

Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass

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Summary

1. Exotic plant species have become increasingly prominent features of ecological landscapes throughout the world, and their interactions with native and exotic taxa in these novel environments may play critical roles in mediating the dynamics of such invasions.

2. Here, we summarize results from comparative and experimental studies that explore the effects of two factors – herbivory and facilitation – on the performance and distribution of an invasive South African grass, *Ehrharta calycina*, in a coastal foredune system in northern California, USA.

3. Using a 2-year exclosure experiment, we show that a native herbivore, black-tailed jackrabbits (*Lepus californicus*), significantly reduced the height, shoot production, fecundity and above-ground biomass of this exotic grass.

4. Data from two comparative studies and a neighbour-removal experiment revealed that *Ehrharta* frequently escaped herbivores by associating with three neighbouring plant species – an exotic perennial grass, *Ammophila arenaria*, an exotic perennial succulent, *Carpobrotus edulis*, and a native perennial shrub, *Baccharis pilularis*. *Ehrharta* growing in association with neighbours was taller, had fewer grazed shoots, produced greater numbers of spikelets and had greater above-ground biomass than unassociated individuals. Furthermore, removing neighbours generally eliminated these benefits in 7 months, although effects differed among neighbour species.

5. An additional neighbour-removal experiment conducted in the absence of jackrabbits indicated that neighbour removals did not have significant impacts on *Ehrharta* height, shoot production, spikelet production or above-ground dry biomass. These results suggest that the primary means by which *Ehrharta* benefits from neighbouring plants is protection from herbivores – either because they are less apparent to herbivores or less accessible – and that *Ehrharta* likely incurred minimal costs from associating with neighbours.

6. *Ehrharta* was more frequently associated with neighbours than expected due to chance, and less frequently found in open dune habitat. These results are consistent with the hypothesis that the effects of herbivory and facilitation have been sufficiently strong to shape the local distribution of this invader in the landscape.

7. *Synthesis*. Our research has demonstrated that herbivory and facilitation have jointly influenced the dynamics of a biological invasion, and highlights the importance of evaluating the effects of multiple interactions on invasions in a single system.

Key-words: associational resistance, biological invasion, biotic resistance, coastal dunes, invasion ecology, invasive exotic grass, mammalian herbivory, plant facilitation

Introduction

Exotic species have become an increasingly prominent feature of ecological landscapes throughout the world (Parker *et al.*

1999; Mack *et al.* 2000; Meyers & Bazely 2003; Lockwood, Hoopes & Marchetti 2007), and their interactions with native and exotic taxa in these novel environments may play critical roles in mediating the dynamics of such invasions. Ideas on this topic have been strongly influenced by two prominent hypotheses. The Enemy Release Hypothesis, originally

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proposed by Darwin (1859) and Elton (1958), predicts that exotic taxa should thrive in their new ranges because they are freed from control by native predators, pathogens and herbivores (Maron & Vila 2001; Keane & Crawley 2002; Agrawal *et al.* 2005; but also Colautti *et al.* 2004). In contrast, the Biotic Resistance Hypothesis proposes that natural enemies and competitors in recipient communities will limit the success of invasive exotic taxa (Elton 1958; Maron & Vila 2001; Levine, Adler & Yelenik 2004). For example, numerous studies have shown that native herbivores can decrease the growth, fecundity and/or population size of exotic plant species (Maron & Vila 2001; Parker, Burkepile & Hay 2006). Given these divergent views on invasion, the key is to understand how the losses and gains of biotic interactions affect the success of exotic species in their introduced landscapes (Mitchell *et al.* 2006).

Facilitation is increasingly recognized as a central force in population and community ecology (Bertness & Callaway 1994; Callaway 1995, 2007; Bruno, Stachowicz & Bertness 2003; Brooker *et al.* 2008) and these interactions may play important roles in mediating the success of exotic species. Although this subject has not received a lot of attention, Simberloff & Von Holle (1999) clearly highlighted the link between facilitation and invasion when proposing the idea of 'invasional meltdowns', where positive interactions can arise between exotic taxa that subsequently facilitate the success of one or both invaders in their novel environment (see also Simberloff 2006). More recently, Badano *et al.* (2007) provided an illustration of the facilitation–invasion linkage by showing that a native cushion plant in high-elevation environments ameliorates stress and thus positively affects performance of two exotic forbs. However, despite these advances, few studies have explored the importance of facilitation by native and exotic vegetation as a means by which exotic plants can escape control by native herbivores (although see Johnson & Cushman 2007; Iponga, Milton & Richardson 2009). Assessing the relative importance of herbivory and facilitation jointly in the same system will greatly enhance our understanding of the factors that determine the success of plant invasions.

In this paper, we explore the influence of herbivory by native mammals and facilitation by native and exotic plants on the success of an invasive South African grass, *Ehrharta calycina* (veldt grass; hereafter referred to as *Ehrharta*), at a coastal dune in northern California. Using both comparative and experimental studies, we address four research questions; (i) Does herbivory by native jackrabbits influence the growth and fecundity of the invasive, exotic grass *Ehrharta*? (ii) Is the vulnerability of *Ehrharta* to jackrabbit herbivory reduced by its association with native and exotic plant species? (iii) Does *Ehrharta* incur costs or receive additional benefits from associating with neighbours in the absence of herbivores? and (iv) Do herbivory and facilitation alter the local distribution of *Ehrharta* in the landscape? Collectively, these questions address the importance of native herbivores and plant facilitation by native and exotic neighbours in mediating the success of a highly invasive exotic grass.

Study system

We conducted our research in a coastal foredune system 2 km north-west of the town of Bodega Bay in Sonoma County, California, USA (38°20'N, 123°3'W). This site is 100–300 m from the Pacific Ocean and is part of Sonoma Coast State Beaches. The area is characterized by a Mediterranean-type climate typical of California's north-central coast, with moderate rainy winters and cool foggy summers with little or no precipitation. The soil is comprised of nearly pure sand, which is fast-draining and nutrient-poor (Barbour *et al.* 1973; Lortie & Cushman 2007; J.H. Cushman, unpublished data). The terrain is low, and strong onshore winds and salt spray dominate the area.

This foredune site is inhabited by a number of dominant perennial species, the primary ones being the exotic grass *Ammophila arenaria* (European beach grass; Poaceae), the exotic succulent *Carpobrotus edulis* (ice plant; Aizoaceae) and the native shrub *Baccharis pilularis* (coyote brush; Asteraceae). The native shrub *Lupinus arboreus* (bush lupine; Fabaceae) is also present but at considerably lower abundance than the other plant taxa. Percent cover of these four species at our study area averaged 16%, 10%, 9% and 5%, respectively (J.H. Cushman *et al.* unpublished data).

Ehrharta calycina (veldt grass; Poaceae) is a tussock-forming perennial grass native to southern Africa that has become widespread in coastal areas of California and in forested areas in western Australia (Smith, Bell & Loneragan 1999; Bossard, Randall & Hoshovsky 2000; Fisher *et al.* 2006). This grass is in an explosive stage of invasion along the central coast of California (Bossard, Randall & Hoshovsky 2000) and the California Invasive Plant Council (<http://www.cal-ipc.org>) has assigned *E. calycina* its highest impact/invasion category, which is reserved for species that have severe ecological impacts and exhibit high rates of dispersal and establishment. In California, it occurs in sandy soils and spreads almost exclusively via seed, although rhizomes are present occasionally. The species typically grows from December to May and produces seed from March to June. Inflorescences of this grass consist of an erect panicle that bears a collection of spikelets, each of which contains three florets, although two are sterile (Hickman 1993; Bossard, Randall & Hoshovsky 2000). Thus, each spikelet produces only one seed and the number of spikelets per plant is an indirect measure of fecundity for this species. At our foredune study site, this exotic grass has not reached the high abundances observed elsewhere – occurring at an average density of 0.52 plants m⁻² (+ 0.1 SE; range = 0.13–1.2; J.H. Cushman *et al.* unpublished data) – perhaps because it is in the early stages of invasion, experiences intense herbivory and/or is subjected to particularly harsh abiotic conditions. *Ehrharta* is regularly found growing in multiple microhabitat types at our site – in the open dune free of neighbouring vegetation as well as growing in association with dominant perennial species, including *Ammophila*, *Carpobrotus*, *Baccharis* and *Lupinus*. When found in association with surrounding vegetation, *Ehrharta* either grows underneath the canopy of shrubs (*Baccharis* and *Lupinus*) or grows amidst and

emerges from non-shrub perennials (*Ammophila* and *Carpobrotus*).

Black-tailed jackrabbits (*Lepus californicus*) and black-tailed deer (*Odocoileus hemionus columbianus*) are by far the most abundant mammalian herbivores at our site (Warner & Cushman 2002; McNeil & Cushman 2005; Huntzinger, Karban & Cushman 2008). Jackrabbits are especially abundant, as indicated by the dense layer of distinctive scat that carpets the dune surface (Barbour *et al.* 1973; J.H. Cushman, unpublished data). They feed almost exclusively on grasses and readily consume *Ehrharta*, although not *Ammophila* (J.H. Cushman personal observation). In contrast, deer browse primarily forbs and shrubs (Warner & Cushman 2002; McNeil & Cushman 2005) and do not feed on *Ehrharta* (J.H. Cushman, personal observation). In addition, jackrabbits are the only mammalian herbivore we have observed during the past 10 years feeding on *Ehrharta* at our site.

Methods

HERBIVORE-EXCLOSURE EXPERIMENT

To address the impacts of herbivory by native jackrabbits on the growth and reproduction of *Ehrharta*, we established an enclosure experiment in June 2000. We selected 20 pairs of *Ehrharta* plants that were roughly of similar size, grew within 1 m of each other and occurred in the open dune, free of neighbouring vegetation. We then randomly selected one plant in each pair to receive fencing that excluded jackrabbits and left the other plant unmanipulated to serve as a control. These enclosures were very effective at protecting *Ehrharta* plants from jackrabbit herbivory and consisted of cylindrical poultry-mesh cages, 45 cm high \times 20 cm wide, anchored into the sand with steel U-shaped stakes.

In June 2000 prior to establishing the enclosures, we quantified the height and spikelet production of all 40 plants used in this experiment. In June 2002, we again sampled these plants and quantified their height, number of spikelets and number of shoots. We also harvested the above-ground biomass of all plants, dried the material at 60 °C for 48 h and then weighed it.

EHRHARTA PERFORMANCE IN DIFFERENT MICROHABITATS

To evaluate how *Ehrharta* performance varied among different microhabitat types, we randomly selected 80 plants in May 2000 and 80 different plants in May 2002 that were equally distributed among four locations: growing in association with one of three dominant plant species (*Ammophila*, *Carpobrotus* or *Baccharis*) or growing alone in the open dune, at least 1 m from other vegetation. We then quantified the height and spikelet production of all 80 *Ehrharta* plants in 2000 and the height and proportion of grazed shoots in 2002.

NEIGHBOUR-REMOVAL EXPERIMENTS

We performed two additional field experiments to determine how *Ehrharta* was affected by growing in close association with other plant species. The first experiment was designed to assess whether neighbouring plant species influenced the level of jackrabbit herbivory experienced by *Ehrharta*. To address this issue, in early October 2001, we selected 10 *Ammophila*, 10 *Carpobrotus* and 10 *Baccharis*

plants that each had a pair of healthy *Ehrharta* plants of roughly similar size growing in association with them. We then removed the neighbouring vegetation surrounding a randomly chosen *Ehrharta* in each pair and left the other unmanipulated to serve as a control. In all cases, we removed the above-ground material of the associated species from within a 20-cm-wide area surrounding the target *Ehrharta* plant. Because of the low cover and species richness of this system, our manipulations of neighbouring vegetation surrounding focal *Ehrharta* plants always involved the removal of only a single neighbouring individual. All plants in this experiment were unfenced and thus accessible to jackrabbit herbivores. In October 2001 and May 2002, we assessed both manipulated and control *Ehrharta* plants with respect to their height, number of shoots and proportion of shoots grazed by jackrabbits. In May 2002, we also quantified the number of spikelets produced per plant and harvested the above-ground biomass of all plants. This material was dried at 60 °C for 48 h and then weighed.

The second experiment sought to determine if, in the absence of jackrabbit herbivory, there were costs or benefits to *Ehrharta* from associating with other plant species (i.e. direct plant–plant interactions). In late October 2001, we selected five *Ammophila*, five *Carpobrotus* and five *Baccharis* plants that each had a pair of healthy *Ehrharta* plants growing amidst their canopy. We then removed a 20-cm swathe of neighbouring vegetation from around a randomly chosen *Ehrharta* in each pair and left the other unmanipulated. Unlike the first neighbour-removal experiment, we then fenced all *Ehrharta* pairs and associated vegetation to exclude jackrabbit herbivores. As before, we quantified the height and number of shoots of all *Ehrharta* plants in both October 2001 and May 2002. We also quantified the number of spikelets produced per plant in May 2002 as well as harvested, weighed and dried all above-ground biomass.

DISTRIBUTION OF EHRHARTA AND ITS PLANT NEIGHBOURS

We assessed the distribution of naturally occurring *Ehrharta* plants in the seven most dominant microhabitat types found at our fore-dune site: *Ammophila*, *Baccharis*, *Carpobrotus*, dead *Carpobrotus*, *Lupinus*, dead *Lupinus* and open dune. To obtain the naturally occurring frequencies of each microhabitat type, in November of 2002 we first established an initial 30-m transect that passed through our study site and then randomly selected 14 points along it. At each of these points, we established 30-m long transects running perpendicular to the initial transect ($n = 14$ transects) to quantify the abundance of each microhabitat type. For all 14 transects, we recorded the length of the transect line intercepting each microhabitat type (to the nearest 0.05 m) and divided by the total transect length to estimate the proportion of each microhabitat type present at the study site. Along each transect, we also recorded the microhabitat of each *Ehrharta* plant occurring within a 0.5-m wide belt on either side of the 14 transects. In total, we sampled 0.042 ha of the study area.

STATISTICAL ANALYSES

We performed all statistical analyses using JMP 8 (SAS Institute, Cary, NC, USA). Data from our jackrabbit-exclosure experiment were first analysed using a two-way MANOVA, with the jackrabbit treatment (present or excluded) and block (pairs 1–20) as the grouping factors. Block was treated as a random effect in all models. The four response variables for this MANOVA were the number of

shoots produced per plant and above-ground dry biomass in 2002 as well as relative change (= log response ratio; $\ln[2002/2000]$) in *Ehrharta* height and the number of spikelets produced per plant. Relative change values are symmetrical around zero, with positive values indicating increases over the 2-year period and negative ones indicating decreases. We log-transformed the shoot number and biomass data prior to analyses to equalize variances. We then proceeded with 'protected' ANOVAS on the individual response variables if the MANOVA generated a significant jackrabbit main effect. As discussed by Scheiner (2001), this approach is an effective method for addressing potential correlations among multiple dependent variables (see Alvarez & Cushman 2002; Cushman, Tierney & Hinds 2004; Johnson & Cushman 2007).

To evaluate how *Ehrharta* performance varied among different microhabitat types, we analysed our data using two separate one-way MANOVAS, with microhabitat type (growing in association with *Ammophila*, *Carpobrotus* or *Baccharis* or in the open dune without neighbours) as the grouping factor and *Ehrharta* height and spikelet production in 2000 as the response variables for the first MANOVA and height and proportion of grazed shoots in 2002 as the response variables in the second. We log-transformed all response variables prior to analysis to equalize variances. As before, we proceeded with 'protected' one-way ANOVAS on each response variable if a MANOVA produced a significant microhabitat term. We performed Tukey–Kramer HSD multiple comparison tests ($\alpha = 0.05$) on all ANOVAS with significant microhabitat main effects. This test corrects for the number of pairwise comparisons being made within an ANOVA.

Both neighbour-removal experiments were analysed with three-way MANOVAS followed by 'protected' ANOVAS as needed, with neighbour treatment (present or removed), neighbour species (*Ammophila*, *Carpobrotus* or *Baccharis*), and block (either 10 or 5) as the grouping factors. Response variables for analyses of the neighbour-removal experiment in the presence of herbivores were the number of spikelets produced per *Ehrharta* plant and above-ground biomass in 2002 as well as relative change ($\ln[2002/2000]$) in height, number of shoots and proportion of grazed shoots. We used the same response variables for analyses of the neighbour-removal experiment in the absence of herbivores, except that proportion of grazed shoots was omitted. We performed Tukey–Kramer HSD multiple comparison tests ($\alpha = 0.05$) on all ANOVAS with significant neighbour treatment \times neighbour species interaction terms. These two experiments were analysed separately because they had different start dates and levels of replication.

To test whether the distribution of *Ehrharta* plants was independent of the distribution of microhabitat types in the foredunes, we conducted a contingency table analysis, using the actual distribution of each microhabitat as the expected frequencies. We then subdivided the contingency table and examined each microhabitat separately using a Bonferroni-adjusted significance level ($0.05/7 = 0.0071$) to account for multiple comparisons.

Results

HERBIVORE-EXCLOSURE EXPERIMENT

Results from a two-way MANOVA indicated that the jackrabbit treatment had an overall significant effect on relative change in *Ehrharta* height and spikelet production ($\ln[2002/2000]$) as well as shoot production and above-ground dry biomass in 2002 ($F_{4,16} = 51.85$, $P < 0.0001$). Subsequent protected

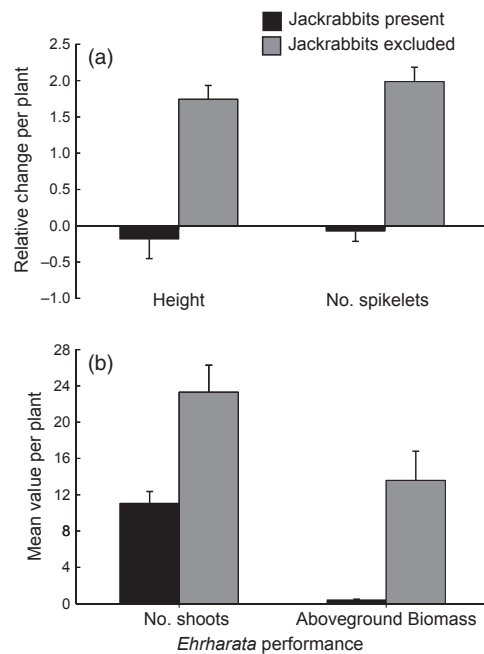


Fig. 1. Mean (± 1 SE) relative change ($\ln[2002/2000]$) in height and spikelet production per plant (a) and mean (± 1 SE) number of shoots and above-ground dry biomass (g) per plant in 2002 (b) for the exotic grass *Ehrharta calycina* as a function of the presence or absence of jackrabbits (*L. californicus*) at a coastal dune site.

ANOVAS showed that excluding jackrabbits resulted in significantly greater change in *Ehrharta* height ($F_{1,19} = 56.97$, $P < 0.0001$), spikelet production ($F_{1,19} = 165.00$, $P < 0.0001$), shoot production ($F_{1,19} = 22.06$, $P = 0.0002$) and above-ground dry biomass ($F_{1,19} = 80.20$, $P < 0.0001$; Fig. 1).

EHRHARTA PERFORMANCE IN DIFFERENT MICROHABITATS

Our results indicate that *Ehrharta* performance varied significantly among the four microhabitats at our study site in both 2000 (MANOVA – $F_{6,150} = 23.50$, $P < 0.0001$) and 2002 (MANOVA – $F_{6,150} = 13.59$, $P < 0.0001$). Subsequent protected ANOVAS showed that *Ehrharta* height and spikelet production varied significantly among microhabitats in 2000 ($F_{3,76} = 57.78$, $P < 0.0001$; $F_{3,76} = 12.13$, $P < 0.0001$; respectively), as did height and proportion of grazed shoots in 2002 ($F_{3,76} = 24.47$, $P < 0.0001$; $F_{3,76} = 20.88$, $P < 0.0001$; respectively). *Ehrharta* plants were taller in both years when they associated with vegetation than when they grew alone in the open dune (Fig. 2a,c). In general, *Ehrharta* was tallest when growing amidst *Ammophila* followed by *Baccharis* and then *Carpobrotus*. Spikelet production in 2000 was greatest when *Ehrharta* grew in association with *Ammophila* and equally low when with *Baccharis*, *Carpobrotus* and in the open dune (Fig. 2b). The proportion of jackrabbit-grazed shoots in 2002 was greatest for *Ehrharta* that grew in the open dune followed distantly by *Carpobrotus*, *Baccharis* and then *Ammophila* (Fig. 2d).

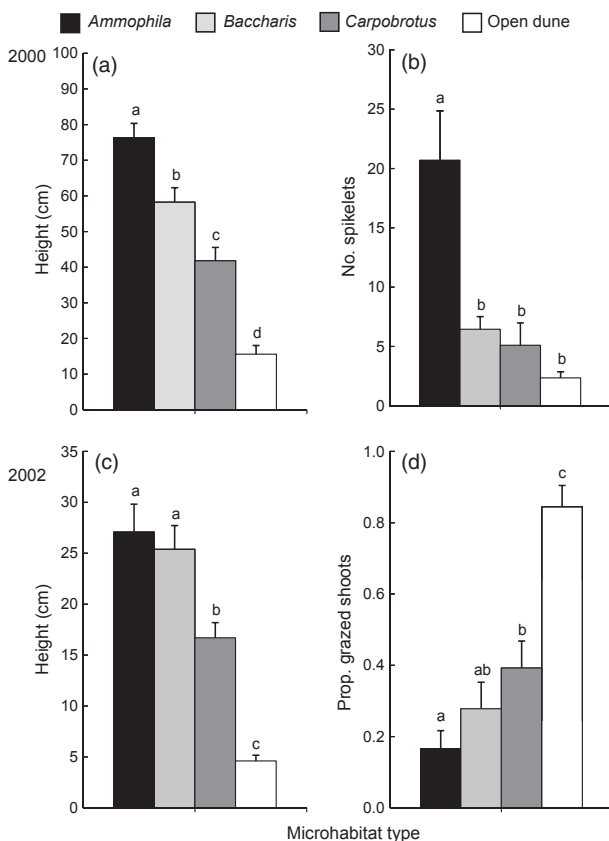


Fig. 2. Mean (+1 SE) height and spikelet production per plant in 2000 as well as height and proportion of grazed shoots per plant in 2002 for the exotic grass *Ehrharta calycina* in four coastal dune microhabitat types. Letters above bars correspond to the result of multiple comparison tests.

NEIGHBOUR-REMOVAL EXPERIMENTS

Results from a three-way MANOVA showed that, in the presence of jackrabbits, removing plant neighbours had an overall significant effect on change in *Ehrharta* height, shoot production and proportion of grazed shoots ($\ln[2002/2000]$) as well as spikelet production and above-ground dry biomass at the end of the experiment ($F_{5,14} = 11.23$, $P = 0.0002$). A protected ANOVA indicated that relative change in shoot production was not affected by the neighbour-removal treatment on its own ($F_{1,9} = 0.66$, $P = 0.4385$), but the treatment did vary significantly among neighbour species (treatment \times neighbour interaction: $F_{2,18} = 7.02$, $P = 0.0056$). Despite this interaction, multiple comparison tests revealed that neighbour removal did not impact relative change in *Ehrharta* shoot production for any of the three neighbour species (Fig. 3a). Relative change in the proportion of shoots grazed by jackrabbits increased significantly when neighbours were removed ($F_{1,9} = 41.18$, $P < 0.0001$), and this effect did not vary among neighbour species (treatment \times neighbour interaction: $F_{2,18} = 1.15$, $P = 0.3360$; Fig. 3b). Neighbour removal also led to significant reductions in relative change of *Ehrharta* height ($F_{1,9} = 28.42$, $P = 0.0005$; Fig. 3c) and spikelet production in 2002 ($F_{1,9} = 8.68$, $P = 0.0163$; Fig. 4a) and these effects

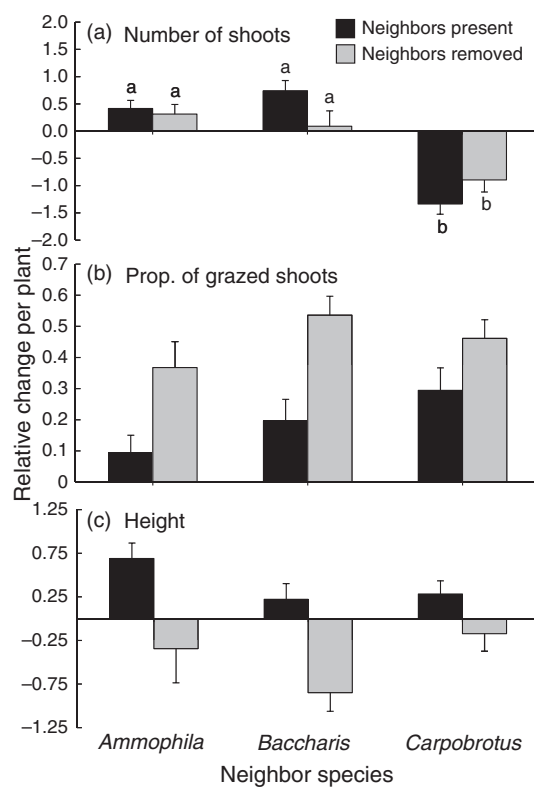


Fig. 3. Mean (+1 SE) relative change ($\ln[2002/2000]$) in number of shoots (a), proportion of grazed shoots (b) and height (c) for the exotic grass *Ehrharta calycina* as a function of the presence or absence of neighbouring plant species (either the exotics *A. arenaria* and *C. edulis* or the native *B. pilularis*). Jackrabbit herbivores had access to the focal *Ehrharta* plants throughout this experiment. Letters above bars correspond to the result of multiple comparison tests.

did not vary among neighbour species (treatment \times neighbour interactions: $F_{2,18} = 1.77$, $P = 0.1994$ and $F_{2,18} = 0.24$, $P = 0.7919$, respectively). Finally, neighbour removal significantly reduced the above-ground biomass of *Ehrharta* in 2002 ($F_{1,9} = 10.60$, $P = 0.0099$), with effects varying among neighbour species (treatment \times neighbour interaction: $F_{2,18} = 6.92$, $P = 0.0059$). Neighbour removal had a negative effect on *Ehrharta* biomass when the plant associated with *Ammophila* and *Baccharis* but not *Carpobrotus* (Fig. 4b).

In contrast to the first neighbour-removal experiment, results from a three-way MANOVA showed that removing plant neighbours in the absence of jackrabbits did not have an overall significant effect on relative change in *Ehrharta* height or shoot production ($\ln[2002/2000]$) nor on spikelet production and above-ground dry biomass in 2002 ($F_{4,5} = 2.36$, $P = 0.1855$).

DISTRIBUTION OF *EHRHARTA* AND ITS PLANT NEIGHBOURS

Ehrharta plants were not distributed independently of the foredune microhabitat types at our site (Fig. 5; $X^2_6 = 144.46$, $P < 0.0001$). Assessing each microhabitat separately, we

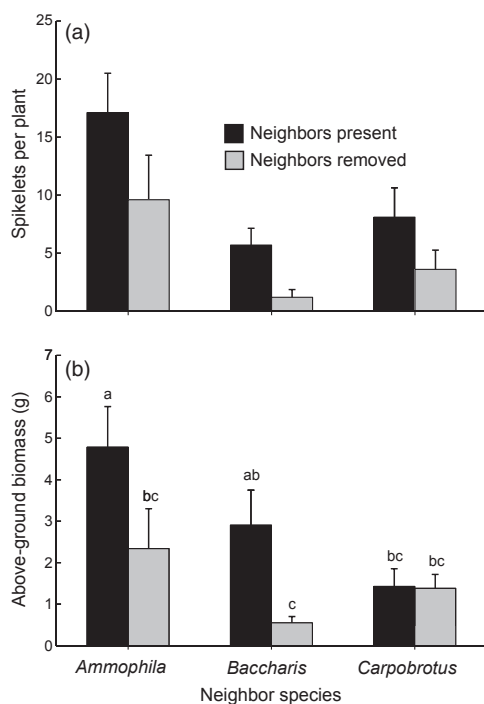


Fig. 4. Mean (\pm 1 SE) spikelets produced (a) and above-ground dry biomass (b) per plant in 2002 for the exotic grass *Ehrharta calycina* as a function of the presence or absence of neighbouring plant species (either the exotics *A. arenaria* and *C. edulis* or the native *B. pilularis*). Jackrabbit herbivores had access to the focal *Ehrharta* plants throughout this experiment. Letters above bars correspond to the result of multiple comparison tests.

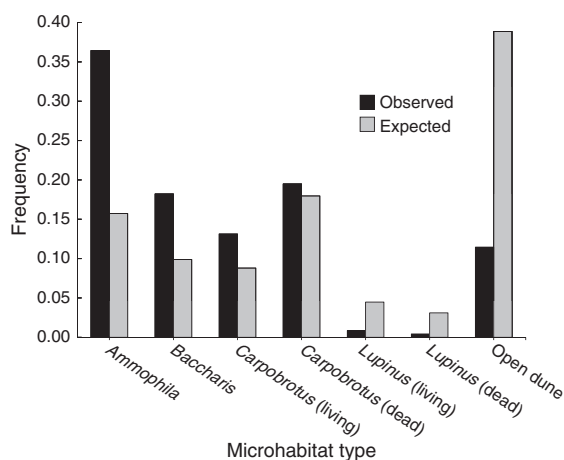


Fig. 5. Observed and expected frequencies of occurrence of the exotic grass *Ehrharta calycina* in seven microhabitat types in a coastal dune system.

found that *Ehrharta* plants were 2.3 times more likely to associate with *Ammophila* ($X^2_1 = 75.12$, $P < 0.0001$), 1.8 times more likely to associate with *Baccharis* ($X^2_1 = 17.91$, $P < 0.0001$), and 1.5 times more likely to associate with live *Carpobrotus* ($X^2_1 = 6.84$, $P = 0.008$, although this was just outside the significance level required by our Bonferroni correction). In contrast, *Ehrharta* was 5.3 times less likely to associate with live *Lupinus* ($X^2_1 = 7.51$, $P = 0.006$), 7.3 times

less likely to associate with dead *Lupinus* ($X^2_1 = 13.84$, $P = 0.0002$), and 3.4 times less likely to occur in open dune habitat ($X^2_1 = 77.83$, $P < 0.0001$). There was no association between *Ehrharta* and dead *Carpobrotus* ($X^2_1 = 0.31$, $P = 0.5774$).

Discussion

Using both field surveys and manipulative experiments, we have examined the importance of herbivory and plant facilitation in jointly mediating a plant invasion. We have shown that intense herbivory by native jackrabbits negatively affected the growth and fecundity of an invasive South African grass in northern California, but that the plant was able to escape control by associating with three neighbouring plant species – an exotic grass, an exotic succulent and a native shrub. Our findings suggest that the effects of herbivores and neighbours have been sufficiently strong and persistent to shape the local distribution of this invader in the landscape. This is one of only a few studies that have evaluated the importance of herbivory and facilitation in the same system as joint forces mediating the success of a plant invasion.

Historically, exotic plants were widely assumed to flourish in their introduced ranges because they escaped the control of herbivores (Elton 1958). However, a review by Colautti *et al.* (2004) revealed that, in their introduced environments, exotic species were no less affected by enemies than native taxa. In support of this finding, our research clearly demonstrates that *Ehrharta* has not escaped from the adverse effects of an influential enemy (Fig. 1). Indeed, a growing number of studies reveal that generalist herbivores can be important regulators of the performance, fecundity and abundance of exotic plant species. For example, Maron & Vila (2001) conducted a literature review of 18 studies from 1986 to 1998 and reported that native herbivores frequently reduced the performance of exotic plants at multiple life-history stages (also see Keane & Crawley 2002). Case & Crawley (2000) used an enclosure experiment to show that rabbit herbivory in Great Britain significantly reduced the survival and seedling recruitment of *Conyza sumatrensis*, an exotic annual forb native to North America. More recently, Iponga, Milton & Richardson (2009) showed that seedling height and canopy area of an invasive tree from South America were reduced substantially by vertebrate herbivores (cattle and various game species) in South Africa. Finally, Parker, Burkepile & Hay (2006) conducted a meta-analysis of published enclosure experiments and found that native herbivores negatively impacted the relative abundance of exotic plant species, measured as percent of total plant cover or biomass. In addition, they found that native vertebrate herbivores had a 3- to 5-fold greater negative effect on the survival of exotic plants than did native invertebrate herbivores. Collectively, these studies indicate that there is an abundance of evidence that contradicts the Enemy Release Hypothesis. In addition, Colautti *et al.* (2004) suggest that evidence purporting to support the Enemy Release Hypothesis has often been accepted uncritically when more compelling alternative explanations existed.

The amount of herbivory experienced by plants can be reduced by associating with specific types of plant species or assemblages (Root 1973; Atsatt & O'Dowd 1976; Hambäck, Agren & Ericson 2000; Milchunas & Noy-Meir 2002; Callaway *et al.* 2005; Baraza, Zamora & Hodar 2006; Alberti *et al.* 2008). Such conditional or context-dependent outcomes are known as associational resistance, and we have shown that they occur in our system, as the performance of *Ehrharta* was typically greater when associating with both native and exotic plant neighbours and decreased rapidly when we removed these neighbours. We hypothesize that *Ehrharta* benefitted from neighbouring plants either because they were less apparent to herbivores or less accessible. Although less powerful due to reduced replication, our second neighbour-removal experiment was critical for understanding this system because it suggested that there was no effect – positive or negative – of removing neighbours in the absence of herbivores. Thus, *Ehrharta* did not appear to receive additional benefits (e.g. facilitation through habitat amelioration) or incur costs from associating with plant neighbours (e.g. interspecific competition), and protection from jackrabbit herbivory was the primary means by which *Ehrharta* benefitted from neighbours.

Although plant neighbours had an indirect positive effect on exotic *Ehrharta* (i.e. facilitation), different neighbour species varied in the magnitude of their effects. Our comparative data from 2 years showed that, in general, *Ehrharta* performance was greatest when associating with the large exotic grass, *Ammophila*, followed closely by the native shrub, *Baccharis*, and then more distantly by the exotic low-growing succulent, *Carpobrotus* (Fig. 2). Results from our neighbour-removal experiment with herbivores present (Figs 3 and 4) partially corroborate these neighbour rankings. *Carpobrotus* was still the least beneficial neighbour for *Ehrharta* to associate with, but *Ammophila* and *Baccharis* were now equally superior neighbours. Both *Ammophila* and *Baccharis* are considerably taller than *Carpobrotus* and we hypothesize that *Ehrharta* benefits more from associating with them simply because they afford greater protection from herbivory. Regardless of the specific rankings, our key finding is that both native and exotic neighbours were able to protect a highly invasive exotic grass from control by native mammalian herbivores.

Our data are consistent with the hypothesis that the joint influence of native herbivores and both native and exotic plant neighbours has been sufficiently strong and consistent to shape the local distribution of an exotic invader. *Ehrharta* inhabited the open dune far less frequently than would be expected due to chance, and was more commonly found occurring in association with plant neighbours (Fig. 5). Furthermore, the spatial patterns detected were consistent with what we would have predicted from our comparative and experimental data on plant neighbours (Figs 2–4) – the local distribution of *Ehrharta* was most positively associated with *Ammophila* followed by *Baccharis* and *Carpobrotus* (Fig. 5). We hypothesize that jackrabbits greatly limited the survival and recruitment of *Ehrharta* in open-dune patches, and that native and exotic plant neighbours provided refuges from this pressure. Other factors undoubtedly play a role in shaping the distribution of *Ehrharta*

as well, including seed trapping by neighbouring plants and variation among microhabitats in abiotic stress at the seedling stage.

Numerous studies have previously documented that native herbivores can influence the spatial distributions of native plants (see review by Maron & Crone 2006). In addition, as reviewed by Callaway (2007), other studies have shown that native plants can positively affect the local distributions of native taxa, and Cavieres *et al.* (2005, 2008) demonstrate that native cushion plants in Chile positively influenced the local distribution of exotic dandelions. However, we know of only two studies that have explored the joint influence of herbivory and facilitation on local plant distributions. Gómez (2005) showed that ungulate herbivores in Spain restricted the distribution of two native herb species in open montane habitat, but found that plants were able to escape this control by associating with native shrubs. Similarly, Johnson & Cushman (2007) showed that intense herbivory by Tule elk in California restricted the local distribution of an invasive exotic grass in open grasslands but that the invader escaped control when associating with a native shrub. Despite the shortage of empirical studies on this topic, we suspect that herbivory and facilitation commonly operate together to affect the local distribution of exotic plant invaders in a wide range of ecosystems throughout the world.

In conclusion, our research has demonstrated that herbivory and facilitation have jointly affected the dynamics of a biological invasion. Using field experiments and comparative studies, we have shown that native mammalian herbivores negatively affect the growth and fecundity of an invasive South African grass in California, that this invader can escape control by associating with both native and exotic plant neighbours, and that both interactions likely have shaped the local distribution of this invader. Our work adds to a growing body of literature indicating that native herbivores commonly impact exotic plant invaders, which offers support for the Biotic Resistance Hypothesis and questions the prevalence of the Enemy Release Hypothesis. This research also points to the important role that facilitation can play in promoting the success of plant invasions, although much more work needs to focus on this critical topic. Finally, our study highlights the value of evaluating the effects of multiple ecological interactions on invasions and the net outcome of these interactions in a single system. Indeed, we believe that understanding the impacts of various forms of global change – such as biological invasions – will require a more integrated approach that considers interactions among native and exotic species as well as positive and negative effects.

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