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Large-scale correlates of alien plant invasion in Catalonia (NE of Spain)

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Abstract

Identification of the main correlates of the invasion process is a fundamental step in alien species management at the regional scale. This paper explores the main climatic, territorial, and anthropic correlates of alien plant species richness and percentage in Catalonia (NE of Spain), by means of GIS techniques. We used floristic data collected in FLORACAT per UTM 10 km × 10 km to set up the number and the percentage of alien species. The association of these variables with climate, topography, landscape, human settlement, and geographic position was explored by means of stepwise regression models applied on the axes obtained from principal component analysis. The significance of the resulting correlates was tested using the modified *t* test of Dutilleul to remove the effects of spatial autocorrelation. PCA reduced the 22 variables to 12 principal components (PC) that explained 90% of the cumulative variance. Regression models were highly significant and captured a high proportion of total variance (adjusted $r^2 = 0.70$ for alien species richness and $r^2 = 0.56$ for alien species percentage). Both alien species richness and percentage were mainly correlated to PC summarising variables concerning climate, habitat and landscape heterogeneity, and potential anthropogenic disturbance. However, while these PC exhibited similar weights on alien species richness, species percentage was mainly determined by climate. Implications for conservation are discussed considering a future scenario of climate warming and increasing land use change in Mediterranean areas.

Keywords: Alien plant invasion; Climate; Native plant richness; Habitat diversity; Man-induced disturbance; Mediterranean region

1. Introduction

Biological invasions have been receiving much attention since the classic study of Elton (1958) and in recent decades they have become one of the most trendy fields of research in ecology (see, for a review, di Castri, 1990; Pyšek and Pyšek, 1995; Pyšek et al., 2002). The introduction of alien species is a world-wide phenomenon with recognised negative effects on the conservation of the native biota and the integrity of ecosystems (Vitousek et al., 1987; Lodge, 1993; Parker et al., 1999), often involving important economic costs (Pimentel et al., 2000), but also providing us with an unparalleled opportunity for ecological studies (Vitousek et al., 1987).

Research has been considered a key factor in order to understand and control the process of invasion. Earlier studies focussed into the history of introduction and the dynamics of invading species at various hierarchical levels (see Rejmánek, 1989, and Kornaš, 1990 for a review). More recently, many studies focussed on the identification of the main factors determining invasion at regional, nation-wide or indeed larger scales (Vilà and Pujadas, 2001; Pyšek et al., 2002). The composition, distribution, and even the history of the naturalised flora are fairly well documented in many regions of Europe

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(di Castri, 1990; Weber, 1997). Large-scale geographical approaches have become possible by the development of GIS technology, but they are limited by the availability, level of detail and heterogeneity of data concerning invaders (Pyšek et al., 2002). Recently, several studies have used this information to address the relationships between patterns of alien species richness and spatial heterogeneity across varying landscape patterns at a regional scale, despite no examples having been found for the Mediterranean region. These studies are commonly performed on a set of selected sites of variable size and geographical distribution (Lonsdale, 1999; Stadler et al., 2000; McKinney, 2002). Several examples using a systematic subdivision of the study area in regular, geographical units are limited to regions in which environmental gradients are not sharp (Deutschewitz et al., 2003).

In this paper we conducted a regional regression analysis aimed at exploring the predictive power of several climatic, topographic, geographical, land-cover and human settlement factors concerning the number and percentage of alien plant species in a systematic subdivision of the study area in regular geographical units. The study has been performed in Catalonia, a region of 32,000 km^2 in the NE of Spain with high plant species richness resulting from sharp climatic, landscape, and socioeconomic gradients. The exotic floristic pool of this region has been studied considerably, and even invasion processes and some of their main driving factors have been outlined in previous works (Casasayas, 1989, 1990). The approximate geographical distribution of all vascular plants in Catalonia is fairly accurately known thanks to FLORACAT, a database of Catalan plant species and communities holding all the vegetation inventories and floristic citations available for the region geographically referred to the Universal Transverse Mercator (UTM) 10 km × 10 km grid (Font and Ninot, 1995). FLORACAT has been used to obtain the number and the percentage of alien species per 10-km UTM. Data sets on climate, topography, geology, land-use and human settlement have been set up at this same spatial resolution using GIS techniques, in order to explore their relative association with both alien species richness and percentage by means of stepwise regression analysis.

2. Materials and methods

2.1. Study site

Catalonia is a region of 32,000 km^2 located in the NE corner of the Iberian Peninsula, on the Mediterranean coast (Fig. 1). The region exhibits highly variable environmental conditions resulting from its topography, with elevations ranging from 0 to 3350 m a.s.l., and geographical situation, receiving Mediterranean, Atlantic and even Saharan influences (Ninyerola et al., 2000). Catalonia is located in the boundary between two phytographic regions –the Eurosiberian and the Mediterra-

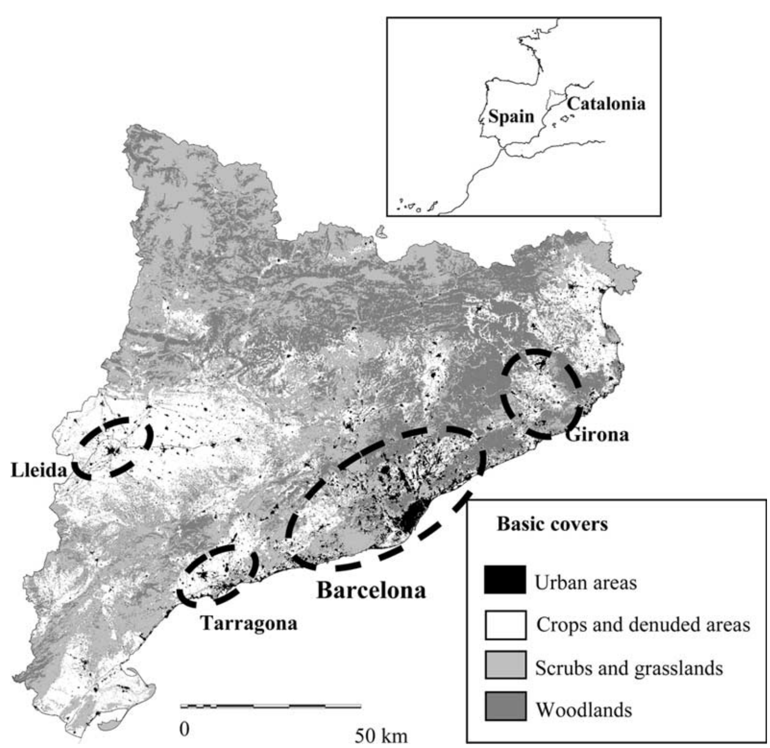

Fig. 1. Basic land cover map of the study area (generalised land cover map of Catalonia, CREAF 1993). Main urban areas are encircled.

nean- in which the Pyrenees impose a sharp topographic-climatic gradient where Mediterranean or Eurosiberian-type biomes gradually change northwards, to subalpine and Alpine types. Rainfall decreases and average temperature increases southwards. A continental gradient can also be observed from the coast, with moist temperate climates, to inland, with contrasting dry conditions.

The landscape structure of Catalonia reflects the typical secular interaction between man and climate in Western Europe and the Mediterranean region, with a historical scenery of forest regression. Indeed, forest currently occupies 40% of the Catalonian surface (Burriel et al., 2001), despite its potential area covering up to 80%. Climacic broad-leaved forests (evergreen *Quercus* ssp. in Mediterranean areas, deciduous *Quercus* ssp. and *Fagus sylvatica* in Submediterranean and Eurosiberian areas) have been mostly substituted by coniferous forests (*Pinus halepensis* and *P. pinea* in Mediterranean areas, and*P. nigra* and *P. sylvestris* in submediterranean and Eurosiberian areas). In recent decades, abandonment of marginal agricultural areas promoted a reversion of this situation, leading to a progressive forest recovery in mountain areas that is, however, challenged by an increasing wildfire frequency. The most favourable plains and plateaux for human settlement exhibit a contrasting situation, with progressive crop intensification and urbanisation. The central coast of Catalonia corresponds to the city of Barcelona and its surrounding area, which is one of the most industrialised and populated areas on the northern Mediterranean coast (MMAMB, 1995). Urban cover doubled in the metropolitan area of Barcelona from 1972 to 1992, and now this process is still accelerating and even expanding towards adjacent areas. Because of this accelerated land cover change, conservation efforts during the last three decades have led to the establishment of a set of designated areas of conservation interest, adding up to 21% of the total land area and belonging to different conservation bodies (National Parks, Natural Parks, Natural Reserves, Hunting Reserves, etc.). All these areas are included in the Plan of Areas of Natural Interest (PEIN) approved by the regional Catalonian government in 1992.

2.2. Alien plant species dataset

The high phytogeographic diversity of Catalonia results in a rich flora, estimated in more than 3200 species (Bolòs et al., 1993). A remarkably long tradition in botany has permitted the accumulation of a great number of floristic records in Catalonia, formerly dispersed in both published work (more than 500 references from journals, books, dissertations, local atlas) and unpublished information (from a botanist network covering all Catalonia). In order to facilitate the development of surveys from the regional to continental level, the FLORACAT project (Font and Ninot, 1995) has been devoted to the gathering, organisation and online exploitation (http://biodiver.bio.ub.es/biocat/homepage.html) of all these floristic data, with the agreement of the Global Biodiversity Information Facility (GBIF) effort (Edwards et al., 2000). FLORACAT is basically the online presentation of a former dataset generated within the ORCA project (Bolòs et al., 1985-2003; http://biodiver.bio.ub.es/orca/), also updated with new citations, vegetation inventories, and revisions of both taxa and sintaxa. Presently, FLORACAT accounts for about 1,200,000 floristic records. FLORACAT and ORCA data are organised following the 10-km UTM grid, which is particularly useful for large-scale studies.

Two response variables concerning the extent of the invasion process in Catalonia were obtained per 10-km UTM cell from FLORACAT: The absolute number of alien species and their percentage (in relation to the overall species richness found in each UTM square). The decision of whether a plant could be considered an alien or not was taken in accordance with Bolòs et al. (1993), who limited the status of alien species to neophytes (i.e., those alien species introduced or naturalised after 1500 A.D.). The number and the percentage of alien species exhibited a positive correlation (Pearson's $r = 0.67$, $p < 0.001$). The number of alien species is a direct measure of the extent of the invasion process, whereas the percentage of species can be related to the potential impact on the ecosystems of receiving areas. Data on both number and percentage of alien plant species were linked to a spatially referred 10-km UTM grid using MiraMon, an in-house developed GIS (Pons, 2002).

2.3. Effect of sampling intensity

FLORACAT is a dataset of heterogeneous origin, with contrasting sampling intensity between UTM squares (Pausas et al., 2003). Sampling intensity is always a potential source of error in studies as such, and its role is not easily assessed because the majority of the related variables provided by databases (i.e. the number of citations, of publications, or researchers) exhibit ambiguous cause–effect relationships with species richness. Indeed, it is difficult to ascertain whether the sampling effort determines the floristic richness or vice versa, because the most diverse areas frequently attract more studies on botany and, in consequence, they accumulate a high number of publications and floristic records. Deutschewitz et al. (2003) used the richness of the 50 most ubiquitous species as a surrogate for sampling intensity in regular, geographic grid cells in the Dessau district (Germany). However, this method does not appear adequate for larger areas with a more intense environmental gradient such as Catalonia, where different biogeographic regions coexist and the presence of the most ubiquitous species cannot be ensured in all UTM cells.

We measured the homogeneity in sampling intensity by comparing several well prospected squares and their immediate surroundings. The ORCA project accounts for 10 control UTM squares distributed within the study area, all of which have been exhaustively sampled with similar intensity for all species groups and by a limited number of researchers. The floristic records of these squares have been published as local floristic catalogues (http://biodiver.bio.ub.es/orca/). We analysed the significance of sampling intensity by comparing species richness of native and alien species between the control squares and the mean value of all (up to 8) their immediate neighbours. We also tested the homogeneity of sampling between alien, native, and total species by comparing the percentage of alien species and the ratio between alien and native species richness in control and neighbouring squares. Comparisons were performed using the non-parametric Mann–Whitney test of ranks because the data showed non-normal distributions.

2.4. Independent variables

A number of variables concerning climate, topography, geology, land-use, and human settlement of Catalonia were set up for the study area (Table 1). Because of the limitations of spatial resolution imposed by data on alien species, all these variables were recalculated for the UTM 10-km grid. All the GIS procedures involving the set up of the independent variables and their combination with the dependent variables were performed using MiraMon.

Climatic variables were calculated from the climatic models of Catalonia, set up by Ninyerola et al. (2000) at a spatial resolution of 180 m using the existing network of meteorological stations and Digital Elevation (DEM) models. We calculated the mean values per UTM square of mean annual temperature, mean minimum temperature in January (considered the coldest month), mean maximum temperature in July (the hottest month), annual rainfall, mean rainfall of January and July, and mean annual solar radiation.

Topographic variables were obtained from the official DEM (30 m pixel size) and the 1:50,000 topographic map of Catalonia, both generated by the Cartographic Institute of Catalonia (ICC). The mean and range (difference between maximum and minimum) of altitudes per UTM square were calculated from the DEM. The 1:50,000 topographic map of Catalonia was used to select a layer of the main streams and their first order tributaries, and to calculate the mean distance to these selected rivers for each UTM square. The mean distance to the coastline was also calculated using the same procedure.

Geological explicative variables were obtained from the official 1:250,000 geological map of Catalonia, a grid of 180 m pixel size that accounts for 10 main bedrock types. The diversity of these bedrock types in each UTM cell was calculated from the relative ground cover of these geological classes and using the Shannon index.

Landscape variables were set up using the Land Use Map of Catalonia (LUMC), generated by the ICC in 1997 by processing multitemporal data captured by the Thematic Mapper (TM) sensor of the Landsat satellite. The resulting 30-m pixel grid, which accounts for 21 landscape categories, has been generated every 5 years from 1987 using a standard procedure (Viñas and Baulies, 1995). We used this map to calculate the relative ground cover per UTM square of woodlands, shrubs, croplands, and urban areas, as indicators of basic landscape categories. We also calculated the relative ground cover of bare soil as an indicator of land disturbance. Land cover diversity was finally estimated by calculating the Shannon index for each UTM square from the initial categories of the LUMC.

Frequency of fires was included as a variable of landscape disturbance because of its recognised effect on plant invasion (D'Antonio, 2000). The mean number of fires per UTM cell in the period 1973–2000 was calculated from the periodicity fire map of Díaz-Delgado and Pons (2001), set up initially for the period 1975–1995 and later completed at CREAF for the period 1996–2000. This map collects all the fires of more than 30 ha that have affected Catalonia at a pixel size of 30 m.

Several *human settlement* variables were also included in the analysis. Mean population density and mean distance to cities larger than 50,000 inhabitants were considered to evaluate the extent of the metropolitan phenomenon, which is presumably a strong correlate of invasion. We used the official urban settlement map of Catalonia (http://www.gencat.net/mediamb/sig/sig-a.htm) that includes the most recent (1999) population census to calculate the population density per UTM square and to select urban areas of more than 50,000 inhabitants. Miramon distance algorithms were then used to calculate the mean distance to these cities per UTM square. The mean distance to the main roads and motorways was calculated for each UTM square with a similar procedure, applied on a selection of the motorways and major roads from the 1:50,000 topographic map of Catalonia.

The percentage of protected area and the mean distance to these areas were enclosed as *conservation planning* variables. Both were calculated for each UTM square using a GIS layer with the official limits of the areas included in the Plan of Areas of Natural Interest of Catalonia (PEIN, http://www.gencat.net/mediamb/sig/sig-a.htm).

The number of native species per UTM cell was added to the model to investigate the association of native flora

Table 1
Initial pool of explicative variables in the study and their corresponding data source

Variables	Data source
Botany	BIOCAT project, http://biodiver.bio.ub.es/biocat/homepage.html
Native species richness	
Geology	Catalan Ministry of Environment (DMA) http://www.gencat.es/mediamb/sig/bases-a.htm
Geological diversity (Shannon Index)	
Climate	Digital Climatic Atlas of Catalonia http://magno.uab.es/atles-climatic/index_us.htm
Mean minimum temperature in January (°C)*	
Mean maximum temperature in July (°C)*	
Mean annual temperature (°C)	
Mean rainfall in January (°C)*	
Mean rainfall in July (°C)*	
Mean annual rainfall (°C)	
Mean annual radiation	
Relief	Cartographic Institute of Catalonia (ICC) 1:50.000 topographic map of Catalonia
Mean altitude (m)*	
Altitude range (maximum-minimum; m)*	
Mean distance to main streams (m)	
Mean distance to coastal line (m)*	
Landscape	Land Cover map of Catalonia, CREAF, http://www.creaf.uab.es/mcsc/
Percentage of urban areas	
Percentage of croplands	
Percentage of woodlands	
Percentage of scrublands	
Percentage of bare soil	
Land cover diversity (Shannon Index)	
Frequency of fires 1973–2000	CREAF (Díaz-Delgado and Pons, 2001)
Human settlement	Catalan Ministry of Environment (DMA) http://www.gencat.es/mediamb/sig/bases-a.htm
Human population density (hab/km^2)	
Mean distance to primary roads (m)	
Mean distance to cities of more than 50.000 hab. (m)*	
Conservation planning	Catalan Ministry of Environment (DMA) http://www.gencat.es/mediamb/sig/bases-a.htm
Percentage of protected areas	
Distance to protected areas (m)	
Geographical position	
UTM X coordinate (km)	
UTM Y coordinate (km)	
X^2 coordinate (km^2)	
Y^2 coordinate (km^2)	
XY coordinate (km^2)	
X^3 coordinate (km^3)*	
X^3 coordinate (km^3)*	
X^2Y coordinate (km^3)*	
XY^2coordinate (km^3)*	

* Indicate those variables removed from the pool because of their high correlations ($r^2 < 0.56$) with other variables.

with the extent of the invasion process. As shown by Lonsdale (1999) and Pyšek et al. (2002), this relationship might be negative, presumably due to competitive effects, or positive, native plant diversity being a suitable surrogate for fine-scale habitat diversity.

Finally, *geographical position* variables were also included in the analysis, thus performing a trend surface analysis in the regression model (Burrough and McDonell, 1998) to account for the spatial variability due to regional gradients. A third-order polynomial, constructed from X and Y coordinates of the centre of each UTM square, was added to the regression model, after rescaling X and Y coordinates by subtracting their means. This procedure avoids colinearity problems derived from the inclusion of the different th-power terms of the polynomial.

2.5. Statistical analyses

The relative association of all the explicative variables with both the number and the percentage of alien species were analysed by separate stepwise regression analysis. The analyses were limited to UTM squares with a land proportion of more than 70% ($n = 319$). To reduce the number of variables in the regression analysis and colinearity between them, a Pearson's correlation matrix was calculated using potential independent variables. A tolerance of a pair wise $r^2 > 0.56$ ($|r| = 0.75$) was used to determine unacceptable colinearity between independent variables, and we then eliminated the less general variable or that with less biological sense (Table 1). This was the case of the mean temperature in January and July, which exhibited a close correlation with the mean annual temperature, and the mean rainfall in January and July, which were highly correlated with mean annual rainfall. Mean and range of elevation were also removed because of their correlation with mean temperature. Of the variables concerning geographical position, X^3, Y^3, X^2Y, and Y^2X terms were removed as they showed a close relationship with either the linear or the quadratic terms. Variables of distance to large cities and to the coastal line were excluded as they were correlated with mean annual temperature.

In order to reduce colinearity between the remaining variables, PCA with varimax rotation was performed to obtain orthogonal axes from the initial variables. The resulting principal components (PC) where then used as explicative variables for the regression analyses. We performed a backward stepwise regression analysis on each dependent variable, using the standardised beta coefficient as the ordination criteria of the importance of PC on either absolute or relative alien plant richness. Because automated stepwise methods do not account for the number of independent variables, they may artificially increase confidence in the overall model and, consequently, the type-I error. Therefore, we adjusted the minimum significance of 0.05 to eliminate variables at each backward step to 0.002 using the method of Bonferroni.

As plant distribution patterns are likely to be influenced by spatial correlation, especially in the case of alien species usually spreading from one or a few introduction points, data squares commonly are not independent and this contradicts basic assumptions of statistical tests. Following Deutschewitz et al. (2003), we tested the significance of PC using the modified *t* test of Dutilleul (Legendre, 2000) that takes spatial autocorrelation into account when calculating the degrees of freedom and corrected the tests for the number of significant regressors (Legendre et al., 2002).We also examined the residual autocorrelation of the regression models by calculating the index of Moran on the standardised residuals.

3. Results

3.1. Sampling intensity among UTM squares

The Mann–Whitney test of ranks detected significant differences between control UTM squares and their immediate neighbours for native species richness (z-statistic = −2.343; $p < 0.05$), but not for alien species richness ($z = -1.814$; $p = 0.075$). The test also failed to detect significant differences for the percentage of alien species ($z = -0.453$; $p < 0.650$) and for the ratio between alien and native species richness ($z = -0.454$; $p < 0.649$) In consequence, it was assumed that there were no significant effects of sampling intensity on alien species richness and percentage, and that sampling effort was similar for native and alien species in all the study area.

3.2. Alien species richness

264 alien (neophyte) species have been recorded in Catalonia. A mean of 37.85 (SD 26.55) alien species was found per 10-km UTM square, with values ranging from 0 to 146. The percentage of alien species ranged from 0 to 21.25, with a mean of 6.85 (SD 4.31). In general, coastal UTM squares contained the highest values of both alien species richness and species percentage (Fig. 2). Alien species richness was concentrated in the north coast of Catalonia, from Barcelona northwards, with other hot spots in the extreme south and values higher than 50 species per square along all the coast and adjacent areas. Alien species percentage showed its highest values mainly in the southern coast and especially around Tarragona conurbation, despite percentages of more than 10% being common along the north coast. Inland areas in northwestern Barcelona and around Lleida also exhibited secondary peaks of species richness and percentage, with a number of squares showing more than 50 alien species that correspond to more than 10% of their plant richness.

3.3. Principal component analysis

The 12 main PC explained more than 90% of the total variance (Table 2). PC1 was a combination of geographical and climatic variables, with main factor loadings on *Y* coordinate (positive) and mean annual temperature (negative). PC2 was mainly correlated with the percentage of woodlands (positive association) and croplands (negative association), whereas PC3 collected the variation due to urban extent (population density and urban cover). PC4 and PC5 were related with the quadratic terms of *X* and *Y* UTM coordinates, respectively. Land cover diversity was the main correlate of PC6, and the percentage of bare soil areas was that of PC7. Other variables summarising PC with factor loadings higher than 0.8 were the percentage of scrublands (PC8), the mean distance to roads (PC9), the frequency of fires (PC10), the mean distance to protected areas (PC11), and native species richness (PC12).

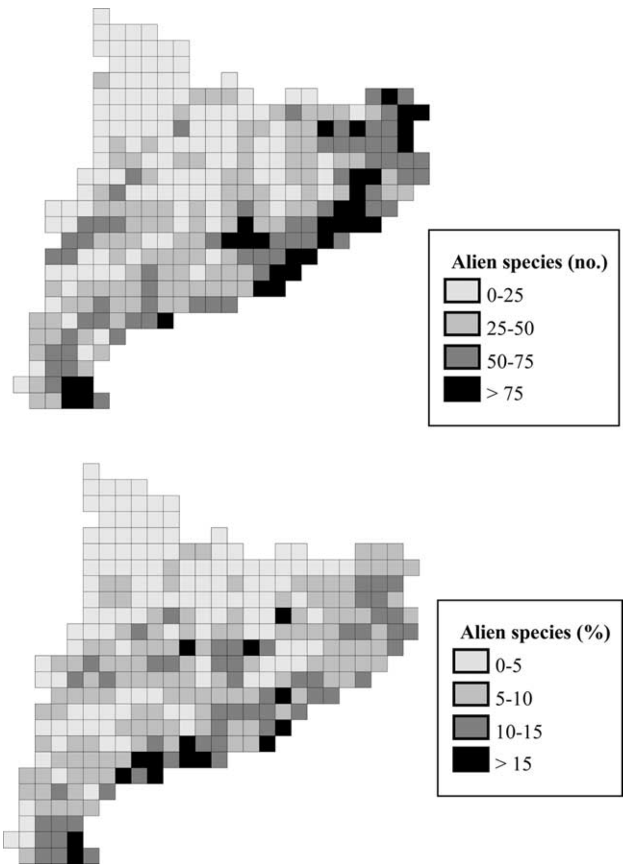

Fig. 2. Number (above) and percentage (below) of alien species per 10-km UTM square in Catalonia.

3.4. Stepwise regression analysis

The regression model performed for the number of alien species captured a high proportion of the total variance ($r^2 = 0.70$, $p < 0.001$). The majority of the first 12 PC were significantly correlated with the dependent variable, except PC5, PC7, and PC11 (Table 3). However, after correcting for spatial autocorrelation and therefore obtaining the appropriate degrees of freedom, only six PC remained significant. Of them, PC1 (latitude, mean temperature, and rainfall) was the first correlated variable, followed by PC12 (native species richness) and PC3 (population density and urban cover). At more distance but also significant we found PC6 (land cover diversity), PC8 (percentage of scrublands), and PC9 (distance to primary roads).

A relatively high proportion of total variance was also captured by the regression model performed on the percentage of alien species ($r^2 = 0.56$, $p < 0.001$). All first 12 PC except PC5, PC7, and PC10 were correlated with the dependent variable. As in the case of alien species richness, only six PC remained significant after correcting for spatial correlation. Of them, PC1 was the first correlated variable. It is followed at considerable distance by PC8, and at much more distance by PC12, PC3, PC6, and PC9.

An analysis of the standardized residuals of the models showed, in general, no failure of normality, linearity, or homocedasticity. The index of Moran calculated on the standardized residuals using 8 neighbours (King's

Table 2
Scores of the main 12 principal components obtained from PCA with marimax rotation on the initial variables of Table 1

	Principal components											
	1	2	3	4	5	6	7	8	9	10	11	12
Native species richness	0.123	0.146	0.076	0.126	0.057	0.094	0.057	0.065	0.021	0.010	0.218	**0.905**
Geological diversity	0.037	0.106	−0.019	−0.004	−0.054	0.124	−0.027	0.021	−0.059	−0.047	0.051	0.111
Mean annual temperature	**−0.745**	−0.227	0.142	0.325	−0.096	0.120	−0.224	−0.248	−0.152	0.126	−0.108	−0.106
Mean annual rainfall	**0.586**	0.487	−0.055	−0.005	0.193	−0.020	0.174	0.141	0.154	−0.088	0.205	0.162
Mean annual radiation	−0.360	−0.261	−0.008	−0.171	−0.043	−0.050	−0.133	0.033	−0.063	0.044	−0.083	−0.119
Distance to main streams	0.027	−0.048	−0.037	0.007	0.129	−0.098	0.077	0.001	0.114	−0.031	−0.031	−0.060
Percentage of urban areas	−0.242	−0.049	**0.714**	−0.045	−0.075	0.358	0.125	−0.124	−0.135	0.036	−0.024	0.031
Percentage of croplands	−0.266	**−0.731**	−0.115	0.093	−0.115	−0.016	−0.125	−0.407	−0.141	−0.110	−0.213	−0.145
Percentage of woodlands	0.235	**0.845**	−0.106	−0.024	−0.157	0.011	−0.197	−0.161	0.049	−0.087	0.148	0.084
Percentage of scrublands	0.231	0.033	−0.119	−0.163	0.182	−0.055	0.096	**0.836**	0.115	0.311	0.119	0.071
Percentage of bare soil	0.209	−0.063	0.074	−0.095	0.139	0.135	**0.918**	0.083	0.078	−0.019	0.068	0.058
Land cover diversity	−0.069	0.017	0.147	0.045	−0.070	**0.935**	0.121	−0.035	−0.157	−0.025	0.042	0.083
Frequency of fires	−0.125	−0.020	−0.007	−0.009	−0.046	−0.019	−0.020	0.187	−0.042	**0.968**	0.019	0.006
Human population density	−0.042	−0.007	**0.991**	−0.013	−0.016	0.032	0.017	−0.025	−0.035	−0.022	0.005	0.048
Distance to primary roads	0.057	0.112	−0.093	0.026	0.131	−0.166	0.075	0.096	**0.927**	−0.044	0.094	0.023
Percentage of protected areas	0.170	0.276	−0.021	0.058	0.089	−0.081	0.171	0.088	0.227	−0.002	0.328	0.257
Distance to protected areas	−0.085	−0.261	0.004	−0.069	−0.139	−0.054	−0.070	−0.118	−0.106	−0.031	**−0.868**	−0.246
UTM X coordinate	0.203	0.277	0.129	0.265	−0.301	0.164	−0.062	−0.172	−0.092	0.107	0.086	0.056
UTM *Y* coordinate	**0.917**	0.175	−0.094	0.004	−0.124	−0.037	0.073	0.063	−0.027	−0.065	0.007	0.056
*X*2 coordinate	−0.100	−0.042	−0.030	**0.954**	0.035	0.042	−0.068	−0.107	0.021	−0.024	0.055	0.110
*Y*2 coordinate	−0.031	−0.028	−0.044	0.053	**0.915**	−0.074	0.145	0.149	0.134	−0.048	0.128	0.061
XY coordinate	−0.423	−0.074	−0.125	0.422	0.291	−0.105	−0.190	−0.068	0.141	0.042	0.040	0.061

Loadings higher than 0.5 are shown in bold.

approach) showed low to moderate levels of autocorrelation, with values of 0.36 for alien species richness and 0.25 for alien species percentage.

Finally, it is also interesting to highlight that alien and native species richness exhibit a moderate and positive linear correlation (Pearson's $r = 0.37$; $p < 0.001$).

4. Discussion

The use of a unique data source such as FLORACAT gave us a sound basis for relatively unbiased discussion of the regional pattern of invasion and its main correlates in Catalonia. It avoided the undesirable effects derived from the use of various, incomplete sources that could differ in criteria of classification of plants and their immigration status, and in methods of data capture (Pyšek et al., 2002). Although FLORACAT shows contrasting sampling effort between areas, this seems not to affect the estimation of alien species richness and percentage according to the Mann–Whitney tests. In consequence, results obtained in the present study can be considered consistent.

We obtained a mean percentage of alien (neophyte) species in Catalonia of less than 7%, clearly lower than in other areas in Europe, such as eastern Germany (17%; Deutschewitz et al., 2003), the Czech Republic (25%; Pyšek et al., 2003), Poland (36%, Tokarska-Guzik, 2003), and the United Kingdom (at least 47%, Preston et al., 2002). The percentage of total alien flora in Spain, including archaeophytes and neophytes, is around 13% (Vilà et al., 2001), which is clearly intermediate between the high values recorded in central and north western Europe (Preston et al., 2002; Deutschewitz et al., 2003; Pyšek et al., 2003) and those of subtropical areas such as north western Kenya (6%, Stadler et al., 2000). Bearing in mind that data capture might be relatively discrepant (i.e., data from Kenya do not include grasses neither woody species), a latitudinal trend is observed as other authors have indicated (Lonsdale, 1999). Environmental constraints can limit the invasion process in southern, dry areas, as it has been suggested for the Mediterranean region (di Castri, 1990; Casasayas, 1990) where the harshness of climatic conditions, a particular pattern of disturbance regime and a long history of biogeographic changes have selected a set of communities especially resistant to invasion (di Castri, 1990). However, socioeconomic factors superposed onto this climatic gradient can also play an important role on plant invasion. Indeed, positive correlations between alien species richness and the Human Development Index and imports have been reported in European and North African countries (Vilà and Pujadas, 2001).

Both the number and the percentage of alien species in Catalonia are moderately explained at a resolution of 10 km × 10 km by a limited set of variables with territorial expression, as can be deduced from the r^2 obtained. The main significant PC are characterized by variables concerning geographical position, climate, habitat and landscape heterogeneity, and potential anthropogenic disturbance.

The PC most correlated with alien species richness and percentage is mainly characterized by latitude, mean temperature, and mean annual rainfall. The climatic component of latitude is evident, since it is correlated with mean annual temperature (Pearson's $r = -0.70$, $p < 0.001$), mean annual rainfall ($r = 0.68$, $p < 0.001$), and even with mean annual radiation ($r = 0.57$, $p < 0.001$) and elevation ($r = 0.67$, $p < 0.001$): the more northwards, the more elevation, and the colder and moister the climate, and this seems to be a disadvantage for alien species according to the negative association of PC1 with alien species richness and percentage. Positive effects of warm climates on representation of alien species in temperate latitudes have been repeatedly described (Kowarik, 1990; Dukes and Mooney, 1999). Elevation, which was highly correlated with mean temperature ($r = -0.98$, $p < 0.001$) and therefore removed from our regression models, has also been found to be closely related with alien regression richness by other authors, who recorded an increase in the number of alien plant species with decreasing altitude in Central Europe (Mihulka, 1998; Pyšek et al., 2002). The Catalonian alien flora is mainly dominated by species of tropical and subtropical origin, most of them presumably unable to complete their life-cycle in cold or high-altitude areas (Casasayas, 1989, 1990). These results are, however, somewhat contradictory to the latitudinal gradient of alien invasion in Europe and Africa previously indicated for national and regional scales, suggesting that climatic effects are modulated by other variables at finer scales.

Indeed, a second component describing variation in alien representation in Catalonia is native species richness that characterises PC12, which exhibit a positive association with alien species richness and negative with alien species percentage. The relationship between native and alien species richness is affected by scale: native species richness increases community resistance against non-native species at local, neighbourhood scales (species interaction level), at least when disturbance levels are moderate to low (Elton, 1958; Levine, 2000), but this pattern is not repeated at coarser scales where positive relationships between native and alien species richness have been reported under moderate disturbance (Lonsdale, 1999; Levine, 2000; Deutschewitz et al., 2003). According to previous studies (Lonsdale, 1999; Pyšek et al., 2002) native richness describes much of the variation in exotic plant richness because of its relationship with the size of the study sites and also with their habitat diversity. Both native and alien species might respond, therefore, to the greater habitat diversity in positive ways (Levine and D'Antonio, 1999; Deutschewitz et al., 2003), with no causal relationships between both groups at landscape or regional scales.

Native species richness is also related to sampling intensity as we demonstrated with the comparison of control and neighbouring UTM squares. However, the effect of sampling on alien representation can be discarded because the same comparison between control and neighbouring squares failed to detect significant differences on alien species richness and percentage. In consequence, and because land area is relatively constant, we can assume that native species richness is a surrogate for habitat diversity in10-km UTM grid. The positive relationship of PC12 with alien species richness would indicate that habitat heterogeneity might increase the number of alien species by providing many opportunities for establishment. This assumption is also supported by the positive association of alien species richness with land cover diversity that characterise PC6.

Alien species percentage is fairly but significantly correlated with both habitat diversity and native species richness, with positive and negative correlations respectively. Beyond the possible forced correlation caused by the inclusion of native species richness in the calculation of alien species percentage, these results would indicate a complex relationship between alien species richness, native species richness and habitat heterogeneity as Pyšek et al. (2002) suggested. According to these authors, a positive relationship can be explained by neophytes invading mostly disturbed, heterogeneous environments where the role of direct competition with native flora can be lower and disturbance would enhance both native and alien establishment. However, disturbance can determine a simplification of native flora at larger spatial scales such as the 10-km UTM grid, because of the spread of a small number of ruderal communities integrated by a reduced pool of native species, and this would lead to an increase in alien species percentage.

A third main component describing alien representation is potential anthropogenic disturbance represented by urban extent (percentage of urban areas and population density) collected by PC3, and also by the distance to primary roads summarised in PC9. Man-induced disturbance (including fragmentation of natural habitats and agricultural intensification, but also trading, gardening, recreational activities, and traffic) has been traditionally considered a key factor for land cover diversity, and, in turn, for the invasion process (Elton, 1958; Kowarik, 1990; Jenkins, 1996; Pyšek, 1998; Hobbs, 2000). In consequence, flora of urban areas is usually richer in alien species than their surroundings (Stadler et al., 2000; Chocholoušková and Pyšek, 2003). On the other hand, the resistance of natural or seminatural habitats to invasion is also known, and this is supported in our study by the positive association of the percentage of scrublands characterising PC8 with both alien species richness and percentage. Natural or seminatural habitats are less prone to invasion than man-modified ecosystems such as human settlements, old fields, roadsides, rangelands and areas near croplands or plantations (Kowarik, 1990; Pyšek, 1998; Tyser and Worley, 1992; Hobbs, 2000; Vilà et al., 2003). This is especially true in the case of European Mediterranean ecosystems (di Castri, 1990; Casasayas, 1990), and particularly in the case of scrubland formations growing in harsh conditions (Vilà et al., 2003).

Although the study has succeeded to explain a relatively high proportion of the total variance (70% for alien species richness, 56% for alien species percentage), results should be interpreted with caution because they do not necessarily imply cause-effect relationships between the independent variables and alien invasion, and there is no evidence that all relevant variables explaining alien representation were enclosed. Difficulties of including all the possible factors affecting a given study variable in regression models have been emphasized by some authors (James and McCulloch, 1990; Nally, 2000), but they are especially important in the case of alien plants, because invasion is commonly the outcome of historical factors that have been playing a role in ecosystems for a long time and that are hardly identifiable nowadays (di Castri, 1990). In this study, unexplained variance exhibits some autocorrelation according to the results of the Moran's index calculated on the residuals of the regression models, but also implicit to the variables that were discarded from these models using the Dutilleul's modified *t* test. Autocorrelation is a typical attribute of geographical data (Lee and Wong, 2001), which is especially interesting in the case of alien plants because it might be related to the colonisation pattern of these species, which commonly spread from a limited number of naturalisation areas that concentrate the majority of introductions and thus become hot-spots of alien species richness. Casasayas (1989, 1990) already indicated the special importance of several trading and transport areas (main ports, railway stations, railways and road systems in general) especially of north-east coast between Barcelona and Girona for alien species introduction in Catalonia. These areas concentrated Catalonian industry and trading activities during the last century, and accumulated most of the first records of alien species.

In summary, the study identified three main groups of factors explaining alien representation in Catalonia: climate, habitat and landscape diversity, and potential man-induced disturbance. According to the regression models (Table 3), these factors have similar importance on alien species richness, whereas the climatic component summarised in PC1 predominates on alien species percentage. The relationship between the extent of invasion and climate may become crucial in the conservation

Table 3
Results of stepwise linear regressions for the two variables studied (β coefficient, t test and significance), and after testing for spatial autocorrelation using Dutilleul's modified t test (t_{mod}, modified t statistic; d_{mod}, modified degrees of freedom; Sig_{mod}, significance)

Dependent variables (adjusted r^2 of model)	β	t	Sig	t_{mod}	df_{mod}	Sig_{mod}
Alien species richness ($r^2 = 0.70$, $p < 0.001$)						
PC1	−0.396	−12.738	***	4.842	23.207	*
PC12	0.381	12.258	***	18.943	146.246	***
PC3	0.362	11.644	***	7.870	84.528	**
PC4	0.287	9.217	***	1.149	10.903	n.s.
PC6	0.283	9.112	***	10.148	122.330	**
PC8	−0.232	−7.458	***	5.181	81.664	*
PC9	−0.191	−6.139	***	8.782	223.727	**
PC10	0.107	3.436	***	0.398	125.192	n.s.
PC2	−0.090	−2.908	**	0.186	28.349	n.s.
Alien species percentage ($r^2 = 0.56$, $p < 0.001$)						
PC1	−0.486	−12.941	***	5.618	17.412	*
PC8	−0.295	−7.859	***	9.024	94.671	**
PC12	−0.223	−5.946	***	9.407	148.062	**
PC2	−0.218	−5.800	***	1.891	38.556	n.s.
PC3	0.218	5.796	***	6.026	101.677	*
PC6	0.217	5.768	***	6.081	130.165	*
PC9	−0.163	−4.336	***	5.699	210.414	*
PC11	−0.130	−3.467	***	2.944	162.308	n.s.
PC4	0.108	2.888	**	0.190	16.732	n.s.

Significance of variables: n.s., non significant; *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

of temperate ecosystems in a future scenario of climate warming (Beerling, 1994; Dukes and Mooney, 1999). Warm, mainly southern, lowland areas in Catalonia appear to be particularly vulnerable to effects of invasions. This argument is reinforced by the evidence that native plant species richness per UTM exhibits significant, negative relationships with mean annual temperature ($r = -0.25$; $p < 0.001$) and radiation ($r = -0.35$; $p < 0.001$). In consequence, the effect of global warming on ecosystems can be highly significant as a result of the simultaneous increase in alien flora and decrease in native flora. These results are particularly interesting regarding the predictions of global change in the Mediterranean region and their effects on biodiversity (Sala et al., 2000). According to our results, an increasing importance of man-modified ecosystems and global warming in the Mediterranean region would determine an intensification and extension of the invasion processes. Recent works highlighted the homogenisation effects of increasing alien species representation (McKinney, 2004), whose ultimate outcome could be an impoverishment of biomes and even the global biosphere with reduced global distinctiveness. A further avenue for future research should be the analysis of the effects of increasing plant invasion, including species homogenisation, in Catalonia as example of a Mediterranean area, using a geographical approach aimed at testing the possible climate- and man-modified landscape-dependences of these effects. Meanwhile, our preliminary results might be useful for the design of a regional strategy for the management and prevention of alien invasions in Catalonia.

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