

Exploring species attributes and site characteristics to assess plant invasions in Spain

Núria Gassó¹*, Daniel Sol¹, Joan Pino¹, Elías D. Dana², Francisco Lloret¹, Mario Sanz-Elorza³, Eduardo Sobrino⁴ and Montserrat Vilà⁵

 ¹CREAF (Centre for Ecological Research and Forestry Applications), Universitat Autònoma de Barcelona. E-08193 Bellaterra, Catalonia, Spain; ²EGMASA (Empresa de gestión medioambiental), E-41092 Sevilla, Spain;
³Gerencia Territorial del Catastro, E-40001 Segovia, Spain; ⁴Departamento de Ingeniería, Producción y Economía Agraria, Escuela Técnica Superior de Ingeniería Agraria, Universidad de La Laguna, E-38200 La Laguna, Spain; ⁵EDB-CSIC (Estación Biológica de Doñana, Centro Superior de Investigaciones Científicas), E-41013 Sevilla, Spain

(Centre for Ecological Research and Forestry Applications), Edifici C, Universitat Autònoma de Barcelona, E-08193 Bellaterra, Catalonia, Spain. Tel.: +34935813345; Fax: +34935814151; E-mail: n.gasso@creaf.uab.es

*Correspondence, Núria Gassó, CREAF

ABSTRACT

Aim Biological invasions are a major component of global change with increasing effects on natural ecosystems and human societies. Here, we aim to assess the relationship between plant invader species attributes and the extent of their distribution range size, at the same time that we assess the association between environmental factors and plant invader species richness.

Location Spain, Mediterranean region.

Methods From the species perspective, we calculated the distribution range size of the 106 vascular plant invaders listed in a recently published atlas of alien plant species in Spain. Range size was used as an estimation of the degree of invasion success of the species. To model variation in range size between species as a function of a set of species attributes, we adopted the framework of the generalized linear mixed models because they allow the incorporation of taxonomic categories as nested random factors to control for phylogenetic relationships. From the invaded site perspective, we determined invader plant species richness as the number of species for each 10×10 km Universal Transverse Mercator (UTM) grid. For each grid cell, we estimated variables concerning landscape, topography, climate and human settlement. Then, we performed a generalized linear mixed model incorporating a defined spatial correlation structure to assess the relationship between plant invader richness and the environmental predictors.

Results From the species perspective, wind dispersal and minimum residence time appeared to favour invasion success. From the invaded site perspective, we identified high anthropogenic disturbance, low altitude, short distance to the coastline and dry, hot weather as the main correlates to UTM grid cell invader richness.

Main conclusions According to these results, an increasing importance of man-modified ecosystems and global warming in the Mediterranean region should facilitate the expansion of plant invaders, especially wind-dispersed species, leading to the accumulation of invasive species in some sites (i.e. invasion hot spots).

Keywords

Biological invasions, climate, life-history traits, man-induced disturbance, Mediterranean region, residence time, seed dispersal, spatial autocorrelation, taxonomic bias.

INTRODUCTION

Biological invasions are a major component of global environmental change (Vitousek *et al.*, 1997; Dukes & Mooney, 1999; Vilà *et al.*, 2006; Thuiller *et al.*, 2007), with increasing effects on the loss of biodiversity (Lodge, 1993), alteration of disturbance regimes (DíAntonio & Vitousek, 1992), changes in the biogeochemical cycles (Vitousek, 1994) and homogenization of Earth's biota (Atkinson & Cameron, 1993). Given that once an alien species is established in a new region, it is extremely difficult to eradicate or control; the most effective method to minimize its impact is to prevent establishment or spread in the first place (Duncan *et al.*, 2003). For this purpose it is needed to predict which alien species have the highest risk to invade and which areas are the most prone to be invaded.

Analyses of regional inventories of alien species can contribute to identify situations associated with high risk of invasion (Cadotte *et al.*, 2006). From a species perspective (species approach, hereafter), one may ask why some naturalized species have been able to attain large distributions whereas others remain localized. This is related to the species potential to invade according to their life-history characteristics (i.e. invasiveness) and introduction event factors such as the pathway of introduction or time since introduction (Pyšek & Richardson, 2007). From an invaded site perspective (site approach, hereafter), one may wonder why invaders are more common in some regions than in others. The regional degree of invasion is related to the properties of the region of introduction that facilitate the survival of non-indigenous species (i.e. invasibility; Lonsdale, 1999) and the intensity to which this species has been introduced (i.e. propagule pressure; Kühn *et al.*, 2003).

Despite the considerable effort that has been devoted in the past to identify the traits that underpin the invasiveness of introduced species (Pyšek & Richardson, 2007) or the characteristics that make some regions more vulnerable to invasion than others (Ohlemüller et al., 2006), surprisingly there have been few studies that included both species and site perspectives (Thuiller et al., 2006) or even focused on both aspects for a single region (Chong et al., 2006; at local scale). Here, we used the species and site approaches as two different ways to comprehend the distribution and invasion extent of invasive plants in Spain as the basis to develop spatially explicit invasion risk protocols and scenarios of plant invasions in the Mediterranean region. In particular, we use empirical models to examine how some life-history traits are related to the regional distribution of invasive plants once introduction event factors and phylogenetic effects are accounted for. We also test a number of climatic, landscape, topographical and anthropogenic factors that could account for variation in invader richness within the study region.

METHODS

Study region

Spain occupies 493,486 km² of the Iberian Peninsula. Its geography is characterized by two central plateaus crossed by three main rivers (Duero, Tajo and Guadiana). These plateaus are surrounded by mountains and two main depressions in the north-east and in the south (the Ebro and Guadalquivir rivers, respectively). It is a mountainous country where elevations over 1500 m a.s.l. are common and the highest peak achieves 3480 m a.s.l. These geographical features condition the distribution of agricultural areas (50.3%, mainly in the centre of the plateaus, along the main river valleys and the coastal plains). The remaining territory is occupied by forests (17.5%, mainly in the north half), scrublands (20.5%), grasslands (7%) and artificial areas (1.3%) (CORINE Land Cover Map of Spain, http://www.fomento.es).

Spain houses a heterogeneous climatic mosaic with three main climatic types: oceanic Mediterranean, continental and Mediterranean maritime (Ninverola et al., 2000). Furthermore, mountainous systems impose sharp topographical-climatic gradients where these three climatic types gradually change to Mountain climate, characterized by cold, strong winds and abundant rainfall or snowfall. Oceanic climate prevails in the north-west and it is characterized by relatively mild winters, warm summers, and generally abundant rainfall spread out over the year. Mediterranean continental climate covers the majority of mainland Spain and it is characterized by wide diurnal and seasonal variations in temperature and by low, irregular rainfall with high rates of evaporation. Finally, Mediterranean maritime climate dominates the eastern and southern coast and it is characterized by rainfall concentrated in spring and autumn, and the moderating effect of the sea over the temperatures. Therefore, in Spain there are up to three main climatic gradients: from north to south, from lowland to summits and from the coast to inland.

Due to its geographical, topographical, climatic and geological characteristics, Spain has a high landscape diversity; and despite a large number of protected areas, natural ecosystems are rather fragmented and deteriorated (Costa *et al.*, 1990; Valladares *et al.*, 2005). Around the middle of the 20th century, large reforestation programs were performed to increase the productivity of the Spanish forests, following a crisis of the rural world and its consequent generalized agricultural field abandonment. Currently, human population in Spain is mostly concentrated in metropolitan areas (e.g. Madrid and Barcelona with 5.6 and 4.6 million inhabitants, respectively), and coastal areas, where urban cover has highly increased in the last 20 years and it is even expanding towards adjacent areas.

Species approach

The identity and distribution of the 106 vascular plant invaders analysed in this study were obtained from the most recently published atlas of alien plant species in Spain (Sanz-Elorza et al., 2004). The cartographic information in the atlas was generated through a 5-year work compilation of bibliographic and herbarium records. The selected list included all vascular neophytes (i.e. established aliens introduced after 1500) identified for Spain, and represent 10.6% of the total number of alien plants listed in the above mentioned atlas. Sanz-Elorza et al. (2004) considered that a plant was invasive according with the definition by Pyšek et al. (2004), that is, an alien species with self-sustainable populations without direct human intervention that produces offspring at considerable distances from the parent plants, and thus has the potential to spread over large areas. For each species we calculated the size of the area of distribution (hereafter range size) as the number of occupied cells in the 10×10 km Universal Transverse Mercator (UTM) grid. This variable was used as an estimation of the degree of invasion success of the species.

We built a data base with six biological and ecological plant traits that, according to the literature (Pyšek *et al.*, 1995; Rejmánek *et al.*, 1995; Goodwin *et al.*, 1999; Lloret *et al.*, 2003), are potentially related with the invasion success of alien species and for which we had sufficient data: seed size (very large (> 10 mm), large (5–10 mm), medium (2–5 mm), small (1–2 mm), very small (< 1 mm)), clonality (yes, no), longevity (annual, biennial, perennial), life-form (Raunkiaer system), dispersal syndrome (wind, animal, water) and pollination type (wind, animal, water). Three factors related to the introduction event were also included in the data base: region of origin (America, Asia, Africa, Europe, Middle East, Oceania, Cosmopolitan (i.e. native to more than one continent)), pathway of introduction (agriculture, gardening, forestry, unintentionally) and minimum residence time (i.e. year of first bibliographic or herbarium record in Spain). All the above information was taken from Castroviejo *et al.* (1986–2000), Casasayas (1989, 1990), Bolós *et al.* (1993) and Sanz-Elorza *et al.* (2004).

We adopted the framework of the generalized linear mixed models (GLMM) (e.g. Blackburn & Duncan, 2001) to model variation in range size between species as a function of the predictors described above. There was a clear taxonomic bias in the set of invasive species, with over 34% of species belonging to just two families (Asteraceae and Poaceae). Because species are linked by phylogeny (Harvey & Pagel, 1991), using species as independent data points may inflate the degrees of freedom (Brändle et al., 2003) and increase the type-I error. Therefore, we accounted for phylogenetic effects by allowing the incorporation of taxonomic categories as nested random factors in the GLMM as a surrogate for phylogenetic relationships. In this way, the likely non-independence of response values of closely related species is, at least partly, controlled by assuming a common positive correlation between introduction outcomes for species within nested taxonomic groups (genera and family, in our case), but a zero correlation between introduction outcomes for species in different groups (a variance components model). There are more sophisticated procedures that allow implementing the complete phylogenetic structure in the statistical models, but we could not use such methods because there was no possibility to have a robust phylogenetic tree that reflected the complete phylogenetic structure. Even if this approach has limitations, we are confident that it contributes to mitigate the problem that invasive species are a non-random subset of all species introduced (see Blackburn & Duncan, 2001).

The response variable (i.e. range size) was right-skewed and could not be normalized with logarithmic or any other transformation. This precluded the use of models with error structure based on the normal distribution. As an alternative, we decided to model invasion success with a Poisson distribution of errors (Crawley, 2002). Poisson errors are recommended to deal with integer (count) variables, which are often right-skewed (Crawley, 2002). The inspection of the residuals showed that this error structure adjusted well to our response variable.

We started modelling invasion success with a model that contained all our predictors and their quadratic terms. Using a backward selection process, we next simplified the model so as to leave only significant predictors (minimum adequate model). The model was run in the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley, 2002; R Development Core Team, 2006).

Site approach

We determined invader plant species richness as the number of species present in each 10×10 km UTM grid as the dependent variable. For each UTM cell, we estimated 18 variables concerning landscape, topography, climate and human settlement. Several authors have highlighted the influence of these variables on the number of invasive plant species in a given area (Kühn *et al.*, 2003; Pyšek *et al.*, 2002; Pauchard & Alaback, 2004; Pino *et al.*, 2005; Stohlgren *et al.*, 2005). All the GIS procedures involving the set up of the explicative variables and their combination with invasive species richness were performed using the in-house software MiraMon (Pons, 2002).

Landscape variables were calculated from the CORINE Land Cover Map of Spain (http://www.fomento.es). We used this map to calculate the following relative ground covers per UTM cell: built-up areas, agricultural areas, forests, scrub-herbaceous vegetation, open spaces, wetlands and water bodies. Land cover diversity was estimated by calculating the Shannon index of the above mentioned land cover categories.

Topographical variables were obtained from the official digital elevations model (DEM) of 100 m pixel size (http://www. opengis.uab.es). We calculated mean altitude (m) and altitude range (difference between maximum and minimum) per UTM cell and, through MiraMon distance algorithms, mean distance to the coastline (m) for each UTM cell.

Climatic variables were calculated from the Digital Climatic Atlas of Spain (Ninyerola *et al.*, 2005; http://opengis.uab.es/wms/ iberia/index.htm), a grid of 200-m pixel size generated from the existing network of meteorological stations and DEM. We calculated the mean values per UTM cell of annual temperature (°C), annual temperature range (i.e. difference between maximum temperature in July as the hottest month, and minimum temperature in January, the coldest month), annual rainfall (mm), summer rainfall (sum of the rainfall in June, July and August) and annual solar radiation (KJ·m⁻²·day⁻¹·µm⁻¹).

Human settlement variables were calculated from maps obtained in the official server of the Spanish Ministry (http:// www.cnig.es). Road length (m) and railway length (m) were also calculated per each UTM cell. We considered human settlement variables as a measure of human footprint (Sanderson *et al.*, 2002) and a surrogate for propagule pressure (Pyšek *et al.*, 2002). Percentage of built-up areas was already calculated as a landscape variable.

Due to the potential heterogeneity of sampling effort within the region and the consequent difficulty to distinguish between absence of invasive species and missing data, the analyses were limited to UTM cells with at least one invasive species present. We also excluded UTM cells with a land proportion of less than 60%. Then, from the total pool of 10,506 UTM cells that cover Spain, only 2517 of them were taken into account in our analysis. To reduce the colinearity in explicative variables, a Pearson's correlation matrix was calculated. Because environmental data are *per se* highly correlated at the regional scale, a tolerance of a pairwise $|\mathbf{r}| > 0.75$ was used to determine unacceptable colinearity between explicative variables, as previous studies have done (Pino *et al.*, 2005). After revising the Pearson's correlation matrix, we excluded mean annual temperature, which was a model whose estimation involved a DEM and thus exhibited a trivially high correlation with mean altitude (r = -0.79, P < 0.001) and summer rainfall (r = -0.74, P < 0.001).

We started modelling invader species richness as a function of the predictors with generalized linear models (GLM). We used Moran's *I* correlograms (Legendre & Legendre, 1998) to evaluate the amount of spatial autocorrelation of the residuals. Moran's *I* is an autocorrelation coefficient and could be regarded as spatial equivalent to Pearson's correlation coefficient. Significance was assessed after 1000 permutations (Bjørnstad, 2004).

Autocorrelated data violate the assumption of independence of most standard statistical procedures, so when positive autocorrelation is present type I errors may be strongly inflated (Legendre, 1993). Moreover, Lennon (2000) pointed out that spatial autocorrelation can alter parameter estimates of linear models by influencing the variance-covariance matrix (Anselin, 1988; Anselin & Bera, 1998), and these biases may seriously distort our understanding of the processes involved in generating the observed ecological patterns. Therefore, with the purpose to control for spatial autocorrelation, we next performed a generalized linear mixed model (GLMM) with a Poisson distribution of errors and a defined correlation structure. We tested different autocorrelation structures, as described in Crawley (2002), and used spatial correlograms to select the one that most effectively eliminated the spatial autocorrelation. The models were run using the glmmPQL procedure of the MASS library on the R statistical package (Venables & Ripley, 2002; R Development Core Team, 2006). As before, we simplified the final model in order to obtain a minimum adequate model with only significant variables.

RESULTS

Species approach

Invasive plants in Spain largely varied in their range size. On average, species range size was of 131.27 UTM cells, ranging from 1 to 824. However, many species had restricted ranges (e.g. *Opuntia monacantha* (Willd.) Haw (Cactaceae), *Leucaena leucocephala* (Lam.) de Wit (Fabaceae), *Pennisetum setaceum* (Forssk.) Chiov. (Poaceae)), whereas a few showed extensive distributions (e.g. *Sorghum halepense* (L.) Pers. (Poaceae), *Amaranthus retroflexus* L. (Amaranthaceae) and *Robinia pseudoacacia* L. (Fabaceae)) (Fig. 1) and see Appendix S1 in Supplementary Material.

Family of the invasive species did not explain any proportion of the variance in range size, while genera explained 48.5% of the variation. After accounting for taxonomic differences, we found that only two out of our nine predictors were significantly related with range size (Table 1), and none of the quadratic terms was significant. First, wind was the dispersal vector related to the largest ranges, followed by animal dispersal (Fig. 2). Second, minimum residence time and range size showed a positive relationship (Fig. 3). Closer inspection showed that, while range size increased with time in species introduced in the last 100 years ($r^2 = 0.272$, P < 0.0001), the relationship turned out



Figure 1 Frequency distribution of range size (number of 10×10 km Universal Transverse Mercator cells where the species is present) of each plant invader.

Table 1 Minimum adequate mixed model accounting for variation in range size of invasive plants in mainland Spain (N = 106 species), controlling for taxonomic relationships. Family and genus of the species were included as nested random factors in the model (not shown) to deal with taxonomic autocorrelation. Dispersal syndrome is a categorical variable with three levels (water, wind and animal); the estimates represent differences of each level with respect to animal dispersion, which is given a value of zero (Crawley, 2002).

Variable	Category	Estimate	Standard error	<i>t</i> -value	Р
Intercept		3.611	0.242	14.909	< 0.001
Dispersal syndrome	Water	-1.721	0.880	-1.955	0.059
	Wind	0.568	0.256	2.219	0.033
Residence time		0.004	0.000	5.623	< 0.001

non-significant for species introduced between 500 and 100 years ago ($r^2 = 0.091$, P = 0.142).

Site approach

On average, only 2.49 invasive species were found per 10×10 km UTM cell, with values ranging from one to 54 species. However, most UTM cells (35.9%) had only one invader. In general, the coastal UTM cells had the highest values of invasive species richness, especially along the Eastern side of mainland Spain, with hot spots (i.e. arbitrarily set up to values higher than 50 species per UTM cell) in the Northern Mediterranean coast (Fig. 4).

A high spatial autocorrelation was detected in the residuals of the initial GLM (Moran's I = 0.70). Thirty percent of this autocorrelation could be removed by using a spatially based GLMM



Figure 2 Range size (number of 10×10 km Universal Transverse Mercator cells where the species is present) of invasive plant species in mainland Spain according to their dispersal syndrome (i.e. animal, 58 species; water, five species; wind, 43 species). Box width indicates the interquartile range, the dark line inside the box indicates where the median is, dashed lines extend until the largest and smallest non-outlier observations, and the small circles represent the observations considered as outliers.

with Gaussian correlation structure. We could not find any model that completely removed the spatial autocorrelation, and thus the results presented here may be conditional on the model adopted. However, we note that the remaining autocorrelation was small (Moran's I < 0.50). The minimum adequate model showed that



Figure 3 Relationship between minimum residence time and range size (number of 10×10 km Universal Transverse Mercator cells where the species is present) of invader plant species in mainland Spain. Range size increased with time in species introduced in the last 100 years ($r^2 = 0.272$, P < 0.0001), the relationship turned out non-significant for species introduced between 500 and 100 years ago ($r^2 = 0.091$, P = 0.142).

six out of 18 predictor variables were significantly related to invasive plant richness. Percentage of built-up areas, road and railway length were all positively related with invasive plant richness, while distance to the coastline, mean altitude and annual rainfall were negatively related with invasive plant richness (Table 2).



Figure 4 Invasive plant species richness (number of species) per 10×10 km Universal Transverse Mercator cell in mainland Spain. White cells have not been considered in the analysis.

Table 2 Minimum adequate mixed model accounting for variationin regional invasive species richness in mainland Spain (N = 2517 10×10 km Universal Transverse Mercator cells), incorporatingGaussian spatial correlation structure.

Variable	Estimate	Standard error	<i>t</i> -value	Р
Intercept	1.349	0.032	41.390	< 0.001
Built-up areas	0.122	0.013	9.127	< 0.001
Road length	0.051	0.016	3.210	0.001
Railway length	0.049	0.016	3.025	0.002
Distance coast	-0.522	0.039	-13.358	< 0.001
Mean altitude	-0.186	0.034	-5.391	< 0.001
Annual rainfall	-0.169	0.028	-5.876	< 0.001

DISCUSSION

Our two approaches allowed for the identification of several factors that underpin the range size of invasive plant species and make some sites more susceptible to invaders than others. Before discussing these findings in detail, we draw attention on an historical factor that can alter our perception of invasion success: the time since the species was first introduced. Species recently introduced showed more restricted distributions because they have had less opportunity to expand their range. Residence time also represents a dimension of propagule pressure: the longer the species is present in the region, the more propagules are spread by human activities and the probability of founding new populations increases (Rejmánek et al., 2005; Hamilton et al., 2005; Pyšek & Jarosík, 2005). Moreover, time since introduction or residence time could not be necessarily the same than time since the first record, as we have assumed on this work, because for species introduced at the same moment, the ones that are more invasive are likely to be recorded earlier. Therefore, time since first record might depend on invasiveness. However, our analysis also reveals that the relationship between invasion success, measured in terms of range size, and time since the first record disappears when considering species introduced more than 100 years ago. This result could be due to the fact that these species would have already reached their maximum spreading area in Spain, according to their potential invasiveness and the characteristics of the recipient-area, or it could be a consequence of the lack of highly reliable historical data before 100 years ago.

Only a few traits seem to be consistently associated with invasion success in plants (Pyšek & Richardson, 2007). From the nine traits we examined, besides minimum residence time, only propagule dispersal syndrome appeared to be related with range size. After correction for minimum residence time and taxonomic affiliation, species dispersed by wind (i.e. anemochory) have the widest range size. Dispersal syndrome has classically been screened as an important determinant of invasiveness (Vermeij, 1996; Richardson *et al.*, 2000; Kolar & Lodge, 2001). In many regional analysis, wind dispersal has been found to be the most effective for invaders to spread (Lloret *et al.*, 2003; Prinzing *et al.*, 2002).

Besides dispersal, none of the other traits classically considered to be associated with invasion success were significant in our analyses. Thus, successful plant invaders do not seem to be characterized by their seed size, clonal strategy, longevity, lifeform or pollination mechanism. The general failure to identify features of successful invaders are in line with suggestions that the outcome of invasions is highly idiosyncratic, although it can also indicate that the ecological attributes of successful alien invaders are not general but habitat-dependent (Thompson et al., 1995). General features of successful invaders, if they exist, should not be many, as adaptations that are useful in some environments are not necessarily appropriate for other environments. Thus, it would seem more likely to find preadaptations to invade specific habitats, rather than a wide variety of habitats (Sol, 2007). Although our analyses consider many of the main hypotheses put forward to explain invasion success in plants, the possibility that we have missed the traits that really matter because they could not be found in the literature or have to be assessed experimentally, should not be completely ruled out.

Compared to the species-level approach, our attempt to identify factors that make some regions more susceptible to invasion than others was much more successful. Even if we did not manage to eliminate completely spatial autocorrelation, it was reduced until a level that it should not alter our main conclusions. The hot spots of invasive plants richness in Spain were localized in coastal NE areas, consistent with a previous analysis of a subregion (Pino *et al.*, 2005). These areas have concentrated an historical and up-to-date high level of development, trading and tourism activities, and hence should be associated with higher rates of species introductions. In agreement with this hypothesis, the coastal north-eastern areas accumulate most of the first records of alien species in Spain (Casasayas, 1989, 1990).

The importance of anthropogenic disturbance is represented by percentage of built-up areas, road and railway length. Man-induced disturbances have 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 *et al.*, 2000). In consequence, flora of urban areas and their surroundings is usually richer in alien species than natural areas (Stadler *et al.*, 2000; Chocholouškova & Pyšek, 2003). Man-modified habitats such as human settlements, old fields, roadsides, rangelands and areas near croplands or plantations are more prone to invasion than natural or seminatural habitats, as found in other studies (Kowarik, 1990; Tyser & Worley, 1992; Pyšek, 1998; Hobbs, 2000; Vilà *et al.*, 2003).

With regard to topographical and climatic factors, mean altitude and annual rainfall were negatively related with invasive plant richness, as it has also been found, at regional and landscape scales, in Central Europe (Mihulka, 1998; Pyšek *et al.*, 2002), in South Central Chile (Pauchard & Alaback, 2004) and USA (Stohlgren *et al.*, 2005; Chong *et al.*, 2006). Low altitudes have been found to have higher propagule pressure (Becker *et al.*, 2005). A recent study (Kleunen *et al.*, 2007) found that plants from low altitudes in their native ranges have a higher naturalization success and more opportunities to be introduced elsewhere because they are used in horticulture. Therefore, the higher invasive species richness in low altitudes might be due to a combination of high propagule pressure and the introduction of plant species adapted to low altitude conditions and dispersed intentionally by humans. Moreover, mean altitude is negatively correlated with mean annual temperature, which has also been found to be closely related with invasive plant richness in other studies (Pino *et al.*, 2005). Therefore, warm and dry climates seem to be advantageous for invasive plants. Spanish invasive 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; Sanz-Elorza *et al.*, 2004).

The negative association of invader richness with altitude, coupled with distance to the coast, is also an indicator for the importance of anthropogenic land uses such as built-up and agricultural areas for invasion because they are clumped at low elevations. Thus, elevation was not only an indicator of microclimate but also indirectly represented the gradient of land use intensity from built-up and intensively managed agricultural areas at low elevations to forest, shrub and herbaceous associations, and extensive farming at high elevations. Given these previous findings, it should not come as a surprise that distance to the coastline was negatively related with invasive plant richness. Close to the coastline we find the mildest climates, and high human presence and therefore, a high propagule pressure and disturbance.

Despite the limitations of our study in terms of reduced number of species traits analysed, potential variation in sampling effort and limitations to consider all country area, by using species and site approaches at regional scale, we have been able to identify some features that underpin range size of invasive species and make some sites more vulnerable to invasion than others. The dispersal syndrome seems to be central in understanding variation among species in their geographical spread, whereas anthropogenic disturbance, propagule pressure and mild climate are all factors explaining patterns of variation in alien species richness, what seems consistent at different scales and regions, as discussed above. Therefore, an important implication of our finding is that an increasing importance of man-modified ecosystems and global warming would facilitate plant invasions (Dukes & Mooney, 1999), increasing the opportunities for the accumulation of invasive plant species in hot spots. Such information is critical to develop invasion risk protocols for future global change scenarios in the Mediterranean region.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 List of invasive plant neophytes from the recently published atlas of invasive plant species in Spain (Sanz-Elorza *et al.*, 2004), indicating their range size (i.e. number of UTM where present).

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