Regional context affects native and alien plant species richness across habitat types

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Abstract

Question: How does large-scale context affect native and alien species richness across different habitat types?

Location: Catalonia, NE Spain.

Methods: We analysed a set of 5309 vegetation plots from the BDBC (Biodiversity Data Bank of Catalonia) database, organized following the UTM (Universal Transverse Mercator) 10 km × 10 km grid. Plots were assigned to the first or second hierarchy of EUNIS (European Nature Information System) habitat classification. For each plot, the number of native plants (including archaeophytes, i.e. alien plants introduced before 1500 AD) and neophytes (alien plants introduced after 1500 AD) was recorded. Neophytes were classified according their Raunkiaer's life form. For each UTM we selected eight predictors related to land cover composition, anthropogenic context and climate. The association of neophyte and native species richness with these predictor variables was explored by generalized linear mixed models for each terrestrial habitat type after controlling for plot area.

Results: A total of 77 different neophyte species were found distributed among the eight habitat types with fitted models. Minimum adequate models on both neophyte and native species richness were highly variable. In general, native species richness responded more to climatic variables, while neophyte species richness was associated more with human landscape factors such as distance to main roads and, secondarily, cropland cover.

Conclusions: Context factors defined on a large scale (10 km) have a significant effect on local native and neophyte species richness for many habitat types in Catalonia. Our results highlight the major influence of climatic context on native species richness and the influence of human landscape context on neophyte species richness in the study region. The inconsistency of results between habitat types suggests that this large-scale effect might be highly idiosyncratic and dependent on species ecology and life form.

Introduction

Biological invasion is a worldwide phenomenon caused by direct and indirect species introduction by humans (Kowarik 2003). The extent of invasion and its impact differs spatially depending on the region and habitat type (Sax 2001; Levine et al. 2003; Rejmánek et al. 2005). In the case of plants, low-altitude regions contain more alien species than high-altitude areas (Arévalo et al. 2005). This is because low-altitude regions experience a milder climate and harbour a greater range of anthropogenic environ-

ments with a higher degree of invasion compared with high-altitude regions, which are generally more preserved (Pino et al. 2005; Vilà et al. 2007; Chytrý et al. 2008b).

Spatially explicit analyses of degree of invasion are needed to face the challenges of future climate and land-use changes (Ibáñez et al. 2006; Thuiller et al. 2006; Nobis et al. 2009; Vilà & Ibáñez 2011). At the coarse scale, regional analyses have focused on correlations between alien species richness and environmental variables (Deutschewitz et al. 2003; Pino et al. 2005; Stohlgren et al. 2005; Gassó et al. 2009). These analyses have identified climate

mildness and surrogates of propagule pressure (i.e. intensity and frequency of introductions) such as population density and urbanization as key determinants of invasion (Deutschewitz et al. 2003; Pino et al. 2005; Kühn & Klotz 2006; Gassó et al. 2009; Nobis et al. 2009). At the fine scale, most studies are based on extensive analysis of large datasets of vegetation plots. These local-scale analyses have shown that anthropogenic habitat types are among the most invaded ones (Chytrý et al. 2005, 2008b; Stohlgren et al. 2005; Maskell et al. 2006; Vilà et al. 2007).

However, some of these analyses have found large differences in the spatial pattern of plant invasions within particular habitat types, depending on their invasion history (Roy et al. 1999; Domènech et al. 2005; Guo 2006) and their environmental context, which includes climate, landscape and human factors at diverse spatial scales (McIntyre & Lavorel 1994; Bartuszevige et al. 2006; Ohlemüller et al. 2006; Chytrý et al. 2008a). Indeed, the degree of invasion by alien plants in forest patches is often explained more by landscape factors than by habitat properties (Bartuszevige et al. 2006; Ohlemüller et al. 2006). In addition, the number of alien plants in vegetation plots of diverse habitats in the Czech Republic was weakly but significantly related to a set of proxies for propagule pressure measured in the immediate context (i.e. a radius of 500 m; Chytrý et al. 2008a). Some regional environmental factors also affect habitat invasion in the few studies available (Ohlemüller et al. 2006).

To date, it is unknown whether, at the local (plot) scale, the environmental and landscape context influences alien and native plant species richness differently (Vilà & Ibáñez 2011). This comparison is needed in order to ascertain the mechanisms behind alien species success and habitat vulnerability to invasion. We know that the association between alien and native species richness is both context- and scale-dependent (Levine & D'Antonio 1999; Brown & Peet 2003; Vilà et al. 2007). This apparent inconsistency suggests that patterns of native and alien plant species across environmental gradients might be driven by different ecological factors. Many alien species are recent colonizers and thus their patterns of distribution and abundance are not yet influenced by geological factors (e.g. glaciations) and speciation rates in the recipient region (Sax 2001; Kühn et al. 2003). Furthermore, both the introduction and spread of alien species are intrinsically human mediated. Thus their occurrence and abundance might be influenced more by anthropogenic processes than by environmental factors.

In the present study, we explored the effect of large-scale context (10 km × 10 km) factors on a set of more than 15 000 vegetation plots classified in EUNIS (European Nature Information System) habitat types. This dataset is recorded in Catalonia, located in the NE of Spain. The

heterogeneous climate, topography and geology found in this area has given rise to a high plant species richness. In this study we address three questions: (1) Is there a significant effect of climate and landscape context factors on the degree of habitat invasion? (2) Is native and alien species richness within habitats associated with the same context factors? and (3) How consistent is the influence of these context factors across habitat types?

Methods

Study area

Catalonia (32 000 km^2), located in NE Spain, is bounded in the north by the Pyrenees and in the east by the Mediterranean Sea. We chose this region for our analysis because of its contrasting topography, climate, dominant vegetation and land uses. Catalonia is located in the boundary between the Eurosiberian and Mediterranean phytographic regions, in which the Pyrenees impose a sharp topographic–climatic gradient where Mediterranean and 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 mild climate, to inland, with contrasting dry conditions (Ninyerola et al. 2000).

The landscape structure of Catalonia is also highly heterogeneous. Forest currently occupies 40% of the Catalonian surface and dominates the mountain ranges. In the last century, abandonment of marginal agricultural areas has led to progressive forest recovery, which is challenged by increasing wildfire frequency. The most favourable plains and plateaux for human settlement show a contrasting situation, with progressive crop intensification and urbanization.

Vegetation plots

The high phytogeographic diversity of Catalonia has resulted in a rich flora, estimated as more than 3200 species (Bolòs et al. 2005). A remarkably long botanical tradition has permitted the accumulation of a great number of floristic records in Catalonia. In order to facilitate the development of surveys from the regional to continental level, the Biodiversity Data Bank of Catalonia (BDBC) has been devoted to the gathering, organization and online exploitation (http://biodiver.bio.ub.es/biocat/homepage. html) of all these floristic data. The BDBC accounts for about 1 200 000 floristic records and 17 000 phytosociological relevés organized following the UTM (Universal Transverse Mercator) 10 km × 10 km grid. We selected those relevés produced between 1975 and 2005, having phytosociological classification, and located in UTM cells

with more than 60% of their area within the borders of Catalonia. This region accounts for a long tradition in the study of alien plants, which led to an early review of its alien flora (Casasayas 1989). Thus, we can be relatively confident that alien species were not excluded from plots, as observed in many old phytosociological studies.

Relevés were assigned to a first or second hierarchical level of EUNIS habitat classification through the phytosociological alliance they belong to (See the Supporting Information, Appendix S1). The size of the plots where relevés were performed ranged from 1 m² to hundreds of m² (Table 1), following the within-habitats variation of the European standards for phytosociological relevés (Chytrý & Otýpková 2003). Further details on the Catalonian data set are given in Vilà et al. (2007).

To assess if the relevés of each UTM cell correctly represent the habitat distribution in the range analysed, the correlation between the number of plots per EUNIS habitat type and the number of UTM cells they belong was calculated (Appendix S2). Results indicate that the number of plots is a good measure of the geographical extent of a particular EUNIS habitat type within the region studied. In this context we can confirm that the selected relevés were representative of the habitats inside the majority of UTM cells in the study. Their distribution was relatively heterogeneous (Fig. 1) and concentrated in the main mountain ranges in the north and south boundaries.

For each plot, the number of native and neophyte (i.e. alien species introduced or naturalized after 1500 AD) species was recorded. Archaeophytes (i.e. alien species introduced before 1500 AD) were pooled with natives as the archaeophytic flora of the Mediterranean Basin is largely unknown and, in many cases, it is difficult to prove whether a species is archaeophyte or native (Chytrý et al. 2008b). Neophytes were classified according their Raunkiaer's life form.

Predictor variables

We selected three variables relative to land-cover composition (cover percentage of forests, scrubland–grassland, and cropland), three of anthropogenic context (cover percentage of built-up areas, human population density and distance to main roads) and two climatic variables (mean annual temperature and annual rainfall), all known to be correlated with both native and alien species richness in Catalonia and Spain (Pausas et al. 2003; Pino et al. 2005; Gassó et al. 2009). As the only spatial reference of vegetation plots was the UTM cell they belong to, these variables were averaged for the UTM 10 km × 10 km grid. Thus, all plots within each UTM cell shared the same values of predictor context variables. All the GIS procedures involving the set-up of environmental variables were performed

using MIRAMON software version 5.4 (http://www.creaf.uab.cat/miramon/index.htm).

These variables were calculated from digital cartography of around 1990, close to the middle point of relevé dates (mean of years 1992.4; SD 5.7). Artefacts caused by discrepancies between relevé and cartography dates were minimized by the fact that context variables were averaged for each UTM 10 km × 10 km grid. The percentage of each land-cover category was calculated from the CORINE (Coordination of Information on the Environment) Land Cover Map of Spain (http://www.fomento.es) of 1990. The percentage of built-up areas, the human population density and the distance to the roads were calculated from the official urban settlement map of Catalonia (http://www20.gencat.cat/portal/site/dmah), which includes population census of 1990 to calculate the population density per UTM square. The mean distance to the main roads and motorways for each UTM square was obtained from distance maps of 200 m pixel size, calculated on a selection of the motorways and main roads from the 1:50 000 topographic map of Catalonia.

Mean annual temperature (°C) and annual rainfall (mm) 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. Mean annual temperature was strongly correlated with annual rainfall ($r = -0.84$, $P < 0.0001$). In order to keep both variables in the analyses, we adjusted annual rainfall by fitting univariate non-linear regressions (generalized additive model with four degrees of freedom) describing the average relationship between mean annual temperature and annual rainfall. We then used the residuals of the univariate regression as a predictor (for more details see Leathwick et al. 2006; Thuiller et al. 2006).

Statistical analyses

Native and neophyte species richness (i.e. species number per plot) were used as dependent variables. Their association with the predictor variables was explored by generalized linear mixed models (GLMM) for each terrestrial habitat type with at least one neophyte species per plot using the open source R software version 2.5.1 (R Development Core Team 2005; http://www.r-project.org). Plot size was included as a covariable in the analyses because it varied largely within some habitat types (Table 1). Furthermore, as each plot belonged to a geographical well-delimited UTM cell, they could not be used as fully independent data points. Therefore, UTM cell identity was considered as a random factor in the model.

Gaussian, linear mixed-effects models (type I) were performed on native species richness using the lme procedure

Table 1. Range size, cumulative area and number of plots per EUNIS habitat type, number of UTM (Universal Transverse Mercator) cells where they are located, number of plots per UTM cell, mean (±SE) alien and native species richness, and proportion of plots with at least one alien species.

EUNIS habitat	Number of plots	Plot size (interquartile range, m²)	Cumulative plot area (m²)	Number of UTM with plots	Number of plots per UTM (mean ± SD)	Number of alien species per plot (mean ± SD)	Number of native species per plot (mean ± SD)	Plots with at least one alien species (%)
B1 Coastal dune and sand habitats	76	12–50	3436	7	5.8 ± 5.26	0.48 ± 0.07	10.15 ± 0.55	42.11
B3 Coastal rocks	44	20–100	29511	2	2.86 ± 2.79	0.18 ± 0.05	12.81 ± 0.93	18.18
E1 Dry grasslands	**1964**	**5–35**	115	**169**	10.72 ± 15.79	**0.09 ± 0.01**	**29.20 ± 0.26**	**8.71**
E2 Mesic grasslands	**310**	**18–50**	4897	**58**	4.65 ± 6.25	**0.11 ± 0.02**	**28.15 ± 0.70**	**10.65**
E3 Wet grasslands	**369**	**7–25**	3906	**81**	4.43 ± 4.81	**0.19 ± 0.03**	**16.29 ± 0.41**	**13.55**
E5.6 Anthropogenic forb-rich habitats	**720**	**10–30**	182686	**123**	5.64 ± 5.61	**0.98 ± 0.06**	**16.65 ± 0.33**	**39.44**
E6 Inland saline grass and herb-dominated habitats	276	20–50	13604	13	8.11 ± 6.88	0.24 ± 0.02	7.42 ± 0.20	22.46
F3 Temperate and Mediterraneo-montane scrub habitats	**339**	**20–50**	8035	**85**	3.27 ± 2.87	**0.06 ± 0.01**	**19.67 ± 0.54**	**5.31**
F5 Maquis, matorral and thermo-Mediterranean brushes	252	50–100	19173	55	4.1 ± 4.45	0.02 ± 0.01	21.18 ± 0.50	1.58
F9.1 Riverine and lakeshore scrub	41	25–80	9235	25	1.42 ± 0.96	0.66 ± 0.17	23.78 ± 2.18	36.58
F9.3 Southern riparian galleries and thickets	41	25–80	14045	14	1.73 ± 1.27	0.43 ± 0.14	13.27 ± 0.97	26.83
G1 Deciduous woodland	**973**	**75–100**	14254	**119**	6.41 ± 8.62	**0.05 ± 0.01**	**27.43 ± 0.34**	**3.18**
G2 Broadleaved evergreen woodland	588	40–100	2157	107	5.13 ± 5.7	0.01 ± 0.01	21.75 ± 0.38	1.19
H3 Inland cliffs, rock pavements and outcrops	452	4–20	1871	82	6.00 ± 7.8	0.01 ± 0.01	9.39 ± 0.20	1.55
H5.6 Trampled areas	**272**	**5–20**	92074	**76**	3.22 ± 3.31	**0.75 ± 0.07**	**14.71 ± 0.53**	**40.81**
I1 Arable land and market gardens	**362**	**30–90**	41587	**90**	3.38 ± 2.93	**1.49 ± 0.09**	**19.65 ± 0.49**	**59.95**

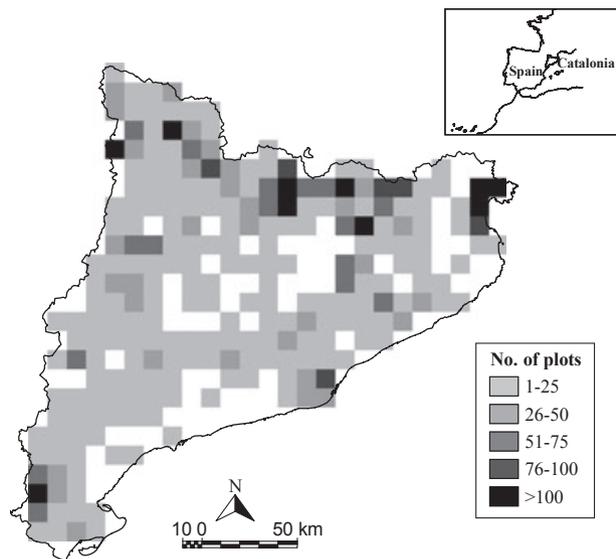Habitat types with fitted models are shown in bold type.

Fig. 1. Map of the study area showing the total number of vegetation plots in each studied UTM (Universal Transverse Mercator) cell.

of the nlme library in the R statistical package (Lindstrom & Bates 1988). In contrast, neophyte species richness was generally right-skewed and it could not be normalized with logarithmic or any other transformation. In consequence, it was modelled with a Poisson distribution of errors (Crawley 2002) after checking that data were not affected by overdispersion. Models were performed using the glmmPQL procedure of the MASS library in the R statistical package (v. 2.12, R Development Core Team). We then explored whether habitat types with fitted and non-fitted models differed in their mean and dispersion (SE) of
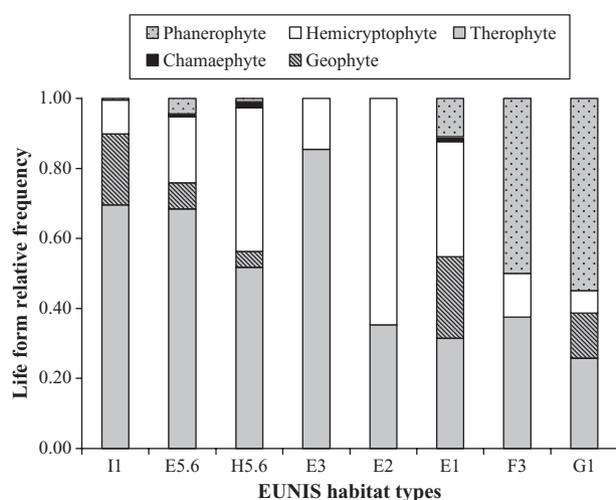
both neophyte and native species richness, in their number of plots and UTM cells. The mean values of these variables were compared between habitat types with and without fitted models, using a non-parametric test of ranks and the Mann–Whitney U statistics.

Results

Only 8 of the 16 original habitat types could be modelled. These habitats showed a significantly higher number of plots and they were present in significantly more UTM cells than those that could not be modelled (Appendix S3). The three least invaded habitats (i.e. F5, H3 and G2) could not be modelled despite their large sample size and wide distribution across the region because, in these habitats, the distribution of neophyte species richness was biased towards zero values.

A total of 77 different neophyte species were found distributed among the eight habitat types with fitted models (Appendix S4). The three most represented species were *Aster squamatus* (found in 87 plots), *Amaranthus retroflexus* (75 plots) and *Bromus catharticus* (68 plots). Only the first species was found in all habitat types.

Therophytes were the most frequent life form in the most anthropogenic modelled habitats, namely arable land and market gardens (I1), anthropogenic forb-rich habitats (E5.6) and trampled areas (H5.6), and in wet grasslands (E3; Fig. 2). In contrast, temperate and Mediterraneo-montane scrub habitats (F3) and deciduous woodland (G1) were dominated by phanerophytes. Hemicryptophytes were mostly concentrated in mesic grasslands (E2), and geophytes were mostly concentrated in dry grasslands (E1).

Predictors for neophyte and native species richness

Minimum adequate models on both neophyte and native species richness showed high variability in the resulting significant variables among habitat types (Table 2). However, climate variables were associated more with native than with neophyte species richness. Indeed, native species richness was positively associated with rainfall and negatively associated with mean temperature in the majority of habitats. In contrast, rainfall and temperature were positively associated with neophyte species richness in only two habitat types. In the majority of habitat types, plot area was significantly associated with native species richness but not with neophyte species richness. The association with native and neophyte species richness was mostly positive and of variable sign, respectively.

Landscape variables showed a heterogeneous pattern of association with native and neophyte species richness, depending on habitat type. Native species richness was

Fig. 2. Relative frequency of Raunkiaer's life forms of alien species per modelled EUNIS (European Nature Information System) habitat type, based on the number of records of each species in the plots.

Table 2. Summary of the minimum adequate models for each habitat type when modelling alien species richness and native species richness.

Eunis	Plot area	Forests (%)	Scrubland (%)	Cropland (%)	Built-up (%)	Distance to main roads	Population density	Mean annual temperature	Annual rainfall
Alien species richness									
E1 Dry grasslands	−40.980***			−0.311*		−0.476**			
E2 Mesic grasslands									0.555*
E3 Wet grasslands	−0.291*	−1.092***				−0.765*			
E5.6 Anthropogenic forb-rich habitats	0.187***			0.316*		−0.276*		0.401*	0.230*
F3 Temperate and Mediterraneo-montane scrubs		0.966*		1.638***					
G1 Deciduous woodland		−1.443***	−1.686***	−0.398***					
H5.6 Trampled areas			0.233*		0.180**	−0.430**		1.136***	
I1 Arable land and market gardens			−0.315*	0.300*		0.161*	0.232***		
Native species richness									
E1 Dry grasslands	−0.028**	0.073**					0.096**		
E2 Mesic grasslands	2.329***	2.339**				−2.682*		−3.083**	5.191***
E3 Wet grasslands	0.831**	4.243***	4.505***					−1.403*	1.430*
E5.6 Anthropogenic forb-rich habitats				5.018*	3.033**	−1.220*		−2.103*	1.804***
F3 Temperate and Mediterraneo-montane scrubs	1.759***							−3.612***	3.521***
G1 Deciduous woodland	1.386***	1.887**						−1.966**	2.167***
H5.6 Trampled areas	3.798***								1.524*
I1 Arable land and market gardens	1.128*								

Model estimates of Student t-statistic are shown only for those variables that remained in the minimum adequate model. See Table 1 for habitat type description.

Significance: *$0.01 < P < 0.05$, **$0.001 < P < 0.01$, ***$P < 0.001$).

positively associated with forest cover percentage in four of the modelled habitats, and with scrubland and cropland cover in anthropogenic forb-rich habitats (E5.6) only. In contrast, neophyte species richness showed both positive and negative associations with forest, scrubland and cropland cover depending on habitat type. Built-up land cover showed a positive association with both native and neophyte species richness in trampled areas (H5.6).

Distance to roads affected both native and neophyte species in a similar way. However, the trend was more generalized for neophytes. The association of neophyte species richness with distance to roads was negative for the majority of habitat types except for two of the most anthropogenic types (I1, arable land and market gardens, and E5.6, anthropogenic forb-rich habitats) and one of the least anthropogenic (G1, deciduous woodland), for which the association was positive or non-significant. Population density was only positively related to neophyte species richness in anthropogenic forb-rich habitats (E5.6) and with native species richness in dry grasslands (E1).

Discussion

Our study shows that the local degree of plant invasion in a given habitat may be significantly affected by large scale (10 km × 10 km) context factors. This complements the view of Chytrý et al. (2008a), who also found some significant effects of context factors on patterns of alien plant invasion in Central European habitats but at a considerably lower spatial scale (500 m radius around plots). In consequence, habitat identity is not the only determinant of the degree of invasion, as spatially explicit factors related to environmental conditions and propagule pressure also modulate habitat invasion (Vilà & Ibáñez 2011). Furthermore, the effect of these environmental factors appears to be largely idiosyncratic in Catalonia, probably because of specific interactions between context, habitats and species. However, some artefacts resulting from the discrepancy between the scale of analysis in plots and UTM cells cannot be discounted. Several recent studies highlight the importance of selecting the appropriate spatial scale for evaluating the distribution and abundance of alien plant invasions and identifying their primary correlates (Foxcroft et al. 2009).

Context factors also had an effect on native species richness, but usually in a different or even opposite way to neophyte species richness. Climate variables were associated more with native than with neophyte species richness. In many habitats, native species richness increased and decreased with increasing annual rainfall and mean annual temperature, respectively, which is in accord with other studies (Pausas & Austin 2001; Pausas et al. 2003) and consistent with the energy-productivity hypothesis

(Allen et al. 2002). In contrast to these effects on native species, temperature and rainfall showed significant associations with neophyte species richness only in two EUNIS habitat types. These associations were always positive, as has also been found for neophyte species richness at the UTM scale (Pino et al. 2005).

The association of landscape factors with both native and neophyte species richness was highly variable among habitat types, indicating that there is no unique set of context correlates of plant species richness across habitats. However, some trends can be highlighted. In general, native species richness was associated less with landscape variables than with neophyte species richness, which, in turn, was especially correlated with human landscape factors. Indeed, forest cover percentage, which was the primary landscape correlate of native species richness, was positively associated with this variable in only four of the eight modelled habitats. In contrast, neophyte species richness was mainly related to distance to main roads and, secondarily, to cropland cover. A number of studies show that the anthropogenic transformation of landscape enhances the introduction of alien species and their spread (Brothers & Spingarn 1992; Hobbs & Huenneke 1992; Pino et al. 2006), because it commonly determines the rarefaction of habitat specialists while encouraging the spread of habitat generalists, including alien species (McKinney 2006; Pino et al. 2009). The negative association between neophyte species richness and distance to roads indicates high propagule pressure associated with transport of commodities (Tyser & Worley 1992; Lippe & Kowarik 2006).

It should be noted that landscape factors showed relatively variable associations with both neophyte and native species richness depending on habitat type. Results might be partially explained by plant life form and ecology (Fig. 2). For example, the relationship with neophyte species richness was positive for arable land and marked gardens (I1), and non-significant for woody habitats (F3 and G1). In the first habitat type, the alien flora is dominated by annual weeds with short life cycles (Boutin & Jobin 1998) and persistent seed banks (Thompson 1992), whose means of introduction might be relatively independent of roads and railways as they are mostly introduced as a crop contaminant (Mohler 2001). In the second case, the neophyte flora is especially rich in woody, long-lived species with specific dispersal mechanisms that are also independent of road networks. The effects of cropland cover on neophyte species richness also suggest some links with species life strategy. Indeed, the significant relationships with neophyte species richness were mostly positive, except for dry grasslands (E1) and deciduous woodland (G1). The neophyte flora of these habitats is dominated by woody species and hemicryptophytes whose introduction

pathways are not determined by cropping activities. The other results regarding the linking of landscape factors with neophyte and native species richness are extremely variable, suggesting complex interactions between landscape, habitat type and species identity that deserve further investigation.

Our study shows that, for several habitats in Catalonia, neophyte species richness is partly explained by coarse-scale (10 km) human landscape factors. These results contrast with those of Chytrý et al. (2008a), who measured a set of variables related to human pressure at a considerably finer scale (500 m around the plots), and found a significant association of these factors with alien species richness for archaeophytes, but not for neophytes. Vilà et al. (2010) found that contrasting alien species richness between similar habitats of Catalonia and the adjacent Balearic Islands match differences in the regional pool of alien species and overall indicators of human development, such as gross domestic product and road density. This suggests that the association between these anthropogenic factors and alien species richness in habitat plots mainly manifests at large scales, as supported by our results.

Our study also highlights that, in sparsely invaded habitats, the influence of environmental and climatic factors on neophyte species richness cannot be explored. Mediterranean forests and maquis (F5 and G2) are among the least invaded habitats in Catalonia (Vilà et al. 2007). Although well represented across the study area (i.e. high number of plots and UTM), more than 98% of the plots of this type are non-invaded. It has been suggested that woody habitats in the Mediterranean Basin are highly resistant to invasion because of environmental constraints (e.g. summer drought) and a long history of anthropogenic disturbances (di Castri 1990). Observational studies have found that Mediterranean woodlands are exposed to invasion when they are subjected to fragmentation and human frequentation (Guirado et al. 2007). However, alien plants are restricted to a narrow area (less than 500 m) on the forest edge (Guirado et al. 2006).

In conclusion, neophyte and native species richness at the local scale in Catalonia are associated with the larger climatic and landscape context. However, this association is relatively inconsistent among habitats, especially when considering anthropogenic landscape variables. Our results reinforce the view that habitat identity is more important as a predictor of invasion than environmental and geographic variables (Chytrý et al. 2008a). There are, however, some observable patterns such as the response to an anthropogenic context, according to the ecology of the alien species introduced in each habitat, and a major dependence on climate by native species. More research is needed on the interaction of species requirements and traits with habitat and landscape properties. These interactions are very diverse and complex but could be an route to improving habitat risk assessments to invasions (Vilà & Ibáñez 2011).

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Supporting Information

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

Appendix S1. Correspondence between the eight EUNIS habitat types with fitted models and the phytosociological alliances to which the plots were originally ascribed. Syntaxonomical nomenclature follows Bolòs et al. (2005). See Table 1 for description of habitat types.

Appendix S2. Number of plots vs number of UTM for each habitat type with indication of those habitat types with fitted (white triangles) and non-fitted (black rhombus) models. The curvilinear relationship between these variables was significant ($y = 59.052e^{0.0216x}$, Spearman $R^2 = 0.83$, $P < 0.001$). See Table 1 for habitat type description.

Appendix S3. Test of ranges comparing a set of descriptive statistics for habitat types with non-fitted (i.e. 'Non-modelled') and fitted (i.e. 'Modelled') models. Non-parametric statistics were performed to test the differences between both categories of habitats.

Appendix S4. List of neophyte species found in the eight modelled EUNIS habitat types, with their family and Raunkiaer's life form (Th: therophyte, H: hemicryptophyte, G: geophyte, Ch: chamaephyte, P: phanerophyte). The number of plots per habitat type where each species was found is indicated. See Table 1 for habitat type description.

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