

PRESENCE OF INVASIVE ALIEN VASCULAR PLANT TAXA IN THE SELECTED NATURA 2000 SITES IN CROATIA

Marina ŠKUNCA^{1*}, Sanela DAMJANOVIĆ², Oleg ANTONIĆ²

SUMMARY

The Natura 2000 (N2000) ecological network, one of the most important tools for preventing further biodiversity loss in the European Union and the world's largest coordinated network of protected areas, is affected by the spread of invasive alien vascular plant taxa (IAPs). The aim of this research was to gain first insights into (1) the presence of IAPs in the selected Croatian N2000 sites designated under the Habitats Directive, and determine (2) potentially the most vulnerable sites. IAPs were recorded in 233 out of 373 of the selected N2000 sites (62%), while 76 of the total 77 IAPs recorded at the time for entire Croatia (99%) were documented in at least one site. In all but one N2000 site in which they were recorded, the IAPs had potentially suitable habitats for the establishment and spread of their populations. Additionally, 92% of the IAPs had potentially suitable habitats in all N2000 sites where they were recorded. In 94% N2000 sites where IAPs were recorded and target habitats were present, at least one recorded IAP could potentially threaten the target habitat(s). Eight species were considered as the potentially most worrisome IAPs recorded in Croatian N2000 sites, while ten sites were identified as the potentially most vulnerable. Avenues for additional research were identified, which could contribute to the improvement of management strategies and the conservation of target species and habitats in Croatian Natura 2000 sites.

KEY WORDS: biological invasions, Habitats Directive, protected areas, site management, threats and pressures, Flora Croatica Database

INTRODUCTION

Invasive alien vascular plant taxa (IAPs) are naturalised plant taxa that exhibit considerable reproductive and dispersal capabilities, which result in significant impacts on native taxa and habitats, various ecosystem services and/or human health (Richardson et al. 2000, Mitić et al. 2008, Nikolić et al. 2014). As per Nikolić (2024) a total of 77 IAPs, belonging to 28 families, have been recorded to date in the flora of Croatia. These taxa are predominantly recorded in areas that have been subjected to direct anthropogenic impact, e.g. discontinuous urban areas, managed broad-leaved forests, complexes of cultivated and arable lands, pastures, transitional woodlands and shrubs (Nikolić et al. 2014). Invasive alien taxa are generally considered one of the main drivers of biodiversity loss (e.g. Brondizio et al. 2019), while the costs to

the European economy are estimated at billions of euros annually (e.g. Haubrock et al. 2021).

The Natura 2000 (N2000) ecological network is a network of terrestrial and marine nature protection sites in the European Union. It consists of Special Areas of Conservation (SACs) and Special Protection Areas (SPAs), which are designated under the Habitats Directive (Council Directive no. 92/43/EEC) and Birds Directive (Council Directive no. 79/409/EEC; 2009/147/EC), respectively. The network's primary objective is the conservation of so-called target species and habitats, as listed in the annexes of the Directives. The network currently covers around 18% of the European total land area across 27 Member States. It is regarded as a vital tool for preventing further biodiversity loss in the EU, and the world's major coordinated network of protected areas

¹ Marina Škunca, MSc, Eurosite – the European Land Conservation Network, Tilburg, The Netherlands

² Sanela Damjanović, MSc, Prof. Oleg Antonić, PhD, Josip Juraj Strossmayer University of Osijek, Department of Biology, Osijek, Croatia

* Corresponding author: Marina Škunca, email: mskunca@eurosite.org

(Guerra et al. 2018, Natura 2000 Barometer 2024). Proclaimed in 2013, the N2000 spans three biogeographical regions in Croatia (continental, alpine and Mediterranean region) and consists of 745 SACs and 38 SPAs, covering almost 37% of the country's total land area (Official Gazette no.80/19, no. 119/23, Natura 2000 Barometer 2024).

The N2000 sites are not immune to the spread of IAPs. Some authors (e.g. Gallardo et al. 2017, Guerra et al. 2018) propose that they may be, in fact, more susceptible to invasion than nationally designated protected areas. This is attributed to the fact that variable human activities are allowed in most of the N2000 sites, as well as relatively recent designation and large area of these sites (e.g. Gallardo et al. 2017, Guerra et al. 2018, Baquero et al. 2021, Ayllón et al. 2022). Therefore, data pertaining to the presence and impact of IAPs on the N2000 network is considered crucial for developing effective strategies to counteract their detrimental impacts on native taxa and habitats of Community interest. In recent years, several studies have been carried out to comprehensively investigate the occurrence of IAPs in N2000 sites at the regional or national level (e.g. Guerra et al. 2018, Lazzaro et al. 2020, Ayllón et al. 2022). The factors influencing this occurrence have also been examined (e.g. Dimitrakopoulos et al. 2017, Guerra et al. 2018, Christopoulou et al. 2021, Baquero et al. 2021, Ayllón et al. 2022), as well as the ecological impacts of IAPs on N2000 habitats (e.g. Lazzaro et al. 2020). However, basic distribution data is still lacking, as is exhaustive research into the effects of IAPs on the N2000 sites, target species and habitats, or a common approach for protecting the N2000 network (Rouget et al. 2016, Guerra et al. 2018, Lazzaro et al. 2020). Despite the growing number of research, mapping, monitoring, and policy-related projects focused on the invasive flora in Croatia over recent decades, both on site-level and nationally, the presence and impact of IAPs on the N2000 is still largely investigated as part of the general floristic research or focused on a limited number of taxa and a geographically limited area (e.g. Novak and Novak 2018 or project "The LIFE CONTRA *Ailanthus* – Establishment of control of the invasive alien species *Ailanthus altissima* in Croatia LIFE19 NAT/HR/001070").

This research aimed to gain first insights into the occurrence of IAPs in Croatian N2000 sites and the potentially most vulnerable sites. Additionally, prospective avenues for additional research were identified, which could contribute to the improvement of management strategies for the sites and the conservation of target species and habitats.

MATERIALS AND METHODS

The research was carried out using the MS Excel 365 and Quantum GIS (QGIS) 3.10.10. (A Coruña).

Data on invasive alien plant taxa

The georeferenced dataset on the spatial distribution of IAPs in Croatia was obtained from the Flora Croatica Database module "Allochthonous plants" (Nikolić 2024). The level of precision of the coordinates is indicated for each observation in the database, with values ranging from very low (0 – Croatia and 1 – region) to very high (11 – GPS, ca. 5-50 m). Only data with a precision of 7 or higher was considered, with 7 representing a precision of 100 to 200 m (Nikolić 2020).

Based on the collected data, an Excel spreadsheet was created for each of the 77 taxa. The data sets were transformed, harmonised and combined to create a point shapefile layer ("IAPs shapefile") projected into the national coordinate system: Croatian Terrestrial Reference System for the Epoch 1995.55 (HTRS96, i.e. EPSG:3765 - HTRS96/ Croatia TM in QGIS), which was used in subsequent analyses in QGIS. The errors resulting from the transposition of coordinates were corrected, while the data with incomplete coordinates or localities outside the Croatian borders were deleted. In the analyses, each taxon was considered individually, whether it was included in the database as a species or as a subspecies (as in the case of the taxa *Angelica archangelica* L. and *Erigeron annuus* (L.) Desf.).

N2000 site selection

The study area comprised the N2000 sites designated in the Republic of Croatia under the Habitats Directive (Council Directive no. 92/43/EEC). A list of proposed Sites of Community Importance (pSCI), Sites of Community Importance (SCI) and Special Areas of Conservation (SAC) (in total 745 sites), their target species and habitats were obtained from the then-current Regulation on the Ecological Network and the Competencies of Public Institutions for Ecological Network Management (Official Gazette no. 80/19). Given the ecology of IAPs, sites listing only marine or subterranean habitats or taxa were excluded from the analyses. On the other hand, sites featuring the target habitats "1130 Estuaries" and "1150 Coastal lagoons" – complex habitats under the substantial freshwater influence, and often including surrounding terrestrial elements – were included. Overall, the study area consisted of 373 selected N2000 sites.

The Web Feature Service (WFS) layer of the N2000 sites was obtained from the Biportal (2021) and saved as a polygon shapefile. Sites excluded from the analyses were removed and 200 m buffer was added around each site

to match accuracy of georeferenced IAPs data. Although this may have resulted in the inclusion of the IAPs localities situated just beyond the boundaries of the sites, we have elected to exercise caution and maintain the buffer zone, given the relatively high probability of the introduction or spread of those IAPs. The resulting "N2000 shapefile" was used in the subsequent analyses. Each site was analysed individually, regardless of any overlaps with other sites.

QGIS shapefile preparation and data analysis

The main objectives were to establish a relationship between (a) data on IAPs and selected N2000 sites, and (b) habitats impacted by the IAPs and (target) habitats identified in the sites.

The habitats impacted by a certain IAP represent those with the highest potential (suitability) for the taxa to establish and spread its population, as described in the literature and FCD (e.g. Nikolić et al. 2014, Nikolić 2024, Vuković et al. 2019, project "The LIFE CONTRA *Ailanthus* – Establishment of control of the invasive alien species *Ailanthus altissima* in Croatia LIFE19 NAT/HR/001070"). Their descriptions were translated to the Level 1 habitat codes listed in the National Habitats Classification (NHC; Appendix 1 of then-current Official Gazette no. 27/21) and added to the "IAPs shapefile".

To evaluate the relationship between IAPs and the potentially suitable target habitats, the N2000 habitat codes were cross-walked to the corresponding NHC Level 1 habitat codes in the "N2000 shapefile", in accordance with the List of Endangered and/or Rare Habitat Types of National and European Significance Present in the Republic of Croatia (Appendix 2 of Official Gazette no. 27/21). Moreover, to ascertain the general presence of potentially suitable habitats for the establishment and spread of IAPs, the "N2000 shapefile" was overlapped with the Map of Natural and Seminatural Non-Forest and Freshwater Habitats of the Republic of Croatia (Bardi et al. 2016), and the column with the NHC Level 1 habitat codes of the present habitats was also added to the "N2000 shapefile". Only "dominant" habitats were considered, i.e. those which covered over 85% of the area of a polygon in which they were recorded. NHC Level 1 habitat codes were used due to the limited country-specific information on the habitats affected and the incomplete data, available at the time in the FCD and additional literature, on the specific habitats or vegetation in which a particular IAP was recorded.

Two analyses were carried out using the two shapefiles prepared in the preceding steps: the final "IAPs shapefile" and the final "N2000 shapefile". An IAP was considered to have potentially suitable habitat for the establishment

and spread of its population in a given N2000 site if it had the NHC code of the impacted habitat identical to the NHC code of the habitat(s) occurring in the N2000 site. The same was true for the target habitats of each N2000 site. Other target habitats, which were not suitable for IAPs, were not considered in subsequent analyses.

RESULTS

Of the 77 taxa of IAPs in Croatia, 76 were recorded in at least one N2000 site. The selected N2000 sites where IAPs were or were not recorded are shown in Figure 1.

IAPs are present in 62% of the selected N2000 sites ($n = 373$). Only three sites recorded more than 50% of the then total Croatian invasive alien flora, 58 N2000 sites recorded more than 20%, while the lowest percentage (10% and less) was found in the highest number of N2000 sites (132).

IAPs presence in the selected N2000 sites

Conyza canadensis (L.) Cronquist was the most recorded IAP, closely followed by *Erigeron annuus* (L.) Desf. and *Robinia pseudoacacia* L., and not so closely by *Ambrosia artemisiifolia* L. The first three species were recorded in ca. 59% of the selected N2000 sites where IAPs were recorded ($n = 233$), while *A. artemisiifolia* in 54%. On the other hand, five IAPs were recorded in only one N2000 site (0.43%), while *Sicyos angulatus* L. was not found in any N2000 site.

In 232 out of 233 N2000 sites, the recorded IAPs had potentially suitable habitats for the establishment and spread of their populations. The only exception was the Blatina site (HR2001009), a small lake near Sobra on the island of Mljet, where no suitable habitat was detected for the only recorded species, *C. canadensis*. Furthermore, 92% of the IAPs had potentially suitable habitats in all N2000 sites where they were recorded. The exceptions, in addition to *C. canadensis*, were *A. artemisiifolia* (124 out of 125 sites), *Bidens subalternans* DC. (34 out of 35 sites), *Conyza bonariensis* (L.) Cronquist (28 out of 29 sites), *Galinsoga parviflora* Cav. (47 out of 48 sites), and *Sorghum halepense* (100 out of 102 sites).

In the total sample of 373 N2000 sites, a total of 69 target habitats were identified. However, no IAPs were recorded in five N2000 sites where one or more of the following four target habitats were designated: "7110* Active raised bogs", "7150 Depressions on peat substrates of the *Rhynchosporion*", "91D0* Bog woodland", "92D0 Southern riparian galleries and thickets (*Nerio-Tamaricetea*)". These target habitats are generally characterised by a limited distribution in Croatia. Of all the N2000 sites where IAPs were recorded, 183 sites had designated target habitats (65 habitats in total). In three

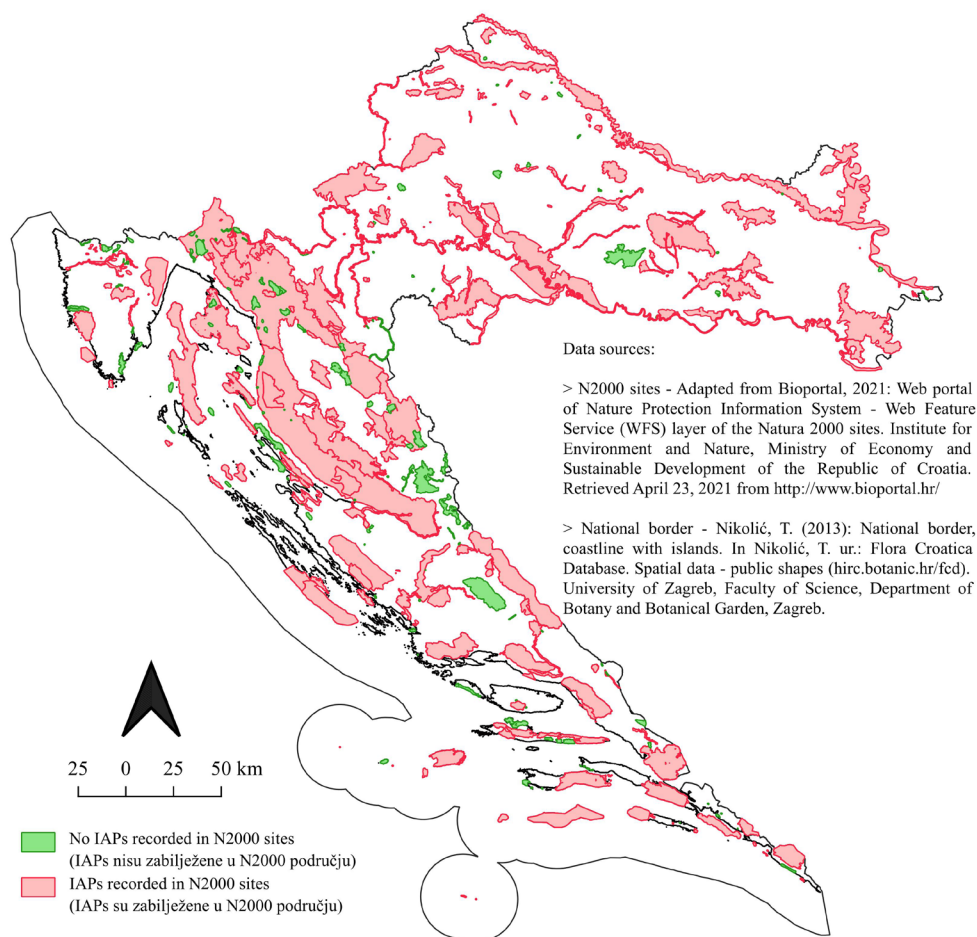


Figure 1 Presence of invasive alien vascular plant taxa (IAPs) in the selected Natura 2000 (N2000) sites (n = 373; including 200 m wide buffer around each site).

of those N2000 sites, the dominant habitats identified in the habitat map (Bardi et. al. 2016) did not match the NHC codes corresponding to the target habitats: "3180* Turloughs" (occasional Lake Blata, HR2000594), "6240* Sub-Pannonic steppic grasslands" (cemetery in Bilje, HR2000728) and "6220* Pseudo-steppe with grasses and annuals of the *Thero-Brachypodietea*" (the island of Susak, HR2000888). Thus, out of 180 N2000 sites where IAPs were recorded and target habitats were present, in 170 sites at least one recorded IAP could potentially threaten the target habitat(s).

A quantitative overview of each IAP in terms of the number and proportion of sites in which it was recorded, as well as of potentially suitable (target) habitats identified across the sites, is provided in Table 1. Based on the obtained results, eight potentially most worrisome IAPs for over a quarter of the Croatian N2000 sites were identified.

N2000 sites in the context of IAPs presence

Of the 76 IAPs recorded in a total of 233 N2000 sites, the highest number of IAPs (around 53%) was recorded in

the proximity of the rivers Neretva (HR5000031), Sava (HR2001311) and Kupa (HR2000642). A further 18 N2000 sites were recorded over a third of the total invasive alien flora, with the higher percentages (over 45%) found in Gorski kotar and northern Lika (HR5000019), Velebit Nature Park (HR5000022) and the upper course of the Drava River (HR5000014). In 32 N2000 sites only one IAP was recorded.

In 228 out of 232 N2000 sites (98%), all the recorded IAPs had potentially suitable habitats for the establishment and spread of their populations. The exceptions are four sites: Lake Sovsko (HR2001512, 8 taxa out of 11 recorded), the settlement of Meja near Bakar (HR2001487, 9 out of 10), Cavtat islands Bobara, Mrkan and Supetar (HR2001047, 2 out of 6) and Lake Blatina near Sobra on the island of Mljet (HR2001009, 0 out of 1). Not surprisingly, the six sites with the highest number of IAPs in general are also the ones with the highest number of IAPs with potentially suitable habitats, with the identical proportion of IAPs recorded. In 31 N2000 sites, only one IAP with potentially suitable habitats was recorded.

Table 1 Presence of invasive alien vascular plant taxa (IAPs) in the selected Natura 2000 (N2000) sites. Abbreviations: N2000 (a) = the number of N2000 sites where a particular IAP has been recorded; SH (a) = the number of N2000 sites where a particular IAP has suitable habitat(s); TH (a) = the number of N2000 sites where the target habitat(s) represent potentially suitable habitat(s) for a particular IAP; N2000 (b), SH (b) and TH (b) = a proportion of the total number of N2000 sites where IAPs have been recorded (%) (n = 233). The taxonomic nomenclature follows the Flora Croatica Database (Nikolić 2024).

IAPs	N2000		SH		TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
<i>Abutilon theophrasti</i> Medik.	42	18.0	42	18.0	7	3.0
<i>Acer negundo</i> L.	44	18.9	44	18.9	36	15.5
<i>Ailanthus altissima</i> (Mill.) Swingle	84	36.1	84	36.1	60	25.8
<i>Amaranthus albus</i> L.	17	7.3	17	7.3	12	5.2
<i>Amaranthus blitoides</i> S. Watson	5	2.1	5	2.1	2	0.9
<i>Amaranthus deflexus</i> L.	25	10.7	25	10.7	17	7.3
<i>Amaranthus hybridus</i> L.	29	12.4	29	12.4	13	5.6
<i>Amaranthus retroflexus</i> L.	101	43.3	101	43.3	33	14.2
<i>Ambrosia artemisiifolia</i> L.	125	53.6	124	53.2	17	7.3
<i>Amorpha fruticosa</i> L.	55	23.6	55	23.6	49	21.0
<i>Angelica archangelica</i> L.	4	1.7	4	1.7	4	1.7
<i>Angelica archangelica</i> L. subsp. <i>archangelica</i>	1	0.4	1	0.4	1	0.4
<i>Artemisia annua</i> L.	8	3.4	8	3.4	6	2.6
<i>Artemisia verlotiorum</i> Lamotte	43	18.5	43	18.5	29	12.4
<i>Asclepias syriaca</i> L.	46	19.7	46	19.7	30	12.9
<i>Aster squamatus</i> (Spreng.) Hieron.	25	10.7	25	10.7	21	9.0
<i>Bidens frondosa</i> L.	59	25.3	59	25.3	43	18.5
<i>Bidens subalternans</i> DC.	35	15.0	34	14.6	22	9.4
<i>Broussonetia papyrifera</i> (L.) Vent.	24	10.3	24	10.3	16	6.9
<i>Carpobrotus edulis</i> (L.) N.E.Br.	4	1.7	4	1.7	3	1.3
<i>Cenchrus longispinus</i> (Kneuck.) Fernald	1	0.4	1	0.4	1	0.4
<i>Chamomilla suaveolens</i> (Pursh) Rydb.	14	6.0	14	6.0	3	1.3
<i>Chenopodium ambrosioides</i> L.	5	2.1	5	2.1	5	2.1
<i>Conyza bonariensis</i> (L.) Cronquist	29	12.4	28	12.0	21	9.0
<i>Conyza canadensis</i> (L.) Cronquist	138	59.2	135	57.9	45	19.3
<i>Conyza sumatrensis</i> (Retz.) E. Walker	25	10.7	25	10.7	8	3.4
<i>Cuscuta campestris</i> Yunck.	11	4.7	11	4.7	3	1.3
<i>Datura innoxia</i> Mill.	13	5.6	13	5.6	5	2.1
<i>Datura stramonium</i> L.	47	20.2	47	20.2	25	10.7
<i>Diploaxis erucoides</i> (L.) DC.	3	1.3	3	1.3	0	0.0
<i>Duchesnea indica</i> (Andrews) Focke	7	3.0	7	3.0	6	2.6
<i>Echinocystis lobata</i> (Michx.) Torr. et A. Gray	57	24.5	57	24.5	42	18.0
<i>Egeria densa</i> Planch.	1	0.4	1	0.4	1	0.4
<i>Eleusine indica</i> (L.) Gaertn.	36	15.5	36	15.5	24	10.3
<i>Elodea canadensis</i> Michx.	6	2.6	6	2.6	5	2.1
<i>Epilobium ciliatum</i> Raf.	11	4.7	11	4.7	4	1.7
<i>Erigeron annuus</i> (L.) Desf.	137	58.8	137	58.8	68	29.2
<i>Erigeron annuus</i> (L.) Pers. subsp. <i>annuus</i>	7	3.0	7	3.0	6	2.6
<i>Erigeron annuus</i> (L.) Pers. subsp. <i>septentrionalis</i> (Fernald et Wiegand) Wagenitz	5	2.1	5	2.1	4	1.7
<i>Erigeron annuus</i> (L.) Pers. subsp. <i>strigosus</i> (Mühlenb. ex Willd.) Wagenitz	4	1.7	4	1.7	3	1.3
<i>Euphorbia maculata</i> L.	31	13.3	31	13.3	12	5.2
<i>Euphorbia prostrata</i> Aiton	32	13.7	32	13.7	10	4.3
<i>Galinsoga ciliata</i> (Raf.) S.F. Blake	31	13.3	31	13.3	17	7.3
<i>Galinsoga parviflora</i> Cav.	48	20.6	47	20.2	28	12.0
<i>Helianthus tuberosus</i> L.	61	26.2	61	26.2	38	16.3
<i>Impatiens balfourii</i> Hook. f.	6	2.6	6	2.6	4	1.7
<i>Impatiens glandulifera</i> Royle	17	7.3	17	7.3	13	5.6
<i>Impatiens parviflora</i> DC.	10	4.3	10	4.3	8	3.4
<i>Juncus tenuis</i> Willd.	26	11.2	26	11.2	19	8.2
<i>Lepidium virginicum</i> L.	22	9.4	22	9.4	18	7.7
<i>Ludwigia peploides</i> (Kunth) P.H. Raven	4	1.7	4	1.7	2	0.9
<i>Mesembryanthemum crystallinum</i> L.	10	4.3	10	4.3	7	3.0
<i>Mesembryanthemum nodiflorum</i> L.	1	0.4	1	0.4	1	0.4

IAPs	N2000		SH		TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
<i>Nicotiana glauca</i> Graham	4	1.7	4	1.7	4	1.7
<i>Oenothera biennis</i> L.	15	6.4	15	6.4	6	2.6
<i>Opuntia ficus-indica</i> (L.) Mill.	16	6.9	16	6.9	13	5.6
<i>Oxalis pes-caprae</i> L.	1	0.4	1	0.4	1	0.4
<i>Panicum capillare</i> L.	21	9.0	21	9.0	14	6.0
<i>Panicum dichotomiflorum</i> Michx.	22	9.4	22	9.4	2	0.9
<i>Parthenocissus quinquefolia</i> (L.) Planchon	55	23.6	55	23.6	50	21.5
<i>Paspalum dilatatum</i> Poir.	2	0.9	2	0.9	1	0.4
<i>Paspalum paspalodes</i> (Michx.) Scribn.	13	5.6	13	5.6	9	3.9
<i>Phytolacca americana</i> L.	37	15.9	37	15.9	33	14.2
<i>Reynoutria japonica</i> Houtt.	36	15.5	36	15.5	28	12.0
<i>Reynoutria sachalinensis</i> (F. Schmidt) Nakai	2	0.9	2	0.9	1	0.4
<i>Reynoutria</i> × <i>bohemica</i> Chrtek et Chrtková	31	13.3	31	13.3	24	10.3
<i>Robinia pseudoacacia</i> L.	137	58.8	137	58.8	80	34.3
<i>Rudbeckia laciniata</i> L.	21	9.0	21	9.0	17	7.3
<i>Solanum elaeagnifolium</i> Cav.	4	1.7	4	1.7	2	0.9
<i>Solidago canadensis</i> L.	39	16.7	39	16.7	34	14.6
<i>Solidago gigantea</i> Aiton	93	39.9	93	39.9	77	33.0
<i>Sorghum halepense</i> (L.) Pers.	102	43.8	100	42.9	17	7.3
<i>Tagetes minuta</i> L.	6	2.6	6	2.6	5	2.1
<i>Veronica persica</i> Poir.	49	21.0	49	21.0	29	12.4
<i>Xanthium spinosum</i> L.	16	6.9	16	6.9	14	6.0
<i>Xanthium strumarium</i> L. subsp. <i>italicum</i> (Moretti) D. Löve	65	27.9	65	27.9	44	18.9

Out of 76 IAPs that were recorded in the N2000 sites, 75 taxa were present in the sites where the target habitats represent their potentially suitable habitats. The only exception was the ruderal weed *Diplotaxis eruroides* (L.) DC, for which the target habitats designated in three N2000 sites – the island of Murter (HR2001050), the Krka estuary (HR3000171) and the lagoon of Morinje (HR3000460) do not represent the potentially suitable habitats. In 26 N2000 sites, target habitats represent potentially suitable habitats for only one IAP.

A quantitative overview of each N2000 site in terms of the number and proportion of IAPs recorded, as well as the number of IAPs with potentially suitable (target) habitats identified in the given site, is provided in Table 2. Based on the obtained results, ten most vulnerable Croatian N2000 sites for over a third of the total recorded IAPs have been identified.

Table 2 The number and proportion of the invasive alien vascular plant taxa (IAPs) recorded within the selected Natura 2000 (N2000) sites. Abbreviations: IAPs (a) = the number of IAPs recorded at a given N2000 site; IAPs-SH (a) = the number of IAPs with potentially suitable habitat(s) in a given N2000 site; IAPs-SH (b) = the number of IAPs for whom the target habitat(s) represent potentially suitable habitat(s) in a given N2000 site; IAPs-SH (b) = a proportion of the total number of IAPs recorded at N2000 sites (%) (n = 76).

N2000 sites	IAPs		IAPs-SH		IAPs-SH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2000132	15	19.7	15	19.7	6	7.9
HR2000364	29	38.2	29	38.2	20	26.3
HR2000369	6	7.9	6	7.9	0	0.0

N2000 sites	IAPs		IAPs-SH		IAPs-SH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2000371	18	23.7	18	23.7	18	23.7
HR2000372	28	36.8	28	36.8	28	36.8
HR2000394	28	36.8	28	36.8	16	21.1
HR2000415	30	39.5	30	39.5	22	28.9
HR2000416	25	32.9	25	32.9	19	25.0
HR2000420	22	28.9	22	28.9	17	22.4
HR2000426	8	10.5	8	10.5	6	7.9
HR2000427	18	23.7	18	23.7	7	9.2
HR2000437	9	11.8	9	11.8	5	6.6
HR2000438	11	14.5	11	14.5	6	7.9
HR2000440	11	14.5	11	14.5	5	6.6
HR2000441	8	10.5	8	10.5	3	3.9
HR2000447	4	5.3	4	5.3	4	5.3
HR2000449	9	11.8	9	11.8	6	7.9
HR2000450	8	10.5	8	10.5	5	6.6
HR2000451	6	7.9	6	7.9	3	3.9
HR2000459	12	15.8	12	15.8	5	6.6
HR2000463	29	38.2	29	38.2	0	0.0
HR2000465	8	10.5	8	10.5	6	7.9
HR2000544	1	1.3	1	1.3	0	0.0
HR2000545	1	1.3	1	1.3	0	0.0
HR2000546	1	1.3	1	1.3	0	0.0
HR2000570	2	2.6	2	2.6	1	1.3
HR2000571	10	13.2	10	13.2	8	10.5
HR2000572	8	10.5	8	10.5	5	6.6
HR2000573	5	6.6	5	6.6	0	0.0
HR2000580	16	21.1	16	21.1	12	15.8
HR2000583	24	31.6	24	31.6	24	31.6
HR2000586	31	40.8	31	40.8	25	32.9

N2000 sites	IAPs		IAPs-SH		IAPs-TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2000591	2	2.6	2	2.6	2	2.6
HR2000592	20	26.3	20	26.3	10	13.2
HR2000593	13	17.1	13	17.1	6	7.9
HR2000594	3	3.9	3	3.9	0	0.0
HR2000596	7	9.2	7	9.2	2	2.6
HR2000601	8	10.5	8	10.5	8	10.5
HR2000604	11	14.5	11	14.5	5	6.6
HR2000605	3	3.9	3	3.9	3	3.9
HR2000609	7	9.2	7	9.2	4	5.3
HR2000616	12	15.8	12	15.8	9	11.8
HR2000619	11	14.5	11	14.5	6	7.9
HR2000623	27	35.5	27	35.5	8	10.5
HR2000632	2	2.6	2	2.6	2	2.6
HR2000634	1	1.3	1	1.3	1	1.3
HR2000635	13	17.1	13	17.1	8	10.5
HR2000637	13	17.1	13	17.1	2	2.6
HR2000641	19	25.0	19	25.0	12	15.8
HR2000642	40	52.6	40	52.6	39	51.3
HR2000648	2	2.6	2	2.6	1	1.3
HR2000670	4	5.3	4	5.3	2	2.6
HR2000707	1	1.3	1	1.3	0	0.0
HR2000728	5	6.6	5	6.6	0	0.0
HR2000780	5	6.6	5	6.6	3	3.9
HR2000799	2	2.6	2	2.6	2	2.6
HR2000871	2	2.6	2	2.6	2	2.6
HR2000874	1	1.3	1	1.3	0	0.0
HR2000888	1	1.3	1	1.3	0	0.0
HR2000917	4	5.3	4	5.3	0	0.0
HR2000918	26	34.2	26	34.2	26	34.2
HR2000919	7	9.2	7	9.2	0	0.0
HR2000929	31	40.8	31	40.8	31	40.8
HR2000931	5	6.6	5	6.6	0	0.0
HR2000932	3	3.9	3	3.9	1	1.3
HR2000933	12	15.8	12	15.8	0	0.0
HR2000936	1	1.3	1	1.3	0	0.0
HR2000937	1	1.3	1	1.3	1	1.3
HR2000942	18	23.7	18	23.7	18	23.7
HR2000943	2	2.6	2	2.6	2	2.6
HR2000944	1	1.3	1	1.3	0	0.0
HR2000946	6	7.9	6	7.9	6	7.9
HR2001004	4	5.3	4	5.3	0	0.0
HR2001005	6	7.9	6	7.9	0	0.0
HR2001006	11	14.5	11	14.5	0	0.0
HR2001009	1	1.3	0	0.0	0	0.0
HR2001010	8	10.5	8	10.5	2	2.6
HR2001011	1	1.3	1	1.3	1	1.3
HR2001012	22	28.9	22	28.9	15	19.7
HR2001016	5	6.6	5	6.6	5	6.6
HR2001017	3	3.9	3	3.9	0	0.0
HR2001021	1	1.3	1	1.3	1	1.3
HR2001031	15	19.7	15	19.7	9	11.8
HR2001042	6	7.9	6	7.9	3	3.9
HR2001045	5	6.6	5	6.6	1	1.3
HR2001046	5	6.6	5	6.6	1	1.3
HR2001047	6	7.9	2	2.6	2	2.6

N2000 sites	IAPs		IAPs-SH		IAPs-TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2001050	19	25.0	19	25.0	12	15.8
HR2001058	8	10.5	8	10.5	6	7.9
HR2001070	30	39.5	30	39.5	0	0.0
HR2001085	14	18.4	14	18.4	6	7.9
HR2001086	10	13.2	10	13.2	3	3.9
HR2001097	7	9.2	7	9.2	7	9.2
HR2001115	12	15.8	12	15.8	12	15.8
HR2001215	15	19.7	15	19.7	0	0.0
HR2001216	20	26.3	20	26.3	0	0.0
HR2001228	13	17.1	13	17.1	0	0.0
HR2001243	8	10.5	8	10.5	0	0.0
HR2001257	4	5.3	4	5.3	0	0.0
HR2001260	5	6.6	5	6.6	5	6.6
HR2001267	4	5.3	4	5.3	0	0.0
HR2001274	1	1.3	1	1.3	1	1.3
HR2001277	4	5.3	4	5.3	0	0.0
HR2001278	4	5.3	4	5.3	2	2.6
HR2001279	3	3.9	3	3.9	2	2.6
HR2001280	2	2.6	2	2.6	2	2.6
HR2001281	14	18.4	14	18.4	3	3.9
HR2001285	6	7.9	6	7.9	0	0.0
HR2001286	1	1.3	1	1.3	0	0.0
HR2001288	6	7.9	6	7.9	0	0.0
HR2001292	7	9.2	7	9.2	6	7.9
HR2001293	18	23.7	18	23.7	12	15.8
HR2001298	9	11.8	9	11.8	5	6.6
HR2001299	1	1.3	1	1.3	1	1.3
HR2001305	2	2.6	2	2.6	2	2.6
HR2001307	30	39.5	30	39.5	23	30.3
HR2001308	30	39.5	30	39.5	11	14.5
HR2001309	22	28.9	22	28.9	22	28.9
HR2001311	41	53.9	41	53.9	41	53.9
HR2001313	21	27.6	21	27.6	15	19.7
HR2001314	16	21.1	16	21.1	11	14.5
HR2001318	1	1.3	1	1.3	1	1.3
HR2001319	8	10.5	8	10.5	4	5.3
HR2001320	2	2.6	2	2.6	0	0.0
HR2001322	3	3.9	3	3.9	0	0.0
HR2001325	3	3.9	3	3.9	2	2.6
HR2001326	18	23.7	18	23.7	9	11.8
HR2001327	3	3.9	3	3.9	0	0.0
HR2001328	18	23.7	18	23.7	8	10.5
HR2001329	22	28.9	22	28.9	11	14.5
HR2001330	14	18.4	14	18.4	0	0.0
HR2001335	19	25.0	19	25.0	13	17.1
HR2001336	4	5.3	4	5.3	0	0.0
HR2001338	1	1.3	1	1.3	1	1.3
HR2001339	5	6.6	5	6.6	2	2.6
HR2001343	3	3.9	3	3.9	1	1.3
HR2001345	8	10.5	8	10.5	5	6.6
HR2001346	12	15.8	12	15.8	7	9.2
HR2001347	9	11.8	9	11.8	3	3.9
HR2001348	1	1.3	1	1.3	0	0.0
HR2001349	8	10.5	8	10.5	0	0.0
HR2001350	17	22.4	17	22.4	0	0.0
HR2001351	13	17.1	13	17.1	11	14.5

N2000 sites	IAPs		IAPs-SH		IAPs-TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2001352	28	36.8	28	36.8	28	36.8
HR2001353	15	19.7	15	19.7	11	14.5
HR2001354	10	13.2	10	13.2	3	3.9
HR2001356	20	26.3	20	26.3	10	13.2
HR2001357	31	40.8	31	40.8	31	40.8
HR2001358	12	15.8	12	15.8	12	15.8
HR2001359	10	13.2	10	13.2	10	13.2
HR2001360	11	14.5	11	14.5	10	13.2
HR2001361	29	38.2	29	38.2	11	14.5
HR2001362	3	3.9	3	3.9	2	2.6
HR2001363	17	22.4	17	22.4	17	22.4
HR2001364	21	27.6	21	27.6	16	21.1
HR2001365	11	14.5	11	14.5	0	0.0
HR2001367	10	13.2	10	13.2	10	13.2
HR2001378	5	6.6	5	6.6	4	5.3
HR2001379	2	2.6	2	2.6	2	2.6
HR2001383	4	5.3	4	5.3	3	3.9
HR2001385	19	25.0	19	25.0	9	11.8
HR2001387	17	22.4	17	22.4	0	0.0
HR2001389	4	5.3	4	5.3	0	0.0
HR2001390	2	2.6	2	2.6	0	0.0
HR2001391	7	9.2	7	9.2	0	0.0
HR2001392	1	1.3	1	1.3	0	0.0
HR2001393	6	7.9	6	7.9	0	0.0
HR2001394	7	9.2	7	9.2	0	0.0
HR2001396	3	3.9	3	3.9	0	0.0
HR2001399	4	5.3	4	5.3	0	0.0
HR2001404	2	2.6	2	2.6	0	0.0
HR2001405	6	7.9	6	7.9	0	0.0
HR2001407	8	10.5	8	10.5	0	0.0
HR2001408	10	13.2	10	13.2	8	10.5
HR2001409	21	27.6	21	27.6	14	18.4
HR2001410	10	13.2	10	13.2	6	7.9
HR2001412	3	3.9	3	3.9	3	3.9
HR2001413	7	9.2	7	9.2	6	7.9
HR2001414	17	22.4	17	22.4	8	10.5
HR2001415	13	17.1	13	17.1	8	10.5
HR2001416	5	6.6	5	6.6	2	2.6
HR2001420	3	3.9	3	3.9	1	1.3
HR2001421	8	10.5	8	10.5	2	2.6
HR2001425	4	5.3	4	5.3	1	1.3
HR2001428	3	3.9	3	3.9	1	1.3
HR2001429	1	1.3	1	1.3	0	0.0
HR2001433	1	1.3	1	1.3	0	0.0
HR2001483	1	1.3	1	1.3	0	0.0
HR2001484	1	1.3	1	1.3	0	0.0
HR2001485	1	1.3	1	1.3	0	0.0
HR2001486	8	10.5	8	10.5	0	0.0
HR2001487	10	13.2	9	11.8	0	0.0
HR2001500	3	3.9	3	3.9	2	2.6
HR2001501	7	9.2	7	9.2	5	6.6
HR2001505	18	23.7	18	23.7	9	11.8
HR2001506	21	27.6	21	27.6	0	0.0
HR2001509	8	10.5	8	10.5	3	3.9
HR2001510	8	10.5	8	10.5	6	7.9
HR2001511	12	15.8	12	15.8	8	10.5

N2000 sites	IAPs		IAPs-SH		IAPs-TH	
	(a)	(b) (%)	(a)	(b) (%)	(a)	(b) (%)
HR2001512	11	14.5	8	10.5	5	6.6
HR3000124	1	1.3	1	1.3	1	1.3
HR3000126	20	26.3	20	26.3	8	10.5
HR3000167	2	2.6	2	2.6	1	1.3
HR3000171	25	32.9	25	32.9	10	13.2
HR3000351	5	6.6	5	6.6	3	3.9
HR3000430	17	22.4	17	22.4	10	13.2
HR3000433	7	9.2	7	9.2	1	1.3
HR3000450	1	1.3	1	1.3	0	0.0
HR3000460	19	25.0	19	25.0	8	10.5
HR4000001	9	11.8	9	11.8	9	11.8
HR4000002	3	3.9	3	3.9	3	3.9
HR4000004	1	1.3	1	1.3	1	1.3
HR4000005	6	7.9	6	7.9	3	3.9
HR4000006	3	3.9	3	3.9	2	2.6
HR4000008	1	1.3	1	1.3	1	1.3
HR4000009	1	1.3	1	1.3	1	1.3
HR4000010	6	7.9	6	7.9	5	6.6
HR4000017	5	6.6	5	6.6	5	6.6
HR4000018	1	1.3	1	1.3	1	1.3
HR4000028	10	13.2	10	13.2	10	13.2
HR4000029	2	2.6	2	2.6	2	2.6
HR4000030	12	15.8	12	15.8	6	7.9
HR5000014	35	46.1	35	46.1	35	46.1
HR5000015	24	31.6	24	31.6	9	11.8
HR5000019	37	48.7	37	48.7	11	14.5
HR5000020	21	27.6	21	27.6	21	27.6
HR5000022	36	47.4	36	47.4	35	46.1
HR5000025	21	27.6	21	27.6	10	13.2
HR5000028	1	1.3	1	1.3	1	1.3
HR5000030	7	9.2	7	9.2	7	9.2
HR5000031	41	53.9	41	53.9	35	46.1
HR5000037	2	2.6	2	2.6	2	2.6
HR5000038	6	7.9	6	7.9	6	7.9

DISCUSSION

Eight potentially most worrisome IAPs recorded in Croatian N2000 sites

When considering the potentially most worrisome IAPs recorded in Croatian N2000 sites, the focus was both on the IAPs recorded in over a third of the sites and those that could potentially threaten the target habitats in over a quarter of the sites. Consequently, eight IAPs were identified: *A. altissima*, *A. retroflexus*, *A. artemisiifolia*, *C. canadensis*, *E. annuus*, *R. pseudoacacia*, *S. gigantea* and *S. halepense*. These eight species can be found throughout the country, although some might be prevalent in certain biogeographical regions — e.g. *S. gigantea* prefers continental region, while *A. altissima* shows greater aggressiveness in the Mediterranean (Novak and Novak 2018).

There are several secrets to their success and the relatively high number of their records in the N2000 sites: high propagule pressure (e.g. *A. altissima*, *A. retroflexus*, *A. artemisiifolia*, *C. canadensis*); combination of generative and vegetative reproduction (e.g. *A. altissima*, *S. gigantea*, *S. halepense*); pioneer character (e.g. *R. pseudoacacia*); high adaptability to a range of environmental conditions (e.g. *A. altissima*, *A. artemisiifolia*, *R. pseudoacacia*); quick growth or vegetative spread (e.g. *A. altissima*, *R. pseudoacacia*, *S. halepense*); and a wide range of seed dispersal vectors (e.g. *S. halepense*) to name a few. In addition, *R. pseudoacacia* has long provided a wide range of ecosystem services: it was deliberately cultivated as a park tree, but also for fuel, erosion control, afforestation of devastated and burned areas, construction wood and bee pastures (Nikolić et al. 2014, Lazzaro et al. 2020, Nikolić 2024). It is our understanding that at least five of these eight species have been considered as transformers (sensu Richardson et al. 2000, Mitić et al. 2008, Nikolić 2024) in other regions of Europe: *A. altissima* (e.g. Török et al. 2003), *A. artemisiifolia* (e.g. Protopopova et al. 2014), *C. canadensis* (e.g. Protopopova et al. 2014), *R. pseudoacacia* (e.g. Török et al. 2003, Lazzaro et al. 2020) and *S. gigantea* (e.g. Török et al. 2003).

None of these eight species were included on the Croatian Black List (Official Gazette no. 13/24), as they are all widely distributed within the country and it is unlikely that their listing on the Black List would effectively prevent, minimise or mitigate their harmful effects. Conversely, although they adhere to a similar set of criteria, the list of Invasive Alien Species of Union Concern includes the species *A. altissima* (Regulation (EU) 1143/2014 and Commission Implementing Regulations (EU) 2016/1141, 2017/1263, 2019/1262, 2022/1203). Four species were mentioned in the reviews listing the most problematic (European) IAPs: e.g. DAISIE's "the 100 most invasive alien species in Europe" (*A. altissima*, *A. artemisiifolia*, *R. pseudoacacia*; Vilà et al. 2009), the "worst invasive plants in protected areas of the world" (*A. altissima*, *R. pseudoacacia*; Foxcroft et al. 2017), the "149 worst alien species for Europe" (*R. pseudoacacia*, *A. artemisiifolia*; Nentwig et al. 2018), and on the EPPO List of Invasive Alien Plants (EPPO 2024), which includes taxa considered most threatening to the Euro-Mediterranean region's taxa and ecosystems (*A. altissima*, *A. artemisiifolia*, *S. gigantea*).

Ten Croatian N2000 sites potentially most vulnerable in terms of IAPs presence

While three Croatian N2000 sites each recorded more than half of the Croatian invasive flora, and the additional 18 sites recorded more than a third, when considering the potentially most vulnerable N2000 sites, the focus was on those sites with potentially suitable target

habitats for the highest number of IAPs. Consequently, ten sites were identified: Sava River near Hrušćica (HR2001311), Kupa River (HR2000642), Danube River downstream of Osijek and Vukovar (HR2000372), wider area of the Krka National Park (HR2000918), the canyon of the Cetina River (HR2000929), the Mosor Mountain (HR2001352), the island of Krk (HR2001357), the upper course of the Drava River (HR5000014), Velebit Nature Park (HR5000022) and the Neretva Delta (HR5000031). Interestingly, only two out of the ten potentially most vulnerable N2000 sites recognised invasive taxa as a negative threat and included it in the Standard Data Form, as defined by the Commission Implementing Decision 2011/484/EU. One ranked invasive non-native taxa as a threat of high importance (the Neretva Delta, HR5000031), while the other ranked them as a threat of medium importance (Velebit Nature Park, HR5000022) (Bioportal 2024).

Riparian zones are among the most endangered ecosystems, exposed to increasing natural and anthropogenic pressures that facilitate the spread of IAPs. Indeed, some authors have suggested that the plant communities of the riparian zones are among those most susceptible to invasion (e.g. Zedler and Kercher 2004, Dimitrakopoulos et al. 2017). Nikolić et al. (2013) reported that a variety of invasive taxa were found in the major river valleys. Additionally, over half of the IAPs identified in Croatia at that time were recorded in inland waters or in the immediate vicinity of inland waters, while almost a third occurred within inland wetlands. Therefore, it is not surprising that seven out of ten potentially most vulnerable Croatian N2000 sites are connected to the (wider) river areas (HR2001311, HR2000642, HR5000014, HR2000372, HR2000929, HR5000031 and HR2000918). It is also noteworthy that a significant number of those sites are situated in close proximity to urban centres. Major ones include Zagreb (Sava) and Varaždin (Drava), both of which are situated at the intersection of the main continental transport corridors. Smaller regional centres include Osijek (Drava), and industrial towns such as Karlovac (Kupa), Sisak (Kupa and Sava) and Slavonski Brod (Sava). In addition, some of the floodplains, as well as wider areas in the vicinity of certain rivers (e.g. Drava, Danube, Krka, Neretva) and encompassed by the aforementioned N2000 sites, have been transformed into agricultural lands, one of the most invaded habitats (Nikolić et al. 2013).

Once regarded as a relatively resilient ecosystem in the face of recently introduced taxa, the European Mediterranean biogeographical region is nowadays considered to be particularly endangered by IAPs, with a high level of invasion predicted for its coastal zone (Foxcroft et al. 2013, Nikolić et al. 2013, Dimitrakopoulos et al. 2017, Radović et al. 2018). Nikolić et al. (2013) reported that

the majority of recorded introductions and naturalisations in the last 20 years occurred in Croatia's Mediterranean region, particularly on the islands, which tend to harbour more alien taxa than the equivalent mainland sites. One of the ten potentially most vulnerable Croatian N2000 sites (HR2001357) is indeed located on the island in the northern Adriatic – the island of Krk. The Standard Data Form (Bioportal 2024) reports a long history of human habitation and a wide range of traditional activities, including extensive sheep grazing and the exploitation of timber. This is coupled with a direct link to the mainland via bridge, industrial and transportation areas (e.g. the floating LNG terminal, Valbiska ferry port, international Rijeka Airport and Marina Puntat), as well as numerous touristic places located on the coast.

It would appear that montane regions have thus far been spared the fate of their lowland counterparts. This is most likely due to the fact that high-elevation and steep areas are often sparsely populated, isolated, situated a considerable distance from alien taxa hotspots, and have limited vehicular traffic and low levels of active landscape maintenance (Dimitrakopoulos et al. 2017). Nikolić et al. (2013) observed that IAPs occurred in a relatively wide altitude range in Croatia, but predominantly below 1100 m a.s.l. As altitude increased, the number of taxa rapidly decreased, with only a few taxa observed at elevations above 1300 m (a few localities on the Velebit Mountain and the Gorski kotar area), and no invasive taxa observed above 1500 m. It was therefore somewhat unexpected to find that two of the ten potentially most vulnerable N2000 sites were situated in mountainous areas (HR2001352 and HR5000022). The former includes the Mosor Mountain (highest peak Veliki Kabal at 1339 m a.s.l.), a part of the central Dalmatian Dinarides mountain range. The Mosor Mountain extends from the town of Split, a major urban centre and a seaport in the northwest, to the lower course of the Cetina River in the southeast (Bioportal 2024). The latter covers the majority of the Velebit Mountain (highest peak Vaganski vrh at 1757 m a.s.l.) and the valley of the karst Zrmanja River, and represents the largest natural protected area in Croatia (Bioportal 2024). The high number of IAPs observed in these two sites may be attributed to a number of factors. Both sites encompass also wider, lower-elevation areas, including those in close proximity to the rivers Cetina and Zrmanja, respectively. They have been inhabited for centuries and are popular hiking destinations, attracting a considerable number of visitors – an important vector promoting alien taxa introductions to protected areas (e.g. Dimitrakopoulos et al. 2017). Relatively well-developed network of roads and pathways, particularly in the lower parts and at the sites' borders, may facilitate the spread of IAPs to less populated and more isolated areas of these sites (e.g. Dimitrakopoulos et al. 2017). Stock breeding with pasturing

represented once the most significant economic activity in the Mosor Mountain area, yet the pastures in the region are now largely abandoned and under succession (Koren et al. 2020). However, agriculture is still somewhat present in both areas (Bioportal 2024), while the fragments of transhumance can still be observed in the mountain areas of Velebit. Finally, the frequent occurrence of forest fires in the Mosor Mountain area, particularly on the southern slopes (Koren et al. 2020), may increase the potential for invasion during at least the first few post-fire years (e.g. Brooks and Lusk 2008).

It can be observed that all ten N2000 sites share a number of common characteristics: they are large sites, generally floristically well-studied, situated in close proximity to urban areas and well connected to them. Furthermore, they attract a significant number of local, regional, and in some cases, international visitors on an annual basis. This is in accordance with previous studies (e.g. Gallardo et al. 2017, Guerra et al. 2018), which reported that the number of IAS was higher in larger N2000 sites with higher accessibility, and which was often related to the probability of receiving visitors in these areas for nature-based tourism or recreation.

A road ahead

To paraphrase Foxcroft et al. (2013), the threat or vulnerability based on the presence of the IAPs is only part of the story. Indeed, there is a complex network of research trajectories that should be pursued in the future.

The preliminary analysis indicates that the ranking of the most vulnerable N2000 sites may differ considerably if the size of a site is considered. This would likely result in the prioritisation of smaller sites – e.g. a coastal lagoon situated in Drašnice cove (HR3000351), small grassland near the settlement of Klasnići (HR2001383), Lake Sovsko (HR2001512) and the Odra River near the settlement of Jagodno (HR2001031); which are generally more vulnerable due to the larger edge/total area ratios (e.g. Foxcroft et al. 2013).

A deeper, regional and local grasp of the IAPs' behaviour (e.g. Lazzaro et al. 2020) and impact (e.g. Hulme et al. 2013, Rouget et al. 2016, Foxcroft et al. 2017, Guerra et al. 2018), which is (1) translated into a robust scientific base, (2) accompanied by a quantitative, systematic and comparable assessment methodology, and (3) coupled with information on so-called invasion debt (sensu Rouget et al. 2016) could greatly assist in informed decision-making and proactive management. The impact of climate change on the growth and spread of IAPs in the N2000 sites also requires further investigation (e.g. Foxcroft et al. 2013, Gallardo et al. 2017).

The actual presence of the IAP in question in a given

N2000 site, habitat type or target habitat could be assessed by using the observations with a precision of 11, which corresponds to the maximum spatial (GPS) precision (precision between 5 and 50 m; Nikolić 2020). However, this could lead to further underestimation of the numbers and distributions of IAPs in Croatian N2000 sites and threats to the (target) habitats, as the dynamics of their invasion already render the differentiation of poorly sampled areas from truly absent areas challenging for invasive alien flora (Radović et al. 2018). By comparing our lists of the N2000 sites where the IAPs were and were not recorded, we could already suspect some of the findings were more the result of the unsystematic sampling or unprecise location than true absence of IAPs in the site. It is anticipated that the use of high-precision observations for these purposes would be more appropriate at the site level, and that they would currently be confined to N2000 sites where detailed research of the vascular flora has already been underway.

Our results suggest only potential presence of potentially suitable (target) habitats in a given N2000 site for a certain IAP. Further and more targeted research could assist in both connecting IAPs to the affected habitats on higher NHC levels, but also in assessing the true impact of a given IAP on the invaded habitats. It is anticipated that the situation will be somewhat improved in the future as a result of an increased input of precisely geo-referenced data to FCD (e.g. Radović et al. 2018).

Distinctions in the potential for invasion (in terms of both possibilities and opportunities) of IAPs across the three Croatian biogeographical regions: continental, alpine and Mediterranean should be further explored to facilitate more reliable comparisons between taxa and provide a clearer basis for threat assessment at the national and international levels.

CONCLUSIONS

Although our study identified several knowledge gaps, it could be argued that these largely reflect the gaps in plant invasion science which have been identified in other European countries and at a global level. We conclude that, to adequately identify the most problematic IAPs and assess the vulnerability of Croatian N2000 sites, a broader set of criteria and additional floristic research (at certain sites) is necessary. A deeper country-specific insight into the ecology of certain IAPs and their interdependence with the range of environmental variables is essential. It is our hope that the findings presented here will provide a basis and inspiration for further, more targeted research in the future. Such research could make a substantial contribution to the improvement of site management and the conservation of the target species and habitats.

ACKNOWLEDGEMENTS

The authors would like to thank Sven Jelaska for his invaluable critical feedback on the manuscript.

REFERENCES

- Ayllón, D., R.A. Baquero, G.G. Nicola, 2022: Differential vulnerability to biological invasions: not all protected areas (and not all invaders) are the same. *Biodiversity and Conservation* 31: 1535–1550. <https://doi.org/10.1007/s10531-022-02407-8>
- Baquero, R.A., D. Ayllón, G.G. Nicola, 2021: Are the EU Biosecurity Legislative Frameworks sufficiently effective to prevent biological invasions in the Natura 2000 Network? A case study in Mediterranean Europe. *Environmental Science & Policy* 120: 21–28. <https://doi.org/10.1016/j.envsci.2021.02.007>
- Bardi, A., P. Papini, E. Quaglino, E. Biondi, J. Topić, M. Milović, M. Pandža, M. Kaligarić, G. Oriolo, V. Roland, A. Batina, T. Kirin, 2016: Karta prirodnih i poluprirodnih ne-šumskih kopnenih i slatkovodnih staništa Republike Hrvatske (Map of Natural and Seminal Natural Non-Forest and Freshwater Habitats of the Republic of Croatia). AGRISTUDIO s.r.l., TEMI S.r.l., TIMESIS S.r.l., HAOP, Zagreb.
- Bioportal, 2021: Web portal of Nature Protection Information System - Web Feature Service (WFS) layer of the Natura 2000 sites. Institute for Environment and Nature, Ministry of Economy and Sustainable Development of the Republic of Croatia. <http://www.bioportal.hr/>
- Bioportal, 2024: Web portal of Nature Protection Information System - Standard Data Form of the Natura 2000 sites: HR2001352 Mosor, HR2001357 Otok Krk, HR5000022 Park prirode Velebit, HR5000031 Delta Neretve. Institute for Environment and Nature, Ministry of Economy and Sustainable Development of the Republic of Croatia. <http://www.bioportal.hr/>
- Braun, M., S. Schindler, F. Essl, 2016: Distribution and management of invasive alien plant species in protected areas in Central Europe. *Journal for Nature Conservation* 33: 48–57. <https://doi.org/10.1016/j.jnc.2016.07.002>
- Brondizio, E.S., J. Settele, S. Díaz, H.T. Ngo (eds.), 2019: Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. IPBES Secretariat, Bonn. <https://doi.org/10.5281/zenodo.3831673>
- Brooks, M., M. Lusk, 2008: Fire management and invasive plants: a handbook. United States Fish and Wildlife Service, Arlington.
- Christopoulou, A., A. Christopoulou, N.M. Fyllas, P.G. Dimitrakopoulos, M. Arianoutsou, 2021: How effective are the protected areas of the Natura 2000 Network in halting biological invasions? A case study in Greece. *Plants* 10: 2113. <https://doi.org/10.3390/plants10102113>
- Dimitrakopoulos, P.G., S. Koukoulas, A. Galanidis, P. Delipetrou, D. Gounaridis, K. Touloumi, M. Arianoutsou, 2017: Factors shaping alien plant species richness spatial patterns across Natura 2000 Special Areas of Conservation of Greece. *The Science of The Total Environment* 601–602: 461–468. <https://doi.org/10.1016/j.scitotenv.2017.05.220>
- EPPO, 2024: Lists of invasive alien plants of the European and Mediterranean Plant Protection Organization (EPPO), a regional Plant Protection Organization (RPPO) for the Euro-Mediterranean region under the International Plant Protection Convention (IPPC, Article IX). https://www.eppo.int/ACTIVITIES/invasive_alien_plants/iap_lists
- Foxcroft, L.C., P. Pyšek, D.M. Richardson, P. Genovesi (eds.), 2013: Plant invasions in protected areas: patterns, problems and challenges. Springer, Dordrecht. <https://doi.org/10.1007/978-94-007-7750-7>

- Foxcroft, L.C., P. Pyšek, D.M. Richardson, P. Genovesi, S. MacFadyen, 2017: Plant invasion science in protected areas: progress and priorities. *Biological Invasions* 19: 1353–1378. <https://doi.org/10.1007/s10530-016-1367-z>
- Gallardo, B., D.C. Aldridge, P. González-Moreno, J. Pergl, M. Pizarro, P. Pyšek, W. Thuiller, C. Yesson, M. Vilà, 2017: Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology* 23: 5331–5343. <https://doi.org/10.1111/gcb.13798>
- Guerra, C., R.A. Baquero, D. Gutiérrez-Arellano, G.G. Nicola, 2018: Is the Natura 2000 network effective to prevent the biological invasions? *Global Ecology and Conservation* 16: e00497. <https://doi.org/10.1016/j.gecco.2018.e00497>
- Haubrock, P.J., A.J. Turbelin, R.N. Cuthbert, A. Novoa, N.G. Taylor, E. Angulo, L. Ballesteros-Mejia, T.W. Bodey, C. Capinha, C. Diagne, F. Essl, M. Golivets, N. Kirichenko, M. Kourantidou, B. Leroy, D. Renault, L. Verbrugge, F. Courchamp, 2021: Economic costs of invasive alien species across Europe. In (Zenni, R.D., S. McDermott, E. García-Berthou, F. Essl, eds.), 2021: The economic costs of biological invasions in the world. *NeoBiota* 67: 153–190. <https://doi.org/10.3897/neobiota.67.58196>
- Hulme, P.E., P. Pyšek, V. Jarošík, J. Pergl, U. Schaffner, M. Vilà, 2013: Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution* 28 (4): 212–218. <https://doi.org/10.1016/j.tree.2012.10.010>
- Koren, T., I. Burić, G. Glavan, R. Verovnik, 2020: The butterfly (Lepidoptera: Papilionoidea) diversity of Mt. Mosor in Dalmatia, Croatia. *Natura Sloveniae* 22 (2): 43–68. <https://doi.org/10.14720/ns.22.2.43-68>
- Lazzaro, L., R. Bolpagni, G. Buffa, R. Gentili, M. Lonati, A. Stinca, A. Acosta, M. Adorni, M. Aleffi, M. Allegrezza, C. Angiolini, S. Assini, S. Bagella, G. Bonari, M. Bovio, F. Bracco, G. Brundu, M. Caccianiga, L. Carnevali, V. Di Cecco, S. Ceschin, G. Ciaschetti, A. Cogoni, B. Foggi, A.R. Frattaroli, P. Genovesi, D. Gigante, F. Lucchese, A. Mainetti, M. Mariotti, P. Minissale, B. Paura, M. Pellizzari, E.V. Perrino, G. Pirone, L. Poggio, L. Polidini, S. Poponessi, I. Prisco, F. Prosser, M. Puglisi, L. Rosati, A. Selvaggi, L. Sottovia, G. Spampinato, A. Stanisci, R. Venanzoni, D. Viciani, M. Vidali, M. Villani, L. Lastrucci, 2020: Impact of invasive alien plants on native plant communities and Natura 2000 habitats: State of the art, gap analysis and perspectives in Italy. *Journal of Environmental Management* 274: 111140. <https://doi.org/10.1016/j.jenvman.2020.111140>
- Mitić, B., I. Boršić, I. Dujmović, S. Bogdanović, M. Milović, P. Cigić, I. Rešetnik, T. Nikolić, 2008: Alien flora of Croatia: proposals for standards in terminology, criteria and related database. *Natura Croatica* 17 (2): 73–90.
- Natura 2000 Barometer, 2024: Web portal facilitated by European Environment Agency (Release version: end 2022 to 12 March 2024). <https://www.eea.europa.eu/data-and-maps/dashboards/natura-2000-barometer>
- Nentwig, W., S. Bacher, S. Kumschick, P. Pyšek, M. Vilà, 2018: More than "100 worst" alien species in Europe. *Biological Invasions* 20: 1611–1621. <https://doi.org/10.1007/s10530-017-1651-6>
- Nikolić, T., 2020: Upute za upotrebu web sučelja baze podataka Flora Croatica, verzija 4.0, rujan 2020. (User Manual: Flora Croatica Web Interface, Ver. 4.0, Sep. 2020). University of Zagreb Faculty of Science, Department of Botany and Botanical Garden, Zagreb. <https://hirc.botanic.hr/fcd/Html/Hr-FC-kako.html>
- Nikolić, T. (ed.), 2024: Alohtone biljke (Allochthonous plants), Flora Croatica Database. University of Zagreb Faculty of Science, Department of Botany and Botanical Garden, Zagreb. The dataset includes observations until June 10, 2021. Retrieved October 10, 2020 - June 10, 2021; April 28, 2024 from <https://hirc.botanic.hr/fcd/InvazivneVrste>
- Nikolić, T., B. Mitić, B. Milašinović, S.D. Jelaska, 2013: Invasive alien plants in Croatia as a threat to biodiversity of South-Eastern Europe: distributional patterns and range size. *Comptes Rendus Biologies* 336 (2): 109–121. <https://doi.org/10.1016/j.crvi.2013.01.003>
- Nikolić, T., B. Mitić, I. Boršić, 2014: Flora Hrvatske – Invazivne biljke. Alfa, Zagreb.
- Novak, N., M. Novak, 2018: Razlike u invazivnosti nekih stranih biljnih vrsta između kontinentalnog i obalnog dijela Hrvatske. *Poljoprivreda* 24 (2): 63–69. <https://doi.org/10.18047/poljo.24.2.9>
- Official Gazette no. 13/24, 2024: Pravilnik o crnoj i bijeloj listi stranih vrsta (Regulation on the Black and White List of Alien Species). Narodne Novine, official Gazette of the Republic of Croatia.
- Official Gazette no. 27/21, 2021: Pravilnik o popisu stanišnih tipova i karti staništa (Regulation on the List of Habitat Types and Habitat Maps). Narodne Novine, official Gazette of the Republic of Croatia.
- Official Gazette no. 80/19, 2019: Uredba o ekološkoj mreži i nadležnostima javnih ustanova za upravljanje područjima ekološke mreže (Regulation on the Ecological Network and the Competencies of Public Institutions for Ecological Network Management). Narodne Novine, official Gazette of the Republic of Croatia.
- Official Gazette no. 119/23, 2023: Uredba o izmjenama Uredbe o ekološkoj mreži i nadležnostima javnih ustanova za upravljanje područjima ekološke mreže (Regulation amending the Regulation on the Ecological Network and the Competencies of Public Institutions for Ecological Network Management). Narodne Novine, official Gazette of the Republic of Croatia.
- Protopopova, V.V., M.V. Shevera, M.M. Fedoronchuk, V.L. Shevchik, 2014: Transformer species in the flora of the Middle Dnipro Region. *Ukrainian Botanical Journal* 71 (5): 563–572. (In Ukrainian) <https://doi.org/10.15407/ukrbotj71.05.563>
- Radović, A., S. Schindler, D. Rossiter, T. Nikolić, 2018: Impact of biased sampling effort and spatial uncertainty of locations on models of plant invasion patterns in Croatia. *Biological Invasions* 20: 3527–3544. <https://doi.org/10.1007/s10530-018-1793-1>
- Richardson, D.M., P. Pyšek, M. Rejmánek, M.G. Barbour, F.D. Panetta, C.J. West, 2000: Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* 6 (2): 93–107. <https://doi.org/10.1046/j.1472-4642.2000.00083.x>
- Rouget, M., M.P. Robertson, J.R.U. Wilson, C. Hui, F. Essl, J.L. Renteria, D.M. Richardson, 2016: Invasion debt – quantifying future biological invasions. *Diversity and Distributions* 22: 445–456. <https://doi.org/10.1111/ddi.12408>
- Török, K., Z. Botta-Dukát, I. Dancza, I. Németh, J. Kiss, B. Mihály, D. Magyar, 2003: Invasion gateways and corridors in the Carpathian Basin: biological invasions in Hungary. *Biological Invasions* 5: 349–356. <https://doi.org/10.1023/B:BINV.0000005570.19429.73>
- Vilà, M., C. Basnou, S. Gollasch, M. Josefsson, J. Pergl, R. Sclera, 2009: One hundred of the most invasive alien species in Europe. In: *Handbook of Alien Species in Europe. Invading Nature - Springer Series in Invasion Ecology*, vol 3. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-8280-1_12
- Vuković, N., V. Šegota, A. Alegro, N. Koletić, A. Rimac, S. Dekanić, 2019: "Flying under the radar" – How misleading distributional data led to wrong appreciation of knotweeds invasion (*Reynoutria* spp.) in Croatia. *BioInvasions Records* 8 (1): 175–189. <https://doi.org/10.3391/bir.2019.8.1.19>
- Zedler, J.B., S. Kercher, 2004: Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences* 23: 431–452. <https://doi.org/10.1080/07352680490514673>