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Lineage and latitudinal variation in *Phragmites australis* tolerance to herbivory: implications for invasion success

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Herbivores play a critical role in plant invasions either by facilitating or inhibiting species establishment and spread. However, relatively few studies with invasive plant species have focused on the role of plant tolerance and how it varies geographically to influence invasion success. We conducted a common garden study using two lineages (native and invasive) of the grass *Phragmites australis* that are prevalent in North American wetlands. Using 31 populations collected across a broad geographic range, we tested five predictions: 1) the invasive lineage is more tolerant to simulated folivory than the native lineage, 2) tolerance to herbivory decreases with increasing latitude of origin of the populations, 3) estimates of tolerance are correlated with putative tolerance traits and plasticity in those traits, 4) a tradeoff exists between tolerance and resistance to herbivory and 5) tolerance has a fitness cost. Response to folivory varied substantially among populations of *P. australis*, ranging from intolerance to overcompensation. Our model selection procedure deemed lineage to be an important predictor of tolerance but, contrary to our prediction, the native lineage was 19% more tolerant to folivory than the invasive lineage. Tolerance for both lineages exhibited a u-shaped relationship with latitude. A tolerance–resistance tradeoff was evident within the invasive but not the native lineage. Also, tolerance was positively correlated with belowground biomass allocation, leaf silica concentrations, specific leaf area and plasticity in stem density, and negatively correlated with the relative growth rate of the population and plasticity in putative resistance traits. Lastly, although we did not detect costs of tolerance, our results highlight that fast growth rates can maintain high fitness in the presence of herbivory. Herbivory and plant defense strategies for *P. australis* lineages in North America exhibit complex biogeographic patterns that cause substantial heterogeneity in enemy release and biotic resistance and, consequently, invasion success.

Keywords: biogeography, biotic resistance, enemy release, invasive plant, plant defenses, tolerance–resistance tradeoff

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Introduction

Natural enemies can play a major role in biological invasions. The well-supported enemy release hypothesis (ERH) predicts that exotic species successfully establish and spread throughout a novel territory by escaping their co-adapted assemblage of natural enemies from within their native range (Maron and Vilà 2001, Keane and Crawley 2002, Colautti et al. 2004, Liu and Stiling 2006). However, there is also ample evidence to suggest that native consumers can exert greater pressure on exotic species relative to co-occurring native species, thus inhibiting invasions (i.e. the biotic resistance hypothesis [BRH]; Elton 1958, Colautti et al. 2004, Levine et al. 2004, Parker and Hay 2005, Beaury et al. 2020).

Most studies of the ERH and BRH have focused on differences in herbivore richness, abundance, damage or resistance between native and invasive plant species, but tolerance to herbivory, i.e. the degree to which a plant can regrow or reproduce following herbivore damage (Strauss and Agrawal 1999), may also play a critical role in determining the success of invasive plant species relative to native species (Rogers and Siemann 2005, Ashton and Lerdau 2008, Ridenour et al. 2008, Fornoni 2011). Given that invasive plant species often grow faster than native species (van Kleunen et al. 2010), greater compensatory growth or tolerance might be expected for the former. Indeed, a meta-analysis by Zhang et al. (2018) found that invasive plant species were more tolerant to generalist herbivores than native plant species, however no differences in tolerance to specialist herbivores were observed. Thus, in addition to escape from coadapted herbivores in their native range and greater resistance to herbivores in their introduced range, plant invasion success may also be attributed to greater tolerance of generalist herbivores (Zhang et al. 2018). However, the relative contribution of each factor to invasion success is poorly understood and more studies are needed that examine different defense mechanisms (i.e. tolerance and resistance) in native-invasive plant systems. Given that resistance and tolerance traits are thought to be functionally redundant defense mechanisms, models for the joint evolution of resistance and tolerance have predicted that plants should adopt either a resistance or tolerance strategy, but not both (van der Meijden et al. 1988, Fineblum and Rausher 1995). However, evidence for such a tradeoff in plants is scarce (Leimu and Koricheva 2006, Więski and Pennings 2014, Puentes and Ågren 2014), with growing empirical support for the evolution of mixed defense strategies (Nunez-Farfan et al. 2007, Carmona and Fornoni 2013, Turley et al. 2013a). In fact, recent studies have suggested that plant tolerance and resistance may be positively correlated due to the sharing of the same molecular and genetic pathways (reviewed by Mesa et al. 2017).

The mechanisms underlying tolerance to herbivory are varied but relatively understudied (Tiffin 2000, Moreira et al. 2012, Siddappaji et al. 2013, Krimmel and Pearse 2016, Quijano-Medina et al. 2019). Plant traits like high photosynthetic rates, growth rates, belowground storage and branching are thought to promote compensatory growth, and therefore tolerance (Meyer 1998, Strauss and Agrawal 1999, Tiffin 2000, Lurie et al. 2017). Life-history traits like longer lifespan and investment in belowground also have been linked to tolerance (Krimmel and Pearse 2016). A more recently documented molecular mechanism includes endoreduplication – the replication of the genome without mitosis, which can enhance the expression of vital genes involved in rapid regrowth in response to herbivory (Siddappaji et al. 2013). In addition to the consistent expression of putative tolerance traits, it has also been suggested that plasticity in these types of compensatory traits can promote increased tolerance to herbivory, shading and drought (Juenger and Bergelson 2000, Valladares et al. 2014, Liu et al. 2016). Herbivore-induced growth is one example of adaptive phenotypic plasticity (Moreira et al. 2012). Tolerance has also been shown to be genetically variable with genotypes within the same plant species ranging from under- to overcompensation (Tiffin and Rausher 1999, Juenger and Bergelson 2000, Siddappaji et al. 2013, Garcia and Eubanks 2019).

Recent studies have shed light on the importance of biogeographic variation in biotic resistance and enemy release (Bezemer et al. 2014, Cronin et al. 2015, Burns 2016, Allen et al. 2017, Bhattarai et al. 2017a, b, Lu et al. 2018, 2019). Continent-wide plant invasions are complicated by spatial variation in the strength of species interactions, particularly with latitude (i.e. the biotic interaction hypothesis [BIH]; Dobzhansky 1950, Janzen 1970, Connell 1971, Pennings and Silliman 2005, Schemske et al. 2009, Cronin et al. 2015). Originally proposed as a possible mechanism generating a latitudinal gradient in species richness, the BIH has been adapted to explain the evolution of increased plant defense to herbivores towards the tropics (i.e. the latitudinal herbivory-defense hypothesis [LHDH]; Coley and Aide 1991, Johnson and Rasmann 2011, Wieski and Pennings 2014). Although the evidence in support of the LHDH is mixed, Moles et al. (2011) cautioned that many of the studies suffered from methodological issues including narrow latitudinal ranges and cross-species comparisons that potentially confound phylogenetic history. To date, most investigations of the LHDH have focused solely on resistance mechanisms, largely ignoring other defense strategies such as plant tolerance (Anstett et al. 2016). To our knowledge, only five studies have examined tolerance to herbivory along a latitudinal cline, with two finding support of the LHDH for resistance and the opposite pattern for tolerance (Lehndal and Ågren 2015a, b), and others finding no relationship between latitude and tolerance (Więski and Pennings 2014, Prendeville et al. 2015, Sakata et al. 2017). However, no studies have considered how tolerance in invasive species and co-occurring native species might differ across a broad geographic range and contribute to invasion success.

The continent-wide invasion of an Eurasian lineage of *Phragmites australis* in North America that now broadly overlaps with the native *P. australis* lineage serves as an ideal system to address how latitudinal heterogeneity in plant defense

strategies influences invasion success (Cronin et al. 2015, Meyerson et al. 2016a). The native and invasive *P. australis* lineages are morphologically, genetically and phenologically distinct, have broadly overlapping distributions and often occur in sympatry, allowing for phylogenetically controlled comparisons across large spatial scales (Cronin et al. 2015). In a common garden experiment in Baton Rouge, Louisiana, USA, we used 13 native and 18 invasive populations of *P. australis* that were collected across 19.5° latitude (Fig. 1, Supplementary material Appendix 1 Table A1.1) to examine plant tolerance to herbivory. We subjected one half of the replicate plants to repeated artificial folivory (40% of leaf tissue removed) and calculated the proportional change in total end-of-season biomass of damaged relative to undamaged plants as our estimate of tolerance. We also measured an array of putative tolerance, resistance and nutritional traits. We tested the following hypotheses: 1) the invasive lineage is more tolerant to simulated folivory than the native lineage; 2) for both lineages, tolerance to herbivory decreases with increasing latitude of origin of the populations; 3) the experimentally derived estimate of tolerance is correlated with putative tolerance traits and plasticity in those traits; 4) a tolerance-resistance tradeoff is evident for both lineages; and 5) increased tolerance incurs a fitness cost.

Methods

Study system

Phragmites australis is a 2–5 m tall perennial grass commonly found in wetlands, estuaries, salt marshes, ponds and rivers on every continent except for Antarctica (Clevering and Lissner 1999). Although present in North American wetlands for millennia (Hansen 1978, Orson 1999), *P. australis* began spreading aggressively, dominating wetlands and negatively impacting native plant species, hydrologic regimes, nutrient cycles and ecosystem function (Chambers et al. 1999, Meyerson et al. 2009, 2010). The rapid spread is attributed to the introduction of an invasive Eurasian lineage (haplotype M; *P. australis australis*) that first appeared in the herbarium record about 150 years ago (Chambers et al. 1999, Saltonstall 2002). Populations of the Eurasian lineage in North America are genotypically diverse (Saltonstall 2003) and despite being clonal, genotypic variation has been identified within patches (McCormick et al. 2010). Additional haplotypes have been introduced from Europe, North Africa (Lambertini et al. 2012, Meyerson and Cronin 2013) and Asia (Lambert et al. 2016), but their known distributions are localized and none were included in this study. Throughout North America,
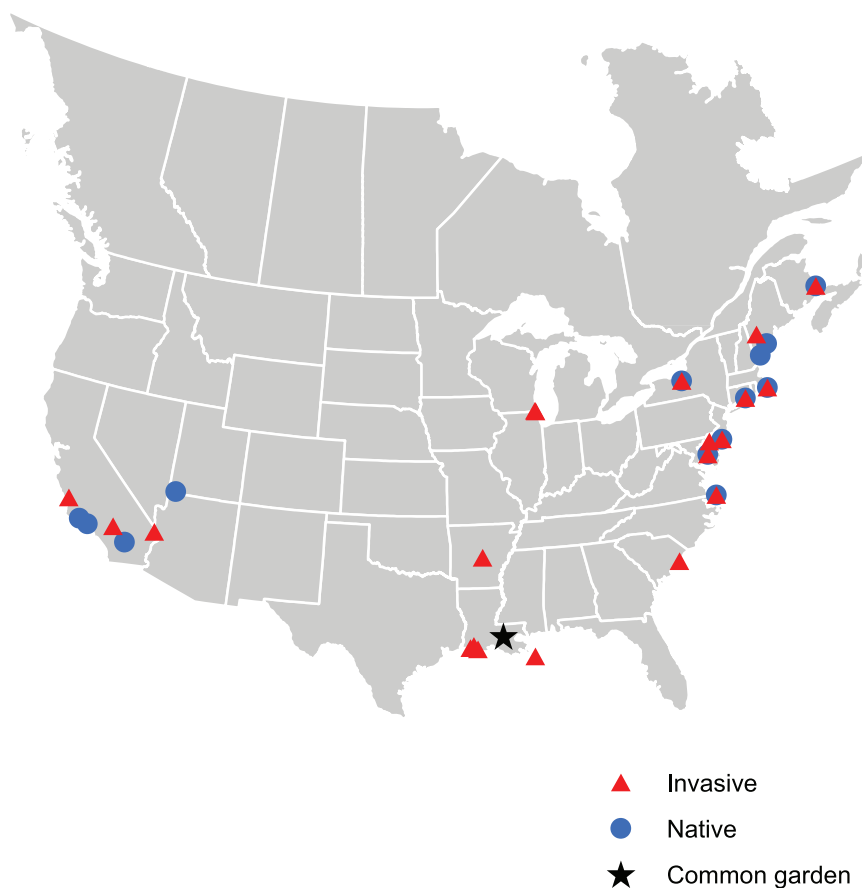

Figure 1. Distribution of *Phragmites australis* populations used in this experiment. See Supplementary material Appendix 1 Table A1 for details.

at least 14 closely related native endemic haplotypes have been identified (Saltonstall 2002, Meadows and Saltonstall 2007, Vachon and Freeland 2011). These native haplotypes have been given subspecies status (*P. australis americanus*) but are collectively referred to as the native lineage.

In Europe where it is considered native, *P. australis* is host to a diverse assemblage of arthropod herbivores with over 170 species identified. In contrast, only 26 herbivore species have been reported in North America (Tewksbury et al. 2002). Within North America, herbivory on *P. australis* is primarily attributed to herbivores introduced from Europe, most prominently stem-galling flies in the genus *Lipara* (Lambert et al. 2007, Allen et al. 2015, Cronin et al. 2015) and the mealy plum aphid *Hyalopterus pruni* (Lozier et al. 2009, Cronin et al. 2015). Based on previous research, there is strong support for the enemy release hypothesis: the invasive lineage suffers substantially less herbivory from each of three major feeding guilds (aphids, stem-gallers and leaf chewers) in its invasive than native range, and in comparison to co-occurring plants of the native lineage in North America (Cronin et al. 2015, Allen et al. 2015, Bhattarai et al. 2017a, b). Because these differences in herbivore abundance or damage between the native and invasive lineages are also manifested under common garden conditions, it suggests greater resistance to herbivory by the invasive than native lineage of *P. australis* and that resistance is genetically based (Lambert and Casagrande 2007, Allen et al. 2017, Bhattarai et al. 2017b). Interestingly, Cronin et al. (2015) found that leaf damage and stem-galler incidence decreased with increasing latitude for the native lineage but not invasive lineage, and these non-parallel latitudinal gradients in herbivory resulted in stronger enemy release at southern than northern latitudes (Cronin et al. 2015). This genotypic and latitudinal variation in herbivory lends credence to a biogeographic investigation into the role of plant tolerance to herbivory in invasion success.

Common garden

The common garden design used in this experiment is detailed in Bhattarai et al. (2017b). Briefly, rhizomes from *P. australis* patches were collected from field sites throughout North America spanning 19°5' of latitude and 55°9' of longitude and planted in a common garden established at Louisiana State University, Baton Rouge, LA (30°35'N, 91°14'W) in 2009 (Fig. 1, Supplementary material Appendix 1 Table A1.1). Plants were grown for at least one year prior to the start of the experiment to minimize the influence of maternal effects. In early March 2014, we potted 10 replicates for each of 31 source populations of *P. australis* (13 native, 18 invasive) in 7.6-liter pots. Each replicate consisted of a single rhizome cutting (10–15 g) potted in sand to standardize nutrients and initial starting conditions. Due to lower than expected propagation success, we added five additional replicate pots for each population in early May 2014. We fertilized each pot with Osmocote (58 g pot^{-1} of 3 month, slow-release in March followed by 58 g pot^{-1} of

9 month, slow-release in June of 15-9-12 NPK) and Ironite (1.7 g pot^{-1}) to ensure that resources were standardized. We repeatedly sprayed the plants with a non-systemic insecticide (Ortho Malathion) to prevent herbivore damage. Finally, we placed potted plants from each population in the same plastic pool (1.2 m diameter) filled with tap water. Plants subjected to different levels of folivory within a population were randomly distributed within pools, and populations were randomly distributed within the common garden.

Folivory treatment and tolerance

We implemented an artificial folivory treatment to simulate the effects of heavy folivory, a common approach in the study of tolerance to herbivory (Marquis 1988, Tiffin and Inouye 2000, Ashton and Lerdau 2008, Vergés et al. 2008, Lurie et al. 2017). *Phragmites australis* lineages vary widely in resistance to folivory (Cronin et al. 2015, Bhattarai et al. 2017b) and, consequently, it would have been difficult to achieve a standardized level of herbivory among source populations without varying herbivore density and/or exposure time. We assigned plants within a population at random to either a folivory or no folivory treatment. Starting in late May 2014, we clipped 40% of the leaf area, followed by a monthly removal of 40% of the new growth until late August. We clipped plants from the top–down to reflect herbivore behavior, because they generally remove the newest, most palatable leaves first. Although 40% folivory is a severe damage treatment, this level of herbivory has been observed in the field (Cronin et al. 2015).

At the end of the growing season (early November in Louisiana), we harvested above- and below-ground plant material, which was then air-dried on benchtops in the greenhouse until completely dried (2 months), and measured with a hanging scale (precision of ± 0.3%). Because flowering frequencies for *P. australis* in the first year following propagation from small rhizome cuttings are quite low, and biomass encapsulates all aspects of asexual reproduction, we used the total dry biomass at the end of the season as our proxy for fitness. Moreover, we had two planting dates owing to the need for supplemental plants, and it was our intention to include a blocking effect for planting date in our statistical models. However, we did not have sufficient replication within the second block to calculate tolerance for each source population. To account for possible differences in final plant size between planting dates, we used least-squares means for plant biomass (above-, belowground and total biomass) computed from a general linear model that included the main and interactive effects of clipping treatment and population, as well the main effect of planting date. From this, we obtained a planting date-independent estimate of plant biomass for each population in both the clipped and unclipped treatments. With these estimates, we calculated tolerance for each population using log-response ratios, where Tolerance$_{total}$ = ln[mean end-of-season total biomass of clipped plants/mean end-of-season total biomass of unclipped plants] (Hedges et al. 1999). A Tolerance$_{total}$ value of zero would indicate no effect of folivory

on end-of-season biomass whereas a Tolerance$_{total}$ > 0 would indicate overcompensation. Overall, the larger the value of Tolerance$_{total}$, the greater the tolerance of that population. We also calculated log–response ratios for aboveground (Tolerance$_{above}$) and belowground (Tolerance$_{below}$) biomass separately to compare the relative impacts of folivory on the shoot and root biomass, respectively. Lastly, we note here that the above method for estimating tolerance necessitated that the population, not the individual pot, was our unit of replication in this experiment, resulting in a single estimate of tolerance for each population. We averaged the estimates for dependent variables at the population-level to avoid pseudo-replication (rhizomes were collected from same pool of plants for each population and thus are not completely independent samples).

Putative tolerance and resistance traits

In addition to population-level measures of tolerance, we also measured a suite of plant functional traits that are widely recognized as correlates of plant tolerance and resistance to herbivore damage. How these traits change in response to a folivore treatment can provide clues as to the mechanisms underlying plant defenses. Putative tolerance traits like relative growth rate (RGR), root–shoot ratio, stem density and photosynthetic rate are closely associated with compensatory ability (Meyer 1998, Strauss and Agrawal 1999, Tiffin 2000). To estimate plant RGR, we divided total end-of-season biomass by the number of days in the growing season. This is a valid measure of RGR because *P. australis* aboveground biomass accumulation in our garden plot increased approximately linearly with time, based on monthly measurements ($R^2 = 0.071$, $p < 0.001$), and a quadratic term was not significant ($R^2 = 0.071$, $p < 0.663$; Supplementary material Appendix 2 Fig. A2.1). Because some plants grew for a longer period of time than others, due to the inclusion of the block of supplementary plants, we used the same statistical procedure to account for the blocking effect on RGR as was done for biomass. In addition to RGR, we measured stem density at the last census of the growing season (late August 2014) and calculated root mass fraction (= belowground biomass/ total biomass; Pérez-Harguindeguy et al. 2016).

High rates of photosynthesis are thought to be a potential mechanism of tolerance, and specific leaf area is a frequently used correlate for photosynthetic ability (Pérez-Harguindeguy et al. 2016). In August 2014, we photographed and subsequently collected the uppermost fully open leaf of three stems per pot. The leaves were dried at 50°C for 72 h before being weighed. We measured leaf area using ImageJ software (Schneider et al. 2012), and calculated specific leaf area as the ratio of area to dry biomass for a leaf (mm^2 mg^{-1}). Using a porcelain pestle and mortar, we ground the dry leaf material into fine powder for leaf chemical analyses.

Foliar nitrogen and carbon serve important physiological and ecological functions, with nitrogen content linked to photosynthetic ability (Evans 1989) and both carbon and nitrogen content shown to influence herbivore performance (Agrawal 2004, Imaji and Seiwa 2010, Cronin et al. 2015). In particular, because nitrogen is often positively correlated with plant RGR and RGR is a putative tolerance trait, plants with high foliar nitrogen content are expected to better compensate for herbivore damage than plants with low nitrogen content (Vergés et al. 2008, Bagchi and Ritchie 2011, Mundim et al. 2012). Therefore, we assayed dried leaf tissues for percent carbon (%C), percent nitrogen (%N) and C:N ratio using an elemental analyzer at Brown University Environmental Chemistry Facilities (<www.brown.edu/ Research/Envchem/facilities/>).

In addition to foliar nutrients, we measured leaf toughness and total phenolics, two putative resistance traits known to correlate with *P. australis* herbivory (Cronin et al. 2015, Bhattarai et al. 2017b). Using a penetrometer, leaf toughness (force [kg] required to push a blunt steel rod [4.8 mm in diameter] through the leaf) was measured on the uppermost fully open leaf on three randomly selected stems per plant. Total phenolics (Nm g^{-1} of dried leaf tissue) were estimated using a modified version of the Folin–Ciocalteu method (Waterman and Mole 1994, Cronin et al. 2015) at the University of Rhode Island, Kingston, RI. Although never before examined in *P. australis* in the context of plant defense, we also analyzed plants for silica content (g kg^{-1}) at the Louisiana State University AgCenter Soil Testing and Plant Analysis Lab, using methods adapted from Kraska and Breitenbeck (2010). Silica is a known herbivore defense in grasses (McNaughton et al. 1985, Massey et al. 2006, Reynolds et al. 2012).

Putative resistance traits sometimes fail to predict, or are only weakly correlated with, true resistance measured in terms of herbivore preference or performance on different plants (Fritz and Simms 1992, Bhattarai et al. 2017b). The best test of tolerance–resistance tradeoffs is with true measures, not putative correlates of each trait. Although we did not measure true resistance in this study, we used data from Bhattarai et al. (2017b) that quantified *P. australis* resistance to a generalist leaf-chewing herbivore, *Spodoptera frugiperda* (fall armyworm; Lepidoptera: Noctuidae) on the same clonal populations used for this study and from within the same common garden. Briefly, in this bioassay, Bhattarai et al. (2017b) reared individual pre-weighed *S. frugiperda* larva on replicate plants of each source population for eight days. Afterward, larval biomass and leaf area consumed were measured and plant palatability to the herbivore (biomass conversion efficiency) was calculated (proportional change in larval fresh mass per unit area of leaf consumed; all measurements ln-transformed). The inverse of this metric was used as a measure of resistance. Between the two experiments, there were 20 overlapping populations that used identical genetic material for plant propagation. Finally, we note that although resistance and tolerance were measured one year apart, our work suggests that population-level resistance is strongly genetically based and relatively fixed over time (Allen et al. 2017, Bhattarai et al. 2017b). Moreover, clonal integrity was maintained in the garden over the years by preventing sexual reproduction (via removal of all panicles prior to

floral maturation) and external contamination of our populations from naturally occurring seed sources was exceedingly unlikely given that the nearest source of *P. australis* was > 100 km away. Thus, we feel confident that these two data sets allow for a valid assessment of a tolerance–resistance tradeoff among *P. australis* populations.

Statistical methods

To test our first two predictions, that the invasive lineage is more tolerant than the native lineage and that tolerance varies geographically (latitude and longitude of origin of the populations), we used Akaike's information criterion corrected for finite sample size (AIC_c) to select the most informative model explaining variation in tolerance (Burnham and Anderson 2002). The full general linear model evaluated the effects of latitude and longitude of origin, lineage and all possible two-way interactions (all fixed effects) on each tolerance metric ($Tolerance_{total}$, $Tolerance_{above}$, $Tolerance_{below}$). Moreover, because plant density may decrease toward the range limits of a species, and because species interactions are likely to be density-dependent, the relationship between plant defense levels and latitude may be non-linear, as predicted by the 'range center' hypothesis (García et al. 2000, Alexander et al. 2007, Gaston 2009, Woods et al. 2012). Thus, we included a quadratic term ($latitude^2$) as a predictor variable in our model-selection procedure. Plant longitude of origin was included in the model to account for possible east-to-west variation in traits which, for the invasive lineage, may be related to its westward spread across North America (Saltonstall 2002, Fig. 1, Supplementary material Appendix 1 Table A1.1). From these variables of interest, we used the dredge function in the MuMIn package (Bartoń 2019) in R (<www.r-project.org>) to generate candidate models containing all possible combinations of longitude, latitude, lineage and all possible two-way interactions, but excluding models containing interactions without the main effects and models containing quadratic latitudinal terms without the linear term. As implemented in the package AICcmodavg ver. 2.1.1 (Mazerolle 2019), candidate models were ranked by AICc from lowest to highest value and models with a Δ_i value (= $AICc_i - AICc_{min}$) of ≤ 2 were deemed to have substantial support (Burnham and Anderson 2002). We also report the AICc weights (w_i) which indicate the weight of evidence (as a proportion) in favor of model *i* being the best model given the set of candidate models.

For our third prediction, that the expression of plant resistance and tolerance traits or plasticity in those traits is related to our experimental measure of tolerance ($Tolerance_{total}$), we used the same model-selection approach as outlined above. First, for each of the ten plant traits (leaf phenolics, silica, %C, %N, C:N, specific leaf area, leaf toughness, root mass fraction, stem density and log-transformed RGR), we calculated the mean for each *P. australis* source population using only the unclipped (control) plants. Trait plasticity for each population was computed as $Plasticity_{trait} = \ln[\text{trait mean for clipped plants/trait mean for unclipped plants}]$

(Liu et al. 2016). Second, we conducted separate principal component analyses (PCA) for the trait means and trait plasticities to reduce the dimensionality of these two data sets (Supplementary material Appendix 2 Table A2.1) (Jolliffe and Cadima 2016). Trait PCs were retained for subsequent analysis if their eigenvalues > 1 (Kaiser 1960). Third, to link trait PCs (response variables) to tolerance, we generated candidate models containing all possible combinations of longitude, latitude, $latitude^2$, lineage, $Tolerance_{total}$ and all possible two-way interactions, but excluding models containing interactions without the main effects and models containing quadratic latitudinal terms without the linear term. We performed the equivalent AICc model selection procedure described above for each trait PC. Finally, if $Tolerance_{total}$ was included in one or more of the top models ($\Delta_i \leq 2$), we plotted the estimated relationship between the trait PC and tolerance from the model with the lowest AICc values. The trait loadings for each PC were plotted adjacent to the tolerance–trait figure to illustrate the traits involved in the tolerance–trait relationship. In order to narrow down the number of traits to consider, we only discuss patterns for traits within a PC that have a Pearson correlation coefficient > 0.5.

Our fourth prediction examined whether a tradeoff exists between plant tolerance and resistance. We tested for a tradeoff by incorporating our measure of resistance (1/biomass conversion efficiency) and the interaction of resistance with *P. australis* lineage (resistance × lineage) into the top model for tolerance resulting from the model selection procedure described above for our first two predictions. This approach allowed us to test for a tradeoff within lineages while accounting for potential biogeographic variation in tolerance.

For our fifth prediction, we tested for the presence of costs associated with tolerance to herbivory using the method outlined by Strauss and Agrawal (1999). For each lineage, we regressed population-level means of total end-of-season biomass for the damaged plants against total end-of-season biomass for the undamaged plants. We also included a quadratic term (total $biomass^2$) to account for the possibility that the costs of tolerance are non-linear and a biomass by lineage interaction to test for different costs between lineages. A negative relationship between biomass of the undamaged and damaged plants would indicate a cost of increased tolerance (Strauss and Agrawal 1999).

Results

Lineage and geographic variation in tolerance to folivory

On average, simulated herbivory (40% removal of new leaf tissue each month) reduced aboveground plant biomass by 14% ($t_{30} = -1.57$, $p = 0.13$), belowground biomass by 19% ($t_{30} = -3.01$, $p < 0.005$) and total biomass by 18% ($t_{30} = -2.43$, $p = 0.02$; Supplementary material Appendix 2 Fig. A2.2). At the population level, the effects of folivory ranged from a 74% reduction to a 72% increase in total

biomass (Supplementary material Appendix 2 Fig. A2.3–4), and this variability was explained in large part by *P. australis* latitude and longitude of origin and lineage.

The top-ranked AICc models were consistent across tolerance metrics, with each of the top models containing the main effects of latitude and longitude of origin, as well as a non-linear latitude term (Table 1). The AICc-best model for Tolerance$_{total}$ (AICc-weight = 0.64) explained 44% of the variation in the response variable (Table 1). The next best model (AICc-weight = 0.36) included the same predictors as above but also lineage. Based on the top model, tolerance increased from east to west, whereby the most westerly population was 1.8 times more tolerant than the most easterly population ($F_{1,27}$ = 4.74, p = 0.038). Moreover, regardless of *P. australis* lineage, we found a strong, u-shaped relationship between tolerance and latitude of origin of the populations ($F_{1,27}$ = 12.86, p = 0.001; Fig. 2A), with a minimum expression of tolerance around 35° latitude. Finally, contrary to our prediction, tolerance for the native lineage was 19% greater than for the invasive lineage (Fig. 3) but the difference was not statistically significant ($F_{1,26}$ = 1.72, p = 0.201). The only model deemed likely for Tolerance$_{above}$ was the same as the AICc-best model for Tolerance$_{total}$ (Table 1) and the patterns were the same as described previously (Fig. 2B, 3).

However, there were differences between above- and belowground tolerances that were primarily rooted in the latter tolerance response being influenced by *P. australis* lineage. The best-supported model for Tolerance$_{below}$ included latitude, latitude^2 and lineage (Table 1). On average, native populations were 21% more tolerant than invasive populations but the difference was marginally significant ($F_{1,27}$ = 3.09, p = 0.090; Fig. 3). Interestingly, one of the top models for Tolerance$_{below}$ contained a lineage × latitude interaction (AICc weight = 0.13; R^2 = 0.41) in which the higher Tolerance$_{below}$ of the native lineage further increased toward lower latitudes (Fig. 2C).

Plant traits and tolerance

Plant traits varied considerably across populations and between treatments, and we report boxplots for each trait in

Supplementary material Appendix 3 Fig. A3.2–12. The first three principal components for plant trait values had eigenvalues > 1 and explained 31, 19 and 12% of trait variation (62% total), respectively (Supplementary material Appendix 3 Table A3.1). The first axis was well correlated with root mass fraction (r = 0.53; % contribution = 9.3%), specific leaf area (r = 0.68; 15.2%), leaf C:N (r = −0.68; 15.2%), leaf silica content (r = 0.76; 18.9%) and growth rate (r = −0.76; 19.1%), the second axis with root mass fraction (r = −0.52; 13.8%), leaf % carbon (r = 0.68; 24.0%) and leaf % nitrogen (r = 0.87; 39.2%), and the third axis with stem density (r = −0.60; 30.0%), leaf toughness (r = 0.54; 24.4%) and leaf phenolic content (r = −0.55; 25.7%). Overall, PC1, PC2 and PC3 are most related to growth/plant structural integrity, nutritional chemistry and resistance traits, respectively.

The primary objective here was to evaluate whether the PCs of trait means and plasticities were related to tolerance while accounting for biogeography (i.e. latitude, longitude) and lineage effects. Of the five resulting top models for PC1 (representing growth/structural integrity), all contained latitude, three contained latitude^2, one contained longitude, three contained tolerance (Tolerance$_{total}$), including the AICc-best model, and two contained either a latitude × tolerance or latitude^2 × tolerance interaction (Table 2). PC1 was positively and significantly related to tolerance ($F_{1,27}$ = 4.86, p = 0.04; Fig. 4A). For PC2 (representing nutritional chemistry), latitude (2 of 3) and lineage (1 of 3) appeared in the AICc-ranked top models but not tolerance (Table 2). Lastly, PC3 (representing resistance traits) included only *P. australis* lineage and tolerance in top models (Table 2), with tolerance negatively correlated with PC3, although it was not significant ($F_{1,28}$ = 0.63, p = 0.43, Fig. 4B).

For our trait plasticities, the first four principal components for plastic trait values had eigenvalues > 1 and explained 26, 21, 17 and 12% of trait variation (75% total), respectively (Supplementary material Appendix 2 Table A2.1). The first axis was highly correlated with plasticity in stem density (r = 0.69; % contribution = 20.8%), leaf % nitrogen (r = −0.51; 11.4%) and leaf C:N (r = 0.92; 36.7%), the second axis with leaf % carbon (r = −0.85; 38.2%) and leaf % nitrogen (r = −0.76; 30.5%), the third axis with stem density

Table 1. Best models (ΔAICc < 2) for the effects of lineage, longitude, latitude, a quadratic term for latitude (latitude^2), and all possible two-way interactions on each *P. australis* tolerance metric (log-response ratio for total biomass [Tolerance$_{total}$], aboveground biomass [Tolerance$_{above}$] and belowground biomass [Tolerance$_{below}$]). The best model was used to show the relationship between latitude and each tolerance variable.

| Dependent variables	Models	AIC$_c$	Δ$_i$	AIC$_c$ Wt	R^2
Tolerance$_{total}$	Longitude + Latitude + Latitude^2	30.76	0.00	0.64	0.44
	Lineage + Longitude + Latitude + Latitude^2	31.88	1.11	0.36	0.47
Tolerance$_{above}$	Longitude + Latitude + Latitude^2	40.49	0.00	1.00	0.46
Tolerance$_{below}$	Lineage + Latitude + Latitude^2	27.78	0.00	0.21	0.37
	Longitude + Latitude + Latitude^2	27.86	0.08	0.20	0.37
	Latitude + Latitude^2	28.28	0.50	0.17	0.30
	Lineage + Longitude + Latitude + Latitude^2	28.46	0.67	0.15	0.42
	Lineage + Latitude + Latitude^2 + Lineage × Latitude^2	28.61	0.83	0.14	0.41
	Lineage + Latitude + Latitude^2 + Lineage × Latitude	28.75	0.97	0.13	0.41
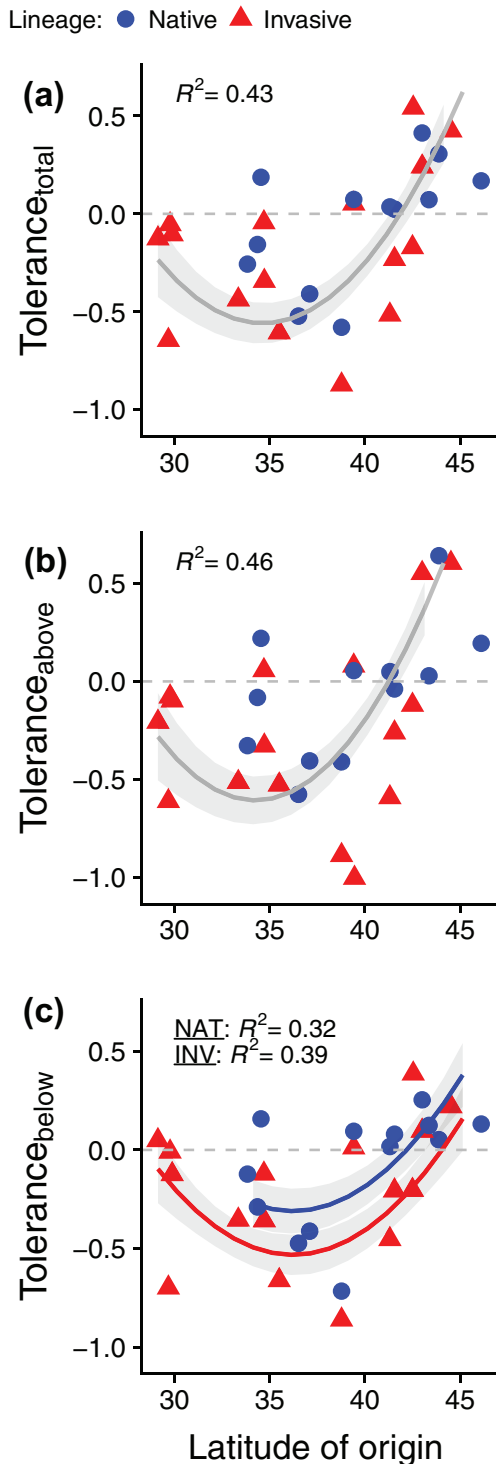
Figure 2. Figure 2. The relationship between tolerance to folivory and latitude of origin of populations of the native and invasive *Phragmites australis* lineages. Tolerance, measured as the log-response ratio of biomass in the clipping treatment relative to the unclipped controls is reported for (a) total biomass (Tolerance$_{total}$), (b) aboveground biomass (Tolerance$_{above}$) and (c) belowground biomass (Tolerance$_{below}$). For Tolerance$_{below}$, a lineage effect was present in the top model (Table 1). Therefore, separate least-squares regression lines are presented for the native (Nat) and invasive (Inv) lineages.
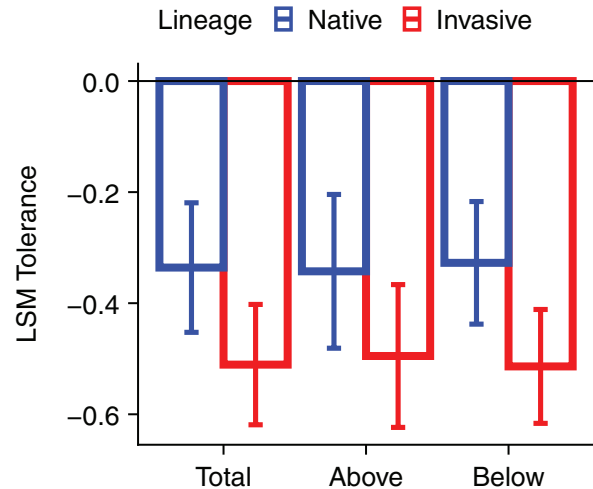

Figure 3. Tolerance to folivory between native (blue) and invasive (red) *Phragmites australis* lineages in North America. (A) Tolerance$_{total}$, (B) Tolerance$_{above}$, and (C) Tolerance$_{below}$. Reported are least-squares means (LSM) ± SE for each lineage, after accounting for the effects of latitude (linear and quadratic terms) and longitude of origin. Only for Tolerance$_{total}$ and Tolerance$_{below}$ did the AICc-best models include lineage as an important predictor of tolerance.

(r = −0.59; 23.5%), leaf toughness (r = −0.54; 19.5%) and root mass fraction (r = 0.68; 31.3%), and the fourth axis with specific leaf area (r = 0.68; 43%).

Model selection for the first trait plasticity axis (PC1) produced six plausible models containing combinations of latitude (3 of 6 models), latitude^2 (2 of 6), lineage (5 of 6), tolerance (5 of 6), tolerance × latitude (1 of 6) and tolerance × lineage (2 of 6) (Table 2). Using the AICc-best model, PC1 (increased stem production) was positively related to tolerance ($F_{1,27} = 8.85$, p = 0.006, Fig. 4C). For PC2 (decreased silica and nitrogen), none of our predictor variables were deemed important. The AICc best model for the third axis (PC3; increased root mass fraction and decreased stem density and leaf toughness) included tolerance as the only predictor variable, to which it was negatively related ($F_{1,28} = 3.05$, p = 0.09, Fig. 4D). Lastly, the AICc-best model to explain PC4 was the intercept-only model and none of the plausible models included tolerance.

Tolerance–resistance tradeoff

After accounting for biogeographical variation in Tolerance$_{total}$, we found a significant relationship between tolerance and resistance that depended on *P. australis* lineage (lineage × resistance interaction: $F_{1,15} = 6.43$, p = 0.02; Fig. 5). When considering each lineage by itself, the negative relationship between tolerance residuals (accounting for longitude and latitude) and resistance was significant for the invasive lineage ($F_{1,10} = 25.0$, $R^2 = 0.71$, p < 0.001) but not for the native lineage ($F_{1,5} = 0.80$, $R^2 = 0.14$, p = 0.41). Overall, the lineage-dependent tradeoff explained 56.9% of

Table 2. AICc-best models (ΔAICc < 2) describing variation in constitutive and plastic plant trait principal components (PC). Model selection was applied to PCs with an eigenvalue > 1. The full model contained plant latitude of origin (linear and quadratic terms), lineage, Tolerance$_{total}$, longitude and all possible two-way interactions. For those models marked with a '†', the relationship between the PC and tolerance is reported in Figure 4.

Trait PC	Models	AIC$_c$	Δ_i	AIC$_c$ Wt	R^2
Trait values					
PC1	Latitude + Latitude^2 + Tolerance†	110.76	0	0.31	0.53
	Latitude + Longitude	111.04	0.28	0.27	0.48
	Latitude	111.96	1.2	0.17	0.41
	Latitude + Latitude^2 + Tolerance + Latitude^2 × Tolerance	112.38	1.62	0.14	0.55
	Latitude + Latitude^2 + Tolerance + Latitude × Tolerance	112.57	1.81	0.12	0.55
PC2	Latitude	111.68	0	0.40	0.08
	Intercept only	111.69	0	0.40	0.00
	Latitude + Lineage	113.15	1.47	0.19	0.11
PC3	Lineage	91.68	0	0.73	0.22
	Lineage + Tolerance†	93.64	1.96	0.27	0.23
Plasticity					
PC1	Lineage + Tolerance†	109.08	0	0.25	0.27
	Latitude + Latitude^2 + Lineage + Tolerance	109.30	0.22	0.22	0.40
	Lineage + Tolerance + Lineage × Tolerance	109.75	0.67	0.18	0.33
	Latitude + Lineage + Tolerance + Latitude × Lineage	110.34	1.25	0.13	0.38
	Tolerance	110.34	1.26	0.13	0.17
	Latitude + Latitude^2 + Lineage + Tolerance + Lineage × Tolerance	111.01	1.93	0.09	0.44
PC2	Intercept	107.38	0	1	0.00
PC3	Tolerance†	99.87	0	0.23	0.10
	Latitude	99.94	0.07	0.22	0.10
	Intercept only	100.5	0.63	0.17	0.00
	Longitude + Tolerance	100.82	0.95	0.14	0.15
	Longitude	101.00	1.12	0.13	0.06
	Latitude + Tolerance	101.19	1.31	0.12	0.14
PC4	Intercept only	91.08	0	0.45	0.00
	Latitude + Longitude	92.78	1.7	0.19	0.11
	Latitude	92.81	1.73	0.19	0.02
	Latitude + Longitude	93.07	1.99	0.17	0.02

the variance in tolerance after accounting for biogeographic variation (using the regression between tolerance residuals).

Costs of tolerance

We found that the relationship between total biomass of damaged plants and total biomass of undamaged plants depended on *P. australis* lineage ($F_{1,27}$ = 5.65, p = 0.025, Fig. 6). The native lineage relationship overlapped with the 1:1 line, indicating complete compensation. In contrast, the invasive lineage exhibited a hump-shaped relationship falling beneath the 1:1 line, indicating under compensation, especially for populations that are genetically predisposed to having large end-of-season biomass. Because populations were allowed to grow over the same time period, faster-growing plants were the least capable of compensating for folivory but maintained high relative biomass in the presence of herbivores. The relationship between total biomass of damaged and undamaged plants for the native lineage does not support the prediction that tolerance is costly, but the non-linear relationship for the invasive lineage suggest that costs of tolerance are only detectable when growth rates in the absence of herbivory are sufficiently high. However, the difference between the native and invasive lineage disappears after removing a particularly

fast-growing invasive population (i.e. the point in Fig. 6 with the highest total biomass; R^2 = 0.45, p = 0.15).

Discussion

The effects of simulated folivory varied substantially among populations of *Phragmites australis*, ranging from relative intolerance to overcompensation. These broad differences in tolerance to herbivory are genetically based and consistent with the intraspecific variation in tolerance found in other plant species (Tiffin and Rausher 1999, Stevens et al. 2007, Hakes and Cronin 2011). However, our study points to a complex geographic pattern of defenses for *P. australis* in North America. Previous work strongly suggests that invasive *P. australis* is substantially more resistant to herbivory than native *P. australis* – plants of the invasive lineage have considerably lower herbivore loads and leaf-tissue losses in the field and lower palatability to leaf chewing and sucking herbivores in common garden experiments than plants of the native lineage (Lambert and Casagrande 2007, Lambert et al. 2007, Allen et al. 2015, 2017, Cronin et al. 2015, Bhattarai et al. 2017a, b). Our current study, which is the first to experimentally quantify variation in tolerance to herbivory between
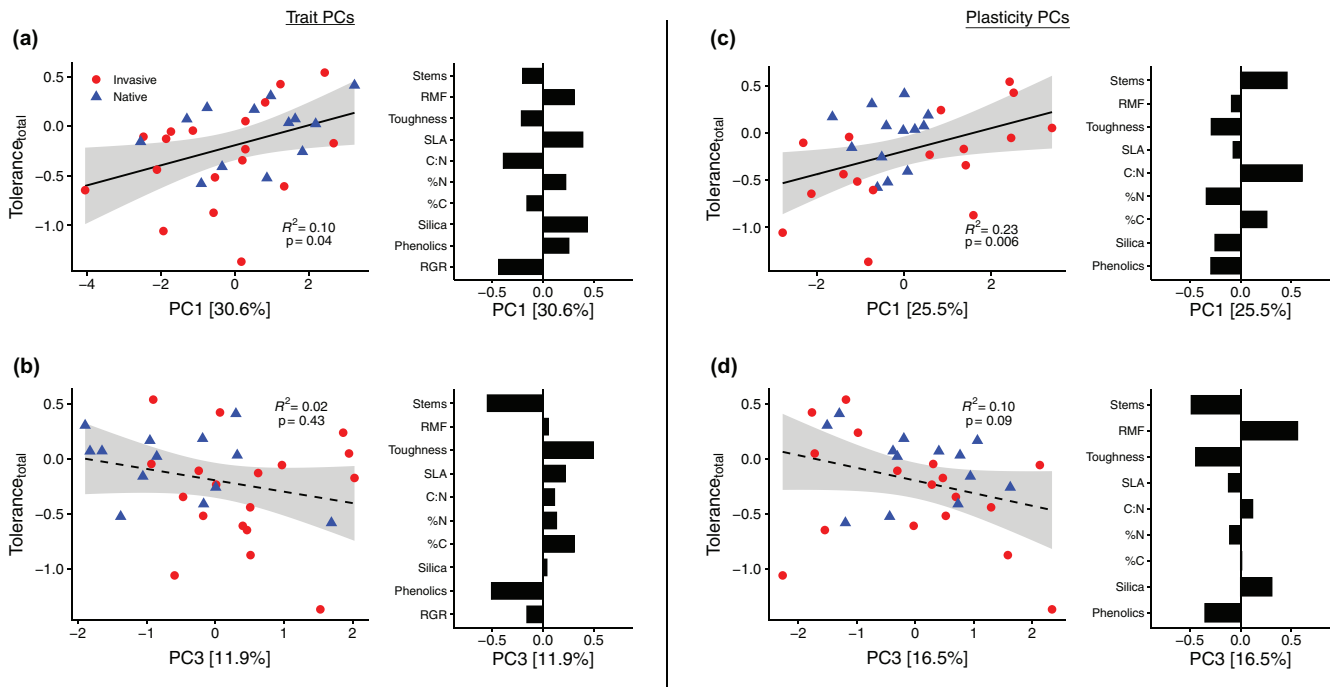
Figure 4. Relationships between *Phragmites australis* tolerance (Tolerance$_{total}$) and trait principal components (left) or plasticity PCs (right). These relationships emerged as important based on the model selection analysis (Table 2). Solid and dashed regression lines indicate significant ($p \leq 0.05$) and nonsignificant ($p > 0.05$) relationships, respectively. The individual trait loadings from the principal components analyses are plotted adjacent to each PC.
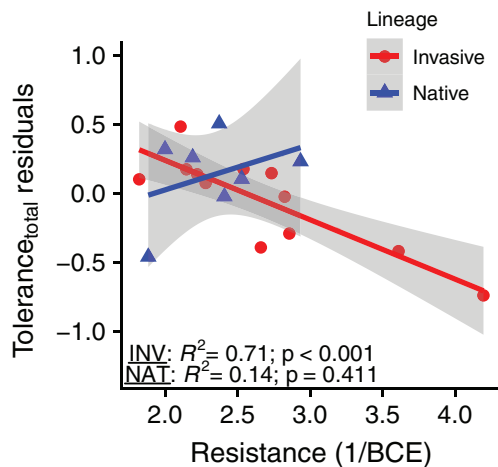

Figure 5 The relationship between *Phragmites australis* tolerance residuals to simulated folivory (Tolerance$_{total}$) and resistance to a generalist leaf chewing insect, *Spodoptera frugiperda*. Residuals were obtained from the regression of tolerance against geographic variables of importance (latitude, latitude2, longitude) and, hence represent the biogeographic-independent effects of tolerance on herbivory. Resistance was measured as the inverse of the change in caterpillar mass per unit area of plant tissue consumed (biomass conversion efficiency [BCE]) and is based on data collected by Bhattarai et al. (2017b). Because there was a significant interaction between *P. australis* lineage and resistance, separate lines are reported for the native (Nat) and invasive (Inv) lineages.

native and invasive lineages of *P. australis*, did not support the prediction that the invasive lineage would be more tolerant to folivory than the native lineage. Instead, we found that the native lineage was 19% more tolerant than the invasive lineage (Tolerance$_{total}$; Fig. 3); although the difference was not statistically significant. Our experimental estimates of total tolerance were positively related to growth-related traits, specifically relative growth rate (RGR), and plasticity in stem density and leaf C:N ratio. Interestingly, we also found that not only does there appear to be a tradeoff in defense strategies between lineages (i.e. native *P. australis* has low resistance but high tolerance whereas invasive *P. australis* has high resistance but low tolerance), but also a defense tradeoff evident among invasive, but not native, populations distributed across the United States (Fig. 4). Finally, defensive strategies in *P. australis* are further complicated geographically because of strong latitudinal variation in tolerance (this study) and resistance (Bhattarai et al. 2017b). Scarcely any other native-invasive plant systems exist where this level of large-scale variation in tolerance and resistance is available (but see Liao et al. 2016). Below, we focus on the causes and consequences of variation in *P. australis* tolerance and conclude with a broader examination of the ramifications of geographic variation in defenses for invasion success.

Tolerance differences between lineages

The enemy release hypothesis attributes invader success to the escape from top–down regulating forces like herbivory
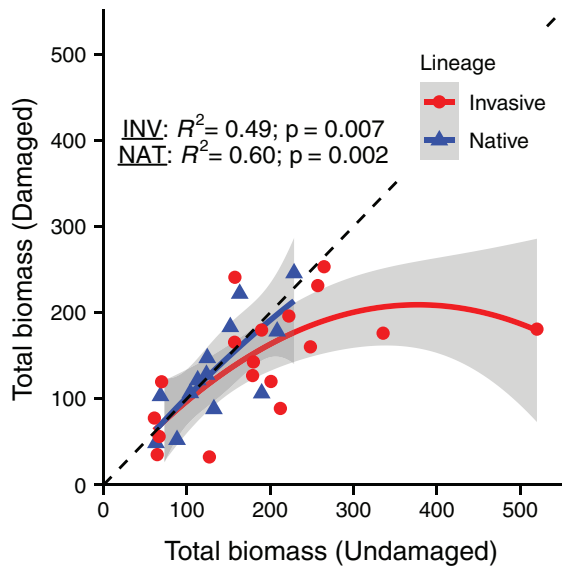
Figure 6. Relationship between total biomass of damaged versus undamaged *Phragmites australis* plants for each lineage. The thin, dashed line (black 1:1 line) represents complete compensation for folivory, while points above and below this line indicate over- and under-compensation, respectively. Separate lines and regression statistics are reported for the native (Nat) and invasive (Inv) lineages..

(Keane and Crawley 2002, Colautti et al. 2004); however, invasive plants may escape specialist herbivores in their home range only to experience increased pressure from generalist herbivores in the invaded range. The shifting defense hypothesis predicts that these differential selection pressures generate variation in defensive strategies between native and invasive plants, with invasive plants evolving increased resistance and tolerance to generalist herbivores (Zhang et al. 2018). Such shifts in defense allocation would likely facilitate invasion success. Although populations sourced from the invaded range tend to be more tolerant than populations sourced from the native range (Abhilasha and Joshi 2009, Wang et al. 2011, Liao et al. 2016, Zhang et al. 2018; but see Bossdorf et al. 2004, de Jong and Lin 2017), understanding how tolerance to herbivory mediates invasion success requires a comparison between co-occurring native and invasive species that share herbivore communities. Many fewer studies have compared tolerance between co-occurring congeneric or confamilial pairs of native and invasive species, with findings of greater tolerance in invasive species (Ashton and Lerdau 2008, Liu et al. 2012), native species (Zas et al. 2011), or no differences between them (Engelkes et al. 2016, Lurie et al. 2017). Our approach is unique in that we compare conspecific native and invasive populations within the invaded range, and we found that native populations tolerate herbivory better on average than invasive populations. Consequently, enemy release, which was previously reported for invasive *P. australis* in North America (Cronin et al. 2015), might be more important than tolerance to generalist herbivores for explaining the spread of the invasive lineage of *P. australis* in North America.

At least two scenarios could explain why the native lineage was generally more tolerant to folivory than the invasive lineage of *P. australis*. First, plants may require time to evolve in response to pressure from novel herbivores and so tolerance may increase with time-since-invasion (Lu and Ding 2012). Although invasive *P. australis* has been in North America for at least 150 years (Saltonstall 2002), it is possible that insufficient time has passed for invasive *P. australis* to achieve tolerance levels similar to native *P. australis*. Second, stands of the native lineage are likely subjected to substantial herbivore spillover from adjacent and often much larger stands of the invasive lineage (Bhattarai et al. 2017a). Even though invasive *P. australis* is less preferred than native *P. australis* (Cronin et al. 2015, Allen et al. 2017, Bhattarai et al. 2017a, b), invasive stands still support large numbers of herbivores. Spillover resulting in elevated herbivore loads on native *P. australis* may have favored the evolution of increased tolerance of herbivory in a relatively short period of time.

The stronger impacts of simulated herbivory on the invasive *P. australis* lineage suggests the possibility that biocontrol agents may limit the spread of the invasive lineage. However, we caution against this interpretation for several reasons. First, releasing a control agent for the invasive lineage (Blossey et al. 2020) has a high probability of spillover to the native lineage (Bhattarai et al. 2016, Cronin et al. 2016, Kiviat et al. 2019). Although our study suggests that the native lineage may be able to tolerate moderate levels of damage if biocontrol agents spillover, spillover from typically much larger invasive stands to less resistant native stands may be substantial. Second, as the proposed biocontrol agents are stem borers, we do not yet know whether tolerance to folivory extends to stem-feeding damage. Finally, it is possible that the invasive lineage may quickly evolve to become more tolerant of the biocontrol agent. Consider the study by Lu and Ding (2012) wherein it was discovered that populations of *Alternanthera philoxeroides*, sourced from regions within the invaded range that had a history of herbivore exposure, were more tolerant to herbivory than those sourced from herbivore-free regions. Generally, enemy release, as mediated by plant defense strategies, is a dynamic process, varying both spatially (Allen et al. 2015, 2017, Cronin et al. 2015, Bhattarai et al. 2017a, b) and temporally (Schultheis et al. 2015) and depending on herbivore feeding guild (Agrawal et al. 2005) and origin (Zhang et al. 2018). The dynamic nature of biological invasions and the idiosyncrasies of plant–herbivore interactions make it difficult to predict the success of a biocontrol agent in reducing the spread of invasive *P. australis* at broad geographic scales.

Latitudinal variation in tolerance

Plant defense theory has long purported that the increasing strength of biotic interactions towards the equator should generate a parallel increase in the expression of plant defense (latitudinal herbivory-defense hypothesis [LHDH]; Coley and Aide 1991, Salgado and Pennings 2005, Moles et al. 2011). Contrary to the predictions of the LHDH, we found

that tolerance of folivory was four times higher for our northernmost populations than for populations at low to intermediate latitudes. This latitudinal cline is genetically based, suggesting local adaptation to the biotic or abiotic environments that is also correlated with latitude (e.g. climate, herbivore abundance). Indeed, herbivores have been shown to impose strong selection pressures on plant defensive strategies (Ehrlich and Raven 1964, Feeny 1975, Futuyma and Slatkin 1983). However, we found a pattern of tolerance that contradicts patterns of herbivory in the field. In a broad geographic survey of herbivory of *P. australis* in Europe and North America, Cronin et al. (2015) found that leaf-chewing damage from herbivores and stem-galling incidence decreased with increasing latitude, but only for the native lineage. These results suggest that among-population variation in tolerance to folivory may not be driven by herbivory pressure. Few studies have investigated broad geographic variation in tolerance, with one study showing the same latitudinal cline as reported herein (Lehndal and Ågren 2015b) and the remaining studies showing no relationship between tolerance and latitude (Więski and Pennings 2014, Prendeville et al. 2015, Sakata et al. 2017).

One alternative explanation for a positive latitude-of-origin versus tolerance relationship is a parallel reduction in growing-season length with increasing latitude. Abbreviated growing seasons may necessitate faster growth rates, higher photosynthetic rates and greater belowground storage of nutrients (Lovelock et al. 2004) – traits often associated with greater tolerance (Meyer 1998, Strauss and Agrawal 1999). Adaptation to a shorter season may therefore indirectly favor selection for greater herbivore tolerance. Similar to this study, Lehndal and Ågren (2015b) found that in a greenhouse experiment, northern populations of *Lythrum salicaria* were more tolerant than southern populations but in field surveys, herbivory was greater on southern than northern plants. The authors proposed that adaptive phenological differences existed among populations of *L. salicaria* in response to latitudinal variation in growing-season length. As a result, northern plants may have been further along in their development at the time of herbivore arrival in comparison to southern plants. If late developmental stages of plants are less susceptible to herbivory than early developmental stages, then northern populations with faster development would appear to exhibit greater tolerance. However, the negative relationship between growing season length and tolerance is not universal. Within a Mediterranean system, delayed flowering time in *Madia elegans* and *Strepanthus* species (i.e. long-growing season) was found to be related to greater tolerance to herbivory (Krimmel and Pearse 2016, Pearse et al. 2017). Moreover, late-season species that were induced into early flowering lost their ability to tolerate herbivory (Krimmel and Pearse 2016). Clearly, additional studies are needed that explore the relationship between growing season length, climate and tolerance to herbivory.

The nonlinear relationship between latitude of origin and tolerance in *P. australis* (measured in terms of aboveground or total biomass) is challenging to explain. Certainly, at a regional to continental scale that encompasses a broad portion of a species range, nonlinearities between latitude or longitude and plant defenses may be expected. Consider the 'range-center' hypothesis which predicts that plant abundance and herbivore pressure are higher near the range center than range margins (Alexander et al. 2007, Woods et al. 2012). It follows that plant defenses should be humped shaped, peaking at the range center. Several studies have tested this hypothesis with mixed support (De Frenne et al. 2012, Woods et al. 2012, Bhattarai et al. 2017b). Bhattarai et al. (2017b) study with *P. australis* found no evidence that resistance or traits associated with resistance were nonlinearly related to latitude. In the current study, the relationship between latitude and tolerance is u-shaped, not humped-shaped as predicted by the range-center hypothesis. Furthermore, there is no evidence that any plant nutritional, resistance or tolerance traits are nonlinearly related to latitude (Cronin et al. 2015, Bhattarai et al. 2017b) that might help to explain the nonlinear latitude–tolerance relationship in *P. australis*.

Plant traits and tolerance

An important goal in the study of plant defenses is to unveil the trait-based mechanisms underlying plant resistance and tolerance to herbivory (Fritz and Simms 1992, Tiffin 2000, Johnson and Rasmann 2011). For plant traits measured in the absence of herbivory, the first principal component was correlated with root mass fraction, specific leaf area, silica content, phenolic content, carbon to nitrogen ratio and growth rate. Taken together, this first trait axis represents a tradeoff between structural integrity and growth that ultimately modulates the effect that folivory has on plant tolerance. For example, phenolics are involved in lignin synthesis (Bhattacharya et al. 2010) and silica is thought to provide similar structural support as lignin at a much lower metabolic cost (Raven 1983). Although silica content has been reported as a defensive compound (Massey et al. 2006, Soininen et al. 2013), there is growing support for its role as a buffer of biotic and abiotic stress to plants (Coskun et al. 2019) and as a promoter of tolerance to herbivory (Johnson et al. 2019). Populations investing in structural integrity also invested in belowground biomass storage, which is widely regarded as a putative tolerance trait (Strauss and Agrawal 1999, Tiffin 2000, de Jong and Lin 2017, Lurie et al. 2017). Moreover, the first axis of plastic trait variation provides additional insight into *P. australis* response to herbivory. Similar to Stevens et al. (2008), increased stem production following herbivory increased compensatory growth. Altogether, our data suggest that investment into storage and structural integrity provide a platform for mobilizing resources towards compensatory stem production in response to herbivory.

Lastly, we found that growth rate was negatively related to tolerance. Growth and tolerance are expected to covary positively (Coley et al. 1985, Gianoli and Salgado-Luarte 2017), but results are currently mixed (Turley et al. 2013b,

Liao et al. 2016, de Jong and Lin 2017). For example, Turley et al. (2013b) found no evolutionary change in *Rumex acetosa* tolerance to herbivory after 26 years without rabbit herbivory, although growth rate decreased by 30%. The authors argued that constitutive growth rate, as opposed to compensatory growth, has evolved as a defense against rabbit herbivory. These results highlight the need to consider how both functional traits and their plasticity serve as mechanisms of tolerance.

Tolerance–resistance tradeoff

In the meta-analysis by Leimu and Koricheva (2006), a tolerance-resistance tradeoff was evident for 'wild' plant species (as compared to crop plants), but only in cases where resistance was measured as a specific trait (e.g. cardenolide concentration) versus an herbivore bioassay. In our study, we found evidence for a tolerance–resistance tradeoff between lineages: the invasive lineage is well known to be substantially more resistant to a wide range of herbivore species than the native lineage (Lambert and Casagrande 2007, Lambert et al. 2007, Allen et al. 2015, 2017, Cronin et al. 2015, Bhattarai et al. 2017a, b) but is less tolerant (this study). We also found evidence for a strong tradeoff among populations within the invasive but not native lineage.

If tolerance and resistance are functionally redundant defenses, a tolerance–resistance tradeoff between native and invasive *P. australis* has the potential to lessen the importance of enemy release as a driver of invasion success. Even though the invasive lineage receives less herbivore damage than the native lineage (Cronin et al. 2015), if the fitness consequences for that damage is greater for the invasive than native lineage, the net impact of herbivores on the two lineages may be more similar than expected based solely on damage levels. However, we doubt this is the case for *P. australis*. The Tolerance$_{total}$ for the invasive lineage is only 19% lower than for the native lineage whereas field-based measures of folivory were 650% greater for the native than the invasive lineage (Cronin et al. 2015). Moreover, a few native populations in the field were so stressed by herbivory that end-of-season aboveground green biomass was practically zero. Additionally, as mentioned earlier, apparent competition between native and invasive populations of *P. australis* is strongly asymmetric, resulting from spillover of herbivores from large invasive stands to smaller, more palatable native stands of *P. australis* (Bhattarai et al. 2017a). Overall, these lines of evidence suggest that if herbivory is substantially high, even relatively tolerant native stands of *P. australis* are likely to suffer severe fitness costs, favoring the invasive lineage.

The presence of a tolerance–resistance tradeoff for the invasive lineage and not the native lineage could be attributed to a few possibilities. First, herbivore communities associated with native *P. australis* are likely much more diverse compared to the invasive lineage due to asymmetric herbivore spillover, high invasive resistance and a more diverse surrounding plant community for native patches. The corresponding diversity in selection pressure is predicted to lead to the adoption of a mixed-defense strategy (Fornoni et al. 2004, Nunez-Farfan et al. 2007, Carmona and Fornoni 2013, Turley et al. 2013a). Second, populations of the invasive lineage exhibit a much broader range of tolerances and resistances than those of the native lineage (Fig. 5), and it is possible from both a statistical and biological perspective that those extremes have high leverage. Consider that the invasive population with the highest resistance in Fig. 4 also has the lowest tolerance; it is possible that only when there is considerable investment in one defense strategy do we see a cost in the other. For the native lineage, all populations show relatively moderate tolerance and resistance. We suggest that to gain a clearer picture of the role of natural enemies in plant species invasion success, more studies are needed that examine a broader diversity of defense strategies, including inducible defenses, for invaders and co-occurring native species that share natural enemies.

Concluding remarks

Our study with *P. australis* illustrates the important role of biogeography for species undergoing large-scale invasions (Bezemer et al. 2014, Cronin et al. 2015). Whether invasion success is linked to superior competitive ability or escape from natural enemies, latitudinal patterns in the distribution and abundance of species (Hillebrand 2004) or interactions among species (Coley and Aide 1991) are likely to cause establishment and spread to vary considerably with latitude. As with several of North America's most well-known invaders, the *P. australis* invasion has occurred at the scale of almost the entire North American continent (Saltonstall 2002). Latitudinal gradients have been described with regard to *P. australis* nutritional condition, structural and chemical defenses, palatability to herbivores, herbivore richness, abundance and damage, pathogen damage, strength of apparent competition and tolerance to folivory (Cronin et al. 2015, Meyerson et al. 2016b, Allen et al. 2017, 2020, Bhattarai et al. 2017a, b). Latitudinal gradients in the invasive lineage are also known to often differ from gradients for the native lineage; sometimes even occurring in the opposite direction (Bhattarai et al. 2017b). This great spatial complexity in the distribution of host defenses has important repercussions for species invasions and plant–herbivore coevolution. Regarding the former, spatial heterogeneity in defense strategies among invasive and co-occurring native plants can cause variation in the strength of enemy release or biotic resistance (Bezemer et al. 2014, Cronin et al. 2015, Lu et al. 2018). This can lead to a spatial mosaic of invader success, which may help explain inconsistent findings regarding the evidence for enemy release (Colautti et al. 2004, Liu and Stiling 2006) and biotic resistance (Colautti et al. 2004, Levine et al. 2004). Thus, we recommend that studies of the role of natural enemies in invasion success need to be repeated in different parts of the invader's range.

A spatial mosaic of plant defenses can result in complex patterns of trait selection and impede adaptation of herbivores to their host plants, especially for mobile herbivores that

might encounter spatially and genetically distinct host–plant patches (Denno 1983, Thompson and Cunningham 2002, Berenbaum and Zangerl 2006). The fall armyworm is one such species. It undergoes an annual migration across most of the central and eastern United States (Nagoshi et al. 2008) and likely encounters populations of *P. australis* that vary tremendously in tolerance and resistance. Another dominant herbivore of *P. australis*, the mealy plum aphid *Hyalopterus pruni* (Lambert and Casagrande 2007, Cronin et al. 2015) alternates generations between *P. australis* and various *Prunus* species (Mook and Wiegers 1999). If these aphids do not always return to the same *P. australis* patch, local adaptation may be difficult. One important consequence of a strong spatial mosaic in plant defenses is that it may be difficult for specialist herbivores to effect widespread control of an invasive plant species (Lu et al. 2013, Harms et al. 2020). Because generalist herbivores are not used in biological control programs, management of these pest plants with biological control agents may not be an option (Cronin et al. 2016). For large-scale invaders in which biological control has not been successful, it would be important to know the pattern of defense distribution.

Data availability statement

Data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.D17D5H> (Croy et al. 2020).

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Supplementary material (available online as Appendix oik-07260 at <www.oikosjournal.org/appendix/oik-07260>). Appendix 1–3.