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What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation?

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ABSTRACT

Effect of invasion by *Impatiens glandulifera* (Balsaminaceae) on the community characteristics and species composition of invaded riparian communities was studied at six rivers in the Czech Republic. Two approaches were used: space for time substitution approach, i.e., comparing invaded and uninvaded sites under the same habitat conditions, and removal of the invader from experimental plots. Differences in the number of species, Shannon diversity index H' and evennes J were compared between invaded and uninvaded plots. Uninvaded plots of the comparative study harboured by 0.23 more species per 16 m^2, and had higher value of H' and J, calculated with species covers as importance values; however only the difference in J was marginally significant ($p = 0.04$). Other effects were not significant, indicating that once *I. glandulifera* is removed, communities recover without any consequences for species diversity. Multivariate analysis did not reveal any effect of invasion on the species composition in terms of species presence but their cover hierarchies changed after the invasion, as *I. glandulifera* became dominant at the expense of tall native nitrophilous dominants. It is concluded that *I. glandulifera* exerts negligible effect on the characteristics of invaded riparian communities, hence it does not represent threat to the plant diversity of invaded areas. This makes it very different from other Central European invasive aliens of a similar performance.

1. Introduction

Research in plant invasion in the past decades improved our knowledge of the patterns of invasion at different scales and substantial progress in understanding the mechanisms of the process was made (Lonsdale, 1999; Rejmánek et al., 2005). Besides traditional issues of species invasiveness and community invasibility, much attention is recently paid to negative effects of alien species on resident vegetation and functioning of invaded ecosystems (Williamson, 1998, 2001; Parker et al., 1999; Byers et al., 2002; Simberloff et al., 2003). Invasive species that change character or condition of an ecosystem over a substantial area are termed transformers (Richardson et al., 2000; Davis, 2003); this happens via excessive use of resources, donation of limiting resources, fire promotion/suppression, promotion of erosion or stabilization of soil surface, or by the accumulation of litter or salt (Richardson et al., 2000). Ecosystem impacts are best documented for invasions of woody species and include e.g., nutrient enrichment (Vitousek and Walker, 1989), increased water loss (Zavaleta, 2000) and changed fire regimes (Brooks et al., 2004). Larger scale effects of plant invasion include homogenization of floras, when originally different phytogeographical units become similar thanks to massive plant invasions (Schwartz et al., 2006).

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At the community level, suppression of native plants is a phenomenon resulting from the dominance invasive species achieve in invaded habitats (Richardson et al., 1989; Pyšek and Pyšek, 1995; Bímová et al., 2004). Surprisingly, studies measuring the community level effects of invasive plants are rather scarce (Tickner et al., 2001). This maybe, at least in part, associated with methodological problems such as the long-term response of invaded community, rare opportunity to observe an ongoing invasion from the beginning (Müllerová et al., 2005) and generally difficult experimentation with alien plants for ethical reasons. Alternative approaches, such as the space for time substitution (Prach et al., 1997; Alvarez and Cushman, 2002; Badano and Pugnaire, 2004) have to be carefully interpreted with awareness of their possible limitations. Nevertheless, studying the community level impacts in situ is desirable as it can provide, by identifying the potential effects of an invading alien, valuable information for landscape management and nature conservation (Gordon, 1998; Manchester and Bullock, 2000).

The present paper, deals with invasion of *Impatiens glandulifera* in the Czech Republic. About one third of the flora of this country is formed by alien species (Pyšek et al., 2002), research on which has been receiving considerable attention recently (Pyšek and Prach, 2003; Mandák et al., 2004; Chytrý et al., 2005). The massive invasion of *I. glandulifera* is considered a conservation problem in riparian habitats (Pyšek and Prach, 1993, 1995). Riparian zones are unique and dynamic ecosystem with complex disturbance regimes (Naiman and Decamps, 1997) and river bank communities are generally considered to be prone to plant invasions (Planty-Tabacchi et al., 1996). The dominance of *I. glandulifera* along riverbanks has been repeatedly reported to cause problems in stream management. Furthermore, as the European tallest annual herb it is highly competitive, and reported to replace native flora in invaded sites (Trewick and Wade, 1986; Perrins et al., 1990, 1993; Hulme and Bremner, 2005). *I. glandulifera* in the Czech Republic is subjected to occasional eradication efforts, but the long-term effects of these rather unsystematic schemes are very limited because the populations usually re-invade within few years (Wadsworth et al., 2000).

The present papers, seeks to determine the effect of invasion by *I. glandulifera* on species composition and characteristics of invaded riparian communities and aims at answering the following questions: Does the invasion cause suppression of species diversity existing in the resident communities prior to the invasion? What are the changes in species composition of these communities following the invasion?

2. Material and methods

2.1. Study species and area

I. glandulifera (Balsaminaceae) is native to the western Himalayas and has become naturalized in northern and Central Europe, temperate North America and New Zealand (Weber, 2003). In Europe, it is one of the most widespread invasive species (Beerling, 1993; Beerling and Perrins, 1993). In the Czech Republic it was first recorded in the vicity of the town Litoměřice (N Bohemia) in 1893 (Slavík, 1995, 1997) and now it is considered invasive (Pyšek et al., 2002). The lag phase in this country was estimated to endure up to 1930s, then the species started to spread exponentially (Pyšek and Prach, 1993) and now it is found along most large rivers (Pyšek and Prach, 1994, 1995). Although there is a good evidence that the plant is able to thrive outside river valleys (Hejda, 2004), the largest populations of the most vigorous plants are found in riparian habitats. Although the competition of invasive species for pollination services with natives is usually species-specific (Moragues and Traveset, 2005), *I. glandulifera* is competitively superior to some resident native species through attracting pollinators by a massive production of nectar (Chittka and Schürkens, 2001).

The study was carried out in the valleys of the Berounka, Sázava, Vltava and Kamenice rivers (Fig. 1, Table 1), in riparian vegetation mostly classified phytosociologically as *Cuscuto europeae–Convolvuletum sepii*, *Chaerophylletum bulbosi* and *Phalaridetum arundinaceae* (Kolbek, 1999). The sampled river banks were nutrient-rich and regularly disturbed by flooding (Grüll and Vaněčková, 1982; Pyšek and Prach, 1995; Hejda, 2004). To evaluate the effect of *I. glandulifera* on the community characteristics of invaded stands, comparative (observational) and experimental approaches were used.

2.2. Comparative study of invaded and uninvaded plots

In 2004–2005, 30 pairs of 4 × 4 m plots were selected in the valleys of six rivers (Fig. 1). Each pair consisted of heavily invaded (with at least 60% of *I. glandulifera* cover) and nearby uninvaded vegetation (further termed "comparative invaded and uninvaded"). Uninvaded plots were selected as to represent the same habitat condition as the corresponding invaded plots (Pyšek and Pyšek, 1995). Some individuals of *I. glandulifera* were present in 23 of the 30 uninvaded plots because in the study system with high invasion dynamics, it was difficult to find a vegetation free of the invading species. Nevertheless, the cover of *I. glandulifera* in uninvaded plots was low (1–5%) and did not affect resident vegetation or exert impact on its species diversity. Invasive species usually affect resident communities only if they are dominant (Richardson et al., 1989; Pyšek and Pyšek, 1995; Bímová et al., 2004). The presence of *I. glandulifera* nevertheless serves as an evidence that habitat conditions in uninvaded plots were suitable for the invasion, hence likely to be invaded in the future. The comparative plots were selected according to the following criteria: (a) The site was heavily invaded by *I. glandulifera*, with its populations as spatially homogenous as possible. (b) The invaded site was adjacent to uninvaded riparian vegetation, and the invaded and uninvaded habitats were as close in terms of site conditions as possible. The space for time substitution approach, often used in studies on vegetation succession (Prach et al., 1997, 2001; Alvarez and Cushman, 2002; Badano and Pugnaire, 2004; Ruprecht, 2005), was therefore justified and the uninvaded plots can be viewed as representing the resident vegetation before the invasion has occurred (Pyšek and Pyšek, 1995). Vegetation in the plots was sampled in July and August 2004 and the percentage cover of each species was estimated.

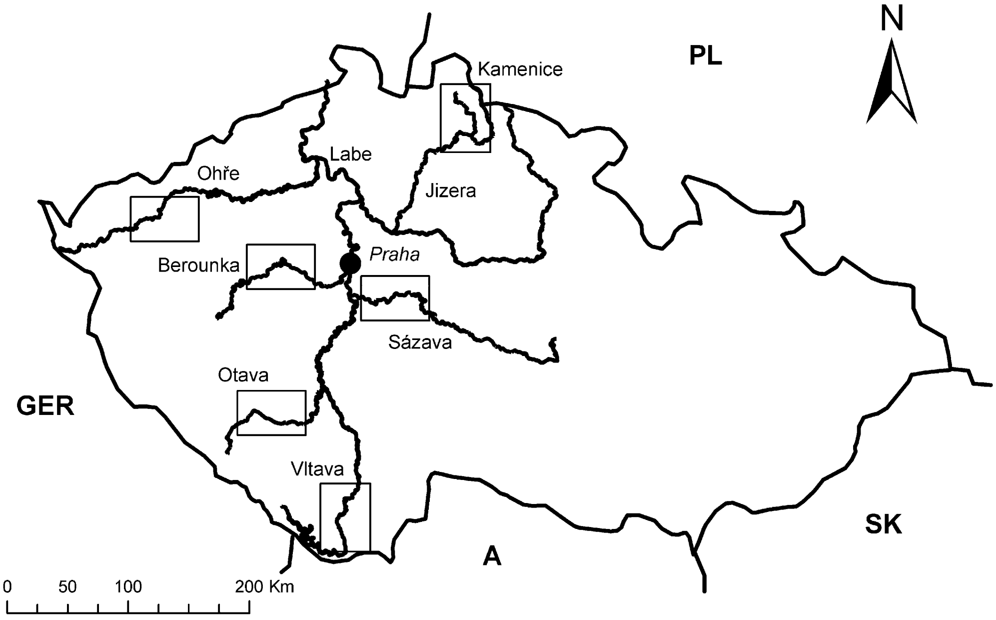

Fig. 1 – Location of the study regions in the Czech Republic. The experimental study was carried out at the river Berounka.

Table 1 – Basic geographical characteristics of the river regions where the comparative data were collected (see Fig. 1)

Area	Position	Altitude (m a.s.l.)	January temperature	July temperature	Annual precipitation	Floods	No. of plots
Berounka	N: 49°55′ E: 14°15′	250	−1.5	16.5	525	1997, 2002	1
Vltava	N: 48°40′ E: 14°20′	400	−2.5	14.5	675	2002	2
Ohře	N: 50°25′ E: 13°10′	400	−3.5	13.5	650	2002	5
Kamenice	N: 50°45′ E: 15°20′	600	−3.5	13.5	1200	2002	1
Sázava	N: 49°50′ E: 14°35′	250	−1.5	15.5	625	2002	6
Otava	N: 49°15′ E: 14°0′	300	−2.5	15.5	550	2002	15

The experimental study was carried out in the Berounka river region. Mean monthly temperatures (°C) are shown. Climate data are based on 50 years average. Floods refer to the most recent in 2002, which was 1-in-500-years flood. Berounka river was also heavily flooded in 1997. Number of plots refers to the pairs (invaded, uninvaded) sampled on the river.

2.3. *Removal experiment*

At the end of April 2003, 10 experimental plots were established in the valley of the Berounka river in the Křivoklátsko Protected Landscape Area, central Bohemia. Each 2 × 1 m plot was divided into two 1 m^2 subplots. Seedlings of *I. glandulifera* were removed from one of the subplots (termed "experimental uninvaded"), the other served as a control (termed "experimental invaded"). The spatial arrangement of subplots within the plot was random. The plots were monitored from May to July to remove plants of *I. glandulifera* penetrating into the uninvaded subplots. At the end of July, when the vegetation was fully developed and no further shifts in the dominance of individual species were observed, species composition was sampled by phytosociological relevés using a seven grade Braun–Blanquet scale (Westhoff and van der Maarel, 1978; Chytrý and Rafajová, 2003).

2.4. *Statistical analysis*

Species richness, Shannon diversity index and evenness index were used as community characteristics. The Shannon diversity index H' was calculated using species covers as importance values. Evenness J was calculated as $H'/\ln S$, where S is the number of species (Magurran, 1983). Differences in the number of species S, Shannon index H' and evenness J between invaded and uninvaded plots were used to measure the effect of invasion on these community characteristics. The respective pairs of invaded and uninvaded plots from the comparative study, and the invaded and uninvaded parts of experimental plots were compared using the paired Wilcoxon signed rank test (Sokal and Rohlf, 1995), because part of he data set, especially the experimental data, exhibited strong deviations from the normal distribution. The aim of the test was to detect whether the mean values of the differences between uninvaded and invaded vegetation were significantly different from zero. Since the presence of *I. glandulifera* was the primary factor distinguishing between invaded and uninvaded plots, this species was excluded from the input data for analyses of species richness and for all multivariate tests. Species of the shrub and tree layers were excluded from analyses, because they were not assumed to be affected by *I. glandulifera* invasion. Only woody species growing in the herb layer (up to ca. 2 m) were retained in the data

Table 2 – Number of species, Shannon diversity index H′ and evenness J as recorded in the studied plots (mean ± SD, n = 10)

Study	Plot	Species number	Diversity *H′*	Evenness *J*
Comparative	Uninvaded	9.2 ± 3.1	1.33 ± 0.46	0.56 ± 0.16
Comparative	Invaded	9.0 ± 2.9	1.19 ± 0.32	0.48 ± 0.08
Experimental	Uninvaded	11.9 ± 3.0	1.53 ± 0.65	0.61 ± 0.21
Experimental	Invaded	10.6 ± 2.5	1.30 ± 0.30	0.56 ± 0.10

Note that *Impatiens glandulifera* was excluded from calculation as comparative and experimental plots cannot be directly compared because of a different size. See text for the statistics.

Table 3 – Results of ordination analyses performed on comparative (CCA) and experimental data (RDA)

Study	Data	Analysis	Explained variance (%)		*F*-ratio	*p*-value	Length of gradient
			1st axis	2nd axis			
Comparative	Cover	CCA	18.1	34.7	1.408	0.094	3.987
Comparative	Presence/absence	CCA	12.1	47	0.965	0.888	4.837
Experimental	Covers	RDA	9.5	19.3	2.278	0.066	2.758
Experimental	Presence/absence	RDA	3.0	9.7	0.621	0.976	2.564

Percentages of variance explained by the first two canonical axis, and the statistics of the Monte-Carlo permutation tests (*F*, *p*) are shown. The selection of the method used was based on the length of gradient of the first ordination axis as obtained by the DCA analysis. Note that *Impatiens glandulifera* was excluded from the analysis.

set, which is a standard approach used in the European phytosociology (Ellenberg, 1988).

To evaluate the differences in species composition attributable to invasion, direct gradient analysis was used. Based on the length of the main gradient in the data (Table 3) estimated by an indirect gradient analysis (DCA), redundancy analysis (RDA) and canonical correspondence analysis (CCA) were identified as appropriate methods for the experimental and comparative data, respectively. Analyses were carried out using the program Canoco (ter Braak and Šmilauer, 1998). For experimental plots, the Braun–Blanquet scale was transformed to percentage covers (Westhoff and van der Maarel, 1978) that served as input data. For comparative plots, species percentages recorded in the field were used. Pairs of experimental subplots and those of relevés from the comparative study were set as block-defining covariables (whole plot level). The Monte-Carlo permutation test (499 permutations) was used to determine the significance of the differences between invaded and uninvaded vegetation (split plot level) for both comparative and experimental data. A two-step analysis was applied: First, presence/absence data were used to test for the effect of invasion on species composition. Second, species covers (%) were used to ascertain the shifts in the dominance of species attributable to invasion.

3. Results

3.1. *Effect of invasion on species richness, diversity and evenness*

Uninvaded comparative plots harboured on average 9.2 ± 3.1 (mean ± SD, $n = 10$) species. This was by 0.2 ± 2.8 more than invaded plots and the difference was not significant ($Z = 0.501$, $df = 29$, $p = 0.6$). In total, 80 and 85 species were recorded in invaded and uninvaded plots, respectively (Appendix). In uninvaded experimental subplots there were on average 11.9 ± 3.0 species, while invaded plots harboured by 1.3 ± 4.6 species less (Table 2). This difference in species number was not statistically significant ($Z = 0.95$, $df = 9$, $p = 0.45$). The total number of species recorded in invaded and uninvaded plots was 34 and 35, respectively (Appendix).

Uninvaded vegetation exhibited higher values of Shannon index H' for the comparative and experimental study (Table 1) but the differences were not significant ($Z = 0.73$, $df = 29$, $p = 0.5$ and $Z = 0.05$, $df = 9$, $p = 0.6$, respectively). Evenness J was higher in uninvaded plots of both comparative and experimental studies; this difference was marginally significant for the comparative data ($Z = 2.128$, $df = 29$, $p = 0.04$) and non-significant for the experimental data ($Z = 0.663$, $df = 9$, $p = 0.55$, respectively).

3.2. *Effect of invasion on species composition*

Invasion had no effect on species composition as demonstrated by non-significant results of ordinations based on presence/absence data (Table 3).

The first axis (λ) of the CCA with species covers from the comparative study separated the species according to their response to invasion and accounted for 18.1% of variation in the data. The Monte-Carlo permutation test for the first axis was non-significant ($p = 0.094$; Table 3). *Galeopsis tetrahit*, *G. speciosa* and *Impatiens noli-tangere* showed the strongest association with invaded plots, while *Phalaris arundinacea* and *Chelidonium majus* exhibited the opposite trend, i.e., a strong affinity to uninvaded plots (Fig. 2).

In RDA with species covers from experimental plots, the first axis was marginally significant ($p = 0.07$) and explained only 9.5% of variation in data (Table 3). *Impatiens parviflora*,

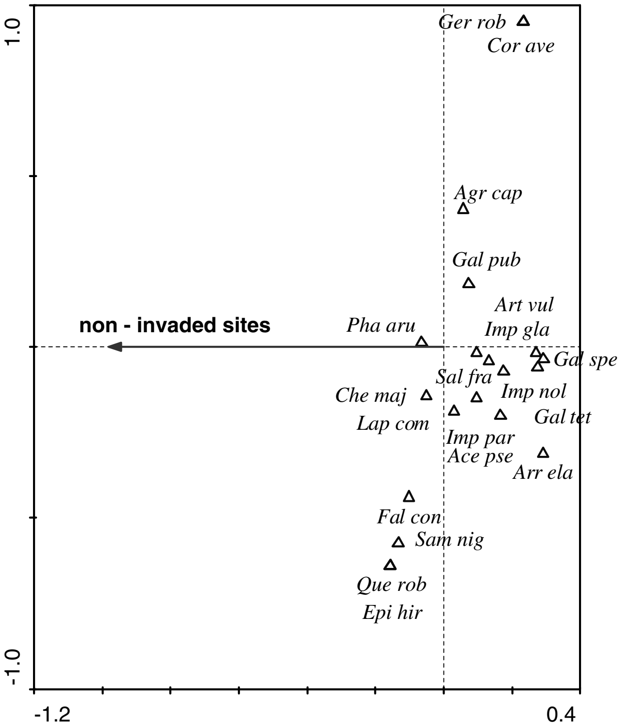

Fig. 2 – CCA ordination diagram (plot of component weights) showing the response of species to the invasion by *Impatiens glandulifera*. Based on species covers from the comparative study (see text for details). *I. glandulifera* was not included in the Monte-Carlo test and is only displayed as a supplementary variable. The 20 species displayed account for more than 10% of variation in the data. Species names are abbreviated, see Appendix for full names.

Poa trivialis, and *Agrostis stolonifera* tended to be more represented in invaded plots, *Cuscuta europaea*, *Silene alba*, and *Arctium lappa* in those from which *I. glandulifera* was removed.

4. Discussion

4.1. Methodological constraints

Measuring the impact of invasive species on resident communities in the field is difficult because the invasion is a long-term process rarely observed from the very beginning (Müllerová et al., 2005), and experimental introductions of alien species into the wild are constrained by ethical reasons. In addition, such studies never mimic the natural process perfectly because factors related to chance and timing, that are of principal importance in biological invasions (Crawley, 1989), cannot be accounted for. Experimental studies are also necessarily constrained by limited time and working capacity, which makes them difficult to perform over large geographical regions.

Alternative options are to compare invaded and uninvaded sites (Levine et al., 2003), i.e., the space for time substitution approach (Alvarez and Cushman, 2002; Badano and Pugnaire, 2004), or to evaluate the invaded community at different covers of the invading species (Kwiatkowska et al., 1997). Advantage of such observational approach is that relatively large data set can be collated, that allows for better coverage of variation in the response of invaded community over a wider range of environments.

The problem with the space for time substitution is that there will always be some uncertainty about the character of invaded plots prior to invasion, i.e., to what extent they are comparable with control uninvaded plots; the plots may differ in factors other than the invasion. In the present study, the uninvaded plots were selected close to invaded stands in habitat conditions matching as closely as possible. An ideal case of such a design would be an ongoing spread of *I. glandulifera* over the site, with part of it already heavily infested, while the other would be still free or almost free of the invader. In fact, repeated visits over several years indicated that some sites of our comparative study were very close to such an ideal situation. We believe that the data presented here provide a sound basis for the assessment of synthetic community characteristics and species composition prior to and after the invasion. It must be also borne in mind that observational studies comparing invaded and uninvaded habitats may be biased by the fact that species diversity in itself can affect the likelihood of invasion, which makes it difficult to separate cause and effect (Levine and D'Antonio, 1999; Hulme and Bremner, 2005). However, this is not valid for our study; we did not find any effect of the invasive species on species diversity of invaded communities hence the objection that species poor stands could have been more easily invaded is irrelevant.

4.2. Effect of invasion on species richness and diversity

By combining the comparative and experimental approaches, the present paper aimed at determining the effects of *I. glandulifera* on resident vegetation. For technical reasons, plots used in the experimental study were smaller, because central parts of such plots would be impossible to sample without seriously disturbing vegetation, e.g., by trampling. On the other hand, it would have been inappropriate to use plots of the same small size for collecting the comparative data, because *I. glandulifera* tends to grow in clusters and the spatial structure of its population would not be properly captured by small plots. Differences in plot size between comparative and experimental studies are, however, irrelevant because the study was aimed at comparing invaded and uninvaded vegetation within the two studies.

The comparative approach quantified changes in species diversity of the community after the invasion, while the experimental study provided some insight into the ability of invaded communities to recover once the invader has been removed. Although both data sets are not directly comparable because of different sizes of sampled plots, which was necessary for technical reasons, the results are sound and indicate very little effect of *I. glandulifera* invasion on the community characteristics. Although a marginally significant influence on Shannon's evenness J' was found in the comparative study, the differences between invaded and uninvaded stands are minor in terms of absolute values (Table 2) or the total number of species present (Appendix). Moreover, the absence of significant differences in community characteristics between plots, from which the invader was removed experimentally, and the control indicates that recovered stands do not suffer from reduced species richness and diversity due to invasion.

These results make *I. glandulifera* rather special if compared to other major invasive species in Central Europe, in particular to those with similar ability to invade rapidly and create dominant stands. *Heracleum mantegazzianum* (Pyšek and Pyšek, 1995) and taxa of the genus *Reynoutria* (Bímová et al., 2004) are the most prominent species building large stands with high cover and they also exhibit affinity to riparian habitats (Pyšek and Prach, 1993; Müllerová et al., 2005). Unlike that of *I. glandulifera*, their effect on the species diversity of invaded communities is very strong. Although studies performed on these species cannot be directly compared with our results because of different sample sizes, the trends they report are unambiguous. Vegetation invaded by *Heracleum mantegazzianum* in the W Bohemia, Czech Republic, studied in a variety of habitats, had on average lower number of species (7.5) and Shannon index H' (0.52) in 25 m^2 plots than uninvaded communities (12.8 and 1.22, respectively). In terms of the total number of species, invaded vegetation supported 40.5% less than uninvaded vegetation (Pyšek and Pyšek, 1995). Similarly, the invasion of three *Reynoutria* taxa sampled in plots of variable size in various types of riparian habitats in N Bohemia, Czech Republic, had a highly significant negative effect on both species number and diversity measured by H' (Bímová et al., 2004). One possible reason for this difference could be the character of *I. glandulifera* cover; although it is high in invaded communities (Appendix), it is not spatially homogeneous as is the case with *Heracleum mantegazzianum* and *Reynoutria taxa*. The patches with lower *I. glandulifera* cover provide other species with an opportunity to survive in the invaded community, even if the total cover assessed at the 1 m^2 scale is high.

In the UK, Hulme and Bremner (2005) conducted an experiment at the scale similar to that of the present study, in terms of the number of plots and their size, and found a highly significant increase in species richness and diversity following the removal of *I. glandulifera*. That the same treatment did not result in a significant effect in the Czech Republic, can be attributed to the difference in cover of the invading species. While in the British study, the cover varied from 80% to 100% (Hulme and Bremner, 2005), it only reached on average 43% in the Czech sites, where the experiment was performed in the year following extensive floods in the summer of 2002. Experimental plots were established in developing populations of *I. glandulifera*, recovering from the effect of floods. This view is supported by that a year later, when the comparative study was carried out, the average cover of *I. glandulifera* in sampled plots was as high as 74%. On the other hand, removal studies usually only cover a limited period of time, mostly a single vegetation period, and provide information on the change in diversity immediately following the removal rather than on long term effects of invasion. It may as well be that what both Hulme and Bremner (2005) and this study recorded is a short term pulse before the competitive hierarchies in the community are established. Subsequent development can lead to the prevalence of native nitrophilous dominants associated with a decrease in species diversity. For this reason, we believe that the comparative study, performed in more balanced communities with established competitive hierarchies and at a larger geographical scale, is more representative of the effect *I. glandulifera* has on invaded riparian vegetation in the Czech Republic. That it was non-significant (with the only exception of evenness for comparative data) indicates that *I. glandulifera* has rather negligible effect on invaded riparian vegetation. Not only *I. glandulifera* but also some other alien and even invasive species, such as *Impatiens parviflora*, were present in the riparian vegetation studied. This needs to be borne in mind when designing actions aimed at the eradication of *I. glandulifera* from riparian sites, because the places from which the invader was removed can become especially prone to invasion by other alien species because of available space and often changed ecosystem characteristics (Ogden and Rejmánek, 2005; Hulme and Bremner, 2005). On the other hand, *I. glandulifera* does not seem to change soil characteristics even when growing with a high cover in invaded communities. In an ongoing study (M. Hejda, in preparation), invaded and uninvaded plots only differed in the former having marginally significantly lower soil pH ($T = 2.24$, $p = 0.052$, $n = 10$), but not in carbon or nitrogen contents.

4.3. *Effect of invasion on species composition*

In the same vein, the effect of *I. glandulifera* on species composition of invaded communities was marginal. The invasion did not alter the species composition in terms of the presence and absence of species; only proportional covers, especially those of dominant species, have slightly changed. This part of the study therefore accords with the assessment of diversity measures and strongly supports the opinion that the impact of *I. glandulifera* is much less dramatic than that of other invasive species. It appears that *I. glandulifera* merely takes over the role of native tall nitrophilous dominants, e.g., *Urtica dioica*, *Chaerophyllum bulbosum*, *Chenopodium album* agg. or *Carduus crispus*, while shorter species in the undergrowth are not principally affected. In invaded communities, *I. glandulifera* can hardly completely eliminate native clonal dominants such as *Urtica dioica*, but under certain conditions it is reported to be a better competitor (Beerling and Perrins, 1993). On the other hand, some native species can effectively reduce the cover of *I. glandulifera*, e.g., the climber *Galium aparine* by overweighing its fragile stems (Prach, 1994).

It has been suggested that the balance between the performance of native and invasive species can be shifted towards the latter by an increased trophic level of the site (Daehler, 2003; Green and Galatowitsch, 2002). The level of impact invasive species exert on native communities is context dependent, and differences in features of invaded habitats may explain some controversy between the results of this study and previous reports. In UK, *I. glandulifera* is reported to form dense monospecific stands in damp woodlands and suppress all other plants (Perrins et al., 1993; Hulme and Bremner, 2005). Riparian communities in the Czech Republic, those in the study area in particular, are supplied with often excessive amount of nutrients. Such conditions support the strong dominance of tall competitive nitrophilous species (Grime, 1979). Shorter species have to cope with competitive pressure from tall dominants, otherwise they are excluded from these communities regardless of *I. glandulifera* invasion. It may be that, unlike in UK where the nutrient load may be generally lower than in largely agricultural Czech landscape, species less resistant to the invasion of *I. glandulifera* do not naturally occur in the type of communities considered in our study.

4.4. *Implications for management*

The results suggest that the invasion by *I. glandulifera* does not represent a major problem for the preservation of native biodiversity. In the light of this conclusion, occasional eradication attempts performed by bodies of nature conservation to preserve biodiversity in affected riparian areas seem questionable, especially if their effect is rather limited and short-term. In addition, as pointed out by Hulme and Bremner (2005), such control efforts may give way to invasions of other alien species. Improved river management and reduced eutrophication of riparian habitats resulting in more natural-like character of river banks can be suggested as a preferable option as it would effectively restrict the occurrence of this invasive species in the study area. The nutrient enrichment, along with the proper disturbance regime, is considered to be a factor that enables alien species to invade a given locality (Lake and Leishman, 2004). On the other hand, large and rare flood events can effectively reduce invasive species' abundances, as observed on large *Tamariscus* stands by Lesica and Miles (2004). In case of *I. glandulifera*, extensive flooding prior to seed germination can also effectively reduce this species' occurrence, since most of the seeds are believed to survive over one winter only (Beerling and Perrins, 1993).

On the other hand, the range of habitats in which this species currently invades in Central Europe is rather narrow but it increases. In Austria, *I. glandulifera* recently started to colonize moist roadsides and forests (Drescher and Prots, 2003) and it the Czech Republic, it starts to invade moist meadows where management has become less intensive or ceased recently (M. Hejda, personal observation). It may as well be that possible invasion into meadow communities composed of less competitive resident species than is the case of the currently invaded riparian habitats will have more profound effect on the characteristics of invaded communities.

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Appendix

Species composition in studied plots invaded by *Impatiens glandulifera* and uninvaded. Mean species covers (%) are shown ($n = 30$ for comparative data and $n = 10$ for the experimental study). Only species with at least 1% cover in at least one treatment are shown. Species are arranged according to the highest cover recorded in any treatment. Nomenclature follows Kubát et al. (2002). AH = annual herb, P = perennial, PP = perennial polycarpic, PM = perennial monocarpic, AG = annual grass, PG = perennial grass, B = biennial, BM = biennial monocarpic, BH = biennial herb, T = tree, S = shrub. Polycarpy and monocarpy is specified only where the information is available.

Species	Life form	Comparative		Experimental	
		Uninvaded	Invaded	Uninvaded	Invaded
Impatiens glandulifera	AH	2.1	80.0	–	43.4
Urtica dioica	PP	25.5	9.4	42.6	16.9
Phalaris arundinacea	PG	30.0	4.7	3.6	8.5
Chenopodium album agg.	AH	0.1	0.8	29.7	18.5
Calystegia sepium	P	8.9	2.8	3.6	1.8
Galium aparine	AH	2.6	1.4	8.1	2.1
Persicaria hydropiper	AH	0.2	0.3	8.0	0.2
Carduus crispus	BH	2.0	1.7	7.9	1.5
Galeopsis tetrahit	AH	–	0.2	7.8	1.7
Myosoton aquaticum	P	2.3	2.4	6.8	7.0
Glyceria maxima	PG	6.2	1.7	–	–
Chaerophyllum bulbosum	AH	0.1	0.0	3.9	4.1
Symphytum officinale	PP	3.5	1.0	0.2	0.1
Filipendula ulmaria	PP	3.3	0.5	–	–
Betula pendula	T	3.0	–	–	–
Cusctuta europaea	AH	0.6	0.3	3.0	1.1
Aegopodium podagraria	PP	2.7	1.3	0.5	0.2

(*continued on next page*)

Appendix – *continued*

Species	Life form	Comparative		Experimental	
		Uninvaded	Invaded	Uninvaded	Invaded
Chenopodium polyspermum	AH	–	–	1.1	2.2
Lamium maculatum	PP	1.7	2.1	0.5	0.5
Bidens frondosa	AH	0.4	0.2	2.0	0.6
Sambucus nigra	S	2.0	0.1	–	–
Saponaria officinalis	P	1.5	–	–	–
Rubus idaeus	S	1.4	0.7	–	–
Agrostis capillaris agg.	PG	1.4	1.2	0.5	0.8
Galeopsis pubescens	AH	1.1	1.2	–	–
Geranium palustre	P	1.0	–	–	–
Populus nigra	T	1.0	–	–	–

Species with less than 1% cover: *Acer pseudoplatanus* (T) 0.03, –, –, –; *Alliaria petiolata* (BM) 0.1, 0.1, 0.4, 0.5; *Alopecurus pratensis* (PG) 0.1, –, –, –; *Anthriscus sylvestris* (P) –, 0.03, –, –; *Arctium lappa* (PM) –, –, 0.2, –; *Arctium tomentosum* (AH, BM) –, 0.1, –, –; *Arrhenaterium elatius* (PG) –, 0.3, –, –; *Artemisia vulgaris* (PP) 0.4, 0.7, 0.7, 0.5; *Aster lanceolatus* agg. (PP) 0.2, –, –, –; *Atriplex nittens* (AH) –, 0.1, –, –; *Capsella bursa-pastoris* (AH) –, –, 0.2, 0.3; *Cardaminopsis halleri* (AH) –, 0.2, –, –; *Chaerophyllum aromaticum* (P) –, 0.03, –, –; *Chaerophyllum hirsutum* (P) 0.2, 0.2, –, –; *Chelidonium majus* (PP) 0.3, 0.1, –, –; *Cirsium arvense* (PP) 0.4, 0.1, –, –; *Cirsium oleraceum* (PP) 0.8, 0.2, –, –; *Crepis paludosa* (P) 0.1, 0.03, –, –; *Cruciata laevipes* (P) 0.1, –, –, –; *Corylus avelana* (T, S) 0.7, –, –, –; *Dactylis glomerata* (PG) 0.3, 0.1, 0.1, 0.2; *Deschampsia cespitosa* (PG) 0,1, –, –, 0.1; *Descurainia sophia* (AH, BM) –, –, 0.1, –; *Echinocystis lobata* (AH) 0.1, 0.1, –, –; *Elymus caninus* (PG) 0.3, 0.2, –, –; *Elytrigia repens* (PG) 1, 0.2, –, –; *Epilobium hirsutum* (P) 0.2, –, –, –; *Epilobium* sp. 0.1, 0.2, –, –; *Equisetum arvense* (PP) 0.1, 0.03, –, –; *Equisetum palustre* (PP) 0.03, –, –, –; *Fallopia conlolvulus* (AH) 0.7, 0.1, –, –; *Festuca gigantea* (PG) 0.03, 0.03, –, –; *Galeopsis pubescens* (AH) 1.1, 1.2, –, –; *Galeopsis speciosa* (AH) –, 0.2, –, –; *Geranium robertianum* (AH, BM) –, 0.03, –, –; *Glechoma hederacea* (PP) 0.3, 0.3, –, –; *Glyceria* sp. (PG) 0.03, 0.2, –, –; *Heracleum sphondylium* (PM) –, 0.03, –, –; *Holcus lanatus* (PG) 0.1, –, –, –; *Holcus mollis* (PG) –, 0.03, –, –; *Hordeum* sp. (AG) –, –, 0.3, –; *Humulus lupulus* (PP) 0.1, 0.2, –, –; *Hypericum perforatum* (PP) 0.2, –, –, –; *Impatiens noli-tangere* (AH) 0.2, 0.5, 0.2, 0.1; *Impatiens parviflora* (AH) 0.1, 0.1, –, 0.2; *Juncus effusus* (P) –, 0.03, –, –; *Lactuca serriola* (AH, BM) 0.1, 0.1, –, –; *Lamium album* (P) 0.4, 0.1, 0.3, –; *Lamium purpureum* (AH) 0.1, –, –, –; *Lapsana communis* (AH) 0.1, 0.1, –, –; *Lycopus europaeus* (P) 0.1, –, –, –; *Lythrum salicaria* (PP) 0.1, 0.1, 0.1, –; *Mentha aquatica* (P) 0.03, –, –, –; *Myosotis arvensis* (AH) –, –, 0.2, 0.1; *Myosotis palustris* agg. (P) 0.03, –, –, –; *Oenothera biennis* (BM) –, 0.1, –, –; *Papaver rhoeas* (AH) –, –, 0.3, –; *Persicaria maculosa* (AH) 0.1, 0.3, 0.3, 0.1; *Persicaria* sp. (AH) 0.1, –, –, –; *Poa trivialis* (PG) 0.03, 0.03, –, 0.1; *Ranunculus repens* (PP) 0.03, 0.1, –, –; *Raphanus raphanistrum* (AH) –, –, –, 0.2; *Reynoutria japonica* (P) –, 0.2, –, –; *Reynoutria sachalinensis* (P) –, 0.3, –, –; *Rorippa palustris* (AH) –, –, 0.5, 0.2; *Rubus idaeus* (S) 1.4, 0.7, –, –; *Rubus saxatilis* (S) 0.1, 0.1, –, –; *Rumex conglomeratus* (P) 0.1, 0.03, –, –; *Rumex hydrolapathum* (P) –, 0,03, –, –; *Rumex obtusifolius* (P) –, –, 0.5, 0.2; *Salix caprea* (T, S) 0.03, –, –, –; *Salix fragilis* (T) –, 0.1, –, –; *Salix viminalis* (T, S) 0.1, –, –, –; *Scrophularia nodosa* (P) 0.2, 0.1, –, –; *Scrophularia umbrosa* (P) 0.1, –, –, –; *Scutellaria galericulata* (P) 0.03, –, –, –; *Securigera varia* (P) 0.2, –, –, –; *Silene latifolia* (PM) 0.2, 0.03, 0.1, –; *Sisymbrium officinale* (AH, BM) –, 0.03, –, –; *Solidago canadensis* (PP) –, –, –, 0.1; *Stachys sylvatica* (PP) 0.3, 0.1, –, –; 0.1; *Tanacetum vulgare* (PP) 0.03, 0.03, –, 0.1; *Thlaspi arvense* (AH) –, –, –, 0.2; *Torilis japonica* (AH) 0.03, –, –, –; *Tripleurospermum inodorum* (AH) –, –, 0.1, –; *Veronica beccabunga* (P) –, 0.03, –, –; *Vicia cracca* agg. (P) 0.1, 0.2, –, –; *Viola arvensis* (AH) –, –, 0.1, —. Species from the upper bush and tree layers were excluded from analyses. Upper bush layer: *Salix viminalis* (T, S) 0.7, 0.5, –, –; *Populus tremula* (T) –, 0.1, –, –; tree layer: *Quercus robur* (T) 0.7, –, –, –.

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