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Geographic variation in leaf traits and palatability of a native plant invader during domestic expansion

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Abstract

Like alien plant invasion, range expansion of native plants may threaten biodiversity and economies, rendering them native invaders. Variation in abiotic and biotic conditions across a large geographic scale greatly affects variation in traits and interactions with herbivores of native plant invaders, which is an interesting yet mostly unexplored issue. We used a common garden experiment to compare defensive/nutritional traits and palatability to generalist herbivores of 20 native (23.64° N–30.18° N) and introduced range (31.58° N–36.87° N) populations of *Reynoutria japonica*, which is a native invader following range expansion in China. We analyzed the relationships among herbivore pressure, climate, plant chloroplast haplotypes, leaf traits, and herbivore performance. Of the 16 variables tested, we observed range differences in 11 variables and latitudinal clines in nine variables. In general, herbivores performed better on the introduced plants than on the native plants, and better on the high-latitude plants than on the low-latitude plants within the introduced populations. Three key traits (leaf thickness, specific leaf area, and carbon-to-nitrogen [C:N] ratio) determined palatability to herbivores and were significantly associated with temperature and/or precipitation of plant provenance as well as with plant haplotypes but not with herbivore pressure. Our results revealed a causal sequence from plant-range-based environmental forces and genetic context to plant quality and palatability to herbivores in *R. japonica*. These findings suggest a post-introduction evolution of *R. japonica*, which may partly explain the colonization success of this important native, but invasive plant.

KEYWORDS

biological invasion, global change, herbivory, knotweed, latitudinal cline, plant ecology, range expansion, species interaction

INTRODUCTION

Plant invasion poses an increasing threat to biodiversity and economies worldwide (Diagne et al., 2021; Kueffer, 2017), which cannot solely be attributed to the invasion of alien plants. Range expansion of native plants across biogeographical regions within a continent can also result in serious ecological and economic consequences (Carey et al., 2012). This expansion, in some cases, is a natural behavior of native species in response to changes in climate and habitat availability (Essl et al., 2019), but it can also be the result of human introduction (Hoffmann & Courchamp, 2016). Ecologists define those species as “native invaders” that are native but have established and expanded dramatically in a new area due to intentional introduction, and have a measured impact on the ecology and economy of the recipient ecosystem (Carey et al., 2012; Simberloff, 2011). Although native invaders and their ecological damages are increasingly prevalent in both natural and managed ecosystems (Carey et al., 2012), very few studies have investigated their range expansion in relation to changes in biotic and abiotic factors in new habitats.

As with alien invasive plants, the shift in interaction with herbivores is a key feature of native plant invaders expanding in their range (Engelkes et al., 2008; Menéndez et al., 2008). For example, native plant invaders may be released from specialist herbivores in the new range (Keane & Crawley, 2002). Such release from specialized enemies can allow for a reallocation of plant resources that exhibits a decrease in defenses but an increase in growth and reproduction following introduction (i.e., the hypothesis of the evolution of increased competitive ability; Blossey & Nötzold, 1995). Despite escaping from specialist herbivores, native plant invaders are still likely to be subjected to frequent attacks by generalists in the expanded range, resulting in altered plant traits that are more palatable to specialists than generalists (i.e., the shifting defense hypothesis; Müller-Schärer et al., 2004). In addition to herbivore specialization, differences in herbivore intensity and climatic factors between original native and expanded ranges can also lead to variation in plant palatability to herbivores (Abdala-Roberts et al., 2016). Considering that native plant invaders may move into different biogeographical zones, plants may alter their morphologies, nutrition, and secondary metabolism to respond to herbivore-intensity alterations and/or climatic constraints (Guo et al., 2023; Hahn & Maron, 2016). So far, there is no comprehensive investigation into the combined effects of biotic and abiotic factors on palatability to herbivores in native plant invaders.

Native plant invaders may develop clines in palatability to herbivores along latitudinal gradients during range expansion. According to the latitudinal herbivory-defense hypothesis (Coley & Aide, 1991), plants will encounter reduced herbivore pressure if they are transferred from low to high latitudes and thus, they may have developed decreased defenses or increased palatability at high latitudes (Rasmann & Agrawal, 2011). In contrast, as predicted by the resource availability hypothesis, poorer resource availability at high latitudes may lead to higher growth costs for plants; limited resources will favor increased defenses and decreased palatability to reduce tissue loss by herbivores at high latitudes (Coley et al., 1985; Hahn & Maron, 2016). Hence, the interaction between plants and herbivores and climatic pressures also impacts predictions of latitudinal patterns in the palatability of native plant invaders.

Numerous studies have demonstrated that some variation in plant traits related to palatability could be the result of genetic differentiation (Bossdorf et al., 2005; Felker-Quinn et al., 2013; Ju et al., 2019; Orians & Ward, 2010; Woods & Sultan, 2022). The genetic context, therefore, should also be considered when we study geographical variation in palatability to herbivores of native plant invaders. Differences in chloroplast haplotypes are often used to explain variation in genetic context underlying variation in plant traits among populations (Qiao et al., 2019). Although chloroplast genes do not directly determine phenotypes related to plant palatability in most cases, they can indirectly influence those phenotypes by altering photosynthesis, which affects the acquisition and allocation of correlative resources (Guo et al., 2014; Kremer et al., 2002).

Here, we report a large-scale study of geographical variation in leaf palatability to generalist herbivores, and related traits of the recently expanding native invader *Reynoutria japonica* (hereafter *Reynoutria*) in China, where *Reynoutria* grows along a large latitudinal gradient, but the northern populations (~31° N–38° N) were intentionally introduced from the southern regions (~22° N–31° N) (Wang, 1996; Zhao, 2021). Following the introduction, *Reynoutria* has successfully naturalized and expanded in natural habitats, resulting in significant biodiversity and agriculture losses in the northern regions (Zhao, 2021). Therefore, this species has become a successful native invader in China. During its human-facilitated expansion, *Reynoutria* escaped from specialist herbivores but was frequently attacked by generalist herbivores (Zhao, 2021). This alteration in herbivore specialization, as proposed by the shifting defense hypothesis (Müller-Schärer et al., 2004), might have selected for a reduction in plant palatability to generalist herbivores. In addition, the altered herbivore pressure as well as lower temperature and less precipitation

at high latitudes compared to low latitudes might also have affected variation in plant palatability (Bi et al., 2024; Moreira et al., 2015; Pennings et al., 2009).

In this study, we assessed palatability of *Reynoutria* to generalists across a latitudinal transect in its native (23.64° N–30.18° N) and introduced ranges (31.58° N–36.87° N) in China using a common garden. We tested leaf palatability of *Reynoutria* to three generalist herbivores (caterpillars of *Spodoptera litura*, *Spodoptera exigua*, and the aphid *Aphis citricola*) that frequently feed upon *Reynoutria* in our collecting sites (Han & Jiang, 2020; Zhang & Zhao, 1996). We hypothesized that (1) native-range and introduced-range *Reynoutria* populations differ in leaf traits and palatability to generalist herbivores, and these tested variables vary in a cline across latitudes within each range; (2) leaf traits of *Reynoutria* determine the performance of generalists; (3) variation in leaf traits of *Reynoutria* is affected by changes in plant source-population herbivore pressure, climate, and chloroplast haplotypes. To our knowledge, this is the first study that simultaneously considered the effects of herbivore pressure, climate, and genetic background on palatability of native plant invaders to herbivores, which could enhance our understanding of how a globally invasive plant behaves at home through range expansion.

MATERIALS AND METHODS

Study species

R. japonica is an important invader worldwide (Bailey et al., 2009; Del Tredici, 2017; Richards et al., 2008), but also is expanding in its native range (Zhao, 2021). *Reynoutria* is a herbaceous perennial native to subtropical and temperate regions in East Asia, including Korea, Japan, and China (Lawson et al., 2021), and has become a problematic alien invader in Europe and North America (Maurel et al., 2013; Parepa et al., 2014; Richards et al., 2008). In China, *Reynoutria* exhibits a wide latitudinal distribution. Due to the lack of studies on the history of expansion of the species, the available literature often considers China as a unified native range of *Reynoutria* (IBCAS, 1998; Lawson et al., 2021; RBG Kew, 2023). However, some researchers have highlighted that *Reynoutria* populations were intentionally introduced from the southern regions (bounded by the Yangtze River) to the northern regions, including Anhui, Henan, and Shandong provinces, as a medicinal and ornamental plant species in the 1990s (Wang, 1996; Zhang et al., unpublished data; Zhao, 2021). We have further substantiated this assertion by our interviews with indigenous residents, researchers, and managers during

the process of plant collection. In the introduced regions, *Reynoutria* has now successfully established itself in farmland and forest habitats, and has caused significant ecological and economic losses (Zhao, 2021). For example, *Reynoutria* has invaded some sesame and corn fields in Henan province, where it crowds out growing space and reduces the yield and quality of the crops. In Anhui province, *Reynoutria* has encroached upon some bamboo forests, forming monocultures that threaten native biodiversity (Y.-J. Zhao, personal observation). Currently, *Reynoutria* has not only spread from its originally introduced sites but also exhibited dispersal potential expanding to higher latitudes. In addition, *Reynoutria* has escaped from specialist herbivores but still suffers great attacks by at least 10 generalist species in the introduced regions (Zhao, 2021). In China, *Reynoutria* has high genetic diversity measured at the ploidy level but also at the chloroplast haplotype level. Our research team has identified four polyploid classes (i.e., tetraploid, hexaploid, octoploid, and decaploid) in China. Among them, octoploid ($2n = 8x = 88$) is the most common type, which includes at least 16 chloroplast haplotypes (Zhang et al., unpublished data). These characteristics make *Reynoutria* a good species to study variation in plant traits and interactions with herbivores, and climatic factors of native plant invaders during range expansion.

We chose the caterpillars of *S. litura* (Lepidoptera: Noctuidae), *S. exigua* (Lepidoptera: Noctuidae), and the aphid *A. citricola* (Hemiptera: Aphidoidae) for plant palatability bioassays; these herbivores are the most common generalist herbivores attacking *Reynoutria* leaves at our collecting sites (Han & Jiang, 2020; Zhang & Zhao, 1996). All three herbivores are cosmopolitan species, and their distribution covers the whole range of *Reynoutria* in China (Eastop & Hille Ris Lambers, 1976; EPPO, 2015). As typical leaf chewers, caterpillars of *S. litura* and *S. exigua* can feed on leaves of >380 plant species from 109 families (Qin et al., 2006), and of ~170 plant species from eight families (Robinson et al., 2010), respectively. Both herbivores frequently attack *Reynoutria* leaves, and can kill the plant in the case of severe damage. *A. citricola* is a polyphagous sucker species but mainly feeds on *Reynoutria*, *Spiraea salicifolia*, and *Malus domestica* (Wang et al., 2008). Adults and nymphs of *A. citricola* can suck sap from leaves and stems, resulting in leaf wrinkling or curling that greatly inhibits plant growth (Wang et al., 2008).

Plant collection and propagation

We collected rhizomes of *Reynoutria* at 10 sites (23.64° N–30.18° N) in the native range, and at 10 sites (31.58° N–36.87° N) in the introduced range that were

>25 km apart along latitudinal gradients between July and August in 2020 in China (Figure 1; Appendix S1: Table S1). At each site, we collected rhizomes from 3 to 5 well-established *Reynoutria* individuals separated by >5 m. We confirmed the introduction history with indigenous residents, researchers, and managers to ensure that the sampled plants in the introduced range were in fact introduced. In total, we collected 98 source rhizomes and stored them at 4°C for at least 30 days to mimic overwintering to induce growth outside of the normal season (Maqbool et al., 2004). In September 2020, we planted source rhizomes (F_1) in a greenhouse at Fudan University (31.35° N, 121.51° E). To eliminate maternal effects, these plants were clonally propagated for two generations (F_2 and F_3) in 3.8-L pots (one propagule per pot) containing a 1:1 mixture of peat soil and vermiculite. We added 5 g of slow-release fertilizer (N:P:K = 14:14:14) to each pot once and watered all pots once every three days. We were able to clonally propagate all source rhizomes. Using cpDNA, we found that all source plants were octoploid with eight distinct chloroplast haplotypes (Appendix S1: Table S1).

In March 2022, we cut 5–7 rhizome fragments of similar size (each weight ~ 7.5 g) from each F_3 individual

(Appendix S1: Figure S1a), transplanted each fragment into a 3.8-L pot and cultured the plants under the same conditions as the source plants. We randomly arranged all pots inside 29 cages with nylon screens (1.2 m × 0.6 m × 0.5 m, aperture = 75 µm) to prevent herbivores (Appendix S1: Figure S1b), and shifted pots between these cages once a week. After two months, we selected five well-grown clonal replicates of each F_3 rhizome (total $98 \times 5 = 490$ clones) for the subsequent experiment (i.e., five replicates for each latitudinal population). We measured plant traits and conducted palatability bioassays of leaf chewers on three of the clonal replicates, and used the remaining two for palatability bioassays of aphids.

Plant traits

We examined nine leaf traits (thickness, specific leaf area [SLA], carbon-to-nitrogen (C:N) ratio, lignin, tannins, alkaloids, coumarins, flavonoids, and pH) that are putatively associated with leaf palatability to generalist herbivores (Agrawal & Weber, 2015; Moles et al., 2011; Pérez-Harguindeguy et al., 2016; Sun et al., 2020). In late May of 2022, we collected the first and the fourth to seventh fully expanded leaves from the top of a plant for the quantification of physical and chemical traits. We first measured total leaf thickness of the five leaves with a micrometer at the same position on the leaf. We oven-dried all leaves at 45°C for 72 h, and then ground the samples into powder and stored them at -20°C. We determined SLA according to the ratio of total area of five leaves to their dry weight, and we quantified the leaf C:N ratio using a Flash-11121-Series Elemental Analyzer (Thermo Finnigan, Milan, Italy). We determined leaf pH using an acidity meter calibrated with standard buffers (Pérez-Harguindeguy et al., 2016). We measured leaf coumarin content using an enzyme-labeled instrument (Ibiogene, Shanghai, China) (Wu et al., 2022), and quantified the contents of leaf lignin, tannins, alkaloids, and flavonoids with commercially available assay kits (Cominbio, Jiangsu, China) following the manufacturer's protocols. For leaf thickness and SLA, we tested three clonal replicates and calculated the mean value for each source rhizome from each site. For measurements of other traits, we had only one replicate sample for each source rhizome because we mixed leaf samples of three clonal replicates to meet the mass (1.0–1.5 g) required for quantification of all chemicals.

Plant palatability bioassay

We employed three indices (larval growth, leaf area consumed, and biomass conversion efficiency) to measure

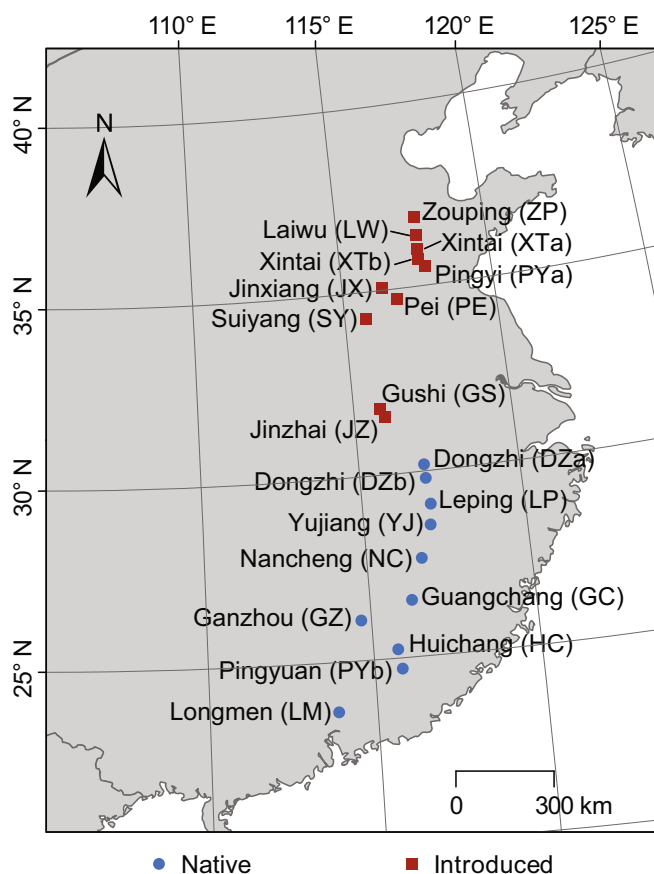


FIGURE 1 Collecting sites of *Reynoutria japonica* populations in the eastern mainland of China. The map projection used is Lambert.

palatability of *Reynoutria* to caterpillars of two moth species. In late May of 2022, we purchased *S. litura* and *S. exigua* from Henan Jiyuan-Baiyun Company in China and reared them with commercial artificial diets provided by the company at 26°C with a relative humidity (RH) of 60% and a photoperiod of 14 h:10 h (L:D). We selected the fifth-instar larvae of *S. litura* and the fourth-instar larvae of *S. exigua* for their palatability bioassay. For the bioassay of *S. litura* (Appendix S1: Figure S1c,e), we collected the third fully expanded leaf from the top of a plant, wrapped wet cotton around the petiole and then placed the leaf in a petri dish (diameter = 15 cm). We added a pre-weighed caterpillar (W_1) to the petri dish and then maintained the dish under the same conditions as for insect source rearing. After 48 h, we removed the caterpillar from the dish and weighed it again (W_2). We calculated caterpillar growth based on the weight gain in fresh biomass during the bioassay ($W_2 - W_1$). We also quantified the leaf area consumed by the caterpillar by extrapolating from the area of leaf remnant and pre-consumption leaf area using Adobe Photoshop CC 2018 and ImageJ (v.1.53) (Rasband, 2014). In addition, we determined the biomass conversion efficiency of each caterpillar (caterpillar growth per ln-transformed unit area of leaf consumed; Bhattarai et al., 2017). We used similar procedures for the palatability bioassay of *S. exigua* (Appendix S1: Figure S1d,e), but for this assay we used the second fully expanded leaf.

We evaluated growth of aphid population size to indicate *Reynoutria* palatability to *A. citricola* (Bhattarai et al., 2017). In late May of 2022, we obtained commercial aphids from Henan Quanying Insect Biology Company of China and reared them on *Malus spectabilis* at 20°C with a RH of 65% and a photoperiod of 14 h:10 h (L:D). We first affixed a gauze-mesh cage (10 cm × 12 cm, aperture = 75 μm) on the upper portion of the stem of a plant (each cage covered apex shoots and the first fully expanded leaf; Appendix S1: Figure S1f,g) and then added 20 mature aphids in the cage and maintained them under the same conditions as for their source rearing. After nine days, we determined the aphid population size by counting the number of both adult and nymph aphids in each cage (Wang et al., 2008).

For the palatability bioassays of caterpillars of two moth species, we tested three replicate dishes and calculated the mean value for clonal replicates from each source rhizome. For the bioassay of the aphid, we tested two replicate cages and calculated the mean value for each source rhizome. We only analyzed petri dishes or cages in which caterpillars or aphids were alive and leaves were not completely consumed.

Data analysis

All analyses were performed with R version 4.1.2 software (R Core Team, 2021). We indicated utilization of non-base R packages when applicable.

Because of collinearity (variance inflation factor > 4, *car* package) between range and latitude, we separately examined the effects of range and latitude on plant traits and herbivore performance (Kabacoff, 2015). We used linear mixed-effects models (LMM) to analyze variation in response variables (leaf thickness, SLA, C:N ratio, lignin, tannins, alkaloids, coumarins, flavonoids, pH, and herbivore performance except for aphid population size) between the native and introduced ranges and among latitudes within each range. Data on aphid population size fitted to a Poisson distribution with overdispersion, so we employed a generalized linear mixed-effects model (GLMM) with the quasi-Poisson distribution to analyze the data (Kabacoff, 2015). In both models, we included “population” as a random effect. We natural-log transformed leaf lignin and SLA, and square-root transformed leaf area consumed by *S. exigua* to normalize the distribution of residuals in the LMM.

To understand the relationships among range, herbivore pressure, climate, plant genetic background, leaf traits, and generalist performance, we used the *piecewise SEM* package to construct a structural equation model (SEM). The SEM was based on the following three logical predictions: (1) herbivore pressure, climatic factors (temperature and precipitation), and plant haplotypes vary between plant ranges; (2) these biotic and abiotic factors affect plant traits; and (3) plant traits affect the performance of generalist herbivores. To simplify the explanatory variables, we used one-by-one simple linear regressions (SLRs) to analyze correlations between nine putative palatability traits of plants and seven variables of generalist performance. We excluded flavonoid content because it was highly correlated with other variables (Spearman's $r > 0.6$ or < -0.6 , Appendix S1: Table S2), and leaf pH and alkaloid and coumarin contents because they had no significant effects on generalist performance (Appendix S1: Table S3). We used principal component analyses (PCA) to summarize 11 temperature variables in one analysis and eight precipitation variables in a second analysis (Appendix S1: Figure S2) with data for our sampling sites in the WorldClim Database (<http://www.worldclim.org>). We also used PCA to summarize seven variables of herbivore performance in a third analysis (Appendix S1: Figure S3). The first principal components (PC1s) of three PCAs explained respectively 68.03%, 85.14%, and 56.08% of the variation in temperature-, precipitation-, and herbivore-performance-related variables

(Appendix S1: Figures S2a,c and S3a). We included temperature PC1, precipitation PC1 and herbivore-performance PC1 (using negative values because of negative correlations between PC1 and herbivore performance) in the subsequent SEM and/or SLR analysis. We used the data on herbivore pressure (proportion of leaf area loss) at the sampling latitudes from Zhao (2021) and the data on chloroplast haplotypes of *Reynoutria* (Appendix S1: Table S1) detected by our knotweed research team. We finally constructed the SEM by evaluating the linear correlations between five plant traits (i.e., leaf thickness, SLA, C:N ratio, and tannin and lignin contents) and herbivore performance, and between plant traits and four predictors (i.e., herbivore pressure, temperature PC1, precipitation PC1, and plant haplotypes; Appendix S1: Figure S4, Table S4) (Pugesek et al., 2009). We determined SEM fitness by Fisher's *C* with a nonsignificant *p* value (Lefcheck, 2016). Furthermore, to reveal the pattern of variation in environmental variables along latitudes, we employed SLRs to analyze linear variation

in temperature PC1 and precipitation PC1 and beta regression (using the *betareg* package) to analyze variation in herbivore pressure across our sampling sites.

RESULTS

Variation in palatability traits

Although the contents of lignin, alkaloids, and coumarins in leaves of *Reynoutria* populations did not differ between the native and introduced ranges (Figure 2d,f,g; Appendix S1: Table S5), leaves in plants from the introduced range had higher SLA and flavonoid content (Figure 2b,h; Appendix S1: Table S5) and lower thickness, C:N ratio, tannin content, and pH than those from the native range (Figure 2a,c,e,i; Appendix S1: Table S5). Within each range, some traits showed significant latitudinal clines. In the native range, only leaf pH significantly decreased with increasing latitude (Figure 2i;

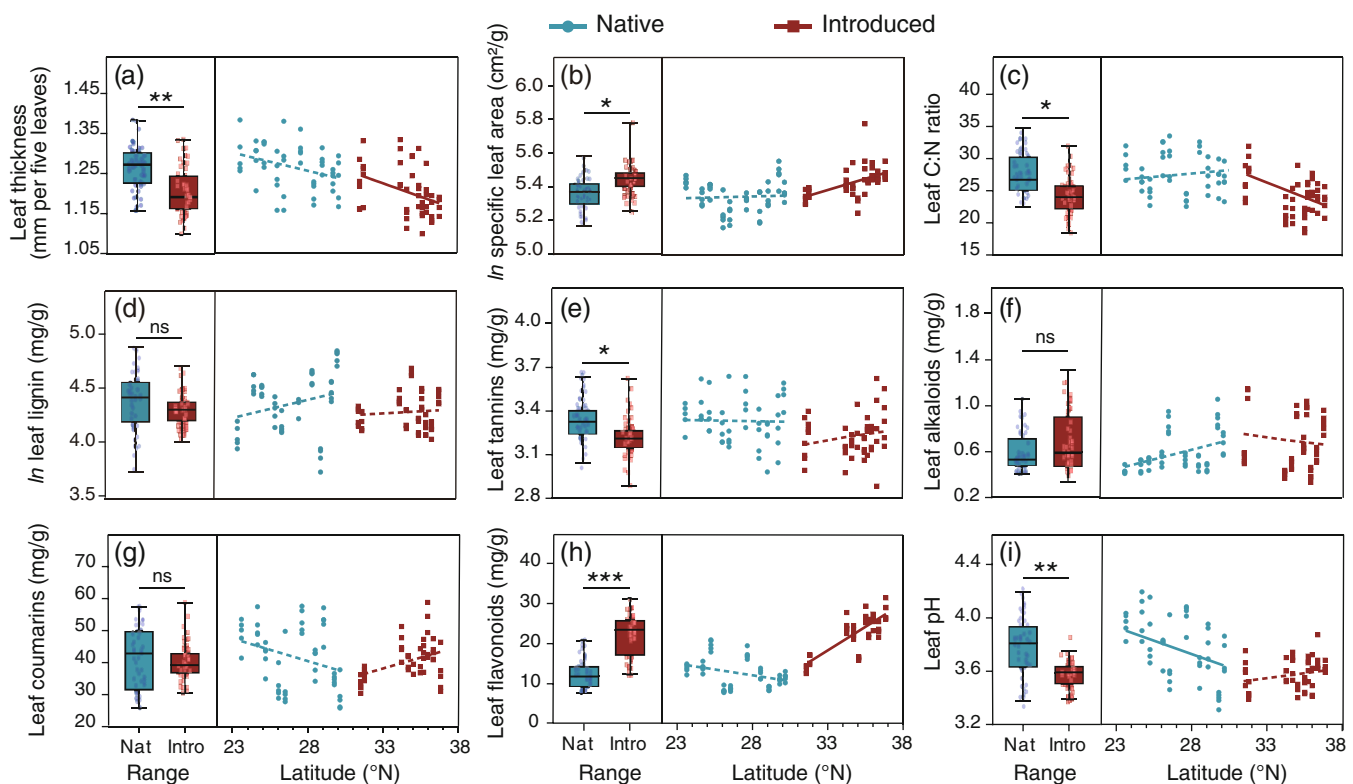


FIGURE 2 Variation in leaf traits in *Reynoutria japonica* between its native (Nat) and introduced (Intro) ranges (shown as boxplots), and among latitudes within each range (shown as scatter plots). The left side of each panel shows the result of range comparison; each boxplot indicates the median and interquartile ranges, whereas the scattered dots show the data distribution; asterisks and ns indicate the degree of significance (^{ns} $p \geq 0.05$, $*p < 0.05$, $**p < 0.01$, $***p < 0.001$). The right side of each panel shows relationships between leaf trait and collection latitudes, separately for each range; we plotted the regression lines, with solid lines indicating significant ($p < 0.05$) slopes and dashed lines nonsignificant ($p > 0.05$) slopes. See Appendix S1: Table S5 for detailed information about estimates \pm SE, *t*-statistic, and df associated with each of the exact *p*-values.

Appendix S1: Table S5). In the introduced range, leaf thickness and C:N ratio significantly decreased with increasing latitude (Figure 2a,c; Appendix S1: Table S5), but the clines of SLA and leaf flavonoid content increased (Figure 2b,h; Appendix S1: Table S5).

Variation in generalist performance

Although the larval growth and biomass conversion efficiency of *S. exigua* feeding on *Reynoutria* leaves were not significantly different between population ranges (Figure 3d,f; Appendix S1: Table S6), the other five indices (larval growth of, leaf area consumed by, and biomass conversion efficiency of *S. litura*, leaf area consumed by *S. exigua*, and aphid colony size of *A. citricola*) showed that all three generalists tended to perform better on plants from the introduced populations than on those from the native populations (Figure 3a–c,e,g; Appendix S1: Table S6). The performance of generalists feeding on native population plants did not differ significantly among plant collection latitudes for any index (Figure 3a–g; Appendix S1: Table S6). Generalists feeding on introduced populations, however, generally performed better on cuttings from high-latitude rhizomes than from low-latitude rhizomes

(although these trends were not significant in performance of *S. exigua*; Figure 3a–g; Appendix S1: Table S6).

Relationships among range, herbivore pressure, climate, plant haplotypes, leaf traits, and generalist performance

The SEM (Figure 4; Appendix S1: Table S7) revealed that of the five palatability traits, increases in leaf thickness and C:N ratio, along with a decrease in SLA, were associated with reduced performance of generalist herbivores, that is, these three traits were key determinants of plant palatability to generalists. Leaf thickness and C:N ratio were positively influenced by temperature PC1 and precipitation PC1, respectively (Figure 4), of the plant origin (i.e., negative correlation with latitude, Appendix S1: Figure S5a,b). All three key palatability traits were significantly affected by plant haplotypes but not by herbivore pressure (Figure 4) at the plant origin (herbivory did not significantly vary across latitudes, Appendix S1: Figure S5c). Finally, aside from herbivore pressure, variation in temperature PC1, precipitation PC1 and plant haplotypes could be attributed to sampling ranges (Figure 4). Altogether, the SEM suggested a causal sequence from

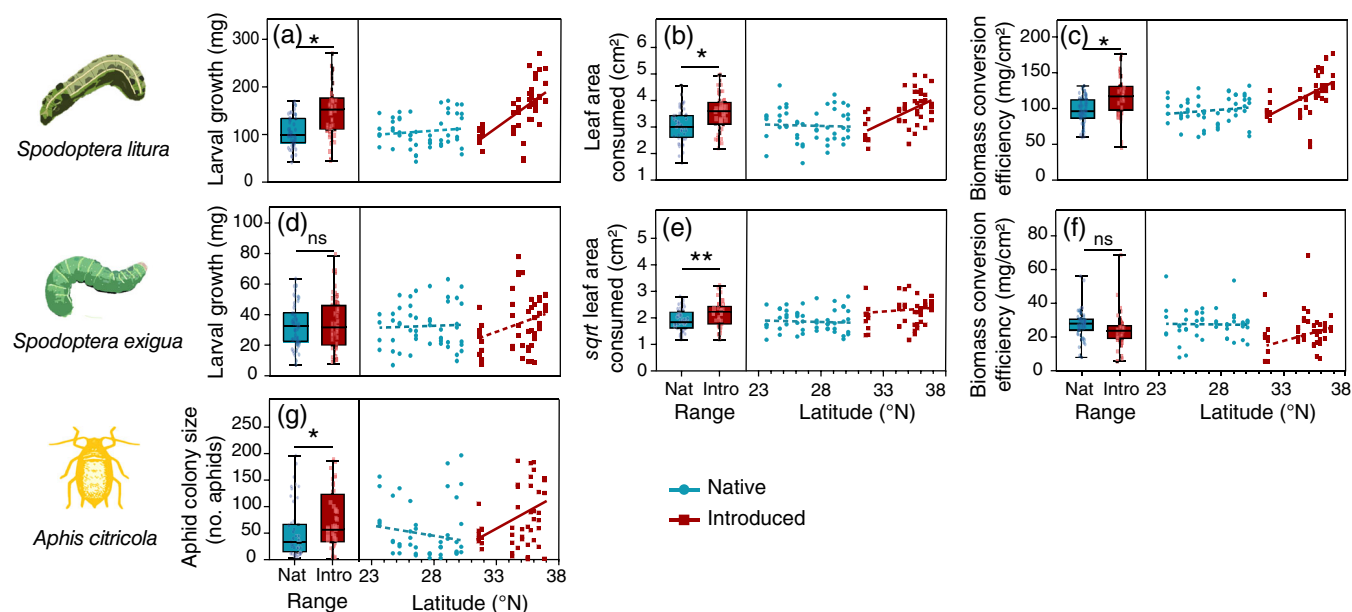


FIGURE 3 Variation in performance of *Spodoptera litura* (a–c), *Spodoptera exigua* (d–f), and *Aphis citricola* (g) feeding on leaves of *Reynoutria japonica* between plant native (Nat) and introduced (Intro) ranges (shown as boxplots) and among latitudes within each range (shown as scatter plots). The left side of each panel shows the result of plant-range comparison; each boxplot indicates the median and interquartile ranges, whereas the scattered dots show the data distribution; asterisks and ns indicate the degree of significance ($^{ns}p \geq 0.05$, $^{*}p < 0.05$, $^{**}p < 0.01$). The right side of each panel shows relationships between herbivore performance and plant-collection latitudes, separately for each plant range; we plotted the regression lines, with solid lines indicating significant ($p < 0.05$) slopes and dashed lines nonsignificant ($p > 0.05$) slopes. See Appendix S1: Table S6 for detailed information about estimates \pm SE, t -statistic, and df associated with each of the exact p -values. Herbivore illustrations by Yu-Jie Zhao.

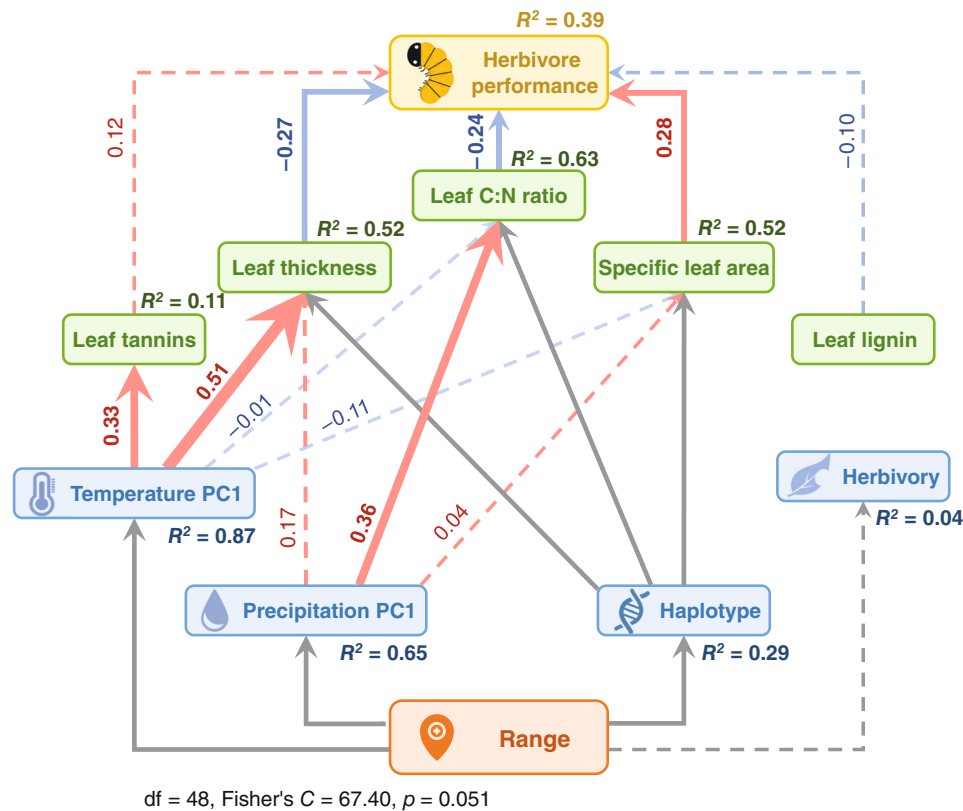


FIGURE 4 Structural equation model showing relationships among plant range, herbivore pressure, climate (temperature PC1, and precipitation PC1), plant haplotypes, leaf traits and herbivore performance. Values next to arrows are standardized path coefficients, and the thickness of arrows corresponds to magnitudes of the coefficients. Red and blue arrows indicate positive and negative relationships, respectively, and gray arrows indicate that the positive/negative correlations are inapplicable. Arrows with dashed lines indicate nonsignificant paths ($p \geq 0.10$). The supporting statistics for each path and for each level of categorical variables are detailed in Appendix S1: Table S7.

geographical range to herbivore pressure, climate, and plant genetic context, and then to palatability traits, which ultimately affected the performance of generalist herbivores.

DISCUSSION

Our results showed an increase in performance of three generalist herbivores feeding on leaves of high-latitude-introduced populations of *Reynoutria* compared with plants from low-latitude native populations in China (Figure 3a–c,e,g), which was consistent with an improved leaf quality in the introduced compared with the native populations (e.g., lower leaf thickness, C:N ratio, tannin content, and higher SLA; Figure 2a–c,e). These findings indicate that *Reynoutria* has increased palatability to generalist herbivores following intentional introduction to the new range by humans. This finding is inconsistent with the prediction of the shifting defense hypothesis that suggests that plants reduce their palatability to generalists due to

their high herbivore pressure in the introduced range (Müller-Schärer et al., 2004). Zhao (2021) found that *Reynoutria* growing in northern introduced regions escaped from specialist herbivores and exhibited greater growth than those in southern, native regions of China. Following this escape from herbivores, the introduced *Reynoutria* populations may have experienced selection for enhanced vigor, which promoted successful colonization and expansion in the new habitats. Our findings, in conjunction with those of Zhao (2021), support the hypothesis of the evolution of increased competitive ability (Blossey & Nötzold, 1995). A recent investigation indicated that introduced plants suffered reduced generalist herbivory in the new habitats, resulting in decreased constitutive defenses but increased induced defenses and growth (Sun et al., 2023). Induced defenses of *Reynoutria* were not examined in this study and needs further research.

Due to the specificity of introduced sites of *Reynoutria*, an unavoidable weakness of our design was that all introduced populations were from higher latitudes but all native

populations were from lower latitudes. Therefore, we had to separately analyze the effects of range and the effects of latitude within each range on plant palatability and related traits. Among all tested traits of *Reynoutria*, the flavonoid content in leaves was higher in plants of introduced populations from higher latitudes than in plants of native populations from lower latitudes (Figure 2h). Within plant range, the flavonoid content in the introduced *Reynoutria* populations increased with increasing latitude (Figure 2h). This finding of leaf flavonoids could be explained on the regional scale by the resource availability hypothesis, that is, plants from higher latitudes are more resistant and less palatable to herbivores (Coley et al., 1985). However, we found lower thickness, C:N ratio, tannin content, pH and higher SLA in leaves of the introduced populations compared with those of the native populations (Figure 2a–c,e,i). Additionally, leaf pH in the native populations, as well as leaf thickness and C:N ratio in the introduced populations, decreased with increasing latitude (Figure 2a,c,i), but SLA in the introduced populations increased with increasing latitude (Figure 2b). These results are inconsistent with the resource availability hypothesis but support the latitudinal herbivory-defense hypothesis on the regional scale, which predicts that plants will reduce their palatability to herbivores at low versus high latitudes (Coley & Aide, 1991; Rasmann & Agrawal, 2011). Furthermore, because of the opposite latitudinal trends (although not always statistically significant) observed in six out of nine traits between the introduced and native populations (Figure 2c,e–i), our findings suggest that *Reynoutria* has altered clinal responses in some traits following introduction from low to high latitudes.

Although plant palatability to herbivores can be indicated by multiple traits, few studies have linked these traits to herbivore performance (Ali & Agrawal, 2012; Zhang et al., 2018). This may lead to redundancy in some tested traits when selecting proxies for palatability traits. Ecologists contend that for generalist herbivores with broad diets, just a few plant traits can dictate herbivore consumption of plant tissues (Coley, 1983; Hanley et al., 2007; Lowman & Box, 1983). We found that leaf thickness, SLA, and C:N ratio were key to *Reynoutria* palatability to generalist herbivores (Figure 4). A shared feature of these three traits is their strong correlation with the physical properties of leaves. For example, thick leaves are difficult to be torn or pierced by herbivore mouthparts (Pérez-Harguindeguy et al., 2016). Leaves with low SLA and high C:N ratio tend to have dense tissue, so these leaves will be hardened, which is associated with the reduced performance of herbivores (Hanley et al., 2007; Ju et al., 2019). Furthermore, low SLA and high leaf C:N ratio typically correspond to lower nutrition for herbivore growth and reproduction, which

may also render leaves less palatable to herbivores (Pérez-Harguindeguy et al., 2016). Because we found that physical and nutritional traits rather than secondary compounds significantly affected generalist herbivores (Figure 4), it means that enhanced physical strength and reduced nutrition are more effective strategies for plants to resist generalists than synthesizing secondary metabolites (Coley, 1983). In other words, physical and nutritional traits of plants may be more robust than secondary compounds in assessing plant palatability to generalists (Hanley et al., 2007; Lowman & Box, 1983).

Because leaf thickness, SLA, and C:N ratio of *Reynoutria* were all significantly influenced by chloroplast haplotypes that varied between plant ranges (Figure 4), differences in three key palatability traits between native and introduced ranges may be partly explained by haplotypes. As mentioned in the introduction, although chloroplast genes typically cannot directly regulate plant palatability traits, they can indirectly affect those traits by affecting photosynthetic resource acquisition and allocation (Guo et al., 2014; Kremer et al., 2002). In addition, different chloroplast haplotypes are often associated with distinct nuclear genotypes (Kremer et al., 2002). Therefore, variation in chloroplast haplotypes can be used to assess the genetic structure of plant populations when nuclear gene differentiation is unknown (Guo et al., 2014; Qiao et al., 2019; Shang et al., 2019). Our findings of variation in plant palatability traits shown in the common garden, as well as the effects of changes in chloroplast haplotypes on that variation, may indirectly imply post-introduction evolution in *Reynoutria* populations. Determining whether this is correct requires additional research.

We found that variation in three key palatability traits of *Reynoutria* was not significantly affected by herbivore pressure at sampling latitudes (Figure 4), which is inconsistent with previous studies (Anstett et al., 2015; Coley & Aide, 1991; Pennings et al., 2009). The lack of effects of herbivore pressure on plant palatability traits may be attributed to following four reasons: (1) Herbivore pressure did not vary significantly between *Reynoutria* ranges (Figure 4) and among latitudes (Appendix S1: Figure S5c), indicating that the allocation of plant resources toward defenses and nutrition are not driven by herbivory (Andrew & Hughes, 2005; Moles et al., 2011); (2) we only included the aboveground herbivore pressure in the analysis but neglected the effects of belowground herbivores and microorganisms; (3) we lacked data on differences in herbivore pressure between specialists and generalists; (4) we measured herbivory at only one time-point, which could not represent the full picture of historic herbivore pressure. All of these are potential reasons why herbivore pressure

failed to predict variation in plant palatability traits (Engelkes et al., 2008; Morriën & van der Putten, 2013).

Many studies have substantiated that alterations in temperature and precipitation can drive variation in plant traits (Abdala-Roberts et al., 2016; Reich & Oleksyn, 2004). We observed that temperature and precipitation differed between plant ranges (Figure 4; Appendix S1: Figure S5a,b), which indirectly linked the variation in leaf traits between native and introduced ranges to the geographic changes in climates. In addition, our findings of the positive effect of temperature on leaf thickness and the positive effect of precipitation on leaf C:N ratio in *Reynoutria* (Figure 4) can be explained by the optimization theory and the adaptive growth hypothesis. The optimization theory posits that plants growing under high versus low temperature conditions tend to increase leaf thickness (Parker & Smith, 1990; Pérez-Harguindeguy et al., 2016). This is because the photosynthetic rate of plants tends to decrease due to insufficient CO₂ supply in hot environments, and increasing leaf thickness is determined as a compromise between the increase in chloroplast surface area for CO₂ dissolution and the decrease in the cost of leaves (Terashima et al., 2005). For the explanation of the variation in C:N ratio, high precipitation at low latitudes with heavy leaching causes major soil nitrogen loss (Reich & Oleksyn, 2004; Zhang et al., 2020); thus, nitrogen becomes a limiting element in soil (Craine et al., 2018). Under the nitrogen-limited environment (e.g., low-latitude native range of *Reynoutria* with high precipitation), according to the adaptive growth hypothesis, plants tend to increase their C:N ratio to promote nitrogen use efficiency and ensure survival priority (Zhang et al., 2020). Furthermore, a lower C:N ratio in plant tissues in the introduced range of *Reynoutria* can facilitate nutrient cycling, thereby promoting the growth of the introduced populations (Zhang et al., 2021). Therefore, the increased palatability of *Reynoutria* in its high-latitude introduced range versus low-latitude native range may be the indirect consequence of plants in response to changes in climates.

Our finding of geographic variation in palatability to generalist herbivores and related traits of the native invader *Reynoutria* was similar to that of invasive alien plants (e.g., Bosssdorf, 2013; Callaway et al., 2022). This suggests that geographic variation in plant characteristics of an introduced plant does not depend on its status (native and alien) that was historically defined by national boundaries of distribution (Valéry et al., 2008). In the current context of rapid global change and frequent species introduction by humans, the native–alien species dichotomy may not be useful in some cases from an applied perspective, although for fundamental evolutionary ecology it incorporates the evolutionary history

(Carey et al., 2012; Davis et al., 2011). The identification of plant status should not only be based on the political boundaries between countries but also take the biogeographical origins of plants and their ecosystem impacts into account (Yazlık & Ambarlı, 2022). That is, the focus of the invasion problem of concern is the adverse effects of species but not their “alien” label defined by humans (Hoffmann & Courchamp, 2016). Given that the expansion of native plants and their ecological damage are increasingly prevalent (Carey et al., 2012), and that plant expansion is profoundly influenced by interactions with herbivores, climate, and other factors in the new ranges (Alpert et al., 2000), it is crucial to consider both abiotic and biotic factors when investigating the mechanisms underlying successful colonization of native invaders. Furthermore, because the juxtaposition of alien plant invasion and native plant expansion caused by human activities is common (Carey et al., 2012), we recommend that land managers not only control alien invaders but also strengthen the management of native invaders across biogeographic regions.

AUTHOR CONTRIBUTIONS

Rui-Ting Ju, Bo Li, Jihua Wu, and Yu-Jie Zhao designed the experiments. Yu-Jie Zhao, Shengyu Wang, Lei Zhang, Peipei Cao, and Jingwen Bi performed the research. Yu-Jie Zhao and Rui-Ting Ju analyzed the data and drew the figures. Yu-Jie Zhao, Zhi-Yong Liao, Yaolin Guo, Christina L. Richards, Oliver Bosssdorf, Jihua Wu, Bo Li, and Rui-Ting Ju contributed to writing and/or revising the paper. All authors read and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Zhao et al., 2024a) are available in Dryad at <https://doi.org/10.5061/dryad.ngf1vhj1g>. Code (Zhao et al., 2024b) is available in Zenodo at <https://doi.org/10.5281/zenodo.13151552>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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