

Research Article

Wide climatic niche and adaptive phenology contribute to the spread of the invasive plant Himalayan balsam (*Impatiens glandulifera* Royle) in Europe

Kristiina Visakorpi¹, Zafar A. Reshi², Oriol Grau³, Anne Muola⁴, Anna Orczewska⁵, Koenraad Van Meerbeek^{6,7}, Bente J. Graae¹

1 Department of Biology, Norwegian Institute of Science and Technology, Høgskoleringen 5, Trondheim, Norway

2 Department of Botany, University of Kashmir, Srinagar-190006, Jammu & Kashmir, India

3 Alt Pirineu Natural Park, C/ de la Riba, 1, 25595 Llavorsí, Catalonia, Spain

4 Division of Biotechnology and Plant Health, Norwegian Institute of Bioeconomy Research, Holtvegen 66, 9016 Tromsø, Norway

5 Institute of Biology, Biotechnology and Environmental Protection, Faculty of Natural Sciences, University of Silesia, ul. Bankowa 9, Katowice, Poland

6 Department of Earth and Environmental Sciences, KU Leuven, Celestijnenlaan 200E, 3001 Leuven, Belgium

7 KU Leuven Plant Institute, KU Leuven, Kasteelpark Arenberg 31, Leuven, Belgium

Corresponding author: Kristiina Visakorpi (kristiina.visakorpi@gmail.com)



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Abstract

Invasive species are one of the greatest threats to biodiversity. However, our understanding of how these species persist and spread in novel environments remains limited. Specifically, the relative importance of species interactions versus environmental conditions and the role of rapid evolutionary adaptation are not fully understood. Here, we investigate the impact of these factors on the distribution of the invasive Himalayan balsam (*Impatiens glandulifera*). We examined whether the climatic niche of the species is pre-adapted to the environmental conditions in the introduced range through niche modeling. Field surveys were conducted to assess the importance of herbivory and competition, and greenhouse treatments were used to investigate local adaptation. We found that the species has not yet fully occupied the suitable climatic space in its introduced range in Europe. Our results suggest that the species may have experienced enemy release while also facing increased biotic pressure at the northern range edge. We identified adaptive differentiation in flowering time, which enhances reproductive success when plants grow in climates similar to their origin. Our results indicate that Himalayan balsam has rapidly adapted to differences in growing season length in its introduced range, with trait plasticity providing an adaptive advantage. Together, these findings suggest that the species may continue to spread across its introduced range in Europe.

Key words: Climate niche, flowering onset, invasive species, local adaptation, phenology, plasticity, species distribution

Introduction

The spread of invasive species is one of the greatest threats to natural ecosystems (IPBES 2023), and the number of new species invasions is steadily increasing (Seebens et al. 2017). In addition to direct human-assisted range expansions (Essl et al. 2019), the rapidly changing climate is exposing many species to new environmental conditions, which facilitate their spread beyond historic range limits (Parmesan

and Yohe 2003). Despite the increasing reshuffling of species ranges due to both human-assisted translocations and climate-assisted range expansions, our understanding of how species persist and spread in novel environments remains limited (Facon et al. 2006; Bridle and Hoffmann 2022).

Predicting the spread of invasive species is difficult, partly because we do not fully understand what sets the limits of species' ranges in general and what allows species to overcome these limits. Species distributions are often expected to be restricted mainly by environmental conditions (e.g., temperature and precipitation). Environmental conditions can be important in assisting the spread of an invasive species, for example, in cases where the climate in the native range matches the climate in the novel introduced range ("climate matching"; Hayes and Barry 2008). Nevertheless, species interactions such as competition or predation can be important in restricting population growth at range margins and thus contribute to setting the limits of species' ranges (Louthan et al. 2015; Stephan et al. 2021). Indeed, when species are introduced into new areas without their natural enemies following them, they can often spread in the new range quickly and become invasive (enemy release hypothesis; Colautti et al. 2004). Similarly, if the introduced species has a higher competitive ability compared to the native species (enhanced weapons hypothesis; Blossey and Notzold 1995), it can also become invasive in the new environment.

In addition to changes in species interactions enabling invasions, rapid evolutionary adaptation could facilitate species in overcoming their range limits. Adaptive evolution should be less common at range edges due to lower genetic variation in marginal populations and potential maladaptive gene flow from the larger core population (Eckert et al. 2008; Sexton et al. 2011). Despite this, many range-edge populations are locally adapted (Bontrager et al. 2021), and rapid evolutionary change in novel environments has been documented in invasive species (Prentis et al. 2008; Buswell et al. 2011). In addition to genetic changes, traits can acclimate to new environmental conditions (i.e., trait plasticity). Plasticity should evolve, especially at range margins, if gene flow and directional selection are strong and if the environment experienced by populations varies (e.g., during range expansion; Chevin and Lande 2011; Usui et al. 2023). Increased plasticity at range margins can facilitate further invasion (Thibert-Plante and Hendry 2011). The relationship between plasticity and adaptation is nevertheless complex, as plasticity itself can be adaptive or maladaptive, and plasticity toward a certain phenotype can either hinder or enhance evolutionary change (Ghalambor et al. 2007). What remains unclear is how often rapid evolution at species' range edges allows species to overcome their limits (Prentis et al. 2008; Sheth et al. 2020) and whether genetic adaptation is an important driver of the success of invasive species (Colautti and Barrett 2013; Vandeputte et al. 2014).

We investigate the factors setting the range limits and facilitating the spread of the invasive plant Himalayan balsam (*Impatiens glandulifera* Royle). Himalayan balsam is a fast-growing annual species in Europe, originating from an altitudinal range of 2000–4000 m in the Himalaya (Beerling and Perrins 1993; Helsen et al. 2021). The first recorded introduction of the species to Europe was in 1839 to the UK, with additional introductions to the continent since (Hagenblad et al. 2015). The current introduced range in Europe covers a large geographic area from the Mediterranean coast to well above the Arctic Circle. Previous studies show that differences in species interactions between the native and introduced ranges are important for invasion success; for example, the lack of natural enemies in Europe (Tanner et al. 2014;

Gruntman et al. 2017), the sensitivity of European flora to the growth-inhibiting chemicals produced by the plant (“allelochemicals”; Gruntman et al. 2014), and the high attractiveness of its flowers to European pollinators (Chittka and Schürkens 2001). Previous work has also shown that the species has high phenotypic plasticity (Pahl et al. 2013) and that the populations from the introduced range in Europe show heritable differences in flowering onset, biomass, and reproductive investment (Kollmann and Bañuelos 2004; Helsen et al. 2020). The extent to which species interactions influence the current distribution of the species in Europe, and whether the observed trait differences between regions contribute to the success of the species across its introduced range, are nevertheless unclear.

In this study, we shed light on the distributional drivers of Himalayan balsam and whether rapid local adaptation allows the species to establish under varied climatic conditions in its introduced range in Europe. First, we describe how climatic conditions differ between the species’ native and introduced ranges by using environmental niche modeling. Second, we investigate how the strength of species interactions changes across species’ introduced range and between the introduced range and a region of the native range by conducting field surveys. Third, we use a common garden experiment to test whether the species has adapted locally in its introduced range in Europe. Specifically, we ask:

- 1) Does the species occupy a different climatic space in its introduced range compared to its native range?
- 2) Does the intensity of herbivory or competition differ between the introduced range and the sampled region in the native range, and how strong are these two biotic drivers at the southern and northern range edges of the species’ introduced range?
- 3) Do traits of the species differ between regions of origin when plants are grown in a common environment?
- 4) Do the plants perform better when grown in environmental conditions corresponding to their origin (potential local adaptation), and is this related to differences in traits?

First, we expected the species to occupy a wider range of climatic conditions in its introduced range compared to its native range (“niche expansion”), because the introduced range covers a larger geographic area and a longer latitudinal gradient than the native range (40°–70° compared to 29°–36°, respectively). Second, we expected herbivory and competitive pressure to be lower in the introduced range, reflecting earlier accounts of enemy release in this species (Tanner et al. 2014; Gruntman et al. 2017). We also expected herbivory and competitiveness of surrounding vegetation to show a latitudinal gradient and be lowest at the northern range edge, because the strength of antagonistic species interactions sometimes decreases with increasing latitude (Roslin et al. 2017). Third, we expected populations to show heritable trait differences between different regions in the introduced range, specifically more drought-resistant traits in plants from the southern edge, traits related to higher competitive ability in plants from the range core, and advanced phenology in plants from the northern edge (Helsen et al. 2020). Fourth, we expected plants to perform better in conditions similar to their place of origin than when grown in other environments, and that this would be related to the observed trait differences between regions.

Materials and methods

Comparing the occupied climate space between the native and introduced ranges

To investigate if Himalayan balsam occupies different climate space in its introduced versus native range, we modeled the climate space occupied by the species in its two ranges using species presence records from the Global Biodiversity Information Facility (GBIF.org 2024) and climate data from WorldClim v2.1 (Fick and Hijmans 2017; 1 km² resolution, 1970–2000). The presence data were first cleaned by removing unlikely and imprecise (<50 km) coordinates, duplicates, and country and capital centroids. The precision of 50 km was chosen because it was the most precise cut-off that allowed enough presence points for the analyses. We selected five bioclimatic variables: precipitation of the warmest quarter, mean temperature of the warmest quarter, maximum temperature of the warmest month, temperature seasonality (standard deviation $\times$ 100), and mean temperature of the coldest quarter. In addition, we included three variables from the Envirem database (same resolution and time period as WorldClim; Title and Bemmels 2018): the Thornthwaite aridity index (describing the difference between precipitation and potential evapotranspiration; Thornthwaite 1948), growing degree days above 0 °C (sum of mean monthly temperature for months with mean temperature >0 °C, multiplied by number of days), and minimum temperature of the warmest month. The selection of the most important climatic factors was made based on what we a priori expected. We chose parameters describing the climate during the growing season rather than annual means, as the species is annual, and thus growing season conditions are likely to be most important for determining survival and reproduction, and therefore local adaptation. Mean wintertime temperature was added because this variable is correlated with minimum temperature in the spring and thus potentially with the likelihood of early growing season frost events (Visakorpi et al. 2024). To identify potentially redundant variables, we examined pairwise correlations between the chosen variables and excluded those with correlation coefficients >0.9. For the remaining six variables, see Suppl. material 1: fig. S1. We built an environmental PCA on the climate data of both ranges, onto which the presence points were projected using a kernel density function (Broennimann et al. 2012; Di Cola et al. 2017). To avoid bias resulting from the significantly higher number of presence points in the introduced range, we thinned the presence points in the introduced range so that the minimum distance between two points was 20 km, resulting in 3650 presence points in the introduced range (versus 79 in the native range; Suppl. material 1: fig. S2). The area for the environmental background data was determined by taking a convex hull around the presence points in both areas (Europe and the Himalaya). To include areas suitable for the species to spread to in the future, we added a 200 km buffer zone around the convex hull. The environmental layers were then cropped into a rectangular shape around the buffer zone. This whole area was used as the background. The radius of the buffer zone was chosen based on previous studies on the potential dispersal distance of the species over 50 years (Wadsworth et al. 2000). We calculated the Schoener's D and Warren's I indices (Warren et al. 2008), which describe the degree of overlap between two niches (in our case, between native and introduced niches; 100% overlap meaning that the two niches are identical). We also estimated the proportion of the niche that has expanded in the introduced range (i.e., novel colonized climates) and the proportion of the niche that has remained unfilled (i.e., not

yet colonized suitable climate space in the introduced range). Niche divergence was tested with niche similarity and equivalency tests. To further analyze whether the introduced range of the species contained novel climatic conditions, we performed a mobility-oriented parity analysis (Cobos et al. 2024) comparing the background climatic conditions in the native range to those in the introduced range.

Field sampling

We conducted field surveys across the species' introduced range and across one region in the native range to describe how the strength of herbivory and competition vary and collected seeds of the plant for the common garden experiment. We sampled six regions in the introduced range and one in the native range during summer 2022 (Table 1; Fig. 1; Suppl. material 1: fig. S3). The sampling in the native range was restricted to a single region (Kashmir) due to logistical and safety reasons. The region of Kashmir covers a large part of the native range, which is overall smaller than the introduced range (Helsen et al. 2021). Nevertheless, our samples from the native range may capture less trait variation than is present among populations. In each region, we sampled 4–7 populations (>20 individuals per population), which were at least 1 km apart, and when possible, not along the same waterway (to avoid sampling related individuals). As much as possible, fieldwork in the introduced range was timed so that the sampling would take place in each region at the same phenological phase (i.e., during seed maturation). To describe the surrounding vegetation of each population, we chose a 3 × 3 m area in the center of each population. We then identified the most common species (up to ten species), estimated their percentage cover, and measured their average height by measuring 2–3 average-sized individuals. To estimate the potential competition from the community, we first estimated the competitiveness of each species as the C-score based on the CSR classification (Grime 1977). We estimated the C-score using three leaf traits (leaf mass per area, leaf area, and leaf dry matter content) following the method of Pierce et al. (2017). Leaf trait values were extracted from the TRY database (Kattge et al. 2020; Suppl. material 1: table S1). Missing values (16% of the data) were imputed using the classification and regression tree method (Buuren and Groothuis-Oudshoorn

Table 1. Overview of the seven sampling regions. From each region, we sampled 4–7 populations (n). The coordinates refer to the closest city (in brackets after the region). Sampling in the introduced range started from the northernmost region (Norway) and continued south to ensure that each location was sampled when seeds were mature but before the first frost in the north. The only exception was the sites around Tromsø, where most of the fieldwork was carried out in early August, but seeds were collected in September. Day length refers to the length of the day at the summer solstice. The number in brackets refers to the populations used in the greenhouse experiment. For the exact location of each sampled population, see Suppl. material 1: table S2, fig. S3.

Region	GPS coordinates (Lat [°], Long [°])	Range	Sampling period	Summer T [°C]	Summer P [mm]	Daylength (h)	n
India (Kashmir, Srinagar)	34.1, 74.3	Native	11–16. July	20.5	207	14.2	7 (5)
Northern Norway (Tromsø)	69.6, 19.0	Introduced north	1–4. Aug, 1–20. Sept	10.4	180	24	7 (4)
Central Norway (Trondheim)	63.4, 10.4	Introduced north	10–12. Aug	12.8	229	20.4	6 (4)
Belgium (Leuven)	50.8, 4.7	Introduced core	22–23. Aug	17.0	201	16.3	6 (4)
Southern Poland (Katowice)	50.3, 19.0	Introduced core	31. Aug – 1. Sept	17.6	306	16.1	4 (4)
Northern Italy (Torino)	45.1, 7.1	Introduced south	12–14. Sept	21.4	199	15.4	4 (3)
Northeastern Spain (Girona)	42.0, 2.8	Introduced south	17–18. Sept	18.1	228	15.1	4 (4)

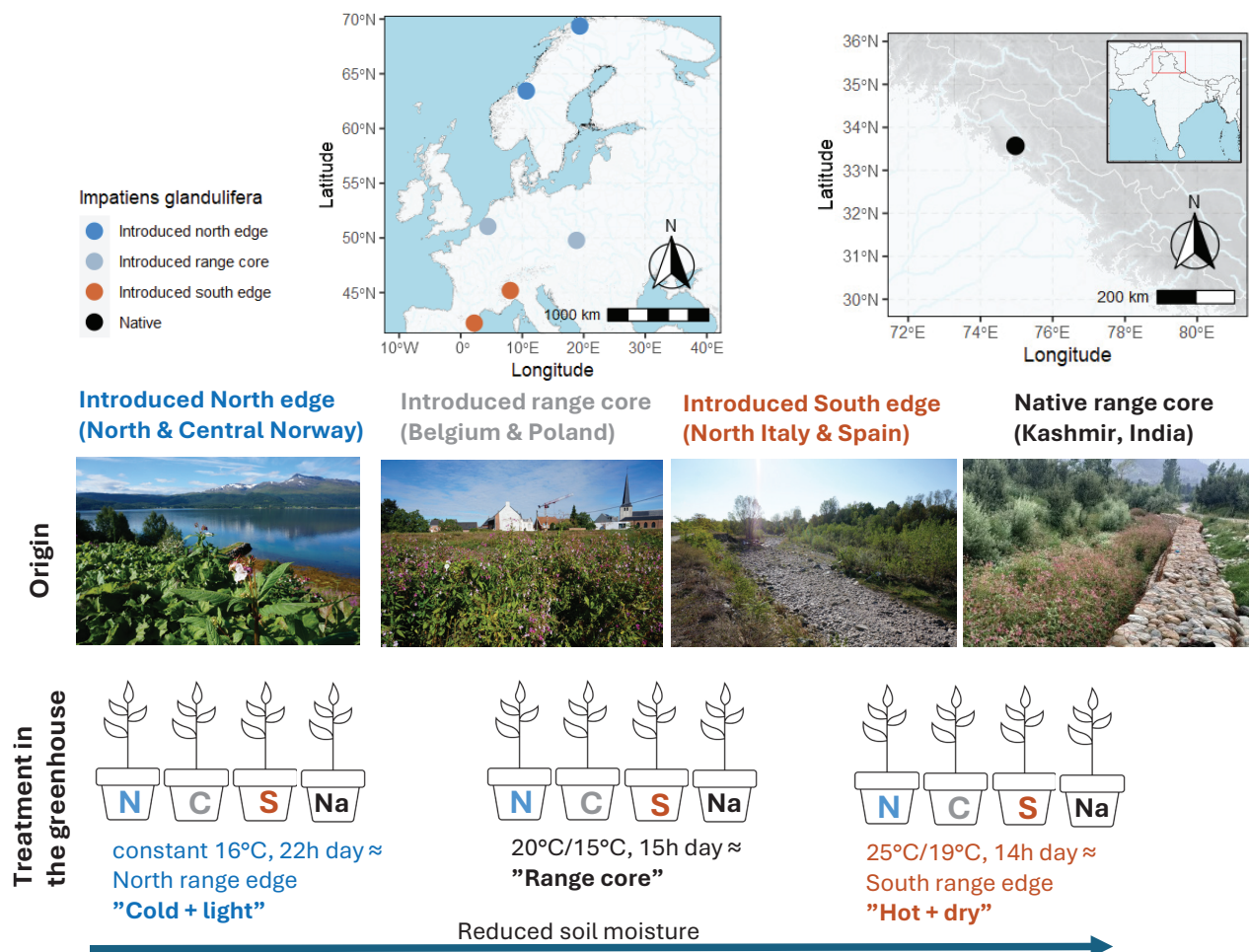


Figure 1. Overview of the sampling regions and the greenhouse setup. The photos show typical conditions at the different sampling regions: the first picture is from Tromsø in early August, where the growing season is short and temperatures are low. The second photo is from the invasive range core in Belgium, where the species grows in dense monocultures. The third photo is from the invasive southern edge in Italy, where the summers are dry and sources of water can dry up completely. The last photo is from the native range in Kashmir. Note that the "Cold + light" treatment refers to increased duration of light (not intensity). The grey areas in the map of the native range show elevations >1500 m a.s.l. See Suppl. material 1: fig. S3 for the locations of each sampled population (n = 4–7 per region).

2011). The leaf trait values were averaged per species and used to calculate community-weighted means of competitiveness for each sampled population.

From each population, we randomly chose 5–8 Himalayan balsam individuals for further measurements. To estimate the level of aboveground herbivory, we counted the number of leaves belonging to different damage categories (0%, 1–10%, 10–25%, 25–50%, 50–75%, >75% of leaf area loss) and the number of aphids, leaf miners, and snails found on the plants. To estimate leaf mass per area (LMA), we collected a randomly chosen leaf from five focal individuals. Leaves were enclosed in moist Ziploc plastic bags and transported back to the lab in a coolbox with ice. The leaves were then scanned, pressed, and air-dried. Leaf area was determined using ImageJ (Abramoff et al. 2004). Leaves were oven-dried at 70 °C for 48 h and weighed. Finally, from each population, we collected up to ten mature seed capsules from 20 randomly chosen individuals located evenly across the population. The seeds were stored in paper bags and transported to the lab at the Norwegian University of Science and Technology, Trondheim, Norway (import permit 2022/8598, Miljødirektoratet).

Greenhouse experiment

To test for potential heritable differences between the sampled regions, we measured the performance and traits of the plants when grown in a common environment in a greenhouse. The seeds collected from the field were placed on Petri dishes with moist Whatman filter paper and sealed with parafilm. The seeds were kept in darkness at 5 °C for 4–5 weeks until most seeds showed signs of germinating (bursting or root formation). Seeds from the introduced range were planted on 12 January 2023. Because seeds from the native range arrived in Norway later, they were planted on 24 February 2023. We planted seeds from 20 individuals from 28 populations (in total 560 plants) into 7.5 L pots filled with standard potting soil. To ensure successful germination, we planted five seeds from one parent plant per pot. All pots were kept under similar conditions for the first 5 days to ensure successful germination (21 °C day/18 °C night, 14:10 light:dark). Subsequently, the seedlings were divided into three treatments corresponding to different climates: northern range edge (average constant 15.8 °C, 22:2 light:dark), range core (average 19.4 °C; 21 °C day/15 °C night, 15:9 light:dark), and southern range edge (average 23 °C; 25 °C day/19 °C night, 14:10 light:dark). Each treatment took place in a separate room within the greenhouse. Temperature and light parameters were chosen so that they roughly corresponded to average summer (May–August) conditions in the northern edge of the introduced range (northern Norway), the core of the introduced range (Belgium), and the southern edge of the introduced range (northern Italy), respectively. The plants were watered every 2 days with similar amounts of water in each treatment, resulting in the driest conditions in the warmest room (evidenced by plants wilting most often in this treatment). As the plants grew the tallest in the range core treatment (see Results), this treatment also corresponded to the highest intraspecific competition. The pots were thinned to two seedlings 2 weeks after germination and to one seedling per pot 4 weeks after germination. Within each greenhouse room, pots were shuffled randomly on 11 February 2023 and 1 March 2023.

We recorded phenology (germination, flowering, and seed maturation), reproductive effort (number of flowers), vegetative growth (growth rate and final biomass), and traits related to competitive ability and drought tolerance (height, LMA, and root/shoot ratio). To measure differences in phenology, we recorded the number of germinating seedlings every 2 days at the beginning of the experiment, calculated the number of flowers once a week, and noted when flowers turned into seedpods. As flowers were not collected when counted (to allow them to turn into seedpods), we used the maximum observed flower number as an estimate of reproductive effort. To estimate vegetative growth, we measured the change in the biomass for half of the plants ($n = 214$). For these plants, we harvested one of the seedlings per pot after the first 2 weeks, cleaned the root system, dried (65 °C, 72 h), and weighed the seedlings. The remaining plant was harvested at the end of the experiment (10–12 June 2023, i.e., after 150 days for the introduced populations and 108 days for the native populations). We used these measurements to estimate early growth rate (biomass gain per day during the first 2 weeks), adult relative growth rate (biomass gain per day after the first 2 weeks, divided by the initial size), root-to-shoot ratio (RSR, final belowground biomass/final aboveground biomass), and total adult biomass. Note that RGR reflects the average daily proportional increase in biomass compared to the initial size of a 2-week-old seedling. Height was measured for each plant as the distance from the soil to the topmost branching point

in the middle of the experiment, 67–68 days after planting. LMA was measured 104–108 days after planting by collecting one leaf from half of the plants ($n = 214$) into a moist plastic bag inside a cool bag. Leaves were scanned immediately after harvest, dried (65 °C, 48 h), and weighed. Leaf area was determined using ImageJ.

Statistical analyses

For variables measured in the field, we tested for differences between the regions in the following response variables: level of herbivory, competitiveness of the surrounding vegetation, height of Himalayan balsam, difference in height between Himalayan balsam and the surrounding vegetation, and LMA of Himalayan balsam. Because we sampled more regions in the introduced range than in the native range, we built two types of models: first, modeling each response variable as a function of the range (native vs. introduced); and second, modeling each response as a function of origin region but only for the introduced range (six levels). For the comparisons between ranges, we built linear mixed-effect models (LMMs) with region as a random effect. For comparisons between regions and for response variables measured at the plant level (herbivory, height, LMA), we built LMMs with population ID (one of the 4–7 populations per region) as a random effect. For comparisons between regions and for response variables measured at the population level (competitiveness of vegetation and height difference), we built linear models. To investigate differences in levels of herbivory (i.e., proportion of leaf area eaten), we used a beta regression model.

To test for the effect of treatment and the region of origin on the traits measured in the greenhouse, we used linear mixed-effect models with the trait as the response variable and treatment, region of origin (both native and introduced, seven levels), their interaction, and the original location in the greenhouse (to account for small environmental variation within the greenhouse rooms during the beginning of the life cycle) as explanatory variables. When possible (i.e., when not resulting in a singular fit), the origin population was a random effect. For three responses (lifecycle length, seed maturation, and LMA), the mixed effect model produced a singular fit, and thus we built linear models with population ID as a fixed instead of a random effect. For continuous response variables (biomass, adult relative growth rate, height, root:shoot, LMA), we built LMMs. Biomass, root:shoot ratio, and RGR were log-transformed because of heteroscedasticity of the model residuals. For count variables (the length of the whole lifecycle, number of days to germination, flowering, or seeding, and number of flowers), GLMMs with Poisson or negative binomial (in case of overdispersion) error distribution with log-link were used. To further clarify the significance of pairwise differences between treatments and origins, we performed Tukey's post hoc test when the main effect Origin or Treatment was significant (Suppl. material 1: tables S5, S6, S8–S13).

Model selection was performed using likelihood ratio tests, starting from a full model and removing variables one at a time (Crawley 2007). The significance of random effects was estimated by comparing models with and without a random effect using likelihood ratio tests. Model assumptions were checked by investigating plots of residual distribution, residuals versus fitted values, and QQ-plots. Overdispersion was detected by comparing the amount of residual deviance to residual degrees of freedom. All analyses were carried out in R version 4.2.2 (R Core Team 2022). For investigating the climatic niches of the species, the packages raster (Hijmans and van Etten 2012), rgbif (Chamberlain and Boettiger 2017), maps (Becker et al. 2023), envirem (Title

and Bemmels 2018), *ecospat* (Di Cola et al. 2017), *GeoThinnerR* (Mestre-Tomás 2025), *CoordinateCleaner* (Zizka et al. 2019), *sf* (Pebesma and Bivand 2023), *mop* (Cobos et al. 2024), *rtry* (Lam et al. 2023), and *ade4* (Dray and Dufour 2007) were used. For statistical analyses, the packages *MASS* (Venables and Ripley 2002), *lme4* (Bates et al. 2015), *emmeans* (Lenth 2025), *betareg* (Cribari-Neto and Zeileis 2010), *lmerTest* (Kuznetsova et al. 2017), and *lmttest* (Zeileis and Hothorn 2002) were used. Data was processed with the help of *dplyr* (Wickham et al. 2020), *reshape2* (Wickham 2007), *tidyr* (Wickham et al. 2023), *lubridate* (Grolemund and Wickham 2011), and *mice* (Buuren and Groothuis-Oudshoorn 2011). The data was visualized with the help of *rnaturalearth* (Massicotte and South 2023), *elevatr* (Hollister et al. 2023), *magrittr* (Bache and Wickham 2022), *ggspatial* (Dunnington 2023), *ggplot2* (Wickham 2009), *ggpubr* (Kassambara 2019), and *gridExtra* (Auguie 2017).

Results

How does the climatic space occupied by the species differ between the native and the introduced range?

The first two axes of the environmental PCA explained 53% and 36% of the variation in climate space, respectively. Despite the lower number of presences recorded from the native range compared to the introduced range in Europe (79 vs. 3560 points after thinning; Fig. 2a, b), the presences in the native range spanned a wider climate space (Fig. 2c). This was true especially toward the region in the climate space described by higher aridity and mean summer temperature and lower seasonality (Fig. 2d). Niche expansion (i.e., the species expanding to new climate space after being introduced to Europe) was low, only 0.04% of the total niche space, and occurred at the cold and wet edge of the niche space (red shaded area in Fig. 2c). Niche unfilling (i.e., the climate space in the introduced range not yet filled by the species) was moderately high (20%), suggesting that the species has more areas in its introduced range in Europe where it can spread (Suppl. material 1: fig. S4). The niche overlap was moderate ($D = 23\%$; $I = 40\%$), and the two niches were not climatically more different from each other than expected by random (equivalency test D , $p = 0.09$; I , $p = 0.71$; similarity test D , $p = 0.04$; I , $p = 0.04$). Based on the mobility-oriented parity analysis, 0.21% of the introduced range contained non-analogous climate conditions compared to the native range, mostly at the higher end values of temperature seasonality (Suppl. material 1: table S3).

How do the strengths of herbivory and competition differ between the native and the introduced ranges and across the introduced range?

Aboveground herbivory was significantly higher in the sampled region in the native range than across the whole invasive range ($22 \pm 2\%$ compared to $1.9 \pm 0.2\%$ leaf area loss; Fig. 3a; Table 2), suggesting that the species might experience lower enemy pressure in the introduced range. Herbivory levels were consistently low across the introduced range, except in the northernmost sampling location, which had a slightly higher rate of herbivory ($3.6 \pm 0.8\%$). The extent of other types of herbivory besides leaf area loss was generally low (Suppl. material 1: fig. S5). Because the sampling took place at the end of the growing season, the amount of herbivory observed reflects the maximum cumulative herbivory experienced by the plant over its lifetime.

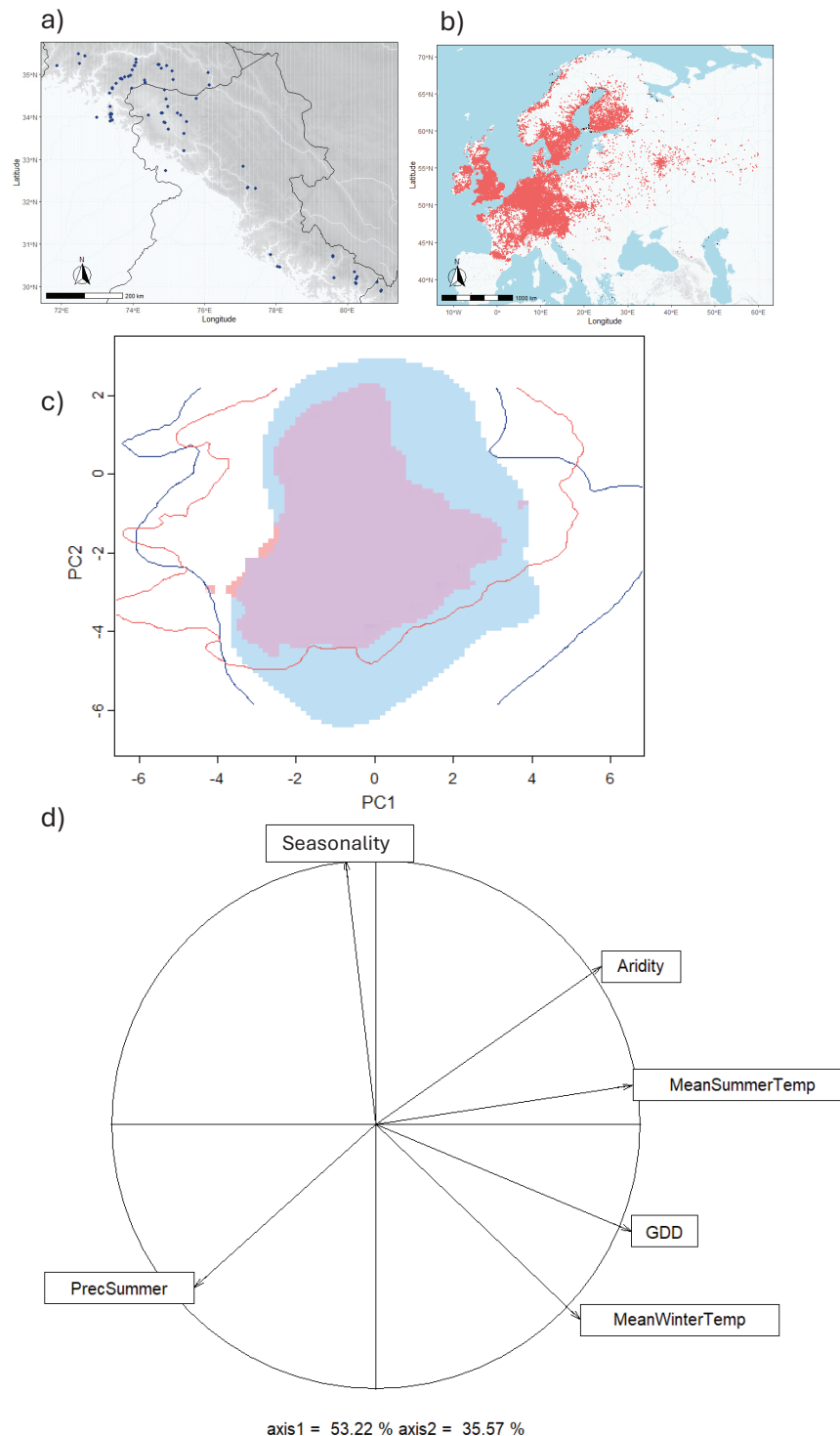


Figure 2. The presence and climatic space occupied by Himalayan balsam. In panel **a**. Blue dots show the presence in the native range, and **b**. Red dots in the introduced range, based on GBIF presence data. After data cleaning, the dataset consisted of 79 observations in the native range and 238,223 observations in the introduced range. For the modeling, the presence points in the introduced range were thinned to 3560 points (see Suppl. material 1: fig. S2). Darker grey in **a** and **b** corresponds to elevation above 1500 m a.s.l. Note that the country borders in panel **a** are not official due to the ongoing border conflict. **c**. Shows the climate space occupied in both ranges: the blue outline corresponds to the available climate space in the native range, and the red outline corresponds to the available climate space in the introduced range. The blue shaded area is the climate niche of the species in the native range only, the red shaded area is the climate niche of the species in the introduced range only, and the purple area is the niche space overlapping between the two ranges. The blue shaded area that lies within the red boundary represents the unfilled niche, i.e., the climate space in the introduced range where the species does not yet occur but could spread. **d**. Shows the climate variables governing the PC axes in panel **c**. Climate variables per region are described in Suppl. material 1: table S4.

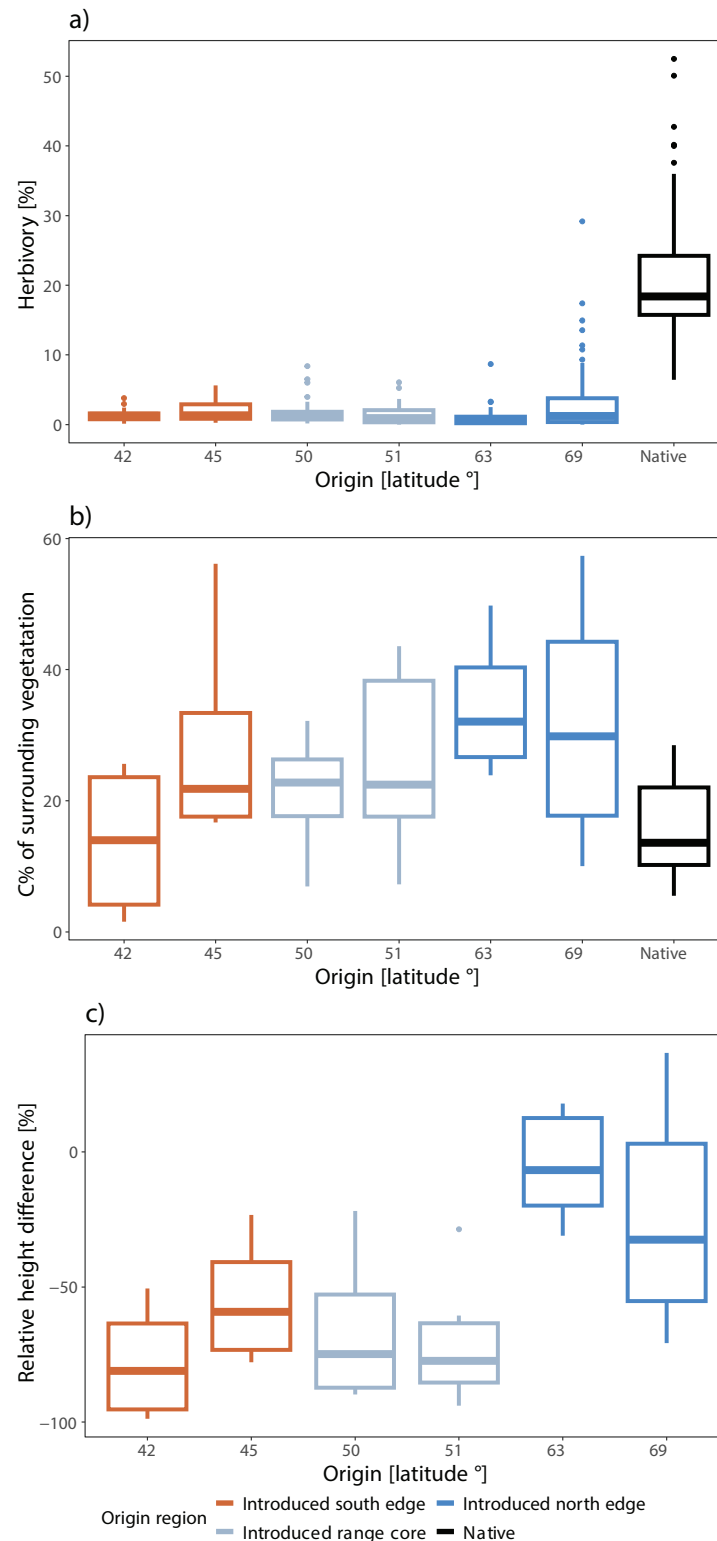


Figure 3. The strength of herbivory and competition in the field. **a.** Shows the level of aboveground herbivory as a percentage of leaf area loss per plant; **b.** The community-weighted mean of competitiveness (as Grime's C%) of the vegetation surrounding the sampled Himalayan balsam individuals; and **c.** The difference in height between Himalayan balsam and the surrounding vegetation (negative values indicate that the surrounding vegetation was shorter than the focal Himalayan balsams). For logistical reasons, the northernmost site was sampled at an earlier point in the growing season (before seed maturation) than the rest of the sites. As the observed herbivory levels reflect cumulative rates over the growing season, and the highest rates were found in the northernmost location, our sampling might have underestimated the difference in herbivory between the northernmost site and the rest. The line in the middle of the box corresponds to the median, and the lower and upper hinges to the first and third quartiles.

Table 2. Test statistics and significance of the fixed effects in the final (most simplified model) per response. The significance of random effects was estimated by comparing models with and without random effects using likelihood ratio tests. Only models with significant fixed effects are shown.

Response	Fixed effects left in the final model	Test statistic	Df num	Df den	p-value fixed	Random effect	p-value random	Model type
Measured in the field (P1 – plants)								
Herbivory%	Range	$\chi^2 = 218.5$	4		<0.001			Beta regression
Herbivory%	Origin region in the introduced range	$\chi^2 = 15.0$	8	-	0.01			Beta regression
Height	Origin region in the introduced range	$\chi^2 = 48.42$	5	-	<0.001	Origin population	<0.001	LMM
Height difference	Origin region in the introduced range	F = 4.75	5	23	0.004			LM
Measured in the greenhouse (F1 – plants)								
Germination	Origin region	$\chi^2 = 29.46$	6	-	<0.001	Origin population		Poisson GLMM
Flowering onset	Origin region * Treatment	$\chi^2 = 107.3$	12	-	<0.001	Origin population		Negative binomial GLMM
Seed maturation	Origin region	$\chi^2 = 32.64$	6	296	<0.001			Negative binomial GLM
	Treatment	$\chi^2 = 37.3$	2	296	<0.001			
Whole lifecycle length	Origin region	$\chi^2 = 143.2$	6	296	<0.001			Negative binomial GLM
	Treatment	$\chi^2 = 29.5$	2	296	<0.001			
Max flowers	Origin region * Treatment	$\chi^2 = 79.54$	12	-	<0.001	Origin population		Negative binomial GLMM
log Biomass	Origin region	$\chi^2 = 37.1$	6	-	<0.001	Origin population	0.001	LMM
	Treatment	$\chi^2 = 85.3$	2	-	<0.001			
log RGR	Origin region	$\chi^2 = 40.11$	6	-	<0.001	Origin population	0.284	LMM
	Location inside the greenhouse	$\chi^2 = 8.81$	3	-	0.032			
log Root:shoot	Origin region	$\chi^2 = 14.89$	6	-	0.021	Origin population	0.717	LMM
	Treatment	$\chi^2 = 7.37$	2	-	0.025			
	Location inside the greenhouse	$\chi^2 = 8.64$	3	-	0.034			
LMA	Origin region * Treatment	F = 3.46	12	-	<0.001			LM
Height	Origin region	$\chi^2 = 30.85$	6	-	<0.001	Origin population	0.001	LMM
	Treatment	$\chi^2 = 299.19$	2	-	<0.001			
	Location inside the greenhouse	$\chi^2 = 16.95$	3	-	0.001			

The competitiveness of the surrounding vegetation was highest at the northernmost sites of the introduced range, whether measured as Grime's C-score or as relative height difference between focal plants and the community, though the difference was significant only for the height difference (Fig. 3b, c; Table 2).

Do traits show heritable differences depending on the region of origin?

Plants from different regions showed significant differences in all measured traits when grown in a common environment in the greenhouse (Table 2). Populations from the northern edge of the introduced range had the fastest life cycle (days to first seed; Fig. 4a; 94.3 ± 1.6 d SEM compared to 120.0 ± 1.7 d SEM in the rest of the populations; Suppl. material 1: table S5) and the highest reproductive effort (48.3 ± 1.7 SEM flowers compared to 29.5 ± 0.9 flowers in the rest of the populations; Fig. 4c; Suppl. material 1: table S6). We observed a potential trade-off between reproductive effort and vegetative growth (Suppl. material 1: table S7), as the northern populations had the slowest relative growth rate (9.1 ± 1.0 g day⁻¹ g⁻¹ SEM compared to 18.3 ± 0.9 g day⁻¹ g⁻¹ SEM on average in other populations; Fig. 4f; Suppl. material 1: table S8), resulting in the lowest biomass at the end of the experiment (40.4 ± 2.7 g SEM compared to 78.4 ± 3.4 g SEM; Fig. 4d; Suppl. material 1: table S9).

Plants from the southern edge of the introduced range had the highest LMA ($32.1 \pm 1.0 \text{ g m}^{-2}$ SEM compared to $28.4 \pm 0.7 \text{ g m}^{-2}$ SEM in the rest; Suppl. material 1: figs S6b, S7b, table S10) and a slightly higher (but non-significant) root/shoot ratio (0.20 ± 0.01 SEM compared to 0.18 ± 0.01 in the rest; Suppl. material 1: fig. S7a, table S11) than the other populations, both of which are likely to confer an advantage in a drier climate. These plants also grew the shortest in all treatments (on average $114.8 \pm 3.6 \text{ cm}$ SEM; Fig. 4e; Suppl. material 1: table S12), despite having the highest final biomass among the introduced populations across treatments ($76.6 \pm 4.7 \text{ g}$ SEM compared to $55.5 \pm 2.9 \text{ g}$ SEM in the rest of the introduced populations).

In contrast to the introduced populations, the native populations did not seem to face a trade-off between phenology and vegetative growth. These plants matured quickly (lifecycle length $99.5 \pm 2.6 \text{ d}$ SEM; Fig. 4a), had a high relative growth rate ($19.0 \pm 2.1 \text{ g day}^{-1} \text{ g}^{-1}$ SEM; Fig. 4f), achieved the highest final biomass ($101.0 \pm 10.3 \text{ g}$ SEM; Fig. 4d), and grew the tallest ($153.7 \pm 4.5 \text{ cm}$ SEM compared to $133.9 \pm 1.7 \text{ cm}$ SEM in the introduced populations; Fig. 4e). The lower reproductive output of these populations (on average 21.5 ± 2.2 flowers) is likely due to the experiment lasting for a shorter time for these plants, as they were planted over a month later.

Do the plants perform better in the conditions corresponding to their climate of origin?

The reproductive output (number of flowers) was highest in the northernmost populations in the treatment corresponding to the conditions at the northern range edge (63.5 ± 2.5 SEM flowers vs. 39.5 ± 3.1 SEM in the warmest treatment; significant Treatment $\times$ Origin; Table 2; Fig. 4c; Suppl. material 1: table S6). Likewise, plants originating from the southernmost populations produced the most flowers in the treatment corresponding to the conditions at the southern range edge, although the difference was not significant (31.5 ± 2.6 SEM flowers compared to 24.3 ± 1.7 in the coldest treatment; Suppl. material 1: table S6). There was no clear trend in the number of flowers produced by the introduced range core populations. The native plants performed worst at the range core conditions (10.9 ± 1.6 SEM flowers compared to 28.1 ± 3.7 SEM at the southern edge and 23.8 ± 4.3 SEM at the northern edge; Suppl. material 1: table S6).

The local advantage in reproductive success was most likely due to changes in flowering onset (significant Treatment $\times$ Origin; Table 2; Fig. 4b). Northernmost populations flowered earliest in the treatment corresponding to the northernmost environment (9.0 ± 1.6 SEM days earlier than in the warmest treatment; Suppl. material 1: table S13), whereas the southernmost populations flowered earliest in the hottest and driest treatment (6.2 ± 2.4 SEM days faster; Suppl. material 1: table S13). Native plants flowered earliest in the warmest treatment and latest in the range core treatment (22.0 ± 4.9 SEM days faster; Suppl. material 1: table S13). Range core populations did not show any trend in flowering onset.

Traits related to vegetative performance were affected by treatment but in a similar way across all populations (no Treatment $\times$ Origin interaction). The final biomass for all populations was lowest in the hottest and driest treatment ($49.8 \pm 3.4 \text{ g}$ SEM compared to $76.4 \pm 3.6 \text{ g}$ SEM in the other treatments; Fig. 4d; Suppl. material 1: table S9), most likely due to the slowest seedling growth rate during the first 2

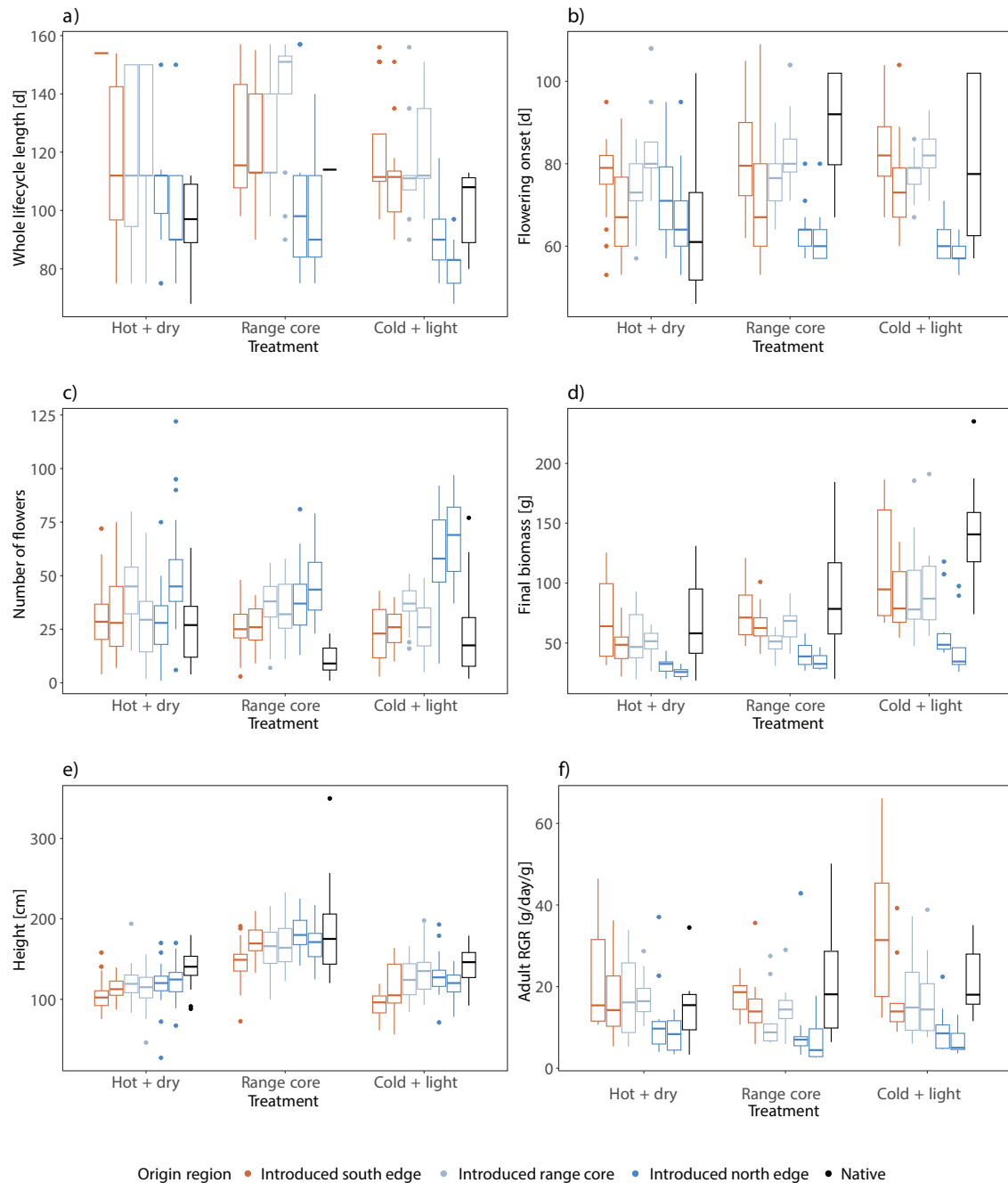


Figure 4. The effect of treatment and region of origin on traits measured in the greenhouse. **a.** Shows the length of the whole lifecycle (days from planting to first seed); **b.** Flowering onset (days from germination to first flower); **c.** Maximum number of flowers; **d.** Final biomass; **e.** Plant height, and **f.** Adult relative growth rate. Boxes are colored by the larger geographic area of origin and ordered so that the southernmost region (42°) is the leftmost box per treatment, and the other regions follow with increasing latitude, with the native region additionally shown as the rightmost box. The faster lifecycle in panel a in the northern populations is due to faster flowering onset (panel b, on average 15.0 ± 0.9 SEM days faster), seed maturation (10.0 ± 2.0 SEM days faster), and germination (1.6 ± 0.2 SEM days faster). The faster lifecycle of native populations was due to faster seed maturation (13.0 ± 3.0 SEM days faster). The line in the middle of the box corresponds to the median, and the lower and upper hinges to the first and third quartiles. For pairwise differences between treatments and origins, see the post hoc test results in Suppl. material 1: tables S5, S6, S8–S13.

weeks (Suppl. material 1: fig. S7c) in this treatment. All plants grew tallest in the treatment corresponding to the range core conditions (168.4 ± 2.5 cm SEM compared to 119.0 ± 2.0 cm SEM at the southern edge and 122.0 ± 2.1 cm SEM at the northern edge; Fig. 4e). This was similar to the field surveys, where the tallest plants

were found in the range core populations (195 ± 5 cm compared to 110 ± 4 cm at the northern edge; Suppl. material 1: fig. S6a), suggesting that height differences are mainly caused by the environment. LMA and root/shoot ratio also showed significant interaction between treatment and origin, but these did not appear to correspond to changes in plant performance (Suppl. material 1: fig. S7, tables S10, S11).

Discussion

In this study, we investigated the factors influencing the distribution and invasion success of Himalayan balsam (*Impatiens glandulifera*), a highly invasive plant species in Europe. We found that the species likely occupies a smaller climate space in its introduced range in Europe compared to its native range in the Himalaya, with 20% of the niche space in the introduced range “unfilled,” i.e., climatically suitable but uninvaded. We observed lower herbivory across the introduced range compared to one of the central regions in the native range. Most traits measured in the greenhouse on first-generation plants showed differences between the sampled regions. Specifically, plants from the northern edge of the introduced range had an earlier onset of various phenological phases and higher reproductive output at the expense of vegetative growth. This difference was plastic and potentially adaptive, as it provided the greatest advantage to northern plants when grown in conditions corresponding to the northern range edge. Plants from the native range were similarly fast in their phenology, but in contrast, also had the highest growth rate and produced the most biomass, potentially suggesting greater vigor compared to plants in the introduced range. Based on our results, we expect that the species is likely to spread to new climatically suitable areas in its introduced range in Europe in the future and could become more dominant, especially at the northern range edge, if the short growing season ceases to be a limiting factor. Below, we discuss these findings.

Himalayan balsam might occupy a wider climatic space in the native range compared to the introduced range

We found that the climatic niche of the species is larger in the native range compared to the introduced range. This was despite the geographic extent of the native area being smaller and having fewer presence records. Nevertheless, the high elevational range (from ca. 500 m a.s.l. up to >4000 m a.s.l.; Suppl. material 1: fig. S8) compensates for the smaller latitudinal extent. Importantly, our climate space modeling revealed that there might still be areas in the introduced range that are suitable for the species but have not yet been invaded. This suggests that the species could spread further in its introduced range (Suppl. material 1: fig. S4). Why the species has not yet invaded all climatically suitable areas could be because 100+ years have not been enough for it to reach these areas (Svenning and Skov 2004). Alternatively, presence records may be missing from these areas, even if the species occurs there. As Fig. 2b shows, the abundance of the species is higher within the boundaries of some countries than others, suggesting that the completeness of online presence records differs between countries. Moreover, the species disperses mainly through waterways, with dispersal also assisted by humans (e.g., through gardening waste; Hagenblad et al. 2015; Helsen et al. 2021), which might create a different distributional pattern than otherwise expected. Finally, the existing imprecision and low number of presence coordinates in the native range call for caution when interpreting the results.

Himalayan balsam experiences low herbivory in the introduced range but higher biotic pressure at the northern range edge

We found higher herbivory pressure in the one sampled region in the native range compared to all of the sampled regions in the introduced range. Previous studies have also found higher rates of herbivory for this species in its native range (Tanner et al. 2014; Gruntman et al. 2017). Together, these studies suggest that the species might have experienced enemy release in its introduced range (Colautti et al. 2004). To confirm whether herbivory is higher across the whole native range, further sampling would be needed.

Surprisingly, we found that herbivory was highest at the northernmost range edge in the introduced range, and there was a trend toward higher competitive ability by the surrounding vegetation toward the northern edge, although this latter trend was not significant. Contrary to our finding, the strength of antagonistic biotic interactions is often found to decrease toward the poles (Roslin et al. 2017, but see Moles et al. 2011). Our results highlight how species interactions could be important in restricting populations at the edges of their range (Louthan et al. 2015) and determining the success of range expansions (Ibáñez et al. 2021).

Himalayan balsam showed higher performance when grown in environmental conditions corresponding to the region of origin

We found that plants from the introduced range had the highest reproductive output when grown in conditions corresponding to the environment of their origin: plants from the northern range edge produced the most flowers when exposed to low temperatures and long days. Plants from the southern range edge also reproduced most successfully in the climate corresponding to their origin (high temperature and short days), though this difference was not significant. These differences were likely driven by corresponding plastic changes in phenology. Flowering of the northern range edge populations was advanced most in the treatment corresponding to the northernmost environmental conditions, and vice versa. Earlier studies on the species have found higher reproductive effort and earlier flowering in populations from the north edge, and these trait differences are maintained in the second greenhouse-grown generation, confirming that they are unlikely due to maternal effects (Kollmann and Bañuelos 2004; Helsen et al. 2020). Earlier flowering in the northern range edge populations has also been documented in other invasive species (Colautti and Barrett 2013; Novy et al. 2013; Van Boheemen et al. 2019).

Even though plants in our experiment performed best in environmental conditions mimicking those of their region of origin, the local plants were not always the best-performing ones. Instead, plants originating from the northernmost population often performed best in several treatments. Our results, therefore, do not fulfill the strict definition of local adaptation (Kawecki and Ebert 2004), which would require local plants to always have the highest performance compared to other genotypes. Nevertheless, it is common that local adaptation is masked in greenhouse experiments. The higher performance of northern populations across several treatments in our experiment could be because the greenhouse environment did not reproduce the different biotic conditions experienced by plants in the field, and the northernmost populations might have had an advantage in the absence of interspecific competition and herbivory. Overall, our results highlight the need to study

the effects of environmental change on ecological communities while considering changes in the surrounding community composition and species interactions.

The mechanism for earlier phenology in plants from northern populations could be that these plants have lower temperature requirements for flower development or that they can take advantage of continuous light to develop faster. Many species exhibit natural genetic variation in how changes in day length affect flowering (Andrés and Coupland 2012). This variation is often due to changes in the expression and activation pathways of genes related to flowering onset (e.g., FLOWERING LOCUS T (FT)) (Andrés and Coupland 2012). Further work is needed to determine whether similar genetic or epigenetic changes have occurred in the northern populations of Himalayan balsam.

The observed change to earlier phenology indicates that the shortness of the growing season in the north is likely a range-limiting factor, as suggested by Beerling and Perrins (1993). Indeed, when seeds from the northernmost location first started maturing in the field, the night temperatures were already below freezing. If freezing temperatures damage flowers or maturing seeds (Ladinig et al. 2013), there is likely very strong selection pressure for early maturation. The earliest record of the species above the Arctic Circle in Norway is from 1986 (artsdatabanken.no, from Bodø, 67°N). If the differences in flowering time are due to in situ evolutionary change, this would have taken place within 36 generations. This is fast, but not unusually so (Maron et al. 2004; Franks et al. 2007; Buswell et al. 2011). It is also possible that pre-adapted individuals have arrived and survived better in the northernmost environment (“climate matching”). Our results cannot separate these two processes. However, if the observed earlier phenology under continuous light is a specific adaptation to a short growing season with continuous light, we cannot think of any other region than the Arctic where this trait change would have been selected for.

The advantage of the plants originating from the southern edge of the introduced range in the treatment simulating the southernmost climate was weaker than for the northernmost plants in the corresponding northern treatment and not statistically significant. This was despite trait differences pointing to a potentially higher drought resistance (slightly higher LMA and root/shoot ratio). The lack of strong advantage of southern plants in the southern treatment could be because the greenhouse experiment did not last as long as the growing season in the southernmost regions (ca. 220 days; Rötzer and Chmielewski 2001), and thus the differences in flowering do not reflect the whole lifetime reproductive output (as individuals that flowered later might not have had time to finish flowering). If the experiment had lasted longer, the plants in the treatment mimicking southern range edge conditions would likely have had time to flower longer and thus to produce more flowers, which might have strengthened the observed pattern. Alternatively, it is possible that the southern populations are simply less locally adapted. The geographic distance between the southern and central European locations is shorter (ca. 1000 km) than between the central and northern European locations (ca. 2000 km), and the central European populations are larger and more connected through human movement. Therefore, it is possible that there is sufficient gene flow between the southern and central European populations to hinder local adaptation (Sexton et al. 2011).

Across all introduced populations, we found a trade-off between investment in reproduction and investment in vegetative growth. This is a common trade-off in many plant species (Colautti and Barrett 2013; Novy et al. 2013; Van Boheemen et al. 2019). Interestingly, plants from the native region grew large

and fast and matured quickly and thus do not seem to be constrained by a trade-off between fast maturation and vegetative growth. They also flowered earliest and produced the most flowers in the hottest treatment. As the native range covers hotter environments compared to the introduced range, it is possible that the native plants, especially those originating from the warm edge of the distribution (low elevation), are better adapted to higher temperatures. We do not know whether the sampled native region is the source of the invasive populations. The species has most likely been introduced to Europe multiple times (Hagenblad et al. 2015); thus, finding the exact origin of any specific European population is likely to be very difficult.

Conclusion

We found that populations of the invasive Himalayan balsam show signs of local adaptation at their northern range edge in Europe by flowering earlier and having higher reproductive output when grown under low temperatures and continuous light. The advanced phenology at the northern range edge suggests that the short growing season might be an important range-limiting factor. If climate warming extends the growing season at the northern range edge, the need for advanced phenology will disappear. If advanced phenology trades off with vegetative growth or with defense against herbivores, a longer growing season would mean that the plants can invest more in growth and/or defense. It is therefore possible that the species could become even more successful in these regions. Even a moderate increase in average temperature might result in a much stronger increase in growing season length, as in the Arctic, light is available for 24 h for most of the season. Fast-growing species that can adapt to take advantage of the long days might quickly become common if spring and autumn frosts disappear. On the other hand, higher rates of herbivory and potentially higher competitive pressure that we found at the northern range edge might slow down further spread of the species.

In contrast, we found only weak signs of potential local adaptation to southern range edge conditions in terms of phenology and reproductive effort. Moreover, all populations of Himalayan balsam grew less well under typical southern range edge conditions. Thus, as northern areas become more suitable for the species, the southern range edge might retract northward with climate warming if hot and dry conditions restrict growth of the species. This is surprising, as the native range of the plant extends to much hotter and drier climates. It might be that the current stock of species in Europe is missing the specific adaptations for hot and dry climates. This highlights the need to further restrict new introductions of the species from its native range, as the newcomers could introduce new genetic material that would not only increase the genetic diversity and vigor of the introduced populations but could also bring in new adaptations enabling the species to withstand an even greater range of environmental conditions.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Author contributions

KV and BJG designed the study. KV and ZAR carried out the fieldwork with the help of OG, AM, AO, and KVM. KV carried out the greenhouse work, analyzed the data, and wrote the first version of the manuscript. All authors contributed substantially to revisions.

Author ORCIDs

Kristiina Visakorpi  <https://orcid.org/0000-0003-2478-0518>

Zafar A. Reshi  <https://orcid.org/0000-0001-9567-7484>

Oriol Grau  <https://orcid.org/0000-0002-3816-9499>

Anne Muola  <https://orcid.org/0000-0003-1828-6425>

Anna Orczewska  <https://orcid.org/0000-0002-7924-9794>

Koenraad Van Meerbeek  <https://orcid.org/0000-0002-9260-3815>

Bente J. Graae  <https://orcid.org/0000-0002-5568-4759>

Data availability

The data underpinning the analysis reported in this paper are deposited in the Zenodo Data Repository at <https://doi.org/10.5281/zenodo.17065505>.

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Supplementary material 1

Supplementary figures and tables

Authors: Kristiina Visakorpi, Zafar A. Reshi, Oriol Grau, Anne Muola, Anna Orczewska, Koenraad Van Meerbeek, Bente J. Graae

Data type: docx

Explanation note: **table S1**. References for the datasets used from the TRY trait database. **figure S1**. Correlation matrix of the climatic variables. **figure S2**. Map of the thinned presence points in the introduced range. **table S2**. Details of all the sampled Himalayan balsam populations. **figure S3**. Map of the populations sampled in the two ranges. **figure S4**. The climatic niche of Himalayan balsam is mapped onto its introduced range in Europe. **table S3**. Summary of the extent of non-analogous environmental conditions in the introduced range. **table S4**. Summary of the climate variables used to investigate the climatic niche of Himalayan balsam in the native vs. introduced range. **figure S5**. The number of aphids, snails, and leafminers found on the surveyed Himalayan balsam plants in the field. **table S5**. Post hoc test results for the whole lifecycle length. **table S6**. Post hoc test results for the number of flowers. **table S7**. Correlation coefficients and p-values for the trade-off between reproduction and growth. **table S8**. Post hoc test results for relative growth rate. **table S9**. Post hoc test results for biomass. **table S10**. Post hoc test results for leaf mass per area measured in the greenhouse. **table S11**. Post hoc test results for root-to-shoot ratio. **table S12**. Post hoc test results for height. **table S13**. Post hoc test results for flowering onset. **figure S6**. Functional traits of the surveyed Himalayan balsam plants were measured in the field. **figure S7**. Functional traits measured from Himalayan balsam plants in the greenhouse. **figure S8**. Histogram of the elevation of the occurrence points of Himalayan balsam in the native range in the Himalayas.

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