitude of the difference between both groups (997 vs. 638 mean NOGC, respectively) was much smaller than that observed with respect to more recently arrived species (see Table 1). This suggests a threshold MRT for an alien species to attain its maximum distribution in Great Britain (see Sakai et al. 2001) and that this threshold is longer than 200 years. More recently, introduced neophytes may be in early stages of invasion and may have not had enough time to attain their potential spread and to integrate fully in the native communities (Pyšek and Jarošík 2005; Cadotte et al. 2006; Celesti-Grapow et al. 2006; Simonová and Lososová 2008). Additionally, an extended temporal lag in the adjustment of exotic distributions with respect to climate is further implicated by our multiple regression models of richness for each plant group (see Table 3). Coefficients of determination continuously increase with the MRT of each group, indicating that equilibration of richness with climate may take more than 500 years.

The notion that climate matching facilitates exotic species spread (e.g., Scott and Panetta 1993; Widrlechner and Iles 2002; Thuiller et al. 2006) received limited support by the data. Specifically, after excluding archaeophytes (due to insufficient information on their regions of origin) and controlling for

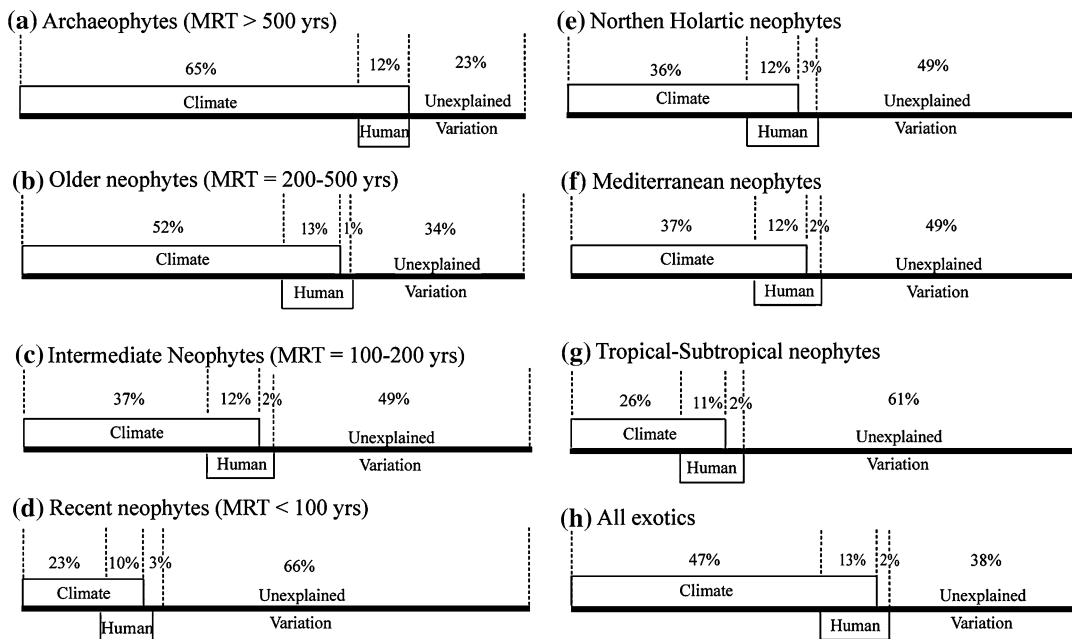


Fig. 4 Partial regression of climatic variables (mean annual temperature + annual precipitation) and the human footprint as predictors of plant species richness for exotic groups

covarying influences of residence time, mean range size differences among northern Holarctic, Mediterranean and tropical–subtropical neophytes were statistically weak, particularly when compared with relationships between range size and MRT. This indeed gives limited support to claims, suggesting that similarity between native and invaded zones is an important determinant of invasibility, at least for the case of Great Britain’s neophyte flora.

The prediction that the association of exotic species richness with environmental gradients would be stronger for groups comprising species with either a longer MRT or a closer environmental matching between the original and invaded regions was also supported by our data. With respect to the influence of MRT, both the descriptive capacity of our multiple regression models (reflected by their R^2 s; see Table 3) and the influence of environment on exotic richness (see Fig. 4) increased strongly from the more recently arrived species groups to those that arrived earlier, which is clearly consistent with the supposition that minimum residence time is a key influence on the relationship between exotic richness patterns and the environment. Similarly, with respect to the region of origin (of neophytes), both model R^2 s

differing in terms of minimum residence time (a–d), for neophytes differentiated according to their region of origin (e–g) and for all species together (h)

and independent influences of environment were higher for temperate groups (i.e., for the richness of northern Holarctic and Mediterranean species) and lower for tropical–subtropical species, although the differences between groups were smaller in this case (see Table 3; Fig. 4). So, there appears to be an effect of the degree of environmental matching between the original and the invaded areas in determining the relationships between exotic species richness and environment, but this effect is secondary to that of minimum residence time. This is further reflected in the stronger differences we found in mean range sizes among species groups defined by MRTs and the smaller differences when the plants were grouped by region of origin.

One question our analysis raises is why should relationships between climate and richness patterns for exotics vary with respect to residence time and place of origin? Terribile et al. (2009) have recently hypothesized that if environmental drivers determine the geographical distribution of species by establishing niche boundaries, then the overlap among ranges (i.e., species richness) will reflect similar effects of these environmental drivers. As discussed earlier, our results suggest that, on average, the longer the MRT

and (to a lesser extent) the higher the environmental matching between original and invaded regions, the greater the possibility for a species to have occupied fully its potential range in the study area. Thus, because potential exotic species' ranges in the target region can be expected to be ultimately determined by environmental constraints (see Scott and Panetta 1993; Widrlechner and Iles 2002; Hamilton et al. 2005; Rejmánek et al. 2005; Thuiller et al. 2006; Wilson et al. 2007; Lambdon et al. 2008; Kuster et al. 2008), these results also suggest a closer link between ranges and environment for the longest established and temperate-zone species. If so, then the mechanism described by Terribile's et al. (2009) hypothesis provides an explanation for the stronger richness–environment relationships we found for these groups; i.e., they were driven by a stronger influence of environmental constraints in determining the range distribution of these species.

Our analyses identified mean annual temperature as the strongest correlate of the richness patterns of all exotic plant groups, a pattern that has also been found for the native plant diversity of Great Britain (Albuquerque et al. 2011). The cool and generally wet macroclimate of this island (see the updated Köppen–Geiger climate classification developed by Kottek et al. (2006)) ensures that water is not limiting to plant richness in most places, which probably explains why annual precipitation has lower explanatory power than temperature in our models (and possibly for its negative sign). This is also consistent with the postulate of the Hawkins' et al. (2003a) conjecture that richness depends on water availability in warm macroclimates, whereas energy is the key driver of richness gradients in temperate macroclimates. It appears that this applies to native plants (Albuquerque et al. 2011) as well as to exotic species.

Finally, in line with the findings of numerous studies reporting that exotic plant establishment tends to be favoured by human-mediated disturbances (e.g., Almasi 2000; Lake and Leishman 2004; Von Holle and Motzkin 2007; Lambdon et al. 2008), we expected exotic plant richness to increase along with human influences. This is what we found (see Table 3), although the signals captured by our partial regression analyses were smaller than those left by climate, with which human footprint overlapped largely (see Fig. 4). Climate has been commonly identified as a primary driver of diversity gradients in

studies conducted at broad geographical extents for native faunas (e.g., Hawkins et al. 2003a and references therein) and floras (e.g., O'Brien 1993, 1998), so an overwhelming influence of climate on the richness patterns of Great Britain's native (Albuquerque et al. 2011) and exotic plant groups is not surprising at the scale of our study. In connection with this, the comparatively smaller signal detected for human influences should not be interpreted to mean that anthropogenic effects are unimportant for exotic plant richness, but as a reflection of the prevailing role of climate in driving biodiversity patterns at broad scale. In fact, human effects have been found many times to be major determinants of exotic richness at finer scales (e.g., see Rejmánek 1996; Almasi 2000; Lake and Leishman 2004). This could also be the case across Great Britain's plant communities and landscapes.

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