

Micro-habitat and season dependent impact of the invasive *Impatiens glandulifera* on native vegetation

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Abstract

The impact of invasive species is often difficult to assess due to species × ecosystem interactions. *Impatiens glandulifera* heavily invaded several habitat types in Central Europe but its impact on native plant communities is rated ambiguously. One reason could be that the impact differs between habitat types or even between environmentally heterogeneous patches (micro-habitats) within one habitat type. In the present study a vegetation survey was performed within heterogeneous riverside habitats in Germany investigating the impact of *I. glandulifera* on native vegetation in dependence of environmental conditions. The vegetation was recorded in summer and spring because of seasonal species turnover and thus potentially different impact of the invasive plant. We found that the cover of *I. glandulifera* depended on environmental conditions resulting in a patchy occurrence. *I. glandulifera* did not have any impact on plant alpha-diversity but reduced the cover of the native vegetation, especially of the dominant species. This effect depended on micro-habitat and season. The native vegetation was most affected in bright micro-habitats, especially those with a high soil moisture. Not distinguishing between micro-habitats, plant species composition was not affected in summer but in spring. However, environmental conditions had a higher impact on the native vegetation than *I. glandulifera*. We conclude that within riparian habitats the threat of *I. glandulifera* to the native vegetation can be rated low since native species were reduced in cover but not excluded from the communities. This might be due to patchy occurrence and year-to-year changes in cover of *I. glandulifera*. The context-dependency in terms of micro-habitat and season requires specific risk assessments which is also an opportunity for nature conservation to develop management plans specific to the different habitats. Particular attention should be given to habitats that are bright and very wet since the effect of *I. glandulifera* was strongest in these habitats.

Keywords

context-dependency, early-flowering spring vegetation, environment, plant community, plant invasion, riverside vegetation

Introduction

Biological invasions are one aspect of anthropogenic global change. Invasive species can alter ecosystems processes, change native community structure and reduce diversity (Ehrenfeld 2010, Vilà et al. 2011). The success of an invader depends, among other things, on its ability to occupy various habitats. A broad tolerance to abiotic site factors can thus facilitate the establishment in different communities. Alternatively, superior fitness within a particular niche can lead to success in particular communities (MacDougall et al. 2009). Ecosystems in turn affect invasion processes (Kueffer et al. 2013) as site specific conditions can modify the performance of the invader and its interaction with other organisms. Since such species \times ecosystem interactions (Kueffer et al. 2013) make it difficult to generalize the impact of an invasive species on native ecosystems it is important to understand such context-dependencies. Knowledge of species \times ecosystem interactions helps to understand species invasions and allows nature conservation authorities to develop more targeted management plans, prioritizing those habitats where an invasive species should have highest impact.

A good model system to study plant species \times ecosystem interactions is *Impatiens glandulifera*. Originating from the Himalayan Mountain ranges, it now occurs all over Europe over a broad range of elevation, geographical latitude, and ecosystem types (Pyšek and Prach 1995, Larsson and Martinsson 1998, Kollmann and Bañuelos 2004, Pacanoski and Saliji 2014, Laube et al. 2015). After introduction to Europe in the 19th century it spread mainly along riverbanks and into wet habitats such as fens, mesotrophic grasslands, and woodland, but also forests out of the riparian zone, and into ruderal vegetation (Beerling and Perrins 1993, Pyšek and Prach 1993, 1995, Čuda et al. 2017). The invasion success of *I. glandulifera* is, among other factors, favored by a strong competitive and allelopathic effect, reducing the growth of native plants as seen in experimental studies (Vrchotová et al. 2011, Gruntman et al. 2014, Ruckli et al. 2014a, Loydi et al. 2015, Bieberich et al. 2018). However, field studies showed ambiguous results. In riparian habitats Cockel et al. (2014) and Hulme and Bremner (2006) found a strong negative impact of *I. glandulifera* on the native vegetation, while others found a weak impact in riparian habitats (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016) and in forests (Čuda et al. 2017). Sometimes the weak effect of *I. glandulifera* is thought to be due to high fluctuations in its population size (Kasperek 2004, Diekmann et al. 2016).

The impact of an invasive species can also depend on environmental conditions because its competitive ability depends on environmental conditions (Amarasekare 2003). Previous studies indicate that high soil nutrient availability and medium light is

beneficial for *I. glandulifera* growth (Andrews et al. 2005, Čuda et al. 2014). In a heterogeneous habitat the competitive environment for *I. glandulifera* and the residents can change from patch to patch determining which of the species becomes dominant and leading to a mosaic of the different species (Amarasekare 2003). Such a patchy occurrence of invasive and native species could facilitate spatial co-existence (Amarasekare 2003) and could be a reason for the overall low impact of the invader as found in some studies (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016, Čuda et al. 2017). Another possibility for species co-existence is temporal niche partitioning. In riparian habitats, especially forests, in the temperate region the plant community in spring often differs compared to summer due to seasonal species turnover with spring communities often being characterized by early flowering geophytes (Ellenberg and Leuschner 2010, Czapiewska et al. 2019).

We hypothesize that within heterogeneous riparian habitats, the impact of *I. glandulifera* on the resident vegetation depends on the environmental conditions at a particular patch (subsequently named micro-habitat) because the growth of *I. glandulifera* also depends on this. Regarding seasonal effects we hypothesize a lower impact of *I. glandulifera* in spring compared to summer because of species turnover, and in particular differences in *I. glandulifera* plant size and cover, thus competition for resources (Grime 1977, Goldberg 1990). In order to test our hypotheses we conducted a field study in Germany within riparian habitats in spring and summer. This is the first study on the impact on spring vegetation and on seasonal differences in the impact of *I. glandulifera* on native vegetation. Here we especially directly link the impact of *I. glandulifera* with environmental conditions.

Materials and methods

Study sites and plot design

Within five riparian field sites ranging from alder woods to abandoned meadows we systematically sampled (Table 1, Fig. 1) the environmental conditions and the vegetation. Each site comprises patches of *Impatiens glandulifera* and heterogeneous micro-habitats regarding tree cover and soil moisture. All sites are located in the region around Bayreuth, Germany at an elevation between 345 m a.s.l. and 426 m a.s.l.. Within each site, plots were arranged on a grid of 20 m × 20 m. Every grid intersection point was used as position for a plot of 2 m × 2 m, independently of environmental condition, *I. glandulifera* or native vegetation cover (Fig. 1). This systematic design allowed us a representative sampling over the whole gradient of environmental conditions and *I. glandulifera* cover and regression analysis instead of comparison between invaded and uninvaded plots only. Across the five sites 114 plots of 2 m × 2 m were established in total (Table 1). In spring two plots were not accessible because of a very high soil water content and one plot was hit by a fallen tree, decreasing the number of replicates to 111 in spring.

Table 1. Field sites used for this study. For each site the main habitat type, the name of the next locality and the adjacent river is given as well as the GPS-location, approximate area and number of established plots.

Main habitat	alder forest	alder swamp forest	abandoned meadow	abandoned meadow	abandoned meadow
Next town	Ludwigschorgast	Neunkirchen	Weidenberg	Pegnitz	Waischenfeld
GPS-location	50°6.66'N	49°55.20'N	49°56.95'N	49°46.84'N	49°49.98'N
	11°35.20'E	11°38.05'E	11°42.15'E	11°32.80'E	11°20.17'E
Area	20000 m ²	7000 m ²	16000 m ²	4000 m ²	9000 m ²
n plots summer	44	17	27	11	15
n plots spring	44	15	27	11	14

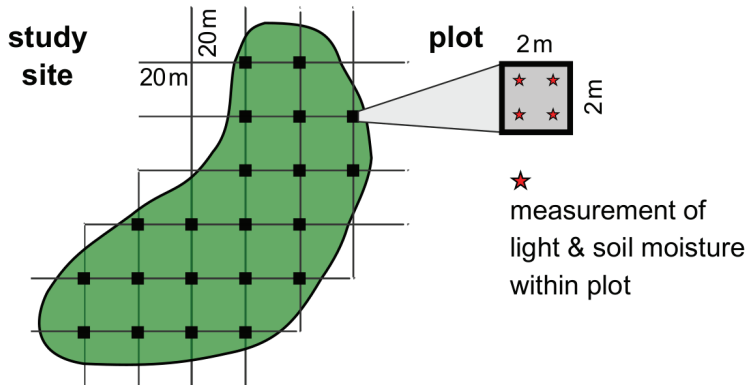


Figure 1. Plot design used for this study. Plots were arranged on a grid laid over the study site. Positions for light and soil moisture measurements within each plot are marked.

Data collection

The herb layer vegetation was surveyed in summer while *I. glandulifera* was flowering (2016-07-12/08-17), and in spring while the spring geophytes were flowering (2017-04-20/05-04). All vascular plant species were determined using standard literature (Schmeil et al. 2011, Eggenberg and Möhl 2013, Jäger et al. 2013, Aas 2017, Jäger 2017), and their cover was estimated according to extended Braun-Blanquet scale (Braun-Blanquet 1964, Reichelt and Wilmanns 1973). Additionally the maximum height of the vegetation, and in summer 2017 the cover of *I. glandulifera* was measured as described in Suppl. materials 1, 2. The environmental variables volumetric soil water content, light (relative photosynthetically active radiation), tree layer species composition and cover, and Ellenberg indicator values were gathered once in each plot in summer. The volumetric soil water content (named soil water content hereafter) was measured on 2017-05-23/05-28 in the uppermost soil layer with a SM-150 sensor (Delta-T Devices). Recordings were taken at four positions per plot and their median was calculated (Fig. 1). Relative photosynthetically active radiation (PAR, Parent and Messier 1996, Gendron et al. 1998) was measured with Quantum sensors (LICOR) when trees were fully foliate (2016-08-03/10-03). In the plot four single point records were taken just above the herb layer (Fig. 1). Simultaneously a reference value was taken at a totally unshaded site nearby

using a second Quantum sensor. This sensor was connected to a BayEOS logger (Bay-CEER, University of Bayreuth) taking records every 30 s and saving them as means over 5 minutes. Relative PAR was calculated with the median of the point records within the plots divided by the particular logged reference matching in time. All light measurements were taken under a homogeneous overcast sky with the sun invisible and no rain, and always between 11:00 and 17:00. The tree layer was characterized estimating the cover of each tree species separately (2017-08-17/09-07) according to extended Braun-Blanquet scale (Braun-Blanquet 1964, Reichelt and Wilmanns 1973). Mean Ellenberg indicator values for light L, soil moisture F, soil nutrients N, and soil reaction R were calculated per plot based on the summer vegetation. Based on additional information included in the F-value, the percentage of plants preferring either periodically wet soils or constantly wet soils was calculated. Hereafter, these parameters are named index of periodically wet soil and index of constantly wet soil.

Statistical analysis

All statistical analyses were done with the software package R 3.5.2 (R Core Team 2018). To find the polynomial model best describing the dependence of cover of *I. glandulifera* on light and soil water content a multiple regression analysis was performed. To identify environmental variables affecting the cover of *I. glandulifera*, we performed an automated model selection (Bartoń 2018) separately for summer and spring vegetation. First of all a global model was built with the cover of *I. glandulifera* as response variable and 13 predictor variables that were expected to affect the cover of *I. glandulifera*: relative PAR (squared because of hump-shaped relationship), soil water content (squared), number of tree species, cover of these tree species occurring at least in 20 plots (*Alnus glutinosa*, *Salix fragilis*, *Acer pseudoplatanus*, *Fraxinus excelsior*, *Betula pendula*), Ellenberg values N, R, and indices for periodically or constantly wet soils. Ellenberg values L, and F were excluded because they correlated with relative PAR and soil water content, (Pearson correlation coefficient 0.549 and 0.544 respectively). All variables were standardized to zero mean and unit variance (VEGAN, (Oksanen et al. 2018)). For analysis of spring vegetation, the cover of *I. glandulifera* was log-transformed to counter heteroscedasticity of the model. The study site was considered as a random factor (NLME, (Pinheiro et al. 2018)). Next a set of models with combinations of all parameters was generated from the global model and the models were weighted by their AICc (MuMIn, (Bartoń 2018)). Models with $\Delta AICc > 2$ were used to calculate the relative importance of each variable as the sum of AICc weights of all models including the variable.

Using the variables resulting from the model selection, we performed a piecewise structural equation model (piecewiseSEM, (Lefcheck 2016)) to test the effects of the environmental variables on *I. glandulifera*, and how in turn *I. glandulifera* affects the resident vegetation (all species except *I. glandulifera*). This also allowed us to infer whether the resident vegetation is more affected by *I. glandulifera* or by the environment based on the regression coefficients of the SEM. The resident vegetation was represented by species number, total

cover (sum of the cover of all resident species in a plot) and the cover of those herbaceous species occurring in more than 20 plots. The construction of the initial models is visualized in Suppl. material 3, Fig. 1. The SEMs were fitted separately for summer and spring vegetation, and within the models the study site was considered as a random factor. For each path in the piecewise structural equation model, a standardized regression coefficient (β) and its significance were calculated as well as conditional R^2 -values for all response variables.

To analyze plant community composition in summer, or respectively spring, we performed a Detrended Correspondence Analysis of the cover of the resident plant species with downweighting of rare species (DCA, package VEGAN (Oksanen et al. 2018)). DCA was confirmed to be appropriate because the DCA-axis gradient length was more than four times the standard deviation. Cover of *I. glandulifera*, as well as environmental parameters, were post-hoc fitted into the DCA result. Additionally, a Constrained Correspondence Analysis (CCA, VEGAN) was performed with the same data constraining the resident community with *I. glandulifera* cover. With an ANOVA-like permutation test (VEGAN) significance of the constraints was tested.

With the summer dataset of the year 2016, we analyzed whether the impact of *I. glandulifera* on the resident vegetation differed between micro-habitat groups. The groups were created by dividing the dataset according to the median of light (23.9 % PAR) and soil water content (51.5 %). Subsequently, they are named moist–bright ($n = 30$), wet–bright ($n = 28$), moist–dark ($n = 27$) and wet–dark ($n = 29$). For each of this groups separately and for the complete dataset impact of *I. glandulifera* on various variables representing the resident vegetation was analyzed: Impact on species number, Shannon-index and total plant cover was tested with linear models. Some parameters in the wet–dark group were log-transformed to counter heteroscedasticity of the models. Impact on cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica* was tested with a quantile regression (R package QUANTREG (Koenker 2018)) because data were not homogenous in variance hence linear regression was not the appropriate test (Cade and Noon 2003). We took the 0.50, 0.75, 0.85 and 0.95 quantiles emphasizing the upper quantiles because after visual inspection of the data we expected *I. glandulifera* to especially restrict maximum cover of other plants. For each quantile regression, standard errors and p -values were calculated by bootstrap analysis. Impact of *I. glandulifera* on community composition was tested with a DCA (with downweighting of rare species) and with CCA (VEGAN).

Results

Vegetation characteristics

I. glandulifera occurred in about 80 % of all plots in summer (87 of 114) and in spring (91 of 111, Fig. 2). Especially in spring the cover of *I. glandulifera* was often very low and rarely above 25 %. In summer *I. glandulifera* reached more than 50 % cover in 28 plots. By summer 2017 the cover of *I. glandulifera* changed largely in few plots (Suppl.

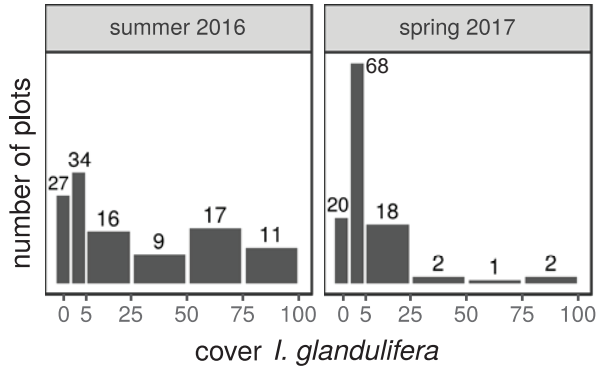


Figure 2. Distribution of cover of *Impatiens glandulifera* in summer 2016 and spring 2017. Shown categories correspond to the Braun-Blanquet scale.

material 1). In summer, *I. glandulifera* plants were higher than the resident vegetation if they reached more than 20 % cover, while in spring *I. glandulifera* was always lower than the resident vegetation (Suppl. material 2). The resident vegetation consisted of in total 128 plant species in summer 2016 and 109 in spring 2017 ranging from 2 to 20 species per plot. None of these plant species was an endangered one. Besides *I. glandulifera* further alien species were recorded: *Lamium argentatum* occurred in 14 plots, sometimes reaching more than 75 % cover. *Fallopia japonica*, *Lysimachia punctata*, *Bidens frondosa* and *Epilobium ciliatum* each occurred in only one plot with always less than 5 % cover. Most frequent native species were typical ones of tall herbaceous vegetation at riparian sites (Fig. 4A, B). Especially *Urtica dioica*, *Filipendula ulmaria*, and *Phalaris arundinacea* in summer, and additionally the geophytes *Ranunculus ficaria* and *Anemone nemorosa* in spring could reach cover of more than 50 %. In spring further early flowering species such as *Corydalis cava*, *Caltha palustris*, *Polygonum bistorta*, *Cardamine amara* and *Alliaria petiolata* occurred.

Relationship between environmental variables, cover of *Impatiens glandulifera* and the resident vegetation

Light (relative PAR) and soil water content spanned nearly the whole gradient from 0–100 %. However, Ellenberg values that correlated with light and soil moisture showed rather smaller gradients (L-value for light 4–7.5, F-value for soil moisture 5.5–9.3) indicating that there were medium light conditions and no sites with dry soils. *I. glandulifera* occurred over the whole range of light and soil water content measured in this study, but in summer it reached high cover mainly at 50–70 % light and 30–40 % soil water content (Fig. 3). The relationship between *I. glandulifera* and light and soil water content was hump-shaped being a typical species reaction on a long environmental gradient (light: linear model: $f(x) = x + x^2 + x^3$, $F_{(3,110)} = 7.221$, $R^2 = 0.142$, $p < 0.001$).

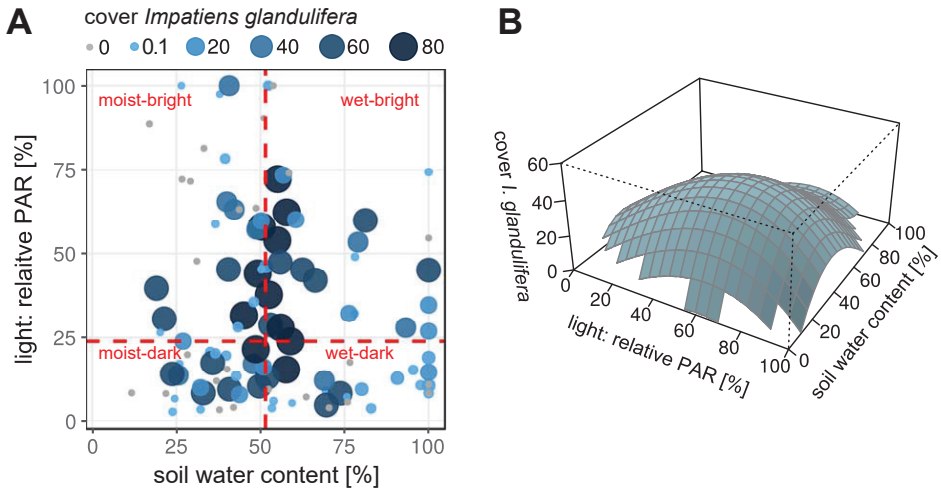


Figure 3. Cover of *Impatiens glandulifera* in summer 2016 in dependence of light and volumetric soil water content. **A** Cover of *I. glandulifera* is represented by point size and color as given in the legend. Grouping the plots into the micro-habitats moist–bright, wet–bright, moist–dark and wet–dark is based on the medians of light and soil water content. **B** Fitted function of the same data shown in 3d-space. $f(\text{cover}) = \text{light} + \text{light}^2 + \text{light}^3 + \text{water content} + \text{water content}^3$. Linear model, $R^2 = 0.208$, $F_{(5,108)} = 6.928$, $p < 0.001$, $n = 114$.

Notably soil water content on its own had only low explanatory power (linear model, $f(x) = x + x^3$, $F_{(2,111)} = 4.88$, $R^2 = 0.064$, $p = 0.009$) but in combination with light the R^2 increased to 0.208 (Fig. 3A, B).

The piecewise SEM revealed that in summer 39 % of the variation in the cover of *I. glandulifera* was explained by the environmental variables identified as important by the model selection ($R^2 = 0.39$, Fig. 4A, Suppl. material 4: Table S1). The reaction of *I. glandulifera* to light was unimodal hence the cover was highest at moderate light ($\beta = -0.294$). The cover of *I. glandulifera* was enhanced by a high Ellenberg value N for nutrients and by periodically wet soils (Fig. 4A). In contrast it was reduced by constantly wet soil and cover of the specific tree species *Acer pseudoplatanus*, *Fraxinus excelsior*, and *Alnus glutinosa*. In turn, *I. glandulifera* had no impact on the number of plant species but on plant cover. It strongly reduced the cover of *U. dioica* ($\beta = -0.387$), slightly that of *F. ulmaria* (not significant, $p = 0.073$) and the total cover of the resident vegetation. Besides the effect of *I. glandulifera* the parameters representing the resident vegetation were mainly directly affected by the environmental variables. For example, the number of plant species increased with the number of tree species and strongly decreased with increasing Ellenberg value N. Cover of *U. dioica* was determined by Ellenberg value N, index of constant wet soil and by cover of *A. glutinosa* similarly to *I. glandulifera*.

The piecewise SEM on spring vegetation showed that 30 % of the variation of the *I. glandulifera* cover was explained by the environmental variables identified as important by the model selection (Fig. 4B, Suppl. material 4: Table S1). As in sum-

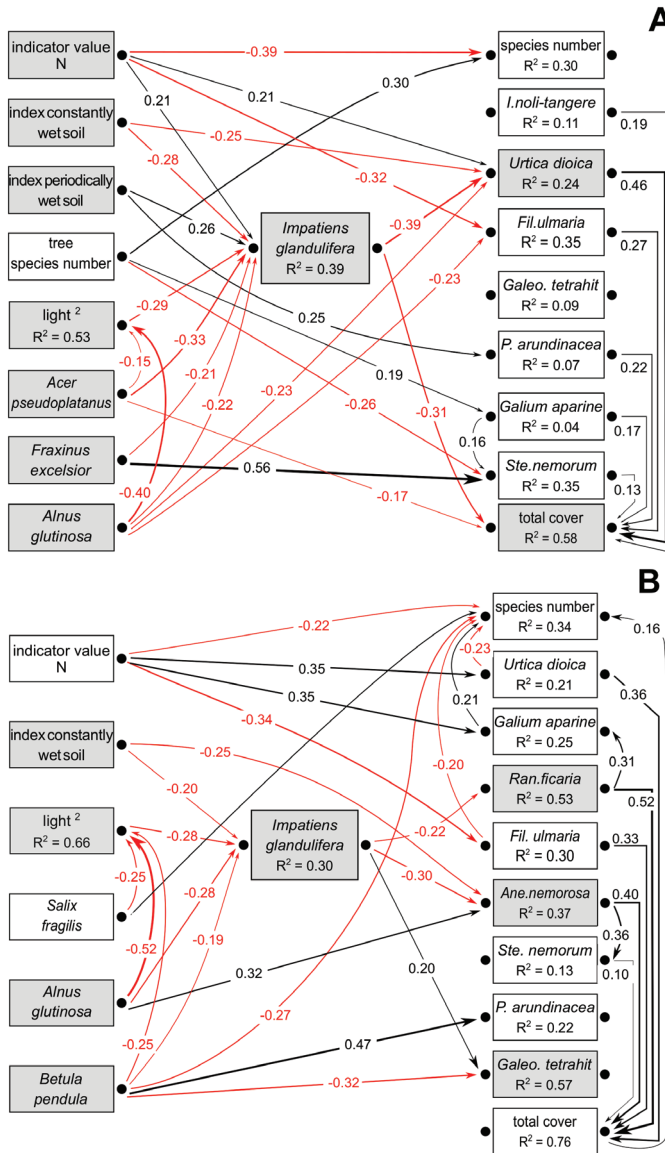


Figure 4. Results of the piecewise structural equation modeling for summer (A) and spring (B). Arrows show significant correlations between the environmental variables shown to be important by the model selection (Suppl. material 4, Table 1), cover of *Impatiens glandulifera* and resident vegetation parameters. Included resident species are the most frequent ones: *Ranunculus ficaria* (*Ran.ficaria*), *Urtica dioica*, *Filipendula ulmaria* (*Fil.ulmaria*), *Galium aparine*, *Anemone nemorosa* (*Ane.nemorosa*), *Phalaris arundinacea* (*Parundinacea*), *Galeopsis tetrahit* (*Galeo.tetrahit*), *Stellaria nemorum* (*Ste.nemorum*) and *Impatiens noli-tangere* (*I.noli-tangere*). Arrows show significant correlations, red arrows negative ones, black arrows positive ones. The thicker the arrows, the higher are the standardized regression coefficients (β), which are stated next to the arrows. R^2 values for the component models are given within the boxes of all response variables. Variables that are directly connected to *I. glandulifera* are highlighted by gray colored boxes. For the spring model cover of *I. glandulifera* was log-transformed. n = 114 plots for summer, n = 111 for spring.

mer, constantly wet soils and cover of the tree species *A. glutinosa* and *Betula pendula* reduced the cover of *I. glandulifera*, and reaction to light was unimodal (Fig. 4B). In contrast to summer, periodically wet soils were not found to be important (model selection, Suppl. material 4: Table S1), and the increase of *I. glandulifera* cover with increasing Ellenberg value N was not significant (SEM, Fig. 4B). Also *I. glandulifera* did not affect *U. dioica* and total plant cover, and the cover of *Galeopsis tetrahit* was even slightly increased. However, the cover of *R. ficaria* and *A. nemorosa* were reduced by *I. glandulifera*. The resident vegetation was mainly directly affected by the environmental variables and by interactions between the resident species. For example, the cover of *R. ficaria* and *G. aparine* were positively correlated and the cover of *U. dioica* and *R. ficaria* reduced the species number.

In summer *I. glandulifera* had no impact on plant community composition: The cover of *I. glandulifera* did not correlate with the axes of a DCA of the resident community ($p = 0.222$, Fig. 5) and was not able to constrain resident community in a CCA ($p = 0.116$, without figure). In contrast the resident plant community in spring was strongly affected by the cover of *I. glandulifera* of the previous summer 2016 ($p < 0.001$, DCA; $p = 0.052$, CCA; Fig. 5), and slightly by current cover in spring 2017 ($p = 0.048$, DCA; $p = 0.551$, CCA). In summer and in spring the resident plant community was also shaped by most of those environmental variables important for the cover of *I. glandulifera* (Fig. 5).

Micro-habitat specific impact of *Impatiens glandulifera* on the resident vegetation in summer

With the summer dataset four micro-habitat groups were created reflecting different conditions of light and soil water content (Fig. 3). These groups differed in their plant community composition (DCA $p = 0.008$, CCA $p = 0.001$). In each group the cover of *I. glandulifera* ranged from 0 to at least 80 % but its mean differed between groups, being highest in the wet–bright group (Table 2). The impact of *I. glandulifera* on plant cover was different between micro-habitat groups (Table 2, Suppl. material 6: Fig. S2). The cover of *I. glandulifera* reduced the total plant cover in all micro-habitat except for the wet–dark group. The cover of *U. dioica* was reduced in the moist–bright and wet–dark groups, as well as the cover of *F. ulmaria* in the two bright micro-habitats. These were exactly those micro-habitats where the highest average cover of these species was observed (Table 2, Suppl. material 6: Fig. S2). In contrast, the cover of *Phalaris arundinacea* was not negatively affected at all, but its cover slightly increased with the cover of *I. glandulifera* under low light conditions. *I. glandulifera* had no impact on plant species number and Shannon-index in any micro-habitat group. In contrast plant species composition was changed under bright conditions especially with high soil water content. Within the wet–bright micro-habitat for example *Calystegia*

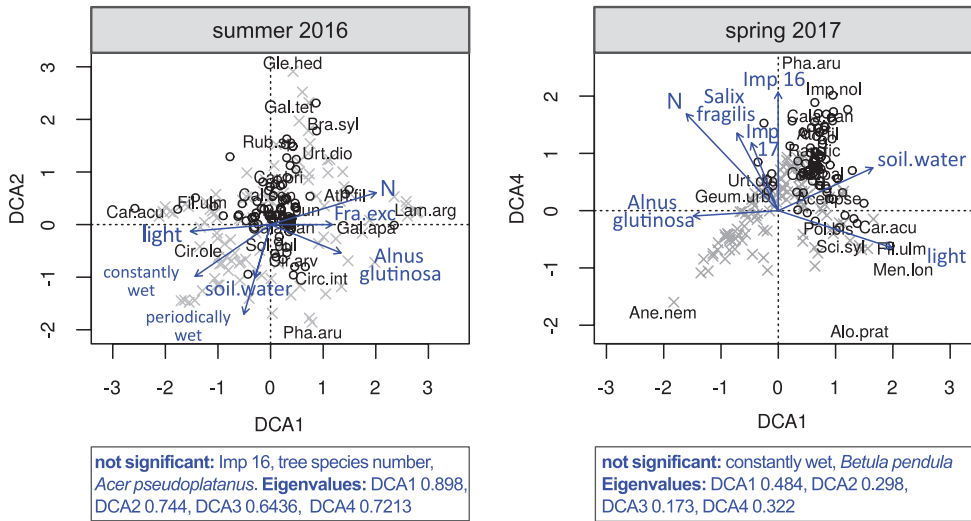


Figure 5. Ordination (DCA) of the resident plant community in summer 2016 and spring 2017. Cover of *I. glandulifera* in summer 2016 (Imp 16) and in spring 2017 (Imp 17) and important environmental variables (Suppl. material 4, Table 1) as well as volumetric soil water content (soil.water) were post-hoc fitted onto the DCA. Significant variables are shown as arrows. Plots are indicated as crosses, species as open circles. Most abundant species are labeled. Not significant environmental variables and Eigenvalues of DCA axes are given in boxes below the plots. $n = 114$ plots for summer, $n = 111$ for spring. For abbreviations of the species names see Suppl. material 5: Table S2.

sepium, *Glechoma hederacea*, and *Polygonum bistorta* tended to occur at high cover of *I. glandulifera* (CCA). In contrast *Carex acutiformis*, *Geranium palustre* and also some species of very wet plots as *Galium elongatum* and *Equisetum fluviatile* occurred at low cover of *I. glandulifera* (Suppl. material 7: Fig. S3). Considering all parameters representing the native vegetation *I. glandulifera* had the lowest impact in the wet–dark micro-habitat where also the cover of *I. glandulifera* was lowest.

Discussion

In this field study, we examined the impact of *Impatiens glandulifera* on native vegetation in riparian habitats depending on micro-site conditions and season. We found that the cover of *I. glandulifera* depended on environmental conditions. *I. glandulifera* did not affect resident plant species alpha-diversity at all. Plant cover in contrast was reduced and species composition changed depending on micro-habitat and season. However, the resident vegetation was more strongly shaped by environmental conditions than by the cover of *I. glandulifera*.

Table 2. Micro-habitat specific impact of *I. glandulifera* on the resident vegetation. With the complete dataset and four subsets representing different micro-habitats regarding light (relative PAR) and soil water content (see also Fig. 3) it was tested whether vegetation parameters depend on cover of *I. glandulifera*. Resulting *p*-values from linear models (total cover, species number, Shannon index), DCA and CCA (species composition) are given. Log-transformations of data are indicated: (log-log) means predictor and response variable transformed, (log) means response variable transformed. For quantile regression (cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica*) 0.50, 0.75, 0.85 and 0.95 quantiles were used (τ). Quantile regressions with ($p < 0.1$) are reported including their regression equation. Bold letters indicate $R^2 > 0.1$ and $p < 0.001$. Number of plots and mean cover of *I. glandulifera* (\bar{x}_{imp}) are given per group. Different letters indicate whether there are differences in the \bar{x}_{imp} between groups (Kruskal-Wallis Anova, $\chi^2 = 10.6$, $df = 3$, $p = 0.014$). See Suppl. material 6, 7: Fig. S2 and S3 for plots of the raw data.

parameter	quantile	complete dataset n = 114 $\bar{x}_{imp} = 23\%$	moist-bright n = 30 $\bar{x}_{imp} = 22\%$ (ab)	wet-bright n = 28 $\bar{x}_{imp} = 39\%$ (a)	moist-dark n = 27 $\bar{x}_{imp} = 20\%$ (ab)	wet-dark n = 29 $\bar{x}_{imp} = 13\%$ (b)
total cover		$F_{(1,112)} = 27.3$, $p < \mathbf{0.001}$, $R^2 = \mathbf{0.189}$	$F_{(1,28)} = 28.44$, $p < \mathbf{0.001}$, $R^2 = \mathbf{0.486}$	$F_{(1,26)} = 9.59$, $p = \mathbf{0.005}$, $R^2 = \mathbf{0.241}$	$F_{(1,25)} = 8.12$, $p = \mathbf{0.009}$, $R^2 = \mathbf{0.215}$ (log)	$F_{(1,27)} = 3.62$, $p = 0.068$, $R^2 = 0.086$ (log)
cover <i>Urtica dioica</i>	τ 0.50					
	τ 0.75		$p = \mathbf{0.023}$, $f(x) = 63 - 0.67x$			
	τ 0.85	$p = \mathbf{0.003}$, $f(x) = 63 - 0.61x$	$p < \mathbf{0.001}$, $f(x) = 87.5 - 0.90x$			
	τ 0.95	$p = 0.052$, $f(x) = 87.5 - 0.67x$	$p < \mathbf{0.001}$, $f(x) = 87.8 - 0.68x$			$p = \mathbf{0.022}$, $f(x) = 63 - 0.69x$
cover <i>Filipendula ulmaria</i>	τ 0.50			$p = 0.056$, $f(x) = 21 - 0.21x$		
	τ 0.75	$p = 0.057$, $f(x) = 21 - 0.14x$	$p = 0.094$, $f(x) = 36 - 0.41x$			
	τ 0.85		$p = \mathbf{0.046}$, $f(x) = 49 - 0.56x$	$p = \mathbf{0.050}$, $f(x) = 63 - 0.62x$		
	τ 0.95	$p = \mathbf{0.030}$, $f(x) = 63 - 0.6x$	$p < \mathbf{0.001}$, $f(x) = 88 - 1.0x$	$p = \mathbf{0.032}$, $f(x) = 88 - 0.81x$		
cover <i>Phalaris arundinacea</i>	τ 0.50	$p = \mathbf{0.039}$, $f(x) = 0 + 0.03x$			$p = 0.053$, $f(x) = 0 + 0.03x$	
	τ 0.75					$p = \mathbf{0.013}$, $f(x) = 2 + 0.57x$
	τ 0.85					$p = 0.052$, $f(x) = 3 + 0.56x$
	τ 0.95	$p = 0.093$, $f(x) = 37.5 + 0.8x$				
species number		$F_{(1,112)} = 2.16$, $p = 0.145$, $R^2 = 0.010$	$F_{(1,28)} = 2.54$, $p = 0.122$, $R^2 = 0.051$	$F_{(1,26)} = 2.76$, $p = 0.109$, $R^2 = 0.061$	$F_{(1,25)} = 1.80$, $p = 0.191$, $R^2 = 0.030$	$F_{(1,27)} = 0.04$, $p = 0.846$, $R^2 = -0.036$ (log-log)
Shannon index		$F_{(1,112)} = 0.52$, $p = 0.472$, $R^2 = -0.004$	$F_{(1,28)} = 0.12$, $p = 0.728$, $R^2 = -0.031$	$F_{(1,26)} = 0.05$, $p = 0.833$, $R^2 = -0.037$	$F_{(1,25)} = 2.86$, $p = 0.103$, $R^2 = 0.067$	$F_{(1,27)} = 0.37$, $p = 0.547$, $R^2 = 0.023$ (log-log)
species composition: DCA		$p = 0.222$	$p = 0.099$	$p = \mathbf{0.032}$	$p = 0.715$	$p = 0.401$
CCA		$p = 0.116$	$p = \mathbf{0.016}$	$p = \mathbf{0.001}$	$p = 0.891$	$p = 0.823$

Patchiness of *Impatiens glandulifera* is associated with environmental conditions

Within our study sites, *I. glandulifera* occurred over a broad range of environmental conditions but it was unevenly distributed within the sites forming invaded and uninvaded patches. Its cover correlated with environmental variables. A positive effect of nutrients and moderate light as well as low importance of soil water content (measured at one point in time), is consistent with literature (Andrews et al. 2005, Čuda et al. 2014). However, we showed that soil water content in combination with light was a good predictor for the cover of *I. glandulifera*, with the cover being highest at moderate light and moderate soil water content. Ellenberg values indicated moreover that constantly high soil moisture had a negative effect on the cover but in summer periodically wet soils were favorable. A high N-supply is also more important in summer than for early establishment in spring. Considering a larger spatial scale, such a patchy occurrence can enable the co-existence of species that would outcompete each other within one patch (Amarasekare 2003). For example, in our study *I. glandulifera* and *U. dioica* coexisted within one study site forming a patchy mosaic.

***Impatiens glandulifera* had no impact on plant diversity but on plant cover**

We found that *I. glandulifera* reduced the cover of the resident vegetation but it had no impact on species composition in summer or on plant species alpha-diversity at all. Thus the resident plant species seem to be able to coexist within *I. glandulifera* stands, albeit reaching only lower cover. Changes in *I. glandulifera* cover from year-to-year as they are reported in literature (Kasperek 2004) and which were also observed in our study, should then enable the resident plants to recover when *I. glandulifera* declines leading to co-existence at a larger time-scale (Stouffer et al. 2018).

I. glandulifera especially reduced the cover of the most dominant native species. Species were most affected in those micro-habitats where their average cover was highest and in each season those species with the highest cover were the most affected ones. These were *Urtica dioica* and *Filipendula ulmaria* in summer, and *Ranunculus ficaria* and *Anemone nemorosa* in spring. We suggest that this is due to competition for space and resources strengthening at high cover. Still, it cannot be ruled out that also less frequent species with lower cover are affected by *I. glandulifera*. Rare occurrence and thus small sample size of a species as well as huge variability result in low statistical power and may lead to an underestimation of the effect of the invader (Davidson and Hewitt 2014).

Similar to other studies comparing plots with and plots without *I. glandulifera*, we are not able to show a causal impact of *I. glandulifera* on native vegetation but only correlations (Hejda and Pyšek 2006). However, in our study the link to environmental conditions can help to disentangle negative correlation because of different spatial niches from negative correlation because of suppression within one spatial niche.

A. nemorosa and *I. glandulifera* could be an example for different spatial niches, because *A. nemorosa* was enhanced by a high cover of *Alnus glutinosa* which in contrast reduced the cover of *I. glandulifera*. *U. dioica* however, seems causally suppressed by *I. glandulifera*. The cover of both species correlated negatively, and according to the SEM they were favored by the same environmental conditions. Experimental studies confirm that *U. dioica* is negatively affected by *I. glandulifera* and that this effect is larger than vice versa (Tickner et al. 2001, Gruntman et al. 2014, Bieberich et al. 2018).

The impact of *Impatiens glandulifera* depended on the micro-habitat

The habitat depending impact of *I. glandulifera* indicates that the impact gets stronger with increasing cover of *I. glandulifera*. This is also indicated by Cockel et al. (2014). In our study the wet–dark micro-habitat with the lowest cover of *I. glandulifera*, was the least affected. The plant species composition was most affected in the wet–bright micro-habitat which had also a strong gradient and highest average cover of *I. glandulifera*. Species that tended to occur only in plots without *I. glandulifera* generally occurred less frequently (for example *Equisetum fluviatile*) while those that tended to occur at high cover of *I. glandulifera* (for example *Glechoma hederacea*) were very common ones.

Micro-habitat specific interactions between native species and an invader can also be due to micro-habitat specific performance of the plant species. If two C-strategists compete for resources, which should be the case with our dominant species, the magnitude of competition is highest under most favorable as well as under most unfavorable environmental conditions (stress-gradient hypothesis, Maestre et al. 2009). In the strongly competitive situation inferiority of the natives in fitness leads to suppression by the invader (MacDougall et al. 2009). We suggest that this can explain the micro-habitat depending impact of *I. glandulifera* on *U. dioica* and *F. ulmaria*. Both natives were most reduced by *I. glandulifera* when they grew under environmental conditions that were, according to the SEM, most favorable for them (*U. dioica* in the moist–bright group and *F. ulmaria* in bright micro-habitats). *U. dioica* was additionally negatively affected by *I. glandulifera* in the wet–dark micro-habitat which was shown by the SEM to be unfavorable for *U. dioica*.

Plant communities in summer and spring were affected differently

Plant species composition in summer was not affected by *I. glandulifera* but in spring it was, despite the fact that *I. glandulifera* plants were smaller than the resident vegetation in spring. The reason could be a seasonally varying allelopathic effect of *I. glandulifera* because it is known, that in spring *I. glandulifera* has a higher content of the allelopathic compound 2-MNQ compared to summer (Ruckli et al. 2014a). In a previous experimental study we showed that *I. glandulifera* has a species-specific allelopathic and competitive impact on native plants especially in the seedlings- and juvenile-stage (Bieberich et al. 2018). Furthermore, cover of *I. glandulifera* from the previous sum-

mer 2016 affected species composition in spring while it did not affect the resident community in summer 2016 itself. Allelopathic legacy effects (Grove et al. 2012) may explain this: 2-MNQ could persist in the soil (Ruckli et al. 2014b) and affect early growing plants even before *I. glandulifera* germinates.

Assessment of the invasiveness of *Impatiens glandulifera*

Negative impact on biodiversity and ecosystem functions, processes and services are the criteria to grade an alien species as invasive (Ehrenfeld 2010, Hulme et al. 2013, Barney et al. 2013). German and European Union nature conservation authorities emphasize the impact on diversity and threat to other species (European Union 2014, Nehring et al. 2015). Taking this study and all available ones into account, the impact of *I. glandulifera* on plant species diversity can be rated to be relatively low (Hejda and Pyšek 2006, Hejda et al. 2009, Diekmann et al. 2016, Čuda et al. 2017) even if some studies showed stronger effects (Hulme and Bremner 2006, Cockel et al. 2014, Kiełtyk and Delimat 2019). Indeed, we found a negative impact on the dominant natives, *U. dioica* and *F. ulmaria*, but they are in general very common and widespread in Central Europe and thus not expected to be threatened (Schreiber 1958, Weber 1995). However, suppression of abundant dominant plant species could lead to changes in ecosystem processes as they account for functions such as primary production and nutrient cycles (Grime 1998).

The micro-habitat and season dependent impact of *I. glandulifera* requires that its invasion risk has to be assessed separately for different habitats. We found the lowest impact in the wet–dark micro-habitat which corresponds to alder swamp-forests. The impact was highest at bright conditions, as abandoned meadows, but especially under high soil moisture as found in marshes or open patches of swamp-forests. Special attention should be given to habitats with rare or specialized communities or with distinct spring communities. For nature conservation this is a great opportunity to develop more targeted management strategies of *I. glandulifera* and invasive species in general with vigorous efforts only in selected habitats.

Conclusion

I. glandulifera can reduce the cover of native plants and especially dominant species depending on micro-habitat and season. Against our expectations, we did not find that the vegetation in spring was less affected than in summer. A threat to the native vegetation is unlikely since the impact on plant alpha-diversity was low, which may be due to the patchy occurrence and year-to-year changes in the cover of *I. glandulifera*. However it has to be kept in mind that a reduction of dominant and frequent native plant species could change ecosystem processes. We suggest that the documented small-scale habitat-dependency is also relevant on larger spatial scales. Wet–dark habitats like swamp-forests should be generally least affected by *I. glandulifera* while wet–bright ones like marshes are most affected.

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Supplementary material 1

Year-to-year changes in cover of *Impatiens glandulifera*

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file describing additional data collection, analysis and results

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl1>

Supplementary material 2

Maximum vegetation height in summer and spring

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file describing additional data collection, analysis and results

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl2>

Supplementary material 3

Figure S1. Initial model of the piecewise structural equation modeling (SEM) for summer (A) and spring (B)

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: Arrows show the hypothesized connections between variables the SEM was started with. Within the SEM all additional significant correlations between variables were then identified and the significance of each path was calculated. The results are shown in Figure 4A, B.

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl3>

Supplementary material 4

Table S1. Result of the automated model selection approach identifying environmental variables that affected the cover of *Impatiens glandulifera* in summer 2016 and spring 2017

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file containing a table with results

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl4>

Supplementary material 5

Table S2. Abbreviations of species names as shown in Figure 5

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: xls-table

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl5>

Supplementary material 6

Figure S2. Micro-habitat specific impact of *I. glandulifera* on the resident vegetation

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: With the complete dataset and four subsets representing different micro-habitats regarding light (relative PAR) and soil water content (see also Fig. 3) it was tested whether vegetation parameters depend on cover of *I. glandulifera*. Results of all statistical tests are given in Table 2. For total cover, species number, and Shannon index linear models were used. Resulting regression lines are shown if $p < 0.001$. For cover of *Filipendula ulmaria*, *Phalaris arundinacea* and *Urtica dioica* quantile regressions were applied using the 0.50, 0.75, 0.85 and 0.95 quantiles. Quantile regression lines are shown in blue color when $R^2 > 0.1$ and $p < 0.001$ or in grey color when $R^2 < 0.1$ and $p > 0.001$.

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl6>

Supplementary material 7

Figure S3. Micro-habitat specific impact of *I. glandulifera* on the resident plant species composition

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: pdf-file

Explanation note: With four data subsets representing different micro-habitats regarding light (relative PAR) and volumetric soil water content (see also Fig. 3) it was tested with DCA and CCA analyses whether the resident species composition changed depending on cover of *I. glandulifera*. In the case of significance cover of *I. glandulifera* is shown as arrow. All statistical results are given in Table 2.

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl7>

Supplementary material 8

Additional information: information on the published datasets

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: table

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl8>

Supplementary material 9

Dataset plant cover

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: table

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Link: <https://doi.org/10.3897/neobiota.57.51331.suppl9>

Supplementary material 10

Dataset environment and vegetation characteristics

Authors: Judith Bieberich, Heike Feldhaar, Marianne Lauerer

Data type: table

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