

Geographic variation in apparent competition between native and invasive *Phragmites australis*

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Abstract. Apparent competition, the negative interaction between species mediated by shared natural enemies, is thought to play an important role in shaping the structure and dynamics of natural communities. However, its importance in driving species invasions, and whether the strength of this indirect interaction varies across the latitudinal range of the invasion, has not been fully explored. We performed replicated field experiments at four sites spanning 900 km along the Atlantic Coast of the United States to assess the presence and strength of apparent competition between sympatric native and invasive lineages of *Phragmites australis*. Four herbivore guilds were considered: stem-feeders, leaf-miners, leaf-chewers and aphids. We also tested the hypothesis that the strength of this interaction declines with increasing latitude. Within each site, native and invasive plants of *P. australis* were cross-transplanted between co-occurring native and invasive patches in the same marsh habitat and herbivore damage was evaluated at the end of the growing season. Apparent competition was evident for both lineages and involved all but the leaf-chewer guild. For native plants, total aphids per plant was 296% higher and the incidence of stem-feeding and leaf-mining herbivores was 34% and 221% higher, respectively, when transplanted into invasive than native patches. These data suggest that invasive *P. australis* has a negative effect on native *P. australis* via apparent competition. Averaged among herbivore types, the indirect effects of the invasive lineage on the native lineage was 57% higher than the reverse situation, suggesting that apparent competition was asymmetric. We also found that the strength of apparent competition acting against the native lineage was comparable to the benefits to the invasive lineage from enemy release (i.e., proportionately lower mean herbivory of the invasive relative to the native taxa). Finally, we found the first evidence that the strength of apparent competition acting against the native lineage (from stem-feeders only) decreased with increasing latitude. These results suggest that not only could apparent competition be of tantamount importance to enemy release in enhancing the establishment and spread of invasive taxa, but also that these indirect and direct herbivore effects could vary over the invasion range.

Key words: *apparent competition; enemy release; Hyalopterus pruni; indirect interactions; invasive plant; latitudinal gradients; Lipara sp.; plant-herbivore interactions.*

INTRODUCTION

Indirect biotic interactions are common in nature and have been shown to strongly influence the structure and dynamics of ecological communities (Wootton 1994). Apparent competition, in which species within the same trophic level negatively interact with each other through the action of shared natural enemies, is widely regarded as one of the most common forms of indirect interactions (Holt and Lawton 1993). Both theory (Holt 1977, Holt and Lawton 1993) and empirical data provide compelling evidence that apparent competition is as important as resource-based competition in structuring ecological communities (e.g., Bonsall and Hassell 1997, Chaneton and Bonsall 2000, Morris et al. 2004).

Apparent competition is an underappreciated but likely important mechanism that may facilitate species invasions (White et al. 2006, Borer et al. 2007, Enge et al. 2013). For example, apparent competition mediated by viral pathogens has been suggested to drive the invasion of California grasslands by competitively inferior introduced annual grasses (Borer et al. 2007). Refuge-mediated apparent competition has recently been proposed as one of the mechanisms for plant invasions (Orrock et al. 2010, Enge et al. 2013). The taller and denser structures of invasive plants are hypothesized to increase the abundance of natural enemies by providing refuge that ultimately causes greater negative impacts on the fitness of neighboring native plants. Reduced fitness of native plants can, in turn, facilitate the invasion success of the invasive plants. Finally, extended leaf phenology of invasive plants can lessen winter starvation of herbivores and has been proposed as a mechanism that could elevate herbivory on sympatric native plants (Smith and Hall 2016).

A more prominent mechanism of plant invasion that involves herbivores is enemy release. This hypothesis

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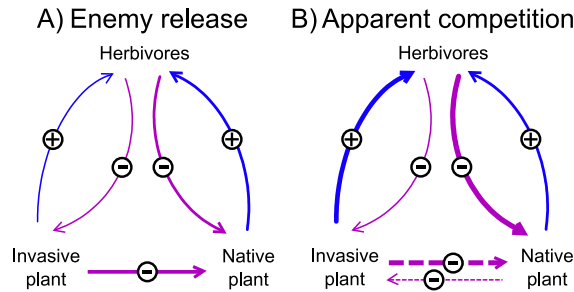


FIG. 1. Schematic diagrams illustrating enemy release and apparent competition in facilitating plant invasions. Solid arrows are direct interactions, broken arrows are indirect interactions and the width of the arrow denotes the strength of the interaction. (A) Invasive plants in the introduced range suffer lower herbivory than the neighboring native plants, which provides the former plants with a competitive advantage (Keane and Crawley 2002). (B) Invasive plants indirectly negatively affect the neighboring native plants by increasing herbivore abundance, which causes greater damage to the native than invasive plants (Holt 1977). [Color figure can be viewed at wileyonlinelibrary.com]

posits that invasive plants in the introduced range are under weaker control from natural enemies than their native competitors (Fig. 1A; Keane and Crawley 2002). Increased herbivore pressure on native plants, because of apparent competition with invasive plants (Fig. 1B), may also result in enemy release. Consequently, although apparent competition and enemy release may drive plant invasions through a difference in herbivore pressure between native and invasive plants, different mechanisms operate. In enemy release, greater herbivore abundance or herbivory on native plants would be caused by greater herbivore preference for the native as compared to invasive plants. It also could result in different herbivore communities on the two plant taxa. In contrast, in apparent competition, invasive plants would actually increase pressure by shared herbivores on the native plants, which could benefit the invasive plants via reduced interspecific competition. The strength of apparent competition has never been assessed relative to the strength of enemy release in species invasions.

The biotic interactions hypothesis posits that species interactions should be stronger at lower than higher latitudes (Schemske et al. 2009). To date, tests of this hypothesis have been restricted to direct species interactions (e.g., predation, mutualism) or interactions through a shared resource (exploitative competition; Schemske et al. 2009). Biogeographic studies involving indirect interactions between species, mediated by another species have not been undertaken. Latitudinal gradients in herbivore pressure and plant defenses, whether positive or negative, appear to be a widespread phenomenon in nature (e.g., Pennings et al. 2001, Cronin et al. 2015, but see Moles et al. 2011) and may underlie latitudinal variation in apparent competition between plant species. Geographic variation in apparent competition between native and invasive plant species is even more likely because invasive species may not have had sufficient time

to evolve latitudinal gradients in traits associated with local herbivore pressure (e.g., defense traits) that parallels the gradients for native plant species (Bezemer et al. 2014, Cronin et al. 2015).

We examined whether apparent competition occurred between native and invasive lineages of the wetland grass *Phragmites australis*, and whether the intensity of apparent competition varied with latitude. The continent-wide spread of an invasive lineage of *P. australis* into North American wetlands inhabited by a native lineage of *P. australis* (Saltonstall 2002) represents an ideal system to study biotic interactions between native and invasive taxa (Cronin et al. 2015, Meyerson et al. 2016). There are two key pieces of information to suggest that the invasive lineage may be a superior apparent competitor than the native lineage of *P. australis* and that the strength of apparent competition is likely to vary with latitude. First, in North America, the native lineage is more palatable to different guilds of herbivores and suffers substantially greater herbivore damage than the co-occurring invasive lineage (e.g., Cronin et al. 2015, Bhattarai et al. 2016). Second, native but not invasive *P. australis* in North America exhibits latitudinal gradients in herbivory (Cronin et al. 2015).

We conducted field experiments, replicated at four coastal wetland sites spanning 900 km (7° latitude) along the Atlantic coast of the United States, to test whether native and invasive *P. australis* interact indirectly with each other through apparent competition. Plants were cross-transplanted between sympatric native and invasive patches and herbivory by different insect feeding guilds was quantified. We tested the following hypotheses. (1) Native plants experience higher herbivory when transplanted into invasive patches than when transplanted into adjacent native patches, supporting the view that invasive *P. australis* is a strong apparent competitor. (2) Because of the greater abundance of herbivores on more palatable native patches (Allen et al. 2015, Cronin et al. 2015), invasive plants transplanted into native patches would also suffer higher herbivory than when transplanted into neighboring invasive patches (i.e., reciprocal apparent competition). (3) Apparent competition would be asymmetric such that native plants would suffer greater herbivory in invasive patches than vice versa. (4) For the invasive lineage of *P. australis*, the positive effects of apparent competition are similar in magnitude to the strength of enemy-release. (5) Finally, the strength of apparent competition acting against the native lineage would be greatest in the south and decrease with increasing latitude (as predicted by the biotic interactions hypothesis; Schemske et al. 2009).

METHODS

Study system

Phragmites australis is a perennial wetland grass that occurs on all continents except for Antarctica (Marks

et al. 1994, Lambertini et al. 2006). The North American native lineage of *P. australis* is 1–2 m in height and is an uncommon but widespread inhabitant of freshwater and brackish marshes (Chambers et al. 1999). A much taller (3–5 m) invasive Eurasian genotype (haplotype *M*) of *P. australis* was introduced to North America in mid-1800s and has since spread throughout the continent (Chambers et al. 1999, Saltonstall 2002). At least 14 genotypes of the native lineage of *P. australis* are distributed across North America and overlap in distribution with the invasive lineage (Saltonstall 2002, Meadows and Saltonstall 2007). Molecular studies show that native and invasive lineages belong to two different clades (Saltonstall and Hauber 2007).

A diverse assemblage of arthropod herbivores, representing a wide range of feeding guilds, has been reported to attack *P. australis* (e.g., Tewksbury et al. 2002, Cronin et al. 2015). Some of the most prominent herbivores of *P. australis* in North America include introduced species such as the mealy plum aphid, *Hyalopterus pruni* (Aphididae; Cronin et al. 2015) and gall-forming flies in the genus *Lipara* (Chloropidae; Lambert et al. 2007, Allen et al. 2015). *Hyalopterus pruni* is the most widespread herbivore of *P. australis* throughout North America and native patches average about 70% more aphids per stem than invasive patches (Cronin et al. 2015). Although fitness costs have not been quantified for aphids, they often undergo severe population outbreaks and cause substantial damage at the patch level (Cronin et al. 2015).

At least three *Lipara* spp. are common along the mid- and north-Atlantic region of the United States and make up 94% of the internal stem feeder guild (Allen et al. 2015, Cronin et al. 2015). Incidence of stem feeders on patches of the native lineage averaged 33%, three times higher than the average on patches of the invasive lineage (Cronin et al. 2015). Incidence of stem-feeders represents a measurement of the fitness costs to the plants because stems occupied by these herbivores fail to produce flowers (Lambert et al. 2007, Allen et al. 2015).

Damage from chewing herbivores is common on both lineages of *P. australis*, with the percentage of stems with chewing damage averaging 24% and 20% for patches of native and invasive lineages, respectively (Cronin et al., unpublished data). However, the actual proportion of leaf area lost to chewers was <1% (Cronin et al. 2015). Similarly, leaf miners (*Dicranoctetes saccharella*; Lepidoptera: Elachistidae) are generally uncommon but incidence levels can reach >50% of the stems (Cronin et al., unpublished data). Even though tissue loss from chewers and leaf miners is low, feeding is more common on upper leaves that likely contribute disproportionately more to plant fitness (e.g., Godschalx et al. 2016).

The biogeography of *P. australis*–herbivore interactions was recently described by Cronin et al. (2015) and Bhattarai et al. (2016). For the native *P. australis* lineage, stem gall incidence and leaf area chewed decreased and aphid abundance increased with increasing latitude. In

contrast, herbivore pressure was constant along the same latitudinal gradient for the invasive lineage. Common garden experiments revealed evidence for genetic-based latitudinal clines in plant defense and palatability traits for both lineages of *P. australis*, and substantial plasticity in these traits that is greater for the invasive than native lineage (Bhattarai et al. 2016).

Field experiment

Our experiments were conducted in the Rachel Carson National Wildlife Refuge, Maine (abbreviated as ME hereafter; 43.298°, –70.579°), Murkwood Conservation Area, Massachusetts (MA; 41.741°, –70.434°), Choptank Wetlands, Maryland (MD; 38.773°, –75.975°), and Mackay Island National Wildlife Refuge, North Carolina (NC; 36.513°, –75.952°). The NC site is near the southern range limit of native *P. australis* on the Atlantic Coast (Cronin et al. 2015). Early in the growing season (late April 2013 for the NC and MD sites; mid May 2013 for the MA and ME sites), we set up a cross-transplantation experiment at each wetland site. Within each site, a pair of native and invasive patches (>40 m in diameter) was selected that were located <1 km apart. In each patch, we established a 30 m long transect. A pair of rhizome clumps were excavated every 3 m along the transect. Each clump of rhizome was transferred to a 19-L nursery pot, filling the pot completely. One of the pots from each pair was returned to its transect of origin and the second pot was transported to the transect of the other patch. As a result, each transect contained 10 potted native and invasive plants that alternated at 3-m intervals. Pots were sunk flush to the ground and all stems were clipped to their base. Therefore, all growth was from new shoots, thus ensuring that all herbivores and damage to plants was post-transplant.

Potted plants were left in the field through to the end of summer to accumulate herbivores and their damage. In early September 2013, we returned to the field sites to quantify herbivory from each of the main feeding guilds. Every stem within a pot was examined for the incidence of internal stem feeders, easily identifiable by the presence of a swelling near the apical portion of the stem or dead apical leaves. Presence of an unknown species of stem borer was also indicated by a tattered apical tip. We also recorded the total number of stems per pot.

Leaves of all potted plants were searched for signs of folivory. We recorded the proportion of leaves with a leaf miner and counted all aphids per stem. Then, we photographed all leaves per stem and all stems per pot. Using ImageJ (Rasband 2014), total remaining leaf area and pre-consumption leaf area were estimated from the digital images. From these quantities, we computed the total leaf area chewed for each experimental plant. Because leaves persist for most of the season, this represents a cumulative measure of chewing damage during the growing season. At the completion of the study, all plant materials were returned to their patch of origin.

Statistical analysis

We tested for differences in herbivore damage (proportion of stems with stem-feeders [gallers and borers combined], proportion of leaves with mining damage, total leaf area chewed, and total number of aphids per plant) between native and invasive plants growing in different patches. For each response variable, a separate linear model was run with site, lineage of the patch (native, invasive [recipient patch lineage effect]), lineage of the potted plant (native, invasive [plant lineage effect]) and patch-by-plant lineage interaction treated as fixed effects. Proportions of stems with stem feeders and leaves with leaf miners were analyzed using generalized linear models with binomial distribution of errors. Number of stems and leaves, respectively, were included in the models as weights. Total number of aphids was analyzed using a generalized linear model with Poisson distribution of errors. Total leaf area chewed was \ln -transformed to meet the normality assumption and analyzed using a general linear model. Quantile-quantile plots were used to examine the distribution of residuals and detect observations with undue influence. In the case of influential observations, we re-ran the analysis excluding those observations. Exclusion of influential observations did not qualitatively alter the results.

Separate Bonferroni-corrected post-hoc analyses were performed to test for the difference in herbivory between patch type for each lineage (e.g., herbivory on potted native plants in an invasive vs. native patch). From this set of analyses, apparent competition was considered to be occurring if herbivory from a particular species or guild was significantly greater for potted plants grown in the patch of the other lineage than in a patch of its own lineage (its natal patch). It is conceivable that herbivory could be less when the plant is grown with the other lineage, resulting in apparent mutualism (e.g., Abrams and Matsuda 1996). All analyses were run in R 3.2.2 (R Development Core Team 2015).

We performed a within-study, meta-analysis to compare the strength of herbivore-mediated indirect interactions between native and invasive *P. australis* mediated by herbivores of different feeding guilds across the study sites. For each site, feeding guild, and *P. australis* lineage, we calculated the strength of the indirect interaction as Hedge's d_{II} = (mean herbivory in the patch of its own lineage – mean herbivory in the patch of the other lineage)/pooled standard deviation (Gurevitch and Hedges 1993). Means and 95% CIs for Hedge's d_{II} were computed for each lineage from the effect sizes for all feeding guilds in the four replicate sites ($n = 16$ effects). If the 95% CI of Hedge's d_{II} was less than and did not overlap zero, it would indicate significant apparent competition. If they were greater than and did not overlap zero, it would indicate significant apparent mutualism. We also compared the strength of these indirect interactions with the strength of enemy release (d_{ER} = [mean herbivory on invasive plants growing in invasive

patch – mean herbivory on native plants growing in native patch]/pooled standard deviation). In this case, enemy release is evident if d_{ER} and 95% CIs < 0. The analysis was performed in MetaWin 2.0 (Rosenberg et al. 2000) using the methods of Gurevitch and Hedges (1993).

Finally, we evaluated whether the intensity of the indirect interactions between native and invasive lineages of *P. australis* varied among sites or with respect to latitude. A separate linear model was performed for each feeding guild evaluating the effects of plant lineage, latitude and lineage \times latitude interaction on the intensity of indirect interactions (estimated as Hedge's d_{II}). Separate regression analyses were performed for each lineage whenever the lineage \times latitude interaction was significant. Although, we had only four sites, we used a linear model to fit a line to the relationship between latitude and d_{II} . The purpose here was to identify whether a latitudinal trend was evident in the data. Finally, we used bootstrapped 95% CIs for the effect sizes to evaluate the variation in the intensity of indirect interactions between sites for the two lineages. Effect sizes that had overlapping 95% CIs were deemed not statistically different.

RESULTS

Along the Atlantic Coast of the United States, we found strong evidence that the invasive lineage had a significant, indirect, negative effect on the native lineage of *P. australis* mediated through their shared herbivores (i.e., apparent competition). For each of the four herbivore feeding guilds, potted native plants that were translocated to a nearby invasive patch suffered greater herbivory than when those potted plants were returned to their patch of origin (Fig. 2; Appendix S1: Table S1). Incidence of stem-feeders was 34% higher ($z = 3.843$, $P = 0.007$, Fig. 2A), the proportion of leaves with leaf-miners was 221% higher ($z = 3.662$, $P = 0.002$, Fig. 2B), and aphid density was 296% higher ($z = 41.783$, $P < 0.0001$, Fig. 2D) when native plants were placed in an invasive patch relative to a native patch. Native plants also had 80% more leaf area chewed in invasive than native patches but this effect was not statistically significant ($P = 0.097$, Fig. 2C).

Similarly, there was evidence that the native lineage had an indirect negative effect on the invasive lineage of *P. australis* through their shared herbivores. Total aphids per plant was 341% higher on potted invasive plants in native than invasive patches ($z = 16.636$, $P < 0.0001$, Fig. 2D). Invasive plants also experienced 30% and 23% higher incidence of stem feeders ($P = 0.096$, Fig. 2A) and total leaf area chewed ($P = 1.00$, Fig. 2C), respectively, in native relative to neighboring invasive patches, although these differences were not significant. Leaf miners showed a trend in the opposite direction (i.e., reduced incidence when invasive plants were transplanted into native patches) but it was not significant ($P = 1.00$, Fig. 2B).

Regardless of recipient patch lineage, native plants suffered greater herbivore damage than invasive plants

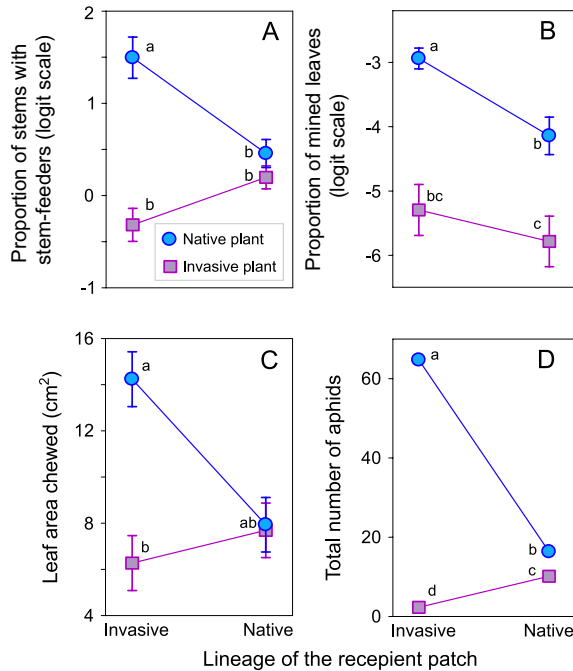


FIG. 2. Herbivory on native and invasive *Phragmites australis* plants transplanted into different (recipient) patches. Least square means (\pm SE) for herbivory for each feeding guild is shown. Herbivory on plants of the same lineage are connected by a line. Symbols with different letters are significantly different from each other ($P < 0.05$). [Color figure can be viewed at wileyonlinelibrary.com]

(Appendix S1: Table S2). After controlling for the effects of patch lineage, native plants had a 50% greater incidence of stem feeders ($z = 6.323, P < 0.0001$), a 620% higher proportion of leaves with leaf miners ($z = 5.804, P < 0.0001$), 53% more total leaf area chewed ($t = 3.334, P = 0.001$), and 573% more aphids per stem than invasive plants ($z = 40.58, P < 0.0001$).

The strength of the indirect interactions between native and invasive *P. australis*, as measured by the mean effect size (Hedge's d_{II} ; averaged across all sites and herbivore guilds), was negative for both lineages (Fig. 3) as expected if apparent competition was occurring between them. The 95% CIs for the mean effect of the native lineage on the invasive lineage (x -axis invasive, Fig. 3) overlapped zero indicating nonsignificant apparent competition. In contrast, the effect size of the invasive lineage on the native lineage (x -axis native, Fig. 3) did not overlap zero, suggesting significant apparent competitive effects. Overall, the strength of the negative effects of the invasive lineage on the native lineage was 57% higher than the strength of the reciprocal relationship, but the difference was not statistically significant ($Q = 0.691, df = 2, P = 0.708$). Finally, the strength of enemy release (d_{ER}) was significantly less than zero (x -axis Inv - Nat; Fig. 3), indicating that the invasive lineage suffers less herbivory on average than the native lineage. The strength of this

direct effect of herbivores was indistinguishable from the effects of apparent competition mediated by the herbivores ($P = 0.708$; Fig. 3).

Among the four wetland sites, we found substantial geographical variation in the strength and direction of herbivore-mediated interactions between native and invasive lineages (Fig. 4A–D). For stem-feeders, the strength of the indirect interaction (Hedge's d_{II}) was negative for both lineages across all sites (i.e., plants suffered greater herbivory when moved to the patches of the other lineage), suggesting apparent competition. In most cases, however, the 95% CIs overlapped with zero (the exception was the negative indirect effect of the invasive lineage on the native lineage in MD). Interestingly, the strength of apparent competition lessened with increasing latitude for both lineages combined ($P = 0.040$, Fig. 4A). For leaf miners, only for the native lineage in the southernmost site, NC, was the indirect effect significant (95% CIs did not overlap zero), i.e., the native plants in the invasive patch had a significantly greater incidence of leaf miners than when native plants were returned to their native patch. With respect to leaf miners, the native lineage exhibited a nonsignificant latitudinal trend in the strength of the indirect effect ($P = 0.274$, Fig. 4B) that was similar to what was found for the stem feeders. Surprisingly, the indirect effect of the native lineage on the invasive lineage was slightly positive at low latitudes (apparent mutualism) and slightly negative (apparent competition) at high latitudes. The relationship was marginally significant ($P = 0.058$, Fig. 4B).

Damage by chewing herbivores showed remarkable variability in the strength and direction of the indirect

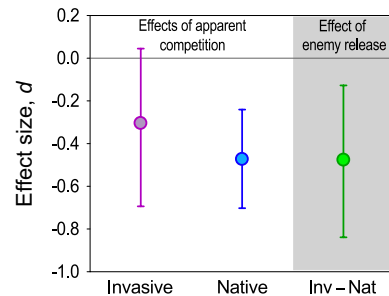


FIG. 3. Effect sizes (Hedge's d_{II} ; mean and 95% confidence intervals) for the strength of apparent competition on invasive and native *Phragmites australis*. Negative values indicate support for apparent competition. For example, for the invasive lineage (x -axis), the mean difference in herbivory of invasive plants grown in their own patch vs. when they are grown in a patch of the native lineage is reported. Because the 95% CIs overlap zero, the indirect negative effect of the native lineage on the invasive lineage is not statistically significant. In contrast, the indirect negative effect of the invasive lineage on the native lineage is significant (95% CIs do not overlap zero). Effect size for enemy release (Hedge's d_{ER}) is reported in the shaded area. It represents the difference in herbivory between invasive and native plants growing in their respective patches (Inv - Nat). The negative d_{ER} and 95% CIs that do not overlap zero indicate that the invasive lineage benefits from significant enemy release. [Color figure can be viewed at wileyonlinelibrary.com]

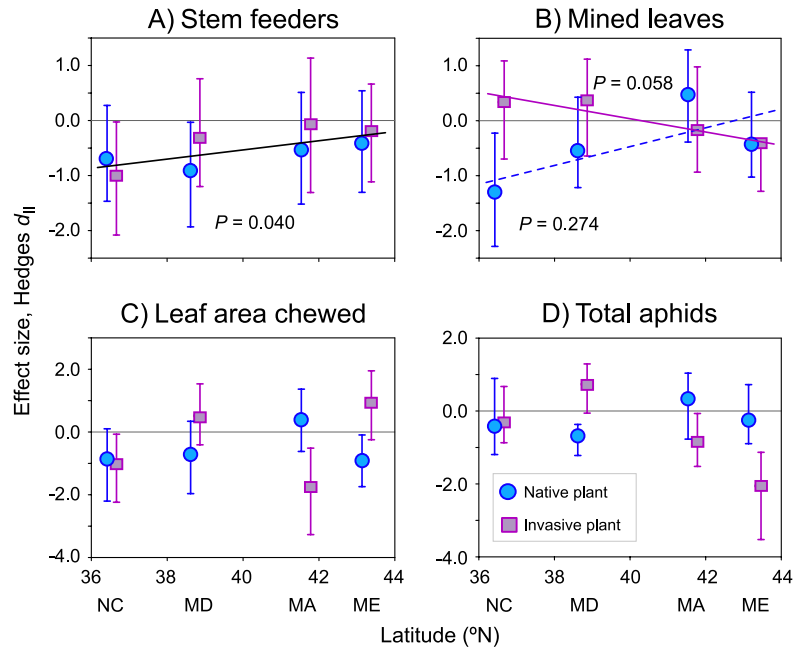


FIG. 4. Spatial variation in the intensity of herbivore-mediated indirect interactions between native and invasive *Phragmites australis*. Each symbol represents an effect size estimated as Hedge's d_{II} and 95% CI for a lineage and site and refers to the indirect effect of the other lineage on the native (circle) or invasive (square) lineage. For example, for the invasive lineage, the mean difference in herbivory of invasive plants grown in their own patch vs. when they are grown in a native patch is reported. The x-axis represents the latitude of the sites (in degrees) and includes abbreviations for the state within which the site occurs (North Carolina, NC; Maryland, MD; Massachusetts, MA; Maine, ME; see *Methods*). Solid lines represent significant ($P < 0.05$) and marginally significant ($P = 0.058$) latitudinal trends fitted as least-square regressions. A nonsignificant latitudinal trend for leaf-miners on native lineage is shown (broken line) because of the marginally significant plant lineage \times latitude interaction ($P = 0.067$). In all plots, a zero effect size reference line is included. [Color figure can be viewed at wileyonlinelibrary.com]

interaction among study sites (Fig. 4C). For native plants, the indirect interaction was negative for NC, MD and ME but positive for MA. The effect size was significant only in ME. In contrast, invasive plants in NC and MA showed evidence of significant apparent competition but non-significant apparent mutualism in MD and ME. For total aphids, native plants showed evidence of apparent competition in NC, MD and ME but apparent mutualism in MA (Fig. 4D). The interaction was significant only in MD. For invasive plants, the effect sizes were negative and significant in MA and ME. No latitudinal trends were evident for chewing damage and aphid density for either lineage.

DISCUSSION

A paradigm of invasion biology is that escape from co-adapted natural enemies in their novel environment is a primary driver of invasion success (Keane and Crawley 2002). A growing list of studies, including this one, suggest that herbivores indirectly influence invasion success and the interactions between native and invasive plants via apparent competition (see also Orrock et al. 2008, 2015, Enge et al. 2013). Furthermore, our study with *P. australis* provides the first evidence that the strength of herbivore-mediated indirect effects is just as strong as the strength of enemy release, and that the

strength of these indirect interactions vary from region to region, and in some cases with latitude. We contend that invasion success of introduced species can be better understood when a broader interaction-network and geographical-scale approach is taken.

As predicted by theory (Holt and Lawton 1993), apparent competition between native and invasive taxa mediated by herbivores appears to be a common phenomenon in natural ecosystems (e.g., Orrock et al. 2008, 2015, Enge et al. 2013). A search of Web of Science using “apparent,” “competition,” “inva*” or “exotic,” and “plant” as keywords yielded 20 publications that evaluated the indirect effects of invasive plants on co-occurring native plants through apparent competition (Appendix S2: Table S1). Seventeen of the 20 studies (85%) provided evidence that invasive plants increase herbivory on native plants by apparent competition. Consistent with those findings, our study suggests that herbivore-mediated apparent competition is one of the mechanisms that may enhance the fitness and spread of the invasive lineage of *P. australis* in North America. For three of four feeding guilds examined in this study (stem-feeders, leaf-miners and aphids), native *P. australis* plants placed in an invasive *P. australis* patch suffered disproportionately greater herbivory than when they were placed in a native patch.

We suggest that two non-mutually exclusive factors may underlie the strong indirect negative effects of the

invasive lineage on the native lineage of *P. australis*. First, for a wide variety of herbivores, the native lineage appears to be a more palatable or preferred host than the invasive lineage (e.g., Lambert et al. 2007, Allen et al. 2015, Cronin et al. 2015, Bhattarai et al. 2016). In our field experiment, native plants averaged 50% greater incidence of stem feeders, 620% higher proportion of leaves with leaf miners, 53% more total leaf area chewed, and 573% more aphids per stem than invasive plants. In controlled common-garden experiments, Bhattarai et al. (2016) found that colony growth rates and survivorship of *H. pruni* aphids were up to an order of magnitude higher on the native than invasive lineage. Similar results were found for larval growth rates, survivorship and biomass conversion efficiency of a generalist chewing herbivore of *P. australis*, the fall armyworm (*Spodoptera frugiperda*). The fact that the native lineage suffers more leaf loss from the entire guild of chewing herbivores (this study; see also Cronin et al. 2015), suggests that other common leaf chewers may also prefer or perform better on the native than invasive lineage. Finally, Allen et al. (2016) found that despite the five-fold difference in the incidence of *Lipara rufitarsis* galls in the field, the two lineages had similar levels of infestation in a common garden. It was suggested that this difference is due to plasticity in the plants that results in the native lineage being the preferred or most palatable host. At present, we know nothing about host preference/performance in the leaf miners.

Native *P. australis* growing in or adjacent to invasive *P. australis* may suffer increased herbivory simply because aphids, chewing herbivores, and possibly other herbivore species that were resident in the invasive patch are likely to switch to their preferred native host. Theory predicts that if invasive taxa are less vulnerable to the herbivores but can sustain a reservoir of these herbivores, they should exclude the more vulnerable native taxa by apparent competition (Orrock et al. 2010). Even in cases where herbivores have no preference, or a higher preference for the invasive lineage, patches of the invasive lineage are often substantially larger than nearby native patches and may serve as a reservoir of herbivores that spillover onto the native patches.

A second possible mechanism promoting the strong herbivore-mediated effect of the invasive lineage on the native lineage of *P. australis* involves the phenological mismatch between them. In deciduous forests, invasive plant species often have extended leaf phenologies that may confer an advantage to them over neighboring native plant species (Fridley 2012, Smith 2013). In a common garden study (see Bhattarai et al. 2016), plant genotypes from the invasive lineage sprouted earlier than genotypes of the native lineage (Bhattarai et al. unpublished data; see also Park and Blossey 2008), which may result in larger populations of herbivores in early spring that are likely to spillover to plants of the more preferred native lineage. Using a mathematical model, Smith and Hall (2016) showed that the combined effect of greater preference by herbivores for native taxa and extended

phenology of invasive taxa could significantly increase the performance of the invader and potentially result in the exclusion of the native apparent competitor.

Interestingly, we found that plants from the invasive lineage of *P. australis* suffered more herbivory (effect size, $d_{II} = -0.304$) when embedded in a native than invasive patch. Although the effect size was not significantly different from zero (Fig. 3), it suggests that apparent competition between the native and invasive lineage may be reciprocal. However, the mean effect size representing the indirect negative impact of the invasive lineage on the native lineage of *P. australis* was 57% greater than for the reciprocal interaction, suggesting that apparent competition is asymmetric. Such asymmetries in the effects of apparent competition are common in the literature (Bonsall and Hassell 1997). However, only one of the twenty studies in our Web of Science search tested whether native taxa affected invasive taxa through apparent competition (Appendix S2: Table S1; White et al. 2008). If native taxa have indirect negative effects on invasive taxa, this could contribute to the ability of a community to resist invasion (e.g., Levine et al. 2004).

A likely explanation for the indirect negative effect of the native lineage on the invasive lineage of *P. australis* is associational susceptibility (e.g., White and Whitham 2000). As pointed out previously, the native lineage supports substantially greater per-stem abundances of all four herbivore guilds. Even though the invasive lineage is generally less palatable/preferred, its risk of attack by herbivores may go up because of its close proximity to native patches. Associational susceptibility has been suggested as the mechanisms underlying apparent competition in a number of systems (e.g., Rand 2003), including other invasive species (e.g., Rand and Louda 2004). We suggest that this associational susceptibility of invasive patches is likely to be inconsequential to the growth and spread of established invasive patches, simply because invasive patches of *P. australis* are often massive in size, sometimes spanning many square kilometers, whereas native patches are typically small, covering tens of square meters or less. Spillover of herbivores in the other direction is likely much more important.

Asymmetrical herbivore-mediated apparent competition is likely to contribute significantly to the competitive superiority of the invasive lineage. Although direct measurements of fitness costs associated with herbivory of *P. australis* lineages have not been documented, these costs are likely to be significant. Stems infested by *Lipara* fail to produce flowers and also suffer from a 55% reduction in stem growth (Lambert et al. 2007, Allen et al. 2015). For plant species, biomass and stem height are strongly related to competitive ability (Gaudet and Keddy 1988). These observations suggest a strong fitness cost of *Lipara* infestation to *P. australis* sexual and asexual reproduction. Although *P. australis* is thought to grow and spread primarily by clonal growth, recent studies have revealed the importance of sexual reproduction in the establishment and expansion of new

patches (e.g., McCormick et al. 2010). With ~80% of the stems unable to produce flowers and biomass production compromised, native plants would likely experience severe fitness costs due to apparent competition with the invasive lineage. Similarly, aphids have been reported to produce massive outbreaks and cause yellowing and early death of aboveground parts (Cronin et al. 2015). Leaf mining and chewing damage are relatively low but the removal of photosynthetic tissues during the early growing season could have a disproportionately large impact on plant fitness (Godschalx et al. 2016).

This study is the first to document geographic variation in the strength of indirect interactions mediated by natural enemies and provide partial support for the biotic interactions hypothesis that posits a negative relationship between latitude and the strength of biotic interactions (Schemske et al. 2009). Damage to native lineages of *P. australis* by stem-feeding and leaf-chewing herbivores decreased but total aphids per stem increased with increasing latitude (Cronin et al. 2015). In comparison, herbivory of the invasive lineage did not vary with latitude (Cronin et al. 2015). These non-parallel latitudinal gradients in herbivory resulted in the invasive lineage suffering much less herbivory than the native lineage in the south (i.e., greater “enemy release”) than the north. In light of this lineage-specific spatial variation in herbivory, we expected herbivore-mediated indirect interactions between native and invasive *P. australis* would also vary with latitude. We did find evidence for a significant latitudinal gradient in stem-feeder-mediated indirect interactions between the two lineages (Fig. 4A). Irrespective of which lineage is being impacted, the effect of the indirect interaction mediated by stem feeders was strongest in the south and decreased within increasing latitude. To our knowledge, this is the only example of a latitudinal gradient in the strength of a species interaction that is mediated through another species. These two pieces of evidence suggest that the importance of herbivory on plant invasion, through direct and indirect ways, is greater in the south. With regard to the other herbivore guilds, significant gradients in herbivore-mediated interactions do not exist, but there is much spatial variation among sites with regard to the strength of these interactions. For example, the effect of the native lineage on aphid pressure on the invasive lineage is almost significantly positive at our MD site (apparent mutualism; Abrams and Matsuda 1996) and significantly negative (apparent competition) at our northernmost sites, MA and ME. One possible explanation for this case of apparent mutualism is that when invasive plants were placed in highly palatable native patches, herbivores were drawn away from the invasive plants. Given that stem feeders and aphids are likely the most important herbivores in this system (Cronin et al. 2015, Allen et al. 2015, Bhattarai et al. 2016), the geographic variation in interactions between lineages of *P. australis*, mediated by these herbivores, is potentially an important source of heterogeneity in *P. australis* invasion success. In the

future, more studies should focus on the geographic variation in complex species interactions, as they are likely to change from region to region owing to large-scale variation in species richness and the strength of direct interactions.

Finally, our study shows that the negative effects of apparent competition on native plants can be as strong as the negative effects of herbivory on native plants (measured in terms of the degree of enemy release; see Fig. 3). Enemy release has long been regarded as one of the most important factors promoting invasion success of introduced plants (Keane and Crawley 2002). Apparent competition is now on the radar of invasion biologists (see Appendix S2: Table S1) and has proven important in the majority of case studies. This indirect interaction has been shown to influence the persistence of co-occurring species in different ecosystems (Bonsall and Hassell 1997, Morris et al. 2004, Cronin 2007). Our study is the first to suggest that these two factors involving natural enemies of invasive taxa may be of equal importance. In addition to these enemy-mediated mechanisms, the invasive lineage of *P. australis* has been shown to be a superior competitor to the native lineage for resources (e.g., Mozdzer and Zieman 2010) and its rate of clonal expansion is strongly correlated with the frequency of disturbances (e.g., Bhattarai and Cronin 2014). Clearly, multiple mechanisms are likely at work in facilitating the invasion and spread of the European invasive lineage in North America. Future studies should focus on partitioning the contributions of these direct and indirect processes in species invasion (e.g., Orrock et al. 2015).

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