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Cross-Continental Shifts of Ecological Strategy in a Global Plant Invader

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ABSTRACT

Aim: Plant invasions are a global problem that requires studying plants and their environmental associations across native and introduced ranges.
Location: 2000 km transects in China, Europe and North America.
Time Period: June 2019–July 2020.
Major Taxa Studied: Japanese knotweed (*Reynoutria japonica*).
Methods: We surveyed 150 populations of Japanese knotweed, a noxious invader of the temperate zone, along 2000 km transects in native China and the introduced ranges of Europe and North America.
Results: We found that larger plants and denser populations in the introduced ranges were associated with shifts in leaf economy and chemical defences. Introduced knotweed populations had higher SLA but reduced leaf chlorophyll, lignin, C:N ratio and leaf toughness along with altered leaf tannins, flavonoids and alkaloids. We found three distinct multivariate knotweed phenotypes primarily in the introduced ranges, and two multivariate knotweed phenotypes mainly in native populations.

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Main Conclusions: Decreased herbivore and pathogen impacts in introduced populations and changes in environmental associations indicate that enemy release and novel habitat conditions might have driven the emergence of novel ecological strategies in this global plant invader.

1 | Introduction

Biological invasions are one of the major threats to global biodiversity (Bellard, Bernery, and Leclerc 2021; IPBES 2023), but they also provide large, unplanned experiments that yield insights into complex ecological and evolutionary processes (Sax and Brown 2000; Richardson and Pyšek 2012; Bailey 2013). Studying the drivers of plant invasions across environmental contexts can provide a fundamental understanding of species responses to novel environments (Moran and Alexander 2014). This knowledge, in turn, can be used to manage and predict invasions, and thus mitigate future biodiversity losses. One main strategy in this context has been to link invader success in different habitats to variation in plant traits (Sodhi et al. 2019; Kaushik et al. 2022; Lau and Funk 2023).

A variety of traits affect the growth, development, reproduction, or survival of plants under different environmental conditions (Violle et al. 2007; Drenovsky et al. 2012). Such traits can be morphological, physiological or phenological, and they often occur in clusters or 'trait syndromes' that are thought to reflect different ecological strategies (Woods and Sultan 2022). One important framework for understanding trait variation is the so-called leaf economics spectrum (Wright et al. 2004), which posits a main axis of trait variation from slow-growing, resource-conservative species to fast-growing species that rapidly take up resources but are less resource-efficient. The fast-growing species have short-lived leaves with, among others, high nitrogen content, photosynthetic capacity and specific leaf area (SLA), whereas the slow-growing species have longer-lived leaves with opposite traits. 'Fast' species are particularly common in nutrient-rich and disturbed habitats (a condition also associated with plant invasion; van Kleunen, Bossdorf, and Dawson 2018), whereas 'slow' species are thought to have an advantage under strong competition, nutrient-poor or other challenging conditions.

An important dimension of plant traits that is not considered in the classic leaf economics spectrum is traits related to defences against natural enemies (Agrawal 2020). Many plant species have morphological defences (surface wax, trichomes, spines and thorns and higher toughness of the leaves) or produce secondary metabolites that act as toxins or reduce tissue palatability to herbivores (War et al. 2012). Chemical defences can be constitutively present in plant tissues, or they can be induced in response to herbivory. Further, chemical defences can be qualitative or quantitative. Secondary metabolites associated with qualitative defences (e.g., alkaloids, glycosides or terpenes) are produced at low concentrations and are typically effective against generalist herbivores whereas quantitative defences (e.g., lignins and tannins) are effective against a wide range of herbivores but require larger doses and high allocation costs (War et al. 2012). Introduced plant populations often experience a release from specialist enemies compared to native populations of the same species, although they continue to be attacked by generalists (Joshi and Vrieling 2005; Liu and Stiling 2006; Halbritter et al. 2012). This change in herbivore pressure during invasion should select on variation in defence traits (Blossey and Notzold 1995), and result in shifts from specialist to generalist defences (Sun et al. 2023), as well as overall reduced defences.

Besides differences between native and introduced ranges, most plant traits also harbour substantial geographic variation within ranges, which is shaped by variation in abiotic conditions, biotic interactions, and the evolutionary history of a species. Studying trait-environment relationships and their links to plants and population performances thus increases our mechanistic understanding of ecological strategies (Verberk, van Noordwijk, and Hildrew 2013; Pearson et al. 2022). Conducting such studies in native versus introduced ranges may detect changes in ecological strategies during a plant invasion. However, few studies so far have undertaken this approach (Colautti, Franks, et al. 2014; Liu et al. 2021; Ricciardi et al. 2021), even for widespread invaders, because of the logistic challenges of sampling at many field locations throughout the native and introduced ranges (Pearson et al. 2022).

Invasive knotweeds (*Reynoutria* spp., Polygonaceae) are listed among the 100 worst invasive alien species in the world by the International Union for Conservation of Nature (Lowe et al. 2004). Native to Eastern Asia, *Reynoutria japonica* Houtt. (Japanese knotweed) and *R. sachalinensis* (F.Schmidt) Nakai (giant knotweed) were introduced to temperate Europe and North America as garden ornamentals in the 19th century (Bailey and Conolly 2000). Hybridization between the two species created the hybrid *R.* × *bohemica* (Chrtek & Chrtková) which can be more aggressive than either parent (Pyšek et al. 2003). The invasive knotweeds inhabit a wide range of habitats including riverbanks, roadsides and urban habitats, and forests (Bímová, Mandák, and Kašparová 2004; Richards, Schrey, and Pigliucci 2012). These species are powerful ecosystem engineers, which can reduce species richness of native communities and disrupt nutrient cycling and ecosystem stability (Maerz, Blossey, and Nuzzo 2005; Murrell et al. 2011; Lavoie 2017; Fogelman et al. 2018). The dominance of introduced knotweed populations, particularly of *R. japonica* and the hybrid, has been attributed to different ecological and evolutionary processes including clonality (Brock and Wade 1992; Gaskin et al. 2014, phenotypic plasticity (Richards et al. 2008; Yuan, Pigliucci, and Richards 2024), hybridization and introgression (Gammon et al. 2007; Grimsby et al. 2007), broad ecological amplitude (Palmer 1994), allelopathy (Murrell et al. 2011; Parepa, Schaffner, and Bossdorf 2012; Parepa and Bossdorf 2016), release from natural enemies (Beerling and Dawah 1993; McIver and Grevstad 2010) and a superior ability to exploit resource fluctuations (Parepa, Schaffner, and Bossdorf, 2013). However, we currently do not know whether these mechanisms play a role in the native range. There are limited data on how traits,

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environmental conditions or local adaptation differ between native and introduced populations (Griffin-Nolan et al. 2024; Maurel et al. 2013; Rouifed et al. 2018). Moreover, the factors that control knotweed performance in situ remain poorly understood. Studies in several locations in Europe have shown that knotweed abundance can be linked to light intensity (Dommanget et al. 2013), disturbance regimes, moisture and soil nitrogen (Bímová, Mandák, and Kašparová 2004) as well as riparian land use (Beerling 1991). In their introduced ranges, knotweeds have been found to harbour a strongly reduced herbivore community compared to co-occurring native plants, with a particular lack of specialist herbivores (Beerling and Dawah 1993; Maurel et al. 2013; McIver and Grevstad 2010).

Here, we evaluated variation in plant performance and plant traits, and their associations with abiotic environmental factors, in natural populations of Japanese knotweed along large latitudinal gradients in its native (China) and introduced ranges (Europe and USA). We tested the following hypotheses: (1) Compared to native populations, knotweed plants in introduced populations show increased performance and shifts in traits related to leaf physical and chemical defences. (2) Introduced populations exhibit different trait syndromes reflecting shifts in ecological strategies that facilitate invasion. (3) Shifts in traits and strategies are associated with changes in the relative importance of different environmental drivers.

2 | Materials and Methods

2.1 | Study Species

The invasive knotweeds include three different taxa: *Reynoutria japonica* (Japanese knotweed), *R. sachalinensis* (giant knotweed) and *R.* × *bohemica* (Bohemian knotweed) (Bailey and Conolly 2000). The latter is a hybrid resulting from a cross between the first two species. The parental species *R. japonica* and *R. sachalinensis* were introduced to Europe from Japan in the 1840s (Bailey and Conolly 2000), and to the United States around 1860 (Del Tredici 2017). After a lag time of ca. 50 years, populations expanded and became invasive in both ranges (Del Tredici 2017). In its native range, Japanese knotweed occurs throughout China, Japan and Korea, whereas the giant knotweed is mostly restricted to Northern Japan and the Sakhalin Island (Russia), (Beerling, Bailey, and Conolly 1994; Bailey and Conolly 2000). Invasive knotweeds are herbaceous perennials that spread predominantly through (fragmented) rhizomes and stems but can also undergo sexual reproduction by seeds when compatible pollen sources are available. Several previous studies suggested that introduced populations of *R. japonica* consisted of a single female genotype in Europe (Hollingsworth and Bailey 2000; Zhang et al. 2016) and the USA (Richards, Schrey, and Pigliucci 2012; Gaskin et al. 2014; Groeneveld, Belzile, and Lavoie 2014) (but see Gammon et al. 2007; Grimsby et al. 2007; Wallendael, Alvarez, and Franks 2021). *Reynoutria japonica* and the hybrid *R.* × *bohemica* are widely distributed and highly invasive, whereas the giant knotweed *R. sachalinensis* is less common and less aggressive (Bailey, Bímová, and Mandák 2007).

2.2 | Field Survey

We conducted a cross-latitudinal survey of 150 Japanese knotweed populations in the native range of China (23.29° N to 36.86° N) and the introduced ranges of North America (34.24° N to 44.94° N) and Europe (44.67° N to 59.94° N; see Table S1 for details about the sampling sites), surveying in each range during the peak growing season. We focused on sampling *R. japonica* but due to morphological similarities, and the natural distribution of the taxa along our transects, we could not rule out the occasional inclusion of hybrids in the introduced ranges. We used morphological and cytological data to confirm taxa identity (see further details in the supplement Data S1). In China, we sampled from Xunwu in Guangdong province to Zouping in Shandong province between 8 July and 16 August in 2020. In Europe, we sampled from Carmagnola, Italy to Uppsala, Sweden between 30 May and 16 June 2019. In the United States, we sampled from Commerce, Georgia to Milford, Maine between 2 and 19 June 2019.

In each range, we surveyed 50 populations along a 2000 km transect (sampling approximately every 40 km; Table S1, see Figure 3). At each site, we measured the width and length of the population and laid a 30 m transect for sampling. We selected five knotweed stems at regular intervals along the transect at 2, 8, 14, 20 and 26 m. When a population was smaller than ~28 m in length, we reduced the distance between stems, but kept stems separated by at least 1 m. For each selected stem, we measured stem density in a one square meter quadrat around the stem, the stem height and diameter. We also collected five fully developed leaves to measure leaf chlorophyll content (Minolta SPAD 502), leaf thickness (Mitutoyo Micrometre Series 293), leaf toughness (Sauter, Gmbh Analog Force Gauge with 8 mm diameter flat head), percent leaf area lost to herbivory, presence of pathogens, specific leaf area (SLA, total leaf area cm^2/leaf dry mass), carbon (C), nitrogen (N), and secondary metabolites (total tannins, alkaloids, lignin and flavonoids content). After completing the leaf measurements in the field, we placed the five leaves of each individual inside a paper bag together with a paper tissue to keep the leaves dry until we reached the lab. All samples were further dried to constant weight in an oven at 60°C, and later stored at room temperature in silica gel bags for about 1 year for the European and US samples, and for 3 months for the Chinese samples before we measured the secondary metabolites (October–December 2020). Therefore, if the drying method affects the concentration of some compounds it should at least affect all samples similarly, so that relative differences were preserved.

We conducted all leaf chemical analyses in the same lab at Fudan University in China. We ground dried leaf samples to the required particle size with a ball mill (MM400, Retsch, Germany) and used a FlashSmart Elemental Analyser (Thermo Scientific, Germany) via thermal combustion and TCD/IR (thermal conductivity and infrared detection) of CO_2/N_2 to analyse total leaf C and N. We analysed all leaf secondary metabolites (total lignin, tannins, alkaloids and flavonoids content) with reagent kits following the manufacturer's protocol (Suzhou Comin Biotechnology Co. Ltd., Suzhou, China) with necessary modifications. Briefly, to measure lignin, we added 4 mg of dried sample (instead of 2 mg in the

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manufacturer's protocol) to a 500 μL mixture of acetic acid/acetyl bromide and 20 μL perchloric acid and incubated it at 80°C for 40 min. After cooling to room temperature, we added a 500 μL mixture of NaOH/acetic and mixed thoroughly, then we took 20 μL of the supernatant and added 980 μL of glacial acetic acid. We measured the absorbance at 280 nm and calculated the lignin content of each sample according to the standard curve. For total tannins, we added 0.1 g ground sample to 1 mL distilled water, incubated the sample in a water bath at 80°C for 30 min, centrifuged it at 12,000 g for 10 min (instead of 8000 g recommended in the protocol), mixed 5 μL of the supernatant with 130 μL of distilled water and added 35 μL mixture of sodium tungstate/phosphomolybdic acid/ phosphoric acid and 30 μL Na_2CO_3 solution. After 30 min at room temperature, we measured the absorbance at 760 nm and calculated the total tannins content. To extract alkaloids, we exposed 0.1 g ground sample in 0.9 mL 80% ethanol and 0.1 mL ammonia solution to low-frequency ultrasound waves for 60 min and centrifuged it at 12,000 g (instead of 8000 g recommended in the protocol) for 10 min. We then mixed 50 μL of the supernatant with 250 μL of citric acid/sodium citrate buffer and 100 μL of bromocresol green/potassium hydrogen phthalate solution. After 5 min at room temperature, we added 500 μL chloroform, and left for another 40 min at room temperature. We used the chloroform layer to measure the absorbance at 416 nm and calculated the alkaloids content according to the standard curve. For total flavonoids, we incubated a mixture of 0.02 g sample and 2 mL 60% ethanol at 60°C for 2 h and then centrifuged it at 12,000 g for 10 min. We mixed 108 μL of the extraction supernatant with 6 μL of $NaNO_2$ solution, 6 μL of $Al(NO_3)$ solution and 80 μL of NaOH solution. After 15 min at room temperature, we measured the absorbance at 510 nm and calculated the total flavonoids contents.

To characterise soil nutrients and soil pH at each sampling site, we collected a soil sample (~50 mL) close to the rhizome of each stem to create a pooled sample for each population. At the third quadrat on each transect, we took a photo of the canopy closure above the stem using a digital camera with a field view of 84°, oriented vertically to get a simple comparative measure across sites (see also Bianchi et al. 2017; Díaz 2023). We used ImageJ (Schneider, Rasband, and Eliceiri 2012) to convert the images into binary forms, with canopy in black and the sky in white, and to calculate percent canopy closure.

2.3 | Environmental Data

We obtained recent climate data (the 1970–2000 averages) for all 150 populations from WorldClim 2 (Fick and Hijmans 2017), at a spatial resolution of 2.5 arcminutes. We used the 19 bioclimatic variables (accessible at: https://www.worldclim.org/data/bioclim.html), which cover different aspects of temperature and precipitation and their temporal variability.

We dried all soil samples at 40°C for 3 days, sieved them through a < 2 mm mesh and milled them to < 63 μm in a planetary ball mill. We analysed the following 11 variables: total soil C, N, Calcium (Ca), Potassium (K), Magnesium (Mg) and Phosphorous (P), as well as plant-available fractions of Ca, K, Mg, P and soil pH. We measured total C and N by elemental analysis via thermal combustion and TCD/IR detection of CO_2/N_2. For total element contents, we digested the samples with a mix of HNO_3, HF and H_2O_2 (4:4:1) in a microwave and measured the elements by ICP-MS (inductively coupled plasmaspectrometry). We tested element recovery of total digestions with certified reference material (BCR2, Columbia River basalt). We extracted plant available elements by the Mehlich 3 procedure (a mix of NH_4NO_3, NH_4F, HNO_3, EDTA and CH_3COOH) and measured them by ICP-OES (inductively coupled plasma-optical emission spectrometry). We measured the soil pH of the sieved material in water (1:2.5).

2.4 | Statistical Analysis

We conducted all analyses in R version 4.3.1 (R Core Team 2023). Prior to the analyses, we examined the relationships between pairs of phenotypic traits with Pearson correlation and arbitrarily discarded one if they were highly correlated with a coefficient > 0.7. Each response variable was subsequently analysed independently, with one exception: to estimate the standing biomass per square meter (cm^3/m^2) we combined stem density, stem height and stem diameter into a composite variable based on the formula:

$$\text{Standing biomass} = \frac{h\left(\frac{Ø}{2}\right)^2 * 3.14}{3} * \text{Stem density}$$

where h is the average stem height in a plot, and Ø is the average stem diameter. Essentially the first term calculates average stem volume, which is multiplied by stem density to estimate total stem biomass (cm^3/m^2) per area.

To visualise climatic differences among ranges, we conducted a standardised and centred PCA (principal component analysis) using the *prcomp* function in the package *factoextra* (Kassambara and Mundt 2020). We generated a PCA biplot of all populations in the climatic space and evaluated climatic variable contributions to the principal components (Figure S1). We conducted an analogous set of analyses, using the soil nutrient data to visualise differences in soil nutrients within and among ranges (Figure S2).

We then tested for range differences in individual variables. For each response variable, we ran a generalised linear mixed model (GLMM) with range as a fixed factor and population as a random factor, using the *lme4* package (Bates et al. 2021). After discovering the extent of hybrids in our collection, and additional ploidy variation within China and the US, we also tested for taxa and ploidy effects on trait variation within each range, but found only minor differences between the two taxa and different ploidies which did not affect our overall findings (see Table S2 and Figure S3). We therefore presented the original, complete and balanced, analysis of all 150 surveyed populations of Japanese knotweed *sensu lato* (*s.l.*) as in our previous work (Richards et al. 2008) and several other studies of Japanese knotweed (e.g., Bailey 2013; Grimsby and Kesseli 2010; Walls, 2010).

For variables that displayed a significant range effect ($p < 0.05$), we conducted Tukey post hoc tests to identify which ranges differed from each other. We used density plots generated in

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ggplot2 (Wickham, Chang, and Wickham 2016) to visualise the variation within and among geographic ranges. To test for differences in herbivory and pathogens among ranges, we fitted a negative binomial generalised linear model (glm.nb) with log function and tested for differences in group means by simultaneous contrast tests using the *linfct* and *mcp* functions in the *multcomp* package (Hothorn, Bretz, and Westfall 2008).

Next, we examined the multivariate structure of our data, potential trait syndromes, and their geographic distributions. We constructed Euclidean distance matrices from scaled and centred mean population traits values and used hierarchical cluster analysis with Ward's linkage to capture similarity and discontinuity among populations (*dist* and *hclust* functions in *stats* package). We used the *clusGap* function (Tibshirani, Walther, and Hastie 2001) in the *cluster* package (Maechler et al. 2022) to determine the optimal number of clusters, and visualised population similarities and clustering through a phenogram with the *dendextend* package (Galili 2015). To understand the contributions of individual variables to the clustering, we ran a linear discriminant analysis (*lda* function in *MASS* package) (Venables and Ripley 2002) and plotted the LDA loadings, together with the population clusters, in two-dimensional ordination space, using the *ggord* package (Beck 2017). We assessed the differences in each trait across clusters with type II ANOVA using the *car* package (Fox and Weisberg 2018), followed by pairwise differences tests (*testInteraction* function, *phia* package) (De Rosario-Martinez 2015). To visualise the relative contributions of variables to specific clusters, we created radial plots, using the *radarchart f*unction in the *fmsb* package (Nakazawa 2023). We first performed the cluster analysis on the complete dataset (including all individuals from the 150 populations). Given that our study was focused on *R. japonica* but inadvertently included some *R.* × *bohemica* individuals, we also re-ran the clustering and LDA analysis with only the octoploid *R. japonica* individuals to evaluate the effect of the hybrids (i.e., 126 populations). We provided these results in the supplement.

Finally, we used the environmental data (climate, soil nutrients, canopy closure) to test for drivers of knotweed variation and compare their relative importance in each range. To avoid collinearity among climate and soil variables, and to reduce the total number of tests, we simplified the 19 bioclimatic variables and 11 soil variables through two principal components analyses, one for climate and one for soil within each range. We evaluated only principal components that explained $>10\%$ of the variation in the data (Figures S1 and S2). We then used model selection to identify the most parsimonious models for explaining variation in each response variable. Initially, we tested a set of global models that included only the climate PCs, the soil PCs and canopy cover, or any possible combinations of these – all either without range, with range (i.e., allowing for different means in each range) or with range interactions (i.e., allowing for different environment relationships in each range). Together with a null model and a range-only model, this resulted in a total of 23 alternative models (Table S3). We used hierarchical model selection with the library *performance* Lüdecke et al. 2021 to rank the models based on their Akaike Information Criterion (AIC) and coefficient of determination (R^2). Because of limited overlap in climate among ranges, environmental effects were partly confounded with the range effects in the global analysis. The most parsimonious global models often included range interactions (Table S3), so we further explored the relative importance of the environmental drivers in each range by fitting separate models for each range that included the effects of climate (within-range climate PCs, Table S4), soil nutrients (within-range soil PCs, Table S5) and light availability (% canopy closure). Then we conducted variance partitioning for each trait in each range, using the *partvar* function with 1000 bootstrap replicates in the *partR2* package (Stoffel, Nakagawa, and Schielzeth 2021).

3 | Results

3.1 | Knotweed Performance Across Ranges

Based on morphological and cytological data, we assigned all samples from China to *R. japonica*. In Europe, most of the populations were also assigned to *R. japonica* while five (out of 50) populations were *R.* × *bohemica*, and one population harboured both *R. japonica* and *R.* × *bohemica* individuals. In the US, we found that 32 populations consisted of only *R. japonica*, 12 populations were assigned to *R.* × *bohemica*, and six populations contained mixtures of *R. japonica* and *R.* × *bohemica* (Table S1).

At the population-level, introduced populations in Europe and the USA produced substantially more standing biomass than native populations in China (Europe: +474%; USA: +300%; Figure 1, Table S6). Plants in introduced populations also differed significantly from those in native populations in most leaf traits: on average, plants in European and USA populations had a higher specific leaf area (Europe +51%, USA +70%), but lower levels of leaf chlorophyll (Europe −35%, USA −15%), leaf toughness (Europe −24%, USA −9%), leaf C:N ratio (Europe −52%, USA −47%) and leaf lignin (Europe −23%, USA −65%). In the USA populations—but not European—plants also had significantly lower levels of leaf tannins (−5%) and flavonoids (−17%) but higher levels of leaf alkaloids (+78%) than native Chinese populations (Figure 1, Table S6). There were no significant differences among ranges in leaf thickness.

There were also significant differences between the two introduced ranges: plants from the USA populations had on average lower standing biomass (−43%), leaf lignin (−34%), tannins (-5%) and flavonoids (-24%) but tougher (+13%) and more chlorophyll (+17%) and alkaloid-rich (+49%) leaves than plants from European populations.

3.2 | Damage From Natural Enemies

Introduced individuals in Europe and North America experienced significantly less damage by herbivores (Europe: −79% less leaf area lost, USA: −76%) compared to individuals in native populations (Figure 2A, Table S6). In addition, only 14% and 17% of the individuals in Europe and the USA respectively showed pathogen lesions compared to the native range where 91% of the individuals exhibited signs of pathogen presence (Figure 2B, Table S6).

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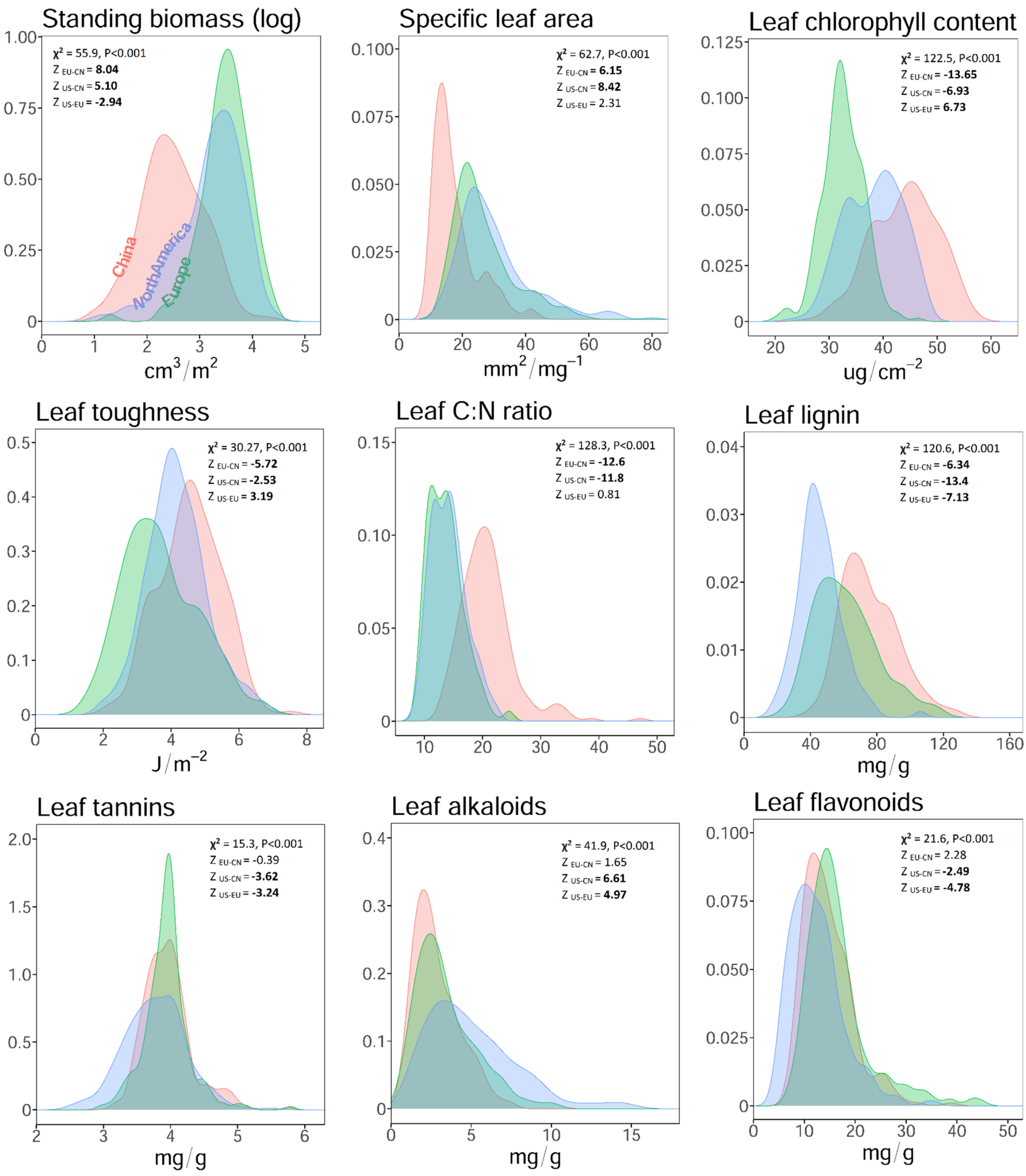

FIGURE 1 | The distributions of traits within populations in the native range of China (red), and the introduced ranges of Europe (green) and North America (blue). The differences among regions are indicated by chi-square (overall differences) and *z*-scores (pairwise range comparisons; CN = China, EU = Europe, US = United States). Significant pairwise range comparisons are in bold.

3.3 | Multivariate Trait Syndromes

The hierarchical clustering analysis based on the complete dataset of Japanese knotweed *s.l.* (150 populations) identified five clusters of observed knotweed trait combinations based on the trait dissimilarity matrix (Figure 3; Figure S4a,b and Table S7). The first two discriminant axes of the LDA explained ~92% of the total variation across clusters (Figure S4c). Cluster 1 (blue area and dots in Figure 3 and Figure S4c) occurred almost exclusively in the native range. These populations had the highest value of C/N, coupled with high levels of leaf toughness and chlorophyll content, as well as increased levels of digestibility-reducing tannins and lignin. This combination of traits defined a conservative growth strategy, with low nutritional quality (high C/N but low SLA levels) and high physical and quantitative chemical defences. Cluster 2 (purple area and dots in Figure 3 and Figure S4c) mainly occurred in the northern area of the native range but also in North America's middle and southern regions. These included individuals with lower amounts of secondary metabolites but relatively high

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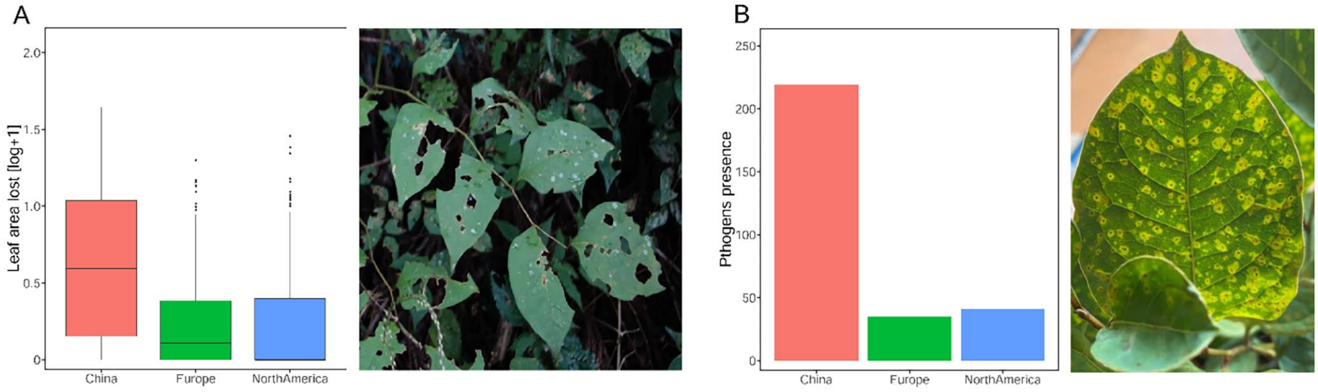

FIGURE 2 | (A) Leaf area lost to herbivores (= trait median) and an image of herbivore attack in the field in China and (B) number of individuals with signs of pathogen presence in native and introduced knotweed populations and an image of pathogen lesions on leaf on a plant in China.

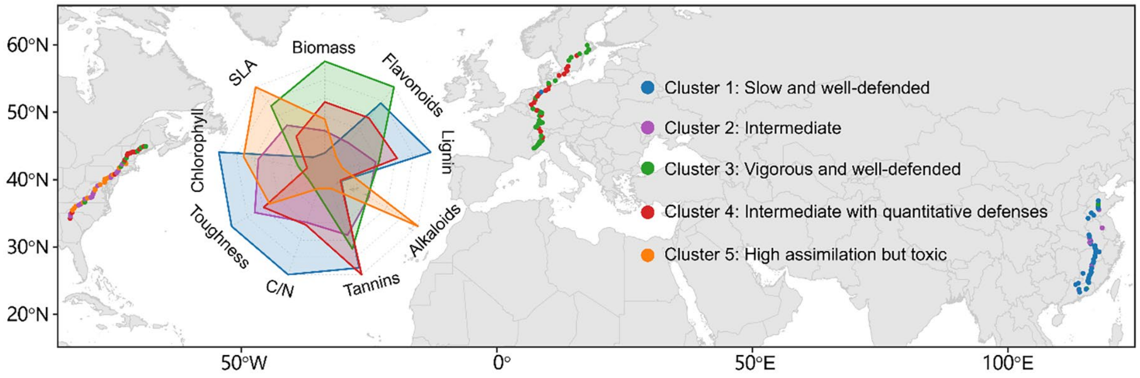

FIGURE 3 | Geographic locations of the 150 knotweed populations surveyed across China (native range), Europe and North America (both introduced range). The symbol colours indicate the predominant multivariate trait syndrome in each population, and the radial plots show the profiles (= traits means) for each of the five trait syndromes.

levels of leaf toughness and intermediate C/N. This combination of traits represented an intermediate level of nutritional quality (C/N levels), with moderate levels of physical defence. Cluster 3 (green area and dots in Figure 3 and Figure S4c) and Cluster 4 (red area and dots in Figure 3 and Figure S4c) occurred only in the introduced ranges of Europe and the northern part of North America. Both clusters contained populations with high standing biomass values, and low levels of leaf chlorophyll and C/N ratio. The two clusters differed in that plants in Cluster 3 had higher values of SLA and flavonoids content, while plants in Cluster 4 displayed higher levels of leaf toughness and tannins. Hence, these two clusters were characterised by a strategy of high nutritional quality and individual biomass, but differed in ways to resist biotic pressure. Cluster 5 (orange area and dots in Figure 3 and Figure S4c) included the fewest populations and only occurred in the middle and southern areas of the USA. They tended to have the highest SLA among the clusters, with relatively high levels of leaf chlorophyll and alkaloid content, intermediate leaf toughness and standing biomass values. This combination of traits is consistent with a classic acquisitive strategy (fast growth), with high nutritional quality (low C/N ratio), and toxins as the chemical defence metabolites (high alkaloid levels).

When we restricted the analysis to only the octoploid *R. japonica* individuals (from 126 populations), the results were similar to those with the full data set (Figure S5), except that cluster 2 (purple) and cluster 4 (red) combined into one cluster resulting in a total of four clusters (Figure S6a,b), and some individuals from China that were previously assigned to the violet ("intermediate") cluster were now assigned to the blue ("slow and well-defended") cluster (Figure S6b,c). The new purple cluster represented an overall intermediate syndrome characterised by high quantitative defences and moderate levels of nutritional quality (Figure S7).

3.4 | Environmental Drivers of Trait Variation

In the global analyses with data combined from all three ranges, there were generally no single best-fit models for explaining trait variation. Instead, we identified several top candidate models for each of the traits analysed (Table S3). The candidate models often included range interactions indicating different relationships between environmental variables and knotweed performance in different ranges. However, because of limited overlap of some environmental variables between different ranges, and therefore the potential (partial) confounding of environmental effects with other range effects, it was difficult to interpret these significant range × environment interactions. We therefore proceeded with separate statistical models for each range to better understand the range-specific responses.

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The range-specific models confirmed that the importance of different environmental factors not only strongly varied among traits but also among ranges. Nevertheless, some general patterns emerged. In all three ranges, specific leaf area and leaf alkaloid content increased with increasing canopy closure, while leaf C:N ratio decreased with increasing canopy closure in both the USA and native China. However, the models of environmental drivers typically explained only between ~10% and 20% of the variation in knotweed performance, leaf traits or leaf secondary chemistry (Figure 4, Table S8).

In China, canopy closure was a strong predictor of SLA and alkaloids which increased with canopy closure, and of leaf lignin, tannins, leaf C:N ratio and leaf toughness which all decreased with increasing canopy closure. In this range, PC1 climate was associated with a decrease in precipitation and winter temperature while PC2 climate was associated with decreasing summer temperature and increasing isothermality (Table S4). Combined, the two climate PCs explained a large portion of the variance in standing biomass, leaf chlorophyll, leaf toughness and leaf flavonoids. PC1 soil was associated with decreasing soil pH and plant-available Ca and Mg fractions while PC3 soil was associated with total available phosphorus in the soil (Table S5). Combined, the soil PCs explained a large amount of the variance in standing biomass, and leaf characteristics: chlorophyll, toughness, lignins, tannins and flavonoids (Figure 4, Table S8).

In Europe, only specific leaf area and alkaloids content were positively associated with canopy closure. Notably, the model explained only ~5% of the variance in total biomass. PC1 climate was associated with a decrease in precipitation, PC2 climate was associated with an increase in temperature, PC3 climate was associated with a decrease in temperature and precipitation seasonality and the temperature annual range (Table S4). Combined, the climate PCs in Europe predicted leaf characteristics: chlorophyll, toughness, C:N ratio, alkaloids, but were less predictive of SLA, lignin and flavonoids. PC1 soil was associated with a decrease in soil nutrients (total soil N and C, plant

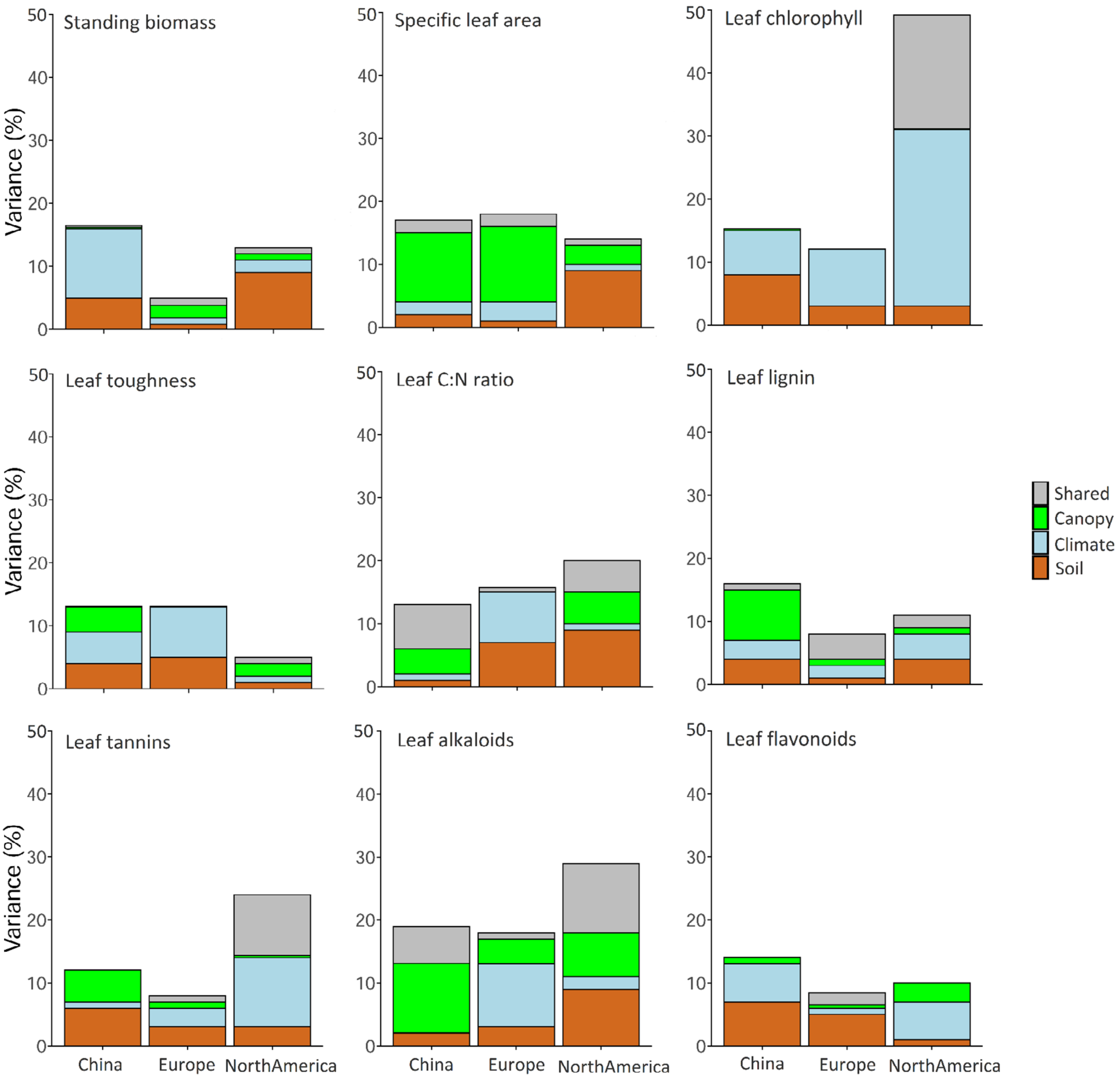
Standing biomass
Specific leaf area
Leaf chlorophyll
Leaf toughness
Leaf C:N ratio
Leaf lignin
Leaf tannins
Leaf alkaloids
Leaf flavonoids

FIGURE 4 | Percentages of variance of performance, leaf traits or leaf secondary chemistry explained by climate and soil variables, or by canopy closure, in native Chinese versus invasive European and North American knotweed populations (within range-specific models). The grey bars represent variances explained by multiple (partially confounded) variables.

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available Mg) and PC2 soil with an increase in soil pH and total Mg (Table S5). Combined soil PCs predicted leaf characteristics: chlorophyll, toughness, C:N ratio and flavonoids (Figure 4, Table S8).

In North America, like in Europe, specific leaf area and alkaloids content increased with increasing canopy closure, whereas leaf C:N ratio showed a negative association with canopy closure. PC1 climate was associated with an increase in temperature seasonality, temperature annual range and a decrease in precipitation while PC2 climate was associated with decreasing summer temperature and the mean temperature of the wettest quarter (Table S4). Combined, the climate PCs in North America strongly predicted leaf chlorophyll, tannins, lignins and flavonoids. PC1 soil was positively associated with soil nutrients (N and C, plant-available Mg and Ca) while PC2 soil was negatively associated with soil pH and total soil Ca. PC3 soil was associated with increasing total soil K (Table S5). The combined soil PCs strongly predicted standing biomass, leaf area, leaf C:N ratio and leaf alkaloids (Figure 4, Table S8).

4 | Discussion

While invasive species provide an opportunity to examine the mechanisms that underlie range expansion and adaptive differentiation (Lee 2002; Leger and Rice 2007; Dlugosch and Parker 2008), researchers have failed to identify traits or combinations of traits that universally confer invasiveness (van Kleunen, Bossdorf, and Dawson 2018; Montesinos 2022; Gioria et al. 2023). This lack of universality is not surprising since the advantage of a given trait or trait combinations is context-dependent (Agrawal 2020). In this study, we sampled populations of Japanese knotweed across a broad environmental gradient in both the native and introduced ranges to more comprehensively evaluate how trait variation is associated with the successful invasion of one of the world's most invasive alien plant species complexes. We found consistent differences in knotweed performance between native and introduced ranges that supported our first hypothesis: introduced plants grew larger with high nutritional value but harboured different combinations of chemical defences compared to native plants. We identified five major ecological strategies, and differences in abiotic and biotic factors that may be driving some of these patterns of trait variation supporting our second and third hypotheses. Combined, our results suggest that enemy release and novel habitat conditions may have driven the emergence of novel ecological strategies in this global plant invader.

4.1 | Trait Divergence Among Ranges

Many plant species that become invasive in their introduced ranges appear to be common but not aggressive in their native ranges (Blossey and Notzold 1995; Colautti, Parker, et al. 2014; Gioria et al. 2023). In a meta-analysis of 53 species, Parker et al. (2013) found that on average, individuals were larger, more fecund, and more abundant in their introduced ranges. Further, Dawson et al. (2012) showed that globally widespread alien species exhibited greater biomass responses to increased resources. Although this may not be a universal pattern across invasive species, previous work on Japanese knotweed (*s.l.*, similar to our collection not exclusively but dominated by *R. japonica*) has indicated that knotweed plants in the introduced ranges are larger and more robust than in their native range (Parker et al. 2013). A comparative field study of native populations in Japan versus introduced populations in France found that the individuals in the introduced range grew taller, had larger leaves, exhibited much lower leaf damage by herbivores and had a more pronounced effect on the plant communities than native individuals (Maurel et al. 2013). Another study compared *R. japonica* individuals from the native area of Japan and introduced areas of France under common garden conditions (Rouifed et al. 2018), and found that individuals from the introduced populations had higher belowground biomass and increased leaf toughness as well as increased competitive effects against *Rubus caesius*. However, the study detected no range differences in aboveground biomass or plant height (Rouifed et al. 2018).

Here, we attempted a more comprehensive comparison of the introduced ranges in Europe and North America to the native range in China. The trait shifts we observed supported an increase in biomass production and high SLA in the introduced ranges. These trait values are consistent with a high photosynthetic capacity of fast growing invasive individuals compared to natives, although a recent study by Griffin-Nolan et al. (2024) found comparable photosynthetic rates between plants from native Japanese populations and those from introduced *R. japonica* populations in France and the USA. Leaf area lost to herbivores and pathogens were much lower in introduced populations compared with native ones, offering support for the enemy release hypothesis (Keane and Crawley 2002). This corroborates several studies which reported overall reduced knotweed herbivory and fewer invertebrates on knotweed stands in the species' introduced range (Beerling and Dawah 1993; McIver and Grevstad 2010; Maurel et al. 2013). The low leaf C:N ratio and reduced investment in quantitative defences (lignin: Europe and USA, and tannins: USA) possibly reflected reduced defences against specialist herbivores. No specialist herbivores have been found on knotweeds in the introduced ranges although biocontrol programs to manage invasive knotweeds with the psyllid *Aphalara itadori*—native to Japan—are currently ongoing in several countries including UK, US, and Netherlands. The latest reports indicated that the insect failed to establish and build large enough populations at the sites where it was released (USDA 2023). Hence, we expect that there was little specialist enemy pressure in populations of introduced knotweeds. The leaf chemical defence traits against specialist herbivores are costly to produce and maintain, and are thought to incur a trade-off with investment into growth. Together, our findings add to the growing evidence of reduction in top-down constraints imposed by herbivores on invasive plant growth (Maurel et al. 2013; Leishman et al. 2014).

We found support for increased plant vigour in both introduced ranges compared to plants in the native range, but the overall patterns differed slightly between the introduced ranges. An increase in production of alkaloids (qualitative defence) in the USA suggested a potential shift in defence to deter generalists (Doorduin and Vrieling 2011). This could reflect knotweed response to herbivory by *Popillia japonica*—the Japanese beetle—which was unintentionally introduced into North America

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around 1916 from Japan and re-established its role as a natural enemy of *R. japonica* where their two ranges overlap (Johnson, Breger, and Drummond 2019). The beetle has become particularly common in the Eastern US, including all regions of our 2000-km US transect (Shanovich et al. 2019). In fact, one study found an increase in cyanogenic glycosides, which inhibited the feeding activity of the Japanese beetle in *R. japonica* populations in Syracuse (New York) (Griffin-Nolan et al. 2024). However, knotweed damage by the Japanese beetle appears to be lower in North America (6.5% leaf area loss) compared to in its native range in Japan (40% leaf area loss; Johnson, Breger, and Drummond 2019).

Unfortunately, we were unable to identify the specific herbivores feeding on knotweed in these populations, so we cannot directly confirm whether a shift from specialist to generalist herbivores has occurred. Individuals in USA populations also had on average lower standing biomass and leaf lignin than plants in Europe, but tougher and more chlorophyll-rich leaves. These differences could reflect the different biotic and abiotic conditions in the two introduced ranges. However, plants from both introduced ranges suffered very little damage from pathogens and herbivores so it is unclear what exactly has driven the differences in defence traits at the time of our study.

A potential caveat of our study is that our field survey was conducted at only one time point, which may not fully capture population differences and their long-term dynamics in terms of performance and functional traits. In 2019, when we conducted the field surveys in the introduced ranges, Europe experienced a drought whereas there were rather wet conditions in the US, and these conditions might explain some of the observed range differences. However, at the time of our sampling the knotweed populations in Europe showed no drought symptoms, and their average performance was in fact higher than in the US, so we assume there was no major problem with the climatic conditions in 2019.

4.2 | Changes in Plant Ecological Strategy Syndromes

Invasion biologists have identified suites of plant traits that are associated with successful invasion (Baker 1965; Blossey and Notzold 1995), but have not often studied how these traits differ between introduced populations and their native sources (Bossdorf et al. 2005; Bock et al. 2015). Our findings are informed by both the leaf economics spectrum and defence syndromes framework. The plant strategies identified by the leaf economics spectrum (Wright et al. 2004) have explained some important differences in ecological strategies across diverse taxa (Agrawal 2020; Joswig et al. 2022), even in the context of future climate scenarios (Cui et al. 2020). However, the concepts have not been much applied within species (Donovan et al. 2011; Anderegg et al. 2018), even though the broad latitudinal and thus environmental ranges occupied by some species may require shifts in plant strategies within species. Globally successful invasive species like Japanese knotweed (*R. japonica, s.l.*) provide an opportunity to explore such shifts on two scales: across broad climatic gradients and between the native and introduced ranges.

Although the leaf economics spectrum defines growth strategies which seem relevant in the context of invasion, Reich (2014) has acknowledged that the framework does not include traits related to dispersal or 'colonisation'. A useful additional framework should therefore be the plant defence syndromes proposed by Agrawal and Fishbein (2006) that consist of nutritional, physical and chemical defence traits. Combining these approaches allows for examining how growth and defence strategies can vary across biotic and abiotic environmental contexts within the range of a species (Agrawal 2020).

We used these frameworks to identify a conservative strategy, and an intermediate strategy in the native range compared to more acquisitive strategies with shifted defences in the introduced ranges. In the native range, the conservative strategy of cluster 1 was demonstrated by high investment in physical and quantitative chemical defence, and low nutritional quality (highest C:N ratio). This strategy is consistent with the slow-growing and 'low nutritional quality' syndromes in previous studies (Aerts and Chapin 1999; Agrawal and Fishbein 2006; Joswig et al. 2022). We also found an intermediate strategy in the native range (Cluster 2), where plants had a slightly higher nutritional quality than in Cluster 1 and contained an intermediate physical defence level with the least values for qualitative defences.

In the native range, *R. japonica* tends to be shorter, and is attacked by a suite of leaf-feeding insects (Yano and Teraoka 1995; Zwölfer 1973) and fungal pathogens such as *Puccinia polygoni-amphibii* var. *tovariae* Arthur, *Aecidium polygoni-cuspidati* Dietel. and *Mycosphaerella polygoni-cuspidati* Hara (Kurose et al. 2013). These natural enemies severely damage the plant and possibly maintain it as an innocuous member of the plant community. This is somewhat reflected by the ecological strategies we found here. However, our sampling of Chinese populations may not fully represent the native range. Ongoing molecular analyses indicated that the Chinese populations are not closely related to the introduced populations in Europe and USA and may not have played a role in the invasion (Zhang et al. 2024). Instead, Japan has been regarded as the main source of introductions (Bailey and Conolly 2000; Del Tredici 2017; Zhang et al. 2024). Unfortunately, we were unable to measure plant phenotypes of Japanese populations in the field, so we could not test whether ecological strategies of Japanese populations were more like the introduced populations in the field. However, our recent work that included offspring from a few additional Japanese populations indicated that Japanese populations are phenotypically different from Chinese populations and more similar to European and US populations when grown in common garden (Cao et al. 2025; Wang et al. 2025). Therefore, we cannot rule out that the phenotypes present in introduced ranges may look like those of the native source populations (island of Kyushu, Japan). Our field survey data alone does not allow us to make inferences about the magnitude of putative trait shifts between introduced populations and their true sources, and the relative importance of evolution versus phenotypic plasticity in what we observed.

Contrary to the strategies in the native range, in the introduced ranges, Cluster 5 was characterised as what might be considered the expected acquisitive and invasive strategy with the highest specific leaf area and leaf chlorophyll content, less defence

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investment against specialists (tannins and lignin) and shift to qualitative defences against generalists (alkaloids). This cluster may be more sensitive to herbivores, and might represent the classic expectation in the introduced ranges of a release from specialist enemy pressure (Blossey and Notzold 1995), as well as a shift in defence to generalist herbivores (Joshi and Vrieling 2005). However, this was the smallest cluster and only consisted of 16 populations in the middle and southern areas of the eastern USA. Clusters 3 and 4 in the introduced ranges were also characterised by high nutritional quality and growth, which may reflect the small enemy pressure that we detected. But each was characterised by investment in different chemical defence metabolites, suggesting the potential to resist different biotic pressure and support for the Shifting Defence Hypothesis (Callaway et al. 2022). Such a shift is consistent with previous studies that demonstrated decreased resistance against specialist herbivores in introduced populations, with increased resistance against generalists (Zhang et al. 2018). However, in the case of clusters 3 and 4 compared to native clusters (1 and 2), the shift was through increased relative investment in flavonoids and tannins (cluster 3) or just tannins (cluster 4) and reduced lignin. Overall, we found a shift from digestibility-reducing compounds in the native “conservative strategy” to different toxins in the invasive, more acquisitive populations.

We found that four of the five clusters occurred in the USA. This diversity in phenotypes could partly reflect additional introduction events to this part of the introduced range (Bailey and Conolly 2000; Del Tredici 2017; Zhang et al. 2024), which could fuel different evolutionary trajectories than in the European range. Although, our study was not designed to examine this hypothesis, we found only a small shift in assignment of strategies when we evaluated only 8x *R. japonica*. Importantly, the populations assigned to cluster 5 were unchanged in this analysis and this strategy was still only present in the USA. Another cross-range study compared French, USA and Japanese populations for a range of leaf traits related to carbon and nitrogen allocation, and found stronger trait shifts between Japan and the USA than between Japan and Europe (Griffin-Nolan et al. 2024). The authors speculated that this could reflect greater genetic changes between populations in Japan and the USA. Our survey of chloroplast markers supports this conjecture since we identified a second haplotype introduced to the USA, and could not resolve the source between Japan, Korea and China (Zhang et al. 2024).

4.3 | Environmental Associations

Prior work has suggested that climatic suitability defined in the native range may not predict invasion success, but so far studies of climatic suitability and invasion success are limited (van Kleunen et al. 2019). Pouteau et al. (2021) recently completed a comprehensive evaluation of 1485 endemic European plant species to characterise their predicted range outside of Europe. They discovered that environmental conditions alone predicted up to two-thirds of successful establishments outside of species' native ranges. The populations we investigated differed in several environmental factors that were associated with knotweed performance. Of note, the climate experienced by the native populations we sampled was systematically different from that in the European and North American ranges, with higher annual, winter and summer temperatures and wetter summer conditions in the native range. The Chinese populations also experienced lower seasonal variation, and lower winter and spring precipitation. In addition, the Chinese sites we sampled were characterised by a reduced soil fertility (lower total soil P, N &C) and mildly acidic soil pH compared to non-native sites. Nonetheless, the introduced European and North American populations included in our study occupied a range of climatic conditions that are also found in southeast Asia (Beerling, Huntley, and Bailey 1995). These results confirm previous work in the native range which reported that Japanese knotweed grows in nutrient-poor habitats, colonising unstable environments such as volcanic soils where it is regarded as a pioneer species (Shimoda and Yamasaki 2016). While we captured variation across a very large latitudinal gradient in each of the ranges, it could be that the native populations we sampled did not capture the full range of environmental conditions occupied by native populations. Since the source of the European and a large part of the subsequent North American invasion has been traced to Nagasaki, Japan (Townsend 1997; Zhang et al. 2024), including the Japanese range will be informative for future work.

Although knotweed traits were significantly associated with several environmental factors, a substantial fraction of the trait variation remained unexplained in our study. This suggested that other, unmeasured factors such as invasion time, disturbance regimes or genomic characteristics may also play significant roles. The variation in population performance that we could explain appeared to be driven by different climatic and soil nutrients factors in the different regions. For example, standing knotweed biomass was explained largely by climate factors in China, but by soil factors in North America, while the combination of factors explained $<5\%$ of the variance in standing biomass in European populations. *Reynoutria japonica* is reported to be vulnerable to summer droughts (i.e., sites with less than 500 mm precipitation per year; Beerling, Bailey, and Conolly 1994). In our study, decreasing summer heat was associated with increased above ground biomass production in both the native and introduced range in the USA. We found that light availability (measured as the percent canopy closure) was among the major factors associated with variation in several knotweed traits, but this was only true in China and Europe, not in the USA. In the introduced ranges, Japanese knotweeds often occur in open and sunny sites and their performance is reduced in closed canopy habitats (Beerling, Bailey, and Conolly 1994; Dommanget et al. 2013; Martin et al. 2020). In the populations we studied, reduced light availability was associated with a reduction in many leaf traits. This was particularly true in China where the sampled populations were on average shadier than in Europe or the US (average canopy closure higher than 50%). SLA and leaf alkaloids were exceptions, which increased with increasing canopy closure in all three ranges. A higher SLA increases the light capture efficiency and is common among many species when grown under reduced light conditions (Liu et al. 2016).

Environmental factors associated with increasing leaf nutritional value and fibre content (measured as C:N ratio, leaf toughness and leaf lignin content) also varied across the ranges: that

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is, with decreasing seasonality (Europe), the annual and winter precipitation as well as winter and summer temperature (China) and summer heat (USA). These traits were also influenced by soil pH (USA) and soil fertility (China—total soil P, Europe and the USA—total N, C and plant available Mg). Climate and soil play important roles in regulating plant metabolites, as their synthesis requires different soil macronutrients including N, P and K, and they are also dependent on an optimum temperature and water availability (Li et al. 2018; Joswig et al. 2022). Similarly, plant metabolites associated with leaf qualitative (alkaloids and flavonoids) and quantitative defences (tannins) also showed variation in response to climate and soil factors within ranges particularly to extreme factors such as drought (Europe) and summer heat (USA). Previous studies have shown that the synthesis of plant metabolic compounds can be altered by different abiotic factors (Yang et al. 2018). Combined, these results highlight differences in abiotic factors across the different ranges which presumably interact with the clear biotic differences and impinge upon trait combinations that we found in the field.

4.4 | Conclusions

Our work is consistent with previous studies that demonstrated invasive knotweed is able to take greater advantage of increased resources than local native species in Europe (Parepa, Fischer, and Bossdorf, 2013, Parepa et al. 2019). Here, we show that this increase in acquisitive strategy is also true when compared to knotweed populations in the native range. Reich (2014) argued that the leaf economics spectrum is often considered as only alternative extremes of the spectrum: slow-growing, resource-conservative species versus fast-growing species that rapidly take up resources but are less resource-efficient. In fact, however, a range of strategies exist in every community. Our work extends the trait-based strategies concept to within species growing under different biotic and abiotic conditions and identifies five discrete combinations that are in line with predictions of the rapid evolution or plastic responses of invasive species. This approach allows for discovery of different strategies that may reflect the local differences in enemy pressure and abiotic conditions.

The changes we have documented in introduced Japanese knotweed (*s.l.*) populations are remarkable, considering that the species are known to have spread largely by clonal fragments with very little genetic diversity (Hollingsworth and Bailey 2000; Richards, Schrey, and Pigliucci 2012; Zhang et al. 2016). Given this lack of genetic diversity, the dramatic differences in phenotype and changes in association of traits with environmental conditions indicate that introduced populations could have resulted from introduction of a "general-purpose genotype" which can accommodate a range of biotic and abiotic conditions through phenotypic or developmental plasticity (Baker 1965; Parker, Rodriguez, and Loik 2003; Richards et al. 2006; Wang et al. 2025). Whatever the genetic make-up of these populations, we were able to identify different strategies employed by this globally invasive plant depending on context. Further studies will decipher how much of these differences are explained by underlying genetic or heritable nongenetic changes, and how much reflect plastic responses to novel environments.

Author Contributions

Madalin Parepa, Bo Li, Oliver Bossdorf and Christina L. Richards conceived the project. Bo Li, Oliver Bossdorf and Christina L. Richards raised funding and supervised the project. Weihan Zhao, Peipei Cao, Madalin Parepa, Zhi-Yong Liao, Shengyu Wang, Jeannie M. Mounger, Conner Richardson, Fatima Elkott, Xin Zhuang, Jingwen Bi, Yujie Zhao, Elodie Kugler, Julia Rafalski, Eva Schloter, Jieren Jin, Zuzana Chumová, Pavel Trávníček and Christina L. Richards performed the field work and lab work. Ramona E. Irimia and Weihan Zhao analysed the data. Ramona E. Irimia, Weihan Zhao, Oliver Bossdorf and Christina L. Richards wrote the manuscript with assistance from all authors.

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Ethics Statement

This study was conducted in accordance with the Academic Integrity Code of NingboTech University.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All relevant data are available on zenodo: https://doi.org/10.5281/zenodo.14603581. All code generated in this study are available on GitHub: https://github.com/weihan-zhao/knotweed_fieldwork.

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