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Weak effects on plant diversity of two invasive *Impatiens* species

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Abstract The study aimed to examine the effect of the invasion of the two congeneric species *Impatiens glandulifera* and *Impatiens parviflora* on species richness and composition across a wide range of communities in North-western Germany. We applied a space-for-time substitution approach, comparing invaded plots with adjacent, environmentally similar uninvaded plots, based on the assumption that the latter represent the situation prior to an invasion. Even though the dominance of the invasive species resulted in a lower Shannon diversity in the invaded plots, species richness was not (*I. parviflora*) or only weakly (*I. glandulifera*) reduced. Also the community composition of the invaded sites was only marginally different. Invaded and uninvaded plots in general had similar habitat conditions, but both *Impatiens* species occurred in slightly shadier sites compared to the uninvaded areas, and the plots invaded by *I. parviflora* tended to have higher nutrient concentrations. These results suggest that dense populations of invading species may often be found at particular microsites. The relatively low impact of *Impatiens* on the vegetation is most likely caused by the annual life strategy of the species: while *I. glandulifera* shows large fluctuations in numbers between years and has a later phenological development than most other species in its habitat, *I. parviflora* establishes preferably in dark and acidic, often disturbed woodlands where it competes with few other species.

Keywords Competition · *Impatiens glandulifera* · *Impatiens parviflora* · Nutrient availability · Space-for-time substitution · Species richness

Introduction

The intentional or unintentional introduction of non-native species to new locations is one of the main components of global change. In many cases, alien species attain a high reproductive success in their new environments, spread rapidly, and become invasive. From an applied point of view, ecologists are mainly interested in and concerned with the potential negative

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effects of biological invasions. Alien plant species may have various effects on species, communities, and ecosystems, for example, altering the abundance and richness of plant and animal species, changing environmental conditions in terms of soil nutrients, litter or light, affecting disturbance or fire regimes, and promoting erosion (Brooks et al. 2004; Dassonville et al. 2008; Ehrenfeld 2010; Vilá et al. 2011; Pyšek et al. 2012).

A phenomenon associated with many plant invasions is that the invasive species attains dominance in its new habitat, leading to the assumption that plant invasions result in a decline of species richness. However, it has been argued that invasive species can also be passengers of disturbance and other environmental changes by being less constrained by these processes than the native species (MacDougall and Turkington 2005). Meta analyses found that invasions often cause a reduction in the number of species, but that the effect is strongly context-dependent and determined by interactions between species traits of the invader and the type of biome invaded (Vilá et al. 2011; Pyšek et al. 2012). In Central Europe, there is a large variation in the impact of alien species on community richness, as for example shown in a study of 13 invasive plant species in the Czech Republic (Hejda et al. 2009) in which *Fallopia japonica* was found to reduce plot species richness by 73 %. Almost the same magnitude of change (77 %) was observed in a study of this species in North-western Germany (Doobe 2015). Quantifying the impact of invasive species on community composition and richness is highly important to guide management priorities into the right direction, given that the financial resources of nature conservation agencies are limited.

There are various approaches for assessing the impact of invasive species. Comparative temporal studies of ongoing invasions are highly informative, but depend on the availability of plot data from sites before they have become invaded, and despite a wealth of relevé data from Central Europe, we only rarely possess precise information about the spatial location of these relevés (but see Müllerová et al. 2005). On the other hand, simple comparisons of invaded and uninvaded sites in a region often disregard that these sites may differ in their environmental conditions or extent of disturbance, implying that there may have been differences in species richness or composition already prior to the invasion. Experimental studies based on the intentional introduction of an invasive plant, apart from widely being considered unethical, generally are too local to provide broad evidence for community level effects of an invasion. A much better experimental approach is the removal of the invasive species from plots and the subsequent monitoring of these plots compared to control sites (see, e.g., Hulme and Bremner 2006). A potential disadvantage is that the removal of a species may alter the environment, for example, through soil disturbance, and thus have an indirect effect on the species assemblage (Zavaleta et al. 2001). Another informative approach is to compare invaded and adjacent uninvaded plots that both are presumably exposed to the same environmental conditions. If plots are carefully selected and measurements verify that habitats are comparable, such space-for-time substitutions can document the impact of invasive species on species richness and composition over a broad range of invaded habitats (Pyšek and Pyšek 1995). However, if species-poor habitats are more prone to invasions than species-rich habitats, it becomes difficult to separate cause and effect (Levine and D'Antonio 1999).

Here, we apply a paired design of invaded and uninvaded plots to examine the impact of the two annual invasive species *Impatiens glandulifera* and *I. parviflora* on species richness and community composition. This study is part of a more extensive project including the screening of the effects of invasive plant species on the vegetation in North-western Germany. We possess only sparse scientific information from this region about the impact of invasive species, which makes it difficult to develop proper management plans. Both *Impatiens* species have been introduced from Asia and become widespread in large parts of Europe. Despite several studies from different countries (*I. glandulifera*: Pyšek and Prach 1995; Hejda and Pyšek 2006; Hulme and Bremner 2006; *I. parviflora*: Trepl 1984; Chmura and Sierka 2006, 2007; Hejda 2012), there is no consensus yet about the impact of *Impatiens* species on species richness. The above literature also does not differentiate between different habitats and therefore cannot answer the question whether the effects are habitat-dependent. In addition, species richness as a response variable is too general to judge whether species with particular traits are affected more strongly than others. In our study, we therefore asked the following questions: (1) Do the environmental conditions in the uninvaded plots differ from those in the invaded plots? (2) To what extent does the invasion of *I. glandulifera* or *I. parviflora* cause a change in plant species richness and community composition? (3) Does the impact of the invasive species differ along the soil and light gradients? And finally, (4) do the shade tolerance and phenology of plant species matter for their sensitivity to an invasion by *Impatiens*?

Materials and methods

Study species and area

The Himalayan Balsam (*I. glandulifera*, Balsaminaceae) is native to the western parts of the Himalayas and was first introduced to Britain in the middle of the 19th century (Beerling and Perrins 1993). It has since then become naturalized in most European countries and is considered as one of the most widespread alien plant species (Kowarik 2010). *Impatiens glandulifera* reaches a height of up to 3 m and is the tallest annual herb of the flora in North-western and Central Europe. It mainly occurs not only on open or half-shady riverbanks and in other riparian habitats, but can also be found in woodlands and disturbed ruderal sites (Cordes et al. 2006; Kowarik 2010; Pahl et al. 2013). Owing to its large seed production (up to 2500 per plant, Koenies and Glavač 1979), it often establishes in dense populations. Its large flowers and extended flowering time in summer and autumn make it one of the most conspicuous plant species along waterways. The species exerts a strong impact not only on the vegetation owing to its dominance, but also to allelopathic effects (Gruntman et al. 2016, but see Del Fabbro et al. 2014).

The Small Balsam (*Impatiens parviflora*) shares several attributes with its congener *I. glandulifera*: it also originates from Middle Asia, naturalized in the 19th century, and is an annual herb that often forms dense populations (Coombe 1956). However, it is much smaller and has a lower seed production, and it has different habitat preferences being predominantly found in forests and forest clearings or at forest edges and paths, more rarely in open ruderal sites (Cordes et al. 2006). *Impatiens parviflora* occurs in a large variety of forest communities on both base-rich and acid, moderately dry to moist sites, and due to its high frequency in urban plantations and parks (Cordes et al. 2006), it is one of the best-known invasive plant species among the public.

The study was carried out in the region of Bremen in the lowlands of North-western Germany. Sites invaded by the species were located on the basis of information from regional floras (e.g., Cordes et al. 2006), nature conservation administrations in Bremen and in the surrounding counties as well as local botanists from the University of Bremen and from conservation societies. Additional sites were found by active searching in suitable areas. For both species, we aimed to sample plots across the whole range of habitats and environmental conditions in which the species occur. When an invaded site was found, plots were sampled only if the following criteria were met: (1) The invaded plot was required to have a cover of *Impatiens* of at least 50 % (then the species can be considered as dominant), while the cover of the species in the adjacent uninvaded plot was allowed to be at maximum 10 %. In fact, the majority of uninvaded plots included some individuals of *Impatiens*—showing the basic habitat suitability of the site for the species—without exerting a strong influence on other species or the environment. (2) Both the invaded and uninvaded plots had to be as homogeneous as possible in terms of their vegetation structure and species composition. (3) Invaded and uninvaded plots had to be highly similar in their overall habitat conditions. Plots were judged as similar if there were no obvious differences in topography, soil type, and shading.

Plots with *I. glandulifera* were sampled mainly in riparian habitats such as riverbanks and floodplains, less often in moist forests. In total, 50 pairs of plots of 10 m^2 (with varying shape, as the species sometimes forms narrow fringes along river banks and forest edges) were examined in July 2014. In each plot, a list of all vascular plants was compiled and their abundance estimated using a refined cover-abundance scale according to Braun-Blanquet (1964). For *I. parviflora* that was exclusively encountered in forests or at forest edges, 30 pairs of plots of 9 (3×3) m^2 size were sampled in June 2013 using the same method as above. The uninvaded plots were situated either directly adjacent to or at a maximum of 5 m from the invaded plots. The sampling date in late spring allowed us to also record the few vernal geophytes occurring in the area, notably *Anemone nemorosa* and *Ranunculus ficaria*. For both *Impatiens* species, the total cover of trees and shrubs (>3 m height) was estimated by eye and used as an inverse surrogate for the light conditions in the plot, which has been shown to be a reliable proxy for measured light availability (e.g., Pannek et al. 2013). The nomenclature of species followed FloraWeb (http://floraweb.de/).

Soil sampling and analysis

To describe the average and variability of edaphic conditions across the sites and to examine whether invaded and uninvaded plots differed in their environmental conditions, soil samples were collected and analyzed. In each plot, a mixed sample was taken from the upper soil (0–10 cm), consisting of three cores from different parts of the plot. The samples were air-dried at room temperature for several days, homogenized by sieving (2 mm), and stored in plastic boxes for further analysis in the laboratory at the University of Bremen. For the determination of calcium (Ca), magnesium (Mg), potassium (K), and plant available phosphorus (P), 5 g of dry soil were mixed with 100 ml acetate-lactate solution and shaken for 4 h. After filtration, the Ca, Mg and K solutions were measured with atomic absorption spectroscopy, while the P solution was measured with flow injection analysis. For the determination of pH, 10 g of air-dried soil were mixed with 25 ml 0.01 M $CaCl_2$ solution, shaken for 1.5 h, and then measured with a pH meter. Total carbon (C) and nitrogen (N) concentrations were determined with the elemental C/N analyzer EuroEA (Hekatech firm) by means of gas chromatography using 5–10 mg of air-dried, fine-ground soil. All laboratory measurements followed the detailed description of methods described by Suchopar (2014). In *I. glandulifera*, there appeared to be large variation in soil moisture at the sites, which we estimated in the field using a coarse 1–5 scale (1—moderately dry, 2—moderately dry to moist, 3—moist, 4—moist to wet, 5—wet).

Statistical analysis

Invaded and uninvaded plots were compared with respect to three measures of plant diversity: species richness, Shannon diversity, and evenness. Species richness was defined as the total number of vascular plants of all vegetation layers in the plot, but excluding *Impatiens* as we wanted to evaluate the impact of the invader on the number of remaining species (the results of analyses including *Impatiens* were almost identical). The Shannon diversity index H' is based on the equation $H' = -\sum P_i \times \ln P_i$, where P_i is the proportion of the cover-abundance value of species i in a plot. Evenness J was calculated as $H'/\ln S$, where S is the total number of species (Magurran 2004). For the comparison of H' and J between invaded and uninvaded plots, *Impatiens* was included as it would have been meaningless to calculate these two diversity indices without considering the high abundance values of the target species in the invaded plots. As the diversity measures mostly did not show a normal distribution, the paired plots were compared with Wilcoxon signed-rank test. In addition, we tested whether the difference in the number of species between invaded and uninvaded plots is correlated with the environmental variables, i.e., whether the effect of the invasive species on species richness depends on the environment or habitat.

To examine whether the responses of single species to the invasion depended on their phenology or light requirements, we correlated the differences in abundance between invaded and uninvaded plots with the Ellenberg indicator values for light (expressing the species' optima; Ellenberg et al. 1992) and to the flowering time as an approximation for the main growing period (data obtained from the data base BiolFlor, Klotz et al. 2002). For these analyses, only species with at least five occurrences in pairs of plots were used. The site conditions (soil variables and light) in the invaded and uninvaded plots were also compared with Wilcoxon signed-rank test. All analyses were carried out with R version 3.1.0 (R Core Team 2014).

The variation in species composition of plots in the datasets with the two species and the impact of the invasion of *Impatiens* on the vegetation were examined with indirect gradient analysis, using the cover-abundance values of species. DCAs revealed that the gradient length of the first ordination axis was higher than 4 in both species and thus identified this method as appropriate for the analysis. *Impatiens* was omitted from the datasets for the purpose of ordination. However, ordination runs including *Impatiens* or based on presence–absence values gave highly similar results. The effect of the invasion on the species composition was assessed by a comparison of the site scores of invaded and uninvaded plots along the ordination axes, applying Wilcoxon signed-rank test. Furthermore, we examined the impact of soil variables (log-transformed if not normally distributed) on the variation in species composition by post hoc tests fitted to the results of the DCA ordination. The significance of these variables was tested with Monte Carlo permutation (with 9999 permutations). All multivariate analyses were carried out with the package Vegan 2.0 10 (Oksanen et al. 2011).

Results

Species richness

In the *I. glandulifera* dataset, species numbers ranged from 4 to 25 in the invaded plots and from 5 to 30 in the uninvaded plots. In the large majority of cases, the invaded plots had fewer species than the uninvaded plots (Fig. 1), resulting in a significant difference of the median values (Table 1). However, the mean decline per plot in the number of species was only 7.4 %. The differences between invaded and uninvaded plots were even more pronounced when comparing the Shannon index H’ or evenness.

Species richness in the *I. parviflora* dataset varied between 3 and 16 in the invaded plots and between 4 and 24 in the uninvaded plots. In most pairs of plots, the number of species did not differ more than 5 (Fig. 1), and the mean decline in species richness in the invaded plots was 5.9 %. while invaded and uninvaded plots did not significantly differ in species richness or evenness, the Shannon index H’ was higher in the uninvaded sites (Table 1).

Species composition

Impatiens glandulifera was primarily found in tall herbaceous vegetation along riversides and ditches, less often in open forests and shrubland along roads and pathways. The most frequent species in both invaded and uninvaded sites were *Urtica dioica*, *Galium aparine*, *Glechoma hederacea*, *Phalaris arundinacea*, and *Calystegia sepium* (Online Appendix Table 3). The invasion of sites by *I. glandulifera* had no pronounced effect on the species composition, as invaded and uninvaded plots are mixed in the DCA ordination diagram without forming distinct clusters (Fig. 2a). Nonetheless, the DCA scores along axis 1 of the majority of invaded plots were situated left of the scores of the uninvaded plots, indicating a weak but systematic shift in species composition ($V = 387$, $p = 0.016$, $n = 50$). The relationship between the

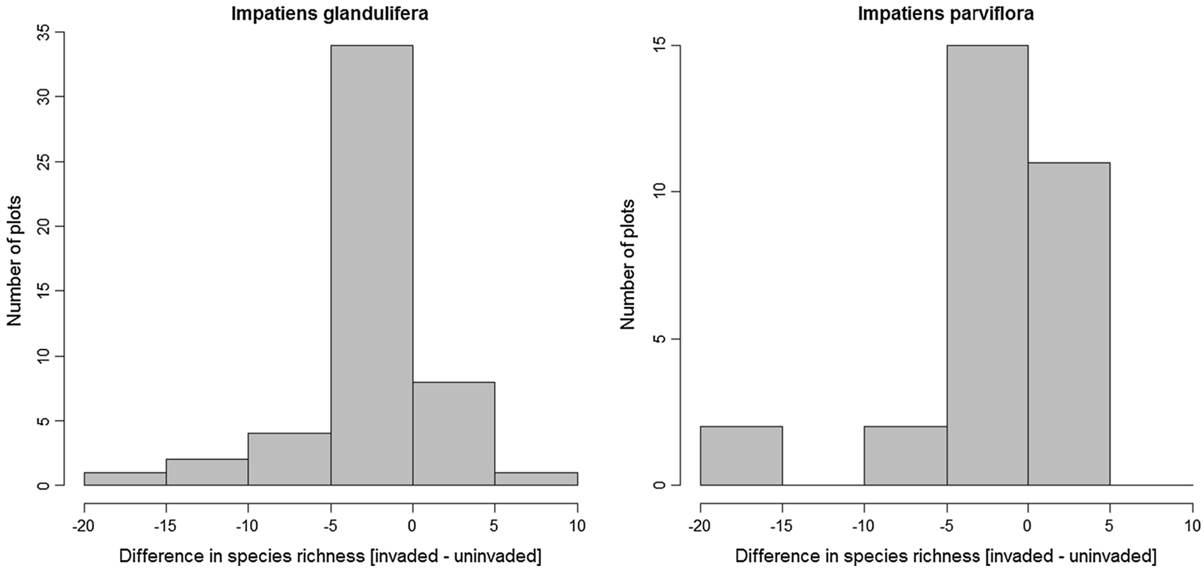

Fig. 1 Difference in species richness between invaded and uninvaded plots for *I. glandulifera* ($n = 50$) and *I. parviflora* ($n = 30$)

Table 1 Species richness, Shannon index and evenness of invaded and uninvaded plots of *I. glandulifera* and *I. parviflora*

	Impatiens glandulifera			*Impatiens parviflora*		
	Invaded plots	Uninvaded plots	Comparison	Invaded plots	Uninvaded plots	Comparison
Total no. of species	100	124		49	59	
Plot species richness						
Median	9.0	10.5	**$V = 193, p = 0.001$**	9.0	10.0	$V = 140, p = 0.240$
Min	4	5		3	4	
Max	25	30		16	24	
Shannon index H'	1.31	1.78	**$V = 121, p < 0.001$**	1.45	1.89	**$V = 67, p = 0.001$**
Evenness	0.57	0.76	**$V = 139, p < 0.001$**	0.65	0.63	$V = 277.5, p = 0.360$

This table shows minimum (min), maximum (max), and median values as well as the results of Wilcoxon signed-rank tests for the comparison of plot types. Significant differences between invaded and uninvaded plots are given in bold

mean difference in abundance between invaded and uninvaded plots and the Ellenberg light value across species was significantly negative ($R^2 = 0.367$, $p < 0.001$, $n = 46$), meaning that the more light-demanding species suffered most from the invasion (Fig. 3). There was also a tendency for late-flowering (and late-developing) species to be less frequent in invaded plots ($R^2 = 0.076$, $p = 0.056$, $n = 47$).

Plots with *I. parviflora* were mainly sampled in forests, at forest edges and along shaded paths. The most frequent companions included *Hedera helix*, *Rubus fruticosus* agg., *Galium aparine* and *Milium effusum*, together with seedlings and saplings of trees such as *Sorbus aucuparia* and *Fraxinus excelsior* (Online Appendix Table 4). Again, plots with or without *I. parviflora* are not clustered in the DCA ordination diagram (Fig. 2b), but the scores along axis 2 showed a systematic difference between plot types (downward shift of invaded sites; $V = 83$, $p = 0.001$, $n = 30$). In contrast to *I. glandulifera*, there was no relationship between the mean difference in abundance between invaded and uninvaded plots and the Ellenberg light value or phenology of the species ($p > 0.05$).

Environment

There was a large variation in environmental conditions across the sites invaded by *I. glandulifera* (Table 2). In the invaded plots, for example, soil pH varied between 3.35 and 7.17 (median 4.96), and the amount of plant available phosphorus ranged from 2.4 to 19.5 mg/100 g soil (median: 6.2 mg/100 g soil). In general, the values of the soil variables were indicative of relatively nutrient-rich conditions. The mean values of the measured edaphic variables did not differ between invaded and uninvaded plots, with the exception of K that showed significantly higher concentrations in the uninvaded plots. *Impatiens glandulifera* occurred both in completely open (without trees and shrubs) habitats and under shady conditions, and plots invaded by the species tended to be less open than the adjacent uninvaded plots (Table 2). When correlating the differences in the number of species between invaded and uninvaded plots with the average values of single environmental variables for the two plots of a pair, no significant results were obtained (Spearman-rank correlation, all p values >0.22). However, species loss was more pronounced in open habitats such as riverbanks and floodplains compared to more shady habitats (Fig. 4).

The DCA ordination diagram of species (Online Appendix Fig. 5) indicates that the main variation in species composition of the habitats invaded by *I. glandulifera* follows a gradient of water availability, from reeds on very wet soils (with, e.g., *Equisetum fluviatile*, *Iris pseudacorus*, *Lythrum salicaria*, and *Sium latifolium*) in the right-hand side of the diagram to more ruderal and shady sites on fresh soils in the left-hand side (including *Galium aparine* and *Heracleum sphondylium*). With increasing soil moisture, there was an increase in C and N contents ($r_s = 0.418, p = 0.003$ and $r_s = 0.487, p < 0.001$, respectively) and in the concentrations of the cations Ca ($r_s = 0.440$, $p = 0.001$) and Mg ($r_s = 0.452, p < 0.001$, all $n = 50$,).

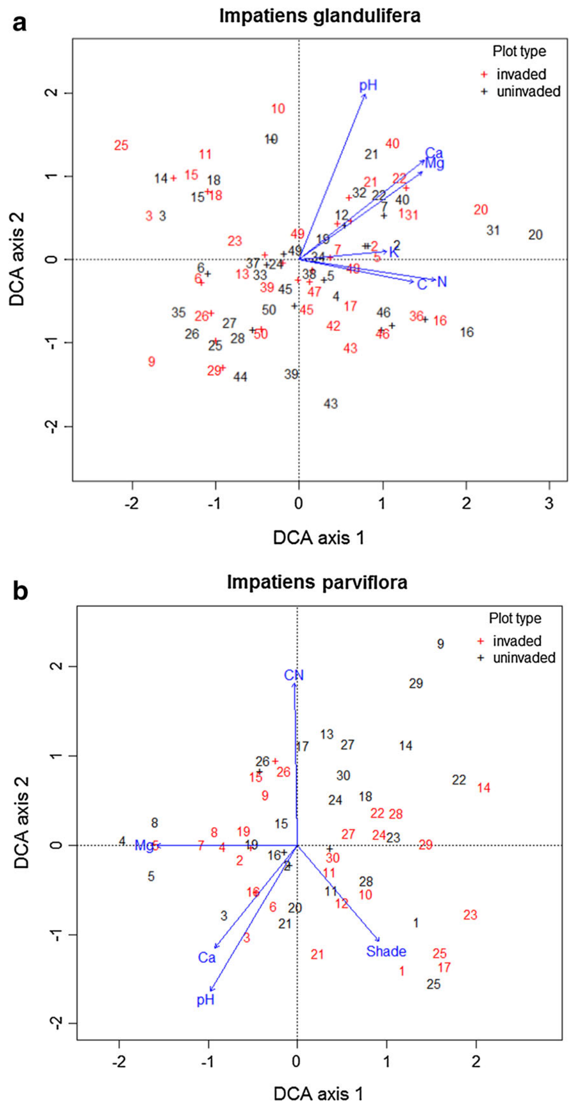

Fig. 2 DCA ordination diagrams of invaded and uninvaded plots of **a** *I. glandulifera*and **b** *I. parviflora*. The uninvaded sites are colored in *black* and the invaded in *red*. To avoid overlapping numbers, some plots are given with "+." Environmental variables were post hoc fitted to the ordination results and displayed as vectors if significant at $p < 0.01$. Ordination statistics: *I. glandulifera*: eigenvalues: axis *1* 0.560, axis *2* 0.394, gradient lengths: axis *1* 4.976, axis *2* 3.535; *I. parviflora*: eigenvalues: axis *1* 0.516, axis *2* 0.389, gradient lengths: axis *1* 4.055, axis *2* 3.812

In sites where *I. parviflora* occurred, there was also a considerable environmental variation across plots, with soil pH varying between 2.82 and 5.38 (median: 3.54) in the invaded plots (Table 2). The Ca concentration was significantly higher in the invaded plots compared to the uninvaded plots, and the same trend was found for K and P. As for the congener, the invaded plots were on average darker than the adjacent uninvaded plots (Table 2). The differences in the number of species between invaded and uninvaded plots were uncorrelated to the average values of environmental variables for the paired plots (Spearman-rank correlation, all p values > 0.37), except for the C/N ratio ($r_s = -0.396$, $p = 0.003$, $n = 30$), i.e., the species loss in invaded plots increased with increasing C/N values. Also for *I. parviflora*, the DCA ordination diagram of species (Online Appendix Fig. 6) probably reflects a gradient in soil water availability, with the moister plots situated in the right-hand side (indicated by, e.g., *Athyrium filix-femina* and *Carex remota*) and the drier ones in the left-hand side of the graph. The vector for shade points into the same direction as the transition from uninvaded to invaded plots, suggesting that the species prefers shadier conditions.

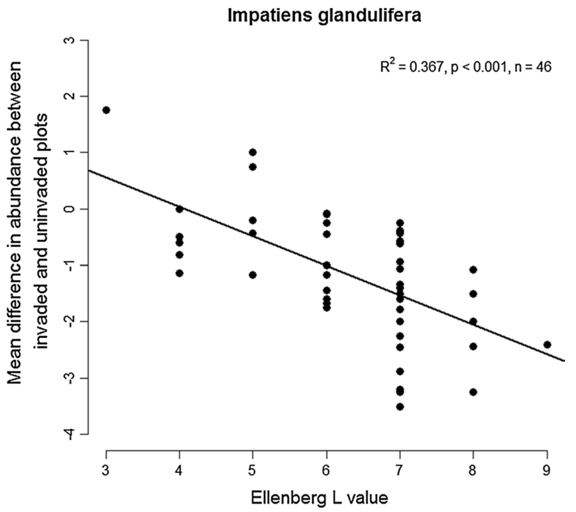

Fig. 3 Relationship between the mean difference in abundance between invaded (by *Impatiens glandulifera*) and uninvaded plots and the Ellenberg indicator values for light across species. The analysis included only species with at least 5 plot occurrences

Discussion

In the absence of detailed plot data on the changes in species richness and composition during an ongoing invasion—proceeding from an uninvaded state to an invaded state, one of the best options for studying the

Table 2 Values of soil parameters and light conditions (as % cover of trees and shrubs) in plots invaded by (a) *I. glandulifera*and (b) *I. parviflora* compared to adjacent uninvaded plots

Soil variable	Invaded plots ($n = 50$)			Uninvaded plots ($n = 50$)			Comparison	
	Min	Max	Median	Min	Max	Median	V	p
(a) *Impatiens glandulifera*								
pH	3.35	7.17	4.955	3.24	6.95	5.065	470	0.228
Ca (mg/100 g soil)	19.8	1174.7	120.3	18.0	886.2	141.1	727	0.390
K (mg/100 g soil)	1.9	47.4	9.2	3.4	67.0	12.7	304.5	**0.001**
Mg (mg/100 g soil)	2.1	60.9	15.1	2.9	74.5	15.2	575	0.550
P (mg/100 g soil)	2.4	19.5	6.2	2.4	20.7	6.1	584	0.971
C (%)	1.8	23.5	6.7	1.4	33.5	5.6	576.5	0.559
N (%)	0.1	1.5	0.4	0.1	1.7	0.4	520.5	0.261
C/N ratio	10.3	36.6	16.9	3.8	31.8	17.0	794.5	0.131
% cover trees and shrubs	0	105	72.5	0	145	50.0	257	**0.039**
Soil variable	Invaded plots ($n = 30$)			Uninvaded plots ($n = 30$)			Comparison	
	Min	Max	Median	Min	Max	Median	V	p
(b) *Impatiens parviflora*								
pH	2.82	5.38	3.54	2.92	5.10	3.40	282	0.314
Ca (mg/100 g soil)	35.6	879.3	118	18.7	640.2	93.8	329	**0.047**
K (mg/100 g soil)	5.6	64.5	17.4	3.7	40.2	14.5	313	0.100
Mg (mg/100 g soil)	5.1	132.7	18.7	3.5	216.9	18.8	281	0.329
P (mg/100 g soil)	0.5	14.5	4.2	0.5	14.7	3.7	323.5	0.063
C (%)	2.1	44.1	15.3	1.2	46.4	11.7	246	0.792
N (%)	0.1	2.0	0.9	0.1	2.0	0.6	255	0.655
C/N ratio	13.3	30.5	19.0	14.7	24.4	18.1	261	0.565
% cover trees and shrubs	25	95	82.5	30	95	70.0	226	**0.029**

This table shows minimum (Min), maximum (Max) and median values as well as the results of Wilcoxon signed-rank tests of the comparison of plot types. Significant differences between invaded and uninvaded plots are given in bold

impact of alien species is the space-for-time substitution, based on a paired design of invaded and adjacent uninvaded plots (for example, Alvarez and Cushman 2002). This approach can be superior to experimental manipulations in that more (and larger) plots can be sampled over a larger range of habitats, but it is based on the assumption of environmental comparability of invaded and uninvaded plots, which is difficult to prove given the large number of variables of potential relevance (related to soil resources, light availability, disturbance, or biotic interactions). Removal experiments with *I. glandulifera* carried out by Hejda and Pyšek (2006) and Hulme and Bramner (2006) indeed included a relatively low number of plots, but found results similar to this study. Here, environmental similarity between invaded and uninvaded plots was largely confirmed, but in *I. parviflora*, invaded plots appeared to have slightly higher nutrient availabilities (Ca, K, and P), most likely because the species preferably establishes in disturbed sites with compacted soil and often increased fertility (Godefroid and Koedam 2010). In *I. glandulifera*, the low K concentration in the soils of invaded plots may be explained by the high uptake of potassium by the species that enables the plants to achieve large height under low irradiance (Andrews et al. 2005). Higher contents of some nutrients (for example in K, Mg, and P) in invaded plots on initially fertile sites were also reported by Dassonville et al. (2008). Thus, the significant difference between invaded and uninvaded plots may not reflect initial differences between the two plot types, but be the consequence of the high growth rate and productivity of the invader. Furthermore, both *Impatiens* species inhabited plots that were

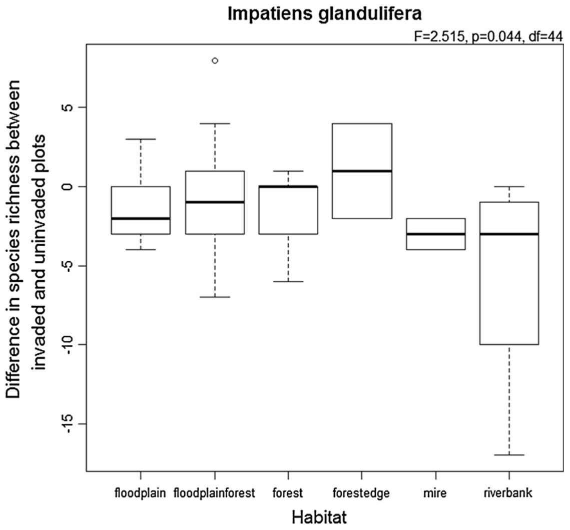

Fig. 4 Mean differences in species richness between plots invaded by *I. glandulifera*and uninvaded plots in different habitat types, analyzed by one-way Anova

significantly shadier than the neighboring uninvaded plots, a feature that was not noticed in the field. *Impatiens parviflora* has been reported to have a high shade tolerance, and *I. glandulifera* appears to show a unimodal response to canopy cover (Čuda et al. 2014), being able to grow fast and outcompete other species also under relatively low irradiance (Andrews et al. 2009). We believe, however, that the above differences are minor and do not invalidate the assumption that the uninvaded plots largely reflect the situation of a plot prior to the invasion. This interpretation is corroborated by the generally weak effects of the presence of *Impatiens* on species richness and composition (see below).

For both species, as expected, the Shannon index and/or evenness were higher in the uninvaded plots compared to the invaded plots, due to the large dominance of the invader at the expense of other species. Mean species richness in *I. glandulifera*-invaded plots showed a significant, but weak (about 7 %) decline, in accordance with findings from the Czech Republic by Hejda and Pyšek (2006) who reported a weak (and nonsignificant) decrease in the number of species in a paired design study. Similar results were found by Hejda et al. (2009), whereas Hulme and Bremner (2006) suggested that large and dense stands of the species may reduce species richness by up to 25 %. The ordination results suggest that also the species composition of the communities remains similar after an invasion. Thus, there is some evidence that the species does not exert a major impact on the vegetation, despite an often extremely high cover of >80 %. We believe this for several reasons: (1) *I. glandulifera* is an annual species, the establishment of which varies strongly over time (Kasperek 2004; also pers. obs.). In some years, the forests and reed communities are colonized by large numbers of plants; in other years, colonization fails almost completely or takes place at another location. Flooding and high ground water during the germination period in early spring impede the establishment of *I. glandulifera* in certain years. These fluctuations prevent a continuous or increasing dominance of the species. (2) In nutrient-rich sites such as reed beds, *I. glandulifera* co-occurs with other tall and fast-growing, perennial species; these are suppressed by the invader, but not fully out-competed. *Urtica dioica*, for example, has been shown to be competitively inferior to *I. glandulifera* (Tickner et al. 2001; Gruntman et al. 2014), but in our study, it was present in 46 uninvaded plots and in the same number of invaded plots. (3) After establishment, the initial growth rate of the species is low, and only in mid summer, growth accelerates and surpasses that of *Urtica* (Koenies and Glavač 1979).

The late phenological development of *I. glandulifera* means that mainly the late summer species are affected negatively. Especially light-demanding species are harmed by the invader (Fig. 3; see also Hulme and Bremner 2006): among the species with 5 or more occurrences in the dataset, all species with Ellenberg L values of 7, 8, or 9 showed a lower mean abundance in the invaded compared to the uninvaded plots. It is thus obvious that species with different traits tend to respond differently to an invasion by *I. glandulifera*. Moreover, Fig. 4 indicates that the effects of the species on general species richness differ between habitats, being more pronounced in open vegetation types. However, also in the floodplains with high nature conservation value, there is no evidence that *I. glandulifera* has contributed to the decline of rare species (Online Appendix Table 3).

The effect of *I. parviflora* on species richness in our study was even less pronounced compared to the congener. Studies from Poland and the Czech Republic give somewhat contrasting results, but largely confirm the weak impact of the species on the phytodiversity of forests (Chmura and Sierka 2006; Łysik 2008; Hejda

2012). While the populations of the species unlike *I. glandulifera* are relatively stable over time without showing strong fluctuations between years, they do not form such a dense and high canopy and thus do not attain a high competitive dominance (Hejda 2012). Furthermore, the species is able to grow on very acidic, nutrient-poor soils in shady forests (Godefroid and Koedam 2010; see also Table 2), which is an environment with few indigenous species in Central Europe. *Impatiens parviflora* thus often invades species-poor (in many cased disturbed) sites with a sparse herb layer (Obidzinski and Symonides 2000) and can be perceived as an unproblematic addition to the forest plant community. It is also unlikely that the species is a threat to the only native representative of the genus, *I. noli-tangere*. Although there is some overlap in habitats (Vervoort et al. 2012), *I. noli-tangere* prefers wetter and more fertile sites than *I. parviflora*, meaning that there is a considerable microsite differentiation between the two species (Godefroid and Koedam 2010; Čuda et al. 2014). When growing together, *I. noli-tangere* appears to have a higher competitive strength than the smaller species (Čuda et al. 2015), although the opposite may be true on drier soils (Skálová et al. 2013).

Conclusions

In summary, the invasion of *I. glandulifera* or *I. parviflora* does not cause a considerable change in plant species richness and composition. Although specific habitats appear to suffer more than others from species loss, even the most affected environments show only a relatively weak reduction in the number of species. Furthermore, there is no evidence that rare species of reed communities and woodlands have disappeared following the invasion of *Impatiens*, in fact most species being negatively affected (in cover) represent widespread, often ruderal, species (Hulme and Bremner 2006).

Our results correspond to the evaluation of the effects of invasive plant species in Germany (Nehring et al. 2013) showing that annual plant invaders in this region do not pose a major threat to phytodiversity. Unlike rhizomatous perennials like *Fallopia* spp. (Doobe 2015) and *Solidago* spp. (see Hejda et al. 2009), they appear not to be able to occupy a habitat over the whole growing season and over many years to such an extent that other plant species are permanently out-competed. This does not necessarily imply that annual plant invaders are unproblematic, because they may still affect animal communities. *I. glandulifera* with its large and nectar-rich flowers has been shown to affect pollinator communities (Bartomeus et al. 2010) and other invertebrate groups (Tanner et al. 2013; Rusterholz et al. 2014). With respect to the vegetation, however, our conclusion is that not all invasive plants with a high competitive dominance have a strong effect on species richness and composition, which is in accordance with a national assessment of the impact of invasive plant species on biodiversity in Germany (Nehring et al. 2013).

In many popular scientific articles, it is argued that plant species classified as invasive need to be extirpated. Accordingly, in our study area, large stands of *I. glandulifera* (but not *I. parviflora*) are regularly mown or otherwise counteracted by the nature conservation authorities, especially in protected areas. Our results, which are largely in correspondence to findings of other authors, suggest that this is not necessary or should only be done if the species attains dominance in areas where rare species are present. Management efforts should rather focus on invasive species shown to have much stronger effects on the vegetation, such as, in our region, *Fallopia* spp.

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