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ORIGINAL PAPER

Multitrophic enemy escape of invasive *Phragmites australis* and its introduced herbivores in North America

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Abstract One explanation for why invasive species are successful is that they escape natural enemies from their native range or experience lower attack from natural enemies in the introduced range relative to native species (i.e., the enemy-release hypothesis). However, little is known about how invasive plants interact with co-introduced herbivores or natural enemies of the introduced herbivores. We focus on *Phragmites australis*, a wetland grass native to Europe (EU) and North America (NA). Within the past 100–150 years, invasive European genotypes of *P. australis* and several species of specialist *Lipara* gall flies have spread within NA. On both continents we surveyed *P. australis* patches for *Lipara* infestation (proportion of stems infested) and *Lipara* mortality from natural enemies. Our objectives were to assess evidence for enemy-release in the invaded (NA) versus native (EU) range and whether *Lipara* infestation or mortality differed between invasive and native *P. australis* genotypes in NA. Enemy-release varied regionally; *Lipara* were absent throughout most of NA, supporting enemy-release of *Phragmites*. However, where *Lipara* were present, the proportion of invasive *P. australis* stems infested with *Lipara* was higher in the introduced (11 %) than native range (<1 %). This difference may be explained by the absence of *Lipara* parasitoids in our NA survey, strongly supporting enemy-release of *Lipara*. In NA, native *P. australis* genotypes exhibited higher *Lipara* infestation (32 %) than invasive genotypes (11 %), largely driven by *L. rufitarsis*. We attribute genotypic differences in infestation to a combination of *Lipara* exhibiting 34 % greater performance (gall diameter) and suffering four times less vertebrate predation on native than invasive genotypes. Our study suggests that complex interactions can result from the co-introduction of plants and their herbivores, and that a multitrophic perspective is required for investigating how biotic interactions influence invasion success.

Keywords Biotic resistance · Chloropidae · Enemy release · Invasive plants · Invasional meltdown · *Lipara* spp. natural enemies

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Introduction

A widely supported explanation for the success of invasive species is that they leave behind their coevolved natural enemies (e.g., herbivores and pathogens) when introduced to a new environment (e.g., Wolfe 2002; Mitchell and Power 2003; Liu and Stiling 2006; Castells et al. 2013), a phenomenon known as enemy-release (Elton 1958; Keane and Crawley 2002). An extension of this hypothesis, known as local enemy-release (Zheng et al. 2012), predicts that invasive species also suffer less damage from natural enemies in the introduced range compared to co-occurring, closely related native species (e.g., Dietz et al. 2004; Parker and Gilbert 2007; Cincotta et al. 2009; Funk and Throop 2009; Zheng et al. 2012; Cronin et al. 2015). This result may be driven by the inability of non-coadapted natural enemies to overcome the novel defenses of invasive species, greater palatability and nutritional quality of native species, or subtle differences in microhabitat. In contrast to the concept of enemy-release, the biotic-resistance hypothesis (Elton 1958; Parker and Hay 2005) predicts that natural enemies in the introduced range cause more mortality to invasive species than co-occurring, closely related native species (e.g., Agrawal and Kotanen 2003; Chun et al. 2010; Morrison and Hay 2011; Fan et al. 2013). This phenomenon is often attributed to the invasive species lacking effective defenses to resist attack by natural enemies with which they do not share an evolutionary history (Morrison and Hay 2011).

A complicating factor of both the enemy-release and biotic-resistance hypotheses is that herbivores from the region of origin of the invasive plant could also be accidentally or intentionally introduced with their invading host plant. Such a scenario does not strictly fit with both hypotheses because the introduced herbivores are presumably already coadapted with the invasive plant and are not native to the recipient community. In the novel environment, the interaction between the invasive plant and introduced herbivore species could be significantly different from in their native range. For example, herbivory of invasive plants by introduced herbivores could be greater in the introduced than native range. Although lower herbivory in the introduced than native range would not represent enemy-release sensu stricto, the resulting advantages to the invasive plant are likely the same. Moreover, novel indirect interactions can potentially lead to net positive effects of herbivory for the invasive host plant in the introduced range (e.g., indirect dispersal through seed predators, see Pearson et al. 2000; Pearson and Ortega 2002), known as the enemy inversion hypothesis (Colautti et al. 2004).

Although tritrophic interactions have received little attention in invasion biology (Harvey et al. 2010), the strength of enemy-release or biotic-resistance may be influenced by higher trophic levels (i.e., predators and parasitoids). Differences in mortality due to natural enemies may represent an explanation for why herbivory varies between invasive and native plants, and between native and introduced ranges. Introduced herbivores may escape their own natural enemies (i.e., enemy-release), allowing them to become more prevalent on host plants in the new range (e.g., Menéndez et al. 2008; Prior and Hellmann 2013). Alternatively, if herbivores feeding on invasive plants suffer greater native natural enemy pressure than those feeding upon closely related native hosts (e.g., Engelkes et al. 2012), this could benefit the invasive plant species through reduced herbivory (i.e., a trophic cascade).

The goal of this study was to assess the evidence supporting enemy-release and biotic-resistance at multiple trophic levels involving the common reed, *Phragmites australis* (Cav.) Trin. ex Steudel (Poales: Poaceae), monophagous gall-forming flies in the genus *Lipara* Meigen (Diptera: Chloropidae), and their natural enemies. Invasive European genotypes of *P. australis* widely overlap with the distribution of rare native genotypes in marshes and wetlands of North America (NA) (Saltonstall 2002). *Lipara* spp. are also introduced from Europe (EU) into NA. To date, there is little information on *Lipara* and their natural enemies in NA. The exceptions are the studies by Lambert et al. (2007) and Park and Blossey (2008) which found evidence suggesting *Lipara* infestation is higher on native than invasive genotypes. However, these studies were based on a comparison of three native and 16 invasive *P. australis* patches from the northeastern United States.

We surveyed 143 *P. australis* patches throughout NA and 21 patches along the Atlantic coast of EU to determine *Lipara* presence, infestation level (proportion of stems infested), performance (gall diameter and adult dry body mass), impact (stem height and flowering frequency), and mortality due to parasitoids and predators. Based on enemy-release and invasion theory, we made the following predictions: (1) infestation of *Lipara* on *P. australis* would be lower in the introduced (NA) compared to native (EU) range (i.e., enemy-release for the plant); (2) *Lipara* infestation, performance, and impact would be lower on invasive relative to native genotypes of *P. australis* in NA (i.e., local enemy-release); and (3) mortality of *Lipara* due to vertebrate and invertebrate natural enemies would be lower in NA than in EU, and on native than invasive genotypes in NA (i.e., enemy-release for the herbivore).

Materials and methods

Study organisms

Phragmites australis is a 2–5 m tall macrophytic grass commonly found in wetlands, rivers, salt marshes, and estuaries on every continent except Antarctica (Clevering and Lissner 1999). Although *P. australis* has been present in NA for millennia (Hansen 1978; Orson 1999), it has spread rapidly during the past 150 years. This spread has been attributed largely to the cryptic invasion of multiple invasive genotypes (Hauber et al. 2011; Howard et al. 2008; Lambertini et al. 2012; Meyerson and Cronin 2013; Saltonstall 2002; for review, see Meyerson et al. 2012), which have had profound ecological impacts, altering hydrology, ecosystem function, and degrading habitat for native species (Saltonstall 2002; Meyerson et al. 2000, 2009). The most abundant and widespread invasive genotype is known as *M* (based on an analysis of chloroplast DNA; Saltonstall 2002), which derives from EU and Asia. There are other introduced genotypes from Europe (e.g., L1 genotype; Meyerson and Cronin 2013) and we lump them all together as European invasive genotypes. Along the Gulf Coast of LA, there are also multiple non-native genotypes (Lambertini et al. 2012; Meyerson et al. 2012) and some are spreading rapidly (Bhattarai and Cronin 2014), the most common of which is known as genotype *I*. Finally, at least 14 native genotypes have been identified in NA (Saltonstall 2002; Meadows and Saltonstall 2007; Vachon and Freeland 2011), which we collectively refer to as "native genotypes" in our analyses. Because herbivory of invasive species has been shown to decrease with greater taxonomic isolation from the resident native community (Dawson et al. 2009; Hill and Kotanen 2009), our study provides a strong and conservative test of the enemy-release and biotic-resistance hypotheses by using distinct native and invasive lineages within a single species.

P. australis is host to a high diversity of arthropod herbivores in EU, where over 170 different species have been identified (Tewksbury et al. 2002). In NA, specialist native herbivores are scarce (Tewksbury et al. 2002) although generalists are common (Cronin et al. unpublished data). However, the majority of herbivore damage is attributed to arthropods accidentally introduced to NA, including three species of *Lipara*: *L. pullitarsis* Doskocil and Chvala, *L. rufitarsis* Loew, and *L. similis* Schiner (Tewksbury et al. 2002; Cronin et al. 2015). The genus *Lipara* is native to EU and northern Asia and all eleven species are monophagous on *P. australis* (Grochowska 2013). *Lipara* are univoltine and a single fully-grown larva overwinters inside the senesced stem. Pupation occurs in the spring, followed shortly thereafter by adult emergence. Once mated, females oviposit on young *P. australis* shoots (Chvala et al. 1974; Reader 2003). Larvae feed internally and generally cause internodes to shorten, widen, and become engorged with nutritious parenchymatous tissue (De Bruyn 1995). Infestation of a stem is associated with strong negative effects on flowering and stem height (Lambert et al. 2007).

Four species of *Lipara* are present in EU where *P. australis* genotypes *M* and L1 are native: *L. lucens* Meigen, *L. pullitarsis*, *L. rufitarsis*, and *L. similis*. *Lipara* infestation levels (proportion of stems infested) in EU are variable; generally less than 5 % of *P. australis* stems are attacked (Reader 2001; Schwarzlander and Hafliger 2000; Skuhravy 1981), although rare outbreaks of infestation levels up to 46 % were reported in a survey of 19 patches over multiple years (Schwarzlander and Hafliger 2000). Moreover, *Lipara* galls in EU are frequently attacked by a high diversity of parasitoids (Nartshuk 2006) and depredated by the harvest mouse (*Micromys minutus*) and blue tit (*Cyanistes caeruleus*) (Mook 1967; Reader 2001; Nartshuk 2007).

Three, and possibly all four, of the EU *Lipara* species have been introduced into NA. *L. lucens* was identified by Sabrosky (1958) from specimens collected in Connecticut in 1931, but neither the original specimens nor any subsequent records are available. *L. similis* was likely introduced in New Jersey via packing material from Holland in 1946 (Sabrosky 1958), while the earliest records for *L. rufitarsis* and *L. pullitarsis* are from Rhode Island in 1998 and New Jersey in 2002, respectively (Tewksbury et al. 2002). To date, investigations of *Lipara* in the northeastern United States report infestation levels to be as high as 80 % (Balme 2000; Blossey 2003; Lambert et al. 2007; Park and Blossey 2008). *L. pullitarsis* was reported as restricted to the invasive genotype (Blossey 2003), whereas both *L. rufitarsis* and *L. similis* have been found inhabiting native and invasive genotypes, with some evidence suggesting they prefer the former (Lambert et al. 2007; Park and Blossey 2008). Furthermore, based on the frequency of damage and the direct impact on sexual reproduction, Cronin et al. (2015) suggested that *Lipara* represent one of the most damaging and important *P. australis* herbivore groups in North America. At present, there is no information on *Lipara* natural enemies in NA.

Study sites

We examined 143 *P. australis* patches throughout NA and 21 patches in Western EU (Fig. 1, Online Resource 1, Online Resource 2) for the presence of *Lipara* galls, as part of a broader herbivore survey (Cronin et al. 2015). Sampling effort in NA was concentrated along the East Coast (where *M* first appeared in herbarium records ca. 150 years ago), the Mississippi River Valley extending from Louisiana to northern Minnesota, and the Western United States. A total of 48 *M*, 1 *L1* (a recently identified invasive genotype in Canada; Meyerson and Cronin 2013), 19 *I*, and 75 native genotype patches were sampled between 2011 and 2014. Patches of different genotypes often occurred in the same watershed but were rarely intermixed. In EU, patches (all genotype *M*) were selected to complement the geographic range of those in NA. Leaf material from each patch was collected for later determination of genotype (based on chloroplast DNA) using the methods of Saltonstall (2002) but with modifications outlined in Kulmatiski et al. (2010).

Data collection

Lipara distribution and infestation level

All *P. australis* patches were inspected by a team of 2–4 investigators for the presence of *Lipara* galls. The minimum inspection period was 5–10 min, but if *Lipara* appeared absent or scarce, 30–60 min was

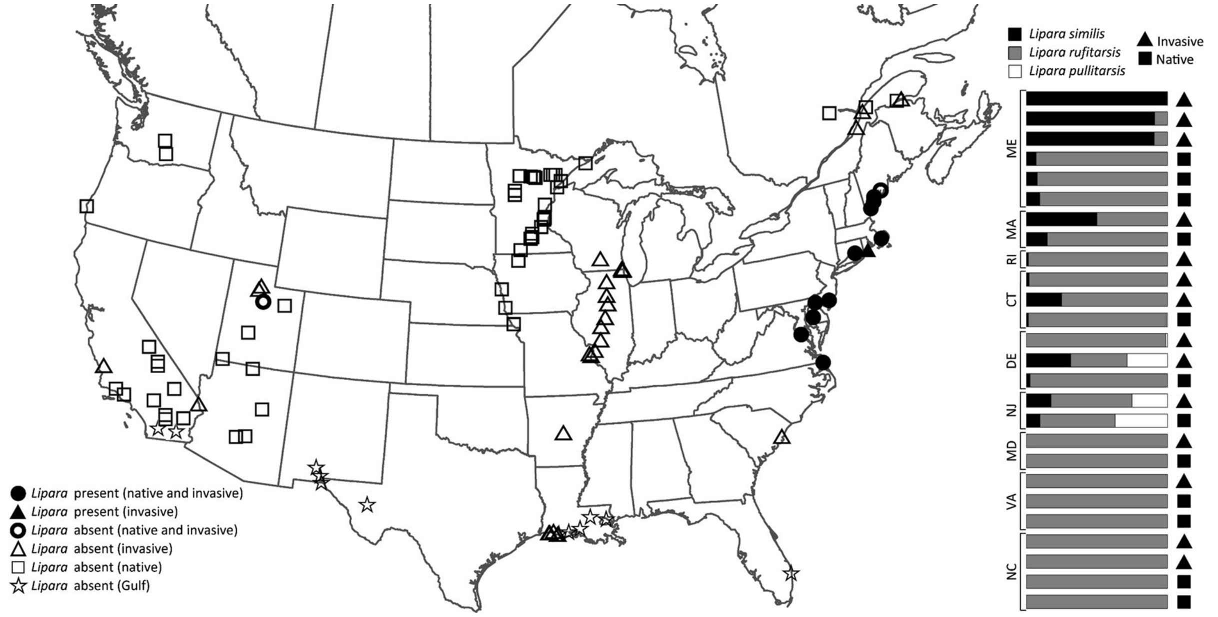

Fig. 1 *Phragmites australis* sampling sites and the distribution of *Lipara* species in North America. The relative abundance (proportion of collected stems inhabited by each *Lipara* species) of *Lipara* species is shown for patches occupied by *Lipara*

spent searching the patch to confirm presence or absence and to maximize gall collection for the study. Sampling in NA was conducted during four different seasons: summer 2012 (July 31–August 20), winter 2013 (March 1–April 20), summer 2013 (August 1–24), and summer 2014 (August 17–26). Most patches were only sampled once, but some were sampled on a second occasion to collect overwintering galls (Online Resource 2). EU patches were visited in summer 2012 (July 22–August 26). We note here that all gall collections were made during the same *Lipara* generation (summer 2012 and winter 2013), minimizing any temporal variability in the data.

The proportion of stems infested with *Lipara* per *P. australis* patch was estimated for all patches in NA and EU where *Lipara* were found (Fig. 1). Within each patch, we walked three separate transects from the edge to interior, examining the three closest stems every 2 m for the presence of a *Lipara* gall, for a total of 150 stems (50 stems per transect). Patch size (estimated by walking the patch exterior with a handheld GPS or using aerial images for very large patches) and stem density (four replicates of stems per 0.25 m^2 quadrat) were also recorded at sites visited in summer 2012. Initial analyses showed that patch size and stem density were unrelated to *Lipara* infestation (Online Resource 3), so these data were no longer collected in subsequent (winter) surveys or included in later analyses.

Lipara species identity, natural enemies, and performance

To examine *Lipara* species composition, parasitism and predation, and performance in native versus invasive *P. australis* patches in NA, galled stems were collected from *Lipara*-infested patches (Fig. 1). In the summer of 2012, 70.1 ± 8.2 galls (mean ± SE; range 13–119; number depended on availability) were collected from each of 17 patches (9 native, 8 invasive; Online Resource 2). All stems were dissected and *Lipara* larvae were identified to species (see Chvala et al. 1974) and examined for parasitism. A second collection of galls (174.0 ± 11.2 per patch; range 65–275) was made during late winter of 2013 from 21 patches (11 native, 10 invasive) in order to rear gall inhabitants. As noted previously, galls from this latter collection (winter) represented the same generation of *Lipara* as the previous (summer) collection. These winter galls were placed in individual Ziploc bags in an environmental chamber (25 °C, 95 % RH, 16:8 h light:dark). Bags were checked weekly and scored based on whether a *Lipara* adult (identified to species), parasitoid, or predator emerged. Galls exhibiting pecking or chewing damage, and from which no *Lipara* emerged, were considered to have been successfully depredated by unidentified mammalian or avian predators. If no *Lipara* emerged, galls were dissected to confirm mortality.

From galls collected in the winter of 2013, *L. rufitarsis* was the only species reared in sufficient numbers to test differences in performance between native and invasive *P. australis* genotypes. We used dry body mass of emerged adults as a proxy for herbivore performance (see Taylor et al. 1998; Tammaru et al. 2002). For each patch with sufficient numbers, 10 male and 10 female *L. rufitarsis* adults were dried in an oven (60 °C for 48 h) and weighted to the nearest 0.1 mg using a Mettler microbalance. Ten individuals of each sex were used because single flies were too light to register an accurate measurement on the scale. Mean gall diameter (another measure of larval performance, see Stille 1984; McKinnon et al. 1999; Sopow and Quiring 2001) for each patch visited in the winter of 2013 was estimated from the average maximum diameter of 10 *L. rufitarsis* galls per patch (measured to the nearest 0.1 mm).

Stem height and flowering

For the most common gall species, *L. rufitarsis*, we assessed whether galled and non-galled stems differed in stem height and flowering frequency, and how this varied with *P. australis* genotype. At each NA patch visited during the winter of 2013 (11 native, 9 invasive, spanning the known range of *Lipara* in NA), the heights of 10 galled and 10 non-galled stems, randomly selected along the sampling transects, were measured to the nearest cm. In addition, flowering of non-galled stems was quantified at all sites where *Lipara* were present by examining 150 random stems along the sampling transects. All galled stems encountered (13 galls minimum, see Online Resource 2) were also scored for presence or absence of flowers.

Data analysis

We tested whether the *Lipara* infestation level (proportion of stems infested) per patch differed among the three phylogeographic groups, NA native (n = 12), NA invasive (n = 14), and EU native (n = 5). We only used sites where *Lipara* was present and the data were analysed using a one-way ANOVA in R version 3.0.3 (R Core Team 2014). The distribution of the proportions of stems infested with *Lipara* galls per patch was normalized using the logit transformation and pairwise differences among phylogeographic groups were assessed with a Tukey's test. To assess whether a particular *Lipara* species was driving differences in infestation levels we compared *Lipara* species composition between native and invasive *P. australis* genotypes in NA (composition data were unavailable for EU). To do this we calculated the infestation level of each individual *Lipara* species as the product of each species' proportional abundance (based on emergences from collected galls) and the proportion of stems infested by all *Lipara* species combined (from the field census). Infestation levels were compared between native (n = 12) and invasive (n = 14) patches for each *Lipara* species using a MANOVA with *P. australis* genotype as the categorical variable. The distribution of infestation levels was normalized using the logit transformation.

Predation by vertebrates was compared between *Lipara*-infested native (n = 11) and invasive (n = 10) *P. australis* patches in NA using a generalized linear model. Whether or not a gall was depredated was the dependent variable with a quasibinomial link function to account for overdispersion (McCullagh and Nelder 1989). *P. australis* genotype (native, invasive) was a fixed factor, and mean gall diameter and patch size were included as covariates in the model. The model was analyzed using R, which provided *t*-statistics as output. Gall size and patch size are known to influence natural enemies (e.g., Weis and Abrahamson 1986; Morrison et al. 2010, respectively) but have never before been tested with *Lipara*. We tested for a difference in predation success (the proportion of attacks resulting in the disappearance or death of *Lipara*) between native and invasive *P. australis* genotypes using a *t* test.

To assess whether adult *L. rufitarsis* body mass differed between *P. australis* genotypes (11 native, 9 invasive patches), we used a two-way ANCOVA in R. Genotype and *L. rufitarsis* sex were fixed factors in the model; the latter was included to account for possible sexual dimorphism within the species. Gall diameter was added as a covariate. Mean diameter of *L. rufitarsis* galls on native and invasive genotypes was also compared using a *t*-test as an additional performance measure.

To examine the potential impact of *L. rufitarsis* on *P. australis*, we tested if the mean height of galled stems was shorter than non-galled stems for both native and invasive genotypes (11 and 9 patches respectively) using *t* tests. The proportional reduction in stem height [= (galled − non-galled)/non-galled] was also compared between genotypes using a *t* test to examine if the mean reduction in stem height was greater for native or invasive *P. australis*. Finally, we calculated the impact of *Lipara* on sexual reproduction at each site as the product of flowering frequency of non-galled stems and the proportion of stems infested by *Lipara* (from the field survey). Because galled stems always failed to flower, this metric represents the proportional reduction in flowering due to the occurrence of galls. We compared *Lipara* impact on sexual reproduction between native (n = 12) and invasive (n = 14) genotypes using a *t* test.

Results

Lipara distribution and infestation level

Lipara were found only on the east coast of NA between latitudes of 36.5° and 43.8°, ranging from northern North Carolina to central Maine (Fig. 1). Galls were absent from all other locations. All three *Lipara* species were found to infest native and invasive *P. australis* genotypes. *L. rufitarsis* was the most widespread species, and the only species found south of New Jersey. *L. similis* increased in abundance in northern invasive patches and was the most dominant *Lipara* species in Massachusetts and Maine. *L. pullitarsis* was present in only five patches from New Jersey to Connecticut. In Europe, *Lipara* were present in all countries surveyed (Online Resource 1), ranging from Portugal (40.6°) to Norway (59.3°), but their overall distribution was patchy (present in only 5 of 21 patches surveyed).

Within the occupied range, the overall proportion of *P. australis* stems infested with *Lipara* differed significantly among NA native, NA invasive, and EU native patches ($F_{2,28} = 25.73$, $P < 0.001$, Figs. 2, 3a). In native *P. australis* patches, 32.0 ± 3.9 % (mean ± SE) of stems had a *Lipara* gall, which was three and 40 times higher than the infestation levels for NA invasive (10.6 ± 2.8 %) and EU native (0.8 ± 0.1 %) patches, respectively (Figs. 2, 3a, all comparisons $P < 0.001$). For the European genotypes, the proportion of stems with galls was over thirteen times higher in the invaded range compared to the native range ($P = 0.002$).

Lipara species composition differed significantly between native and invasive genotypes in NA when analysed using MANOVA (Wilks's Lambda $F_{3,22} = 3.87$, $P = 0.023$, Fig. 4). This difference in species composition was brought about by *L. rufitarsis*, which was over five times more abundant in native than invasive *P. australis* patches ($F_{1,24} = 12.04$, $P = 0.002$; Fig. 4). 92 ± 7.7 % of galls collected from native *P. australis* were identified as containing *L. rufitarsis*, compared to only 67 ± 20.8 % of the invasive *P. australis* galls. Infestation levels of *L. similis* ($F_{1,24} = 0.08$, $P = 0.782$) and *L. pullitarsis* ($F_{1,24} = 0.01$, $P = 0.946$) did not differ significantly between native and invasive *P. australis* genotypes (Fig. 4).

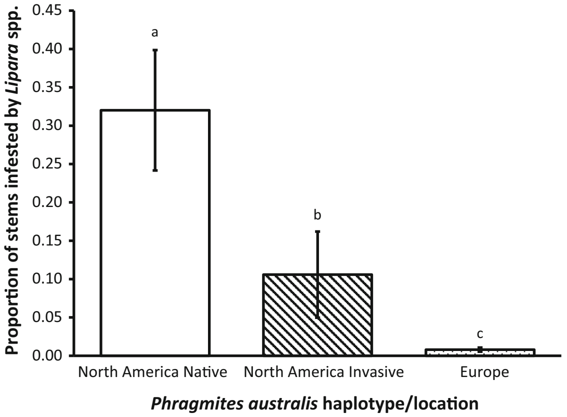

Fig. 2 Mean proportion of stems infested by *Lipara* (±95 % CI) in North American native, North American invasive, and European *Phragmites australis* patches. Different letters indicate significant differences between genotype means ($P < 0.05$)

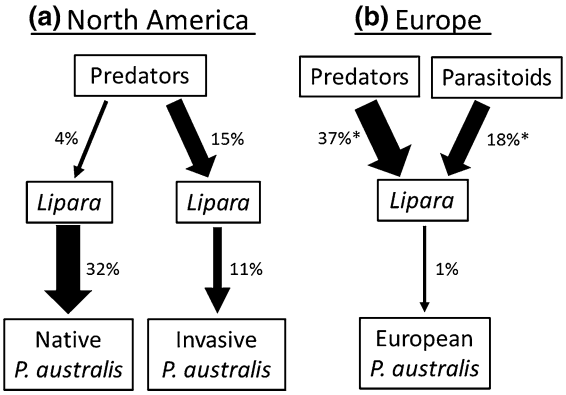

Fig. 3 Schematic diagram illustrating biotic interaction strengths between *Phragmites australis*, *Lipara*, and predators/parasitoids of *Lipara* in North America and Europe, at sites where *Lipara* were present. Parasitoids were absent in North America. Arrow thickness represents the strength of each interaction, which is also shown by the percentage beside each line (i.e., % of *Lipara* galls depredated or parasitized; % of *P. australis* stems infested by *Lipara*). *Predation and parasitism of *Lipara* in Europe is based on an overall average of 25 data points collated from Abraham and Carstensen 1982; Athen and Tsharntke 1999; Tscharntke 1994; Schwarzlander and Hafliger 2000; Reader 2001, 2003 (Online Resource 4)

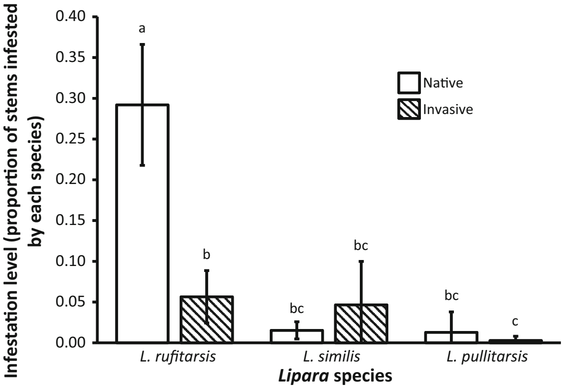

Fig. 4 Mean proportion of collected stems inhabited by each *Lipara* species (±95 % CI) in North American native and invasive *Phragmites australis* patches. *Different letters* indicate significant differences between means ($P < 0.05$)

Lipara parasitism and predation

Of the 1663 NA galls inspected, we found no evidence of mortality from arthropod parasitoids or predators. In contrast, vertebrate predators successfully attacked 14.8 ± 6.2 % of *Lipara* galls on the invasive genotype and 3.5 ± 2.6 % of galls on native genotypes, however this fourfold difference was non-significant ($t = -0.75$, $P = 0.464$, Figs. 3a, 5a). Gall diameter ($t = -0.68$, $P = 0.684$) and patch size ($t = 0.21$, $P = 0.837$) were not related to the successful predation level. Not all attacked galls (as evidenced by pecking or chewing damage) resulted in the death of the *Lipara* inhabitant. Seventy ± 22.7 % of attacks on galls of invasive genotype and 66 ± 32.3 % of attacks on native genotypes resulted in the disappearance or death of *Lipara*; a difference that was non-significant ($t_{13} = -0.21$, $P = 0.840$).

Lipara performance

Dry body mass of *L. rufitarsis* adults was 13 % higher for individuals reared from native than invasive genotypes, but this result was non-significant ($F_{1,35} = 0.95$, $P = 0.337$). Female *Lipara* (2.6 ± 0.2 mg) weighed almost twice as much as males (1.4 ± 0.1 mg) ($F_{1,35} = 197.34$, $P < 0.001$). A marginally significant positive correlation between the covariate gall diameter and body mass was detected ($F_{1,35} = 3.48$, $P = 0.071$, Fig. 5b). If we removed gall diameter as a covariate in the model, genotype also became significant ($F_{1,36} = 7.00$, $P = 0.012$) suggesting that differences in *Lipara* performance between genotypes is due to the effects of genotype on gall size. *L. rufitarsis* galls were 34 % larger on the native than invasive genotypes ($t_{18} = 5.75$, $P < 0.001$, Fig. 5b).

P. australis stem heights and flowering

Stems of the invasive *P. australis* genotypes with a *L. rufitarsis* gall were 55 ± 6.6 % shorter than non-galled stems ($t_{10} = 7.82$, $P < 0.001$). In comparison, native stems with galls were 30 ± 6.3 % shorter than

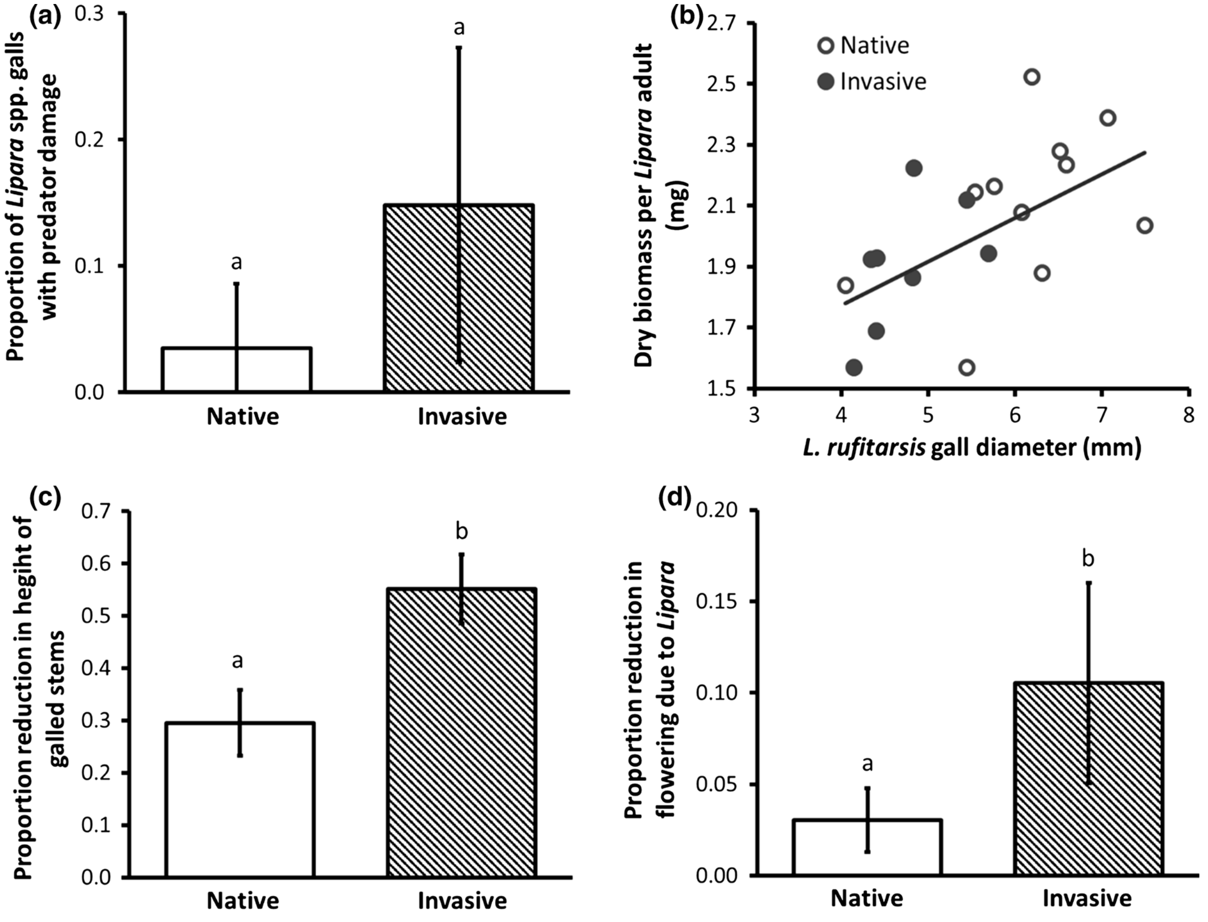

Fig. 5 For native and invasive *Phragmites australis* genotypes in North America, the **a** proportion of *Lipara* galls attacked by mammal or bird predators; **b** relationship between gall diameter and dry body mass of *L. rufitarsis*; **c** proportional reduction in height of stems infested by *L. rufitarsis*; and **d** proportional reduction in flowering frequency due to *L. rufitarsis*. Reported are the means ± 95 % CI per patch. *Different letters* indicate significant differences between genotype means ($P < 0.05$)

non-galled stems ($t_8 = 10.59$, $P < 0.001$). The degree of reduction in stem height when a gall was present was significantly greater for the invasive than native genotype ($t_{16} = 5.53$, $P < 0.001$, Fig. 5c). No galled stems were observed to have flowered. Invasive *P. australis* genotypes suffered a 10.5 ± 2.7 % reduction in flowering due to *Lipara*, almost 3.5 times greater than the 3.0 ± 0.9 % reduction suffered by native genotypes ($t_{24} = -2.43$, $P = 0.023$, Fig. 5d). However, flowering of non-galled stems was over twofold higher in patches of invasive than native genotypes ($t_{24} = -3.03$, $P = 0.006$).

Discussion

Despite a recent increase in the number of studies involving multi-species introductions into the same community (e.g., Rand and Louda 2004; Lau and Strauss 2005; Dangremond et al. 2010; Green et al. 2011; Stricker and Stiling 2012), our understanding is still limited as to how species interactions change between the native and introduced ranges and the potential implications for invaded native communities. With invasive species expected to become more prevalent (Levine and D'Antonio 2003), it is also likely that trophic interactions involving multiple introduced species will become commonplace. The tritrophic interactions between *P. australis*, *Lipara* spp. and their natural enemies in EU and NA are summarized in Fig. 3. Support for our first prediction varied regionally; *P. australis* was released from *Lipara* throughout most of NA (Fig. 1), but our study also showed that along the Atlantic coast the attack of invasive *P. australis* by introduced *Lipara* species was higher in the novel than ancestral range. Escape from their predators and parasitoids in the introduced range likely allowed *Lipara* to achieve higher infestation levels (proportion of stems infested) in NA than EU, supporting our third prediction of enemy-release for the gall-forming herbivores. In the novel range, we found that invasive *P. australis* suffered lower attack from the introduced *Lipara* than closely related native *P. australis*, supporting the local enemy-release hypothesis and our second prediction. Such a result is likely due to a lack of coevolutionary history between native *P. australis* and introduced *Lipara*, but native predators that cause higher mortality of *Lipara* on invasive plants could also contribute to the difference in herbivory between native and invasive plants in the novel range. Our study points to the complex interactions that arise when two or more interacting species are introduced into a novel environment, and that a multitrophic framework is required when investigating the influence of biotic interactions on invasion success.

The enemy inversion hypothesis posits that the effects of introduced herbivores on invasive plants may be reduced or even reversed due to novel interactions in their new environment (Pearson et al. 2000; Pearson and Ortega 2002; Colautti et al. 2004). Our study did not support this prediction. *Lipara* herbivory on European genotypes of *P. australis* was over thirteen times higher in their introduced range (NA) in comparison to their native range (EU). We postulate that the higher infestation level in NA found in our study may be driven by classical enemy-release of *Lipara* from their EU arthropod predators and parasitoids. The total absence of parasitism in our sampled galls provides stark contrast to parasitism rates in EU previously reported to be 15–26 % for *L. rufitarsis* (Reader 2001, 2003; Tscharntke 1994), 22 % for *L. similis* (Schwarzlander and Hafliger 2000; Tscharntke 1994), 0–59 % for *L. pullitarsis* (Abraham and Carstensen 1982; Athen and Tsharntke 1999; Tscharntke 1994), and averaging 18 % across all *Lipara* species and studies (Fig. 3b, Online Resource 4). Moreover, Nartshuk (2006) reported 33 parasitoid species attacking galls of these *Lipara* species in EU. We found no evidence that any of these natural enemies of *Lipara* have been introduced to NA, nor does it seem that native parasitoids have incorporated these novel prey into their host range. Furthermore, predation on *Lipara* galls by unidentified mammalian or avian predators on the invasive and native *P. australis* genotypes in NA was over two and nine times lower, respectively, than found for *Lipara* galls in EU where the attack rate averaged 37 % across 3 years (Reader 2001).

Based on our study, the distribution of *Lipara* in NA is restricted to the Atlantic coast from North Carolina to Maine. This finding expands the known range of *Lipara*, previously reported as far south as New Jersey (Tewksbury et al. 2002). Moreover, unpublished reports by experts on *P. australis* (Rohal and Hazelton, pers. comm.) suggest that *Lipara* (species as yet unidentified) are present in Utah. Given the vast area that *P. australis* covers in NA, it is no surprise that

Lipara has recently begun appearing in isolated areas further west of its site of arrival on this continent, potentially facilitated by the spread of the invasive genotype. Interestingly, contrary to the report by Blossey (2003), we did find *L. pullitarsis* infesting stems of native *P. australis* genotypes. No *Lipara* were found at any of the surveyed patches north of Yarmouth, Maine (43.8°) (Fig. 1; see also Lambert et al. 2007). However, *Lipara* (species unidentified) were present in Norway during our European survey at a latitude of 59.3° and are common at high latitudes (Chvala et al. 1974). This distribution suggests *Lipara* may be able to tolerate colder conditions and that their current northern distribution in NA might not be limited by physiological tolerances. In contrast, physiological tolerances may be limiting the southern extent of *Lipara* in NA. A single *L. similis* observation in Israel (approximately 31.7°) (Nartshuk 1984) is the only location worldwide in which *Lipara* has been reported further south than our North Carolina patches (36.5°), suggesting that *Lipara* may not be tolerant of hotter climates, such as the Gulf Coast region or southwestern United States.

Lipara appear to have considerable impact on *P. australis* sexual reproduction and growth in NA; flowering of infested stems was zero regardless of genotype, suggesting a strong negative effect of *Lipara* on sexual reproduction of infested stems, which is important to the spread of *P. australis* (Brisson et al. 2008; McCormick et al. 2010). *Lipara* reduced flowering by 10.5 % for the invasive genotype and 3.0 % for native genotypes, a difference of over threefold. Furthermore, heights of *L. rufitarsis*-infested stems of native and invasive genotypes were also 30 and 55 % shorter than non-galled stems, respectively (see also Lambert et al. 2007). At present, it is unknown whether *L. rufitarsis* caused reductions in stem height, or if ovipositing females simply selected stems predisposed to achieving shorter heights. Some support is provided for the latter, as *L. rufitarsis* prefer stems with a small basal diameter (De Bruyn 1993, 1994; Tscharntke 1994), a trait strongly correlated with stem height (Reader 2001). Long-term effects of *Lipara* and other herbivores on the population-level response of native and invasive *P. australis* genotypes are currently unknown and should be a focus of future research efforts, particularly for potential biological control agents.

We found support for local enemy-release of invasive *P. australis* in the introduced range relative to co-occurring native genotypes. Native *P. australis* genotypes suffered threefold greater herbivory from *Lipara* than co-occurring invasive genotypes in NA, which was attributed to a fivefold greater infestation level of *L. rufitarsis* in native compared to invasive patches. The pattern of higher herbivory of native genotypes was consistent with previous studies of three native *P. australis* patches from the northeastern United States (Lambert et al. 2007; Park and Blossey 2008) and is consistent with findings involving other invasive species (e.g., Dietz et al. 2004; Parker and Gilbert 2007; Cincotta et al. 2009; Funk and Throop 2009; Zheng et al. 2012). Cronin et al. (2015) also found that native *P. australis* genotypes in NA suffered greater herbivory from the entire guild of internal feeding herbivores than the invasive genotype, and the same pattern was observed for the widespread and abundant non-native aphid, *Hyalopterus pruni,* and all chewing herbivores combined. These results suggest that native *P. australis*-inhabited marshes are susceptible to invasion by *Lipara* and possibly other introduced herbivores. Although invasive *P. australis* suffers lower herbivory compared to native genotypes, this does not fit within the strict definition of enemy-release or biotic-resistance, because *Lipara* are also introduced to NA. However, the ecological implications of such a pattern on invasion success are the same—an advantage to the invasive plant in its novel range. We suggest that the conceptual framework of enemy-release and biotic-resistance be expanded to also include the effects of introduced herbivores, and that further studies are needed examining novel communities inhabited by multiple interacting native and introduced species.

We offer several possible explanations for why *Lipara*, and possibly other introduced herbivores of *P. australis*, are responsible for greater levels of herbivory on native than invasive genotypes in NA. First, the difference in infestation levels could be explained by the influence of higher trophic levels (i.e., natural enemies; see Fig. 3). We found higher levels of predation by vertebrates on galls of the invasive genotype (14.8 %) relative to galls of native genotypes (3.5 %). While this difference was not statistically significant, the large effect size suggests *Lipara* feeding on native genotypes may be released from top-down pressure, whereas invasive *P. australis* may benefit from greater top-down control of herbivores (i.e., a trophic cascade; see Fig. 3). To our knowledge, this study is the first to show that higher trophic levels may impact invasion success in this manner. Second, the invasive genotype has coevolved with *Lipara* in EU and Asia and may therefore have evolved resistance to attack by *Lipara*. In contrast, *Lipara* have only recently been introduced to NA and native genotypes have had little time to adapt defenses to these novel herbivores. For example, the putative defense trait of leaf toughness is greater in invasive than native *P. australis* genotypes (Cronin et al. 2015). Such coevolved plant–herbivore interactions provide bottom-up control of native herbivores, but may allow for outbreaks of newly-associated introduced herbivores (Desurmont et al. 2011; Gandhi and Herms 2009). Thus, a lack of a coevolutionary history with *Lipara* could result in a lack of specialized defenses with which native *P. australis* genotypes can resist infestation. Furthermore, differences in palatability or nutritional quality may contribute to the difference in herbivory between native and invasive *P. australis* genotypes. Gall diameter and body mass, often indicators of host nutritional quality (e.g., Stille 1984; Taylor et al. 1998; McKinnon et al. 1999; Sopow and Quiring 2001; Tammaru et al. 2002), were 34 % and 13 % higher, respectively, on native than invasive genotypes. Third, previous studies have shown that *L. rufitarsis* is more commonly found infesting *P. australis* shoots with a thin basal diameter (De Bruyn 1993, 1994; Tscharntke 1994). The typically thinner stems of the native genotypes (Lambert et al. 2007) may predispose them to attack by *L. rufitarsis*.

The pattern of greater herbivory on native than invasive genotypes of *P. australis* in NA is emerging as a common phenomenon across multiple species and guilds of introduced herbivores (this paper; Lambert et al. 2007; Lambert and Casagrande 2007; Park and Blossey 2008; Cronin et al. 2015; but see Saltonstall et al. 2014). This trend suggests that *Lipara* and perhaps other herbivore species may be involved in an invasional meltdown (Simberloff and Von Holle 1999), the process whereby multiple invasive species facilitate one another's spread or exacerbate their impact on native species. Invasive plant species have been shown to facilitate the growth and spread of introduced herbivore populations, leading to negative effects on closely related native plant species via apparent competition (Colautti et al. 2004; Rand and Louda 2004; Lau and Strauss 2005; Dangremond et al. 2010; Lambert and Dudley 2014). Likewise, introduced generalist herbivores can also indirectly facilitate the growth and spread of invasive plant species by preferentially feeding on their native competitors (Parker et al. 2006; Relva et al. 2010). An alternative outcome is invasional antagonism, where invasive species inhibit one another through competition (Belote and Weltzin 2006) or herbivory (La Pierre et al. 2010; Stricker and Stiling 2012). In the situation of *P. australis*, despite the impact of *Lipara* on sexual reproduction, it is unlikely that *Lipara* are limiting the spread of invasive *P. australis* due to the plant's rapid clonal growth, high stem density, and greater biomass and flowering frequency relative to native genotypes (see Mozdzer et al. 2013 for review). However, the sheer pervasiveness of the invasive genotypes combined with the escape from parasitoids that *Lipara* has experienced in NA has possibly facilitated the spread of these herbivores to the relatively rare native *P. australis* genotypes. A key research need is to determine effects of herbivory on competitive outcomes among invasive and native genotypes at the population level, and if the higher relative level of herbivory experienced by native genotypes is contributing to their decline and disappearance in eastern NA.

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