

Biogeography of a plant invasion: plant–herbivore interactions

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Abstract. Theory predicts that native plant species should exhibit latitudinal gradients in the strength of their interactions with herbivores. We hypothesize that if an invasive plant species exhibits a different latitudinal gradient in response to herbivores (e.g., a nonparallel gradient), it can create large-scale heterogeneities in community resistance/susceptibility to the invasive species. We conducted a study of latitudinal variation in the strength of herbivory and defenses of native genotypes of *Phragmites australis* in North America (NA) and Europe (EU) and European invasive genotypes in NA. Within NA, we tested whether (1) invasive genotypes are better defended and suffer less herbivory than co-occurring native genotypes, (2) herbivory and defenses of native *P. australis* decreases with increasing latitude; and (3) invasive genotypes exhibit either no latitudinal gradient, or a nonparallel latitudinal gradient in herbivory and defenses compared to native genotypes. For the European genotypes, we tested two additional hypotheses: (4) defenses, nutritional condition, and herbivory would differ between the native (EU) and invasive ranges (NA) and (5) latitudinal gradients in defenses and herbivory would be similar between ranges. Within NA, chewing damage, internal stem-feeding incidence, and aphid abundance were 650%, 300%, and 70% lower, respectively, on invasive than native *P. australis* genotypes. Genotypes in NA also differed in nutritional condition (percent N, C:N ratio), but there was little support for invasive genotypes being better defended than native genotypes. For the European genotypes, herbivory was significantly lower in the invaded than native range, supporting the enemy-release hypothesis. Defense levels (leaf toughness and total phenolics) and tissue percent C and percent N were higher in the invaded than native range for European genotypes. Overall, latitudinal gradients in *P. australis* nutritional condition, defenses, and herbivory were common. Interestingly, chewing damage and stem-feeder incidence decreased with latitude for native *P. australis* genotypes in NA and EU, but no latitudinal gradients in response to herbivores were evident for invasive genotypes in NA. Nonparallel latitudinal gradients in herbivory between invasive and native *P. australis* suggest that the community may be more susceptible to invasion at lower than at higher latitudes. Our study points to the need for invasion biology to include a biogeographic perspective.

Key words: biotic resistance; enemy-release hypothesis; herbivory; invasive species; latitudinal gradients; *Phragmites australis*; plant defenses.

INTRODUCTION

Following their introduction, many biological invaders spread over broad spatial scales. In a number of notable North American examples, such as the Asian tiger mosquito (*Aedes albopictus*), Norway rat (*Rattus norvegicus*), and common reed (*Phragmites australis*), biological invasions have occurred at the scale of the whole continent. To date, the preponderance of studies focusing on the causes of invasion success have been limited to the scale of a single community or ecosystem (see Vila and Weiner 2004, Colautti et al. 2007, Kimbro et al. 2013). Besides comparisons between the native and invaded ranges of a species (e.g., Maron et al. 2007, Callaway et al. 2011), a biogeographic approach to

understanding variation in invasion success has rarely been undertaken (e.g., He et al. 2013, Ordóñez and Olff 2013).

A common biogeographical backdrop for continent-wide biological invasions is a latitudinal gradient in species richness within the invaded range (Hillebrand 2004). One longstanding hypothesis for the origin of the latitudinal richness gradient is the “biotic interactions hypothesis,” which posits that species interactions are stronger and more specialized at lower latitudes, promoting greater diversification rates and species richness (Schemske et al. 2009). In support of this hypothesis, levels of plant defenses against herbivores have been shown to decrease with increasing latitude (e.g., Coley and Aide 1991, Salgado and Pennings 2005, Więski and Pennings 2014). In a recent meta-analysis by Moles et al. (2011), 39% of the studies showed higher herbivory at lower latitudes. However, methodological flaws were common to these studies, making it difficult

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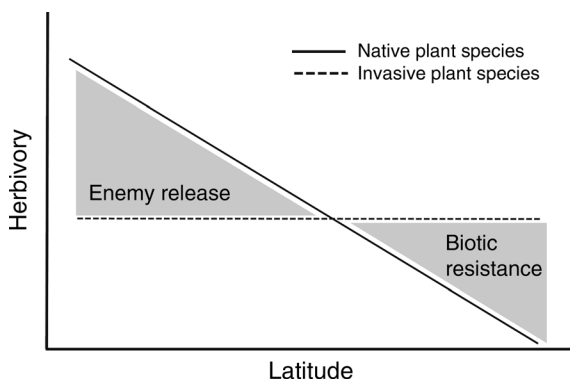


FIG. 1. Hypothetical relationship between latitude and herbivory for a native plant species (solid line) and invasive plant species (dashed line). Invasive species (or genotypes) exhibit proportionately less herbivory than native species (or genotypes) at southern latitudes (i.e., leading to enemy release within invaded communities) than northern latitudes (i.e., leading to biotic resistance within invaded communities).

to assess the ubiquity of gradients in herbivory and other species interactions (Schemske et al. 2009, Moles et al. 2011). Common flaws include narrow latitudinal ranges of study and the comparison of different species at different latitudes. The latter flaw means that phylogenetic constraints could potentially underlie observed latitudinal patterns.

For invasive plant species with continent-wide distributions, this potential latitudinal heterogeneity in the strength of species interactions could greatly influence the establishment, growth, or spread of invasive species populations (Bezemer et al. 2014). One expectation from this hypothesis is that stronger species interactions should make the local community more resistant to invasion (Levine et al. 2004, Freestone et al. 2013). Much research has been conducted on whether the local herbivore assemblage inflicts greater damage on the invasive than native species (i.e., biotic resistance) or vice versa (i.e., biotic susceptibility). Meta-analyses suggest that both scenarios are common (e.g., Chun et al. 2010).

We suggest here that one possible explanation for these mixed results is that latitudinal (or geographic) variation in species interactions (e.g., resistance traits, herbivore pressure) could cause latitudinal (geographic) variation in the importance of biotic resistance or susceptibility. For example, Freestone et al. (2013) demonstrated that predation on invasive tunicates was much greater in marine communities at southern than northern latitudes, suggesting greater biotic resistance to invaders at lower than higher latitudes. Complicating the situation further, it is plausible that the latitudinal cline in the strength of species interactions (e.g., herbivory) may differ between native and invasive species, owing to differences in the species' adaptation to the local environment. Consider the hypothetical example in Fig. 1 in which an invasive plant species

comes from a region where it was adapted to moderate levels of herbivory (e.g., a mid-latitude location). In the southern regions of the invaded range, the invader may be less defended and suffer greater herbivory than native plants, making the plant community more resistant to invasion. In northern regions, the invader may be better defended than local native plants and therefore the community may be more susceptible to invasion. These nonparallel relationships in herbivory between native and invasive plants can create significant large-scale heterogeneities in invasibility.

We conducted a study of the latitudinal variation in herbivory of native genotypes of the common reed (*Phragmites australis*; Poaceae) in North America (NA) and Europe (EU) and European invasive genotypes in NA. What makes this system unique and ideally suited for this type of study is that, in NA, native and invasive genotypes co-occur in marshes along the Atlantic Coast, allowing for phylogenetically controlled comparisons within and among regions. A transect of *P. australis* patches spanning 19°–22° of latitude was established on each continent. Over two years, we conducted surveys of *P. australis* nutritional condition, putative defenses, and herbivory from three different feeding guilds (leaf chewers, internal stem-feeders, and aphids). Two separate sets of hypotheses were tested, one involving co-occurring native and invasive genotypes in NA, and the other involving the European genotypes in the native (EU) and invasive (NA) ranges. Within NA, we tested three main hypotheses: (1) NA wetlands are relatively susceptible to invasion by European genotypes of *P. australis* because these genotypes are better defended and experience reduced herbivory in comparison to co-occurring native genotypes; (2) as predicted by theory, herbivory and defenses of native *P. australis* in NA decreases with increasing latitude; (3) the invasive genotypes in NA exhibit either no latitudinal gradient, or a nonparallel latitudinal gradient in herbivory and defenses compared to the native genotypes. For the European genotypes in the native and invasive ranges, we tested two additional hypotheses: (4) defenses, nutritional condition, and herbivory differed between the native and invasive ranges. In particular, we test whether the European genotypes escaped their natural enemies when they invaded NA. (5) European genotypes in their native and invasive ranges exhibit similar latitudinal gradients in defense and herbivory as the North American native genotypes. Based on our results, we evaluated whether biotic resistance or susceptibility varied significantly with latitude.

METHODS

Study system

P. australis is a large (3–5 m tall) perennial grass that is distributed across all continents except Antarctica (Lambertini et al. 2006). It is associated with freshwater and brackish wetlands where it grows clonally and forms dense monospecific stands. In NA, *P. australis* is native

and widely distributed (Saltonstall 2002). However, ~150 years ago, an introduced European genotype (haplotype M) appeared in herbaria records. By the 1960s, the introduced genotype was widespread in eastern NA (Chambers et al. 1999, Saltonstall 2002). Multiple introduction events at coastal ports led to the establishment of haplotype M in NA (Saltonstall 2002, Lambertini et al. 2012, Meyerson and Cronin 2013). Introduced genotypes have since spread south to the Gulf Coast and west to the Pacific Coast (Saltonstall 2002, Meyerson et al. 2009, 2010a, Lambertini et al. 2012).

Saltonstall (2002) identified 27 distinct haplotypes worldwide, 11 of which were endemic to NA. Haplotype M, which is native and widespread throughout EU and parts of Asia, is likely the ancestral haplotype for the species (see also Lambertini et al. 2006). Several additional native and invasive genotypes have since been discovered in NA (Meadows and Saltonstall 2007, Lambertini et al. 2012, Meyerson and Cronin 2013). These new invasive genotypes are closely related to haplotype M. There are no widespread invasive genotypes reported in EU.

Using published literature, Tewksbury et al. (2002) tabulated the known herbivore diversity associated with *P. australis* in EU and NA. Over 140 species were identified from EU and only 26 from NA. Of the species currently reported to feed on *P. australis* in NA, the majority are introduced, including the gall flies in the genus *Lipara* (Chloropidae; Lambert et al. 2007) and the mealy plum aphid *Hyalopterus pruni* (Lozier et al. 2009).

The impact that herbivores have on *P. australis* fitness is not well studied but the evidence suggests it can be substantial. *H. pruni* are widespread on *P. australis* throughout EU and NA, and can achieve massive and sustained outbreaks (Tscharntke 1989, Lambert and Casagrande 2007). In native NA patches, these multi-year outbreaks have resulted in premature senescence and failure of whole patches to flower for consecutive years (J. T. Cronin, *personal observation*). The proportions of stems galled by *Lipara* spp. have reached as high as 80%, with no galled stems successfully producing flowers (Lambert et al. 2007). Several lines of evidence suggest that sexual reproduction has been very important in the spread of *P. australis* (e.g., Alvarez et al. 2005, Kettenring and Mock 2012). Finally, there have been reports of locally intense herbivory of *P. australis* from a diversity of other herbivores (Tewksbury et al. 2002).

Census procedure

In NA, we conducted our research at widely separated *P. australis* patches along a south-to-north transect from the Louisiana Gulf Coast (29.8° N) to central Quebec, Canada (48.4° N; Appendix A: Table A1). In cases where more than one *P. australis* genotype occurred in the same marsh, we included a representative patch from each genotype. Using this approach, we had paired

invasive-native patches (including genotypes M1 in the Gulf and L1 at La Pocatière, Quebec, Canada; Lambertini et al. 2012, Meyerson and Cronin 2013) of similar latitude, herbivore species pools, and environmental conditions. Below a latitude of 36.5° N, native patches have never been found. Thirteen native and 17 invasive patches were located along the NA transect. A comparable transect was established in EU that extended from southern Portugal (37.1° N) to southern Norway (59.3° N) and traversed the Atlantic coastline (Table A1). Patches along the EU transect were clustered in seven trios (<5 km apart) that represented different regions on the continent (Table A1). Genotypes were determined by DNA analysis according to the protocol of Saltonstall (2002) with modifications by Kulmatiski et al. (2011).

In July–August 2011, May–June 2012, and July–August 2012, we conducted surveys of each patch to assess (1) patch characteristics (patch size, stem density), (2) plant nutritional condition (percent carbon, percent nitrogen, carbon:nitrogen ratio [C:N ratio]) (3) putative defense levels (leaf toughness, total phenolics), and (4) herbivory. We focused on the presence of or damage from three main feeding guilds: chewing herbivores (proportion of leaf area consumed over the growing season), internal stem-feeders (proportion of stems with gall formers or borers), and sucking herbivores (specifically, the number of *H. pruni* aphids per stem). Herbivores were separated into feeding guilds because the damage they inflict is not comparable and they may respond differently to latitude (Pennings et al. 2009). Although the composition of the chewing guild likely changes across latitudes, the aphids and the dominant component of the internal stem-feeder guild (*Lipara* spp.) are present throughout most of the latitudinal range of this study. Details of the census methods are provided in Appendix B.

Statistical analyses

Two sets of statistical tests were performed with these census data. The first set of tests involved whether the nutritional condition, defenses, and herbivory of *P. australis* populations in NA varied with genotype (native vs. invasive) and latitude (henceforth referred to as the “native and invasive genotypes in NA comparison”). We were particularly interested in whether native and invasive genotypes exhibited parallel or nonparallel responses to the latitudinal gradient. The second set of analyses focused on whether the nutrition, defense, and herbivory of *P. australis* along a latitudinal gradient differed with respect to the range of the European genotypes, in either the continent of origin (EU) or in its invasive range (NA) (henceforth referred to as the “European genotypes in their native and invasive ranges comparison”).

The statistical procedure was the same for each comparison. For each nutritional trait (percent C, percent N, C:N ratio), putative defense trait (total

TABLE 1. Best-fit models for *Phragmites australis* nutritional condition, defense levels, and herbivory based on an AIC_c selection procedure from separate mixed-effects models.

Dependent variable	North America native vs. invasive genotype	European genotypes in native and invasive ranges
Plant nutrition/defense		
Percent C	Y, [L], L × Y	Y, R, L, S, Y × R, Y × L, Y × S, L × S
Percent N	Y, G, L, G × L, G × Y, L × Y	[Y], R, L, S, Y × L, L × S
C:N ratio	Y, G, L, S, Y × G, Y × L	[Y], R, L, S, Y × L, L × S
Phenolics	Y, G, L	Y, R, [L], R × L, Y × H
Leaf toughness	Y, G, [L], S, Y × G, Y × L	Y, H, [L], S, R × Y, L × Y
Herbivory		
Proportion of leaves with chewing damage	Y, G, L, S, G × L	Y, L, S, T, [L × Y]
Proportion of stems with internal feeders	Y, G, [L], P, S, G × L, L × P	
Aphid density	Y, G, L, S, C, G × L, G × Y, Y × S	Y, R, L, S, C, T, F, R × S, S × Y
	G, T	R, L, P, S, T, F, L × S

Notes: Abbreviations are Y, year or census period (repeated measure); G, genotype; R, range (Europe or North America); L, latitude (°N); P, patch size (ln-transformed); S, stem density (no./m²; ln-transformed); C, percent carbon; N, percent nitrogen; T, leaf toughness (kg of force); F, total phenolics (nmol/g; ln-transformed). Factors in brackets were not statistically significant ($P \leq 0.05$) but were retained in the model because of the underlying structure (i.e., Y as a repeated measure) or because its interaction with another factor was an important source of variation in the model (an interaction term in the model must be accompanied by the main factors in the model).

phenolics, leaf toughness), and herbivory traits from two herbivore guilds (proportion of leaf area consumed, proportion of stems with internal stem-feeders), we used a separate repeated measures mixed-model ANOVA. Census date for the measurement of plant nutritional and defense traits, and year (July–August 2011 and July–August 2012) for the measurement of herbivory traits were treated as repeated measures. Genotype (native or invasive) and range (EU or NA) were fixed factors; latitude, patch size (m²), and stem density (number of stems/m²) were used as covariates in the model. In the mixed-models for herbivory traits, we also included all of the nutritional and defense traits as covariates. A repeated measure (year) was not included in the mixed model for aphid herbivory, i.e., the total number of aphids per stem, as we only had an estimate for aphid numbers in 2012.

For each dependent variable, we used Akaike's information criteria corrected for finite sample size (AIC_c) to select the most informative model (Burnham and Anderson 2010; Appendix C: Table C1). Details of the selection procedure and statistical methods are provided in Appendix B.

Finally, one issue of concern with this study was that the latitudinal ranges of the native and invasive genotypes in NA and the European genotype in EU were not exactly the same (Table A1). To confirm that the differences in the latitudinal ranges among these three phylogeographic groups of *P. australis* did not bias our conclusions about the effects of genotype (i.e., native vs. invasive ranges) and latitude on plant traits, we conducted an additional set of analyses in which we controlled for latitudinal range (for details, see Appendix B). For each comparison, only the patches that were in the range of overlap for the phylogeographic groups were included in the models. Based on our analyses (see Appendix C: Table C2), controlling for latitudinal range

did not alter our results. We therefore only report on the full data set below.

RESULTS

Native and invasive genotypes in North America

Nutrition and defense traits.—Nutritional and defense levels of *P. australis* in NA varied over time, differed between genotypes in all cases except for percent C, and were linearly related to the latitudinal gradient (Table 1, Fig. 2, Appendix C). In general, *P. australis* leaves in the early season census (May–June 2012) were characterized by slightly higher percent C (1%; $F_{1,33} = 25.7$, $P < 0.001$), 26% higher percent N ($F_{1,45} = 11.0$, $P = 0.002$), 21% lower C:N ratio ($F_{1,42} = 20.9$, $P < 0.001$), 21% lower total phenolics ($F_{1,49} = 383.0$, $P < 0.001$), and 37% lower leaf toughness ($F_{1,46} = 4.9$, $P = 0.031$) than *P. australis* leaves in the late-season censuses (July–August 2011, 2012; Table 1). Percent N was 15% higher in the invasive than native *P. australis* genotypes (Fig. 2B inset) and increased with increasing latitude (Fig. 2B), but the difference between genotypes diminished at higher latitudes (as indicated by a significant genotype × latitude interaction in the most probable model; Table 1). Owing to the relatively invariant response of percent C to genotype or latitudinal variation (Fig. 2A), the C:N ratio exhibited the opposite relationship to that of percent N (Fig. 2C). Here, the native genotypes had a 13% higher C:N ratio overall (Fig. 2C inset); the difference was generally greatest at lower latitudes. Finally, with regard to putative defenses, the native genotypes had 4% more total phenolics but leaf toughness was 21% lower than in the invasive genotypes (Fig. 2D, E insets). For both genotypes, total phenolics decreased with increasing latitude, whereas leaf toughness did not exhibit any obvious latitudinal trends (Fig. 2D, E).

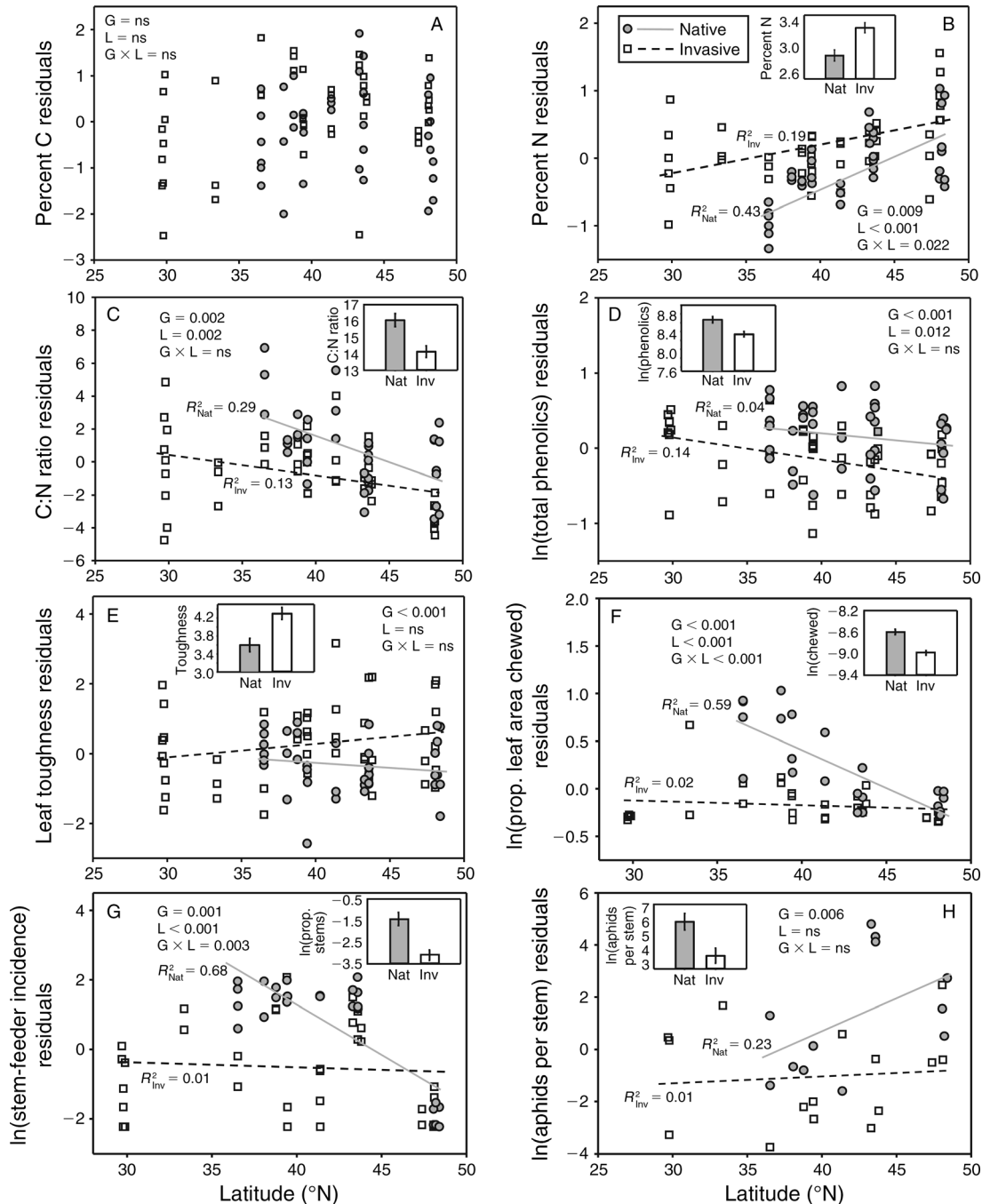


FIG. 2. For North American native (Nat; gray circles) and invasive (Inv; white squares) genotypes of *Phragmites australis*, the relationships between latitude (°N) and (A–C) plant nutritional condition (percent C, percent N, C:N ratio), (D, E) defense levels (total phenolics, leaf toughness), and (F–H) measures of herbivory from three different feeding guilds (proportion [prop.] of leaf area chewed, internal stem-feeder incidence [proportion], and aphids [no./stem]). To emphasize the effects of genotype and latitude independent of all other factors in the best models determined by AIC_c (see Table 1), a repeated-measures mixed-model ANOVA was conducted with these two variables removed. The residuals from this analysis are plotted in the main panels with respect to genotype and latitude. Each data point is based on the mean value per patch per time period. *P* values are reported for the effects of genotype (G), latitude (L), and the G × L interaction; ns stands for not significant. If a significant latitude effect was evident, separate regression lines were fit to each genotype and the associated R^2 was reported (R^2_{Nat} , R^2_{Inv}). Inset bar graphs depict the least-squares means ± SE of plant nutritional condition, defense levels, and herbivory measures for the native (Nat; gray bar) and invasive (Inv; white bar) genotypes from the best models determined by AIC_c values (see Table 1). Bar graphs are only reported if genotype was a factor in the best models determined by AIC_c values.

Herbivory.—Although the proportion of stems with herbivore chewing damage in NA averaged 0.28 ± 0.04 over two years (range: 0.0–0.91, $n = 56$), the mean percentage of total leaf area consumed for a patch was quite low and never exceeded 0.1% per patch (Appendix D; Fig. D1). Two models describing the variation in chewing damage were equally plausible (AIC_c weights of 0.30); both models included genotype, latitude, and a genotype \times latitude interaction as significant factors (Table 1, Appendix C). On average, native genotypes suffered 6.5 times more chewing damage than the invasive genotypes (0.013% vs. 0.002%; $F_{1,24} = 44.3$, $P < 0.001$; Fig. 2F inset). Whereas the invasive genotypes suffered similar levels of chewing damage across the 19° latitudinal gradient, the native genotypes exhibited a strong linear decline in herbivory with increasing latitude, and a significant genotype \times latitude interaction was present in the best models (Appendix C; Fig. 2F). Estimated chewing damage for the native genotypes at the southern limit of population distributions in NA (Mackay Island, North Carolina, USA) was 3.1 times higher than at the northernmost population (Hebertville, Quebec, Canada). Finally, chewing damage increased with a decrease in stem density or an increase in patch size, but the proportion of the variation in chewing damage explained by those linear relationships was quite low (Appendix E; $R^2 < 0.13$).

Very similar results were found for internal stem-feeders. Proportion of infested stems reached a maximum of 73% and averaged $20.5\% \pm 2.9\%$. Overall, 94% of the infested stems from our NA transect were inhabited by a *Lipara* species. Although our model selection procedure yielded no clear-cut best model, all plausible models ($\Delta_i \leq 2$) included year, genotype, latitude, genotype \times latitude, stem density, patch size, and percent C (Appendix C). On average, native genotypes had three times the internal stem-feeder incidence of the invasive genotypes ($33\% \pm 5\%$ and $11\% \pm 3\%$, respectively; $F_{1,25} = 13.6$, $P < 0.001$; Fig. 2G inset). For the native genotypes, internal stem-feeder incidence declined from an estimated 80% in the southernmost populations to 3% in the northernmost populations (Fig. 2G). As with chewing damage, internal stem-feeder incidence of the invasive genotypes did not vary systematically with latitude. Finally, internal stem-feeder incidence tended to increase with an increase in percent C and a decrease in stem density (Appendix E).

H. pruni was present at every site in the NA and EU transects. Mean numbers of *H. pruni* per stem in a patch reached as high as 4847 individuals per stem with 100% of the stems infested (mean of patch means = 400.8 ± 156.9 [mean \pm SE]). AIC_c values indicated no clear-cut best models but all plausible models included genotype, and two of the top four models included latitude (Appendix C). Consistent with the other herbivore guilds, aphid densities per stem were 70% greater on native than the invasive genotypes (Fig. 2H inset) and a

latitudinal gradient in aphid abundance was most evident for the native genotypes (Fig. 2H). In contrast to the other two herbivore guilds, aphids were more prevalent at higher than lower latitudes. Across the latitudinal range of the native genotypes, aphid densities were predicted to increase from a mean of 459 individuals per stem in the south to 2297 individuals per stem in the north, a five-fold increase. Finally, aphid abundance tended to increase with leaf toughness (Appendix E).

European genotypes in their native and invasive ranges

Nutrition and defense traits.—Based on the best-fit models (Appendix C), European genotypes in the invaded range averaged 2.3% higher percent C, 10% higher percent N, and 9% lower C:N ratio than the same genotypes in the native range (Fig. 3A–C insets). Levels of putative defenses were higher in NA than EU (5% for phenolics, 71% for leaf toughness; Fig. 3D, E insets). Consistent with our findings from NA, percent C and percent N increased, and the C:N ratio decreased with increasing latitude (Fig. 3A–C). Neither of the defense traits (phenolics, leaf toughness) varied with latitude (Fig. 3D, E).

Herbivory.—As in NA, chewing damage in EU was also quite low. The proportion of stems with chewing damage was 0.16 ± 0.03 (range 0.0–0.78, $n = 42$), and only $0.002\% \pm 0.001\%$ (range: 0.0–0.00016) of the total leaf area per patch was consumed in a given year. Among the most likely models (Appendix C), of which no single model stood out as best, latitude, stem density, and leaf toughness were the most common factors identified as contributing to variation in the proportion of leaf area consumed. As with the NA native vs. invasive comparison, chewing damage declined with increasing latitude and increasing stem density (Fig. 3F, Appendix E). Also, damage decreased with increasing leaf toughness, although the relationship was relatively weak ($R^2 = 0.08$, Appendix E). The range of the genotypes (NA or EU) was a factor in three of the 10 best models but chewing damage in EU was only 0.8% higher than in NA.

There was substantial evidence for one best model explaining variation in internal stem-feeder incidence (Appendix C; Akaike weight of 0.92). Based on this model, the European genotypes suffered 37% less internal stem-feeder incidence in the invaded range than the native range (0.16 ± 0.02 in EU, 0.11 ± 0.03 in NA; Fig. 3G inset). There was a general decline in internal stem-feeder incidence with increasing latitude and this appears to be more strongly driven by the European genotypes in the native range (Fig. 3G); although a range \times latitude interaction term did not contribute to model fit. Internal stem-feeder incidence also decreased with increasing stem density, total phenolics, and leaf toughness, but increased with increasing percent C (Appendix E).

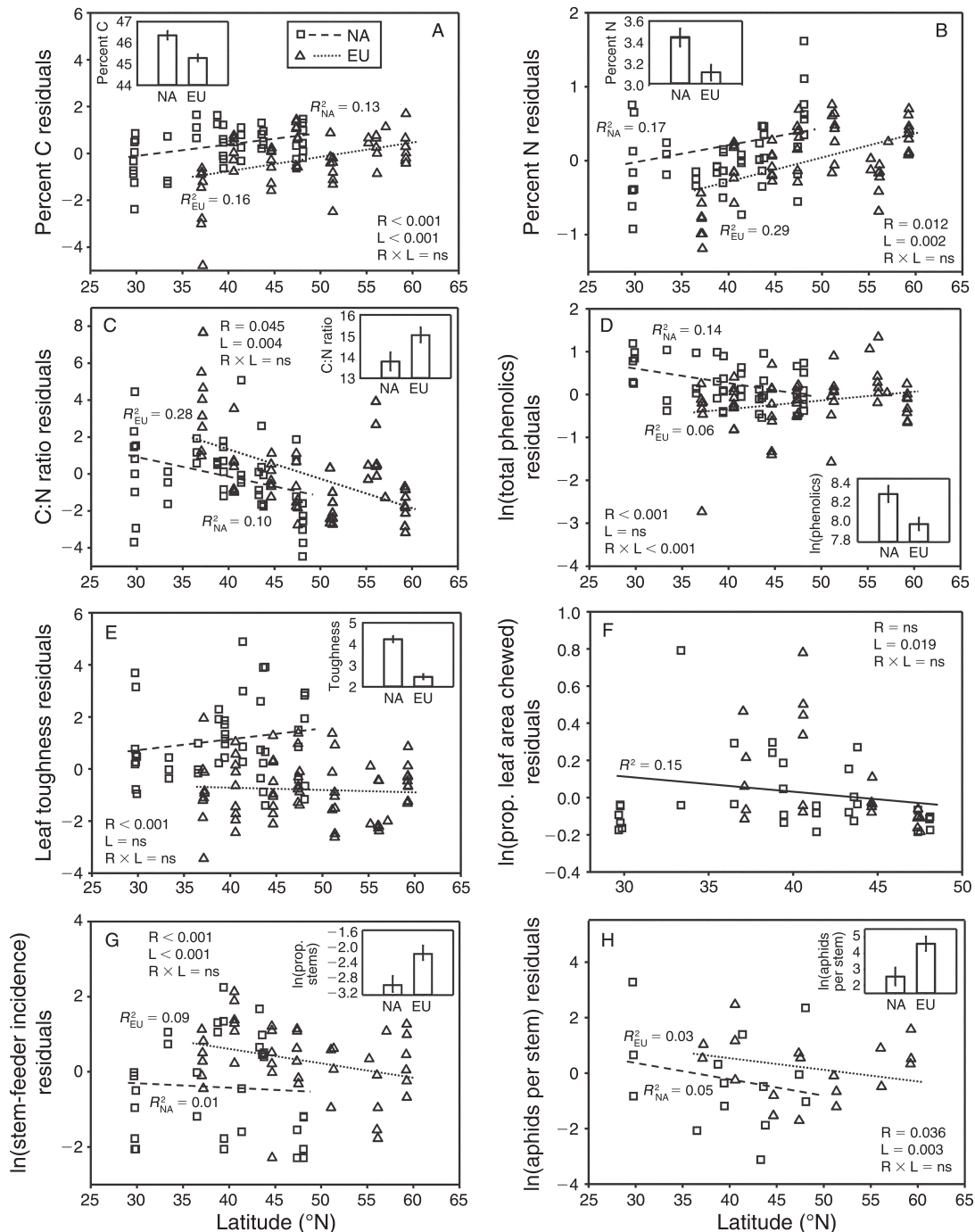


FIG. 3. For the European genotypes of *P. australis* in the native range (EU; triangles) and the invasive range (NA; squares), the relationships between latitude (°N) and (A–C) plant nutritional condition, (D, E) defense levels, and (F–H) herbivory from three different feeding guilds. To emphasize the effects of range and latitude independent of all other factors in the best models determined by AIC_c (see Table 1), a repeated-measures mixed-model ANOVA was conducted with these two variables removed. The residuals from this analysis are plotted in the main panels with respect to range and latitude. Each data point is based on the mean value per patch per time period. *P* values are reported for the effects of range (*R*), latitude (*L*), and the *R* \times *L* interaction; ns stands for not significant. If a significant latitude effect was evident, separate regression lines were fit to each range and the associated R^2 was reported (R^2_{EU} , R^2_{NA}). Inset bar graphs depict the least-squares means \pm SE of plant nutritional condition, defense levels, and herbivory measures for each range (EU and NA; white bars) from the best models determined by AIC_c values (see Table 1). Bar graphs are only reported if genotype was a factor in the best models determined by AIC_c values.

Finally, based on the most plausible set of models, the number of aphids per stem was seven times lower in NA (12.9 ± 1.7 vs. 98.5 ± 1.6 ; Fig. 3H) than in EU (Fig. 3H inset), and there was an overall trend toward declining aphid abundance with increasing latitude (Appendix E; Fig. 3H). Aphid numbers were negatively related to total phenolics ($R^2 = 0.29$). As stem density and leaf toughness increased, and patch size decreased, aphid numbers per stem tended to increase (Appendix E).

DISCUSSION

P. australis, with its continental scale invasion and broad overlap of native and invasive genotypes, afforded us the unique opportunity to investigate the biogeography of species interactions and its potential impact on invasion success. Consistent with the literature (Schemske et al. 2009, Moles et al. 2011), we found strong evidence that traits associated with plant–herbivore interactions commonly varied with latitude. Of greatest novelty and significance, we found that gradients in herbivory were prevalent for native *P. australis* genotypes in NA and EU but mostly nonexistent for the invasive genotypes in NA. The resulting nonparallel responses between native and invasive genotypes along the same latitudinal gradient have the potential to generate important spatial heterogeneities in invasion success. Cryptic plant invasions such as the one involving invasive genotypes of *P. australis* are scarce in the literature (but see Laverne and Molofsky 2007). However, parallels do exist involving multiple invasive genotypes or aggressively spreading hybrids of native and invasive species (*Spartina* spp. [Ayres et al. 2004], *Typha x. glauca* [Ciotir et al. 2013]). In these cases, geographic variation in plant–herbivore interactions across the range of overlap of these genotypes may be affecting their invasion success. Overall, our findings suggest that the field of invasion biology would benefit from a broader scale, biogeographic perspective to the research (Bezemer et al. 2014).

Latitudinal variation in nutrition and defense traits

Native genotypes of *P. australis* in NA and EU, and the invasive genotypes in NA exhibited similar latitudinal patterns with respect to nutritional condition. Percent C and percent N generally increased with increasing latitude. This response is consistent with global patterns of soil and foliar element levels (Reich and Oleksyn 2004, Lovelock et al. 2007, Xu et al. 2013). Although other explanations are possible, a N gradient may arise because of the necessity for plants to grow faster in the abbreviated northern growing season, which would require more nutrients to achieve that growth (Lovelock et al. 2007). Higher concentrations of foliar N would then allow for greater photosynthetic rates and increased accumulation of C (Reich and Oleksyn 2004). Additionally, atmospheric CO₂ levels, which are positively correlated with latitude (Denning et al. 1995), are expected to stimulate photosynthesis (Elser

et al. 2010). Interestingly, the C:N ratio decreased with increasing latitude, owing to the steeper latitudinal gradient in N than C.

A latitudinal gradient in putative chemical but not physical defenses was also found in *P. australis*. Total phenolics, which represent a broad class of compounds, are known to have variable effects on herbivory (Close and McArthur 2002). In NA populations (native and invasive), total phenolics declined with increasing latitude. Interestingly, phenolics in EU patches of *P. australis* exhibited a positive correlation with latitude. It also represented the only trait for the European genotypes that exhibited qualitatively different relationships with latitude in the native and invasive ranges (Fig. 3). At present, we do not know what biotic, abiotic, or genetic factors (e.g., founder effects) have led to this difference between continents for the same genotypes. In their literature review, Moles et al. (2011) found that for only 7 of 23 studies (30%), a significant phenolic–latitude relationship was evident; the majority of these relationships were positive (five of seven responses). Finally, although a longer lifespan of leaves at southern latitudes is predicted to favor greater leaf toughness (Wright et al. 2004), we found no evidence that *P. australis* leaf toughness varied with latitude.

Herbivory on Phragmites in North America and Europe

This study is the first to provide a broad geographic assessment of the impact of herbivores on *P. australis* in EU and NA. Across both continents, leaf damage from chewing herbivores was widespread but cumulative tissue loss during the year was exceedingly low, $\leq 0.01\%$. Although chewers tended to focus on younger leaves that may contribute more to plant fitness than older leaves (McKey 1979), it seems unlikely that this level of damage would have any measurable impact on *P. australis* fitness. In contrast, herbivory from internal stem-feeding herbivores and aphids may incur substantial fitness costs to *P. australis*. Internal stem-feeders in the genus *Lipara* made up the majority of this guild and internal stem-feeder incidence averaged 33% for patches of NA native genotypes, 11% for the NA invasive genotypes, and 16% for the EU native genotype. The highest patch-level infestation was 73% (NA native population) and is comparable to maximal infestation levels reported in the past (Tewksbury et al. 2002). *Lipara* gall formers, which were introduced to NA in the last century from EU, are known to prevent flowering and possibly reduce final stem heights (Lambert et al. 2007, Park and Blossey 2008).

In comparison, *H. pruni* was ubiquitous along the NA and EU latitudinal transects and achieved very high stem densities in some patches (>4800 individuals). *H. pruni* is cyclically parthenogenetic and a particularly serious introduced pest of dried plum (*Prunus domestica*) in California and other *Prunus* species throughout NA (Lozier et al. 2009). The impact of *H. pruni* on the fitness of its secondary host *P. australis*, is difficult to assess;

however, the Webhannet native patch sustained the highest aphid abundances in both years of our study and exhibited almost complete mid-season senescence in the following two years. Tscharnke (1989) reported similarly heavy aphid impacts on *P. australis* in EU.

The two most prevalent factors affecting herbivory were genotype (or range) and latitude. We found that herbivory from chewers, internal stem-feeders, and aphids was 0.8%, 37%, and 700% lower, respectively, for European genotypes in the invasive range (NA) than in the native range (EU). Superficially, these results support the enemy-release hypothesis in which a species or genotype leaves behind its coadapted natural enemies and experiences reduced herbivory in its invaded range compared to its native range (Keane and Crawley 2002). However, the two guilds that exhibited the greatest reduction in herbivory in the invasive range, the aphids and majority of internal stem-feeders (i.e., all *Lipara* spp.), were also introduced into NA. Therefore, the mechanism underlying lower herbivory in NA than EU may not be attributed to these specific herbivores being poorly adapted to invasive *P. australis* in NA. One plausible explanation is that herbivory is lower for the European genotype in its invaded range than its native range because it is better defended against herbivory (more total phenolics and greater leaf toughness; Fig. 3D, E). Interestingly, this finding runs counter to the evolution of increased competitive ability (EICA) hypothesis proposed by Blossey and Notzold (1995). According to the EICA hypothesis, release from herbivory in the invaded range should allow plants to reallocate resources from defenses to growth and competitive ability. Despite substantially lower herbivory on invasive *P. australis*, there is no evidence for a trade off between defenses and growth in invasive genotypes. In general, there has been relatively little support in favor of the EICA hypothesis (Felker-Quinn et al. 2013).

Within NA, typically within the same marsh system, invasive patches of *P. australis* experienced substantially lower herbivory than native patches—650% lower chewing damage, 300% lower internal stem-feeder incidence, and 70% lower aphid densities. These results are consistent with garden studies, which showed that native genotypes were much more vulnerable to *Lipara* and aphid herbivory than invasive genotypes (Lambert and Casagrande 2007, Park and Blossey 2008).

Latitudinal gradients in herbivory

Despite mixed support from the literature (see Schemske et al. 2009, Moles et al. 2011), we found strong evidence that the strength of *P. australis*–herbivore interactions varies with latitude. In our study, native *P. australis* in NA and EU exhibited latitudinal gradients in the levels of herbivory from each of the three herbivore guilds. With the exception of aphid densities in NA, which exhibited a positive relationship to latitude, all other comparisons revealed a negative

relationship between herbivory and latitude. These results fit perfectly with the findings presented by Pennings et al. (2007, 2009) and summarized by Moles et al. (2011), that herbivory is greater at lower than higher latitudes among coastal marsh plants.

The latitudinal patterns in herbivory of native *P. australis* were independent of any effects of latitude on plant nutrition or defense traits. At this point in time, we do not know the underlying mechanism driving these latitudinal patterns. Clearly, temperature varies considerably over the 19° and 22° latitudinal range of the NA and EU transects, respectively. In fact, if we substituted annual mean temperature, or a number of other climate variables from the BIOCLIM database (Hijmans et al. 2005) for latitude, our model-selection results generally indicate a strong climate effect on *P. australis* nutrition, defenses, and herbivory (J. T. Cronin, *unpublished data*). A simple possible explanation may be that with a longer growing season at lower latitudes, herbivores may have more time to feed and produce more generations than at higher latitudes (Coley and Barone 1996). We generally controlled for salinity and elevation in our selection of sites, but patches could vary with regard to a variety of other edaphic and community or ecosystem variables that were not accounted for in our measures of plant nutrition, defense, and patch characteristics.

Interestingly, no latitudinal gradient was evident among invasive patches in NA, despite being widely distributed along the east coast of NA for >50 years (Saltonstall 2002). Studies of invasive species distributions have investigated the formation of parallel clines in response to a latitudinal gradient in various life history traits (e.g., Huey et al. 2000, Maron et al. 2007). To our knowledge, this is the first study to examine whether gradients in the strength of species interactions vary in parallel between native and invasive species (or genotypes). Also, because our native vs. invasive comparison occurred along the same transect, we were able to rule out the possibility that latitudinal differences between genotypes were due to differences in biotic interactions or the abiotic environment (see Schemske et al. 2009, Moles et al. 2011).

The absence of a gradient in herbivory on invasive *P. australis* could be due to insufficient time for the genotype to evolve in response to selective pressure from the local herbivore community. However, the preponderance of evidence suggests that invasive species can adapt quickly to local selection pressures and develop genetically based clines with regard to latitude in <100 years (e.g., Kilkenny and Galloway 2013, Novy et al. 2013). However, hybridization, high rates of gene flow, or multiple introductions of invasive genotypes could all counteract local adaptation and cline formation. Currently, there is evidence that all three mechanisms are active in *P. australis* populations in North America (Meyerson et al. 2010b, 2012, Lambertini et al. 2012, Meyerson and Cronin 2013, Saltonstall et al. 2014).

Despite the above constraints on local adaptation, common garden experiments have indicated that there is a genetic basis to differences among genotypes in nutritional, morphological, defense traits, and palatability to herbivores (G. P. Bhattarai, W. J. Allen, L. A. Meyerson, and J. T. Cronin, *unpublished data*). However, differences among latitude of origin are mostly due to phenotypic plasticity. To date, several studies have found evidence of genetically based clines in traits associated with plant–herbivore interactions (e.g., Salgado and Pennings 2005, Maron et al. 2007, Pratt et al. 2014).

Nonparallel latitudinal gradients in herbivory, as observed for native and invasive *P. australis* in NA, can have important yet unexplored implications for the field of invasion biology (Bezemer et al. 2014). First, as illustrated in Fig. 1, nonparallel herbivore impacts across a latitudinal gradient can result in spatial variation in herbivore pressure within the invaded community; this may help to explain the inconsistent findings in support of the biotic resistance hypotheses (Chun et al. 2010). For example, we found strong evidence that invasive genotypes in NA experienced less herbivore pressure from chewers and gallers than native genotypes in NA (i.e., biotic susceptibility), but only at lower latitudes (see Fig. 2F, G). If the study were restricted to northeastern NA, we would have found no difference in herbivory between native and invasive genotypes and therefore no evidence of biotic susceptibility. Given that many of our most notable invasive species are distributed across broad geographic extents, the evaluation of the biotic-resistance hypothesis should be conducted across multiple regions. We also acknowledge here that other types of species interactions, such as pathogen–host interactions or competition, can potentially generate large-scale spatial heterogeneity in invasion success if these interactions vary in a nonparallel way with regard to latitude.

Second, if herbivores are important factors affecting invasion success (i.e., establishment, growth, spread), then nonparallel latitudinal gradients in herbivory between co-occurring native and invasive plants can generate important spatial heterogeneity in invasion success (Bezemer et al. 2014). Although there is evidence from field and common garden studies to suggest that herbivores can strongly impact *P. australis* biomass, sexual reproduction, and the survival of above-ground standing crop (see *Methods*), we know relatively little about the long-term effects of herbivores on *P. australis* clones in nature. However, if short-term effects of herbivory translate into long-term impacts on *P. australis* growth and spread, we would predict that invasion success could be greater at lower than higher latitudes. The reason for this prediction is that the invasive genotypes exhibited proportionately less herbivory than native genotypes at southern latitudes (i.e., communities are more susceptible to invasion) than

northern latitudes (i.e., communities are more resistant to invasion).

Although this would be a challenging hypothesis to test, we do have data on one aspect of invasion success—the growth rates of established invasive genotypes. Using historical aerial imagery from wetlands along the Gulf and Atlantic Coasts of the United States, Bhattarai and Cronin (2014) found no relationship between latitude and the rate of invasive *P. australis* patch growth. Currently, we have no data on the differences in colonization success, patch growth rates, or proliferation of new patches of native and invasive genotypes along a latitudinal gradient. We conclude with the suggestion that latitudinal patterns in nonnative species distributions (nonnative species are more common in temperate than tropical and polar regions [e.g., Lonsdale 1999, Sax 2001, Fridley et al. 2007], and nonnative species occur at higher latitudes in their invaded than native ranges [Guo et al. 2012]) may be another factor contributing to heterogeneous selection pressures, such as herbivory. Of course, we would expect that nonparallel gradients between native and invasive species (or genotypes) would be transient, and become parallel as the invader adapts to the local environment.

Finally, although it was not one of the primary objectives of this study, we provide a brief assessment of the factors, other than genotype (or range) and latitude, which contributed to the variation observed in herbivory. Interestingly, percent N, a common indicator of nutritional quality (e.g., Price 1991), was not an important factor for incidence of any herbivore guild. Percent C, however, was positively correlated with gall incidence in both NA and EU. Galls are often C sinks and a number of studies have demonstrated that gall formers have the capacity to stimulate photosynthetic rates of neighboring leaves (e.g., Fay et al. 1993, Dorchin et al. 2006). Therefore, it seems likely that herbivory by *Lipara* spp. on *P. australis* is changing percent C in *P. australis* leaves rather than responding to it.

The two plant defenses, total phenolics and leaf toughness, were associated with herbivory from all three herbivore guilds. In EU, leaf chewing damage and internal stem-feeder incidence declined with increasing leaf toughness, and internal stem-feeder incidence and aphid abundance declined with increasing total phenolics. Similar patterns were observed in NA but those defensive traits were not retained in the best-fit models. Overall, these findings support the viewpoint that leaf toughness and total phenolics are resistance traits affecting herbivores (Denno et al. 1990, Salgado and Pennings 2005). Interestingly, aphid colony size increased with leaf toughness. It remains an open question whether aphids respond to plants with tougher leaves or, through the action of their feeding, cause plant leaves to become tougher. Lastly, for chewers and internal stem-feeders on both continents, herbivory declined with increasing stem density. Explanations for this pattern

include the possibility that dense patches have a microclimate that is not conducive to high herbivore fitness, or that dense patches inhibit herbivore movement or support higher predator densities.

Management of P. australis in North America

Management of invasive *P. australis* in NA poses serious challenges. Invasive genotypes have become dominant components of wetland communities and continue to spread rapidly in eastern NA (Chambers et al. 1999, Bhattarai and Cronin 2014). In comparison, endemic native genotypes are relatively rare, often grow in close proximity to invasive genotypes, and are at risk of displacement by or hybridization with invasive genotypes (e.g., Meyerson et al. 2010b, 2012, Saltonstall 2011). Despite efforts to the contrary (reviewed in Hazelton et al. 2014), we suggest that the biological control of invasive *P. australis* using insect herbivores is ill advised. All herbivore guilds, including *Lipara* spp. and *H. pruni* that are derived from the native range of the invasive genotypes, are more abundant (this study) and perform better on the native than invasive genotypes (Lambert and Casagrande 2007, Lambert et al. 2007; W. P. Allen, G. P. Bhattarai, L. A. Meyerson, and J. T. Cronin, *unpublished data*; for a possible exception, see Saltonstall et al. 2014). In general, there are very few examples in the literature where biological control agents exhibit sufficient specificity at the subspecies level (but see Goolsby et al. 2013).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A–E are available online: <http://dx.doi.org/10.1890/14-1091.1.sm>