

## Comparison of native and non-native *Impatiens* species across experimental light and nutrient gradients

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**Background and aims** – The success of invasive species over resident species is often assigned to their trait attributes and their ability to respond plastically towards fluctuating environmental conditions. To elucidate the role of differentiated trait responses towards environmental conditions promoting invasion success, we conducted a congeneric study with three *Impatiens* species, one of which is native to Central Europe (*I. noli-tangere*), while the other two are introduced and considered invasive (*I. parviflora* and *I. glandulifera*). We hypothesised that plasticity in plant traits increases from high resource environments to low resource environments, and we expected the two invasive species to exhibit higher trait plasticity than the native species.

**Methods** – Monocultures of the three species were grown in pots with nine combinations of light and nutrient availability (ambient, medium and high light plus N-limited, balanced and P-limited). We then measured species responses with respect to biomass allocation traits, growth rates and reproduction. We conducted multivariate analysis of trait responses via path analysis and structural equation modelling, and determined phenotypic plasticity indices (PIs) for plant traits across the nine treatments.

**Key results** – The performance of invasive *Impatiens* species is more prone to unfavourable nutrient conditions than to adverse light conditions. Following our initial model, we expected similar trait responses and trait-trait relationships for the three species, regardless of absolute biomass allocation patterns or whether they were native or non-native. Instead, we found that the three congeneric *Impatiens* species exhibited contrasting responses to light and nutrient treatments, leading to different trait-trait relationships. Specifically, *I. noli-tangere* and *I. parviflora* exhibited similar responses and trait-trait relationships, whereas those of *I. glandulifera* differed. Treatment effects on plant traits showed that the non-native *I. parviflora* was the most plastic species; however, this result was not consistent across all traits.

**Conclusions** – The success of invasive species over their native congeners is based on a combination of similar trait responses to environmental site conditions, but the invasive species exhibit higher trait plasticity, facilitating establishment.

**Key words** – Congeners, plasticity, N-limitation, non-native species, P-limitation, structural equation modelling, trait responses.

### INTRODUCTION

The adverse effects of invasive species on native ecosystems have been documented by many studies (Elton 1958, Lockwood et al. 2008, Vilà et al. 2011). Examples of adverse effects include changes to nutrient cycling and hydrology, degradation of terrestrial environments and changes to species composition, due to competitively superior invasive species suppressing resident native species (D'Antonio & Kark 2002, Hejda et al. 2009, Pyšek & Richardson 2010, Gaertner et al. 2011, Pyšek et al. 2012). Abiotic and biotic factors

regulate whether an invasive species is introduced, able to colonise and, ultimately, to naturalise (sensu Richardson et al. 2000). Such factors include propagule pressure, environmental conditions of the resident site and competitive pressure of the resident community, respectively. While only a small percentage of all introduced species becomes established, explanations for differential invasion success remain unsatisfactory (di Castri 1989, Richards et al. 2006). However, some plant characteristics have been demonstrated to promote invasion success. Examples include tall stature, high growth rate, high fecundity and efficient dispersal (Morav-

cová et al. 2010, van Kleunen et al. 2010). A meta-analysis by González et al. (2010) showed that, compared to native species, invasive species exhibit higher growth and production rates in both low and high resource environments. The authors explained invasion success in low versus high nutrient conditions by higher resource use efficiency, threshold element ratios and trait plasticity. Various studies have demonstrated that invasive species are often phenotypically more plastic in their response to fluctuating environmental conditions than their non-invasive or native congeners (Daehler 2003, Burns & Winn 2006, Richards et al. 2006, Funk 2008). Plasticity is understood as the capacity of a single genotype to produce different phenotypes in different environments (Sultan 2000). The plasticity of morphological and physiological traits only contributes to invasion success if it enables the invader to adapt to fluctuating environmental conditions, minimise negative abiotic effects and take advantage of favourable environments (Richards et al. 2006). Thus, measuring how plants respond to more than one environmental helps us to elucidate how plasticity contributes to invasion processes (Burns 2004, Williams et al. 2008, Skálová et al. 2012).

Aikio & Markkola (2002) studied the phenotypic plasticity of the root-to-shoot ratio under different nutrient and light availability. The authors concluded that the phenotypic plasticity of a plant trait decreases from low resource environments to high resource environments, and is intermediate when resources are uncorrelated. Accordingly, the 'Optimal Resource Theory' (Bloom et al. 1985) and the 'Theory of Functional Equilibrium' (Brouwer 1962) predict that biomass should be allocated to either the roots or shoots, depending on which organ is experiencing the greatest resource limitation, but that biomass should be proportionally distributed under non-limiting conditions. In a study with fluctuating light and nutrient availability, plasticity should increase towards resource limited treatments (i.e. when light and nutrient availability are lowest) and should decrease when these resources are highly abundant.

Plasticity studies often use congeneric species (Sultan 2001, Brock et al. 2005, Sultan et al. 2009, Skálová et al. 2012). The congeneric, or phylogenetic approach, involves comparing two or more closely related species with respect to various parameters, including their functional traits, competitive ability, coexistence and others (Feng & Fu 2008, Godefroid & Koedam 2010, He et al. 2012). Closely related species share many physiological and morphological traits and, therefore, more likely compete for the same resources (Matesanz et al. 2011, but see also Beltrán et al. 2012 for phenotypic trait divergence allowing coexistence). The benefit of the congeneric approach lies in the minimisation of bias associated with certain parameters, such as phylogenetic distances, life history traits and dispersal mode (Burns 2004, van Kleunen et al. 2010). However, despite their general similarity, congeners may also differ with respect to adaptive strategies and ecological breadth, with competitively superior species having broader ranges compared to narrow-ranged inferior species (Milla et al. 2011). Consequently, congeneric studies have the potential to reveal why certain species are more successful than others, despite both sharing similar traits. In the field of invasion biology, this approach has been

used to disentangle what causes the success of some invasive species over their native congeners (Godefroid & Koedam 2010, Skálová et al. 2013, Čuda et al. 2014). For example, Burns (2004) found that closely related dayflower species differed in their response to nutrient and water availability, with the invasive species showing higher growth rates than their non-invasive congeners under high nutrient regimes, despite growth responses being similar under low nutrient availability. In contrast, Ugoletti et al. (2011) did not detect differences between native and invasive *Impatiens* species with respect to photosynthetic, growth and reproductive characteristics.

While it was shown that invasive species performed better in environments with high light and nutrient availability (Holdredge et al. 2010), their negative effects on native species decreased in stressful environments (Richardson et al. 2012). Light represents a distinct physical entity, whereas 'nutrients' is a generic term encompassing all macro- and micronutrients essential for plant growth. Yet, the type of nutrient that is limiting promotes different responses in plants. For instance, phosphorus-limitation influences reproduction and productivity more than nitrogen-limitation (Fenner 1986, Wassen et al. 2005 cited by Olde Venterink 2011). Nitrogen-limitation supports the relationship between decreasing growth rate and increasing biomass N:P ratio (i.e. growth rate hypothesis, see Thompson et al. 1997, Sterner & Elser 2002, Güsewell 2004). Wassen et al. (2005) showed that P-enrichment causes an increase in productivity and a loss of species due to the competitive exclusion of species adapted to formerly P-limited conditions. Furthermore, Lannes et al. (2012) demonstrated that alien species decrease while endangered species increase along a gradient of low to high vegetation N:P ratio. The resource competition theory by Tilman (1982) predicts that native species should be competitively subordinate to invasive species, during invasive species establishment, if the latter species has fewer requirements for resources to sustain higher growth rates and reproductive outputs under resource-limited conditions.

Here, we conducted a congeneric study with three *Impatiens* species, one of which is native to Europe, North America and Asia whereas the other two have been introduced and are considered invasive (DAISIE 2015). We evaluated differences in trait responses to light and nutrient gradients among the three species via path analysis and structural equation modelling (SEM, Grace 2006). This procedure allowed us to compare the trait responses and trait-trait relationships of the species. This information was expected to help identify differences in the response patterns between native and invasive congeners. We used causal networks to describe the processes of trait responses and trait-trait interactions, rather than bivariate relationships. This is because bivariate relationships have limited predictive power due to it not being possible to infer underlying mechanisms from bivariate plots and bivariate relationships (Adler et al. 2011, Grace et al. 2014). Canal networks have been successfully used to identify links between fitness-related traits and the invasiveness of plant species (Godoy et al. 2012), plant and insect traits (Frenette-Dussault et al. 2013), and soil properties and species richness (Laughlin et al. 2007).

Furthermore, we questioned which traits of which species are more plastic in response to light and nutrient gradients, with the expectation that trait plasticity increases towards resource limited treatments and vice versa (Aikio & Markkola 2002). In general, we expected the trait plasticity of the invasive species to exceed that of the native species (see Richards et al. 2006). The study design included a light gradient reaching from low light to high light conditions, and a nutrient gradient comprising N-limitation, balanced conditions (no limitations of either N or P), and P-limitation. Specifically, we addressed the following questions: (1) do species responses towards the light and nutrient treatments differ, (2) are there performance-differences between the invasive and non-invasive species, and (3) do the two invasive species exhibit higher trait plasticity than their native congener? Our results are expected to provide new insights into the factors that drive the relative success of establishment by invasive plant species.

## MATERIALS AND METHODS

### Study species

The three study species belong to the genus *Impatiens* (Balsaminaceae), with *I. noli-tangere* being native to Central Europe, whereas *I. glandulifera* and *I. parviflora* have been introduced from Asia (Kowarik 2010). The three annual plant species exhibit ballistic dispersal, form transient seed banks and have shallow root systems (Coombe 1956, Perrins et al. 1993, Hatcher 2003, Clements et al. 2008).

*Impatiens noli-tangere* L. (Touch-me-not Balsam) is native to Central Europe, North America and Asia (Russia, Japan and Kamchatka). It occurs from the lowlands up to 1,300 m a.s.l. in sites with moist to wet soils, on the edges of rivers, streams and lakes and in moist forests and clearings (Hatcher 2003). It is a nitrophilous species and mainly occurs in partial shade (Ellenberg indicator values for nitrogen 6, light 4, Ellenberg et al. 1991). According to Falińska (1979, in Hatcher 2003), *I. noli-tangere* has a variable phenotype that is influenced by shade, moisture and nutrient levels, with taller-growing, heavier plants occurring under higher soil fertility, better light conditions and higher water levels. The species is considered to be in decline locally (Tichý 1997, Čuda et al. 2014), and rarely reappears at sites where it has been lost (Hatcher 2003).

*Impatiens parviflora* DC. (Small Balsam) is native to the mountain ranges of Central Asia (Altai to Hindukush) and has been cultured in the botanical gardens of Germany and Switzerland, from where it escaped horticulture in the 19<sup>th</sup> century (Trepl 1984). Today, it is considered the most abundant and widespread neophyte in the forests of Central Europe. It is common in mesic broad-leaved forests, forest edges and ruderal habitats, where it grows on a wide range of mineral soils that are moist but not waterlogged (Coombe 1956). According to Ellenberg et al. (1991), *I. parviflora* and *I. noli-tangere* share similar ecological requirements, but the local amplitude of the invasive species is much broader, ranging from sites with high light conditions to shaded sites, from dry to moist conditions and from nutrient-poor to nutrient-rich soils (Kowarik 2010, Dobravolskaitė 2012). When

both species occur at the same site, *I. noli-tangere* is competitively subordinate, especially under non-optimal conditions, such as semi-dry soil (Essl & Walter 2005, Chmura & Sierka 2006).

*Impatiens glandulifera* Royle (Himalayan Balsam) is tolerant of a wide variety of soil textures and structures. Originating from the western Himalaya regions, it reached Europe as an ornamental plant, where its spread had been facilitated by its use as fodder plant for bees (Hagen 1991, Kowarik 2010). It grows in full sunlight, and is considered shade tolerant (Ellenberg indicator values for light 5 and for nitrogen 7, Ellenberg et al. 1991), but is adversely affected by light conditions < 30% full daylight. Plants under shaded conditions have higher biomass production and higher leaf area ratios than individuals in open sites (Beerling & Perrins 1993). Pyšek & Prach (1995) reported the rapid spread of *I. glandulifera* in the Czech Republic. Skálová et al. (2012) suggested that it is a highly invasive plant, while the DAISIE-Initiative classified it as one of the 100 of the worst invaders (DAISIE 2015). In response to climatic changes, *I. glandulifera* is expected to extend northwards and to higher elevations (DAISIE 2015).

### Experimental design

In April 2012, seedlings of the three species were collected in a natural forest understorey about 3 km from the campus area of the University of Oldenburg, Germany (between 53°9'36.0"N 8°7'55.0"E and 53°9'34.57"N 8°8'1.70"E). We used seedlings because the germination rates of previously collected seeds were too low to provide enough individuals to conduct the experiment. The individuals of each species were collected from each the same population in the understorey of a deciduous forest, with pH of 5.0 (SE ± 0.26, measured in water and pH of 5.7 ± 0.3 measured in CaCl<sub>2</sub>, samples were taken from the topsoil [0–10cm], n = 5) and canopy openness of about 4% [SE ± 0.45], n = 5). The canopy openness was measured by determining the black–white threshold with Sidelook 1.1 (v. 1.1, <http://www.appleco.ch/>) and calculating the percentage of open sky with Gap Light Analyzer (Frazer et al. 1999). Distances between collection points ranged between 38 and 45 m, with similar conditions at the site collection points. Thus, any environmentally induced differences on the phenotypes at the local scale of our study were excluded. Furthermore, Pahl et al. (2013) showed that *Impatiens glandulifera* exhibits no local adaptation. The collection point was chosen as soon after germination as possible, but when seedlings were big enough to withstand the procedure of transplanting (about 1.5 to 2 cm tall). After collection, all seedlings were grown under the same soil and light conditions for three weeks. Then, twenty seedlings of each species were randomly assigned to each treatment, and each individual was transplanted into a 2 L pot filled with quartz sand. Glass fibre strings were placed near the roots and channelled through the pot into the saucer to avoid water stress, especially during the initial phase of growth when the root system was still poorly developed. Plants were watered by adding tap water into the saucer when needed. Nutrients were applied once a week by watering the plants with a nutrient solution. The study was conducted in a greenhouse,

where the pots were arranged as a  $3 \times 3$  factorial design, with light and nutrients as the factors.

The three light treatments were ambient light (no shade cloth, mean irradiance level of 60 consecutive midday measurements days at  $408 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE  $\pm 32.3$ , range  $808.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), medium light ('M', 40% of ambient light, mean  $150 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE  $\pm 9.65$ , range  $258 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and low light ('L', 26% of ambient light, mean  $110 \mu\text{mol m}^{-2} \text{s}^{-1}$  SE  $\pm 7.09$ , range  $188 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Mean temperature was 19, 23 and  $22^\circ\text{C}$  (HL, ML and LL, SE  $\pm 0.2$ ,  $0.2$  and  $0.19$ ). Shade cloth was stretched around parts of the greenhouse in which all individuals of the M and L treatments were grown. Light levels were measured with Delta-T Logger, Delta-T Devices Ltd., Cambridge, UK with PAR special sensor (Quantum sensor type Q2, Skye Instruments, Wales). To enable insects to access the experimental plants and pollinate the flowers, the greenhouse was open at two sides. The shade cloth was lifted at times when there was no direct sunlight and throughout the nights to early morning to ensure insects had access to all parts of the experiment. Nutrient treatments consisted of three N:P supply ratios (1.7, 15 and 135 mass-based, see also Olde Venterink & Gusewell 2010). Results of another greenhouse experiment conducted with *I. nolitangere* and *I. parviflora* revealed tissue nutrient N:P ratios of about 4, 11 and 27 in response to resource N:P ratios of 1.8, 14.5 and 45, respectively (data not shown). This indicates N-limitation (vegetation N:P < 10), balanced nutrient conditions (vegetation N:P 10–20) and P-limitation (vegetation N:P > 20), see Gusewell (2004).

Nutrients were supplied once a week as salt solutions starting on 15 May 2012. Nitrogen was supplied as  $\text{NH}_4\text{NO}_3$  ( $48.62 \text{ mg L}^{-1}$ ,  $143 \text{ mg L}^{-1}$  and  $429 \text{ mg L}^{-1}$  for the three treatments, respectively) and phosphorus as  $\text{KH}_2\text{PO}_4$  ( $43.93 \text{ mg L}^{-1}$ ,  $13.18 \text{ mg L}^{-1}$  and  $4.83 \text{ mg L}^{-1}$ , respectively). All other nutrients were supplied every two weeks in constant amounts (totals per pot: 400 mg K, 133 mg Ca, 57 mg S, 14 mg Fe, 8 mg Cu, 3.2 mg Mo, 2 mg Mn, 0.2 mg Bo and 0.08 mg Co).

The experiment consisted of nine treatments; namely, three light and three nutrient treatments. The light treatments consisted of high light, medium light and low light, herein-after referred to as 'H', 'M' and 'L'. Nutrient treatments corresponded to N-limited conditions, balanced nutrient supply and P-limited conditions, which were abbreviated as 'N', 'bal' and 'P'. Thus, the nine treatment-combinations were HN, Hbal, HP and MN, Mbal, MP, and LN, Lbal and LP. All treatments were carried out with 20 replicate pots. The total number of pots were three species  $\times$  three light treatments  $\times$  three nutrient treatments  $\times$  20 replicates = 540.

### Harvest and measured plant traits

The plants were harvested when symptoms of senescence appeared. The main harvest took place between 5 and 21 Aug. 2012. During the experiment, senescent leaves were collected if they presented a high level of deterioration; specifically, a yellow-brown colour on more than 70% of the leaf area (Ugoletti et al. 2011). The aboveground shoot was cut off and the leaf and stem mass were separated, and subsequently dried at  $70^\circ\text{C}$  for 72 h and weighted. We did not measure the

seed mass of plants, but we did determine the number of capsule insertion points along the stem for each individual at the date of harvest. The remaining capsules were removed from the stem leaving a distinct mark, which we used to determine the exact number of capsules for each individual. Ugoletti et al. (2011) showed that the number of capsules and seeds was equally high for *I. glandulifera* and *I. parviflora*. Thus, in the present study, the number of capsule insertion points was used to infer the potential reproductive capacity of each species.

Two leaves per individual were collected, and their dry weight and area was determined (flatbed scanner and computer software ImageJ, Rasband 2014). Specific Leaf Area (SLA) was calculated as the area of the two leaves divided by their dry weight ( $\text{mm}^2 \text{mg}^{-1}$ , Pérez-Harguindeguy et al. 2013). The stem length of all stems, including those of second order stems, was measured each week for each individual. Then, the Relative Growth Rate of the stem between each measurement was calculated according to Hunt (1990) as  $\text{RGR}_{\text{Stem}} = (\log W_2 - \log W_1) / (t_2 - t_1)$ , with  $W_2$  and  $W_1$  representing the stem length at the sequential times  $t_2$  and  $t_1$ , respectively. This information was used to calculate the mean Relative Growth Rate of the stem ( $\text{RGR}_{\text{Stem}}$ ,  $\text{cm}$ ).

### Statistical analysis

**Univariate variance analyses** – To test for effects of light and nutrient treatments on the response variables, analysis of variance (ANOVA) was carried out with species, light and nutrients as factors with three levels each. Variables were transformed (log, boxcox) if necessary to meet the assumptions of ANOVA, analysis was conducted with R (R Core Team 2014).

**Multivariate path analyses** – To evaluate differences and similarities of the three species with respect to their trait responses to the environmental drivers (light and nutrient availability) in a multivariate way, three separate path analyses were conducted with nutrients and light as independent variables and plant traits as dependent variables (i.e. with error terms).

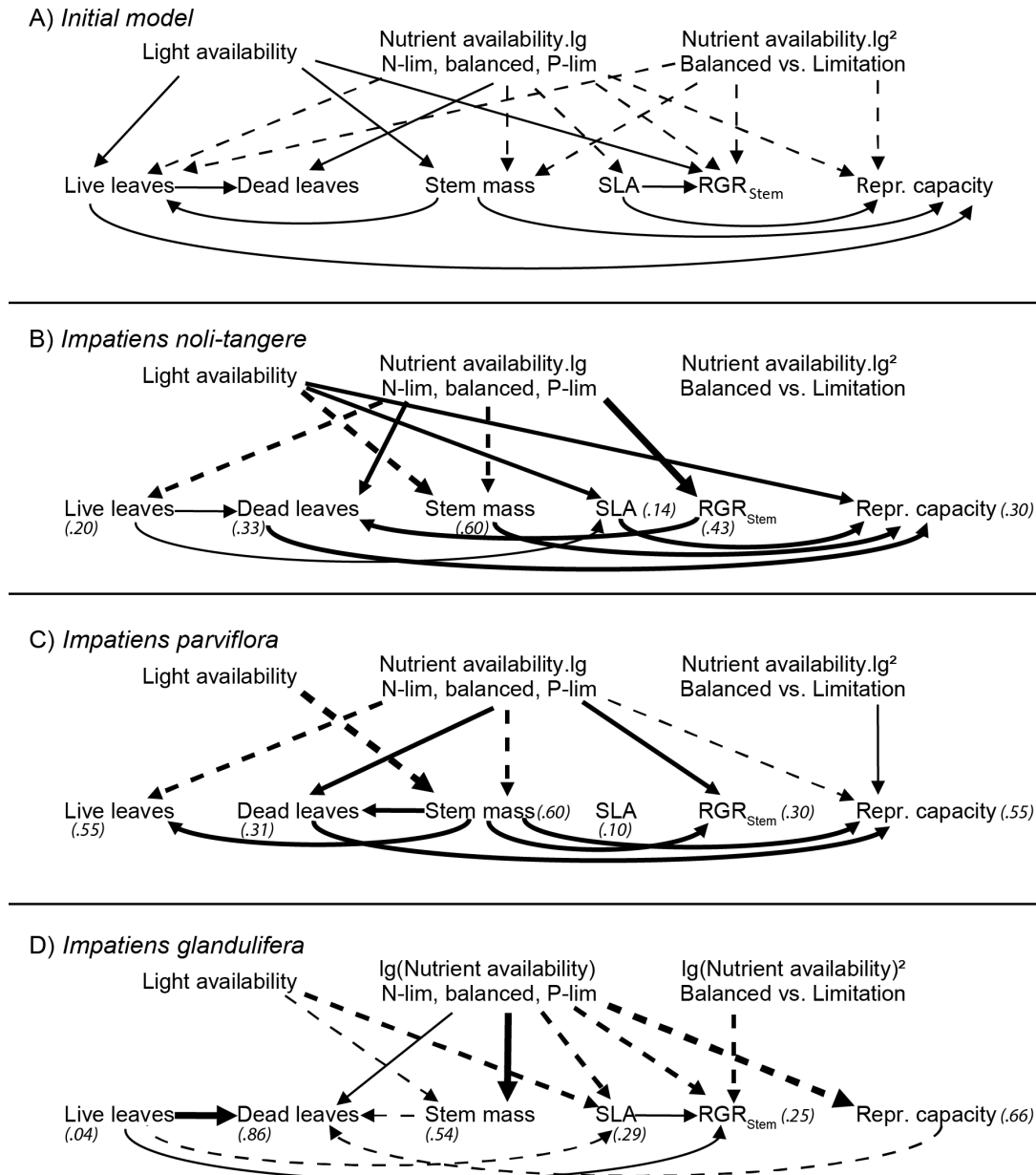
Ecological studies are often required to examine influences and responses simultaneously. Path analysis has been proven as a successful statistical tool for evaluating independent variables (e.g. environmental variables) exerting influences on dependent variables (e.g. plant traits) and examining of interactions between dependent variables (e.g. trait-trait interactions) is possible (Grace 2006). Path models and structural equation models (SEMs) have been applied to test response-effect linkages for plants, identifying key response and effect traits at the community level with respect to various ecosystem processes, like decomposition and productivity (Lavorel & Grigulis 2012, Lienin & Kleyer 2012, Minden et al. 2012). Here, we used this statistical tool to evaluate the similarities and differences in congeneric species responses to light and nutrient availability. We also assessed species dependent differences in trait-trait relationships, like trade-offs and allometries.

Path analysis partitions the correlation among variables, and measures both direct and indirect effects on response variables (Grace 2006). The expected covariance structure of

the hypothetical model is compared to the actual covariance matrix. The path coefficient values are standardised partial regression coefficients that are assigned to direct or indirect pathways (Grace 2006). SEM (Structural Equation Modeling) was used to test the hypothesis that the measured covariance structure adequately describes the expected covariance structure. Via maximum likelihood estimates, a test statistics was generated that was distributed as a  $\chi^2$  approximation (Backhaus et al. 2003). A good fit of the model to the data results in a non-significant P-value, a  $\chi^2/df \sim 1$ , a comparative

fit-index (CFI) of  $> 0.95$  and a root mean square error of approximation (RMSEA) of  $< 0.05$ – $0.08$  (good to fair model, Byrne 2001, Backhaus et al. 2003, Arbuckle 2007). Analysis was conducted using Amos 22 (Amos Development Corporation 2013).

For the model, light availability was represented by the metric values 100, 40 and 26, where 100 refers to high light conditions and 26 to low light conditions. In other words, the variable ‘light availability’ reflects a continuous gradient from high light to low light availability. N-limitation initially



**Figure 1** – Initial model (A) and final models for *I. noli-tangere* (B), *I. parviflora* (C) and *I. glandulifera* (D). The figures include the relationship between the environment (Light availability, Nutrient availability.lg and Nutrient availability.lg²) and traits, in addition to trait-trait relationships. Path coefficients between variables are standardised partial regression coefficients of direct effects. All paths within the interval -0.2 to 0.2 were excluded (see table 1 for total effects). Arrow widths are proportional to the standardised path coefficient (except for the initial model), positive relationships are indicated by solid lines, negative relationships are indicated by dashed lines, error terms for dependent variables were omitted, all pathways are significant at  $p < 0.05$ .  $R^2$  values are given for all dependent variables, and represent the total variance explained as a result of all predictors pointing to that variable.

**Table 1 – Assumptions of the initial model and the results of the path analyses for *I. noli-tangere*, *I. parviflora* and *I. glandulifera*.**

Expected positive (+) and negative (-) relationships between variables are indicated for the initial model. For the final models, we present standardised coefficients for the total effects of the environmental parameters (light availability, Nutrient availability.lg and Nutrient availability.lg<sup>2</sup>) on plant traits, as well for trait-trait relationships; all paths are significant at  $p < 0.05$ .  $R^2$  values for dependent variables are presented in fig. 1.

Initial model			Final model – <i>Impatiens noli-tangere</i>				
Cause		Target	Cause		Target	Total	
Light availability	+ →	Live leaves	Light availability	→	Live leaves	-.20	
Light availability	+ →	Stem mass	Light availability	→	Dead leaves	-.06	
Light availability	+ →	RGR <sub>Stem</sub>	Light availability	→	Stem mass	-.62	
			Light availability	→	SLA	.28	
			Light availability	→	RGR <sub>Stem</sub>	-.03	
			Light availability	→	Repr. capacity	.21	
Nutrient availability.lg	- →	Live leaves	Nutrient availability.lg	→	Live leaves	-.40	
Nutrient availability.lg	+ →	Dead leaves	Nutrient availability.lg	→	Dead leaves	.40	
Nutrient availability.lg	- →	Stem mass	Nutrient availability.lg	→	Stem mass	-.42	
Nutrient availability.lg	- →	SLA	Nutrient availability.lg	→	SLA	-.10	
Nutrient availability.lg	- →	RGR <sub>Stem</sub>	Nutrient availability.lg	→	RGR <sub>Stem</sub>	.64	
Nutrient availability.lg	- →	Repr. capacity	Nutrient availability.lg	→	Repr. capacity	-.03	
Nutrient availability.lg <sup>2</sup>	- →	Live leaves					
Nutrient availability.lg <sup>2</sup>	- →	Stem mass	Nutrient availability.lg <sup>2</sup>	→	Stem mass	-.19	
Nutrient availability.lg <sup>2</sup>	- →	RGR <sub>Stem</sub>					
Nutrient availability.lg <sup>2</sup>	- →	Repr. capacity	Nutrient availability.lg <sup>2</sup>	→	Repr. capacity	-.07	
Live leaves	+ →	Dead leaves	Live leaves	→	Dead leaves	.32	
			Live leaves	→	SLA	.25	
			Live leaves	→	RGR <sub>Stem</sub>	.17	
Live leaves	+ →	Repr. capacity	Live leaves	→	Repr. capacity	.18	
			Dead leaves	→	Repr. capacity	.38	
Stem mass	+ →	Live leaves					
Stem mass	+ →	Repr. capacity	Stem mass	→	Repr. capacity	.37	
SLA	+ →	RGR <sub>Stem</sub>					
SLA	+ →	Repr. capacity	SLA	→	Repr. capacity	.25	
			RGR <sub>Stem</sub>	→	Dead leaves	.39	
			RGR <sub>Stem</sub>	→	Repr. capacity	.15	
Final model – <i>Impatiens parviflora</i>			Final model – <i>Impatiens glandulifera</i>				
Cause		Target	Total	Cause		Target	Total
Light availability	→	Live leaves	-.26	Light availability	→	Live leaves	-.19
Light availability	→	Dead leaves	-.29	Light availability	→	Dead leaves	.03
Light availability	→	Stem mass	-.62	Light availability	→	Stem mass	-.27
				Light availability	→	SLA	-.31
Light availability	→	RGR <sub>Stem</sub>	-.25	Light availability	→	RGR <sub>Stem</sub>	-.12
Light availability	→	Repr. capacity	-.37	Light availability	→	Repr. capacity	-.10
Nutrient availability.lg	→	Live leaves	-.62	Nutrient availability.lg	→	Dead leaves	.41
Nutrient availability.lg	→	Dead leaves	.37				
Nutrient availability.lg	→	Stem mass	-.42	Nutrient availability.lg	→	Stem mass	.66
				Nutrient availability.lg	→	SLA	-.31
Nutrient availability.lg	→	RGR <sub>Stem</sub>	.33	Nutrient availability.lg	→	RGR <sub>Stem</sub>	-.07
Nutrient availability.lg	→	Repr. capacity	-.23	Nutrient availability.lg	→	Repr. capacity	-.79
Nutrient availability.lg <sup>2</sup>	→	Live leaves	-.20				
Nutrient availability.lg <sup>2</sup>	→	Dead leaves	-.09	Nutrient availability.lg <sup>2</sup>	→	Dead leaves	.16
Nutrient availability.lg <sup>2</sup>	→	Stem mass	-.19	Nutrient availability.lg <sup>2</sup>	→	Stem mass	-.19
Nutrient availability.lg <sup>2</sup>	→	SLA	.31	Nutrient availability.lg <sup>2</sup>	→	SLA	-.18
Nutrient availability.lg <sup>2</sup>	→	RGR <sub>Stem</sub>	.18	Nutrient availability.lg <sup>2</sup>	→	RGR <sub>Stem</sub>	-.39
Nutrient availability.lg <sup>2</sup>	→	Repr. capacity	-.12	Nutrient availability.lg <sup>2</sup>	→	Repr. capacity	-.18
Live leaves	→	RGR <sub>Stem</sub>	-.29	Live leaves	→	Dead leaves	.76

reflected its N:P ratio of 1.7, balanced conditions based on an N:P ratio of 15 and P-limitation based on an N:P ratio of 135, which resulted in a linear increase of the numerical values. However, as the response towards this gradient was unimodal (for example, with a higher growth rate in the balanced treatment and a lower growth rate at each end of the gradient), we log-transformed and centred the values in the nutrient treatment. This new variable was used with equidistant values for model creation ('Nutrient availability.lg'). In this variable, the N:P ratio of 1.7 was transformed to -2.18, the N:P ratio of 15 to -0.006 and the N:P ratio of 135 to 2.19. The metric, interval-scaled variables were transformed, rather than being coded as categorical variables, which kept them on a continuous scale. This strategy allowed Pearson's  $r$  correlation coefficient to be calculated, which equals the regression coefficients of direct effects in path analysis with standardised estimates. Furthermore, we squared the values of the new variable to create a third independent variable, 'Nutrient availability.lg<sup>2</sup>', using values of 4.76, 4.36  $e^{-5}$  and 4.79 for N:P ratios of 1.7, 15 and 135, respectively. Squaring of the values allowed us to distinguish between limited and balanced nutrient conditions.

The initial model (fig. 1A & table 1) described the hypothesised relationships for light and nutrient availability in relation to plant traits. The environmental variables were considered exogenous, with no response to any other variable. Trait variables were considered endogenous, responding to other variables and with measurement errors.

We expected Leaf mass, Stem mass and  $RGR_{Stem}$  respond positively to high light availability and we expected a variable response to nutrient limitation. Specifically, we expected the decrease in productivity to be more pronounced under P-limitation compared to N-limitation, given that growth rates depend more strongly on P than on N. For instance, in the model, we expected Live leaves, Stem mass, SLA and  $RGR_{Stem}$  to respond negatively to Nutrient availability.lg (Ågren 2008). Individuals subject to P-limitation might also struggle with maintaining living leaf tissue. This issue could lead to a shorter leaf life span (and more dead leaf mass, Fujita et al. 2014), without shed leaves being replaced, resulting in decreased living leaf biomass compared to the other nutrient treatments. P-limitation more severely impacts the reproduction of plants compared to N-limitation, with N-limited plants having more conservative leaf economic traits (i.e. low SLA, Fujita et al. 2014). Liebig's law of the minimum (Liebig 1840, 1855) states that biomass production is limited by the least available element; thus, we expected Live leaves, Stem mass,  $RGR_{Stem}$  and Reproductive capacity to respond negatively to the independent variable Nutrient availability.lg<sup>2</sup>, in which both N- and P-limitation are represented by values of  $\sim 5$  and balanced nutrient conditions by values of  $\sim 0$ , respectively. For the trait-trait relationships, we expected an allometric relationship between Stem mass and Leaf mass, represented by a direct relationship from Stem mass to Live Leaves and an indirect to Dead leaves via Live leaves. Following Garnier (1992), we expected an allometric relationship between SLA and  $RGR$ , and SLA and Reproductive capacity.

For model interpretation, for instance, a positive relationship between light availability and any trait indicates that al-

location to this trait was highest under high light conditions. A positive or negative relationship between Nutrient availability.lg and any trait indicates the highest and lowest trait values under P- and N-limited conditions, respectively. Finally, a positive relationship between Nutrient availability.lg<sup>2</sup> and any trait indicates the highest trait values under P- or N-limited conditions, whereas a negative relationship describes the highest trait values under balanced nutrient conditions.

**Phenotypic plasticity** – To test whether plasticity increased from low resource environments to high resource environments (sensu Aikio & Markkola 2002), we tested for significant differences between the mean trait values for each species in the treatments with the lowest resources (i.e. low light and N-limited; and low light and P-limited) and in the treatment with the highest resource (i.e. high light, balanced nutrient conditions). We then tested whether the change in trait means was positive (increase towards high resource environment) or negative (decrease towards high resource environment).

To test whether the invasive species showed greater trait plasticity than the native species across all treatments, the phenotypic plasticity index (PI: ranging from 0 to 1) was calculated for each response variable as the difference between the maximum mean value and the minimum mean value divided by the maximum mean value across the levels of a treatment (i.e.  $[\text{mean}_{\max} - \text{mean}_{\min}] / \text{mean}_{\max}$ ). To evaluate the rate of plastic response depending on the type of environmental condition, PI was calculated for each treatment factor (light, nutrients), as well as among all treatment combinations (Valladares et al. 2000a, 2000b).

## RESULTS

### Univariate responses

Species as a factor showed the strongest effect on almost all response traits (see F-values in table 2). Values for Live leaves, Dead leaves and Stem mass were highest for *I. glandulifera*, all other trait values (SLA,  $RGR_{Stem}$ ) were highest for *I. noli-tangere*, only Reproductive capacity was highest in *I. parviflora* (see means in electronic appendix). The experimental setup forbid us to disentangle the effects of light and temperature, which show a high covariation in this study. Thus, in the following we assume that the measured trait responses to 'light' are actually trait responses to a combination of 'light and temperature'.

Traits showed different responses to light and nutrient regimes. Posthoc-tests showed no effect of light on Dead leaves and  $RGR_{Stem}$ , whereas allocation to living leaves and stems, as well as investment in reproduction were highest in the low light treatment. Stem mass and living leaf mass were highest under N-limitation, both regardless of species, whereas turnover rates of leaves (i.e. dead leaf mass) were highest under P-limitation.

Across species the response to nitrogen limitation yielded in highest allocation to Live leaves and Stem mass, whereas under P-limitation values were highest for Dead leaves and  $RGR_{Stem}$  (electronic appendix). Especially the reproductive capacity of *I. glandulifera* decreased strongly under P-limitation, but was higher under N-limitation compared to balanced



**Table 2 – ANOVA results (degrees of freedom, F-values and significance levels) for the effects of Species (S), Light (L) and Nutrients (N) on plant traits.**Significance levels: \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ .

Source	Df	Live leaves	Dead leaves	Stem mass	SLA	RGR <sub>Stem</sub>	Repr. capacity
Species	2	101.63***	134.22***	537.94***	451.26***	249.83***	24.22***
Light	2	15.78***	18.53***	88.53***	21.13***	8.31***	11.38***
Nutrients	2	90.59***	48.09***	187.62***	8.77***	24.74***	81.54***
S × L	4	2.45*	4.68**	11.58***	29.21***	2.68*	6.11***
S × N	4	31.48***	2.67*	25.99***	11.96***	32.47***	34.67***
L × N	4	12.99***	1.16	7.27***	12.13***	5.61***	2.81
S × L × N	8	3.21*	1.09	2.36*	5.59***	2.66**	1.48

nutrient conditions. The reverse was found for the other two species: here, reproductive capacity was highest under balanced conditions, followed by N- and P-limitation and was highest under low light conditions for all species. Across all measured traits, *I. glandulifera* showed significant differences to *I. noli-tangere* in the interaction between species and nutrients, whereas *I. parviflora* took an intermediate position. There was no clear pattern in trait responses for the interactions between species and light.

### Multivariate path analyses

The three separate models exhibited good consistency with the data with  $P = 0.36$  ( $\chi^2/\text{df}$ : 1.08, CFI: 0.99, RMSEA: 0.02) for *I. noli-tangere*,  $P = 0.26$  ( $\chi^2/\text{df}$ : 1.18, CFI: 0.99, RMSEA: 0.03) for *I. parviflora* and  $P = 0.44$  ( $\chi^2/\text{df}$ : 1.00, CFI: 1.0, RMSEA: 0.008) for *I. glandulifera*. The description of the final models focused on direct effects, but also considers standardised total effects for interpretation where necessary (fig. 1 & table 1).

Light availability had strongest effects on Stem mass across species; however, opposite to our expectation, the response was negative. Specifically, allocation to stem mass was lowest in the high light treatments and highest in the low light treatments. Also, opposite to our initial expectation, allocation to Live leaves decreased in the high light treatment; however, this response was quite weak compared to Stem mass. SLA and the reproductive capacity of the three species responded differently to the light treatments. Specifically, the higher the light conditions, the higher SLA and Reproductive capacity in *I. noli-tangere*, whereas *I. parviflora* showed no significant response (for SLA) and *I. glandulifera* responded negatively.

The responses to the different types of nutrient limitation (i.e. either N or P [Nutrient availability.lg] or balanced versus limited nutrient conditions [Nutrient.availability.lg<sup>2</sup>]) were similar for *I. noli-tangere* and *I. parviflora* and for *I. parviflora* and *I. glandulifera*, respectively. For example, Stem mass responded negatively to P-limitation for both *I. noli-tangere* and *I. parviflora*, whereas Stem mass responded positively for *I. glandulifera*. The reproductive rate of the two invasive species strongly declined under P-limitation, whereas the native species only showed a very weak response to P- and N-limitation (table 1 & fig. 1B–D). *Impatiens glandulifera* SLA showed a strong negative response to nutrient availability (i.e. low SLA-values under P-limitation), whereas the na-

tive congener showed a much weaker response, while that of *I. parviflora* was insignificant.

The trait-trait relationships of *I. noli-tangere* and *I. parviflora* were similar to those recorded for the environment, whereas the trait-trait relationships *I. glandulifera* differed. All expected trait-trait relationships were positive in the initial model, with these outputs being confirmed by the final *I. noli-tangere* model. In contrast, trait-traits relationships were mostly allometric for *I. parviflora*, and positive, negative or non-significant for *I. glandulifera*. For example, an increase in Stem mass lead to a simultaneous increase in Reproductive capacity in *I. noli-tangere* and *I. parviflora*, whereas there was no significant relationship for *I. glandulifera*. Also, Dead Leaves and RGR<sub>Stem</sub> yielded strong allometric relationships for *I. noli-tangere* and *I. parviflora*, whereas *I. glandulifera* showed no relationship. Overall, the three species showed different patterns of trait-environment and trait-trait relationships, for which *I. noli-tangere* and *I. parviflora* were more similar in their responses, while *I. glandulifera* noticeably differed.

### Phenotypic plasticity

The hypothesis that plasticity increased from low resource environments to high resource environments was tested for each trait for each species between the treatment with the highest resource abundance (Hbal) and the most resource limited treatments (low light, N- or P-limited). However, our analyses revealed no clear relationships initially (table 3). No trait showed the patterns described by Aikio & Markkola (2002) for any of the three species. Specifically, the authors found an increase in trait plasticity from high resource environments to low resource environments. In our study, most trait values increased from Hbal to either LN or LP (18 out of 36 groups). For eight out of 36 tested groups, the patterns were reversed, with 10 out of 36 tested groups producing insignificant differences between the treatment combinations Hbal and LN, and Hbal and LP. By separately analysing N- and P-limited treatments, a higher number of significant increases in trait values in the nitrogen limited treatment were obtained. Comparison of the three species indicated that trait plasticity was consistently lower under higher resource conditions and higher under lower resource conditions for *I. parviflora*. Consequently, our expectations were met for a particular species (namely *I. parviflora*), but not for a particular trait or a set of traits.



**Table 3 – T-test results of the trait values between the different environments.**

The trait expressions for each species were tested for high light and balanced nutrient conditions (Hbal) against either low light and N-limited (LN), or low light and P-limited (LP) treatments, respectively. The mean trait values ( $\bar{x}$ ) for treatments are given, and the increase or decrease in trait values between the treatments is indicated by  $\searrow$  and  $\nearrow$ , respectively. Significance levels: \*:  $p < 0.05$ , \*\*:  $p < 0.01$ , \*\*\*:  $p < 0.001$ , ns: not significant.

<i>Impatiens noli-tangere</i>	$\bar{x}$ Hbal			$\bar{x}$ LN	$\bar{x}$ Hbal			$\bar{x}$ LP
Live leaves [g]	.09	$\nearrow$	***	.21	.09	$\searrow$	*	.06
Dead leaves [g]	.15		ns	.13	.15	$\nearrow$	**	.22
Stem mass [g]	.17	$\nearrow$	***	.28	.17		ns	.17
SLA [mm mg <sup>-1</sup> ]	78.7		ns	75.7	78.7	$\searrow$	***	64.4
RGR <sub>Stem</sub> [cm day <sup>-1</sup> ]	.0043	$\nearrow$	**	.0035	.0044	$\nearrow$	***	.007
Repr. capacity [no.]	16.40		ns	14.35	16.40	$\searrow$	*	10.10
<i>Impatiens parviflora</i>	$\bar{x}$ Hbal			$\bar{x}$ LN	$\bar{x}$ Hbal			$\bar{x}$ LP
Live leaves	.08	$\nearrow$	*	.14	.08	$\searrow$	*	.04
Dead leaves	.08		ns	.11	.08	$\nearrow$	***	.22
Stem mass	.20	$\nearrow$	***	.68	.20	$\nearrow$	*	.29
SLA	57.2	$\nearrow$	*	66.7	57.2	$\nearrow$	***	71.7
RGR <sub>Stem</sub>	.0029	$\nearrow$	***	0.04	.0029	$\nearrow$	*	.0038
Repr. capacity	18.15	$\nearrow$	***	48.0	18.15		ns	21.95
<i>Impatiens glandulifera</i>	$\bar{x}$ Hbal			$\bar{x}$ LN	$\bar{x}$ Hbal			$\bar{x}$ LP
Live leaves	.16	$\nearrow$	***	.31	.16		ns	.15
Dead leaves	.31	$\searrow$	**	.21	.31	$\nearrow$	***	.50
Stem mass	.75	$\nearrow$	***	1.27	.75	$\searrow$	***	.47
SLA	38.2		ns	41.6	38.2		ns	37.4
RGR <sub>Stem</sub>	.0025		ns	.0022	.0025	$\searrow$	**	.002
Repr. capacity	4.00	$\nearrow$	***	23.75	4.00	$\searrow$	**	0.00

The mean Plasticity index (PI, table 4; see electronic appendix for means and relative standard deviations) across all treatments was greatest for *I. parviflora* in the light treatment (0.44). The PI for Reproductive capacity of *I. glandulifera* was maximal (1), and besides this, the maximum PI was found for Live leaves in the same species. Dead leaves had lower plasticity in the light treatment compared to the nutrient treatment. However, the opposite pattern was detected for SLA, with this trend being consistent for all three species. The PI values of Live leaves and Dead leaves for *I. noli-tangere* and *I. parviflora* were lower in the light treatment compared to the nutrient treatment. Furthermore, the PI values for Leaf mass, Stem mass and Reproductive capacity were greater in the light treatment for these two species. The patterns detected for these traits was generally reserved for *I. glandulifera*. Across species, the greatest plasticity for *I. parviflora* traits was associated with nutrient conditions, whereas the greatest plasticity for *I. glandulifera* was associated with light conditions. Total plasticity values were based on individual treatment combinations (three light  $\times$  three nutrient treatments), and represented the highest possible plasticity. The highest plasticity values were obtained for *I. parviflora*, followed by *I. glandulifera* and *I. noli-tangere*.

## DISCUSSION

This study demonstrated that three congeneric *Impatiens* species exhibited contrasting responses to light and nutri-

ent treatments. Our results indicate that these three species use different strategies, which might contribute to their respective success or failure at establishing at specific sites. In particular, the multivariate path analyses showed that *I. noli-tangere* and *I. parviflora* have similar responses towards both the nutrient- and light-treatments, whereas *I. glandulifera* exhibited a different response. Measures of plasticity revealed that *I. parviflora* traits are most plastic at the extreme ends of the light/nutrient gradients (Hbal vs. LN and LP). This species exhibited the greatest plasticity in response to nutrients when all treatments were taken into account. *Impatiens glandulifera* traits exhibited the greatest plasticity towards light, whereas the native *Impatiens* species had the lowest plasticity.

ANOVA and path analysis results did not support the conclusions of Holdredge et al. (2010), who showed that invasive *Phragmites* species performed better than their native congeners in high light environments. The trait responses of the two invasive *Impatiens* species, especially *I. glandulifera*, towards high light levels were mostly negative. This result indicates that allocation towards certain organs (e.g. Leaf mass, Stem mass and Reproductive capacity) decreased under high light conditions. These findings support those of Andrews et al. (2009) and Skálová et al. (2012), who detected increased biomass allocation, stem length and Root/Shoot ratio in invasive *Impatiens* species compared to their native congeners in treatments with differing light conditions. In contrast, we found that the trait responses of *I. noli-tangere*

towards both N and P limitation were mostly insignificant, whereas those of the two invasive species were mostly negative. These results indicate that the performance of invasive species decreased under nutrient limited conditions, supporting the conclusions of Richardson et al. (2012). Consequently, we conclude that the performance of the two invasive *Impatiens* species is more vulnerable to unfavourable nutrient conditions compared to light conditions. Contrasting patterns in trait-trait relationships were detected between *I. glandulifera* and the other two *Impatiens* species. Biomass allocation to one organ is accompanied by simultaneous allocation to all other organs in plants (see Müller et al. 2000, and Minden & Kleyer 2011 for case studies), with traits being organised in a correlation network rather than acting as uncoupled plant characteristics (Kleyer & Minden 2015). Some of the trait-trait relationships detected in our study met the expectations of the initial model, such as the positive relationship between Live leaves and Stem mass for *I. parviflora*. Other relationships proved non-significant, like that between Stem mass and Reproductive capacity for *I. glandulifera*. Most trait-trait relationships were only significant for one of the three species. This result indicates that, even though the three species are closely related, they differ in their allocation patterns to biomass, growth and/or reproduction.

Godefroid & Koedam (2010) pointed out the difficulty in comparing results of different studies conducted with *Impatiens* species to identify distinctive patterns that contribute to the success or decline of species within this genera. Indeed, a literature review revealed contradictory response patterns by the three species. For instance, in a comparative study in Belgian forests, Godefroid & Koedam (2010) found that the site characteristics of monospecific and combined stands of *I. noli-tangere* and *I. parviflora* caused different species responses to light conditions. While *I. noli-tangere* preferentially grew in well-lit sites, *I. parviflora* cover steadily declined with light intensity. The authors concluded that *I. parviflora* preferentially grows shaded dry, acidic, nutrient-poor soil. Čuda et al. (2014) in the Czech Republic obtained slightly different results, showing that *I. noli-tangere* performed well under moderately shaded conditions, *I. parviflora* preferred shaded and dry sites, and *I. glandulifera* avoided the extremes of full sunlight and deep shade, primarily occurring in intermediate shade. In a greenhouse experiment with seeds from Czech populations, Skálová et al. (2012) found that *I. parviflora* seedlings survival decreased under full sunlight, followed by *I. glandulifera* and *I. noli-tangere*. The authors also reported that shade adversely affected *I. glandulifera* biomass production. In contrast, a study in Lithuanian forests found that *I. parviflora* cover decreased under low light conditions, with biomass increasing under higher light conditions (Dobravolskaitė 2012). Our results showed an increase in biomass production in the low light treatment, regardless of species, but that light had no effect on  $RGR_{Stem}$ , as found by Skálová et al. (2012).

The study by Kollmann & Bañuelos (2004) may explain these contrasting patterns. The authors conducted a comparative study of *I. glandulifera* seeds over a range of latitudinal gradients from Sweden to the Czech Republic. The authors found that region had marked effects as a factor on biomass production, plant height and time until flowering, with the

highest values being obtained for individuals from southern populations and the lowest values in northern populations. Although similar evidence is not available for *I. noli-tangere* and *I. parviflora*, the contradictory results obtained by the various studies indicate that the north-south latitudinal gradient in the distribution of all three species across Europe may represent a 'performance gradient', reflecting differing trait responses in these three species. This assumption concurs with patterns of biomass production and degree of coverage at natural sites, in addition to trait plasticity associated with the three species, but to a lesser extent. Skálová et al. (2012) found that *I. glandulifera* seedlings exhibit the highest trait plasticity (0.67), followed by *I. noli-tangere* and *I. parviflora* (average trait plasticity of 0.50 and 0.45, respectively). *Impatiens parviflora* adult plants exhibited higher trait plasticity compared to *I. glandulifera*, with the native species expressing the lowest trait plasticity (Skálová et al. 2013). Both studies by Skálová et al. (2012, 2013) were performed with plant material from Czech populations. Elemans (2004) compared *I. parviflora* to herb species from Dutch populations, and found that the invasive exhibited the highest plasticity for almost all traits, attributing it to the species' high plastic response to light. Ruprecht et al. (2014) showed that two groups of native and non-native species (including *I. glandulifera*) were equally plastic but that, interestingly, the two annual invasive species had a more plastic reproductive response across different environments than their non-invasive alien congeners.

The high trait plasticity of the invasive species supports previous studies demonstrating that high phenotypic plasticity confers to invasion success, with non-natives often showing higher trait plasticity than native and non-invasive congeners (Richards et al. 2006, Davidson et al. 2011). Our study also supports this phenomenon, as the trait plasticity of *I. parviflora* and *I. glandulifera* are higher than that of the native species, with the highest mean plasticity occurring in *I. parviflora*. We tested plasticity in two ways. First, we tested the hypothesis that plasticity increases from high resource environments to low resource environments (Aikio & Markkola 2002). Specifically, we tested for significant differences in the trait values of the low resource treatments against the high resource treatment, and the direction for each trait and species. Second, we calculated the plasticity index across all treatments, as proposed by Valladares et al. (2000a). Both calculations revealed *I. parviflora* had the highest trait plasticity. The first approach assumes that plants growing in a resource saturated environment grow near their maximal rate, with there being minimal requirements or gain by varying the traits contributing to this rate. In contrast, plants growing in a resource depleted environment might benefit strongly from their ability to vary the traits contributing to critical processes, such as growth rate. Plasticity might bear costs (e.g. information acquisition costs or production costs, DeWitt et al. 1998). However, in general, a phenotypically plastic plant has a higher fitness than a phenotypically fixed plant. If two species have similar plastic traits, their plasticity does not generate a competitive advantage over one another; rather, their competitive abilities would be the same as if plasticity was absent. In our study, *I. parviflora* minimised the negative effects of low resource abundance by

its higher plasticity in response to this limitation. Thus, we would expect this species to be more successful if directly competing with *I. noli-tangere*. This assumption supports the conclusions of Godefroid & Koedam (2010) who, based on response curves, showed that *I. parviflora* adapts better to fluctuating environmental conditions and minimises its negative effects. The authors further concluded that *I. parviflora* is able to colonise *I. noli-tangere* habitats to the detriment of the native species, but not vice versa.

Using the plasticity index (PI) calculated by Valladares et al. (2000a), we determined the degree of plastic response for the measured traits. For example, PI was always greater in the light treatments compared to the nutrient treatments for SLA and  $RGR_{Stem}$ , regardless of species. In contrast, both *I. noli-tangere* and *I. parviflora* exhibited greater plasticity for leaf allocation traits in the nutrient treatment, while Stem mass and Reproductive capacity had greater plasticity in the light treatments, and *I. glandulifera* showed the opposite pattern. Brock et al. (2005) studied the phenotypic plasticity of two *Taraxacum* species in response to light quality (red:far-red light ratio, R:FR) and quantity (PAR). The authors found nonsystematic differences in trait plasticity between the two species, with neither species showing greater plasticity. In our study, *I. parviflora* had the greatest mean plasticity, but plasticity was not consistent across all traits, as found by other studies (Williams et al. 1995, Sultan 2001, Funk 2008). Thus, we conclude, that a species may show a high trait plasticity among distinct environments, and simultaneously lower plasticity among other environments and that plasticity may be unevenly distributed across traits.

## CONCLUSIONS

We found that native and non-native *Impatiens* species responded differently to light and nutrient conditions. Based on our initial model, we expected the three species to exhibit similar trait responses and trait-trait relationships, regardless of native and non-native distinctions or absolute biomass allocation patterns (i.e. *I. glandulifera* produces higher absolute biomass than the other two species). Instead, we found that the three congeneric *Impatiens* species exhibited contrasting responses to light and nutrient treatments, along with differing trait-trait relationships among the three species. Specifically, *I. noli-tangere* and *I. parviflora* were more similar in their responses and trait-trait relationships compared to *I. glandulifera*.

Furthermore, our study revealed that the performance of the two invasive *Impatiens* species is more vulnerable to unfavourable nutrient conditions compared to light conditions. However, the trait responses of the two invasive species were more plastic towards environmental fluctuations. For instance, *I. parviflora* had the highest mean plasticity, with this species being able to minimise the negative effects of low resource abundance by its higher plasticity in response to this limitation.

Overall, the three species exhibited different patterns of trait-environment and trait-trait relationships, with *I. noli-tangere* and *I. parviflora* being more similar in their responses than *I. glandulifera*. Thus, we conclude that the success of invasive species over their native congeners is based on

a combination of similar responses to environmental conditions, but with invasive species exhibiting higher trait plasticity. Closely related species are not necessarily ecologically similar (He et al. 2012), as we demonstrated for *I. glandulifera* and its congeners here. *Impatiens glandulifera* responded differently to light and nutrient conditions compared to the other two species. Thus, even though it is regarded as being highly invasive in some areas and may coexist with the other two *Impatiens* species (Skálová et al. 2012), we expect *I. glandulifera* to occupy different microsites than the other species (Čuda et al. 2014), and which can be observed in nature. We do expect habitat overlap between *I. noli-tangere* and *I. parviflora*, due to the two species exhibiting similar responses to the environment. However, in the long-term, particularly under adverse environmental conditions, *I. parviflora* would be more successful, because it yields greater benefits from its greater trait plasticity under fluctuating environmental conditions. In conclusion, our study demonstrates that a combination of trait characteristics and plasticity regulate the existence and distribution of species from the same genus, particularly native versus invasive species.

## SUPPLEMENTARY DATA

Supplementary data are available in pdf at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consist of means and relative standard deviation (RSD, %) of trait values of *Impatiens noli-tangere*, *I. parviflora* and *I. glandulifera* in each treatment combination.

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