

Research Article

“Flying under the radar” – how misleading distributional data led to wrong appreciation of knotweeds invasion (*Reynoutria* spp.) in CroatiaNina Vuković¹, Vedran Šegota¹, Antun Alegro^{1,*}, Nikola Koletić¹, Anja Rimac¹ and Stjepan Dekanić²¹University of Zagreb, Department of Biology, Division of Botany, Marulićev trg 20/II, 10000 Zagreb, Croatia²Perceptives Ltd., Koprivnička ulica 38, 10000 Zagreb, CroatiaAuthor e-mails: nina.vukovic@biol.pmf.hr (NV), vedran.segota@biol.pmf.hr (VS), antun.alegro@biol.pmf.hr (AA), nikola.koletic@biol.pmf.hr (NK), anja.rimac@biol.pmf.hr (AR), stjepan@perceptives.org (SD)

*Corresponding author

Citation: Vuković N, Šegota V, Alegro A, Koletić N, Rimac A, Dekanić S (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>

Received: 15 January 2018**Accepted:** 29 October 2018**Published:** 12 February 2019**Handling editor:** Giuseppe Brundu**Thematic editor:** Stelios Katsanevakis**Copyright:** © Vuković et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS**Abstract**

Knotweeds were introduced into Europe in the 19th century and soon after became aggressive invaders. While *R. japonica* and *R. sachalinensis* arrived from Asia, their hybrid *Reynoutria* × *bohemica* is believed to originate from the introduced range. Revised material shows that *R. × bohemica* has occurred in Europe since at least 1872, but was frequently misidentified as one of the parents. For that reason, the hybrid was detected relatively late in many European countries, meaning that it was silently spreading throughout the region for a long time. The present study was conducted in Croatia, where the parental species have been recorded since the 19th century, the hybrid, however, not being recognized until very recently, although it has probably been present for decades. As a result, the current knowledge of the distribution of knotweeds in Croatia is mostly erroneous. We revised specimens from Croatian herbaria and performed an extensive field survey across the whole of the territory of Croatia to collect new data. In this paper, we present accurate distribution maps of the three taxa, produced after a thorough revision, showing a result remarkably different to that previously known. In contrast to previously recorded distributions, we found that *R. × bohemica* is by far the most widespread, *R. japonica* is occasional, and *R. sachalinensis* is extremely rare. *R. × bohemica*, unlike its parents, occurs in Mediterranean Croatia as well. Compared to *R. × bohemica*, *R. japonica* occurs more frequently along watercourses. Taking into account that the studied taxa have different behaviour, ecological preferences, spreading ability and consequently different invasiveness, they should be analysed separately in any attempt to explain, manage and/or limit their spread. Therefore, the accuracy of their past and future identification is of major importance.

Key words: distribution maps, invasive plants, *Reynoutria* × *bohemica*, *Reynoutria japonica*, *Reynoutria sachalinensis*

Introduction

Members of the genus *Reynoutria* (Polygonaceae: Asian knotweeds) were introduced into Europe in the early 19th century for ornamental purposes (Bailey and Conolly 2000). At the time, they were regarded as extremely desirable garden plants and spread all over the continent through trade and exchange of material among nurseries and gardens (Bailey and Conolly 2000). Following their distribution throughout the region, the species

eventually escaped into the wild and became successfully naturalized, soon to be recognized as aggressive invaders all over the introduced range (Bailey and Conolly 2000), and their negative impacts on resident communities became widely documented (Padula et al. 2008; Maurel et al. 2009; Aguilera et al. 2010; Maurel et al. 2013).

Two species native to Eastern Asia are currently widespread in Europe; *Reynoutria japonica* Houtt. [*Fallopia japonica* (Houtt.) Ronse Decr., *Polygonum cuspidatum* Siebold and Zucc.], most frequently occurring as *R. japonica* var. *japonica* and occasionally as *R. japonica* var. *compacta* (Hook f.) Moldenke, and its close relative *R. sachalinensis* (F. Schmidt.) Nakai [*Fallopia sachalinensis* (F. Schmidt) Ronse Decr., *Polygonum sachalinense* F. Schmidt].

In 1983, a hybrid between *R. japonica* var. *japonica* and *R. sachalinensis* was described from the Czech Republic, and named *R. × bohémica* Chrtek and Chrtková (Chrtek and Chrtková 1983). Although records of the hybrid started to occur in many European countries from the point of its description onward, revised herbarium material shows that it has been present in European horticulture since at least 1872, and has been naturalized since at least 1954, with botanists being completely unaware of its existence (Bailey and Wisskirchen 2006). Revisions of the genus in a number of national floras have shown that it was silently present in many European countries for a long time, although detected only relatively recently (Fojcik and Tokarska-Guzik 2000; Mandák et al. 2004; Bailey and Wisskirchen 2006; Jogan 2006; Tiébré et al. 2007a; Balogh et al. 2008; Padula et al. 2008; Strgulc Krajšek and Jogan 2011). Despite the time-lag between its occurrence and recognition, in a number of European countries the hybrid is already recognized as a significant component of the *Reynoutria* complex, e.g. in France (Schnitzler et al. 2008), Belgium (Tiébré et al. 2007a), Germany and Switzerland (Krebs et al. 2010), UK (Bailey et al. 1996, 2007), Czech Republic (Mandák et al. 2004).

Asian knotweeds are tall, robust, rhizomatous perennials, with erect, bamboo-like stems arising from a strong, woody rhizome, forming dense, impenetrable crowns up to 2–3 m in height (over 5 m in case of *R. sachalinensis*). They produce more or less broad leaves, alternating along flexuous branches, with small, creamy white flowers arranged in clusters arising from axillary panicles in late summer. Following senescence in winter, tall woody stems persist creating dense thickets (Child 1999; Balogh 2008). The literature suggests that all European clones of *R. japonica* are male-sterile, possibly even originating from a single plant, spread throughout Europe by vegetative means (Hollingsworth and Bailey 2000; Krebs et al. 2010).

Although similar in appearance, the two parental species can be distinguished relatively easily. The main differences refer to the size, shape



Figure 1. Scanned leaves of all three Asian knotweeds present in Croatia. From left to right: *R. japonica*, *R. × bohemica*, *R. sachalinensis*. Photographs by Nikola Koletić.

and hairiness of the leaves: *R. japonica* has relatively small (10–18 cm), broadly ovate leaves with a truncate base and absent (or very inconspicuous) hairs, while *R. sachalinensis* has much larger, elongated leaves (30–45 cm), with a distinctly cordate base and long hairs on the leaf underside (Figure 1) (Bailey and Wisskirchen 2006; Balogh 2008; Bailey et al. 2009). In contrast, the hybrid *R. × bohemica* shows intermedium morphology ranging between the parents and can be easily misidentified (Figure 1). The morphology of hybrids is additionally affected by backcrosses with the parental species, increasing the genetic and phenotypic diversity of the complex (Mandák et al. 2005; Tiébré et al. 2007b; Bailey 2013).

The exact time of arrival of Asian knotweeds to Croatia is not known. Current data from the Flora Croatica Database (FCD, Nikolić 2017) show that *R. japonica* and *R. sachalinensis* have been present since the 19th century and the early 1970s, respectively. According to the same database, *R. japonica* is a very common plant (over 300 records, Figure 2), while *R. sachalinensis* is rare, registered only at seven localities: five in the city of Zagreb (Marković ZA-16275 ZA-16276, ZA-16277; Dujmović et al. 2016; Mitić et al. 2016), one in the city of Rijeka (Karavla 1997), and one on the foothills of Bansko Brdo Hill (Purger and Csiky 2008) (Figure 2). The FCD does not provide any information on the variety of *R. japonica* – it is listed only as a species, since the distinction of varietal ranks is not supported in the database.

Nevertheless, from personal experience we knew that *R. × bohemica* also occurs in Croatia, and we hypothesized that it is perhaps more widespread than the parents. However, in the absence of literature on the occurrence of

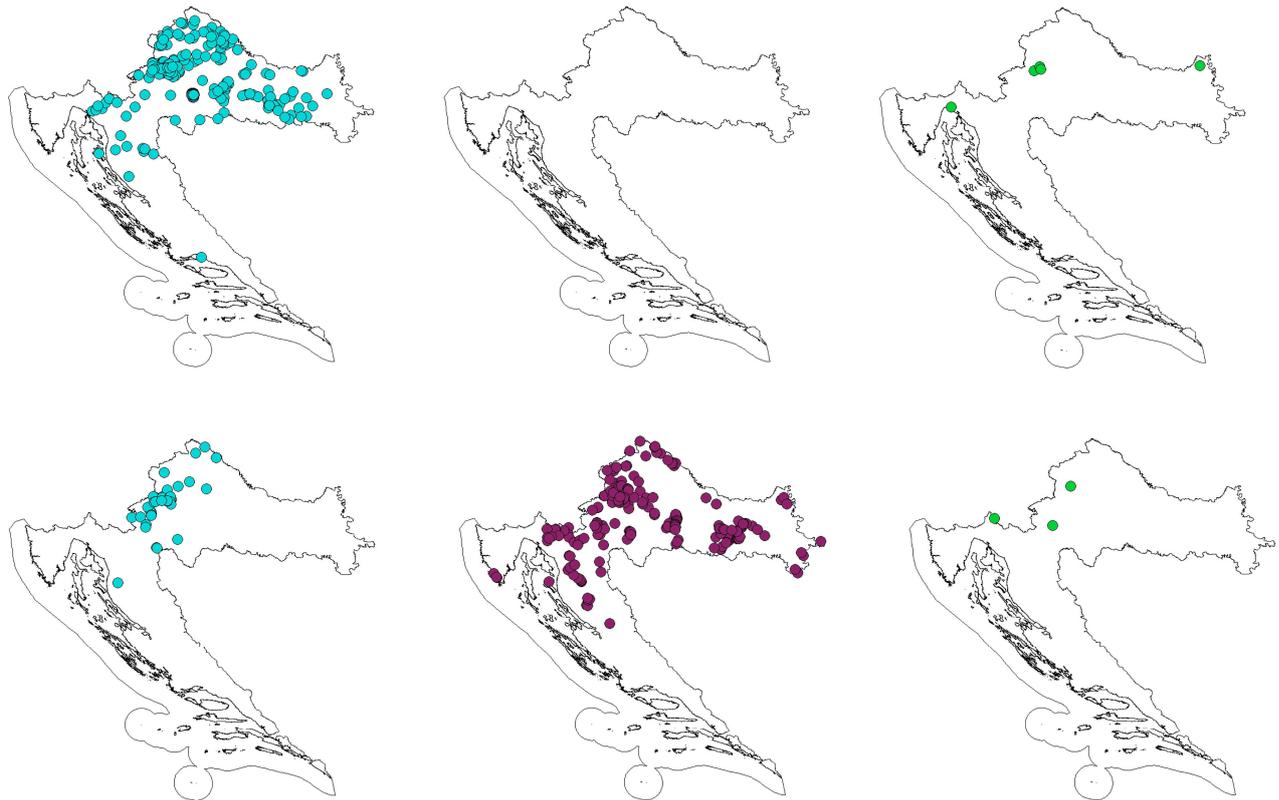


Figure 2. Above – the distribution of knotweeds in Croatia before the study (obtained from the FCD), below – the distribution of knotweeds in Croatia after the study in 2016 (obtained from fieldwork and herbarium collections). Blue – *R. japonica*, purple – *R. × bohemica*, green – *R. sachalinensis*. Literature data from the FCD that could not be checked in the field are not shown in the maps representing the situation after 2016.

the hybrid in Croatia, we additionally hypothesized that *R. × bohemica* was usually erroneously identified as one of the parents. To address this issue, we performed a comprehensive study of the distribution of all three taxa in Croatia. We aimed to obtain realistic distributions of knotweeds in Croatia and compare their occurrences with regards to the habitats and land use types.

Materials and methods

We examined plant material from major herbarium collections in Croatia (ZA, ZAHO, CNHM, ZAGR), in order to revise specimens of *Reynoutria*, i.e. find and correct any erroneously identified plant material.

We performed an extensive survey across Croatia from June to November 2016, during which we closely examined and identified knotweeds found in the field, using the identification key from Bailey and Wisskirchen (2006). The survey was performed during participation in the national water monitoring scheme; therefore, the area of investigation encompassed the whole state territory. Within the course of the water monitoring, we set out to visit the network of localities previously designated for the monitoring scheme, scattered all across Croatia. Although our target sites were freshwater habitats, we performed the survey by travelling along the main traffic network and paid particular attention to

the occurrence of knotweeds anywhere in the landscape. Every observed patch of knotweeds was recorded and identified according to the morphology of the leaves. The associated habitat and land-use types were recorded as well, and classified into four main categories 1) meadows, 2) by house/building, 3) along watercourse and 4) along path/road; while the size of the patches was estimated. In cases of troublesome field identification, samples of the stems with leaves were collected and labelled, instantly pressed and stored in the herbarium, to be identified afterwards by examining the hairiness of the leaves and the presence of extrafloral nectaria. In addition, we recorded geographical coordinates of all sites with knotweeds, using a GPS device, and subsequently produced accurate distribution maps of all three taxa (Figure 2).

The existing records for *R. sachalinensis* in the FCD were very scarce, hence we checked the identification of these plants, and included the revised data in the distribution map. The distribution map of *R. japonica* relies solely on our own field data and existing herbarium records, due to the large amount of literature data that could not be confirmed with certainty.

Results

Revision of altogether 27 herbarium sheets with herbarium material from Croatia showed that approximately one third of the previously collected plants had been erroneously identified. Table 1 shows the data on the sheets with specimens from Croatia found in our collections. Although *R. × bohemica* was previously not recorded in any of the herbaria examined, we found it collected on eight sheets; in most cases misidentified as *R. japonica*, but also as *R. sachalinensis*. Half of the specimens (14 sheets) in the herbaria were collected prior to the description of the hybrid. Among them, we found three herbarium sheets in which *R. × bohemica* was designated as *R. sachalinensis* (Table 1). As for the specimens collected after the description of the hybrid (13 sheets), we found five herbarium sheets where *R. × bohemica* was identified as *R. japonica* (Table 1).

During the survey, we recorded the presence of knotweeds at 238 sites (Supplementary material Table S1), containing monodominant stands. *R. japonica* was only exceptionally found in the same localities as *R. × bohemica*, but never in the same patch. The hybrid was by far the most commonly found (210 sites, Figure 2), followed by *R. japonica* (25 sites, Figure 2). *R. sachalinensis* was found only at three localities; the city of Karlovac, the town of Donja Stubica and near the town of Čabar (Figure 2). Only one plant was found in Karlovac, growing next to a building, while up to 10 young plants were recorded in Donja Stubica, in a neglected front yard of a house. The patch near Čabar was much larger and comprised clonal individuals growing between the road and the River Čabranka, covering approximately 200 m². Notably, we did not manage to confirm the presence

Table 1. Revised data from the herbarium *exsiccata* collected prior to our study (collections ZAGR, CNHM, ZA), with times of collection. Records above the dotted line were collected after the description of the hybrid.

Collection	Label	Revised as	Locality	Year
ZAGR	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Trsje	2015
ZAGR	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Trsje	2015
ZAGR	<i>R. japonica</i>	<i>R. × bohemica</i>	City of Zagreb, Maksimir	2015
ZAGR	<i>R. japonica</i>	<i>R. × bohemica</i>	City of Zagreb, Maksimir	2015
ZAGR	<i>R. japonica</i>	<i>R. × bohemica</i>	City of Zagreb, Maksimir	2015
ZAGR	<i>R. japonica</i>	<i>R. × bohemica</i>	City of Zagreb, Maksimir	2015
ZAGR	<i>R. japonica</i>	<i>R. japonica</i>	City of Čakovec, Kolodvorska St.	2015
CNHM	<i>R. japonica</i>	<i>R. japonica</i>	Sjeverni Velebit Mt., Krasno	2007
CNHM	<i>R. japonica</i>	<i>R. japonica</i>	Sjeverni Velebit Mt., Krasno	2007
CNHM	<i>R. japonica</i>	<i>R. japonica</i>	Sjeverni Velebit Mt., Krasno	2007
CNHM	<i>R. japonica</i>	<i>R. × bohemica</i>	Žumberak Mt., Čunkova draga	1995
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Sveti Ivan Žabno	1997
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Sloboština	1992
ZA	<i>R. sachalinensis</i>	<i>R. × bohemica</i>	City of Zagreb, Mlinovi	1973
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Zelenjak	1972
ZA	<i>R. sachalinensis</i>	<i>R. × bohemica</i>	City of Zagreb, southwards of The Square of Sports	1971
ZA	<i>R. sachalinensis</i>	<i>R. × bohemica</i>	City of Zagreb, between Moskovska St. and Zagorska St.	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Podsused	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Gračani	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Samobor	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Krapina	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Kustošak	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb, Kustošak	1971
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Samobor	1970
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Samobor	1970
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Samobor	1968
ZA	<i>R. japonica</i>	<i>R. japonica</i>	City of Zagreb	*

* No year indicated. Collector was active in the 19th century

of *R. sachalinensis* at localities previously registered in the FCD. After the revision of the herbarium material and searching in the field to confirm the literature records, we excluded all localities from the city of Zagreb, due to erroneous identification (Marković ZA-16275, ZA-16276, ZA-16277; Dujmović et al. 2016; Mitić et al. 2016), and attributed these records to *R. × bohemica*. The records from Rijeka (Karavla 1997) and Bansko Brdo (Purger and Csiky 2008) remain unresolved. Our study, which covered the whole of Croatia, did not reveal any significant presence of knotweeds in the Mediterranean part, only *R. × bohemica* being found, in southern Istria and the island of Rab.

Knotweeds were mostly found in ruderal sites strongly influenced by humans, often by paths and roads, frequently near houses and in gardens (Figure 3). In many cases they were growing very close to freshwater ecosystems; on the open banks of rivers and streams, along embankments, under bridges etc. (Figure 3). It seems that *R. japonica* occurs more often along watercourses than *R. × bohemica* (34% and 22% of the total number of localities, respectively).

Our observations have shown that, although very widespread and frequent plants, they mostly occur in small clonal stands or individually. Nevertheless, we did observe some extremely dense patches with numerous

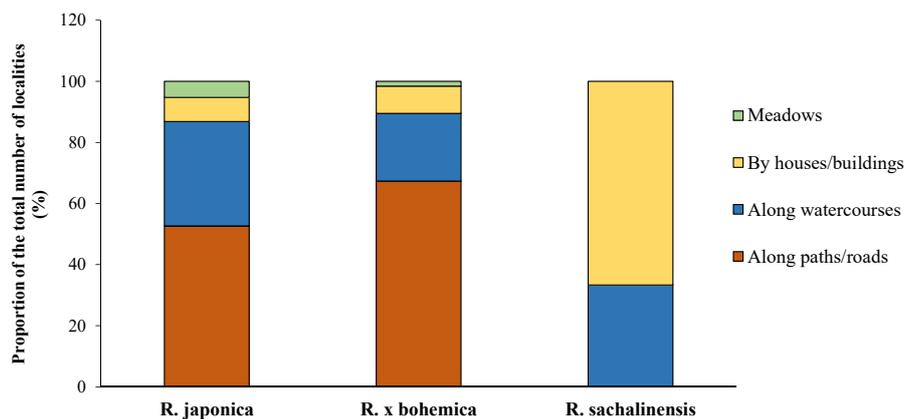


Figure 3. Occurrence of Asian knotweeds in main habitat and land use types in Croatia as recorded in our field study and on herbarium sheets from Croatian collections. Total number of localities: *R. japonica* = 38, *R. × bohemica* = 190, *R. sachalinensis* = 3.

individuals in some cases, typically by watercourses. We recorded three large monotypic patches of knotweeds. The largest one consisted solely of *R. japonica*, expanding approximately seven kilometres along the riverbanks of the River Krapinica, from the town of Krapina to the town of Durmanec (NW Croatia). The other two large patches were composed of *R. × bohemica*. One was detected in the settlement of Kašina, eastwards of Mt Medvednica in Central Croatia, where bohemian knotweeds were growing along the wider area of the Kašina stream. Here we observed a belt of *R. × bohemica* growing alongside the stream for 5 kilometres, occasionally forming dense, monodominant patches. Another large patch was recorded in Međimurje (NW Croatia), between the settlements of Dekanovec and Domašinec. Here, a significant surface of the grassland was colonized by *R. × bohemica*, forming a more or less continuous patch of approximately 200 m².

Discussion

Species distribution

Our study shows that former knowledge on the presence and distribution of *Reynoutria* species in Croatia was largely incorrect. Prior to our study, *R. japonica* was recorded as being widespread in Croatia, *R. sachalinensis* was recorded in seven localities, while *R. × bohemica* was not recorded at all. After conducting a revision of the herbarium collections and an extensive survey in the field, we found *R. × bohemica* occurring very abundantly in Croatia, being by far the most widespread of all three taxa. *R. japonica* is significantly less widespread, although still relatively frequent, while *R. sachalinensis* is extremely rare, with only three sites that can be confirmed with certainty. Furthermore, we hypothesize that *R. sachalinensis* was first introduced into the check list of Croatian flora based on the herbarium examples from the ZA collection (Marković ZA-16275,

ZA-16276, ZA-16277), which in fact contain *R. × bohemica*, meaning that *R. sachalinensis* was mistakenly listed as a member of the Croatian flora. The confusion happened at the time simply because the hybrid was still unknown in the 1970s, when the material was collected. Unfortunately, this record was subsequently transferred into the first checklist of Croatian flora (Marković 1994) and remained in it until recent times. Prior to our study, this misidentification was noticed by Hlavati Širka et al. (2013), who were performing a revision on the distribution of *R. sachalinensis* in Serbia and neighbouring countries and encountered the hybrid while searching for the parent. Unfortunately, this discovery did not find its way to a broader audience, so *R. × bohemica* remained unregistered in the FCD up to date.

The revelation of new localities occupied by *R. × bohemica* after revisions and thorough identification aligns Croatia with what is observed in other parts of Europe (e.g. Bailey et al. 1996, 2007; Fojcik and Tokarska-Guzik 2000; Mandák et al. 2004; Jogan 2006; Tiébré et al. 2007a; Balogh et al. 2008; Padula et al. 2008; Schnitzler et al. 2008; Krebs et al. 2010; Strgulc Krajšek and Jogan 2011). In addition, the Croatian situation shows that the prevalence of the hybrid can easily be masked by its parents, and brings out the possibility that the *Reynoutria* taxa are being wrongly appreciated in the neighbouring countries as well.

As for *R. japonica* var. *compacta*, we did not find any evidence of the occurrence of this variety in the Croatian flora. The FCD database does not provide information on the varietal rank; therefore, we could not distinguish between the two varieties regarding previous records. On the other hand, all stands registered during our fieldwork were, without exception, composed of *R. japonica* var. *japonica*. *R. japonica* var. *compacta* is considered a dwarf, alpine variant of *R. japonica* (Bailey and Connolly 2000), generally occurring much more rarely than the typical variety across the whole of the introduced range (Bailey and Connolly 2000; Mandák et al. 2004; Padula et al. 2008; Strgulc Krajšek and Jogan 2011). We believe that this variety does not occur in Croatia, or is extremely rare.

Our revision of localities of *R. sachalinensis* in Croatia did not firmly confirm its presence in any of the previously reported sites. We excluded the records from Zagreb as erroneously identified, and reclassified them as *R. × bohemica*. Locating the record from Rijeka (Karavla 1997) was troublesome; we did not manage to determine the exact locality, due to the incorrect citing of the literature within the paper. As for Bansko Brdo (Purger and Csiky 2008), we visited the locality but failed to find the plant, due to the imprecise description of the site. Around Bansko Brdo however, we recorded many stands of *R. × bohemica*.

Although we did not focus on their spread potential, we have seen that the three taxa differ in their ability to colonize the space. As well as being

registered at the most sites, *R. × bohemica* frequently formed larger patches, with two out of the three largest ones (in Međimurje and Kašina, NW Croatia) completely comprised of hybrid individuals. By contrast, *R. japonica* was normally found solitarily or in small patches of a few individuals, and ultimately is less widespread. Interestingly, the largest stand along the river Krapinica was completely composed of *R. japonica*, and such abundance is probably the result of the residence period; *R. japonica* was first recorded near Krapina as early as 46 years ago (Marković ZA-16256), and represents one of the earliest known records of Asian knotweeds in Croatia. Obviously, the continuous vegetative spread along the watercourse from that point onward has resulted in the large, clonal stand at this particular site. *R. sachalinensis* was very restricted in its occurrence; only a solitary plant was registered in the city of Karlovac, while fewer than 10 plants were found in the neglected front yard of a house in the town of Donja Stubica, and one larger patch occupying approximately 200 m² was recorded near the town of Čabar. These observations led us to believe that the hybrid is able to spread more efficiently than either of the parents; *R. japonica* spreads less fast but still relatively successfully, and *R. sachalinensis* is very limited in its spread. A similar conclusion was reached by Mandák et al. (2004), when comparing the temporal occurrence of herbarium records of all three taxa in the Czech Republic.

Reasons for scarce occurrence of knotweeds in the Mediterranean part of Croatia may be due to their ecology, as high temperatures combined with summer droughts are probably limiting factors for these species (Bailey and Wisskirchen 2006). Although we did not particularly study their ecological behaviour, we noticed that they frequently occur along watercourses, sometimes forming dense patches. Similar habitat preference was also observed in the Czech Republic, Hungary, Italy, Slovenia, Serbia (Mandák et al. 2004; Balogh 2008; Padula et al. 2008; Strgulc Krajšek and Jogan 2011; Anđelković et al. 2013). It is quite possible that these gigantic herbs have a high demand for water, making it difficult for them to thrive in the Mediterranean climate. Bailey and Wisskirchen (2006) have addressed this topic by comparing *Reynoutria*-dominated communities in France and found that *R. × bohemica* spreads more deeply into areas with a Mediterranean climate than *R. japonica*. They also found that *R. × bohemica* is confined to the immediate vicinity of watercourses in the Mediterranean areas, most probably to escape the detrimental effect of summer droughts.

Methodological considerations

Although we found knotweeds in types of habitats similar to those previously reported (e.g. Mandák et al. 2004; Balogh 2008; Tiébré et al. 2008), the number of records on the watercourses may be underestimated

in our study, due to the methodology of the survey. We mostly conducted our search travelling along the network of roads, searching for knotweeds in the landscape, and thus managed to map the records along roads in detail. On the other hand, knotweed sites along watercourses were recorded in a more random way; since the watercourses were visited mainly at the crossings with the roads, or at the specific sites within the national scheme for water monitoring, the courses not being surveyed completely. We believe that use of the watercourses as corridors for the survey would reveal even more monodominant sites of knotweeds within these habitats. Therefore, to get a better overview on the average population size of Asian knotweeds in Croatia, our recommendation would be to focus on the watercourses in any future studies. These habitats seem to support the development of monocultures of knotweeds, most probably for two reasons; first is the availability of water, and second is water management in Croatia, where the watercourses are often heavily managed, with artificial banks or embankments regularly maintained by mowing. This practice removes natural vegetation and prevents the establishment of many plant species, providing a highly disturbed environment relatively free from competition, suitable for plant invasions. The fact that Asian knotweeds are more productive on riverbanks under intensive light conditions (Dommanget et al. 2013) and that they are very effectively spread by vegetative means (Bímová et al. 2003) indicates the importance of managed watercourses as their habitats and highlights the role of water management in the knotweed invasion.

Factors influencing the distribution of knotweeds

It is widely acknowledged that invasion success is generally regulated by multiple factors (Richardson and Pyšek 2006; Holzmüller and Jose 2009). Vegetative regeneration (when present) may play an important role. Although we did not study the role of vegetative spread in invasion success of knotweeds, we observed cases where knotweeds were able to establish a stand by rooting from plant remains cut during maintenance and left by the road. Also, we have seen successful renewal of knotweeds after heavy disturbances following land preparation, from small rhizome fragments, only a few centimetres long. Our observations are in line with the existing literature in pointing out the key role of vegetative spread in knotweed invasiveness, and it has been well documented that all three taxa have a great capability of vegetative regeneration from rhizome and stem (Child 1999; Bímová et al. 2003; Pyšek et al. 2003). Notably, when compared, wild hybrids of *R. × bohemica* have shown the largest success in vegetative regeneration (Child 1999; Bímová et al. 2003), followed by *R. japonica*, while *R. sachalinensis* was the least successful in vegetative regeneration (Child 1999; Bímová et al. 2003). Regeneration success could be influenced

by long-term crossings and back-crossings, during which new genotypes are created broadening the genetic pool of the complex, providing novel survival and establishment strategies for hybrid generations. Knotweed hybridization results with novel ploidy levels (Mandák et al. 2003), increasing the genetic diversity of the complex, and arguably, some hybrid populations may be more invasive than the parents as a result of this increased diversity (Pyšek et al. 2003; Bailey et al. 2007; Tiébré et al. 2007a).

The combination of successful vegetative propagation (Bímová et al. 2003), high competitive capacity (Mandák et al. 2004), allelopathic activity (Murrell et al. 2011), functional traits (Herpigny et al. 2012), sexual reproduction (Tiébré et al. 2007b) and creation of new genotypes (Pyšek et al. 2003; Bailey et al. 2007; Tiébré et al. 2007a) certainly contribute to the success of this invasive complex, while the interplay between all these influencing factors is what determines the distribution of particular taxa in Croatia.

Implications of misidentifications

The overall impact and significance of knotweeds should not be ignored, even at sites with individual occurrences. They are plants of gigantic habitus, high biomass and thick growth. Even solitary plants occupy a large amount of space, preventing the growth of any other species, and studies have already shown that knotweeds significantly reduce plant diversity in invaded areas (Padula et al. 2008; Maurel et al. 2009; Aguilera et al. 2010; Maurel et al. 2013). Taking into account that they may also exhibit allelopathic properties (Vrchetová and Šerá 2008; Murrell et al. 2011), they should be regarded as dangerous pests, with a high potential for spreading and a negative impact on resident communities.

Unfortunately, the examination of existing literature has revealed decades of misidentification of *Reynoutria* spp. in Europe (Mandák et al. 2004; Balogh 2008; Sirbu and Oprea 2008; Padula et al. 2008; Strgulc Krajšek and Jogan 2011). To our knowledge, comprehensive studies capable of determining the extent of such misidentifications are mostly lacking. Although there are many examples of different authors highlighting the doubtfulness of historical data (Balogh 2008; Sirbu and Oprea 2008; Padula et al. 2008; Strgulc Krajšek and Jogan 2011), the only extensive herbarium and field study reviewing the distributional status of the three taxa was performed in the Czech Republic (Mandák et al. 2004). Our study has shown a strikingly large amount of erroneous distribution data in Croatia, completely changing the current perspective about their distribution, demonstrating the importance of correct identification. In our opinion, after long periods of such misidentifications, the distribution data for *R. japonica*, *R. × bohemica* and *R. sachalinensis* could be largely erroneous even across a wider area, particularly in neighbouring countries, where *R. × bohemica* was recorded relatively late. Consequently, any

further analysis will be of doubtful value unless the data are acquired with proper identification. We provide our considerations on a recent study by Jovanović et al. (2018), who analysed the distribution of knotweeds within South-eastern Europe, including Croatia, and offered conclusions about their future spread and impact on protected areas. However, based on our results, the previous data from Croatia were largely erroneous and therefore the study from Jovanović et al. (2018) should be updated. Furthermore, a confirmation of the identity should be obtained prior to performing any analyses on the distributional data of *Reynoutria* taxa, while the analyses based on datasets from geographical areas with uncertain knotweed identity should be avoided.

Although all three taxa deserve increased attention, previous studies have already highlighted the possibility of the hybrid being more invasive than the parents (Bímová et al. 2003; Mandák et al. 2004; Bailey and Wisskirchen 2006; Parepa et al. 2014; Buhk and Thielsch 2015), which is consistent with our finding that the hybrid is the most widespread in Croatia. Furthermore, the hybrid is genetically more diverse (Pyšek et al. 2003; Bailey et al. 2007; Krebs et al. 2010), apparently of a broader ecological niche (Bailey and Wisskirschen 2006; Krebs et al. 2010), more difficult to control (Bímová et al. 2001) and possibly posing a greater threat to biodiversity than either of the parents. Therefore, instead of continuous neglecting, in our opinion the hybrid identity should be systematically revealed on all geographical scales.

Conclusions

The case of Asian knotweeds represents an interesting phenomenon; the introduction of parental species into a new range resulting in the creation of a hybrid that is more invasive than the parents is a story that goes beyond the usual impacts of invasive plants. From the perspective of conservation biology, it might seem irrelevant to distinguish among three taxa with almost the same habitus; they might have the same impact on the resident flora and act as a single threat to biodiversity in areas where they co-occur. We believe, however, it is important to determine the right identity of these plants and comparatively study their ability to spread. Taking into account that the studied taxa have different behaviour, ecological preferences, ability to spread and invasiveness and show different responses to various control measures, they should be analysed separately in any attempt to explain, manage and/or limit their spread. Therefore, the accuracy of their past and future identification is of major importance. Moreover, understanding these differences may lead to an explanation of the astonishing success of *R. × bohemica*. Currently available data imply that the hybrid is more aggressive, much more successful in colonizing the space, and better adapted to a wider range of

climatic conditions, and therefore, in terms of plant invasions, represents a better, “improved” version of the parents.

In recent times, the advances of modern science, particularly regarding data collection and analysis, have provided many options for making assumptions based on spatial modelling and predictions. Since knotweeds have managed to confuse botanists in Europe for decades, special attention must be paid to the problem of their identification, before any conclusions based on their distributional data are made. Without proper caution, it is likely that wrong assumptions will be made regarding their impact on certain geographic areas or ecosystems, based on analyses of doubtful datasets.

We believe that any future studies of knotweeds in Croatia and potential control efforts should focus on watercourses. According to the currently available data, watercourses are very frequently invaded and seem to support the development of monospecific stands, but at the same time, these habitats may be insufficiently surveyed in our study. As for current management practices, Croatian watercourse management in the present form might be promoting the spread of knotweeds, by creating a highly disturbed environment, suitable for their establishment and dominance. In our opinion, the first measure in preventing the spread of these invasive taxa is taking this knowledge into account in any future water management strategies.

Acknowledgements

The authors would like to thank the anonymous reviewers for their most valuable critical comments on the manuscript.

References

- Aguilera AG, Alpert P, Dukes JF, Harington R (2010) Impacts of the invasive plant *Fallopia japonica* (Houtt.) on plant communities and ecosystem properties. *Biological Invasions* 12: 1243–1252, <https://doi.org/10.1007/s10530-009-9543-z>
- Anđelković A, Živković M, Novković M, Pavlović D, Marisavljević D, Radulović S (2013) Invasion pathways along the rivers in Serbia – the eastern corridor of *Reynoutria* spp. *Plant Protection* 64: 178–188
- Bailey JP (2013) The Japanese knotweed invasion viewed as a vast unintentional hybridization experiment. *Heredity* 110: 105–110, <https://doi.org/10.1038/hdy.2012.98>
- Bailey JP, Connolly AP (2000) Prize-winners to pariahs – A history of Japanese Knotweed s.l. (Polygonaceae) in the British Isles. *Watsonia* 23: 93–110
- Bailey JP, Wisskirchen R (2006) The distribution and origins of *Fallopia* × *bohemica* (Polygonaceae) in Europe. *Nordic Journal of Botany* 24: 173–200, <https://doi.org/10.1111/j.1756-1051.2004.tb00832.x>
- Bailey JP, Bímová K, Mandák B (2007) The potential role of polyploidy and hybridization in the further evolution of the highly invasive *Fallopia* taxa in Europe. *Ecological Research* 22: 920–928, <https://doi.org/10.1007/s11284-007-0419-3>
- Bailey JP, Bímová K, Mandák B (2009) Asexual spread versus sexual reproduction and evolution in Japanese Knotweed s.l. sets the stage for the “Battle of the Clones”. *Biological Invasions* 11: 1189–1203, <https://doi.org/10.1007/s10530-008-9381-4>
- Bailey JP, Child LE, Connolly AP (1996) A survey of the distribution of *Fallopia* × *bohemica* (Chrtek & Chrtková) J. Bailey (Polygonaceae) in the British Isles. *Watsonia* 21: 187–198
- Balogh L (2008) Japanese, giant and Bohemian knotweed (*Fallopia japonica*, *Fallopia sachalinensis* and *Fallopia* × *bohemica*). In: Botta-Dukát Z, Balogh L (eds), The most important invasive plants in Hungary. Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátót, Hungary, 255 pp

- Balogh L, Dancza I, Király G (2008) Preliminary report on the grid-based mapping of invasive plants in Hungary. In: Rabitsch W, Essl F, Klingenstein F (eds), *Biological Invasions – from Ecology to Conservation*. *Neobiota* 7, pp 105–114
- Bímová K, Mandák B, Pyšek P (2001) Experimental control of *Reynoutria* congeners: a comparative study of a hybrid and its parents. In: Brundu G, Brock J, Camarda I, Child L, Wade M (eds), *Plant invasions: species ecology and ecosystem management*. Backhuys, Leiden, pp 283–290
- Bímová K, Mandák B, Pyšek P (2003) Experimental study of vegetative regeneration in four invasive *Reynoutria* taxa (Polygonaceae). *Plant Ecology* 166: 1–11, <https://doi.org/10.1023/A:1023299101998>
- Buhk C, Thielsch A (2015) Hybridisation boosts the invasion of an alien species complex: Insights into future invasiveness. *Perspectives in Plant Ecology, Evolution and Systematics* 17: 274–283, <https://doi.org/10.1016/j.ppees.2015.05.001>
- Child LE (1999) *Vegetative Regeneration and Distribution of Fallopia japonica and Fallopia × bohemica: Implications for Control and Management*. PhD Thesis, Loughborough University, UK, 240 pp
- Chrtěk J, Chrtěková A (1983) *Reynoutria × bohemica*, nový krizenec z celedi Rdesnovitých [*Reynoutria × bohemica*, new hybrid from the family Polygonaceae]. *Casopis Narodního Muzea* 152: 120
- Dommanget F, Spiegelberger T, Cavaillé P, Evette A (2013) Light Availability Prevails Over Soil Fertility and Structure in the Performance of Asian Knotweeds on Riverbanks: New Management Perspectives. *Environmental Management* 52: 1453–1462, <https://doi.org/10.1007/s00267-013-0160-3>
- Dujmović M, Grgurić G, Migić I, Paradžik M, Petković A, Romac L, Zupčić IM, Šegota V (2016) *Reynoutria sachalinensis*. In: Nikolić T (ed), *Flora Croatica Database*. Faculty of Science, University of Zagreb. <http://hirc.botanic.hr/fcd> (accessed September 2015)
- Fojcik B, Tokarska-Guzik B (2000) *Reynoutria × bohemica* (Polygonaceae) – nowy takson we florze Polski [*Reynoutria × bohemica* (Polygonaceae) – new taxon in the flora of Poland]. *Fragmenta Floristica et Geobotanica Polonica* 7: 63–71
- Herpigny B, Dasonville N, Ghysels P, Mahy G, Meerts P (2012) Variation of growth and functional traits of invasive knotweeds (*Fallopia* spp.) in Belgium. *Plant Ecology* 213: 419–430, <https://doi.org/10.1007/s11258-011-9989-9>
- Hlavati Širka V, Lakušić D, Šinžar-Sekulić J, Nikolić T, Jovanović S (2013) *Reynoutria sachalinensis*: a new invasive species to the flora of Serbia and its distribution in SE Europe. *Botanica Serbica* 37: 105–112
- Hollingsworth M, Bailey JP (2000) Evidence for massive clonal growth in the invasive weed *Fallopia japonica* (Japanese Knotweed). *Botanical Journal of the Linnean Society* 133: 463–472, <https://doi.org/10.1111/j.1095-8339.2000.tb01589.x>
- Holzmüller EJ, Jose S (2009) Invasive plant conundrum: What makes the aliens so successful? *Journal of Tropical Agriculture* 47: 18–29
- Jogan N (2006) Japonski dresnik (*Fallopia japonica*) – rastlina leta 2006 [Japanese knotweed (*Fallopia japonica*) – plant of the year 2006]. *Proteus* 68: 437–440
- Jovanović S, Hlavati-Širka V, Lakušić D, Jogan N, Nikolić T, Anastasiu P, Vladimirov V, Šinžar-Sekulić J (2018) *Reynoutria* niche modelling and protected area prioritization for restoration and protection from invasion: A Southeastern Europe case study. *Journal for Nature Conservation* 41: 1–15, <https://doi.org/10.1016/j.jnc.2017.10.011>
- Karavla J (1997) Parkovni objekti u općini Rijeka. In: Bertović S, Generalović M, Karavla J, Martinović J (eds), *Priroda i parkovni objekti u općini Rijeka* [Park objects in the Rijeka County. In: Bertović S, Generalović M, Karavla J, Martinović J (eds), *Nature and park objects in the Rijeka County*]. *Šumarski list* 3–4: 133–160
- Krebs C, Mahy G, Matthies D, Schaffner U, Tiébré M-S, Bizoux J-P (2010) Taxa distribution and RAPD markers indicate different origin and regional differentiation of hybrids in the invasive *Fallopia* complex in central-western Europe. *Plant Biology* 12: 215–223, <https://doi.org/10.1111/j.1438-8677.2009.00219.x>
- Mandák B, Bímová K, Pyšek P, Štěpánek J, Plačková I (2005) Isoenzyme diversity in *Reynoutria* (Polygonaceae) taxa: escape from sterility by hybridization. *Plant Systematics and Evolution* 253: 219–230, <https://doi.org/10.1007/s00606-005-0316-6>
- Mandák B, Pyšek P, Bímová K (2004) History of the invasion and distribution of *Reynoutria* taxa in the Czech Republic: a hybrid spreading faster than its parents. *Preslia* 76: 15–64
- Mandák B, Pyšek P, Lysák M, Suda J, Krahulcová A, Bímová K (2003) Variation in DNA-ploidy levels of *Reynoutria* taxa in the Czech Republic. *Annals of Botany* 92: 265–272, <https://doi.org/10.1093/aob/mcg141>
- Marković Lj (1994) Polygonaceae. In: Nikolić T (ed), *Flora Croatica. Index Florae Croatiae*. Pars 1. *Natura Croatica* 3, Suppl. 2: 1–116
- Maurel N, Salmon S, Ponge J-F, Machon N, Moret J, Muratet A (2009) Does the invasive species *Reynoutria japonica* have an impact on soil and flora in urban wastelands? *Biological Invasions* 12: 1709–1719, <https://doi.org/10.1007/s10530-009-9583-4>

- Maurel N, Fujiyoshi M, Muratet A, Porcher E, Motard E, Gargominy O, Machon N (2013) Biogeographic comparisons of herbivore attack, growth and impact of Japanese knotweed between Japan and France. *Journal of Ecology* 101: 118–127, <https://doi.org/10.1111/1365-2745.12026>
- Mitić D, Majnarić M, Mitić B (2016) *Reynoutria sachalinensis*. In: Nikolić T (ed), Flora Croatica Database. Faculty of Science, University of Zagreb. <http://hirc.botanic.hr/fcd> (accessed September 2015)
- Murrell C, Gerber E, Krebs C, Parepa M, Schaffner U, Bossdorf O (2011) Invasive knotweed affects native plants through allelopathy. *American Journal of Botany* 98: 38–43, <https://doi.org/10.3732/ajb.1000135>
- Nikolić T (2017) Flora Croatica Database. Faculty of Science, University of Zagreb. <http://hirc.botanic.hr/fcd> (accessed September 2015)
- Padula M, Lastrucci L, Fiorini G, Galasso G, Zoccola A, Quilghini G (2008) Prime segnalazioni di *Reynoutria* × *bohemica* Chrtek & Chrtková (Polygonaceae) per l'Italia e analisi della distribuzione del genere *Reynoutria* Houtt [First records of *Reynoutria* × *bohemica* Chrtek & Chrtková (Polygonaceae) in Italy and the analysis of distribution of the genus *Reynoutria* Houtt]. *Atti della Società italiana di scienze naturali e del Museo civico di storia naturale di Milano* 149: 77–108
- Parepa M, Fischer M, Krebs C, Bossdorf O (2014) Hybridization increases invasive knotweed success. *Evolutionary Applications* 7: 413–420, <https://doi.org/10.1111/eva.12139>
- Purger D, Csiky J (2008) Biljke Banskog brda [The plants of BANSKO BRDO HILL]. University of Pécs, Pécs, Hungary, 58 pp
- Pyšek P, Brock JH, Bímová K, Mandák B, Jarošík V, Koukolíková I, Pergl J, Štěpánek J (2003) Vegetative regeneration in invasive *Reynoutria* (Polygonaceae) taxa: the determinant of invisibility at the genotype level. *American Journal of Botany* 90: 1487–1495, <https://doi.org/10.3732/ajb.90.10.1487>
- Richardson DM, Pyšek P (2006) Plant invasions: Merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography* 30: 409–431, <https://doi.org/10.1191/0309133306pp490pr>
- Schnitzler A, Bailey J, Hansen CN (2008) Genotypic and phenotypic variation in a *Fallopia* × *bohemica* population in north-eastern France. In: Tokarska-Guzik B, Brock J, Brundu G, Child L, Daehler CC, Pyšek P (eds), Plant invasions: Human perception, ecological impacts and management. Backhuys, Leiden, pp 133–134
- Sîrbu C, Oprea Ad (2008) Two alien species in the spreading process in Romania: *Reynoutria* × *bohemica* Chrtek & Chrtková and *Grindelia squarrosa* (Pursh) Dunal. *Cercetări agronomice în Moldova* 41: 41–50
- Strgulc Krajšek S, Jogan N (2011) Rod *Fallopia* Adans. v Sloveniji [The genus *Fallopia* Adans. in Slovenia]. *Hladnikia* 28: 17–40
- Tiébré M-S, Bizoux J-P, Hardy OJ, Bailey JP, Mahy G (2007a) Hybridization and morphogenetic variation in the invasive alien *Fallopia* (Polygonaceae) complex in Belgium. *American Journal of Botany* 94: 1900–1910, <https://doi.org/10.3732/ajb.94.11.1900>
- Tiébré M-S, Vanderhoeven S, Saad L, Mahy G (2007b) Hybridization and Sexual Reproduction in the Invasive Alien *Fallopia* (Polygonaceae) Complex in Belgium. *Annals of Botany* 99: 193–203, <https://doi.org/10.1093/aob/mcl242>
- Tiébré M-S, Saad L, Mahy G (2008) Landscape dynamics and habitat selection by the alien invasive *Fallopia* (Polygonaceae) in Belgium. *Biodiversity and Conservation* 17: 2357–2370, <https://doi.org/10.1007/s10531-008-9386-4>
- Vrchotová N, Šerá B (2008) Allelopathic properties of knotweed rhizome extracts. *Plant, Soil and Environment* 54: 301–303, <https://doi.org/10.17221/420-PSE>

Supplementary material

The following supplementary material is available for this article:

Table S1. Details of a survey conducted in 2016 in Croatia: location name and coordinates, occupied habitat, survey date and source of data (fieldwork or herbaria). The survey consisted of detailed mapping of *Reynoutria japonica*, *R.* × *bohemica* and *R. sachalinensis*.

This material is available as part of online article from:

http://www.reabic.net/journals/bir/2019/Supplements/BIR_2019_Vukovic_etal_Table_S1.xlsx