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Alien species in different habitat types of Slovenia: analysis of vegetation database

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Abstract

Background and purpose: *Invasion by alien plant species is considered as one of major threats to biodiversity. Actual invasion of different habitats in particular country is important for understanding processes that are important in invasion ecology as well as for the nature conservation.*

Materials and methods: *Vegetation relevés stored in a database Vegetation of Slovenia were translated into 30 EUNIS habitat types which enables comparison with similar studies in other European countries. Out of the 18 606 plots stored in the database stratified resampling yielded 6 517 relevés. For each vegetation plot we calculated mean relative species richness per plot and total cover of archeophytes, neophytes and native species.*

Results: *Most invaded habitat type with the highest species percentages of alien species (archaeophytes and neophytes) is arable land (I1). In addition, archaeophytes occur in higher percentages in trampled areas, anthropogenic herb stands, mesic grasslands, and moist tall-herb stands. Neophytes are on the other hand highly represented in arable land, trampled areas, but also riverine scrubs and wet and moist tall-herb stands.*

Conclusions: *Pattern across different regions in Europe is very similar with anthropogenous habitats being the most invaded by alien species.*

INTRODUCTION

Alien species have become a major interest of the research community because they pose a threat to local biodiversity, especially when they invade natural vegetation. Alien species are species that occur in certain area as a result of accidental or intentional introduction based on human activity (*1*). Many alien species appear only ephemerally, even require repeatable human introductions and are called casual alien species (or ephemerophytes). Naturalized alien species are successfully establishing stable/permanent populations and in some cases become invasive by reproducing and spreading over large areas. Part of invasive species become transformers by changing natural plant communities or even ecosystems (*1,2*). Native species on the other hand are species that have origin in particular area and are present there without human impact or has arisen de novo in the area (*3*). Their natural areal is conditioned by natural characteristics.

According to the residence time (the time since introduction) we classify an alien species either as an archaeophyte (introduced before 1500 AD) or as a neophyte (introduced after 1500 AD) (*4,5*). Classification of an archaeophyte species is less clear than neophyte species although both categories are well defined. Classification of species as archaeophytes can be fuzzy and different researchers classify same species

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into different categories. Usually species are not classified based on evidence (paleobotanical or fossil) and intuition or uncritical copying of older sources is present (*3*). Distinction is especially difficult in the south of Europe as most of archeaeophytes originate from southern Europe or Middle East (*6*). Archaeophytes are present since their arrival accompanying humans in the region for hundreds or even thousands of years, have become well adapted and are included into plant communities, whereas neophytes still immigrate, occupy different habitats and expand their areal (*7*). On the contrary some archaeophytes are experiencing shrinking of their newly acquired territory because of the loss of suitable habitats (such as intensification of farming) (*8,9*).

Growing amount of floristic and vegetation data enables quantitative assessment of level of invasion of alien species in different habitats (*10*). In the last decade some studies, using large vegetation databases, have dealt with this question on regional (*11-17*) or continental scale (*18*) and they have found major differences with regard to residence time of alien species and different characteristics of particular habitat types, but also altitude and time.

In Slovenia there have been two papers published dealing with alien plant species on a national scale. Jogan, et al. (*19*) published a list of Slovenian alien plant species with data on first recording, present distribution, estimations of naturalization, frequency of occurrence and trends. They had classified alien species into two groups according to the time of introduction: as archaeophytes or neophytes. Archaeophytes were further divided into two categories: most probable (97 species) and potential archaeophytes (127 species) because of before-mentioned lack of direct evidence for such species.

In addition a list of nationally important invasive species list has been formed. According to this list Zelnik (*20*) analysed frequency of invasive species in particular habitats (not using EUNIS classification), using 3500 floristic records. He also evaluated the potential of these species for further invasion in habitats. More focus has been put on analysing synanthropic vegetation that is highly susceptible to invasion by alien plant species (*21-23*).

The aim of the present study is to test data from Slovenian vegetation database (*24*) to analyse the presence of most widespread alien species in various habitats, find the level of invasion of different plant communities and to compare our results to patterns in other European studies.

Study area

Slovenia is a transient country between central and south-eastern Europe (the Balkans) from 46° 52' 36'' to 45° 25' 19'' N and from 13° 22' 32'' to 16°36' 38'' E. On an area of 20 273 km^2, Slovenia has been phytogeographically divided according to climate into: submediterranean, prealpine, alpine, predinaric, dinaric and subpannonian region (*25*). According to diverse topography (altitudes 0-2 864 m a.s.l.) precipitation values range from less than 900 mm in the northeast subpannonian region to more than 3 200 mm in the Alps. Similarly, mean annual temperatures range from around 0 °C in the Alps to over 12 °C in the coastal region (*26*).

The characteristics mentioned are reflected also in floristic and vegetation diversity. Although most of the country's area is covered by forests many other vegetation types are found – from species poor mires, bogs and saline vegetation through diverse grasslands to alpine habitats. Šilc and Čarni (*27*) listed 588 plant associations recorded in Slovenia, belonging to 51 classes. Flora of Slovenia comprises 3 452 taxa (*28*). Assessment of alien species of Slovenia lists 343 neophytes (including casual aliens e.g. ephemerophytes) and 224 archaeophytes (most probable and potential ones), which means that about 10 % of Slovenian flora is alien to the area (*19*).

Methods

We used vegetation dataset from Vegetation database of Slovenia (*24*) in Turboveg software (*29*) where vegetation plots sampled according to Braun-Blanquet (*30*) method are stored. Vegetation plots of all vegetation types were selected that were attributed to syntaxa by original authors. To avoid oversampling of particular areas or vegetation types we performed stratified resampling: one relevé of one particular association from one plot (0.75 x 1.25 degrees) was selected. If more relevés complied with the selection terms one was randomly selected. This yielded 6 517 relevés out of 18 606 stored in database in December 2015. For each relevé list of species, altitude, plot size and habitat was exported.

For interpretation of phytosociological syntaxa to EUNIS habitat we used crosswalk between two hierarchical typologies (alliances and habitat types) by Schaminée, et al. (*31*). Each vegetation plot was assigned to one of 71 unique EUNIS habitat types and subsequently narrowed to 30 habitat types (Table 2). We assigned them to Level 2, but in some cases Level 3 was used where subtypes with different invasion levels were included and to allow comparison with results of Chytrý, et al. (*11*). There is a distinction in classification of ruderal vegetation between previous studies (*11, 14*), where annual ruderal vegetation was classified within J6 habitat type (Waste deposits), while recently (*31*) all ruderal vegetation is classified as E5.1 (Anthropogenic herb stands).

Cryptogams and species determined to genus level were deleted and species in various strata were merged into one. Taxonomy and nomenclature of plant species are in accordance with Martinčič, et al. (*28*) and syntaxa in accordance with Šilc and Čarni (*27*). Closely related species and taxonomically difficult for determination were aggregated according to Martinčič, et al. (*28*). For listing of archaeophyte and neophyte species we used classification by Jogan, et al. (*19*). For further analyses we used only the group of most probable archaeophytes. For each veg-

Table 1. *Mean species number, mean relative species richness and total sum cover in percentage of archaeophytes, neophytes and native species in vegetation plots assigned to 30 EUNIS habitat types.*

			Mean species number				Mean relative species richness per plot			Cover aliens species		
		Nr. plots	Neophytes	Archeo-phytes	Natives	Neophytes	Archeo-phytes	Natives	Neophytes	Archeo-phytes	Natives
A	**– Marine habitats**										
A2	– Littoral sediment	A2	47	0.0±0.0	0.1±0.3	4.8±2.5	0.0±0.0	1.0±3.3	99.0±3.3	0.0±0.0	0.2±0.6	57.9±24.5
B	**– Coastal habitats**										
B1	– Coastal dunes and sandy shores	B1	1	0.0±0.0	0.0±0.0	5.0±0.0	0.0±0.0	0.0±0.0	100.0±0.0	0.0±0.0	0.0±0.0	89.0±0.0
C	**– Inland surface waters**										
C1	– Surface standing waters	C1	63	1.0±1.5	0.0±0.0	12.1±12.9	5.3±8.2	0.0±0.0	94.6±8.3	9.2±17.0	0.0±0.0	60.4±28.5
C2	– Surface running waters	C2	7	0.0±0.0	0.0±0.0	7.9±3.7	0.0±0.0	0.0±0.0	100.0±0.0	0.0±0.0	0.0±0.0	30.6±13.8
C3	– Littoral zone of inland surface waterbodies	C3	311	0.4±0.9	0.2±0.5	12.0±6.8	2.9±5.7	1.1±3.2	96.0±6.8	2.9±10.1	0.9±5.4	68.8±18.7
D	**– Mires, bogs and fens**										
D1	– Raised and blanket bogs	D1	61	0.0±0.0	0.0±0.0	6.8±4.0	0.0±0.0	0.0±0.0	98.4±12.7	0.0±0.0	0.0±0.0	75.8±25.4
D2	– Valley mires, poor fens and transition mires	D2	22	0.0±0.0	0.0±0.0	8.5±5.0	0.0±0.0	0.0±0.0	100.0±0.0	0.0±0.0	0.0±0.0	49.5±28.6
D4	– Base-rich fens and calcareous spring mires	D4	87	0.1±0.1	0.0±0.0	14.3±7.7	0.1±0.6	0.0±0.0	99.9±0.6	0.1±0.3	0.0±0.0	69.8±18.3
D5	– Sedge and reedbeds, normally without free-standing water	D5	36	0.1±0.4	0.2±0.4	18.8±4.1	0.7±2.1	1.0±1.9	98.3±2.6	0.3±0.8	0.5±0.9	75.4±12.0
E	**– Grasslands and lands dominated by forbs, mosses or lichens**										
E1	– Dry grasslands	E1	361	0.2±0.4	0.5±0.5	40.3±14.3	0.6±1.7	1.3±1.5	98.1±2.6	0.4±1.4	1.5±2.1	81.8±13.3
E2	– Mesic grasslands	E2	315	0.4±0.7	0.9±0.8	31.1±13.0	1.3±2.9	2.9±3.2	95.8±5.0	1.1±4.3	4.5±7.3	81.9±14.6
E3	– Seasonally wet and wet grasslands	E3	214	0.2±0.5	0.2±0.4	28.4±21.1	0.7±2.2	0.5±1.3	98.7±2.5	1.4±8.2	0.4±0.9	75.3±21.3
E4	– Alpine and subalpine grasslands	E4	196	0.1±0.3	0.2±0.4	27.1±14.1	0.1±0.7	0.4±1.0	99.5±1.3	0.1±1.1	0.6±3.0	75.7±18.0
E5	– Woodland fringes and clearings and tall forb stands											
E5.1	– Anthropogenic herb stands	E5.1	601	0.9±1.2	1.8±1.3	17.0±6.5	4.9±6.1	9.3±7.0	85.8±9.4	6.0±16.1	7.4±11.5	67.2±18.4
E5.2	– Thermophile woodland fringes	E5.2	115	0.1±0.2	0.5±0.5	31.6±9.0	0.2±0.7	1.6±1.7	98.2±1.9	0.1±0.4	1.1±1.1	78.6±12.1
E5.4	– Moist or wet tall-herb and fern fringes and meadows	E5.4	259	1.1±1.5	1.0±1.0	17.9±5.8	5.3±8.1	4.7±4.5	90.0±9.2	12.5±24.5	2.4±3.0	73.3±17.9
E5.5	– Subalpine moist or wet tall-herb and fern stands	E5.5	56	0.0±0.0	0.4±0.5	28.3±12.0	0.0±0.0	1.4±2.0	98.6±2.0	0.0±0.0	1.4±2.6	84.6±9.1
F	**– Heathland, scrub and tundra**										
F2	– Arctic, alpine and subalpine scrub	F2	112	0.0±0.0	0.1±0.2	36.9±15.6	0.0±0.0	0.1±0.5	99.9±0.5	0.0±0.0	0.1±0.4	90.7±8.8
F3	– Temperate and mediterranean-montane scrub	F3	164	0.2±0.5	0.3±0.5	24.1±10.7	0.7±1.9	1.5±2.4	97.7±3.0	0.4±1.6	0.7±1.0	83.9±11.3
F4	– Temperate shrub heathland	F4	1	0.0±0.0	0.0±0.0	27.0±0.0	0.0±0.0	0.0±0.0	100.0±0.0	0.0±0.0	0.0±0.0	84.0±0.0
F9.1	– Riverine scrub	F9.1	68	1.6±1.7	0.4±0.7	30.2±18.3	5.4±5.0	1.1±1.9	93.6±6.0	4.7±6.2	1.0±2.1	87.0±8.5
F9.2	– [Salix] carr and fen scrub	F9.2	12	0.3±0.4	0.0±0.0	20.3±5.6	1.0±1.8	0.0±0.0	98.9±1.8	3.6±10.4	0.0±0.0	92.1±6.5
G	**– Woodland, forest and other wooded land**										
G1	– Broadleaved deciduous woodland	G1	1952	0.2±0.7	0.3±0.5	42.5±17.6	0.5±2.0	0.9±2.0	98.6±3.0	1.0±6.0	1.4±5.9	92.6±7.1
G2	– Broadleaved evergreen woodland	G2	2	0.0±0.0	0.5±0.5	24.0±0.0	0.0±0.0	2.0±2.0	98.0±2.0	0.0±0.0	1.0±1.0	92.5±0.5
G3	– Coniferous woodland	G3	475	0.1±0.1	0.2±0.4	41.9±20.1	0.1±0.2	0.6±1.6	99.3±1.6	0.1±0.3	0.8±2.9	91.3±10.3
G5	– Forest clearings	G5	10	0.3±0.6	0.3±0.6	25.1±7.8	1.0±2.1	1.0±2.1	98.0±3.5	0.6±1.3	0.6±1.3	86.5±8.4
H	**– Inland unvegetated or sparsely vegetated habitats**										
H2	– Screes	H2	122	0.0±0.0	0.1±0.2	20.9±9.9	0.0±0.0	0.1±0.7	99.9±0.7	0.0±0.0	0.1±0.5	58.4±21.4
H3	– Inland cliffs, rock pavements and outcrops	H3	254	0.1±0.3	0.1±0.2	12.5±7.1	0.4±2.2	0.3±2.2	99.3±3.3	0.1±0.5	0.1±0.3	35.5±19.6
H5.6	– Trampled areas	H5.6	162	1.4±0.9	0.7±0.9	9.4±4.2	12.9±8.3	5.9±7.0	81.3±10.4	12.7±16.5	2.2±5.1	46.2±18.0
I	**– Regularly or recently cultivated agricultural, horticultural and domestic habitats**										
I1	– Arable land and market gardens	I1	430	2.3±1.6	3.7±1.9	16.6±6.2	10.3±7.2	16.6±7.7	73.1±9.2	15.2±20.3	13.7±12.6	48.3±16.7

Table 2. *Fifteen neophytes and archaeophytes in vegetation of Slovenia that occur in the highest number of different EUNIS habitat types. Species are sorted from highest number of occupying habitats downwards.*

Neophytes	Number of EUNIS habitats	Archaeophytes (most probable)	Number of EUNIS habitats	Archaeophytes (possible)	Number of EUNIS habitats
Erigeron annuus	17	*Dactylis glomerata*	20	*Trifolium repens*	17
Solidago gigantea	16	*Cirsium arvense*	14	*Corylus avellana*	15
Conyza canadensis	11	*Cynodon dactylon*	7	*Cirsium vulgare*	13
Rudbeckia laciniata	11	*Setaria pumila*	7	*Picris hieracioides*	13
Galinsoga parviflora	10	*Amaranthus lividus*	5	*Arrhenatherum elatius*	12
Oxalis fontana	9	*Euphorbia helioscopia*	5	*Verbena officinalis*	12
Ambrosia artemisiifolia	8	*Castanea sativa*	4	*Cichorium intybus*	11
Impatiens glandulifera	8	*Portulaca oleracea*	4	*Rumex crispus*	11
Impatiens parviflora	8	*Centaurea cyanus*	3	*Capsella bursa-pastoris*	10
Echinocystis lobata	7	*Artemisia absinthium*	2	*Tanacetum vulgare*	10
Medicago sativa	7	*Carduus acanthoides*	2	*Trisetum flavescens*	10
Solidago canadensis	7	*Celtis australis*	2	*Chelidonium majus*	9
Amaranthus retroflexus	6	*Chenopodium ficifolium*	2	*Humulus lupulus*	9
Chamomilla suaveolens	6	*Chenopodium murale*	2	*Myosotis arvensis*	9
Helianthus tuberosus	6	*Consolida regalis*	2	*Chenopodium album* agg., *Setaria viridis*	8

etation plot we calculated the absolute species richness, mean relative species richness per plot and total cover of archeophytes, neophytes and native species (*11,18,32,33*). Absolute numbers of alien species and their cover are presented for rough estimation but were not used in further comparisons due to problems of sampling plot size.

We calculated regression and correlation between all three groups of species (neophytes, archaeophytes and natives). For statistical analyses we added 0.5 to species number and then square–root transformed it.

Dataset management was done in Juice program (*34*) and statistical analyses were performed in Statistica (*35*).

RESULTS

In the selected data subset there were 100 neophytes (4.6 %), 54 archaeophytes (2.5 %), and altogether 2182 taxa. Mean percentage of neophytes per vegetation plot is 2.22 % (±5.16), archaeophytes 3.01 % (±5.76), and native species 94.75 % (±9.21).

The highest proportion of alien species (archaeophytes and neophytes) occur on arable land (I1). In addition, archaeophytes occur in higher percentages (about 5 % or more) also in trampled areas, anthropogenic herb stands and moist tall-herb stands. Neophytes are on the other hand highly represented (more than 10 %) in arable land, trampled areas, but also riverine scrubs and wet and moist tall-herb stands. Habitats with low invasion of alien species are marine and coastal habitats, mires, bogs and fens and high altitude habitats (herb stands and scrubs). Comparison of invaded habitats based on cover does not change their ranking, but moist tall herb stands and standing waters stand out with higher cover of neophytes (e.g. *Elodea canadensis*, *Impatiens glandulifera*, *Rudbeckia laciniata*, *Solidago canadensis*, *S. gigantea*) compared to their rather low species proportion. Mesic grasslands have high cover of archaeophytes, mostly due to grass *Dactylis glomerata*.

Most frequent neophytes in the dataset are: *Erigeron annuus*, *Veronica persica*, *Galinsoga parviflora*, *Oxalis fontana*, and *Solidago gigantea* while archeophytes with highest frequency are: *Dactylis glomerata*, *Cirsium arvenses*, *Cynodon dactylon*, *Setaria pumila*, and *Amaranthus lividus*. Archaeophytes and neophytes with broadest habitat range are presented in Table 2.

Number of alien species versus native species reveals that alien species numbers are highest in intermediate species rich habitats, while the numbers are lower in extreme cases (species poor or rich habitats). Relationship was not significant for archaeophytes ($r = 0.1202$, $p = 0.5268$) and neophytes ($r = -0.1115$, $p = 0.5576$), but polynomial curve indicates slight increase of species number in the centre of x-axis. Both alien species categories are most represented in arable land. Archaeophytes are overrepresented also in woodland fringes and clearings, mesic grasslands, while neophytes in riparian forests, trampled communities, tall herb fringes and surface standing waters (Table 1, Figure 1). On the other hand there was strong relationship between number of archaeophytes and neophytes ($r = 0.7243$, $p < 0.001$).

DISCUSSION

Archaeophyte and neophyte species with highest number of occupied habitats in Slovenia were found in 20

and 17 out of 30 different habitat types respectively (Table 2). The difference between percentages per plot and per dataset is negative for neophytes (2.2 – 4.5) while for archaeophytes it is positive (3.0 – 2.5), which indicates that archaeophytes occupy more habitats and plots due to longer residence time because they had more time to disperse and adapt (*7*). Neophyte species are present in the area for shorter period of time (compared to archaeophytes) and thus all haven't yet become established in all suitable sites (*18*). Lower occurrence of neophytes in many habitats (and also frequency in particular vegetation plots) is attributed to a lag phase (*36*) and the increase of neophyte numbers is expected due to new introductions and spreading to many new habitats (anthropogenic and natural) as in other countries (*37*). By contrast archaeophytes are shifting from anthropogenous to more natural habitats in recent time (*13*).

The relative proportions of archaeophytes are in most cases higher than that of neophytes across habitat types; notable exceptions are standing waters, riverine scrub and trampled areas. Also, the relationship between the number of archaeophytes and the number of neophytes (Figure 1) is strongly positive which confirms that high number of archaeophyte species is a good predictor for neophytes invasion (*18*).

Comparing percentages of neophyte species that occur in many habitat types (more than one third) in different vegetation datasets across tested European regions, Slovenia exhibits low value (5 %). The highest proportion is in Great Britain (17.8 %) but appears much lower in other regions: Czech Republic 9.4 %, E Romania 6.7 %, and Catalonia 3.7 % (*16,18*). These results place Slovenia amid the other regions and indicate possible maximum value at about 10 % for continental Europe obtained with this type of data.

Composition of 20 neophyte species, occurring in highest number of habitats in Slovenia, is far more similar to that of E Romanian and Czech lists of species (11 and 10 same species, respectively) while it is very different from the ones of Catalonia and Great Britain (only 3 same species) (*16,18*), which shows great geographical dependence. Not one species appears on all of the 5 mentioned top lists, but a few appear on four of them, namely *Veronica persica*, *Robinia pseudacacia*, *Chamomilla suaveolens* and *Conyza canadensis*.

A high number of occupied habitats does not necessarily mean that a species is also invasive in means that it drastically changes natural plant communities; they can only be naturalized and constantly present only with low abundance. The examples in Slovenia beside aforementioned *Veronica persica* are *Oxalis fontana*, found in 21 habitat types, and *Chamomilla suaveolens*, found in 13 habitat types, both considered only potentially invasive (*19*). On the other hand species such as water plants (*Elodea canadensis, Pistia stratiotes*), highly constrained by their physiological characteristics, can express substantial abundance in favourable habitat types but cannot invade

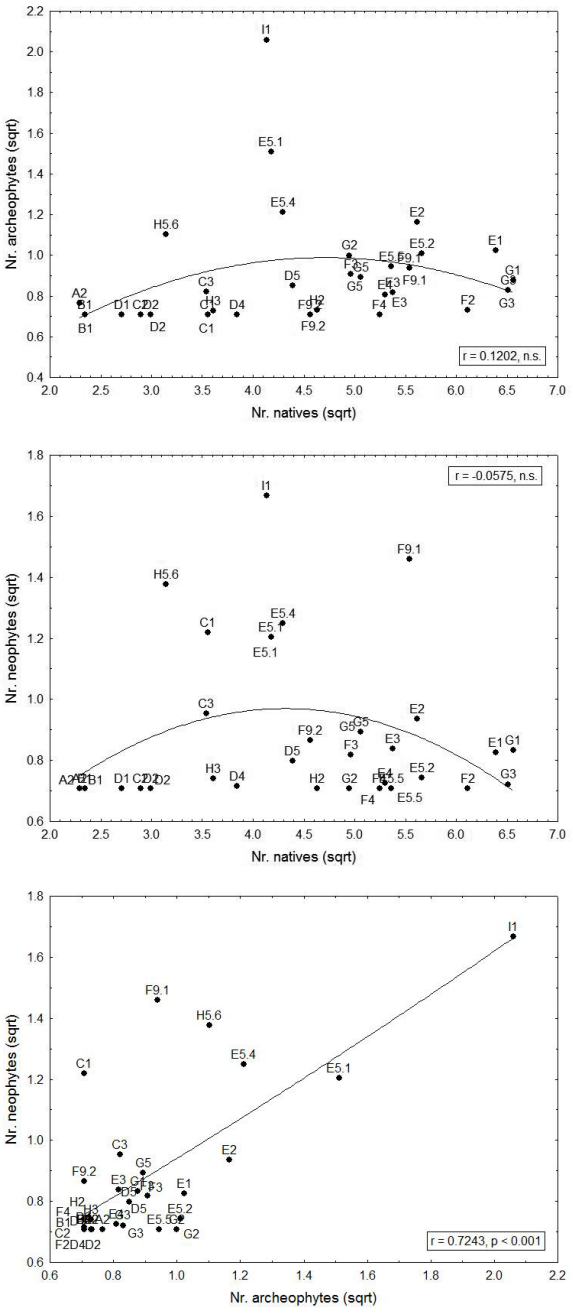

Figure 1. *Relationships between mean number of archaeophytes, neophytes and native species in different habitats. Labels refer to EUNIS habitat types (Table 1).*

many different ones. Habitat generalists among neophytes are not necessarily invasive species, but the number of habitats in which they occur can provide general information on the magnitude of their potential of invasion (*16*).

According to surveys based on vegetation data only few neophyte species occurred in the analysed plots from 5 European regions (Catalonia, Czech republic, Great Britain, Slovenia, E Romania), namely: *Conyza canadensis, Helianthus tuberosus, Juncus tenuis, Chamomilla sua-*

Table 3. *Lists of 20 most spread neophyte species according to percent of occupied habitat types per country. Species in bold occur in more than 3 countries. For Basque country only relative ecological amplitude of neophytes (percentage of alliances) was available.*

Slovenia		East Romania		Czech Republic		Catalonia		Great Britain		Basque Country	
	%	(Sîrbu et al. 2012)	%	(Chytrý et al. 2008)	%	(Chytrý et al. 2008)	%	(Chytrý et al. 2008)	%	(Campos et al. 2013)	%
Erigeron annuus	57	***Erigeron annuus ssp. annuus***	56	*Epilobium adenocaulon*	72	*Aster squamatus*	45	*Acer pseudoplatanus*	74	*Conyza sumatrensis*	52
Solidago gigantea	53	***Conyza canadensis***	44	*Impatiens parviflora*	68	***Conyza canadensis***	45	*Picea sitchensis*	68	*Aster squamatus*	50
Conyza canadensis	37	*Xanthium orientale* ssp. *italicum*	39	*Agrostis gigantea*	52	*Conyza bonariensis*	35	*Brassica napus* ssp. *napus*	58	***Conyza canadensis***	50
Rudbeckia laciniata	37	***Galinsoga parviflora***	36	***Conyza canadensis***	52	*Conyza sumatrensis*	35	*Lolium multiflorum*	58	*Cyperus eragrostis*	39
Galinsoga parviflora	33	*Medicago sativa*	36	***Robinia pseudacacia***	48	*Xanthium strumarium* ssp. *italicum*	32	***Veronica persica***	58	*Paspalum distichum*	30
Oxalis fontana	30	***Amaranthus retroflexus***	33	*Trifolium hybridum*	48	***Amaranthus retroflexus***	29	*Epilobium adenocaulon*	53	*Cortaderia selloana*	30
Ambrosia artemisiifolia	27	***Veronica persica***	33	*Bidens frondosa*	44	*Artemisia verlotiorum*	29	*Impatiens glandulifera*	53	*Paspalum vaginatum*	28
Impatiens glandulifera	27	*Armoracia rusticana*	31	***Erigeron annuus***	44	*Sorhum halepense*	29	***Chamomilla suaveolens***	53	*Solanum chenopodioides*	28
Impatiens parviflora	27	*Artemisia annua*	31	*Juncus tenuis*	40	*Amaranthus blitoides*	26	*Aesculus hippocastanum*	47	***Robinia pseudoacacia***	27
Echinocystis lobata	23	*Juncus tenuis*	31	*Medicago sativa*	40	*Chenopodium ambrosioides*	26	*Picea abies*	47	*Paspalum dilatatum*	27
Medicago sativa	23	*Oenothera biennis*	31	***Solidago canadensis***	40	***Robinia pseudacacia***	26	*Epilobium brunnescens*	42	*Medicago sativa sativa*	27
Solidago canadensis	23	***Chamomilla suaveolens***	28	*Aster novi-belgii* group	36	*Amaranthus hybridus*	23	*Senecio viscosus*	42	*Sporobolus indicus*	25
Amaranthus retroflexus	20	*Xanthium spinosum*	28	*Cytisus scoparius*	36	*Cyperus eragrostis*	23	*Brassica rapa*	37	*Bromus catharticus*	23
Chamomilla suaveolens	20	*Ambrosia artemisiifolia*	25	*Lupinus polyphyllus*	36	*Euphorbia nutans*	23	*Claytonia perfoliata*	37	*Stenotaphrum secundatum*	23
Helianthus tuberosus	20	*Lycium barbarum*	25	***Chamomilla suaveolens***	36	*Euphorbia prostrata*	23	*Claytonia sibirica*	37	*Buddleja davidii*	22
Robinia pseudacacia	20	***Oxalis fontana***	25	***Oxalis fontana***	36	*Sporobolus indicus*	23	*Geranium pyrenaicum*	37	*Centranthus ruber* ssp. *ruber*	22
Veronica persica	20	***Robinia pseudacacia***	25	*Acorus calamus*	32	*Bidens frondosa*	19	*Cardaria draba*	37	***Veronica persica***	19
Galinsoga ciliata	17	***Solidago canadensis***	25	***Galinsoga parviflora***	32	*Bromus willldenowii*	19	*Rhododendron ponticum*	37	*Echinochloa crus-galli*	17
Hemerocallis fulva	17	*Amaranthus albus*	22	*Rumex thyrsiflorus*	32	*Coronopus didymus*	19	*Veronica filiformis*	37	*Baccharis halimifolia*	17
Juncus tenuis	17	*Cuscuta campestris*	22	***Veronica persica***	32	*Datura stramonium*	19	*Castanea sativa*	32	*Oxalis latifolia, Fallopia japonica, Dittrichia viscosa*	16

Table 4. *Most invaded habitat types by neophytes in different European regions according to vegetation database analyses. Habitat types are listed in decreasing order for particular region.*

Slovenia	Slovakia (Medvecka et al. 2014)	E Romania (Sîrbu et al. 2012)	Basque Country (Campos et al. 2013)	Catalonia (Chytrý et al. 2008)	Czech Republic (Chytrý et al. 2008)	Great Britain (Chytrý et al. 2008)	NW Poland* (Myśliwy 2014)	Hungary** (Botta-Dukát 2009)
I1	G1.C	G1.C, G5.2	A2	I1	H3	G3	I1.3	Riverine shrublands and woodlands
H5.6	E5.41	I1.5, J4, J6.1	C2.5 & C3.5	C3 & D5	E5.1	I1	H5.6	Open sand grasslands and poplar-juniper thickets
E5.4	E2.8	I1	E5.1 (*Balloto-Conion*)	H5.6	H5.6	B1 & B2	I1.5	Steppe woodlands
C1	I1	E5.4	G1	E5.1	I1	E5.1	J4.2	Mesic decidious woodlands in lowlands
E5.1	E5.1B	E5.6	E5.4	B1 & B2	C1	C3 & C5	E1	Eu- and mesotrophic wet meadows and sedge beds
F9.1	G1.1	H5.6	E5.1 (*Galio-Alliarion*)	F9	C3 & C5	G1 & G4	E2	Collin and montane hay meadows
F9.2	F3	C1	E2.2	E3 & E5.4	G5	FA	FA	Dry and semi-dry closed grasslands
C3	E5.43	C3, D5	G1.7	A2.5 & D6 & E6	F3	F3	E5.1	Dry, closed *Quercus* woodlands
E3	E5.1A		C3.3 & E3.1	C1	F9	E2	G5.1	Fens
E2	F9.21		E5.1 (*Convolvulo-Agropyrion*)	H2	A2 & D6 & E6	E3 & E5.4	E5.2 & E5.4	Mesic decidious woodlands of hills and mountains

* Based on floristic list made in EUNIS habitats as sampling unit.
** Based on grouped habitats in wider categories from MÉTA survey.

veolens, Solidago canadensis. It is important to bear in mind that vegetation databases store different data than floras or checklists (often missing casual alien species) and that this can limit the generalization of certain patterns or even lead to misleading conclusions (*15*). Although alien flora from vegetation plots of the same habitats differs between regions pattern of habitat invasion is determined by the characteristics of the habitat rather than the particular alien plant species (*18*).

Habitats rich in native species are predicted as also being more invasible (*38, 39*). Habitats with low number of native species indicate sites with environmental conditions that inhibit successful establishment of many native species as well as potential aliens (*40*). In Slovenia number of neophyte or archaeophyte species per plot are similar to the observed pattern in Catalonia (*14*) with highest numbers of alien species at intermediate numbers of native species.

Most of the invaded habitats in Slovenia, where on average almost every vegetation plot contains at least one neophyte (surface standing waters, anthropogenic herb stands, moist and wet forbs, riverine scrub, trampled areas and arable land) (Table 1) have also been found as the most invaded in other surveys (*13,15,16,18,41*). High level of invasion in most of these habitat types is probably a consequence of the intrinsic susceptibility to invasion due to the fluctuating resources (due to lessened competition and/or increased input of resources by natural or anthropogenic means) as hypothesized by Davis, et al. (*42*). Beside the habitats own susceptibility an important factor for higher alien species invasion is a strong and/or regular propagule pressure (*43*).

Differences in most invaded habitats between regions can be interpreted by regional differences in climate, topography and geology (*44*), land-use history (*45,46*) and introduction history (*47*) but also by differences in datasets (e.g. lack of urban habitats in Great Britain dataset, (*18*)) and scale of study (*15*).

Pattern across different regions is very similar with anthropogenous habitats being most invaded by alien species. In several countries forests are most invaded. In Slovakia, Romania and Hungary (Table 4) these are *Salix* dominated forests along rivers that are known as being very prone to invasion of alien species and good corridors for their spread (*48*). Temperate and boreal softwood riparian woodlands (G1.1) have by far the highest mean levels of invasion per plot among forest habitats in Europe (*33*). The reason that in Slovenia riparian forests are not as high on the list of invaded habitats is that we did not separate them as a particular category from other deciduous forests (as Chytrý, et al. (*18*)). Slovenia is the third most forested country in Europe with relatively well preserved forests. Nevertheless analysis of forest stands of Slovenia revealed that riparian forests (*Salix* and *Populus* forests) are the most invaded (*49*). In Slovenia standing waters are high on the list of invaded habitats. In our data set, neophyte species that occur in this habitat type are

mostly *Elodea canadensis* and occasionally *Rudbeckia laciniata, Solidago canadensis* and *S. gigantea*. Standing waters in the database are presented by plant communities (*Nyphaeetum albo-luteae* and *Ceratophyllo-Nupharetum*) in oxbows along Mura river. In Czech Republic the most frequently present neophyte in standing waters is also *Elodea canadensis* (*18*). For Slovenia according to floristic records Zelnik (*20*) states that the species is more common in running waters than in standing ones. Spicer and Catling (*50*) state that *E. canadensis* is more characteristic of eutrophic standing or slowly running waters (ponds, accumulation lakes, ditches) but a survey of the species in Slovenian watercourses (*51*) did not show that it is very invasive, but the invasion by *E. nuttallii* is expected (*20*). It seems *E. canadensis* mostly occupies standing waters, though it does not yet exhibit a tendency to cover larger surfaces. Special case of invasion of this habitat in Slovenia is *Pistia stratiotes* that survives in thermal stream (*52*) but this habitat is not included in vegetation database.

Coastal habitats are in Slovenia limited to few protected areas and the rest of the coast is highly urbanized by port industry and intensive tourism. Saline habitats are very prone to alien invasion but coastal regions can differ considerably in the level of the invasion. Coastal communities of Basque country are the most invaded habitat while saline habitats in Catalonia are less invaded and in Great Britain less invaded even in comparison to inland halophytic habitats in Czech Republic (Table 4). As saline habitats in Slovenia are localised and not open to free visit there is less disturbance and possible propagule pressure. Floristic data from Slovenia highlight only *Aster squamatus* and *Robinia pseudoaccacia* as invasive species in coastal wetlands (*20*).

CONCLUSION

The results of the invasion level across different habitat types using data from the Slovenian vegetation database show great similarity with other regions in Europe. Most invaded habitat types are those under strong human influence – arable land, trampled areas, anthropogenic herb stands; and some (semi-)natural habitats: riverine scrub and wet and moist tall herb stands. The composition of top most spread alien species is more similar to geographically closer regions (E Romania, Czech Republic) and a lot different than in more distant ones (Great Britain, Catalonia). Regarding the percentage of alien species that occur in more than a third of habitat types results place Slovenia amid other continental regions in Europe. Changes in the ratios (especially regarding neophytes) will be important for future research.

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Appendix: *All neophytes and archaeophytes in vegetation of Slovenia that occur in different EUNIS habitat types. Species are sorted alphabetically. ?-marks doubtful archaeophytes that were not included into analyses.*

Neophytes	Number	Archaeophytes		Number
Abutilon theophrasti	1	*Amaranthus lividus*		5
Acer negundo	2	*Anagallis foemina*	?	1
Acorus calamus	2	*Anthemis arvensis*	?	4
Aesculus hippocastanum	3	*Anthemis cotula*	?	5
Ailanthus altissima	2	*Arrhenatherum elatius*	?	12
Althaea hirsuta	1	*Artemisia absinthium*		2
Amaranthus albus	1	*Asparagus officinalis*	?	2
Amaranthus cruentus	2	*Berberis vulgaris*	?	6
Amaranthus deflexus	1	*Campanula rapunculus*	?	5
Amaranthus hybridus	4	*Capsella bursa-pastoris*	?	10
Amaranthus powellii	2	*Cardaria draba*	?	1
Amaranthus retroflexus	6	*Carduus acanthoides*		2
Ambrosia artemisiifolia	8	*Carduus nutans*	?	3
Antirrhinum majus	1	*Carduus pycnocephalus*	?	1
Artemisia verlotiorum	1	*Castanea sativa*		4
Asclepias syriaca	1	*Celtis australis*		2
Aster novae-angliae	1	*Centaurea cyanus*		3
Atriplex hortensis	1	*Chaerophyllum bulbosum*	?	1
Barbarea intermedia	1	*Chelidonium majus*	?	9
Bidens cernua	2	*Chenopodium album agg.*	?	8
Bidens frondosa	4	*Chenopodium ficifolium*		2
Buddleja davidii	1	*Chenopodium murale*		2
Cerastium tomentosum	1	*Chenopodium opulifolium*		1
Chamomilla suaveolens	6	*Chondrilla juncea*	?	1
Chenopodium ambrosioides	2	*Cichorium intybus*	?	11
Cirsium helenioides	1	*Cirsium arvense*		14
Commelina communis	3	*Cirsium vulgare*	?	13
Consolida ajacis	1	*Consolida regalis*		2
Conyza albida	1	*Cornus mas*	?	4
Conyza bonariensis	2	*Corylus avellana*	?	15
Conyza canadensis	11	*Cynodon dactylon*		7
Coronopus didymus	1	*Dactylis glomerata*		20
Datura stramonium	1	*Digitaria ischaemum*	?	3
Deutzia scabra	1	*Digitaria sanguinalis*	?	6
Draba muralis	1	*Dipsacus fullonum*	?	4
Duchesnea indica	3	*Dipsacus laciniatus*	?	3
Echinocystis lobata	7	*Dipsacus pilosus*	?	1
Eleusine indica	3	*Eragrostis minor*	?	4
Elodea canadensis	2	*Eragrostis pilosa*	?	2
Erigeron annuus	17	*Euphorbia exigua*	?	1
Erucastrum gallicum	1	*Euphorbia falcata*	?	3
Euphorbia humifusa	2	*Euphorbia helioscopia*		5
Euphorbia lathyris	1	*Euphorbia peplus*	?	4
Euphorbia maculata	2	*Foeniculum vulgare*	?	3
Euphorbia nutans	1	*Galeopsis tetrahit*	?	6
Fallopia sachalinensis	1	*Galium tricornutum*	?	1
Fraxinus americana	1	*Hedysarum hedysaroides*	?	5
Galeobdolon argentatum	1	*Hesperis candida*	?	5
Galinsoga ciliata	5	*Humulus lupulus*	?	9
Galinsoga parviflora	10	*Kickxia elatine*	?	1
Galium saxatile	1	*Kickxia spuria*	?	2
Helianthus tuberosus	6	*Lactuca viminea*	?	1
Hemerocallis fulva	5	*Logfia arvensis*	?	1
Impatiens glandulifera	8	*Logfia minima*	?	1
Impatiens parviflora	8	*Mentha pulegium*	?	5
Juncus tenuis	5	*Mentha spicata*		1
Lepidium virginicum	3	*Microrrhinum litorale*	?	2
Lindernia dubia	1	*Misopates orontium*	?	2
Lupinus polyphyllus	1	*Myosotis arvensis*	?	9
Mahonia aquifolium	1	*Nepeta cataria*	?	1
Medicago sativa	7	*Onobrychis arenaria*	?	2
Narcissus pseudonarcissus	1	*Onobrychis viciifolia*	?	2
Nycandra physalodes	1	*Physalis alkekengi*	?	4
Ornithogalum nutans	1	*Picris echioides*	?	4
Oxalis articulata	1	*Picris hieracioides*	?	13
Oxalis fontana	9	*Portulaca oleracea*		4
Panicum capillare	4	*Ranunculus arvensis*	?	2
Panicum dichotomiflorum	1	*Raphanus raphanistrum*	?	3
Parthenocissus inserta	2	*Rapistrum rugosum*	?	1
Parthenocissus quinquefolia	3	*Reseda luteola*	?	1
Phalaris canariensis	1	*Ribes nigrum*	?	2
Philadelphus coronarius	1	*Rumex crispus*	?	11
Phytolacca americana	1	*Salvia verticillata*	?	4
Pinus strobus	1	*Scandix pecten-veneris*	?	1
Polygonum orientale	1	*Sclerochloa dura*	?	1
Populus canadensis	1	*Sempervivum tectorum*	?	4
Ribes rubrum	2	*Setaria pumila*		7
Robinia pseudacacia	6	*Setaria verticillata*		1
Rudbeckia hirta	1	*Setaria viridis*	?	8
Rudbeckia laciniata	11	*Sisymbrium orientale*	?	2
Salvinia natans	1	*Tanacetum vulgare*	?	10
Sarothamnus scoparius	2	*Trifolium repens*	?	17
Scirpus georgianus	1	*Trisetum flavescens*	?	10
Sedum spurium	1	*Valerianella carinata*	?	1
Senecio inaequidens	1	*Valerianella dentata*	?	1
Sisyrinchium bermudiana agg.	1	*Verbena officinalis*	?	12
Solanum lycopersicum	2	*Veronica agrestis*	?	2
Solanum tuberosum	2	*Veronica polita*	?	3
Solidago canadensis	7	*Veronica triphyllos*	?	1
Solidago gigantea	16	*Vicia dasycarpa*	?	1
Tagetes erecta	1	*Vicia sativa*	?	3
Tagetes minuta	1	*Vicia striata*	?	1
Tanacetum parthenium	1			
Thuja orientalis	1			
Trifolium incarnatum	1			
Veronica filiformis	1			
Veronica persica	6			
Viola cornuta	1			
Xanthium italicum	2			