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Original article

Pre-adaptation or genetic shift after introduction in the invasive species *Impatiens glandulifera*?☆

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ABSTRACT

Invasive exotic plants often grow fast, reproduce rapidly and display considerable phenotypic plasticity in their invasive range, which may be essential characteristics for successful invasion. However, it remains unclear whether these characteristics are already present in native populations (pre-adaptation hypothesis) or evolve after introduction (genetic shift hypothesis).

To test these hypotheses we compared means and phenotypic plasticity of vegetative and reproductive traits between populations of *Impatiens glandulifera* collected from either the invasive (Norway) or native range (India). Seeds were sown and the resulting plants were exposed to different experimental environments in a glasshouse. We also tested whether trait means and reaction norms harbored genetic variation, as this may promote fitness in the novel environment.

We did not find evidence that invasive populations of *I. glandulifera* grew more vigorously or produced more seeds than native populations. Phenotypic plasticity did not differ between the native and invasive range, except for the number of nodes which was more plastic in the invasive range. Genetic variation in the slope of reaction norms was absent, suggesting that the lack of change in phenotypic plasticity between native and invasive populations resulted from low genetic variation in phenotypic plasticity initially harbored by this species. Post-introduction evolution of traits thus probably did not boost the invasiveness of *I. glandulifera*. Instead, the species seems to be pre-adapted for invasion.

We suggest that differences in habitat between the native and invasive range, more specifically the higher nutrient availability observed in the new environment, are the main factor driving the invasion of this species. Indeed, plants in the more nutrient-rich invasive range had greater seed mass, likely conferring a competitive advantage, while seed mass also responded strongly to nutrients in the glasshouse. Interactions between habitat productivity and herbivore defense may explain the lack of more vigorous growth in the new range.

1. Introduction

Biological invasion is a global phenomenon causing ecological, economic and social disruption (Davis et al., 2000). Alien invasive species often outcompete native species, affecting biodiversity and altering the structure and function of invaded ecosystems (Vitousek et al., 1996; Bossdorf et al., 2005). Identifying traits or mechanisms responsible for species invasiveness is crucial to predict the fate, spread and impact of invasive species and to take sound management decisions.

Numerous studies have identified traits associated with invasiveness in plants (e.g. Theoharides and Dukes, 2007; Hayes and Barry, 2008; Whitney and Gabler, 2008; van Kleunen et al., 2010). These include – among others – vigorous growth, abundant

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☆ Shared first authorship between EME and KPA. KPA and BJG designed the study. KPA, PAD and ZAR collected samples in the wild. KPA set up the experiment. EME did the measurements in the glasshouse and wrote the manuscript with help from KPA and IN. JT and EME did statistical analysis. All coauthors commented on the manuscript. All authors have approved the final article.

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reproduction and high phenotypic plasticity (i.e. the ability of an organism to change its phenotype in response to different environments) of morphological and physiological traits (Richards et al., 2006; Whitney and Gabler, 2008; van Kleunen et al., 2010; Godoy et al., 2011). However, where in the invasion pathway such traits originate is still unclear. According to the pre-adaptation hypothesis, species become invasive if characteristics that promote invasiveness are already present in the native range (Lee and Gelembiuk, 2008; Mason et al., 2008; Hejda et al., 2009; Schlaepfer et al., 2010). Alternatively, the genetic-shift hypothesis states that invasive phenotypes arise from rapid evolution after introduction (DeWalt et al., 2004; Caño et al., 2008; Lande, 2009; Qing et al., 2011; Colautti and Barrett, 2013). In the latter case, the small size of an introduced population typically first causes reduced genetic diversity (founder effect) which can be accompanied by inbreeding (Kaufman and Smouse, 2001; DeWalt et al., 2004; Maron et al., 2004; Bossdorf et al., 2005; Caño et al., 2008; Prentis et al., 2008; Qing et al., 2011). Post-introduction natural selection by – and local adaptation to – the abiotic and biotic conditions in the invasive range will further change the species genotype, giving rise to a novel micro-evolutional trajectory (Kaufmann and Smouse, 2001; Blair and Wolfe, 2004; DeWalt et al., 2004; Maron et al., 2004; Bossdrof et al., 2005; Caño et al., 2008; Feng et al., 2008; Barney et al., 2009; Qing et al., 2011; Li et al., 2015).

To distinguish whether a species is pre-adapted to invasion or has evolved after introduction, its traits need to be compared between native and invasive populations along a common environmental gradient (DeWalt et al., 2004; Maron et al., 2004; Caño et al., 2008; Qing et al., 2011; Moroney et al., 2013). Different trait means and different reaction norms to the environmental gradient indicate a genetic shift in respectively the traits themselves and their phenotypic plasticity (and indicate pre-adaptation otherwise). Such shifts can occur if genetic variation in trait means or trait plasticity exists in the introduced populations and if this variation yields a fitness advantage in the novel environment.

Some previous studies found evidence for pre-adaptation (e.g. DeWalt et al., 2004), while others support the genetic shift hypothesis (e.g. Qing et al., 2011). However, different studies used different approaches. While all studies compared trait means (e.g. Siemann and Rogers, 2001; Hejda et al., 2009; Schlaepfer et al., 2010), fewer compared also the phenotypic plasticity of traits between native and invasive populations, using either plasticity indices (e.g. DeWalt et al., 2004) or the slope of the reaction norm to environmental treatments (e.g. Maron et al., 2004; Caño et al., 2008; Qing et al., 2011; Moroney et al., 2013). Plasticity indices provide quick estimations but are weaker for statistical comparison, whereas reaction norms are more reliable since they are the most direct way of exploring phenotypic plasticity (Valladares et al., 2006). Studies testing pre-adaptation vs. genetic shift on new species should therefore use the best available methodology.

Here we investigate mechanisms underlying the invasion of a major invasive species in Europe, *Impatiens glandulifera*. We determine whether high competitiveness, abundant reproduction and high phenotypic plasticity were already present before invasion (pre-adaptation) or evolved after introduction (genetic shift) by comparing offspring from the native and the invasive range. Importantly, we also test for the presence of genetic variation in trait means and trait plasticity, which to our knowledge has not been done before in alien invasive species and could shed more light on the causes for possible changes in phenotypic plasticity during the invasion process.

2. Materials and methods

2.1. Study species and populations

The Himalayan balsam, *I. glandulifera* Royle (Balsaminaceae), is a widespread, often riparian forb native to the western Himalaya from Kashmir to Garhwal (India) (Hulme and Bremner, 2006). After introduction in Great Britain in 1839 it spread through Europe (Beerling and Perrins, 1993), where it increased dramatically in abundance and distribution during the past 30–40 years. The species is classified as one of the 100 most invasive species in Europe (DAISIE, 2008). It occurs in many different habitats, but thrives best under high nutrient and water availability (Beerling and Perrins, 1993; Pyšek and Prach, 1995). *I. glandulifera* commonly reaches a height of up to 2.5 m and the plants in the invasive range are generally taller than in the native range (Beerling and Perrins, 1993; Pyšek and Prach, 1995; Clements et al., 2008; Tanner et al., 2014). The species is annual, does not reproduce vegetatively and has a limited seed bank; successful seed production and recruitment each year is therefore crucial for maintenance and spread of populations (Skálová et al., 2012). Seeds are dispersed by ballistochory (Willis and Hulme, 2004), but long-distance dispersal often occurs by water currents, small rodents or man's deliberate or inadvertent spread (Beerling and Perrins, 1993).

The current study used the offspring from four populations of *I. glandulifera* (see Table 1 for population's coordinates and characteristics), two from the native range (Kashmir, India) and two from the invasive range (Trondheim, Norway). The latter were chosen at the northern end of the invasive range in order to have maximal differences in environmental conditions relative to the native range (Table 1). This maximizes the selective pressure on the plants and thus the chance to detect any realized genetic shift (DeWalt et al., 2004; Maron et al., 2004; Bossdorf et al., 2005; Caño et al., 2008; Qing et al., 2010; Colautti and Barrett, 2013). Moreover, the Species Map Service (Norwegian biodiversity information center and GBIF-Norway, 2007–2014) indicates the presence of *I. glandulifera* around Trondheim since 1949, which is considered sufficiently long for genetic shifts to be expressed (Lee, 2002).

During August and September 2011, mature seeds from a large number of capsules were collected from 30 randomly selected maternal plants in each population. After measuring their height, these plants were harvested and oven dried for 72 h at 60 °C to determine the aboveground biomass. The average number of seeds per capsule was obtained by dividing the total number of collected seeds by the number of collected capsules. The average seed mass was obtained by dividing the mass of all collected seeds by the total number of seeds. In each population, four PRS probes (Plant Root Simulator, Western Ag Innovations Inc., Saskatoon, Canada) were inserted vertically into the soil at 5 cm depth to measure soil nitrogen availability during six weeks of the growing season (mid-June to end of July 2011). These probes consist of an ion exchange resin membrane that is charged. When buried, soil ions displace the counter-ions at a rate that depends on their diffusion rate in the soil. The quantity of soil ions absorbed during a burial period is a function of all soil properties controlling nutrient availability in soil. After six weeks the PRS probes were removed from the soil and the amount of nitrogen per surface area of membrane was measured. Average soil nitrogen availability per population was calculated from the amount of nitrogen per surface area of membrane measured on the four PRS probes in every population. During the same period, two data loggers (DS 1921G, NexSens Technology, Fondriest environment Inc., Beavercreek, Ohio, USA) per population measured the top soil temperature at 2 cm depth every hour. All populations were located along roads and were assumed to have experienced similar disturbance regimes.