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Deconstructing the native–exotic richness relationship in plants

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ABSTRACT

Aim Classic theory suggests that species-rich communities should be more resistant to the establishment of exotic species than species-poor communities. Although this theory predicts that exotic species should be less diverse in regions that contain more native species, macroecological analyses often find that the correlation between exotic and native species richness is positive rather than negative. To reconcile results with theory, we explore to what extent climatic conditions, landscape heterogeneity and anthropogenic disturbance may explain the positive relationship between native and exotic plant richness.

Location Catalonia (western Mediterranean region).

Methods We integrated floristic records and GIS-based environmental measures to make spatially explicit 10-km grid cells. We asked whether the observed positive relationship between native and exotic plant richness ($R^2 = 0.11$) resulted from the addition of several negative correlations corresponding to different environmental conditions identified with cluster analysis. Moreover, we directly quantified the importance of common causal effects with a structural equation modelling framework.

Results We found no evidence that the relationship between native and exotic plant richness was negative when the comparison was made within environmentally homogeneous groups. Although there were common factors explaining both native and exotic richness, mainly associated with landscape heterogeneity and human pressure, these factors only explained 17.2% of the total correlation. Nevertheless, when the comparison was restricted to native plants associated with human-disturbed (i.e. ruderal) ecosystems, the relationship was stronger ($R^2 = 0.52$) and the fraction explained by common factors increased substantially (58.3%).

Main conclusions While our results confirm that the positive correlation between exotic and native plant richness is in part explained by common extrinsic factors, they also highlight the great importance of anthropic factors that – by reducing biotic resistance – facilitate the establishment and spread of both exotic and native plants that tolerate disturbed environments.

Keywords

Anthropic factors, biological invasions, biotic resistance, Catalonia, exotic plants, ruderal plants.

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INTRODUCTION

Ever since Elton (1958), species-rich communities have been thought to be more resistant to the establishment of non-indigenous exotic species than species-poor communities, a

theory known as the ‘biotic resistance hypothesis’. The rationale of the hypothesis is that as more species are present in a community, the niches will be better filled and the competition for resources will be stronger (Case, 1990; Lonsdale, 1999; Levine *et al.*, 2004). Several studies have indeed documented negative

relationships between the number of native and naturalized non-native species (exotic hereafter) at small spatial scales, often with resolutions of 10 m² or less (Knops *et al.*, 1999; Levine, 2000; Kennedy *et al.*, 2002), and microcosm and mesocosm experiments have confirmed that these patterns truly reflect a higher resistance of species-rich communities (Stachowicz *et al.*, 1999, 2002; Levine, 2000; Naeem *et al.*, 2000; Fargione & Tilman, 2005).

Scaling the biotic resistance hypothesis up to landscape or regional scales, we would expect that regions with high native richness should contain fewer exotic species than regions with low native richness (Elton, 1958). If so, the implications for conservation policies would be important as it would mean that more diverse regions should be regarded as less susceptible to biological invasions. However, observations at broad spatial scales show that the correlation between exotic and native species richness is not negative but is often positive (Planty-Tabacchi *et al.*, 1996; Lonsdale, 1999; Stohlgren *et al.*, 2003; Perelman *et al.*, 2007). These seemingly conflicting results constitute what Fridley *et al.* (2007) refer to as a paradox.

This paradox may be a matter of spatial scale. As we move from smaller plots to larger regions, the relative effect of biotic interactions diminishes and environmental factors gain importance in shaping regional biodiversity (Levine & D'Antonio, 1999; Shea & Chesson, 2002). If these environmental factors also facilitate the establishment of non-indigenous species, then this could explain the positive relationship between species diversity and invasion success seen on broad spatial scales (Byers & Noonburg, 2003; Fridley *et al.*, 2004; Herben *et al.*, 2004; Kumar *et al.*, 2006; Stohlgren *et al.*, 2006). The nature of such extrinsic factors is not known yet, although some possibilities have been advanced. First, a structurally heterogeneous region may provide a greater array of microenvironments for native species (Davies *et al.*, 2005), and at the same time increase the chances that the invader encounters a favourable niche not monopolized by native species. Second, climatic conditions can also influence both native and exotic species richness by limiting the number of species that can persist in the region when these are most extreme. For example, the low tolerance of many plants to low temperatures should decrease the diversity of both exotic and native plant species in very cold sites, and this could lead to a positive native–exotic richness relationship in regions with high geographic variation in climatic characteristics. Finally, almost all documented patterns of native–exotic richness relationships have been reported in highly developed countries, and although human activities increase the rates of extinction of native species, they can also produce a 'positive correlation' between exotic and native species richness by a variety of mechanisms. For example, human settlements, which are the source for exotic propagules, are usually placed in fertile areas with suitable climates where native species richness is often high (McKinney, 2001). Moreover, human activities themselves may create new niche opportunities for both exotic and native species adapted to disturbances as well as facilitate the transport (intentionally or unintentionally) and spread of exotic and native plants (Pyšek, 2002). All this could be translated into a higher diversity

of both exotic and native plants in the localities most influenced by human activities.

Two previous macroecological analyses provide some credence to the existence of common factors causing native and exotic species to be positively correlated on large spatial scales. In a response article, Rejmánek (2003) showed that the positive native–exotic plant richness relationships reported by Stohlgren *et al.* (2003) in their analysis in the USA were negative when human population density and latitude were included in a model predicting exotic plant richness. Subsequent analyses of the same data by Taylor & Irwin (2004) further confirmed that the positive association between native and exotic plant richness was entirely explained by the effects of latitude and the economic activity of the state. Although these previous studies are consistent with the hypothesis that native and exotic species richness are not causally related, the large scale of the analyses makes it difficult to draw firm conclusions. In addition to the difficulties of estimating accurate values of environmental factors in large sampling units when the environment is heterogeneous, there are serious doubts that the signature of community-level interactions may be detected at such large scales. To address the paradox that regions with higher native species richness also support larger numbers of naturalized exotic species, we need to scale down the level of analysis to the landscape level, where the effects of biotic resistance and common extrinsic factors may be more clearly inferred.

Here, we conduct a landscape-level analysis to ask to what extent climatic conditions, landscape heterogeneity and degree of anthropogenic disturbance may explain the positive native–exotic plant richness relationships seen in a particularly well-sampled region from the western Mediterranean basin (Pausas *et al.*, 2003; Pino *et al.*, 2005). Albeit relatively small (32,114 km²), the region presents a remarkable diversity of native vascular plant species (with more than 3200 species), resulting from sharp climatic, landscape and socioeconomic gradients, and harbours a high number of well-established exotic plants (around 450 species; Vilà *et al.*, 2010). Both the native and exotic floristic composition of the region have been exhaustively studied in recent years, confirming that spatial variation in plant richness is associated with climatic conditions, landscape heterogeneity and the degree of anthropogenic disturbance (Pausas *et al.*, 2003; Pino *et al.*, 2005). Thus, the study region provides an ideal opportunity to test the hypothesis that extrinsic factors account for the positive relationship between native and exotic species richness.

We explored the factors underlying the positive relationship between natives and exotics with two conceptually distinct approaches. As proposed by Shea & Chesson (2002), we first investigated whether the above pattern results from the addition of several negative correlations corresponding to different environmental conditions. We used a cluster analysis to classify each grid cell into homogeneous groups based on climatic conditions, landscape heterogeneity and anthropic factors, and then examined whether the native–exotic richness relationships turns out negative or non-significant when examined within these homogeneous groups. In the second approach, we used struc-

tural equation modelling (SEM) to assess to what extent the climate, landscape and anthropogenic factors explain the positive native–exotic richness relationship. SEM provides a strong framework for such an analysis because it allows us to disentangle causal effects from spurious influences associated with common causes. These analyses were repeated by dividing native plants into those associated with human-disturbed (i.e. ruderal) habitats and those that are not, making it possible to explore in more detail the influence of anthropic factors on the positive relationship between native and exotic plant richness.

METHODS

Study area

Catalonia is a region of 32,000 km² located in the north-east of the Iberian Peninsula, near the Mediterranean coast. The region exhibits highly variable environmental conditions resulting from its complex topography, with elevations ranging from 0 to 3350 m a.s.l., and geographical location between Mediterranean, Atlantic and Saharan influences (Ninyerola *et al.*, 2000). The Catalonian landscape is highly heterogeneous as a result of the transformations caused by centuries of human occupation. In the last century, crop intensification increased in lowlands and urban areas concentrated in coastal areas, especially around the city of Barcelona (MMAMB, 1995). In contrast, crop abandonment and cessation of forest cutting led to the dominance of woodland in mountain areas, often shaped by the increasing frequency of wildfires.

The data

The environmental complexity of Catalonia results in a rich flora, estimated as at least 3200 species (Bolòs *et al.*, 2005). We obtained information on the number of exotic and native plant species from the Catalonian Database of Biodiversity (Banc de Dades de Biodiversitat de Catalunya, BDBC; <http://biodiver.bio.ub.es/biocat/>; Font & Ninot, 1995), a project that gathers and organizes all available floristic data from Catalonia. At present, the BDBC accounts for about 1,200,000 floristic records. This information is made spatially explicit by associating the record with 10-km Universal Transverse Mercator (UTM) grid cells distributed all over the region.

In the BDBC, a plant species is considered exotic when it has been accidentally or intentionally transported and introduced by humans in a region that is outside the species' native range. However, not all the exotic species currently detected in Catalonia are included in the BDBC. Exotic plants may be classified as casual, naturalized or invasive (Richardson *et al.*, 2000; Pyšek *et al.*, 2004), corresponding to the classical stages of introduction, establishment and spread (Duncan *et al.*, 2003). The BDBC only includes citations in which the author confirms the naturalization of the species (e.g. through field observation of reproduction of the species and long-term persistence of the population), systematically excluding all casual species (*sensu* Richardson *et al.*, 2000; Pyšek *et al.*, 2004). Consequently, throughout the text

the term 'exotic species' refers to naturalized non-indigenous species. In the BDBC database there is no distinction between naturalized and invasive species, given the difficulties of drawing a clear separation between these two categories. However, we note that our operational definition of exotic species is still appropriate, as the biotic resistance hypothesis primarily focuses on the establishment stage (see Fridley *et al.*, 2007). Given the long history of human occupation in the region and the difficulties of tracing back old introductions, we considered only as exotic species those established after the year AD 1500.

Native plants were classified as ruderal and non-ruderal. Our operational definition of a native ruderal was a species characteristic of the phytosociological class Rudero-Secalietaea (*sensu* Braun-Blanquet & Braun-Blanquet, 1931) or its lower-level orders, alliances or associations, which include those plants most heavily influenced by human activities in the region (Rivas-Martínez *et al.*, 2001; Bolòs *et al.*, 2005).

Variables describing climate, topography, geology, land use and human settlement were obtained for each 10-km grid using the MiraMon GIS (Pons, 2002). Climatic variables were calculated from the climatic models of Catalonia set up by Ninyerola *et al.* (2000) at a spatial resolution of 180 m using the existing network of meteorological stations and digital elevation models (DEM). For each 10-km square, we calculated the mean annual temperature, mean minimum temperature in January (considered the coldest month), mean maximum temperature in July (the hottest month), annual rainfall, mean rainfall of January and July, and mean annual solar radiation. Topographic variables were obtained from the official DEM (30-m pixel size) and the 1:50,000 topographic map of Catalonia, both generated by the Cartographic Institute of Catalonia (ICC). The mean and range (difference between the maximum and minimum) of altitudes per 10-km square were calculated from the DEM. Geological explicative variables were obtained from the official 1:250,000 geological map of Catalonia, a grid of pixel size 180-m that accounts for 10 main bedrock types. Landscape variables were set up using the Land Use Map of Catalonia (LUMC), generated by the ICC in 1997 by classifying LANDSAT images. The resulting 30-m pixel grid was used to calculate the relative ground cover per 10-km square of woodlands, shrubs, croplands and urban areas, as indicators of basic landscape categories. We also calculated the relative ground cover of bare soil excluding beaches and rocky areas, which, at the scale (pixel size) of the LUMC, is mostly related with human-derived land disturbance. Geological and land-cover diversity were measured using Shannon diversity indices within each grid cell. Several human settlement variables were also included in the analysis. Mean population density and mean distance to cities larger than 50,000 inhabitants were considered to evaluate the extent of the metropolitan phenomenon. We used the official urban settlement map of Catalonia (<http://dadesobertes.gencat.cat/en/dades-obertes/cartografia.htm>) that includes the most recent (1999) population census to calculate the population density per 10-km square and to select urban areas of more than 50,000 inhabitants. MiraMon distance algorithms were then used to calculate the mean distance to these cities per 10-km square. The mean distance to the primary roads

and motorways was calculated for each 10-km square with a similar procedure, applied on a selection of the motorways and primary roads from the 1:50,000 topographic map of Catalonia.

Data analysis

We modelled native and exotic species richness as a function of climatic conditions, landscape heterogeneity and degree of anthropogenic disturbance using 10-km grid cells with more than 70% of land cover ($n = 295$ cells). We used two distinct modelling approaches. First, we asked whether the positive relationship between total natives and exotics resulted from the addition of several negative correlations corresponding to different environmental conditions (Shea & Chesson, 2002). To classify the grid cells in homogeneous groups (hereafter, 'group') as a function of the environmental variables, we used a robust measure of k -means cluster analysis as implemented in the R package 'fpc' (R Development Core Team, 2010). k -mean clustering or partitioning splits the data into k clusters around medoids. The algorithm is based on the search for k representative objects or medoids among the observations of the dataset. After finding a set of k medoids, k clusters are constructed by assigning each observation to the nearest medoid. The goal is to find k representative objects that minimize the sum of the dissimilarities of the observations to their closest representative object (Crawley, 2002). Variables were rescaled for comparability and the appropriate number of clusters were identified by visual inspection of the plot showing the within-groups sum of squares as function of the number of clusters extracted. Once we had classified each square in a homogeneous group with the k -means partitioning, we then modelled the richness of exotic plants (response variable, square-root transformed) as a function of the richness of native plants (predictor) with a least-square regression, including 'group' as a factor. In this way we could fit a different line for each homogeneous group and test whether the slope relating exotic and native species richness turned out negative. To deal with spatial autocorrelation, we computed the Moran's I of the residuals of all models, and whenever there was evidence of autocorrelation we controlled for latitude and longitude in the model by fitting linear models using generalized least squares (GLS, hereafter) where the errors are allowed to be correlated (Crawley, 2002). We used the 'nlme' package in R to perform the GLS models. Diagnostic plots were examined to check for outliers and heteroscedasticity, as well as to ensure the normality of errors (Crawley, 2002).

The second method we used was structural equation modelling (SEM), a multivariate statistical method useful for describing the direct, indirect and spurious dependences among a set of variables (Li, 1975; Grace, 2006). We decomposed the correlation between exotic and native richness as a function of the factors defining the extrinsic environmental factors. Given the strong correlation between some environmental predictors and the risk of model under-identification (Grace, 2006), we opted to reduce data dimensionality with a principal component analysis (PCA) using a 'varimax' rotation, as implemented in the R package 'psych'. We followed the common practice of extract-

ing enough factors to explain 90% of the variance (Crawley, 2002). Although this implies the consideration of some factors that explain a small fraction of environmental variance (Table 1), these may still be relevant if they describe factors that have a great influence on plant richness. The factors extracted by the PCA were then used instead of the actual variables in SEM. We performed SEM using AMOS 16.0 (Arbuckle, 2006), fitting general structural equation models by the method of maximum likelihood with multinormal errors. The analysis was performed considering total, ruderal and non-ruderal native species separately. The fit of the models was evaluated with a chi-square test comparing the observed and predicted covariance matrices. A non-significant chi-square indicates that the data fit the model (Grace, 2006). SEM does not allow correction for spatial autocorrelation. As an alternative, we validated each path by using spatially explicit GLS as explained above.

Although the BDBC represents one of the most comprehensive and accurate accounts of the floristic composition currently available for any region of its size, the sampling effort may vary among grid cells and hence affect the estimates of exotic and native species richness. These biases have been shown to have a negligible effect on the estimates of exotic species richness but a significant one on native species richness estimates (Pino *et al.*, 2005). To ensure that our conclusions were not affected by sampling biases, we repeated all the analyses excluding the grids in the lower quartile of total species richness. The remaining subset included 221 grid cells, each containing at least 459 species. The results were qualitatively similar to those obtained with the complete data set and are presented in Appendix S1 in the Supporting Information.

RESULTS

General patterns

The analyses revealed a positive, albeit weak, association between native and exotic plant richness in the study region, either considering spatial autocorrelation (GLS: estimate = 0.004, $P < 0.001$, Moran's $I = -0.10$) or not [least square regression (LSR): estimate = 0.003, $P < 0.001$, $R^2 = 0.11$, Moran's $I = 0.62$]. Interestingly, this association was primarily driven by the effect of ruderal native plants, as evidenced by the fact that the coefficient of determination of the model increased substantially when exotic plant richness was compared with ruderal native plant richness (LSR: estimate = 0.03, $P < 0.001$, $R^2 = 0.52$, Moran's $I = 0.54$; GLS: estimate = 0.03, $P < 0.001$, Moran's $I = -0.08$) and was close to zero when the comparison was with non-ruderal native plant richness (LSR: estimate = 0.002, $P < 0.001$, $R^2 = 0.04$, Moran's $I = 0.60$; GLS: estimate = 0.003, $P < 0.001$, Moran's $I = -0.17$; see Appendix S1 for additional analyses).

Environmental groups

Using all climatic, landscape and anthropic variables in the model (see Table 1 for variables names), the k -means

Table 1 Scores of the 10 principal components (PCs) explaining more than 90% of the total variance obtained from principal components analysis with ‘Varimax’ rotation on the initial variables. Bold scores correspond to values larger than 0.75 to facilitate the interpretation of the PCs. Principal components are sorted in descending order of explained variance.

	PC1	PC5	PC2	PC4	PC8	PC3	PC9	PC7	PC6	PC10
Land use Shannon diversity index	−0.24	0.12	0.35	–	−0.16	0.23	−0.19	0.20	–	0.73
Geologic Shannon diversity index	–	–	–	–	–	–	–	0.97	–	–
Distance to main roads	0.24	0.15	−0.20	–	0.89	–	0.13	–	–	−0.11
Distance to main cities	0.80	0.14	−0.26	–	–	–	0.27	−0.13	–	0.16
Distance to main rivers	0.11	–	–	–	0.11	–	0.95	–	–	–
Distance to the sea	0.92	–	−0.14	–	–	–	–	–	–	–
Solar radiation	−0.13	−0.82	–	0.10	–	−0.26	−0.11	–	–	–
Mean January temperature	−0.93	−0.12	0.15	–	–	–	–	–	–	0.19
Mean July temperature	−0.83	−0.46	–	–	−0.14	−0.13	–	–	–	–
Mean annual temperature	−0.90	−0.33	–	–	−0.12	−0.13	–	–	–	–
January precipitation	0.39	0.83	–	–	–	0.15	0.13	–	–	0.16
July precipitation	0.69	0.6	–	–	–	–	–	–	–	−0.10
Annual precipitation	0.55	0.74	–	–	0.17	–	–	–	–	–
Mean altitude	0.90	0.28	–	–	0.19	0.12	–	–	–	–
Altitudinal range	0.78	0.42	–	0.14	0.24	–	–	–	–	0.15
Population density	−0.15	−0.13	0.90	–	−0.11	–	–	–	–	–
No. habitats	–	–	–	–	–	–	–	–	0.99	–
% Forest	0.11	0.76	–	−0.14	0.14	−0.42	−0.24	0.18	–	−0.12
% Scrub	0.55	–	−0.15	0.72	0.21	–	–	–	–	0.20
% Agriculture	−0.44	−0.64	−0.11	−0.39	−0.26	0.14	0.12	−0.16	–	−0.15
% Urban land use	−0.37	–	0.74	–	−0.10	0.25	–	–	–	0.27
% Bare soil	0.38	0.13	0.13	–	0.12	0.84	–	–	–	0.14
Fire frequency	−0.26	–	–	0.91	–	–	–	–	–	−0.15
Variance explained:	0.31	0.17	0.08	0.07	0.05	0.05	0.05	0.05	0.05	0.04

clustering analysis identified four environmentally homogeneous groups (see Table S1). These groups define cells that were primarily characterized by low precipitation (Group 1), reduced human impact (Group 2), high environmental heterogeneity and human population density (Group 3), and high altitude and low human population density (Group 4). We re-examined the relationship between native and exotic plant richness within each of these groups by including ‘group’ as a predictor in the model. The analysis revealed notable differences between groups in exotic plant richness (Fig. 1 and Fig. S1). Specifically, Group 4, characterized by high altitude and low human population density, was significantly different from all other groups regardless of spatial autocorrelation ($P < 0.05$; Fig. 1). Further, Group 3, which was best defined by human-altered conditions, was only significantly different from Groups 1 and 2 when spatial autocorrelation was not taken into account ($P = 0.001$; with spatial autocorrelation $P = 0.12$). Yet despite these differences, the relationship between native and exotic plant richness remained positive (rather than negative) within all the groups (Fig. 1), regardless of considering spatial autocorrelation (GLS: estimate = 0.01, $P < 0.001$, Moran’s $I = 0.01$) or not (LSR: estimate = 0.04, $P < 0.001$, Moran’s $I = 0.17$), and did not significantly differ between groups (interaction between native plant richness and groups: $P > 0.6$).

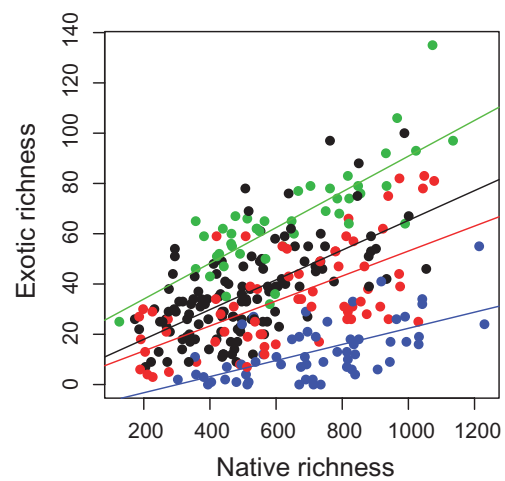


Figure 1 Native–exotic richness relationship for each environmental group. Each group is plotted with a different colour (Group 1, low precipitation, black; Group 2, reduced human impact, red; Group 3, high environmental heterogeneity and human population density, green; Group 4, high altitude and low human population density, blue).

Common environmental causes

The PCA over climatic, landscape and anthropic variables extracted 10 principal components, which together explain

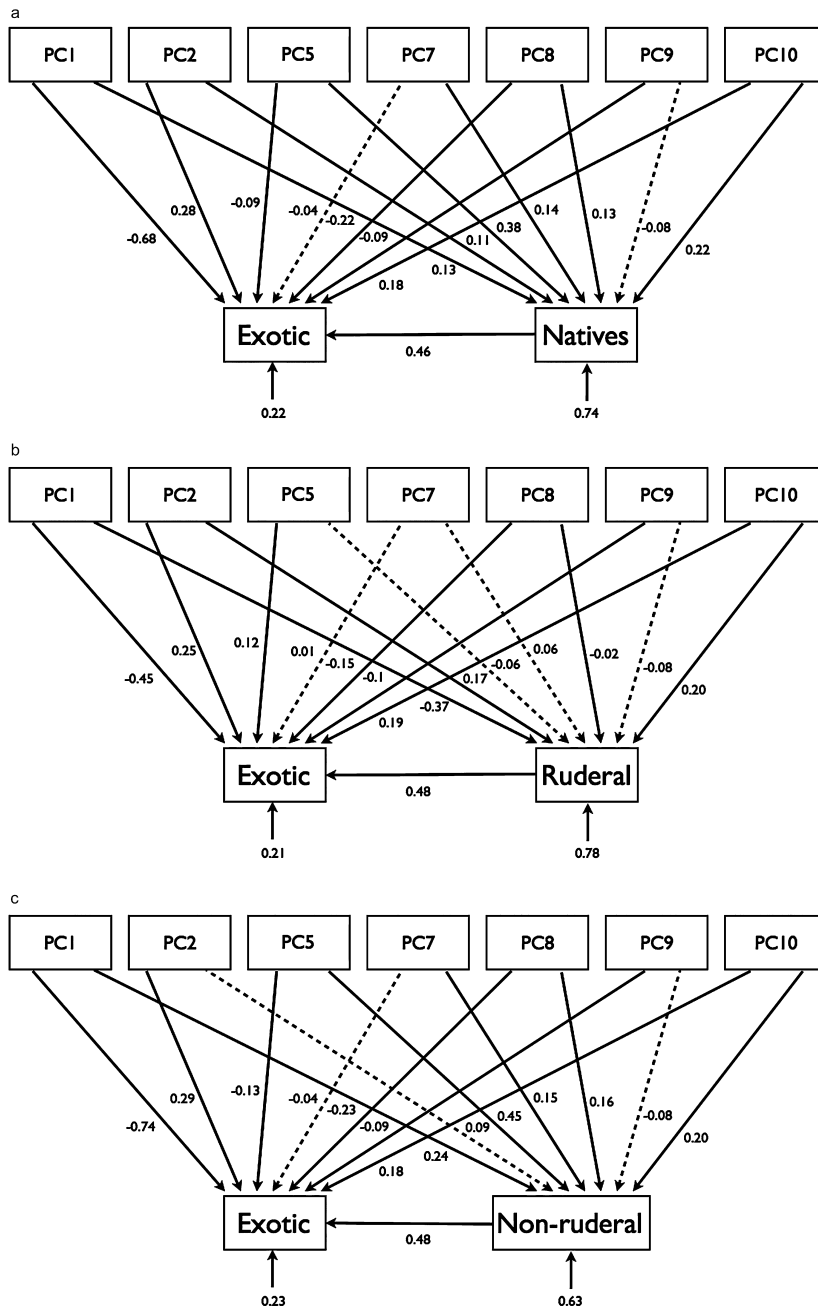


Figure 2 Structural equation model using the principal factors from a principal components (PC) analysis loading into (a) native–exotic, (b) ruderal–exotic, and (c) non-ruderal–exotic richness relationship. The standardized paths presented are comparable within each model, but not among models. Dotted lines represent non-significant paths.

more than 90% of the variance (Table 1 and S2). Each of those 10 factors explains at least a 4% of the variance. We used SEM to decompose direct and spurious effects of these factors on the correlation between exotic and native plant richness. We restricted the analysis to the seven components with significant effects on exotic and/or total native richness (see Appendix S2 for the minimum adequate GLS models). The model using the total native plants fitted well to the data ($\chi^2 = 0.1$, d.f. = 28, $P < 0.9$). All factors except PC7, characterized mainly by geological diversity, and PC9, which mainly reflects the distance to rivers, had significant effects on both exotic and native species richness (Fig. 2a), although PCs 8 and 9 turned out to be non-significantly associated with native plant richness when spatial

autocorrelation was accounted for (see Appendix S2). Most of these common factors had path coefficients of different signs, indicating that they had opposite effects on exotic and native plant richness. For example, while exotic plant richness primarily increased with drier climatic conditions (i.e. higher temperatures and/or lower precipitation; PC 1), native plant richness increased in colder and rainier areas. Likewise, short distances to primary roads and a high percentage of agricultural areas primarily favoured exotic plant richness, whereas an increased availability of natural habitats (e.g. forests) favoured native plant richness (PCs 8 and 5).

Nevertheless, two factors (PC2, reflecting human pressure, and PC 10, which includes landscape heterogeneity) had path

coefficients with the same sign, and hence could be regarded as common causes explaining the positive correlation between native and exotic plant richness. Species richness of both native and exotic plants increased with human density and with the degree of heterogeneity in land use. Yet these common causes only explain 17.2% of the correlation between exotic and native plant richness, and hence cannot completely account for the positive sign of the correlation. Not surprisingly, the direct effect of native richness on exotic richness remained significantly positive even when the common causal effect of these factors was taken into account in the model (Fig. 2a).

When the analysis was restricted to ruderal native plants, the path model again fitted well to the data ($\chi^2 = 0.1$, d.f. = 28, $P < 0.9$). Ruderal and exotic plant richness continued to be simultaneously affected by PCs 2 and 10 (Fig. 2b), which respectively describe human disturbance and landscape heterogeneity, but now the most important common cause was PC 1 (see Appendix S2 for GLS models accounting for spatial autocorrelation). This suggests that species richness of both native and exotic plants decreases in cold, wet, forest-dominated sites far from the main human settlements. Note that although the path coefficient between ruderal and exotic richness is similar to the native–exotic one, this path coefficient is a standardized regression coefficient and, therefore, indicates the number of standard deviations of change in exotic plant richness expected from a unit change in ruderal plant richness. Hence, both paths (ruderal–exotic and native–exotic) are not directly comparable because native plants (ranging from 200 to 1200 species per cell) are one order of magnitude higher than ruderal plants (from 10 to 200), reflecting the higher correlation of exotic with ruderal than with all natives or non-ruderal plants (unstandardized paths are: exotic–natives = 0.04, exotic–ruderal = 0.34 and exotic–non-ruderal = 0.03).

Interestingly, the fraction of the correlation between exotic and ruderal plant richness that was accounted for by common causal effects of the environmental factors increased substantially (from 17.2 to 58.3%) when compared with the model comparing exotic plant richness with all native plant richness. In contrast, common causes only accounted for 15.1% of the correlation between exotic and native plant richness when the latter were restricted to non-ruderal native plant richness (Fig. 2c, Fig. S2 and Appendix S1).

DISCUSSION

It has been proposed that the positive relationship between exotic and native species richness at broad spatial scales may result from adding several negative relationships across different environmental conditions (Shea & Chesson, 2002). We found that in Catalonia the proportion of exotic species relative to native species differed across environmentally homogeneous regions, being lower in forested mountain areas with high rainfall, low temperatures and little human pressure and higher in coastal areas with high population density. Yet within environmentally homogeneous areas, the slope of the relationship between native and exotic species richness always remained

positive, lending little support to the view that the relationship only arises from the addition of several negative correlations corresponding to different environmental conditions.

Nevertheless, our path analyses identified a set of common factors at the landscape scale that seem to favour both native and exotic richness. As anticipated, habitat heterogeneity was one of the primary factors (see also Davies *et al.*, 2005). In general, as the heterogeneity of the locality increased, so did the number of native and exotic species it contained. The proximity to main cities also correlated positively with both native and exotic richness, consistent with previous findings (Pino *et al.*, 2005; Vilà *et al.*, 2007), although exotic plants (but not native plants) appeared to be particularly diverse in agricultural landscapes and in areas close to primary roads. These results add to previous evidence that some environmental conditions favouring native species richness also favour exotic species richness (Gilbert & Lechowicz, 2005; Perelman *et al.*, 2007).

Despite the existence of common environmental factors, the relationship between native and exotic richness continued to be positive even after statistically controlling for all these factors. Likewise, Gilbert & Lechowicz (2005) and Perelman *et al.* (2007) found, in finer-scale surveys, that when covarying habitat factors were held constant with statistical techniques, exotic and native richness were still positively correlated across sites. In contrast, studies conducted in the USA at coarse scale revealed that the positive relationship disappears after taking into account latitude and anthropic variables (Rejmánek, 2003; Taylor & Irwin, 2004). It seems unlikely that our discrepancies with these previous works are caused by having missed any relevant extrinsic factor, because we used the same general factors that were used in these studies. In addition, the sampling units used in our study (cells of 10×10 km) were much smaller than those used in the previous studies, allowing a more precise estimation of climatic conditions, landscape heterogeneity and degree of anthropogenic disturbance. Finally, our analyses are less likely to have been biased as a result of richness–area relationships because, unlike previous studies, we used sampling units of similar size.

Why do environmental factors explain relatively little of the variation in the positive relationship between total native and exotic plants? One interesting finding is that among native plants, those that shared more common environmental factors with exotic species tended to be ruderal species associated with human disturbances, which represented a large fraction of native plant diversity in the study region. This observation highlights the importance of considering anthropic factors in resolving the invasion paradox. We believe that two anthropic processes may be particularly important. On the one hand, human activities may facilitate the expansion of plants – mainly exotic but also native (Pyšek, 2002) – by increasing propagule pressure (e.g. by increasing unintentional transport and release of seeds and vegetative propagules). Most studies reporting invasion resistance from richer plant communities are experimental and hence control for propagule pressure (Friedley *et al.*, 2007). However, observational studies reporting positive native–exotic relationships have uncertain histories of propagule pressure (Stohlgren *et al.*, 2006). If species-rich areas also receive a

higher propagule pressure, patterns of biotic resistance to establishment will be difficult to detect. The finding that species richness of both ruderal native and exotic plants increases in warm, low-elevation environments close to human settlements gives credence to this possibility. The obvious difficulties in accurately measuring propagule pressure in plants (Lockwood *et al.*, 2005) might have detracted from our ability to resolve the actual sign and strength of the natives–exotics relationships.

On the other hand, anthropic processes operating at small scales, notably the urbanization of wildlands, may alter competition regimes by a variety of factors, such as increasing extinction risk of native species, creating new niche opportunities for newcomers and generating environmental heterogeneity that may allow resource partitioning. All these factors may reduce biotic resistance and facilitate the entrance of exotic and native plants pre-adapted to such altered conditions (Callaway, 2007; Verdú & Valiente-Banuet, 2008; Altieri *et al.*, 2010). If so, we should not expect a negative relationship between the native–exotic species richness in such ecosystems, even when common causal factors are taken into account.

The role of competition in governing the establishment of exotic species in natural communities has also been called into question by other authors (Duncan *et al.*, 2003; Levine *et al.*, 2004; Gilbert & Lechowicz, 2005; Perelman *et al.*, 2007) based on a number of additional arguments. The first is that while closely related species compete more strongly than species belonging to distantly related taxa, exotic species are unlikely to encounter close relatives in the recipient community when they come from distant regions (Valiente-Banuet & Verdú, 2007). Second, although biotic resistance may reduce the establishment of individual exotic plants, ecological interactions rarely enable communities to resist invasion but instead constrain the abundance of exotic species once they have successfully established (reviewed in Levine *et al.*, 2004). Third, the biotic resistance of a community depends not only on the species richness, but also on the abundance of the species present and their function in the ecosystem (Tilman, 1997). Finally, once the first exotic plants have become established, this may lead to an invasion meltdown (Simberloff & Von Holle, 1999). All these arguments may contribute to explaining the lack of evidence for the biotic resistance hypothesis in previous regional comparisons of exotic and native plant richness (e.g. Perelman *et al.*, 2007).

The fundamental prediction of the biotic resistance hypothesis is that, all else being equal, communities with higher native richness should contain fewer exotic species than communities with fewer species (Elton, 1958). However, in the real world all else is never equal. Almost all documented positive patterns of native–exotic richness relationships have been reported in developed countries, where the human impact on both native and exotic flora is usually high. Our results confirm that the positive relationship between native and exotic plants is in part driven by common extrinsic factors that affect both native and exotic species. However, the results also highlight the great importance of anthropic factors, which may not only provide novel niche opportunities and increase propagule pressure, but may also alter competition regimes and hence facilitate the invasion of

those exotic and native plants that are able to live close to human settlements. Thus, the positive native–exotic richness relationship may not only emerge as a matter of spatial scale, but because, in human-made ecosystems, competition probably plays a less important role in organizing plant communities.

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REFERENCES

- Altieri, A.H., Van Wesenbeeck, B.K., Bertness, M.D. & Silliman, B.R. (2010) Facilitation cascade drives positive relationship between native biodiversity and invasion success. *Ecology*, **91**, 1269–1275.
- Arbuckle, J.L. (2006) *Amos* (version 7.0). SPSS, Chicago, IL.
- Bolòs, O., Vigo, J., Masalles, R.M. & Ninot, J.M. (2005) *Flora Manual dels Països Catalans*. Pòrtic, Barcelona.
- Braun-Blanquet, G. & Braun-Blanquet, J. (1931) Recherches phytogéographiques sur le Massif du Gross Glockner (Hohe Tauern). *Revue de Géographie Alpine*, **19**, 675–735.
- Byers, J.E. & Noonburg, E.G. (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology*, **84**, 1428–1433.
- Callaway, R.M. (2007) *Positive interactions and interdependence in plant communities*. Springer, Dordrecht, The Netherlands.
- Case, T.J. (1990) Invasion resistance arises in strongly interacting species-rich model competition communities. *Proceedings of the National Academy of Sciences USA*, **87**, 9610–9614.
- Crawley, M.J. (2002) *Statistical computing. An introduction to data analysis using S-plus*. John Wiley and Sons, Chichester, UK.
- Davies, K.E., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. & Rice, K.J. (2005) Spatial heterogeneity explains the scale dependence of the native–exotic diversity relationship. *Ecology*, **86**, 1602–1610.
- Duncan, R.P., Blackburn, T.M. & Sol, D. (2003) The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 71–98.
- Elton, C. (1958) *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Fargione, J.E. & Tilman, D. (2005) Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, **8**, 604–611.
- Font, X. & Ninot, J.M. (1995) A regional project for drawing up inventories of flora and vegetation in Catalonia (Spain). *Annali di Botanica*, **53**, 99–105.
- Fridley, J.D., Brown, R.L. & Bruno, J.F. (2004) Null models of exotic invasion and scale-dependent patterns of native and exotic species richness. *Ecology*, **85**, 3215–3222.

- Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, **88**, 3–17.
- Gilbert, B. & Lechowicz, M.J. (2005) Invasibility and abiotic gradients: the positive correlation between native and exotic plant diversity. *Ecology*, **86**, 1848–1855.
- Grace, J.B. (2006) *Structural equation modeling and natural systems*. Cambridge University Press, Cambridge.
- Herben, T., Mandák, B., Bímová, K. & Münzbergová, Z. (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology*, **85**, 3223–3233.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.
- Knops, J.M.H., Tilman, D., Haddad, N.M., Naeem, S., Mitchell, C.E., Haarstad, J., Ritchie, M.E., Howe, K.M., Reich, P.B., Siemann, E. & Groth, J. (1999) Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecological Letters*, **2**, 286–293.
- Kumar, S., Stohlgren, T.J. & Chong, G.W. (2006) Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*, **87**, 3186–3199.
- Levine, J.M. (2000) Species diversity and biological invasions: relating local processes to community pattern. *Science*, **288**, 761–763.
- Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.
- Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.
- Li, C.C. (1975) *Path analysis: a primer*. Boxwood, Pacific Grove, CA.
- Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- McKinney, M.L. (2001) Effects of human population, area and time on non-native plant and fish diversity in the United States. *Biological Conservation*, **100**, 243–252.
- MMAMB (Mancomunitat de Municipis de l' area Metropolitana de Barcelona) (1995) *Metropolitan dynamics in the Barcelona area and region*. AMB, Barcelona.
- Naeem, S., Knops, J.M.H., Tilman, D., Howe, K.M., Kennedy, T. & Gale, S. (2000) Plant diversity increases resistance to invasion in the absence of covarying extrinsic factors. *Oikos*, **91**, 97–108.
- Ninyerola, M., Pons, X. & Roure, J.M. (2000) A methodological approach of climatological modeling of air temperature and precipitation through GIS techniques. *International Journal of Climatology*, **20**, 1823–1841.
- Pausas, J.G., Carreras, J., Ferré, A. & Font, X. (2003) Coarse-scale plant species richness in relation to environmental heterogeneity. *Journal of Vegetation Science*, **14**, 661–668.
- Perelman, S.B., Chaneton, E.J., Batista, W.B., Burkart, S.E. & León, R.J.C. (2007) Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *Journal of Ecology*, **95**, 662–673.
- 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.
- Planty-Tabacchi, A., Tabacchi, E., Naiman, R., Deferrari, C. & Decamps, H. (1996) Invasibility of species-rich communities in riparian zones. *Conservation Biology*, **10**, 598–607.
- Pons, X. (2002) *MiraMon*. Sistema d'Informació Geogràfica i software de Teledetecció, Centre de Recerca Ecològica i Aplicacions Forestals, CREAF, Bellaterra. <http://www.creaf.uab.cat/miramon/index.htm>.
- Pyšek, P. (2002) Alien and native species in Central European urban floras: a quantitative comparison. *Journal of Biogeography*, **25**, 155–163.
- Pyšek, P., Richardson, D.M., Rejmánek, M., Webster, G.L., Williamson, M. & Kirschner, J. (2004) Alien plants in checklists and floras: towards better communication between taxonomists and ecologists. *Taxon*, **53**, 131–143.
- R Development Core Team (2010) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org>.
- Rejmánek, M. (2003) The rich get richer – responses. *Frontiers in Ecology and the Environment*, **1**, 122–123.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D. & West, J.C. (2000) Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, **6**, 93–107.
- Rivas-Martínez, S., Fernández-González, F., Loidi, J., Lousa, M. & Penas, A. (2001) Syntaxonomical checklist of vascular plant communities of Spain and Portugal to association level. *Itinera Geobotanica*, **14**, 5–341.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.
- Stachowicz, J.J., Whitlatch, R.B. & Osman, R.W. (1999) Species diversity and invasion resistance in a marine ecosystem. *Science*, **286**, 1577–1579.
- Stachowicz, J.J., Fried, H., Osman, R.W. & Whitlatch, R.B. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology*, **83**, 2575–2590.
- Stohlgren, T.J., Barnett, D.T. & Kartesz, J.T. (2003) The rich get richer: patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment*, **1**, 11–14.
- Stohlgren, T.J., Jarnevich, C., Chong, G.W. & Evangelista, P.H. (2006) Scale and plant invasions: a theory of biotic acceptance. *Preslia*, **78**, 405–426.
- Taylor, B.W. & Irwin, R.E. (2004) Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of Sciences USA*, **101**, 17725–17730.

- Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.
- Valiente-Banuet, A. & Verdú, M. (2007) Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters*, **10**, 1029–1036.
- Verdú, M. & Valiente-Banuet, A. (2008) The nested assembly of plant facilitation networks prevents species extinctions. *The American Naturalist*, **172**, 751–760.
- 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., Pino, J., Montero, A. & Font, X. (2010) Are island plant communities more invaded than their mainland counterparts? *Journal of Vegetation Science*, **21**, 438–446.

SUPPORTING INFORMATION

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

Appendix S1 Analysis including only cells with more than 459 species.

Appendix S2 Autocorrelation in individual SEM Paths.

Figures S1 Native-Exotic richness relationship for each environmental group for Appendix S1 analysis.

Figures S2 Structural equation model for Appendix S1 analysis.

Table S1 *k*-means clustering medoids.

Table S2 Scores of the PCA for Appendix S1 analysis.

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BIOSKETCH

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