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Plant invasions are context-dependent: multiscale effects of climate, human activity and habitat

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ABSTRACT

Aim Understanding the conditions that promote biological invasions is a critical step to developing successful management strategies. However, the level of invasion is affected by complex interactions among environmental factors that might change across habitats and regions making broad generalizations uninformative for management. We aimed to quantify the context-dependent association of climate and human activity at landscape scale (i.e. disturbance and propagule pressure) with the level of plant invasion at local scale across different stages of invasion, habitat types and bioclimatic regions.

Location Mainland Spain.

Methods Based on an extensive database of vegetation plots (~50,000), we used hierarchical Bayesian models to test how climate and human activity at a landscape scale (i.e. land-cover variables) are associated with establishment (i.e. presence) and dominance (i.e. relative species richness and abundance in invaded plots) of non-native plants across nine habitat types and three bioclimatic regions.

Results The association of climate with establishment and dominance of non-native plants varied depending on habitat type but not bioclimatic region. These associations also varied depending on the stage of invasion under consideration. Establishment of non-native species was more likely close to the coast, while their dominance increased in wet and warm continental areas. Human activity variables were associated with establishment and dominance similarly across bioclimatic regions. Non-native species establishment and abundance peaked in human-altered landscapes. Different habitats showed different susceptibilities to establishment versus dominance by non-native species (e.g. woodlands had medium levels of establishment, but very low dominance).

Main conclusions This study highlights how complex interactions among climate, human activity and habitats can determine patterns of invasions across broad landscapes. Successful management of plant invasions will depend on understanding these context-dependent effects across habitats at the different stages of the invasion process.

Keywords
Bayesian, biological invasions, establishment, hierarchical, level of invasion, propagule pressure, stages of invasion.

INTRODUCTION

Biological invasions pose a major threat to the native biota and ecosystem functioning (Vilà *et al.*, 2011). Thus, prevention and management of invasions are critical for the conservation of natural and semi-natural ecosystems. Successful management of biological invasions relies on understanding the mechanisms behind the invasion process. Recent

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conceptual models have suggested that invasions are affected by multiple interacting factors, including abiotic conditions, human activity, and habitat type, which may act at different scales and stages of invasion (Catford *et al.*, 2009; Milbau *et al.*, 2009). Such complexity hampers our ability to disentangle the mechanisms underlying invasions and thus the forecasting of future invasions. Climatic effects on invasion are perhaps the most commonly studied within abiotic factors. This approach can be successful at large scales to the extent that climatic patterns shape the macroenvironmental conditions determining species distribution from continental to regional scales (Pearson & Dawson, 2003; Milbau *et al.*, 2009). Human activity can also clearly affect patterns of invasion (Ibáñez *et al.*, 2009a; Vilà & Ibáñez, 2011; González-Moreno *et al.*, 2013b). For example, human land-covers types such as built-up areas or crops are highly associated with plant invasions due to the increased propagule pressure and disturbance that benefit non-natives establishment (Ohlemüller *et al.*, 2006; Gassó *et al.*, 2009; Gavier-Pizarro *et al.*, 2010). In addition, the level of plant invasion has also been shown to vary among habitat types at a local scale (Vilà *et al.*, 2007; Ibáñez *et al.*, 2009a) with anthropogenic, mesic, and nutrient-rich habitats being more invaded than natural, dry and nutrient-poor habitats (Chytrý *et al.*, 2008b). These differences among habitats, partly explained by biotic interactions and human influence at a local scale, highlight the paramount importance of habitat type for influencing invasions on top of the combined effects of climate and human activity at larger spatial scales.

The effects of climate, human activity and habitat type on plant invasions are likely interactive rather than additive, further complicating efforts to understand the relative importance of different drivers of invasion (Catford *et al.*, 2009; Jiménez-Valverde *et al.*, 2011). Patterns of invasion appear highly idiosyncratic when different habitat types are modelled separately (Gassó *et al.*, 2012). For example, identical climates may result in a different level of invasion depending on the habitat type and bioclimatic region (i.e. biogeographical region sensu EEA, 2008) (Ibáñez *et al.*, 2009b). In addition, the effects of human activity, derived from land-cover variables, may also vary across bioclimatic regions. For example, regions often have distinct landscape compositions as a result of the interaction of human activities and their climatic drivers. In regions with a predominance of agricultural land and dispersed human settlements, crops may be the most important source of non-native propagules. In contrast, in highly urbanized regions, ornamental plants may be the source of most non-native plants, while crops could help to buffer the spread of these species into natural habitats (González-Moreno *et al.*, 2013b). Given these complex interactions, a comprehensive understanding of the invasion process is critical and may even require new analytical approaches that account for those interactions.

Ecological theory and conceptual models of invasions also suggest that the relative importance of climate, human activity and habitat type shaping invasions will depend on the stage of the invasion process under consideration (Catford *et al.*, 2009; Leung *et al.*, 2012). For example, initial establishment of a single species may be driven by propagule pressure from the neighbouring landscape (i.e. human activity), while subsequent dominance may be more dependent on the existence of suitable climatic and local conditions (i.e. habitat type) for plant and population growth (Catford *et al.*, 2009; Leung *et al.*, 2012). The framework of invasion stages for single species can also be applied to groups of non-native species invading plant communities (Catford *et al.*, 2011; Polce *et al.*, 2011). Following the initial establishment of a particular non-native species within a community, this species might increase in abundance at the time that new non-native species are establishing and becoming abundant (i.e. increase in non-native species richness and abundance, respectively). Developing a better understanding of how the combination of climatic conditions, human activity and habitat characteristics affects both the establishment and dominance of non-native species in the community will be critical to inform more targeted management actions (Polce *et al.*, 2011; Leung *et al.*, 2012).

In this study, we used an extensive database of vegetation plots (~50,000) and hierarchical Bayesian statistical models to investigate how climate, human activity and habitat type interact to explain local patterns of non-native species establishment (i.e. presence) and dominance (i.e. richness and abundance) across mainland Spain. We used data on native and non-native plant species presence and abundance as proxy of invasion success (Catford *et al.*, 2012). Specifically, we asked the following questions: (1) Does the relationship between climate and plant invasions vary across bioclimatic regions and habitats? (2) Does the association of human activity (in terms of land-cover variables) with plant invasions depend on the regional bioclimatic context? and finally, (3) Do these associations and the relative importance of climatic conditions and human activity depend on the metric of invasion (presence, richness and abundance of non-natives, as surrogates of the invasion stages establishment and dominance)? To answer these questions, we compared the results of two modelling approaches: a hierarchical model (context-dependent) that nested the effects of climate across bioclimatic regions and habitat types and allowed variation of human activity variables along bioclimatic regions and a classical non-hierarchical model (non-context-dependent) that included the different driving variables in an additive and independent fashion. Finally, we discuss the benefits of hierarchical models to investigate current determinants of the level of plant invasion and the potential to identify the current and future incidence of plant invasions.

METHODS

Plant species dataset

To quantify plant invasions across mainland Spain, we used data from the Information System of Iberian and Macaronesian

Vegetation (SIVIM) (Font *et al.*, 2012; see Appendix S1 for database characteristics). We gathered 53,345 relevés (plots, hereafter) from 1970 to 2011 that had a phytosociological alliance assignment and location accuracy at least of 10 Km UTM. Our selection covers most environmental gradients across mainland Spain and therefore a wide range of plant communities. A higher density of plots was located in mountain and coastal areas compared to plateau and large valleys (Fig. 1). According to a survey gap analysis based on multivariate environmental similarity surface index (MESS) (Elith *et al.*, 2010; Rossi, 2012, see code in Appendix S3), the dataset provided a good coverage of the entire environmental conditions of the study area with only exception in rare areas with extremely high precipitation (north-western Spain), urban development (Madrid) and agriculture cover (Guadalquivir basin in southern Spain). Plot size was variable, but with ranges per habitat type following European standards (Appendix S1). Despite the long time frame of the dataset, we found little association between level of invasion and time of collection (Appendix S1). Furthermore, we did not find any significant bias in the sampling through time across different habitats, regions or geographical areas.

Table 1 Summary of climate (averages period 1971–2007) and human activity at landscape-scale characteristics (CORINE land-cover maps) in different bioclimatic regions in mainland Spain

	Alpine	Atlantic	Mediterranean
Annual precipitation (mm)	965.56	1301.72	552.38
Summer precipitation (mm)	218.42	173.43	70.99
Winter minimum temperature (°C)	−5.56	1.1	0.77
Temperature seasonality (SD)	6.46	4.85	6.46
Urban cover (%)	1	5.38	7.13
Agriculture cover (%)	3.53	12.12	30.63
Grassland cover (%)	47.72	45.41	29.11
Woodland cover (%)	28.85	29.78	17.12
Land-cover diversity	1.07	1.08	1.26

For each plot, we identified the bioclimatic region (i.e. Alpine, Atlantic and Mediterranean; Fig. 1, Table 1, details in Appendix S1) (EEA, 2008) and the habitat type following a classification based on the Level 1 of the European Nature Information System of 2007 (EUNIS). We identified the habitat type using a cross-walk table between the phytosociological alliance assigned in SIVIM and the most likely EUNIS habitat type as in Vilà *et al.* (2007) and Chytrý *et al.* (2008b): coastal, aquatic (inland surface waters), grasslands, scrubland including heathlands, woodlands, rocky, ruderal, agriculture and saline habitats (Appendix S2). This classification informs the type of both native community and the human influence at a local scale. We developed the cross-walk table using expert knowledge and habitat information provided by Rivas-Martínez *et al.* (2002) and Rodwell *et al.* (2002). Our expertise on the species composition of the phytosociological alliances guaranties the validity of grouping them in broad habitat types.

Relaying on the strong association between the number of introductions and the incidence of invasive species (Catford *et al.*, 2011, 2012; Polce *et al.*, 2011), we calculated three widely used metrics in invasion ecology: (1) presence–absence of non-native species in all plots, (2) relative non-native species richness in invaded plots, calculated as the number of non-native species within a plot in relation to the total number of species and (3) relative non-native abundance in invaded plots calculated as the accumulated percentage of non-native vegetation cover divided by the cover of all species. Only non-natives introduced after 1500 a.c. were considered. We did not restrict the study to only invasive species as we might have missed species limited to early stages in the invasion process (Catford *et al.*, 2012). These different metrics are surrogates for different stages of invasion, with presence representing the establishment stage and

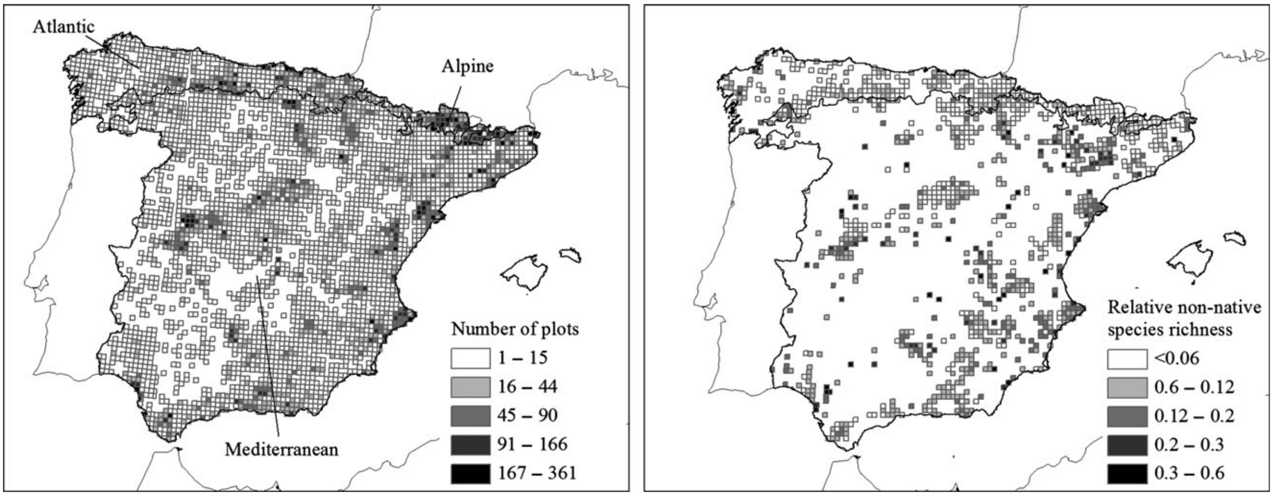

Figure 1 Number of vegetation plots and mean relative non-native species richness at invaded plots per 10-km UTM grid in mainland Spain.

richness and abundance indicating a dominance stage (Catford *et al.*, 2011; Polce *et al.*, 2011). The presence–absence of any non-native plant would inform about the likely recruitment of at least an individual plant irrespective of its ability to reproduce and become naturalized. In contrast, an increase in abundance of the species or the recruitment of new species would inform about a later phase in the invasion process where given suitable ecological conditions, non-native species are expanding and ultimately becoming dominant in the community.

Climate and human activity data

We selected several climatic and land-cover variables (our proxy for human activity at landscape scale). All variables selected have been commonly used in plant invasion studies (description in Appendix S2). The geographical location of each plot was only known within the 10-km UTM grid. We therefore characterized the climate and human activity context of each plot at the grid level. We discarded UTM grids with size lower than 60 km^2 or <60% of land (versus ocean) to ensure comparable values of predictors and to avoid possible misplacement of plots located at UTM borders.

We obtained climate data from the UNEX Spatial Data Infrastructure (http://ide.unex.es), which provides average monthly precipitation, minimum and maximum temperature at 1-km grid across Spain for the period 1971–2007. From this dataset, we extracted the following biologically relevant climate variables per UTM grid using the R-package DISMO: annual precipitation, summer precipitation (i.e. warmest quarter of the year), precipitation seasonality (i.e. coefficient of variation), annual temperature, winter minimum temperature (i.e. coldest month), summer maximum temperature (i.e. warmest month) and temperature seasonality (i.e. standard deviation). We also calculated the distance from each grid cell border to the coast to reflect a gradient in climate continentality.

Finally, we extracted the following human activity variables for each grid from the CORINE Land-cover Map (2006): percentage of urban (including major transport infrastructures), agriculture, woodland and grasslands land cover and the Shannon diversity index of these land-cover types (land-cover diversity, hereafter).

Model development

We modelled initial establishment of non-native species (i.e. presence data in 53,345 plots) and subsequent dominance (i.e. richness and abundance data in 8146 invaded plots) to test whether these different stages are associated with different variables (Catford *et al.*, 2011; Polce *et al.*, 2011). For each of these two stages of invasion, we constructed hierarchical generalized linear models (HGLMs) to allow the associations with climate to vary among bioclimatic regions and habitats, and human activity variables to depend on bioclimatic region. We compared the results of this model structure with a more traditional approach using non-hierarchical generalized linear models (GLMs) in which we included all the sets of variables and models with only habitat, climate or human activity variables. In contrast to the context-dependent associations considered in the HGLMs, GLMs just test the independent effects of the variables included. We fit all models using a Bayesian framework, which is useful for complex models or when sample sizes within subgroups are highly variable (Clark, 2004; see Appendix S3 for details).

Modelling the presence of non-native species

The presence–absence of non-native species at each plot was estimated from a Bernoulli distribution with probability of being present p_{i}:

$$N_i \sim \text{Bernoulli}(p_i)$$

$$\text{Logit}(p_i) = \alpha_{\text{habitat}(i)} + \beta X_i + e_{g(i)}$$

where α_{habitat} represents the intercept for each habitat type. Random effects for each UTM grid, *g*, were estimated from the same grid level distribution. The matrix of explanatory variables, X_i, included all the climate and human activity variables, and their associated coefficients, β, were estimated using a hierarchical and non-hierarchical approach (Fig. 2).

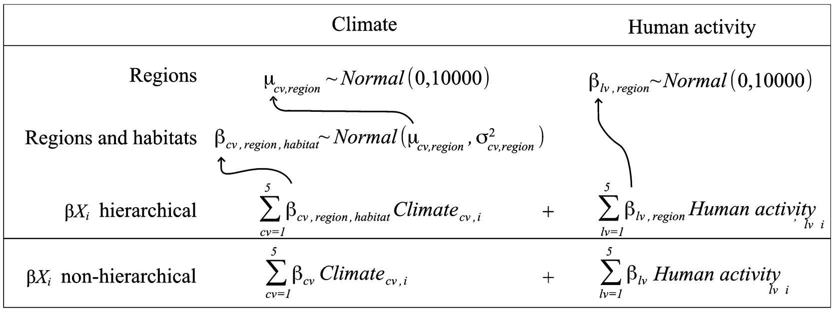

Figure 2 Model structure that defines the vector of coefficients associated with each climate and human activity predictor (βX_i) using both hierarchical and non-hierarchical approaches. In the hierarchical section, the level region defines the association of each climate and human activity variable in each bioclimatic region. The level region and habitats represent the vector of coefficients associated with each combination of climate variables across regions and habitat types.

Modelling the richness and abundance of non-native species

Non-native species richness at each plot, $\text{NNSR}_{i,}$ was modelled using a binomial distribution with parameters TR_i, total species richness, and $q_{i.}$, the probability of being non-native:

$$\text{NNSR}_i \sim \text{Binomial}(q_i TR_i)$$
$$\text{Logit}(q_i) = \alpha_{\text{habitat}(i)} + \beta X_i + e_{g(i)}$$

To ensure positive values and also improve convergence, non-native species relative abundance, NNSRA_i: $\text{NNSA}_i/\text{TA}_i$, (non-native species abundance/total vegetation abundance), was modelled using a log-normal distribution with mean μ_{Ai} and variance σ_{A}:

$$\text{NNSRA}_i \sim \text{ Log-Normal}(\mu_{Ai}, \sigma_A^2)$$
$$\mu_{Ai} = \alpha_{\text{habitat}(i)} + \beta X_i + e_{g(i)}$$

The habitat-related intercepts, α_{habitat}, the vector of coefficients associated with climate and human activity variables, β, and the plot level random effects, e_g, were modelled following the same approach described above.

Variable selection

We tested the collinearity among the predictors using pairwise Pearson's correlation tests (Appendix S2). First, we selected variables that had a pairwise correlation lower than 0.75 in both datasets (i.e. in all plots and in invaded plots). Among the variables with correlations >0.75, we selected those with the strongest ecological meaning and explanatory power. This process resulted in the following climate variables: annual precipitation, summer precipitation, winter minimum temperature, temperature seasonality and distance to the coast. Human activity variables were not highly correlated, and thus we included them all. All variables were standardized by subtracting the mean (centred) and dividing by the standard deviation (standardized) to improve model convergence and aid interpretation of coefficient estimates (Gelman & Hill, 2007).

Model comparison and validation

We implemented four non-hierarchical (GLM) models: (1) only climate variables, (2) only human activity variables, (3) only habitat type and (4) all variables (i.e. full model). We compared these models with the hierarchical model (HGLM), which included all variables but allowed climate effects to vary among habitats and regions and human activity effects among regions. We used the deviance information criteria (DIC) to compare the performance of the models (Spiegelhalter *et al.*, 2002). First, we compared the performance of the five models to identify the best-fit model. Then, we compared the first three models to quantify the relative importance of climate variables, human activity variables and habitat type on the presence, richness and abundance of non-natives. Finally, we compared the relationships estimated using the HGLM with those of the GLMs to test for the importance and differences of context-dependent relationships versus independent ones.

Preliminary analyses using the Moran's Index did not detect significant spatial autocorrelation in the models' residuals at any distance bigger than 10 km ($I < 0.1$). Therefore, we proceeded without modelling spatial random effects. It is possible that there is spatial autocorrelation in patterns of invasion within 10-km grid cells, but we could not test this because we lacked more precise information for plots location.

We randomly set apart 20% of total plots for model validation and calibrated the models with the remaining 80%. Goodness-of-fit of the validation data was calculated using the sum of squares errors (SSE, predicted–observed) for each model. Models that minimized this value were considered to fit better the data. For the presence model, we also calculated the area under the curve (AUC), a widely used method to evaluate presence–absence data models (Jiménez-Valverde *et al.*, 2011). Models with AUC > 0.5 discriminate the presences and absences better than chance.

Final models were run in OpenBUGS 3.2.1 (Lunn *et al.*, 2009). Models were run until convergence of the parameters was ensured (~50,000 iterations), after which posterior distributions of the parameters were calculated from 100,000 iterations (code of the models in Appendix S3).

RESULTS

Model comparison

The hierarchical model (HGLM) considering all context-dependent effects performed better than all classical non-hierarchical models (GLMs) across all metrics according to DIC values (i.e. smallest DIC value, Table 2). Differences were greater for the presence of non-native species than for richness or abundance. Validation of the models with independent data yielded similar model rankings, except for richness (Table 2).

Models including the three groups of variables together (i.e. climate, human activity and habitat type) performed better than models considering only a group of variables for all non-native plant metrics (Table 2). The difference in DIC between climate and human activity models was rather low in comparison to the difference with the habitat model for all metrics. Validation of the models with independent data yielded similar results.

The association of climate, human activity and habitat type with non-native plant metrics

The two types of models, GLMs and HGLM, provided different insights about the association of non-native plant metrics with climate, human activity and habitat type. The hierarchical model tested regional and habitat-dependent association of these variables with non-native plant metrics, whereas the classical non-hierarchical model estimated their association

Table 2 Comparison of models used to explain presence, relative richness and abundance of non-native plant species at invaded plots in mainland Spain using habitat type, climate and human activity variables. Best indicators for each plant invasion metric are shown in bold

			Calibration				Validation	
	Model	DIC	DIF	pD	AUC	SSE	AUC	SSE
Presence	All hierarchical	**30150**	0.00	1059	**0.82**	**4254.61**	**0.78**	**1147.83**
	All non-hierarchical	30830	0.02	1038	0.81	4379.33	0.77	1169.46
	Habitat	30940	0.03	1147	0.82	4367.25	0.77	1170.76
	Climate	33200	0.10	1150	0.78	4753.87	0.71	1263.78
	Human activity	33260	0.10	1174	0.78	4753.92	0.71	1261.99
Richness	All hierarchical	**16660**	0.00	297.6		4804.64		1077.34
	All non-hierarchical	16670	0.00	280.4		4839.52		**1064.28**
	Habitat	16780	0.01	382.5		**4596.59**		1091.85
	Human activity	17100	0.03	381.9		4988.25		1094.51
	Climate	17110	0.03	399.2		4962.87		1098.45
Abundance	All hierarchical	**−20100**	0.00	494.9		**116.64**		**28.55**
	All non-hierarchical	−20000	0.00	439.3		120.92		28.99
	Habitat	−19980	0.01	456.5		121.24		29.04
	Human activity	−19510	0.03	446.6		129.67		30.93
	Climate	−19510	0.03	466.4		130.43		31.31

DIC, deviance information criteria; DIF, increment in relative DIC compared to best model; pD, effective number of parameters; AUC, area under the curve; SSE, sum of square errors.

independently. In the following subsections, we compare the results for both types of models.

Association of climate with non-native plant metrics

Considering independent effects (i.e. non-hierarchical model), the significance of the climate predictors varied between the presence of non-native species and the richness and abundance of non-native species models (Fig. 3). Presence of non-native species was positively correlated to summer precipitation and proximity to the coast (Fig. 3). In contrast, both richness and abundance were positively associated with high annual precipitation and negatively with summer precipitation (Fig. 3). Furthermore, richness was also positively associated with temperature seasonality and winter minimum temperature (Fig. 3).

Although the independent effects of some climate variables on non-native plant metrics were not significant (Fig. 3), the hierarchical analyses revealed significant associations within specific habitat types (Table 3, Appendix S2 – Table S8–S10). For instance, the effect of annual precipitation on presence was different among habitat types: in grasslands, rocky and agriculture habitats, presence was associated with low annual precipitation, whereas in coastal, scrubland, woodland and ruderal habitats, it was associated with high annual precipitation (Table 3). These habitat-specific associations were more prevalent with presence than with richness or abundance of non-native species (Table 3).

The effect of climate across regions was very consistent for non-native plant metrics within each habitat type (Table 3). We only found divergence in the association of summer precipitation with presence, which was positive in the Mediterranean region for most habitats and highly variable in the Alpine and Atlantic regions (Table 3, Appendix S2 Table S8).

Association of human activity with non-native plant metrics

Considering independent associations (i.e. non-hierarchical model), the presence of non-native species was positively associated with agriculture and urban land cover and negatively with woodland land cover (Fig. 3). The pattern was different for richness and abundance of non-native species, which were negatively associated only with grassland land cover (Fig. 3). Richness also showed a negative association with land-cover diversity.

For human activity variables, we hypothesized that their association with non-native plant metrics would vary regionally. We found that most associations were in fact only significant in the Mediterranean region (Fig. 4). For instance, presence of non-native species was only associated with urban land cover and land-cover diversity in the Mediterranean region.

Non-native plant metrics across habitat types

Presence, richness and abundance of non-natives were significantly different among habitat types in the non-hierarchical model (Fig. 3, Appendix S2 – Table S6). Agriculture and ruderal habitats had the highest presence, richness and abundance of non-native species, whereas scrublands had the lowest. Differences among several habitats varied depending on the non-native plant metric under consideration (Fig. 3). For instance, woodlands showed medium presence values of non-native species, but very low richness and abundance;

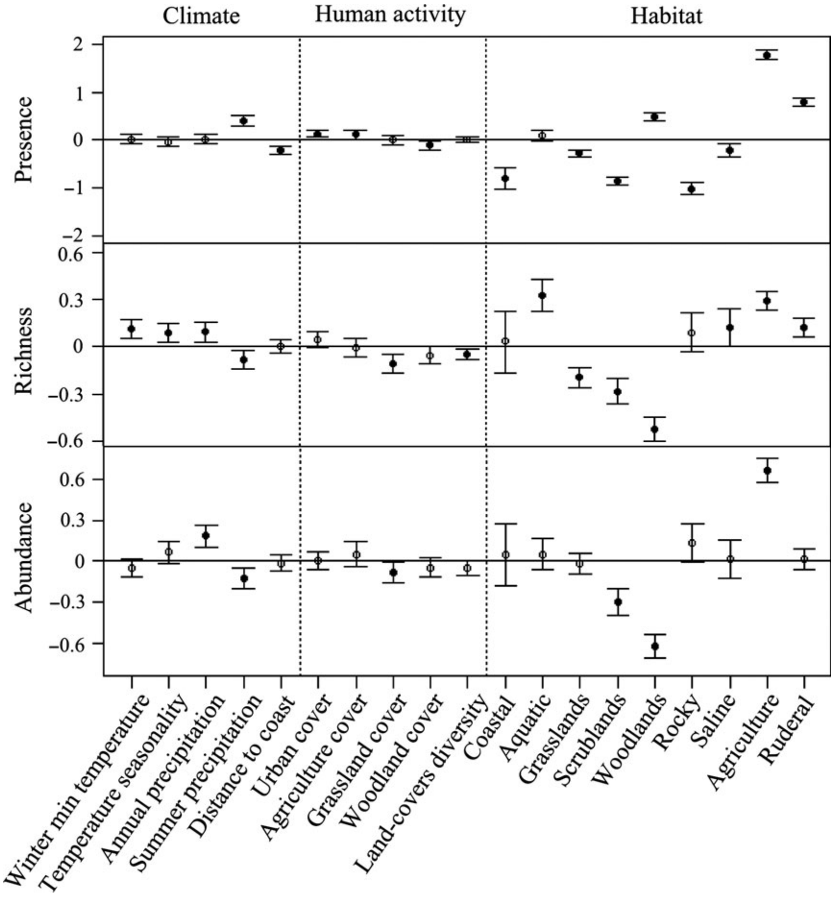

Figure 3 Posterior means (with credible intervals) of the independent mean coefficients for habitat, climate and human activity variables in the non-hierarchical models for the presence of non-native species and their relative richness and abundance at invaded plots in mainland Spain. Filled dots indicate that the 95% credible interval around the parameter mean values did not include zero. To facilitate comparison, habitat coefficients are centred around the mean of all habitat coefficients.

aquatic habitats had medium presence and abundance values, but rather high richness. These trends were similar for the hierarchical model (Appendix S2: Fig. S2 and Table S7).

DISCUSSION

Conceptual models to explain invasion success have pointed to the combination of having enough propagules and a suitable environment, biotic and abiotic (Chytrý *et al.*, 2008a; Catford *et al.*, 2009). In our work, climate was used to estimate abiotic suitability (Thuiller *et al.*, 2005), human activity at a landscape scale was used as a proxy for propagule availability (Chytrý *et al.*, 2008a; González-Moreno *et al.*, 2013b), and habitat type represented both characteristics of the native community and the human influence at a local scale (Chytrý *et al.*, 2008a). Among these variables, we found habitat type to be the single most important factor associated with invasion. Furthermore, these factors are likely interactive rather than additive and might act at different spatial scales and stages (Catford *et al.*, 2009; Milbau *et al.*, 2009; Jiménez-Valverde *et al.*, 2011). However, few empirical studies have quantified these complex patterns (Gassó *et al.*, 2012). Here, we have explored how a hierarchical modelling approach can quantify the context-dependent association of these variables with the presence and abundance of non-native plants (i.e. our proxy for plant invasion). We found that the associations of climate and human activity with non-natives patterns were mainly dependent on the habitat type, but not on the bioclimatic region. Furthermore, non-native plant metrics across habitats varied depending on the metric of invasion. As the different metrics could be considered surrogates for different stages of invasion, our results reinforce that different stages might be controlled by different factors (Catford *et al.*, 2009; Polce *et al.*, 2011).

Climate and plant invasions

At large scales, climate is the most important abiotic aspect shaping non-native species distribution (Thuiller *et al.*, 2005; Broennimann *et al.*, 2007). In our study, non-native species were more likely to be present in areas with high summer precipitation and close to the coast (i.e. the Atlantic part of the study area), reflecting higher presence in mesic areas without extreme seasonality (Polce *et al.*, 2011). Presence of non-natives in coastal areas could also be enhanced by the increased propagule pressure associated with higher human influence in these regions (Gassó *et al.*, 2009; González-Moreno *et al.*, 2013b). Still, we already accounted by human activity by adding the land-cover variables and considered distance to the coast as a good proxy for low seasonality. In contrast, higher richness and abundance of non-natives was associated with higher climate seasonality, but also with higher wet and warm conditions. Thus, although it is more likely to find at least one non-native species close to the

Table 3 Sign of the coefficients for climate variables across bioclimatic regions and habitat types in the full hierarchical models explaining presence of non-native species, relative richness and abundance at invaded plots in mainland Spain. Only results for combinations of climate variables and bioclimatic region with at least one significant coefficient for habitat type are shown. For full results, see Appendix S2

Model		Winter Minimum temperature		Temperature seasonality		Annual precipitation			Summer precipitation			Distance to coast	
Region	Habitat type	Atl	Med	Atl	Med	Alp	Atl	Med	Alp	Atl	Med	Alp	Med
Presence	Coastal	n.s.	–	n.s.	n.s.	n.s.	+	n.s.	n.s.	–	+	n.s.	n.s.
	Aquatic	–	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grassland	+	n.s.	n.s.	+	–	–	–	n.s.	n.s.	+	n.s.	–
	Scrubland	+	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	–	+	n.s.	n.s.
	Woodland	–	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.
	Rocky	n.s.	n.s.	n.s.	n.s.	n.s.	–	–	n.s.	n.s.	+	n.s.	–
	Agriculture	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.	+	+	n.s.	–
	Ruderal	n.s.	+	n.s.	+	n.s.	+	n.s.	n.s.	n.s.	+	–	–
Richness	Grassland	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.
	Scrubland	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.
	Saline	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.
	Agriculture	n.s.	+	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Ruderal	+	+	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
Abundance	Coastal	n.s.	n.s.	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Aquatic	n.s.	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Grassland	n.s.	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Scrubland	n.s.	n.s.	+	n.s.	n.s.	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Woodland	n.s.	–	+	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Rocky	n.s.	–	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Saline	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	–	n.s.	n.s.
	Agriculture	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	+	–	n.s.	n.s.	n.s.	n.s.
	Ruderal	n.s.	+	n.s.	n.s.	n.s.	n.s.	+	–	n.s.	n.s.	n.s.	n.s.

Alp, Alpine; Atl, Atlantic; Med, Mediterranean; +, positive association; –, negative association; n.s., non-significant association.

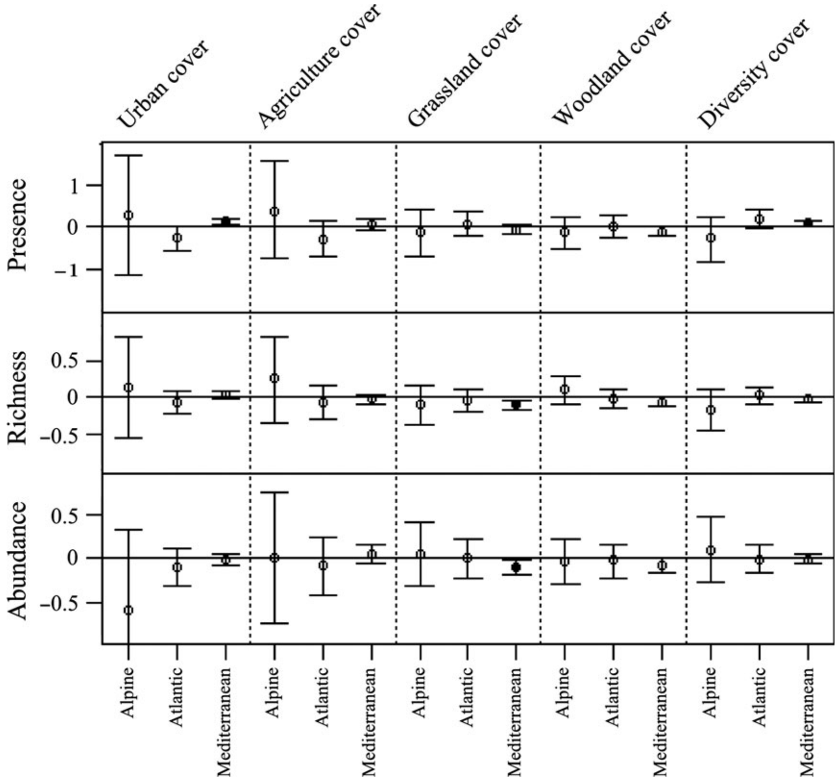

Figure 4 Posterior means (with credible intervals) of the coefficients for human activity variables across bioclimatic regions in the hierarchical models for the presence of non-native species and their relative richness and abundance at invaded plots in mainland Spain. Filled dots indicate that the 95% credible interval around the parameter mean values did not include zero.

coast, wet areas towards the interior are also hubs for non-native species diversity and abundance.

Climate variables that were not significantly associated with non-native plant metrics independently (i.e. non-hierarchical model) were found to be important in specific habitats (i.e. hierarchical model). Climatic effects on plant invasions are mediated by the ecological characteristics of different habitats such as biotic resistance or abiotic constraints. For instance, we found higher presence of non-native species with low annual precipitation in grasslands, rocky and agriculture habitats, whereas the opposite trend was relevant in coastal, scrubland, woodlands and ruderal habitats. In contrast to more open habitats, an increase in annual precipitation might counteract the competition for water in woody habitats and the excess of salinity in coastal habitats. Although the mechanisms underlying these interactions require further research, our results suggest that considering habitat-dependent effects seems fundamental to understand and predict plant invasions (Gassó *et al.*, 2012).

There was high consistency in the associations of climate variables with all non-native plant metrics across bioclimatic regions. Within specific habitat types, only the association of summer precipitation with presence showed divergences for coastal and scrubland habitats. In the humid Atlantic region, presence was enhanced in relative drier environments (lower summer precipitation), whereas in the drier Mediterranean region, we found the opposite trend. This finding agrees with plant invasion being enhanced in mesic conditions (i.e. intermediate temperature and moisture levels) (Polce *et al.*, 2011).

Human activity and plant invasions

Besides suitable climatic conditions, plant invasions are facilitated by increasing disturbance levels and propagule pressure of non-native species from regional to landscape scales. Such patterns are highly associated with human land covers (i.e. agriculture or urban), while natural areas (i.e. higher grassland and woodland cover) might act as a buffer to plant invasions (Ohlemüller *et al.*, 2006; Carboni *et al.*, 2010). We found the same pattern for all non-native plant metrics: invasive plants were negatively associated with natural areas and positively associated with human-altered areas. Unlike other studies (e.g. Pino *et al.*, 2005; Marini *et al.*, 2009; González-Moreno *et al.*, 2013b), we found a negative association of land-cover diversity and non-native richness. Diverse landscapes usually enhance local non-native species richness by increasing variability of ecological conditions; however, if the number of land covers characterized is low, land-cover diversity could show the pattern of the most predominant land-cover type (i.e. agriculture land cover).

As for the relationships with climate variables, we also found that the relationships between invasion and human activity were highly consistent spatially, exhibiting similar relationships across bioclimatic regions. In fact, we found that human activity variables were only significant in the Mediterranean region probably due to its higher human alteration and disproportionate number of plots (five times more samples in the Mediterranean than in the Atlantic). Considering the high consistency found for climate and human activity effects across bioclimatic regions, we suggest that broad patterns of plant invasion could be feasibly extrapolated among neighbouring regions.

Habitat types and plant invasions

Following previous studies, anthropogenic habitats (i.e. agriculture and ruderal) yielded the highest values of non-natives metrics and natural habitats the lowest values (i.e. scrubland) (Vilà *et al.*, 2007; Chytrý *et al.*, 2008b). Nevertheless, for several habitats there were some discrepancies. For instance, woodlands showed high non-native species presence, but extremely low richness and abundance. The few shade-tolerant non-native species that could overcome the limitation of light availability in woodlands are very likely to survive even if it is in low numbers (Martin *et al.*, 2009). However, the species able to invade woodlands are generally rare or might be still in an incipient phase of expansion (Martin *et al.*, 2009; González-Moreno *et al.*, 2013a), reflecting low local richness and abundance. Thus, further research should confirm if the potential differences between the presence and abundance of non-native plants are mediated by their different traits in relation to the habitat they invade or by the stage of the invasion process.

Analysis of multispecies invasion

Several metrics have been proposed to quantify the level of plant invasions such as the richness or abundance of non-native species (Catford *et al.*, 2012). We have found different patterns of climate, human activity and habitat type associations with each metric, suggesting that different variables control the overall presence and abundance of non-native species, our proxies for establishment and dominance during multispecies invasions (Catford *et al.*, 2011; Polce *et al.*, 2011). We expected higher importance of human activity at a landscape scale (i.e. proxy for propagule pressure) than climate (i.e. defining suitable abiotic conditions) in the establishment stage. Nevertheless, both groups of variables showed similar importance for predicting the establishment and dominance of non-native species. Further studies could explore whether these patterns are also similar in other stages of the invasion process such as transport or expansion (Blackburn & Duncan, 2001; Leung *et al.*, 2012) or consider the human activity predictors at a finer scale (González-Moreno *et al.*, 2013b).

Modelling strategies to understand the context-dependence of invasions

Our model results have shown how a hierarchical approach better reflects plant invasions than non-hierarchical models. Although proven a powerful modelling strategy (Pearson *et al.*, 2004; Diez & Pulliam, 2007; Vicente *et al.*, 2011), hierarchical modelling has been rarely used to model biological invasions (Ibáñez *et al.*, 2009a, 2014; Diez *et al.*, 2012). Hierarchical modelling can accommodate the frequently proposed issue of considering the invasion process across spatial scales (Collingham *et al.*, 2000; Pearson & Dawson, 2003; Milbau *et al.*, 2009). Climate, topography and human activity at regional level might drive invasion variability at large scales while local variability may be determined by changes in biotic interactions, disturbance or microclimate which are highly associated with habitat type (Milbau *et al.*, 2009).

Hierarchical models can also be used to test the consistency in the associations of plant invasions and environmental variables. Context-dependent associations are usually assessed by calibrating the same model with different datasets (Broennimann *et al.*, 2007; Gassó *et al.*, 2012). This modelling strategy is problematic when the number of categories is large due to the increasing number of parameters to estimate, the unbalanced number of samples per category and the difficulty to interpret differences. Hierarchical models can partially solve these problems, especially when the data have a nested structure and when partial pooling of information across groups is likely to be helpful. Because these are common characteristics of ecological studies, hierarchical approaches may be widely useful for quantifying context-dependent patterns of invasion and developing predictions of invasion risk.

Concluding remarks

It is important to consider the stage of the invasion process when managing new introductions (Simberloff, 2009). Areas with high establishment probability might not be the ones with higher dominance of non-native species (Catford *et al.*, 2011). These invasion hotspots regarding establishment might be colonized by only a few widespread species, but not highly abundant because of environmental constraints. Screening non-native species presence together with richness and abundance provides a simple method to anticipate successful plant invasions and not only potential establishment.

Although future patterns of invasions will not necessarily mirror past invasions, given our stage of knowledge, the information we can obtain from past invasions is our best bet on how future invasions may develop. Given this information, hierarchical models can help management of plant invasions through a better accountability of context-dependent effects (i.e. the interactions between climate suitability, human activity and the conditions of the local habitat). The outputs from these models might be used to develop invasion risk scenarios within particular habitats and bioclimatic regions, delivering more detailed information to prevent future invasions.

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SUPPORTING INFORMATION

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

Appendix S1 Database characteristics.

Appendix S2 Complementary tables and figures.

Appendix S3 Modelling details, Openbugs, and MESS codes

Figure S1 Number of plots, proportion of plots with non-natives presence and mean relative richness and abundance of non-native species at invaded plots across habitat types.

Figure S2 Posterior means of the independent mean coefficients for habitat type in the hierarchical models.

Table S1 Cross-walk table between the alliance and the most likely EUNIS habitat type.

Table S2 List of non-native species included in the database.

Table S3 Variables used as predictors in the models.

Table S4 Pearson's correlation coefficients independent variables used in the models.

Table S5 Number of plots for each combination of habitat type and bioclimatic region.

Table S6 Confidence intervals of paired habitat coefficient differences for the non-hierarchical model.

Table S7 Confidence intervals of paired habitat coefficient differences for the hierarchical model.

Table S8–10 Posterior mean of the coefficients for climate variables across bioclimatic regions and habitat types in the hierarchical models.

BIOSKETCH

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