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Latitudinal trends in growth, reproduction and defense of an invasive plant

Li Xiao · Maxime R. Hervé · Juli Carrillo · Jianqing Ding · Wei Huang

Abstract Invasive plants often occupy an array of habitats along wide latitudinal scales which differ considerably in climatic conditions and herbivory. Variation in plant traits across latitude may play an important role in invasion success, yet few studies have tested whether there is a latitudinal pattern in invasive plant traits. Here, we sampled individuals of the invasive plant *Phytolacca americana* at 15 field sites spanning 10° of latitude from 25.72° to 36.15°N in central and southern China. We measured traits related to growth (plant height, canopy width, number of branches and stem diameter), reproduction (fruits per raceme and racemes per plant) and anti-herbivory defense (leaf, stem, root and fruit saponin). Overall, we found no latitudinal patterns for plant size, reproductive output or defense in growth tissues. However, growth architecture was significantly related to latitude: number of stems increased, while stem diameter decreased with increasing latitude. Reproductive architecture was also significantly related to latitude: with increasing latitude, plants produced fewer fruits per raceme, but more racemes per plant. We also found defense in reproductive tissue (fruit saponin) increased with increasing latitude.

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These findings provide an important latitudinal perspective for resource allocation and adaptive strategy in invasive *P. americana* that may aid in management recommendations at regional scales.

Introduction

Discovering mechanisms driving plant invasions is fundamental to invasion biology and is crucial for invasive plant management (Mitchell et al. 2006; Kuebbing and Nuñez 2015). Invasive plants often occupy a wide range of habitats in the introduced range which differ considerably in climatic conditions and biotic pressures (Hejda et al. 2009; Richardson and Pyšek 2012). Heterogeneity in the environment over large geographic scales can facilitate adaptation to local conditions by invasive plants and the formation of geographic clines; this may also promote rapid evolution at later stages of plant invasion (Prentis et al. 2008; Colautti and Barrett 2013; Bezemer et al. 2014). Studies on the performance of invasive plants along geographic clines may increase our understanding of how the invasion process is driven by multiple abiotic and biotic variables with the added benefit of facilitating management recommendations at more regional scales (Cronin et al. 2015; Hughes et al. 2016).

Geographical gradients in species traits are often attributed to a number of biotic and abiotic factors (Schemske et al. 2009; Maron et al. 2014). For example, latitudinal gradients in species interaction become stronger towards the equator, and the strength of selection on species traits is expected to increase in tropical regions (Dobzhansky 1950; Coley and Barone 1996; Schemske et al. 2009). For plant–herbivore interactions, the Latitudinal Herbivory-defense Hypothesis (hereafter LHDH, Coley and Aide 1991) predicts that increasing herbivore pressure at lower latitudes should select for greater investment in plant defenses (Pennings et al. 2001, 2009; Rasmann and Agrawal 2011). Indeed, the diversity and abundance of herbivores including both generalists and specialists can themselves exhibit latitudinal gradients (Mitchell et al. 2006; Bezemer et al. 2014; Cronin et al. 2015; Allen et al. 2017; Bhattarai et al. 2017). Thus, biotic factors, including herbivory and pathogen pressure, may play a determinant role in latitudinal trends of plant traits (Schemske et al. 2009). For example, the lower herbivory damage observed on the invasive plant *Arctium minus* at higher latitudes potentially contributed to its enhanced growth and seed production (Kambo and Kotanen 2014). Latitudinal trends in plant traits are also characterized by changes in abiotic factors such as temperature, precipitation, and the duration of the growing season. Invasive populations at high latitude may experience lower mean temperatures, lower precipitation, and a shorter season for active growth and development than low latitude populations, resulting in earlier phenologies, smaller seeds, and slower growth rates (Kollmann and Bañuelos 2004; Montague et al. 2008; Leiblein-Wild and Tackenberg 2014).

A growing number of studies have reported such latitudinal trends in growth, reproduction or defense in invasive plants (Bezemer et al. 2014; Cronin et al. 2015; Li et al. 2015; Liu et al. 2016). For example, in common garden experiments, the northern populations of the invasive plants *Solidago altissima* and *Solidago gigantea* had smaller size and produced flowers earlier than plants from southern populations (Weber and Schmid 1998). Similar latitudinal trends in growth and reproduction were also found in transplant experiments for *Impatiens glandulifera* (Kollmann and Bañuelos 2004) and *Lythrum salicaria* (Colautti et al. 2010). Latitudinal clines in defense may differ between native and invasive species, as invasive species can sometimes escape suppression by natural enemies from their native ranges (The enemy release hypothesis, hereafter ERH, Elton 1958). For example, Cronin et al. (2015) surveyed invasive and native populations of *Phragmites australis* and found that chewing damage and stem boring decreased with increasing latitude for native genotypes only, while chemical defenses (leaf phenolics) decreased with latitude for both native and invasive genotypes in the introduced range. To date, sufficient evidence has indicated that strategies of resources allocation among the traits of growth, reproduction and defense can influence colonization, establishment and spread of invasive plants in the introduced range (Sakai et al. 2001; Theoharides and Dukes 2007; Huang et al. 2010; Oduor et al. 2011; Yang et al. 2014; Zheng et al.

2015). However, latitudinal trends in these traits of invasive plants have rarely been investigated simultaneously (but see Kambo and Kotanen 2014), which limits our understanding of how invasive plants allocate resources along latitudinal gradients from a whole plant perspective.

Here, we examined the relationships among growth, reproduction and defense of *Phytolacca americana* across latitudes between central and southern China. *Phytolacca americana* is considered an aggressive plant pest due to its invasiveness and toxicity to mammals, and currently occupies a wide range of habitats in central and southern China (Xu et al. 2012; Ma 2013). A recent study suggests that the successful invasion of *P. americana* may result from a lack of natural enemies in its introduced range and corresponding evolution away from defense and towards growth, since plants sampled from the invaded range grew larger and produced more seeds than plants from the native range in the absence of herbivory (Huang and Ding 2016). However, field surveys in the introduced range found that *P. americana* is frequently attacked by foliar insects (e.g. caterpillars and beetles) associated with an indigenous congener, *Phytolacca acinosa,* and the abundance of generalist herbivores is higher in the southern compared to the northern range (Huang W., personal observation). Moreover, Huang and Ding (2016) found that there was no significant difference in growth and reproduction among invasive populations collected from 9 sites spanning 25–32°N in China, suggesting the invasion success of *P. americana* across latitudes is not associated with genetic evolution of plant trait variation, whereas the plastic response to environmental gradients may play a large role in its successful invasion. Overall, variation in abiotic and biotic factors across the broad-scale distribution of *P. americana* provides an excellent opportunity to study latitudinal trends in growth, reproduction and defense traits and the influence of abiotic and biotic factors on *P. americana* invasion at large scale geographic ranges.

In this study, we tested for latitudinal variation in *P. americana* plant traits by sampling 34 populations along a 10° latitudinal transect (Table S1, Fig. 1). Specifically, we asked whether there are latitudinal clines in herbivory, plant defense and growth in this invasive plant, and which biotic and abiotic factors are associated with variation in plant growth, reproduction and defense along latitudes.

Materials and methods

Study organism

Phytolacca americana L. (Phytolaccaceae) [Pokeweed], native to North America, is an herbaceous perennial shrub (Mitich 1994). It was introduced to China for ornamental purpose and first reported in 1935 in Zhejiang province (Xu et al. 2006, 2012). Currently, it is widely distributed in disturbed areas, abandoned fields, roadsides, and forest edges in central and southern China from temperate to subtropical zones (Ma 2013). *Phytolacca americana* is thought to exert a significant detrimental impact on coastal forest ecosystems by decreasing biodiversity (Zhai et al. 2010; Fu et al. 2012). Furthermore, it has largely replaced an indigenous congener *P. acinosa* which has been used as traditional Chinese medicine for more than 2000 years. Because *P. americana* is similar in appearance to *P. acinosa*, but considerably more toxic than *P. acinosa*, this has led to human poisoning by accidental usage (Kim et al. 2005).

Geographical survey

In 2013, we conducted a geographical survey at 15 field sites spanning 10° of latitude from 25.72° to 36.15°N in central and southern China (Table S1, Fig. 1). At each survey site, 2–5 quadrats were randomly established in different habitats including along active and abandoned farmland sites, roadsides, and sites alongside rivers and forest edges. Each quadrat was separated by at least two kilometers (Table S1). Only one quadrat was selected at Xinyang, Henan and Shouxian, Anhui due to intense human disturbance (Table S1, Fig. 1). To eliminate possible effect of altitude, all quadrats were less than 300 m above sea level (Table S1). We started field surveys at the southernmost site (Jiangxi province) in late July and ended at the northernmost site (Shandong province) in mid-August, completing all surveys within 3 weeks. This schedule corresponded with peak seed production at each site (Huang W., personal observation).

Fig. 1 Sampling sites (n = 15) for the invasive plant *Phytolacca americana* in central and southern China. At each field site, 2–5 quadrats were established which were separated by at least two kilometers (n = 34)
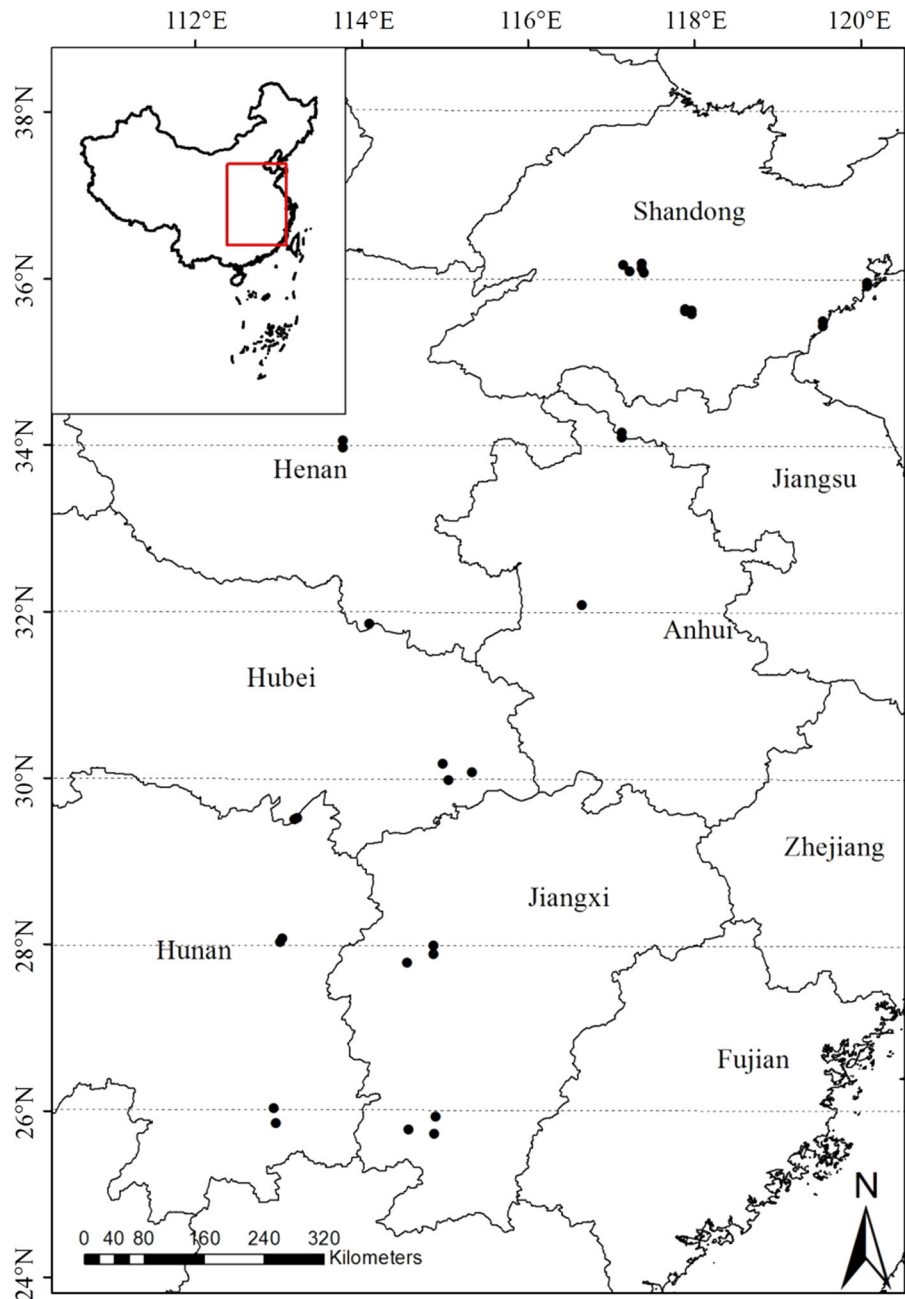
Measurements

Each quadrat (10 × 10 m) contained at least 10 individuals and was without evident disturbance caused by mammals and humans, where we could accurately evaluate plant traits with an adequate number of non-disturbed individuals. For growth traits, we measured plant height, canopy width and stem diameter, and recorded the number of branches. To evaluate plant height, we measured the perpendicular distance from the soil at its base to the top leaf in its natural position. To measure canopy width, we set two range poles to mark the extreme edges of the canopy and measured the widest point of the canopy. We measured stem diameter at 1 cm above the soil at its base and defined an individual branch as the

secondary stem arising from the main stem. For reproductive traits, we recorded the number of fruits per raceme and number of racemes per plant. To evaluate the number of fruits per raceme, we selected two racemes at the two widest points of each plant and counted the number of fruits. All above plant growth and reproductive traits were investigated on all plants within each quadrat (716 plants, 10–42 individuals per quadrat, Table S1).

Triterpenoid saponin is an important secondary metabolite in plants that serves as a defense against insects and pathogens and is the main active insecticidal component in *P. americana* (Augustin et al. 2011; Szakiel et al. 2011). To examine latitudinal trends in defense of *P. americana*, we measured triterpenoid saponin (hereafter saponin) in the leaves, stem, roots and fruits. We randomly selected five plants for saponin analysis within each quadrat (170 plants = 34 quadrats × 5 individuals). These five plants were at least 2 m apart from each other and from quadrat margins. We sampled leaves, main stem, roots and fruits (ca. 30 g) of each plant and stored the samples in individual Ziploc bags filled with silica gel. Leaves, main stem and mature fruits were detached at an intermediate height on each plant, and the taproot was dug out at around 10 cm depth. All samples were dried separately at 60 °C for 5 days, ground to a powder using a small medicinal mill, then stored in sealed tubes at − 20 °C until analyze. The modified methods of Huang and Fan (2010) were used to analysis saponin content. Briefly, samples (100 mg) were extracted in 5 ml methanol for 1 h at room temperature and then ultrasonically extracted for 30 min (500 W, 40 Hz). Insoluble materials were removed by centrifugation (5 min, 10,000 rpm, 4 °C). We estimated saponin content using spectrophotometry by mixing 0.2 ml of test solution with 0.2 mL of 5% vanillin-acetic acid solution and 0.8 mL perchloric acid solution, heating the solution for 15 min at 60 °C, immediately cooling them with ice and measuring their absorbance at 550 nm. We used oleanolic acid (Sigma-Aldrich) as a standard.

Environmental variables

Impact of latitude on plant growth, reproduction and defense may be determined by multiple abiotic and biotic factors that are highly correlated with latitude. Thus, to identify associations between abiotic factors and traits of *P. americana* across latitude, we downloaded climate data from Weather China Database (http://en.weather.com.cn/). The raw data were extracted from the climate stations nearest to each site. We selected variables known to be important for plant growth and reproduction, including annual mean temperature and total annual precipitation (Moles et al. 2014). To identify associations between biotic factors and plant traits across latitude, we measured percentage of leaf damage on plants sampled for chemical analysis (170 plants = 34 quadrats × 5 individuals). We recorded the number of total leaves and number of insect-damaged leaves on each plant. Then, we collected, scanned and digitized all damaged leaves and measured damaged leaf area using Digimizer software (MedCalc Software bvba; Mariakerke, Belgium). The percentage of damaged leaf area caused by insects was calculated as $\sum$ damaged leaf areas/(average leaf area × number of total leaves). In the geographical survey, we only recorded leaf damage since we did not observe insect or pathogen damage to stems, fruit or roots.

Statistical analysis

In this study, we measured four growth variables, two reproductive variables and four defensive variables. To reduce the dimensionality and explore the possible relationship between variables, principal component analyses (PCA) were conducted on the variables related to plant growth (PCA_G), reproduction (PCA_R) and defense (PCA_D) separately. Analyses were performed at the plant scale. The scores of the resulting PCA (axes 1 and 2) were used as representative variables that were linear combinations of the plant original variables and used for the following analyses.

To examine the impact of latitude on *P. americana* traits, representative variables were analyzed using Wald tests applied to linear mixed models (LMM). One model was built on each of the representative variables. They all included latitude as an independent variable, and site and quadrat as random factors (with quadrat nested within site). To test for an association between latitude and biotic environmental variables, insect damage was analyzed using Wald tests applied to LMM as described above. To test for an association between latitude and abiotic environmental variables, temperature and precipitation were analyzed using

Pearson correlation (raw data was extracted from climate stations at each site).

To evaluate the relative importance of each environmental variable on *P. americana* traits, linear models and model selection procedures were conducted for each plant variable. Firstly, a LM was built that included as independent variables temperature, precipitation, insect damage and latitude (to determine the effect of latitude beyond these three other variables). Models were based on mean values per site since temperature and precipitation were measured at the site scale. Secondly, an automatic selection procedure based on AICc (Akaike Information Criterion corrected for small samples, (Burnhan and Anderson 2002) was performed with every possible model, including 0 and all of the environmental variables (combinations = 16). Then, model averaging was performed considering all models with a difference in AICc (ΔAICc) less than two units compared with the best model (with lowest AICc, Johnson and Omland 2004). Results are reported with AICc, ΔAICc, and Akaike weight (AICc-W), which indicates the plausibility that a given model is the best model (Burnhan and Anderson 2002), and coefficient of determination R^2, which indicates the proportion of the total variation in plant trait that is explained by a given model. Furthermore, the relative importance of each environmental factor to plant trait was also calculated based the average model.

All analyses were conducted using R 3.2.0 (R Foundation for Statistical Computing, Vienna, Austria) with 'vegan', 'RVAideMemoire', 'lme4', 'car', 'MuMIn' packages (Fox et al. 2011; Bates et al. 2015; Oksanen et al. 2017; Hervé 2018).

Results

In the PCA_G analysis, the first two axes explained 64% and 21% of the total variation, respectively (Fig. 2a). The first axis positively related to plant height, canopy width, number of branches and stem diameter, thus was defined as a composite measure of "Plant size"; the second axis represented the trade-off between number of branches and stem diameter, and thus was defined as a composite measure of "Growth architecture" (Fig. 2a). Higher values on the first and second axes indicated bigger plants (axis 1), a greater number of branches and smaller stem diameters (axis 2). In the

PCA_R analysis, the first two axes explained 68% and 32% of the total variation, respectively (Fig. 2b). The first axis positively related to the number of fruits per raceme and number of racemes per plant, thus was defined as "Reproductive output"; the second axis represented the trade-off between these two traits, and thus was defined as "Reproductive architecture" (Fig. 2b). Higher values on the first and second axes indicated higher reproductive output (axis 1), and a greater number of fruits per raceme but smaller number of racemes per plant (axis 2). In the PCA_D analysis, the first two axes explained 55% and 24% of the total variation, respectively (Fig. 2c). The first axis negatively related to leaf-, stem- and root-saponin concentration, thus was defined as "Defense in growth tissues"; the second axis negatively related to fruit-saponin concentration, thus was defined as "Defense in reproductive tissue". For clarity, the sign of the coordinates on these two axes was inverted (Fig. 2c). In these cases, a higher value corresponds to a higher defense level, in growth tissues (first axis) and in fruits (second axis).

No significant effect of latitude was found on plant size ($\chi^2 = 1.198$, $P = 0.274$, Fig. 3a). However, growth architecture was significantly and positively related to latitude ($\chi^2 = 4.313$, $P = 0.038$, Fig. 3b). Plants at higher latitude had more branches and lower stem diameter than those at lower latitude. There was no significant effect of latitude on reproductive output ($\chi^2 = 3.056$, $P = 0.080$, Fig. 3c), while reproductive architecture was strongly and negatively related to latitude ($\chi^2 = 6.260$, $P = 0.012$, Fig. 3d). Plants at higher latitudes had less fruits per raceme, but more racemes per plant than those in the lower latitude. Plant defense in growth tissues was not affected by latitude ($\chi^2 = 2.513$, $P = 0.113$, Fig. 3e). However, plant defense in the reproductive tissues showed a significant positive correlation with latitude ($\chi^2 = 8.607$, $P = 0.003$, Fig. 3f). For environmental factors, annual mean temperature ($R^2 = 0.806$, $P < 0.001$) and annual precipitation ($R^2 = 0.307$, $P = 0.032$) were both strongly and negatively correlated with latitude (Fig. S1a, b). Furthermore, the percentage of insect-damaged leaf area was negatively correlated with latitude ($\chi^2 = 3.824$, $P = 0.050$, Fig. S1c).

Overall, there were no consistent impacts of environment factors on plant traits (Table 1). For growth traits, the best set of models explaining plant
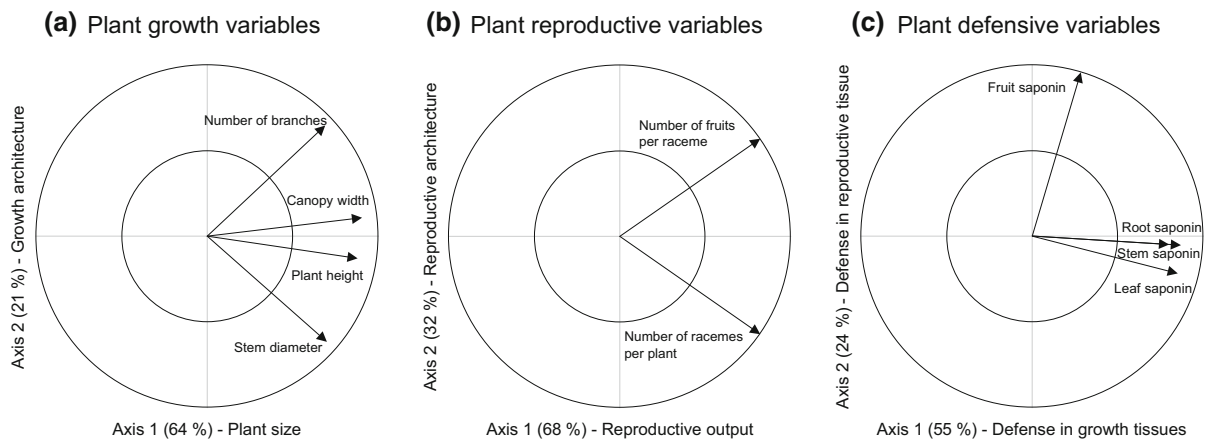
(a) Plant growth variables   **(b)** Plant reproductive variables   **(c)** Plant defensive variables

Fig. 2 Correlation circle plots for the results of principal component analyses (PCA) on the variables of growth (PCA$_G$), reproduction (PCA$_R$) and defense (PCA$_D$) of *Phytolacca americana*, separately. In the PCA$_G$ (**a**), first and second axes were defined as composite measures of "Plant size" and "Growth architecture", respectively. In the PCA$_R$ (**b**), first and second axes were defined as composite measures of "Reproductive output" and "Reproductive architecture", respectively.

In the PCA$_D$ (**c**), first and second axes were defined as composite measures of "Defense in growth tissues" and "Defense in reproductive tissue", respectively. The sign of the scores on PCA$_D$ axes 1 and 2 were inverted to ensure a positive correlation between original and new variables. PCA axes were used as representative variables for further correlation analyses with latitude. The radii of the centered and outer circles are 0.5 and 1 respectively

size included latitude, precipitation and insect damage. The averaged model explained 18% of variability and precipitation was the most important predictor (0.33). In contrast, the best set of models explaining growth architecture included latitude, temperature and precipitation. The average model explained 26% of variability and latitude was the most important predictor (0.50). For reproductive traits, the best set of models explaining reproductive output and architecture included latitude, temperature and insect damage. The average model explained 24% of variability in reproductive output and insect damage was the most important predictor (0.41), while the average model explained 39% of variability in reproductive architecture and latitude was the most important predictor (0.57). For plant defense traits, the model which best explained defense in growth tissue only included insect damage. The average model explained 24% of variability. In contrast, the model which explained defense in reproductive tissue included latitude and temperature. The average model explained 40% of variability and the latitude was a more effective predictor than temperature.

Discussion

Through a large-scale geographic survey, we found that some *P. americana* traits related to growth, reproduction and defense were strongly correlated with latitude. Moreover, we found temperature, precipitation and herbivory were all correlated with latitude. Together these results suggest that *P. americana* exhibits latitudinal trends across its introduced range and such latitudinal trends appear to be driven by abiotic and biotic factors.

Plant growth

Plants are generally expected to have smaller size at higher latitudes than at lower latitudes due to less favorable growing conditions (Moles et al. 2009). Such latitudinal trends in plant growth have been demonstrated in many invasive plants (Weber and Schmid 1998; Kollmann and Bañuelos 2004; Colautti et al. 2010). However, inconsistent with expectations, we found there was no significant latitudinal pattern in the plant size of *P. americana*. One explanation for this latitudinal trend is that reductions in precipitation at higher latitudes potentially contributes to enhanced growth as *P. americana* grows well in soil with moderate moisture (USDA Natural Resources
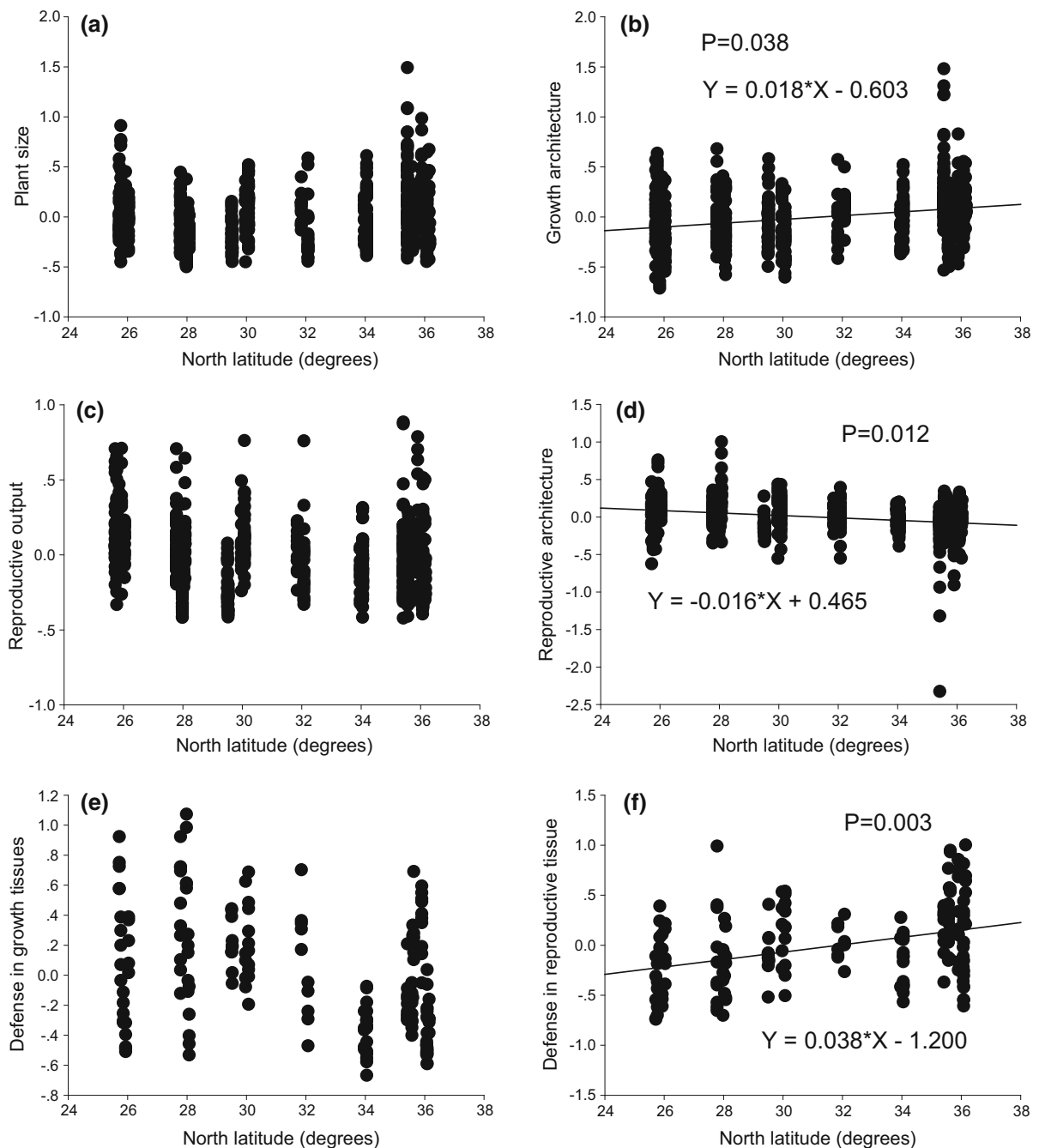
Fig. 3 Relationships between latitude and representative variables (PCA axes) for *Phytolacca americana*. The representative variables included plant size (**a**), growth architecture (**b**), reproductive output (**c**), reproductive architecture (**d**), defense in growth tissues (**e**) and defense in reproductive tissue (**f**). Higher values in the growth architecture represent a greater number of branches and lower the stem diameter, while higher values in reproductive architecture indicate a higher the number

of fruits per raceme and lower number of racemes per plant. Each point represents the mean value of all individuals in a quadrat (34 quadrats, 10–42 replicate individuals per quadrat, 716 individuals). Pearson correlation coefficients and *P* values adjusted by False Discovery Rate method are given. Lines through points indicate significant correlation between latitude and representative variables

Table 1 Models testing relationships of *Phytolacca americana* traits along latitude to abiotic and biotic factors for fixed predictors and the average model

Plant trait	Model	Inter	Latitude	Tempera	Precipita	Insect	AI	ΔA	AIC	R²
Plant size	1	− 0.002					− 15.22	0.00	0.236	0.00
	2	0.168			− 0.00018		− 14.82	0.40	0.193	0.17
	3	0.103				− 0.06051	− 14.53	0.69	0.167	0.15
	4	− 0.348	0.01085				− 13.63	1.59	0.107	0.10
	Average model	0.034	0.00180 (0.20)		− 0.00006 (0.33)	− 0.01654 (0.30)				0.18
Growth architecture	1	− 0.594	0.01819				− 13.95	0.00	0.265	0.24
	2	0.249		− 0.01660			− 13.30	0.66	0.191	0.21
	3	− 0.015					− 12.95	1.00	0.161	0.00
	4	− 0.998	0.02570		0.00017		− 12.11	1.84	0.105	0.34
	Average model	− 0.306	0.01046 (0.50)	− 0.00460 (0.33)	0.00003 (0.21)					0.26
Reproductive output	1	− 0.009					− 19.81	0.00	0.218	0.00
	2	0.686	− 0.01803			− 0.06855	− 19.40	0.41	0.177	0.36
	3	0.346	− 0.01114				− 18.96	0.85	0.142	0.14
	4	− 0.165		0.00979			− 18.46	1.35	0.111	0.12
	5	− 0.152		0.01616		− 0.06496	− 18.28	1.52	0.102	0.31
	Average model	0.169	− 0.00593 (0.40)	0.00312 (0.28)		− 0.02493 (0.41)				0.24
Reproductive architecture	1	0.464	− 0.01451				− 24.48	0.00	0.220	0.29
	2	0.733	− 0.01997			− 0.05438	− 24.48	0.00	0.220	0.45
	3	− 0.199		0.01261			− 23.18	1.30	0.115	0.23
	Average model	0.264	− 0.00953 (0.57)	0.00351 (0.31)		− 0.02084 (0.41)				0.39
Defense in growth tissue	1	− 0.311				0.18530	9.50	0.00	0.326	0.26
	2	0.012					10.72	1.22	0.177	0.00
	Average model	− 0.074				0.09175 (0.52)				0.24
Defense in reproductive tissue	1	− 1.208	0.03829				− 2.76	0.00	0.419	0.40
	2	0.551		− 0.03386			− 0.94	1.82	0.169	0.33
	Average model	− 0.648	0.02541 (0.66)	− 0.00849 (0.33)						0.40

The intercept, corrected Akaike Information Criterion (AICc), AICc difference (ΔAICc), Akaike weights (AICc-W) and R² are given for each model. AICc and ΔAICc are used to determine the best set of models. Akaike weights indicate the plausibility that a given model is the best model. R² indicates the proportion of the total variation in the plant trait explained by the model. Values in parentheses indicate the relative importance of each environment variable

Conservation Service, http://plants.usda.gov/java/charProfile?symbol=PHAM4).

Although there was no change of *P. americana* plant size with latitude, we found that the growth architecture of plants was significantly and positively related to latitude, and that this latitudinal trend can be explained by temperature. Plant growth architecture plays an important role in resource capture, and the

variations of growth architecture can be modified by multiple environmental factors such as light, temperature or water conditions (Stützel and Kahlen 2016). Our findings that *P. americana* had more branches and lower stem diameter at higher latitudes may indicate an architecture adaptation to environmental factors at higher latitudes. For example, the number of branches in *Stipa baicalensis* increased significantly with increasing latitude (Zhang et al. 2015), likely because low temperature can increase the production of tillers (Friend 1965; Chaturvedi et al. 1981). Future studies should incorporate more environmental variables to clarify the impact of abiotic factors on invasive plants over large geographic scales and provide greater predictability for their range expansion.

Plant reproduction

Reproductive traits are important for the establishment and spread of invasive plants (Burns et al. 2013; Moravcová et al. 2015). In this study, *P. americana* reproductive output (number of fruits per raceme and number of racemes per plant) showed no significant latitudinal trends, however, its reproductive architecture showed a significant negative relationship with increasing latitude, with less fruits per raceme, but more racemes per plant at higher latitude. The raceme production in *Trifolium repens* showed a similar latitudinal pattern, with populations from lower latitude producing higher raceme number per plant (Fraser 1991). This latitudinal trend of reproductive architecture may be affected by different abiotic factors across latitudes, such as light or temperature conditions. As shown in a recent study, low red/far-red ratios reduced growth of the main floral raceme while increased floral branching of *Brassica napus* (Rondanini et al. 2014). Plant reproductive performance can also be affected by temperature, for example, *Macadamia integrifolia* produced a higher number of flowers per raceme under warmer condition (Stephenson and Gallagher 1986). At high latitudes, *P. americana* produces more racemes but less fruits per raceme, which may disperse the risk of feeding by herbivorous animals.

Plant defense

It is often assumed that investment in defense should be greater at lower latitudes (LHDH, Coley and Aide 1991) since the diversity, density, and activity of natural enemies are often thought to be higher in tropical areas (Schemske et al. 2009; Rasmann and Agrawal 2011; but see Moles et al. 2011). In our study, although leaf damage of *P. americana* showed a latitudinal trend, the overall damage level was quite low due to a lack of natural enemies in the introduced range. Triterpenoid saponin content in *P. americana* vegetative tissue (e.g., leaves, stems, and roots) also showed no relationship with latitude. Thus, within the introduced ranges of invasive plants escaping natural enemies, the primary agent of selection for the LHDH could be missing. Conversely, a latitudinal trend in plant defense may be driven by variation in abiotic factors along latitude. As shown in our study, plant defense in reproductive tissues was positively related to latitude, and negatively related to temperature. Saponins in plants can play an important role in improving the resistance to low temperature stress (Zhao et al. 2016). At high latitudes, triterpenoid saponin in reproductive tissues of *P. americana* may facilitate plant tolerance of low temperature, suggesting *P. americana* can quickly adapt to local environmental conditions by changing defense strategies and which in turn may accelerate its invasion.

Phenotypic plasticity

Trait variation can be either genetically based or a plastic response to environmental gradients (Maron et al. 2004; Alexander et al. 2009; Richardson and Pyšek 2012; Colautti and Barrett 2013). An important limitation of our study is that we only conducted field surveys without experimental manipulations of populations and environments, which makes it difficult to disentangle ecological versus contemporary evolutionary (genetic) effects on variation in growth, reproduction, and defense traits along latitude. But, in a previous common garden experiment with *P. americana*, we found that there was no significant difference in total biomass, fruit mass or leaf damage among invasive populations spanning 25–32°N in China (Huang and Ding 2016). Similar to our study, Liu et al. (2016) found latitudinal clines in growth and reproduction of the invasive plant *Spartina alterniflora* across latitude, however, that geographic variation in traits disappeared in a common garden, indicating that the rapid spread of *S. alterniflora* has probably been facilitated by phenotypic plasticity in

growth and reproductive traits. Moreover, Allen et al. (2017) found that there were no latitudinal gradients in herbivory in invasive *P. australis* both in a field survey and common garden experiments, suggesting that enemy release of *P. australis* may also be driven by a plastic response, which may play a large role in invasion success. Together, our results suggest that the latitudinal trends in traits of *P. americanain* in the introduced range are more likely to be a plastic phenotypic response to abiotic and biotic factors, which may in turn contribute to its environmental tolerance and invasiveness across a wide range, although reciprocal transplant experiments may be necessary to test this prediction.

Impact of plant age

Plant growth and reproduction traits are expected to be correlated with plant age due to the annually steady growth of plant size, however, the correlation between plant growth and age can be quite weak (Van Pelt 2008), especially for adult plants. In our study we did not measure plant age but randomly established quadrats within the site and measured all individuals in each quadrat. However, variation in the plant age along the gradient is potential confounding factor that could affect the traits. Thus, future experiments are needed to determine the potential influence of plant age in explaining the observed latitudinal trends.

In summary, we found that some traits in growth, reproduction and defense of *P. americana* exhibit latitudinal trends in the invasive range and that the impacts of abiotic and biotic factors on latitudinal trends of *P. americana* are dependent on the nature of the specific plant traits. Plants at high latitudes had more branches and higher saponin contents in fruits which may be a plastic response and enhance resistance to harsh environments. Understanding resource allocation of *P. americana* at different latitudes may help in developing effective control measures which may vary based on the characteristics of invasive plant growth and reproduction.

Author contributions JD and WH conceived the project and designed experiments. LX and WH carried out field survey. WH and MRH analyzed data with interpretation from all authors. All authors wrote the first draft of the manuscript and revised subsequent versions.

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