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Factors associated with invasiveness in the genus *Impatiens*: interaction of species traits, competition and environment

Faktory ovlivňující invazivnost v rodě *Impatiens* (netýkavka): interakce vlastností druhů, kompetice a podmínek prostředí

Ph.D. Thesis

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Consultant: RNDr. Hana Skálová, CSc.

Prague 2017

I hereby declare and confirm with my signature that the doctoral dissertation is exclusively the result of my own autonomous work based on my research and the literature published. I also declare that no part of the thesis has been used for any other degree or diploma. All literature sources I used when writing this thesis have been properly cited.

Prague, July 2017 Jan Čuda

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Abstract

The aim of this thesis was to identify factors that contribute to invasiveness of species in the genus *Impatiens*. This genus is horticulturally attractive and includes several species that are known to have naturalized outside their native ranges, while others did not escape, in spite of being frequently cultivated. When looking for traits associated with invasiveness, it is useful to focus on congeneric species. Their traits and dispersal modes are less influenced by phylogeny, than when comparing unrelated species or even complete floras. This helps to account for traits that favour invasive species over native ones and thus identify potential invaders more precisely. A superior invader performance is attributed to a competitive advantage over native species that can lead in extreme case to competitive exclusion of the latter. Invasive and native species compete only if their niches overlap and the strength of competition depends on niche similarity. Importantly, invasive species are considered to be able to maintain their high competitiveness over a wide range of environmental conditions, while native ones often have narrower environmental optima. Lastly, competitive outcome can vary over life stages and depends on the degree of species dominance, which is rarely taken into account. Spread and resulting distribution of invaders is further affected by distributional and environmental constrains in the secondary range. As a result, many invasive species have naturalized in riparian habitats, characterised by patchy environment with range of microhabitats, reduced competition in disturbed sites and easy propagule transport.

The aims of my PhD. thesis were

- to identify traits associated with invasiveness and assess the role of planting frequency within selected *Impatiens* species
- search for microsite differentiation in one native and two invasive *Impatiens* species that coexist in the field
- investigate competition of these species under manipulated environmental conditions, varying plant densities and different life stages in an experimental garden;
- determine factors that affect distribution and abundance of *Impatiens glandulifera* along river corridors.

The results can be summarized as follows: (i) juvenile traits, namely heavy seed, fast seedling growth, and germination postponed to the period of more favourable conditions were more strongly associated with invasiveness than adult traits, such as fecundity and final biomass; (ii) frequently planted species naturalized more easily; (iii) niches of invasive and native species partially overlapped; (iv) in mixed stands, abundances of all species were negatively related to those of the other congeners, and the coexistence in one locality is possible due to different

microhabitat use; (v) competitive interactions had stronger effects on plant fitness than had environmental settings; (vi) the most invasive representative, *Impatiens glandulifera*, was competitively superior across all experimental conditions and its dominance increased over time, while the native *I. noli-tangere* is being outcompeted from shared part of its niche; (vii) the largest populations of *I. glandulifera* were located in flooded patches in the vicinity of the rivers, specifically flooded patches had twice as many individuals as those that were not flooded; (viii) populations in tributaries were twice as far from the main river than those not associated with tributaries.

Based on these results I conclude that more *Impatiens* species might invade in the future if their planting becomes more widespread. Juvenile traits are of crucial importance, because establishment determines the success of these mostly annual aliens. Niche width and species performance shape the pattern of coexistence among native and invasive species. Native *I. noli-tangere* will be restricted to wet and shady parts of the niche, while competitively superior *I. glandulifera* will reduce these native populations when growing together in mixed stands. The other very successful invasive species, *I. parviflora*, is competitively inferior and has negligible impact on the native species. In terms of landscape dynamics, flooding accounts for the dominance of *I. glandulifera* along rivers due to spreading the seed, disturbing native vegetation and increasing the nutrient availability.

Abstrakt

Cílem předkládané disertační práce bylo určit, které faktory ovlivňují invazivnost v rodě *Impatiens* (netýkavka). Netýkavky jsou velmi atraktivní rostliny; některé zdomácněly mimo původní areál výskytu, zatímco jiné ne, přestože byly často pěstovány. Pokud pátráme po vlastnostech, které podporují invazivnost, je výhodné srovnávat druhy jednoho rodu, tzv. kongenery. Díky blízké příbuznosti jsou jejich vlastnosti a způsob rozšiřování méně ovlivněny fylogenezí, než při srovnání nepříbuzných druhů či dokonce celých flór. Srovnání kongenerů umožňuje přesnější určení vlastností, které invazní druhy zvýhodňují oproti druhům domácím, a zároveň přesnější rozpoznání druhů s invazním potenciálem. Intenzita kompetice mezi původními a invazními druhy závisí na míře překryvu jejich nik. Invazní druhy jsou obvykle vysoce kompetitivní v širokém rozsahu podmínek prostředí, zatímco domácí druhy často mají užší ekologické optimum. Výsledek kompetice se navíc může v různých fázích životního cyklu lišit a závisí na míře dominance (vyjádřené např. pokryvností), což bývá zřídka zohledněno. Rozšíření invazního druhu v nepůvodním areálu také ovlivňují místní podmínky prostředí, způsoby a rychlost šíření. Mnoho invazních druhů proto zdomácnělo podél vodotečí, které poskytují celou řadu příhodných mikrostanovišť, na nichž je kompetice ze strany domácích druhů snížena v důsledku disturbancí, a diaspory jsou snadno šířeny vodou.

Cílem mé disertační práce bylo:

- nalézt vlastnosti podporující invazivnost u vybraných druhů netýkavek (*Impatiens*), s přihlédnutím k frekvenci pěstování
- zjistit, zda se liší niky jednoho původního a dvou invazních druhů, které se v přírodě vyskytují společně
- prozkoumat kompetiční vztahy těchto tří druhů v pokusné zahradě za různých podmínek prostředí a hustoty kompetitorů v průběhu celého životního cyklu
- určit faktory, které ovlivňují rozšíření a početnost *I. glandulifera* podél řek

Výsledky mé disertační práce lze shrnout následovně: (i) vlastnosti rostlin v časné vývojové fázi (velká hmotnost semen, rychlý růst semenáčů a klíčení situované do příznivého období) přispívaly k invazivnosti silněji než vlastnosti dospělců (plodnost a celková biomasa); (ii) často pěstované druhy snadněji zdomácňují; (iii) niky invazních a domácího druhu se překrývají; (iv) pokryvnosti všech druhů byly negativně ovlivněny pokryvnostmi kongenerů, společný výskyt druhů v rámci jedné lokality je možný díky rozdílnému využití mikrostanovišť; (v) na fitness rostlin má silnější vliv kompetice než podmínky prostředí; (vi) silně invazní druh *Impatiens glandulifera* je nejsilnějším kompetitorem bez ohledu na podmínky prostředí, což vede k tomu,

že domácí *I. noli-tangere* je kompetičně vylučována ze společné části niky; (vii) největší populace *I. glandulifera* vytváří v zaplavovaných plochách v blízkosti řek, kde byl zaznamenán dvojnásobný počet jedinců oproti plochám nezaplavovaným; (viii) populace ležící na přítocích byly dvakrát tak daleko od mapovaných řek, než ty ležící mimo přítoky.

Na základě těchto výsledků předpokládám, že se počet invazních druhů netýkavek v budoucnosti zvýší, pokud budou často pěstovány. Stěžejní význam mají časná stádia vývoje, protože úspěšné uchycení a růst semenáčů je základním předpokladem úspěchu u těchto převážně jednoletých druhů. Šíře niky a kompetiční síla druhu ovlivňují společný výskyt původních a invazních druhů. Domácí *I. noli-tangere* bude v místech, kde roste společně s kompetičně silnější *I. glandulifera*, vytlačena do vlhké a stinné části niky. Druhý velmi úspěšný invazní druh *I. parviflora* je ze zkoumaných druhů kompetičně nejslabší a tudíž má malý vliv na původní druh. Dynamika výskytu *I. glandulifera* v krajině je ovlivněna povodněmi, které rozšiřují semena, narušují domácí vegetaci, zvyšují zásobu živin, což ve výsledku umožňuje dominanci netýkavky v břehových porostech.

1 Introduction

1.1 Rationale of the study, approaches and research questions

The question, why some alien (syn. exotic, non-native, non-indigenous) species are more successful than the others still remains in the centre of interest of invasion ecology. The success of species as invaders has been traditionally attributed to their biological and ecological traits, such as fast growth, great biomass, long-distance dispersal, fecundity, etc. (Pyšek and Richardson 2007, van Kleunen et al. 2010, Pellock et al. 2013[1]). Classical approach of comparing whole floras when looking for traits linked with invasiveness can be limited by great variability among the species pools, in other words it is hard to find some common traits responsible for invasiveness among woody plants, grasses and herbs that have different life strategies (Crawley et al. 1996, Pyšek and Richardson 2007). Phylogenetic relatedness among species can be accounted for by phylogenetic corrections (Sakai et al. 2001), i.e. including phylogenetic distance among species into multispecies comparisons (Burns 2004, van Kleunen et al. 2010). This helps to differentiate between traits characteristic for the whole family (e.g. small seeds in *Orchidaceae*) from those that really promote invasiveness (e.g. small seed in genus *Pinus*, see Rejmánek and Richardson 1996). Nevertheless, phylogenetic corrections should be understood rather as a conceptual decision, which interpretation we want to prioritize, because after use of phylogenetic corrections we lose information about evolutionary background (Westoby et al. 1995).

Further, it is known that invasiveness is not equally distributed across individual phylogenetic lineages, e.g. that there are many invaders in Poaceae and Fabaceae, but only a few in Orchidaceae family (Daehler 1998; Lambdon et al. 2008a; Pyšek et al. 2017). Importantly, Moravcová et al. (2010) found that there is a big variance within the phylogenetic groups and that most variation in invasiveness is linked to variation among species within genera. Therefore predictions of invasiveness should be done at lower phylogenetic levels, optimally within a genus (Moravcová et al. 2010, Pyšek et al. 2014). However, this technique has some limitations, as such a genus should have enough species to allow for statistical testing and needs to contain species of different invasive status in a particular region (ideally invasive, naturalized, casual, and present but not escaping from cultivation into the wild) together with native representative(s) (Burns 2004). Comparison of phylogenetically related species has been made in a number of congeneric or confamilial groups, such as *Crepis* and *Centaurea* (Muth and Pigliucci, 2006, 2007), *Eucalyptus* (Radho-Toly et al. 2001), *Impatiens* (Perrins et al. 1993, Perglová et al. 2009, Skálová et al. 2011, 2012, 2013), *Iridaceae* (van Kleunen and Johnson 2007), *Oenothera* (Mihulka et al. 2006), *Plantago* (Matsuo 1999), *Pinus* (Rejmánek and Richardson 1996, Grotkopp et al. 2002, Gallien et al. 2016), Poaceae (Harris 1967, Bilbao and Medina 1990, Smith and Knapp 2001) and *Rubus* (McDowell 2002). However, most of these studies took into account less than four species which impedes broader generalisation.

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[1] References cited in the Introduction are included after the Synthesis chapter (p. 85)

Invasiveness is determined not only by the traits alone, the traits act in concert with dispersal pathways (Carlton 1996). The number of individuals released into a region to which they are not native is called propagule pressure (Lockwood et al. 2005) or introduction effort (Blackburn and Duncan 2001). Within plant invaders, intentional introductions play a major role (Mack 2003, Hulme 2011) and ornamental plants are the main source of deliberate introductions (Lambdon et al. 2008a, Pyšek et al. 2012b). The frequency of planting directly affects the propagule pressure, species planted more commonly are more likely to naturalize (Dehnen-Schmutz et al. 2007, Pyšek et al. 2015). Importantly, horticulture prefers species that do not need excessive gardening care: germinate easily, grow vigorously and fast, reproduce easily and grow in a wide range of environments (Mack 2000, Wiens and Graham 2005). In addition, all these characteristic are known to support invasion success as well as competitive ability (Pyšek and Richardson 2007).

A high competitiveness of invasive species is well documented (Sakai et al. 2001, van Kleunen et al. 2010); in general invasive species are believed to be more competitive than natives (Vilà et al. 2011) but the outcome of the competition varies depending on external factors (Daehler 2003). Success of invasive species is usually associated with better performance for a given trait (e.g. better germination). Alternatively, the invader brings a novel characteristic, not present in the resident community, such as different life form (Vilà and Weiner 2004), allelopathy (Callaway and Aschehoug 2000), presence or absence of mycorrhiza (Štajerová et al. 2009) or nitrogen fixation (Vitousek et al. 1987). Except favourable traits mentioned above, high competitiveness is supported by other mechanisms, e.g. lack of enemies in the new range (Keane and Crawley 2002). The superiority of invasive species is not universal, but depends on environmental set up and changes of species fitness along environmental gradients – typically water availability, shading and nutrient supply (Burns 2004, Molina-Montenegro et al. 2012, Skálová et al. 2013) or climatic conditions, e.g. frost tolerance (Beerling 1993). Performance and competitive output is species-specific, however, some general trend were detected, e.g. invasive species are less represented with increasing altitude, in mountain areas (McDougall et al. 2011, Pyšek et al. 2011). Nevertheless, this pattern can be confounded with propagule pressure (Dark 2004, Jodoin et al. 2008), because human activities in mountains are reduced compared to lowland (e.g. density of roads is lower, arable land is mostly missing). Alternatively, some invasive species are known to little interact with resident biota (MacArthur 1972, MacDougall et al. 2009). Their niches differ from those of native species, in other words they use an ecological space (resources, space, time) not used by native species (empty niche hypothesis, Elton 1958, Lambdon et al. 2008b). Nevertheless, the majority of invaders has some impact on resident biota and most negative effects belong to the category of competitive interactions (Levine et al. 2004, Kumschick et al. 2015).

The intensity of competition depends on many factors. First, it has been suggested that closely related species, e.g. plants from the same genus, occupy similar niches. According to Hardin (1960) the intensity of competition increases with niche similarity and two species with identical niches cannot coexist (Hutchinson 1957). Therefore, the most intense competition is expected among closely related species (Darwin 1859, Elton 1946, Violle et al. 2011). This is supported by floristic data from invaded areas, where invasive species from the same family as native species were under-represented (Rejmánek and Richardson 1996, Daehler 2001). Second, the competition intensity increases with the density of competitors. The density of competition has two components, total density (e.g. number of all individuals per m^2) and the proportion of the competitors. The majority of studies on invasive plants did not take invader density into account, or considered the invasive species dominant (Leger and Espeland 2010). There is a limited information about invader effect if its density, or cover is low (but see Hejda 2013, Hejda et al. 2017). Finally, the effect of competition can vary among life stages with supposed strongest effect in juvenile stages due to strong thinning effects (Goldberg et al. 2001).

Competitiveness of an alien species is important when it spreads from human-altered landscapes, where the naturalization process usually starts (Richardson et al. 2000). Alien populations spread typically along roads, railways and rivers that act as transport vectors and also provide suitable sites for establishment due to disturbances in their vicinity (Mack 2003). Riparian sites, one of the most invaded habitats worldwide (Richardson et al. 2007, Pyšek et al. 2010), are most suitable for alien species' naturalization. First, river corridors are an efficient and diverse vector of spread – propagules flow downstream, can be transported along animal migratory paths upstream or beyond river corridors. Mud helps seed to stick on animals and on machinery, facilitating spread of species that are not equipped for epichory. Second, riparian habitats are a very diverse mosaic of environmental conditions, with sufficient water and nutrient supply. Third, floods disturb native vegetation, provide space by creating gaps and facilitate establishment of alien species in environment that is highly competitive for light (Naiman and Décamps 1997). Some alien species with a wide environmental valence spread after establishment further from river corridors. This is documented by increasing ratio over time of non-riparian to riparian localities in *Acer negundo* (Erfmeier et al. 2010), *Fallopia japonica*, *F. sachalinensis*, or *Impatiens glandulifera* (Pyšek and Prach 1993).

To provide further insights into a complex process of plant invasion, this thesis aims to integrate diverse factors that contribute to invasiveness in selected species of the genus *Impatiens* from the Balsaminaceae family (Fig. 1). In the presented papers, multiple factors that are known to affect invasiveness were studied, such as biological traits, propagule pressure, residence time, environmental constrains and competition with native species. The genus *Impatiens* was chosen as a suitable study system, because it includes both successful invaders and species that do not invade. The congeneric approach enabled to compare the traits of species unbiased by different phylogeny, therefore we could identify potential invasive species from this genus more precisely. We also included a native species to determine whether or not (i) successful invaders have similar traits with the native species, (ii) niches of the native and invasive species overlap, i.e. how strongly native and invasive species interact with each other, and (iii) whether the invasive species are competitively stronger that the native one under varying environmental conditions and competitors' density.

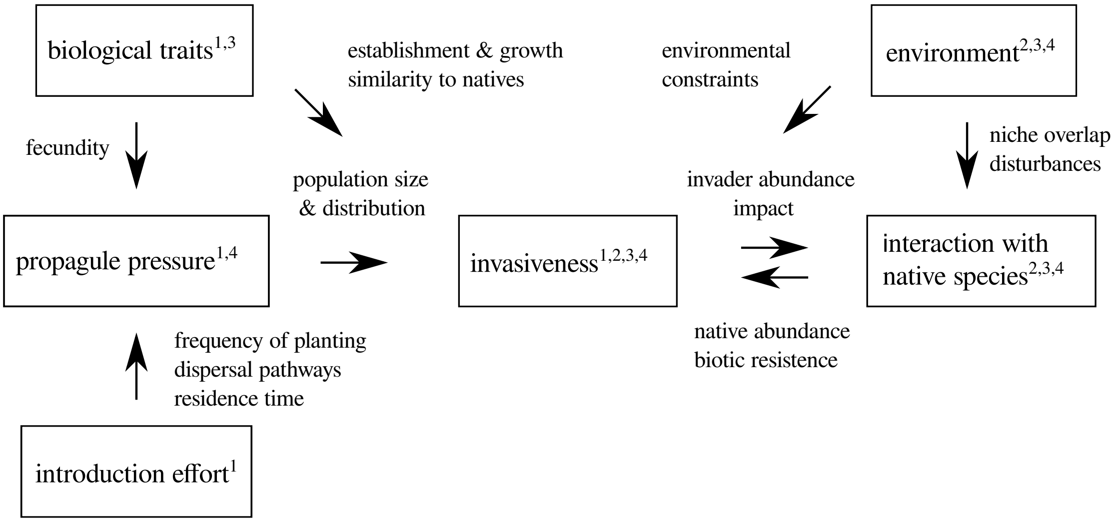


Fig. 1. Assumed relationships between invasiveness and factors that were investigated in the Ph.D. thesis. Superscripts denotes studies, where particular factors were investigated (1 = Study 1, etc.).

Thus, the broad aims of my dissertation were to identify traits associated with invasiveness of selected *Impatiens* species (Study 1), find evidence for niche differentiation and competitive interactions in one native and two invasive *Impatiens* species that coexist in the field (Study 2), and quantify the competition of these three species under manipulated environmental conditions, varying plant densities and different life stages in an experimental garden (Study 3). Finally, to capture the spatio-temporal trends in the dynamics of the most invasive of the studied species, *Impatiens glandulifera*, and infer about possible future avenues of its invasion, I aimed at determining factors that affect its distribution and abundance along river corridors and spread beyond (Study 4).

1.2 Study species

The genus *Impatiens* is in the Balsaminaceae family and contains two genera: the species-rich *Impatiens* and monotypic *Hydrocera* (Fischer 2004). *Impatiens* belongs to one of the largest genera of the flowering plants with ~1000 species (Yu et al. 2016). The representatives of the genus occur predominantly in the tropics and subtropics of the Old World (Grey-Wilson 1980) and has five diversity hotspots: tropical Africa, Madagascar, southern India and Sri Lanka, the eastern Himalayas, and south-east Asia (Yuan et al. 2004). The genus is taxonomically very complicated (Hooker 1908, Grey-Wilson 1980) and every year several new species are described. Most species occur in tropical and subtropical mountain forest areas with abundant precipitation, and only a few are able to grow in drought and direct sunlight (Janssens et al. 2009). A few species are native to the temperate zone (most notably *I. noli-tangere* and *I. capensis*), however many species from subtropical Asia occur in high mountains. Asian species are predominantly annuals that overwinter as seeds, hence are able to cope with temperate conditions (Adamowski 2008, Yu et al. 2016).

The genus is horticulturally very attractive (see Fig. 2), *I. walleriana* and *I. hawkerii* belong to the most frequently planted ornamentals in the world (Morgan 2007). *Impatiens balsamina* has been cultivated for ~4000 years in India, but other species have been grown approximately for last 150 years (Grey-Wilson 1983). Planting of several species in the 19th century resulted in several worldwide invasions. *Impatiens glandulifera*, native in Himalaya, is naturalized in Europe, North America, Russia, and New Zealand (Beerling and Perrins 1993), its occurrence has been recently documented in South America, Colombia (GBIF 2017, see Fig. 3F). *Impatiens parviflora*, native to central Asia, is naturalized in Europe, North America, East Asia (Mattews 2008, GBIF 2017, Fig. 3H). *Impatiens balfourii*, native in Himalayas, is naturalized in Europe, North America, Japan, and Australia (Adamowski 2009, GBIF 2017, Fig. 3A). Two more thermophilous species, *I. balsamina*, native to India and *I. waleriana*, native to east Africa, are naturalized in tropics and subtropics all around the world, but were found in some warmer temperate regions as well (Adamowski 2008, GBIF 2017, Fig. 3B and 3J respectively). Invasion of most of these species started by escape from cultivation, only *I. glandulifera* was, in addition to this pathway, intentionally spread by beekeepers due to its massive nectar production until late fall (Hegi 1912, Hartmann et al. 1995, Chittka and Schürkens 2001). *Impatiens* species that occur in the temperate zone are mostly annuals and spread exclusively by seed (Adamowski 2008, Matthews et al. 2015). Seed is dispersed actively by capsule dehiscence up to several meters, depending mainly on plant's height, and passively, e.g. as a soil contaminant, by epizoochory, on tires along roads, by water flow, with garden waste and by logging machinery (Coombe 1956, Beerling and Perrins 1993, Hatcher 2003).

Eradication of all invasive balsam species from small areas is possible by pulling, mowing or grazing before the seed set (Matthews et al. 2015). Herbicide use is problematic due to their common occurrence along waterways, and it is not necessary, because mechanical control is effective, if done properly. Further, the biocontrol agent, rust *Puccinia komarovii* var. *glanduliferae,* was released in the UK in 2014 (Tanner et al. 2015), however was able to overwinter only in some populations of *I. glandulifera* in 2016 (Varia et al. 2016).

We used 10 *Impatiens* species: *I. balfourii* Hook. f., *I. balsamina* L., *I. capensis* Meerb., *I. edgeworthii* Hook. f., *I. flemingii* Hook. f., *I. glandulifera* Royle, *I. noli-tangere* L., *I. parviflora* DC., *I. scabrida* DC. and *I. walleriana* Hook. f. (Fig. 2, Table 1) to search for traits associated with invasiveness (Study 1), three of them that occur in the Czech Republic (*I. glandulifera*, *I. noli-tangere*, *I. parviflora*) to explore niche partitioning and coexistence in the field (Study 2) and competition in the experimental garden in detail (Study 3).

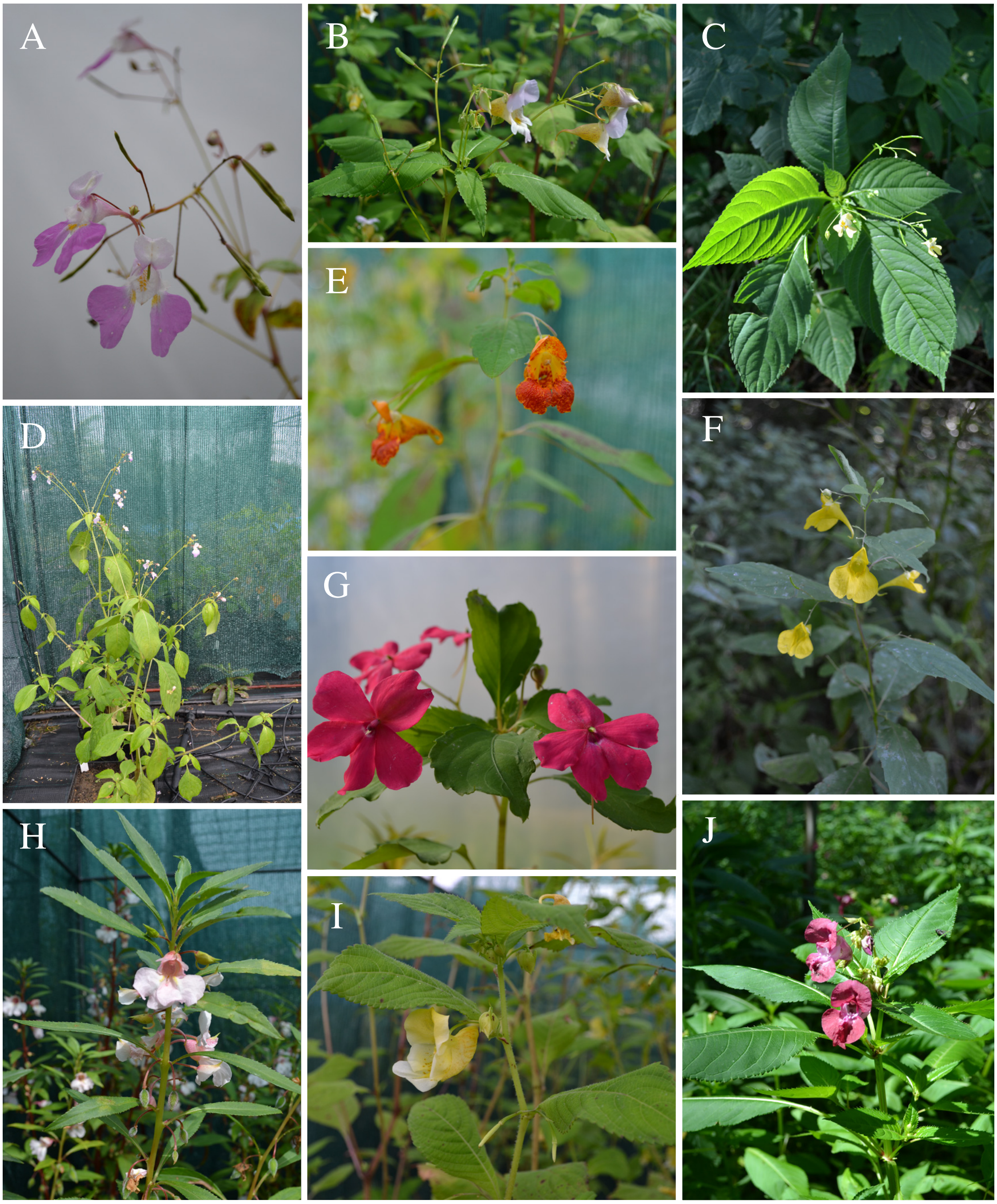
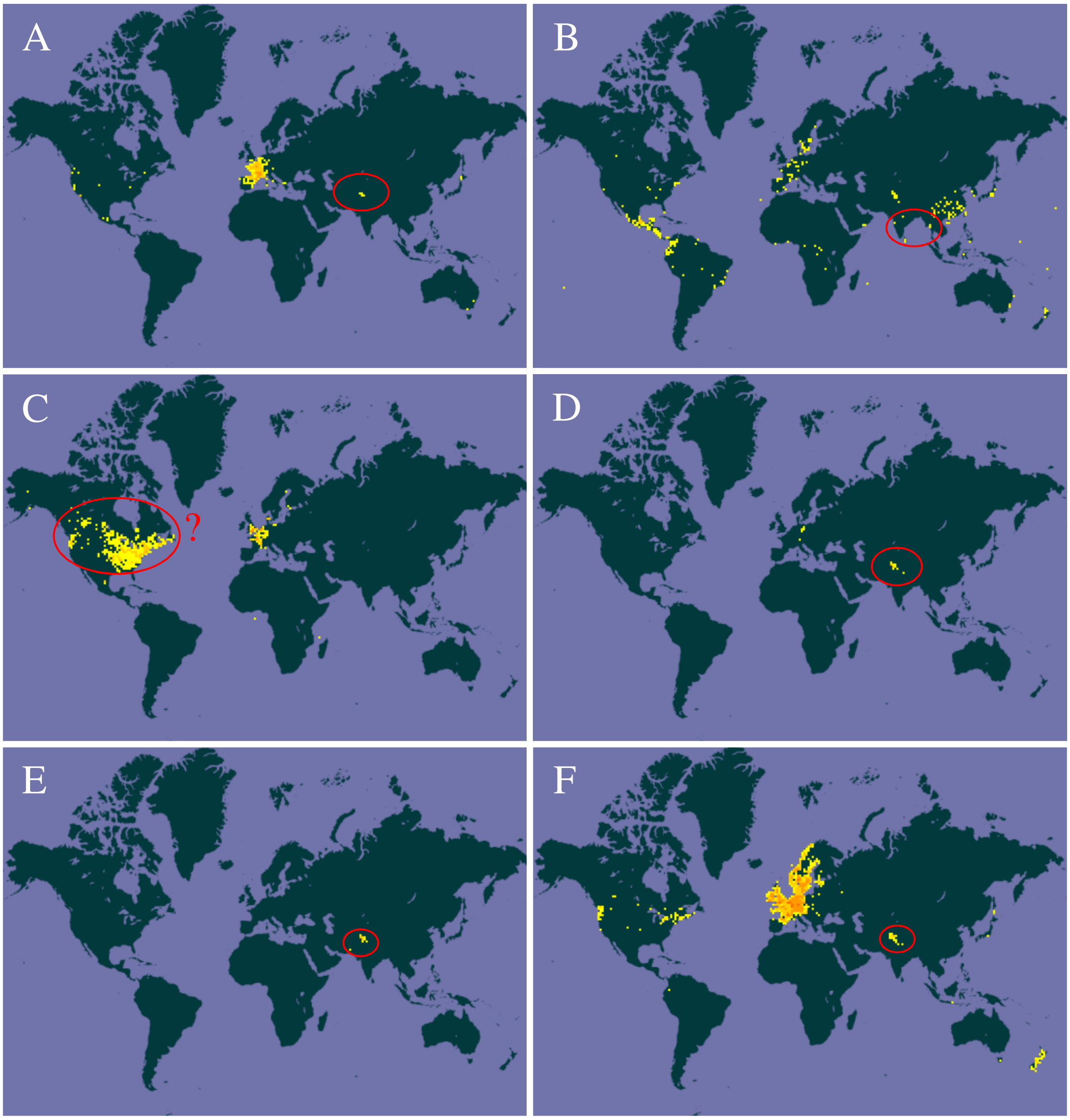


Fig. 2. *Impatiens* species that were studied in the Ph.D. thesis. **A**: *I. balfourii*, **B**: *I. edgeworthii*, **C**: *I. parviflora*, **D**: *I. flemingii*, **E**: *I. capensis*, **F**: *I. noli-tangere*, **G**: *I. walleriana*, **H**: *I. balsamina*, **I**: *I. scabrida*, **J**: *I. glandulifera*

The most prominent invader, *I. glandulifera,* was used to analyse its distributional pattern across the landscape (Study 4). The species were included based on their invasion status in Europe, seed availability and frequency of planting. All naturalized and commonly planted species were covered, only *Impatiens hawkeri*, despite being frequently cultivated, was not included, because it is propagated from stems cuttings and not from seed as the other species (Morgan 2007).



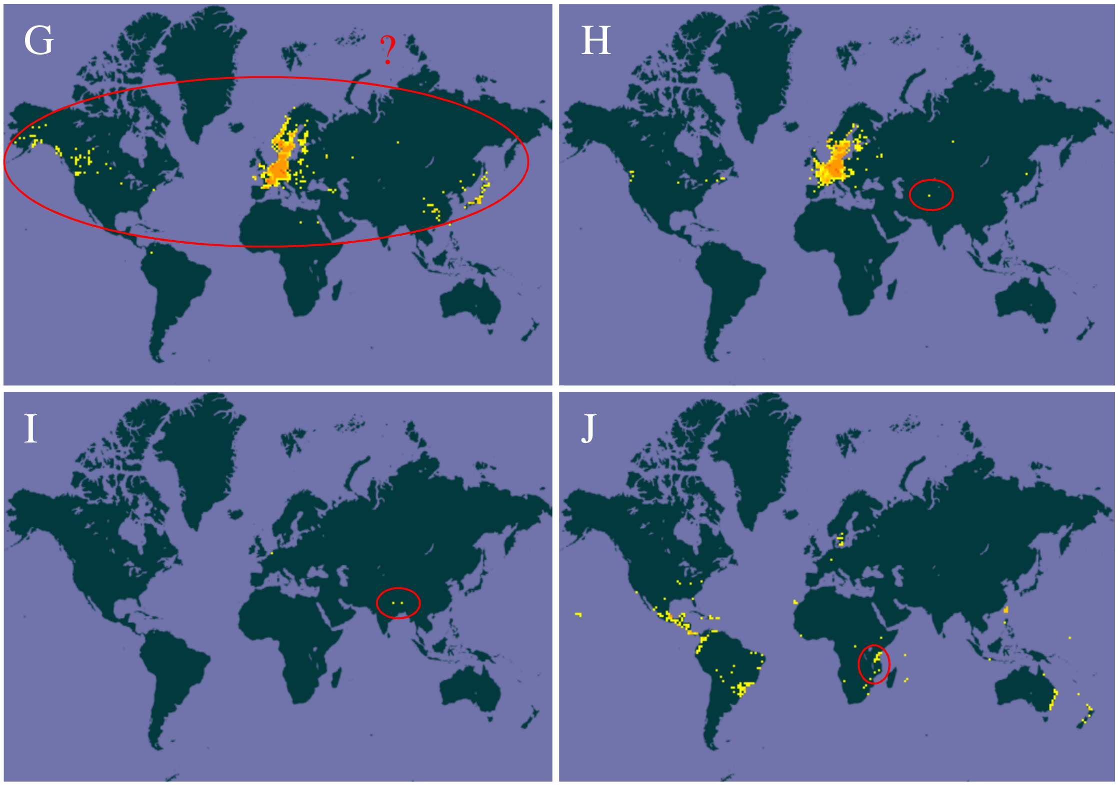


Fig. 3. Distribution of the 10 *Impatiens* species that were studied in the Ph.D. thesis. **A**: *I. balfourii*, **B**: *I. balsamina*, **C**: *I. capensis*, **D**: *I. edgeworthii*, **E**: *I. flemingii*, **F**: *I. glandulifera*, **G**: *I. noli-tangere*, **H**: *I. parviflora,* **I**: *I. scabrida*, **J**: *I. walleriana*. Native range of each species indicated by red circle, based on Adamowski (2008) and http://www.efloras.org. Extent of the native ranges labelled with question mark is unclear. Maps obtained from Global Biodiversity Information Facility (www.gbif.org).

Table 1. Overview of *Impatiens* species included in the study and information about their invasion. Based on data taken from Study 1.

Species	Native range	Invaded range	Invasion status in Europe	First record in cultivation
I. balfourii Hook.f.	W Himalaya	S & W Europe, Japan, N America, SE Australia	naturalized	1901, France
I. balsamina L.	India, Myanmar	tropical and warm temperate regions	casual	2000 BC India, 1542 Europe
I. capensis Meerb.	N America	W, C & N Europe, E Asia, W N America?	naturalized	<1822 Great Britain
I. edgeworthii Hook. f.	W Himalaya	Germany	casual	?1983, Germany
I. flemingii Hook.f.	NW Himalaya	none	not escaped	no data
I. glandulifera Royle	W Himalaya	Europe, Asia, N America, New Zealand, Japan	naturalized	1839, Great Britain
I. noli-tangere L.	Europe, N & E Asia, W N America	-	native	-
I. parviflora DC.	C Asia	Europe, N America, E Asia	naturalized	1830, Switzerland
I. scabrida DC.	Himalaya	Czech Republic, Sweden, Norway, Netherlands	casual	1836
I. walleriana Hook. f.	E Africa	Tropical and warm temperate regions	not escaped	1883, Europe

1.3 Data sources

Detailed description of data acquisition, datasets structure and data analysis is provided in particular Method sections in the studies forming the core of the thesis (p. 19–75). Here I summarize general information about data for each study to illustrate the variety of methods used to build as complete as possible picture of invasion within the genus studied. The data were collected by using various methods: field, experimental garden, climatic chambers and databases.

In Study 1 traits of 10 selected species, which are supposed to be beneficial to plant fitness and potentially related to ability to naturalize or invade, were measured directly in an experimental garden and climatic chambers. The aim was to capture the species performance over the whole life cycle, i.e. seed, seedling and adult traits. The following traits were measured: seed mass; time since seed sowing to germination; seed germination in laboratory; seedling emergence in the experimental garden; seedling growth rate; total seedling biomass; seedling root/total biomass ratio; adult aboveground biomass; height and fecundity. Invasion success of *Impatiens* species was characterized by two variables: (i) invasion status in Europe (from DAISIE 2017), taken as the prevailing stage of the invasion process reached in countries where the species was recorded and (ii) the number of global temperate regions in which the species is known to occur as naturalized (from the GloNAF database; van Kleunen et al. 2015, Pyšek et al. 2017). Finally, the frequency of planting was estimated on a rough scale (none, rare, common) based on the knowledge of cultivation of the given species in the past, seed availability on internet and availability on botanical gardens seed lists to quantify the propagule pressure.

In Study 2 niche differentiation, coexistence and competition between two invasive (*I. glandulifera* and *I. parviflora*) and native (*I. noli-tangere*) species was studied in 84 permanent plots 1 × 1 m in size, distributed in five localities in the Czech Republic. Localities were chosen to harbour mixed populations of the three species to cover all factorial combinations of the species' presence and absence. The plots were sampled for four years and the following parameters were measured: number of all *Impatiens* individuals; cover of all vascular plant species (including *Impatiens*); bare soil cover;, soil moisture; tree canopy cover; total soil carbon and nitrogen content; slope. From species data obtained in the plots (with the *Impatiens* species excluded) mean Ellenberg indicator values (EIV) were calculated, which were further used as surrogates for actual field measurements.

In Study 3 competition between the same species as in Study 2 was measured in detail in an experimental garden to verify and extend the results obtained in the field. The experiment was designed as a full factorial one: seeds of one or two species were sown in 5-liter pots to achieve two different total densities of seedlings (high and low) that correspond to the range of densities typically observed in the field. Within each total density level, three ratios of target plants to competitor plants, high (1 : 5), medium (1 : 1) and low (5 : 1) were established. This resulted into 24 species/density/competition combinations, that were replicated under four combinations of water and light (both low and high) supply. In total, the experiment consisted of 960 pots (4 environmental treatments × 24 species-density-competition combinations × 10 replicates). Plants were counted and measured since the seedling emergence in 3 weeks intervals, and were harvested in July. For each pot, data were obtained on mean species height; number of individuals; total aboveground biomass; and number of capsules of each species.

In Study 4 distribution and abundance of *Impatiens glandulifera* was mapped in more than 1200 patches along four rivers and their tributaries. Both individual plants and discrete populations were mapped by a GPS device by systematically walking along the rivers. Total number of *I. glandulifera* individuals in each patch was calculated as a product of patch area and plant density that was scored on a three-grade scale (scattered, common, dominant). The patches were further characterized in terms of the distance from the riverbank; height above the river surface; degree of soil disturbance; flooding regime; and habitat type. Data about flooding were extracted from the DIBAVOD database (DIBAVOD 2016).

2 Juvenile traits as determinants of naturalization

(Study 1)

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Research article

Juvenile biological traits of *Impatiens* species are more strongly associated with naturalization in temperate climate than their adult traits

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ABSTRACT

Potentially invasive species can be identified before they start to spread by comparing their traits with those of successful invaders. A powerful tool for delimiting the traits associated with invasiveness are analyses of a number of species of the same genus, where it is more likely to detect relevant differences because of elimination of biases that constrain the search for such traits in whole floras. Since the influence of traits on invasion success may differ with respect to the stage of the plant's life cycle, comparative studies should address the whole life cycle, including early stages. Here we studied which biological traits are associated with the ability to naturalize within the genus *Impatiens*, how frequency of planting affects naturalization success, and whether naturalized species with biological traits similar to the native representative of this genus are more successful. The genus *Impatiens* includes a number of cultivated species popular in horticulture, among them several widespread invaders. We used one native and 10 alien annual taxa. This data set involved all commonly cultivated species, and representatives of different invasion status in Europe. In garden experiments and climatic chambers we measured seed mass, time to germination, percentage of seeds germinated, seedling growth rate, total seedling biomass, seedling root/total biomass ratio, adult biomass and fecundity. These traits and planting frequency were used to explain the invasion success of the species, expressed as (i) invasion status in Europe and (ii) the number of global temperate regions in which the species has been reported as naturalized. The frequency of planting was used as a proxy of propagule pressure to separate this potentially biasing factor known to affect plant invasiveness from the effect of plant traits. We found that both species traits and frequency of planting were correlated with naturalization. Species naturalized in many temperate regions of the world had heavier seeds, high seedling growth rate and allocated low proportion of seedling biomass to roots. Importantly, common planting was more strongly correlated with naturalization success than with biological traits. *Impatiens* species naturalized in Europe exhibited better seed germination in the common garden, and it took a longer time for the seeds to germinate. Species escaped from cultivation but occurring only as casuals in Europe had heavy seeds and invested more resources into shoots than roots, whereas species not escaping from cultivation were characterized by fast seed germination and light seed. In general, traits linked to early stages of the life cycle were more strongly associated with invasion success than those of the adults. Frequently planted species tend to naturalize more easily than those planted scarcely. The successful invaders share traits similar to the one native *Impatiens* species in Europe and those with traits distinct from it do not invade. Our results indicate that many *Impatiens* species represent potential invaders should their planting become more widespread; this prediction is supported by the fact that *Impatiens* species included in the experiment completed their life cycles in an experimental garden in central Europe.

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1. Introduction

Effort to identify biological traits associated with plant species invasiveness has been central to plant invasion ecology (Roy, 1990; Pyšek and Richardson, 2007; van Kleunen et al., 2010a). As the traditional methodical approach towards identifying the role of species traits, comparisons of complete regional floras, is constrained by great variability within the species pools which makes it difficult to detect the respective traits (Moravcová et al., 2010), discovering which species traits promote invasiveness is thus more realistic at the generic or familial level (Rejmánek and Richardson, 1996; Burns, 2004; Cadotte et al., 2006; Pyšek and Richardson, 2007; van Kleunen et al., 2010b). Searching for traits linked to invasiveness in related species is also justified by the fact that most variation is observed among species within genera (Moravcová et al., 2010). This indicates that the predictions of species invasiveness should be done at the species level (Pyšek et al., 2009, 2014a; Moravcová et al., 2010).

Up to now, comparisons of closely related species have been used to reveal traits associated with invasiveness in several genera or families, including *Pinus* (Rejmánek and Richardson, 1996; Grotkopp et al., 2002; Matzek, 2011), *Senecio* (Sans et al., 2004), *Rubus* (McDowell, 2002), *Oenothera* (Mihulka et al., 2006), *Eucalyptus* (Radho-Toly et al., 2001), *Lespedeza* (Woods et al., 2009), *Crepis* and *Centaurea* (Muth and Pigliucci, 2006; Muth and Pigliucci, 2007), *Impatiens* (Perrins et al., 1993; Perglová et al., 2009; Skálová et al., 2011, 2012, 2013), *Iridaceae* (van Kleunen and Johnson, 2007). For details and other studies see review by Pyšek and Richardson (2007). To date, however, few studies have included more than four species within the genus, which somewhat limits the possibility to detect important traits and generalize beyond the specific circumstances of a given study (but see Rejmánek and Richardson, 1996; Grotkopp et al., 2002; Muth and Pigliucci, 2006, 2007; van Kleunen and Johnson, 2007; Matzek, 2011).

Traits of invasive species have been found to differ from those of the native and non-invasive alien species (van Kleunen et al., 2010b), but the relevance of such traits for invasiveness is not the same throughout the whole life cycle. For example, the relative importance of two key concepts related to invasion from the perspective of community ecology, limiting similarity (Abrams, 1983) and competition displacement (Brown and Wilson, 1956), is thought to change during the invasion process, with trait similarity being more important for establishment (Williamson, 2006; Funk and Vitousek, 2007) and dissimilarity for naturalization and invasion (Blackburn et al., 2011; Richardson and Pyšek, 2012). However, studies assessing traits along the complete species' life-cycle are rather rare (but see Radford and Cousens, 2000), despite the well known importance of early life stages, such as seed germination (Moravcová et al., 2010; Chrobock et al., 2011; Skálová et al., 2011) and seedling growth (Grotkopp and Rejmánek, 2007; Skálová et al., 2012) for population establishment and the beginning of invasion (van Kleunen and Johnson, 2007). The importance of seed and juvenile traits for invasion success was demonstrated e.g. for pines (Richardson, 2006).

Finally, it has been well established that whether a species becomes naturalized or invasive in a new region depends on the propagule pressure, a factor that acts in concert with species traits (Richardson and Pyšek, 2006; Pyšek et al., 2015). Propagule pressure is a function of reproduction and dispersal. Since the majority of naturalized and invasive species recruit from deliberately introduced plants (Mack, 2003; Hulme, 2011; Pyšek et al., 2011), horticulture represents the most important pathway of introduction (Groves et al., 2005; Dehnen-Schmutz et al., 2007a; Pyšek et al., 2012), and the frequency of planting can directly affect propagule pressure. Moreover, horticulture selects plants with fast growth and easy reproduction, namely high seed production, easy and massive germination or vigorous clonal reproduction, minimum gardening care, resistance to pathogens and other enemies and wide environmental tolerance (Mack, 2000). Studies searching for traits related to invasiveness revealed just the same traits (Pyšek and Richardson, 2007; van Kleunen et al., 2010b). In addition, plants introduced intentionally could have been preadapted to the local conditions by horticultural selection before they were launched on the market. Thus the probability of naturalization of such plants is greater (Milbau and Stout, 2008; Pyšek et al., 2011) and the process, including subsequent invasion, can be accelerated by horticulture (Pyšek et al., 2002; Hulme, 2011). Repeated introductions, which are typical of deliberately introduced plants, also increase the probability of naturalization and invasion (Richardson, 2006).

In this paper, we address the importance of traits for invasion success by using one native and 10 alien taxa of the genus *Impatiens*, all but one of which are annuals. We included all species within the genus that are commonly cultivated in the temperate climate. The genus includes ~1000 species (Grey-Wilson, 1980; Fisher, 2004), many of which are being introduced as popular ornamentals, and some have become invasive in various parts of the world (Adamowski and Tokarska-Guzik, 2008). The most prominent example is *I. glandulifera*, a highly invasive annual in temperate regions (Beerling and Perrins, 1993; Hejda and Pyšek, 2006; Clements et al., 2008). *Impatiens parviflora* has also invaded the temperate zone (Trepl, 1982; Hejda, 2012) while *I. walleriana*, the only perennial among the tested species, invades in the tropics (CABI, 2014; Pacific Islands Ecosystems at Risk, 2013). The other invasive species are *I. balfourii*, rapidly increasing its range in southern Europe (Adamowski, 2009; Schmitz and Dericks, 2010), *I. capensis*, with an invaded range in western and central Europe and eastern Asia (Perrins et al., 1993; Adamowski and Tokarska-Guzik, 2008), and *I. balsamina*, which has become widely naturalized in many areas of the warm temperate zones and the tropics. *Impatiens balsamina* has been grown for ~4000 years in India (Grey-Wilson, 1983), but other *Impatiens* species have been grown for only the last ~150 years. The high number of planted *Impatiens* species (~90 species worldwide, according to their presence in horticultural databases; Plant Finder of the Royal Horticultural Society; PlantFiles of Dave's Garden; HortiPlex Plant Database of GardenWeb), together with the fact that many of them have become invaders, some of them widespread, makes the genus a suitable model group to ask what drives the performance of those that succeeded. As the genus includes both successful invaders and species that do not invade despite being planted provides an opportunity to compare species traits of closely related species unbiased by phylogenetic effects. Moreover, the presence of both native and invasive *Impatiens* species in our study area of central Europe makes it possible to assess the role of invaders' biological similarity to the native species, and whether or not it is beneficial for naturalization in the new range. To obtain insights into the mechanisms of invasion within the genus, we thus ask the following questions: (i) Which biological traits are associated with the ability to naturalize in the genus *Impatiens*? (ii) What is the role of the frequency of planting in the probability of becoming naturalized? (iii) Are the traits of the native species, that is successful in a given settings, close to those of the successfully naturalized species?

2. Material and methods

2.1. Study species

We selected nine alien species of *Impatiens*, and one cultivar (further termed 'species' for simplicity), differing in their invasion

Table 1
Overview of the *Impatiens* species with their characteristics. Invasion status (naturalized = established in DAISIE terminology) is taken from DAISIE (2015), number of global temperate regions where naturalized from the GloNAF database (van Kleunen et al., 2015 see text for details). Planting frequency was based on the knowledge of cultivation of the given species in the past, seed availability on Internet and availability on botanical gardens seed lists (Index semina 2009 and 2010). Information on the first report of cultivation, region of native distribution and invaded range is according to [1]Adamowski and Tokarska-Guzik (2008), [2]the Global Biodiversity Information Facility (www.gbif.org), [3]Tropicos (www.tropicos.org), [4]Baade and Gutte (2008), [5]Kalveram (2014), [6]http://waarneming.nl/waarneming/view/51036938. Seed sources: [1]Antwerp Botanic Garden, [2]Botanical Garden Graz, [3]Botanical Garden in Krefeld, [4]Botanical Garden of the Masaryk University, [5]Botanical Garden of the Regensburg University, [6]Botanical Garden of the University of Agronomic Science and Veterinary Medicine in Bucharest, [7]Botanical Garden of the University of Hohenheim, [8]Botanical Garden und Botanical Museum Berlin-Dahlem, [9]Ecological-Botanical Garden in Bayreuth, [10]Siauliai University Botanic Garden, [11]Station of Nature Research and Environmental Education – Marijampole, [12]W. J. Beal Botanical Garden of the Michigan State University; seeds were obtained via seed lists from years 2009 (in the table marked by *) and 2010.

	Invasion status in Europe	Number of naturalized temperate regions globally	Planting frequency	Cultivation	Region of native distribution	Invaded range	Seed sources
I. balfourii Hook. f.	Naturalized	6	Rare	1901, France	W Himalaya[1]	S & W Europe, Japan, N America, SE Australia[1, 3]	4, 6, 9
I. balsamina L. (incl. *I. balsamina* 'alba')	Casual	34	Common	2000 BC India, 1542 Europe[1]	India, Myanmar[1]	tropical and warm temperate regions[1], recently also Scandinavia and Canada[3]	1, 4, 5, 6, 7*, 8, 10; 11*(*I. balsamina* 'alba')
I. capensis Meerb.	Naturalized	10	Rare	<1822 Great Britain[1]	N America[1]	W, C & N Europe, East Asia, N America[1, 3]	12
I. edgewothii Hook. f.	Casual	1	None	?1983, Germany[5]	W Himalaya[1]	Germany[4, 5]	8
I. flemingii Hook. f.	Not escaped	0	None	No data	NW Himalaya[2]	No data	2*
I. glandulifera Royle	Naturalized	45	Common	1839, Great Britain[1]	W Himalaya[1]	Europe, Asia, N America, New Zealand, Japan[1, 3]	Field; Czech Rep. (50°18′4.315″ N, 16°5′22.730″E)
I. noli-tangere L.	Native	0	–	–	Europe, N & E Asia, W N America[1, 3]	–	Field; Czech Rep. (50°21′28.501″ N, 16°9′48.858″ E)
I. parviflora DC.	Naturalized	30	Common	1830, Switzeland[1]	C Asia[1]	Europe, N America, E Asia[1,3]	Field; Czech Rep. (50°6′42.770″ N, 15°10′10.635″ E)
I. scabrida DC.	Casual	0	Rare	1836	Himalaya[1]	Czech Republic[1], Sweden[3], Netherlands[6]	1, 4, 5; 3, 7*, 11 (under the name *I. cristata*)
I. walleriana Hook. f.	Not escaped	9	Common	1883, Europe[1]	E Africa[1]	Tropical and warm temperate regions[1, 3]	11*

status (sensu Richardson et al., 2000) in Europe: four are naturalized (i.e., create self-sustaining populations), three casual aliens (depend on repeated introductions by humans for their occurrence in the wild) and two are only planted and not escaping from cultivation, and the native species *I. noli-tangere* (Table 1). The cultivar *I. balsamina* 'alba' was included in the study because it exhibited the most vigorous growth and highest fecundity in comparison with of all other cultivars of *I. balsamina* (*I. b.* 'flore', and *I. b.* 'violacea') and the botanical species of *I. balsamina* in a pilot experiment. All species were annuals, except for *I. walleriana*, which is perennial, but it is commonly planted from seed as an annual plant in the temperate zone. The majority of species included in the study have been cultivated since ~1850s, but only some of them to great extent such as *I. balsamina* and *I. walleriana* recently, and *I. glandulifera* in the past (Table 1).

2.2. Invasion success

We used two variables to describe the invasion success of the *Impatiens* species studied: First, (i) invasion status in Europe (from DAISIE, 2015), taken as the prevailing stage of the invasion process reached in countries where the species was recorded. According to DAISIE we distinguished whether a species is naturalized ('established' in DAISIE terminology), casual or did not escape from cultivation; this reflects the realized invasion potential in the target region of Europe. The second was (ii) the number of global temperate regions in which the species is known to occur as naturalized. Here, we restricted data to naturalization in temperate regions only, because this corresponds to experimental conditions under which *Impatiens* species were grown in our experimental garden. The data on naturalization was taken from the GloNAF database, the most comprehensive resource containing information on naturalized alien floras in 843 regions of the world (van Kleunen et al., 2015).

2.3. Frequency of planting

We included for each species the estimate of the frequency of planting in Europe, a proxy for propagule pressure, which is known to affect the invasion success (e.g. Dehnen-Schmutz et al., 2007a; Pyšek et al., 2015) and therefore could bias the effect of plant traits. The frequency of planting was scored on a rough scale (none; rare; common) based on the knowledge of cultivation of the given species in the past, seed availability on internet and availability on botanical gardens seed lists (Index Seminum 2009 and 2010).

2.4. Species traits

For the study species, we measured traits that are supposed to be beneficial to plant fitness and potentially related to ability to naturalize or to invasiveness. Our aim was to cover plant performance over the whole life cycle, by including not only traits of adult plants that are most commonly addressed in studies on invasiveness, but also traits related to seeds, and seedling stage. We measured the following traits in the three experiments: (i) experimental garden – mostly adult traits (adult aboveground biomass – further referred as 'adult biomass'; fecundity and seed mass), (ii) climatic chambers – seedling traits (seedling growth rate; total seedling biomass; and seedling root/total biomass ratio), (iii) experimental garden – seed germination (time since seed sowing to germination and seed germination rate). We measured also adult plant height, but we decided not to include it in analyses, because we consider the adult plant's biomass a better proxy of competitive strength, and both measures were closely correlated ($r = 0.73$; also see Fig. 3F).

2.5. Seed sources

Seeds of *Impatiens* species occurring in the Czech Republic (*I. noli-tangere*, *I. parviflora* and *I. glandulifera*) were collected in summer 2011 in eastern and central Bohemia in the field; seeds of the other species were obtained from botanical gardens making seeds available via seed lists (Index Seminum) in 2009 and 2010 (Table 1). Seeds from the botanical gardens were sown in 2011 and plants grown in a glasshouse at the Institute of Botany CAS, Průhonice, Czech Republic, to obtain sufficient number of seeds for the experiments, to check species identity and avoid possible maternal effects (Roach and Wulff, 1987). After collection, seeds of *I. noli-tangere* and *I. capensis* were kept in a refrigerator at 3 °C on heat-sterilized wet river sand in Petri-dishes, as dry storage decreases the seed germination considerably (Perglová et al., 2009). Seeds of other species were stored in paper bags at room temperature.

2.6. Seed germination in the experimental garden

Twenty seeds were placed in a 10 cm × 10 cm × 15 cm pot filled with heat-sterilized common garden soil and covered by a thin layer (0.5 cm) of soil, in 10 replicates per species. For *I. flemingii* we were able to establish only seven replicates, because of the low number of available seeds. This germination experiment was established on 24 October 2012 in the experimental garden of the Institute of Botany CAS in Průhonice (49°59′38.972″ N, 14°33′57.637″ E; mean annual temperature 8.6 °C; mean annual precipitation 610 mm). The germination of seeds was recorded by counting the emerged seedlings once a week from 31 January 2012 to 4 June 2013; the recording ceased when the number of seeds germinated between the two counts was negligible. These data were used to compute mean time to germination (MTG), further referred to as 'time to seed germination', which was computed as: $\mathrm{MTG} = \sum(n \times d)/N$, where n is the number of seeds germinated between scoring intervals, d is the incubation period in days since beginning of the experiment, and N is the total number of seeds germinated in the treatment.

2.7. Seed mass and seedling growth

Seeds were weighed on a micro-balance with a precision of 10^{-4} g in groups of 10 in 15 replicates (*I. flemingii* only in 13 replicates, due to the low number of available seeds). The seeds were placed on heat-sterilized wet river sand into Petri-dishes and kept at 5 °C. The germinating seeds (with about 2 mm radicles) were transplanted into the plastic trays with individual 39 ml wells filled with sterilized river sand. Ten seeds per species were used, each planted in one well. Trays were put on the plastic plates and supplied with 50% Knop solution, which was maintained at the level of 1–2 cm during the experiment to provide plants with optimal conditions.

To achieve stable nutrient supply, conductivity of the solution was measured three times a week and nutrient solution or demineralized water was added to keep the conductivity at 1770 μS/cm. The nutrient solution was changed about every 10 days to prevent the growth of algae. The seedlings were cultivated in climatic chambers (Vötsch 1014) under a 16/8 h light/darkness regime, with mean humidity of 70% during the light and 80% during the dark period. The temperatures used simulated the gradually changing daily temperatures recorded in the field in spring from a minimum of 5 °C to a maximum of 19 °C (for details see Skálová et al., 2012). Seedling height was measured since the release of the cotyledons from the testa two times a week. After 10 measurements (~1 month in total) the seedlings were harvested and separated into roots and shoots. The biomass was dried at 70 °C for about 24 h and weighed.

2.8. Adult traits

Individuals were grown separately, 10 replicates per species, in 20 cm × 20 cm × 23 cm pots with ~5 L of heat-sterilized common garden soil. Plants were watered daily by a micro-drip system (Hunter Industries, San Marcos, USA) to provide full water supply. To avoid full sunshine, shading net transmitting 50% of incident radiation was used, to meet the *Impatiens* species' general requirement of partial shade (Morgan, 2007; Čuda et al., 2014). Plants were harvested individually, when the first symptoms of senescence appeared, and their height was measured. Peduncles were separated from the shoot biomass, counted, and considered as a substitute for the number of capsules; they were dried separately from the remaining shoot biomass at 70 °C for about 24 h and weighed. Fecundity was expressed as the number of seeds, which was calculated as the number of capsules × average number of seeds in the capsule, derived from seed counts in ~60 capsules (from 45 to 96) per species. The capsule sampling for seed counts was done continuously throughout the whole fruiting season, as the number of seeds in capsule varies over time (J. Čuda, personal observation). This experiment was carried out in the experimental garden of the Institute of Botany CAS, in 2012.

2.9. Data analysis

We analyzed the data obtained from experiments both by univariate and multivariate methods. First, we conducted separate analyses of variance in seed mass, time to seed germination, total seedling biomass, seedling root/total biomass ratio, adult biomass and fecundity, using species identity as the only predictor. These were followed by post hoc Tukey HSD tests. Meeting the assumptions of linear models was checked by means of regression diagnostic plots. This resulted in logarithmic transformation of some response variables (seed mass, adult biomass and fecundity) in order to improve the homogeneity of variance. Seed germination from the common garden was analyzed due to its binomial nature by means of Generalized linear models (GLM) of quasi-binomial family, since also considerable overdispersion was detected (dispersion parameter $\Phi = 3.35$). The seedling growth rate was computed as the species-specific regression slope derived from the linear mixed effect models fit to square-root transformed seedling height. Linear mixed effect models (LME) were used due to repeated measures of individual plants with time since planting and its interaction with species identity as fixed effects and random intercepts and slopes of time since planting for each measured individual. The post hoc tests cannot be conducted both in LME and quasi-binomial GLM analyses and therefore we specified the species identity predictors by use of treatment contrasts with *I. noli-tangere* set as a reference species and tested the differences of coefficient estimates of alien species from those of the native *I. noli-tangere* by means of Wald tests (Crawley, 2007). The residual degrees of freedom necessary for the Wald tests were calculated for LME-analysis by Kenward–Roger approximation (Halekoh and Højsgaard, 2012).

We used the obtained species traits, i.e., model estimates of species-specific coefficients (with exception of *I. walleriana*, which was missing in some of the experiments due to zero seed germination) as the main dataset for multivariate analyses (estimates of fixed effects were used in the case of seedling growth and back-transformed estimates were used in the case of seed germination rates in the common garden). The variation in the species traits was summarized by means of principal component analysis (PCA).

The main aim of the multivariate analysis was to relate the traits of nine (*I. walleriana* was excluded because it did not complete the life cycle, thus some traits were missing) alien species and their frequency of planting to their naturalization, expressed

Table 2
Correlation matrix of species traits and frequency of planting with ability of species to naturalize. Supporting information to Fig. 1.

	Naturalized regions	Naturalized	Casual	Not escaped
Seed mass	0.79	0.19	0.52	−0.75
Time to seed germination	0.51	0.54	0.37	−0.99
Seed germination	0.38	0.77	−0.2	−0.68
Seedling growth rate	0.75	0.4	−0.17	−0.29
Total seedling biomass	0.45	−0.03	0.25	−0.21
Seedling belowground/total biomass ratio	−0.55	0.23	−0.49	0.23
Adult biomass	−0.25	−0.12	0.24	−0.1
Fecundity	−0.6	−0.53	0.29	0.32
Planted not	−0.53	−0.58	0.33	0.33
Planted rare	−0.48	0.26	−0.45	0.15
Planted common	0.95	0.26	0.15	−0.45

as the naturalization status in Europe and the number of geographic temperate regions worldwide where naturalized. Since there is no clear causality between the species traits, and the measures of naturalization and frequency of planting (i.e., no response and predictor dataset), we decided to use co-inertia analysis to test for association between these two datasets (Dray et al., 2003). We utilized RV-coefficient, a multivariate extension of R^2, as a measure of agreement among the two datasets (Robert and Escoufier, 1976). The significance of its value was assessed by permutation tests with 9999 replications.

All analyses were conducted in R 3.1.1 statistical environment (available at www.r-project.org). Besides the base installation packages, we used packages: lme4 1.1-7 for fitting LME model; pbkrtest 0.4-1 for calculating the Kenward–Roger approximation of residual degrees of freedom of LME model; and ade4 1.6-2 for conducting the Co-inertia analysis and testing the significance of RV-coefficient by permutation test (Dray and Dufour, 2007). The ordination diagrams were drawn CANOCO v. 5.0 (ter Braak and Šmilauer, 2012).

3. Results

3.1. *The relationship of biological traits and frequency of planting with the species' ability to naturalize*

The species traits and the frequency of species' planting were closely correlated with the measures of naturalization success; the multidimensional correlation coefficient was 0.697, $P = 0.019$. Different biological traits were important in affecting the species' naturalization in Europe, and the number of temperate regions where it has become naturalized globally (Fig. 1, see also Table 2). In general, seedling traits were more strongly correlated with main gradients of the ability to naturalize than were the adult traits (biomass and fecundity). High frequency of planting was strongly positively correlated with the number of naturalized temperate regions worldwide ($r = 0.95$, see Fig. 1 and Table 2) and negatively with not escaping from cultivation in Europe ($r = -0.45$).

Species naturalized in many temperate regions of the world were positioned close to each other within the trait space (*I. glandulifera*, *I. parviflora*, *I. balsamina* incl. *I. balsamina* 'alba', and *I. capensis*; see Fig. 2 and Table 2) and had heavy seed, high seedling growth rates and low proportion of total seedling biomass allocated to roots. On the contrary, species naturalized in few or no temperate regions showed much scatter in their traits. For instance, *I. flemingii* and *I. scabrida*, not reported as naturalized anywhere in the world, had shorter time to seed germination and low seed mass (see Table 2 for details). Common planting of *Impatiens* species was more strongly associated with naturalization success than were their biological traits ($r = 0.95$; see Table 2 and Fig. 1).

Plants naturalized in Europe exhibited high seed germination ($r = 0.77$, see Table 2), and long times to seeds to germinate; species known only to occur as casuals had heavy seeds and allocated more resources into shoots than roots (Fig. 1, see Table 2 details). Species not reported to escape from cultivation had short times to germination and light seeds. Commonly planted species are likely to escape from cultivation (see Table 2), the only exception being *I. walleriana* that does not escape although commonly planted.

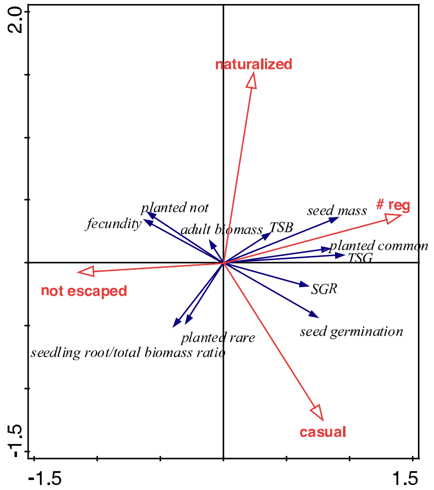

Fig. 1. Relationship between species traits, planting frequency (blue arrows) and their ability to naturalize (red). Co-inertia ordination diagram. Permutation test of co-inertia ("correlation" between species traits, planting frequency and naturalization) $P = 0.02$, RV coefficient (multidimensional correlation coefficient) = 0.697. First two axes explained 69% and 19% of total variability. Abbreviations: SGR – seedling growth rate; TSG – time to seed germination; TSB – total seedling biomass; # reg – number of temperate regions where species is naturalized; naturalization status in Europe (naturalized, casual, not escaped); planted (common, rare, not) – planting frequency. Biomass was transformed by natural logarithm. Native *I. noli-tangere*, *I. balsamina* 'alba' (due to missing values of invaded and naturalized regions) and *I. walleriana* (due to low germination resulting in missing species traits) were excluded from the analysis.

3.2. *Differences in traits between native and alien species*

The native species, *I. noli-tangere*, did not substantially differ in biological traits from the alien species studied. Its position in the multidimensional space derived from biological traits lies among those of the other species (Fig. 2), and exhibited similar values of all traits (Fig. 3A–H). Traits of the two most invasive species in central Europe, *I. glandulifera* and *I. parviflora*, and *I. balsamina*, especially *I. balsamina* 'alba' were more similar to those of the native species than were traits of the other aliens, and the same was true for the

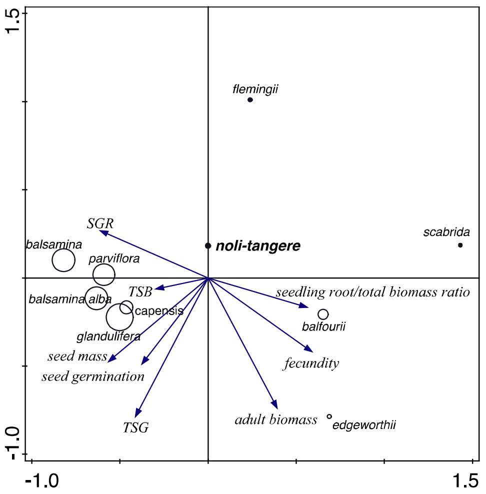

Fig. 2. Relationships of traits of *Impatiens* species. PCA ordination diagram. First two axes explained 49% and 19% of total variability, respectively. Diameter of circles is proportional to the number of naturalized temperate regions worldwide for each species; note that this variable was not included in the analysis. Species symbolized by solid circles are not known to be recently naturalized anywhere; native species, *I. noli-tangere*, is in bold. The same symbol size is used for *I. balsamina* 'alba' and for *I. balsamina* as there are no data about the naturalization of *I. balsamina* 'alba'. Abbreviations: SGR – seedling growth rate; TSG – time to seed germination; TSB – total seedling biomass.

native species' close relative *I. capensis*. On the contrary, traits of species which do not invade (*I. flemingii*, *I. scabrida*, see Figs. 2 and 3) were different from those of the native *I. noli-tangere* as well as from those that invade.

4. Discussion

4.1. *Biological traits associated with naturalization within* Impatiens

Impatiens species naturalized in many temperate regions had heavier seeds than less broadly distributed species, which contradicts the results of some previous studies that invasive species have on average lighter seeds (Rejmánek and Richardson, 1996; Moravcová et al., 2010; but see Crawley et al., 1996). Generally heavy seeds disperse worse than light seeds; this relationship was observed both among (Harper et al., 1970) and within species (Morse and Schmitt, 1985; Cappuccino et al., 2002). The trade-off between seed mass and dispersal capacity drives the balance between the probability of species' establishment and spread. In the *Impatiens* species studied dispersal seems to be less important than establishment, or alternatively, seed mass may not be so closely related to seed dispersal. The explanation could be that invasive *Impatiens* species effectively disperse over long distances by soil movements, animal activity, forestry machines (Coombe, 1956), and by water flow (Lhotská and Kopecký, 1966); these modes of dispersal are not much affected by seed mass. In a similar vein, species in cultivation are dispersed with garden waste (Adamowski and Tokarska-Guzik, 2008) where differences in seed mass are unlikely to play a role as well. The seemingly surprising negative relationship between naturalization success and fecundity is probably due to the general inverse relationship between seed mass and fecundity. One possible explanation is that the advantage gained from producing large seed outweighs possible constraints from a lower seed number, resulting from the trade off between the number and mass of the seed per plant (Westoby et al., 1992).

Heavy seeds are also advantageous for germination and seedling development, hence plant establishment (Baskin and Baskin, 1998). This is supported by the pattern found in our study where the seedlings of heavy-seeded species had higher germination rates and grew faster. The high performance of large-seeded *Impatiens* can be related to light requirements of the majority of species; i.e., their preference of shaded sites (Morgan, 2007). Shade-preferring plants in general tend to have larger seeds, ensuring enough stored reserves before the plant develops sufficient leaf area (Walters and Reich, 2000).

In our data, there was a strong relationship between *Impatiens* seed mass and time to seed germination; similarly to Tomback and Linhart (1990), who found that heavy seeds need a longer chilling period in order to overcome dormancy. This is one of the mechanisms involved in winter seed survival that is very important in temperate regions to ensure proper timing of germination (Baskin and Baskin, 1998). Proper seed germination is crucial for establishment of *Impatiens* species populations, as a mechanism to avoid winter frosts to which they are rather sensitive (Beerling, 1993; Skálová et al., 2011). The low hardiness of *Impatiens* species probably causes their limited spread in colder regions, despite many of them being cultivated; the importance of hardiness in general for plant invasion has been previously documented (Dehnen-Schmutz et al., 2007b; Hanspach et al., 2008).

The most successful invaders in Europe, *I. glandulifera* and *I. parviflora*, are both superior to their non-invasive congeners in at least one particular trait. *Impatiens glandulifera* is much taller and both its seedlings and adults produce much more biomass than all other species, making its individuals highly competitive. *Impatiens parviflora* had the highest germination rate of all species, indicating its perfect adaptation to local (climatic) conditions, which could be related to one of the earliest introduction dates to Europe of all species tested (Table 1). The invasion success of *I. parviflora* is also ascribed to its extreme plasticity (Skálová et al., 2012, 2013) and wide environmental tolerance, especially to shade and drought (Coombe, 1956; Čuda et al., 2014), enabling growth both in spruce plantations and along river banks (Sádlo et al., 2007). We suggest that *I. parviflora* is an example of a species filling an empty niche not occupied by a native species (Hejda, 2012), which compensates for its low competitiveness (Skálová et al., 2013; Čuda et al., 2015).

The ability to naturalize of *I. balfourii* and *I. capensis* may be limited by poor seedling growth, which is not offset by the high germination of seeds. However, *I. balfourii* is highly invasive in western Europe and is currently spreading in southern Europe (Adamowski, 2009), which may be due to higher spring temperatures. Similarly *I. capensis* invades areas with a mild temperate climate in western Europe (Adamowski and Tokarska-Guzik, 2008; GBIF, 2012). Unclear is the future of invasion of *I. edgeworthii*, because this species has both traits of a successful invaders and species, which do not invade, but the growing number of records from Germany indicates its potential to spread (Baade and Gutte, 2008; Weiss, 2013; Kalveram, 2014).

The two proxies of naturalization were not associated with the same traits: for example the number of regions where the species is naturalized showed relatively weak relationship to seed germination, but the species naturalized in Europe were strongly positively linked with this trait. Invasive species in Europe (*I. parviflora*, *I. capensis*, *I. glandulifera*) had higher seed germination and germinated later than non-invasive species, similar to the pattern reported for *Senecio* species (Radford and Cousens, 2000). Conversely, *I. flemingii*, which is not known to escape from cultivation, had low seed germination and an extremely short time to germinate. Differences in predictive power between both measures of naturalization most likely reflect their nature: the

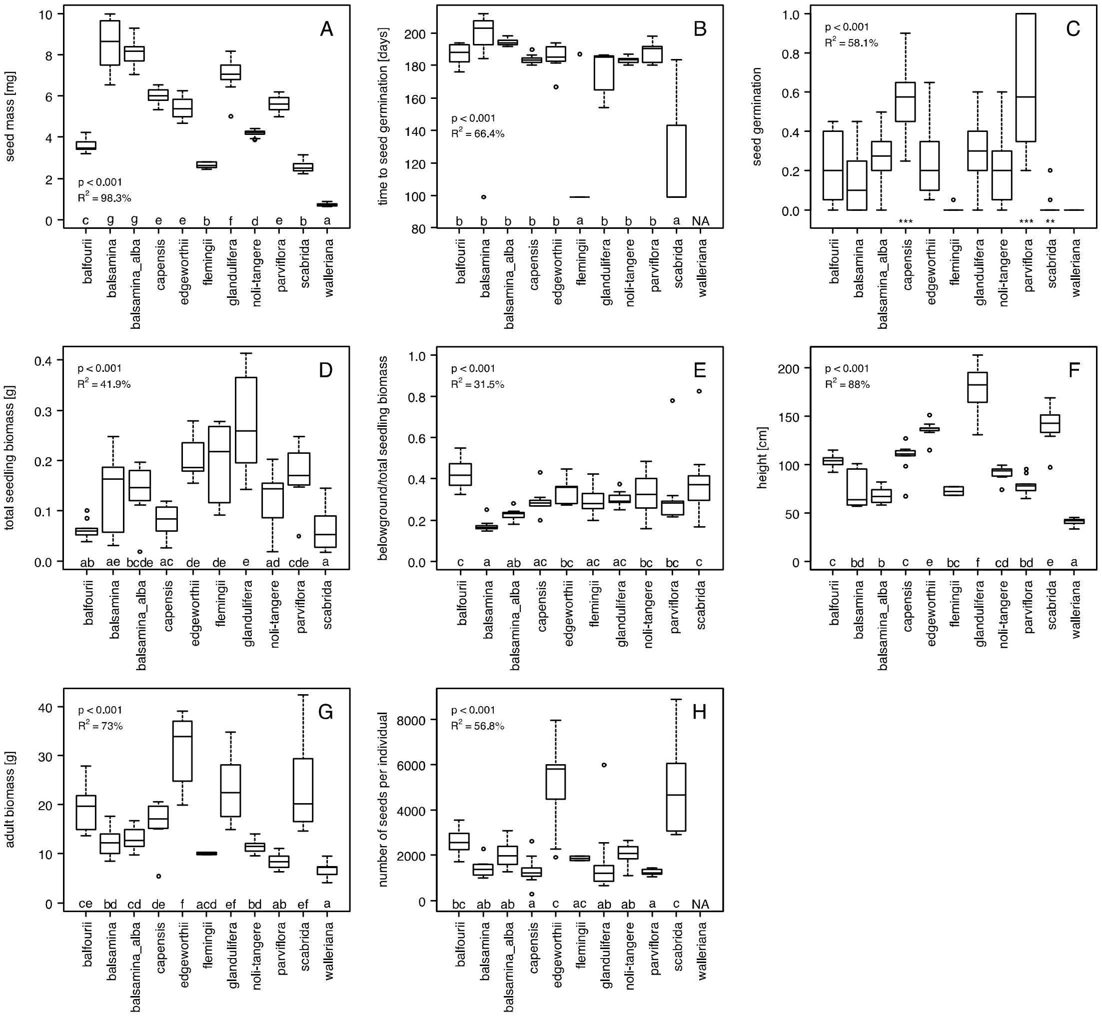

Fig. 3. (A–H) Comparison of traits of *Impatiens* species within the study during the whole life cycle. Overall *P*-value of the test and R^2 (in case of seed germination likelihood pseudo-$R^2 - R^2_L$, Menard, 2000) noted by each graph. Results of Tukey HSD post hoc comparisons indicated by letters below each boxplot. Post hoc tests for seed germination (C) were not conducted, since they are not defined for quasibinomial GLM. Model coefficients of non-native species significantly different from native *I. noli-tangere* are marked by asterisks ($^{***}P < 0.001$; $^{**}P < 0.01$). Total seedling biomass includes both the above- and belowground biomass (D), adult biomass shows the aboveground biomass only (G).

naturalization status in Europe is a qualitative trait related to the ability to become naturalized in a new region, whereas the number of temperate regions globally relates also to the species' ability to become widespread. Therefore, the latter relates not only to ability to naturalize but also provides some indication of invasiveness at the global scale.

Both measures of naturalization were positively associated namely with delayed germination, followed by rapid growth of seedlings (see Fig. 1 and Table 2). This indicates that the seed and seedling traits were more closely associated with successful naturalization within *Impatiens* than the traits of adult plants, such as biomass and fecundity. The importance of early life stages for invasiveness (Grotkopp and Rejmánek, 2007; van Kleunen and Johnson, 2007; Dawson et al., 2011; Skálová et al., 2012) and fitness in general is crucial especially for annuals that have to succeed in early life stages to reach the only reproduction in their life, while perennial plants can persist in early life stages for many seasons before they reproduce. All but one species in our study were annuals that have very poor or non-existing seed banks (Perglová et al., 2009); this makes the early life stage even more critical because their persistence at a site is crucially dependent on successful reproduction and establishment in a given year.

4.2. Commonly planted species are more likely to become naturalized

Our results support the assumption that frequency of planting contributes to successful naturalization of plant species. This is in accord with findings of previous studies that frequent planting increases propagule pressure and therefore promotes species invasiveness (Groves et al., 2005; Dehnen-Schmutz et al., 2007a; Pyšek et al., 2015). For *Impatiens*, planting was among the most important correlates in comparison with the biological traits of species, regardless of the measure of naturalization. Similarly, Hanspach et al. (2008) found that propagule pressure, expressed as the number of botanical gardens in Germany where an alien species was planted, was among the most important predictors of its naturalization success.

Interestingly, common planting was strongly correlated with naturalization in temperate regions worldwide (see Table 2), while in Europe the effects of common and rare planting were of lesser importance.

4.3. Successful aliens differ in traits from unsuccessful ones

In our model system the species that were more similar to the native *I. noli-tangere* tend to become naturalized in Europe and those that are most different do not. Nevertheless, the majority of naturalized species had traits similar to each other, and different from non-invasive species, while the native species possess traits intermediate between these two groups. However, since our data set includes only one native species, the aforementioned pattern needs to be taken with caution. Interestingly, the invasive aliens *I. parviflora* and *I. glandulifera*, long established in central Europe, and also *I. capensis*, were the most similar to the native *I. noli-tangere* when considering all traits together. The same time to seed germination for all four species, including the native, indicates that the right timing of germination is crucial for successful performance of invaders in the temperate zone (Hanspach et al., 2008). *Impatiens capensis*, closely relative to native *I. noli-tangere* (Yuan et al., 2004) seems to be limited in its spread to continental Europe by its poor seedling performance (Beerling and Perrins, 1993; Skálová et al., 2012). In Europe it is invasive predominantly in the western part of the continent (Adamowski and Tokarska-Guzik, 2008; GBIF, 2012), where seasonality and also diurnal fluctuations are less pronounced as the temperature is buffered by oceanic water masses. In the same vein, *I. flemingii* and *I. scabrida*, which markedly differ in their traits from the native species, do not represent a potential threat, because they are limited by climatic conditions; their seeds germinate too early.

In conclusion, it is important to stress that 9 of 10 alien *Impatiens* species included in the experiment completed their life cycles in an experimental garden in central Europe (the only exception being *I. walleriana*). This indicates that those species up to now not reported as naturalized are unlikely to be limited by the regional climate as to their escape from cultivation, and that the majority of *Impatiens* species represent potential invaders should their planting become more widespread. For prediction, it is important to emphasize that invasiveness in *Impatiens* is associated namely with the traits of early life stages, such as high seed mass, delayed germination and fast seedling growth, while the traits of adult plants are of lesser importance.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ppees.2016.02.007.

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3 Coexistence of native and invasive *Impatiens* species

(Study 2)

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ORIGINAL PAPER

Habitat requirements, short-term population dynamics and coexistence of native and invasive *Impatiens* species: a field study

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Abstract The genus *Impatiens* (Balsaminaceae) includes three widespread species in the Czech Republic, central Europe: the native *I. noli-tangere*, and two invasive species, *I. parviflora* and *I. glandulifera*, differing in the dynamics of invasion. They all occur in similar habitats and share basic life-history characteristics, which make them a suitable model for studying species traits associated with invasiveness. In this study we investigated differences in habitat requirements of these *Impatiens* species, their coexistence and short-term population dynamics in the field. We established 84 1 × 1 m permanent plots in five localities where all three species co-occurred. In each plot vascular plant species were determined, their cover estimated and all individuals of *Impatiens* species counted. Site characteristics including tree canopy cover, soil moisture, nitrogen and carbon content, and slope were measured directly. Nutrients, light, humidity and soil reaction were estimated using Ellenberg indicator values. The presence of *I. noli-tangere* was strongly correlated with high soil moisture, that of *I. parviflora* with high tree canopy cover and low soil moisture. *Impatiens glandulifera* exhibited a unimodal response to tree canopy cover, avoiding both very shaded and fully open sites. The current-year abundances of all species were negatively related to those of congeneric species. These results suggest that the coexistence of *Impatiens* species in the same habitat is due to microsite differentiation. Further spread of *I. glandulifera* to new habitats, and reduction of the native *I. noli-tangere* niche, can be expected in areas where the latter species co-occurs with competitively strong invasive congeners.

Keywords Balsam · Canopy cover · Congeneric species · Ellenberg indicator values · Microsite differentiation · Soil moisture

Introduction

Many studies show that some invasive species are competitively superior to native species (Baker 1965; Roy 1990; Mack et al. 2000; Vilà et al. 2011), reduce native biodiversity and change the functioning of invaded ecosystems (Vitousek and Walker 1989; Hejda et al. 2009a; Pyšek and Richardson 2010; Vilà et al. 2010; Gaertner et al. 2011). The success of invasive species has been traditionally attributed to

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their biological and ecological traits, such as tall stature, high biomass, high growth rate and fecundity, and efficient dispersal (Pyšek and Richardson 2007; Moravcová et al. 2010; van Kleunen et al. 2010). It has also been suggested that invasive plants are phenotypically more plastic than non-invasives or natives, hence able to grow and reproduce in a wide range of environmental conditions (Pigliucci 2005; Berg and Ellers 2010; Skálová et al. 2012), which may result in broadening their habitat niche in the invaded range (Richards et al. 2006; Hejda et al. 2009b).

Invasive species often belong to families not present in the local flora (Rejmánek 1996; Daehler 2001). This might reflect a release of invasive species from strong inter-specific competition upon their introduction to a new range (Darwin 1859; Maherali and Klironomos 2007; but see Cavender-Bares et al. 2009). Thus, particularly strong competition is expected if there is a native congener present in the new range (Dayan and Simberloff 2005).

The competitive advantage of an invasive plant may also depend on various environmental factors (Shea and Chesson 2002; Suding et al. 2004; Vinton and Goergen 2006), as species abundances in a community result from inter-specific interactions, which can differ along environmental gradients (Tilman 1982). Available studies suggested that the negative effect of invasive plants on natives was decreased in stressful environments (Richardson et al. 2012), while the success and impact of invasive plants on the natives was enhanced by increased nutrient levels (Green and Galatowitsch 2002, Holdredge et al. 2010, Witkowski 1991) or greater light intensity (Molina-Montenegro et al. 2012). Indeed, recent studies indicated a considerable role of the characteristics of recipient habitats in plant invasions (Chytrý et al. 2008a, b; Pyšek et al. 2010), that interact with climate and propagule pressure. Thus, gradients of sites ranging from entirely dominated by invasive plants to invader-free that can be found in the field, depending on local conditions, represent a suitable model for studying the interactions among invasive and native species.

To get better insight into processes driving the performance of invaders in invaded communities we use three annual species of the genus *Impatiens* (Balsaminaceae) occurring in central Europe. The species were the native *I. noli-tangere* and two aliens differing in their invasion status: a highly invasive *I. glandulifera* and less invasive *I. parviflora*. Using congeners minimizes phylogenetic biases (Burns 2004; Grotkopp and Rejmánek 2007; van Kleunen et al. 2010) as well as those associated with other traits such as life history or dispersal mode. Congeneric studies also have the potential to reveal traits associated with invasiveness, possible microsite differentiation, or shifts in realized niches to avoid competition, thus separating the effect of niche from that of differences in fitness (MacDougall et al. 2009). The three species we address in our study co-occur in some sites, which minimized habitat- and community-related biases because species from the same habitats tend to be similar to each other in terms of ecology, and different from species in other habitats (Morgan and Smith 1979; Franks and Farquhar 1999). So far the coexistence in the field of species within the *Impatiens* genus has only been studied for *I. noli-tangere* and *I. parviflora*. These studies revealed considerable habitat overlap and impending competition due to the spread of the latter congener (Vervoort and Jacquemart 2012) and marked differences in the environmental optima of the two species (Godefroid and Koedam 2010). However, *I. noli-tangere* and *I. parviflora* may come often into competition with *I. glandulifera* in the near future because the latter spreads from river banks into the surrounding habitats where the former two typically occur (Malíková and Prach 2010). In addition, investigating species that coexist allows detailed study of the role of site-specific factors such as microrelief, soil moisture and shading, which likely shape invader performance, while eliminating the potentially confounding effects of environmental factors linked to geography, geology and climate.

Our study is the first to investigate interactions among all three *Impatiens* congeners commonly co-occuring in central Europe. Because we conducted the study over a period of four years, we were able to assess mid-term trends in the population dynamics of these annual species. We ask (1) what site-specific environmental conditions determine the presence or absence of the *Impatiens* species (2) what are the main abiotic and biotic factors that determine the short-term population dynamics of these species in the field, and (3) under which combination of the studied factors is the coexistence of *Impatiens* species possible?

Materials and methods

Study species

The three annual species of *Impatiens* (Balsaminaceae) occurring in the Czech Republic possess similar biological characteristics (Perglová et al. 2009; Skálová et al. 2012), but differ in their origin and invasion status. *Impatiens noli-tangere* is a European species native to the study region, the two introduced species occur as naturalized or invasive in a number of European countries (Lambdon et al. 2008) and both are classified as invasive in the Czech Republic (Pyšek et al. 2012b). However, the occurrence of *I. parviflora* is stabilised, while *I. glandulifera* is still spreading rapidly (Williamson et al. 2005; Pyšek et al. 2012a). The species are often found growing together in the same habitats.

Impatiens noli-tangere (N) is widely distributed across the whole Czech Republic except for the driest areas and mountains over 1,000 m a.s.l. It grows in damp, fertile soils in partly shaded sites in forests, clearings and along rivers (Slavík 1996; Hatcher 2003). The species germinates in April, flowers from July to August and sets seed from mid-July to the end of August. It may be suppressed by competition from *I. parviflora* (Tichý 1997; Chmura and Sierka 2007), which is also capable of outcompeting native species from the herb layer (Faliński 1998).

Impatiens parviflora (P), native to Central Asia, grows on nutrient-rich soils, but with lower nitrogen levels than is characteristic for soils preferred by *I. noli-tangere* (Godefroid and Koedam 2010). It is recorded from 45 habitat types in the Czech Republic, growing as a dominant species in nitrophilous herbaceous vegetation of mesic sites, alluvial forests, oak-hornbeam forests, ravine forests, spruce plantations and *Robinia pseudoacacia* plantations (Pyšek et al. 2012a). It germinates in April, flowers from mid-June to November and sets seed from late June to November (Coombe 1956). Studies reporting the impact of *I. parviflora* on species richness of invaded communities yielded rather ambiguous results, with negative (Obidzinski and Symonides 2000) but also no effect (Hejda 2012) on the numbers of co-occurring plant species reported.

Impatiens glandulifera (G), native to Himalayas, is highly invasive in Europe (Adamowski 2008). In the Czech Republic it is a dominant species of nitrophilous herbaceous fringes of lowland rivers. It also finds optimum conditions on loamy and sandy riverbanks and in riverine reed vegetation, and invades on fresh soil heaps, in forest clearings and margins and along forest roads. In total, it occurs in 16 habitat types (Pyšek et al. 2012a). The plants germinate in April, flower from the late July until the first frosts, and set seed from the end of August. Until recently its invasion in the Czech Republic has been restricted to floodplains and surroundings of villages with nutrient-rich humus and permanently moist soils. However, in the last decades the species has started to widen its habitat niche by spreading outside floodplains, such as in forest clearings and abandoned meadows (Malíková and Prach 2010; Pyšek et al. 2012a). As one of the tallest European herbs (up to 250 cm), *I. glandulifera* is competitively superior, and by suppressing native flora in invaded sites (Beerling and Perrins 1993; Pyšek and Prach 1995; Hulme and Bremner 2005; Clements et al. 2008) it changes the composition of invaded communities (Hejda and Pyšek 2006; Hejda et al. 2009a). Competition for pollinators with native plant species (Chittka and Schürkens 2001, Vervoort et al. 2011) and allelopathy (Vrchotová et al. 2011) were also suggested to play a role in this species' invasion.

Study sites and sampling

Habitat requirements and coexistence of *Impatiens* species were studied at five sites in the Czech Republic (Table 1). The sites were chosen because they hosted populations of all three *Impatiens* species under study. In August 2008, we established plots 1 × 1 m in size, covering all factorial combinations of the species' presence and absence. At each locality, we set plots with only one of the three *Impatiens* species present (N, P, G), with two co-occurring species (NP, NG, PG), and with all three species (NPG). Each combination was replicated 2–3 times in each site, depending on the availability of mixed populations at the scale of the plot. In total, 84 plots were established in the five sites (Table 1). The minimum distance between plot margins was 3 m, maximum distance 1 km. The plots were sampled once a year in August, i.e. at the peak of *Impatiens* vegetative development, from 2008 to 2011, which corresponds to the time when also other vegetation in the study sites was fully developed. Since one plot was destroyed, 83 were available for analyses.

In each plot, all *Impatiens* plants were counted, and percentage covers of *Impatiens* species, other vascular plant species and bare soil were estimated. Cover values below 10 % were estimated in increments of one (i.e., 1, 2, … 10 %) and cover values above 10 % were estimated in increments of ten (i.e., 20, 30, … 100 %). Plant species nomenclature follows Kubát et al. (2002).

During each sampling we measured soil moisture using a Moisture meter HH2 device with probe Theta Probe ML2× (Delta-T Devices, UK); moisture was measured in the four corners of the plot and average values were calculated. Tree canopy cover (hereafter called canopy cover) and slope (in °) were measured in May 2009. Canopy cover served as a proxy of light availability and was estimated based on a hemispherical photograph (Guevara-Escobar et al. 2005). We used a digital Canon 350D camera with objective Sigma 8 mm F3.5 EX DG Circular Fisheye with default camera settings. The camera was situated in a vertical position in the plot centre, 1 m above the surface, with the bottom of the photograph situated to the north. To minimize error due to direct sunlight, we took photos within 1 h in early morning or late evening, when the sun was low above the horizon. Photographs were converted in the program SideLook (Nobis 2005) to bitmaps using blue colour channel, whereby we achieved the maximum contrast between tree canopies and the sky. The bitmap image was then analysed in the program Gap Light Analyser 2.0 (Frazer et al. 1999). In May 2011 soil samples were taken from the upper soil horizon (0–5 cm) at the edge of the each plot to avoid damage to the seedlings in the plot, and content of total nitrogen and total carbon was recorded following Ehrenberger and Gorbach (1973).

Using species data obtained from the plots (with the *Impatiens* species excluded) we calculated mean Ellenberg indicator values (EIV) for light, moisture, soil reaction and nutrients (Ellenberg et al. 1992) using the programme Juice 7.0 (Tichý 2002). The calculation was based on species presence as weighting by species abundances was shown not to provide more accurate results (see Käfer and Witte 2004). Temperature and continentality were excluded because of the minimum variability among plots. EIV describe the response of a given species to edaphic and climatic factors, using a 9- or 12-point ordinal scale, and comparing it with other species (Godefroid and Dana 2007). These indicator values are derived from field distributions of plant species in central Europe and can therefore potentially act as surrogates for actual field measurements (Thompson et al. 1993).

Statistical analysis

The relationships between particular *Impatiens* species and accompanying species were explored by multivariate analysis (DCA) in the Canoco for Windows 4.5 program. The *Impatiens* species were projected into the charts as supplementary variables ex post. The design of analysis was restricted by covariables (locality and year). Species cover was square-root transformed. An ordination diagram was produced in CanoDraw for Windows 4.0 (ter Braak and Šmilauer 2002).

The effect of site characteristics on the presence of *Impatiens* species was tested by using generalized linear models (GLM) with binomial error structure and subsequent Chi square tests of predictor significance. The aim of these analyses was to determine the

Table 1 Characteristics and numbers of plots in individual sites; climatic characteristics are taken from Tolasz (2007)

Site	Prevailing habitat	GPS coordinates		No. of plots	Altitude (m a.s.l.)	Mean annual temperature (°C)	Mean annual precipitation (mm)
		N	E				
Volyně	Alluvial forest	49°08′30″	13°53′44″	18	460	7	500
Čelina	Deciduous forest	49°43′52″	14°20′40″	18	300	8	500
Třebsín	Mixed forest	49°51′34″	14°27′56″	16	280	8	550
Krhanice	Mixed forest	49°51′30″	14°34′56″	15	350	8	550
Potštejn	Alluvial forest	50°04′15″	16°19′25″	16	340	7	650

The number of plots varies because not all combinations were present in all sites to allow for the complete replications (see text for details) minimal adequate model. Significant predictor variables were chosen by backward selection, beginning with the maximal model (containing all main effects and interactions), then proceeding by the elimination of non-significant terms (using deletion tests from the maximal model) and retention of significant terms (Crawley 2008). As carbon and nitrogen contents were strongly correlated ($r = 0.97$, $P < 0.001$), we used sample scores of the first canonical axis from PCA analysis (referred to as C&N) in the statistical analyses. In order to avoid pseudoreplication due to abundances of individual species and soil moisture being recorded every year, and canopy cover, slope, and C&N only once, we used averages for all EIVs and directly measured soil moisture in the models. The presence of *Impatiens* species in the plot was expressed as 0, 0.25, 0.5, 0.75 or 1 based on absences/presences over the four years of recording (coded 0 if species was absent and 1 if present throughout the whole period). As locality never had a significant effect in the preliminary analyses, we did not include it in the models. Because we expected a non-linear response of species to EIV for moisture and light, soil moisture and tree canopy, we also included squared functions of these variables. For all models we included only two-way interactions, because of non-orthogonal field data. Separate models were built for the directly measured characteristics (soil moisture, tree canopy, slope, C&N) and EIV (light, moisture, soil reaction, nutrients); there was no collinearity within either group. Variability explained by GLMs was computed using Nagelkerke R^2, which represents pseudocoefficient of determination used for GLM (Nagelkerke 1991). Finally we compared both models according to the amount of variability they explained (based on Nagelkerke R^2) and added significant factors from the model which explained less variability, i.e. from the model using EIV variables, to that with directly measured characteristics.

To compare the ecological requirements of the species and predict their coexistence we used GLM models with explanatory variables identified as significant by the minimal adequate models for all species, i.e. canopy cover, soil moisture, and C&N.

Short-term population dynamics were investigated using linear models (LM) to test the effect of directly measured site characteristics, bare soil cover and abundance of the congener on the abundance of the target species. The abundance of the target species in the previous year was used as a covariable. Only plots where a given *Impatiens* species was present were involved in the analyses. The numbers of individuals were log-transformed to achieve normality. Minimal adequate models for individual species were obtained by using backward selection according to same criteria. The analyses were carried out in program R 2.12.2 (R Development Core Team 2011).

Results

Site characteristics

In total, 125 plant species (other than *Impatiens*) were recorded in the plots. The most common species were *Urtica dioica* (recorded in 55 % of the 84 plots), *Oxalis acetosella* (46 %), *Galeobdolon luteum* (40 %), *Poa trivialis* (37 %), *Fraxinus excelsior* (34 %), and *Stellaria nemorum* (30 %). The floristic composition was relatively heterogeneous with centroids of all three *Impatiens* species occurrence located closely together (Fig. 1). The first two axes explained together 12.8 % and covariables 9.1 % of variability in data. As indicated by visual inspection of the DCA plot, all *Impatiens* species grow together with *G. luteum*, *I. noli-tangere* with *Galeopsis speciosa*, *U. dioica* and *Chrysosplenium alternifolium*, while *I. parviflora* occurs with *Stellaria holostea*, *S. media*, *F. excelsior* and *Dryopteris filix-mas*. *Impatiens glandulifera* often grows in the same plots as *Festuca gigantea* and *P. trivialis* (Fig. 1).

The minimum adequate models based on characteristics directly measured in the field explained more variability than those based on EIVs (Table 2). As none of the factors estimated by EIV had a significant effect in the model for *I. glandulifera*, combined models were only constructed for *I. noli-tangere* and *I. parviflora*. However, adding of EIV variables to the direct-measurement model for *I. parviflora* did not significantly increase the proportion of explained variability. For *I. noli-tangere*, the quadratic term of EIV for moisture significantly increased explained variability, but in general, EIV variables had a poor explanatory power (Table 2).

The occurrence of *I. noli-tangere* was positively related to directly measured soil moisture and to the canopy cover × C&N interaction, and marginally also to canopy cover. The occurrence of *I. parviflora*

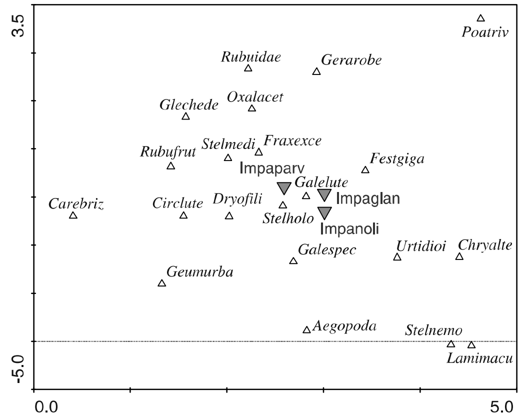

Fig. 1 Relation of *Impatiens* species to accompanying species; DCA ordination diagram. The first two axes explained 7.0 and 5.8 % of total variability. Length of gradient = 3.893. *Impatiens* species were projected as supplementary variables. Covariables (site and year) explained 9.1 % of variability. Only species with weight more than 3 % displayed. Full species names: *Aegopodium podagraria*, *Carex brizoides*, *Circaea lutetiana*, *D. filix-mas*, *F. gigantea*, *Fraxinus excelsior*, *G. luteum*, *G. speciosa*, *Geranium robertianum*, *Geum urbanum*, *Glechoma hederacea*, *C. alternifolium*, *I. glandulifera*, *I. noli-tangere*, *I. parviflora*, *Lamium maculatum*, *O. acetosella*, *P. trivialis*, *Rubus fruticosus*, *Rubus idaeus*, *S. holostea*, *S. media*, *S. nemorum*, and *U. dioica*

responded positively to canopy cover and negatively to soil moisture, and that of *I. glandulifera* positively to canopy cover and C&N, and negatively to the quadratic term of canopy cover (Table 2). These results indicate that *I. noli-tangere* is likely to occur at shaded sites with wet soils, whereas *I. parviflora* is associated with dry shaded sites (Fig. 2a, b). The maximum probability of the occurrence of *I. glandulifera* is at sites with tree-canopy cover between 55 and 72 % irrespective of soil moisture; such unimodal response indicates that this species avoids both very shaded and fully open sites. The area with overlap of more than 50 % probability of the occurrence of all three species is rather narrow (Fig. 3).

There was a good correspondence between measured canopy cover, EIV for light based on the presence of accompanying species, and the EIV for light assigned to individual *Impatiens* species. *I. glandulifera* has the highest EIV for light of the three congeners; this also holds true for the value computed by using accompanying species, and accordingly, this species occurred in plots with the lowest canopy cover (Table 3). On the other hand, the high EIV for moisture assigned to *I. glandulifera* does not accord with EIVs derived from accompanying species, which are comparable among all three species, and it is even contradicted by direct measurements suggesting that *I. noli-tangere* is more demanding of wet soils. The high EIV value of *I. glandulifera* for nutrients does not correspond to the direct measurements either.

Short-term population dynamics

For all three *Impatiens* species, the abundances in the previous year (expressed as the number of individuals and used as a covariate) had no effect on the abundances in the year sampled. The abundance of *I. noli-tangere* was negatively affected by that of *I. glandulifera* in the same year (Table 4). This negative effect of a congener was even stronger for *I. parviflora*, which was highly significantly suppressed by both *I. noli-tangere* and *I. glandulifera*. For the two invasive species the negative effect of the other congener's abundance was mutual, because *I. glandulifera* was also highly significantly suppressed by *I. parviflora* (Table 4). In terms of abiotic factors, the abundance of *I. parviflora* was negatively related to soil moisture and positively, but marginally significantly, to its quadratic term. The abundance of *I. glandulifera* decreased with moisture and was positively affected by the slope × C&N interaction, increasing in sites rich in C&N on steep slopes.

Coexistence of Impatiens species

The area of coexistence of all three *Impatiens* species is quite limited (Fig. 3). The invasive species occupy rather dry parts of gradient, in comparison with native *I. noli-tangere*, which is more moisture demanding. *Impatiens noli-tangere* seems to be outcompeted from mild shade to very shady and sunny parts of gradient by *I. glandulifera*, a species that is a stronger competitor. On the contrary *I. parviflora* coexists with *I. noli-tangere* in sites that are too dry and shaded for the native congener. The latter two species seem to coexist, rather than compete, in marginal parts of their niches. The two invasive species compete in open sites where the light-demanding *I. glandulifera* can survive, negatively affecting each other (Table 4). We suggest that *I. glandulifera* is suppressed by a dense cover of its congener's seedlings in spring and *I. parviflora* by shading from *I. glandulifera* adults in summer.

Table 2 Minimum adequate models based on characteristics directly measured in the field (moisture, canopy cover, slope, C&N) and derived from Ellenberg indicator values (mean EIV per plot for moisture, light, pH and nutrients) for presence of three *Impatiens* species in the field plots

	I. noli-tangere				*I. parviflora*					*I. glandulifera*				
	D.f.	Effect	*P*	EV (%)		D.f.	Effect	*P*	EV (%)		D.f.	Effect	*P*	EV (%)
Directly measured				**38.5**					**37.0**					**40.1**
Moisture	1,78	+	**<0.001**	22.4	Canopy cover	1,80	+	**0.001**	19.4	Canopy cover	1,79	+	**0.002**	18.1
Canopy cover × C&N	1,78	+	**0.011**	9.9	Moisture	1,80	–	**0.001**	17.7	Canopy cover^2	1,79	–	**0.002**	15.3
Canopy cover	1,78	(+)	0.069	0.7						C&N	1,79	+	**0.050**	6.6
C&N	1,78		0.495											
Ellenberg indicator values				**18.7**					**16.8**					
EIV moisture^2	1,80	–	**0.002**	18.1	EIV moisture	1,81	–	**0.004**	15.8					
EIV moisture	1,80		0.558											
Combined model				**54.7**										
Moisture	1,76	+	**<0.001**	22.4										
EIV moisture	1,76	+	**0.002**	14.6										
EIV moisture^2	1,76	–	**0.012**	8.6										
Canopy cover	1,76	(+)	0.069	5.4										
Canopy cover × C&N	1,76		0.133											
C&N	1,76		0.495											

Non-significant variables were excluded during the model simplification (slope and EIVs for light, pH and nutrients). Combined model was only run for *I. noli-tangere*, where adding EIV variables to directly measured variables significantly increased the variance explained in the model

Bold values significant at ($p \leq 0.05$) results

Discussion

Accompanying species and site characteristics

The heterogeneous floristic composition of the study plots without clear community differentiation shows that native and invasive *Impatiens* species occur in similar plant communities, as previously reported for two of the species addressed in our study, *I. noli-tangere* and *I. parviflora* (Vervoort and Jacquemart 2012). The limited community differentiation indicates that both invasive *Impatiens* species are able to colonize semi-natural communities harbouring the native *I. noli-tangere*. Despite this, we found a weak pattern in the species composition of communities in which the three *Impatiens* species occur. *Impatiens noli-tangere* is associated with hydrophilous species typical of forest springs (e.g. *C. alternifolium*) and nitrophilous forest margins or clearings (e.g. *G. speciosa*). *Impatiens parviflora* grows together with shade-tolerant species (e.g. *D. filix-mas*, *Stellaria media*) and *I. glandulifera* with species able to withstand shading by its canopy (*P. trivialis*, *F. gigantea*). Similar species composition of *Impatiens*-invaded plots was reported by Hejda and Pyšek (2006).

Impatiens noli-tangere performed well at moist, slightly shaded sites. Its performance increased with high carbon and nitrogen contents. *Impatiens parviflora* preferred shaded but dry sites (Godefroid and Koedam 2010). *I. glandulifera* occurred in mild shade, avoiding both extremes—full sunlight and deep shade. This corresponds to the results of Maule et al. (2000) who found the highest biomass of *I. glandulifera* at the margin of the forest. On the other hand, these authors found no correlation of biomass with other environmental factors including nutrient availability, which appears to play a role in our study. In terms of the effect of canopy cover, the results reported here represent a field confirmation of our previously

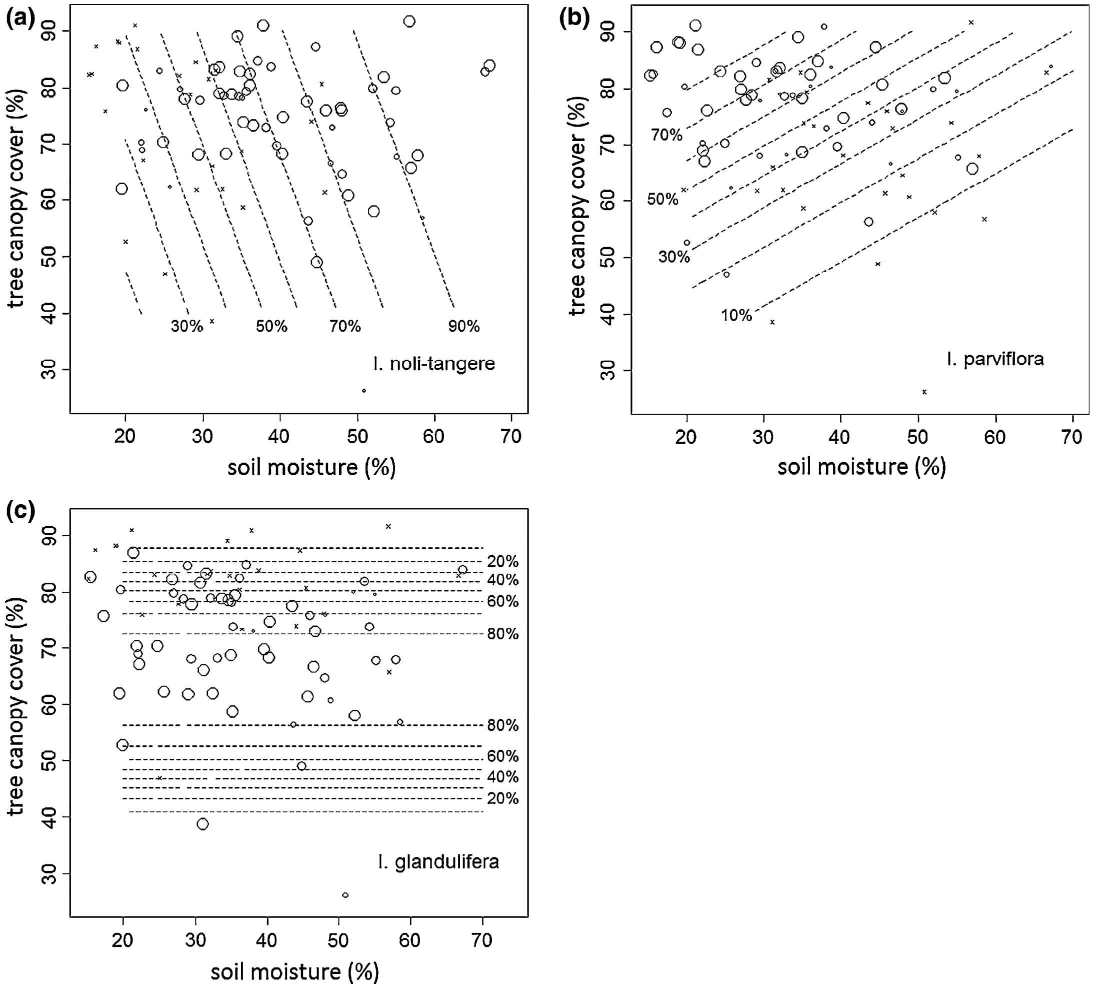

Fig. 2 a–c Occurrence of *Impatiens* species tested by GLM prediction models with tree canopy cover and soil moisture as explanatory variables in 83 permanent plots during the 4 years of observation; x indicates absence of the species in the plot and circles its presence (with the *smallest circles* indicating presence in 1 year and the largest in all 4 years); *dashed isolines* indicate occurrence probability

conducted cultivation experiments. We observed a superior performance of *I. glandulifera* under various environmental conditions except simulated canopy shade where biomass of its seedlings was comparable with that of *I. noli-tangere* and *I. parviflora*. On the other hand, simulated canopy shade stimulated shoot elongation, which enabled *I. glandulifera* to overtop the congeners. The competitive advantage of *I. glandulifera* may be, however, limited by the fragility of rapidly elongated stems (Skálová et al. 2012, 2013). The positive relationship to C&N content and negative relationship to canopy cover may be explained by using NO_3^- as osmoticum in stems and higher and synchronised germination in nutrient rich soils (Andrews et al. 2009). It needs to be emphasized that the patterns reported above are valid only for sites with populations of all three *Impatiens* species growing together in conditions comparable to those of our study. The site characteristics covered by our experimental plots do not span the entire ecological niche of the species, which is wider, especially in *I. parviflora* that invades a number of habitat types (Sádlo et al. 2007;

Pyšek et al. 2012a). Nevertheless, the habitats assessed in this study are representative of the ongoing invasion and are a useful model system to study the relationships between invading species and competing native congeners.

The absence of a relationship between the occurrence of *I. glandulifera* and soil moisture is rather surprising as the species is commonly reported as requiring high soil moisture (Ellenberg et al. 1992; Beerling and Perrins 1993; Pyšek and Prach 1995; but see Maule et al. 2000). Typical sites invaded by *I. glandulifera* are riparian habitats, which are generally rich in alien species (Richardson et al. 2007; Chytrý et al. 2008a; Lambdon et al. 2008; Pyšek et al. 2010). Riparian habitats provide suitable conditions for germination, establishment and growth of nutrient-demanding, fast-growing invasive plants (Davis et al. 2000; Blumenthal et al. 2009) and water streams serve as a vector for propagule dispersal (Foxcroft et al. 2007; Richardson et al. 2007; Foxcroft et al. 2011). The rather weak effect of soil moisture on the presence of *I. glandulifera* in our study suggests that the role of streams in the dispersal of propagules may be more important than ecological affinity of this species to riparian habitats. Seeds of *I. glandulifera* are easily transported by water (Lhotská and Kopecký 1966) and massive spread along rivers typically occurs shortly after the river has been colonized, followed by later spread into more distant sites outside the river corridor (Malíková and Prach 2010). Recent colonization of habitats such as woodland clearings, observed in the last two decades, can be explained by the combined effect of moisture and light conditions to which *I. glandulifera* seems to respond differently than thought.

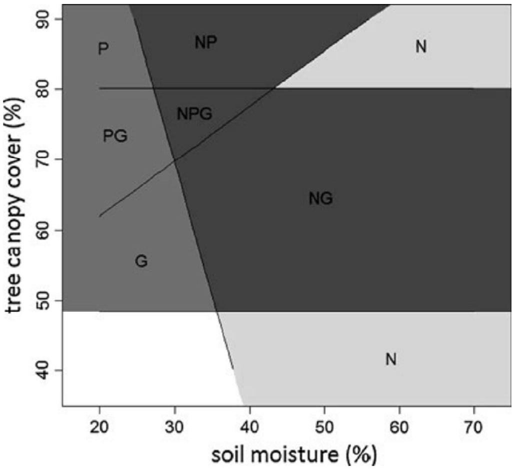

Fig. 3 Areas with a high probability of occurrence of the three *Impatiens* species in relation to tree canopy cover and soil moisture, with indication of their possible coexistence. The *lines* represent 50 % probability of the given species occurrence, the *letters* denote areas with more than 50 % probability of occurrence of individual species (N = *I. noli-tangere*, P = *I. parviflora*, G = *I. glandulifera*). *Light grey area* refers to a combination of light and moisture under which only the native species occurs; *medium grey* where invasive species occur, and *dark grey* is the area where native and invasive species grow together and compete

Directly measured characteristics were better predictors of the occurrence of the *Impatiens* species than variables based on Ellenberg indicator values, which confirms that indicator values provide only a rough estimate of environmental conditions. Another explanation could be the low number and stochastic

Table 3 Site characteristics directly measured in the field, Ellenberg indicator values (EIV) for the *Impatiens* species, and averaged EIVs calculated based on species occurring in the plots (in brackets)

	I. noli-tangere	*I. parviflora*	*I. glandulifera*
Canopy cover (%)	73.94 ± 1.32, 58	77.05 ± 1.31, 57	70.90 ± 1.85, 59
Moisture (%)	40.13 ± 1.65, 189	31.18 ± 1.53, 164	36.02 ± 1.64, 192
Nitrogen (%)	0.49 ± 0.03, 58	0.60 ± 0.04, 57	0.54 ± 0.03, 59
Carbon (%)	7.09 ± 0.41, 58	9.37 ± 0.60, 57	8.26 ± 0.51, 59
Slope (°)	13.45 ± 2.68, 58	19.54 ± 2.45, 57	16.62 ± 2.57, 59
EIV light	4 (4.59 ± 0.12), 190	4 (4.52 ± 0.11), 164	5 (4.86 ± 0.10), 192
EIV moisture	7 (5.87 ± 0.09), 190	5 (5.72 ± 0.09), 163	8 (6.00 ± 0.10), 192
EIV nutrients	6 (6.67 ± 0.09), 190	6 (6.48 ± 0.09), 164	7 (6.67 ± 0.10), 192
EIV soil reaction	7 (6.11 ± 0.08), 190	7 (5.87 ± 0.11), 157	7 (6.03 ± 0.10), 192

The figures are mean ± S.E., number of observations

Table 4 Minimum adequate models for abundances, expressed as the numbers of individuals, of the *Impatiens* species as recorded in the field plots

Factor	*I. noli-tangere*			Factor	*I. parviflora*			Factor	*I. glandulifera*		
	Direction	EV (%)	Pr (>F)		Direction	EV (%)	Pr (>F)		Direction	EV (%)	Pr (>F)
G number	–	4.0	**0.017**	G number	–	15.7	**<0.001**	P number	–	6.4	**0.001**
				Moisture	–	11.9	**<0.001**	Moisture	–	6.0	**0.002**
				N number	–	7.6	**<0.001**	Slope × C&N	+	3.8	**0.011**
				Moisture^2	+	2.3	**0.049**	C&N	(–)	2.1	0.061
								Slope			0.203

N—*I. noli-tangere*, P—*I. parviflora*, G—*I. glandulifera*

From directly measured variables were tested: moisture, canopy cover, slope, C&N and bare land cover, only variables which passed to final minimal model displayed here. The direction of effects and explained variance (EV) are indicated. Significant effects are in bold

occurrence of species in small-size plots. The results thus indicate limited suitability of Ellenberg indicator values, at least for studies investigating subtle differences in the responses of congeneric species with largely similar ecology to environmental conditions on a small scale (see also Smart and Scott 2004; Tichý et al. 2010).

Short-term population dynamics

The fact that the numbers of plants in our study plots cannot be used as a predictor of species' abundances in the following year can be due to several reasons. The production of seed per plant in *Impatiens* species may vary between years as the allocation to reproduction depends on environmental conditions (Daumann 1967; Skálová et al. 2013). The relationship between abundances in subsequent years can be further masked by seed rain from the surroundings of the plots and by the seed bank, which is developed in *I. noli-tangere* (Perglová et al. 2009) and sometimes also in *I. glandulifera* (Beerling and Perrins 1993).

The abundances of *I. noli-tangere* and *I. parviflora* were negatively affected by that of *I. glandulifera*, which was shown to overtop the shorter congeners from the seedling stage under most conditions (Skálová et al. 2012, 2013) and provide effective shade due to extremely high SLA (Andrews et al. 2009). On the other hand, the number of *I. glandulifera* plants decreased with increasing abundance of the other invasive species, *I. parviflora*. Such a negative effect imposed by a less vigorous species may be caused by the fact that both species produce a comparable amount of biomass at the seedling stage, especially in the shade and low moisture where *I. parviflora* competes successfully (Skálová et al. 2012). The number of *I. parviflora* plants was suppressed in moderately wet sites, but increased in very wet sites. Moisture therefore has different effects on this species' abundance versus its presence or absence; the latter is determined by a negative monotonic relationship indicating that the occurrence consistently decreased towards low-moisture conditions. A different sensitivity of plants in individual life stages may thus serve as an explanation for this seeming contradiction.

Surprisingly, the number of *I. glandulifera* plants decreased with increasing moisture, therefore exerting a stronger effect on this species' abundance than on its presence in plots, where the relationship was not significant. Higher abundances in dry sites may result from smaller plants produced under water limitation and less severe self-thinning due to lower competition for light (Yoda et al. 1963; Morris and Myerscough 1991). Overall, the negative effect of moisture on *I. glandulifera* abundance, together with the fact that this factor did not affect this species' presence in plots, suggests that the generally assumed dependence of this species on wet habitats needs to be revisited.

Species coexistence and its possible implications for future invasion dynamics

The differences in microsite requirements indicate that long-term coexistence of these species in the same locality is possible (Shmida and Ellner 1984; Huston and Deangelis 1994; VivianSmith 1997). In our study, the overlap of conditions under which two or all three species can coexist is rather limited (Fig. 3). This, together with negative effects among individual species, suggests that the *Impatiens* species coexist at the locality scale in separate microsites rather than commonly forming mixed populations. The observed coexistence in mixed stands thus seems to be transient rather than permanent. *I. parviflora* was previously reported to have no effect on the diversity of native vegetation (Hejda 2012). This corresponds to our result that the native *I. noli-tangere* is not negatively affected by the presence of *I. parviflora*, despite a considerable habitat overlap of the two species (Vervoort and Jacquemart 2012). The co-existence of *I. noli-tangere* with *I. parviflora* may be also facilitated by post-invasion trait divergence, which results in increased size, earlier germination, increased phenotypic plasticity and increased shade-avoidance syndrome of the *I. noli-tangere* plants growing together with *I. parviflora* (Dostál et al. 2012). Where the three congeners occur together, spread of *I. glandulifera* is likely to be favoured due to its negative effect on the population dynamics of both *I. noli-tangere* and *I. parviflora*. On the other hand, invasion dynamics of *I. glandulifera* can be constrained by the presence of *I. parviflora* in some situations.

The species-coexistence patterns might change if shade-tolerant *I. glandulifera* populations with potentially superior performance in forests are selected. The existence of drought-adapted genotypes is possible and would explain the lack of relationship between the presence of *I. glandulifera* and soil moisture. The existence of locally adapted genotypes, reported for the closely related species *I. capensis* (Dudley and Schmitt 1995; Donohue et al. 2001; Heschel et al. 2002), points to the possibility of this mechanism acting in *I. glandulifera* and contributing to broadening its habitat niche. Such locally adapted genotypes in *I. glandulifera* are indicated by results of our previous studies on frost resistance and timing of germination as a response to spring temperatures at invaded sites (Skálová et al. 2011).

The coexistence of the *Impatiens* species in the field might be further determined by disturbances, both natural and anthropogenic, that are frequent in riparian and forest ecosystems and allow for population regeneration in created gaps. *Impatiens noli-tangere* is likely to profit from small-scale soil disturbances that trigger recovery from the seed bank (Perglová et al. 2009), while the spread of *I. glandulifera* is encouraged by larger disturbances creating open space by removing tree canopy (Maule et al. 2000). Disturbances also accelerate soil decomposition and result in an increase of soil NO_3^- accessible to plants, a process contributing to synchronous emergence of seedlings (Andrews et al. 2009). It can be hypothesized that disturbed sites occasionally colonized by *I. glandulifera*, such as forest clearings or margins of abandoned wet meadows, serve not only as a reservoir for further spread, but may select for populations suited to spreading beyond the forest border. Succession towards shrub/woodland on nutrient-rich stands proceeds quickly and the process may impose selection for more shade-tolerant *I. glandulifera* populations.

We predict that the colonization of new habitats by *I. glandulifera* will continue in the near future, while the realized niches of its congeners in sites where populations of the three species occur together will become restricted. The results of this study suggest that the displacement of the native *I. noli-tangere* will be towards very wet parts of the moisture gradient, either strongly shaded or completely open, and that of *I. parviflora* towards dry shaded habitats. This scenario is supported by the fact that *I. glandulifera* was the most competitive of the three species in terms of establishment and survival of seedlings in experimentally manipulated field plots (Skálová and Pyšek 2009). We conclude that both niche and fitness differences (MacDougall et al. 2009) play a role in shaping the pattern of coexistence among native and invasive *Impatiens* species.

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4 Competition among native and invasive *Impatiens* species

(Study 3)

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Research Article

Competition among native and invasive *Impatiens* species: the roles of environmental factors, population density and life stage

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Abstract. Many invasive species are considered competitively superior to native species, with the strongest competition expected in species with similar niches and/or in closely related species. However, competition outcome is strongly context-dependent as competitive strength varies along environmental gradients, and life stages, and also depends on abundances. To explore the importance of these factors, we examined competition effects in an experiment with three *Impatiens* species (Balsaminaceae) widespread in central Europe and sharing similar life-history characteristics and habitats: the native *I. noli-tangere*, and two invasive species, *I. parviflora* and *I. glandulifera*. We compared their competitive strength and reciprocal impacts under two levels of water and light availability, two overall planting densities and three competitor densities. We assessed species performance (ability to complete the life-cycle, biomass and fecundity) and temporal competition dynamics in a garden pot experiment. Environmental variables had lower explanatory power than overall planting and competitor density, which indicates the importance of competitive interactions when evaluating plant performance and potential invasion success. Despite poor and delayed germination, the invasive *I. glandulifera* attained dominance even at a high competitor density and was competitively superior across all treatments, exceeding the height of both congeners. *Impatiens parviflora* was competitively weakest, having a negligible impact on both native *I. noli-tangere* and invasive *I. glandulifera*. The intermediate competitive strength of the native *I. noli-tangere* probably results from its intermediate height, and good germination rate and timing. The difference in height among species increased during the experiment when *I. glandulifera* was involved; this species continues growing until autumn, enhancing its competitive superiority. The results provide a mechanistic understanding for the competitive exclusion of native *I. noli-tangere* that occurs in stands with *I. glandulifera*, but the limited impact of *I. parviflora* on *I. noli-tangere* in their mixed stands.

Keywords: Alien species; balsam; competition; congeners; plant density; shading levels; water availability.

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Introduction

Non-native species have to overcome numerous barriers to naturalize and become invasive in the introduced range (Richardson *et al.* 2000; Blackburn *et al.* 2011). While immediately after introduction into a new range the species need to cope with the local environment, especially climatic conditions (Wiens and Graham 2005), later on different mechanisms involving interactions, or their absence, with resident biota come into play. It has been suggested that some invading species can exploit resources not used by plants in resident communities (empty niche hypothesis; Elton 1958; Lambdon *et al.* 2008), which results in minimizing or even avoiding competitive interactions with co-occurring species (MacArthur 1972; Crawley 1987; MacDougall *et al.* 2009). On the other hand, the outcome of interactions with resident organisms, especially competition (Levine *et al.* 2004), have been repeatedly found to be important for successful invasion of local communities (Sakai *et al.* 2001; Levine *et al.* 2004; Vilà and Weiner 2004; Maherali and Klironomos 2007; Hierro *et al.* 2011). In particular case studies, competitive advantage of invading species is often attributed to traits such as high germination rate, good survival, fast growth, early or late flowering, high fecundity and tall stature (Baker 1965; Pyšek and Richardson 2007; Kubešová *et al.* 2010; Moravcová *et al.* 2010; van Kleunen *et al.* 2010; Pellock *et al.* 2013).

Nevertheless, alien invaders were not found to be significantly competitively superior to native species in an analysis of available case studies (Daehler 2003). The outcome of competition depended on the environmental context (Daehler 2003), e.g. on water availability (Franzese and Ghermandi 2014), shading (Molina-Montenegro *et al.* 2012) or nutrient supply (Powell and Knight 2009). The competitive hierarchy of alien and native species changes along environmental gradients (Milberg *et al.* 1999; Shea and Chesson 2002; Pathikonda *et al.* 2009), with competitive strength of invaders usually decreasing towards more extreme conditions, such as, for example, high altitudes (Daehler 2005; Alexander *et al.* 2011; Pyšek *et al.* 2011). However, many invasive species possess a high phenotypic plasticity which makes them capable of adapting to a wide range of environmental conditions (Funk 2008; Berg and Ellers 2010). This corresponds to invasive plants often being generalists with a broad tolerance of ecological conditions, but exploiting resources less effectively than specialists (Richards *et al.* 2006).

The strength of competition between species depends on the degree to which their niches overlap (Hutchinson 1957), with two species occupying the same niche unable to co-exist over the long term (Hardin 1960). The strongest competition is expected in closely related species (Darwin 1859; Elton 1946; Maherali and Klironomos 2007; Violle *et al.* 2011). Nevertheless, some studies have found no linkage between the relatedness of competing species and the competition strength (Cahill *et al.* 2008) or reported even an opposite pattern, with less intense competition between closely related species (Diez *et al.* 2008; Mayfield and Levine 2010). Strong competition was suggested as the reason why invasive species from families with numerous members in native floras are under-represented in floras of target regions (Rejmánek 1996; Daehler 2001).

Despite some studies testing for the competitive superiority of invasive plants over native plants under a range of environmental conditions (Powell and Knight 2009; Molina-Montenegro *et al.* 2012; Franzese and Ghermandi 2014), the competitive relationships between these two groups of species have rarely been tested along the gradient of competitor densities (but see Leger and Espeland 2010). Moreover, studies focusing on a reciprocal impact of native species on invasive species are still the exception rather than the rule (Leger and Espeland 2010; Carvallo *et al.* 2013).

The rationale of our study stems from the well-established notion that high-density results in severe competition for resources (Antonovics and Levin 1980; Silvertown and Charlesworth 2009). Invasive species often gain an advantage over their native competitors under high resource supply, but stressful conditions can reverse the hierarchy, leading to a competitive advantage of natives (Daehler 2003). Density-dependent effects may differ across life stages, with the strongest effect found in the emergence stage (Goldberg *et al.* 2001). For intraspecific competition, high plant density usually decreases biomass and the number of individuals (Antonovics and Levin 1980). On the other hand, density effects have rarely been found to be significant in interspecific competition (Connolly *et al.* 1990, but see Antonovics and Fowler 1985).

To obtain a deeper insight into competitive interactions between native and invasive species under manipulated environmental conditions, varying plant densities and different life stages, we used three annual *Impatiens* species occurring in Central Europe: native *I. noli-tangere* and invasive *I. glandulifera* and *I. parviflora*. Using congeners minimizes phylogenetic biases (Burns 2004; Grotkopp and Rejmánek 2007; van Kleunen *et al.* 2010) as well as those associated with other traits such as life history or dispersal mode. Due to the overlap of the species' niches, which brings them into direct contact in the field (Čuda *et al.* 2014), we expected strong interspecific competition to occur (Matesanz *et al.* 2011). It is of interest to understand the ecological interactions among the *Impatiens* species because highly invasive *I. glandulifera*, which has historically colonized river banks, is currently spreading into novel habits such as clearings and roadsides distant from the river courses (Hejda and Pyšek 2006; Čuda *et al.* 2014). Since environmental conditions and dispersal vectors in these novel habitats differ from those acting in river corridors, the competitive interactions among this invader and co-occurring species might be changing. It is thus necessary to establish the competitive hierarchies of the three species across a range of seed availability and environmental conditions. A previous study (Čuda *et al.* 2014) revealed that shade, and moisture drive *Impatiens* distributions in the field. As such, we assessed these factors in a common garden experiment designed to capture the reciprocal effects of competition between species. Specifically, we answer the following questions. (i) What is the effect of density-dependent congeneric competition and environmental conditions on the ability of plants to complete their life-cycle? (ii) How do these factors affect plant biomass and fecundity? (iii) How does the effect of competition change over time with respect to the life stages?

Methods

Studied species

All three studied *Impatiens* (Balsaminaceae) species are annuals with similar biological characteristics (Coombe 1956; Beerling and Perrins 1993; Hatcher 2003) and habitat preferences (Slavík 1997), but with different origin and invasion status in the Czech Republic (Pyšek *et al.* 2012*a*). They partly differ in germination rates and stratification demands (Perglová *et al.* 2009), but in the field the majority of seedlings emerge within one month (April) (J. Čuda, pers. obs). The presence of all three species is dependent on disturbances and they therefore often occur in early successional herbaceous communities. At the same locality, the spatial pattern of the occurrence of individual *Impatiens* species is driven by canopy closure and water availability (Čuda *et al.* 2014).

Impatiens noli-tangere L., a native species, grows in damp forests, at clearings, along watercourses and around springs (Slavík 1997). It is recorded from 39 habitat types in the Czech Republic (Sádlo *et al.* 2007). Its height varies depending on local conditions from 20 to 120 cm (Hatcher 2003). The plants flower from July to August and set seed from mid-July to end of August. It is reported that it may be suppressed by competition from invasive *I. parviflora*, with which it often co-occurs (Tichý 1997; Faliński 1998; Chmura and Sierka 2007) as well as by competition from *I. glandulifera* (Vervoort *et al.* 2011; Čuda *et al.* 2014).

Impatiens parviflora DC., an invasive species, is characterized by a height similar to that of *I. noli-tangere* (Coombe 1956) and a broad ecological amplitude, being recorded from 45 habitat types in the Czech Republic (Sádlo *et al.* 2007; Pyšek *et al.* 2012*b*). It often grows as a dominant in nitrophilous herbaceous vegetation at shady mesic sites, in alluvial forests, oak-hornbeam forests, ravine forests and spruce or *Robinia pseudoacacia* plantations (Pyšek *et al.* 2012*b*). The plants flower from mid-June to October, setting seed from late June until the first autumn frosts.

Impatiens glandulifera Royle, a highly invasive species, occurs predominantly along rivers, but has been recently colonizing forest clearings and margins, wet ditches, forest roads and ruderal sites. It is recorded from 16 habitat types (Sádlo *et al.* 2007; Pyšek *et al.* 2012*b*; Pahl *et al.* 2013) but the number is expected to increase due to the ongoing spread. The plants flower from late July until the first frosts, setting seeds from late August. Due to high seed production (Moravcová *et al.* 2010) and tall stature up to 3 m (Adamowski 2008), it is highly competitive and able to replace the native flora in invaded sites.

Seed collection

Seeds were collected from large established populations, extending over 2500 m^2 in July and August 2011. Seeds of *I. glandulifera* were collected in Bohuslavice nad Metují (50°18′4.315″N, 16°5′22.730″E) along a riverbank and a meadow margin partly shaded by trees; *I. parviflora* and *I. noli-tangere* in Velký Osek (50°6′42.770″N, 15°10′10.635″E) in a flooded forest and forest gaps. Due to the low seed production, seeds of *I. noli-tangere* were collected also in Peklo by Nové Město nad Metují (50°21′28.501″N, 16°9′48.858″E) in a flooded forest and clearings and mixed together with those from Velký Osek. Altogether at least 15 000 seeds from at least 1000 individuals of each species were taken. After the collection, seeds of *I. noli-tangere* were kept in refrigerator at 3 °C on heat-sterilized wet river sand in the Petri-dishes as dry storage decreases the seed germination considerably (Perglová *et al.* 2009). Seeds of *I. parviflora* and *I. glandulifera* were stored in paper bags at room temperature.

Experimental design

The experiment was carried out in the experimental garden of the Institute of Botany ASCR in Průhonice (49°59′38.972″N, 14°33′57.637″E), 320 m above sea level, temperate climate zone, where the mean annual temperature is 8.6 °C and the mean annual precipitation is 610 mm. The seeds of the three *Impatiens* species were sown, separately or in pairs, into $20 \times 20 \times 23$ cm^3 pots with ~5 L of heat-sterilized common garden soil in early November 2011. Sowing seeds in the autumn ensured cold stratification, required for breaking the dormancy of the seeds (Perglová *et al.* 2009). Seeds were homogeneously dispersed on the soil surface and covered with a thin layer (0.5 cm) of soil. Seeds were sown to achieve two different total densities of seedlings that correspond to the range of densities typically observed in the field (J. Čuda, unpubl. data): high density (60 seedlings per pot) and low density (12 seedlings per pot). Within each density level, we sowed seeds to create three ratios of target plants to competitor plants, such that target plants experienced high (1 : 5), medium (1 : 1) and low (5 : 1) levels of competition from their congeners. Including also no-competitor (monospecific) controls resulted in 24 species-density-competition combinations (see Table 1).

In order to test the influence of environmental factors on species performance and competitive interactions, plants were grown under two water and shading levels in a full factorial design, hereafter referred to as moderate shade/low water; deep shade/low water; moderate shade/high water and deep shade/high water treatments. Due to logistic reasons plants exposed to the same treatment were grown together in the same experimental bed. The experimental design therefore consisted of a total of four experimental beds. Plants under high water treatment were watered twice a day in the morning and evening with tap water. The low water treatments were watered only when plant wilting was noticed. The aim was to induce water stress in the low water treatment and to provide full water supply in the high water treatment. The average soil moisture was 21.2 % in the low water treatments and 29.6 % in the high water treatments. The moisture was measured only once in every fifth pot (to obtain information about the difference between the treatments, not for the purpose of an analysis) on 20 June 2012, one day after the last rain and ~6 h after watering the plants in the morning. Shading levels were achieved by using a green garden shading net transmitting 10 and 65 % of incident radiation, without any significant change in light spectrum, for deep and moderate shade, respectively.

In total, the experiment consisted of 960 pots (4 environmental treatments × 24 species-density-competition combinations × 10 replicates). In all four beds, pots containing *I. glandulifera* plants (both no-competitor controls and pairs) were placed in separate sections, separated by 1 m from pots without it, to avoid unwanted shading by tall *I. glandulifera*. Pots were randomized within the sections and separated by 20 cm.

Unfortunately, very low emergence of *I. glandulifera* seedlings was recorded in the deep shade/high water bed. This was probably due to an anomalous warm episode in January when some of the seeds of *I. glandulifera* germinated and were killed afterwards by frost. The frost affected only this one bed probably because it was located lower on the slope than the others and could be exposed to cooler air accumulating in the lower part of the garden. Thus, we excluded the bed from all analyses.

The first sampling was carried out on 3–4 April 2012, after the seedlings emerged in the majority of pots, and the number of plants was recorded. Later samplings were done in 3-week intervals: April 26–27, May 14–16, June 4–5, and the number of plants and their mean height (taken as the height of the layer with the maximum density of leaves) were recorded. Plants were harvested in July, when they reached maximum size and the first symptoms of senescence appeared in *I. noli-tangere* and *I. parviflora*: after recording the same characteristics as on previous samplings, the plants were clipped at soil level and sorted by species. As capsules are

Table 1. Seed doses of target species and competitor under different levels of total plant and competitor density. *The number of seeds was increased in species where we expected poor germination (Perglová *et al.* 2009) to achieve comparable numbers of emerged seedlings. In *I. noli-tangere* the number of seeds was enhanced from two to four and from six to eight, and in *I. parviflora* from two to three and from six to seven.

Total density	Competitor density	Number of seeds of target species	Number of seeds of competitor	Final ratio (target : competitor)
High	High	10	50	1 : 5
	Medium	30	30	1 : 1
	Low	50	10	5 : 1
	No competitor	60	0	1 : 0
Low	High	2*	10	1 : 5
	Medium	6*	6*	1 : 1
	Low	10	2*	5 : 1
	No competitor	12	0	1 : 0

released after seed maturation and only peduncles remain attached to the stem, we used peduncles as a proxy of the reproductive output. The peduncles were clipped from the plants, and counted. For technical reasons (extreme time demand), peduncles were analysed only in 60 % of the sections in each of moderate shade/low water and deep shade/low water treatments. The complete biomass, i.e. that of vegetative parts and peduncles, was dried at 70 °C for 24 h and weighed.

Datasets and statistical analyses

We arranged the data collected during the experiment into three datasets (Table 2).The first one, hereafter 'vegetative dataset', was used to analyse the effects of experimental conditions on 'life-cycle completion' (number of individuals per species in the pot at the time of harvest divided by the number of sown seeds) and on the average biomass of the individual (further referred to as 'biomass'). Because almost all surviving individuals were fruiting at the time of the harvest, we took the number of surviving individuals as equal to the ability to complete the life-cycle. The second one, hereafter 'reproductive dataset', focused on the effects of experimental conditions on the average number of capsules produced by an individual (further referred to as 'fecundity'). The third one, hereafter 'temporal dataset' was used to explore changes in plant height under competition for light among the *Impatiens* species over the duration of the experiment. The response variable was the height ratio of the target species (t) to the competitor (c) and target species and calculated as $t/(c + t)$. Unlike the simple ratio target species/competitor species known to have the Cauchy distribution, this response variable comes from a β distribution, which can be approximated by normal distribution (and thus linear regression can be used; Sokal and Rohlf 1987). All *Impatiens* species were tested separately in all analyses.

All three datasets were analysed by means of linear regressions. The competitor density was expressed as the number of emerged competing individuals in the pot and used as a continuous variable in the analyses. The effects of environmental treatment and competitor identity were further tested by Tukey HSD post-hoc comparisons. Some of our response variables were ratios (life-cycle completion and temporal variation), where the underlying statistical distribution generating the data is binomial or β, respectively, however, the observed values lay within the range of 0.2–0.8, where linear approximation of functional relationships and assumption of normal distribution of errors is relatively reasonable (Crawley 2007). The assumptions of linear regression were checked by plotting the diagnostic graphs (Crawley 2007). All response variables with the exception of the life-cycle completion and temporal variation analyses had to be log-transformed in order to meet the assumption of homogeneity of variance. The estimates of life-cycle completion differed in their precision among the pots, since they were based on different numbers of seed sown or capsules produced (respectively). This was reflected in the analysis by setting these totals as weights in the corresponding linear regressions. We included the pot identity in the analysis of the temporal dataset in order to account for hierarchical structure in data (i.e. four repeated measurements from an individual pot, see Table 2). Given the pseudoreplication of our environmental treatments, responses to environmental conditions should be interpreted with caution. All computations were undertaken in the R 2.15.3 statistical environment (R Core development team, available at www.r-project.org).

As some response variables (biomass and fecundity) were calculated as the mean value per individual, they were strongly influenced by total density according to the law of constant final yield (Harper 1977). Because individuals from the low-density treatment are bigger

Table 2. Overview of analyses within the study. Life-cycle completion = number of individuals per species in the pot at the time of harvest divided by the number of sown seeds; biomass = mean weight of individual at the time of harvest; fecundity = mean number of capsules per individual at the time of harvest; temporal variation = mean height of individuals of target species divided by mean height of individual of competitor at the four time-sequential measurements. [1]Shade and water levels.

Analysis	Response variables	Explanatory variables	Data
(1) Life-cycle completion	Number of individuals in the time of harvest/number of seeds	Density, environmental treatment[1], competitor identity, competitor density	Vegetative dataset
(2) Biomass	Mean weight of individual	Density, environmental treatment[1], competitor identity, competitor density	Vegetative dataset
(3) Fecundity	Mean number of capsules per individual	Density, shading treatment, competitor identity, competitor density	Reproductive dataset
(4) Temporal variation	Target species height/(target species + competitor height)	Pot (covariable), time, density, environmental treatment[1], competitor identity, competitor density	Temporal dataset

Table 3. The influence of three strongest factors from analysis of particular species (according to explanatory power) on *Impatiens* fitness. D.f., residual degrees of freedom; E.V. total, variability explained by the model. For effects direction and explained variability by the particular factor **[see Supporting Information—Tables S1–S4]**. For the explanation of response variables see Table 2; factors are described in Methods.

	Life-cycle completion	Biomass	Fecundity	Temporal variation
I. noli-tangere				
Factor 1	Environment	Density	Density	Time × competitor identity
Factor 2	Density × environment	Competitor identity	Competitor identity	Time × density
Factor 3	Environment × competitor identity	Environment	Shading	Time × competitor density
D.f.	371	351	139	862
EV total (%)	35.5	54.7	55.0	58.7
I. parviflora				
Factor 1	Environment	Competitor density	Competitor identity	Competitor identity
Factor 2	Competitor identity	Density	Density	Time
Factor 3	Environment × competitor density	Competitor identity	Competitor density	Time × competitor density
D.f.	346	341	139	772
EV total (%)	27.7	58.8	50.2	49.4
I. glandulifera				
Factor 1	Environment × competitor identity	Density	–	Time
Factor 2	Competitor identity	Competitor identity	–	Time × competitor identity × environment
Factor 3	Density × competitor identity	Environment	–	Time × environment
D.f.	284	277	115	689
EV total (%)	23.9	22.7	14.9	70.7

and more fecund, we focused on the effects of competition density and environment (Figs 2A–C and 3A and B). In the results (Table 3), we present only the influence of the three strongest factors (explaining the majority of variance) to each response variable **[see Supporting Information for details]**.

Results

Effect of competition and environment on life-cycle completion

Life-cycle completion was affected more strongly by environment than by competition (Table 3) **[see Supporting Information—Table S1]**. The highest proportion of *I. noli-tangere* individuals completed their life-cycle under high water and high total density (Fig. 1A). *Impatiens parviflora* performed better in deep shade (Fig. 1B), but poorly in competition with *I. glandulifera*, with the negative effect of the latter species being significant in all environments. The lowest number of *I. glandulifera* individuals completed their life-cycle in competition with *I. parviflora*, but only in moderate shade treatments (Fig. 1C).

Effect of competition and environment on biomass and fecundity

Unlike life-cycle completion, biomass and fecundity was affected more strongly by competition than by environment (Table 3) **[see Supporting Information—Tables S2 and S3]**. Biomass per individual of all three species was higher in low than high total density treatments **[see Supporting Information—Table S2]**. *Impatiens glandulifera* had considerably higher biomass than the other species and was the strongest competitor, in terms of reducing the other species' biomass (Fig. 2A–C). Competition with *I. parviflora* increased the biomass of *I. noli-tangere* in all environments relative to the control (Fig. 2A). *Impatiens parviflora* was the weakest competitor with its biomass reduced by both competitors. This decrease was proportional to the competitor density (Fig. 2B). The biomass of *I. glandulifera* increased by competition with *I. parviflora* and was reduced by competition from *I. noli-tangere*. In the high water treatment, the biomass of *I. glandulifera* was low irrespective of competitors (Fig. 2C).

Fecundity, i.e. the number of capsules per individual, was higher in *I. noli-tangere* and *I. parviflora* under lower densities **[see Supporting Information—Table S3]**. The fecundity of *I. noli-tangere* was higher in competition with *I. parviflora*

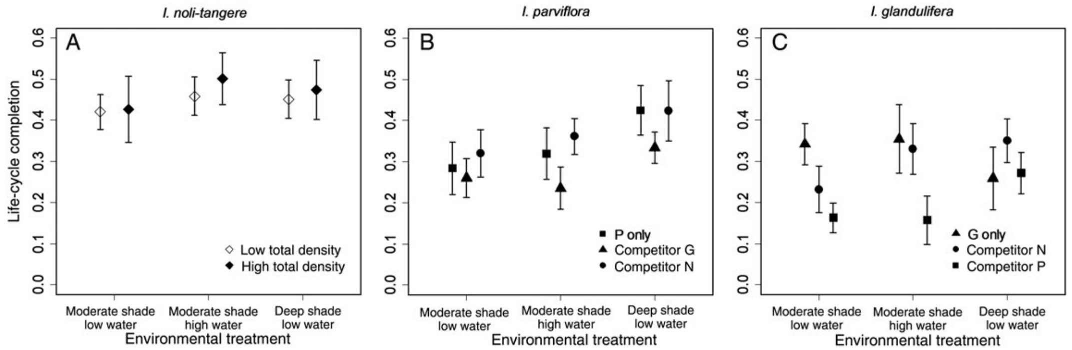

Figure 1. (A–C) Effect of competition (competitor identity and competitor density), total plant density (low and high) and environmental conditions (water and shading) on life-cycle completion rate (number of individuals per species in the pot at the time of harvest divided by the number of sown seeds). Symbols show species mean value under interspecific competition or without it; error bars show the 95 % confidence intervals. Species abbreviations: N = *I. noli-tangere*, P = *I. parviflora*, G = *I. glandulifera*. Each graph shows the pair of most important variables (according to the explanatory power). Sixty seeds were sown into pots with high total plant density and 12 into pots with low total density (A).

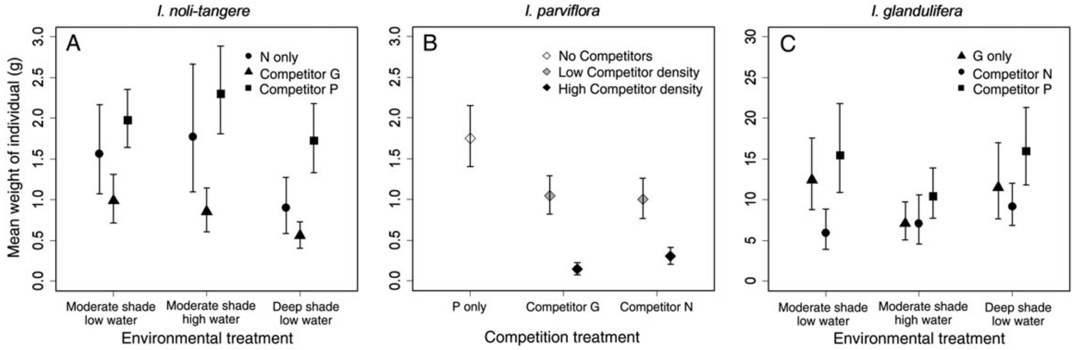

Figure 2. (A–C) Effect of competition (competitor identity and competitor density) and environmental conditions (water and shading) on biomass. Symbols show species mean value under interspecific competition or without it; error bars show the 95 % confidence intervals. Species abbreviations: N = *I. noli-tangere*, P = *I. parviflora*, G = *I. glandulifera*. Each graph shows the pair of most important variables (according to their explanatory power). To visualize the effect of competitor density (B), we divided this continuous variable into two categories: low competitor density = under mean competitor number and high competitor density = above mean competitor number.

and lower in that with *I. glandulifera* than without competitors in addition, *I. noli-tangere* plants were more fecund under moderate than deep shade (Fig. 3A). *Impatiens parviflora* was less fecund if the density of competitors was high; both congeners had such negative effects (Fig. 3B). None of the tested factors affected the fecundity of *I. glandulifera* (Table 3) **[see Supporting Information—Table S3]**.

Temporal variation in competition due to the differences in species height

The height of the target plant, as well as the height ratio, expressed as the mean height of the target plant divided by mean height of the competitor + mean height of the target plant, was strongly influenced by competition in *I. noli-tangere* and *I. parviflora* during the experiment (Table 3) **[see Supporting Information—Table S4]**. *Impatiens glandulifera* overtopped both congeners from the early stages of the experiment and this difference became more pronounced with time. On the contrary, competition from both congeners did not affect the height of *I. glandulifera.* The plants of native *I. noli-tangere* competing with *I. parviflora* were taller throughout the experiment and the height ratio did not change markedly (Fig. 4).

Discussion

Performance as a function of competition, density and environment

Our results indicate that environmental variables and competition play a different role in the plant life-cycle

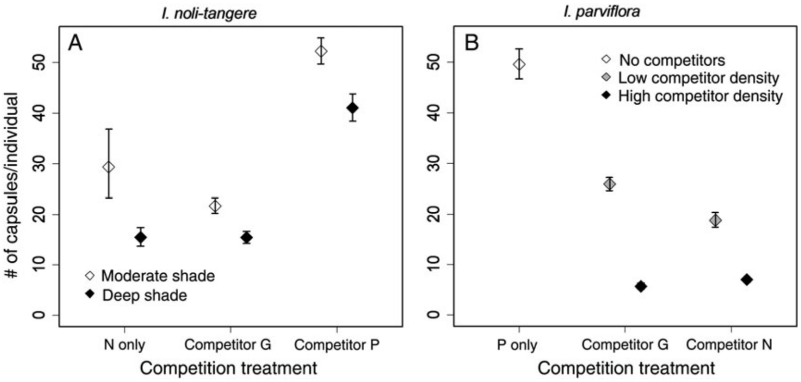

Figure 3. (A, B) Effect of competition (competitor identity and competitor density) and environmental conditions (shading) on fecundity (number of capsules per individual). Symbols show species mean value under competition; error bars show the 95 % confidence intervals. Each graph shows the pair of most important variables (according to their explanatory power). To visualize the effect of competitor density (B), we divided this continuous variable into two categories: low competitor density = under mean competitor number and high competitor density = above mean competitor number. We omitted the graph for *I. glandulifera* for which no significant effects of competition were found.

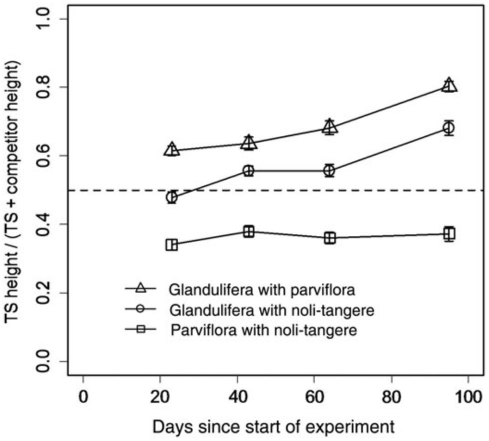

Figure 4. The temporal competition dynamics expressed as change in the ratio in target species height/(target plant + competitor height). TS, target species. At zero time the first seedlings emerged; height was first measured 22 days later. Triangle: *I. glandulifera* (target) with *I. parviflora* (competitor), circle: *I. glandulifera* with *I. noli-tangere*, square: *I. parviflora* with *I. noli-tangere*. The dashed line represents equal height of both competitors.

completion and growth response of the three *Impatiens* species. Overall, competition was a more important factor than environmental conditions for all variables except for the life-cycle completion of plants over the growing season, which points to the importance of competitive interactions in evaluation of plant fitness and potential invasion success. This suggests that for the studied *Impatiens* species, the environment plays a role in early stages of the invasion process while competition becomes more important when it comes to the naturalization phase (Blackburn *et al.* 2011) and could act as a mechanism preventing the non-native species from colonizing the resident communities (Levine *et al.* 2004; Davies *et al.* 2010).

Life-cycle completion

Life-cycle completion was surprisingly little affected by total plant density (with the only exception being a suppression of *I. parviflora* at high densities), indicating rather negligible self-thinning in our experimental populations. This contradicts reports from field studies, where a strong thinning to adult plant densities of *I. glandulifera* between 25 and 30 individuals/m^2 from a seed rain of ∼5000–6000 seeds/m^2 was observed (Perrins *et al.* 1990). The stronger thinning in the field can be attributed to seed predation and impact of other enemies (Dostál 2010), disturbances and large spatio-temporal heterogeneity in environmental factors, especially in soil moisture—factors from which plants are protected in an experimental garden. There is also a difference in the spatial pattern of seedling emergence; as seed dispersal in the field is random, seeds may emerge in dense patches, where it is impossible for the majority of plants to survive until maturity.

In contrast, environment had strong effect on life-cycle completion. *Impatiens glandulifera* performed poorly in moderate shade, if competing with the other invasive congener, *I. parviflora*; this could result from intensified light stress in the seedling stage due to a lack of shading by the low-statured seedlings of *I. parviflora*. Such a conclusion is supported by the fact that in the field *I. glandulifera* avoids full sunlight (Čuda *et al.* 2014). The native species *I. noli-tangere* generally showed the best performance of all three congeners in terms of the proportion of individuals that completed the life-cycle, which indicates that it may be better adapted to local conditions than the two alien species (Alexander *et al.* 2011). The number of individuals of *I. noli-tangere* that completed the life-cycle increased under high water supply (Čuda *et al.* 2014).

Biomass and fecundity

In contrast to life-cycle completion, biomass and fecundity were strongly influenced by competition and slightly by environment. As expected, density had a strong negative effect on the biomass and fecundity of all species, which is in accordance with the law of constant final yield (Harper 1977), except for the fecundity of *I. glandulifera.* Although *I. glandulifera* was the poorest among all the species studied in terms of the life-cycle completion, the surviving plants were able to dominate the pots regardless of the competitor presence and abundance. The fecundity of *I. glandulifera* plants was not significantly affected by the congeners, both native and invasive, which also indicates this species' competitive superiority. The biomass of *I. glandulifera* decreased in competition with the native *I. noli-tangere*, but its fecundity remained unaffected despite a close correlation of the number of capsules with biomass. This contradiction can be interpreted as a sign of plasticity in allocation of assimilates into the seed production (Berg and Ellers 2010). Due to the limited occurrence of *I. glandulifera* in woodlands (Beerling and Perrins 1993), reflecting a higher demand for light than is available under dense canopies (Maule *et al.* 2000; Čuda *et al.* 2014), we expected lower fecundity of plants exposed to shade. However, the seed production was similar in both shading treatments. The ability of *I. glandulifera* to produce seeds until the very end of the growing season contributes to its superiority over its congeners. The biomass of *I. glandulifera* was not negatively influenced by low water supply (similar to Maule *et al.* 2000; Skálová *et al.* 2013; Čuda *et al.* 2014), despite this species being traditionally considered a water-demanding plant (Beerling and Perrins 1993). On the other hand, the biomass of *I. glandulifera* decreased in the high water treatment, a phenomenon possibly associated with the high water content in its stems. Water is important to maintain turgor in the supporting structures. High water content, ∼96 %, is maintained by nitrate accumulation, which is used as an osmoticum in stems and leaves (Andrews *et al.* 2009). If water supply is insufficient, the plants have to invest more into cellulose in the stem structure. This opinion is supported by the plants reaching similar height in the low and high water treatments. High water content due to nitrate accumulation in place of organic molecules in stems enables the species to achieve substantial height at low irradiance (Andrews *et al.* 2009) or for instance to invest the assimilates into increased fecundity. The biomass and fecundity of *I. parviflora* were reduced in competition with both congeners, more so if the competition was intense; this shows that this is the weakest competitor of the three species. The native *I. noli-tangere* produced less biomass and fewer capsules when grown alone than in competition with *I. parviflora*. This means that *I. noli-tangere* suffers more from intraspecific competition than from interspecific competition with *I. parviflora* and, therefore, it has limited impact on *I. noli-tangere* under most conditions except for strong water limitation (Skálová *et al.* 2012). This is contrary to Tichý (1997) and Faliński (1998), who supposed that *I. parviflora* could influence *I. noli-tangere* by competition, but did not test this hypothesis experimentally. Biomass and fecundity of *I. noli-tangere* decreased across all environmental treatments in competition with *I. glandulifera* and increased with *I. parviflora* compared with monospecific control. This indicates an intermediate position of the native species in the competitive hierarchy within the members of the genus occurring in the studied region, and its ability to resist the competition by the less invasive alien congener. However, its ability to resist is context specific. For example the presence and timing of disturbances is very important, because the species differ in the time of setting seeds. In general, *I. parviflora* suppresses *I. noli-tangere* in very dry conditions (Skálová *et al.* 2012) and *I. glandulifera* outcompetes it wherever *I. noli-tangere* is able to survive.

Temporal variation in competition due to the difference in species height

Although *I. glandulifera* was not the tallest at the beginning of the experiment, it overtopped both congeners rather early and its superiority increased during the growing season. The ability of *I. glandulifera* to grow through the whole vegetation period facilitates its competitive dominance and also increases its propagule pressure, because plants flower and fruit from July to the first frost (Beerling and Perrins 1993). On the other hand, the height ratio between *I. parviflora* and *I. noli-tangere* was relatively consistent, with *I. parviflora* being shorter all the time.

Conclusions

The results suggest that the effect of competitor density on the performance of invasive *Impatiens* species exceeds that of environmental factors. Competitive interactions with co-occurring congeners may be thus a more important predictor of the invasion success of an invasive species and its population dynamics than its response to abiotic factors, and should be taken into account when evaluating their invasion potential.

The high invasiveness of *I. glandulifera* seems to result from its competitive dominance over the other congeners across varying environmental conditions of light and moisture. A main mechanism underlying this species' success is fast growth resulting in tall stature, which enables the plants to exploit available light and ability to still growing over the whole vegetation period. On the other hand, success of *I. parviflora* is definitely not caused by its competitive strength, but probably by its ability to avoid competition by tolerance of extreme conditions. Competitive exclusion of the native species *I. noli-tangere* is likely to occur from the stands with co-occurring *I. glandulifera*, but in mixed stands with the other invasive congener, *I. parviflora*, the impact on the native species will probably be limited.

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Contributions by the Authors

All listed authors wrote the manuscript; J.Č., H.S. and P.P. designed the experiment; J.Č. and H.S. collected the data and Z.J. conducted the statistical analyses.

Conflict of Interest Statement

None declared.

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Supporting Information

The following additional information is available in the online version of this article –

Table S1. Effects of experimental conditions on life-cycle completion (the proportion of survived individuals from seed to maturity).

Table S2. Effects of experimental conditions on the average biomass of the individual.

Table S3. Effects of experimental conditions on fecundity (the average number of capsules produced by an individual).

Table S4. Effects of experimental conditions on the temporal variation, i.e. changes in the height ratio of the target species to the competitor during the duration of the experiment.

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5 Effect of floods on abundance and spread of *Impatiens glandulifera*

(Study 4)

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BIODIVERSITY RESEARCH

Floods affect the abundance of invasive *Impatiens glandulifera* and its spread from river corridors

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ABSTRACT

Aim Riparian habitats are amongst the most invaded ecosystems world-wide. The great abundance of invasive species in river corridors is attributed to the efficient transport of alien species' propagules and reduced competition from native plants due to regular flooding. Once an invasive species has become established, river corridors can serve as stepping stones for spread into other habitats. We have chosen the Himalayan balsam *Impatiens glandulifera* Royle, highly invasive annual in riparian areas, as a model for spread of invasive species from linear river corridors.

Location Central Europe.

Methods We mapped its distribution and recorded its abundance in over 1200 patches along four rivers in central Europe, differing in the time of balsam's introduction (1900–1995). The patches were characterized in terms of the distance from the riverbank, height above the river surface, degree of soil disturbance and flooding regime.

Results The patches at sites subject to flooding had twice as many individuals as those that were not subject to flooding, regardless of their distance from the riverbank and height above the river surface. There was a strong effect of the river identity, with river invaded 20 years ago being less infested than those invaded earlier. The distance from the riverbank at which the populations occurred differed and did not depend on river identity/residence time. The patches in tributaries were on average two times further from the bank of the main river than those located elsewhere.

Main conclusions Flooding is an important factor affecting the abundance of *I. glandulifera*, and accounts for its spread and dominance along river corridors probably due to spreading the seeds, increasing nutrient availability and disturbing native vegetation. It is likely that the number of *I. glandulifera* populations will increase in the future, especially along small water courses.

Keywords
disturbance, flood, Himalayan balsam, niche broadening, residence time, riverbank.

INTRODUCTION

Riparian habitats are generally considered to be very susceptible to plant invasion (Planty-Tabacchi *et al.*, 1996, 2001; Pyšek *et al.*, 2010) and are among the most invaded ecosystems world-wide (Richardson *et al.*, 2007; Hejda *et al.*, 2015). The high number and abundance of invasive species in river corridors is attributed to several mechanisms such as connectivity of waterways and transport of propagules (Johansson *et al.*, 1996; Leuven *et al.*, 2009; Säumel & Kowarik, 2013), increased human influence in the vicinity of rivers favouring the spread of invasive plants (Stromberg *et al.*, 2007), reduced competition from native species due to regular disturbances, which enables propagules of invasive

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plants to become established (Planty-Tabacchi *et al.*, 1996; Hufbauer *et al.*, 2012) and an heterogeneous patchy environment providing a wide range of microhabitats (Planty-Tabacchi *et al.*, 1996). In the riparian zone, floods are the main agent influencing competitive hierarchy, but it is difficult to predict the composition of the vegetation because floods typically vary in their extent and periodicity (Naiman & Decamps, 1997). Furthermore, floods transport propagules faster, more effectively and over longer distances than regular water flow (Gurnell *et al.*, 2008) and even beyond the river corridor. Importantly, rivers also transport heavy, non-buoyant, propagules (Goodson *et al.*, 2003).

Easily invasible river corridors can also serve as stepping stones for invasion of adjacent habitats. It is reported that in the initial phase of their invasion some species, such as *Fallopia japonica*, *F. sachalinensis* (Pyšek & Prach, 1993), *Helianthus tuberosus* (Řehořek, 1997), *Phragmites australis* (Jodoin *et al.*, 2008; Brisson *et al.*, 2010), *Acer negundo* (Erfmeier *et al.*, 2010) and *Impatiens glandulifera* (Pyšek & Prach, 1993), occur in riparian localities and subsequently spread into a range of adjacent non-riparian habitats. This indicates that the predominant habitat of an invader may change during invasion and this is especially the case for easily invasible narrow linear habitats along which their propagules are easily transported, such as waterways, road margins and railway corridors (Thébaud & Debussche, 1991; Ernst, 1998; Hansen & Clevenger, 2005; Brisson *et al.*, 2010). Such broadening of the ecological niche in the invaded range is associated with a number of factors; an invading species' characteristics and the permeability of the receiving habitat (Parendes & Jones, 2000; Hansen & Clevenger, 2005), number of habitats occupied in their native range (Otte *et al.*, 2007), invading species' residence time in the region (Kowarik, 1995; Crooks, 2005), phenotypic plasticity (Geng *et al.*, 2007) and adaptations to local conditions (Sakai *et al.*, 2001).

In this study, we focused on the factors determining the abundance of the invasive annual *Impatiens glandulifera* along four rivers in the Czech Republic, central Europe, and its spread from the river corridors into surrounding habitats. Its invasion of riparian habitats in the region studied was very fast, and it only took 100 years to colonize the majority of the big rivers in the Czech Republic (Pyšek & Prach, 1995a, b; Rydlo, 1999). Its abundance along these rivers has increased with residence time (Malíková & Prach, 2010) and the largest populations are still confined to river corridors, but there are many reports of it spreading into adjacent habitats (Hejda, 2004; Malíková & Prach, 2010; Pahl *et al.*, 2013; Kostrakiewicz-Gierałt & Zając, 2014). This is associated with this species' tolerance of a wide range of environmental conditions (Beerling & Perrins, 1993), including relatively low soil moisture (Čuda *et al.*, 2014) and shading (Andrews *et al.*, 2009; Skálová *et al.*, 2012, 2013), and is supported by it being highly competitive (Bottollier-Curtet *et al.*, 2013; Skálová *et al.*, 2013; Gruntman *et al.*, 2014).

The ecological hypothesis behind the study is thus that the ecology of the species has been changing in recent decades and its spread from the river corridors is not random but determined by the characteristics of the colonizing populations and landscape features such as habitat structure in the areas adjacent to the rivers. In this study, we examine how the distribution of this species along rivers and beyond is associated with river identity (linked with the year of introduction), constraints on dispersal (distance from river surface, flooding regime), disturbance and the type of habitat adjacent to river corridors. We address the following questions: (1) Which factors determine the abundance of *I. glandulifera*, expressed in terms of the numbers of individuals in a patch? (2) What determines the maximum distance of *I. glandulifera* from a riverbank? (3) Which of the habitats adjacent to rivers are invaded?

METHODS

Species studied

Impatiens glandulifera Royle is an annual that grows up to 3 m high, native to the Himalayas and invasive in Europe, Asia (Russian Far East and Japan), North America, Japan and New Zealand (Adamowski, 2008). Due to its tall stature and high seed production, it is highly competitive in a wide range of light and moist conditions (Čuda *et al.*, 2015). It reduces the species diversity of the communities it invades (Hulme & Bremner, 2006; but see Hejda & Pyšek, 2006), attracts pollinators away from other plants (Chittka & Schürkens, 2001; but see Bartomeus *et al.*, 2010) and by increasing the erosion of riverbanks promotes its persistence (Greenwood & Kuhn, 2014). Nevertheless, all aspects of the impact of *I. glandulifera* are not fully understood yet and its suggested competitive ability can be overestimated due to it temporarily occurring in large quantities (Kasperek, 2004) and conspicuousness in bloom. *Impatiens glandulifera* is recorded from 16 types of habitats in the Czech Republic (Sádlo *et al.*, 2007), with the largest populations occurring along rivers, but is also recorded in a range of other habitats, such as forest clearings and margins, ruderal sites, wet ditches, abandoned meadows, margins of arable fields, road ditches and railway embankments (Pyšek & Prach, 1995b), away from rivers it occurs most often at human-disturbed sites (Usher *et al.*, 1986). In the Czech Republic the species is missing only in drier areas with sparse river network (Slavík, 1996). The species tolerates a wide range of substrata, and it is able to grow on alluvia, mineral soil, peat and even colliery spoil (Beerling & Perrins, 1993). *Impatiens glandulifera* occurs mainly in early successional vegetation or disturbed sites, as it requires bare soil for seedling establishment (Sinker *et al.*, 1985). It is very frost sensitive (Beerling, 1993; Kollmann & Bañuelos, 2004; Skálová *et al.*, 2011), but as it rapidly completes its annual life cycle, it is able to survive at altitudes as high as 1010 m a.s.l. in the Czech Republic (Anonymous, 2013) and 1180 m a.s.l. in Austria

(Drescher & Prots, 2003). More than half of unripe seeds are capable to germinate and sustain high propagule pressure, for example when early frosts occur (Janczak & Zieliński, 2012). Seedbank does not persist more than one season according to Perglová *et al.* (2009), but Beerling & Perrins (1993) report germinable seeds after 18 months. Balogh (2008) suggests that seed buried by river sediments may remain germinable for much longer time. Competitive ability is enhanced especially by early and synchronous germination promoted by massive cotyledons (Kurtto, 1992; Skálová *et al.*, 2011), together with subsequent fast growth (Beerling & Perrins, 1993). The species is further favoured by a wide phenotypic plasticity (Kurtto, 1996; Skálová *et al.*, 2012; but see Elst *et al.*, 2016) and by the lack of diseases, pests and herbivores in the invaded range (Beerling & Perrins, 1993; Schmitz, 1991; but see Tanner *et al.*, 2015). In the past, the plant was propagated and distributed by gardeners and beekeepers, and migration among distantly located populations has been inferred from reports about seed exchange (Kurtto, 1996) and using molecular techniques (Hagenblad *et al.*, 2015). The first occurrence outside cultivation in the Czech Republic was recorded in 1896 near the town of Litoměřice, and in 1900, it was first found at a riparian site on the bank of the river Svitava (Pyšek & Prach, 1995b). The plants flower from late July until the first frost and set seed from late August until November and the seed rain density is ~5000–6000 seeds m^{-2} (Beerling & Perrins, 1993); Koenis & Glavač (1979) found a maximum of 32,000 seeds m^{-2} in Germany. Seeds are dispersed actively by explosive capsule dehiscence up to 5 m (Beerling & Perrins, 1993) and passively by water flow (Lhotská & Kopecký, 1966; Love *et al.*, 2013). The seeds are also dispersed with soil by logging machinery or animals along forest roads and clearings, as well as by ants and small rodents (Beerling & Perrins, 1993), birds (Heintze, 1932) and maybe even fish (Boedeltje *et al.*, 2015). Whole plants or seedlings can be transported downstream during floods (Hejda & Pyšek, 2006; Balogh, 2008), as they are able to root at the nodes. The maximum rate of spread was estimated to 38 km $year^{-1}$ in England, and the ballistic spread is limited up to 2 m $year^{-1}$ (Perrins *et al.*, 1993); according to Williamson *et al.* (2005), the average rate of spread was 3.66 km $year^{-1}$ between 1934 and 1995 in the Czech Republic.

Field methods

We mapped the occurrence of *I. glandulifera* along four rivers and their tributaries in the Czech Republic, central Europe (Table 1). The segments of the rivers (158 km in total) selected had similar geomorphologies and land use in the surrounding valley, but differed in the year of first recorded occurrence of *I. glandulifera*, from which the beginning of the invasion of these sites was inferred. The populations were recorded at flowering by systematically walking along both riverbanks and mapping plants growing there. In open plain terrain, such as grasslands and arable fields across which seed is likely to be dispersed, but are unsuitable for the establishment of new populations due to frequent disturbances, we were able to distinguish the species safely at distances of several hundred metres using binoculars. Every tributary flowing into the river segments studied was searched for the presence of *I. glandulifera* up to 500 m from the confluence; only tributaries where the species was present were searched. We assume all occurrences in a tributary originated from the populations located along the main river, as there are no records in the literature of an earlier occurrence in the tributaries along the rivers we sampled (Pyšek & Prach, 1995b). These authors collected information on the majority of published and unpublished localities and herbarium specimens of the species in the Czech Republic. In the field, we distinguished two types of records based on the character of the patches of *I. glandulifera*: (1) a point occurrence described by the GPS coordinates in the centre of the patch used to record isolated individuals or small groups of plants (up to 3 m in diameter); (2) occurrence of approximately rectangular patches, parallel to a river, specified by two points measured farthest from the river, which describe the length (2–800 m) of the rectangle; the width of the rectangle (1–100 m) was estimated visually. To record large stands of irregular shape, we used more than one rectangle; subsequently the patches closer than 5 m to each other (limit to the distance of spread of this species by seed) were merged and considered as a single patch. In total, we mapped 1738 patches that were subsequently merged into 1210 patches of *I. glandulifera*.

The density of *I. glandulifera* in patches was scored on a three-grade scale: (1) scattered (at least one plant per every 10 m), (2) common (more than one plant per one square metre; cover up to 50%), and (3) dominant (cover > 50%). The location of plants was recorded using a GPS device (Garmin GPSMAP 62 and Garmin eTrex Legend) with positioning accuracy of about 3 m in open terrain. We recorded the type of habitat in which each patch of *I. glandulifera* was recorded, using an ad hoc classification of 10 types of habitats and their transitions: riverbank, roadside, dense woodland, sparse woodland, managed grassland, non-managed grassland, arable field, forest clearing, ruderal site and railway embankment; see legend of Table 2 for the descriptions of the habitats.

Data preparation and statistical analyses

The coordinates of occurrences of *I. glandulifera* in the field were processed in ArcGIS (ESRI, 2015). Point occurrences were assigned the distance to the nearest riverbank, vertical distance from river surface (Conrad *et al.*, 2015), estimated patch area (Network analyst, ESRI, 2015) and information about flooding based on data from the DIBAVOD database (DIBAVOD, 2016). We used five-year flooding data because this is frequent enough to have an effect on the abundance and distribution of *I. glandulifera*. A patch was considered to be subject to flooding, when its centroid was inside a five-year flood zone. For larger patches, rectangular shapes were

Table 1 Characteristics of the four rivers studied. Information is from [1]Pyšek & Prach (1995b), [2]Rydlo (1999), [3]www.chmi.cz and [4]Tolasz (2007).

River	Berounka	Jizera	Vltava	Svitava
Year of first record of *Impatiens glandulifera*[1,2]	1995	1908	1955	1900
Observed segment (Initial and terminal point)	Beroun (49.9668514N, 14.0751342E) – Praha Lahovice (49.9948236N, 14.4002472E)	Železný Brod (50.6416033N, 15.2546714E) – Dražice (50.3074172N, 14.8460869E)	Český Krumlov (48.8122000N, 14.3135367E) – České Budějovice (48.9727486N, 14.4694411E)	Rájec-Jestřebí (49.4068964N, 16.6344569E) – Adamov (49.2962761N, 16.6638542E)
Length of the observed segment (km)	32	70	38	18
Mean flow rate (m^3 s^{-1}) (location)[3]	39.4 (Lahovice)	12.6 (Sovenice)	26.4 (České Budějovice)	5.2 (Bílovice n. S.)
Altitudinal range of mapped segment	216–197 m a.s.l.	270–195 m a.s.l.	489–385 m a.s.l.	279–235 m a.s.l.
Mean annual temperature[4]	8.5	7.5–8.5 °C (from upper to lower part)	7.5	7.5–8.5 °C
Mean annual precipitation[4]	525–500 mm	850–575 mm	625 mm	625 mm
Description of the mapped segment	Few small tributaries, flow rather laminar, few weirs, river surrounded by a wooded area with equal percentages of meadows, arable land and urbanized areas.	Upper part: many small tributaries, flow more turbulent, surrounded by a mosaic of forest and meadows. Lower part (from Turnov): flow laminar, few smaller tributaries, surrounded by an increasing percentage of arable land and decrease in forestation, and a high number of ruderal sites.	Many tributaries, flow very turbulent, valley first forested and canyon-shaped, then increasing portion of meadows and urbanized land. This segment closest to potential natural conditions.	Many tributaries, flow rather laminar, the segment includes intensively cultivated agricultural land, urbanized areas and a forested valley.

generated from the GPS data and assigned the same characteristics as point occurrences based on polygon centroids. We added the maximum distance of the patch from the riverbank.

The data were then analysed using program R 3.2.0 (R Development Core Team, 2016), starting with Generalized Least Squares models (Liang & Zeger, 1986) from NLME package (Pinheiro *et al.*, 2016). We checked the data for spatial correlation using coordinates as covariates in the models, but there was no apparent relationship in the models for the number of individuals or the distance from the riverbank. As no spatial correlation was detected, we used an analysis of variance. The total number of individuals in each patch was calculated as a product of patch area and plant density estimated for the following categories: scattered = 1 individual m^{-2}; common = 11 individuals m^{-2}; dominant = 40 individuals m^{-2} (Čuda *et al.*, 2014). The degree of soil disturbance in patches was arbitrarily assigned to the invaded habitat using a three-degree scale (1 = low, 2 = middle and 3 = high, see Table 2 for details of habitat classification). Patches with *I. glandulifera* mostly occurred at the boundary of two or three types of habitats (Table S1 in Supporting Information); thus, the degree of soil disturbance was averaged across habitats if there was more than one habitat in the invaded patch.

We used two measures of the distance from the riverbank: (1) the distance of the patch centroid to specify 'mean distance' of the whole patch from the riverbank, which we used as a predictor in analyses using the number of individuals as a response variable; (2) the maximum distance of the patch, that is, that of the most distant individuals in the patch from the riverbank, which we used as a response in other analyses (Table 3). The mean distance was the best characterization for all the individuals in a patch, but the maximum distance was a more suitable measure for assessing the penetration of *I. glandulifera* in adjacent habitats. Using the mean distance results in a patch extending 100 m from the riverbank having the same distance as a single plant growing 50 m from the riverbank. For patches < 5 m from each other that were merged into a single patch, we computed the 'mean value' of each variable to be used in the models: mean distance of the patch from the riverbank = mean distance of merged patches weighted by the length of the patches; maximum

Table 2 Area of habitat, number of patches with *Impatiens glandulifera* in each habitat and the degree of soil disturbance arbitrarily assigned to each habitat. Note that *I. glandulifera* mostly occurred in transitions between habitats (ecotones), for example sparse woodland on riverbanks (see habitat transitions in Table S1).

	Area occupied (%)	Number of patches (%)	Degree of soil disturbance
Sparse woodland	36	30	2
Riverbank	22	19	3
Non-managed grassland	9	5	1
Managed grassland	9	6	1
Roadside	5	9	3
Dense woodland	5	8	1
Clearing	4	3	3
Ruderal site	3	11	3
Railway embankment	3	5	3
Arable field	2	3	3

Definitions of the habitats: **sparse woodland** – solitary trees and shrubs, alder carrs; **riverbank** – habitat close to a riverbank with specific riparian vegetation; **non-managed grassland** – mainly abandoned meadows; **managed grassland** – mowed or grazed grasslands, mainly meadows (*I. glandulifera* occurred predominantly at the margins); **roadside** – narrow strip of land on either side of a road or track disturbed by passing vehicles and mowing; **dense woodland** – shady forests and woody plantations; **clearing** – woodland habitat with nutrient enrichment, high disturbance and partial shade; **ruderal site** – ruderal area subject to regular disturbance, such as soil heaps, abandoned industrial field, etc.; **railway embankment** – similar habitat to roadside, but differing in substrate (riprap) and regular herbicide spraying; **arable field** – mainly field margins, but *I. glandulifera* is able to penetrate into crops (typically those with a wider spacing during early development, such as maize or rape).

Table 3 Overview of response and explanatory variables used in maximal models in this study, ordered as we used them in the ANOVA models. We also included all two-way interactions among the predictors and quadratic terms of selected factors, which are marked with asterisks.

Response variables	Explanatory variables included in the maximal models
Number of individuals in patch	River, mean distance of patch from riverbank*, vertical distance from river surface*, subject to flooding (Y/N), degree of soil disturbance
Maximum distance of patch from riverbank	River, tributary (Y/N)

distance = similar to mean distance; vertical distance above the river surface = similar to mean distance; position of the tributary = assigned as tributary patch when at least 50% of merged patches were in the tributary; degree of soil disturbance = mean disturbance calculated for the merged patches; flooding = patch considered to be subject to flooding when at least 50% of merged patches were in the flood zone; number of individuals = total number of individuals in merged patches.

Both response variables, the number of individuals and maximum distance from riverbank, were log-transformed to achieve a normal distribution and homogeneity of variance, and three outlying observations were not included in the analysis. The assumptions of all regressions were checked by plotting diagnostic plots (Crawley, 2013). In models where the response was the maximum distance of a patch, we analysed data for patches that were and were not subject to flooding each based on the five-year flooding data, because of interference between the response and flooding. We excluded the results for the river Berounka from the analysis of the distance from the riverbank, because there were no flooded patches in its tributary and therefore we could not test the interaction between the position of a patch in a tributary and flooding. All models included only two-way interactions, because the field data were non-orthogonal (see Table 3). In case of quantitative explanatory variables, we also included their quadratic terms. The model containing all terms and their interactions was further reduced by backward selection to obtain a model that only contained the significant factors. The deletion of terms was validated step by step by comparing the original and simplified models (Crawley, 2013). The differences among levels of categorical predictor 'river', which was the most important predictor in the analyses, were further tested using Tukey HSD *post hoc* comparisons, with river identity as the only predictor.

RESULTS

Number of individuals

About half of the patches with *I. glandulifera* (48%) were situated in areas subject to flooding relatively close to the riverbank (median distance of patch from riverbank was 18.4 m and 42.2 m for patches that were subject and not subject to flooding, respectively). River identity was the best predictor of abundance of *I. glandulidera* expressed as the estimated number of individuals. There were smaller groups of individuals along the river invaded 20 years ago than along the one invaded more than 60 years ago, but there was no significant difference between rivers invaded 60 and 100 years ago (Table 4, Fig. 1). In patches subject to flooding, there were more than twice as many plants than in those not subject to flooding (Fig. 1). The effect of flooding was highly significant even when distance and vertical distance from river surface were included in the models as covariates. The number of individuals was significantly associated with soil disturbance, with the highest numbers recorded at the least disturbed sites. The number of individuals was negatively associated with the mean distance from the riverbank. Environmental factors accounted for 14.7% of the variation in the data.

Table 4 Number of individuals in patch in response to factors included in the minimal model. Response was log-transformed by analysis of variance; maximal model was simplified by backward deletion of non-significant terms. Explained variance is displayed for significant terms only.

	d.f.	Explained variance	Effect	Significance
River	3	3.6%		< 0.001
Mean distance of patch from riverbank	1	0.9%	–	< 0.001
Vertical distance from river surface	1	0.6%	–	0.003
Subject to flooding	1	3.4%	+	< 0.001
Degree of soil disturbance	2	3.4%	–	< 0.001
River × Degree of soil disturbance	6	1.2%		0.013
Mean distance of patch from riverbank × Subject to flooding	1			0.082
Mean distance of patch from riverbank × Degree of soil disturbance	2	0.5%		0.030
Vertical distance from river surface × Subject to flooding	1	0.9%		0.001
Residuals	1191			

Maximum distance from riverbank

The maximum distance of patches from the riverbank differed for the different rivers (Table 5, Fig. 2a, b). *Impatiens glandulifera* occurred significantly further from the riverbank of the tributaries than of the main rivers. However, when testing the effect of tributary for each river separately, it was significant for patches not subject to flooding on all rivers (Fig. 2a), but for those subject to flooding only for the river Jizera (Fig. 2b).

Habitats invaded

The most common type of habitat occupied (based on the percentage of the area occupied) was sparse woodland (36%) and riverbank (22%) followed by non-managed grassland (9%) (Table 2). We found *I. glandulifera* typically under solitary or scattered trees along rivers, in alder and willow carrs and at the fringes of forests (Table S1). The typical occurrence of *I. glandulifera* is in tree/shrub and herb/grassland boundaries in habitats that provide plants with partial shade. The largest stands of *I. glandulifera* located far from riverbanks (100 m and more) were found in forest clearings. We often found this species growing alongside roads and railways and in ditches, and it also occurred in grasslands that were rarely mowed or grazed, such as abandoned meadows, but hardly at all if they were regularly mowed or grazed. *Impatiens glandulifera* was often recorded at ruderal sites, such as abandoned industrial zones in the vicinity of rivers, soil dumps and rubbish heaps. Patches at ruderal sites were over-represented in terms of numbers (11%), but occupied only 3% of the area invaded along the rivers (Table 2). It was rarely found in crops (2% of the area invaded; maize, wheat, barley, rape and soya), where it occurred mainly at field margins. It was abundant along riverbanks, but rarely occurred on the shores of ponds.

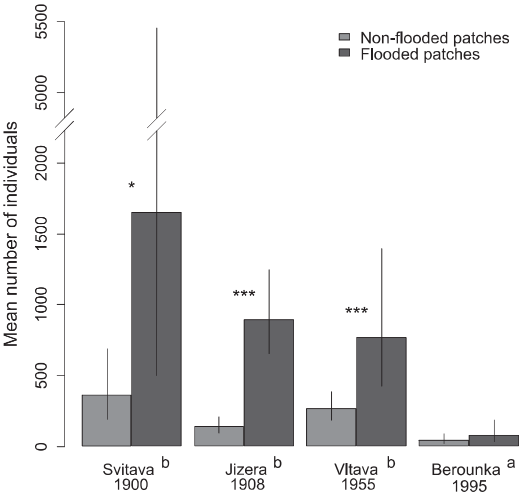

Figure 1 Number of individuals of *Impatiens glandulifera* in patches that were and were not subject to flooding along four rivers in central Europe that were initially colonized by *I. glandulifera* in different years (noted under river name). Bars show mean number of individuals in patches predicted by ANOVA model with merged river and flooding as the only predictor (resulting in categorical variable with eight levels = all possible combinations of river and flooding); error bars show 95 confidence interval. Values predicted by models on logarithmic scale were back-transformed using an exponential function. Letters beside river names show differences among rivers tested by Tukey HSD *post hoc* comparisons. Asterisks above bars show significant differences between patches that were and were not subject to flooding along each river tested separately using Student's *t*-test.

DISCUSSION

Number of individuals

Most patches with *I. glandulifera* were located close to rivers, often in areas that are subject to flooding, which corresponds with the reported habitat preferences of this species (Beerling & Perrins, 1993; Pyšek & Prach, 1995a).

There were approximately twice as many individuals in patches that were subject to flooding as in those that were not. This holds true in models where patch mean distance and vertical distance from river surface were included as covariates and indicates that there is a direct effect of

Table 5 Maximum distance from riverbank of patch in areas that were or were not subject to flooding in response to factors included in the minimal model. River Berounka was excluded from this comparison, because there were no patches along tributaries that were subject to flooding.

	Not subject to flooding				Subject to flooding			
	d.f.	Explained variance	Effect	Significance	d.f.	Explained variance	Effect	Significance
River	2	11.9%		< 0.001	2	7.4%		< 0.001
Tributary (Y/N)	1	6.4%	+	< 0.001	1	3.4%	+	< 0.001
Residuals	585				502			

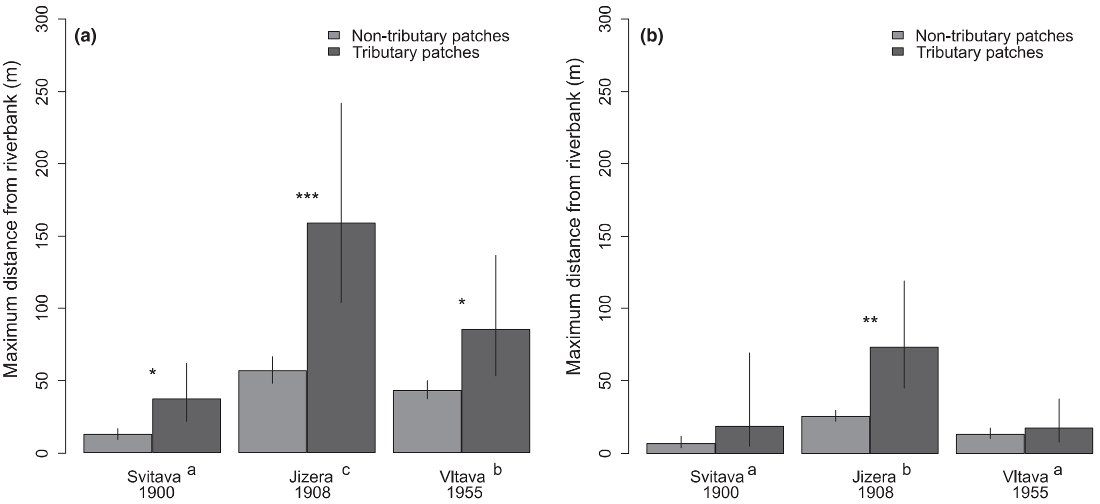

Figure 2 (a, b) Mean maximum distances of patches from riverbanks that were not (a) and were subject to flooding (b) along three rivers in central Europe that were initially colonized by *Impatiens glandulifera* in different years (noted under river name) and according to whether or not the patches were in a tributary. Bars show mean distance of patches predicted by ANOVA model with merged river and tributary as the only predictor (resulting in categorical variable with six levels = all possible combinations of river and tributary); error bars show 95 confidence interval. Values predicted by models on logarithmic scale were back-transformed using an exponential function. Letters beside river names show differences among rivers tested using Tukey HSD *post hoc* comparisons. Asterisks above bars show significant differences between patches along a tributary and along the river for each of the rivers studied based on Student's *t*-tests. River Berounka was excluded from this comparison because none of the patches along the tributary of this river were subject to flooding.

flooding on *I. glandulifera* not influenced by the proximity of a river. Floods act as dispersal vector for seeds (Lhotská & Kopecký, 1966; Goodson *et al.*, 2003) and disturb native vegetation (Planty-Tabacchi *et al.*, 1996), but can also have a detrimental effect on some invasive species, depending on their biology (Predick & Turner, 2008; Schmiedel & Tackenberg, 2013). *Impatiens glandulifera* is very susceptible to spring and early summer floods (Kasperek, 2004), because as an annual it has shallow roots and can be easily damaged by the water flow. Kasperek (2004) recorded extreme fluctuations in *I. glandulifera* abundance due to flooding and water-ground table regression in reed communities with large quantities in some years and a sharp decline in others. Also Dajdok *et al.* (1998) report the destruction of the majority of localities along the Odra river in Poland due to a June flood, only the individuals on the top of the riverbanks survived. In spite of this, 1 year later single individuals emerged and 2 years later *Impatiens* was abundant in the locality (Dajdok *et al.*, 2003). Analogously Blažková (2003) reports the total destruction of *I. glandulifera* stands along Berounka river, due to a flood in August; there were only two *I. glandulifera* individuals alive 2 months after the flood, but she suggests that seeds were probably spread to new sites. According to Köppl (2002) the floods in Tichá Orlice river accelerated spread of the species to more distant sites (~25 m from the riverbank), although populations under trees and shrubs in the river vicinity were heavily damaged. This author also reports that highest abundance the species reached at flood created sand alluvia (Köppl, 2002). The winter floods from melting snow are more common in the Czech Republic than summer floods (Elleder, 2007); winter floods transport seeds and disturb the soil but do not harm *I. glandulifera* plants. As we demonstrated above, the timing of flood is critical, and it has the most detrimental effect just before the seed set when it can drastically lower the species' abundance. Therefore, flooding can be viewed as an opportunity for eradication of *I. glandulifera* from small watersheds. However, it is necessary to keep in mind that only few surviving or newly emerging individuals are able to restore the population, and Kasperek (2004) shows changes in cover from '+' to '5' in *I. glandulifera* cover on the Braun–Blanquet scale from 1 year to the next, which corresponds to an increase from a few individual to a dominant stand with 75–100% cover. Water flow creates a seed–soil mixture, which sediments out downstream (Gurnell *et al.*, 2008) and provides ideal conditions for seed germination. Seeds of *I. glandulifera* do not float on the surface of the water but are transported along the riverbed (Lhotská & Kopecký, 1966); however, long-term inundation of seed reduces germination considerably (Janczak & Zieliński, 2012). The great amount of seeds dispersed over floodplains, together with massive seed production, contribute to the dominance of this species in areas subject to flooding. The spread of *I. glandulifera* in flooded areas can be also promoted by nutrient enrichment from flooding. Although the species is known to tolerate poor nutrient conditions, overall fitness and especially fertility are much lower in nutrient-poor soils than in the rich ones (Kostrakiewicz-Gierałt, 2015; Minden & Gorschlüter, 2016). This view is supported by Elst *et al.* (2016), who attribute the balsam success in its new ranges to the fact that it colonized habitats with higher nitrogen availability than in the native distribution areas. Last but not least, stands of *I. glandulifera* promote soil erosion (Greenwood & Kuhn, 2014) and as there are almost no other species in these stands that would stabilize the soil, erosion ensures the persistence of *I. glandulifera* once a site is colonized. *Impatiens glandulifera*, despite being an annual, is known to be able to persist at a site for 70 years (Larsson & Martinsson, 1998), but such long-term persistence could be also caused by recolonization. Populations close to the human settlements usually diminish after few years, mainly due to the damage of habitats or lack of repeated introduction in the vicinity of settlements in northern countries, such as Latvia (Helmisaari, 2006).

There is currently greater abundance of *I. glandulifera* growing along the rivers that were colonized earlier than along the river Berounka, which was colonized later. Species with long residence times are more widespread (e.g. Rejmánek, 2000; Wilson *et al.*, 2007) and more likely to become invasive (Pyšek & Jarošík, 2005). However, in this study the rivers invaded more than 60 years ago did not differ in the level of abundance of *I. glandulifera*. Another explanation of the lack of difference in rivers invaded long time ago could be the extremely fast spread of *I. glandulifera* during the last decades, which seems to be somewhat unrelated to the time of introduction (Wade, 1997); the number of localities increased eight times between 1990–2009 in Polish Carpathians that were invaded in the mid-1960s (Zając *et al.*, 2011). It is necessary to treat our results with caution because the data are only for four rivers, and residence time and river identity are confounded. Although the invasion of *I. glandulifera* has proceeded rapidly and along some rivers all suitable habitats appear to be occupied, only repeated sampling of the same site will reveal whether it has ceased increasing in abundance along these rivers (e.g. Dostál *et al.*, 2013).

Maximum distance from riverbank

River identity and whether or not the patch is located in a tributary were the most important predictors of the maximum distance of *I. glandulifera* from a riverbank in both patches subject and not subject to flooding, but plants along rivers invaded early did not spread further from the riverbank than those occurring along more recently invaded rivers. This contradicts the results of Malíková & Prach (2010). Differences in our results may be due to our using GPS devices to more accurately measure the spatial parameters of *I. glandulifera* populations.

Patches along tributaries were generally further from bank of the main river than other patches; this was true for patches not subject to flooding on all four rivers. We found no indication that *I. glandulifera* colonized tributaries earlier than the rivers (based on the list of historical localities in Pyšek & Prach, 1995b); therefore, it is assumed that *I. glandulifera* gradually spreads upstream. We are aware that there is a possibility that some of the tributaries could be colonized downstream, for example from plants escaping from the private gardens (e.g. Kurtto, 1996; Priede, 2008). Given a thorough documentation of the initial spread of this conspicuous species in the Czech Republic that did not indicate early occurrences on the tributaries (Pyšek & Prach, 1995b), we believe that the greater distance of the patches from riverbanks along tributaries is due to the habitats there favouring its long-term persistence. It is thus important to take into account the persistence of small vulnerable populations that cannot be maintained by propagules from a neighbouring upstream population (Love *et al.*, 2013). This assumption is supported by the short-term persistence of unconnected populations, compared with connected ones, as recorded for *Heracleum mantegazzianum* (Pergl *et al.*, 2012). For *I. glandulifera*, small forest populations persisted for 4 years (Čuda *et al.*, 2014), but 3 years later they were out-competed by shrubs (J. Čuda, unpublished data). Annual plants with a short-term seed bank, although competitively strong at maturity, such as *I. glandulifera* (Perglová *et al.*, 2009), require stable conditions for continuous year-to-year survival, or the possibility of spreading quickly to form new stands when conditions are not suitable. We also recorded a sharp decline in abundance and area occupied by *I. glandulifera* population in the mixed forest far from the riverbank during the extreme drought in 2015, in an experiment lasting 3 years (Čuda *et al.*, under review). This view is supported by results of Malíková (2003), who found a very high persistence (94%) of *I. glandulifera* populations along streams and rivers, but negligible persistence at non-riparian localities (9%).

Invaded habitats and possible management practices

Impatiens glandulifera was dominant especially in flooded zone in the close vicinity of the river, in accordance with the results of Balogh (2008) who reports that the species is concentrated in highly productive and moderately disturbed habitats. We observed similar patterns in its distribution far from riverbanks. This species is able to grow at sites exposed to direct sunlight if well supplied with water. In such conditions, it grows on eyots, gravel and sand alluvia or directly on riverbanks if its roots can access the groundwater (Beerling & Perrins, 1993; Balogh, 2008). Otherwise, *I. glandulifera* prefers partially shaded sites (Skálová *et al.*, 2013; Čuda *et al.*, 2014), such as among sparse shrubs, scattered trees, forest gaps, clearings and margins; however, fully shaded sites, such as dense young spruce plantations or closed forest, are an effective barrier against its spread. Canopy shade can be further enhanced by shading due to geomorphology; for instance, *I. glandulifera* rarely occurs in deep forested valleys. Under canopies, *I. glandulifera* plants are protected from early spring/late autumn frosts (Beerling, 1993; Skálová *et al.*, 2011).

It needs to be emphasized that the spread of *I. glandulifera* is effectively blocked in traditionally managed landscapes. The exponential increase in abundance after WWII (Pyšek & Prach, 1993) was probably due to abandonment of traditional management. This is especially true for edge habitats, such as riverbanks, forest fringes and road margins that are often invaded by exotic species (Hansen & Clevenger, 2005). Unification of small fields by agricultural cooperatives during the 1950s–1960s (Blažek & Kubálek, 2008) led to the abandonment of labour-intensive management of narrow strips of the land that was difficult to cultivate by machinery. This, together with the increase in the input of nutrients, accumulating in those ecotonal habitats, probably contributed to the increase in the rate of spread of *I. glandulifera* since the 1960s (see Pyšek & Prach, 1995a). The positive effect of management is evident in Switzerland, where river banks are continuously managed and there are very few dense stands of *I. glandulifera* along river banks (Z. Rumlerová, personal observation). In particular, it is effectively blocked in areas grazed by cattle, horses and sheep; at sites where it was present before grazing plants are consumed and trampled (Larsson & Martinsson, 1998; Helmisaari, 2006). In contrary, Matthews *et al.* (2015) consider grazing as a limited tool for species eradication, because most of the grazers consume other plants before eating *I. glandilufera*. Cockel & Tanner (2011) point out that grazing along watercourses during the seed release can create further disturbances that favour the spread of the species. During the fieldwork, we recorded only a few individuals growing along grazed or mowed riverbanks, despite otherwise suitable conditions and a nearby source of propagules. *Impatiens glandulifera* is unable to become established in continuously grazed or mowed areas completely and densely covered by grass (Pyšek & Prach, 1995a; Larsson & Martinsson, 1998), and short statured vegetation is supported by grazer generalists, such as cattle. We consider grazing as a potentially effective management tool, if it is applied in proper time, ideally several times during the season (but not during the seed release); animals also heavily damage the fragile stems. Continuous grazing over more seasons prevents species to retrieve, while single-shot eradication is pointless and can even enhance spread of the species.

Together, these results provide us with a holistic picture of *I. glandulifera* future potential distribution; the centre of its occurrence will be along the rivers colonized long ago. Floods can have ambiguous effect on abundance of the species, depending on the timing, but in general seem to promote species dominance by spreading the seeds, increasing the nutrient availability and disturbing the native vegetation. The spread will proceed along smaller currently uncolonized watercourses; however, smaller scattered populations will temporarily occur in a wide range of other habitats. It is relatively easy to manage the species in the small areas, if the eradication is systematic (Saegesser *et al.*, 2016); if so, it pays back to follow a sharp decline of the population in particular years that is periodically caused by flooding in riparian and by drought in non-riparian ones.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Maps showing the occurrence of *Impatiens glandulifera* along four river segments within the study. The diameter of the circle indicates the total number of individuals in thousands in every 3 km of watercourse; red sector of the circle represents proportion of individuals in areas subject to flooding, green sectors are those that were not subject to flooding. Projection: S-JTSK/Krovak East North - EPSG:5514.

Figure S2 Map showing the occurrence of *Impatiens glandulifera* along a short segment of the river Jizera. Red circles represent patches in areas subject to flooding, green circles are patches that were not subject to flooding; the diameter of the circles indicates the number of individuals in thousands in the patch. The zones that were subject to flooding over a five-year period are plotted in red. Picture also shows some typical occurrences of patches more distant from the riverbank: this species often spreads along railway embankments (green dots on the right and bottom left), small water courses and forest margins (green dots on the left). Projection: S-JTSK/Krovak East North - EPSG:5514.

Figure S3 Abundant growth of *Impatiens glandulifera* along a railway line close to the river Jizera.

Table S1 Percentages of transitions between habitats present in patches with *Impatiens glandulifera*. Those with more than 2% of the total number of particular transitions are in bold.

BIOSKETCHES

Jan Čuda, Zuzana Rumlerová, Hana Skálová and **Petr Pyšek** are members of a research team focusing on various aspects of biological invasions, such as species invasiveness, competition among native and invasive species, dynamics of alien species' spread, impact of invasive plants and macroecological patterns of biological invasions.

Josef Brůna focuses on using remote sensing and spatial analysis for monitoring of vegetation dynamics.

Author contributions: J.Č., P.P. and H.S. conceived the idea, J.Č. and Z.M. collected the data, J.Č. and J.B. conducted data analyses, and all authors contributed to the writing.

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6 Synthesis

6.1 Summary of main results

Before interpreting the results from a broader perspective of the current invasion ecology, I will briefly summarize the main findings obtained in particular studies (Table 2). This summary shows which *Impatiens* species were included, what were the approaches used to obtain the data, which questions were asked and what were the answers based on the results of the studies.

Table 2. Overview of the *Impatiens* species studied, data sources, questions and answers related to particular studies.

	Study species	Data from	Question	Answer
Study 1	*I. balfourii*, *I. balsamina*, *I. capensis*, *I. edgeworthii*, *I. flemingii*, *I. glandulifera*, *I. noli-tangere*, *I. parviflora*, *I. scabrida*, *I. walleriana*	Experimental garden, climatic chambers & databases (GloNAF, DAISIE)	Which biological traits are associated with the ability to naturalize in the genus *Impatiens*?	Juvenile traits: heavy seed, high seedling growth rates and low proportion of seedling biomass allocated to roots
			What is the role of the frequency of planting in the probability of becoming naturalized?	High frequency of planting was positively correlated with number of naturalized regions worldwide.
			Are the traits of the native species, that is successful in a given settings, close to those of the successfully naturalized species?	Traits of successful invaders were similar to those of the native congener.
Study 2	*I. glandulifera*, *I. noli-tangere*, *I. parviflora*	Field	What site-specific environmental conditions determine the presence or absence of the *Impatiens* species?	Occurrence of *Impatiens* was predominantly driven by moisture and shading.
			What are the main abiotic and biotic factors that determine the short-term population dynamics of these species in the field?	*Impatiens* abundance was determined by congeneric competition; invasive *I. glandulifera* exerted the strongest negative impact on both congeners.
			Under which combination of the studied factors is the coexistence of *Impatiens* species possible?	Area of coexistence was quite limited, however possible in moderately shaded habitats with sufficient water supply.

Study 3	*I. glandulifera*, *I. noli-tangere*, *I. parviflora*	Experimental garden	What is the effect of density-dependent congeneric competition and environmental conditions on the ability of plants to complete their life-cycle?	Life-cycle completion was more affected by abiotic factors, in *I. noli-tangere* positively by high moisture, in *I. parviflora* by deep shade and in *I. glandulifera* by deep shade and congeneric competition.
			How do these factors affect plant biomass and fecundity?	Biomass and fecundity were more influenced by competitive interactions that the environment, *I. glandulifera* was strongest competitor irrespectively of environmental set up.
			How does the effect of competition change over time with respect to the life stages?	*I. glandulifera* overtopped both congeners from the early stages of the experiment and this difference became more pronounced with time.
Study 4	*I. glandulifera*	Field & database (DIBAVOD)	Which factors determine the abundance of *I. glandulifera*, expressed in terms of the numbers of individuals in a patch?	Abundances were two times higher in flooded patches than in non-flooded. River invaded 20 years ago was infested less than those infested more than 60 years ago.
			What determines the maximum distance of *I. glandulifera* from a riverbank?	Patches located on tributaries were two-times further from the riverbank than the other patches.
			Which of the habitats adjacent to rivers are invaded?	Most common habitat was riverbank with scattered trees and non-managed grasslands, from those further from riverbank the most common were forest fringes and clearings.

6.2 Traits associated with invasiveness in the genus *Impatiens* and the role of planting frequency

Two proxies representing species invasiveness, the number of naturalized temperate regions globally and invasive status of species in Europe reflected different relationship to species traits. This was caused by the nature of both measures: the number of naturalized regions worldwide (GloNAF, van Kleunen et al. 2015, Pyšek et al. 2017) is a quantitative measure that represents a species' ability to become widespread, while invasion status in Europe (DAISIE 2017) is a qualitative variable that shows its ability to naturalize in at least some regions within this continent. However, some patterns were universal: juvenile traits (seed and seedling traits) were more important than the adult traits (adult biomass and fecundity) and frequency of planting had positive effect on the naturalization success. The crucial importance of an early phase of development for naturalization success (van Kleunen and Johnson 2007, Skálová et al. 2012) can be explained by life strategy of these species, of which all but *I. walleriana* are annual. Annuals have to succeed in their early life-stages as they have the only chance to reproduce, while perennials can wait in juvenile stage for many years before they reproduce. All of the species involved in the study possess the ruderal life-strategy (*sensu* Grime 1977), i.e. they colonize disturbed environment, grow fast and fruit early and massively. The majority of *Impatiens* species require partial shade and grow in moist habitats that are often well supplied with nutrients (Grey-Wilson 1983, Morgan 2007). The establishment in shaded habitats places demands on nutrient reserves in seed; shade-tolerant species usually have large seed that ensure enough nutrients until the plant develops sufficient leaf area (Walters and Reich 2000).

The frequency of planting was a stronger predictor of naturalization than the biological traits. The number of temperate regions in the world where a species have naturalized was strongly positively correlated with the frequency of its planting. Further, all alien species planted in experimental garden completed their life cycle, which suggests that they have potential to survive under local environmental conditions. This shows that more species could become naturalized if they were planted more commonly. Easy seed shipping and cultivation together with increasing popularity of *Impatiens* as ornamental plants suggest than many species of this genus represent potential invaders. This is supported by successful establishment outside cultivation of some not yet widespread *Impatiens* species; some of those included in my study are already naturalized regionally, such as *I. edgeworthii* in Germany (Weiss 2013, Kalveram 2014). Others are recently spreading and becoming globally distributed, such as *I. balfourii* (Fig. 3A, GBIF 2017).

6.3 Niche partitioning and coexistence of native and invasive *Impatiens* species

Three *Impatiens* species co-occur in the field and compete, nevertheless, there was a marked microsite differentiation among them. Soil moisture and shading were the most important factors that influenced their occurrence. Native *I. noli-tangere* performed best in moist and shaded conditions, while in more open stands it was displaced by the competitively stronger *I. glandulifera*. The invasive *I. parviflora* performed best in dry and shaded sites that represent ecological pessima of other *Impatiens* species (Perrins et al. 1993, Godefroid and Koedam 2010). *Impatiens glandulifera* exhibited a unimodal response to shading and surprisingly its presence was not affected by soil moisture, which is surprising for a species confined to watercourses and considered a wetland plant (Beerling and Perrins 1993, Prach 1994). All localities were selected to harbour mixed populations of all three species, thus the patterns found can be generalized only for sites where all three species co-occur. The ecological niches of the three *Impatiens* species are wider, especially in *I. parviflora* which tolerates even dry and shady conditions and invades many habitat types in central Europe (Sádlo et al. 2007, Pyšek et al. 2012a).

Our results imply that the area of coexistence of all three species is rather limited because of the microsite differentiation (Shmida and Ellner 1984, VivianSmith 1997). In the field, the populations of the three species will form rather separate than mixed populations with mixture zone dependent on year-to-year variation of local conditions. Existence of mixture zones can be further explained by colonization abilities of all three species (Coombe 1956, Beerling and Perrins 1993, Hatcher 2003) – they rapidly occupy free and unstable habitats created by disturbances (Kasperek 2004). As a result, the native *I. noli-tangere* will be competitively displaced from less shaded and drier parts of its niche when competing with *I. glandulifera*. The second invasive species, *I. parviflora,* is not competitively stronger than the native congener thus obviously will have a limited impact on its population dynamics (Vervoort et al. 2011).

6.4 Detailed insights into competition: environmental conditions, density and life-stage

We focused on three different outcomes of competition in the manipulated experiment in the common garden: life cycle completion, performance (biomass and fecundity) and temporal variation in height. Environment was more important for life-cycle completion, while species fitness expressed as species biomass, fecundity and temporal variation in height was more strongly influenced by competition. This suggests that competition among congeneric species affects their performance, which can be further translated into invasion success (see Pyšek and Richardson 2007 for review). In *Impatiens*, environment works as a filter in early life stages; while after the populations are established competition comes into play. When we extend this knowledge on invasion stages (Richardson et al. 2000, Blackburn et al. 2011) then environment is important in the phase of establishment (i.e. whether the species remains casual), while competition becomes more important during the later stages of the invasion process (codetermining whether it reaches the naturalized or invasion status).

The effects of competition on life-cycle completion observed in the common garden were consistent with results from the field (Study 2). The native *I. noli-tangere* performed and survived better under sufficient moisture, *I. parviflora* and *I. glandulifera* in a deeper shade. The native species completed its life cycle more successfully than the invaders, which indicates that it is better equipped to cope with local conditions than the invasive species (Alexander et al. 2011). The biomass and fecundity were more influenced by competition; invasive *I. glandulifera* was competitively strongest regardless of competitors and environmental conditions. The native congener, *I. noli-tangere* was competitively intermediate and *I. parviflora* was inferior. Interestingly, the biomass of *I. glandulifera* was affected by native *I. noli-tangere*, while its fecundity remained unaffected. This can be explained by a plastic response of *I. glandulifera*, which is able to relocate nutrients to seed production (Berg and Ellers 2010) and maintain a high propagule output. Another interesting finding is that plants in moist and dry environment had similar height and fecundity, but those in high water had lower biomass. Plants in high water supply can probably afford to invest less cellulose into their stems (forming larger cells and thicker cell walls) because stems are kept in an upright position by the water turgor.

6.5 Distribution of *Impatiens glandulifera* and its spread from river corridors

Flooding has a positive effect on the size of *I. glandulifera* populations; there were twice as many individuals in flooded plots than in non-flooded, regardless of distance from riverbank and elevation above river surface. The flood combines three important positive effects on populations of *I. glandulifera* that act by spreading seed (Gurnell et al. 2008), disturbing native vegetation, and supplying nutrients (Planty-Tabachi et al. 1996). Seed production in monoculture *I. glandulifera* stands is enormous, the seed rain is reported to reach 32,000 seeds per square meter (Koenis and Glavač 1979). During the flood non-floatable seeds are transported along riverbed, create a seed-rich mixture with soil and sediment out downstream (Lhotská and Kopecký 1966). Seeds germinate synchronously (Beerling and Perrins 1993), seedlings create dense canopy cover in several weeks that impede growth of other plants. Mature plants have shallow root system that promotes soil erosion (Greenwood and Kuhn 2014). This blocks succession and facilitates persistence of the species once it is established. The role of disturbances seems to be pivotal, because the species was found to grow in drier, but disturbed habitats. As a result *I. glandulifera* hardly colonizes stands with dense vegetation, such as mowed or grazed meadows, where there is a limited space for establishment (Larsson and Martinsson, 1998).

Impatiens glandulifera spreads further from riverbanks in tributaries, which is in agreement with its habitat requirements (Beerling and Perrins 1993, Pyšek and Prach 1995). Water spreads seed only downstream, but riparian habitats provide ideal conditions for growth and establishment and gradual spread upstream, because of stable water supply, shading by riparian trees and newly created stands with bare soil (Pyšek and Prach 1993). Importantly, if some small patchy populations are destroyed, they can be quickly saturated by recolonization from neighbouring populations upstream (Love et al. 2013). The connectivity of watersheds surely contributed to the persistence of this annual species with short-term seed bank (Perglová et al. 2009). This is strongly supported by data of Malíková (2003), who found very high persistence of populations along watercourses (94%), but poor in other localities (9%). Our results support this view, we found non-riparian populations to be less abundant and often located in transient habitats, such as soil heaps, clearings and ruderal places that will change due to succession.

7 Conclusions: current state of invasion and outlook on future trends

Congeneric comparison proved to be a useful tool for more precise description of differences between successful invaders and species that do not invade, because of smaller variation in traits caused by shared evolutionary history. One signal from the set of studies presented in this thesis is that we can expect further invasions in the genus *Impatiens*, fuelled by its horticultural popularity and frequent planting. This belief is supported by a historical experience with common cultivation and intentional spread into the wild that contributed to the invasion of *I. glandulifera* in the past. Nevertheless, the inconspicuous *I. parviflora*, a small-statured species that spread without human help, became the most common invasive *Impatiens* species in the central Europe. The mechanism of spread of *I. parviflora* is still not fully understood, but has to be rather effective as this species is commonly found in remote and isolated woodlands.

However, there is an evidence of some newly naturalized species, such as *I. edgeworthii*, starting to spread in Germany. This species is only locally common and still could be eradicated before it becomes more widespread. Moreover, I suggest that some species that are already invasive are extending their secondary ranges and becoming more abundant *–I. balfourii, I. glandulifera and I. parviflora*. These three species, currently widespread in Europe, will probably become more common in the temperate zone all around the globe. This is likely to happen in North America, where all three of them already occur, but their distribution is still somewhat limited. The existence of suitable habitats and climatic match is guaranteed as native *Impatiens* species occur in North America, similarly as in Europe.

Juvenile traits were crucial for invasion success that is largely driven by population establishment and early phase of development of these annual plant species. Three congeneric species, one native and two invasive, that are common in temperate Europe, partly overlap in their niches. Native *I. noli.-tangere* is being competitively excluded from part of its niche by competitively stronger *I. glandulifera*, while competitively inferior *I. parviflora* has limited impact. *Impatiens parviflora* is an example of species with discrepancy between its relatively minor impact and extensive area invaded, nevertheless studies that account for its impacts are contradictory and it is better to adopt the precautionary principle. *Impatiens glandulifera* and *I. parviflora* are very successful invasive species that are characterised by the same suite of traits: high seed germination rate, big phenotypic plasticity, and fast dispersal. These two invasive annuals, although belonging to the same genus, differ markedly in their life strategies that resulted in their recent massive invasion. This points to that every invasion event is unique and broader generalisations are applicable only to some extent.

Impatiens parviflora is able to grow in dry shady sites with low competition from native herb species. There is a limited number of species of shady understories in central Europe. None of them is an annual species forming monocultures, thus it seems that *I. parviflora* took and advantage of occupying an empty niche. Similarly, more light-demanding *I. glandulifera* requires bare soil to establish, therefore it grows in disturbed sites. However, after establishment it is highly competitive, with synchronous germination early in the season, fast growth and tall stature in particular. Populations are mainly located along watercourses with strong affinity to flooded sites. This is consistent with general pattern that invasions often start in riparian habitats. The reason is that flood spread seeds over long distance downstream and out of the river corridor, create gaps for establishment and bring nutrients that are needed to maintain high propagule pressure. Populations further from the rivers were smaller, unconnected and seem to be transient due to environmental stochasticity or succession of perennial species.

8 References[2]

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Author contributions

Study 1: Čuda J, Skálová H, Janovský Z & Pyšek P (2016) Juvenile biological traits of *Impatiens* species are more strongly associated with naturalization in temperate climate than their adult traits. *Perspectives in Plant Ecology, Evolution and Systematics* 20: 1–10.

JČ and PP conceived the idea, JČ and HS collected the data, ZJ and JČ analysed the data, JČ wrote the first draft of the paper and all authors took share in the subsequent writing.

Study 2: Čuda J, Skálová H, Janovský Z & Pyšek P (2014) Habitat requirements, short-term population dynamics and coexistence of native and invasive *Impatiens* species: a field study. *Biological Invasions* 16: 177–190.

JČ and HS conceived the idea and did the fieldwork, ZJ and JČ analysed data, JČ wrote the first draft of the paper and all authors contribute to the subsequent writing.

Study 3: Čuda J, Skálová H, Janovský Z & Pyšek P (2015) Competition among native and invasive *Impatiens* species: the roles of environmental factors, population density and life stage. *AoB Plants* 7: plv033.

JČ, PP and HS conceived the idea, JČ and HS collected the data, ZJ and JČ analysed the data,

JČ wrote the first draft of the paper and all authors took share in the finalizing of the paper.

Study 4: Čuda J, Rumlerová Z, Brůna J, Skálová H & Pyšek P (2017) Floods affect the abundance of invasive *Impatiens glandulifera* and its spread from river corridors. *Diversity and Distributions* 23: 342–354.

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In revision

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