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Regional assessment of plant invasions across different habitat types

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Abstract

Questions: 1. Which habitats have the highest degree of invasion? 2. Do native species-rich communities have also a high degree of invasion? 3. Do the patterns of association between native and alien species richness vary between habitats.
Location: Catalonia region (NE Spain).
Methods: We conducted a large regional analysis of 15 655 phytosociological relevés to detect differences in the degree of invasion between European Nature Information System (EUNIS) habitats representative of temperate and Mediterranean European areas.
Results: Alien species were present in less than 17 % of the relevés and represented less than 2% of the total number of species per habitat. The EUNIS habitats with the highest alien species richness were arable land and gardens followed by anthropogenic forb-rich habitats, riverine and lakeshore scrubs, southern riparian galleries and thickets and trampled areas. In contrast, the following habitats had never any alien species: surface running waters, raised and blanket bogs, valley mires, poor fens and transition mires, base-rich fens, alpine and sub-alpine grasslands, sub-alpine moist or wet tall-herb and fern habitats, alpine and sub-alpine scrub habitats and spiny Mediterranean heaths. There was a unimodal relationship between the mean native and mean alien species richness per EUNIS habitat with a high number of aliens in habitats with intermediate number of native species and a low number of aliens at both extremes of the native species gradient. Within EUNIS habitats, the relationship was positive, negative or non-significant depending on the habitat type without any clear pattern related to the number of native species. Alien species richness was not related to plot size, neither between habitats nor within habitats.
Conclusions: The analysis emphasised that the habitats with a higher degree of invasion were the most disturbed ones and that in general habitats rich in native species did not harbour less invaders than habitats poor in native species.

Keywords: Alien plant; EUNIS; Mediterranean community; Relevé; Species richness; Vegetation type.

Abbreviations: EUNIS = European Nature Information System; UTM = Universal Transverse Mercator.

Introduction

Biological invasions are threatening the conservation of native species and habitats worldwide. However, not all native species are threatened to the same degree by invaders and not all habitats are equally invaded (Lonsdale 1999). Habitat differences in the degree of invasion depend on alien species traits compared to native species, environmental and biotic characteristics of the recipient habitat and the propagule pressure with which alien species are entering into the recipient habitat (Rejmánek et al. 2005).

Several studies have compared differences in the diversity of alien and native species within habitats at the landscape scale (Levine et al. 2003) and in general have found that habitats with a high number of native species also harbour a high number of alien species (Stohlgren et al. 1999; Stohlgren & Chong 2002; Brown & Peet 2003). This positive relationship can be explained by the similarity of both groups of species in the abundance of propagules entering a community (Levine 2000) or by both groups of species occurring in resource rich and moderately disturbed sites (Davis et al. 2000). Most of the patterns have been observed in surveys conducted after *a priori* verification of highly invaded habitats, e.g. riparian habitats (DeFerrari & Naiman 1994; Planty-Tabacchi et al. 1996; Stohlgren & Chong 2002). Consequently, they are probably biased towards immigration driven systems characterized by processes leading to resource release and entrance of new species through intermediate intensity disturbances (Brown & Peet 2003). Moreover, most surveys, even if they have been conducted at a large scale, are performed within habitat types (e.g. Gilbert & Lechowicz 2005), not verifying if there are differences in the degree of invasion between habitats (but see Stohlgren et al. 1999). It is possible that in some habitats, especially those with low diversity, alien and native species respond differently to environmental and disturbance parameters (McIntyre & Lavorel 1994).

In this study we take advantage of the habitat classification of the European Nature Information System

(EUNIS) developed and managed by the European Topic Centre for Nature Protection and Biodiversity (ETC/NPB in Paris), the European Environment Agency (EEA) and the European Environmental Information Observation Network (EIONET). This habitat type classification is a comprehensive, pan-European system that covers all types of habitats from terrestrial to aquatic and from natural to artificial; URL: http://eunis.eea.eu.int/index.jsp . Therefore, we used EUNIS classification to compare the relationship between alien and native species richness within habitats and between habitats. Our main questions were: 1. Which habitats have the highest degree of invasion? 2. Do native species-rich communities have also a high degree of invasion? 3. Do the patterns of association between native and alien species richness vary between habitats? Our main hypothesis was that habitats and plots with a large number of native species also have a large number of alien species, especially for highly disturbed habitats. To the best of our knowledge this is one of the largest regional analyses of native-alien richness association between and within habitats. Furthermore, it adds to the knowledge of the degree of plant invasion in Spain (Sanz-Elorza et al. 2004).

Material and Methods

Study area

Catalonia (ca. 32 000 km^2) is situated at 40°30' N - 42°40' N and 0°15' E - 3°15' E. This region was chosen because of its contrasting topography, climate, dominant vegetation and land use; altitudes range from 0 to 3350 m a.s.l. It receives Mediterranean, Atlantic and Saharan influences. Catalonia forms a boundary between two phytographic regions – the Eurosiberian and the Mediterranean. Rainfall decreases and mean temperature increases southwards. A continental gradient can also be observed from the coast, with moist temperate climates, to inland, with contrasting dry conditions (Ninyerola et al. 2000).

The landscape structure of Catalonia reflects the typical secular interaction between man and climate in western Europe and the Mediterranean region. Forest currently occupies 40% of the region (Burriel et al. 2001). Broad-leaved forests (evergreen *Quercus* spp. in Mediterranean areas, deciduous *Quercus* spp. and *Fagus sylvatica* in sub-Mediterranean and Eurosiberian areas) have been mostly substituted by coniferous forests (*Pinus halepensis* and *P. pinea* in Mediterranean areas and *P. nigra* and *P. sylvestris* in sub-Mediterranean and Eurosiberian areas). In recent decades, abandonment of marginal agricultural areas is leading to a progressive afforestation challenged by an increasing wildfire frequency. In the favourable plains and plateaux for human settlement progressive crop intensification and urbanization have occurred. The central coast of Catalonia is one of the most populated and industrialised areas along the northern Mediterranean coast (Anon. 1995).

Species database

The high phytogeographic diversity of Catalonia results in a rich flora with more than 3200 species (Bolòs et al. 1993). Due to a long tradition in botany many floristic records have accumulated, available in both published work (more than 500 references from journals, books, dissertations and local atlases) and unpublished information (mainly Ph.D. and M.Sc. theses). The FLORACAT project (Font & Ninot 1995) has been devoted to the gathering, organisation and online exploitation of these floristic data, with the agreement of the Global Biodiversity Information Facility (GBIF) effort (Edwards et al. 2000), URL: http://biodiver. bio.ub.es/biocat/homepage.html and http://www. gencat.net/mediamb/pn/e-bdbiodiversitat.html

Presently, FLORACAT accounts for ca. 1 200 000 floristic records and 17 000 phytosociological relevés organised following the 10 km UTM grid. From the total of FLORACAT relevés, we selected 15 655 relevés with phytosociological assignment. They were used to calculate the number of alien, native and total species, and the percentage of alien species per relevé. A species was considered an alien if it originated in another region outside Spain and when it was introduced accidentally or deliberately by man. Only neophytes (i.e. introduced after the 15th century) were considered. Each relevé was assigned to a first or second hierarchical level of EUNIS habitat classification (Table 1) through the phytosociological alliance it belongs to. The correspondence among alliances and EUNIS classes was established by expert knowledge and it is summarized in Table 2. Publication

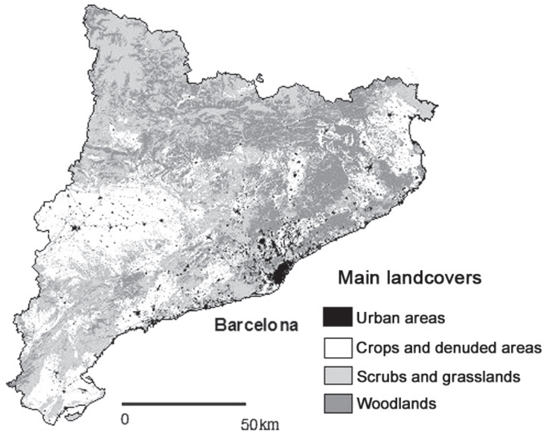

Fig. 1. Study area with main land cover types (Anon.1993).

Table 1. *F*-values and Correlation coefficient (r^2) and of the multiple regression number of alien species = number of native species + plot area for EUNIS habitats represented in the FLORACAT relevés of Catalonia (NE Spain). *P*-values for the number of native species are variable once the effect of plot area has been accounted for. *N* = sample size for each habitat; No aliens = no occurrence of alien species in the habitat; + = positive correlation, - = negative, NS = non-significant.

EUNIS habitat type	*F*	*P*	r^2	*N*	
B - Coastal habitats					
B1 - Coastal dune and sand habitats	15.39	0.01	0.11	254	+
B3 - Rock cliffs, ledges and shores, including the supralittoral	20.99	0.04	0.21	152	+
C - Inland surface water habitats					
C1 - Surface standing waters	6.86	0.0007	0.16	61	NS
C2 - Surface running waters			No aliens	126	
C3 - Littoral zone of inland surface waterbodies	0.91	0.19	0.10	224	+
D - Mire, bog and fen habitats					
D1 - Raised and blanket bogs			No aliens	153	
D2 - Valley mires, poor fens and transition mires			No aliens	229	
D4 - Base-rich fens			No aliens	46	
D6 - Inland saline and brackish marshes and reedbeds	7.56	0.0002	0.10	116	+
E - Grassland and tall-forb habitats					
E1 - Dry grasslands	2.11	0.05	0.001	2205	NS
E2 - Mesic grasslands	2.18	0.04	0.007	335	-
E3 - Seasonally wet and wet grasslands	41.30	<0.0001	0.17	407	-
E4 - Alpine and sub-alpine grasslands			No aliens	1344	
E5 - Woodland fringes and clearings and tall-forb habitats					
E5.2 - Thermophile woodland fringes	5.21	0.87	0.04	194	NS
E5.5 - Sub-alpine moist or wet tall-herb and fern habitats			No aliens	104	
E5.6 - Anthropogenic forb-rich habitats	34.21	<0.0001	0.07	860	-
E6 - Inland saline grass and herb-dominated habitats	4.96	0.002	0.01	506	+
F - Heathland, scrub and tundra habitats					
F2 - Arctic, alpine and sub-alpine scrub habitats			No aliens	369	
F3 - Temperate and mediterraneo-montane scrub habitats	3.22	0.03	0.01	386	-
F4 - Temperate shrub heathland	0.8	0.21	0.00	100	NS
F5 - Maquis, matorral and thermo-Mediterranean bushes	0.62	0.55	0.00	348	NS
F6 - Garrigue	3.21	0.88	0.01	651	NS
F7 - Spiny Mediterranean heaths (phrygana, hedgehog-heaths and related coastal cliff vegetation)			No aliens	141	
F9 - Riverine and fen scrubs					
F9.1 - Riverine and lakeshore [*Salix*] scrub	1.31	0.66	0.01	63	NS
F9.3 - Southern riparian galleries and thickets	1.04	0.46	0.002	48	NS
G - Woodland and forest habitats and other wooded land					
G1 - Broad-leaved deciduous woodland	8.1	0.0002	0.01	1091	+
G2 - Broad-leaved evergreen woodland	6.7	0.003	0.02	688	+
G3 - Coniferous woodland	1.32	0.24	0.00	176	NS
H - Inland unvegetated or sparsely vegetated habitats					
H2 - Screes	2.34	0.43	0.01	293	NS
H3 - Inland cliffs, rock pavements and outcrops	4.21	0.004	0.01	548	-
H5.6 - Trampled areas	7.83	0.001	0.04	313	-
I - Regularly or recently cultivated agricultural, horticultural and domestic habitats					
I1 - Arable land and market gardens	18.15	<0.0001	0.08	397	-

date of relevés considered in this study ranged from 1926 to 2003 with 1993 as the mode. There was no correlation between date of publication and number of alien species ($r^2 = 3.5 \times 10^{-4}$).

There was a large variation in plot size both between and within habitats; Plot size accounted for species composition and diagnostic species, and were representative of differences in size and abundance of species (Fig. 2). There were significant differences in mean plot size between first order EUNIS habitat classes ($F_{7,\ 12254} = 680.59$, $p < 0.0001$); inland surface water habitats (C) had the smallest and woodland habitats (G) the largest plots. However, mean plot sizes within habitats agreed with European standards (Chytrý & Otýpková 2003).

Data analysis

We tested if the number of alien and native species was significantly different between habitats by a General Linear/Non-linear Model (Anon. 1999) with a logarithmic link function and a Poisson error distribution. Due to the large number of *post-hoc* multiple tests, pair-wise differences between habitats were corrected with the Bonferroni test (Cabin & Mitchell 2000).

Native and alien species richness relationships were investigated at two scales: among habitats and within habitats. In the analysis among habitats the sample units were the mean number of species per plot for each habitat. In contrast, in the analysis within habitats each plot was a sample unit.

Table 2. Correspondence of the EUNIS habitats with the syntaxonomic alliances originally identifying the relevés. Syntaxonomical nomenclature follows Bolòs & Vigo (1984) and Rivas-Martínez et al. (2001). See Table 1 for description of habitat types.

EUNIS	Alliance	EUNIS	Alliance	EUNIS	Alliance
B1	*Alkanno-Malcolmion parviflorae*	E4	*Arabidion coeruleae*	F6	*Gypsophilion hispanicae*
	Ammophilion arundinaceae		*Elymion medioeuropaeum*		*Lepidion subulati*
	Crucianellion maritimae		*Festucion eskiae*		*Rosmarino-Ericion*
	Saginion maritimae		*Festucion gautieri*		*Thymo longiflori-Siderition leucanthae*
B3	*Crithmo-Limonion*		*Festucion scopariae*		*Thymo-Teucrion verticillati*
	Medicagini-Lavaterion arboreae		*Festucion supinae*	F7	*Genistion lobelii*
C1	*Isoetion*		*Laserpitio-Ranunculion thorae*	F9.1	*Salicion pentandrae*
	Lemnion minoris		*Nardion strictae*		*Salicion triandro-fragilis*
	Littorellion uniflorae		*Primulion intricatae*	F9.3	*Rubo ulmifolii-Nerion oleandri*
	Potamion pectinatae		*Salicion herbaceae*		*Tamaricion africanae*
	Ruppion maritimae	E5.2	*Aegopodion podagrariae*	G1	*Alno-Padion*
C2	*Callitricho-Batrachion*		*Atropion belladonnae*		*Alno-Ulmion*
	Cardamino-Montion		*Bromo ramosi-Eupatorion cannabini*		*Fagion sylvaticae*
	Cratoneurion commutati		*Epilobion angustifolii*		*Fraxino-Carpinion*
	Potamogetonion eurosibiricum		*Geranion sanguinei*		*Populion albae*
C3	*Glycerio-Sparganion*		*Trifolion medii*		*Quercion pubescenti-petraeae*
	Magnocaricion elatae	E5.5	*Adenostylion alliariae*		*Quercion robori-petraeae*
	Phragmition australis		*Arction lappae*		*Tilio-Acerion*
D1	*Oxycocco-Ericion tetralicis*	E5.6	*Bidention tripartitae*	G2	*Quercion ilicis*
D2	*Caricion nigrae*		*Bromo-Oryzopsion miliaceae*	G3	*Abieti-Piceion*
D4	*Caricion davallianae*		*Carrichtero-Amberboion*		*Deschampsio-Pinion*
D6	*Juncion maritimi*		*Chenopodion muralis*		*Pino-Juniperion sabinae*
E1	*Aegilopion*		*Convolvulion sepium*	H2	*Androsacion alpinae*
	Agropyro-Lygeion		*Dauco-Melilotion*		*Andryalo-Glaucion*
	Alysso-Sedion		*Euphorbion peplis*		*Calamagrostion arundinaceae*
	Aphyllanthion		*Galio-Alliarion*		*Cystopteridion*
	Brachypodion phoenicoidis		*Glaucio-Cakilion*		*Galeopsion pyrenaicae*
	Corynephorion canescentis		*Hordeion leporini*		*Glaucion flavi*
	Helianthemion guttati		*Onopordion acanthii*		*Iberidion spathulatae*
	Mesobromion erecti		*Onopordion arabici*		*Pimpinello-Gouffeion*
	Ononidion striatae		*Rumicion alpini*		*Scrophularion sciaphilae*
	Phlomidio-Brachypodion retusi		*Salsolo-Peganion*		*Senecion leucophylli*
	Saturejo-Hyparrhenion hirtae		*Silybo-Urticion*		*Stipion calamagrostis*
	Sedo-Scleranthion		*Sisymbrion officinalis*	H3	*Adiantion capilli-veneris*
	Stipion capensis	E6	*Arthrocnemion fruticosi*		*Androsacion vandellii*
	Taeniathero-Aegilopion geniculatae		*Limoniastrion monopetali*		*Anomodontion europaeum*
	Thero-Airion		*Limonion galloprovincialis*		*Antirrhinion asarinae*
	Thero-Brachypodion		*Plantaginion crassifoliae*		*Asplenion petrarchae*
	Tuberarion guttatae		*Suaedion braun-blanquetii*		*Bartramio-Polypodion australis*
	Xerobromion erecti		*Suaedion brevifoliae*		*Homalothecio-Polypodion serrulati*
E2	*Agrostion stoloniferae*		*Thero-Salicornion*		*Hypno-Polypodion vulgaris*
	Arrhenatherion elatioris		*Thero-Suaedion*		*Parietario-Centranthion rubri*
	Cynosurion cristati	F2	*Juniperion nanae*		*Phagnalo-Cheilanthion fragrantis*
	Deschampsion mediae		*Loiseleurio-Vaccinion*		*Saxifragion mediae*
	Violion cornutae		*Rhododendro-Vaccinion*	H5.6	*Agropyro-Rumicion crispi*
E3	*Calthion palustris*	*F3*	*Berberidion vulgaris*		*Echio-Galactition*
	Imperato-Erianthion		*Genistion purgantis*		*Polygonion avicularis*
	Isoetion		*Pruno-Rubion ulmifolii*		*Trifolio-Cynodontion*
	Juncion acutiflori		*Rubion subatlanticum*	I1	*Caucalidion platycarpae*
	Lythrion tribracteati		*Sambuco-Salicion capreae*		*Diplotaxion erucoidis*
	Molinio-Holoschoenion vulgaris		*Sarothamnion scoparii*		*Panico-Setarion*
	Molinion coeruleae		*Ulici-Ericion ciliaris*		*Polygono-Chenopodion polyspermi*
	Nanocyperion flavescentis	F4	*Calluno-Genistion*		*Scleranthion annui*
	Paspalo-Polypogonion semiverticillati	F5	*Cistion laurifolii*		*Secalion mediterraneum*
			Cistion mediomediterraneum		
			Oleo-Ceratonion		

Because in general it has been observed and modelled that the association between native and alien species richness is scale-dependent with negative relationships in small plots and positive relationships in large plots (Shea & Chesson 2002; Fridley et al. 2004; Sax & Gaines 2003) the correlation between alien and native species was tested once the effect of area has been accounted for by a multiple regression analysis of the form: number of alien species = area + number of native species. In the analysis among habitats we also compared if the habitats with positive, negative or non-significant relationships differed in plot size by a Kruskall-Wallis test (Herben et al. 2004).

Results

The number of alien species per relevé was 0.29 ± 0.006 (mean ± SE) ranging from 0 to 12 species per plot and representing 1.95 ± 0.05 % of the total number of species per relevé. The occurrence of alien species (i.e. percentage of plots with aliens) within a certain habitat type was also low (16.79 ± 3.24 %). Among all invaded habitats, there was a positive relationship between the degree of occurrence in a habitat and mean alien richness in this habitat (number of alien species = 0.02×, occurrence –0.089, $r^2 = 0.869$) but not with mean native species richness (Number of native species = – 0.72×, occurrence +19.31, $r^2 = 0.035$).

Of the inventoried habitats, the following never had aliens: surface running waters (C2), raised and blanket bogs (D1), valley mires, poor fens and transition mires (D2), base-rich fens (D4), alpine and sub-alpine grasslands (E4), sub-alpine moist or wet tall-herb and fern habitats (E5.5), alpine and sub-alpine scrub habitats (F2) and spiny Mediterranean heaths (F7) (Fig. 3). We are confident that this lack of aliens was not related to the sampling effort because the number of relevés in habitats without aliens was not under-represented compared to habitats with aliens (mean ± SE, 314 ± 151.08 and 547.62 ± 116.07, respectively, *t*-test = 1.06, $p = 0.297$).

Of the 24 EUNIS habitat types that were invaded there were significant differences in alien species richness among habitats ($\chi^2 = 8959.09$, $p < 0.0001$). The habitats with the highest alien richness were arable land and gardens (I1) followed by anthropogenic forb-rich habitats (E5.6), riverine and lakeshore scrubs (F9.1), southern riparian galleries and thickets (F9.3) and trampled areas (H5.6) (Fig. 3). Differences among habitats in the percentage of alien species followed the same pattern (Fig. 4).

In contrast, the number of native species per relevé was 20.80 ± 0.09 (mean ± SE) ranging from 1 to 102 species per plot. As expected, there were also significant differences in native species richness among habitats ($\chi^2 = 5886.63$, $p < 0.0001$). The habitats with the highest native richness were different from the ones with highest alien richness: dry and mesic grasslands (E1 and E2, respectively), broad-leaved deciduous woodlands (G1), garrigues (F6), and coniferous forests (G3) (Fig. 3). The habitats with the lowest number of native species were inland surface water habitats (C1, C2 and C3), inland saline and brackish marshes and reedbeds (D6) and inland saline grass and herb dominated habitats (E6) (Fig. 3).

There was not a significant linear relationship between mean native and mean alien species richness per habitat type even when we included plot area in the analysis ($F = 0.339$, $p = 0.715$). Plots without alien species were not more native species-rich than plots with alien species (mean ± SE, 20.87 ± 0.09 and 20.47 ± 0.22 respectively, *t*-test = 1.76, $p = 0.08$). Similarly, habitats which were never invaded do not harbour more native species than habitats where invasions occur (mean ± SE, 17.84 ± 1.7 and 17.71 ± 1.4 respectively, *t*-test = 0.052, $p = 0.96$). The same lack of association was found when plots or habitats without aliens were excluded from the analysis. The relationship between mean native and alien species richness per habitat type appears to be unimodal (hump-

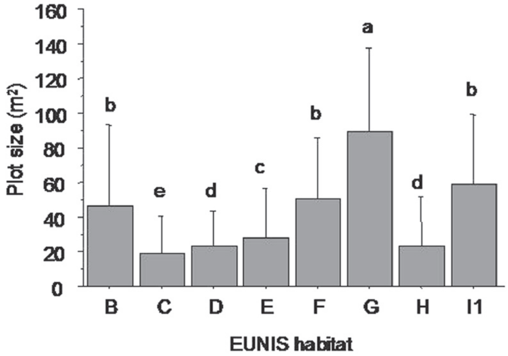

Fig. 2. Plot sizes (mean + SD) in relevés grouped according to main EUNIS habitats in Catalonia. See Table 1 for EUNIS type classification. Different letters above columns indicate significant differences among habitats according to pair-wise Bonferroni tests.

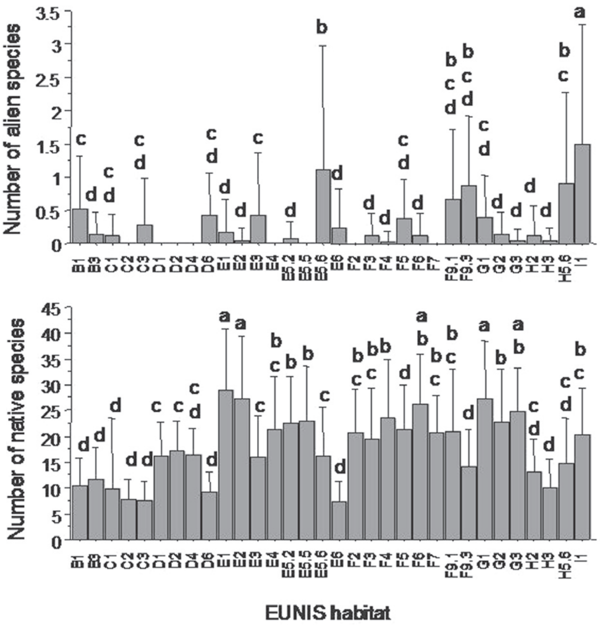

Fig. 3. Native and alien species richness (mean + SD) for different EUNIS habitats in Catalonia. See Table 1 for EUNIS type classification. Different letters above columns indicate significant differences among habitats according to pair-wise Bonferroni tests.

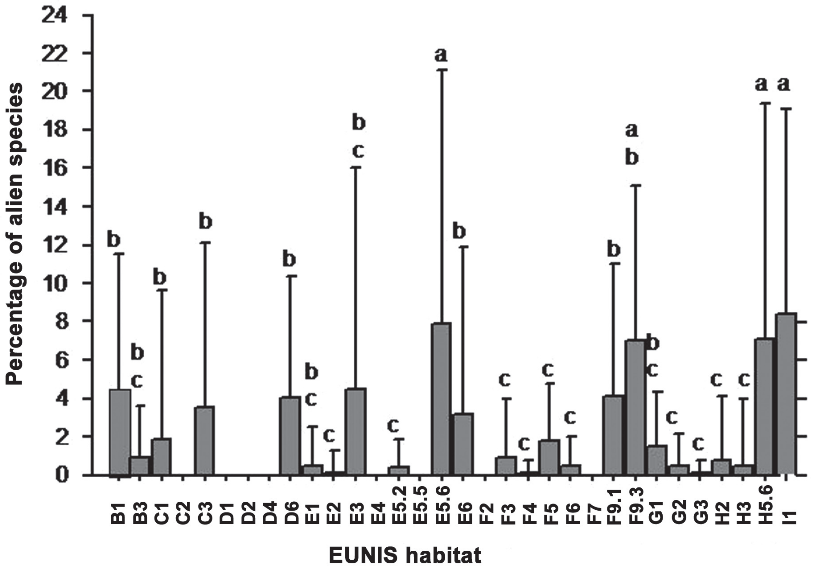

Fig. 4. Percentage of alien species per plot (mean + SD) for different EUNIS habitats in Catalonia. See Table 1 for EUNIS type classification. Different letters above columns indicate significant differences among habitats according to pair-wise Bonferroni tests.

shaped), with the highest number of alien species at intermediate values of native species richness and the lowest number of alien species at both extremes of low and high native species richness (Fig. 5).

For the 24 invaded EUNIS habitat types we found a positive association between native and alien species in seven types, a negative association in seven and a non-significant relationship in ten types (Table 1). There were non-significant differences in mean plot size between those habitats with positive, negative and non-significant alien-native relationships (Kruskall-Wallis, $H = 3.16$, $p = 0.206$).

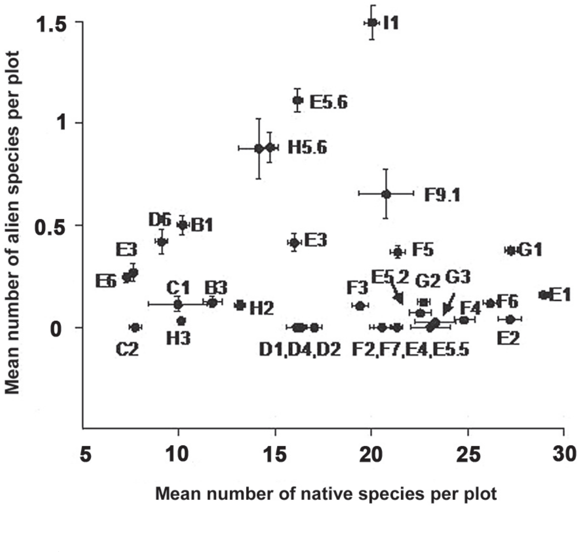

Fig. 5. Relationship between mean (± SE) number of native and mean (± SE) alien species for EUNIS habitats in Catalonia. See Table 1 for EUNIS type classification.

Discussion

The mean number of alien species was low (representing less than 2% per relevé) matching results for similar phytosociological database analysis (Rejmánek et al. 2005; Chytrý et al. 2005). For Catalonia, alien richness analysis conducted at the scale of UTM grid squares of floristic mapping has found larger percentages (Pino et al. 2005). Similarly, local field surveys conducted in several regions of Spain have found percentages of alien species higher than 10% probably because field surveys were deliberately biased towards highly invaded areas such as riverine (Sobrino et al. 2002) or coastal habitats (Campos et al. 2004). We are confident that this low value of alien representation in relevés is not due to under-representation of relevés with high number of aliens because in Catalonia there is a strong tradition of vegetation research in anthropogenic habitats (Masalles et al. 1997; Casasayas 1990). There is not a trend towards low sampling of relevés with few aliens. In fact, there is not a significant relationship between the number of relevés per habitat type and number of alien species per relevé ($r^2 = 0.002$, $p = 0.808$). Furthermore, the analysed database is extensive enough (15 655 phytosociological relevés across a 32000-km^2 area) to be certain that it is representative of all vegetation types of the region. As in other European phytosociological surveys, sampling was conducted in sites where there is a high probability of including presumed diagnostic species (Chytrý 2001).

The total lack of alien species in certain habitats such as in sub-alpine and alpine habitats mirror observation analysis in which there is a decrease of alien species richness with altitude and low temperatures (DeFerrari & Naiman 1994; Pyšek et al. 2002; Pino et al. 2005). This negative correlation does not necessarily imply a causal relationship between temperature and alien species richness, or with components of invasibility (i.e. community susceptibility to invasion) at high elevations but could also be related to lower propagule pressure in such habitats due to remoteness and low human activities (Pyšek et al. 2002). In contrast, the habitats with the highest frequency and number of alien species are anthropogenic habitats such as agricultural, ruderal and trampled areas together with riparian habitats, all of them being frequently disturbed areas (DeFerrari & Naiman 1994; Planty-Tabacchi et al. 1996) with usually a high propagule pressure due to their closeness to urban areas and communication networks.

Contrary to expected, we did not find a positive association between native and alien species richness between EUNIS habitats. The relationship appears to be unimodal, indicating a high number of aliens in habitats with intermediate number of native species and low number of aliens at both extremes of the native species gradient. The relationship might be better viewed as an area below an upper boundary of an envelope filled with data points than a line of fitted values. This type of association mirrors observational patterns of plant species diversity-productivity relationships when data from different habitats along a productivity gradient and a broad range of variation in species richness are analysed (Mittelbach et al. 2001). In fact, our analysis encompasses the whole range of local variation in alien and native species richness across habitats within Catalonia.

Within EUNIS habitats, the native-alien species richness relationship was positive, negative or non-significant, independent of plot size. This result is consistent with studies conducted in other regions which have also found that the relationship between native and alien species depends on the vegetation type (Planty-Tabacchi et al. 1996; Stohlgren et al. 1999; Brown & Peet 2003; Cully et al. 2003); emphasising that hot spots of native plant diversity are not immune to alien species invasion (Stohlgren et al. 1999; MacDougall & Turkington 2005). Furthermore, correlation values, even if significant, were very low indicating that at the local scale alien species richness can not be predicted by native species richness (MacDougall et al. 2006). Habitats with low alien species richness could be independent of native species richness but might reflect environmental constraints as well as dispersal limitations (MacDougall & Turkington 2005). Observations are not tests of causality. The mechanisms underlying the relationship between native and alien species richness across and within habitats could only be elucidated with large-scale, long-term experimental manipulation of plant species richness and environmental limiting factors.

Conclusions

By analysing thousands of phytosociological relevés expanding a broad range of habitats, we found the percentage of alien species to be low indicating that at the local scale, and when floristic surveys are not biased towards sampling the most invaded habitats, aliens are not very common, compared to values found at the regional scale, where the percentage of aliens comprise a large amount of rare aliens increasing the total diversity of the flora (Sax & Gaines 2003).

As previously stated, the habitats with a higher degree of invasion were the most disturbed (e.g. riparian) and anthropogenic (e.g. agricultural, trampled). Contrary to our expectations, these habitats were not the most native species rich. In fact, patterns of association between native and alien species richness were highly idiosyncratic within habitats emphasising that native species richness is not a good indicator of the degree of invasion, and that alien species richness is probably more dependent on environmental and invasion event factors (e.g. propagule pressure, residence time) than on biotic factors.

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