Effects of past landscape and habitat changes in plant invasion provide evidence of an invasion credit

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Contribution to the project

The MSc project was initiated in February 2014.

The student (Maria Clotet Fons) contributed to the different parts of the study as follows:

- Literature research: Totally by the student.
- Data compilation: The database on alien species distribution was obtained by the supervisors through field work in 2012. The student compiled the cartography of potential correlates of alien species invasion, and assembled the database of variables using GIS tools
- Statistical analyses: Totally by the student, with the help of supervisors
- Manuscript writing: Totally by the student, with revisions by supervisors.

The MSc project follows *Biological invasions* guidelines.

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Abstract

Habitats differ in the invasion degree due to habitat properties and current spatial context. Historical context effects (i.e. land use change legacy) have been little studied and can be modulated by the invasion credit (the delayed increase in habitat invasion after changes in the land use). In this study we considered historical context to know if habitat changes affect the diverse components of plant invasion (introduction, establishment and spread) and to find evidence of invasion credit. The study is performed in the Barcelona province and consists in 531 sampling points distributed along 9 different habitats where we sampled the abundance (cover percentage) of each recorded alien plant species. Habitat and current and historical (past landscape and changes) spatial context variables were used to create the best model explaining introduction and establishment (presence and richness) and spread (mean abundance) of alien species in sampling points. The results show that alien species presence and richness are mostly influenced by habitat and topography but also by the number of changes, which suggests an effect of the land use legacy. The relationship between the historical landscape and alien species abundance provides evidence of an invasion credit. In conclusion, we have found evidence of an invasion credit in the spread stage while there is an effect of the historical legacy in the introduction and establishment. However, habitat invasion is a complex process affected by several factors such as species traits, the introduction event and residence time that should be considered in further studies.

Key words: invasion degree, habitat invasion, invasion credit, land use legacy.

Introduction

Alien species invasions are one of the most important threats for native species and habitats worldwide. However, not all native species are threatened to the same degree by invaders and not all habitats are equally invaded (Lonsdale 1999). It is known that the level of invasion of a given habitat (i.e., the actual number or proportion of alien plant species present in a habitat) strongly depends on habitat type (Crawley 1987; Vilà et al. 2007). However, these differences might be determined by either habitat invasibility, the spatial context of the invaded habitat or both (Chytrý et al. 2005).

Habitat invasibility has been defined as the relative number or proportion of alien plants when all of the context effects (climatic, topographic or landscape variables) are held constant (Chytrý et al. 2008). It has been found to be the most important factor in determining the level of invasion in large-scale studies (Chytrý et al. 2008). The most invaded habitats are those more influenced by human activity. In contrast, the least invaded are nutrient-poor habitats and those in the most extreme environmental conditions (Chytrý et al. 2005; Vilà et al. 2007; Chytrý et al. 2008). Therefore, the most important factor determining the invasion process is intrinsic disturbance regime and nutrient availability in habitats. The hypothesis of fluctuating resource availability states that disturbance returns resources to the system or decreases their consumption by eliminating resident vegetation (Davis et al. 2000) and these processes favour the introduction of alien species.

The level of invasion of a given habitat might also be determined by the spatial context (Gassó et al. 2012). Some context factors such as climate, topography and surrounding landscape have been identified as correlates of habitat invasion (Deutschewitz et al. 2003; Pino et al. 2005; Bartuszevige et al. 2006; Kumar et al. 2006; Catford et al. 2011; Vilà and Ibáñez 2011; Gassó et al. 2012; González-Moreno et al. 2013).

Many of these context factors are associated to environmental constraints (climatic and topographic) that can limit the invasion process in different regions. For example, temperature constraints habitat invasion in Catalonia due to tropical and subtropical origin of the majority of its alien species (Pino et al. 2005; Gassó et al. 2012).

The heterogeneity of the surrounding landscape is also an important context factor in determining alien plant invasions (Deutschewitz et al. 2003; Pino et al. 2005; Bartuszevige et al. 2006; Kumar et al. 2006; Catford et al. 2011; González-Moreno et al. 2013). Propagule pressure, defined as the number of individuals introduced and the number of introduction attempts (Colautti et al. 2006), and disturbance level can be influenced by the surrounding landscape (Vilà and Ibáñez 2011; Basnou et al. 2014).

Propagule pressure is commonly assessed through proxy variables such as the density and distance to the main roads, and the distance to the urban zones or its cover percentage in the surrounding landscape (Chytrý et al. 2008). The shorter the distances to the main roads and the urban zones, the higher the propagule pressure in terms of individuals and species (Gassó et al. 2012; González-Moreno et al. 2013; Basnou et al. 2014).

It is important to consider at which distance context affects the invasion process. Some studies have concluded that the extent of the surrounding landscape has the maximum influence in the invasion process at smaller extents (250m) (Kumar et al. 2006). However, it should be noted that the scale at which spatial context affects the invasion process strongly varies among factors (Milbau et al. 2009). Climatic requirements are the determinants for the establishment of alien plants at a regional scale. Other factors such as topography and land use and cover become important at landscape scales, whereas soil type, disturbance regime or biotic interactions are the most important factors determining alien plants establishment and spread at local, habitat scale.

In addition, it should be taken into account that habitat and spatial context might change over time and these changes might strongly affect the level of invasion of a site (Vilà and Ibáñez 2011). A number of recent works indicate that the invasion degree of habitats might be strongly related with their historical legacy (Vilà et al. 2003; Domènech et al. 2005; Pino et al. 2006; DeGasperis and Motzkin. 2007; Mosher et al. 2009; Pretto et al. 2010; Aragón and Morales 2013; Basnou et al. 2014). However, very little is known about how this legacy affects the invasion process. Recently, it has been proposed that it is a complex combination of two processes that might occur at contrasting time scales: landscape and habitat changes and the invasion process itself.

The invasion process is made up by different stages that might take place over time depending on the characteristics of the species and the spatial context (Theoharides and Dukes 2007). These processes are introduction, establishment and spread. The introduction depends, basically, on the propagule pressure, climate conditions, resource availability and species traits. The establishment and spread depend basically on specific processes of local adaptation but also on interactions with other plants or other trophic levels, disturbance regime, patch attributes and connectivity among different populations (Theoharides and Dukes 2007). Not all species finish this process as many of them are extirpated from the recipient areas during the introduction and establishment processes (Pysek et al. 2004), but even species that do so might take some time (e.g. years or decades) to complete this process from introduction to spread after changes in habitats and landscapes.

When this happens, there might be the so called invasion credits which are defined as the delayed increase in the richness and abundance of alien species after habitat change (Kowarik 1995; Vilà and Ibáñez 2011). Invasion credit is a particular case of immigration credit experienced by a committed increase of species richness after a forcing event (Jackson and Sax 2010).

There are no empirical evidences of invasion credits in habitat invasions but there are some studies suggesting their existence. Domènech et al. (2005) found that time since abandonment is really important in determining species composition in a particular area and in determining the vulnerability of a site to be invaded. Several related features such as direction (trajectory towards more degraded or more restored land-use), and intensity (magnitude of the land-use change) of change, and number of stages (number of land-use steps) can also modify the introduction, establishment and spread of alien species at a site (Domènech et al. 2005). Mosher et al. (2009) also found that the land use history plays an important role on the pattern, extent and timing of the woody plant invasion process.

The major problem in studies as such is that time series information is rarely available and this makes the investigation of the invasion credit very limited to few studies. A solution is to assess the relationship of current data of presence, richness and abundance of alien species with the information about context and habitat conditions in the past obtained by photointerpretation, as explored in colonization credit (Basnou et al. 2014) and extinction debt (Kuussaari et al. 2009) studies.

The aim of the study is to know how habitat and landscape changes influence the invasion process in the case of alien plants. We have used information about the past (in 1956 and 1993) and the present (2009) landscape obtained by photointerpretation and other variables related with the topography, climate and changes over time. To model the different phases in the invasion process, we have used presence and richness, as indicators of the introduction and establishment, and abundance, as indicator of the spread of alien plants. The specific questions of the study are: (1) which is the relative effect of habitat properties, and current and historical spatial context in the introduction, establishment and spread of alien species in an area?; (2) are the introduction, establishment and spread driven by the present or the past landscape?; and (3) is there any evidence of an invasion credit?

We expect that there is an important effect of the habitat properties and propagule pressure in the introduction and establishment of alien plant species (Theoharides and Dukes 2007). On the other hand, we expect landscape characteristics to be the most important factors in determining the spread of alien species, due to the importance of the landscape in the spread of alien species (Vilà and Ibáñez 2011). The spread of alien plants is expected to be more related to the past than to the present landscape (Domènech et al. 2005; DeGasperis and Motzkin 2007; Vilà and Ibáñez 2011). Finally, we expect to find some evidences of invasion credit due to the high number of changes in the landscape, basically croplands abandonment that the study zone has suffered since 1956 which might have enhanced the introduction, establishment and spread of alien plants. Moreover, the establishment and spread of these species might take several years or decades due to biological and ecological constraints, and also to limitations in propagule pressure (Vilà and Ibáñez 2011).

Materials and methods

Study area

The Barcelona province (772437,5 ha) is located into Catalonia, in the NE corner of the Iberian Peninsula (1º 39’ 55’’-1º 56’ 11” N, 1º 20’ 4”-2º 46’ 39” E; *Fig.1*). The region exhibits highly variable environmental conditions resulting from its topography, with elevations ranging from 0 to 2590 m.a.s.l. and geographical situation receiving Mediterranean, Atlantic and even Sahara influences (Ninyerola et al. 2000).

The province exhibits high landscape heterogenity. In the highest areas of the northern most limit, close to Pyrenees, landscapes are dominated by forests, while coastal areas and pre-coastal plains are highly dominated by built-up areas, especially close to Barcelona. The centre of the province shows a set of mountain ranges mostly dominated by forests, especially in the east, combined with a set of inland plains and platforms mostly occupied by croplands and shrublands. Forests are the dominant land cover category (50% of the province area) followed by croplands (21%), urban zones (12,8%) and shrublands (11%) (Land Cover Map of Catalonia, LCMC, 2009: http://www.creaf.uab.es/mcsc/).

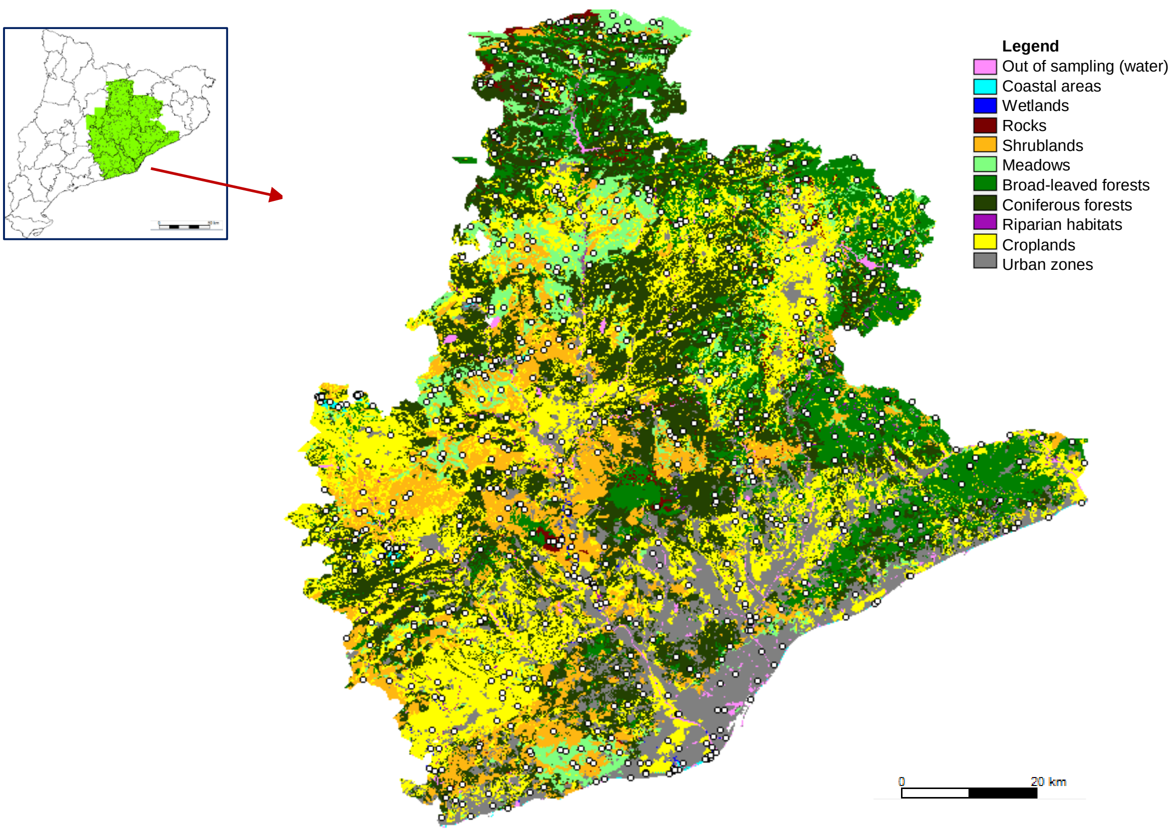

Figure 1. The Barcelona Province in the NE corner of the Iberian Peninsula. Colours represent habitats studied, while points represent the sampling plots.

Floristic sampling

The invasion degree of main habitats in the study area was assessed during the year 2012. A set of sampling points were selected on a digital coverage of the most important habitat types in the Barcelona Province (coastal habitats, broad-leaved forests, coniferous forests, croplands, meadows, riparian habitats, rocks, shrublands, urban habitats and wetlands), obtained by reclassifying the Cartography of Habitats in Catalonia (UB, 2010). Points (n=531) were stratified across the different habitat types, proportionally to the logarithm of their importance in the province. This allowed to have a good representation of the entire study area but also to have enough replicates of the studied habitats. Presence and abundance [i.e. species cover percentage following the Braun-Blanquet scale (Braun-Blanquet et al. 1932)] of each alien plant were recorded in a plot of 5 m radii on each sampling point.

Modelling species presence, richness and abundance

General linear models (GLM) were performed using presence (invaded and non invaded), richness (number of alien species) and abundance of alien species as dependent variables. Only non-native species introduced after 1500 B.C. (i.e. neophytes) were considered. Presence and richness have been used as proxies of the introduction and establishment stage in the invasion process, while abundance has been used as a proxy for the spread of alien plant invasion.

A set of potential correlates of alien species presence, richness and abundance were obtained per sampling plot. These variables were classified into three different categories: habitat, current context and historical context (*Table 1*).

- Habitat variables: habitat type, herbaceous cover, shrub cover and tree cover, all obtained in the field sampling.
- Current context, with the following sub-categories.
    - Climate: mean annual temperature, mean annual solar radiation and annual rainfall. All of them obtained from the Climatic Digital Atlas of Catalonia (http://www.opengis.uab.cat/acdc/catala/cartografia.htm).
    - Topography: latitude, longitude, elevation, aspect, slope, distance to the main streams, distance to large urban areas (>40.000 inhabitants) and distance to the main roads. Elevation, aspect and slope were obtained based on the Digital Elevations Model (DEM) of Catalonia. The other variables were obtained from the Catalan government webpage (http://www.gencat.cat).

- Current landscape in a radius of 50m, 500m and 1000m from the sampling points. The variables calculated at each distance were percentages of the different land uses classified into urban, agricultural and natural for the maps of 2009. Land use data was obtained from different editions of the Land Cover Map of Catalonia (LCMC, 2009).
- Current alien plant species richness per UTM 10km in 2009 (EXOCAT, 2012) as proxy of current propagule pressure at landscape level.

- Historical context and changes.
  - Historical landscape in a radius of 50m, 500m and 1000m from the sampling points. The variables calculated at each distance were percentages of the different land uses classified into urban, agricultural and natural for the maps of 1956 and 1993. Land use data was obtained from different editions of the Land Cover Map of Catalonia (LCMC, 1993) and from the Land Cover Map of the Barcelona Province of 1956 (LCMB, 1956).
  - Number of changes among the different years, years of stability and direction of the changes were calculated for two different radius: 10m and 50m. Layers of the land-use in two different years (1956 and 1993) were obtained by photointerpretation.

First, a Pearson's correlation matrix was calculated using the potential independent variables in order to reduce the number of variables in the regression analysis and the colinearity among them. A tolerance of a pair wise $r^2 > 0.56$ ($|r| = 0.75$) was used to determine unacceptable colinearity between predictor variables. From the most correlated variables, those with a best ecological meaning and explanatory power (those with the least colinearity with the rest of the factors) were selected (*Table 1*).

Table 1. Predictor variables classified into the different types and the extent of the measurement. Those with a (*) were the ones selected to create the full models.

Variable	Data Source
Habitat	
Habitat type.*	Field sampling (CREAF, 2012)
% herbaceous cover.*	
% shrub cover.*	
% tree cover.*	
Current context	
Climatic	
Mean annual temperature.	Climatic Digital Atlas of Catalonia (2004) http://magno.uab.es/atles-climatic/index_us.htm
Mean annual solar radiation.*	
Annual rainfall.*	
Topographic	
Latitude.	
Longitude.*	
Elevation.*	Digital Elevations Model (DEM) of Catalonia.
Aspect.*	
Slope.*	
Mean distance to the main streams.*	Catalan government webpage http://www.gencat.cat
Mean distance to the main roads.*	
Mean distance to large urban areas.*	
Landscape	
Croplands % 2009.* (100m, 500m* and 1000m)	Land Cover Map of Catalonia (LCMC) CREAF (2009), http://www.creaf.uab.es/mcsc/
Urban % 2009.* (100m, 500m* and 1000m)	
Alien plant per UTM richness in 2010	EXOCAT (2012)
Historical context and changes	
Landscape	
Croplands % 1956.* (100m, 500m* and 1000m)	Land Cover Map of Catalonia (LCMC) CREAF (1956, 1993), http://www.creaf.uab.es/mcsc/
Urban % 1956.* (100m, 500m* and 1000m)	
Croplands % 1993.* (100m, 500m* and 1000m)	
Urban % 1993.* (100m, 500m* and 1000m)	
Alien plant per UTM richness in 1989	Casasayas (1989)
Changes	
Number of changes.*	Land Cover Map of Catalonia (LCMC) CREAF (1993), Land Cover Map of Barcelona Province (LCMB) CREAF (1956) http://www.creaf.uab.es/mcsc/
Years of stability.*	
% of progressive changes between 1956 and 2009*	
% of regressive changes between 1956 and 2009*	
% of no changes between 1956 and 2009*	
% of progressive changes between 1993 and 2009*	
% of regressive changes between 1993 and 2009*	
% of no changes between 1993 and 2009*	

A binomial distribution of errors was used for the presence models while a Poisson one was used for richness and a Gaussian one was used for abundance.

We performed three different types of generalized linear models (GLM): (1) partial models for (a) climatic and topographic variables, (b) habitat variables, (c) landscape and alien plant species variables and (d) changes variables; (2) full models and (3) interaction models among habitat and the other variables.

The partial models were constructed to compare the explanatory power of the different groups of variables and, consequently, to know which was the most important group of variables in explaining our response variables. The full models were constructed to detect the most important variables in predicting the presence, richness and abundance. In the interaction analyses the objective was to know if the responses to the variables differed depending on the habitat type.

In the case of the full model, the steps followed were:

1. Creation of the full model.
2. Selection of the significant variables of the full model.
3. Creation the new model with the significant variables.
4. Selection of the best model (with the lower AICc value) with those significant variables.

In the interactions analyses, habitat was reclassified into three categories (urban, croplands and natural (the other habitats in the database)). In this case the steps followed were:

1. Creation of the full model
2. ANOVA analyses
3. Post-hoc analyses (Tukey) for the significant variables in the ANOVA.

The selection of the models was done using the Akaike's information criterion corrected for a large number of predictors (AICc) and the *dredge* process. The Akaike's information criterion is an indicator of the goodness of fit and the complexity of the model. This value is lower with the best fitted model and in the model with lower complexity. The *dredge* process selects the best model with the lower AICc value.

It is important to consider that presence analyses were done with the whole number of sampling data (n=531) while richness and abundance analyses were only done with the samples where their values were ≥1 (n=151). The reason is that the residuals of the analyses were not normal and the results were biased (the models were not representative of our data) if we used all of the database for the richness and abundance analyses.

In all models we tested the spatial autocorrelation by calculating the I Moran's index of the residuals of the best model for each dependent variable.

All statistical analyses were performed with the R-CRAN software (R Development Core Team 2009). We used the packages MuMin, Effects and Corrgram for the selection of the best models, the ANOVA analyses and the creation of the correlogram for the autocorrelation analyses, respectively.

Results

Partial models

Habitat variables were the most important ones in explaining the presence of alien plants because of their low AICc value (*Fig.* 2a). The topographic variables were the most important ones in explaining richness of alien plants (*Fig. 2b*). Finally, landscape variables were the most important ones in explaining the abundance of alien plants (*Fig. 2c*).

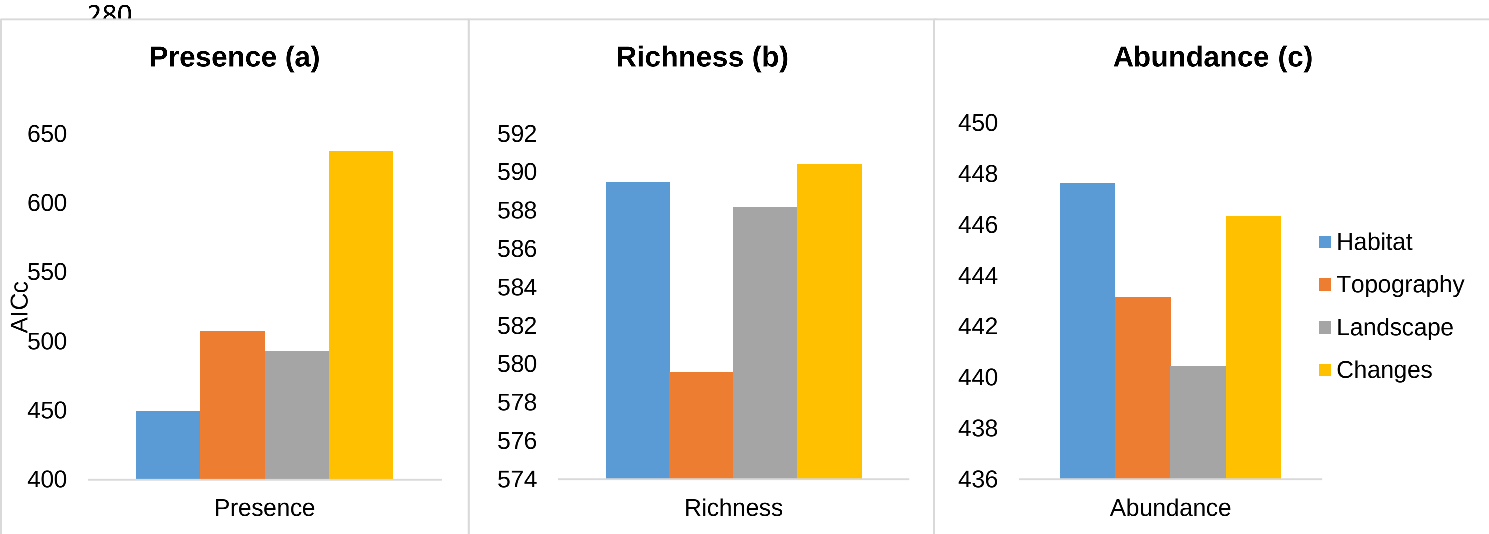

Figure 2*.* AICc values of the best model for each dependent variable (presence (a), richness (b) and abundance (c)) and for each partial model (topography, habitat, landscape and changes). Low AICc values indicate high explanative power of the corresponding models.

Full models

The presence in each site was, basically, explained by topographic (longitude, elevation and distance to urban zones) and habitat variables (habitat type and shrub cover). The mean number of changes in a 50 m radium was also significantly related with the presence (*Table 2*).

Alien plant richness was explained by two topographic variables (longitude and elevation). No habitat, landscape or changes variables were significantly related with alien plant richness.

Abundance was mainly explained by historical landscape variables such as the croplands percentage in 1956 and 1993. No topographic, habitat or changes variables were significant in explaining the abundance of alien plants.

Comparing the best partial models for the three groups of variables, that of presence showed the lowest AICc value followed by that of abundance while that of richness had the highest AICc value. This means that the best model for richness explained less than those of abundance and presence.

There was no autocorrelation in the models for the three dependent variables, namely presence (Annexes; *Fig. 1*), richness (Annexes; *Fig 2*) and abundance (Annexes; *Fig. 3*).

Table 2. Variables included in the best models for each dependent variable. P value, sign and type of each explanatory variable and AICc of each final model.

Model	P value	Estimate	Variable type	AICc
Presence				402.97
Longitude	0.0157	+1.370e-05	Topographic	
Elevation	2.45e-07	-3.030e-03	Topographic	
Distance to urban zones	0.00032	-3.112e-05	Topographic	
Habitats referring to croplands				
Coastal areas	0.00291	-2.415e+00	Habitat	
Coniferous forests	1.26e-07	-3.192e+00	Habitat	
Deciduous forests	1.35e-07	-3.326e+00	Habitat	
Meadows	0.0121	-1.537e+00	Habitat	
Riparian habitats	0.0812	-6.956e-01	Habitat	
Rocks	0.0011	-3.521e+00	Habitat	
Shrublands	4.30e-09	-3.981e+00	Habitat	
Urban zones	0.7543	-1.518e-01	Habitat	
Wetlands	0.0245	-1.160e+00	Habitat	
Shrub cover	0.0395	+1.028e-02	Habitat	
Number of changes	0.0539	+5.470e-01	Changes	
Richness				537.8
Longitude	0.0278	+4.869e-04	Topographic	
Elevation	0.0153	-5.688e-06	Topographic	
Abundance				444.63
Croplands percentage 1956	0.0267	+1.194	Landscape	
Croplands percentage 1993	0.0359	-1.126	Landscape	

Models with interactions

In the case of presence, there were significant (or marginally significant) interactions between habitat and elevation, aspect, slope, distance to the main streams, alien plant richness in 1989, number of changes in the 1956-2009 period, urban percentage in 1993, progressive changes in 1993-2009 and regressive changes 1956-2009 (*Table 3*). There was a positive association between distance to the rivers and alien species presence (i.e. invasion risk) in the case of croplands, while this relation was negative in natural habitats (Annexes; *Fig. 4*). The differences between the general interaction p-values and the post-hoc test are probably due to the use of the conservative Tukey test for the post-hoc analyses.

Table 3. Significant interactions among habitat and different predictor variables for presence. Test post hoc for each pair of habitats (croplands vs. natural, croplands vs. urban and urban vs. natural) and p-value for the general interaction.

Dependent Variable	Interaction with habitat	Croplands-Natural	Croplands-Urban	Urban-Natural	P-value
Presence					
	Elevation	0.966	0.395	0.407	0.061
	Aspect	0.145	0.658	0.423	0.051
	Slope	0.655	0.247	0.322	0.092
	Distance to the main streams	0.0136	0.714	0.271	0.0012
	Alien plant richness 1989	0.657	0.303	0.404	0.075
	Number of changes 1956-2009	0.859	0.322	0.354	0.046
	Urban percentage 1993	0.306	0.187	0.435	0.060
	Progressive changes 1993-2009 (%)	0.374	0.184	0.280	0.013
	Regressive changes 1956-2009 (%)	0.553	0.288	0.419	0.087

In the case of richness there were significant interactions between habitat and elevation and also between habitat and slope, annual radiation, and progressive and regressive changes between 1956 and 2009. However, in the post-hoc tests, only elevation and annual radiation showed significant interactions. As for elevation, post-hoc tests detected significant differences between croplands and urban habitats.

Croplands showed a positive relationship between species richness and elevation while this relation was negative for urban habitats (Annexes; *Fig. 5*). On the other hand, differences between natural and urban habitats were observed for annual radiation, and progressive and regressive changes for the 1956-2009 period (*Table 4*). In the case of annual radiation, the association with alien species richness was negative in natural habitats and positive in urban habitats (Annexes; *Fig. 6*). For progressive and regressive changes in 1956-2009, the association with alien plant species richness was positive in urban habitats but negative in natural ones (Annexes; *Fig. 7 and Fig. 8*).

Table 4. Significant interactions among habitat and different predictor variables for richness. Test post hoc for each pair of habitats (croplands vs. natural, croplands vs. urban and urban vs. natural) and p-value for the general interaction.

Dependent Variable	Interaction with habitat	Croplands-Natural	Croplands-Urban	Urban-Natural	P-value
Richness					
	Elevation	0.070	0.010	0.682	0.011
	Slope	0.089	0.961	0.318	0.084
	Annual radiation	0.247	0.179	0.028	0.021
	Progressive changes 1956-2009 (%)	0.313	0.985	0.063	0.050
	Regressive changes 1956-2009 (%)	0.333	0.881	0.043	0.046

For alien species abundance, there were significant interactions between habitat and the percentage of croplands in 1993, the number of changes in the 1956-2009 period, and progressive changes in 1956-2009 and 1993-2009 periods. However, only the number of changes was significantly different comparing croplands and urban zones in a post hoc analysis (*Table 5)*. The association between species abundance and the number of changes was positive in croplands but negative in urban habitats (Annexes; *Fig. 9*).

Table 5. Significant interactions among habitat and different predictor variables for abundance. Test post hoc for each pair of habitats (croplands vs. natural, croplands vs. urban and urban vs. natural) and p-value for the general interaction.

Dependent Variable	**Interaction with habitat**	**Croplands-Natural**	**Croplands-Urban**	**Urban-Natural**	**P-value**
Abundance					
	Croplands percentage 1993	0.097	0.820	0.135	0.041
	Number of changes 1956-2009	0.302	0.016	0.119	0.019
	Progressive changes 1956-2009 (%)	0.579	0.857	0.867	0.039
	Progressive changes 1993-2009 (%)	0.579	0.857	0.867	0.071

Discussion

Our results indicate that habitat type is the most important factor determining alien species presence and richness, while the historical surrounding landscape is the primary correlate of species abundance. These results suggest that habitat and context effects on habitat invasion are different for the diverse invasion stages (i.e. introduction, establishment and spread) considered in the study. Finally, the association between species abundance and the past landscape suggests the presence of an invasion credit (*sensu* Vilà and Ibáñez 2011) in the spread stage.

Results regarding the studied proxies of species introduction and establishment (i.e. species presence and richness) agree with those by Chýtry et al. (2008) who found that habitat invasibility is the most important factor determining habitat invasion by alien plants. However, it should be noted that the successive introduction and establishment of alien species (assessed using alien species richness) is only explained by two context factors (longitude and elevation) and this suggests that the introduction and establishment of the diverse alien species might follow a relatively random pattern, not clearly associated to context factors.

Habitat invasibility has been reported in several studies as the major factor determining the invasion process (Chytrý et al. 2005; Gassó et al. 2012), which matches with our results. The most invaded habitats are urban areas followed by croplands, riparian habitats and coastal habitats. These results agree with those by Chytrý et al. (2005) and Vilà et al. (2007) who found a major number of alien plants in those habitats with more disturbance level, and also with those by Chytrý et al. (2008) who found the same pattern in all European habitats. These results are supported by the hypothesis of fluctuating resource availability and the propagule pressure: in disturbed habitats, there are more resources available because of the removal of the resident vegetation that favours the introduction and establishment of alien plants (Davis et al. 2000).

The role of habitat invasibility on the invasion of our study habitats is modulated by context factors, as shown by the significant interactions of habitat type with diverse variables (*Table 4*). In any case, the low number of significant interactions in the post-hoc analysis seems to indicate a lack of a specific pattern for each type of habitat and that this modulating effect on habitat type is not strong. It is important to consider that these analyses were performed with a reduced number of habitat categories (urban, natural and croplands) which can be the cause of these results. Repeating the analysis with more habitat categories could give more significant results because of the high heterogeneity of the natural habitat group. However, this alternative is currently constrained from the low number of samples per extended habitat type, and new samplings would be needed.

Our study also detected significant effects of context factors on the diverse stages of the invasion process (basically introduction and establishment), as also found in previous studies (e.g. Chytrý et al. 2005; Pino et al. 2005; Walter et al. 2005; Vilà et al. 2007). Elevation is known to be important in determining alien species richness, our proxy of alien species introduction and establishment, and high richness of alien plants in low elevations is reported in many papers at diverse scales (Aragón and Morales, 2003; Chytrý et al. 2005; Pino et al. 2005; Vilà et al. 2007). This finding can be explained by the fact that alien plants in Catalonia have their origin in the tropical and subtropical regions so they need to be in the lower zones, with a warmer climate (Casasayas 1989).

As for longitude, the positive relationship with species presence and richness found in our study can be explained by the distribution of the population or by the regional plant richness in the study zone. In relation to this, Pino et al. (2005) found that large scale (UTM 10-km) alien species richness was higher in the north-eastern than in the south-western coast of Catalonia. Moreover, the higher presence and richness of alien species can also be related with some socioeconomic causes such as the higher dynamism of the north-eastern coast in Catalonia (Vilà and Pujadas 2001).

The distance to urban areas, another important context factor in our study, is negatively related with the introduction and establishment (i.e. presence) of alien plants (the less distance to urban zones, the more likely the presence of alien plants). These results are supported by those by Pino et al. (2006) and Deutschewitz et al. (2003) who found that the number of alien plants at a landscape scale was positively associated with urban cover, which is considered a proxy of the disturbance level and propagule pressure. Urbanized regions show higher alien species frequency, richness and abundance and, consequently, they are responsible for higher alien propagule pressure in habitats (Catford et al. 2011). Also, it is known that human altered habitats are a common reservoir of non-native species because disturbance reduces the competition and increases the number of safe sites for alien species establishment (Pino et al. 2006; Gavier-Pizarro 2010; Vilà and Ibáñez 2011; González-Moreno et al. 2013).

We have found that landscape properties are the only correlates for species abundance, considered as a proxy of species spread, and it is supported by the significant interactions relating landscape and its changes with alien plant abundance (Theoharides and Dukes 2007; Vilà and Ibáñez 2011). The association with current landscape had been previously reported both for particular species (e.g. Domènech et al. 2005) and for the whole alien species community (González-Moreno et al. 2013) and can be explained by the great importance of the surrounding landscape heterogeneity on the incidence of plant invasions (Vilà and Ibáñez 2011). Landscape heterogeneity positively affects propagule pressure and, consequently, facilitates the spread of alien plant species (González-Moreno et al. 2013). However, it seems that current landscape has no effect in the first stages of invasion (i.e. introduction and establishment), differing from Mosher et al. (2009) and Aragón and Morales (2003) who suggested that previous land use could influence the first stages of invasion. This fact shows that there are differences in the factors driving the different stages in the invasion process which is according with Theoharides and Dukes (2007).

What is new in our study is the identification of significant yet secondary effect of the historical context on the diverse components of the invasion stages. This effect is reflected in two main results: the positive relationship between the presence of alien plants and the number of changes in the landscape and the relationship between species abundance and the past landscape.

The first result suggests that land use legacy has a noticeable effect on the invasion degree of habitats in the Barcelona province, as locally reported by Vilà et al. (2003) and Domènech et al. (2005) for *Opuntia spp.* and *Cortaderia selloana*. These results corroborate that habitat instability across time favours the spread of exotic species in Mediterranean habitats (Basnou et al. 2014). These changes in the habitat may have facilitated both the introduction and the establishment of the alien plant species that we can now find in the sampling points.

However, there is no significant association between the presence of alien plants and the type of change (either regressive or progressive). This means that what is really important is the occurrence of the change rather than its type (Domènech et al. 2005), and this result differs from those reported by Vilà and Ibáñez (2011), who found that regressive changes were more associated with an increasing number of alien plants while the progressive ones were more associated with a reduction in alien plants.

The second result, i.e. the abundance of alien plants associated with the intensity of the past land use, provides evidence of the invasion credit (*sensu* Vilà and Ibáñez 2011) in the spread stage. This result suggests that croplands in 1956 provided opportunities for alien species establishment as commonly in croplands (Davis et al. 2000; DeGasperis and Motzkin 2007), and these species would have started their spread later in time thus originating the invasion credit in the spread stage.

The negative relationship between the percentage of croplands in 1993 and the alien plant abundance can only be explained in a metropolitan context of progressive landscape urbanization, in which recent croplands correspond to the least transformed areas in the last year. Then, the relative stability of these areas might have affected alien species spread through a lower disturbance pressure on habitats, which might have determined less resources available and higher competition with resident species (Davis et al. 2000) than in highly disturbed landscapes.

Conclusions and further studies

We can conclude that habitat properties and current and historical context have effects on the habitat invasion, but depending on the diverse stages (introduction, establishment and spread) of the invasion process. Introduction and establishment are mostly affected by habitat invasibility, but also by some current context variables as found by some previous studies. The influence of landscape changes shows an effect of the historical context in these invasion stages. Spread, on the other hand, is mainly related to the past landscape fact that provides evidences of an invasion credit in this stage of the invasion process.

However, we have to consider that richness and abundance analyses have been done only for plots with alien species presence. This constraints the interpretation of the results and it is important to consider richness and abundance basically for metropolitan regions with high population density and high landscape transformation.

This study sets some bases that had been little studied but are relevant in the invasion process. However, the invasion process is really complex and there are several factors affecting it. In our study we have added the historical context and changes until now to the previous work but there are some other factors such as the introduction event, the invasiveness or the residence time of particular species that should be considered. All of these factors can modify the time at which we can consider that a species is established in a place and at which this specie starts the spread stage (Alpert et al. 2000, Pysek and Jarosik 2005). Including these factors in further research would help to improve our knowledge about the invasion process of Mediterranean habitats by alien plants and its associated factors.

References

Andreu J, Pino J, Basnou C, Guardiola M, Ordóñez JL(2012) EXOCAT: Les espècies exòtiques a Catalunya.

Aragón R, Morales JM (2003) Species composition and invasion in NW Argentinian secondary forests: Effects of land use history, environment and landscape. *Journal of vegetation science*. 14: 195-204.

Basnou C, Iguzquiza J, Pino J (2014) Examining the role of past and present landscape on exotic plant invasions in Mediterranean coastal habitats. *Landscape and Urban Planning*. → submitted

Bartuszevige AM, Gorchov DL, Raab L (2006) The relative importance of landscape and community features in the invasion of an exotic shrub in a fragmented landscape. *Ecography*. 29: 213-222.

Braun-blanquet J, Fuller GD, Conrad H (1932) Plant sociology. The study of plant communities. McGraw-Hill, New York and London.

Casasayas T (1989) La flora al·lòctona de Catalunya. Catàleg raonat de les plantes vasculars exòtiques que creixen sense cultiu del NE de la Península Ibèrica. PhD Thesis, Universitat de Barcelona, Barcelona.

Catford JA, Vesk PA, White MD, Wintle BA (2011) Hotspots of plant invasion predicted by propagule pressure and ecosystem characteristics. *Diversity and distributions*. 17:1099-1110.

Chytrý M, Jarosik V, Pysek P, Hájek O, Knollova I, Tichý L, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology*. 89: 1541-1553.

Chytrý M, Pysek P, Tichý L, Knollová I, Danihelka J (2005) Invasions by alien plants in the Czech Republic: a quantitative assessment across habitats. *Preslia.* 77: 339-354.

Colautti RI, Grigorovich IA, Macisaac HJ (2006) Propagule pressure: a null model for biological invasions. *Biological invasions*. 8: 1023-1037.

Crawley MJ (1987) What makes a community invasible? Pages 429–543 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. Colonization, succession and stability. Blackwell Scientific Publications, Oxford, UK.

Davis MA, Grime JP, Thompson K (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of ecology*. 88: 528-534.

Degasperis B, Motzkin G (2007) Windows of opportunity: historical and ecological controls on *Berberis thunbergii* invasions. *Ecology*. 88: 3115-3125.

Deutschewitz K, Lausch A, Kühnm I, Klotz S (2003) Native and alien plant species richness in relation to spatial heterogeneity on a regional scale in Germany. *Global ecology & biogeography*. 12: 299-311.

Domènech R, Vilà M, Pino J, Gesti J (2005) Historical land-use legacy and *Cortaderia selloana* invasion in the Mediterranean region. *Global change biology*. 11: 1054-1064.

Gavier-pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS (2010) Housing is positively associated with invasive exotic plant richness in New England, USA. *Ecological applications.* 20: 1913-1925.

Gassó N, Pino J, Font X, Vilà M (2012) Regional context affects native and alien plant species richness across habitat types. *Applied vegetation science*. 15: 4-13.

González-moreno P, Pino J, Carreras D, Basnou C, Fernández-rebollar I, Vilà M (2013) Quantifying the landscape influence on plant invasions in Mediterranean coastal habitats. *Landscape ecology*. 28: 891-903.

Jackson ST, Sax DF (2010) Balancing biodiversity in a changing environment: extinction debt, immigration credit and species turnover. *Trends in ecology and evolution*. 25: 153-160.

Kowarik I (1995) Time lags in biological invasions with regard to the success and failure of alien species. In: PYŠEK, P., PRACH, K., RÉJMANEK, M and WADE, M. (eds). Plant invasions. SPB Academic Publishers, Amsterdam, pp 15-38.

Kumar S, Stohlgren TJ, Chong GW (2006) Spatial heterogeneity influences native and non-native plant species richness. *Ecology*. 87: 3186-3199.

Kuussaari M, Bommarco R, Heikkinen RK, Helm A, Krauss J, Lindborg R, Öckinger E, Pärtel M, Pino J, Rodà F, Stefanescu C, Teder T, Zobel M, Steffan-dewenter I (2009) Extinction debt: a challenge for biodiversity conservation. *Trends in ecology and evolution*. 24: 564-571.

Milbau A, Stout JC, Graae BJ, Nijs I (2009) A hierarchical framework for integrating invasibility experiments incorporating different factors and spatial scales. *Biological invasions*. 11: 941-950.

Mosher ES, Silander JA, Latimer AM (2009.) The role of land-use history in major invasions by woody plant species in the northeastern North American landscape. *Biological invasions*. 11: 2317-2328.

Ninyerola M, Pons X, Roure JM (2000) A methodological approach of climatological modelling of air temperature and precipitation through GIS techniques. *International Journal of Climatology.* 20: 1823-1841.

Pino J, Font X, Carbó J, Jové M, Pallarès L (2005) Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological conservation*.122: 339-350.

Pretto F, Celesti-grapow L, Carli E, Blasi C (2010) Influence of past land use and current human disturbance on non-native plant species on small Italian islands. *Plant ecology*. 210: 225-239.

Pysek P, Richardson DM, Rejmánek M, Williamson M, Kirschner J (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*. 53: 131-143.

Pysek P, Jarosik V (2005) Residence time determines the distribution of alien plants. Pages: 77-96 in Inderjit, editors. Invasive plants: ecological and agricultural aspects. Birkhäuser Verlag, Basel, Switzerland.

Theoharides KA, Dukes JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New phytologist*. 176: 256-273.

Vilà M, Ibáñez I (2011) Plant invasions in the landscape. *Landscape ecology*. 26: 461-472.

Vilà M, Pino J, Font X (2007) Regional assessment of plant invasions across different habitat types. *Journal of vegetation science.* 18: 35-42.

Vilà M, Pujadas J (2001) Land-use and socio-economic correlates of plant invasions in European and North African countries. *Biological* conservation. 100: 397-401.

Walter J, Essl F, Englisch T, Kiehn M (2005) Neophytes in Austria: habitat preferences and ecological effects. *Biological invasions.* 6:13-25.

Annexes

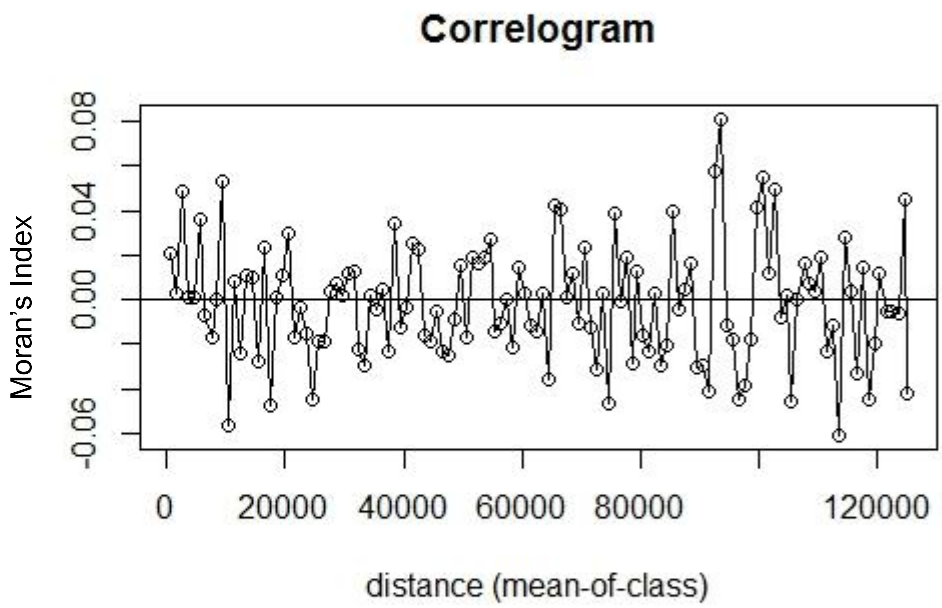

Figure 1. Correlogram for the full model of alien species presence.

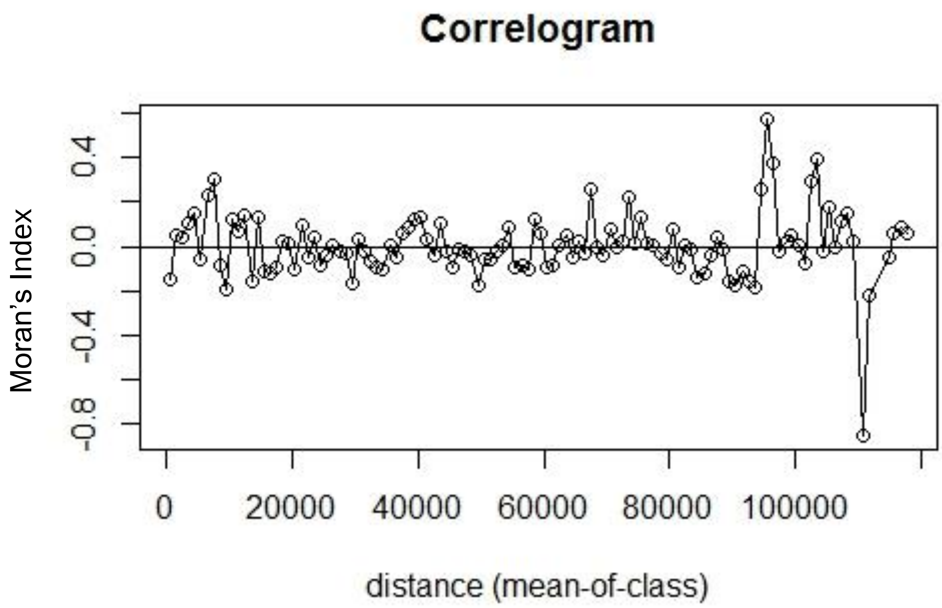

Figure 2. Correlogram for the full model of alien species richness.

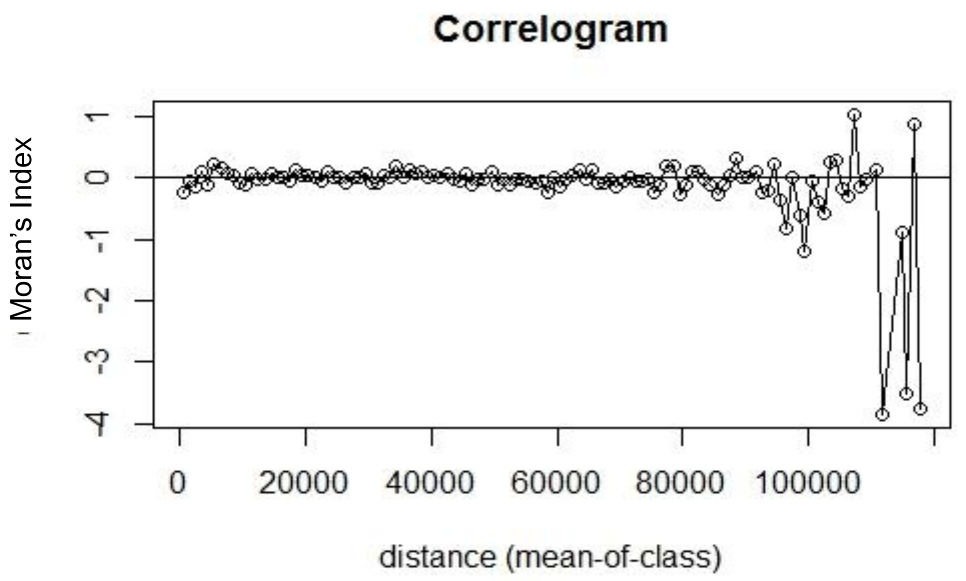

Figure 3. Correlogram for the full model of alien species abundance.

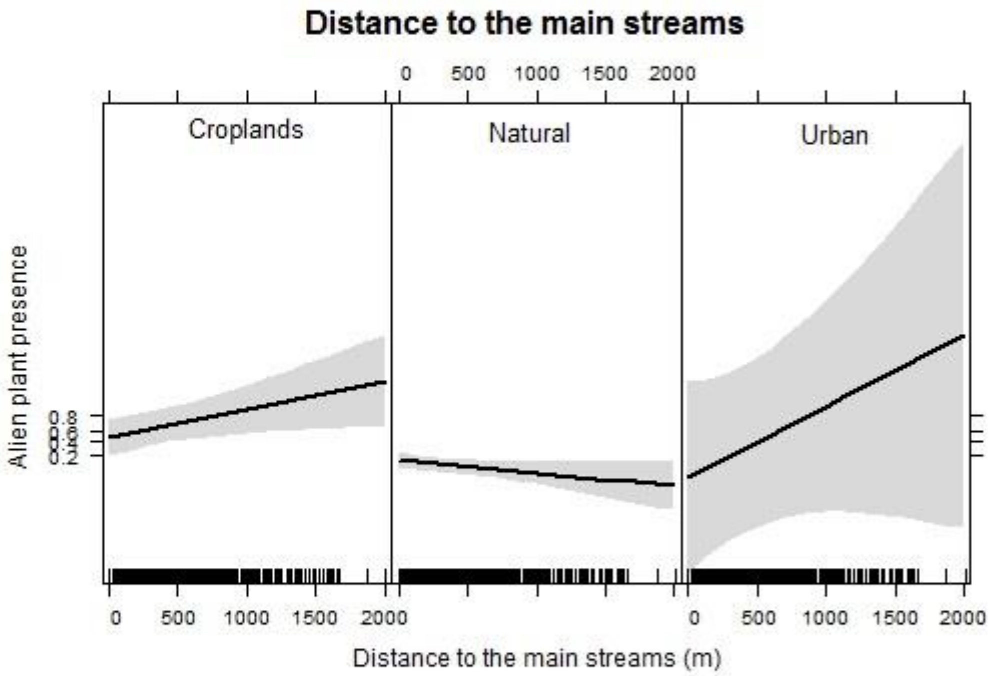

Figure 4. Interaction graph between distance to the main streams and habitat. Relation between distance to the main stream and alien plant presence for the three habitats used in this analyses (Croplands, natural and urban).

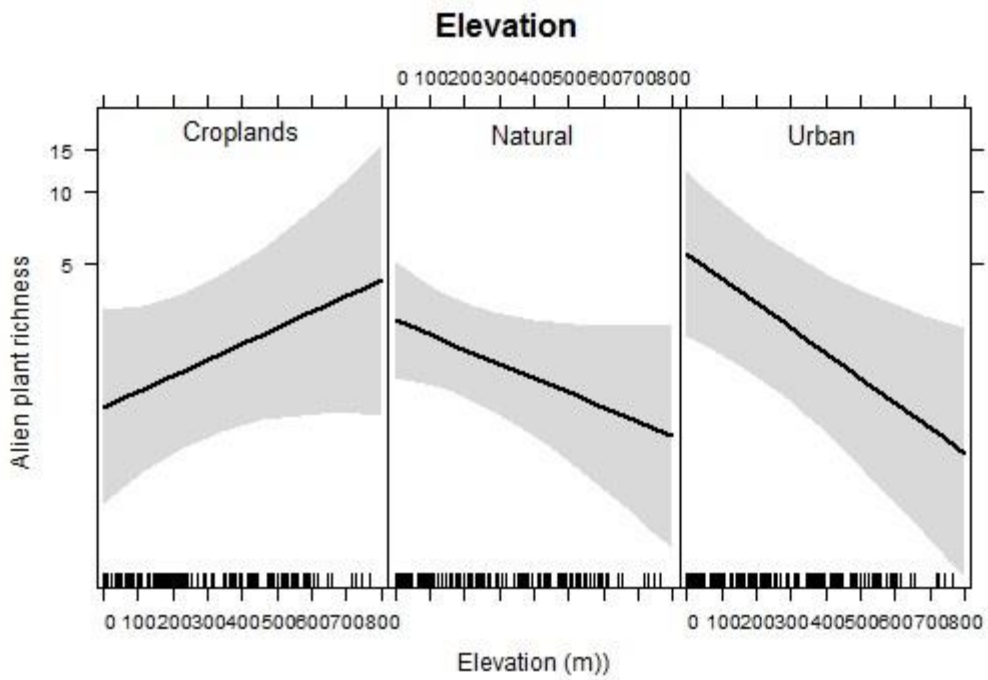

Figure 5. Interaction graph between elevation and habitat. Relation between elevation and alien plant richness for the three habitats used in this analyses (Croplands, natural and urban).

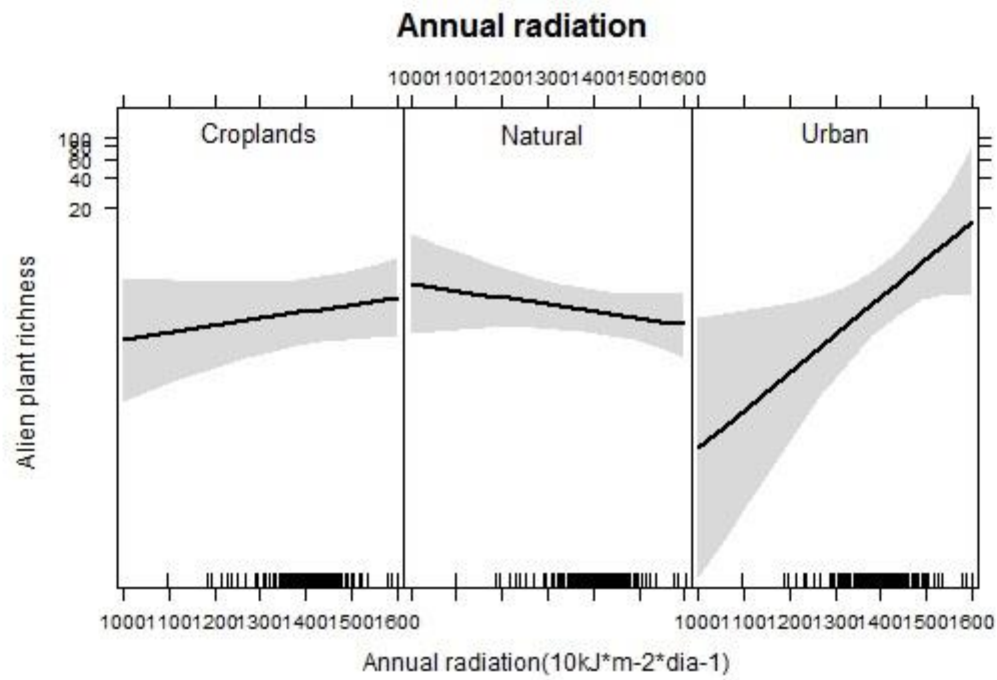

Figure 6 Interaction graph between annual radiation and habitat. Relation between annual radiation and alien plant richness for the three habitats used in this analyses (Croplands, natural and urban).

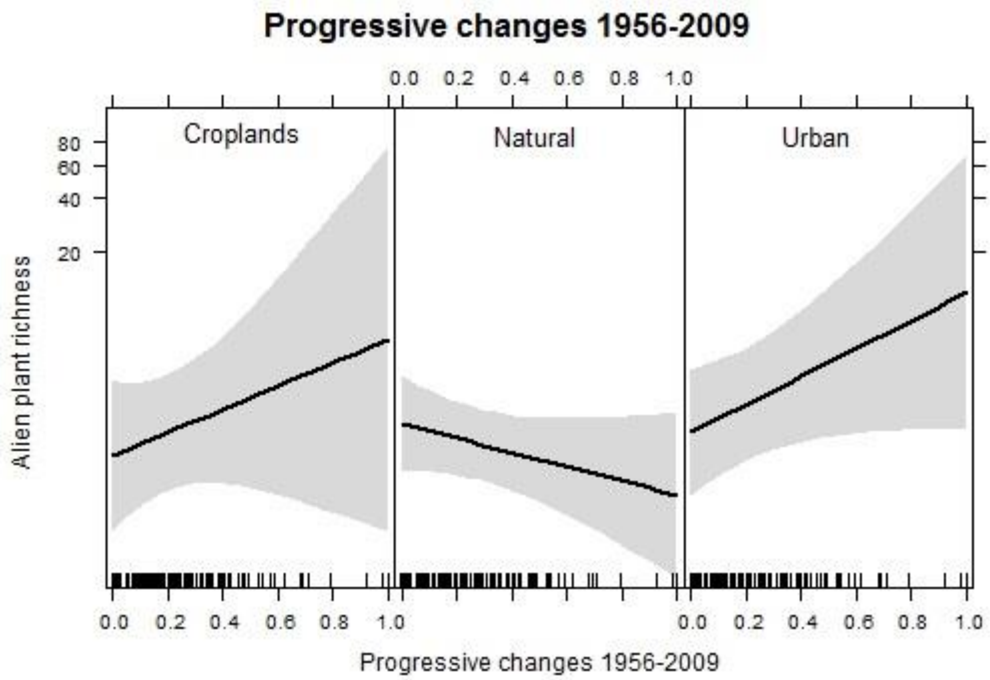

Figure 7. Interaction graph between progressive changes 1956-2009 and habitat. Relation between progressive changes 1956-2009 and alien plant richness for the three habitats used in this analyses (Croplands, natural and urban).

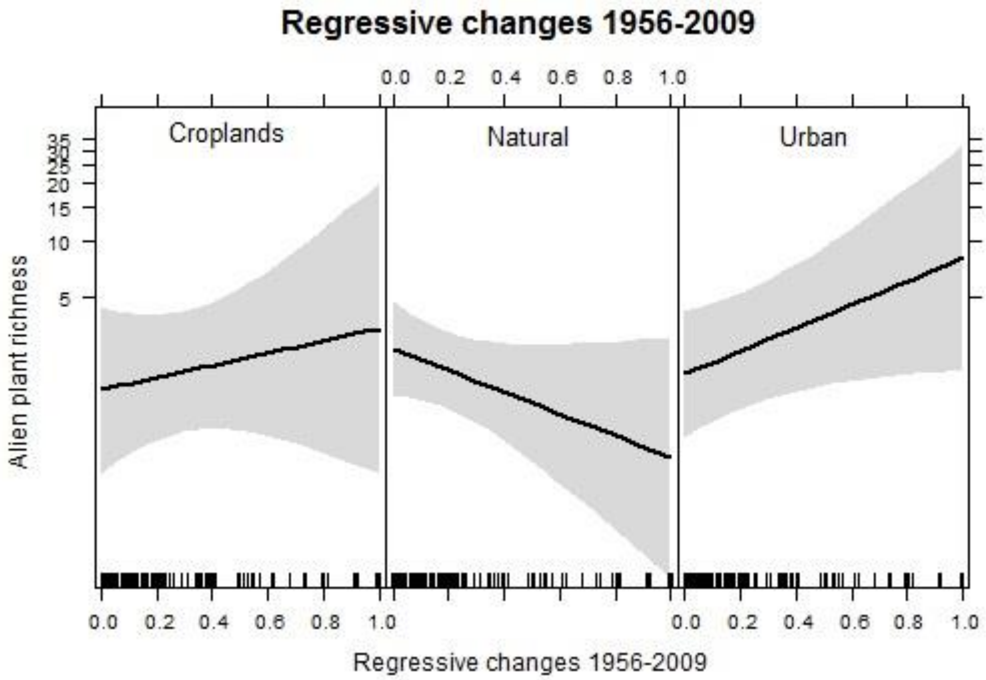

Figure 8. Interaction graph between regressive changes 1956-2009 and habitat. Relation between regressive changes 1956-2009 and alien plant richness for the three habitats used in this analyses (Croplands, natural and urban).

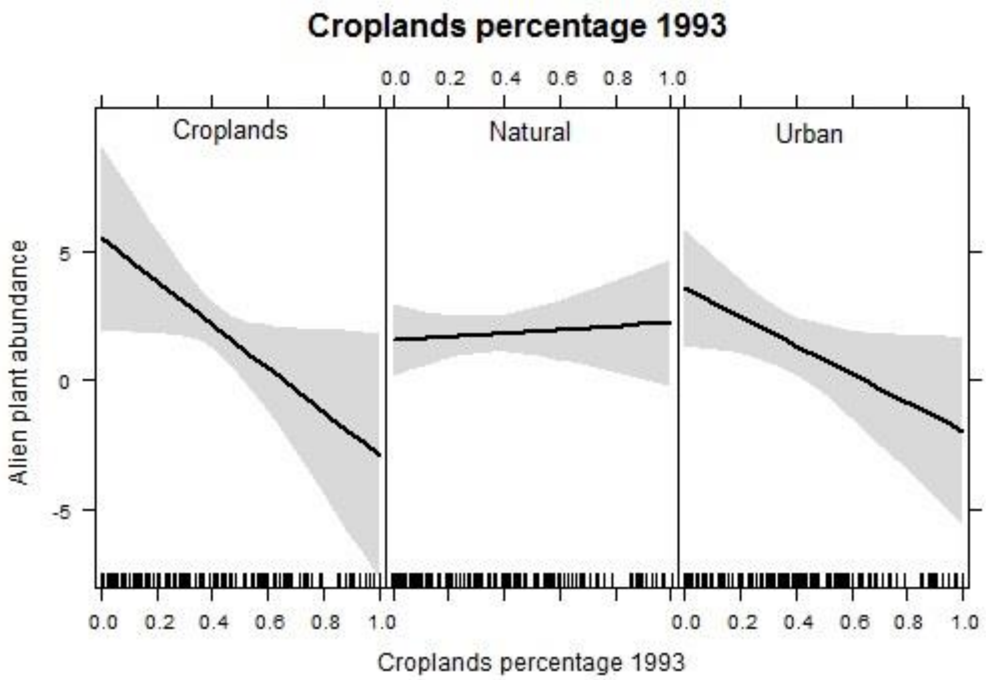

Figure 9. Interaction graph between croplands percentage 1993 and habitat. Relation between croplands percentage 1993 and alien plant abundance for the three habitats used in this analyses (Croplands, natural and urban).