

The spread of *Impatiens parviflora* DC. in Central European oak forests – another stage of invasion?

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Abstract

In this study, we examine the pattern of occurrence of *Impatiens parviflora* in Central European oak forests over time and its ecological requirements within these types of communities. Research was based on phytosociological data collected in 3776 relevés. A modified TWINSpan algorithm was used to distinguish the groups of oak forests. The ecological preferences of the *I. parviflora* and studied communities as well as differences between invaded and non-invaded vegetation plots were analyzed using mean weighted Ellenberg indicator values (EIVs). Finally, both the temporal pattern of *I. parviflora* participation and changes in its coverage in the studied communities were analyzed. Our study confirmed a high adaptability of this species with respect to temperature, moisture, soil reaction and nutrients and determined its broad ecological optimum in oak forests. However, it also revealed both a greater sensitivity of some communities within Central European oak forests to the invasion of *I. parviflora* and differences in habitat conditions between invaded and non-invaded vegetation plots. This suggests that the habitat niche of *I. parviflora* within oak forests is not accidental. The analysis of temporal changes in the frequency of *I. parviflora* confirmed a 20% increase in relevés over the last 50 years. However, we did not identify any statistically significant rise in the coverage of *I. parviflora* in oak forests specifically during the studied period.

Keywords: invasive plants; long-term changes; plant species composition; forest vegetation; ecological amplitude; small balsam

Introduction

Processes connected with the invasiveness of alien plant and animal species are currently one of the most important factors influencing biological diversity [1–4]. Their consequences on the functioning of the world's ecosystems are difficult to estimate and are still the subject of scientific debate [5–13]. In response to changes caused by geographically alien species, different preventive actions have been taken. However, they usually ignore species for which control would be inefficient or time-consuming due to the species' high seed production, persistence of their seed bank, ability to increase their range effectively or the lack of unequivocal evidence supporting an ecologically or economically negative impact. One of these types of species is *Impatiens parviflora* (small balsam) – the most commonly observed alien plant in Central European deciduous forests [14–16]. Nevertheless, it is considered to be an invasive species of lesser importance [17], probably owing to its inconspicuous

root system (typical of annual plants) and consequently to its weaker ability to compete with native species [8,18–21].

On account of its wide spread, *I. parviflora* has become the subject of many experimental and field studies. However, they very often result in contradictory findings and ambiguous conclusions. It seems that the main problem is the character of a significant amount of ecological research conducted under controlled conditions [22–29], whose outcomes are then extrapolated to the occurrence of the species in the natural environment. Similarly, ambiguous or even contradictory results can be derived from studies conducted on relatively small areas due to the high ecological plasticity of *I. parviflora*, which contributes to its reproductive success across ecosystems that differ in terms of soil reaction, fertility, moisture, and light availability.

Although the species has been present in Europe since 1830 [14], its dispersion seems to have accelerated during the last few decades [30–32] – in particular, the first decade of the 21st century [19,33,34]. This increasing frequency of *I. parviflora* refers particularly to both “saturation” of the area, where only scattered locations of the species were found previously, and penetration into new types of habitats,

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including even very unfavorable railway embankments [35], field crops [36], and rock outcrops [37].

In respect to the ecological diversity of occupied habitats, *I. parviflora* is probably one of the most flexible vascular plants. Within natural communities such as oak-hornbeam forests and riparian forests the species is of primary importance due to both its common occurrence in the herb layer and potential impact on other species [38,39]. Nevertheless, in recent years, its increasing participation in other types of forest communities (e.g., beech and oak forests) has been observed [19,34].

This led the authors to analyze the occurrence patterns of this species in oak forests in a broader Central European context. The choice of oak forests was not accidental. The communities which are included in the *Quercion petraeae* Issler 1931 and *Quercion roboris* Malcuit 1929 alliances are a distinctive syntaxonomic unit in Central Europe which feature an absolute domination of *Quercus petraea* or *Q. robur* with well-known floristic and ecological diversity [40–42]. For this reason, they are a model subject for a study on the variability of phytocoenoses. Most of the known communities of oak forests developed under ecological conditions which would seem to be unfavorable to the occurrence of *I. parviflora*, e.g., xeric or acid habitats. Therefore, we can formulate a hypothesis that *I. parviflora* will occur more frequently in mesophilous oak forests rather than those which are of thermo- or acidophilous character.

This study is an attempt to create a synthetic view of the ecological conditions of *I. parviflora* occurrence in the oak forests of Central Europe and to scrutinize the rate of its invasion, on the basis of more than 3000 relevés, covering the period from 1930 to 2010, and originating from the vegetation databases and fieldwork within the studied area.

Material and methods

Relevé data

The study is based on the analysis of phytosociological relevés representing Central European oak forests, collected according to the Braun-Blanquet approach [43] and originating from the vegetation databases of Austria [44] – 260 relevés; the northern part of Germany [45] – 1030 relevés; the Czech Republic [46,47] – 1191 relevés; Poland [48] – 869 relevés; and Slovakia [49] – 149 relevés. Additionally, 312 relevés were obtained directly from the authors' field investigations [42]. All of them were stored and maintained using Turboveg 2.94 software [50]. The entire data set used in the analysis contained 3776 relevés (35 duplicates were excluded) and covered a wide range of Central European oak forests, from the Baltic coast in Germany, throughout the Polish and German lowlands, the Sudetes range (both in Poland and the Czech Republic), to Western Slovakia and Austria.

The nomenclature follows Tutin et al. [51] for vascular plants, Ochyra et al. [52] for bryophytes and Szwejkowski [53] for liverworts. Due to the regionally different taxonomic approach, we merged some species into aggregates (marked as “agg.”), which were established a priori by database content corresponded with Chytrý and Tichý [54] and Świerkosz et

al. [55]. The moss layer was included in the analysis, but we excluded lichens, because they have been recorded sporadically throughout the databases. The nomenclature of syntaxa follows J.M. Matuszkiewicz [56] and Roleček [40,41].

Numerical analyses

We performed the analysis of 3776 relevés using JUICE software [57] with a modified TWINSpan algorithm and Total Inertia as a measure of cluster heterogeneity [58]. We transformed the cover abundance scale into a three-step interval scale (pseudospecies cut levels 0%, 5%, and 25%). We merged different layers for the same species using the procedure implemented in JUICE [59,60]. As a measure of fidelity, the Φ coefficient for clusters of equal size was used [61–63]. Only species with both a significant concentration in a particular cluster (using a Fisher's exact test at the significance level $P < 0.05$) and the Φ coefficient of ≥ 20 were considered to be diagnostic, regardless of their frequency. All fidelity values were multiplied by 100. The constant species were defined as species with a frequency of at least 50% in any particular cluster. The final classification of the relevés was based on the TWINSpan results. The number of clusters was chosen according to the crispness analysis [64].

As there were no direct measurements available we used mean weighted Ellenberg indicator values (EIVs) to explain differences in the species composition between clusters as well as to recognize the ecological tolerance of *I. parviflora* within oak forests [65]. The EIVs were calculated using *indicator values* option in the JUICE program. The normality of the EIVs' distribution was tested with the Shapiro–Wilk test. The structure of the data set was analyzed with a detrended correspondence analysis (DCA) using Canoco software (version 5.0 Biometris, Wageningen, České Budějovice). The gradient length of the first DCA axis (5.156 SD units) indicated an application of the unimodal ordination techniques. Scaling by segments and square-root transformation of species cover data were used in the DCA.

A correlation analysis using sample scores of the first four DCA axes was performed to identify a statistical relationship between the mean weighted EIVs and the distribution of samples in an ordination space. The association between variables was expressed by Spearman's rank correlation coefficient. In order to identify the statistical significance between variables, a forward selection procedure and a modified permutation test with 499 unrestricted permutations were conducted using MoPeT_v1.0.r script prepared in R software [66,67]. The Kruskal–Wallis test (with a post-hoc Mann–Whitney *U*-test) of the mean EIVs using PAST software [68] was performed to examine the statistical relationship between distinguished oak forest communities. Finally, differences in the statistical significance of EIVs between relevés with and without the analyzed species were tested using the Mann–Whitney *U*-test.

In order to recognize the ecological amplitude of *I. parviflora* within oak forests, we selected relevés with the occurrence of this species, including: 158 relevés from Poland, 104 relevés from the Czech Republic, 49 relevés from Germany, and 3 relevés from Austria. In the relevés from Slovakia, *I. parviflora* was not reported. The frequency of EIVs among the relevés was calculated using PAST software

[68]. Additionally, using the same data set and software, we analyzed the changes in the coverage of *I. parviflora* within the relevés in the following years. As a measure of the coverage, the mean percentage of *I. parviflora* in each relevé, consistent with the Braun-Blanquet scale (r – 0.1%, “+” – 0.5%, 1 – 2.5%, 2 – 15%, 3 – 37.5%, 4 – 62.5%, 5 – 87.5%), was used. The analysis was performed separately for acidophilous (217 relevés) and thermophilous oak forests (97 relevés). The statistical significance of changes in the coverage of *I. parviflora* was identified using Sperman’s rank correlation test.

The analysis of changes in the share of *I. parviflora* over time was possible for 3222 relevés which included information about date. Of them, only 299 were characterized by the occurrence of *I. parviflora*. Due to the varying number of relevés made each year, we primarily focused on decades. However, relevés made between 1930 and 1960 were treated together because of their small number within the databases and the lack of *I. parviflora*. The years 1960, 1970, 1980, 1990, 2000, and 2010 were established as the last years of each decade. The number of relevés with the occurrence of the small balsam in particular countries was counted for each year. Analyses were conducted in PAST software [68].

Results

TWINSPAN analysis

Numerical analysis using the TWINSPAN algorithm enabled us to distinguish 11 groups of Central European oak forests with the participation of *I. parviflora*, which differ in floristic composition, as well as geographical range (Fig. 1). The species composition of the oak forests is presented in the shortened synoptic table with the modified fidelity Φ coefficient and the percentage frequency as superscript (Appendix S1).

Cluster 1 contains relevés from Brandenburg (northeastern Germany). Due to the large share of *Fagus sylvatica* in the tree layer and mesophilous species in the herb layer, it can be identified with the stands of (sub-)Atlantic lowland oak forests included in *Fago-Quercetum petraeae*, which prefer mesic or moderately wet habitats. Cluster 2 contains relevés from the northwestern part of Germany and northern Poland. A higher share of hygrophilous and/or sub-Atlantic species indicates its resemblance to the stands of *Betulo pendulae-Quercetum roboris molinietosum*, which are not influenced by coastal eolian processes. Cluster 3 contains relevés mainly from Poland and refers to the lowland stands of *Holco mollis-Quercetum roboris* typical of wet habitats. This cluster also comprises relevés originating from the Czech Republic and Austria. Cluster 4 contains relevés mainly from Poland and northeastern Germany. They represent stands of *Betulo pendulae-Quercetum roboris prunetosum* occurring on dunes and cliffs. Within these acidophilous oak forests, species preferring various habitat conditions, including sub-Atlantic, hygrophilous and nitrophilous species, occur. Cluster 5 contains relevés originating from Poland and the Czech Republic. This cluster shows a strong similarity to *Potentillo albae-Quercetum petraeae*, typical of mesic and calcium carbonate-rich habitats with a share of boreal species. In cluster 6, relevés from Slovakia, the Czech Republic, and Poland were included. The species composition of this cluster is in accordance with the thermophilous oak forest from the alliance *Quercion petraeae* such as *Melico pictae-Quercetum roboris*. However, it also shows a strong transition towards oak-hornbeam forests represented by *Melico uniflorae-Quercetum petraeae*. Cluster 7 contains relevés from Austria and the Czech Republic and represents phytocoenoses of *Genisto pilosae-Quercetum petraeae*. This association prefers very dry and steep south-facing outcrops, which is reflected in the large share of drought-adapted acidophytes. In Cluster 8, relevés from the Czech Republic, Poland, and Austria were

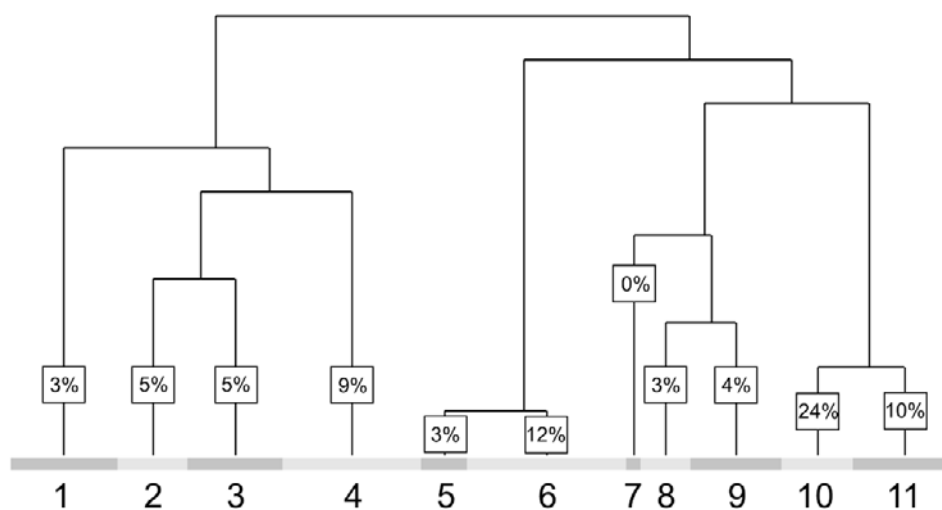


Fig. 1 Dendrogram of numerical classification for the 3776 vegetation plots of Central European oak forests. Explanation: 1 – *Fago-Quercetum*; 2 – *Betulo pendulae-Quercetum molinietosum*; 3 – *Holco mollis-Quercetum*; 4 – *Betulo pendulae-Quercetum prunetosum*; 5 – *Potentillo albae-Quercetum*; 6 – *Melico pictae-Quercetum* and *Melico uniflorae-Quercetum*; 7 – *Genisto pilosae-Quercetum*; 8 – *Viscario vulgaris-Quercetum*; 9 – *Sorbo torminalis-Quercetum*; 10 – *Calamagrostio arundinaceae-Quercetum*; 11 – *Luzulo luzuloidis-Quercetum*. In squares there is the frequency of *I. parviflora* in each cluster.

included. Due to the large share of acidophytes and slightly thermophilous species, this cluster shows a strong resemblance to *Viscario vulgaris-Quercetum petraeae*, typical of rocky and nutrient-poor habitats. Cluster 9 contains relevés of oak forests typical of rocky and sunny slopes and refers mainly to *Sorbo torminalis-Quercetum*. Cluster 10 shows a strong similarity to *Calamagrostio arundinaceae-Quercetum petraeae*, which prefers mesic habitats and is distinguishable in Poland and Germany with single relevés originating from the Czech Republic, as well. Cluster 11 represents typical phytocoenoses of *Luzulo luzuloidis-Quercetum petraeae* with a share of moderately acidophilous species, reported in the Czech Republic and Poland.

Impatiens parviflora occurred in relevés within all clusters except for cluster 7, which represented the driest type of oak forest *Genisto pilosae-Quercetum*. The species reached the highest frequency (24%) in *Calamagrostio arundinaceae-Quercetum* (cluster 10), where it also played a diagnostic role. It was also quite common in *Melico pictae-Quercetum* (cluster 6; 12% frequency) and *Luzulo luzuloidis-Quercetum* (cluster 11; 10% frequency; Appendix S1).

Main environmental gradients

Differences in the species composition of particular vegetation types enabled the general identification of the main environmental factors causing this diversity (Fig. 2). The first DCA axis explained 1.8% of the species variance, and the second one 1.1%. The correlation of mean EIVs with the distribution of the studied samples along the axes of DCA revealed that three factors – soil reaction (ρ 0.66, $P < 0.01$), temperature (ρ 0.62, $P < 0.01$), and moisture (ρ -0.88, $P < 0.01$) – were responsible for the arrangement of analyzed samples along the first DCA axis, whereas soil reaction (ρ 0.59, $P < 0.05$), temperature (ρ -0.35, $P < 0.01$), and nutrients (ρ -0.60, $P < 0.01$) influenced the arrangement of studied samples along the second DCA axis. Although

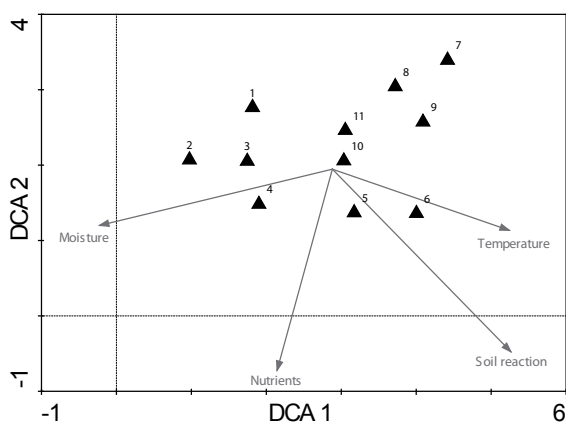


Fig. 2 The passive projection of statistically important Ellenberg indicators onto the DCA diagram. Explanation: 1 – *Fago-Quercetum*; 2 – *Betulo pendulae-Quercetum molinietosum*; 3 – *Holco mollis-Quercetum*; 4 – *Betulo pendulae-Quercetum prunetosum*; 5 – *Potentillo albae-Quercetum*; 6 – *Melico pictae-Quercetum* and *Melico uniflorae-Quercetum*; 7 – *Genisto pilosae-Quercetum*; 8 – *Viscario vulgaris-Quercetum*; 9 – *Sorbo torminalis-Quercetum*; 10 – *Calamagrostio arundinaceae-Quercetum*; 11 – *Luzulo luzuloidis-Quercetum*.

the arrangement of samples along the third and the fourth axes was correlated to particular EIVs (light, temperature, moisture, and nutrients), these axes did not contribute to the variation within the analyzed data set.

The Kruskal–Wallis test revealed that general differences in all analyzed EIVs between the distinguished vegetation groups were statistically significant. However, the results of the post-hoc test indicated that clusters with the highest frequency of *I. parviflora* (clusters 6, 10) did not differ significantly from each other with respect to light conditions and nutrient availability. The results confirmed that the small balsam reached the lowest frequency or was absent in phytocoenoses which were marked by both high availability of light (clusters 7, 8, 9) and the most unfavorable light conditions (cluster 1). In respect to the content of nutrients, *I. parviflora* was common in phytocoenoses preferring intermediate (clusters 6, 10) or increased (cluster 4) fertility of soil, whereas it was absent or rarely recorded in vegetation plots typical of less fertile habitats (clusters 1, 7, 8, 9). Fig. 3 illustrates the EIVs for distinguished plant communities.

The ecological optimum of *Impatiens parviflora*

The analysis of mean EIVs for 314 relevés with the occurrence of *I. parviflora* revealed that habitat conditions prevailing within oak forests were highly diversified. Nevertheless, the species had specific optima within the range between 25 and 75 percentile for the EIVs for light 5.45–5.94, temperature 5.40–5.78, continentality 3.01–3.87, and moisture 4.74–5.08 (Fig. 4). The optimum for the EIVs for nutrients was not very clear due to its wide range from 3.46 to 5.55 (Fig. 4). Interestingly, with reference to the EIVs for soil reaction, the species seemed to have two ecological optima (Fig. 4), because its occurrence increased in communities which were acidophilous (from 3.0 to 4.2) and mesophilous in character (from 5.6 to 6.4). All of the analyzed EIVs were characterized by a non-normal distribution.

The comparison of relevés with and without the presence of *I. parviflora* revealed statistically significant differences between them with respect to all analyzed EIVs except for moisture (Tab. 1). This suggests that the habitat niche of *I. parviflora* within oak forests is not accidental.

The coverage of *Impatiens parviflora* within studied plots

There were no statistically significant correlations between the years in which particular relevés were made and the coverage of *I. parviflora* within documented vegetation plots of oak forests (Fig. 5).

Changes in the participation of *Impatiens parviflora* over time

The analyses of phytosociological data, which were obtained from databases, revealed that the small balsam was reported for the first time in Central European oak forests in the Czech Republic in 1963 (Údolí střední Berounky: Háj u Plzně). In the mid-1960s it was also recorded in Poland (Strzelińskie Hills, Sudety foreland) and once again in the Czech Republic (Praha: Kunratický les). However, these were only singular observations, and their share within the total number of relevés in Central Europe did not exceed 2% per decade. In 1981–1990, there was a substantial increase in the frequency of *I. parviflora* to 9.8% and it has since

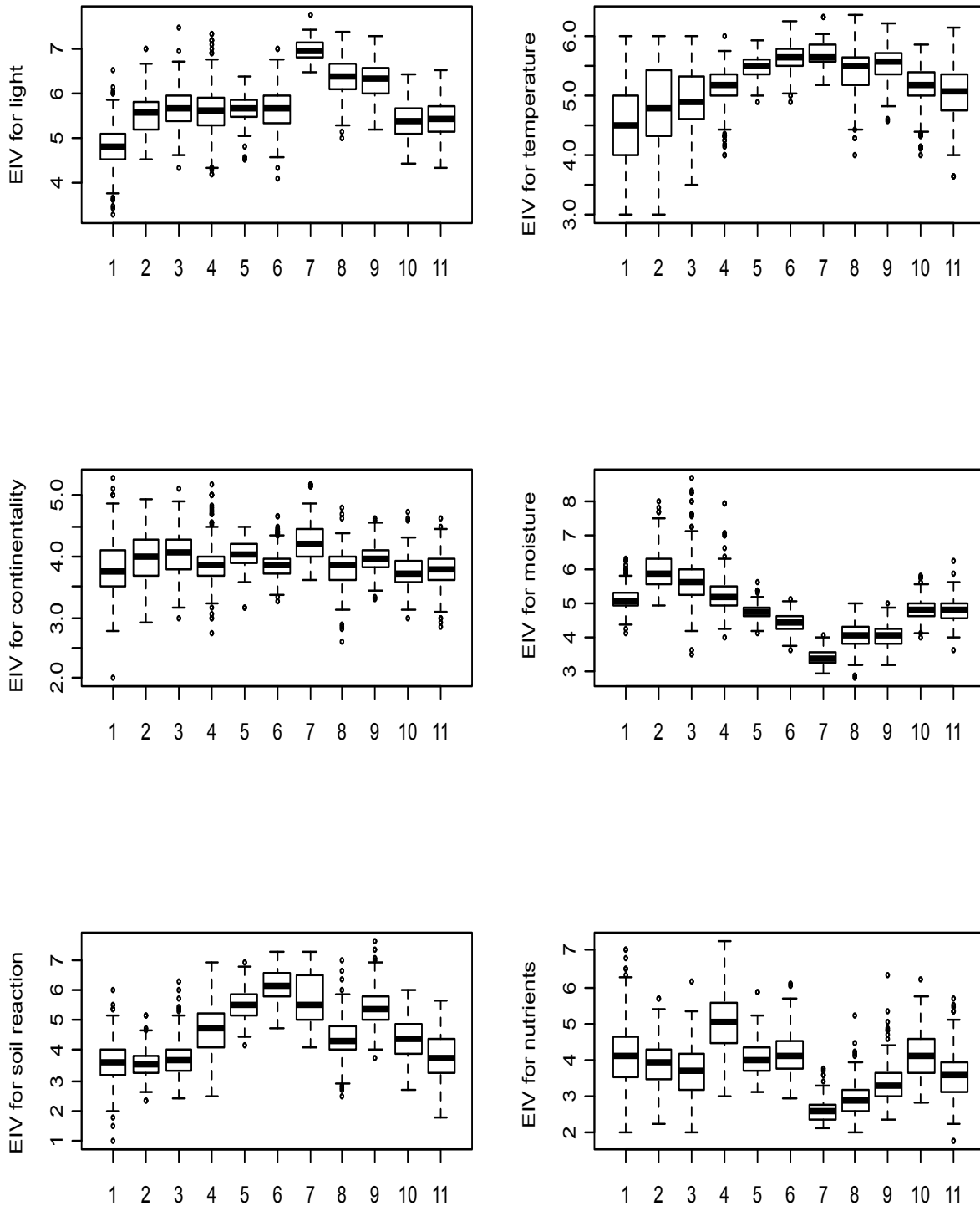


Fig. 3 Box-and-whisker plot of Ellenberg indicator values (EIVs) for distinguished plant communities. The central line of each box indicates the median value; the boxes, the lower (25%) and upper (75%) quartiles, and the whiskers, the range of values. The numbers of clusters correspond to the Fig. 2.

become even higher, reaching 20.6% in 2001–2010 (Fig. 6). The exponential increase in the number of relevés with the occurrence of *I. parviflora* was observed in each of the analyzed countries independently (Fig. 7). This means that the observed trend is not just an artefact resulting from the method of sampling and the differences between regions do not indicate a misinterpretation of this phenomenon (Fig. 6).

Discussion

Impatiens parviflora as a component of ecologically diversified Central European oak forests

Impatiens parviflora has spread into many plant communities across Europe. However, its occurrence in acidophilous and thermophilous oak forests has not yet been studied

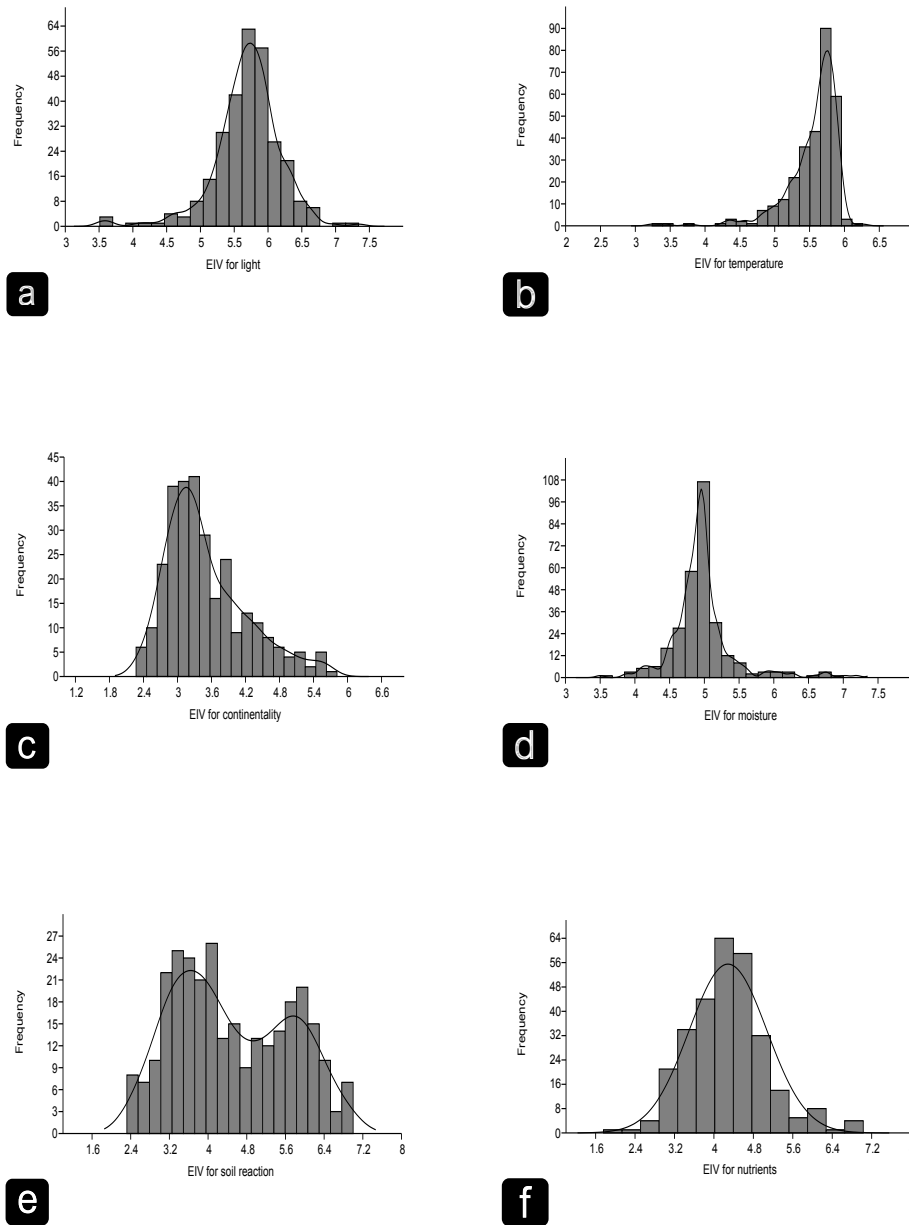


Fig. 4 Frequency histograms of the distribution of mean EIVs for 314 vegetation plots of Central European oak forests with the occurrence of *I. parviflora*. A black line shows Kernel's density for each value.

Tab. 1 Statistical significance of differences in the mean EIVs between relevés invaded and non-invaded by *I. parviflora* calculated using the *U* Mann–Whitney test.

EIV	<i>U</i>	<i>N</i> ₁ , <i>N</i> ₂	<i>z</i>	<i>P</i>	Monte Carlo <i>P</i>
Nutrients	333700	3451, 314	−11.28	1.58E-29	0.000
Light	470500	3462, 313	−3.86	0.000	0.000
Temperature	476800	3460, 314	−3.59	0.000	0.000
Soil reaction	480800	3457, 314	−3.36	0.001	0.001
Continentality	487300	3462, 314	−3.04	0.002	0.003
Moisture	529100	3462, 314	−7.08	0.435	0.430

U, *z* – test statistics; *N*₁, *N*₂ – the number of relevés non-invaded and invaded by *I. parviflora*, respectively; differences are statistically important with *P* and Monte Carlo *P* ≤ 0.05.

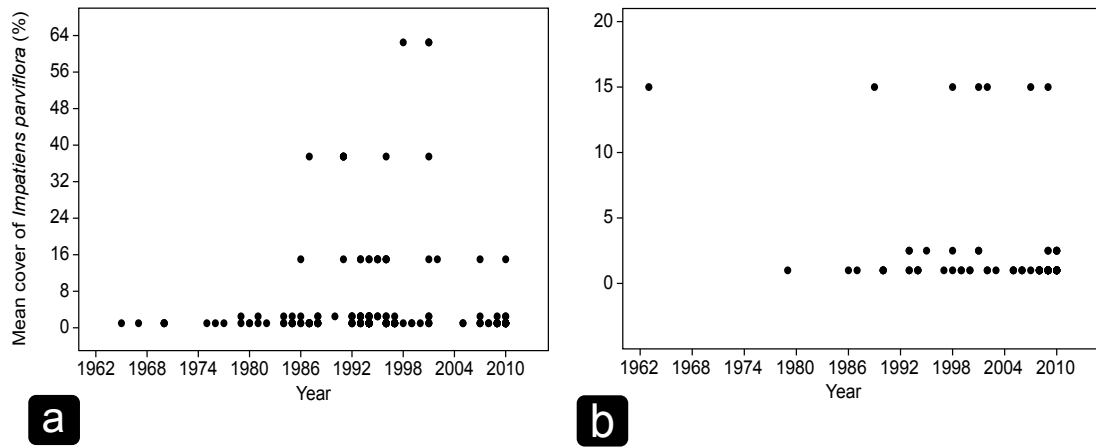


Fig. 5 The mean cover of *I. parviflora* in vegetation plots of Central European acidophilous (a) and thermophilous (b) oak forests over 50 years.

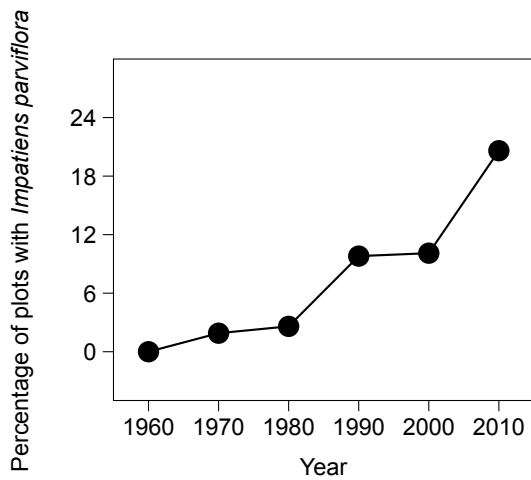


Fig. 6 The percentage of relevés of Central European oak forests with *I. parviflora* ($N = 3222$) in each decade. Before 1960, *I. parviflora* had not been present in oak forest vegetation plots.

thoroughly. The analysis conducted in this study revealed a large variety of oak forest communities of the alliances *Quercion petraeae* and *Quercion roboris*, with the participation of *I. parviflora* in the herb layer. The group of relevés was divided into 11 clusters (Fig. 1). Each of them can be identified with a particular type of single forest community or, eventually (Cluster 6), a group of similar communities.

Obtained results revealed that *I. parviflora* was reported in the majority of Central European oak forests within the aforementioned alliances, regardless of their ecological preferences (Appendix S1). The occurrence of *I. parviflora* in both acidophilous oak forests preferring moderately dry or mesic habitats and thermophilous oak forests within base-rich habitats is in accordance with previous knowledge about this species [20,25,34,69–73]. However, its presence in the lowland, wet oak forests has been heretofore questioned [69,71,73]. Moreover, *I. parviflora* was observed in xerophilous oak forests on rocky and sunny habitats over acidic (*Viscario vulgaris-Quercetum*) and neutral (*Sorbo torminalis-Quercetum*) substrates, though the species did not occur in extremely dry phytocoenoses of *Genisto*

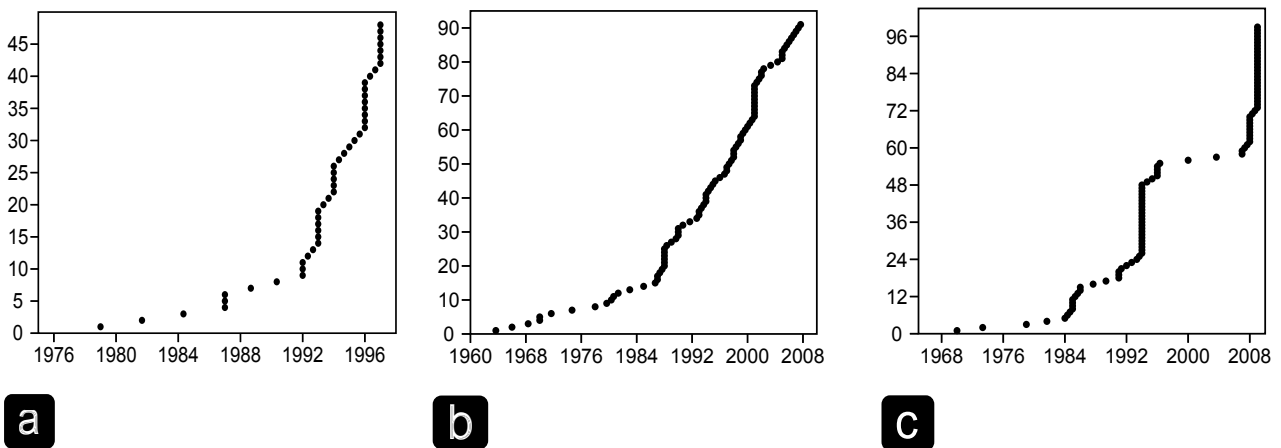


Fig. 7 The number of phytosociological relevés (3-pt average) of German (a), Czech (b), and Polish (c) oak forests with *I. parviflora* occurrence.

pilosae-Quercetum, which confirms its high sensitivity to excessive drought [21]. Therefore, it mainly prefers flat areas or slopes of northern exposition [42,69,71], which reflects its high frequency in *Calamagrostio arundinaceae-Quercetum phytocoenoses* (Fig. 1, Appendix S1).

The tolerance of *Impatiens parviflora* to habitat factors within oak forests

The analysis on the basis of EIVs revealed that there is a wide range of ecological tolerance of *I. parviflora* with respect to nutrients, soil reaction, light availability, and moisture within oak forests.

In the case of content of nutrients in the soil (EIV for N), it can adapt to different habitats, from infertile sites up to richly fertile places, with its optimum found on soils of intermediate fertility [74]. Therefore, it is difficult to agree with the results of the studies in which a clear correlation of biomass [26,28], coverage or abundance of species [72,75] with an increase in nutrient content was observed without taking into account other ecological factors. Rather, our results correspond with the outcomes of research conducted by Chmura et al. [71], who did not confirm any correlation between the number of individuals and the content of organic nitrogen in the soil. Therefore, it can be assumed that other physiochemical properties of soils, including the C/N ratio as an example, which are indirectly connected with the content of nutrients, may become more important [71,76].

In reference to soil pH, *I. parviflora* prefers both acidic soils and soils with weakly basic conditions. It seems that it has two optima for occurrence (Fig. 4), which confirms the conclusion of Chmura et al. [71], and refutes the results obtained by Węglarski [76], who stated that *I. parviflora* reached an optimum only in acidic habitats. This diversity can perhaps be attributed to the capability of *I. parviflora* to develop mycorrhiza. According to Chmura and Gućwa-Przepióra [77], specimens with well-developed mycorrhiza prefer more alkaline soils with higher values of pH and magnesium content.

On account of the light conditions in the studied oak forest communities, the *I. parviflora* optimum is about 5.7, which locates this species between semi-shade plants and plants preferring generally well-lit habitats [74]. This result neither confirms an often-cited statement that *I. parviflora* is a shade-tolerant species [76,78,79], nor the opposite one – that it is definitely a light-demanding species [28,69,80]. Our outcomes indicate a wide tolerance of this species to different light conditions, which is in accordance with both laboratory [23] and field studies [81]. Its high genetic [82] and phenological plasticity [38,72] seem to allow the local populations of *I. parviflora* to adapt and function both in places of low illumination, even if it results in decrease in biomass and growth of individuals [28], as well as rapid expansion under well-lit conditions [72]. However, in the latter case, expansion is usually limited by competition from other vascular plant species, which also benefit from the increase in insolation [7,14,21,34,38,83,84], or by other ecological factors, e.g., reduced C/N ratio.

The optimum of *I. parviflora* in relation to the EIV for moisture indicates a moist-site indicator, mainly occurring on fresh soils of average dampness. However, its ecological

amplitude is wide, and includes habitats with dry and moderately moist (but not swampy) soils. This conclusion is generally consistent with the current knowledge on the ecology of *I. parviflora*, but calls attention to its occurrence in wet habitats, which have been considered to be hitherto unfavorable to this species [69,71,73]. Interestingly, the research on mycorrhiza of *I. parviflora* [77] revealed that arbuscule richness in root fragments where mycorrhiza was present was found to be positively correlated with Ellenberg moisture. This may explain the higher resistance of certain subpopulations to increasing soil moisture, and the occurrence of *I. parviflora* in wet types of oak forests of Central Europe, such as *Holco mollis-Quercetum* or *Betulo pendulae-Quercetum*.

The spread of *Impatiens parviflora* into oak forest communities

The increasing role of *I. parviflora* in the herb layer of oak forests was firstly noted in Poland by Jakubowska-Gabara [85], who documented a rise in the share of this species at 4 of the 11 investigated sites of *Potentillo albae-Quercetum* in western and central Poland. Matuszkiewicz [86] indicated a similar process in oak forests in the Ojcowski National Park between 1950 and 2000. In southwest Poland, Reczyńska [34] noted that *I. parviflora* was the only neophyte occurring mainly sporadically in the herb layer of acidophilous oak forests in the Polish part of the Sudetes. However, she also indicated a significant rise in frequency of the small balsam in the Sudetic relevés from 14.2% (in 1965–2003) to 24.7% (in 2009–2011) [42]. Therefore, our outcomes indicate that the increase in frequency of the small balsam refers to most oak forest communities in Central Europe.

According to different concepts of invasion ecology [87,88], the invasion of an environment by new species is influenced by three factors: the number of propagules entering the new environment (propagule pressure), the characteristics of the new species, and the susceptibility of the environment to invasion by a new species (invasibility) [89,90].

There is a belief that *I. parviflora*, due to its natural occurrence in the moist forests of Central Asia, can penetrate only into forest communities of a similar nature within its secondary range [15]. In the case of Central Europe, these are oak-hornbeam or riparian forests, where its presence is well documented, [21,91] and, more recently, mesophilous beech forests [21].

Even if we assume that thermo- and acidophilous oak forests have been far more resistant to the penetration of *I. parviflora* than moist forests, the fluctuating resources theory of invasibility should be taken into account [90]. In this view, resistance is not a static or permanent attribute but a condition that can fluctuate over time. Furthermore, the establishment and persistence of an invader is in many cases not the result of replacement of a resident species, due to competition or disturbance, but occurs because of the use of open sites, available nutrients and space [92].

Another issue is the impact of spreading invaders on plant communities. For *I. parviflora* and many other invasive species, the effect of their presence depends on the coverage reached in a particular community. As was stated by Powell et al. [4], the time scale also plays a crucial role

for consideration. In the studied oak forests between 1960 and 2010, there was no statistically significant correlation between the coverage of *I. parviflora* and the year in which the relevé was made. Hence, it suggests that the presence of *I. parviflora* does not seem to have any serious influence on oak forests. The obtained results correspond to outcomes of Hejda et al. [8] and Hejda [21], who stated that the small balsam did not determine the diversity and composition of the herbal layer in forest communities. The results may

therefore indicate that, despite the increasing range of *I. parviflora* and its penetration into new types of communities, it rarely becomes dominant. This suggests the low competitive ability of this species [8,18,21]. Nevertheless, we can conclude that some communities within oak forests of Central Europe are clearly more sensitive to the invasion of *I. parviflora* than others and the occurrence of small balsam within them is not accidental.

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Authors' contributions

The following declarations about authors' contributions to the research have been made: substantial contribution to the idea and design of research: KR, KŚ; field data collection: KR, KŚ; analysis and interpretation of data: KŚ, KR, ZD; writing the manuscript: KR, KŚ, ZD.

Competing interests

The following declarations about authors' competing interests have been made: ZD is associate editor of the *Acta Societatis Botanicorum Poloniae*; other authors: no competing interests.

Supplementary material

The following supplementary material for this article is available online at <http://pbsociety.org.pl/journals/index.php/asbp/rt/suppFiles/asbp.2015.039/0>:

1. Appendix S1: summarized synoptic table of oak forest communities in Central Europe.

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