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ORIGINAL ARTICLE

Performance of the herb *Verbascum thapsus* along environmental gradients in its native and non-native ranges

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ABSTRACT

Aim We evaluated whether the performance of individuals and populations of the invasive plant *Verbascum thapsus* differs between its native and non-native ranges, across climate gradients, and in response to its position in a global-scaled niche model.

Location India (Kashmir) and Switzerland (native range) and Australia and USA (Hawaii, Montana and Oregon) (non-native range).

Methods We measured population characteristics (density of flowering individuals, population size), plant traits (plant height, number of flowering branches) and seed germination for 50 populations of *V. thapsus* growing along elevational gradients in six mountain regions around the world (two in the native range, and four in the non-native range). We fitted linear regression models to determine the relationship of plant and population level performance variables to range, region, climate and probability of occurrence from a global niche model.

Results Plant height, number of flowering branches and population density of *V. thapsus* did not differ consistently between the native and non-native ranges, but the area covered by populations in the non-native range was on average two orders of magnitude larger than the area of native populations. Within and among regions, individual plant performance traits responded variably to precipitation and mean annual temperature, depending on the climatic range of the observed populations; however, performance was greater for populations that had a greater modelled probability of occurrence. Seed germination under controlled conditions was highest between 20 and 35 °C and consistent across populations, although germination at low temperatures was substantially higher for native populations from Kashmir.

Main conclusions The introduction of *V. thapsus* to its non-native range is not associated with consistent increases in plant performance. Instead, plant performance is more strongly influenced by position within the climate niche of the species, position along environmental gradients, and climatic or other differences among regions. We demonstrate that individual-level and population-level performance traits can yield different predictors of plant performance. Therefore, future studies comparing plant performance in native and non-native ranges should include both plant and population characteristics and should also sample the target species from multiple regions in both ranges and along environmental gradients that comprehensively represent the niche of the species.

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Keywords

Biennial herb, climate, elevation, invasion, invasive plants, niche model, non-native, phenotypic plasticity, *Verbascum*.

INTRODUCTION

Invasive species are often observed to grow larger or produce more offspring in areas where they have been introduced than in their native range. Possible reasons for this include that they escape natural enemies from their native range, alter resource allocation, exhibit novel allelopathic compounds, or they are fortuitously introduced to more favourable environmental conditions (Crawley, 1987; Blossey & Nötzold, 1995; Callaway & Aschehoug, 2000; Jakobs *et al.*, 2004; Ebeling *et al.*, 2008; Alba *et al.*, 2011; Flory *et al.*, 2011; Parker *et al.*, 2013). Differences in performance have been attributed to both evolutionary changes and phenotypic plasticity (Lee, 2002; Parker *et al.*, 2003; Blair & Wolfe, 2004; Bossdorf *et al.*, 2005). However, evidence that plants grow better in the introduced range is inconsistent, with many species varying widely in performance within both the native and introduced ranges (Thébaud & Simberloff, 2001; Maron *et al.*, 2004; Hierro *et al.*, 2005; Williams *et al.*, 2008; Alexander *et al.*, 2009, 2012; Firn *et al.*, 2011; Kueffer *et al.*, 2013; Parker *et al.*, 2013).

To determine whether a species behaves differently in the invaded range, it is necessary to compare its performance with that in the native range (Reinhart *et al.*, 2003; Maron *et al.*, 2004; Alexander *et al.*, 2009; Colautti *et al.*, 2009; Richardson *et al.*, 2010). However, the performance of a species varies widely according to environmental conditions, making the interpretation of range comparisons difficult unless many locations are considered (Kueffer *et al.*, 2013). For example, many species exhibit clinal variation in traits along environmental gradients, such as temperature and growing season length, in both the native and non-native ranges (Reinartz, 1984a; Alexander *et al.*, 2009; Colautti *et al.*, 2009; Keller *et al.*, 2009). Sampling from different positions along an environmental gradient in different ranges could confound comparisons between ranges because climate may have a larger effect on traits than range differences (Colautti *et al.*, 2009). This problem can be overcome by sampling from numerous regions in the native and non-native ranges of the species, and by sampling along environmental gradients within regions (Kueffer *et al.*, 2013). Mountains are excellent systems for this purpose because they have steep environmental gradients over short distances, and offer opportunities to replicate study designs across multiple, independent mountain ranges (Pauchard *et al.*, 2009).

We illustrate this approach by testing for differences in the performance of an invasive species, *Verbascum thapsus* (Scrophulariaceae), between its native and non-native ranges, and along climatic gradients within ranges. *Verbascum thapsus* is a monocarpic biennial herb (occasionally annual or perennial) native to Eurasia, which has been widely transported and planted by humans (Wilhelm, 1974). It can grow under a broad range of climatic conditions (Parker *et al.*, 2003), although it requires open disturbed soil to establish (Gross & Werner, 1978, 1982; Reinartz, 1984b). It occurs in all 50 states of the USA, is considered a noxious weed in Colorado and Hawaii (USDA, NRCS, 2011), and has become one of the most common species in mountain regions around the world (Seipel *et al.*, 2012). The success of this species in naturalizing in mountain regions may be because its seed can germinate across a variety of temperatures (Semenza *et al.*, 1978; Baskin & Baskin, 1981), and because it can respond plastically to environmental variation (Gross & Werner, 1978; Parker *et al.*, 2003; Ansari & Daehler, 2010; von Arx *et al.*, 2014). For example, observational studies of the species indicate different flowering phenology along latitudinal gradients (Reinartz, 1984a). Furthermore, *V. thapsus* may have adapted genetically to new conditions in the non-native range, where plants reportedly grow faster and are better defended than native conspecifics in common gardens under certain environmental conditions (Alba *et al.*, 2012; Kumschick *et al.*, 2013).

Whether *V. thapsus* performs differently between its native and non-native ranges remains unclear. Our null expectation is that, after accounting for climatic differences, there are no differences in performance between ranges; alternatively performance will be greater (e.g. individuals grow larger or populations cover a larger area) in the non-native range. We measured plant and population characteristics associated with performance within populations of *V. thapsus* along environmental gradients in six regions around the world in order to address the following questions. (1) Does the performance of *V. thapsus* at the plant or population level differ between ranges (native versus non-native)? (2) Do plant and population level responses differ in response to climate gradients, their position within the global climatic niche of the species, or among regions? To address these questions we combined the analysis of individual plant-level and population-level responses along climate gradients using a multiple region, biogeographical approach. This allowed us to determine whether performance differences in *V. thapsus* are linked to its native versus non-native status in a region, or whether performance is best explained simply by climate (including the position in the climatic niche of the species).

MATERIALS AND METHODS

Population data

A total of 50 populations of *Verbascum thapsus* were sampled in six mountain regions (see Appendix S1 in Supporting

Information for coordinates of each population). We sampled two sites at the western and eastern end of the native range – the Swiss Alps (hereafter Switzerland) and Indian Kashmir (hereafter Kashmir) – and four in the non-native range – the island of Hawaii (Big Island), USA (hereafter Hawaii), New South Wales, Australia (hereafter Australia), the Wallowa Mountains in Oregon, USA (hereafter Oregon), and the northern part of the Greater Yellowstone Ecosystem in Montana, USA (hereafter Montana). We followed the same standard protocol to sample three replicate populations at low, middle and high elevations of the elevational range occupied by the species in each region. Populations were located using information from previous surveys (Seipel *et al.*, 2012), and by reconnaissance and input from local botanists, which allowed us to determine the entire elevational range that *V. thapsus* occupied in each region. The total elevational gradient occupied was then divided into equally spaced low, middle and high elevational bands. Within the elevational bands, populations were selected near roadsides and were characteristic of established (large and conspicuous) populations in each region (Seipel *et al.*, 2012). We chose the largest available populations near roads because non-native species worldwide are most common near roadsides (Seipel *et al.*, 2012), and because the largest populations are likely to be the oldest, the most stable, and represent optimal performance at a given elevation. Populations in Switzerland were scattered and rare, which made it difficult to find enough elevational replicates, so we sampled populations continuously along the elevational range that the species occupied. Populations from all the regions covered much of the known climatic niche of the species, with mean annual temperature ranging from 2.3 to 20.0 °C among populations and annual precipitation ranging from 388 to 1508 mm (Appendix S1).

At each population centre we recorded the global positioning (GPS) coordinates and elevation above sea level. The relationship between climate and elevation differs around the world such that elevation in metres above sea level is not comparable between regions (Körner, 2007). We therefore related performance to climate within and among regions, rather than to elevation. We extracted average minimum, mean and maximum monthly temperatures and precipitation from the WorldClim database of interpolated climate layers for the years 1950–2000 at a 0.167° (1 km × 1 km) resolution (Hijmans *et al.*, 2005). To check for errors resulting from the coarse resolution of these global-scale data, we compared the values from WorldClim with more precise data in regions (Switzerland, Montana and Oregon) where these were available (Zimmermann & Kienast, 1999; PRISM Climate Group, 2004). The differences at a given site were on average less than 10% of mean annual temperature and total annual precipitation. For consistency we present results obtained using WorldClim.

All populations were sampled towards the end of the growing season, after the peak of flowering or when plants had begun to senesce. The extent of each population, defined as an interconnected group of individuals with gaps of less than 10 m apart, was estimated by measuring its length and width. The minimum distance between any two sampled populations in this study was 300 m (in Australia), and the average distance between populations within a region was 40 km (1 SD = ± 32 km).

To estimate the number of plants flowering per square metre, we randomly selected ten 1-m^2 plots, either along a transect traversing the entire length of the population or along a 100-m transect within the population if it was very large. To select the plot locations, we randomly sampled integers without replacement to locate positions along the length of the transect, and chose at random to place the plot on either the left or right side of the transect line. In each plot we recorded the number of flowering individuals of *V. thapsus* and the number of all individuals of all life stages.

Individual morphological traits

We report two important traits frequently used as measures of individual plant performance in studies of *V. thapsus* and other invasive species (e.g. Parker *et al.*, 2003). We measured plant height in centimetres, from the ground to the tip of the inflorescence, which is correlated with total inflorescence length (also recorded though not reported, $r = 0.76$) and with capsule number in Hawaii ($r = 0.70$; C. Daehler, unpublished). We also counted the number of flowering branches along the central (longest) flowering stem. The number of flowering branches varies as a result of reduced apical dominance, and is also positively correlated with capsule production (Lortie & Aarssen, 2000). Individual plant height and number of flowering branches assessments within a population were chosen by randomly selecting 20 points along the transect and measuring the first mature individual to the left or right of the transect (chosen at random). If the plants were scattered and scarce (less than 20 individuals per population), we recorded all available flowering individuals.

Seed collection and germination trials

We collected seeds from each sampled individual in Switzerland, Kashmir, Montana, Oregon and Australia to investigate whether the temperature dependency of germination varied among ranges and regions. Seeds were collected from the same individuals measured (a maximum of 20), at the same time as the other measurements were recorded. After harvesting, seeds were cleaned, pooled by population and thoroughly mixed, and immediately sent to Montana State University herbarium (MONT), where they were stored at room temperature for approximately 6 months. Germination tests were conducted using a thermo-gradient table consisting of six parallel aluminium plates (101.6 cm long × 15.2 cm wide × 1.0 cm thick). Temperature was controlled by a 200 W fluid loop chiller and a 260 W fluid heater at opposite ends, thereby creating a temperature gradient. Temperatures at six locations along the length of the plates were maintained at 5.0, 11.5, 21.0, 29.0, 35.0 and 42.0 (± 0.1 °C). Lots of 50 seeds were used for each population, one lot for each of the six temperatures (300 seeds total per population) and were sorted without regard to size or colour. Seed lots were weighed, then placed in covered 5-cm diameter plastic boxes lined with one sheet of germination paper (Anchor Paper Co., Minneapolis, MN, USA), wetted with distilled water, and kept moist by the addition of distilled water as needed. The positions of the plastic boxes were randomized within temperatures on the thermo-gradient table at the start, and positions rotated every day. Seeds were subjected to the best light regime for germination (12 h dark and 12 h light; see Baskin & Baskin, 1981). Germination was defined as protrusion of the radical and was recorded at 11:00 h daily for 15 days, a time frame sufficient for most seeds to germinate (Semenza *et al.*, 1978). The germination trial was repeated three times over 6 months in 2011. Percentage germination was calculated using only viable seeds. The viability of seeds that did not germinate was evaluated visually. Seeds were considered viable when there was a lack of fungus or rot, and the seeds were firm when squeezed with tweezers.

Data analysis

Climatic niche model based on the global distribution of Verbascum thapsus

To relate the performance of *V. thapsus* populations to their position within the climatic niche of the species, we first fitted a global niche model using presence–absence of *V. thapsus* from a large dataset from Eurasia, North America and Australia with a resolution of 0.5° (*c.* 50 km) and approximately 37,000 data points (Petitpierre *et al.*, 2012). We assume that climate variables broadly predict the fundamental niche of the species. All data were analysed using R 3.0.1 (R Development Core Team, 2013). Using multiple logistic regression we fitted *V. thapsus* presence–absence to linear and quadratic terms of mean annual temperature (BIO1), total annual precipitation (BIO12), their interaction, and BIOCLIM variables that were less than 70% correlated with mean annual temperature and average annual precipitation (Graham, 2003; see Table 1 and Appendix S2 for correlation of BIOCLIM variables). These variables included mean diurnal temperate range (BIO2), mean temperature of the wettest quarter (BIO8), and precipitation seasonality (BIO15). All BIOCLIM variables were downloaded from WorldClim at a resolution of 0.16667° and aggregated to a resolution of 0.5° by averaging the values for each of the nine corresponding cells (Hijmans *et al.*, 2005; Petitpierre *et al.*, 2012). To characterize the global niche, we selected the best model from all combinations of the full model using Akaike's information criterion (AIC) implemented through a forward and backward stepwise procedure (Burnham & Anderson, 2002; Venables & Ripley, 2002). We validated the global niche model that had the lowest AIC in two ways. First, we divided the data 100 times into two subsets by randomly sampling from the data without replacement, using 80% of the data to fit the model and 20% for calculating the areas under the curve (AUC) of the receiver operating characteristic function (DeLong *et al.*, 1988; Tuszynski, 2009). Then we cross-validated the global niche model, calculating the AUC to evaluate how well the global niche model predicted the distribution of *V. thapsus* with two datasets that were 50 times finer (1 km^2) in resolution in two regions. The two 1-km^2 grid datasets of presence–absence were from Hawaii (C. Kueffer and C. Daehler, unpublished data) and Switzerland (Swiss Biodiversity Monitoring, 2001–2007, http://www.biodiversitymonitoring.ch/; Weber *et al.*, 2004). After validation we then extracted interpolated global probabilities of occurrence for populations in the field survey based on the values of the BIOCLIM variables included in best model.

Analysis of variation in response to climate and between ranges

We modelled the mean population response of plant height, number of flowering branches, seed germination, population density and population size using multiple linear regression, to determine whether characteristics of populations (size and density) and individuals (plant traits and seed germination)

Table 1 The best global probability of occurrence models for *Verbascum thapsus* assessed using Akaike's information criterion (AIC) values and highest weight (w) calculated based on the log-likelihood (LL) and number of model parameters (K). The response is presence–absence of *V. thapsus* in 36,637 approximately 50 km × 50 km grid cells from Australia, North America and Eurasia. Deviance explained (D^2) by each model is 1 − residual deviance/null deviance. Explanatory variables are polynomial forms of climate variables extracted from the BIOCLIM database (BIO1, mean annual temperature; BIO12, total annual precipitation; BIO2, mean diurnal temperature range; BIO8 temperature during the wettest quarter; BIO15 precipitation seasonality). Coefficient estimates and a model summary are given in Appendix S2.

Model	LL	K	AIC	ΔAIC	w	D^2
BIO1 * BIO12 + BIO2 + BIO8 + BIO15	−6991.5	15	14013	0	1	0.58
BIO1 * BIO12 + BIO15 + BIO2	−7219.6	13	14465	452.1	0	0.57
BIO1 * BIO12 + BIO15	−7264.3	11	14551	537.6	0	0.57
BIO1 + BIO12 + BIO15 + BIO8 + BIO2	−7469.9	11	14962	948.8	0	0.56
BIO1 * BIO12 + BIO8	−8350.3	11	16723	2709.6	0	0.54
BIO1 * BIO12	−8623.6	9	17265	3252.1	0	0.53

varied between the native and non-native ranges, among different regions, by climate, and as a function of the global probability of occurrence.

The factors 'region' with six levels and 'range' (native versus non-native) with two levels are nested and collinear. First, we fitted eight separate models to evaluate how range, region, climate and global probability of occurrence characterize the data (see Table 2). We compared the models using AIC, whereby the best model was that with the lowest AIC value or the model that was most parsimonious with no greater than a 2 point AIC difference from the model with the lowest AIC (Burnham & Anderson, 2002). When continuous climate variables were included in the models with the lowest AIC, we used general additive models to fit the individual-level and population-level responses to mean annual temperature, average annual precipitation and probability of occurrence from the global niche model using the gam() function in the MGCV package (Wood, 2006). Models were fitted for each predictor independently (Guisan *et al.*, 2002). The general additive models had four basic dimensions, resulting in four knots that allow for four changes in the relationships between traits across the climate range. Four knots (*k*) were selected by comparing model fit beginning with three knots, the models were refit with a higher *k* up to *k* = 6. If no statistical statistically important changes were detected the lower *k* was preferred (Wood, 2006), which was generally four knots for all responses.

We determined how much variation was accounted for by region, range, climate, and global probability of occurrence, based on all possible regressions with variables from the best models of plant traits and population characteristics. Variation explained was determined by R^2 using the hierarchical partitioning function hier.part() in the R package HIER.PART (Chevan & Sutherland, 1991; Walsh & Mac Nally, 2013). To determine whether the response variables – plant density, population area, plant height and flowering branch number – were independent from each other, we used Spearman's nonparametric correlation tests.

RESULTS

Global niche model and sampled populations

The best global niche model contained a quadratic form of mean annual temperature and total annual precipitation and their interaction, plus quadratic forms of mean diurnal temperature range, mean temperature during the wettest quarter of the year and precipitation seasonality (Table 1, Fig. 1). Of these variables, precipitation seasonality, total annual precipitation and mean annual temperature accounted for the largest effects on *V. thapsus* occurrence (Appendix S2). Internal validation supported the global niche model (AUC = 0.953; 95% CI = ± 0.006). External validation using the local dataset from Hawaii supported the global niche model, but external validation using local data from Switzerland was less strong (AUC = 0.86 and 0.59, respectively).

The sampled populations varied widely in their fitted probability of occurrence based on the global niche model (Fig. 1). *Verbascum thapsus* occurred with highest probability in climates with a mean annual temperature of 9 °C, 1050 mm of average precipitation annually, and low seasonal variability in precipitation. Populations sampled in both the native and non-native ranges had both low and high probabilities of occurrence and a similar range of values (0.01–0.94, Fig. 1).

Response of population density and area to range, region and climate factors

The density of flowering individuals in plots with at least one plant was similar between ranges (3.1 vs. 2.1 plants per m^2 for native and non-native, respectively; $t = 0.667$, d.f. = 48, $P = 0.508$; Fig. 2). While the maximum population density recorded was in a non-native region (15.1 plants per m^2; Oregon), the maximum average regional density was recorded in Kashmir (4.3 per m^2) in the native range; and

Table 2 Results of model selection (Akaike's information criterion values) for multiple linear regression models of plant density, population extent, plant height and number of flowering branches in 50 populations of *Verbascum thapsus*. The models had different combinations of variables including a quadratic form of mean annual temperature (MAT), a quadratic form of total annual precipitation (TAP), probability of occurrence derived from a global niche model (PO), the region of origin (*n* = 6), and the range of origin (native or non-native). *K* is the number of parameters in the model. The factor region was nested in the factor range. Best models are indicated in bold type-face and are summarized in Appendix S3.

Model	*K*	Plant density	Population area	Plant height	Flowering branch number
Intercept only	2	**235.4**	128.4	1371.8	398.9
MAT × TAP + PO	5	238.9	116.1	1350.2	341.9
MAT × TAP + PO + Region	6	237.6	103.2	**1294.1**	**304.2**
MAT × TAP + PO + Range	6	238.1	103.2	1344.1	332.2
Range	3	235.8	**96.4**	1368.3	394
Region	3	235.7	102.4	1327.1	323.9
PO	3	236.1	130.2	1358	391.5
MAT × TAP	4	237.3	114.6	1367.3	356.2

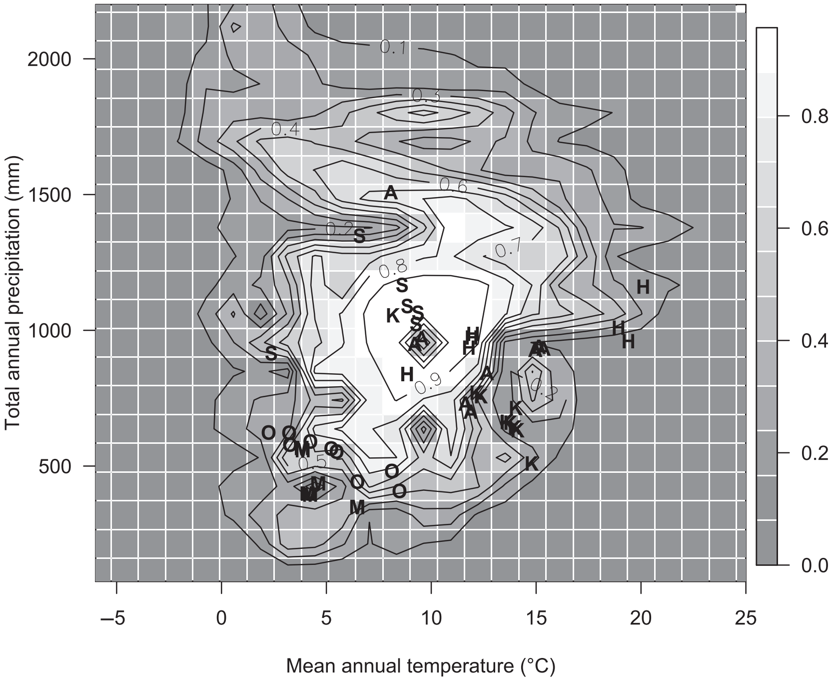

Figure 1 Climatic niche (estimated as probability of occurrence) of *Verbascum thapsus* derived from a global logistic regression model with quadratic terms of mean annual temperature, total annual precipitation, mean diurnal temperature range, mean temperature of the wettest quarter, and precipitation seasonality (see Table 1) based on presence–absence distribution data from Eurasia, North America and Australia. The climate of each population is indicated by letters and denotes the six study regions (A, Australia; H, Hawaii; K, Kashmir; M, Montana; O, Oregon; S, Switzerland). Elevational gradients within regions are always arranged by temperature, i.e. low-elevation (warmer) sites are on the right, and high-elevation (cooler) sites on the left of the panel. Grey shading and contour lines refer to probability of occurrence in the global climatic model.

Kashmir was the only region to differ from all the other regions ($t = 2.362$, d.f. $= 44$, $P = 0.023$; Fig. 2, Appendix S3b). Climate, probability of occurrence, region, and range were poor predictors of density. The best-fit model was an intercept only model (Table 2). The density of plants was not significantly correlated with plant height ($r_s = -0.240$, $P = 0.092$), but was negatively correlated with the number of flowering branches ($r_s = -0.47$, $P < 0.001$). The lowest mean number of flowering branches was in Kashmir, where the populations were on average the most dense (Table 3, Fig. 2).

The only characteristic that differed consistently between the native and non-native ranges was the average area covered by a population ($F_{1,36} = 35.4$, $P < 0.001$; Fig. 2), this being two orders of magnitude greater in the non-native range (1380 m^2 vs. 19.4 m^2). Range characterized the differences in area better than region, and better than climate (Table 2, Appendix S3a). Plant height and number of flowering branches were not correlated with population area (plant height: $r_s = -0.12$, $P = 0.48$; flowering branches: $r_s = -0.089$, $P = 0.62$).

Response of plant-level performance to range, region and climate factors

Mean individual plant performance of *V. thapsus* did not differ significantly between the native and non-native ranges, and variation within populations and within regions was high (Table 3). Plants were neither larger in the non-native range nor had more flowering branches (number of flowering branches: $F_{1,44} = 1.77$, $P = 0.19$; plant height: $F_{1,44} = 2.26$, $P = 0.14$; Table 3). Plant height and number of flowering

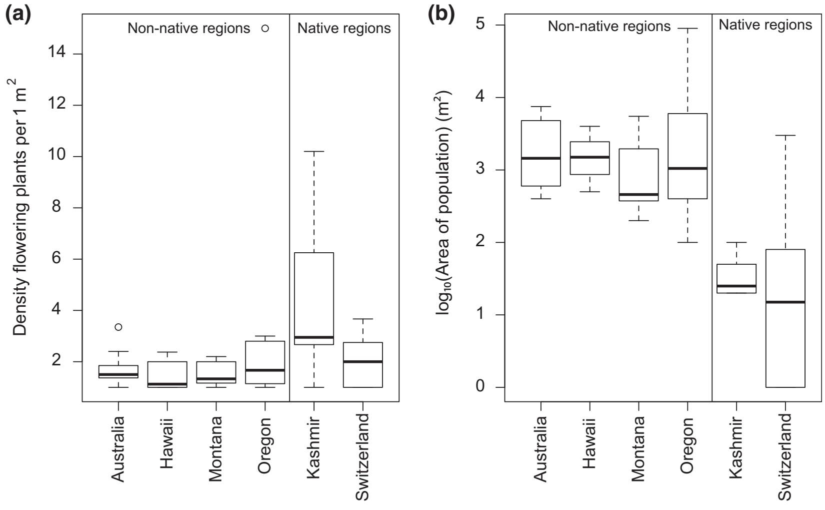

Figure 2 Population density and area (size) of *Verbascum thapsus* in each region. Density (a) is the average number of flowering individuals in 1-m^2 plots that contained at least one plant. The area that a population covered (b) was calculated as the product of the length and width of a population. Bars of the boxplot indicate 95% of the data, the box 50% of the data and the heavy black line the median.

Table 3 The mean (± 1 SD) plant height (cm) and number of flowering branches of *Verbascum thapsus* in the native and non-native ranges (bold type), and within each region. The number of individual plants recorded within each region is provided, with the number of populations in parentheses.

Range	Region	Plant height (cm)	Flowering branches	Number of individual plants
Native		**116 (37)**	**1.7 (0.9)**	
	Kashmir	101 (34)	1.2 (0.2)	186 (9)
	Switzerland	140 (28)	2.5 (0.9)	63 (6)
Non-native		**102 (32)**	**2.2 (1.0)**	
	Australia	87 (17)	2.7 (0.9)	168 (9)
	Hawaii	132 (30)	3.0 (1.1)	174 (9)
	Montana	109 (39)	1.5 (0.6)	160 (7)
	Oregon	89 (21)	1.6 (0.6)	161 (9)

Table 4 Generalized additive models of *Verbascum thapsus* plant height and number of flowering branches predicted by regression splines with four knots ($k = 4$). *P*-values test whether the patterns significantly differs from zero based on *F*-tests with the effective estimated degrees of freedom (d.f.) and residual degrees of freedom (Res d.f.). The predictors include mean annual temperature (MAT), total annual precipitation (TAP) and probability of occurrence from a global niche model (PO). Deviance explained (D^2) by the model is calculated as 1 − residual deviance/null deviance.

Response	Explanatory variable	d.f.	Res d.f.	*F*-value	*P*	D^2
Flowering branches	MAT	2.91	46	3.923	0.0156	0.22
	TAP	2.99	46	12.44	<0.001	0.47
	PO	1	46	3.079	0.0862	0.65
Plant height	MAT	2.91	46	1.872	0.149	0.13
	TAP	2.97	46	2.966	0.043	0.20
	PO	2.33	46	3.853	0.0238	0.20

branches differed strongly between regions (number of flowering branches: $F_{5,40} = 6.8$, $P = 0.001$; plant height: $F_{5,40} = 2.26$, $P = 0.005$). Models of plant height and number of flowering branches that contained region performed better than models that contained range, and the best models also included mean annual temperature, average annual precipitation and global probability of occurrence (Table 2).

Plant height and the number of flowering branches varied with climate, with observed maximal performance at 11.7 °C mean annual temperature and *c.* 1000 mm total annual precipitation, which coincided approximately with populations with the highest probability of occurrence derived from the global niche model (Fig. 3). Both plant performance traits increased in response to increases in probability of occurrence (Fig. 3, Table 4). Generalized additive models with four dimensions accounted for 6–47% of the total deviation in plant height and flowering branch number (Table 4, Fig. 3). Plant height and flowering branch number increased in response to mean annual temperature up to approximately 9 °C, and were highly variable thereafter, but only flowering branch number significantly varied in response to mean annual temperature (Table 4). The responses of plant height and number of flowering branches to total annual precipitation varied in slope at different portions of the total annual precipitation range (Fig. 3). Based on the hierarchical partitioning of variance, the most important factors accounting for variation in plant traits were differences among regions, average annual precipitation, mean annual temperature, and probability of occurrence from the global niche model (Fig. 4).

Germination trials

Seeds of *V. thapsus* from the various populations showed similar germination characteristics, with highest germination rates (> 80%) after 15 days at between 20 and 35 °C (Fig. 5). Germination was low at lower incubation temperatures in all regions except Kashmir (native), where 60% of seed germinated after 15 days compared to less than 10% of seed from all other regions (Appendix S3e). Across all regions, mean annual temperature was not a significant predictor of seed germination (Appendix S3). Mean seed size was 0.43 mg (1 SD = ± 0.0085), and was positively correlated with mean annual temperature of the populations ($r_s = 0.57$, $P = 0.004$), but not with average annual precipitation ($r_s = 0.27$, $P = 0.21$; Appendix S3e).

DISCUSSION

Comparisons between native and non-native populations are essential to test the assumption that invasive species perform better in their non-native range. Our study included populations from multiple regions and broad environmental gradients in both the native and non-native ranges and measured multiple traits at the individual and population level. We show that there are no consistent differences in the performance of *V. thapsus* between ranges – with the exception of population size, which was larger in the non-native range. These findings have implications for understanding the global invasion of *V. thapsus*, and more generally for the design and interpretation of comparative studies of invasive species.

Population characteristics differ between ranges

Populations of *V. thapsus* were spatially larger in the non-native than in the native range (Fig. 2), suggesting that population-level processes contribute to the success of this species. Alba *et al.* (2012) also reported a greater number of large populations in the non-native range, which they attribute to more available habitat in the non-native range than in the native range. These authors also found that small differences in individual-level traits did not explain the population size differences, consistent with the results of our study. One possible explanation for this could be that demographic rates such as field germination and establishment of seedlings, which we did not assess, are more important for population dynamics than variation in plant size or

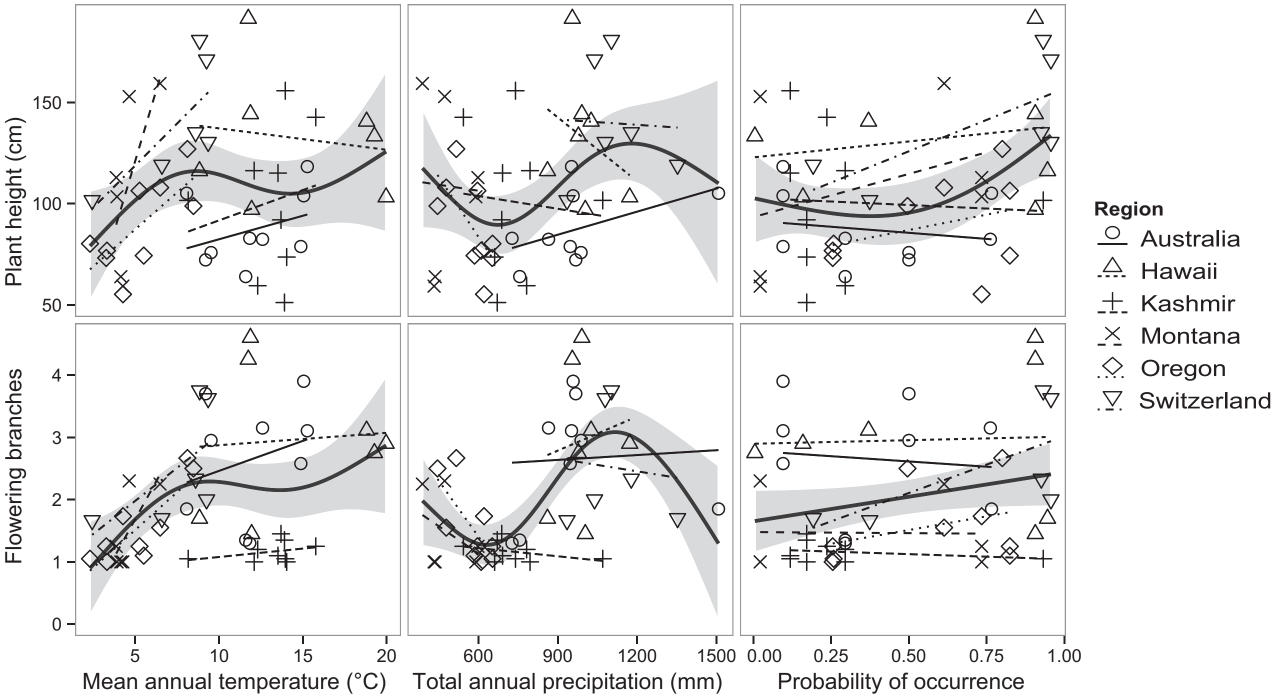

Figure 3 The response of *Verbascum thapsus* plant height (cm) and number of flowering branches to mean annual temperature, total annual precipitation and global probability of occurrence. Symbols identify each region and the different line types indicate linear trends of populations within each of the six regions. The heavy black line is a general additive model of the response with four dimensions (four knots), and the grey shaded area indicates the 95% confidence interval of the mean response. Model statistics are given in Table 4.

fecundity. Whatever the explanation, our data suggest that performance of individual plants, measured as morphological traits that presumably correlate with fitness, do not necessarily translate into population performance (see also van Kleunen & Fischer, 2005); therefore, the performance of populations should be assessed directly based on population characteristics, or ideally on estimates of demographic rates (e.g. Williams *et al.*, 2010).

High variability in the performance of *Verbascum thapsus* individuals

Plant traits of *V. thapsus* were more influenced by regional and climate differences than by the native or non-native status of the plants (Fig. 4). Based on the modelled climatic niche, plant performance traits peaked at the centre of the niche distribution, and we found a positive relationship between plant performance traits and probability of occurrence (Fig. 3).

Verbascum thapsus traits varied with mean annual temperature and total annual precipitation, both along gradients within some regions, and in response to climatic differences between regions (Fig. 3). Such clinal patterns, often observed along gradients of elevation or latitude, are common in the native and non-native ranges of invasive species (Maron *et al.*, 2004; Pergl *et al.*, 2006; Alexander *et al.*, 2009; Colautti *et al.*, 2009; Alba *et al.*, 2011; Alba & Hufbauer, 2012). In our study, plant size increased in response to mean annual temperature in populations with a mean annual temperature of < 10 °C (see Fig. 3), which is consistent with Parker *et al.* (2003), who found a negative trend in height of *V. thapsus* with elevation in the Sierra Nevada of California. However, we found no overall significant relationship between plant height and mean annual temperature because of large variation in the warmer climates covered by this study. Nonetheless, in subtropical Hawaii plants were largest and had the greatest number of flowering branches at the warmer sites. The cooler, high-elevation populations in Hawaii have a climate that falls in the centre of the modelled niche, and the high performance and invasiveness of *V. thapsus* in Hawaii (Daehler, 2005; Ansari & Daehler, 2010) might reflect the response of the species to the local climate (possibly further promoted by an aseasonal (subtropical) climate that allows plants to grow throughout the year). This illustrates how a global niche model can be used to locate the position of a local environment within the niche space of a species, and thereby contribute to predicting plant performance.

Regional differences in plant performance of *V. thapsus* were partially explained by the position of regions in the global niche model (Figs 3 & 4), but much of the variation among regions remained unexplained. Indeed, plant species occasionally perform better, based on demographic rates, outside the centre of their distribution or climate niche (Angert, 2009; Gerst *et al.*, 2011), making it difficult to predict how the species might perform in another area

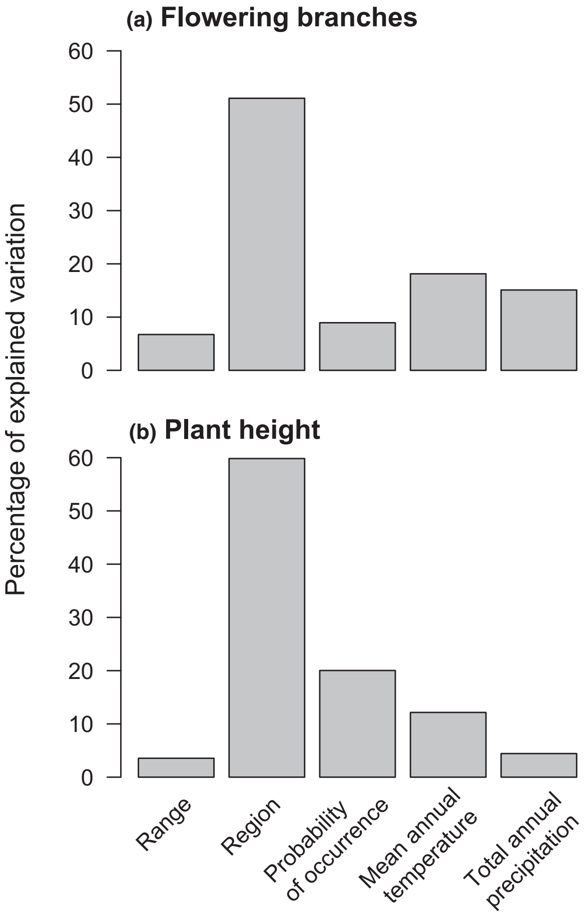

Figure 4 Percentage of variation (R^2) explained by each explanatory variable from all possible combinations of explanatory variables in regression models of *Verbascum thapsus* for (a) plant height and (b) number of flowering branches calculated using the HIER.PART package in R. The predictors include: range (native versus non-native), sample region (six total: four non-native and two native), mean annual temperature, total annual precipitation, and probability of occurrence derived from a global niche model.

(Alexander *et al.*, 2009). These factors could include anthropogenic or natural disturbance regimes, differences in invasion time and history, soil, herbivory or climate extremes and may suggest that variation in plant or population performance (e.g. plant density in Kashmir) is driven to a large extent by unmeasured local factors.

Our results confirm that *V. thapsus* traits vary substantially in response to climate (Figs 3 & 4; agreeing with Reinartz, 1984a; Parker *et al.*, 2003; Alba *et al.*, 2012). This response is more likely to be explained by high phenotypic plasticity than genetic differentiation, given that little genetic differentiation has been found along elevational gradients in other studies (Parker *et al.*, 2003; Ansari & Daehler, 2010, 2011). Indeed, one of the reasons for the success of *V. thapsus* around the world may be that it is a 'Jack of all trades' (Richards *et al.*, 2006), at least with respect to temperature, but possibly also aridity (von Arx *et al.*, 2014). However, there is some evidence of genetic differentiation among regions based on our seed germination tests, and results from other common garden experiments (Alba *et al.*, 2012; Kumschick *et al.*, 2013). Although germination at different temperatures was similar among regions, a native region (Kashmir) showed considerably better germination at low temperatures than all other populations. Genotypes from Kashmir might be adapted to germination at lower temperatures, although maternal effects can also not be excluded as a possible explanation. Such low temperature germination seems to be absent from all non-native populations, which may reflect the history of spread, with introductions in the New World being of predominantly European origin (Wilhelm, 1974). In line with these results indicating differences between genotypes, *V. thapsus* from western North America (i.e. including Montana and Oregon) has been shown to grow faster and produce more biomass than European plants in a common garden experiment, but only when growing without competition from other species and under drought stress (Kumschick *et al.*, 2013).

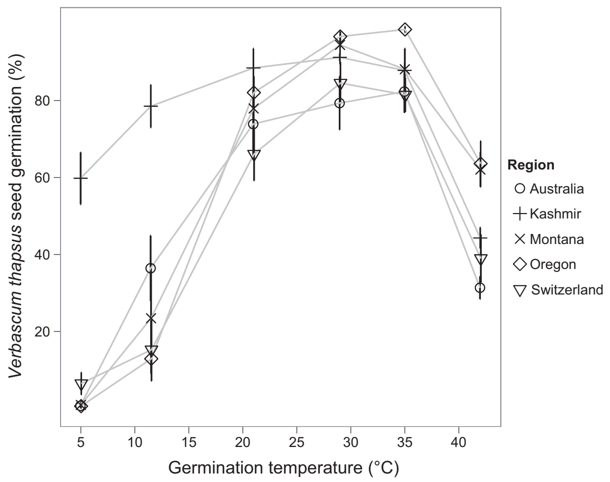

Figure 5 Seed germination of *Verbascum thapsus* along a temperature gradient. Percentage seed germination was calculated from the number of viable seeds that germinated in 15 days. Grey lines indicate regional trends in germination. Symbols indicate mean germination in each of the different regions. Black bars indicate ± 1 SE.

Potential biases

By including multiple regions and broad climate gradients in both the native and non-native range, we avoided potential biases of many previous studies that compared the performance of non-native species between the native and non-native ranges (Kueffer *et al.*, 2013). However, by always choosing the largest and most conspicuous populations in each region, we might have introduced bias if the patterns we report do not reflect average trends. To minimize this problem, we selected populations close to main roads where non-native species often establish first in mountains (Seipel *et al.*, 2012). Future studies might prefer a more randomized sampling of populations, though this is logistically difficult.

Range comparisons in invasion biology: accounting for variation to improve inference

Invasion biology has tended to concentrate on trait differences between native and non-native ranges as a means of understanding invasion success. However, our study indicates that such comparisons can be misleading for a number of important reasons. Crucially, differences in performance between different locations within the native or non-native range may be greater than the overall difference between ranges (Leger & Rice, 2003; Leifso *et al.*, 2012; Kueffer *et al.*, 2013). This may be due to genetic variation among populations in the native or non-native ranges, or other local factors such as abiotic or biotic interactions that affect plant performance at a particular site. Therefore, multiple regions from the native and non-native ranges should be included in comparative studies to avoid confounding differences between ranges with differences between regions. In particular, underlying environmental gradients affect the performance of plant species, and can confound the interpretation of performance differences between the native and non-native range (Colautti *et al.*, 2009; Kueffer *et al.*, 2013). A better understanding of such within-range variation will help to explain why problematic invaders in some regions are more innocuous than in other regions (Melbourne *et al.*, 2007; Kueffer *et al.*, 2010; Firn *et al.*, 2012), and lead to better predictions of invasion success. For example, our results indicate that globally fitted climate niche models can help to broadly predict plant performance and potentially target regions where a species is likely to become problematic. However, the generality of this observation needs further testing (compare, e.g., Angert, 2009 and Bradley, 2012), especially since individual plant performance might not predict performance at the population level, which ultimately shapes invasion success and impact. Overall, generalizations about changes in performance of a given invasive species require information about individual and population performance from replicated regions spanning relevant environmental gradients across the whole native and non-native ranges.

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SUPPORTING INFORMATION

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

Appendix S1 Population name, location, and climate of populations.

Appendix S2 Details of the global-niche model of *Verbascum thapsus*.

Appendix S3 Model summaries of population characteristics and seed germination.

BIOSKETCH

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