BIODIVERSITY RESEARCH

European map of alien plant invasions based on the quantitative assessment across habitats

Milan Chytrý[1]*, Petr Pyšek[2,3], Jan Wild[2], Joan Pino[4], Lindsay C. Maskell[5] and Montserrat Vilà[6]

[1]*Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czech Republic,* [2]*Institute of Botany, Academy of Sciences of the Czech Republic, CZ-25243 Průhonice, Czech Republic,* [3]*Department of Ecology, Faculty of Science, Charles University, Viničná 7, CZ-12801 Praha, Czech Republic,* [4]*Center for Ecological Research and Forestry Applications (CREAF) and Unit of Ecology, Department of Animal and Plant Biology and Ecology, Autonomous University of Barcelona, E-08193 Bellaterra, Spain,* [5]*Centre for Ecology and Hydrology, Lancaster Environment Centre, Library Avenue, Bailrigg LA1 4AP, UK,* [6]*Biological Station Doñana (EBD-CSIC), Avenida María Luisa s/n, Pabellón del Perú, E-41013 Sevilla, Spain*

*Correspondence: Milan Chytrý, Department of Botany and Zoology, Masaryk University, Kotlářská 2, CZ-61137 Brno, Czech Republic.
E-mail: chytry@sci.muni.cz

ABSTRACT

Aim Recent studies using vegetation plots have demonstrated that habitat type is a good predictor of the level of plant invasion, expressed as the proportion of alien to all species. At local scale, habitat types explain the level of invasion much better than alien propagule pressure. Moreover, it has been shown that patterns of habitat invasion are consistent among European regions with contrasting climates, biogeography, history and socioeconomic background. Here we use these findings as a basis for mapping the level of plant invasion in Europe.

Location European Union and some adjacent countries.

Methods We used 52,480 vegetation plots from Catalonia (NE Spain), Czech Republic and Great Britain to quantify the levels of invasion by neophytes (alien plant species introduced after AD 1500) in 33 habitat types. Then we estimated the proportion of each of these habitat types in CORINE land-cover classes and calculated the level of invasion for each class. We projected the levels of invasion on the CORINE land-cover map of Europe, extrapolating Catalonian data to the Mediterranean bioregion, Czech data to the Continental bioregion, British data to the British Isles and combined Czech–British data to the Atlantic and Boreal bioregions.

Results The highest levels of invasion were predicted for agricultural, urban and industrial land-cover classes, low levels for natural and semi-natural grasslands and most woodlands, and the lowest levels for sclerophyllous vegetation, heathlands and peatlands. The resulting map of the level of invasion reflected the distribution of these land-cover classes across Europe.

Main conclusions High level of invasion is predicted in lowland areas of the temperate zone of western and central Europe and low level in the boreal zone and mountain regions across the continent. Low level of invasion is also predicted in the Mediterranean region except its coastline, river corridors and areas with irrigated agricultural land.

Keywords

Biological invasions, CORINE land cover, EUNIS habitat classification, habitat type, non-native species, risk assessment.

INTRODUCTION

Invasions by alien plants and their actual or potential impacts on biodiversity, economy and human welfare are serious environmental and conservation issues at the global scale (Mack *et al.*, 2000; Hulme, 2006; Pyšek *et al.*, 2006). In spite of the intensive recent research on alien plants, any spatially explicit quantification of the level of invasion is still missing at the regional scale and especially so for Europe. Habitat characteristics and propagule pressure of alien plants can be suitable predictors of the level of invasion at particular sites (Lonsdale, 1999; Chytrý *et al.*, 2008a), and are potentially appropriate for mapping the levels of invasion at large scales.

Propagule pressure, i.e. the rate of spread of propagules of alien plants to new areas (Williamson, 1996; Lonsdale, 1999; Lockwood *et al.*, 2005; Colautti *et al.*, 2006; Daehler, 2006), is

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difficult to quantify for multispecies assemblages at the regional scale. Propagule pressure can be estimated by using proxy variables such as the density of human population, number of visitors in nature reserves, proportion of urban or industrial land cover, road density, or the intensity of traffic and trade (Pino *et al*., 2005; Thuiller *et al*., 2005). However, an extensive analysis of the representation of alien plant species in central European habitats has indicated that the effect of propagule pressure measured through such proxy variables is low compared to the effect of habitat type (Chytrý *et al*., 2008a). This analysis has also shown that at the regional scale habitat type appears to be the most effective predictor of the level of invasion in a given site. To some extent, the effect of habitat integrates the effects of climate, geography (e.g. some habitats are typical of mountains, others of lowlands) and propagule pressure because some habitats are more common in human affected areas with intense and frequent introductions of alien species, others in less disturbed areas with low human impact. Although habitat types can predict the level of invasion with a very fine resolution, current knowledge of the broad-scale patterns of plant invasion in Europe is mainly based on the numbers of alien species by administrative regions (Weber, 1997; Lambdon *et al*., 2008), which cannot be simply scaled down to the landscape level.

Within an international project ALARM (Settele *et al*., 2005), focused on identifying large-scale environmental risks for Europe, we have quantified proportional representation of alien plant species in different habitats of three areas encompassing the major climate types of Europe and with a contrasting history of human impact: Catalonia, Czech Republic and Great Britain (Chytrý *et al*., 2005, 2008b; Maskell *et al*., 2006; Vilà *et al*., 2007). This analysis was based on several thousands of vegetation plots from different habitats in each region. It demonstrated that while habitats within individual regions strongly differ in the proportion of aliens to all species, there is a considerable degree of consistency of the invasion patterns between regions. Although the composition of the alien flora of Catalonia, Czech Republic and Britain is very different, as is their climate and other characteristics, generally the same habitats (with few exceptions) are either strongly/ frequently or weakly/rarely invaded by alien plants in each of these three regions (Chytrý *et al*., 2008b). This finding suggests that reasonable estimations of the level of invasion for Europe can be obtained by extrapolating Catalonian, Czech and British data to other countries.

In this study, we combine the quantitative data on the proportion of alien species in different habitats of three above-mentioned regions with a land-cover map to construct the first map of the level of alien plant invasion for Europe.

METHODS

Database on the level of habitat invasion

In this paper, we use the term *level of invasion* for the actual proportion of alien plant species among all plant species occurring in a given habitat. The level of invasion results from both the habitat properties and the propagule pressure (Chytrý *et al*., 2005, 2008a; Hierro *et al*., 2005; Richardson & Pyšek, 2006). This term is different from *habitat invasibility*, which is the habitat's susceptibility to invasion imposed by abiotic and biotic constraints under the assumption of constant propagule pressure (Lonsdale, 1999).

The level of plant invasions in European habitats was assessed using vegetation plots originally sampled for the purposes of phytosociological classification (Font & Ninot, 1995; Chytrý & Rafajová, 2003) or long-term monitoring (Smart *et al*., 2003). The data set included 52,480 vegetation plots ranging in size from a few square metres to a few hundred square metres, sampled since the 1970s, from three regions representing contrasting climates typical of large parts of southern, central and western Europe: (1) Catalonia (Mediterranean–submediterranean climate; Vilà *et al*., 2007); (2) Czech Republic (subcontinental; Chytrý *et al*., 2005) and (3) Great Britain (oceanic; Maskell *et al*., 2006). Details on the complete data set and procedures used to standardize across regions are described in Chytrý *et al*. (2008b).

Alien species recorded in vegetation plots were identified using national literature (Preston *et al*., 2002; Pyšek *et al*., 2002b; Sanz-Elorza *et al*., 2004), and the percentage of neophytes (species introduced after AD 1500; see Pyšek *et al*., 2004 for definition) among the total number of species was calculated for each plot. Vegetation plots were assigned to 33 habitat types of EUNIS (Davies & Moss, 2003; see Chytrý *et al*., 2008b for details), which is a standard classification of European habitats developed by the European Environment Agency (http://eunis.eea.europa.eu/). For each of the three regions, the level of invasion of each habitat was expressed as the mean proportion of neophytes, averaged across all vegetation plots from that habitat. The level of invasion was consistently high in human-made, frequently disturbed habitats with fluctuating nutrient availability (arable land, ruderal vegetation, trampled areas) and coastal, littoral and riverine habitats (Chytrý *et al*., 2008b). The only difference between the data used in the current paper and those presented by Chytrý *et al*. (2008b) is that in the current paper we divided the habitat I1 arable land in the Mediterranean area into I1-1 Irrigated arable land, woody crops and gardens, and I1-2 Non-irrigated arable land (herbaceous crops, especially cereals), because these subtypes strongly differ in the level of invasion. The proportion of neophytes in these two subclasses was estimated based on the vegetation plots from Catalonia (FLORACAT database, Font & Ninot, 1995) at 15.7 ± 10.6% (mean ± standard deviation) for the former and 3.3 ± 6.4% for the latter. For the extra-Mediterranean parts of Europe where the period of summer drought is absent, this distinction was not made because the differences in the proportion of neophytes between irrigated and non-irrigated arable land are not so pronounced.

Biogeographical and land-cover classification and map construction

We classified Europe following the European biogeographical regions (European Topic Centre on Biological Diversity, 2006, http://dataservice.eea.europa.eu/dataservice/metadetails.asp?id=839). Quantitative data on the level of invasion obtained from

Figure 1 Delimitation of areas where the level of invasion was mapped, based on different data sources: 1, Catalonian data, 2, Czech data, 3, British data, 4, mean of Czech and British data. Boundaries between the areas follow the map of European biogeographical regions (European Topic Centre on Biological Diversity, 2006) and the areas correspond to 1, Mediterranean region, 2, Continental and Pannonian regions, 3, British Isles and 4, remaining part of Atlantic and Boreal region.

vegetation plots assigned to EUNIS habitats were used for extrapolations within particular biogeographical regions as follows: (1) the Mediterranean region was based on the Catalonian data; (2) Continental and Pannonian regions, including embedded patches of the Alpine region, on the Czech data; (3) British Isles on the British data; and (4) the remaining part of the Atlantic region and the Boreal region, including the embedded patches of the Alpine region, on average values obtained from British and Czech data (Fig. 1). We believe that this averaging provided a good approximation for the areas of Atlantic region on the European continent, because of their transitional biogeographical position between oceanic and subcontinental climates. Average values from the British and Czech data also provide a reasonable extrapolation for the Boreal region, because Scottish and Czech mountains contain most of the habitats typical of the Boreal region, such as coniferous forests, alpine grasslands and mires. Anatolian, Arctic, Black Sea, Macaronesian and Steppic biogeographical regions were omitted because of the lack of appropriate vegetation data to justify extrapolation.

CORINE land-cover data (Moss & Wyatt, 1994) were obtained from the European Environment Agency (raster data with 250×250 m resolution, version 8/2005). This data set does not cover Iceland, Norway, Andorra, Switzerland, Serbia, Montenegro, Kosovo, Belarus, Ukraine, Moldova and Russia; therefore these countries were not mapped.

EUNIS habitat types were transferred to CORINE land-cover classes. Since most of the CORINE classes correspond to more than one EUNIS habitat (Petit *et al.*, 2001; Slootweg *et al.*, 2005), proportional contribution of the relevant EUNIS habitats was estimated for each CORINE land-cover class (Table 1), based on the description of the CORINE classes (Bossard *et al.*, 2000) and the delimitation of the EUNIS habitats (Chytrý *et al.*, 2008b).

The level of invasion for individual CORINE classes was expressed as an average value of the corresponding EUNIS habitats, weighted by their proportional contributions as given in Table 1. Values were computed for the CORINE classes in each of the biogeographical regions following the above criteria and used as input data for map construction. The level of invasion was visualized using three categories: < 1, 1–5 and > 5% of alien (neophyte) species. Boundaries of the categories were arbitrarily set up to allow for optimum visualization with roughly equal number of pixels in each category. All GIS analyses and map visualizations were done in the ArcGIS 9.2 program (http://www.esri.com).

Table 1 Cross-tabulation of the EUNIS habitat types and the CORINE land-cover classes used for mapping the habitat levels of invasion onto the CORINE land-cover map. Percentage contributions of habitat types to each land-cover class were estimated based on expert judgement, following the description of the land-cover classes by Bossard *et al.* (2000). Percentages are related only to the vegetated parts of the CORINE classes (e.g. excluding the non-vegetated parts of urban fabric). Habitat types and their delimitations follow Chytrý *et al.* (2008b) except type I1, which is divided into two subtypes for the Mediterranean areas; for the extra-Mediterranean areas, undivided type I1 is used with summed values of the two subtypes.

	EUNIS habitat type																																
CORINE land-cover class	A2.5 & D6 & E6 Saline habitats	B1 & B2 Coastal sediments	B3 Rock cliffs	C1 Surface standing waters	C2 Surface running waters	C3 & D5 Sedge and reedbeds	D1 Raised and blanket bogs	D2 Fens and transitional mires	D4 Base-rich fens	E1 Dry grassland	E2 Mesic grassland	E3 & E5.4 Wet grasslands	E4 Alpine and subalpine grasslands	E5.1 Anthropogenic herb stands	E5.2 Thermophile woodland fringes	E5.3 Pteridium aquilinum fields	E5.5 Subalpine moist or wet tall-herb and fern stands	F2 Arctic, alpine and subalpine scrub	F3 Temperate scrub	F4 Temperate shrub heathland	F5 Maquis	F6 Garrigue	F7 Spiny mediterranean heaths	F9 Riverine and fen scrub	FA Hedgerows	G2 Broadleaved evergreen woodland	G3 Coniferous woodland	G1 & 4 Broadleaved deciduous and mixed woodland	G5 Disturbed woodland	H2 Screes	H3 Cliffs	H5.6 Trampled areas	I1-1 Irrigated arable land, woody crops and gardens	I1-2 Non-irrigated arable land (herbaceous crops)
111 Continuous urban fabric	.	.	.	.	.	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50	.	.
112 Discontinuous urban fabric	.	.	.	.	.	.	.	.	.	10	10	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.	.	20	20	.
121 Industrial or commercial units	.	.	.	.	.	.	.	.	.	15	15	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40	.	.
122 Road and rail networks and associated land	.	.	.	.	.	.	.	.	.	15	15	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40	.	.
123 Port areas	.	.	.	.	.	.	.	.	.	10	20	.	.	30	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	40	.	.
124 Airports	.	.	.	.	.	.	.	.	.	30	30	.	.	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.
131 Mineral extraction sites	.	.	.	.	.	.	.	.	.	.	.	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	20	10	.	.
132 Dump sites	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
133 Construction sites	.	.	.	.	.	.	.	.	.	.	.	.	.	70	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.	.
141 Green urban areas	.	.	.	.	.	.	.	.	.	10	30	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.	.	15	.	.
142 Sport and leisure facilities	.	.	.	.	.	.	.	.	.	10	30	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	25	.	.
211 Non-irrigated arable land	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100
212 Permanently irrigated land	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.
213 Rice fields	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.
221 Vineyards	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.
222 Fruit trees and berry plantations	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.
223 Olive groves	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.
231 Pastures	.	.	.	.	.	.	.	.	.	20	50	25	.	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
241 Annual crops associated with permanent crops	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50	50

Table 1 *Continued*

CORINE land-cover class	A2.5 & D6 & E6 Saline habitats	B1 & B2 Coastal sediments	B3 Rock cliffs	C1 Surface standing waters	C2 Surface running waters	C3 & D5 Sedge and reedbeds	D1 Raised and blanket bogs	D2 Fens and transitional mires	D4 Base-rich fens	E1 Dry grassland	E2 Mesic grassland	E3 & E5.4 Wet grasslands	E4 Alpine and subalpine grasslands	E5.1 Anthropogenic herb stands	E5.2 Thermophile woodland fringes	E5.3 Pteridium aquilinum fields	E5.5 Subalpine moist or wet tall-herb and fern stands	F2 Arctic, alpine and subalpine scrub	F3 Temperate scrub	F4 Temperate shrub heathland	F5 Maquis	F6 Garrigue	F7 Spiny mediterranean heaths	F9 Riverine and fen scrub	FA Hedgerows	G2 Broadleaved evergreen woodland	G3 Coniferous woodland	G1 & 4 Broadleaved deciduous and mixed woodland	G5 Disturbed woodland	H2 Screes	H3 Cliffs	H5.6 Trampled areas	I1-1 Irrigated arable land, woody crops and gardens	I1-2 Non-irrigated arable land (herbaceous crops)
	EUNIS habitat type																																	
242 Complex cultivation patterns	.	.	.	.	.	.	.	.	.	10	20	10	.	.	.	.	.	.	.	10	5	5	.	.	.	.	.	.	10	.	.	.	10	20
243 Land principally occupied by agriculture, with significant areas of natural vegetation	.	.	.	.	.	.	.	.	.	10	20	10	.	.	.	.	.	.	.	10	5	5	.	.	.	.	.	.	10	.	.	.	10	20
244 Agro-forestry areas	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.	.	.	.	.	.	10	10	.	.	.	.	.	.	.	.	.	.	20	30
311 Broad-leaved forest	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.
312 Coniferous forest	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.	.
313 Mixed forest	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.	.
321 Natural grassland	5	.	.	.	.	.	.	.	.	25	30	25	5	.	5	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
322 Moors and heathland	.	.	.	.	.	.	15	20	15	.	.	.	.	.	.	.	.	25	.	25	.	.	.	.	.	.	.	.	.	.	.	.	.	.
323 Sclerophyllous vegetation	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	30	10	.	.	30	.	.	.	.	.	.	.	.
324 Transitional woodland/shrub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	30	.	.	.	.	.	20	.	.	.	50	.	.	.	.	.
331 Beaches, dunes and sand plains	.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
332 Bare rock	.	.	50	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	50	.	.	.
333 Sparsely vegetated areas	.	.	.	.	.	.	.	.	.	40	.	.	40	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	20	.	.	.	.
334 Burnt areas	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	100	.	.	.	.	.
411 Inland marshes	10	.	.	.	.	70	.	10	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
412 Peatbogs	.	.	.	.	.	.	30	50	20	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
421 Salt marshes	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
422 Salines	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
423 Intertidal flats	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
511 Water courses	.	.	.	.	80	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.
512 Water bodies	.	.	.	100	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

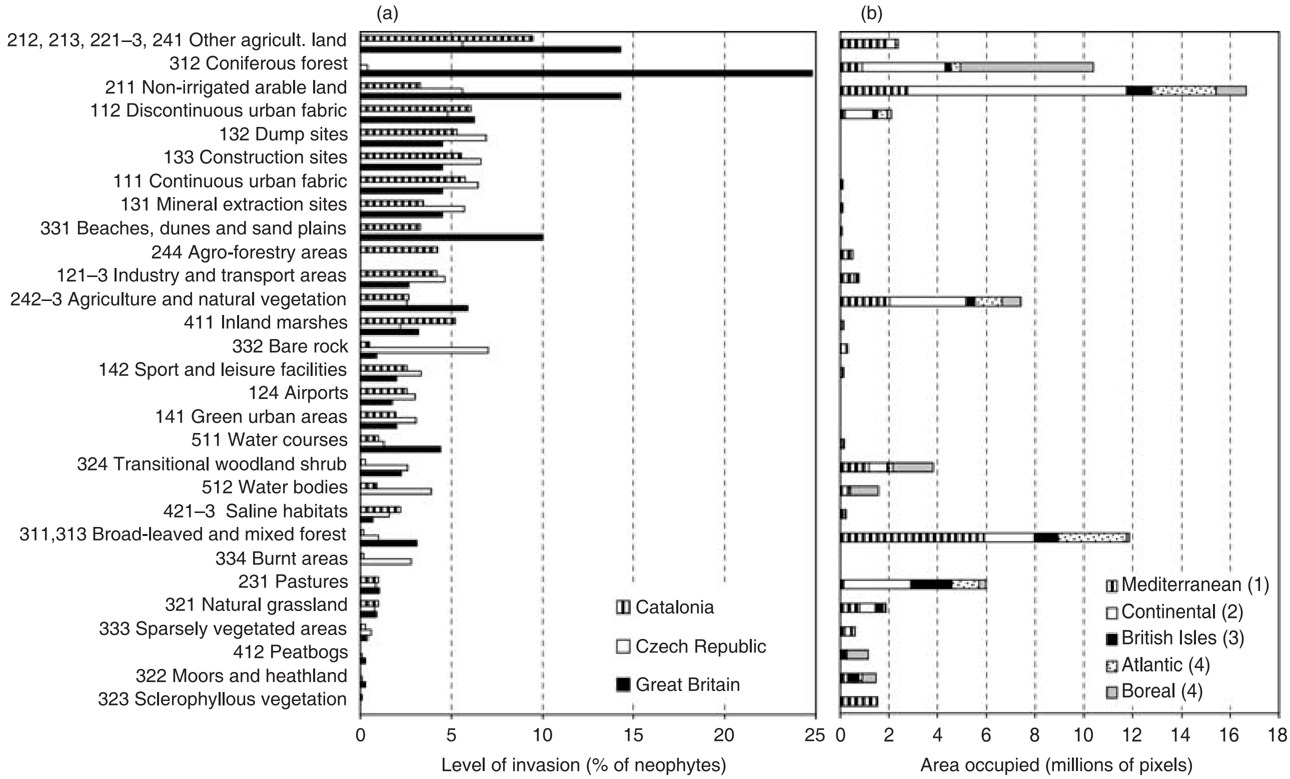

Figure 2 Level of invasion (mean percentage of neophytes among the total number of species recorded in vegetation plots) in the CORINE land-cover classes in the three European regions considered (a), and the area occupied by individual land-cover classes in different biogeographical regions (b). Land-cover classes are ordered by decreasing mean of the level of invasion across the three regions. Similar land-cover classes with the same predicted levels of invasion were merged. Zero values in (a) for classes 244 and 323 in the Czech Republic and Britain mean the absence of these classes, not zero level of invasion. Areas occupied by each land-cover class are quantified in millions of 250×250 m pixels assigned to each class. Numbers in brackets next to the labels of the biogeographical regions refer to numbers used in Fig. 1.

As quantitative contributions of the EUNIS habitats to CORINE land-cover classes (Table 1) were estimated by expert judgement, we tested how possible errors in these estimates might affect the resulting map. For this purpose, we randomly added or subtracted 5% to the non-zero values in Table 1, then standardized the table to the row totals equal to 100%, and re-calculated the level of invasion for each pixel of the map. We repeated this procedure 100 times and counted the mean percentage of pixels for which the classification into the three categories used for the visualization of the level of invasion differed from that based on the expert judgement shown in Table 1. Then we did the same analysis after randomly changing the non-zero values by 10% and 20%.

RESULTS

The highest levels of neophyte invasion among the CORINE land-cover classes (Fig. 2a) are predicted on various types of arable land and in urban and industrial areas. A high level of invasion is also associated with coniferous forests in Britain but not elsewhere. The lowest levels of invasion are typical of sclerophyllous vegetation, peatbogs, moors and heathlands. Rather low levels are also found in natural and seminatural grasslands, deciduous forests, and coniferous forests outside Britain. The areas occupied by each land-cover class (Fig. 2b) indicate which classes have a dominant effect on the predicted map of the level of invasion. Most extensive land covers are different classes of agricultural land, forests, pastures and transitional woodland/shrub. Some classes are relatively common in some regions (e.g. sclerophyllous vegetation in the Mediterranean region and peatbogs in the Boreal region) but rare elsewhere.

The European map of the level of invasion by neophytes (Fig. 3), based on the estimates presented in Fig. 2a, predicts the highest levels of invasion in moderately dry and warm low-land areas, both in western Europe (e.g. south-eastern England or north-western France) and in agricultural regions in central and eastern Europe (e.g. northern Germany, Poland, Czech Republic, Hungary and the lower Danube valley). In contrast, low levels of invasion are predicted for the Boreal biogeographical region, Scotland, montane zones throughout the continent and the Mediterranean region (including the sub-Mediterranean zone) where higher levels of invasion are predicted only along the coastline, in areas with irrigated agricultural land or along rivers.

The tests involving random change of values in the EUNIS-CORINE cross-tabulation (Table 1) by 5%, 10% and 20% resulted in mean changes in the classification of the map pixels to the categories of the level of invasion for 2.0%, 4.9% and 7.2% pixels, respectively. Given that an error of 20% for all values in Table 1 is very unlikely, this analysis confirmed that the resulting

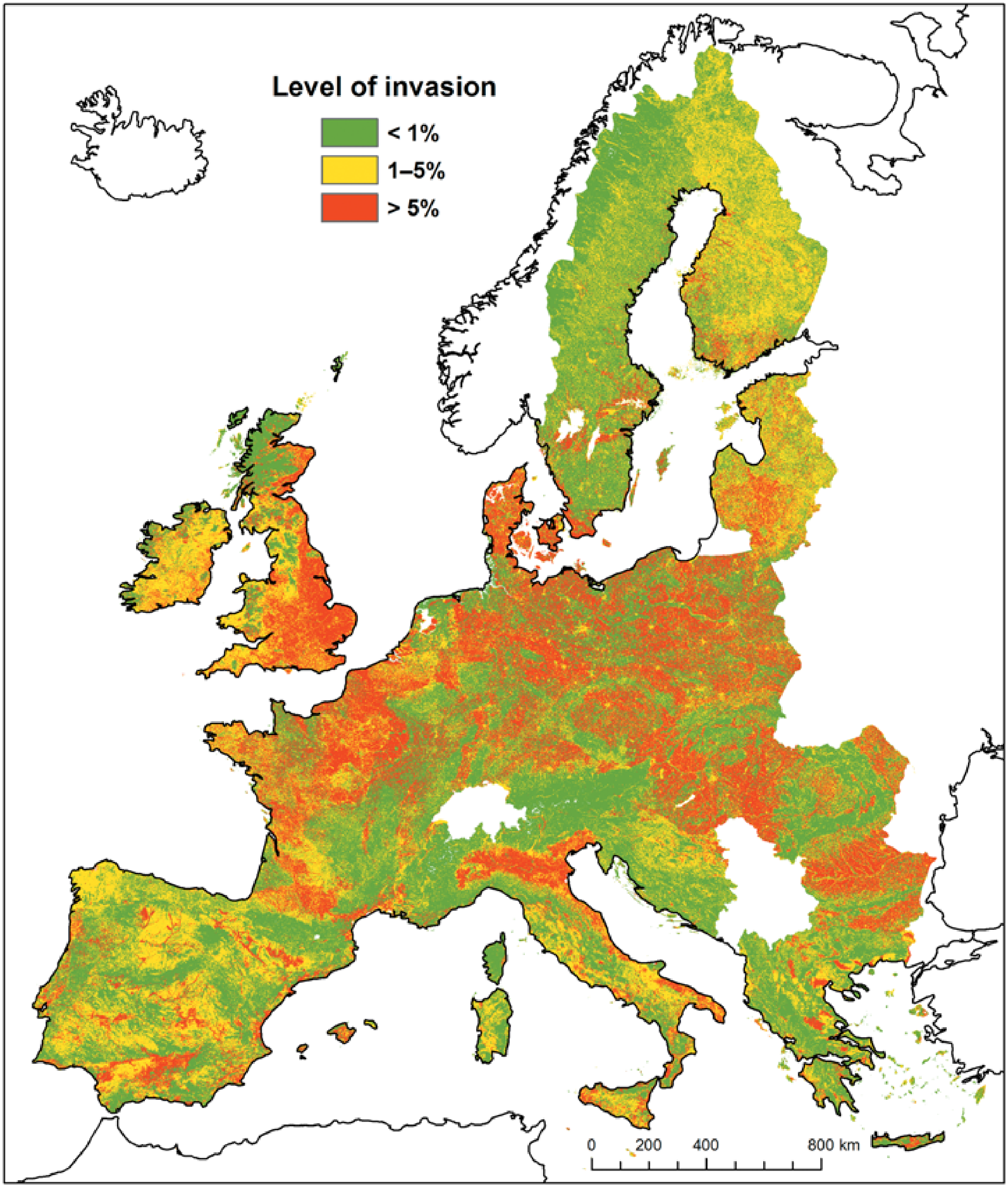

Figure 3 European map estimating the level of invasion by alien plants, based on the mean percentage of neophytes in vegetation plots corresponding to individual CORINE land-cover classes (see text for details). Within the mapping limits, areas with non-available land-cover data or insufficient vegetation-plot data are blank.

European invasion map is robust with respect to possible errors in the expert-based EUNIS-CORINE cross-tabulation.

DISCUSSION

Methodological considerations

Mapping the levels of invasion typical of different habitat types onto land-cover classes enabled us to create the first predictive map of the level of invasion by alien plants (neophytes) for Europe (Fig. 3). The mapping based on habitat types is justified, because they were shown to be much better predictors of the level of invasion than other environmental and propagule pressure variables (Chytrý *et al.*, 2008a).

Our results are based on vegetation-plot data, which provides a fine-resolution estimation of the level of invasion; however, the map resolution (pixels of 250 × 250 m) is coarser than the size of the vegetation plots sampled. Each pixel of the map contains a plot-scale estimation of the level of invasion for the dominant land-cover class of that pixel, which is not the same as the proportion of alien to all species occurring in the whole pixel. Alien-to-all-species proportions are scale-dependent, being usually low in small plots but tending to increase when the size of the basic sampling units increases. For example, Czech vegetation plots contain, on average, 2.3% of neophytes while the whole flora of the country contains 26.8% of neophytes, and similar scale effects are found within individual habitats (Pyšek *et al*., 2002b; Chytrý *et al*., 2005; Sádlo *et al*., 2007). Therefore the percentage values displayed on the map (Fig. 3) represent only the fine-scale level of invasion in the predominant land-cover class, but not the total alien flora of the pixel (for which values would be mostly higher), and they cannot be directly compared with maps based on the floras of counties (e.g. Stohlgren *et al*., 2006a) or grid squares of several square kilometres as used in floristic mapping (e.g. Deutschewitz *et al*., 2003; Pino *et al*., 2005).

Many surveys have shown that, at the large scale, there is a positive correlation between the number of alien and native plant species (Pyšek *et al*., 2002a; Kühn *et al*., 2003; Pino *et al*., 2005; Maskell *et al*., 2006; Palmer, 2006; Stohlgren *et al*., 2006a). Positive rather than negative relationships are also more common at the scale of vegetation plots (Stohlgren *et al*., 2006b) and this holds also for the plots used as the basis for this study (Chytrý *et al*., 2005; Vilà *et al*., 2007). Therefore we did not define the level of invasion by using the absolute numbers of alien species in a plot, because in that case the resulting map of the level of invasion would be similar to the map of native species richness. The proportion of alien to all species, as used in this study, reflects deviations from the positive alien–native relationship, which is indeed a dominant trend in our data set.

An alternative measure of the level of invasion would be the total cover of alien species, which is usually of greater importance for conservation managers than alien species numbers due to its potential negative impact on native species diversity (Crall *et al*., 2006). However, the alien-to-all-species proportion used in this study is positively correlated with the total cover of aliens in our data ($P < 0.001$ for most habitats). We can therefore conclude that to some extent, the map of the level of invasion (Fig. 3) also reflects the pattern of alien plant cover.

The extrapolation used in the current study, especially predicting the level of invasion in the Boreal region on the basis of data from the Atlantic and Continental regions, can result in a slight bias or lower accuracy of the map. However, given that most habitat types of the Boreal region have their close analogues in the Atlantic or Continental regions (Bohn & Neuhäusl, 2000–03), we believe that our extrapolations are sufficiently robust. Similarly, reasonable extrapolations to the Alpine region can be made based on the assessment of corresponding habitat types occurring in the adjacent regions. Still, future studies on the level of local invasion in other European regions would be desirable for validation of the map and its further improvement.

Pattern of plant invasions across Europe

The spatial pattern of the level of plant invasions in Europe, as presented in the map (Fig. 3), is directly derived from the land-cover distribution. At the same time, however, it shows a clear relationship to the macroclimatic patterns of temperature and precipitation. This is not surprising, because the distribution of land cover at the European coarse resolution is mainly driven by climate (Thuiller *et al*., 2004). Low levels of invasion are predicted in humid areas with cool summers, such as north-western British Isles, northern Europe and mountainous areas or upland plateaus across the continent. In contrast, warm areas in lowlands are most invaded, especially in south-eastern Britain, northern France, central Europe north of the Alps and the Danube and Po basins. The Mediterranean region is less invaded than temperate Europe but it shows high levels of invasion on its coastline, in large conurbations, and in intensively used agricultural systems subjected to irrigation. The relatively low levels of invasion in the Mediterranean Basin are in contrast with the high levels in other mediterranean areas of the world, such as California (Stohlgren *et al*., 2006a). This difference within the biome could be due to a long history of human presence and prehistoric invasions in the Mediterranean Basin, which makes its ecosystems relatively resistant against current invasions, and also due to the fact that the Mediterranean Basin is more of a donor than receptive area of species introductions during the colonization of the New World (di Castri, 1989).

The level of invasion is also associated with human population density; it is low in sparsely populated areas in Sweden, Finland or central Spain, and in mountainous areas throughout the continent. In fact, European plant species richness is positively correlated with human population density at a coarse resolution (Araújo, 2003), indicating that most people have settled in areas with environmental conditions conducive to high species richness (Kühn *et al*., 2004; Luck, 2007). It is therefore difficult to separate the effect of environmental factors, biotic factors (e.g. species interactions) and human activities on species diversity. Since we defined the level of invasion as the proportion of aliens to all species rather than absolute number of alien species, the coincidence of the high level of invasion with high human population density may reflect the positive influence of human activities on invasions, e.g. creating disturbed habitats susceptible to invasions or increased propagule pressure (Chytrý *et al*., 2008a). However, the effects of human population density can also be confounded by the fact that human population is concentrated in warm lowland areas, while most alien plants seem to be preadapted to mild climate areas at low altitudes (Pyšek *et al*., 2002a; Stohlgren *et al*., 2006a; Chytrý *et al*., 2008a).

Future outlook

Our study provides a preliminary coarse approach to the spatially explicit assessment of the level of alien plant invasion in Europe based on existing vegetation-plot data. The map can be improved in many respects in the future, e.g. by including vegetation-plot data from other areas, by increasing the number of plots from the least representative habitats, by refining the correspondence between habitats and land-cover classes or by accounting for levels of impacts depending on the habitat type. Still it is a robust product for public awareness and immediate applications in modelling the future level of alien plant invasions in Europe, which will involve the projection of the quantitative data from vegetation plots onto classes of future land-cover change scenarios (Settele *et al*., 2005; Rounsevell *et al*., 2006; Spangenberg, 2007), assessment of the expected trends of the invasion level within habitats, and modelling the effects of climate changes on the level of invasion (Thuiller *et al*., 2005; Gritti *et al*., 2006).

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