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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