

2-1-2017

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

Ganesh P. Bhattarai
Louisiana State University

Laura A. Meyerson
University of Rhode Island

James T. Cronin
Louisiana State University

Follow this and additional works at: https://digitalcommons.lsu.edu/biosci_pubs

Recommended Citation

Bhattarai, G., Meyerson, L., & Cronin, J. (2017). Geographic variation in apparent competition between native and invasive *Phragmites australis*. *Ecology*, *98* (2), 349-358. <https://doi.org/10.1002/ecy.1646>

This Article is brought to you for free and open access by the Department of Biological Sciences at LSU Digital Commons. It has been accepted for inclusion in Faculty Publications by an authorized administrator of LSU Digital Commons. For more information, please contact ir@lsu.edu.

Received Date : 28-Jun-2016

Revised Date : 08-Oct-2016

Accepted Date : 31-Oct-2016

Article type : Articles

Running Head: Apparent competition and plant invasion

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

Ganesh P. Bhattarai^{1,3,4}, Laura A. Meyerson², and James T. Cronin¹

¹ *Department of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803
USA*

² *Department of Natural Resources Sciences, University of Rhode Island, 1 Greenhouse
Road, Kingston, RI 02881 USA*

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1002/ecy.1646](https://doi.org/10.1002/ecy.1646)

This article is protected by copyright. All rights reserved

³ Present address: Department of Entomology, Kansas State University, Manhattan, KS
66506 USA

⁴ E-mail: bhattaraigp@gmail.com

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

26
27 *Keywords:* apparent competition, indirect interactions, invasive plant, latitudinal gradients,
28 enemy release, plant-herbivore interactions, *Hyalopterus pruni*, *Lipara sp.*

30 INTRODUCTION

31 Indirect biotic interactions are common in nature and have been shown to strongly
32 influence the structure and dynamics of ecological communities (Wootton 1994). Apparent
33 competition, in which species within the same trophic level negatively interact with each other
34 through the action of shared natural enemies, is widely regarded as one of the most common
35 forms of indirect interactions (Holt and Lawton 1993). Both theory (Holt 1977, Holt and Lawton
36 1993) and empirical data provide compelling evidence that apparent competition is as important
37 as resource-based competition in structuring ecological communities (e.g., Bonsall and Hassell
38 1997, Chaneton and Bonsall 2000, Morris et al. 2004).

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

51 A more prominent mechanism of plant invasion that involves herbivores is enemy
52 release. This hypothesis posits that invasive plants in the introduced range are under weaker
53 control from natural enemies than their native competitors (Fig. 1A; Keane and Crawley 2002).
54 Increased herbivore pressure on native plants, because of apparent competition with invasive
55 plants (Fig. 1B), may also result in enemy release. Consequently, although apparent competition
56 and enemy release may drive plant invasions through a difference in herbivore pressure between
57 native and invasive plants, different mechanisms operate. In enemy release, greater herbivore
58 abundance or herbivory on native plants would be caused by greater herbivore preference for the
59 native as compared to invasive plants. It also could result in different herbivore communities on

60 the two plant taxa. In contrast, in apparent competition, invasive plants would actually increase
61 pressure by shared herbivores on the native plants which could benefit the invasive plants via
62 reduced interspecific competition. The strength of apparent competition has never been assessed
63 relative to the strength of enemy release in species invasions.

64 The biotic interactions hypothesis posits that species interactions should be stronger at
65 lower than higher latitudes (Schemske et al. 2009). To date, tests of this hypothesis have been
66 restricted to direct species interactions (e.g., predation, mutualism) or interactions through a
67 shared resource (exploitative competition) (Schemske et al. 2009). Biogeographic studies
68 involving indirect interactions between species, mediated by another species have not been
69 undertaken. Latitudinal gradients in herbivore pressure and plant defenses, whether positive or
70 negative, appear to be a widespread phenomenon in nature (e.g., Pennings et al. 2001, Cronin et
71 al. 2015; but see Moles et al. 2011) and may underlie latitudinal variation in apparent
72 competition between plant species. Geographic variation in apparent competition between native
73 and invasive plant species is even more likely because invasive species may not have had
74 sufficient time to evolve latitudinal gradients in traits associated with local herbivore pressure
75 (e.g., defense traits) that parallels the gradients for native plant species (Bezemer et al. 2014,
76 Cronin et al. 2015).

77 We examined whether apparent competition occurred between native and invasive
78 lineages of the wetland grass *Phragmites australis*, and whether the intensity of apparent
79 competition varied with latitude. The continent-wide spread of an invasive lineage of *P. australis*
80 into North American wetlands inhabited by a native lineage of *P. australis* (Saltonstall 2002)
81 represents an ideal system to study biotic interactions between native and invasive taxa (Cronin
82 et al. 2015, Meyerson et al. 2016). There are two key pieces of information to suggest that the
83 invasive lineage may be a superior apparent competitor than the native lineage of *P. australis*
84 and that the strength of apparent competition is likely to vary with latitude. First, in North
85 America, the native lineage is more palatable to different guilds of herbivores and suffers
86 substantially greater herbivore damage than the co-occurring invasive lineage (e.g., Cronin et al.
87 2015, Bhattarai et al. 2016). Second, native but not invasive *P. australis* in North America
88 exhibits latitudinal gradients in herbivory (Cronin et al. 2015).

89 We conducted field experiments, replicated at four coastal wetland sites spanning 900 km
90 (7° latitude) along the Atlantic coast of the United States, to test whether native and invasive *P.*

91 *australis* interact indirectly with each other through apparent competition. Plants were cross-
92 transplanted between sympatric native and invasive patches and herbivory by different insect
93 feeding guilds was quantified. We tested the following hypotheses. (1) Native plants experience
94 higher herbivory when transplanted into invasive patches than when transplanted into adjacent
95 native patches, supporting the view that invasive *P. australis* is a strong apparent competitor. (2)
96 Because of the greater abundance of herbivores on more palatable native patches (Allen et al.
97 2015, Cronin et al. 2015), invasive plants transplanted into native patches would also suffer
98 higher herbivory than when transplanted into neighboring invasive patches (i.e., reciprocal
99 apparent competition). (3) Apparent competition would be asymmetric such that native plants
100 would suffer greater herbivory in invasive patches than vice versa. (4) For the invasive lineage of
101 *P. australis*, the positive effects of apparent competition are similar in magnitude to the strength
102 of enemy-release. (5) Finally, the strength of apparent competition acting against the native
103 lineage would be greatest in the south and decrease with increasing latitude (as predicted by the
104 biotic interactions hypothesis; Schemske et al. 2009).

105

106 **METHODS**

107 *Study system*

108 *Phragmites australis* is a perennial wetland grass that occurs on all continents except for
109 Antarctica (Marks et al. 1994, Lambertini et al. 2006). The North American native lineage of *P.*
110 *australis* is 1-2 m in height and is an uncommon but widespread inhabitant of freshwater and
111 brackish marshes (Chambers et al. 1999). A much taller (3-5 m) invasive Eurasian genotype
112 (haplotype *M*) of *P. australis* was introduced to North America in mid-1800s and has since
113 spread throughout the continent (Chambers et al. 1999, Saltonstall 2002). At least 14 genotypes
114 of the native lineage of *P. australis* are distributed across North America and overlap in
115 distribution with the invasive lineage (Saltonstall 2002, Meadows and Saltonstall 2007).
116 Molecular studies show that native and invasive lineages belong to two different clades
117 (Saltonstall and Hauber 2007).

118 A diverse assemblage of arthropod herbivores, representing a wide range of feeding
119 guilds, has been reported to attack *P. australis* (e.g., Tewksbury et al. 2002, Cronin et al. 2015).
120 Some of the most prominent herbivores of *P. australis* in North America include introduced
121 species such as the mealy plum aphid, *Hyalopterus pruni* (Aphididae; Cronin et al. 2015) and

122 gall forming flies in the genus *Lipara* (Chloropidae; Lambert et al. 2007, Allen et al. 2015).
123 *Hyalopterus pruni* is the most widespread herbivore of *P. australis* throughout North America
124 and native patches average about 70% more aphids per stem than invasive patches (Cronin et al.
125 2015). Although fitness costs have not been quantified for aphids, they often undergo severe
126 population outbreaks and cause substantial damage at the patch level (Cronin et al. 2015).

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

133 Damage from chewing herbivores is common on both lineages of *P. australis*, with the
134 percentage of stems with chewing damage averaging 24% and 20% for patches of native and
135 invasive lineages, respectively (Cronin et al. unpublished data). However, the actual proportion
136 of leaf area lost to chewers was <1% (Cronin et al. 2015). Similarly, leaf miners (*Dicranoctetes*
137 *saccharella*; Lepidoptera: Elachistidae) are generally uncommon but incidence levels can reach
138 >50% of the stems (Cronin et al. unpublished data). Even though tissue loss from chewers and
139 leaf miners is low, feeding is more common on upper leaves that likely contribute
140 disproportionately more to plant fitness (e.g., Godschalx et al. 2016).

141 The biogeography of *P. australis* – herbivore interactions was recently described by
142 Cronin et al. (2015) and Bhattarai et al. (2016). For the native *P. australis* lineage, stem gall
143 incidence and leaf-area chewed decreased and aphid abundance increased with increasing
144 latitude. In contrast, herbivore pressure was constant along the same latitudinal gradient for the
145 invasive lineage. Common garden experiments revealed evidence for genetic-based latitudinal
146 clines in plant defense and palatability traits for both lineages of *P. australis*, and substantial
147 plasticity in these traits that is greater for the invasive than native lineage (Bhattarai et al. 2016).

148 149 *Field experiment*

150 Our experiments were conducted in the Rachel Carson National Wildlife Refuge, Maine
151 (abbreviated as ME hereafter; 43.298°, -70.579°), Murkwood Conservation Area, Massachusetts
152 (MA; 41.741°, -70.434°), Choptank Wetlands, Maryland (MD; 38.773°, -75.975°), and Mackay

153 Island National Wildlife Refuge, North Carolina (NC; 36.513°, -75.952°). The NC site is near
154 the southern range limit of native *P. australis* on the Atlantic Coast (Cronin et al. 2015). Early in
155 the growing season (late April 2013 for the NC and MD sites; mid May 2013 for the MA and
156 ME sites), we set up a cross-transplantation experiment at each wetland site. Within each site, a
157 pair of native and invasive patches (> 40 m in diameter) was selected that were located < 1 km
158 apart. In each patch, we established a 30-m long transect. A pair of rhizome clumps were
159 excavated every 3 m along the transect. Each clump of rhizome was transferred to a 19-L nursery
160 pot, filling the pot completely. One of the pots from each pair was returned to its transect of
161 origin and the second pot was transported to the transect of the other patch. As a result, each
162 transect contained 10 potted native and invasive plants that alternated at 3 m intervals. Pots were
163 sunk flush to the ground and all stems were clipped to their base. Therefore, all growth was from
164 new shoots, thus ensuring that all herbivores and damage to plants was post-transplant.

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

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

178 179 *Statistical analysis*

180 We tested for differences in herbivore damage (proportion of stems with stem-feeders
181 [gallers and borers combined], proportion of leaves with mining damage, total leaf area chewed
182 and total number of aphids per plant) between native and invasive plants growing in different
183 patches. For each response variable, a separate linear model was run with site, lineage of the

184 patch (native, invasive [= recipient patch lineage effect]), lineage of the potted plant (native,
185 invasive [= plant lineage effect]) and patch-by-plant lineage interaction treated as fixed effects.
186 Proportions of stems with stem feeders and leaves with leaf miners were analyzed using
187 generalized linear models with binomial distribution of errors. Number of stems and leaves,
188 respectively, were included in the models as weights. Total number of aphids was analyzed using
189 a generalized linear model with Poisson distribution of errors. Total leaf area chewed was *ln*-
190 transformed to meet the normality assumption and analyzed using a general linear model.

191 Quantile-quantile plots were used to examine the distribution of residuals and detect observations
192 with undue influence. In the case of influential observations, we re-ran the analysis excluding
193 those observations. Exclusion of influential observations did not qualitatively alter the results.

194 Separate Bonferroni-corrected post-hoc analyses were performed to test for the difference
195 in herbivory between patch type for each lineage (e.g., herbivory on potted native plants in an
196 invasive versus native patch). From this set of analyses, apparent competition was considered to
197 be occurring if herbivory from a particular species or guild was significantly greater for potted
198 plants grown in the patch of the other lineage than in a patch of its own lineage (its natal patch).
199 It is conceivable that herbivory could be less when the plant is grown with the other lineage,
200 resulting in apparent mutualism (e.g., Abrams and Matsuda 1996). All analyses were run in R
201 3.2.2 (R Development Core Team 2015).

202 We performed a within-study, meta-analysis to compare the strength of herbivore-
203 mediated indirect interactions between native and invasive *P. australis* mediated by herbivores
204 of different feeding guilds across the study sites. For each site, feeding guild and *P. australis*
205 lineage, we calculated the strength of the indirect interaction as Hedge's d_{II} = (mean herbivory in
206 the patch of its own lineage – mean herbivory in the patch of the other lineage)/pooled standard
207 deviation (Gurevitch and Hedges 1993). Means and 95% CIs for Hedge's d_{II} were computed for
208 each lineage from the effect sizes for all feeding guilds in the four replicate sites ($N = 16$ effects).
209 If the 95% CI of Hedge's d_{II} was less than and did not overlap zero, it would indicate significant
210 apparent competition. If they were greater than and did not overlap zero, it would indicate
211 significant apparent mutualism. We also compared the strength of these indirect interactions with
212 the strength of enemy release (d_{ER} = [mean herbivory on invasive plants growing in invasive
213 patch – mean herbivory on native plants growing in native patch]/pooled standard deviation). In
214 this case, enemy release is evident if d_{ER} and 95% CIs < 0 . The analysis was performed in

215 MetaWin 2.0 (Rosenberg et al. 2000) using the methods of Gurevitch and Hedges (1993).

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

226

227 RESULTS

228 Along the Atlantic Coast of the US, we found strong evidence that the invasive lineage
229 had a significant, indirect negative effect on the native lineage of *P. australis* mediated through
230 their shared herbivores (i.e., apparent competition). For each of the four herbivore feeding guilds,
231 potted native plants that were translocated to a nearby invasive patch suffered greater herbivory
232 than when those potted plants were returned to their patch of origin (Fig. 2; Appendix S1: Table
233 S1). Incidence of stem-feeders was 34% higher ($z = 3.843$, $P = 0.007$, Fig. 2A), the proportion of
234 leaves with leaf-miners was 221% higher ($z = 3.662$, $P = 0.002$, Fig. 2B), and aphid density was
235 296% higher ($z = 41.783$, $P < 0.0001$, Fig. 2D) when native plants were placed in an invasive
236 patch relative to a native patch. Native plants also had 80% more leaf area chewed in invasive
237 than native patches but this effect was not statistically significant ($P = 0.097$, Fig. 2C).

238 Similarly, there was evidence that the native lineage had an indirect negative effect on the
239 invasive lineage of *P. australis* through their shared herbivores. Total aphids per plant was 341%
240 higher on potted invasive plants in native than invasive patches ($z = 16.636$, $P < 0.0001$, Fig.
241 2D). Invasive plants also experienced 30% and 23% higher incidence of stem feeders ($P = 0.096$,
242 Fig. 2A) and total leaf area chewed ($P = 1.00$, Fig. 2C), respectively, in native relative to
243 neighboring invasive patches, although these differences were not significant. Leaf miners
244 showed a trend in the opposite direction (i.e., reduced incidence when invasive plants were
245 transplanted into native patches) but it was not significant ($P = 1.00$, Fig. 2B).

246 Regardless of recipient patch lineage, native plants suffered greater herbivore damage
247 than invasive plants (Appendix S1: Table S2). After controlling for the effects of patch lineage,
248 native plants had a 50% greater incidence of stem-feeders ($z = 6.323$, $P < 0.0001$), a 620% higher
249 proportion of leaves with leaf-miners ($z = 5.804$, $P < 0.0001$), 53% more total leaf area chewed (t
250 $= 3.334$, $P = 0.001$), and 573% more aphids per stem than invasive plants ($z = 40.58$, $P <$
251 0.0001).

252 The strength of the indirect interactions between native and invasive *P. australis*, as
253 measured by the mean effect size (Hedge's d_{II} ; averaged across all sites and herbivore guilds),
254 was negative for both lineages (Fig. 3) as expected if apparent competition was occurring
255 between them. The 95% CIs for the mean effect of the native lineage on the invasive lineage (x -
256 axis = Invasive, Fig. 3) overlapped zero indicating non-significant apparent competition. In
257 contrast, the effect size of the invasive lineage on the native lineage (x -axis = Native, Fig. 3) did
258 not overlap zero, suggesting significant apparent competitive effects. Overall, the strength of the
259 negative effects of the invasive lineage on the native lineage was 57% higher than the strength of
260 the reciprocal relationship, but the difference was not statistically significant ($Q = 0.691$, $d.f. = 2$,
261 $P = 0.708$). Finally, the strength of enemy release (d_{ER}) was significantly less than zero (x -axis:
262 Inv - Nat; Fig. 3), indicating that the invasive lineage suffers less herbivory on average than the
263 native lineage. The strength of this direct effect of herbivores was indistinguishable from the
264 effects of apparent competition mediated by the herbivores ($P = 0.708$; Fig. 3).

265 Among the four wetland sites, we found substantial geographical variation in the strength
266 and direction of herbivore-mediated interactions between native and invasive lineages (Fig. 4A-
267 D). For stem-feeders, the strength of the indirect interaction (Hedge's d_{II}) was negative for both
268 lineages across all sites (i.e., plants suffered greater herbivory when moved to the patches of the
269 other lineage), suggesting apparent competition. In most cases, however, the 95% CIs overlapped
270 with zero (the exception was the negative indirect effect of the invasive lineage on the native
271 lineage in MD). Interestingly, the strength of apparent competition lessened with increasing
272 latitude for both lineages combined ($P = 0.040$, Fig. 4A). For leaf miners, only for the native
273 lineage in the southernmost site, NC, was the indirect effect significant (95% CIs did not overlap
274 zero) – i.e., the native plants in the invasive patch had a significantly greater incidence of leaf
275 miners than when native plants were returned to their native patch. With respect to leaf miners,
276 the native lineage exhibited a non-significant latitudinal trend in the strength of the indirect effect

277 ($P = 0.274$, Fig. 4B) that was similar to what was found for the stem feeders. Surprisingly, the
278 indirect effect of the native lineage on the invasive lineage was slightly positive at low latitudes
279 (apparent mutualism) and slightly negative (apparent competition) at high latitudes. The
280 relationship was marginally significant ($P = 0.058$, Fig. 4B).

281 Damage by chewing herbivores showed remarkable variability in the strength and
282 direction of the indirect interaction among study sites (Fig. 4C). For native plants, the indirect
283 interaction was negative for NC, MD and ME but positive for MA. The effect size was
284 significant only in ME. In contrast, invasive plants in NC and MA showed evidence of
285 significant apparent competition but non-significant apparent mutualism in MD and ME. For
286 total aphids, native plants showed evidence of apparent competition in NC, MD and ME but
287 apparent mutualism in MA (Fig. 4D). The interaction was significant only in MD. For invasive
288 plants, the effect sizes were negative and significant in MA and ME. No latitudinal trends were
289 evident for chewing damage and aphid density for either lineage.

290

291 DISCUSSION

292 A paradigm of invasion biology is that escape from co-adapted natural enemies in their
293 novel environment is a primary driver of invasion success (Keane and Crawley 2002). A
294 growing list of studies, including this one, suggest that herbivores indirectly influence invasion
295 success and the interactions between native and invasive plants via apparent competition (see
296 also Orrock et al. 2008, Enge et al. 2013, Orrock et al. 2015). Furthermore, our study with *P.*
297 *australis* provides the first evidence that the strength of herbivore-mediated indirect effects is
298 just as strong as the strength of enemy release, and that the strength of these indirect interactions
299 vary from region to region, and in some cases with latitude. We contend that invasion success of
300 introduced species can be better understood when a broader interaction-network and
301 geographical-scale approach is taken.

302 As predicted by theory (Holt and Lawton 1993), apparent competition between native
303 and invasive taxa mediated by herbivores appears to be a common phenomenon in natural
304 ecosystems (e.g., Orrock et al. 2008, Enge et al. 2013, Orrock et al. 2015). A search of Web of
305 Science using ‘apparent’, ‘competition’, ‘inva*’ or ‘exotic’, and ‘plant’ as keywords yielded 20
306 publications that evaluated the indirect effects of invasive plants on co-occurring native plants
307 through apparent competition (Appendix S2: Table S1). Seventeen of the 20 studies (85%)

308 provided evidence that invasive plants increase herbivory on native plants by apparent
309 competition. Consistent with those findings, our study suggests that herbivore-mediated apparent
310 competition is one of the mechanisms that may enhance the fitness and spread of the invasive
311 lineage of *P. australis* in North America. For three of four feeding guilds examined in this study
312 (stem-feeders, leaf-miners and aphids), native *P. australis* plants placed in an invasive *P.*
313 *australis* patch suffered disproportionately greater herbivory than when they were placed in a
314 native patch.

315 We suggest that two non-mutually exclusive factors may underlie the strong indirect
316 negative effects of the invasive lineage on the native lineage of *P. australis*. First, for a wide
317 variety of herbivores, the native lineage appears to be a more palatable or preferred host than the
318 invasive lineage (e.g., Lambert et al. 2007, Allen et al. 2015, Cronin et al. 2015, Bhattarai et al.
319 2016). In our field experiment, native plants averaged 50% greater incidence of stem-feeders,
320 620% higher proportion of leaves with leaf-miners, 53% more total leaf area chewed, and 573%
321 more aphids per stem than invasive plants. In controlled common-garden experiments, Bhattarai
322 et al. (2016) found that colony growth rates and survivorship of *H. pruni* aphids were up to an
323 order of magnitude higher on the native than invasive lineage. Similar results were found for
324 larval growth rates, survivorship and biomass conversion efficiency of a generalist chewing
325 herbivore of *P. australis*, the fall armyworm (*Spodoptera frugiperda*). The fact that the native
326 lineage suffers more leaf loss from the entire guild of chewing herbivores (this study; see also
327 Cronin et al. 2015), suggests that other common leaf chewers may also prefer or perform better
328 on the native than invasive lineage. Finally, Allen et al. (2016) found that despite the five-fold
329 difference in the incidence of *Lipara rufitarsis* galls in the field, the two lineages had similar
330 levels of infestation in a common garden. It was suggested that this difference is due to plasticity
331 in the plants that results in the native lineage being the preferred or most palatable host. At
332 present, we know nothing about host preference/performance in the leaf miners.

333 Native *P. australis* growing in or adjacent to invasive *P. australis* may suffer increased
334 herbivory simply because aphids, chewing herbivores and possibly other herbivore species that
335 were resident in the invasive patch are likely to switch to their preferred native host. Theory
336 predicts that if invasive taxa are less vulnerable to the herbivores but can sustain a reservoir of
337 these herbivores, they should exclude the more vulnerable native taxa by apparent competition
338 (Orrock et al. 2010). Even in cases where herbivores have no preference, or a higher preference

339 for the invasive lineage, patches of the invasive lineage are often substantially larger than nearby
340 native patches and may serve as a reservoir of herbivores that spillover onto the native patches.

341 A second possible mechanism promoting the strong herbivore-mediated effect of the
342 invasive lineage on the native lineage of *P. australis* involves the phenological mismatch
343 between them. In deciduous forests, invasive plant species often have extended leaf phenologies
344 that may confer an advantage to them over neighboring native plant species (Fridley 2012, Smith
345 2013). In a common garden study (see Bhattarai et al. 2016), plant genotypes from the invasive
346 lineage sprouted earlier than genotypes of the native lineage (unpublished data; see also Park and
347 Blossey 2008) which may result in larger populations of herbivores in early spring that are likely
348 to spillover to plants of the more preferred native lineage. Using a mathematical model, Smith
349 and Hall (2016) showed that the combined effect of greater preference by herbivores for native
350 taxa and extended phenology of invasive taxa could significantly increase the performance of the
351 invader and potentially result in the exclusion of the native apparent competitor.

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

364 A likely explanation for the indirect negative effect of the native lineage on the invasive
365 lineage of *P. australis* is associational susceptibility (e.g., White and Whitham 2000). As pointed
366 out previously, the native lineage supports substantially greater per-stem abundances of all four
367 herbivore guilds. Even though the invasive lineage is generally less palatable/preferred, its risk
368 of attack by herbivores may go up because of its close proximity to native patches. Associational
369 susceptibility has been suggested as the mechanisms underlying apparent competition in a

370 number of systems (e.g., Rand 2003), including other invasive species (e.g., Rand and Louda
371 2004). We suggest that this associational susceptibility of invasive patches is likely to be
372 inconsequential to the growth and spread of established invasive patches, simply because
373 invasive patches of *P. australis* are often massive in size, sometimes spanning many square
374 kilometers, whereas native patches are typically small, covering tens of square meters or less.
375 Spillover of herbivores in the other direction is likely much more important.

376 Asymmetrical herbivore-mediated apparent competition is likely to contribute
377 significantly to the competitive superiority of the invasive lineage. Although direct
378 measurements of fitness costs associated with herbivory of *P. australis* lineages have not been
379 documented, these costs are likely to be significant. Stems infested by *Lipara* fail to produce
380 flowers and also suffer from a 55% reduction in stem growth (Lambert et al. 2007, Allen et al.
381 2015). For plant species, biomass and stem height are strongly related to competitive ability
382 (Gaudet and Keddy 1988). These observations suggest a strong fitness cost of *Lipara* infestation
383 to *P. australis* sexual and asexual reproduction. Although *P. australis* is thought to grow and
384 spread primarily by clonal growth, recent studies have revealed the importance of sexual
385 reproduction in the establishment and expansion of new patches (e.g., McCormick et al. 2010).
386 With ~80% of the stems unable to produce flowers and biomass production compromised, native
387 plants would likely experience severe fitness costs due to apparent competition with the invasive
388 lineage. Similarly, aphids have been reported to produce massive outbreaks and cause yellowing
389 and early death of aboveground parts (Cronin et al. 2015). Leaf mining and chewing damage are
390 relatively low but the removal of photosynthetic tissues during the early growing season could
391 have a disproportionately large impact on plant fitness (Godschalx et al. 2016).

392 This study is the first to document geographic variation in the strength of indirect
393 interactions mediated by natural enemies and provide partial support for the biotic interactions
394 hypothesis that posits a negative relationship between latitude and the strength of biotic
395 interactions (Schemske et al. 2009). Damage to native lineages of *P. australis* by stem-feeding
396 and leaf-chewing herbivores decreased but total aphids per stem increased with increasing
397 latitude (Cronin et al. 2015). In comparison, herbivory of the invasive lineage did not vary with
398 latitude (Cronin et al. 2015). These non-parallel latitudinal gradients in herbivory resulted in the
399 invasive lineage suffering much less herbivory than the native lineage in the south (i.e., greater
400 “enemy release”) than the north. In light of this lineage-specific spatial variation in herbivory, we

401 expected herbivore-mediated indirect interactions between native and invasive *P. australis*
402 would also vary with latitude. We did find evidence for a significant latitudinal gradient in stem
403 feeder mediated indirect interactions between the two lineages (Fig. 4A). Irrespective of which
404 lineage is being impacted, the effect of the indirect interaction mediated by stem feeders was
405 strongest in the south and decreased within increasing latitude. To our knowledge, this is the
406 only example of a latitudinal gradient in the strength of a species interaction that is mediated
407 through another species. These two pieces of evidence suggest that the importance of herbivory
408 on plant invasion, through direct and indirect ways, is greater in the south. With regard to the
409 other herbivore guilds, significant gradients in herbivore-mediated interactions do not exist, but
410 there is much spatial variation among sites with regard to the strength of these interactions. For
411 example, the effect of the native lineage on aphid pressure on the invasive lineage is almost
412 significantly positive at our MD site (apparent mutualism; Abrams and Matsuda 1996) and
413 significantly negative (apparent competition) at our northernmost sites, MA and ME. One
414 possible explanation for this case of apparent mutualism is that when invasive plants were placed
415 in highly palatable native patches, herbivores were drawn away from the invasive plants. Given
416 that stem feeders and aphids are likely the most important herbivores in this system (Cronin et al.
417 2015, Allen et al. 2015, Bhattarai et al. 2016), the geographic variation in interactions between
418 lineages of *P. australis*, mediated by these herbivores, is potentially an important source of
419 heterogeneity in *P. australis* invasion success. In the future, more studies should focus on the
420 geographic variation in complex species interactions, as they are likely to change from region to
421 region owing to large-scale variation in species richness and the strength of direct interactions.

422 Finally, our study shows that the negative effects of apparent competition on native plants
423 can be as strong as the negative effects of herbivory on native plants (measured in terms of the
424 degree of enemy release; see Fig. 3). Enemy release has long been regarded as one of the most
425 important factors promoting invasion success of introduced plants (Keane and Crawley 2002).
426 Apparent competition is now on the radar of invasion biologists (see Appendix S2: Table S1)
427 and has proven important in the majority of case studies. This indirect interaction has been
428 shown to influence the persistence of co-occurring species in different ecosystems (Bonsall and
429 Hassell 1997, Morris et al. 2004, Cronin 2007). Our study is the first to suggest that these two
430 factors involving natural enemies of invasive taxa may be of equal importance. In addition to
431 these enemy-mediated mechanisms, the invasive lineage of *P. australis* has been shown to be a

432 superior competitor to the native lineage for resources (e.g., Mozdzer and Zieman 2010) and its
433 rate of clonal expansion is strongly correlated with the frequency of disturbances (e.g., Bhattarai
434 and Cronin 2014). Clearly, multiple mechanisms are likely at work in facilitating the invasion
435 and spread of the European invasive lineage in North America. Future studies should focus on
436 partitioning the contributions of these direct and indirect processes in species invasion (e.g.,
437 Orrock et al. 2015).

438

439 **ACKNOWLEDGEMENTS**

440 We thank W. Allen, R. Andrews, A. Chow, J. Croy, D. Landau, M. Hoff, K. O'Brien, S.
441 Spry, T. Williams, and R. Young for their assistance, and two anonymous reviewers for valuable
442 suggestions on previous draft of the manuscript. Funding was provided to JTC and LAM by
443 National Science Foundation DEB Awards 1049914 and 1050084, and to GPB by the Louisiana
444 Environmental Education Commission, LSU Biograds, and Sigma Xi GIAR.

445

446 **REFERENCES**

- 447 Abrams, P. A., and H. Matsuda. 1996. Positive indirect effects between prey species that share
448 predators. *Ecology* **77**:610-616.
- 449 Allen, W. J., L. A. Meyerson, D. Cummings, J. Anderson, G. P. Bhattarai, and J. T. Cronin.
450 2016. Biogeography of a plant invasion: drivers of latitudinal variation in enemy release.
451 *Global Ecology and Biogeography* in press.
- 452 Allen, W. J., R. E. Young, G. P. Bhattarai, J. R. Croy, A. M. Lambert, L. A. Meyerson, and J.
453 T. Cronin. 2015. Multitrophic enemy escape of invasive *Phragmites australis* and its
454 introduced herbivores in North America. *Biological Invasions* **17**:3419-3432.
- 455 Bezemer, T. M., J. A. Harvey, and J. T. Cronin. 2014. Response of native insect communities to
456 invasive plants. *Annual Review of Entomology* **59**:119-141.
- 457 Bhattarai, G. P., and J. T. Cronin. 2014. Hurricane activity and the large-scale pattern of spread
458 of an invasive plant species. *PLoS ONE* **9**:e98478.
- 459 Bhattarai, G. P., L. A. Meyerson, J. Anderson, D. Cummings, W. J. Allen, and J. T. Cronin.
460 2016. Biogeography of a plant invasion: genetic variation and plasticity in latitudinal
461 clines for traits related to herbivory. *Ecological Monographs* DOI: 10.1002/ecm.1233.
- 462 Bonsall, M., and M. Hassell. 1997. Apparent competition structures ecological assemblages.

463 Nature **388**:371-373.

464 Borer, E. T., P. R. Hosseini, E. W. Seabloom, and A. P. Dobson. 2007. Pathogen-induced
465 reversal of native dominance in a grassland community. *Proceedings of the National*
466 *Academy of Sciences* **104**:5473-5478.

467 Chambers, R. M., L. A. Meyerson, and K. Saltonstall. 1999. Expansion of *Phragmites australis*
468 into tidal wetlands of North America. *Aquatic Botany* **64**:261-273.

469 Chaneton, E. J., and M. B. Bonsall. 2000. Enemy-mediated apparent competition: empirical
470 patterns and the evidence. *Oikos* **88**:380-394.

471 Cronin, J. T. 2007. Shared parasitoids in a metacommunity: indirect interactions inhibit
472 herbivore membership in local communities. *Ecology* **88**:2977-2990.

473 Cronin, J. T., G. P. Bhattarai, W. J. Allen, and L. A. Meyerson. 2015. Biogeography of a plant
474 invasion: plant-herbivore interactions. *Ecology* **96**:1115-1127.

475 Enge, S., G. M. Nylund, and H. Pavia. 2013. Native generalist herbivores promote invasion of a
476 chemically defended seaweed via refuge-mediated apparent competition. *Ecology Letters*
477 **16**:487-492.

478 Fridley, J. D. 2012. Extended leaf phenology and the autumn niche in deciduous forest invasions.
479 *Nature* **485**:359-362.

480 Gaudet, C. L., and P. A. Keddy. 1988. A comparative approach to predicting competitive ability
481 from plant traits. *Nature* **334**:242-243.

482 Godschalx, A. L., L. Stady, B. Watzig, and D. J. Ballhorn. 2016. Is protection against florivory
483 consistent with the optimal defense hypothesis? *BMC Plant Biology* **16**:32.

484 Gurevitch, J., and L. V. Hedges. 1993. Meta-analysis: combining the results of independent
485 experiments. Pages 378-398 in S. M. Scheiner and J. Gurevitch, editors. *Design and*
486 *Analysis of Ecological Experiments*. Chapman and Hall. New York.

487 Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities.
488 *Theoretical Population Biology* **12**:197-229.

489 Holt, R. D., and J. H. Lawton. 1993. Apparent competition and enemy-free space in insect host-
490 parasitoid communities. *American Naturalist* **142**:623-645.

491 Keane, R. M., and M. J. Crawley. 2002. Exotic plant invasions and the enemy release hypothesis.
492 *Trends in Ecology and Evolution* **17**:164-170.

493 Lambert, A. M., K. Winiarski, and R. A. Casagrande. 2007. Distribution and impact of exotic

- 494 gall flies (*Lipara* sp.) on native and exotic *Phragmites australis*. *Aquatic Botany* **86**:163-
495 170.
- 496 Lambertini, C., M. Gustafsson, J. Frydenberg, J. Lissner, M. Speranza, and H. Brix. 2006. A
497 phylogeographic study of the cosmopolitan genus *Phragmites* (Poaceae) based on
498 AFLPs. *Plant Systematics and Evolution* **258**:161-182.
- 499 Levine, J. M., P. B. Adler, and S. G. Yelenik. 2004. A meta-analysis of biotic resistance to exotic
500 plant invasions. *Ecology Letters* **7**:975-989.
- 501 Marks, M., B. Lapin, and J. Randall. 1994. *Phragmites australis* (*P. communis*): threats,
502 management and monitoring. *Natural Areas Journal* **14**:285-294.
- 503 McCormick, M. K., K. M. Kettenring, H. M. Baron, and D. F. Whigham. 2010. Extent and
504 reproductive mechanisms of *Phragmites australis* spread in brackish wetlands of
505 Chesapeake Bay, Maryland (USA). *Wetlands* **30**:67-74.
- 506 Meadows, R. E., and K. Saltonstall. 2007. Distribution of native and introduced *Phragmites*
507 *australis* in freshwater and oligohaline tidal marshes of the Delmarva peninsula and
508 southern New Jersey. *The Journal of the Torrey Botanical Society* **134**:99-107.
- 509 Meyerson, L. A., J. T. Cronin, and P. Pysek. 2016. *Phragmites* as a model system for studying
510 plant invasions. *Biological Invasions* **18**:2421-2431.
- 511 Moles, A. T., S. P. Bonser, A. G. B. Poore, I. R. Wallis, and W. J. Foley. 2011. Assessing the
512 evidence for latitudinal gradients in plant defence and herbivory. *Functional Ecology*
513 **25**:380-388.
- 514 Morris, R. J., O. T. Lewis, and H. C. J. Godfray. 2004. Experimental evidence for apparent
515 competition in a tropical forest food web. *Nature* **428**:310-313.
- 516 Mozdzer, T. J., and J. C. Zieman. 2010. Ecophysiological differences between genetic lineages
517 facilitate the invasion of non-native *Phragmites australis* in North American Atlantic
518 coast wetlands. *Journal of Ecology* **98**:451-458.
- 519 Orrock, J. L., H. P. Dutra, R. J. Marquis, and N. A. Barber. 2015. Apparent competition and
520 native consumers exacerbate the strong competitive effect of an exotic plant species.
521 *Ecology* **96**:1052-1061.
- 522 Orrock, J. L., M. S. Witter, and O. Reichman. 2008. Apparent competition with an exotic plant
523 reduces native plant establishment. *Ecology* **89**:1168-1174.
- 524 Orrock, J. L., R. D. Holt, and M. L. Baskett. 2010. Refuge-mediated apparent competition in

525 plant-consumer interactions. *Ecology Letters* **13**:11-20.

526 Park, M. G., and B. Blossey. 2008. Importance of plant traits and herbivory for invasiveness of
527 *Phragmites australis* (Poaceae). *American Journal of Botany* **95**:1557-1568.

528 Pennings, S. C., E. L. Siska, and M. D. Bertness. 2001. Latitudinal differences in plant
529 palatability in Atlantic coast salt marshes. *Ecology* **82**:1344-1359.

530 R Development Core Team. 2015. R: A language and environment for statistical computing. R
531 Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.

532 Rand, T. A. 2003. Herbivore-mediated apparent competition between two salt marsh forbs.
533 *Ecology* **84**:1517-1526.

534 Rand, T. A., and S. M. Louda. 2004. Exotic weed invasion increases the susceptibility of native
535 plants attack by a biocontrol herbivore. *Ecology* **85**:1548-1554.

536 Rasband, W. S. 2014. ImageJ. U. S. National Institutes of Health, Bethesda, Maryland, USA,
537 <http://imagej.nih.gov/ij/>, 1997-2014.

538 Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: Statistical Software for Meta-
539 Analysis. Version 2. Sinauer Associates, Massachusetts.

540 Saltonstall, K. 2002. Cryptic invasion by a non-native genotype of the common reed, *Phragmites*
541 *australis*, into North America. *Proceedings of the National Academy of Sciences*
542 **99**:2445-2449.

543 Saltonstall, K., and D. Hauber. 2007. Notes on *Phragmites australis* (Poaceae: Arundinoideae) in
544 North America. *Journal of the Botanical Research Institute of Texas* **1**:385-388.

545 Schemske, D. W., G. G. Mittelbach, H. V. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a
546 latitudinal gradient in the importance of biotic interactions? *Annual Review of Ecology,*
547 *Evolution and Systematics* **40**:245-269.

548 Smith, L. M. 2013. Extended leaf phenology in deciduous forest invaders: mechanisms of impact
549 on native communities. *Journal of Vegetation Science* **24**:979-987.

550 Smith, L. M., and S. Hall. 2016. Extended leaf phenology may drive plant invasion through
551 direct and apparent competition. *Oikos* **125**:839-848.

552 Tewksbury, L., R. Casagrande, B. Blossey, P. Häfliger, and M. Schwarzländer. 2002. Potential
553 for Biological Control of *Phragmites australis* in North America. *Biological Control*
554 **23**:191-212.

555 White, E. M., J. C. Wilson, and A. R. Clarke. 2006. Biotic indirect effects: a neglected concept in

556 invasion biology. Diversity and Distributions **12**:443-455.
557 White, E. M., N. M. Sims, and A. R. Clarke. 2008. Test of enemy release hypothesis: the native
558 magpie moth prefers a native firewood (*Senecio pinnatifolius*) to its introduced congener
559 (*S. madagascariensis*). Austral Ecology **33**:110-116.
560 White, J. A., and T. G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder
561 herbivore. Ecology **81**:1795-1803.
562 Wootton, J. T. 1994. Predicting direct and indirect effects: an integrated approach using
563 experiments and path analysis. Ecology **75**:151-165.
564

565 SUPPORTING INFORMATION

566 Supporting information may be available online at: <http://onlinelibrary.wiley.com/doi/xx>.

567 FIGURE LEGENDS

568 **Fig. 1.** Schematic diagrams illustrating enemy release and apparent competition in facilitating
569 plant invasions. Solid arrows are direct interactions, broken arrows are indirect interactions and
570 the width of the arrow denotes the strength of the interaction. (A) Invasive plants in the
571 introduced range suffer lower herbivory than the neighboring native plants which provides the
572 former plants with a competitive advantage (Keane and Crawley 2002). (B) Invasive plants
573 indirectly negatively affect the neighboring native plants by increasing herbivore abundance
574 which causes greater damage to the native than invasive plants (Holt 1977).

575 **Fig. 2.** Herbivory on native and invasive *Phragmites australis* plants transplanted into different
576 (recipient) patches. Least square means (\pm SE) for herbivory for each feeding guild is shown.
577 Herbivory on plants of the same lineage are connected by a line. Symbols with different letters
578 are significantly different from each other ($P < 0.05$).

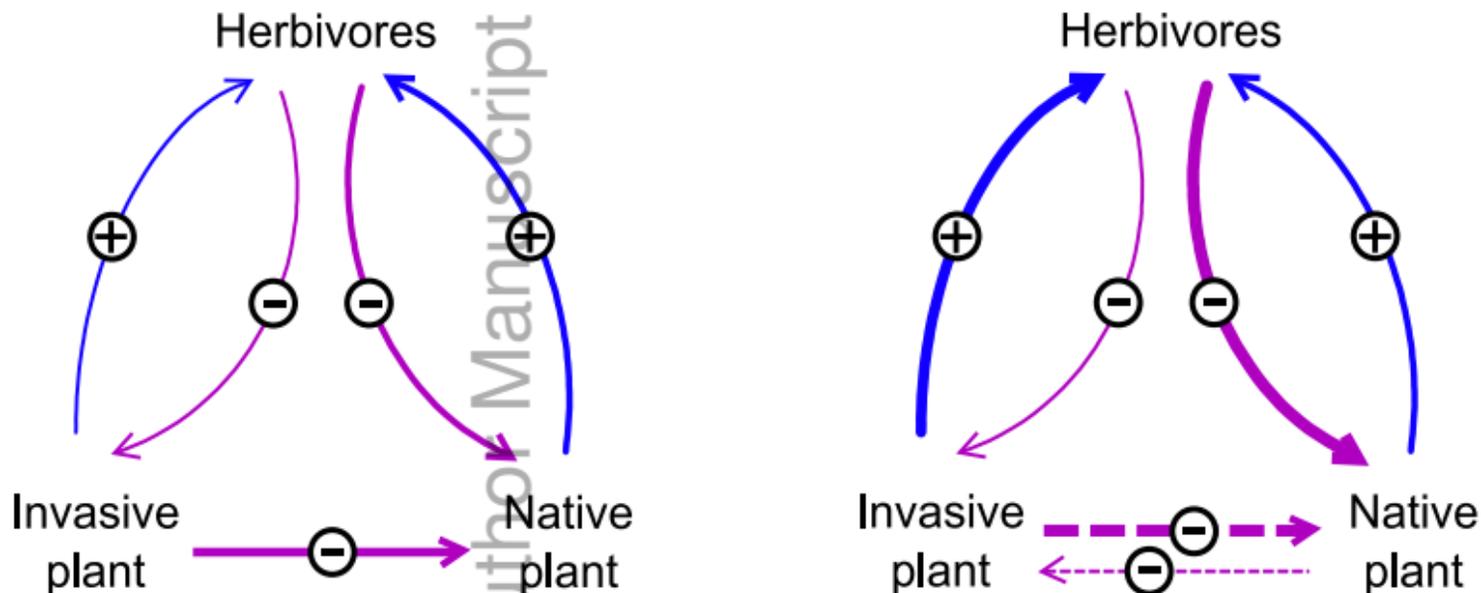
579 **Fig. 3.** Mean effect sizes (Hedge's $d_{II} \pm 95\%$ confidence intervals) for the strength of apparent
580 competition on invasive and native *P. australis*. Negative values indicate support for apparent
581 competition. For example, for the invasive lineage (x -axis), the mean difference in herbivory of
582 invasive plants grown in their own patch versus when they are grown in a patch of the native
583 lineage is reported. Because the 95% CIs overlap zero, the indirect negative effect of the native
584 lineage on the invasive lineage is not statistically significant. In contrast, the indirect negative
585 effect of the invasive lineage on the native lineage is significant (95% CIs do not overlap zero).
586

587 Effect size for enemy release (Hedge's d_{ER}) is reported in the shaded area. It represents the
588 difference in herbivory between invasive and native plants growing in their respective patches
589 ("Inv - Nat"). The negative d_{ER} and 95% CIs that do not overlap zero indicate that the invasive
590 lineage benefits from significant enemy release.

591 **Fig. 4.** Spatial variation in the intensity of herbivore-mediated indirect interactions between
592 native and invasive *P. australis*. Each symbol represents an effect size estimated as Hedge's $d_H \pm$
593 95% CI for a lineage and site and refers to the indirect effect of the other lineage on the native
594 (circle) or invasive (square) lineage. For example, for the invasive lineage, the mean difference
595 in herbivory of invasive plants grown in their own patch versus when they are grown in a native
596 patch is reported. The x -axis represents the latitude of the sites (in degrees) and includes
597 abbreviations for the state within which the site occurs (see Methods). Solid lines represent
598 significant and marginally-significant latitudinal trends fitted as least-square regressions. A non-
599 significant latitudinal trend for leaf-miners on native lineage is shown (broken line) because of
600 the marginally-significant plant lineage \times latitude interaction ($P = 0.067$). In all plots, a zero
601 effect size reference line is included.

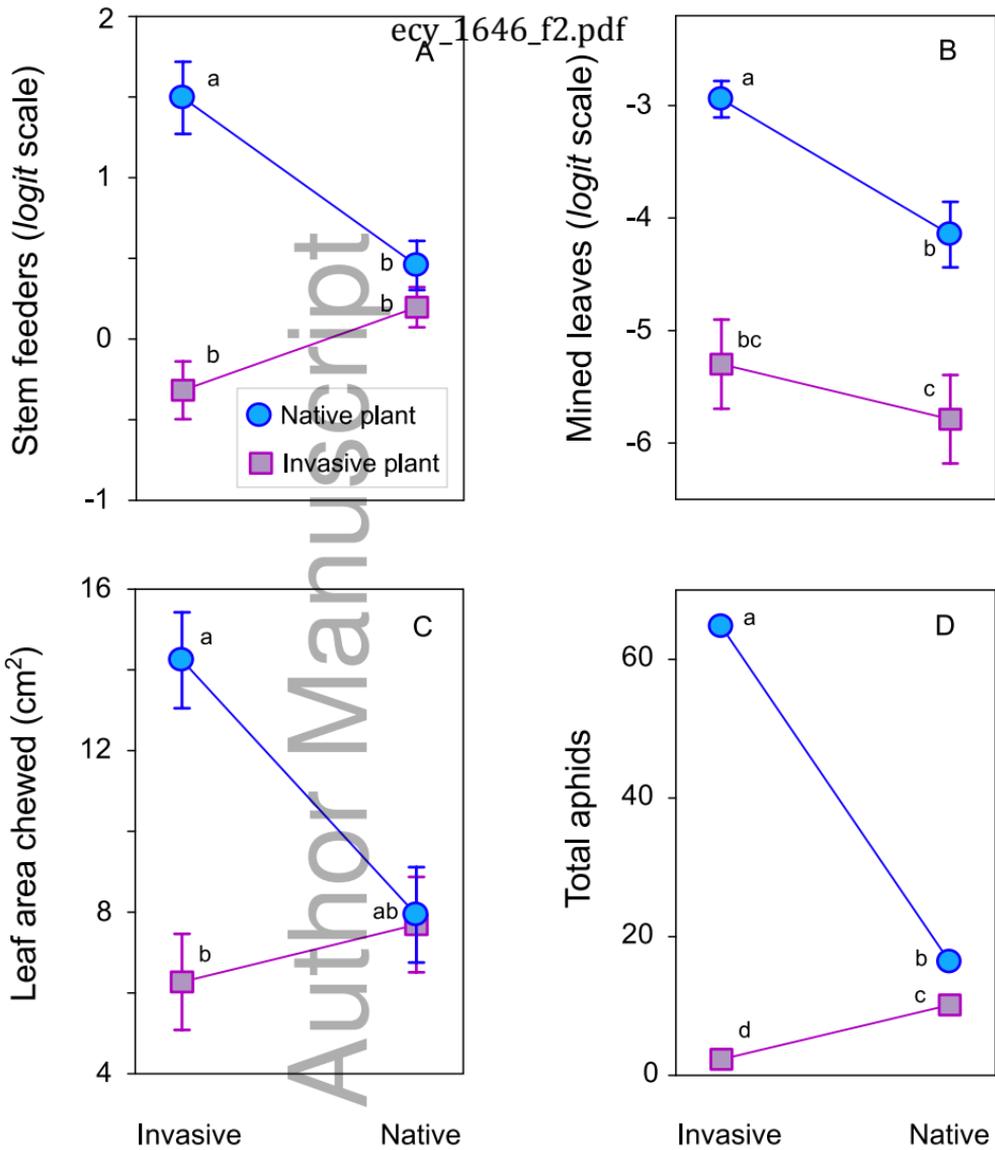
Author Manuscript

A. Enemy release ecy_1646_f1.pdf B. Apparent competition



This article is protected by copyright. All rights reserved.

Figure 1



This article is protected by copyright. All rights reserved.

Figure 2

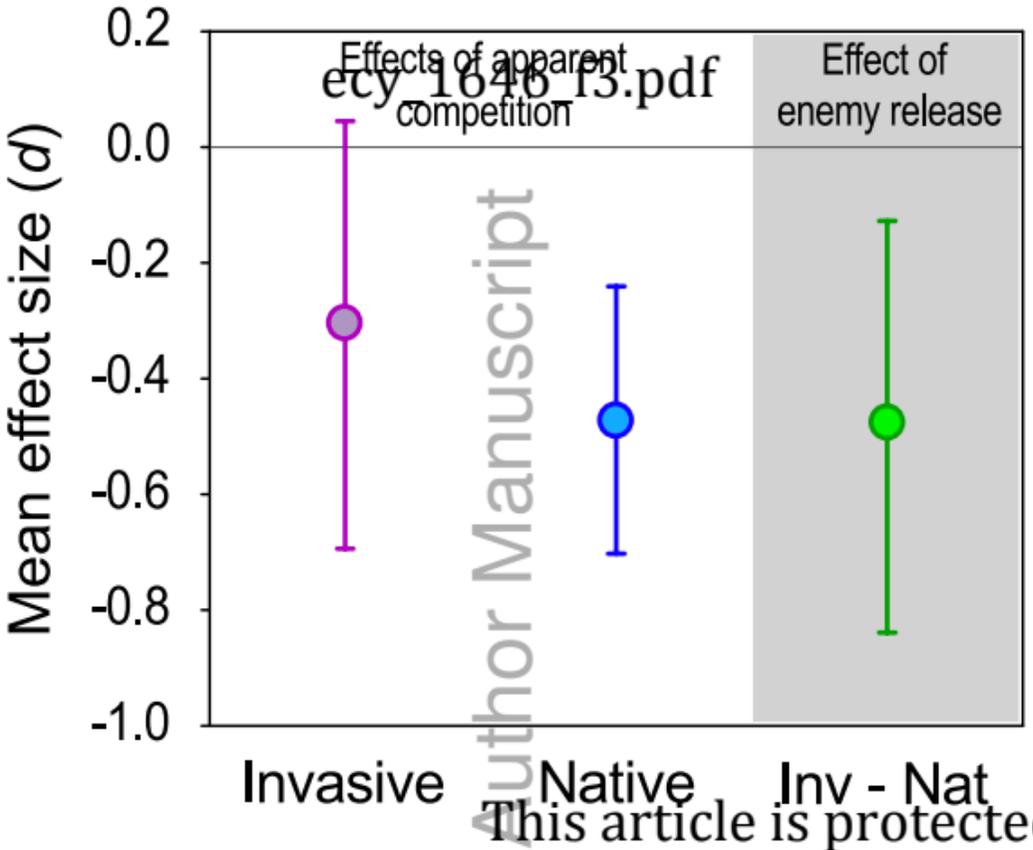
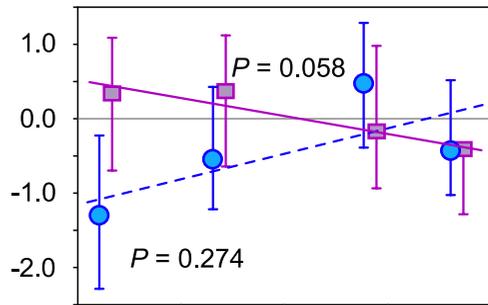
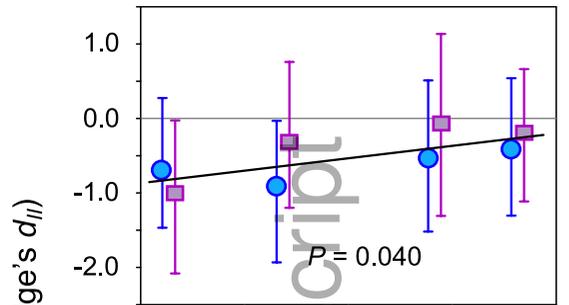
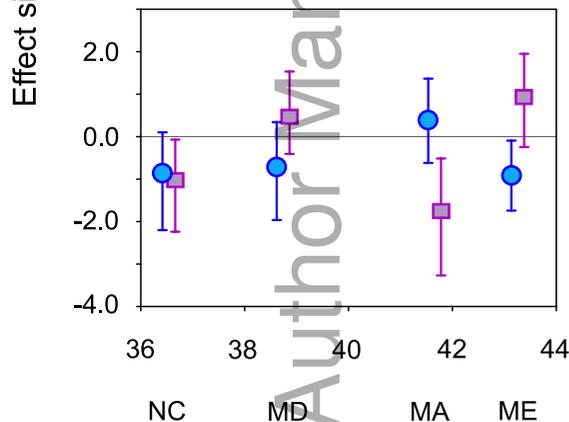


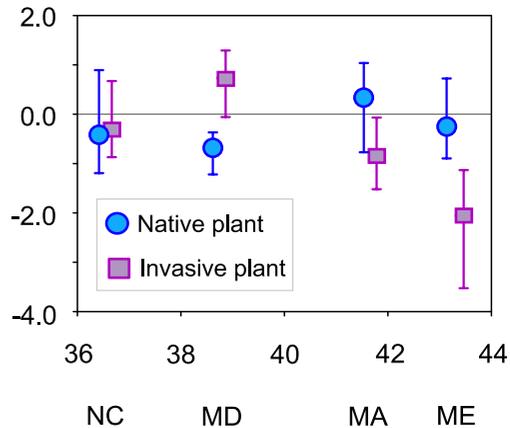
Figure 3



C. Leaf area chewed



D. Total aphids



Latitude

This article is protected by copyright. All rights reserved