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LETTER

Coexistence between native and exotic species is facilitated by asymmetries in competitive ability and susceptibility to herbivores

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Abstract

Differences between native and exotic species in competitive ability and susceptibility to herbivores are hypothesized to facilitate coexistence. However, little fieldwork has been conducted to determine whether these differences are present in invaded communities. Here, we experimentally examined whether asymmetries exist between native and exotic plants in a community invaded for over 200 years and whether removing competitors or herbivores influences coexistence. We found that natives and exotics exhibit pronounced asymmetries, as exotics are competitively superior to natives, but are more significantly impacted by herbivores. We also found that herbivore removal mediated the outcome of competitive interactions and altered patterns of dominance across our field sites. Collectively, these findings suggest that asymmetric biotic interactions between native and exotic plants can help to facilitate coexistence in invaded communities.

Keywords

Biodiversity, conservation, diversity, extinction, invasion, invasive species, non-native, plant insect interaction, predation, trade-off.

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INTRODUCTION

Plant invasions are a nearly ubiquitous feature of the modern world, as all regions of the globe and most local communities contain exotic plant species (Lonsdale 1999; Sax & Gaines 2003). While exotic plants can have significant impacts on the structure and function of ecosystems (Chapin *et al.* 1997; Vilà *et al.* 2011), their role in causing extinctions is less certain. At global and regional scales, there is little evidence to suggest that plant-mediated extinctions of other plants are a common consequence of invasions (Davis 2003; Sax & Gaines 2003, 2008). At local scales, extirpation of native plants as a consequence of exotic plant invasions are likely to be a more common outcome (Hejda *et al.* 2009; Vilà *et al.* 2011), but detailed studies often fail to find evidence that this has occurred (e.g. Mills *et al.* 2009). In most communities, invasions took place before detailed ecological records were collected, so it is difficult to know how native diversity may have changed following invasions (Sax & Gaines 2003; Thomaz *et al.* 2012). What is clear, however, is that coexistence between natives and exotics is common at both local and regional scales in plant communities worldwide (Lonsdale 1999; Stohlgren *et al.* 1999) and that this coexistence has often occurred over decades or centuries (Sax & Gaines 2008; Heard *et al.* 2012). In spite of the commonness of long-term coexistence between natives and exotics, the mechanisms facilitating this remain largely unresolved (Adler 1999; Shea & Chesson 2002; MacDougall *et al.* 2009). Examining the mechanisms by which natives and exotics coexist can therefore provide an important means by which to advance ecological understanding.

Trade-offs or asymmetric differences in functioning among species can facilitate coexistence (Grime 1979; Huston 1994; Chesson 2000; Chase & Leibold 2003; Kneitel & Chase 2004; Adler *et al.* 2010; Knapp & Kühn 2012) and such trade-offs may explain native and exotic coexistence in invaded communities (Adler 1999; Daehler 2003; Stachowicz & Tilman 2005). Both theoretical and empirical research suggests that coexistence in invaded communities is most likely when exotics are differentiated from native species, i.e. they exhibit functional or niche differences (Shea & Chesson 2002; Chase & Leibold 2003; MacDougall *et al.* 2009). Indeed, this work is entirely consistent with longstanding views on the importance of differentiation among species in promoting coexistence (e.g. Hutchinson 1959). More specifically, fundamental trade-offs in species characteristics, such as those between growth rates and investment in herbivore defenses (Coley *et al.* 1985), could be important in understanding coexistence between native and exotic plant species. As a group, exotic species are often competitively superior to natives (Blossey & Notzold 1995; Levine *et al.* 2003; Vilà *et al.* 2011). In contrast, and contrary to the expectations of the enemy release hypothesis (Crawley 1987), recent experiments and meta-analyses show that exotic plant species are typically more, not less, impacted by herbivores than are natives (Agrawal & Kotanen 2003; Parker *et al.* 2006; Chun *et al.* 2010). While these asymmetries in competitive ability and herbivore susceptibility are well established, little empirical work has been done to examine whether they facilitate coexistence in invaded plant communities (but see HilleRisLambers *et al.* 2010). Instead, most empirical studies have focused on either competitive ability or herbivore susceptibility, but not both (e.g. Agrawal *et al.* 2005). Empirically examining both factors together could yield surprises, as theoretical modeling suggests that there may be significant interactions between competition and herbivory that impacts native and exotic species' coexistence (Adler 1999; Adler *et al.* 2010; Orrock *et al.* 2010).

While empirical studies that simultaneously examine the influence of competition and herbivore susceptibility could advance our understanding of coexistence between native and exotic species, there are several reasons why such studies are uncommon. First, the motivation for conducting such studies is greater in communities where there is evidence that natives and exotics have coexisted over time, but long-term records of invaded communities are uncommon (Strayer *et al.* 2006). Second, the utility of such studies is limited unless the entire community can be manipulated, because without whole system manipulation it is difficult to determine the relative strength of competition, predation, and their interactive effects (Gurevitch *et al.* 2000; Chase *et al.* 2002; HilleRisLambers *et al.* 2010). Finally, whole system manipulations are difficult in most systems since plant herbivory often manifests through diffuse predatory guilds of insects, vertebrates, and pathogens (Ritchie & Olff 1999). As a result, invasion biologists and ecologists have been challenged to find systems in which to experimentally study the drivers of native and exotic coexistence.

One habitat type where we can overcome the aforementioned limitations is the strandline plant community. These communities are found along beaches, where they occur between intertidal and terrestrial zones, are strongly influenced by disturbance, and have been invaded by numerous exotic species over time (Heard *et al.* 2012). In particular, the strandline plant communities of Narragansett Bay (in Rhode Island and Massachusetts, USA) are a model system for examining native and exotic coexistence for several reasons. These communities have been invaded by numerous exotic plant species, making them comparable to plant communities worldwide (Lonsdale 1999; Maron & Vila 2001). Further, high-resolution surveys of these communities over the last decade (1998–2009) show that despite increases in exotic richness and cover at sites over time, native species richness and cover have not significantly declined, indicating that native and exotic species are coexisting within these communities (Heard *et al.* 2012). Finally, these communities are easy to manipulate, as the majority of plants are herbaceous annuals and perennials (Heard *et al.* 2012) and herbivory is primarily driven by insects (Heard personal observation).

In this study, we examine the hypothesis that trade-offs between native and exotic species in competitive ability and herbivore susceptibility affect species coexistence in invaded plant communities. Specifically, we tested the hypothesis that exotic species are more susceptible to herbivores, but competitively superior to natives and that this trade-off facilitates coexistence. We tested this hypothesis using a combination of observational and experimental field studies. We predicted that there are significant interactions between herbivory and competition and that suppression of competitors and/or herbivores would reduce native and exotic coexistence.

MATERIALS AND METHODS

Study site

This study was conducted in the strandline plant communities of Narragansett Bay, Rhode Island and Massachusetts. Narragansett Bay is the largest estuary in New England, with over 412 km of shoreline and a surface area of *c.* 380 km^2. Strandlines are common, highly heterogeneous, terrestrial plant communities with substrates ranging from course sand to cobble stones. They have similar vegetation and physical properties to foredune and shingle beach communities (Heard *et al.* 2012).

Observational study design

We conducted three observational field surveys to determine if there were differences in the rates and magnitude of insect herbivory on native and exotic plants. First, to determine the overall mean frequency of herbivory on native and exotic plant species we conducted a broad-scale field survey across 24 strandline plant communities (Fig. S1) in July 2009 and July 2010, at the time of peak biomass. At each site, we established a 100 m transect parallel to the shoreline along which we placed 10–1 m^2 quadrats at 10 m intervals (five above and five below the transect line). Within each quadrat, we recorded the number of individuals of each plant species present. We also recorded the number of individuals from each species (101 species in total) that showed any sign of herbivory damage (i.e. leaf mining scars, chew marks, leaf scrapes, and missing portions of the leaf). We calculated the mean frequency of herbivory across our sites for native species as a group, by dividing the total number of individuals of any native species with signs of herbivory by the total number of individuals of native species observed; we calculated the frequency of herbivory in exotic species in the same way.

Second, we compared rates of herbivory over time for six pairs of native and exotic species (Table 1). We used con-generic and con-familial pairs in our analyses to compare damage between species that were closely related, but had different geographic origins (Agrawal & Kotanen 2003; Agrawal *et al.* 2005). We selected these particular native-exotic pairs because they were the only ones prevalent across our field sites. Herbivory rates for each species-pair were examined at two sites where both species were present. At each site, 20 individuals of each species were randomly selected in early June of 2009 and 2010, and observed repeatedly *c.* every two weeks until the end of July. For each individual plant, one leaf was randomly selected and tracked for herbivore damage (i.e. each leaf was scored for whether it showed signs of herbivory impacts, as described above) – a protocol modified from Cappuccino & Carpenter (2005).

Third, we quantified percentage of leaf-area damaged by insect herbivores for each of the 12 species comprising our species-pairs. We did this by harvesting each leaf that was tracked from the individuals described above, plus an additional three leaves randomly

Table 1 Six pairs of con-generic and con-familial native and exotic species used for herbivory and competition studies. All pairs of species were used for herbivory studies, but only pairs 1–3 were used for competition studies. C : N indicates mean carbon-to-nitrogen ratios for species. Herbivory frequency indicates mean frequency of herbivory per species found across sites. Leaf area consumed indicates mean percentage of leaf area eaten per species found across sites

Pair #	Family	Native	C : N in leaves	Herbivory frequency (%)	Leaf area consumed (%)	Exotic	C : N in leaves	Herbivory frequency (%)	Leaf area consumed (%)
1	Chenopodiacae	Atriplex prostrata	14.2	42.5	3.2	Chenopodium album	11.4	80.0	18.1
2	Brassicaceae	Cakile edentula	13.9	59.0	24.6	Raphanus raphinistrum	11.9	100.0	26.3
3	Asteraceae	Solidago sempervirens	21.4	65.0	4.9	Lactuca serriola	19.6	95.0	30.0
4	Rosaceae	Rosa carolina	32.4	52.5	8.3	Rosa rugosa	23.6	87.5	29.7
5	Asteraceae	Ambrosia artemisifolia	24.0	57.5	4.2	Artemisia vulgaris	9.4	97.5	20.3
6	Fabaceae	Lathryus maritimus	9.6	52.5	7.1	Melilotus alba	11.9	95.0	31.3

selected from each of these individual plants ($n = 160$ leaves/species). All leaves were harvested at the end of our herbivory monitoring study in the first week of August. We then visually scored each leaf for percent leaf-area removed by herbivores to the nearest 10% (Agrawal & Kotanen 2003; Agrawal *et al.* 2005).

We also examined differences in Carbon-to-Nitrogen (C : N) ratios within the six pairs of native and exotic species. Differences in these ratios between native and exotic plants may provide an important basis for differentiation in competitive abilities (i.e. growth over time) and leaf-area consumed (Agrawal & Kotanen 2003; Mediavilla & Escudero 2003; Agrawal *et al.* 2005; Leishman *et al.* 2007). We conducted this work using the leaves on which we assessed the magnitude of herbivory damage, allowing us to examine the relationship between leaf-area consumed and C : N ratios. All C : N ratios were determined using elemental combustion in the Brown University Environmental Chemistry Laboratory for Environmental Studies.

Experimental study design

We performed a field experiment to determine if there were differences in the competitive ability of native and exotic plants, which we approximated by comparing differences in plant growth rates (i.e. changes in percent cover over time). A factorial competition experiment was run in 2009 and 2010 for three of the six pairs of native and exotic species (Table 1). We used these three pairs because they were the only ones abundant enough across field sites to allow for sufficient replication. In 2009, there were four experimental treatments: (1) removal of all species within 30 cm of the focal plant, (2) removal of all native species within 30 cm of the focal plant, (3) removal of all exotic species within 30 cm of the focal plant and (4) removal of no species within 30 cm of the focal plant (control plots). Removal of plants, by weeding, was conducted at the beginning of June and repeated weekly until monitoring ceased at the end of August. The response of each focal plant was measured as change in percent cover of a 0.5 m^2 plot over time. In 2009, the six focal species were each studied at three sites, and at each site the four treatments were replicated six times ($n = 432$). In 2010, we conducted the same experiment, but added four additional treatments to examine how insect herbivory altered plant performance. These treatments were identical to those described above, except that we applied insecticide (2–3 mL of 2% Talstar solution) weekly to each plot. Each of the eight treatments in this study were replicated five times at each of sites where these species were studied ($n = 720$).

In addition to examining species pairs, we also examined competitive interactions between native and exotic species in the broader community over the 2010 growing season in the presence and absence of herbivores. At six field sites, we established a 150 m transect parallel to the shoreline along which we placed 15–1 m^2 quadrats at 10 m intervals. We randomly selected 5 of these 15 quadrats as herbivore removals and applied an insecticide spray weekly (2–3 mL of 2% Talstar solution) to suppress insect herbivory, leaving the remaining 10 quadrats as controls. Within both control and experimental plots, we measured species identity and percent cover every two weeks from May through August 2010.

Statistical analyses

We used analyses of variance (ANOVA) to examine the frequency and magnitude of herbivory across sites, chi-squared tests to compare the total number of field sites where the mean frequency of herbivory damage on exotics was higher than on natives, and repeated measures analysis of variance (rm ANOVA) to evaluate changes in the frequency of herbivory over time. We used Monte Carlo simulations ($n = 1000$) to randomly separate species into two distinct groups to examine the possibility that differences in herbivory between natives and exotics would be likely to occur between randomly separated groups of species.

We used ANOVA to determine if there were significant differences in mean C : N ratios for native and exotic species. We used linear regression to determine if C : N ratios in individuals correspond with the total amount of leaf area eaten. Linear regression analyses were conducted separately for natives, for exotics, and for all species combined; we also determined these relationships for each individual species examined.

We used ANOVA and *post-hoc* Tukey analyses to examine native and exotic performance between treatments in the competition experiments. We compared the interactive effects of herbivory and competition on native and exotic species within our weeding study using factorial ANOVA and interactive diagrams (Gurevitch *et al.* 2000). We calculated the overall effect size and relative importance of both competition and herbivory for native and exotic species (Gurevitch *et al.* 2000; Chase *et al.* 2002). We also examined changes in the ratio of exotic-to-native richness and cover over time in observational and experimental plots (Heard *et al.* 2012) with rm ANOVA.

All analyses were carried out in R 2.10.1 (R Foundation for Statistical Computing, Vienna, Austria) and JMP version 8 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Herbivory on native and exotic plants

In our survey of species present across 24 field sites, the mean frequency of herbivory was *c.* two times higher for exotic species than natives in both 2009 and 2010 (Fig. 1). At individual sites, the frequency of herbivory was higher across exotic species than native species at 22 of 24 sites in 2009 ($\chi^2 = 16.667$, $P < 0.0001$) and 23 of 24 sites in 2010 ($\chi^2 = 20.167$, $P < 0.0001$). These differences in average frequency of herbivory between native and exotic species were unlikely to occur as a consequence of randomly splitting all species found across sites into two random groups, as Monte Carlo simulations revealed that differences in frequency of herbivory between these two random groups were not significantly different ($t = 0.09$, $P = 0.9342$).

In our comparison of six pairs of con-generic and con-familial native and exotic species, we found that frequency of herbivory and leaf-area consumed were always greater on the exotic member of a species pair (Table 1). These differences were apparent not just at the end of the season, but also over the course of growing season in both 2009 and 2010 (Fig. 2a, b). By the end of the growing season, among those leaves with herbivory damage, the average leaf-area consumed was more than twice as high on exotics than natives (Fig. 2c). The differences in frequency of leaves with damage together with percentage of leaf-area removed on damaged leaves combine to produce nearly an order of magnitude difference in the net fraction of total leaf material removed between exotics (24.6%) and natives (3.4%).

C : N ratio in native and exotic plants

Comparisons of C : N ratios in leaves of the six pairs of native and exotic species indicate that C : N ratios are significantly

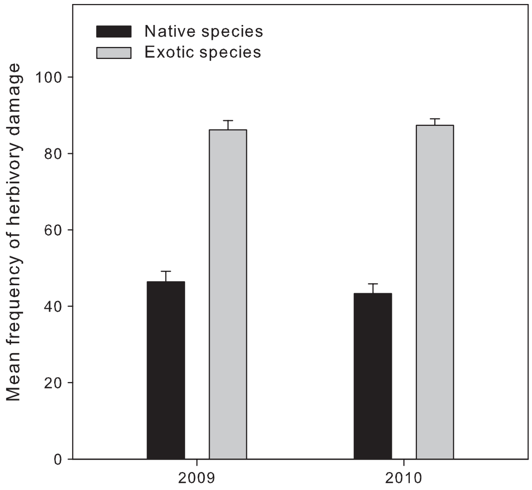

Figure 1 Mean frequency of herbivory on plants across 24 sites was approximately two times higher on exotic than native species in 2009 ($F_{1,46}$ = 112.8, $P < 0.0001$) and 2010 ($F_{1,46}$ = 205.8, $P < 0.0001$).

higher for natives than exotics (Fig. 3a). We also found significant negative relationships between the total amount of leaf area eaten and C : N ratios among the six native species (Fig. 3b), among the six exotic species (Fig. 3c), and among all 12 species ($R^2 = 0.33$, $P < 0.0001$). Most species showed qualitatively similar patterns of variation among individual plants, with negative trends between C : N ratios and leaf-area consumed observed for 11 of 12 species (Fig. S2).

Effects of competition and herbivory on native and exotic plants

In our weeding and herbivory suppression experiments with three pairs of species we found both similarities and differences in native and exotic responses to treatments. When all competitors were removed and herbivory was not suppressed, both natives and exotics responded similarly, by showing a significant reduction in percent cover relative to plots were competitors were retained (Fig. 4a, d). In contrast, when all competitors were removed and herbivory was suppressed then natives, but not exotics, showed a marginally significant increase in percent cover relative to plots were competitors were retained (Fig. 4a, d). In plots where only native competitors were removed, but exotic competitors were retained, both natives and exotics showed no significant changes in cover relative to plots were native competitors were retained; this was the case regardless of whether herbivores were suppressed (Fig. 4b, e). In plots where exotic competitors were removed, but native competitors were retained, and herbivores were suppressed, natives showed increases in percent cover relative to plots were exotic competitors were retained (Fig. 4c). In contrast, in plots where exotic competitors were removed, native competitors were retained, and herbivores were not suppressed, natives, but not exotics, showed significant increases in percent cover relative to plots were exotic competitors were retained (Fig. 4c, f). Effect size estimates, examining the relative importance of competition and herbivory, also showed that there were significant interactions between competition and herbivory (Fig. S3). Finally, results of removing competitors in the presences of herbivores were quantitatively similar in 2009 and 2010 (Fig. S4).

In our examination of native and exotic richness and cover across quadrats, where all species present were examined, we found that the fate of native relative to exotic species was mediated by the presence or absence of herbivores. In particular, we found that suppression of insect herbivores selectively favored exotic species and significantly increased the exotic-to-native ratios of richness and cover over the course of the growing season (Fig. 5). In contrast, in the presence of herbivores, the richness and cover of native and exotic species was relatively stable over the course of the growing season (Fig. 5).

DISCUSSION

We found strong asymmetries in competitive ability and herbivore susceptibility between native and exotic species in our experiments and observational studies. Among our paired focal species, remov-

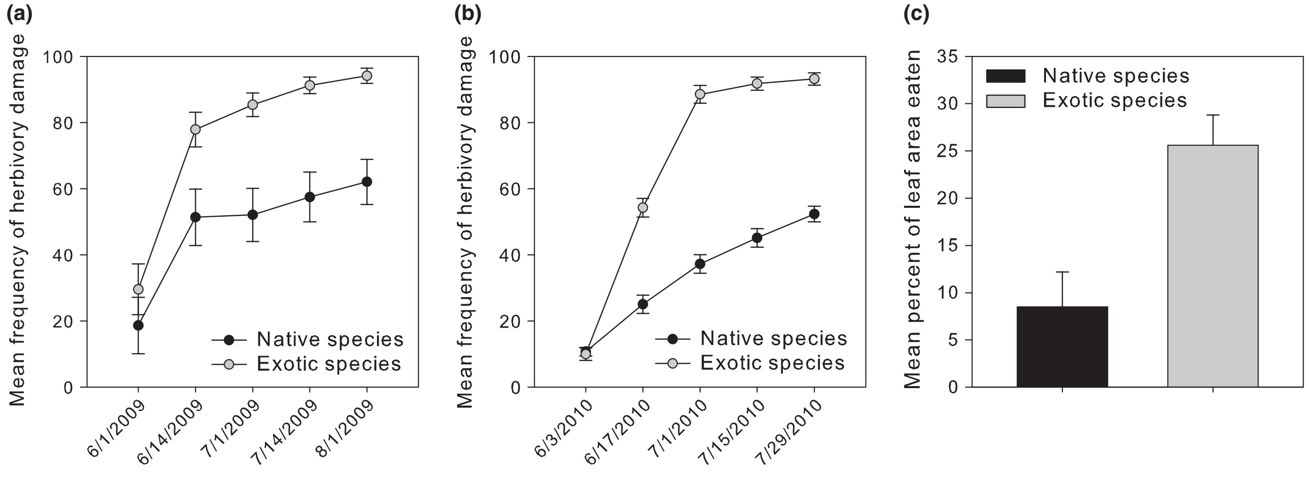

Figure 2 Variation in the frequency of herbivory and mean leaf area consumed between six con-generic and con-familial pairs of native and exotic species. (a, b) The mean frequency of herbivory between natives and exotics was similar early in each growing season, became differentially greater on exotics relative to natives over the course of each season, and was significantly different by the end of each season – 2009 ($F_{1,10}$ = 22.6, $P < 0.0001$) and 2010 ($F_{1,10}$ = 43.4, $P < 0.0001$). (c) The mean percentage of leaf area removed by the end of the growing season was almost four times higher on exotics than natives in 2009, in 2010, and when the years were combined, as shown here ($F_{1,11}$ = 18.8, $P = 0.0015$).

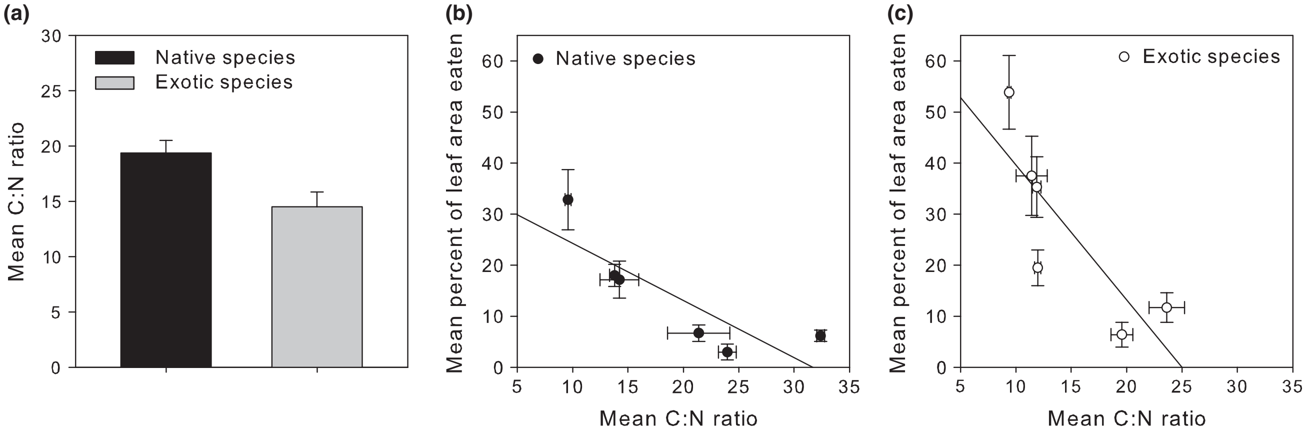

Figure 3 Variation in mean C : N ratios between six con-generic and con-familial pairs of native and exotic species and their relationship with the total percentage of leaf area eaten. (a) C : N ratios were significantly higher for native than exotic species, indicating that exotic leaves had proportionately higher nitrogen levels ($F_{1,68} = 7.5$, $P = 0.0078$). (b,c) Mean C : N ratios were negatively associated with the mean percentage of leaf area consumed for native ($r^2 = 0.71$; $P < 0.035$) and exotic species ($r^2 = 0.68$; $P < 0.043$).

ing exotics increased native growth rates, but removing natives did not have a comparable effect on exotics (Fig. 4). In contrast to this exotic advantage in competitive interactions, exotics were preferentially preyed upon by herbivores (Table 1, Figs. 1 & 2). These two findings help to explain the results of our herbivore suppression treatments on plots of otherwise unmanipulated vegetation, where over the course of the growing season, plots without herbivore suppression showed relatively stable ratios of native-to-exotic richness and cover, but plots with suppressed herbivory became increasingly exotic dominated (Fig. 5). Together, these findings suggest that coexistence between natives and exotics in this system is possible because greater herbivory pressure on exotics prevents them from manifesting what would otherwise be a competitive advantage that is strong enough to displace native species. Consequently, this work is novel because it combines the pieces needed to demonstrate empirically that a particular trade-off (i.e. growth rates and susceptibility to herbivory) can help to facilitate coexistence between native and exotic species. It provides specific support for the suggestion that trade-offs between native and exotic species in competitive ability and predator susceptibility may be required for coexistence (Adler 1999; Chesson 2000; Kneitel & Chase 2004) and is generally consistent with previous empirical and theoretical research suggesting, (1) that herbivory can limit the importance of competition in communities and may be the principal factor regulating species diversity at the local scale (Sih *et al.* 1985; Hulme 1996) and (2) that there are likely to be interactive effects between herbivory and competition, as well as growth rates and investment in herbivore defenses, that influence species coexistence (Coley *et al.* 1985; Gurevitch *et al.* 2000; Chase *et al.* 2002; Viola *et al.* 2010). Finally, our findings are consistent with previous work that has showed that exotic species are more frequently preyed upon by herbivores (Agrawal & Kotanen 2003; Agrawal *et al.* 2005; Parker *et al.* 2006; Chun *et al.* 2010) and is consistent with work that has showed that exotics can have strong competitive advantages over natives (Blossey & Notzold 1995; Levine *et al.* 2003; Vilà *et al.* 2011).

The differences in competitive ability and herbivory rates between natives and exotics are likely influenced by the differences we observed in C : N ratios. Exotic species, on average, had lower C : N ratios in their leaves than con-generic and con-familial native taxa (Table 1; Fig. 3). Further, among both natives and exotics, the species with the highest herbivory rates were the ones that had the greatest levels of Nitrogen relative to Carbon in their leaves (Fig. 3). These findings are consistent with previous work that has shown that increased nitrogen levels within plants (relative to competitors) can increase relative growth rates and competitive ability, while simultaneously increasing susceptibility to herbivores (Mediavilla & Escudero 2003; Leishman *et al.* 2007). To the degree that differences in C : N ratios represent niche differentiation, our findings are consistent with work suggesting that coexistence between natives and exotics is most likely when they occupy different niches (Shea & Chesson 2002; Chase & Leibold 2003; MacDougall *et al.* 2009). These findings are also consistent with research that suggests that fast-growth plants (e.g. exotics) should experience more damage from herbivores than slow-growing plants (e.g. natives), which invest more heavily in defensive chemistry (Coley *et al.* 1985).

Some of our observed results are best explained by the advantages, not disadvantages, that 'competitors' can provide to focal species. This is particularly true for interpreting some of our competitor removal experiments; when all native and exotic competitors were removed, focal species actually grew significantly less than in control plots where all competitors were retained (Fig. 4a, d). This finding is consistent with the hypothesis that in the presence of strong herbivory pressure, neighbors may provide a facilitative advantage through associational defenses, by reducing the herbivory that a focal plant experiences because herbivores are attracted to neighboring plants (Hay 1986). If herbivores are attracted to dense aggregations of exotics, potentially because of their higher nitrogen levels, this could explain our finding that focal exotic species did marginally better when exotic competitors were removed, but native competitors were retained (Fig. 4f).

While asymmetries in competitive ability and herbivore susceptibility observed between native and exotic species in these communities are likely to be important in facilitating coexistence, it is likely that other factors are important as well. For example, habitat heterogeneity has been shown to facilitate coexistence between native and exotic species in invaded communities (Huston 1994; Orrock

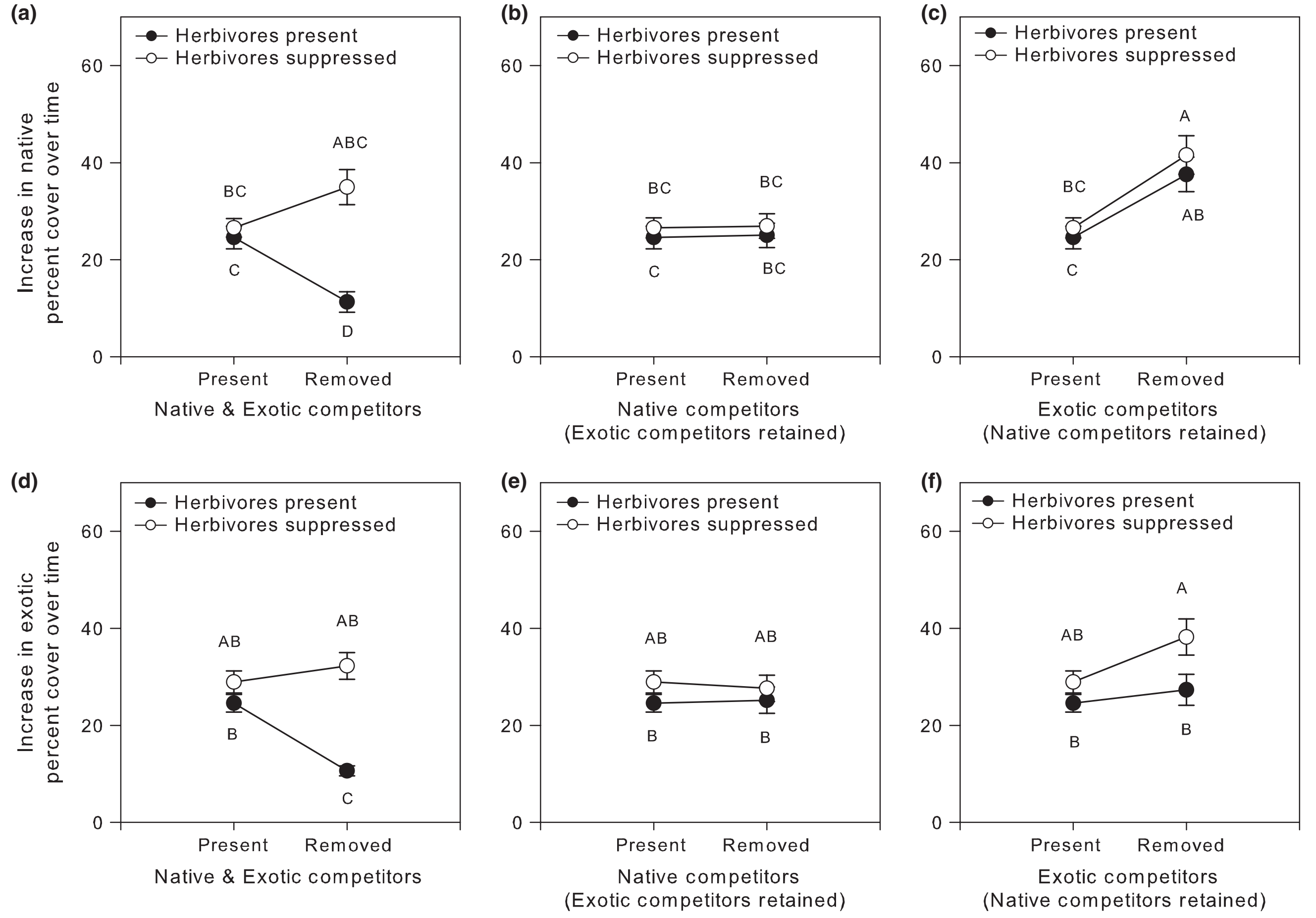

Figure 4 Interactive diagrams from a 2010 (June-August) factorial weeding-based competition experiment manipulating the presence of plant competitors and insect herbivores. Panel letters indicate *post-hoc* Tukey values, where different letters indicate significant differences. Analyses were conducted separately for natives and exotics. (a, d) Removal of all competitors significantly reduces percent cover for both natives ($P < 0.001$) and exotics ($P < 0.001$) in the presence of herbivores. (b, e) Removal of native competitors, but retention of exotics, had no significant impacts on native ($P = 0.81$) and exotic plants ($P = 0.74$) in the presence or absence of herbivory. (c, f) Removal of exotic competitors, but retention of natives, significantly increased native plant cover over time in the presence and absence of herbivores ($P < 0.001$; $P < 0.001$); percent cover of exotics increased marginally only when herbivores were removed ($P = 0.09$).

et al. 2010). In the case of strandline plant communities, it is likely that habitat heterogeneity plays an important role, as these communities are highly prone to disturbance from storms that can alter shoreline topography and create unique microhabitats (Heard *et al.* 2012). Additionally, as strandline communities are frequently disturbed, it is likely that resources are available in a 'fluctuating' manner that may have promoted invasion (Davis *et al.* 2000) and could be important in promoting coexistence. Indeed, the relative role of competition, for example, may be of reduced importance at our study sites if the system is not at a competitive equilibrium (Huston 1994). Further, because the relative influence of biotic interactions in promoting coexistence is likely to vary in relationship with the productivity of particular sites (Grime 1979; Huston 1994, 2004; Guo & Berry 1998) differences in productivity among our sites could influence the relative importance of the processes we observed. It is also important to emphasize that the patterns we observed, i.e. in strandline plant communities, which are found at the marine-terrestrial interface, are highly stressful, and have pulses of resources, may not be generally applicable to other ecosystems. Finally, coexistence between native and exotic species at the sites we studied could be a temporary phenomenon. This possibility is difficult to rule out, but patterns of coexistence over the past decade show that that while there has been an increase in the dominance of exotic species, this has not occurred at the expense of native diversity or cover (Heard *et al.* 2012). This suggests that if coexistence is transient in this system than the dynamics are playing out over a very long time period.

To date, we have lacked the empirical foundation to determine whether asymmetries in competitive ability and herbivore susceptibility between native and exotic species may facilitate coexistence in invaded plant communities. Recent research has been unable to answer this question as long-term records of coexistence between native and exotic species remain sparse (Strayer *et al.* 2006) and because the entire community of herbivores and competitors are often difficult to manipulate (Gurevitch *et al.* 2000; Chase *et al.* 2002). Here, we have provided observational and experimental evidence that functional differences exist between native and exotic species in competitive ability and herbivore susceptibility in the plant communities we studied, ones that have been invaded for over 200 years (Heard *et al.* 2012). Collectively, these findings complement existing invasion theory (Stohlgren *et al.* 1999; Shea & Chesson 2002; MacDougall *et al.* 2009) and provide a specific example of how asym-

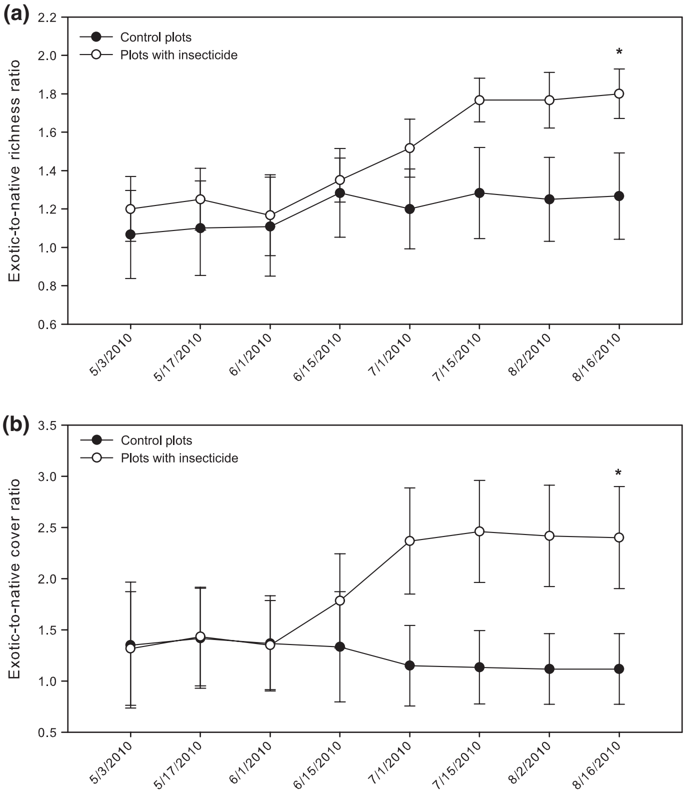

Figure 5 Changes in the ratios of exotic-to-native richness and cover from six strandline plant sites over the 2010 growing season. (a, b) The ratios of exotic-to-native richness ($F_{1,88} = 12.8$, $P < 0.01$) and cover ($F_{1,88} = 18.9$, $P < 0.01$) were significantly different by the end of the growing season on plots where herbivores were suppressed with insecticide, but stayed relatively constant over the growing season on plots where herbivores were not manipulated.

metric functional differences between native and exotic species may help to facilitate long-term coexistence in invaded communities. Finally, our results also provide support for the hypothesis that there can be important ecological differences between native and exotic species in invaded communities (Adler 1999; Agrawal & Kotanen 2003; Vilà *et al.* 2011; Knapp & Kühn 2012). This argument furthers the current debate over the validity of utilizing native-exotic dichotomies in ecological studies (Davis *et al.* 2011; Knapp & Kühn 2012) and provides a novel example of how these functional differences can influence community composition.

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AUTHORSHIP

MJH & DFS conceived the ideas, MJH conducted experiments and collected data, MJH & DFS analyzed the data, MJH & DFS wrote the manuscript.

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