WHY ARE SOME PLANT SPECIES BECOMING EXTINCT WHILE OTHERS SPREADING?

ANDRZEJ URBISZ

Institute of Biology, Faculty of Natural Sciences, Biotechnology and Environmental Protection University of Silesia in Katowice, ul. Jagiellońska 28, 40-032 Katowice, Poland
Corresponding email: andrzej.urbisz@us.edu.pl

Abstract

The research was carried out in the Kraków-Częstochowa Jurassic Upland (Southern Poland). Two groups of plants were distinguished in the vascular flora of this area, each consisting of 32 species: probably extinct and invasive. All species were described in respect of 33 traits related to their morphology, anatomy, reproduction biology, phenology, chorology, taxonomy, habitat requirements, life strategy and response to human impact. The objective of this study is to answer the question which traits of plant species determine their extinction or spreading. To demonstrate statistically significant differences between invasive and extinct species, Pearson's chi-square test was applied. The statistically significant differences were found for 16 traits. The compared groups of plants differed the most in terms of stem height, human use, the degree of hemeroby, urbanity, the number of sites, types of plant communities in which they occur, the nitrogen content in the substrate and the life strategy. Statistically significant differences were also determined for the pollination method, anatomical structure of leaves, dicliny, the type and weight of a diaspore, duration of the flowering period, taxonomic affinity with a family and the soil moisture value. It has been found that invasive species are mostly medium-sized plants (0.5–2 m high), often cultivated by man, abundant on anthropogenic habitats; they are nitrophilous, mesophilic, self-pollinating and C-strategists. On the other hand, extinct species are up to 0.5 m high. They are not crop plants and occur mostly on natural and semi-natural habitats, on substrates with low content of nitrogen and they are CSR-strategists.

Key words: Plant traits, Extinct species, Invasive species, Vascular plants, Poland.

Introduction

In recent years, many researchers have drawn attention to the declining biodiversity all over the world. Many species are not able to adapt to large-scale intensive environmental changes, caused mainly by human activity. On the other hand, some species referred to as invasive increase their range of occurrence, and often adapt to new habitats. They are defined as species of alien origin, established in an initially alien region, produce viable progeny, often in large numbers, and spread over a considerable distance from their parent plants (Pyšek *et al.*, 2004). Invasive species pose a widely recognised threat to biodiversity (e.g. Sax *et al.*, 2002; Gurevitch & Padilla, 2004; Sax & Gaines, 2008; Khan *et al.*, 2010; Downey & Richardson, 2016; Bomanowska *et al.*, 2017). Along with the use of biological resources, alien species have been identified as the most important cause of species extinction (Bellard *et al.*, 2016). Even though the number of hitherto extinct plant species is not large on the global scale, it seems that the near future may witness its rapid growth (Gilbert & Levine, 2013). Many scientists have been trying to determine which traits cause the spread or extinction of species (e.g. Lodge, 1993; McKinney, 1998; McKinney & Lockwood, 1999; Moravcova *et al.*, 2015). Results of this research are not always explicit and unambiguous (Kolar & Lodge, 2001). Successful colonisation of new areas results not only from various species traits related to their habit, taxonomic affinity, genetic variability, reproduction, habitat requirements, but also from the way they are used by man and the stage of their invasion (or extinction).

The objective of this study was to determine which of the 33 traits analysed (Tables 1 and 2) differentiate the extinct species from the invasive ones to the greatest extent.

Materials and Methods

Study area: The Kraków-Częstochowa Jurassic Upland, also known as the Polish Jurassic Highland, is a 2,615 km^2 macroregion, situated in southern Poland, between the city of Kraków and the city of Częstochowa – Fig. 1 (Kondracki, 1988).

The landscape features characteristic limestone rocks, deposited by the Upper Jurassic sea ca. 150 m years ago. The average altitude ranges from 300 to 450 m a.s.l., and the highest point is Mt Góra Zamkowa (Castle Mountain) (515 m a.s.l.).

The soil cover consists mainly of poor podzolic soils, developed from sand and loam. More fertile brown soils, formed on loess, dominate only in the central and eastern parts. Nutrient-rich calcareous rendzinas, associated mainly with limestone rocks, are also common here (Musierowicz, 1961).

The Kraków-Częstochowa Jurassic Upland is located at the border between watersheds of the Vistula and the Oder – the main rivers in Poland. There are no large water bodies in the study area, and the network of surface watercourses is relatively scarce.

The climatic conditions vary. The mean annual precipitation in the northern part is 600–700 mm, and 700–800 mm in the southern part of the study area. The average annual temperature is about 7.5°C; the coldest month is January (mean temperature –3°C) and the warmest – July (17°C). The average snow cover duration is about 80 days; the growing season lasts on average 210 days in the western part of the area and 200 days in the east (Kruczała, 2000).

Table 1. Values of chi-square distribution (χ^2) for the analysed traits of the extinct and invasive species in the study area (df – number of degrees of freedom, p – significance level).

No.	Trait name		χ^2	
1.	Life form	16.74026	df=9	p=.05294
2.	Stem height (cm)	25.26654	df=4	p=.00004***
3.	Leaf persistence	5.396364	df=2	p=.06733
4.	Leaf anatomy	19.82455	df=9	p=.01903*
5.	Leaf form	13.31890	df=11	p=.27299
6.	Life span	10.85812	df=5	p=.05427
7.	Pollination type	23.39478	df=10	p=.00938**
8.	Seed dispersal type	27.23861	df=18	p=.07463
9.	Type of reproduction	4.615385	df=4	p=.32908
10.	Dicliny	9.904762	df=4	p=.04206*
11.	Fruit type	14.46377	df=8	p=.07045
12.	Diaspore type	19.76381	df=8	p=.01127*
13.	Diaspore weight (mg)	9.538653	df=4	p=.04896*
14.	Duration of flowering (months)	12.96381	df=6	p=.04361*
15.	Basic chromosome number	4.476191	df=4	p=.34538
16.	Maximum ploidy level	4.411956	df=5	p=.49175
17.	Cultivation	29.09091	df=1	p=.0000***
18.	Hemeroby	60.00000	df=9	p=.00000***
19.	Urbanity	41.72107	df=4	p=.00000***
20.	Number of localities	60.12121	df=4	p=.00000***
21.	Number of inhabited floristic zones (natural range)	9.683761	df=6	p=.13862
22.	Family	42.23077	df=27	p=.03123*
23.	Number of species within the genus (in the world)	3.401399	df=4	p=.49303
24.	Number of species within the genus (in the study area)	2.526316	df=4	p=.63993
25.	Plant sociology (class)	44.29139	df=16	p=.00018***
26.	Light value (L)	7.730397	df=7	p=.35697
27.	Temperature value (T)	10.00751	df=5	p=.07502
28.	Continentality value (K)	2.839890	df=5	p=.72465
29.	Moisture value (F)	20.59024	df=9	p=.01460*
30.	Reaction of soil value (R)	12.45989	df=8	p=.13183
31.	Nitrogen value (N)	34.33485	df=8	p=.00004***
32.	Salinity value (S)	4.105263	df=2	p=.12840
33.	Life strategy	44.73693	df=6	p=.00000***

Fig. 1. Location of the study area.

Data analyses: Two groups of plants were distinguished in the vascular flora of the Kraków-Częstochowa Jurassic Upland (Urbisz, 2004, 2008), each consisting of 32 species (Table 2): 1) probably extinct species in this area and 2) invasive species. Invasive species are listed after Tokarska-Guzik *et al.* (2012), whereas species whose presence in the study area has not been confirmed after 1980 are considered extinct (Urbisz, 2004, 2008).

All species were studied in terms of 33 selected traits (Frank & Klotz, 1990; Ellenberg *et al.*, 1992; Klotz *et al.*, 2002; Rutkowski, 2004; Urbisz, 2004; The Plant List, 2013) related to their morphology, anatomy, reproduction biology, phenology, chorology, taxonomy, habitat requirements, life strategy and response to human impact (Tables 1 and 2).

To demonstrate statistically significant differences between invasive and probably extinct species, Pearson's chi-square test was applied (StatSoft, 2014). The significance levels were defined as follows: * = p<0.05, ** = p<0.01 and *** = p<0.001.

Table 2. Differentiation of the studied species based on the analysed traits.

Species name																				Trait numbers													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
Extinct species																																	
Anacamptis pyramidalis	G	II	s	m	lang	p	i	w	s	so	ka	s	n/a	2	IV	2	0	om	1	1	3	or	II	I	FB	8	7	2	3	9	2	0	csr
Astragalus arenarius	H	I	n/a	n/a	gefie	p	i	wev	s	so	hu	s	n/a	2	II	2	0	om	1	1	1	fa	V	II	SS	7	7	7	2	7	1	0	cs
Bupleurum falcatum	H	III	s	ms	lang	p	is	ewhm	s	so	spf	tf	IV	3	II	2	0	om	1	1	3	ap	IV	II	TG	6	6	6	3	9	3	0	csr
Carex arenaria	G	II	i	s	gras	p	w	wes	vvs	so	nu	fzb	III	6	I	2	0	omb	2	1	3	cy	V	V	SS	6	6	2	3	2	2	1	cs
Catabrosa aquatica	H	II	w	em	gras	p	w	we	sv	so	nu	fzb	II	4	II	6	0	om	1	1	1	po	I	I	BT	8	5	5	9	7	8	1	cs
Cerastium brachypetalum	H,T	I	w	s	norm	a	is	wh	s	gm	ka	s	I	3	IV	5	0	omb	2	1	3	ca	IV	III	SS	9	7	4	3	8	2	0	sr
Dactylorhiza sambucina	G	I	s	m	lang	p	i	w	s	so	ka	s	n/a	3	IV	2	0	om	1	1	3	or	III	III	FB	7	5	4	4	5	2	0	csr
Drosera anglica	H	I	s	c	lang	p	sk	w	sv	so	ka	s	I	2	II	4	0	ao	1	1	3	dr	IV	II	SC	8	4	3	9	3	2	0	s
Eleocharis ovata	T	I	w	e	rohr	a	w	we	s	so	nu	fzb	I	3	I	2	0	om	2	1	3	cy	IV	III	IN	8	6	4	8	n/a	5	0	r
Festuca altissima	H	III	w	m	gras	p	w	we	s	so	nu	fzb	III	2	II	2	0	om	2	1	2	po	V	IV	QF	3	5	3	5	4	6	0	cs
Gentiana asclepiadea	H	III	n/a	n/a	norm	p	i	w	sv	so	ka	s	I	3	III	4	0	m	1	1	2	ge	V	II	MA	7	n/a	4	6	7	2	0	c
Gratiola officinalis	H	I	w	e	norm	p	i	w	sv	so	ka	s	I	3	II	4	0	om	1	1	3	sc	II	I	MA	7	7	5	8	7	4	1	csr
Hieracium echioides	H	III	w	m	lang	p	isa	wea	s	so	nu	fzb	I	2	II	4	0	om	1	1	3	as	V	IV	SS	8	6	6	2	6	1	0	csr
Hydrocotyle vulgaris	H	II	w	ey	voll	p	s		sv	so	spf	f, tf	II	2	III	8	0	om	1	1	3	hy	IV	I	SC	7	5	2	9	3	2	1	s
Lathyrus montanus	G	I	s	m	gefie	p	i	s	sv	so	hu	s	V	3	II	2	0	om	1	1	2	fa	IV	III	QF	n/a	5	2	5	3	2	0	csr
Lathyrus palustris	H	III	s	m	gefie	p	i	s	sv	so	hu	s	I	2	II	6	0	om	1	1	4	fa	IV	III	MA	8	6	n/a	8	8	3	0	csr
Linosyris vulgaris	H	II	s	ms	gras	p	is	we	sv	so	nu	fzb	IV	2	II	4	0	om	1	1	2	as	I	I	FB	8	7	5	2	8	2	0	csr
Montia fontana	H,T	I	w	e	lang	ap	s	s	sv	so	ka	s	IV	3	II	2	0	omb	1	1	8	por	II	I	IN	8	4	2	9	5	4	0	r
Orchis coriophora	G	I	n/a	n/a	lang	p	i	w	s	so	ka	s	n/a	2	IV	2	0	om	1	1	3	or	II	III	MA	8	7	4	7	4	2	0	csr
Orchis palustris	G	II	n/a	n/a	lang	p	i	w	s	so	ka	s	I	2	V	2	0	om	1	1	3	or	II	III	SC	9	6	5	9	8	2	1	csr
Orchis ustulata	G	II	s	ms	lang	p	i	w	sv	so	ka	s	n/a	2	V	2	0	om	1	1	2	or	II	III	FB	7	5	5	4	n/a	3	0	csr
Potamogeton acutifolius	A	II	w	a	lang	ap	wh	h	sv	so	sastf	fch	n/a	3	III	2	0	n/a	n/a	1	2	pot	III	IV	P	7	6	4	11	5	6	0	n/a
Potamogeton nodosus	A	IV	w	a	lang	p	wh	h	vvs	so	sastf	fch	n/a	3	III	4	0	n/a	n/a	1	5	pot	III	IV	P	6	6	5	12	8	5	0	n/a
Pulsatilla pratensis	H	I	s	ms	mgef	p	i	we	s	so	samu	fch	V	2	II	2	0	om	1	1	1	ra	III	II	FB	7	6	5	2	7	2	0	csr
Pulsatilla vernalis	H	I	i	ms	gefie	p	i	we	s	so	sanu	fch	n/a	3	II	2	0	om	1	1	3	ra	III	II	PP	7	n/a	5	4	5	2	0	csr
Rhynchospora fusca	H,G	I	s	e	gras	p	w	e	sv	so	nu	fzb	II	2	IV	2	0	ao	1	1	3	cy	V	II	SC	8	5	2	9	1	2	0	s
Spiranthes spiralis	G,H	I	s	ms	schup	p	i	w	s	so	ka	s	I	3	III	2	0	om	1	1	3	or	III	I	FB	8	6	2	4	5	2	0	csr
Thesium ebracteatum	G	I	n/a	n/a	lang	p	i	va	sv	so	nu	fzb	n/a	2	II	4	0	om	1	1	2	sa	IV	II	SS	7	3	6	4	2	2	0	n/a
Traunsteinera globosa	G	II	s	m	lang	p	i	w	s	so	ka	s	n/a	2	V	2	0	om	1	1	2	or	I	I	SA	7	3	4	5	8	3	0	csr
Veronica catenata	H,T	II	n/a	lang	voll	a	is	whas	sv	so	ka	s	I	5	II	4	0	omb	1	1	3	sc	V	IV	BT	8	7	3	9	7	7	0	cs
Veronica praecox	T	I	w	ms	voll	a	is	wha	s	so	ka	s	I	3	II	2	0	om	1	1	3	sc	V	IV	SS	8	8	5	2	8	1	0	sr
Zannichellia palustris	A	II	i	a	graz	p	h	e	sv	mo	sastf	fch	n/a	5	II	4	0	n/a	n/a	1	7	za	I	I	R	6	6	5	12	8	8	5	n/a

Table 2. (Cont'd).

Species name	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
												Trait numbers																					
											Invasive species																						
Acer negundo	P	V	s	m	gefie	p	iw	w	sv	do	spf	tf	V	1	III	2	2	0	mb	4	IV	ac	IV	III	QF	(5)	6	6	6	7	7	0	c
Amaranthus retroflexus	T	II	s	m	voll	p	iw	we	s	mo	ka	s	II	3	IV	2	2	1	mbcp	3	III	am	III	III	C	5	7	6	4	2	7	1	cr
Anthoxantum aristatum	T	I	w	m	gras	a	w	we	s	so	nu	fzb	II	3	II	2	2	0	mbc	3	II	po	II	II	S	7	6	2	n/a	2	3	0	r
Aster novi-belgii	H	III	s	m	lang	p	is	we	sv	gm	nu	fzb	II	2	III	6	6	1	bc	4	IV	as	IV	III	A	9	6	2	6	7	9	0	c
Bidens frondosa	H,G	III	s	em	gefie	a	is	e	s	so	nu	fzb	V	2	II	4	4	0	mbcp	3	III	as	III	III	BT	7	6	n/a	5	7	8	0	cr
Bunias orientalis	H,T	III	s	m	fied	a	is	we	s	gm	nu	f	I	4	II	2	2	0	bcp	2	V	br	IV	I	C	5	6	5	n/a	4	5	0	cr
Conyza canadensis	T	V	s	n/a	gelap	a	i	v	v	mo	be	f	I	3	II	2	2	0	mbcp	2	V	as	IV	I	A	7	8	n/a	n/a	8	7	0	cr
Echinocystis lobata	A	IV	w	a	lang	a	n/a	sh	v	do	v	v	n/a	4	III	4	4	1	n/a	n/a	II	cu	I	I	P	7	7	5	9	8	7	0	n/a
Elodea canadensis	H	III	w	n/a	lang	p	is	w	sv	so	ka	s	I	4	IV	2	3	0	mbcp	3	III	hych	IV	IV	n/a	7	6	n/a	12	5	7	0	c
Epilobium ciliatum	H	III	n/a	ym	norm	bp	is	wea	s	gm	nu	f,fzb	n/a	4	II	3	3	0	mb	3	IV	on	II	II	A	7	7	4	5	5	6	0	cr
Erigeron annuus	T	II	s	ym	voll	a	is	wea	s	so	nu	fzb	I	6	III	4	4	0	cp	3	V	as	II	II	C	7	7	3	4	5	7	0	c
Galinsoga ciliata	T	II	s	m	voll	a	is	wea	s	so	v	v	I	6	IV	6	4	0	cp	3	V	as	III	I	A	7	6	n/a	6	7	5	0	c
Galinsoga parviflora	G	IV	s	m	voll	p	is	wesm	vvs	so	spf	tf	n/a	3	III	2	2	1	bc	3	II	ap	III	II	n/a	8	7	n/a	6	8	5	0	c
Helianthus tuberosus	H	V	w	m	gefie	bh	is	ewm	s	so	ka	s	V	3	III	2	2	0	mb	3	II	ba	V	II	C	9	7	2	2	8	7	0	c
Heracleum mantegazzianum	H	IV	s	ye	norm	a	i	s	s	so	ka	s	V	2	II	2	2	0	mbcp	2	V	ba	V	II	QF	5	5	5	5	6	n/a	0	sr
Impatiens glandulifera	T	II	s	y	norm	a	i	s	s	so	ka	s	V	2	III	4	4	0	mbc	2	V	ba	V	II	PI	6	6	5	6	5	n/a	0	sr
Impatiens parviflora	H	II	w	m	rohr	p	w	e	ssv	so	ka	s	I	4	IV	2	2	1	bc	1	IV	ju	V	IV	C	6	7	3	3	4	5	0	csr
Juncus tenuis	H,T	III	s	m	gras	abh	w	we	s	so	nu	fzb	V	3	III	4	4	0	bc	3	IV	po	V	III	EA	8	5	4	5	4	8	0	c
Lolium multiflorum	H	IV	n/a	n/a	gefin	p	i	s	sv	so	hu	s	V	3	III	4	4	0	mb	3	IV	fa	IV	I	QF	5	7	5	5	5	n/a	0	c
Lupinus polyphyllus	N	IV	s	ms	lang	p	is	v	v	so	be	f	n/a	4	III	4	4	0	mbc	4	III	so	IV	I	FB	9	8	6	6	3	4	0	c
Lycium barbarum	H	II	s	m	gefie	p	is	e	sv	so	hu	f	I	5	III	4	4	0	mb	3	IV	fa	IV	I	C	8	7	3	3	8	3	0	c
Onobrychis viciifolia	G,T	II	s	y	gefin	p	is	v	sv	so	ka	s	I	3	II	4	4	0	cp	1	IV	ox	V	II	n/a	6	6	3	5	6	5	0	r
Oxalis fontana	N,P	V	s	m	norm	p	is	v	ssv	so	stf	f	n/a	3	II	4	4	0	mb	2	IV	ro	II	II	n/a	8	6	n/a	5	5	n/a	0	c
Padus serotina	G	IV	w	em	norm	p	wis	wem	vvs	gd	nu	fzb	n/a	3	III	8	8	1	mbcp	3	IV	pol	I	II	n/a	8	7	2	2	5	7	0	c
Reynoutria japonica	G	IV	s	em	norm	p	wis	wem	v	do	nu	fzb	II	3	III	2	2	1	mbcp	3	V	pol	I	II	A	7	6	4	4	8	7	0	c
Reynoutria sachalinensis	P	IV	s	me	gefie	p	i	vw	sv	so	hu	s,tf	V	2	II	2	2	0	mbc	2	V	fa	II	I	A	8	6	5	5	8	7	0	c
Robinia pseudacacia	H,G	IV	w	m	fied	is	is	weas	sv	so	nu	fzb	V	3	IV	4	4	0	bcp	3	III	as	IV	III	A	6	6	5	n/a	n/a	6	0	c
Rudbeckia laciniata	H,G	IV	w	m	lang	is	is	wea	sv	gm	nu	fzb	I	3	II	6	6	0	mbc	2	IV	as	IV	III	A	8	6	5	6	n/a	7	0	c
Solidago canadensis	H,G	III	w	m	lang	is	is	wea	sv	gm	nu	fzb	I	2	II	4	4	0	mbc	5	IV	as	IV	IV	A	8	6	6	7	7	7	0	c
Solidago gigantea	H,G	III	w	m	lang	a	is	wha	s	so	ka	s	III	12	II	4	4	0	bcp	3	V	sc	V	IV	C	8	n/a	3	5	5	7	0	cr
Veronica persica																																	

Explanations to table 2: 1. life form (Frank & Klotz, 1990): A – hydrophyte, G – geophyte, H – hemicryptophyte, N – nanophanerophyte, P – phanerophyte, T – therophyte; 2. stem height in cm (Rutkowski, 2004): I – <25, II – 25-50, III – 51-100, IV – 101-200, V – >200; 3. leaf persistence (Klotz et al., 2002): i – persistent green, s – summer green, w – overwintering green; 4. leaf anatomy (Klotz et al., 2002): a – hydromorphic, c – succulent, e – helomorphic, m – mesomorphic, s – scleromorphic, y – hygromorphic; 5. leaf form (Klotz et al., 2002): fied – pinnatifid, gefie – pinnate, gelap – lobate, gras – grass-like, lang – long-leaf, mgef – bipinnate, norm – simple, rohr – tubular, schup – scale-like, voll – full; 6. life span (Klotz et al., 2002): a – annual, b – biennial, h – pluriennial-hapaxanthic, p – pluriennial-pollakanthic; 7. pollination type (Frank & Klotz, 1990): a – apogamy, h – hydrophily, i – entomophily, k – cleistogamy, s – self-pollination, w – anemophily; 8. seed dispersal type (Frank & Klotz, 1990): a – myrmecochory, e – epizoochory, h – hydrochory, m – anthropochory, s – autochory, v – endozoochory, w – anemochory; 9. type of reproduction (Klotz et al., 2002): s – by seed/by spore, ssv – mostly by seed, rarely vegetatively, sv – by seed and vegetatively, v – vegetatively, vvs – mostly vegetatively, rarely by seed; 10. dicliny (Klotz et al., 2002): do – dioecious, gd – gynodioecious, gm – gynomonoecious, mo – monoecious, sru – hermaphroditic; 11. fruit type (Klotz et al., 2002): be – berry, hu – legume, ka – capsule, nu – nut, Po – pome, sanu – aggregate nutlets, sastf – aggregate drupelets, spf – schizocarp, stf – drupe, v – vegetative; 12. diaspore type (Klotz et al., 2002): f – fruit, fch – fruitlet, fzb – fruit with appendage, s – seed, tf- mericarp, v – vegetative; 13. diaspore weight in mg (Klotz et al., 2002): I – <0.25, II – 0.25-0.5, III – 0.51-1.0, IV – 1.01-2.0, V – >2.0; 14. basic chromosome number (Klotz et al., 2002): 1-12; 15. maximum ploidy level (Klotz et al., 2002): 2 – diploid, 3 – triploid, 4 – tetraploid, 5 – pentaploid, 6 – hexaploid, 8 – octoploid; 17. cultivation (Rutkowski, 2004): 0 – no, 1 – yes; 18. hemeroby (Klotz et al., 2002): a – ahemerobic, b – b-euhemerobic, c – a-euhemerobic, m – mesohemerobic, o – oligohemerobic, p – polyhemerobic, t – metahemerobic; 19. urbanity (Klotz et al., 2002): 1 – urbanophobic, 2 – moderately urbanophobic, 3 – urbanoneutral, 4 – moderately urbanophilic, 5 – urbanophilic; 20. number of localities (Urbisz, 2004): I – <11, II – 11-30, III – 31-90, IV – 91-270, V – >270; 21. number of inhabited floristic zones in natural range (Klotz et al., 2002): 1-8; 22. family (Mirek i in., 2002): ac – Aceraceae, am – Amaranthaceae, ap – Apiaceae, as – Asteraceae, ba – Balsaminaceae, br – Brassicaceae, ca – Caryophyllaceae, cu – Cucurbitaceae, cy – Cyperaceae, dr – Droseraceae, fa – Fabaceae, ge – Gentianaceae, hy – Hydrocotylaceae, hych – Hydrocharitaceae, ju – Juncaceae, on – Onagraceae, or – Orchidaceae, ox – Oxalidaceae, po – Poaceae, pol – Polygonaceae, por – Portulacaceae, pot – Potamogetonaceae, ra – Ranunculaceae, ro – Rosaceae, sa – Santalaceae, sc – Scrophulariaceae, so – Solanaceae, za – Zannichelliaceae; 23. number of species within the genus (The Plant List, 2013): I – <11, II – 11-30, III – 31-90, IV – 91-270, V – >270; 24. number of species within the genus in the study area (Urbisz, 2004): I – 1, II – 2-3, III – 4-9, IV – 10-27, V – >27; 25. plant sociology (Ellenberg et al., 1992): A – Artemisietea, BT – Bidentetea tripartiti, C – Chenopodietea, EA – Epilobietea angustifolii, FB – Festuco-Brometea, IN – Isoëto-Nanojuncetea, MA – Molinio-Arrhenatheretea, P – Potamogetonetea, Pl – Plantaginetea, PP – Pulsatillo-Pinetea, QF – Querco-Fagetea, Pl – Plantaginetea, S – Secalietea, SA – Sesleritea albicantis, SC – Scheuchzerio-Caricetea, SS – Sedo-Scleranthetea, TG – Trifolio-Geranietea sanguinei; 26. light value (Ellenberg et al., 1992): 1(deep shade)-9 (full light); 27. temperature value (Ellenberg et al., 1992): 1(alpine-subnival)-9 (Mediterranean); 28. continentality value (Ellenberg et al., 1992): 1(euoceanic)-9 (eucontinental); 29. moisture value (Ellenberg et al., 1992): 1(strong soil dryness)-12(underwater); 30. reaction of soil value (Ellenberg et al., 1992): 1(extremely acidic)-9 (alkaline); 31. nitrogen value (Ellenberg et al., 1992): 1(least)-9 (excessive supply); 32. salinity value (Ellenberg et al., 1992): 0(no)-9 (extreme salinity); 33. life strategy (Frank & Klotz, 1990): c – competitors, cr –competitors/ ruderals, cs –competitors/stress-tolerators, csr – competitors/stress-tolerators/ruderals, r – ruderals, s – stress-tolerators, sr – stress-tolerators/ruderals; n/a – data not available

Results and Discussion

Of the 33 analysed traits of extinct and invasive species, statistically significant differences were determined for 16 traits (Table 1). The largest differences (p<0.001) between the compared groups of plants were found for the stem height, the human use, the degree of hemeroby, urbanity, the number of sites, types of plant communities in which they occur, the nitrogen content in the substrate and the life strategy.

Extinct species rarely reach a height of more than 0.5 m (e.g. *Bupleurum falcatum*, *Festuca altissima*, *Gentiana asclepiadea*), which is the almost lower limit of invasive species, only one invasive species (*Anthoxantum aristatum*) has a stem less than 25 cm high. None of the 32 species that are probably extinct in the study area is commonly cultivated, while as many as 20 of the 32 invasive species are (or were recently) planted by man. Extinct species are mainly oligo- and mesohemerobic – those are mostly urbanophobes. Invasive species, on the other hand, are meso- and euhemerobic, mostly urbanoneutral. The largest number of localities, at which currently extinct species occurred in the past is 6, while 18 invasive species occur at least at 100 sites, and only one species (*Solidago graminifolia*) has fewer than 10 sites. All extinct species belong to natural or seminatural phytosociological classes, while as many as 19 invasive species are classified into syntaxa comprising anthropogenic communities and another 6 invasive species (*Epilobium ciliatum*, *Heracleum mantegazzianum*, *Padus serotina*, *Reynoutria japonica*, *R. sachalinensis* and *Robinia pseudacacia*) do not show any definite phytosociological affinity. The compared groups of species very clearly differ in their requirements regarding the nitrogen content in the substrate. Almost all extinct species are confined to nitrogen-poor habitats, while invasive species are nitrophilous. An important trait that differentiates extinct from invasive species is the type of life strategy. While the former group (15) is dominated by CSR-strategists, most of the species (20) in the latter are C-strategists (Table 2).

Statistically significant differences between the compared groups of species were also found for the pollination method (p<0.01), anatomical structure of leaves, dicliny, the type and weight of a diaspore, duration of the flowering period, taxonomic affinity with a family and the soil moisture value (p<0.05) – Table 1.

Most of the extinct species were pollinated exclusively by insects. While invasive species can be pollinated by insects, but are self-pollinated also (e.g. *Bidens frondosa*, *Conyza canadensis*, *Helianthus tuberosus*, *Heracleum mantegazzianum*, *Padus serotina*, *Solidago canadensis*, *S. gigantea*). Among the invasive species, plants with mesomorphic leaves (17 spp.) dominate, while extinct species are more diverse in this respect. Almost all extinct species (30 spp.) have bisexual flowers, while 8 invasive species have unisexual flowers. A seed is the dominant type of diaspore in extinct species, while in invasive species it is a piece of fruit connected with other parts of the plant (e.g. corolla, calyx or stipules). Diaspores were found to weigh more than 2 mg

in the case of 12 invasive species, and in only 2 extinct ones (*Lathyrus montanus*, *Pulsatilla pratensis*). On the other hand, a short flowering period (up to 2 months) occurs in as many as 15 extinct species, and in only 7 invasive species. Most of the extinct species belong to the family Orchidaceae, while invasive species belong to Asteraceae. While invasive species occur most frequently on habitats with medium moisture content (F=5–8), nine extinct species occur on dry habitats (F=2–3) and 10 species occur on very humid habitats or are aquatic plants (F=9–12) – Table 2.

When trying to answer the question what traits cause one plant species extinct while another become invasive, it should be considered that it is not a single trait but their entire complex. Furthermore, the analysed traits are very diverse. Some of them are closely related to the morphology and anatomy of a given species and the way it propagates, while others are related to its habitat, life strategy, taxonomic affinity, frequency of occurrence or the use by man.

The obtained results confirm that invasive species are statistically taller than the extinct ones. Most of the former are 0.5–2 m tall, allowing them to compete effectively with most of the native herbaceous species. This relationship is also confirmed by other authors (Moravcova et al., 2015; Pyšek et al., 2015). According to Williamson & Fitter (1996), invasive species are also characterised by a larger leaf surface area, higher proportion of phanerophytes and species with the height greater than the width. Although statistically no significant difference was determined in the present research for life forms between the compared groups of species, the obtained p value (0.05294) is only slightly higher than that required for its determination. Four phanerophytes were identified in the group of invasive species (*Acer negundo*, *Lycium barbarum*, *Padus serotina* and *Robinia pseudacacia*) and none in the group of the extinct ones. Lavergne et al. (2004) compared pairs of species from the Mediterranean region of France belonging to the same genera, one endemic and one widespread species. Endemic species were found in the vegetation layers of a lower height, smaller vegetation cover and with a smaller number of co-occurring species. They were also characterised by a lower height of the leaf and inflorescence layer. Of the leaf traits analysed in this study, a statistically significant difference between the compared groups of plants was found only in the case of anatomical structure of leaf lamina – mesomorphic leaves occurred more often in invasive species than in the extinct ones. This proves that the latter generally avoid both extremely dry and wet habitats.

When comparing the extinct and invasive species in the study area, no significant difference was found in relation to the number of species that reproduce vegetatively, even though some authors (Richardson et al., 1990; Reichard & Hamilton, 1997) suggest that invasive species tend to propagate this way. However, this applies mainly to species from aquatic or waterlogged habitats (Rejmánek et al., 2005). Compared to extinct species, invasive species are more likely to develop entomophily (insect pollination) or

self-pollination and unisexual flowers. Williamson & Fitter (1996) reported a higher contribution of entomophilous species among species of alien origin domesticated in the UK, compared to native species. On the other hand, according to the aforementioned authors, unisexual flowers are more common among native species. The self-pollination seems to be one of the most important traits that differentiates the compared groups of plants – it is present in as many as 20 invasive and in only 9 extinct species (*Bupleurum falcatum*, *Cerastium brachypetalum*, *Drosera anglica*, *Hieracium echioides*, *Hydrocotyle vulgaris*, *Linosyris vulgaris*, *Montia fontana*, *Veronica catenata*, *V. praecox*). Diaspores of invasive species are not usually seeds alone, but fruits that are often connected with other parts of the plant. Analysis of the diaspore weight in both groups of plants revealed that diaspores heavier than 2 mg were more common in invasive species (Table 2). Whereas the research carried out on the genera *Pinus* and *Banksia* has shown that their invasive species have lighter seeds than non-invasive ones (Richardson *et al*., 1990; Rejmánek & Richardson, 1996). Moravcova *et al*. (2015) observed that invasive species mostly had seeds (diaspores) lighter than 80 mg. Other authors did not find statistically significant differences in seed weight between endemic and widespread species (Lavergne *et al*., 2004). It appears that the optimal weight of diaspores in invasive species ranges from a few to several dozen milligrams, but the colonisation success is determined mostly by their shape. The question whether the duration of the flowering period differentiates the extinct species from the invasive ones cannot be answered unambiguously. This is indicated by the results of the presented research, which show that it lasts up to 2 months in as many as 15 extinct species, and only in 7 invasive ones (*Acer negundo*, *Aster novi-belgii*, *Bidens frondosa*, *Impatiens glandulifera*, *Robinia pseudacacia*, *Rudbeckia laciniata*, *Solidago gigantea*). However, no such correlation was found by other authors (Williamson & Fitter, 1996; Kolar & Lodge, 2001).

The obtained results showed no statistically significant difference between the compared groups of species as regards the basic number of chromosomes and the level of ploidy (Table 1). It is likely that selected DNA sequences should be analysed for the presence of specific genes that determine the traits of invasive or extinct species.

One of the most important factors that helps invasive species to succeed is the impact of human activity on the spreading of their diaspores. Because they are often relocated, transported and cultivated, they can colonise new areas considerably faster and compete more effectively with other species. The strong influence of this phenomenon on the expansion of species distribution is also indicated by other authors (Lodge, 1993; McKinney, 1998; McKinney & Lockwood, 1999). Obviously, the fact that a given species is used by man is not sufficient to classify it as invasive, but it makes it much easier to increase its prevalence in a new area. On the other hand, none of the analysed extinct species was

widely cultivated and it can be assumed that this significantly accelerated the disappearance of their sites in the study area. Extinct species – are hardly found on artificial habitats and differ from invasive species also in terms of hemeroby and urbanity. Human activity is also associated with another characteristic, i.e. incidence of species (expressed as a number of species' sites), which was also confirmed by Williamson & Fitter (1996). It is obvious that very rare species are more likely to become extinct compared to common species, which in many cases become invasive (McKinney & Lockwood, 1999). On the other hand, the size of the natural range of a species, expressed in a number of vegetation zones in which it occurs seems to be of lesser importance. No statistically significant difference was found between the compared groups.

It is interesting to compare extinct and invasive species based on their taxonomic affinity. Some authors indicate that certain families, e.g. Poaceae, comprise a larger number of invasive species compared to other families (Daehler, 1998; Pyšek, 1998). Taxonomic affinity, i.e. taxonomic position of the compared groups of species in a given family is statistically significant also on a regional scale. The family of Asteraceae proved to be particularly abundant in invasive species, while Orchidaceae are represented by the largest number of extinct species (Table 2). This is confirmed by the fact that most of the invasive species belong to families represented by species that prefer habitats created by man (McKinney & Lockwood, 1999). No clear difference was found between extinct and invasive species for the number of species within a specific genus. Also according to Moravcova *et al*. (2015), the taxonomic affiliation of species is of minor importance in predicting their invasiveness.

On the other hand, the type of vegetation preferred by the analysed species is very important. Extinct species occurred on grasslands, meadows and on aquatic and littoral habitats, while invasive species were mostly found in anthropogenic communities (*Artemisietea*, *Chenopodietea*). This confirmed the results of other authors who found that communities with medium moisture were more susceptible to invasion compared to dry or wet communities (Rejmánek, 1989; Rejmánek *et al*., 2005).

Of the seven analysed habitat parameters, statistically significant differences between extinct and invasive species were found only in the case of nitrogen content and the soil moisture value. Other authors also reported the importance of soil fertility as a factor differentiating invasive species from the native ones (Williamson & Fitter, 1996).

The next difference relates to life strategies. The obtained results showed that invasive species were usually C-strategists, while extinct species were CSR-strategists. Other authors state that stress-tolerant species (S) are unlikely to become invasive due to their slow growth (Pyšek *et al*., 2015).

Based on the available literature data, it is not possible to list universal traits that distinguish extinct species from invasive ones. Most authors search for

specific traits of a species that can be used to predict their invasive nature. They compare invasive with non-invasive species of alien origin (Kolar & Lodge, 2001; Moravcova *et al.*, 2015), native (Williamson & Fitter, 1996), endemic (Lavergne *et al.*, 2004) or vanishing ones (McKinney & Lockwood, 1999). Due to the fact that the listed groups of plants vary in terms of ecological characteristics and the number of species, the obtained results are not always explicit. Nevertheless, it can be assumed that the traits of invasive species that enable them to increase their range of occurrence and to colonise new habitats are most often contrasting with those of extinct species. The survival success of species is mainly supported by traits that enable these plants to survive in an environment transformed by human activity.

In conclusion, it has been found that invasive species are mostly medium-sized plants (0.5–2 m high), usually cultivated by man, abundant on anthropogenic habitats, nitrophilous, mesophilic, self-pollinating and C-strategists. On the other hand, extinct species are up to 0.5 m high; they are not crop plants, often occupy extreme habitats (mainly natural or semi-natural), on a substrate with low content of nitrogen and they are CSR-strategists.

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