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Spread of *Impatiens glandulifera* from riparian habitats to forests and its associated impacts: insights from a new invasion

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Summary

Impatiens glandulifera is a globally successful invader that primarily spreads along riparian habitats; however, during the last ~20 years, it has started to colonise forests, but little has been published on impacts of this recent spread. Several factors may have contributed to this phenomenon: (i) high propagule pressure from large and widespread riparian populations, (ii) extensive anthropogenic and natural disturbances in the forest ecosystems, (iii) increased use of forest machinery efficiently spreading the seeds together with (iv) a wide environmental tolerance of the species. The impacts of *I. glandulifera* on native communities in forests are manifold. Contrasting effects are reported on native plant species diversity, richness and growth of saplings of co-occurring species, as well as negative effects on soil mycorrhizal fungi. We suggest that the eradication of *I. glandulifera* populations in forests is more feasible than along watercourses because the recolonisation in forests is limited and, in some cases, populations are outcompeted by woody species during succession.

Keywords: disturbance, Himalayan balsam, habitat expansion, invasive alien plant, management, niche broadening, woodland.

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Introduction

Invasive species pose a major threat to native biodiversity and the functioning of invaded ecosystems (Mack *et al*., 2000; Pyšek *et al*., 2012a; Kumschick *et al*., 2015), and thus represent a major component of global environmental change (Vitousek *et al*., 1997). Species must overcome a series of barriers to become naturalised or invasive (Blackburn *et al*., 2011); therefore, with the aim of informing management decisions, intensive research has been focused on identifying mechanisms determining invasion success (Mack *et al*., 2000; Pyšek *et al*., 2015). In our study, we deal with one of the most invasive plant species in Europe, *Impaties glandulifera*, and review factors related to its recent spread. This species' invasion typically started along rivers (Pyšek & Prach, 1995), but recently it has expanded into other habitats, particularly forests (Čuda *et al*., 2017a). Consequently, much attention has been paid to its invasion in riverine habitats, while

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other habitats were mostly overlooked. To our knowledge, there is no paper summarising the spread of *I. glandulifera* into forests. In this paper, we aim to: (i) determine vectors of spread, (ii) analyse factors that enabled spread into forests, (iii) assess impacts on forest ecosystems and (iv) provide management recommendations.

Species invasion history and its current distribution

Impatiens glandulifera Royle is an annual invasive species that originates from the Himalayas, where it grows in ditches between fields, along roads, on pastures, along forest edges, in mixed forest and forest gaps up to 4000 m a.s.l. (Polunin & Stainton, 1984). It typically occurs in scrublands and pastures of the Himalayan cedar (*Cedrus deodara*) mixed forest zone (Balogh, 2008). The species was intentionally introduced as an ornamental garden plant (Beerling & Perrins, 1993), and in the 19th century, it was also recommended for 'naturalizing or making wild innumerable beautiful natives of many regions of the earth in our woods, wild and semi-wild places, rougher parts of pleasure grounds' (Robinson, 1870). Nowadays, *I. glandulifera* is still cultivated (Fig. 1), although it is listed among invasive alien species of Union concern (EC, 2017) and classified as a highly invasive species all around the world (CABI, 2019). In addition to its ornamental use, it was also spread by beekeepers as a valuable late source of nectar at the end of summer (Showler, 1989). The species was first introduced to the UK in 1839 (Beerling & Perrins, 1993), although some sources claim it was introduced 2 years earlier (Jernelöv, 2017). Since its initial introduction, the species has spread throughout mainland Europe, where it became naturalised around the 1900s (Pyšek & Prach, 1995), and later on it invaded other parts of the world: North America, New Zealand and Japan (CABI, 2019). In addition, it took approximately 40 years to form stabilised populations in European countries (Table 1). *Impatiens glandulifera* is currently recorded from 46 countries worldwide: most of Europe (only some southern countries remain uninvaded), Russian Federation (European part and far East), Japan, China (Hunan), US east and west coast and Alaska, Canada (present in eight provinces), New Zealand, Tasmania, and Argentina (CABI, 2019; GBIF.org, 2019). At the national scale, *I. glandulifera* distribution and spread has been well documented in the UK (Beerling & Perrins, 1993), Czech Republic (Pyšek & Prach, 1995), Finland (Kurtto, 1996), Sweden (Larsson & Martinsson, 1998) and Austria (Drescher & Prots, 2003).

In the Czech Republic, *I. glandulifera* was present in 284 (41.8%) of the 679 grid cells

Fig. 1 Several individuals of *I. glandulifera* that were maintained unmown in a lawn close to the Jizera river, Czech Republic, in 2015. Photo Credit: J. Čuda. [Colour figure can be viewed at wileyonlinelibrary.com].

(~12.0 km × 11.1 km resolution) in 1992 (Pyšek & Prach, 1995). Recently, it has been recorded from 521 (76.7%) grid cells (Pladias, 2019). In the UK, it was recorded from over 20.9% (i.e. over 600 of the 2858 land-containing grid cells at a 10 km × 10 km resolution) in 1992 (Beerling & Perrins, 1993); currently, it is present in 55.9% (1599 grid cells; Online Atlas of the British and Irish flora, 2019). This indicates a rapid invasion in both countries. The massive recent increase in abundance of *I. glandulifera* may be explained by spread outside of riverine habitats. Pyšek and Prach (1995) showed that the invasion in several European countries was accelerated between 1960 and the 1990s irrespective of the date of species introduction. The synchronous invasion in Europe was probably supported by land use changes (e.g. eutrophication and abandonment of traditional river-bank management) that occurred in different countries around the same time period (Pyšek & Prach, 1995; Larsson & Martinsson, 1998). Due to its tendency to colonise species-poor and degraded communities, *I. glandulifera* represents an increasing threat to habitats such as native deciduous forests and hydrophilous tall herb communities in Ireland (Gioria *et al*., 2018).

Vectors of spread

Impatiens glandulifera reproduces exclusively by seeds that are spread autonomously by explosive capsule dehiscence up to 3–5 m from the mother plant and these distances can be much larger when dispersed by water flow along rivers (Beerling & Perrins, 1993). Seed rain density is ~5000–6000 seeds / m^2 in the UK (Beerling & Perrins, 1993). In Germany, plants were more fecund with a maximum of 32 000 seeds / m^2

Table 1 Invasion of *I. glandulifera* in selected European countries

Country	Date of introduction[1]	Year of naturalisation[2]	Recent status[3]	Forests[4]	References
UK	1839, Kew Gardens	1848 escape; in 1855 naturalised between Haresfield and Denham	Invasive	Yes	Coombe, 1956[1]; Balogh, 2008[2]; Britten, 1900[2]; Irvine, 1855[2]; Beerling & Perrins, 1993[3]; Maule *et al*., 2000[4]
Sweden	1842, Stockholm	1873, in Lund	Invasive	Yes	Larsson & Martinsson, 1998[1,2,4], Jernelöv, 2017[3]
Austria	1845, surrounding of Linz	1884, Wien; 1898, Weidling river near Klosterneuburg	Invasive	Yes	Drescher & Prots, 2003[1,2,4]; Walter *et al*., 2005[3]
Czech Republic	1846, Červený Hrádek u Jirkova	1896, escaped near Litoměřice; by 1903 Jizera river near Turnov	Invasive	Yes	Slavík, 1996[1]; Kudrnáč, 1903[2]; Pyšek *et al*., 2012b[3]; Čuda *et al*., 2017b[4]
Finland	1870, Botanical Garden of the University of Helsinki	1947, Vaasa (west coast)	Invasive	?	Kurtto, 1996[1]; Erkamo, 1949[2]; Niemivuo-Lahti, 2012[3]
Belgium	1891, along river Zenne	1920′ in the valley of river Dijle	Invasive	Yes	Verloove, 2012[1,2]; Branquart, 2019[3]; Vervoort *et al*., 2011[4]

The listed countries are ordered according to their date of introduction. Superscripts in the references refer to the column linking the reference.

(Koenies & Glavač, 1979). The first records from the early spread phase in the 1920s are from sites 'where garden waste was dumped', these sites were often close to rivers (Jernelöv, 2017) which facilitated further spread. Ripe seeds do not float, but roll on the river bed and sediment downstream, especially during floods (Čuda *et al*., 2017a). However, the intact capsules can float and more than 40% of unripe white seeds are able to germinate (Prots & Drescher, 2010). Apart from spread along river banks, seeds also spread unintentionally via contaminated soil, with mud on machinery wheels and worker's boots (Dawson & Holland, 1999), and possibly also on the legs of browsing animals. The seeds are also transported with top soil to construction areas (Drescher & Prots, 2003), especially if river gravel is used for road reinforcement (Hartmann *et al*., 1995). The volume of transported soil does not need to be large due to massive seed production. Trepl (1984) found 22 seeds of closely related *I. parviflora* in 1 L of soil collected from wheels of construction vehicles. Rusterholz *et al*. (2012) reported that *I. glandulifera* spreads with garden waste into forests in Switzerland. Nevertheless, intentional spread cannot be excluded, for example seeds are still sold on eBay.

Spread into forests: effects of a broad habitat range and management actions

The spread of *I. glandulifera* into European forests has accelerated over the last 20 years (Gaggini *et al*., 2018; J. Sádlo, F. Krahulec, pers. comm.). This has been illustrated by the increasing number and size of *I. glandulifera* populations found in forests (Fig. 2; Čuda *et al*., 2017a). Notably, *I. glandulifera* often grows in forests and forest gaps in the native range (Drescher & Prots, 2000), while in Europe, until recently, it was confined to rivers and their close surroundings because rivers and water streams are the main dispersal vectors (Čuda *et al*., 2017a).

Due to high propagule pressure and increased opportunities for transportation, *I. glandulifera* can reach sites that are distant from riverbanks. In general, the invasion of *I glandulifera* into forests is facilitated by its ability to grow in shade. It tolerates a wide range of irradiances, from 0.3% to 100% open-ground photosynthetically active radiation (Maule *et al*., 2000). However, as the biomass production is positively correlated with available light and decreases with increasing distance from the forest edge, deep shade is most likely to act as a limiting factor (Maule *et al*., 2000). Similarly, Čuda *et al*. (2014) found that *I. glandulifera* tolerates canopy closure of almost 90%, but prefers mild shading. However, other studies have shown that *I. glandulifera* manifests great phenotypic plasticity with respect to light availability (Skálová *et al*., 2012) and is able to maintain high fitness and competitiveness in shady and relatively dry conditions (Čuda *et al*., 2015). This is explained by its ability to achieve substantial growth at low irradiance levels and thus reduced photosynthesis. In such conditions, nitrate, which functions as a vacuole osmoticum, may be used to compensate for the shortage of organic compounds to maintain a positive turgor for cell

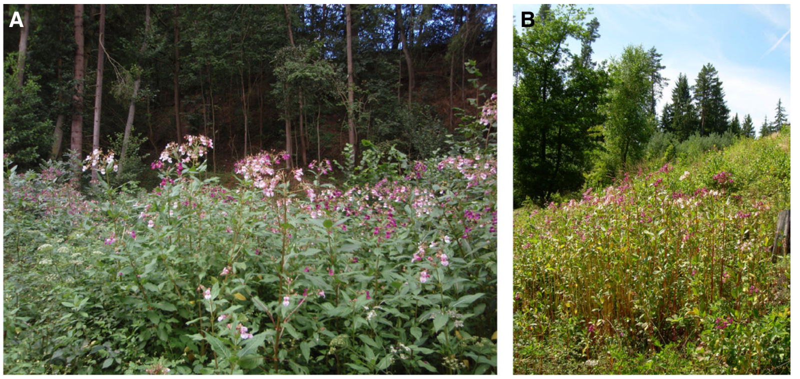

Fig. 2 (A, B) Stands of *I. glandulifera* in the forest gap near the village of Čelina in 2008 and in a clearcut in mixed forests by the Jizera river, Czech Republic in 2015. Photo Credit: J. Čuda. [Colour figure can be viewed at wileyonlinelibrary.com].

expansion during growth (Blom-Zandstra & Lampe, 1985). In addition, less energy is required for the uptake and transport of nitrates to the vacuoles than for the synthesis of organic acids and sugars: malate is twice and hexose seven times more costly than KNO_3 (Andrews *et al*., 2005). Thus, *I. glandulifera* is able to withstand low irradiance and maintain high fitness, if it grows in nitrogen-rich stands (Andrews *et al*., 2005). Therefore, its spread may possibly also be facilitated by atmospheric nitrogen depositions.

In forests, increased nutrient and light availability typically occurs in logging areas and clearings, which brings about extensive soil disturbances and often temporal waterlogging. Such conditions are optimal for the establishment of *I. glandulifera*, as they create open spaces for germination and release nutrients, similar to river banks disturbed by floods. In addition, large amounts of soil contaminated with seeds are unintentionally transported on logs and wheels over large distances. Forest management has been intensified recently as a response to the decimation of spruce plantations by bark beetle. These outbreaks have been recently reported in Austria, Czech Republic, Germany, Slovakia and also in North America (Hlásny *et al*., 2019).

Impacts on forests

Only during the last decade, studies started to address the impact of *I. glandulifera* in forests. For example, Ammer *et al*. (2011) established two experimental sites in Germany (Bavaria) in an area formerly dominated by *Picea abies* that was affected by bark beetles and subsequent windthrow resulting in two big clearcut gaps (~5000 m^2). The authors found no significant effect of *I. glandulifera* on the survival of *Picea abies*, *Abies alba* and *Betula pendula* seedlings and suggest that the effect of the common native competitor (*Rubus fruticosus*) was stronger than that of the invader. In contrast, Ruckli *et al*. (2014) found reduced root biomass and lower survival rates of *Acer pseudoplatanus* saplings in invaded sites in Switzerland and lower arbuscular mycorrhiza root colonisation. The authors reported no effect of increased soil moisture and phosphorus on sapling survival in invaded sites. Instead, they attributed the negative effect to the influence of allelopathic compounds (naphthoquinones) released into the soil that show antimicrobial and antifungal effects (Ruckli *et al*., 2014). Čuda *et al*. (2017b) compared invaded (i.e. invaded more than 5 years), uninvaded and removal plots in a mixed forest in the Czech Republic over a 3 year period. They found a minor effect of *I. glandulifera* on plant community composition, but no effect on plant species richness and litter, and only a marginal effect on soil characteristics. These authors explain the changes in community composition by reduced light due to shading by *I. glandulifera* in the invaded sites (by 56%), and they suggest that only marginal effects on soil but no other parameters are explained by large annual fluctuations of invader biomass and population size. Gaggini *et al*. (2018) tested the effect of *I. glandulifera* on plant and fungal communities and reported that invaded and uninvaded sites differed in fungal and plant community composition. In addition, activity of the soil bacterial community in uninvaded sites was lower in comparison with invaded sites in late spring. Impact on fungi is presumed to be linked with allelopathy and an increase in soil moisture (Gaggini *et al*., 2018).

These studies illustrate that ambivalent impacts of *I. glandulifera* on native organisms are often reported, but with negative effects prevailing. Most of the studies, both in riparian habitats (e.g. Hulme & Bremner, 2006; Hejda *et al*., 2009) and forests (e.g. Rusterholz *et al*., 2017; Gaggini *et al*., 2019), show changes in community composition. Decreased species diversity may be predominantly attributed to shading (e.g. Čuda *et al*., 2017b) and increased soil moisture or allelopathic compounds by *I. glandulifera* (Gaggini *et al*., 2018). Lastly, dispersal of *I. glandulifera* into forests is typically linked with extensive disturbances, for example bark beetle outbreaks, windthrows and clear-cuts (Ammer *et al.*, 2011; Ruckli *et al.*, 2014).

Methodological constraints of studies

There are several methodological constraints related to the studies reported above which should be kept in mind. If invaded and uninvaded sites are compared (e.g. Gaggini *et al.*, 2018), they may differ in other factors besides the presence of an invader, and such different conditions may be a reason why the invasive species is absent. In other studies (e.g. Čuda *et al.*, 2017b), it is usually uncertain when the site was invaded. Rusterholz *et al.* (2017) point out the importance of the residence time of an invader at a site, because in their study the impact of *I. glandulifera* on vegetation manifested with a delay of 13 years. Most of the studies assess the impact in one vegetation season (sometimes only once) and relatively early after the invasion. However, Čuda *et al.* (2017b) report that the impact of *I. glandulifera* removal on soil characteristics, which is highly significant in the first season, may disappear in the following seasons. Impact may also vary across habitats. For example, Gaggini *et al.* (2019) showed that it was more pronounced in coniferous than in broad-leaved forests. Lastly, soil characteristics are more stable in forests than in riparian habitats, where they may change quickly due to water-level fluctuations and flooding (Baldwin & Mitchell, 2000).

Species-rich plant communities containing weak competitors, such as fresh meadows and road embankments (Kiełtyk & Delimat, 2019), seem to be more affected than species-poor and competitively strong riparian vegetation (Hejda *et al.*, 2009) or competitively poor but shade tolerant forest understorey (Čuda *et al.*, 2017b). The movements of populations and changing density and extent of the stand (Kasperek, 2004) contribute to fluctuating impact across the years. This reduces the impact of an annual species such as *I. glandulifera* in comparison with perennial species that remain in the same place and have a higher potential to displace co-occurring native species (Hejda *et al.*, 2009). Ideally, plots should be established along the invasion chronosequence, as well as, along environmental gradients (Gruntman *et al.*, 2017). To obtain the most representative results, data on an invader's impact should be collected across multiple sites and various environmental conditions, for example habitats, countries, climates or human influence (Kumschick *et al.*, 2015).

Further spread and management recommendations

We expect further spread of *I. glandulifera* into forests in central Europe (the majority of evidence comes from here), as well as in other regions where it is already widespread. The potential of this species to continue invading these habitats is high due to *I. glandulifera*'s ability to maintain massive seed production under various conditions, its increasing distribution, and the current forest management practices which facilitate its establishment. The number of sites suitable for establishment is increasing at present, especially due to the current bark beetle outbreaks that greatly disturb forests and increase the proportion of clearings. The species ruderal strategy represents an advantage due to its fast spread and growth, but at the same time, it acts as a constraint due to its persistence in a site (i.e. populations of annual species need to recover every year from seeds). We suggest sites that are most threatened by invasion of *I. glandulifera* comprise those that provide optimum conditions for creating dominant and persistent populations of this species and those that are not threatened by rapid population declines. Such sites are characterised by occasional disturbances, high nutrient supply and stable light and moisture conditions, for example forests spring areas and bogs. *Impatiens glandulifera* prefers partially shaded sites (Beerling & Perrins, 1993) and this also protects the seedlings from early spring frosts, which may damage whole stands (J. Čuda, personal observation). In contrast to periodically disturbed riparian sites, *I. glandulifera* may be outcompeted in forests due to succession by woody species and standard forest management aimed at suppressing all species apart from timber.

To prevent further spread of *I. glandulifera*, it is important to minimise soil disturbances and control the transport of soil contaminated by seeds into forests. This can be achieved by using gentler machinery, cable cranes in steep slopes and by timing logging during periods without mud (e.g. when the soil is frozen or dry). We also highly recommend detecting the presence of *I. glandulifera* in sites disturbed by machinery a year following the work and any plants detected should be manually removed before they set fruit. Furthermore, managing *I. glandulifera* populations in forests is more feasible than along watercourses because they are more isolated and cannot be saturated by seeds from upstream. Small and isolated populations or solitary individuals may be extirpated by hand pulling. Re-rooting of plants left on the ground is less probable due to drier soils and a generally thicker litter layer in comparison with riparian habitats. Due to the species annual life strategy, we recommend logging before seed release and the sites should be monitored up to 4 years, especially since the seeds were reported to stay viable for a long time in some localities (Skálová *et al.*, 2019).

Conclusions: should we be worried?

In conclusion, we reveal several key factors that contribute to the spread of *I. glandulifera* into forests: (i) a high propagule pressure from large and widespread riparian populations, (ii) extensive anthropogenic and natural disturbances in forest ecosystems, and (iii) increased use of heavy forest machinery over the past 30 years that has a high potential to spread seeds. The impacts on riparian habitats and in forests seem to be comparable and depend on the dominance of *I. glandulifera* and its residence time in the community. In our opinion, we should be worried about the increasing number of *I. glandulifera* populations, despite their somewhat limited impact. The greatest threat of *I. glandulifera* is the release of allelopathic compounds that affects soil fungi and arbuscular mycorrhiza and may thus alter nutrient cycling. Importantly, management of *I. glandulifera* occurring in forests outside the flooding zones seems to be more feasible since populations are still small and less interconnected than in riparian habitats, and seed dispersal is limited.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 Schematic overview of the impacts of *I. glandulifera* in studies discussed in the section 'Impact on forests'. Superscripts show two cases, where means were not shown in the article but were calculated from data presented: [1]mean for coniferous and deciduous forest taken together; [2]mean for coniferous and deciduous forest together in June.