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Warwick J. Allen
Louisiana State University

Laura A. Meyerson
University of Rhode Island

David Cummings
University of Rhode Island

John Anderson
University of Rhode Island

Ganesh P. Bhattarai
Louisiana State University

See next page for additional authors

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Authors

Warwick J. Allen, Laura A. Meyerson, David Cummings, John Anderson, Ganesh P. Bhattarai, and James T. Cronin

RESEARCH
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Biogeography of a plant invasion: drivers of latitudinal variation in enemy release

Warwick J. Allen^{1*†}, Laura A. Meyerson², David Cummings², John Anderson², Ganesh P. Bhattarai^{1‡} and James T. Cronin¹

¹Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA, ²Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA

ABSTRACT

Aim The relationship between herbivory and latitude may differ between native and invasive plant taxa, which can generate biogeographical heterogeneity in the strength of enemy release. Our aim was to compare latitudinal gradients in herbivory between native and invasive plants and investigate whether gradients are driven by local adaptation or phenotypic plasticity.

Location North America.

Methods Using sympatric native and invasive lineages of the wetland grass *Phragmites australis* and the specialist gall-fly *Lipara rufitarsis*, we conducted a field survey to examine whether the relationship between herbivory (the proportion of stems galled) and latitude was parallel between lineages. In a subsequent common garden experiment, we assessed whether latitudinal gradients in herbivory were genetically based or driven by phenotypic plasticity.

Results In the field, *L. rufitarsis* herbivory on the native *P. australis* lineage increased from 27% of stems galled in southern populations (36.5°) to 37% in northern populations (43.6°), whereas there was no relationship for the invasive lineage. Similar relationships were evident in the common garden experiment, indicating a genetic basis to latitudinal variation in herbivory. Moreover, the invasive lineage suffered five times less herbivory than the native lineage on average, supporting the enemy release hypothesis. However, a genetic basis to this pattern was absent in the common garden experiment, suggesting that local environmental conditions were responsible for the enemy release observed in nature. Specifically, stem height, diameter and density during the *L. rufitarsis* oviposition period appeared to be important drivers of herbivory.

Main conclusions Non-parallel gradients in herbivory may help explain the equivocal results of other studies that examine enemy release and biotic resistance at local scales, and can be an important mechanism promoting biogeographical variation in invasion success. We suggest that these latitudinal patterns in herbivory and other species interactions are likely to be a common phenomenon across a range of invaded systems.

Keywords

Chloropidae, invasive plants, latitudinal gradients, *Lipara*, phenotypic plasticity, *Phragmites*, plant–herbivore interactions, plant traits.

*Correspondence: Warwick J. Allen, Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA.

E-mail: warwick.j.allen@gmail.com

[†]Present address: Warwick J. Allen, The Bio-Protection Research Centre, Lincoln University, PO Box 84, Lincoln, 7647, New Zealand

[‡]Present address: Ganesh P. Bhattarai, Department of Entomology, Kansas State University, Manhattan, KS, 66506, USA

INTRODUCTION

One of the most general and recognizable patterns in ecology is the latitudinal diversity gradient (Pianka, 1966; Hillebrand, 2004). Ecologists have hypothesized that this phenomenon should contribute to the evolution of stronger species interactions (e.g. herbivory, competition, parasitism, mutualisms) at lower than higher latitudes (Dobzhansky, 1950; Coley & Aide, 1991; Schemske *et al.*, 2009). However, a meta-analysis by Moles *et al.* (2011) found a significant negative latitudinal gradient in herbivore damage for only 37% of studies, while an additional 21% reported a significant positive latitudinal gradient. Clearly, there is substantial variation in the presence and direction of latitudinal gradients in herbivory, which may have important implications for other ecological processes.

Although evidence regarding the presence and direction of latitudinal gradients is mixed, it is undoubted that species interactions are often important in the establishment and spread of invasive species (Shea & Chesson, 2002; Mitchell *et al.*, 2006). For example, the enemy release hypothesis is a major and intuitive hypothesis within invasion ecology, consisting of two key predictions: (1) invasive species escape from herbivores which were present in their native range, and (2) invasive species suffer less damage from natural enemies in their introduced range relative to co-occurring native species (Elton, 1958; Keane & Crawley, 2002). Empirical evidence for the first prediction is generally strong (Colautti *et al.*, 2004; Liu & Stiling, 2006), but support for the second prediction is equivocal (Colautti *et al.*, 2004; Agrawal *et al.*, 2005; Parker & Gilbert, 2007; Chun *et al.*, 2010). In this paper, we focus only on the latter prediction. An alternative to enemy release is the biotic resistance hypothesis. In this scenario, natural enemies in the introduced range cause greater damage to invasive species than co-occurring native species (Elton, 1958). Interestingly, evidence supporting this hypothesis is also mixed (Levine *et al.*, 2004; Parker *et al.*, 2006).

Inconsistent support for these contrasting hypotheses (i.e. enemy release and biotic resistance) may stem from the fact that the majority of studies testing them have generally focused on small spatial scales (i.e. a single geographical area). Whereas native species are expected to evolve latitudinal gradients in the strength of species interactions (Dobzhansky, 1950; Coley & Aide, 1991), expectations for latitudinal gradients involving invasive species could be considerably different. For example, invaders may have had insufficient time to evolve a parallel gradient in interaction strength. Invasive species also often have reduced genetic variation compared with their native range (Dlugosch & Parker, 2008), which can hinder local adaptation. Moreover, they may be subjected to different selection pressures relative to co-occurring native species (e.g. herbivory levels), which can result in differing evolutionary trajectories. Thus, if sympatric native and invasive plant taxa exhibit dissimilar or non-parallel relationships between herbivory and latitude, this

could lead to heterogeneity in the strength of enemy release or biotic resistance at a biogeographical scale (Bezemer *et al.*, 2014; Cronin *et al.*, 2015), which may confound smaller-scale studies. For example, Cronin *et al.* (2015) examined latitudinal gradients in herbivory from several herbivore guilds on co-occurring native and invasive lineages of the wetland grass *Phragmites australis* (Cav.) Trin. ex Steudel (Poaceae) in North America. Chewing damage and incidence of internal feeding herbivores was lower on average for the invasive than the native lineage. However, damage decreased with increasing latitude for the native lineage but not for the invasive lineage. Consequently, enemy release was strongest for the invasive lineage at southern latitudes (i.e. lower biotic resistance).

However, it remains unclear whether non-parallel latitudinal gradients in herbivory are genetically based (i.e. owing to natural selection and local adaptation) or phenotypically plastic responses to the local environment (e.g. Woods *et al.*, 2012; Hiura & Nakamura, 2013; Bhattarai *et al.*, 2016). Combining field surveys and common garden studies is a powerful approach to disentangling these two influences (e.g. Woods *et al.*, 2012; Hiura & Nakamura, 2013; Bhattarai *et al.*, 2016). For instance, a gradient observed in the field that disappears in the common garden would suggest that phenotypic plasticity is the underlying cause for the gradient. Alternatively, the absence of a gradient in the field but the presence of one in the common garden would suggest that environmental variability obscures evidence of local adaptation.

The goal of this study was to compare the strength and direction of latitudinal gradients in herbivory between native and invasive plants and to investigate whether gradients have an underlying genetic basis or are due to plastic responses to local environmental conditions. We focused on native and invasive lineages of *P. australis* and a specialist gall-forming fly, *Lipara rufitarsis* Loew (Diptera: Chloropidae). We surveyed 25 *P. australis* populations (12 native, 13 invasive) along the east coast of North America from North Carolina (36.5°) to Maine (43.6°) to examine biogeographical variation in the proportion of stems with galls of *L. rufitarsis*. We also ran a complementary common garden experiment examining *L. rufitarsis* herbivory of 59 *P. australis* populations sourced from throughout North America. Based on the enemy release hypothesis and previous studies suggesting the existence of non-parallel latitudinal gradients between the two lineages in this system (Cronin *et al.*, 2015; Bhattarai *et al.*, 2016), we tested the following predictions: (1) native and invasive *P. australis* lineages will exhibit non-parallel latitudinal gradients in the proportion of stems with galls (i.e. biogeographical heterogeneity in relative strength of herbivory); (2) the proportion of stems with galls will be lower on the invasive than the native lineage in the field (i.e. the enemy release hypothesis); (3) the same patterns will be reflected in a complementary common garden experiment (i.e. patterns of herbivory have a genetic basis); and (4) the proximal mechanism underlying variation in the proportion

of stems with galls is related to stem characteristics at the time of *L. rufitarsis* oviposition.

METHODS

Study organisms

Phragmites australis is a model organism for studying plant invasions (Meyerson *et al.*, 2016). It is a large-statured perennial grass which forms dense stands in the littoral zone of lakes, rivers and fresh- and saltwater marshes, and is virtually cosmopolitan in its distribution (Lambertini *et al.*, 2006). A native lineage of *P. australis* has been present in North America for millennia and consists of at least 14 different haplotypes (Saltonstall, 2002, 2016; Meadows & Saltonstall, 2007; Vachon & Freeland, 2011). However, an invasive lineage of *P. australis* from Europe has spread throughout North America since first appearing in herbarium records around 150 years ago (Chambers *et al.*, 1999; Saltonstall, 2002; Howard *et al.*, 2008; Meyerson *et al.*, 2009, 2012). There is an additional Gulf Coast lineage (Hauber *et al.*, 2011; Meyerson *et al.*, 2012) that is found outside the range of *Lipara* (Allen *et al.*, 2015) and thus was not included in this study. The co-occurrence of conspecific lineages enables robust and conservative comparisons between native and invasive plants by minimizing phylogenetic differences between taxa.

Herbivory of *P. australis* in North America is mostly attributed to accidentally introduced arthropods, including three species of monophagous and univoltine *Lipara* gall-flies introduced from Europe: *Lipara pullitarsis* Daskočil and Chvala, *L. rufitarsis* and *L. similis* Schiner (Tewksbury *et al.*, 2002; Allen *et al.*, 2015). *Lipara* adults emerge in the spring, mated females oviposit on young *P. australis* shoots and the resultant larvae feed internally to induce distinctive cigar-shaped galls in the apical parts of the stems (Chvala *et al.*, 1974). A single fully grown larva overwinters inside the senesced stem before pupation occurs in the spring. All three *Lipara* species in North America attack the native and invasive lineages of *P. australis* (Allen *et al.*, 2015), although higher herbivory has consistently been reported on the former, with up to 80% of stems per population with galls (Balme, 2000; Lambert *et al.*, 2007; Park & Blossey, 2008; Allen *et al.*, 2015). *Lipara rufitarsis* is the most widespread and abundant species, occurring from North Carolina to Maine and inhabiting 79% of all galls (Allen *et al.*, 2015). Stems infested by *Lipara* have a reduced size and never produce a panicle (Lambert *et al.*, 2007; Park & Blossey, 2008; Blossey, 2014; Allen *et al.*, 2015). Based on the frequency of damage and the direct impact on sexual reproduction, *Lipara* represents one of the most damaging and important herbivores of *P. australis* in North America (Cronin *et al.*, 2015).

Field survey

To examine latitudinal variation in the proportion of stems with *L. rufitarsis* galls, we surveyed 25 *P. australis* populations (12 native, 13 invasive) along the East Coast of the United

States (Appendix S1 in Supporting Information), where the invasive European lineage first appeared in herbarium records (Saltonstall, 2002). Populations were selected to cover the entire known latitudinal range of *L. rufitarsis* in North America (36.5° to 43.6°, 789 km; Allen *et al.*, 2015). Determination of lineage was made using chloroplast DNA and the methods of Saltonstall (2002), with modifications outlined in Kulmatiski *et al.* (2010). In many locales, populations of both native and invasive *P. australis* lineages occurred in the same watershed but were rarely intermixed.

Sampling was conducted when galls were apparent during late summer (28 July–30 August 2012). For each *P. australis* population, the proportion of stems with a *Lipara* gall was estimated by walking a single transect from the edge of the patch to the interior and examining the three closest stems every metre for the presence of a gall (150 stems in total). To estimate the proportion of stems with a *L. rufitarsis* gall, all galls were collected during the survey, transferred to individual Ziploc bags, and reared in an environmental chamber (25°C, 95% relative humidity, 16:8 h light:dark) (see Allen *et al.*, 2015). *Lipara* were identified to species based on gall and insect morphology, following Chvala *et al.* (1974). In this study, we focused exclusively on *L. rufitarsis* because it was the only *Lipara* species that was widespread and abundant enough to test our predictions.

Common garden experiment

A complementary experiment was conducted at an established common garden at the University of Rhode Island, Kingston, RI (41.49° N, −71.54° W). We collected data from 59 populations of *P. australis* (24 native, 35 invasive), initiated with small cuttings of rhizome material collected from natal populations throughout North America, and ranging in latitude from 29.1° to 46.1° (1889 km) (Appendix S2). Native populations belonged to eight different haplotypes, whereas all of the invasive populations used were haplotype M (Saltonstall, 2002, 2016), the predominant invasive haplotype in North America. Six native and seven invasive populations overlapped with those from the field study.

Each population was represented by 12.6 ± 1.2 pots (mean \pm SE; range 3–38) and was planted between 2005 and 2011 in 19-l nursery pots containing Metromix® soil (Sungro Horticulture, Agawam, MA, USA). At yearly intervals, the potted plants were split and repotted to prevent the roots from becoming potbound. Replicate pots within each population were randomly distributed among outdoor plastic pools that were filled with fresh water and were regularly fertilized with Mega Green organic fertilizer (Hydrolysate Company of America LLC, Isola, MI). Plants were grown in the common garden for at least 2 years prior to implementation of the experiment. Because we removed panicles before seeds dehisced, only clonal rhizomatous growth occurred in the garden. Thus, unless somatic mutations occurred over a relatively short time period, it is highly unlikely that evolution took place in response to the local (garden) environment.

Consequently, any variation among common garden populations was expected to be due to genetic differences that originated in the natal location. Furthermore, by growing the plants under identical conditions from small amounts of rhizome material for at least 2 years prior to the start of our study, maternal effects that might drive differences in herbivory were minimised.

To assess herbivory of *L. rufitarsis* on *P. australis* populations under homogeneous environmental conditions, we first removed all senesced stems from the common garden in the winter of 2012–13. We then seeded the garden on 18 April 2013 with 800 *L. rufitarsis* galls, sourced from an invasive *P. australis* population 8 km from the common garden (41.38° N, -71.51° W; Appendix S1). The collected galls were evenly spread throughout the common garden, at a rate of about one gall per pot. *Lipara rufitarsis* were left to naturally emerge, mate and select stems for oviposition. Plants and galls were allowed to develop naturally over the year.

The proportion of stems infested with *Lipara* per *P. australis* source population was quantified by inspecting each senesced stem for the presence of a gall during April 2014 (the year after the garden was seeded with *L. rufitarsis*). The number of stems examined per population averaged 125.5 ± 14.3 (range 10–432). We set a minimum criterion of 10 stems for a population to be included in the analyses. All galls were collected and inhabitants reared in the laboratory to determine *Lipara* species identity.

To investigate the proximal factors that affect *L. rufitarsis* herbivory, we collected data on *P. australis* stem characteristics during the period when adult female *L. rufitarsis* were selecting plants for oviposition (25 May to 10 June 2013; based on Chvala *et al.*, 1974). Stem density, height and diameter were the traits quantified; these were selected because they are known to influence oviposition and performance of gall-forming herbivores (e.g. Prado & Vieira, 1999; Santos *et al.*, 2008), including *Lipara* (De Bruyn, 1994; Blossey, 2014). The number of stems per pot were counted and converted to number/m². Stem height (measured from the base to the highest point of the stem) and stem diameter (measured at the first internode above the soil using digital calipers) were obtained for a single randomly selected stem in each pot. We set a minimum criterion of three replicate pots for a population to be included in the analyses.

Data analysis

Field survey

We tested whether there were latitudinal gradients in the proportion of stems galled by *L. rufitarsis* and whether they differed between native and invasive *P. australis* lineages. We used a generalized linear model (GLM) with a logit link function and binomial distribution of errors, and included lineage and latitude as explanatory variables. A quadratic term (latitude²) was also included to evaluate whether the relationship between the proportion of stems with galls and latitude was nonlinear. A nonlinear latitudinal gradient may

be expected based upon the range centre hypothesis (Alexander *et al.*, 2007; Woods *et al.*, 2012), which posits that higher plant abundance and herbivore pressure nearer the range centre than the range margins could lead to unimodal patterns in herbivory. Furthermore, the invasive lineage and *Lipara* both first appeared in the mid-Atlantic (around the centre of our study range) and then spread north and south (Saltonstall, 2002). Consequently, a unimodal relationship may also be expected for the invasive *P. australis* lineage if time since invasion is an important driver of latitudinal gradients in herbivory (see Bhattarai *et al.*, 2016). Possible interactions between lineage and latitude and lineage and latitude² were also tested, as they were deemed to be potentially important based on previous studies with *P. australis* which showed that non-parallel latitudinal gradients in herbivory between the native and invasive lineage are common (Cronin *et al.*, 2015; Bhattarai *et al.*, 2016).

We used the Akaike information criterion corrected for small sample size (AICc; a measure of the relative quality of a statistical model) to select the most informative model (Burnham & Anderson, 2010). Candidate models ($n = 13$) were constructed from the full model (lineage, latitude, latitude², lineage \times latitude, and lineage \times latitude²) using all possible combinations of the variables, but with the restriction that interaction terms could only be included if their main effects were also present in the model. Candidate models were ranked by AICc from lowest to highest value and models with a ΔAICc value ($= \text{AICc}_i - \text{AICc}_{\text{min}}$; the change in AICc between the current and top model) of two or less were deemed to have substantial support (Burnham & Anderson, 2010). We also report the AICc weights which indicate the weight of evidence (as a proportion) in favour of model i being the best model given the set of plausible candidate models. Finally, if the most highly supported model(s) included a lineage \times latitude or lineage \times latitude² interaction as an important explanatory variable, we subsequently performed separate GLMs for each lineage to characterize relationships between the proportion of stems galled and latitude. Goodness of fit is reported as $1 - (\text{residual deviance}/\text{null deviance})$, comparable in interpretation to the coefficient of determination (R^2) for linear models (Menard, 2000).

Common garden experiment

Using the same GLM and AICc model selection approach outlined above, we tested whether the proportion of stems with a gall was influenced by *P. australis* lineage, latitude and stem characteristics during the *L. rufitarsis* oviposition period. The proportion of stems with a gall was weighted by the total number of stems examined per population to account for potential effects of stem density on our response variables. Thus, our full model included lineage, latitude, latitude², stem density, height and diameter at oviposition, as well as interactions between lineage and each of the other explanatory variables ($n = 275$ candidate models). For each continuous explanatory variable present in the most likely

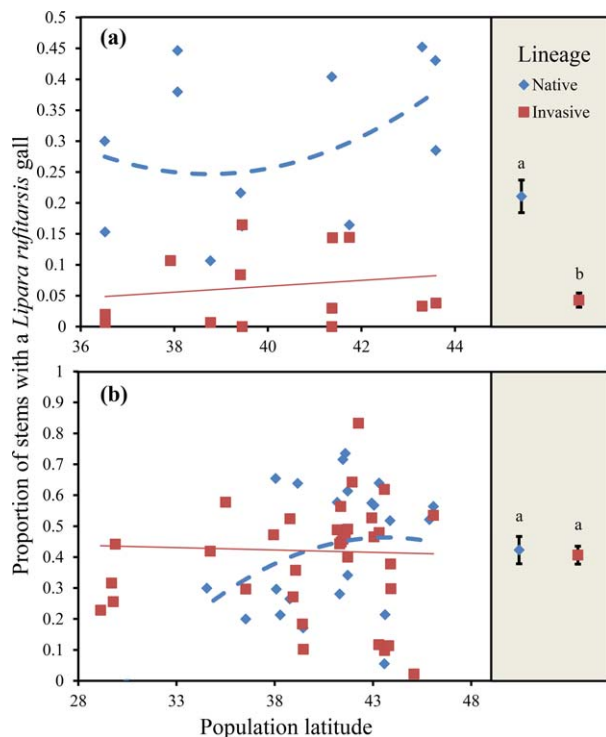


Figure 1 Relationship between latitude and the proportion of stems galled by *Lipara rufitarsis* for populations of the native and invasive *Phragmites australis* lineages in (a) the field survey and (b) the common garden experiment. Regression lines are fitted using parameter estimates from separate generalized linear models for each lineage (solid line, invasive; dashed line, native) or from least-squares regression for nonlinear relationships. Thick lines denote significant relationships between the proportion of stems galled and latitude ($P < 0.05$; see Appendix S3). Symbols in the shaded portion of the figure depict the mean (\pm SE) proportion of stems galled for each lineage independent of latitude. Different lowercase letters indicate significant differences between means ($P < 0.05$).

model(s), we again performed separate GLMs for each *P. australis* lineage to characterize relationships with the proportion of stems galled. For variables which did not interact with lineage in the most likely model(s), we performed a single GLM with the *P. australis* lineages combined. Finally, for each explanatory variable in the top AICc models across all analyses, we reported effect sizes (i.e. proportional differences in means or strength of relationship slopes) (Burnham & Anderson, 2010). All analyses were performed in R 3.3.1. (R Development Core Team, 2016) using the MuMIn package (Barton, 2016).

RESULTS

Field survey

Variation in the proportion of stems galled by *L. rufitarsis* in the field was best explained by a single model (AICc = 325.7, $R^2 = 0.674$, AICc weight = 1.0). This was the full model, including lineage, latitude, latitude², lineage \times latitude and

lineage \times latitude² as influential explanatory variables. In the field, the proportion of stems galled by *L. rufitarsis* on native *P. australis* populations (0.29 ± 0.04 , mean \pm SE) was nearly five times higher than on invasive *P. australis* populations (0.06 ± 0.02) (Fig. 1a). The relationship between the proportion of stems galled by *L. rufitarsis* and latitude depended upon the *P. australis* lineage (i.e. the lineage \times latitude and lineage \times latitude² interactions were present in the most likely model). The quadratic relationship between the proportion of stems galled for the native lineage and latitude (based on a separate GLM for this lineage only) was weakly U-shaped and increased from 0.27 at the southernmost site to 0.37 at the northernmost site (latitude²: $z = 4.30$, $R^2 = 0.134$, $P < 0.001$; Fig. 1a). Conversely, the proportion of stems galled for the invasive lineage increased by 68% over its latitudinal range, but this increase was non-significant ($z = 1.78$, $R^2 = 0.028$, $P = 0.075$; Fig. 1a).

Common garden experiment

A single plausible model (Δ AICc ≤ 2) explained variation in *L. rufitarsis* herbivory in the common garden (AICc = 584.4, $R^2 = 0.640$, AICc weight = 1.00) and included all terms except the lineage \times stem height interaction. Whereas *P. australis* lineage was an influential variable, the average proportion of stems with a *L. rufitarsis* gall was only slightly higher on the native (0.43 ± 0.03) than invasive (0.40 ± 0.03) lineage of *P. australis* (Fig. 1b), representing a 30% and six-fold increase in herbivory in comparison with the field, respectively. As with the field survey, the effects of lineage on the proportion of stems with galls varied with latitude (i.e. lineage \times latitude and lineage \times latitude² interactions). Separate GLMs for each lineage indicated that the native lineage had a significant nonlinear but generally positive correlation between the proportion of stems galled and latitude (latitude²: $z = 3.29$, $R^2 = 0.047$, $P = 0.001$; Fig. 1b, Appendix S3). The proportion of stems galled doubled (from 0.23 to 0.46) from the southern to the northern end of the native lineage distribution (1281 km). In contrast, no relationship was detected between the proportion of stems galled and latitude for the invasive lineage ($z = 0.79$, $R^2 = 0.001$, $P = 0.430$; Fig. 1b). Importantly, these non-parallel latitudinal gradients observed in the common garden were consistent with those observed in the field.

Stem characteristics during the *L. rufitarsis* oviposition period were very influential in explaining the proportion of stems with galls per source population in the common garden experiment. First, *L. rufitarsis* herbivory was strongly and negatively correlated with mean stem height, regardless of *P. australis* lineage ($z = -15.95$, $R^2 = 0.362$, $P < 0.001$; Fig. 2a, Appendix S3), decreasing by 82% over the range of stem heights. Second, basal stem diameter was weakly and positively correlated with the proportion of stems galled, but the slope of the relationship depended on *P. australis* lineage (lineage \times stem diameter interaction in the top model). The correlation was steeper for the invasive ($z = 6.72$, $R^2 = 0.095$,

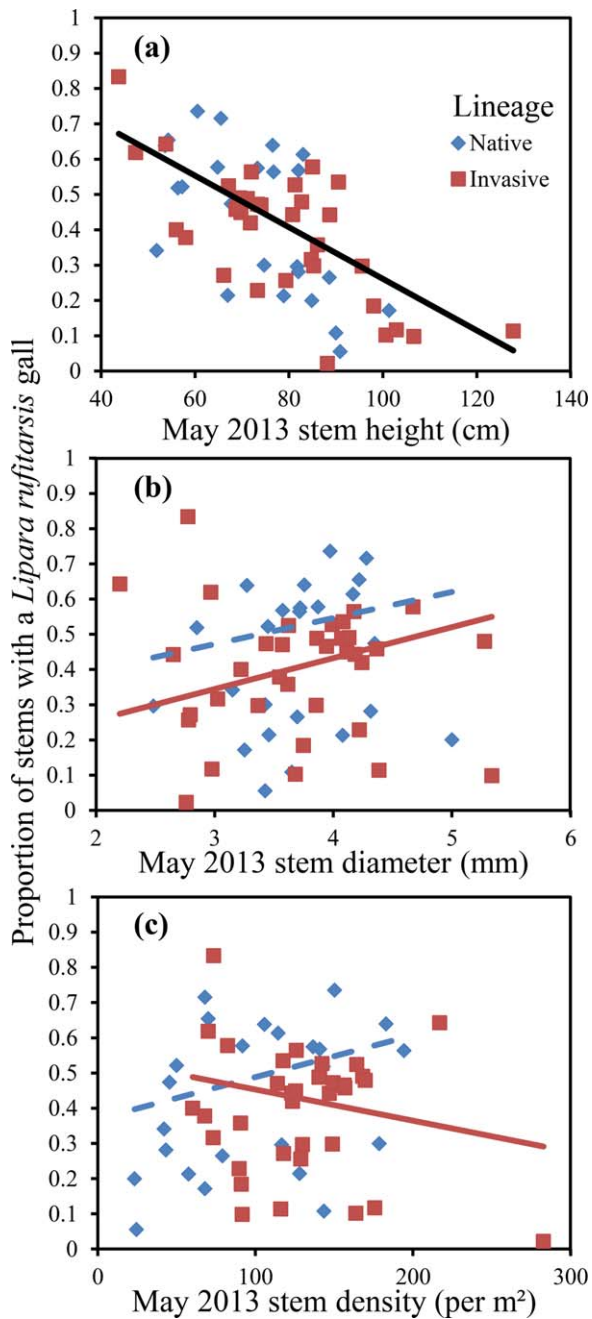


Figure 2 Relationship between the proportion of stems galled by *Lipara rufitarsis* and (a) stem height (cm), (b) stem diameter (mm), and (c) stem density (per m²) during the *L. rufitarsis* oviposition period for the native and invasive lineages of *Phragmites australis* in the common garden experiment. Regression lines are fitted using parameter estimates from generalized linear models for each stem characteristic. Individual lines for each lineage (solid line, invasive; dashed line, native) are shown if the stem characteristic had a significant interaction with lineage in the most likely model. Thick lines denote significant relationships between *L. rufitarsis* herbivory and stem characteristics ($P < 0.05$; see Appendix S3).

Table 1 Mean (\pm SE) stem height (cm), diameter (mm) and density (per m²) for the native and invasive *Phragmites australis* lineages in the common garden experiment.

	<i>Phragmites australis</i> lineage	
	Native	Invasive
Stem height (cm)	73.50 ^a \pm 2.77	74.97 ^a \pm 2.30
Stem diameter (cm)	3.71 ^a \pm 0.11	3.61 ^a \pm 0.11
Stem density (per m ²)	99.96 ^a \pm 10.50	124.88 ^b \pm 6.16

Different lowercase letters indicate significant differences between lineage means for each stem characteristic ($P < 0.05$).

$P < 0.001$) than native ($z = 3.35$, $R^2 = 0.048$, $P < 0.001$) lineage, increasing by 97% and 43% over the range of stem diameters for each lineage, respectively (Fig. 2b, Appendix S3). Third, the native lineage exhibited a positive correlation ($z = 4.88$, $R^2 = 0.103$, $P < 0.001$) and the invasive lineage exhibited a negative correlation ($z = 4.77$, $R^2 = 0.048$, $P < 0.001$) between stem density and the proportion of stems with galls (Fig. 2c, Appendix S3). The proportion of stems galled increased by 51% over the range of native stem densities and decreased by 39% over the range of invasive stem densities.

Because stem characteristics during *L. rufitarsis* oviposition were important predictors of the proportion of stems galled in the common garden, we tested how each stem characteristic varied with respect to lineage, latitude (and the quadratic latitude²) and their interaction using analysis of covariance (ANCOVA). Stem density was 25% higher for the invasive (124.9 \pm 6.2 per m²) than native (100.0 \pm 10.5 per m²) lineage ($F_{1,53} = 5.84$, $P = 0.019$; Table 1). However, stem height and stem diameter did not differ between *P. australis* lineages, and none of the stem characteristics varied with latitude of origin of the *P. australis* populations ($P > 0.05$ for all tests).

DISCUSSION

The native lineage of *P. australis* exhibited a positive relationship in the field between herbivory from a specialist stem gall-fly (*L. rufitarsis*) and latitude, whereas no relationship with latitude was detected for the invasive lineage. These non-parallel gradients resulted in stronger enemy release of invasive *P. australis* from *L. rufitarsis* at more northern latitudes. Latitudinal gradients observed in the field were reflected in the common garden experiment, suggesting an underlying genetic basis to these biogeographical patterns. However, *P. australis* lineage was relatively unimportant in determining the proportion of stems galled per population in the common garden experiment. Instead, stem characteristics (height, diameter, density) measured during the *L. rufitarsis* oviposition period were the primary determinants of herbivory. This result suggests that the strong difference in the proportion of stems galled between native and invasive *P.*

australis lineages observed in the field was not genetically based but rather driven by the effects of local environmental conditions on plant growth and the subsequent response of *L. rufitarsis*. Along with the studies by Cronin *et al.* (2015) and Bhattarai *et al.* (2016), our study suggests that genetically based latitudinal gradients in herbivory and qualitative differences in those gradients between sympatric native and invasive plant taxa may be widespread. Moreover, these biogeographical patterns can help explain the equivocal results of other studies that examine enemy release and biotic resistance at local scales, and may be an important mechanism promoting biogeographical variation in invasion success.

Non-parallel latitudinal gradients in *L. rufitarsis* herbivory

Although evidence to date is limited to a single plant system, *P. australis*, this study lends support to the idea that enemy release is dependent on biogeography (see also Cronin *et al.*, 2015; Bhattarai *et al.*, 2016). Our prediction that native and invasive *P. australis* lineages exhibit non-parallel latitudinal gradients in the proportion of stems with *L. rufitarsis* galls was supported. In the field, we found that the proportion of stems with galls in native *P. australis* populations increased by 37% from our southernmost to our northernmost populations, whereas there was no relationship between the proportion of stems galled and latitude for the invasive lineage. Thus, the difference in herbivory between the two lineages diverged with increasing latitude, resulting in stronger enemy release in the north than the south. These non-parallel gradients between native and invasive lineages were reflected in the common garden experiment. Due to the controlled environment in the common garden, these biogeographical patterns are genetically based rather than the result of phenotypic plasticity, thus supporting our third prediction.

Cronin *et al.* (2015) and Bhattarai *et al.* (2016) have previously described biogeographical heterogeneity in the strength of enemy release of invasive *P. australis* in the field and common garden, respectively. These studies focused on oligophagous and generalist herbivores [the mealy plum aphid, *Hyalopterus pruni* (Geoffroy) and the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), respectively] or the combined effects of entire herbivore guilds (leaf chewers, internal stem feeders), whereas the current study focused on an obligate specialist of *P. australis*. We expected that local adaptation by native and invasive *P. australis* to a specialist herbivore would be more likely than adaptation to oligophagous or generalist herbivores (Anstett *et al.*, 2014). However, for the native lineage, *H. pruni* exhibited a genetically based negative latitudinal gradient, *L. rufitarsis* a genetically based positive latitudinal gradient and *S. frugiperda* showed no evidence of a gradient. Interestingly, the invasive lineage only exhibited a genetically based negative latitudinal gradient for *H. pruni* aphids. These findings concur with those of Kim (2014) who found no clear distinction between specialist and generalist herbivores

in the likelihood that their host plants evolved a genetically based latitudinal gradient in susceptibility to attack. *Lipara rufitarsis*, *H. pruni*, the guild of leaf chewers and the guild of internal stem feeders all exhibited non-parallel latitudinal gradients in herbivory in which a gradient was evident for the native lineage but not the invasive lineage. Ultimately, this consistent pattern indicates there is a tremendous amount of spatial heterogeneity in enemy release or biotic resistance for the invasive lineage of *P. australis*.

We offer some possible mechanisms that could lead to non-parallel latitudinal gradients in *L. rufitarsis* herbivory of native and invasive *P. australis* lineages. First, *Lipara* have only been present in North America for less than 100 years (Sabrosky, 1958; Tewksbury *et al.*, 2002), meaning that both *P. australis* lineages have had approximately the same period of time to evolve latitudinal gradients in response to *Lipara* herbivory. However, because the native lineage has been present in North America for millennia, it is possible that there are pre-existing latitudinal gradients in some plant traits which may be important in determining outcomes of plant–herbivore interactions. For example, leaf tissue nitrogen content, a key nutrient for many herbivores (Mattson, 1980), increased with latitude for native but not invasive *P. australis* in the field and common garden (Cronin *et al.*, 2015; Bhattarai *et al.*, 2016). Unfortunately, we did not quantify nitrogen content in this study, so were unable to assess whether this gradient is related to *L. rufitarsis* herbivory. Second, local adaptation to herbivores may be more likely for native than invasive *P. australis* populations because they have higher haplotype diversity within North America (Saltonstall, 2002, 2016). Moreover, native populations tend to be more isolated from one another and thus potentially experience less gene flow relative to invasive populations. However, this possibility is contradicted by Bhattarai *et al.* (2016), who observed a genetically based negative correlation between latitude and palatability to *H. pruni* aphids for the invasive *P. australis* lineage. Third, a number of studies with replicate common gardens have found that latitudinal gradients in traits associated with plant–herbivore interactions are phenotypically plastic (Woods *et al.*, 2012; Bhattarai *et al.*, 2016) and that invasive taxa are more plastic than native taxa (Richards *et al.*, 2006; Davidson *et al.*, 2011; Bhattarai *et al.*, 2016). Thus, expression of latitudinal gradients may depend upon complex interactions between plant lineage and local environmental conditions, and the patterns observed in this study may be altered under different common garden conditions. Finally, herbivore source latitude could also be an important factor driving the presence and direction of latitudinal gradients. The *L. rufitarsis* used in our common garden experiment came from a single invasive *P. australis* population in Rhode Island, so may be co-adapted to plants from that latitude (Pennings *et al.*, 2001). Indeed, Bhattarai *et al.* (2016) demonstrated major differences in the direction and strength of latitudinal gradients using locally sourced *H. pruni* aphids in replicate common gardens in Rhode Island and Louisiana.

Because of the strong effect of *L. rufitarsis* on plant fitness through prevention of flowering (Lambert *et al.*, 2007; Allen *et al.*, 2015) such biogeographical heterogeneity in the strength of enemy release could potentially result in corresponding heterogeneity in establishment and spread of invasive *P. australis*. However, the effects of herbivores (including *L. rufitarsis*) on the fitness and demography of *P. australis* are largely unexplored. Moreover, there have been few studies that have quantified the establishment, fitness and spread of *P. australis* at different latitudes, which could more directly test whether biogeographical gradients in the strength of enemy release translate into gradients in invasion success. However, a recent study by Hughes *et al.* (2016) demonstrated that stem density of the invasive lineage was highest at more northern latitudes, consistent with our findings of stronger enemy release for more northern populations. In contrast, a study of historical aerial imagery from the east coast of North America found no latitudinal variation in the rate of increase of invasive *P. australis* populations (Bhattarai & Cronin, 2014), suggesting there may be no corresponding variation in invasion success of *P. australis*.

Enemy release for the invasive *P. australis* lineage

Although it has long been argued that leaving behind co-adapted natural enemies can facilitate invasions, invasion success may ultimately depend on whether the non-native plant species can withstand the impact of herbivores in their new range (Elton, 1958; Keane & Crawley, 2002). In support of this hypothesis (our second prediction), we found that the proportion of stems galled by *L. rufitarsis* was lower on the invasive than the native *P. australis* lineage in the field. This result is consistent with previous studies involving *Lipara* and other herbivores of *P. australis* in North America (Lambert & Casagrande, 2007; Lambert *et al.*, 2007; Park & Blossey, 2008; Allen *et al.*, 2015; Cronin *et al.*, 2015, 2016). Because differences in herbivory could be expected to be less likely within than between species, we suggest that our study presents a conservative and phylogenetically controlled test of the enemy release hypothesis, which also accounts for biogeographical variation in plant–herbivore interactions.

Despite the strong evidence for enemy release of invasive *P. australis* from *L. rufitarsis* in the field, there was almost no difference (just 3%) in the proportion of stems galled between native and invasive *P. australis* in the controlled common garden experiment. These data suggest that there is no genetic basis for the difference in *L. rufitarsis* herbivory between lineages observed in our field survey. This finding is somewhat surprising, because the invasive lineage has had a much longer co-evolutionary history with all three introduced *Lipara* species (all of which originate from Europe) than the native lineage and is therefore more likely to have evolved defences against attack. Multiple other studies have previously documented contrasting results between field and common garden patterns of herbivory (Park & Blossey, 2008; Woods *et al.*, 2012; Hiura & Nakamura, 2013), generally

attributed to the variable influence of local environmental conditions in the field (i.e. phenotypic plasticity). Thus, the discrepancy between our field and common garden studies suggests that the strong enemy release observed in the field is likely to be the result of phenotypic plasticity or legacy effects (e.g. *Lipara* herbivory is historically higher in association with native than invasive populations in the field), rather than genetic differences between native and invasive *P. australis* lineages. Many studies have demonstrated that invasive taxa are more phenotypically plastic than native taxa (Richards *et al.*, 2006; Davidson *et al.*, 2011), including within *P. australis* (Mozdzer & Magonigal, 2012; Bhattarai *et al.*, 2016; Douhovnikoff *et al.*, 2016). In this study, the invasive lineage demonstrated a nearly six-fold difference in the proportion of stems galled between the field survey and common garden experiment. Thus, it is possible that the enemy release observed in the field was driven by a strong plastic response to local environmental conditions on the part of the invasive lineage.

Lipara rufitarsis herbivory depends on stem characteristics

Plant morphological traits have often been shown to be useful predictors of attack and damage by gall insects and herbivores in general (e.g. De Bruyn, 1994; Prado & Vieira, 1999; Santos *et al.*, 2008). In support of our fourth prediction, we found that stem characteristics during the oviposition period of *L. rufitarsis* were strongly correlated with the subsequent proportion of stems galled. Most importantly, the proportion of stems galled was much higher in those native and invasive populations that had shorter and thicker stems. However, neither of these stem characteristics varied between lineages or with latitude. Thus, differences in latitudinal gradients between the native and invasive lineage cannot be attributed to variation in stem height or diameter.

Host plant density is often cited as an important factor driving oviposition and herbivory of many gall-forming insects (e.g. Abrahamson *et al.*, 1983; Cuevas-Reyes *et al.*, 2004), and previous studies have found *Lipara* herbivory to be both positively correlated (Blossey, 2014) and unrelated (Allen *et al.*, 2015) to stem density. In this study, we found that the proportion of stems galled by *L. rufitarsis* and stem density were positively correlated for the native lineage and negatively correlated for the invasive lineage. Taken together, these results suggest that for the native *P. australis* lineage, any competitive advantage gained through increased stem density may be negated by increased herbivory from *L. rufitarsis*. In contrast, the invasive lineage experiences decreased *Lipara* herbivory at higher stem densities.

These stem characteristics are likely to be strongly influenced by the local environment. In nature, the native and invasive lineages of *P. australis* in North America often occupy different microhabitats related to salinity, hydrology, disturbance and nutrient availability (e.g. Vasquez *et al.*, 2005; Holdredge *et al.*, 2010; Price *et al.*, 2014). For example,

native *P. australis* populations may be more prevalent in nutrient-poor environments, where they are better able to compete (Holdredge *et al.*, 2010). This environment could result in a higher proportion of short, stressed stems, thus making the native lineage more attractive to *L. rufitarsis* for oviposition (De Bruyn, 1994). In a well-fertilized and watered common garden, plants were subjected to homogeneous environmental conditions and were not nutrient- or water-limited or exposed to varying salinity levels. Therefore, lineage-specific patterns in the field (driven by microclimatic effects on stem characteristics) may be negated in a common garden.

CONCLUSIONS

We find that enemy release of the invasive *P. australis* lineage from *L. rufitarsis* is likely to be a plastic response, driven by stem characteristics that are modified by local environmental conditions rather than being the result of genetic differences between native and invasive lineages. Latitudinal variation in the strength of the enemy release is subsequently generated by local adaptation of the native but not invasive lineage along a latitudinal gradient. The result is non-parallel latitudinal variation in herbivory by *L. rufitarsis* such that the invasive lineage suffers proportionately less herbivory than the native lineage (i.e. greater enemy release) at high than low latitudes. Biogeographical variation in enemy release is widespread in *P. australis* for both generalist and specialist herbivores (this study; Cronin *et al.*, 2015; Bhattarai *et al.*, 2016). Unfortunately, the *P. australis* system is the only one in which the biogeography of enemy release has been explored. However, we suggest that herbivory of many co-occurring native and invasive plants with respect to latitude is likely to be dissimilar owing to many factors including different phylogenies, historical distributions and co-evolutionary histories with local herbivores. Moreover, this latitudinal heterogeneity in enemy release or biotic resistance can result in corresponding heterogeneity in the establishment and spread of invasive species. On these grounds, we argue for a broader, biogeographical perspective to the study of invasive species. Moreover, because invasive species can evolve rapidly in response to environmental gradients (Maron *et al.*, 2004; Li *et al.*, 2015; Bhattarai *et al.*, 2016), and native and invasive species may differ in evolutionary trajectories, differences in enemy release and biotic resistance are likely to be transient. Thus, future studies in this area should investigate temporal as well as spatial variability in interactions between invasive and native plant species. Finally, the majority of studies examining biogeographical variation in species interactions have focused on herbivory (Schemske *et al.*, 2009). However, the importance of non-parallel latitudinal gradients for invasive and native taxa remains unexplored with respect to other species interactions such as mutualisms, competition and multi-trophic interactions, which may ultimately be important in explaining invasion success.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site:

Appendix S1 List of *Phragmites australis* field populations surveyed for the proportion of stems galled by *Lipara*.

Appendix S2 List of *Phragmites australis* populations used for the common garden experiment at the University of Rhode Island.

Appendix S3 Results from generalised linear model analyses for the effects of latitude, latitude² and stem characteristics during the *Lipara rufitarsis* oviposition period on the proportion of stems galled of the native and

invasive lineages of *Phragmites australis* in the common garden experiment.

BIOSKETCH

Warwick Allen is a post-doctoral fellow at The Bio-Protection Research Centre, Lincoln University, New Zealand. This work was carried out during his PhD at Louisiana State University. His research interests include the causes and consequences of biological invasions, with a specific focus on the role of direct and indirect species interactions on the success of invasive species and biological control.

This research group aims to study the role of multi-trophic interactions, plant genetics, plasticity and biogeography in driving plant invasions at large spatial scales. They are also members of PhragNet, a global research network that uses *Phragmites australis* as a model organism for studying plant invasions.

Editor: Angela Moles