

Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats

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Abstract Landscape pattern might be an important determinant of non-native plant invasions because it encompasses components influencing the availability of non-native plant propagules and disturbance regimes. We aimed at exploring the relative role of patch and landscape characteristics, compared to those of habitat type and regional human influence on non-native plant species richness. For this purpose, we identified all non-native plant species in 295 patches of four coastal habitat types across three administrative regions in NE Spain differing in the degree of human influence. For each patch, we calculated several variables reflecting habitat patch geometry (size and shape), landscape composition (distribution of land-cover categories) and landscape configuration (arrangement of patches). The

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last two groups of variables were calculated at five different spatial extents. Landscape composition was by far the most important group of variables associated with non-native species richness. Natural areas close to diverse and urban landscapes had a high number of non-native species while surrounding agricultural areas could buffer this effect. Regional human influence was also strongly associated with non-native species richness while habitat type was the least important factor. Differences in sensitivity of landscape variables across spatial extents proved relevant, with 100 m being the most influential extent for most variables. These results suggest that landscape characteristics should be considered for performing explicit spatial risk analyses of plant invasions. Consequently, the management of invaded habitats should focus not only at the stand scale but also at the highly influential neighbouring landscape. Prior to incorporate landscape characteristics into management decisions, sensitivity analyses should be taken into account to avoid inconsistent variables.

Keywords Non-native plants · Level of invasion · Land-use and land-cover change · Landscape configuration · Spatial heterogeneity · Species richness · Urban area

Introduction

There is increasing interest in disentangling local and geographic effects on the distribution and abundance

of non-native plant invasions (Chytrý et al. 2008a; Marini et al. 2009; Catford et al. 2011). Although significant advances have been made, several aspects remain largely unexplored. For instance, we still do not have a thorough understanding of the effects of patch and landscape characteristics (Vilà and Ibáñez 2011) compared to those of the regional degree of human influence or habitat type (Chytrý et al. 2008a; Catford et al. 2011). Regions with heavy human influence have an overall increase in the probability of non-native plant arrival and establishment (Pyšek et al. 2010; Kueffer et al. 2010) that can be driven among other causes to a high use of ornamental species for gardening and restoration. Furthermore, within particular regions, the level of plant invasion among habitat types has proven to be different with water and nutrient rich habitats being more invaded than dry and stressful habitats (Chytrý et al. 2008b).

The main landscape characteristics associated with invasion are related to human land-cover such as built-up areas or transportation infrastructures edges (Sullivan et al. 2005; Gassó et al. 2009; Gavier-Pizarro et al. 2010). These human-altered areas are a common reservoir of non-native species (Ohlemüller et al. 2006; Gavier-Pizarro et al. 2010) that can enhance the non-native propagule pressure on nearby natural areas. Except landscape composition (i.e. distribution of land-cover categories), the analysis of other landscape characteristics related to its configuration (e.g. habitat fragmentation) and habitat patch geometry (e.g. size and shape) have received less attention (Deutschewitz et al. 2003; Kumar et al. 2006). The exploration of these variables could give new insights into secondary invasions from land-use areas other than urban (Vilà and Ibáñez 2011).

Another aspect that still requires attention is the spatial extent (i.e. buffer area from the focal sampling unit) at which landscape characteristics influence local invasions (Kumar et al. 2006). It is well known that the influence of landscape characteristics on many ecological processes is dependent on the extent. For instance, the effect of habitat fragmentation on plant pollination and predation varies depending on the size of the landscape under consideration (Steffan-Dewenter et al. 2001). In this case, the influence of habitat fragmentation on pollination occurred at an extent of up to 1,000 m from the sampled patch, while the influence on predation took place at a larger extent (2,500 m). The few studies exploring the effect of extent on plant

invasions point to maximum influence at smaller extents (~ 250 m) (Kumar et al. 2006; Bartuszevige et al. 2006).

In this paper, we first explore the influence of patch and landscape characteristics on non-native species richness at different spatial extents and then we analyse their importance compared to the regional degree of human influence and habitat type controlling for climatic variability. The study was conducted in three coastal regions in Spain differing in their degree of human influence. Mediterranean coastal areas have a large number of habitats of high conservation concern which have been included in the Habitats Directive 92/43/EEC of the European Council (Campos et al. 2004). Nevertheless, Mediterranean coastal areas are in general heavily invaded and under intensive human use, especially tourism-related activities (Chytrý et al. 2008b; Sobrino et al. 2009). Specifically, we ask: (i) Are patch and landscape characteristics more important than the regional degree of human influence or habitat type in explaining non-native species richness?, (ii) Which patch and landscape characteristics are the most relevant to non-native species richness? And finally, (iii) at what spatial extent does landscape characteristics have maximum influence on non-native species richness?

Methods

Study sites

The study was conducted in three administrative regions of Spain: Menorca Island, Girona, and Barcelona. The three regions were selected to represent a gradient from low to high human influence, respectively (Table 1). Menorca Island, declared Biosphere Reserve in 1993, belongs to the Balearic archipelago and it is located within the same latitude as the mainland regions. Balearic Islands are considered to be para-oceanic, as they were connected to the continent during the Messinian period (between 5.70 and 5.35 million years ago). Due to this pre-historical geographical connexion and the historical and current trade and transport between all these regions, they share an important component of both native and non-native flora. The climate of the three regions is typically Mediterranean, with warm, dry summers and mild winters. They also share a similar cultural

Table 1 Geographic characteristics of the three study regions

	Mainland		Island
	Barcelona	Girona	Menorca
Latitude (N)	41.2–41.6	41.7–42.4	39.8–40.1
Longitude (E)	1.7–2.8	2.8–3.2	3.8–4.2
Coast length (km)	187.7	332.9	432.5
Population density (hab/km ²) ^a	4711.3	335.8	136.5
Road length (km/km ²) ^b	2.52	2.94	1.33
Urban area (km ² /km ²) ^b	0.43	0.27	0.09
Mean temperature	16.3	15.9	16.8
Mean precipitation	636	609	608

^a Coastal municipalities (Spanish National Statistics Institute 2011)

^b Within 2,000 m coastal strips

landscape as a result of the typical interaction between man and environment at the Western Mediterranean region. Forests and shrublands dominate the hilly areas, as a result of agricultural land abandonment in the mid-twentieth century. In contrast, lowlands and coastal areas are intensively cultivated or urbanised.

Floristic survey

Non-native plant species (according to Bolós et al. 1993) were identified at the patch level in four types of coastal habitats: dunes (sand-covered shorelines), rock-outcrops (sea cliffs), shrublands (evergreen sclerophyllous shrub vegetation) and forests (pine/oak woodlands). The vegetation patches were selected from the most recent land-cover map for each region: the land-cover map of Catalonia (www.creaf.uab.cat/mcsc, based on images from 2005) for Barcelona and Girona, and the land-cover map of Menorca (<http://www.obsam.cat/>, based on images from 2002) for Menorca. These land-cover maps depict any distinct vegetation patch with a minimum area of 500 m². First, we randomly selected an initial set of 50 patches of the land-cover maps for each habitat and study region with at least 60 % of their area within a 500-m strip along the coast. Second, within this initial set, between 23 and 28 patches per habitat type and study region were selected to set up a gradient of patch area and human influence in the surroundings (percentage of urban and road area within 1 km radius). In Barcelona, we were able to sample only 16 rock-outcrop patches due to availability and accessibility

constraints. Finally, a total of 295 patches ranging from 0.05 to 80 ha were sampled.

Patches were sampled from April to June 2010 depending on the regions, starting with the warmest (Menorca and southern Barcelona) and ending with the coldest (northern Barcelona and Girona). Within each region, patches were also sampled from south to north following the plant phenology. We performed an intensive prospection of each patch to identify all non-native species growing therein. Prospection was done by three or more trained botanists walking through all its area with no time limit, to be reasonably sure that none non-native species was missed. Only neophytes (i.e. introduced after 1500AC) were considered. We did not consider archaeophytes (i.e. introduced before 1500AC) due to the controversy of classifying some of them as native or non-native (Khadari et al. 2005). We then calculated non-native species richness per patch (i.e. total number of non-native species) as this is a good estimator of the level of plant invasion (Catford et al. 2011).

Explanatory variables

We characterized each patch with several patch and landscape variables (Table 2) commonly found to be associated to plant invasions at both grid and plot level (Deutschewitz et al. 2003; Pino et al. 2005; Ohlemüller et al. 2006; Kumar et al. 2006; Gavier-Pizarro et al. 2010). Patch and landscape variables were inferred from the most recent land-cover map for each region mentioned above. We calculated a set of patch variables, describing the geometry of the sampled patches; landscape composition variables, indicating the main land-cover categories; and landscape configuration variables, reflecting the arrangement of patches in the landscape surrounding the sampled patches (Table 2).

Patch variables included patch area, patch edge, and two shape complexity variables: patch shape index and patch fractal index. As composition variables we calculated the relative percentage of each land-cover type and three land-cover diversity indices: Shannon and Simpson indices and land-cover richness. Configuration variables have been rarely used in plant invasion studies. We selected two broadly used indices to quantify each of these relevant aspects: the amount of edge in the landscape (i.e. edge density and landscape shape index), the number and size of

Table 2 Variables used as predictors of non-native species richness in coastal habitats with indication of the landscape extent (i.e. buffer area from the focal patch) selected

Variable	Extent (m)	Description	Data source
Habitat type		Four coastal habitats: dunes, rock-outcrops, shrublands and forests	
Region		Three regions to represent a gradient of human influence: Barcelona, Girona and Menorca	
Patch characteristics			
Patch edge (m)		Perimeter of the focal patch	Land-cover map of Catalonia 2005 (www.creaf.uab.cat/mcsc) and land-cover map of Menorca 2002 (http://www.obsam.cat/)
Patch area (ha) ^a		Area of the focal patch	
Patch fractal index (dim.) ^a		Two times the logarithm of the patch perimeter divided by the logarithm of patch area	
Patch shape index (adim.)		Perimeter of the patch divided by the minimum perimeter possible of a circle of the corresponding patch area	
Landscape composition			
Natural land-cover (%)		Forests, shrublands and open areas	
Low-density urban land-cover (%) ^a	100	Mixed garden and buildings areas such as single-family housing areas and touristy resorts	
High-density urban land-cover (%) ^a	100	Built areas such as villages and cities	
Agricultural land-cover (%) ^a	100		
Water land-cover (%) ^a	100		
Shannon land-cover diversity index			
Simpson land-cover diversity index ^a	100		
Land-cover richness		Number of land-cover types in the landscape	
Landscape configuration			
Edge density (m/ha) ^a	100	Total length of edge in the landscape divided by the total landscape area	
Patch density		Number of patches in the landscape	
Landscape shape index (adim.)		Total length of edge in the landscape divided by the minimum total length of edge possible	
Mean patch area (ha) ^a	250	Mean area of all patches in the landscape	
Mean fractal index (adim.) ^a	250	Mean fractal index of all patches in the landscape	
Mean shape index (adim.)		Mean shape index of all patches in the landscape	
Climate			WorldClim (Hijmans et al. 2005)
Mean annual temperature (°C)			
Mean minimum temperature (°C January) ^a			
Mean maximum temperature (°C July)			
Annual precipitation (mm) ^a			
Mean annual radiation (W m ⁻²) ^a			ASTER GDEM 2009

dim dimensionless

^a Variables included in the final analysis to avoid collinearity

patches (i.e. patch density and mean patch area), and the mean patch-shape complexity (i.e. mean shape index and mean fractal index) (McGarigal et al. 2002).

We calculated configuration variables and land-cover diversity indices using a land-cover map with the following classification: urban, natural, water, and agricultural. For the rest of variables regarding landscape composition we split the urban land-cover into low-density urban (i.e. mixed garden and buildings areas such as single-family housing areas and tourist resorts) and high-density urban (mainly built-up areas) as we were interested in the relative importance of both predictors. We calculated composition and configuration variables at five buffer distances (hereafter extent) from each sampled patch edge (100, 250, 500, 1,000 and 2,000 m) using ArcGIS 9.2 and FRAGSTATS (McGarigal et al. 2002).

Finally, to control for climate variability, we calculated several climate variables. For the centroid of each patch, we obtained mean annual temperature, mean minimum temperature in the coldest month (January), mean maximum temperature in the hottest month (July), and annual rainfall from the WorldClim dataset (Hijmans et al. 2005) at 30 arc-second resolution (approximately 1 Km²). We calculated mean annual solar radiation at the centroid of each patch in GRASS based on the ASTER Global Digital Elevation Model (<http://gdem.ersdac.jpacesystems.or.jp>) of 30 m resolution.

Statistical analyses

We used variance-partition techniques (Mood 1969) and multimodel inference (Burnham and Anderson 2002) of generalized linear models (GLMs) to analyse the relationship between non-native species richness and region, landscape, habitat and patch variables. Climate variables were also included in the models as covariates to control their effect. We modelled the error terms of the GLMs using a negative binomial distribution, which is typically used for count data when overdispersion occurs (Gelman and Hill 2007).

Prior to both the partitioning and the multimodel inference modelling, for each landscape variable, we selected the extent that was most influential on non-native species richness (Table 2). The selection was based on the Pearson's correlation coefficient between each landscape variable and non-native species richness at each buffer distance (Fig. 3). Then, we checked

the collinearity among the selection of predictors by pair-wise Pearson's correlation tests (Supplementary Material 1). First, we selected variables that had a pair-wise correlation lower than 0.6 and then selected the ones with best ecological meaning and explanatory power. With regard to patch variables, patch area was correlated with patch edge and patch shape index with the fractal index. For final models, we used the non-correlated indices patch area and patch fractal index. Taking landscape composition variables into account, we found natural land-cover to be negatively correlated to urban land-cover and land-cover diversity. Thus, we kept high- and low-density urban land-cover, agricultural land-cover and water land-cover. The three land-cover diversity indices were correlated. We selected only the Simpson diversity index. Most landscape configuration variables were also highly correlated. We selected edge density, mean patch area and mean fractal index. Climate variables were highly correlated and thus we selected only mean annual precipitation, mean minimum temperature in the coldest month and mean annual solar radiation.

Deviance partitioning

Variance-partition techniques indicate the variability explained by the single and shared effects of different groups of variables (Mood 1969). Assuming that the deviance is a good measure of the variability explained by a model, we set up GLMs including a different subset of non-collinear variables: patch and landscape variables (i.e. including variables regarding patch geometry, landscape composition and landscape configuration), only regions, only habitat type, only climate variables and the combination of the four groups of variables. The deviance explained by each model was then used to identify the single and shared effects on non-native species richness by simple equation systems (Carrete et al. 2007). Following the same approach, we also partitioned the deviance of non-native species richness accounted by patch and landscape characteristics within patch geometry, composition and configuration variables.

Multimodel inference

Multimodel inference is a model selection method that allowed us to identify the best possible models and to rank all independent variables according to their

influence on non-native species richness (Burnham and Anderson 2002). We performed multimodel inference based on the all-subsets selection of GLMs using Akaike's information criterion corrected for a large number of predictors (AICc).

We selected the best model (smallest AICc) for each block of non-collinear predictors (i.e. patch geometry, composition, configuration, and climate). Then, we repeated the procedure, combining the best variables of each block and the factors habitat type and region to establish the set of best candidate models. For each candidate model in the final selection, we calculated the Akaike weight of evidence (w_i) to rank the predictors in order of importance (i.e. the closest to 1) in their relation to non-native species richness (Burnham and Anderson 2002; Grueber et al. 2011). The weight of evidence was calculated within the set of best models given the selected predictors: all models within four AICc units from the best model. This threshold is within the limits adopted in other studies (Grueber et al. 2011), and allowed the presence of all groups of variables.

Moreover, to avoid a possible correlation between the predictor and the response variable due to random or unexpected noise, we performed a permutation procedure (100 times) to calculate the unbiased weight of evidence (Dw_{+i}) (Thuiller et al. 2007). Only predictors with Dw_{+i} higher than zero had a certain explanatory power on the dependent variable (Thuiller et al. 2007).

We also used multimodel inference to estimate regression coefficients and their confident intervals (with the adjusted standard error) within the best models subset ($\Delta AICc < 4$) (Burnham and Anderson 2002; Burnham and Anderson 2004). We calculated the coefficient for a given predictor as the sum across all possible models where the predictor was present, of the predictor's coefficient multiplied by the w_i (Burnham and Anderson 2002).

To explore the differences in non-native species richness among coastal habitat types and regions, we used the best candidate model (smallest AICc), including the factors habitat type and region. We tested significant differences among levels within each factor using a post hoc normal test with multiplicity correction by the joint distribution of all the statistics (Westfall 1997).

Due to the characteristics of the data and the generally aggregated pattern of plant invasions, it is very likely to find spatial autocorrelation in the

residuals of the GLMs. Spatial autocorrelation could generate an underestimation of the confidence intervals in the regression coefficients. In preliminary analyses using the Moran's Index, we detected significant spatial autocorrelation in the model's residuals at distances smaller than 1,000 m. Thus, for each GLM in the multimodel inference procedure we tested the spatial autocorrelation in the model's residuals by the Moran's index. When the spatial autocorrelation was proven to be significant ($p < 0.05$) we included a spatial autocovariate in the model considering the inverse distance among patches up to 1,000 m (Augustin et al. 1996; Dormann et al. 2007).

All statistical analyses were performed with the R-CRAN software (R Development Core Team 2009). We used the package MuMIn for some procedures of the multimodel inference method and the package VEGAN as the base code for deviance-partition.

Results

Differences on non-native species richness among regions and among habitat types

Across all the regions, we found 125 non-native species. The most abundant species were *Carpobrotus edulis* (L.) L. Bolus, *Agave americana* L., *Pittosporum tobira* (Thunb.) W.T. Ayton and *Opuntia ficus-indica* (L.) Mill., which occur in 31, 26, 24 and 23 % of the patches, respectively.

Considering the best model that included habitat type and region (Supplementary Material 1), non-native species richness of patches was significantly higher in the two mainland regions, Barcelona and Girona, than in Menorca Island (Fig. 1). However, we found no differences in non-native species richness between Barcelona and Girona. Invasion across coastal habitat types was significantly different (Fig. 1). Non-native species richness was greater in forests than in rock-outcrops, while the richness of shrublands and dunes was not significantly different from those two.

Partitioning the influence of region, patch and landscape characteristics and habitat type on plant invasions

The variability of non-native species richness was explained mainly by patch and landscape variables,

and by region (Fig. 2). Both sets of predictors also had a high shared effect. In contrast, habitat type had very low single effect and its explanatory power was shared mainly with patch, landscape and region variables (Fig. 2).

Considering patch and landscape variables separately, the deviance-partition analysis revealed that the composition of the landscape surrounding the patch explained most of the deviance (Fig. 2). Patch geometry and configuration variables showed very little single effect on non-native species richness and a similar amount was shared with composition variables.

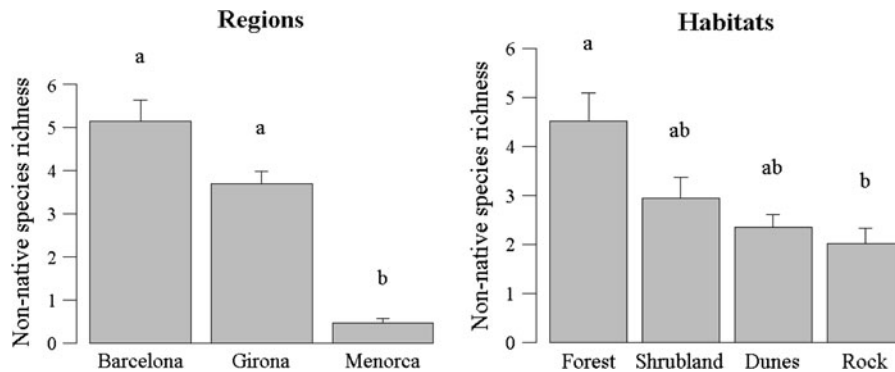


Fig. 1 Mean (+SE) non-native species richness for each region and habitat type. Letters indicate significant differences ($p < 0.05$) between regions and between habitats according to

Patch and landscape characteristics influencing plant invasions

The best patch and landscape predictors explaining non-native species richness were Simpson land-cover diversity index, percentage of agricultural land-cover, and mean fractal index (Table 3). Land-cover diversity showed a positive association with non-native species richness while the association with agricultural land-cover and mean fractal index was negative. Patch area, edge density and percentage of urban land-cover also had a significant positive effect on

post hoc test corrected for multiple hypothesis based on the best model including habitat, region, landscape and climate variables selected by AICc criteria

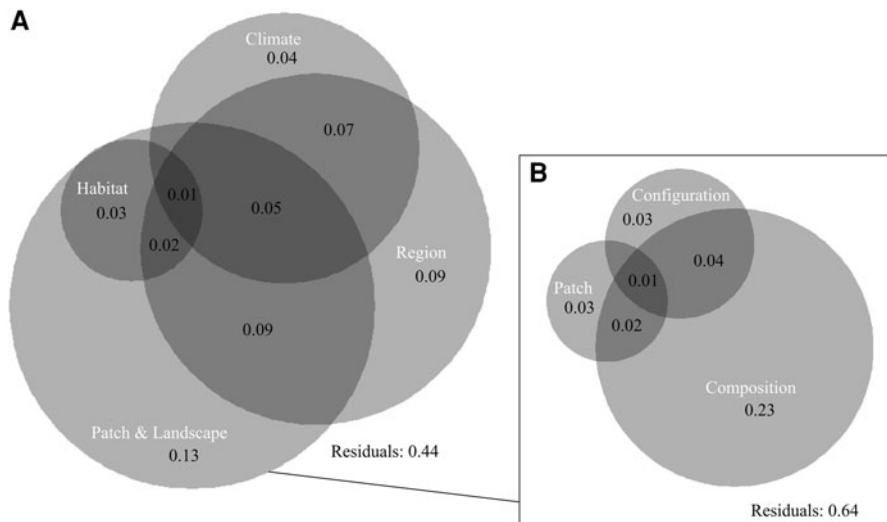


Fig. 2 Deviance partitioning of non-native species richness using generalized linear models among **A** region, climate, habitat type, and patch and landscape predictors, and **B** patch and landscape predictors: patch geometry, landscape composition, and landscape configuration. Each circle corresponds to a

group of variables. Numbers within circles are the proportion of deviance explained by each set of predictors alone (non-overlapped part of circles) or shared. Residuals indicate the deviance non-explained by the models

non-native species richness. Regarding the percentage of urban land-cover, low-density urban land-cover showed higher importance than high-density land-cover (Table 3).

The landscape extent relevant to plant invasions

Landscape composition and configuration variables showed different patterns of influence on non-native species richness, depending on the spatial extent. The most influential extent for landscape composition variables was 100 m around patches with a slight linear decrease in influence at larger radii (Fig. 3). By contrast, for configuration variables changes were more diverse (Fig. 3). A group of variables including mean shape complexity in the landscape (i.e. mean shape and fractal index) and patch density showed a unimodal response with maximum influence at 250–500 m. Edge density and landscape shape index showed a linear response. Landscape shape index and patch density had a positive effect on non-native species richness at smaller extents but changed to negative above 1,000 m.

Discussion

The relative importance of patch and landscape characteristics influencing plant invasions

Plant invasions could be seen as a spatial hierarchical process where ecological factors affect invasions at different scales (McDonald and Urban 2006; Milbau et al. 2009). For instance, regional human influence and climate might control variability in non-native species richness at the regional scale (2,000–200 km), landscape characteristics might influence from the landscape to the local scale (200–1 km), while patch characteristics and habitat type influence invasion at the local scale. Following this hierarchical approach, we found patch and landscape characteristics the most important group of variables influencing non-native species richness in comparison to regional human influence and habitat type. The importance of landscape characteristics found is in line with the medium spatial scale of the study area (<200 km) (Milbau et al. 2009). Coarser scales such as continental, would probably found a more relevant role of climate

Table 3 Multimodel inference results: non-corrected and unbiased weight of evidence, averaged and standardized coefficient estimates (β) and confidence intervals (95 % CI)

Variable	Type	Weight	Unbiased weight	β Averaged	Adjusted SE	Lower CI	Upper CI
Intercept				1.103	0.182	0.747	1.460
Spatial autocovariate				0.074	0.015	0.045	0.104
Region	Region	1.000	0.820	–	–	–	–
Agricultural cover	Composition	1.000	0.784	–0.243	0.083	–0.405	–0.082
Patch area	Patch	0.976	0.736	0.097	0.041	0.017	0.177
Simpson land-cover diversity index	Composition	1.000	0.713	0.263	0.078	0.111	0.414
Mean fractal index	Configuration	1.000	0.711	–0.158	0.052	–0.260	–0.057
Edge density	Configuration	0.856	0.645	0.148	0.068	0.014	0.282
Low-density urban cover	Composition	0.790	0.591	0.117	0.057	0.006	0.227
High-density urban cover	Composition	0.674	0.411	0.096	0.050	–0.002	0.195
Habitat type	Habitat	0.587	0.354	–	–	–	–
Patch fractal index	Patch	0.457	0.243	–0.083	0.057	–0.194	0.028
Mean min. temperature	Climate	0.231	0.015	0.110	0.126	–0.138	0.357

Predictors are sorted by importance according to the unbiased weight of evidence. Regression coefficients for the categorical variables habitat and region are not shown. Significant averaged coefficients are shown in bold. See Table 2 for a complete description of variables

of region, habitat, patch, landscape (configuration and composition), and climate predictors for non-native species richness in Mediterranean coastal habitats

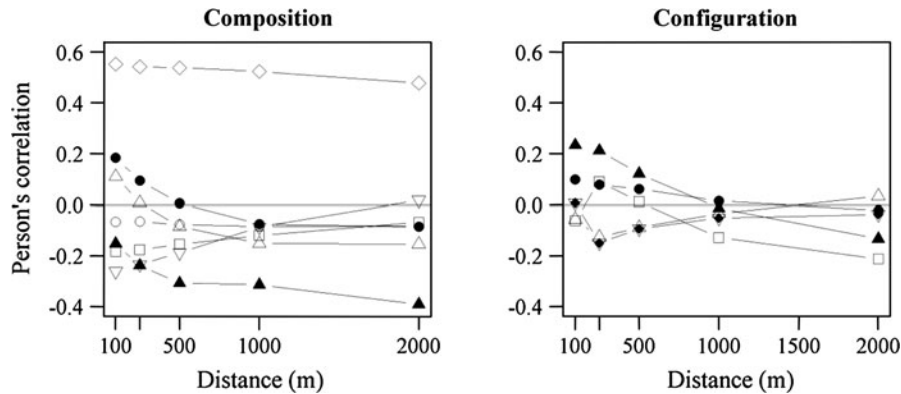


Fig. 3 Pearson's correlation coefficient between non-native species richness and landscape composition and configuration variables at each spatial extent (100, 250, 500, 1,000, 2,000 m around sampled patch). For configuration variables, the land-cover classification used considers urban, agricultural, natural and water land-covers. Composition: □ agricultural land-cover,

○ water land-cover, ▽ natural land-cover, ◇ urban land-cover, ▲ land-cover richness, △ Shannon land-cover diversity, ● Simpson land-cover diversity. Configuration: □ patch density, ● edge density, ▲ landscape shape index, △ mean patch area, ▽ mean shape index, ◆ mean fractal index

(Pearson et al. 2004) or regional human influence. The effect of landscape variables is mainly related to an increased propagule pressure from fragmented human-altered areas (Chytrý, et al. 2008a; Catford et al. 2011; Vilà and Ibáñez 2011). Human-altered areas such as gardens, artificial edges or communication networks are usually heavily invaded (Vilà et al. 2007; Chytrý et al. 2008b) and can easily become the source of propagules to nearby natural areas.

The identity of the region was, after patch and landscape variables, the most important factor explaining non-native species richness in Mediterranean coastal habitats. Non-native species richness was higher in Barcelona and Girona regions than in the Menorca Island. This result was also found for a broader geographic area in Catalonia and Balearic regions using a regional database of vegetation relevés and it was attributed to the higher human influence in the mainland regions than in Menorca (Vilà et al. 2010). Stronger regional human influence could encompass factors known to increase non-native plant invasions such as higher propagule pressure from human-altered habitats and an intense use of non-native plants for ornamental or restoration purposes (Simberloff 2009). Indeed, density of human population and that of road networks are larger in Catalonia than in the Balearic Islands (Vilà et al. 2010; Table 1). However, in Menorca, these effects might be confounded with insularity, which might alter the arrival and establishment of non-native plant species.

Classical works suggested that islands tend to be more heavily invaded than their mainland counterparts (Elton 1958; Lonsdale 1999; Pyšek and Richardson 2006). However, other studies confirm our findings supporting that communities in non-oceanic islands tend to be less invaded by non-native plants than in the mainland (Teo et al. 2003; Atwood and Meyerson 2011). Furthermore, even when islands were found to be more invaded these differences could be explained by other factors not directly linked to insularity, but to differences in anthropic disturbances (Yiming et al. 2006). Thus, after accounting for landscape characteristics and climate differences, our results suggest that the difference in regional human influence is the most important aspect explaining the differences in plant invasions across regions. Other factors not explored in this study that could account for difference in invasion might be related to differences in invasion history (Teo et al. 2003; Yiming et al. 2006; Vilà et al. 2010). However, its relative importance should be considered rather low due to the intensive trade and transport among regions.

Although we found significant differences among habitats, habitat type alone did not explain a high amount of deviance in non-native species richness. On the contrary, previous studies have found habitat type to be the foremost factor explaining differences in plant invasions (Chytrý et al. 2008a; Gassó et al. 2012). One reason for this discrepancy could be the environmental similarity among the habitats assessed

in our study. Furthermore, habitat type encompasses a range of factors known to affect plant invasions (Chytrý et al. 2009; Catford et al. 2011). The partition analyses revealed that habitat type shared its explained deviance with landscape, region and climatic variables. Therefore, although habitat type might not be the most important predictor, it might be used as a simple estimate of invasion risk when information on the landscape or climate is scarce.

Patch and landscape characteristics influencing plant invasions

Landscape composition variables were more important predictors of non-native species richness than landscape configuration or patch variables. The importance of landscape composition on plant invasions has been widely confirmed in many studies (Vilà and Ibáñez 2011). Land-cover diversity and the percentage of urban and agricultural land-cover were the most important landscape predictors of non-native species richness. Highly diverse landscapes support the idea that a larger gradient of environmental conditions allows the establishment and spread of many different non-native species. In turn, these landscapes could provide a greater pool of non-native species with the potential to reach natural vegetation patches (Pino et al. 2005; Marini et al. 2009).

Urban land-cover usually has a positive effect on plant invasion both at plot and grid level (Pino et al. 2005; Gassó et al. 2009; Gavier-Pizarro et al. 2010; Vilà and Ibáñez 2011). However, not all urban areas contribute the same to plant invasion. Patches surrounded by low-density urban areas showed higher non-native species richness than high-density urban areas. These results support previous findings by Gavier-Pizarro et al. (2010) within administrative regions in New England (USA). The low-density urban land-cover is characterized by fragmented and disturbed natural areas within a loose matrix of gardening and housing areas. Therefore, the probability of non-native ornamental species spreading from gardening and housing areas into adjacent natural areas is higher in a low-density urban landscape matrix.

Agricultural land-cover was negatively associated with non-native species richness, as found in other studies (Ibáñez et al. 2009; Marini et al. 2009). The effect of agricultural land-cover depends on the

surrounding landscape and habitat type (Vilà and Ibáñez 2011). In human-influenced landscapes, as in our study, agriculture could act as a buffer against invasion. Especially in forests, where invasion into the interior is driven mainly by shade-tolerant ornamental species, agriculture areas could act as a barrier to their expansion (Cadenasso and Pickett 2001). Furthermore, non-native species of agricultural origin may not invade natural areas but remain as weeds in crops (Vilà et al. 2004).

The effect of landscape configuration and patch characteristics on plant invasions has been traditionally less explored (Vilà and Ibáñez 2011). The low importance of these variables found in contrast to landscape composition variables underpins their idiosyncratic effects on plant invasions. As in previous works by Kumar et al. (2006) and Bartuszevige et al. (2006), we found that patches surrounded by fragmented landscapes (i.e. high edge density) underwent heavier invasions. Edges are usually highly invaded and thus might play an important role both as sources and sinks of non-native propagules (Vilà and Ibáñez 2011). Mean landscape-shape complexity (i.e. mean fractal index) had a negative association with non-native plant richness. To our knowledge, the only study available exploring this attribute found a positive association (Kumar et al. 2006). Our opposite finding might be explained by less shape complexity of anthropogenic landscapes (mainly urban and agricultural) than natural landscapes. In fact, there was a negative correlation between mean shape complexity and urban land-cover (Supplementary Material 1).

Finally, the only patch characteristic influencing non-native species richness was patch area. The positive relationship found between patch size and non-native species richness might be simply trivial (i.e. the larger patch area the more opportunities for random establishment of non-native species), but it might also reflect higher microhabitat diversity of large patches compared with that of small ones. This finding contradicts previous studies where the relationship was not significant (Cully et al. 2003) or even negative (Ohlemüller et al. 2006; Guirado et al. 2006). The lack of effect of patch shape complexity is in line with other studies (Bartuszevige et al. 2006; Vilà and Ibáñez 2011; but see Ohlemüller et al. 2006). These results confirm the variability of the influence of patch characteristics on non-native species richness in

comparison to propagule pressure proxies such as landscape composition variables.

The landscape extent relevant to plant invasions

We found high variability in the association of landscape characteristics with non-native species richness considering the spatial extent of study. The sensitivity of landscape indices to the spatial extent is a major concern when trying to elucidate the importance of landscape characteristics in ecological processes (Baldwin et al. 2004; Kumar et al. 2006; Bailey et al. 2007). While previous studies have found 250 m to be the most influential extent in plant invasions (Sullivan et al. 2005; Kumar et al. 2006; Bartuszevige et al. 2006), our findings suggest that the major influence occurs at smaller spatial extents (100 m) for most of the variables. In highly altered systems such as in our study area, the immediate neighbouring space is probably the most relevant extent to invasion because it might reflect a direct link with disturbance and species dispersal. For example, adjacent urban areas might facilitate the arrival of ornamental plant species without the need of long-distance dispersal events or an increase in human frequentation.

We also found that landscape configuration variables caused more diverse changes across spatial extents than did landscape composition variables. While composition variables showed slightly linear decrease in association, most of the configuration variables showed also unimodal responses to the extent (i.e. maximum association at 200–250 m). This finding reinforces the idiosyncratic effect of landscape configuration variables on non-native species richness, and the importance of performing sensitivity analyses to detect the most relevant landscape extent for each landscape predictor (Kumar et al. 2006). Other aspects on the sensitivity of landscape indices not explored in this study that might require further research are the type of landscape (e.g. urban vs. agriculture landscapes), the landscape thematic resolution (i.e. classification scheme of land-cover types) and the sampling resolution (Baldwin et al. 2004; Kumar et al. 2006).

Conclusions

Landscape composition was the most important determinant of non-native plant invasions in Mediterranean

coastal areas. Natural areas close to diverse and urban landscapes are highly vulnerable to plant invasions while surrounding agricultural areas could buffer this effect. Within highly invaded systems the effect of landscape composition is clearly more evident than the variability in regional human influence, habitat type, patch geometry or landscape configuration. The prevalence of this pattern might also depend on the range of climatic conditions, habitat similarity and the stage of invasion under consideration. Thus, our findings indicate that invasion-risk analyses must take into account the landscape matrix, especially in terms of land-cover diversity and human alteration (Hulme 2006).

Our study also advocates that plant-invasion risk analyses considering landscape characteristics should include sensitivity analyses in order to test differences across spatial extents (Kumar et al. 2006; Pauchard and Shea 2006). Our study yielded a wide variability in the strength of association of landscape variables with non-natives species richness at different spatial extents. Thus, a measure of landscape characteristics at a single spatial extent might lead to erroneous conclusions about the susceptibility of an area to invasion. Once the spatial extent that maximizes plant invasions is identified, it could be used to target the management of non-native species. Usually, the management of non-native species focus on the stand scale (Pauchard and Shea 2006) although other approaches have been applied at the landscape scale (e.g. vehicles or weed cleaning) or even at broader scales (e.g. import regulation). Our study suggests that management of the neighbouring landscape (i.e. 100–250 m) should be a priority to control plant invasions at the local scale.

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