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Research article

Cross-continental variation of herbivore resistance in a global plant invader

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While successful plant invasions often occur in novel environments, invasive species usually occupy broad niches within their native and introduced ranges. A better understanding of the process of invasion therefore requires a wide sampling of ranges, and a good knowledge of introduction history. We tested for differentiation in herbivore resistance among 128 introduced (European, North American) and native (Chinese, Japanese) populations of the invasive Japanese knotweed *Reynoutria japonica* in two common gardens in the native range: one in Shanghai and the other in Yunnan. In both common gardens, we found that herbivore resistance of plants from introduced populations differed from that from native populations in China but not from native populations in Japan, the putative source of introduction. Compared to native Chinese populations, plants from native Japanese populations and introduced European and North American populations had thicker leaves in both common gardens, and a lower C:N ratio but higher flavonoids content in the Shanghai garden. Variation in herbivore resistance was more strongly associated with climate of collecting sites for populations from the native range than for those from introduced ranges. Our results support the hypothesis that introduction of particularly resistant plants from Japan may have played a key role in driving biogeographic variation in herbivore resistance. Our study

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highlights the importance of understanding introduction history to interpret the biogeographic divergence of global plant invaders.

Keywords: common garden, invasion history, plant defense, plant invasion, rapid evolution, *Reynoutria japonica*

Introduction

The number of invasive plant species has increased dramatically over the past two centuries (Seebens et al. 2017), causing exceedingly negative impacts on the environment (Castro-Díez et al. 2019) and economy (Bradshaw et al. 2016, Diagne et al. 2021, Fantle-Lepczyk et al. 2022) in the invaded ranges. In the context of globalization and climate change, one-sixth of the world's land surface is expected to be highly vulnerable to invasion (Early et al. 2016), and the number of new invasive species is likely to increase over time (Seebens et al. 2017, 2021). Thus, a comprehensive understanding of the mechanisms that underlie the successful invasions of alien species is an urgent issue in ecology and evolution (Pyšek et al. 2020).

Many eco-evolutionary hypotheses attempting to explain biogeographic differences between native and introduced populations assume novel abiotic or biotic environmental conditions to be the key drivers (Cripps et al. 2006, Monti et al. 2016). For example, the enemy release hypothesis (ERH) states that plant populations in the introduced ranges experience decreased regulation by herbivores and other natural enemies (Keane and Crawley 2002). Since resistance to enemies can be costly (Koricheva 2002), altered enemy pressure may lead to rapid shifts in growth and defense allocation (Bossdorf et al. 2005, Buswell et al. 2011, Li et al. 2022). The evolution of increased competitive ability (EICA) hypothesis therefore predicts that reduced herbivore pressure will select for individuals that allocate fewer resources to herbivore defenses in favor of increased allocation to growth and reproduction, thus becoming more competitive than their native conspecifics (Blossey and Nötzold 1995, Lin et al. 2015). However, despite rich evidence for enemy release (Rotter et al. 2019, Xiao et al. 2020), especially from specialist herbivores, the evidence in support of EICA is so far mixed (Bossdorf et al. 2005, Rotter and Holeski 2018). Lower herbivore resistance has been observed in several invasive plant species (Siemann and Rogers 2001, Huang and Ding 2016), but similar or even higher resistance was also found in others (Alba et al. 2011, Bhattarai et al. 2017, Lin et al. 2019). Some of these mixed results might be attributed to the different costs of resistance to specialists compared to generalist herbivores (Zhang et al. 2018) and the changes in herbivore community composition in the introduced ranges of invasive plants (Müller-Schärer et al. 2004, Endriss et al. 2022; shifting defense hypothesis, SDH). Hence, individual studies on specific herbivores may find limited support for the EICA hypothesis, while more general answers may require meta-analyses across multiple independent studies (Zhang et al. 2018, Callaway et al. 2022).

Besides biotic conditions, novel selection pressures and thus biogeographic divergence in performance may also result from altered abiotic conditions in introduced populations (Buswell et al. 2011, Lee and Kotanen 2015). Climatic conditions often differ between native and introduced ranges of invasive species (Early and Sax 2014, Boci et al. 2016). Previous studies have already demonstrated climate-driven trait differentiation between native and introduced plant populations (Alexander 2013, Woods and Sultan 2022). Furthermore, clinal patterns along climatic gradients are frequently regarded as evidence of adaptation to climatic factors in both native and introduced ranges (Hulme and Barrett 2013, Bock et al. 2015). In the introduced range, such adaptation may be facilitated by the introduction of pre-adapted genotypes (Neuffer and Hurka 1999, Keller and Taylor 2008) or by post-introduction evolution (Hulme and Barrett 2013, Bock et al. 2015). However, to distinguish between the two mechanisms, a good knowledge of introduction history is required.

The key method to test for phenotypic divergence between native and introduced populations is common garden experiments. However, these experiments face several challenges (van Kleunen et al. 2018, Woods and Sultan 2022). First, invasive species usually occupy broad climatic niches both in their native and introduced ranges (Brandenburger et al. 2020, Liu et al. 2020). Comparisons of only a few populations in common gardens may lead to wrong conclusions simply because the studied populations do not represent their respective ranges well enough (Lucas et al. 2024). Second, to understand if traits have diverged post-introduction, introduced plants must be compared to the sources of the introduction in the native range (van Kleunen et al. 2010, Levis and Pfennig 2016). Third, because of widespread genotype-by-environment interactions (Richards et al. 2006), the results of common garden studies may, to some extent, be garden-specific. For instance, differences in abiotic and biotic conditions (e.g. climate, interacting species) might influence absolute values of growth and defense traits and their relative differences between plant origins (Qin et al. 2013, Yang et al. 2021). To make things even more complicated, selection pressures imposed by changes in herbivores can interact with the effects of climatic differences. Climate can directly affect plant defenses through physiological constraints and altered resource availability (Coley 1985, Wright et al. 2004), but also influence the diversity and composition of herbivore communities (Maron et al. 2014, Zhang et al. 2016a, Loughnan and Williams 2019). Therefore, to understand the invasion success of alien plants and predict habitat vulnerability to future invasion, we need to understand the impacts of enemies and climatic

conditions, and their interactions, on the herbivore resistance of invasive plant populations. So far, however, few previous studies have addressed the relationships between climate and herbivore resistance when comparing native with introduced populations (Xiao et al. 2020).

Here, we worked with the invasive Japanese knotweed *Reynoutria japonica* and built on a previous cross-continental field survey of the species that provided plant materials, along with important metadata, which allowed us to establish two large common gardens in different climatic zones of the native range. Previous studies have shown lower levels of genetic diversity in introduced *R. japonica* populations than in native populations, which suggests limited potential for evolutionary changes (Hollingsworth and Bailey 2000, Jugieau et al. 2024, Zhang et al. 2024). However, introduced populations occupy a broad range of environmental conditions, and harbor significant phenotypic variation even when grown in common garden conditions (Richards et al. 2008, Zhang et al. 2016b). These heritable differences might have resulted from underlying epigenetic processes, which have been hypothesized to play an important role in invasion (Bossdorf et al. 2008, Mounger et al. 2021). The worldwide sampling efforts and relatively clear invasion history of introduced knotweed can therefore provide an excellent model to explore the roles of different mechanisms that drive biogeographic variation in herbivore resistance and resistance traits (leaf traits and leaf chemistry). We here tested the following hypotheses: 1) introduced populations have lower herbivore resistance than native populations, 2) introduced populations behave more similarly to native Japanese populations (the putative source of the introduced populations) than to native Chinese populations, and 3) traits of native populations are more strongly associated with climates of collecting sites than those of introduced populations.

Material and methods

Study system

Japanese knotweed, *Reynoutria japonica* (Polygonaceae), is native to eastern Asia and was introduced to Europe in the early 1840s and to North America in the 1870s as an ornamental (Bailey and Conolly 2000). Along with its sister species *R. sachalinensis*, it has become widely naturalized in both introduced ranges (Barney 2006, Del Tredici 2017). *Reynoutria japonica*, *R. sachalinensis* and their hybrid *R. bohemica* spread rapidly along river banks and roadsides, often forming dense pure stands encompassing hundreds of square meters or larger (Bímová et al. 2004, Rouifed et al. 2014). Knotweed invasion seriously threatens the biodiversity and integrity of native ecosystems (Stoll et al. 2012, Mincheva et al. 2014), which causes substantial economic damage (Reinhardt et al. 2003). As a major environmental threat in Europe and North America, Japanese knotweed is listed among the 100 world's worst invasive alien species by IUCN (Lowe et al. 2000).

In the native ranges, *R. japonica* is attacked by more than 180 natural enemies (Shaw et al. 2009). Some of the most damaging herbivores include the leaf beetles *Gallerucida bifasciata* (specialist) and *Popillia japonica* (generalist), leaf sucker *Aphalara itadori* (specialist), leaf-rolling weevil *Euops chinensis* (specialist), stem miner *Lixus elongatus* (specialist) and the sawfly *Allantus luctifer* (specialist) (Defra 2009, Li et al. 2012, Johnson et al. 2019, Grevstad et al. 2020). In its introduced range, a survey in western North America found no specialist herbivores on knotweed (McIver and Grevstad 2010). In North America, the Japanese beetle *P. japonica* was unintentionally introduced and has re-established its associations with *Reynoutria* spp. in their overlapping introduced ranges (Johnson et al. 2019). Nevertheless, leaf area loss to herbivores was much lower in North America and Europe than those reported in Japan and China, suggesting partial enemy release (Maurel et al. 2013, Johnson et al. 2019, Irimia et al. 2025). Maurel et al. (2013) indicated that the success of *R. japonica* in the introduced ranges could be seen as a plastic response to an environment with fewer enemies.

Sample collection

The plant materials we used came from a cross-latitudinal survey of 150 Japanese knotweed populations in the native range of China and the introduced ranges of North America and Europe (Irimia et al. 2025). We surveyed 50 populations in each range along a 2000 km transect (approximately every 40 km). The surveys in Europe and North America were carried out in 2019, and the one in China was done in 2020. Our survey ranged from Guangdong province in the south to Shandong province in the northeast in China, northern Italy to central Sweden in Europe, and Georgia to Maine in the United States (Fig. 1, Supporting information). For full details on the field survey, please see Irimia et al. (2025). Briefly, at each sampling site, we confirmed the knotweed taxon based on morphological characters (Bailey et al. 2009), laid a 30 m transect for sampling, selected five knotweed stems at regular intervals along the transect and collected rhizomes from these individual stems.

In addition to the main field survey, we collected six native *R. japonica* populations from around Nagasaki in Japan, which was believed to be the source of European and North American introductions (Bailey and Conolly 2000, Del Tredici 2017). Our recent phylogenetic analysis based on chloroplast DNA (Zhang et al. 2024) has supported this hypothesis. Between 28 April and 4 May 2021, we collected rhizomes from 5–8 individuals separated by at least 6 m in each Japanese population. In 2021, the rhizomes from Japan, Europe and North America were imported and grown under quarantine conditions in a greenhouse for one growing season at Xishuangbanna Tropical Botanical Garden, as required by administrative regulations. We planted the Chinese rhizomes under the same greenhouse conditions during the same period. Because of legal restrictions, only one rhizome per North American population could be imported prior to setting up the experiment.

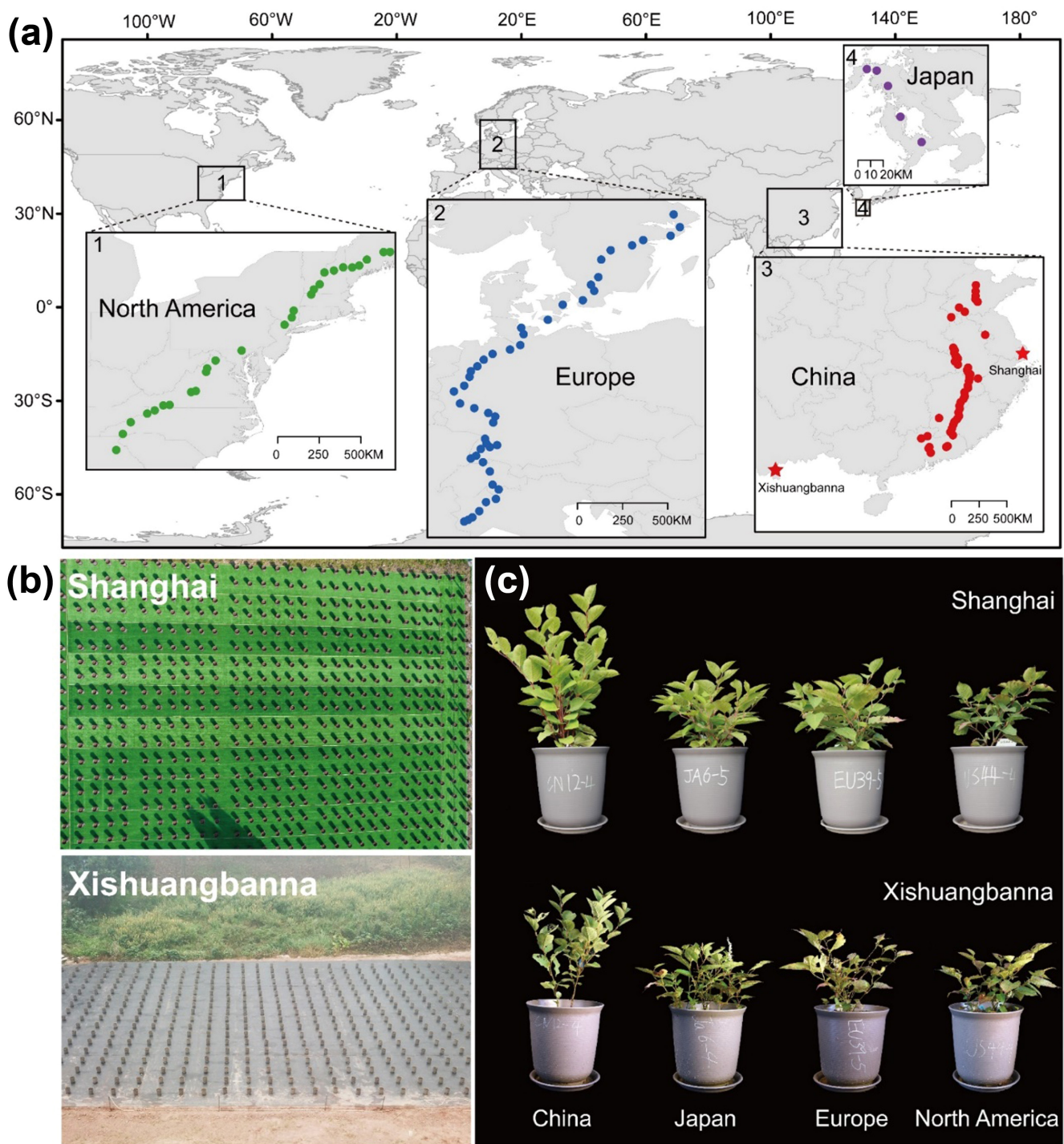


Figure 1. Geographic origins of the studied Japanese knotweed *Reynoutria japonica* populations, the two common gardens and typical performances of knotweed plants from different ranges in the two gardens. (a) The geographic locations where rhizomes of *R. japonica* had been collected in the introduced ranges of North America (1; $n = 27$ populations) and Europe (2; $n = 46$) and in the native ranges of China (3; $n = 50$) and Japan (4; $n = 5$). The stars in panel 3 show the locations of the two common gardens. (b) Aerial photos of the common gardens in Shanghai and Xishuangbanna. (c) Typical growth differences between the two gardens and among plants from different ranges in mid-July 2022.

Common garden experiments

To test for phenotypic variation among knotweed plants from different ranges and populations, we set up two outdoor common gardens, one at Fudan University in Shanghai (31°20'N, 121°30'E) and the other at Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (21°54'N, 101°16'E) in Yunnan province (Fig. 1). The two common garden locations differed in their climatic conditions, with warmer and moister conditions in Xishuangbanna (average March–October temperature 24.1°C; average monthly precipitation 171 mm) compared to Shanghai (average temperature 20.3°C; monthly precipitation 116 mm) (<http://www.nmic.cn/>; Yu et al. 2021). The Fudan common garden was near the center of the native range distribution of *R. japonica*, and the Xishuangbanna common garden was near its southern limits. Both gardens were set up in open areas on flat ground covered with weed barrier fabrics (Fig. 1).

In February 2022, after the parental plants had been grown in the greenhouse for one growing season, two rhizome fragments were cut from each individual. The two rhizome fragments from each individual were then randomly assigned to the Shanghai and Xishuangbanna common gardens, and were kept at 4°C for another four weeks to facilitate sprouting success. One day before transplanting the rhizomes, we clipped all rhizome fragments to a similar size of 3–10 g (at least one intact node), removed the fine roots and determined the fresh weight of each cutting as a measure of initial size. On 11 March 2022, all rhizomes were treated with fungicide and planted separately into 20-litre pots filled with the same potting soil (Pindstrup substrate 5–20 mm, Pindstrup Mosebrug) in both gardens. Based on rhizome availability, we eventually grew a total of 518 *R. japonica* individuals in the Shanghai garden (27 individuals from 27 North American populations; 218 individuals from 46 European populations; 239 individuals from 50 Chinese populations; 34 individuals from 5 Japanese populations); and 463 individuals in the Xishuangbanna garden (16 individuals from 16 North American populations; 190 individuals from 46 European populations; 232 individuals from 50 Chinese populations; 25 individuals from 5 Japanese populations; Supporting information). In each garden, we arranged the plants in five blocks, with one individual from each population in each block – North American populations were the exception, and were instead evenly distributed across blocks, as we only had one individual per North American population. We randomly assigned individuals to blocks and their positions within blocks. The distance between pots was at least 90 cm to avoid aboveground interference. To prevent nutrient depletion, we added 10 g Osmocote fertilizer (Osmocote plus 801, N:P:K 16:8:12, Everris International) to each pot at the beginning of the experiment. Throughout the experiment, we watered the plants whenever the soil was dry. To avoid loss of water and nutrients, all pots were individually placed on plastic trays. The pots, soils and fertilizers used were identical in both common gardens.

Herbivore damage and resistance traits

To quantify variation in plant herbivore resistance, we estimated the degree of herbivore damage experienced by each individual in each garden, determined the levels of leaf secondary metabolites (lignin, flavonoids, alkaloids) and measured additional leaf traits that are often associated with palatability to herbivores (leaf toughness, leaf thickness, leaf C:N ratio) (Feng et al. 2011, Lin et al. 2015). All plants were exposed to naturally occurring herbivores and no insecticides were applied during the experimental period. We inspected the plants daily at different times, and more often when we noticed an increase of herbivores during the growing season. We found that two beetle species (*Apogonia* sp. and *Adoretus* sp., Coleoptera) and one caterpillar species (*Lymantria* sp., Lepidoptera) caused the majority of the damage in the Xishuangbanna garden. Herbivore diversity and abundance were much lower in the Shanghai garden, but we found several beetle species (mainly Coccinellidae, Chrysomelidae and Attelabidae, Coleoptera) and caterpillar species (mainly Noctuidae and Geometridae, Lepidoptera). The beetles usually caused skeleton-like holes throughout the leaves (Supporting information), while the caterpillars usually consumed a big part of each leaf (Supporting information). In addition, we could further identify the caterpillar damage by the presence of the caterpillars, feces or cocoons on the plants (Supporting information).

In the middle of the growing season, we estimated herbivore damage – separately for beetle and caterpillar damage – as the percentage of leaf area eaten on each plant (Supporting information). Two days later, we sampled five fresh, fully developed leaves (the 1st, 2nd, 4th, 5th and 6th leaves from the top) from the tallest shoot of each plant and measured the thickness of each leaf with a digital micrometer in both gardens, and its toughness with a penetrometer (FA10, SAUTER) in the Shanghai garden and with a mechanical testing machine (ZQ990A, Dongguan Zhiqu Precision Instrument) in the Xishuangbanna garden. We then estimated the leaf thickness and toughness for each plant as the averages of the five measurements. We measured all plant traits in the Xishuangbanna and Shanghai common gardens from 14 to 21 July 2022, and 24 to 31 July 2022, respectively. All plants grew for four months in both common gardens.

Finally, we dried all leaves at 60°C for 72 h to analyze for leaf chemistry. After grinding samples to the required particle size with a ball mill, we measured total C and N with an organic elemental analyzer (FlashSmartElemental Analyzer, Thermo-Fisher Scientific) via thermal combustion and TCD/IR detection of CO₂/N₂. Then, we measured leaf lignin, alkaloids and total flavonoids using the MZS-1-G, SWJ-1-Y and LHT-1-G test kits (Suzhou Comin Biotechnology), respectively. After acetylation, the phenolic hydroxyl group in lignin had a characteristic absorption peak at 280 nm. Alkaloids can react with bromocresol green indicator to generate green compounds with a maximum

absorption peak at 416 nm. In alkaline nitrite solution, flavonoids can form red complexes with aluminum ions with a characteristic absorption peak at 510 nm. Then, we used the photometric method to measure the absorbance of the sample solution at each wavelength using an enzyme-labeled instrument (Synergy2, Biotek Instrument), and calculated the content of each chemical compound group (more details in Irimia et al. 2025).

Statistical analyses

To test for between-range differences in plant traits and herbivore damage within each common garden, we fitted linear mixed models in R ver. 4.2.1 (www.r-project.org), with range (China, Japan, Europe, North America) as a fixed effect, and population and block as random effects. To account for variation in initial rhizome size, our models included initial rhizome weight as a covariate. We assessed the significance of fixed effects through type III Wald X^2 tests using the R-package 'car' (Fox and Weisberg 2018). For traits that displayed a significant range effect ($p < 0.05$), we then conducted Tukey post hoc tests with the *emmeans* and *pairs* functions (Lenth 2022). Where necessary, we log-transformed herbivore damage data to normalize the distribution of residuals.

To test for associations between leaf traits and herbivore damage, we calculated population-level Spearman's correlation coefficients for each pairwise combination of resistance trait (leaf traits and leaf chemistry) and herbivore damage for each garden using the 'Hmisc' package (Hauke and Kossowski 2011).

Finally, we tested whether the climatic conditions of population collecting sites were associated with the resistance traits of native and introduced populations. For this, we obtained eight bioclimatic variables (1970–2000 averages at a spatial resolution of 30 s) from the WorldClim database (Fick and Hijmans 2017) that seemed particularly meaningful for characterizing growing and overwintering conditions for knotweed plants: annual temperature (bio1), temperature seasonality (bio4), maximum temperature of the warmest month (bio5), minimum temperature of the coldest month (bio6), mean annual precipitation (bio12), precipitation of the wettest month (bio13), precipitation of the driest month (bio14) and precipitation seasonality (bio15). We simplified these climate data through a principal component analysis (PCA) using the *prcomp* function. The first and second principal components ('climate PC1' and 'climate PC2' hereafter) explained 54% and 21% of the variance in the eight climatic variables across all populations, respectively, with climate PC1 mainly related to mean temperature as well as heat and precipitation extremes, and climate PC2 related to temperature minima and seasonality (Supporting information). We then performed population-level linear regression analyses with either climate PC1 or climate PC2 as explanatory variables and the common-garden averages of the resistance traits of native or introduced populations as dependent variables (Moreira et al. 2018).

Results

We found that, on average, the traits of plants from introduced populations generally differed from those of native populations. However, these overall patterns were largely driven by the native populations from China, which were distinct from introduced European and North American populations across many traits. Chinese populations differed from Japanese populations for fewer traits, but European and North American populations were almost always indistinguishable from the native Japanese populations across measured traits.

Range differences in herbivore damage

The average levels of herbivore damage differed considerably between the two common gardens: in Xishuangbanna, the percentages of leaf area eaten by beetles and caterpillars were respectively three and 19 times higher than those in Shanghai (Fig. 2). In Shanghai, plants from Chinese populations experienced significantly higher levels of caterpillar herbivory than those from European or North American populations (Fig. 2b), and the same was true for beetle damage in Xishuangbanna, where the Chinese populations were also most strongly attacked (Fig. 2c). Chinese populations experienced less caterpillar damage than European populations in Xishuangbanna, but we never found any significant differences between the two introduced ranges, or between Japanese populations and the introduced populations, in the two common gardens.

Range differences in resistance traits

Plants from native Chinese populations were also distinct from other populations in their resistance traits. In both common gardens, Chinese populations had significantly thinner leaves than introduced populations (Fig. 3a, d). In the Shanghai garden, Chinese populations also had higher leaf C:N ratios and lower leaf flavonoids than populations from both introduced ranges (Fig. 3c, 4c). Moreover, Chinese populations had tougher leaves than European populations in the Shanghai garden (Fig. 3b) and higher leaf C:N ratios than North American populations in the Xishuangbanna garden (Fig. 3f). We did not find differences in leaf lignin and leaf alkaloids between native and introduced populations (Fig. 4a, b, d, e), and there were no significant differences in leaf traits between native populations from Japan and the introduced populations (Fig. 3, 4).

Correlations between resistance traits and herbivore damage

In the Shanghai garden, leaf damage by caterpillars was negatively correlated with leaf thickness and leaf flavonoids but positively with leaf C:N ratios (Table 1). In contrast, in the Xishuangbanna garden, beetle herbivory was negatively correlated with leaf thickness and flavonoids, but caterpillar herbivory was positively correlated with leaf thickness (Table 1).

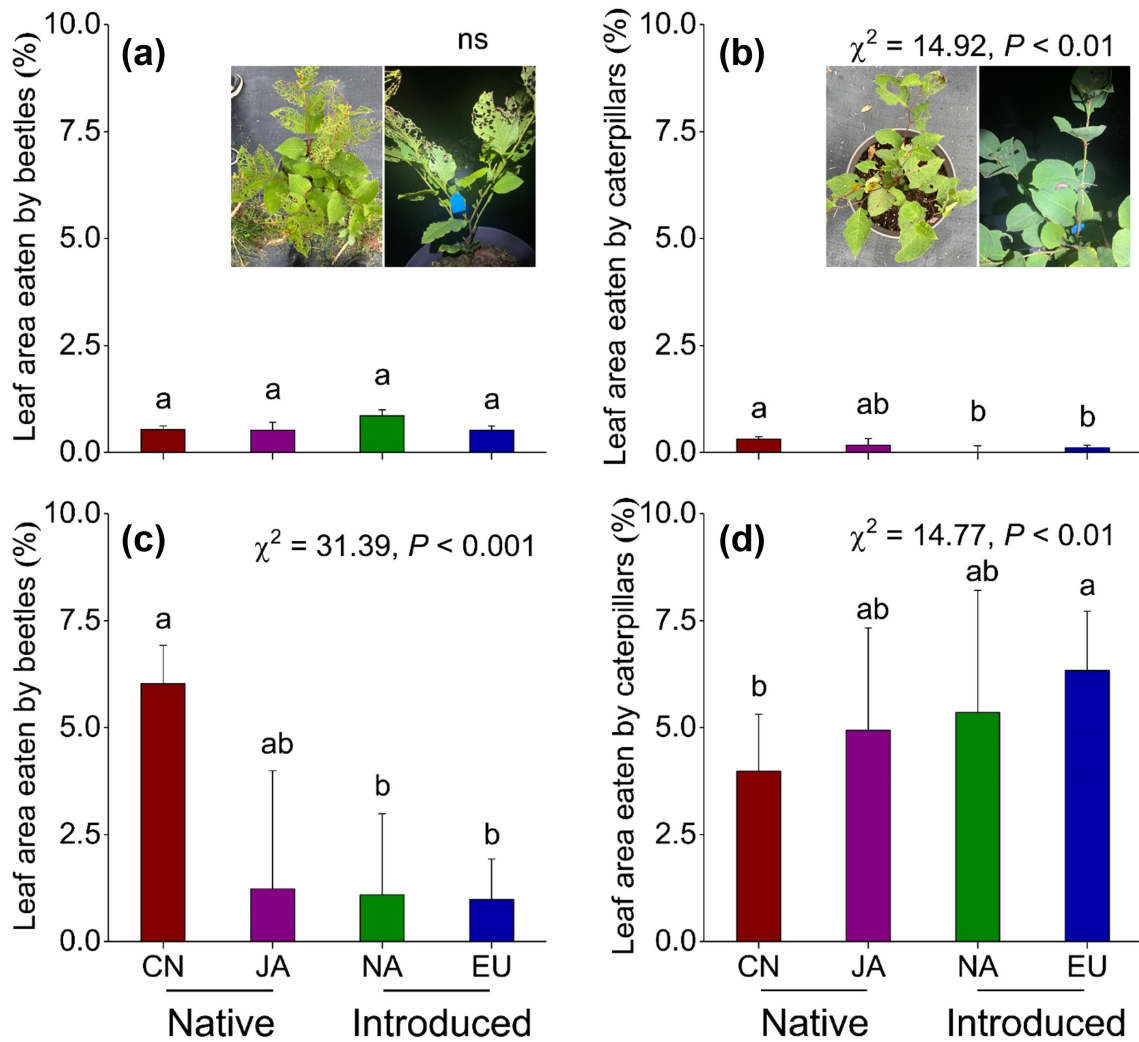


Figure 2. Average values of herbivore damage observed in *Reynoutria japonica* plants from China (CN), Japan (JA), North America (NA) and Europe (EU) when grown in common gardens in Shanghai (a, b) and Xishuangbanna (c, d). (a, b) show typical herbivores and their feeding characteristics in the Xishuangbanna common garden. The values are adjusted means (bars) and SEs (error bars) from ANOVA, with different letters above error bars indicating significant group differences based on Tukey's HSD post hoc tests. χ^2 and the significance are shown, and ns indicates non-significant differences ($p > 0.05$).

Correlations between climates of collecting sites and resistance traits

We found that variation in resistance traits was generally significantly associated with climates of collecting sites in native populations but much less frequently in introduced populations (10 versus 3 correlations in native versus introduced populations; Table 2). In both common gardens, leaf thickness was negatively correlated with climate PC1 but positively correlated with climate PC2 for native but not introduced populations. The leaf C:N ratios of native populations were negatively related to climate PC1. Only in the Xishuangbanna garden did leaf C:N ratios of introduced populations positively correlate to climate PC2. For native populations, leaf flavonoids were positively related to climate PC1 but negatively

associated with PC2 in both gardens. For introduced populations, we found a positive climate PC1-flavonoids correlation in Xishuangbanna and a negative correlation of flavonoids with climate PC2 in Shanghai (Table 2).

In other words, native populations from warmer, humid sites with low seasonal variability in temperature tended to have thicker leaves with higher C:N ratios and lower flavonoids contents when grown in either common garden (Table 2). In contrast, for introduced populations, climate associations were rarer and more variable: in Shanghai, higher flavonoids contents of introduced populations were associated with collecting sites with colder winter temperature and high seasonality, whereas in Xishuangbanna, lower flavonoids contents were associated with warm and humid collecting sites (Table 2).

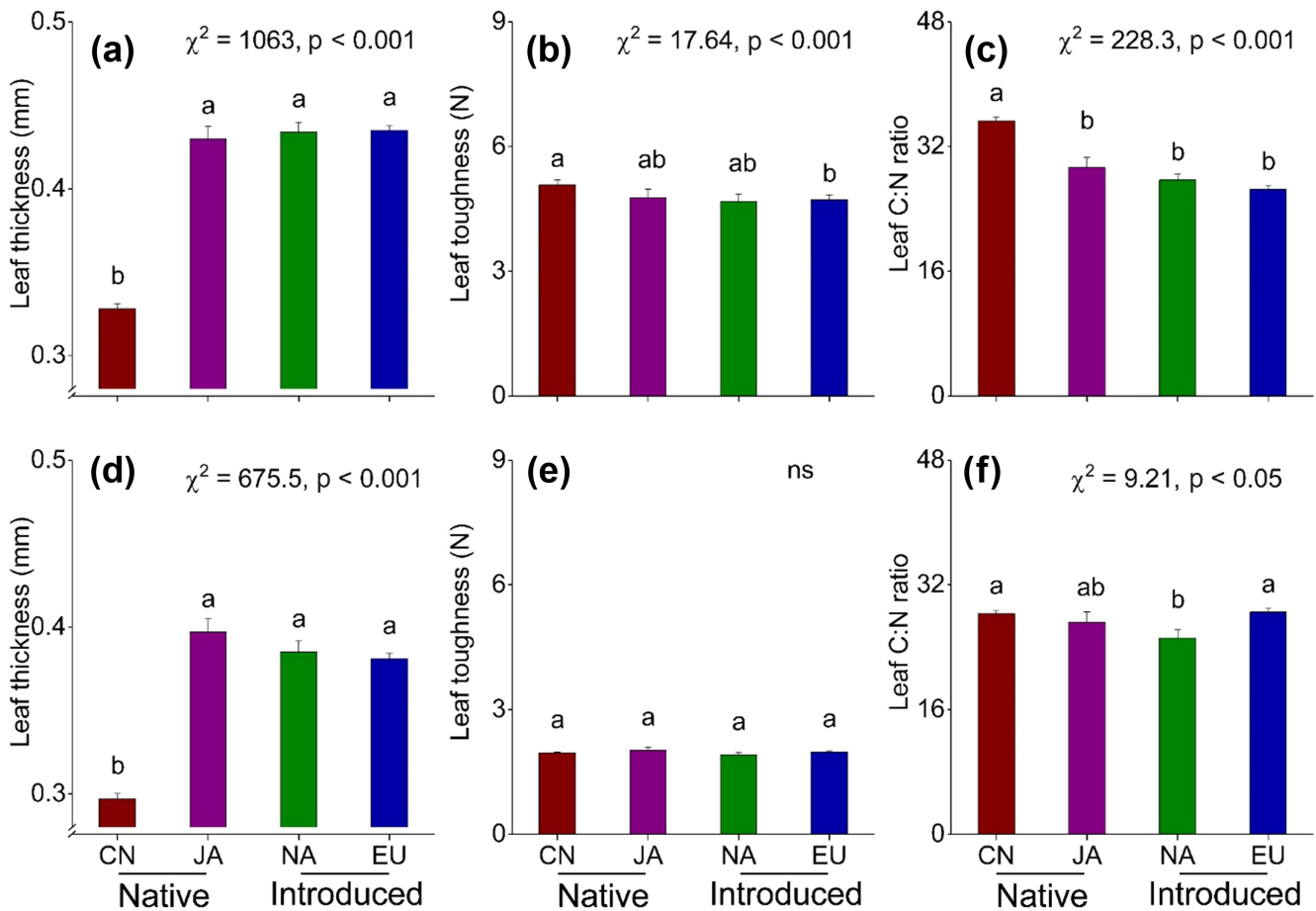


Figure 3. Average values of leaf traits observed in *Reynoutria japonica* plants from China (CN), Japan (JA), North America (NA) and Europe (EU) when grown in common gardens in Shanghai (a–c) and Xishuangbanna (d–f). The values are adjusted means (bars) and SEs (error bars) from ANOVAs, with different letters above error bars indicating significant group differences based on Tukey's HSD post hoc tests. χ^2 and the significance are shown, and ns indicates non-significant differences ($p > 0.05$).

Discussion

Successful plant invasions are often assumed to involve evolutionary changes in plant traits. However, the power of previous common garden comparisons to identify evolutionary change has remained limited. Here, we tested for differentiation in herbivore resistance among 128 native and introduced populations of invasive knotweed, *Reynoutria japonica*, in two common gardens in the native range. We found no support for our first hypothesis that introduced populations have lower herbivore resistance, although plants from introduced populations in Europe and North America differed in several resistance traits compared to native populations. We found stronger support for our second hypothesis that the resistance traits of introduced populations were more similar to those of their native source Japanese populations. Our study supports that a Japanese source of knotweed invasions rather than post-introduction evolution may explain overall differences among ranges in knotweed resistance traits. Finally, we also supported the third hypothesis that traits from native populations were more strongly associated with their climates of collecting sites than those from introduced populations.

Range differences in herbivore resistance

In this study, we found that *R. japonica* plants from introduced European and North American populations were significantly different in many leaf traits from native Chinese populations, but they were not significantly different in leaf traits from the putative source Japanese populations (Wang et al. 2025). In the context of invasions more broadly, our results show that inconsistent conclusions might be made depending on which native populations are compared to introduced populations. While numerous biogeographic comparisons studies have been conducted without knowing the actual source of introductions (Colautti and Lau 2015), our results demonstrated the importance of accounting for invasion history when deciphering the mechanisms underlying the differences in evolutionary related studies (Colautti and Lau 2015, Brandenburger et al. 2020).

Specifically, we found no significant differences in herbivore damage or in many herbivore resistance traits such as leaf C:N ratios, leaf toughness, leaf flavonoids, lignin or alkaloids between introduced European and North American and native Japanese populations in both common gardens. Our results

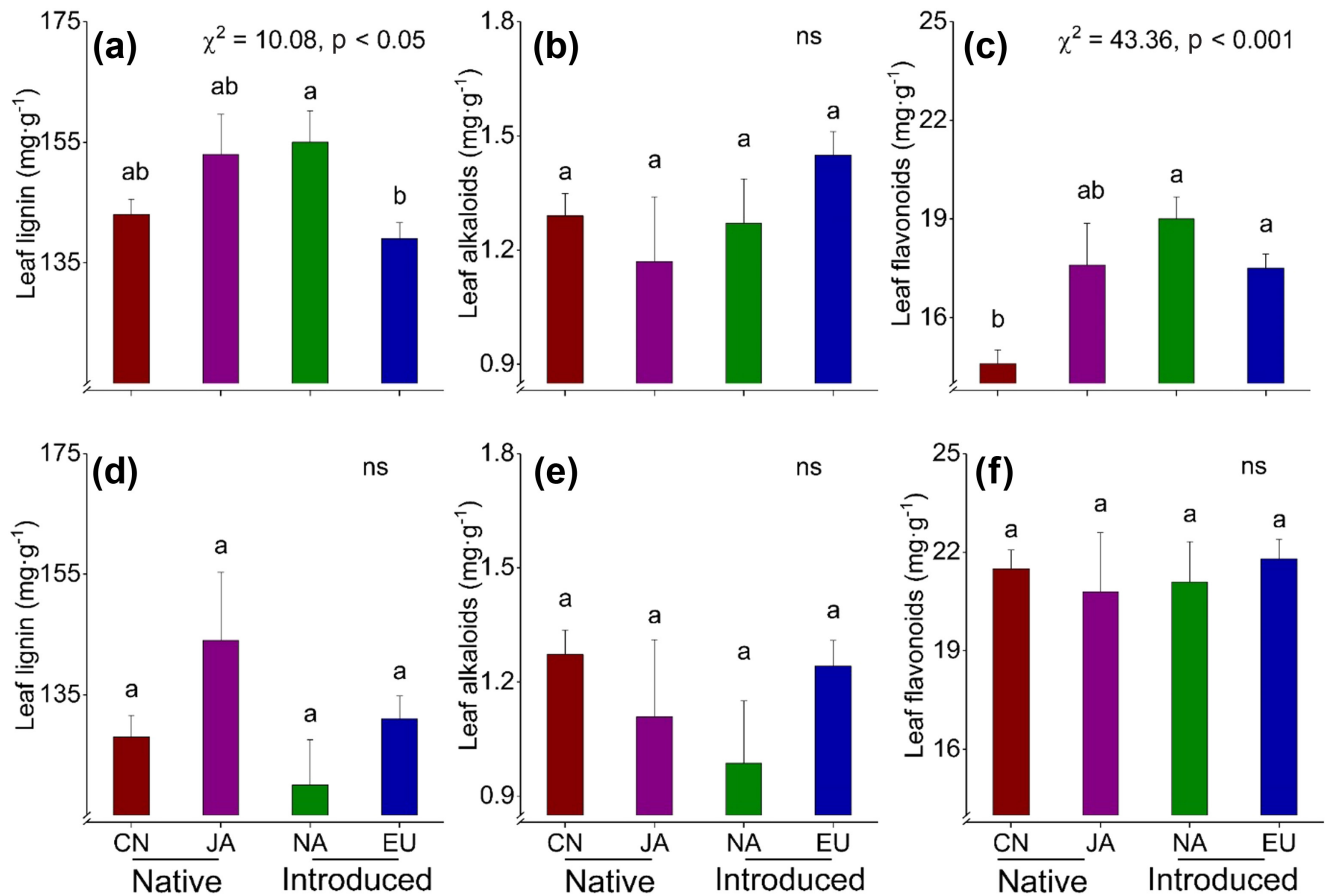


Figure 4. Average values of leaf chemistry observed in *Reynoutria japonica* plants from China (CN), Japan (JA), North America (NA) and Europe (EU) when grown in common gardens in Shanghai (a–c) and Xishuangbanna (d–f). The values are adjusted means (bars) and SEs (error bars) from ANOVAs, with different letters above error bars indicating significant group differences based on Tukey's HSD post hoc tests. χ^2 and the significance are shown, and ns indicates non-significant differences ($p > 0.05$).

thus failed to support the EICA prediction that introduced populations have evolved lower herbivore resistance than their native conspecifics (Blossey and Nötzold 1995). Several studies with other invasive species have also found no differences (e.g. *Lepidium draba*, Cripps et al. 2009, *Rorippa austriaca*, Huberty et al. 2014), or even higher (e.g. *Chromolaena odorata*, Liao et al. 2014, *Brassica nigra*, Oduor et al. 2011) resistance of introduced populations. Such inconsistencies with the EICA prediction may be due to the type of plant defense traits studied or herbivores used (Zhang et al. 2018,

Endriss et al. 2022). For *R. japonica*, none of the native knotweed specialist herbivores occur in North America (McIver and Grevstad 2010). Although there have been attempts to introduce the specialist knotweed psyllid *Aphalara itadori* in the UK (since 2010), Canada (since 2014; Grevstad et al. 2020), and the United States (since 2020; USDA 2023), we found no evidence that the European and North American knotweed populations used in this study were attacked by specialist herbivores in the field. Our previous field surveys and the work of others showed that European and North

Table 1. Spearman's correlation coefficients (r_s) between leaf traits and leaf herbivory, tested across 128 native and introduced populations of Japanese knotweed *Reynoutria japonica* when grown in two different common gardens in Shanghai and Xishuangbanna, respectively. Significant correlations are in bold. Significance levels: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

	Thickness	Toughness	C: N ratio	Lignin	Alkaloids	Flavonoids
<i>Shanghai</i>						
% leaf area eaten by beetles	0.13	−0.06	−0.11	−0.11	0.10	−0.07
% leaf area eaten by caterpillars	−0.40***	0.12	0.34***	−0.14	0.05	−0.35***
<i>Xishuangbanna</i>						
% leaf area eaten by beetles	−0.30**	−0.13	−0.06	0.06	0.00	−0.31***
% leaf area eaten by caterpillars	0.19*	−0.08	−0.03	0.15	0.03	0.11

Table 2. Associations between climates of collecting sites (first two PCs from a PCA of eight bioclimatic variables, Supporting information) and variation in leaf traits across native (N; Chinese and Japanese) and introduced (I; European and North American) Japanese knotweed *Reynoutria japonica* populations, when grown in two common gardens respectively in Shanghai and Xishuangbanna in China. The values are regression coefficients (β) and their significance levels (p values < 0.05 in bold) and adjusted model R^2 from linear regressions.

		Climate PC1			Climate PC2		
		β	p	R^2	β	p	R^2
<i>Shanghai</i>							
Thickness	N:	-0.01	0.013	0.09	0.02	0.001	0.18
	I:	0.00	0.855	0.00	0.00	0.747	0.00
C: N ratio	N:	-1.29	0.022	0.08	0.79	0.170	0.02
	I:	-0.40	0.157	0.01	-0.30	0.286	0.00
Flavonoids	N:	1.57	0.002	0.16	-1.86	< 0.001	0.23
	I:	-0.35	0.187	0.01	-0.64	0.015	0.07
<i>Xishuangbanna</i>							
Thickness	N:	-0.01	0.016	0.09	0.02	< 0.001	0.22
	I:	0.00	0.641	0.00	0.00	0.984	0.00
C: N ratio	N:	-2.00	< 0.001	0.28	0.89	0.075	0.04
	I:	0.56	0.189	0.01	1.38	0.001	0.16
Flavonoids	N:	2.73	< 0.001	0.30	-2.61	< 0.001	0.27
	I:	1.19	0.002	0.14	0.41	0.298	0.00

American knotweed populations had significantly lower herbivore attacks than native Chinese and Japanese populations (Maurel et al. 2013, Irimia et al. 2025).

In fact, we are only aware of one previous common garden study with native and introduced populations of *R. japonica* (Rouifed et al. 2018), which compared five native Japanese and five introduced French populations in a greenhouse common garden in the introduced European range. They also found that introduced populations did not differ in their composition of secondary metabolites, stem stiffness and leaf thickness, but had even higher leaf toughness than native Japanese populations. As the Japanese populations used in our experiments – as well as those used in Rouifed et al. (2018) – were from the putative source region of knotweed introductions to Europe and North America, our results indicated that the introduction of plants with particular resistance profiles, rather than post-introduction evolution, might have underlain the trait divergence between the native and introduced ranges, and may have played a role in the invasion success of *R. japonica*.

Overall, we found that herbivore damage varied substantially between the two common gardens and was related to different leaf traits. Part of these divergent results might have resulted from the different herbivore communities in the two common gardens, e.g. different herbivores may have different feeding preferences (Van der Meijden 1996, Yang et al. 2014). For instance, in the Shanghai garden, damage by caterpillars was negatively associated with leaf thickness and flavonoids but positively with leaf C:N ratios, whereas in Xishuangbanna, the same type of damage was only positively associated with leaf thickness. In Xishuangbanna, for example, we found that beetle damage was associated with different traits than damage by caterpillars: beetles preferred plants with thinner leaves and lower flavonoid levels, whereas caterpillars preferred plants with thicker leaves. The beetles and caterpillars that caused the most damage were not specialists to *R. japonica*, and demonstrated quite different preferences

on leaves from different ranges. The beetles that caused the most damage were in most cases leaf-feeding *Apogonia* sp. and *Adoretus* sp. that preferred plants from the native Chinese compared to the introduced European or North American populations. The caterpillar *Lymantria* sp. that caused the heaviest damage preferred plants from European rather than from Chinese populations. The average herbivore damage in the Shanghai common garden was relatively low, and it was not possible to further attribute the herbivory damage to specific beetle or caterpillar species. This limitation might have contributed to the inconsistent patterns of herbivory damage we found across the two gardens. Our results highlight the importance of quantifying herbivory damage into more refined categories, to better understand variation of herbivore defenses.

Besides the herbivore communities, the two common gardens also differed in climatic conditions, including temperature, precipitation and solar radiation. Since leaf traits could also respond to other environmental drivers, e.g. drought or UV radiation (Barton and Boege 2017, Li et al. 2022), this might have further contributed to the divergent herbivory–leaf trait relationships. More generally, our results demonstrated the environmental contingency of common garden results, when testing for variation in herbivore resistance (Maron et al. 2004, Qin et al. 2013, Yang et al. 2021), and hence the value of working with multiple common gardens.

Associations between climates of collecting sites and herbivore resistance

We found that the climatic conditions at the collecting sites were significantly associated with resistance traits in both common gardens, but only for populations from the native range. For populations from the introduced range, there were only very few significant associations. Many previous studies of invasive plants have documented the development of parallel clinal patterns in ecological traits among

populations of native and introduced ranges (Rosche et al. 2019, Hodgins et al. 2020) and have usually interpreted this as evidence for rapid post-introduction evolution and adaptation. However, there are also studies of successful invasive plants with unparalleled (Bhattarai et al. 2017, Yang et al. 2021) or no clinal patterns at all (Endriss et al. 2018, Sun and Roderick 2019). Our results also provide little evidence for post-introduction differentiation of introduced European or North American populations with climate.

A simple reason for the observed lack of heritable trait differentiation could be that there was too little heritable variation for natural selection to act on. The majority of invasive *R. japonica* populations are thought to be clonal descendants of a single introduced individual (Hollingsworth and Bailey 2000, Richards et al. 2012, Zhang et al. 2016b; Jugieau et al. 2024). However, so far this knowledge is based on low-resolution molecular studies of a limited number of populations, and we clearly need broader and higher-resolution population genomic analyses to evaluate this explanation. In particular, plants like *R. japonica* that are polyploid and have large genomes often maintain high intra-genomic diversity that can contribute to the evolution of gene expression repatterning even within clonal offspring of a single individual (Ainouche et al. 2012, Ferreira de Carvalho et al. 2017, Mounger et al. 2021). Moreover, several studies have reported that high rates of somatic mutation may allow asexual species to maintain genetic variation and adapt to changing environmental conditions. Mutations in structural or regulatory portions of the genome can have large effects on phenotype, and mutation may be common enough to fuel adaptation even in the short time frame of an invasion (Dlugosch et al. 2016, Estoup et al. 2016, Mounger et al. 2021). Such mutations could be particularly important for the quantitative traits and plastic responses that are involved in adaptation, considering the increased opportunities for mutations to occur in the multiple genes that are involved (Lande 2015).

In any case, an alternative explanation for the lack of climate-related differentiation could be that adaptation has never occurred. Although rapid evolutionary changes have frequently been reported for invasive plants, examples from the invasion literature show that geographic clines usually develop 50–150 generations after introduction (Moran and Alexander 2014). Many of these examples came from short-lived plants. However, *Reynoutria japonica* was introduced to Europe ca 170 years ago and some years later to North America, and began to expand rapidly only in the past 50–100 years (Bailey and Conolly 2000). As a perennial, it is possible that there has not been enough time for evolutionary patterns to emerge. Again, genomic approaches will help to answer this question.

Our phylogenetic analysis and biogeographic reconstruction of the knotweed plants supported the contention that all European and almost all North American populations originated from the southern-most island of Kyushu, Japan (Zhang et al. 2024). Therefore, the phenotypic differences observed between Chinese and European/North American populations cannot be used as evidence of rapid evolutionary

change. Instead, we found conspicuous differences in plant traits among native source (Japanese) populations and native non-source (Chinese) populations, although for some traits the native sources could not be differentiated. However, in the two common gardens we maintained, there was no evidence of divergence of the introduced plants from the source populations in Japan despite the passing of ~ 170 years since introduction (Wang et al. 2025). One limitation of our study was that, for biosafety reasons, we could not grow plants from the introduced populations in the location of the source populations, or grow Japanese populations in the introduced habitats. Such comparisons may reveal evolved differences between the introduced populations and their source of introduction. Furthermore, including more Japanese populations in future studies will help provide valuable information about this part of the native range.

Conclusion

Our study combined replicate common gardens and a biogeographical approach with samples spanning an exceptionally large climatic gradient from both introduced and native ranges to understand within- and among-range variation in herbivore resistance in the invasive plant *R. japonica*. We found that the resistance traits of introduced European and North American populations differed from most native Chinese populations but were generally similar to native Japanese populations that are the putative source of the introductions. Thus, we found little evidence for post-introduction evolution. Instead, we found evidence that plants with particular resistance profiles were introduced to Europe and North America, which may have played a role in the invasion success of *R. japonica*. Our study highlights the importance of accounting for invasion history when deciphering the mechanisms underlying the biogeographic divergence of important traits during invasion.

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Author contributions

Peipei Cao and **Zhi-Yong Liao** contributed equally to this publication. **Peipei Cao**: Data curation (lead); Formal analysis (lead); Investigation (lead); Writing - original draft (lead); Writing - review and editing (equal). **Zhi-Yong Liao**: Data curation (lead); Formal analysis (equal); Investigation (lead); Writing - original draft (equal); Writing - review and editing (equal). **Shengyu Wang**: Formal analysis (supporting); Investigation (lead); Writing - original draft (supporting). **Madalin Parepa**: Formal analysis (supporting); Writing - original draft (supporting). **Lei Zhang**: Investigation (supporting). **Jingwen Bi**: Investigation (supporting). **Yujie Zhao**: Investigation (supporting). **Yaolin Guo**: Investigation (supporting). **Tiantian Lin**: Formal analysis (supporting); Writing - original draft (supporting). **Stacy B. Endriss**: Formal analysis (supporting); Writing - original draft (supporting). **Jihua Wu**: Writing - review and editing (supporting). **Rui-Ting Ju**: Conceptualization (equal); Funding acquisition (lead); Supervision (equal); Writing - review and editing (equal). **Christina L. Richards**: Conceptualization (equal); Funding acquisition (lead); Writing - review and editing (equal). **Oliver Bossdorf**: Conceptualization (equal); Funding acquisition (lead); Supervision (equal); Writing - review and editing (equal). **Bo Li**: Conceptualization (lead); Funding acquisition (lead); Supervision (equal); Writing - review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.qbzk18r4> (Cao et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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