COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Responses to invasion and invader removal differ between native and exotic plant groups in a coastal dune

Susan M. Magnoli · Andrew R. Kleinhesselink · J. Hall Cushman

Abstract The spread of exotic, invasive species is a global phenomenon that is recognized as a major source of environmental change. Although many studies have addressed the effects of exotic plants on the communities they invade, few have quantified the effects of invader removal on plant communities, or considered the degree to which different plant groups vary in response to invasion and invader removal. We evaluated the effects of an exotic succulent, iceplant (*Carpobrotus edulis*), on a coastal dune plant community in northern California, as well as the community responses to its removal. To assess possible mechanisms by which iceplant affects other plants, we also evaluated its above- and belowground influences on the germination and growth of a dominant exotic annual grass, *Bromus diandrus*. We found that iceplant invasion was associated with reduced native plant cover as well as increased cover and density of some exotic plants—especially exotic annual grasses. However, iceplant removal did not necessarily lead to a reversal of these effects: removal increased the cover and density of both native and exotic species. We also found that *B. diandrus* grown in iceplant patches, or in soil where iceplant had been removed, had poorer germination and growth than *B. diandrus* grown in soil not influenced by iceplant. This suggests that the influence of iceplant on this dune plant community occurs, at least in part, due to belowground effects, and that these effects remain after iceplant has been removed. Our study demonstrates the importance of considering how exotic invasive plants affect not only native species, but also co-occurring exotic taxa. It also shows that combining observational studies with removal experiments can lead to important insights into the influence of invaders and the mechanisms of their effects.

Keywords Biological invasions · Community effects · Iceplant (*Carpobrotus edulis*) · Invader removal · Residual effects · Restoration · Sand dunes

S. M. Magnoli · A. R. Kleinhesselink · J. H. Cushman (✉)
Department of Biology, Sonoma State University,
Rohnert Park, CA 94928, USA
e-mail: cushman@sonoma.edu

Present Address:
S. M. Magnoli
W. K. Kellogg Biological Station, Michigan State University,
Hickory Corners, MI 49060, USA

S. M. Magnoli
Department of Plant Biology, Michigan State University,
East Lansing, MI 48824, USA

Present Address:
A. R. Kleinhesselink
Department of Wildland Resources, Utah State University,
Logan, UT 84322, USA

Introduction

Biological invasions are a global phenomenon and have been widely recognized as a source of environmental change (Mack et al. 2000; Hulme 2003; Ruiz and Carleton 2003; Hulme 2006; Lockwood et al. 2007; Simberloff et al. 2013). Exotic invasive species directly threaten native taxa through competition, predation, and herbivory (Mack et al. 2000), and can also act as ecosystem engineers, altering processes such as nutrient cycling and fire regimes (D'Antonio and Vitousek 1992; Ehrenfeld 2003). Environmental management programs often prioritize exotic plant removal as a first step towards restoration and conservation, making it imperative from both a theoretical and an applied

standpoint to determine the effects of invasive plants on the communities they invade.

Although many studies have assessed the effects of invasive plants on communities by observational means, comparing invaded and uninvaded vegetation (Levine et al. 2003; Powell et al. 2011; Vilà et al. 2011), few have combined observational studies with removal experiments in the same system (Powell et al. 2011) to examine both the effects of invasion and the consequences of invader removal. Removal experiments can enhance studies of invader impacts, especially since exotic taxa can often have residual or legacy effects on communities even after removal (i.e., Corbin and D'Antonio 2004, 2011; Conser and Connor 2009). Such residual effects of invasion are likely when exotic plants alter the physical, chemical, or microbial characteristics of the soil they inhabit (Corbin and D'Antonio 2004, 2011). In some systems, invader removal results in increased abundance of other, non-target exotic plants (Alvarez and Cushman 2002; Erskine Ogden and Rejmanek 2005; Larson and Larson 2010). This could be due to reduced competition, disturbance (Hobbs and Huenneke 1992) caused by invader removal, or residual effects of invaders that benefit other exotics. Determining whether invaders continue to affect communities after removal, and examining the mechanisms by which such effects occur, is critical for developing effective approaches for restoring invaded systems.

In addition to using a combination of approaches to study the impacts of invaders, it is critical to examine how the effects of invasion vary among different plant groups in the community. Plants with different life histories, life forms, and geographic origins vary in their responses to invasion and the disturbance created by invader removal (Hobbs and Huenneke 1992; McIntyre et al. 1995; Alvarez and Cushman 2002; Cushman and Gaffney 2010). For instance, invasive plants can alter the environment so as to facilitate other invaders (Simberloff and Holle 1999 and references therein; Cushman et al. 2011). In other cases, invasive species suppress other invaders and can even facilitate the establishment of native species (MacDougall and Turkington 2005).

Iceplant, *Carpobrotus edulis* (Aizoaceae), a South African succulent, is a prevalent invader of dune, scrub, and grassland habitats in coastal Mediterranean-type climates throughout the world (D'Antonio 2006). Such climates are often home to a high diversity of endemic species and as a consequence are considered biodiversity "hotspots" (Cowling et al. 1996; Myers et al. 2000). The effects of iceplant on plant communities include competing with native species (D'Antonio and Mahall 1991) and changing patterns of species diversity (Maltez-Mouro et al. 2009). In addition, modification of the soil under iceplant may be a

mechanism by which it affects other species. For example, D'Antonio (1990a) found that iceplant decreased soil pH, cations, and nitrate, and Vilà et al. (2006) found that it increased soil organic matter content. Not surprisingly, iceplant removal is often undertaken in efforts to conserve and restore habitats (Albert 1995). Despite these activities, it is unclear whether native plant communities will recover quickly after iceplant removal or whether residual effects of invasion on soils will persist after removal (Andreu et al. 2010). Without knowing the extent of iceplant's effects on plant communities, it is difficult to justify or guide restoration practices.

We conducted a comparative study and two field experiments to evaluate the effects of iceplant and its removal on a coastal dune ecosystem in northern California. Specifically, we addressed the following questions. (1) How does iceplant invasion affect plant community composition, and do native and exotic taxa vary in response to invasion? (2) How does iceplant removal affect community composition? (3) Does iceplant affect the community through above- or belowground mechanisms, and do effects persist after iceplant removal? Examining the community-level and residual effects of iceplant will provide insight into the ecological effects of an invasive exotic species, improve the efficacy of restoration practices, and contribute to the conservation of native plant species in fragile coastal ecosystems.

Methods

Study system

We conducted our research in a coastal hind-dune ecosystem on Bodega Head, a small peninsula in Sonoma County, CA, USA, 105 km north of San Francisco (38°19′N, 123°3′W). This region experiences a Mediterranean-type climate, with 90 % of the rainfall occurring between October and April (Barbour et al. 1973). Our 500 × 100 m study area consisted of a hind-dune trough and surrounding ridges located within Sonoma Coast State Beaches, adjacent to the UC Davis Bodega Marine Reserve. Hind dunes typically support more vegetation and experience less harsh abiotic conditions (i.e., wind and salt spray) than foredunes, which lie between hind dunes and the ocean. Dune soils are sandy, fast-draining, and poor in organic matter and nitrogen (Barbour et al. 1973; McNeil and Cushman 2005; Lortie and Cushman 2007; Cushman et al. 2010).

Iceplant is a succulent, mat-forming perennial native to South Africa. It was introduced to California in the early 1900s as a dune stabilizer and has since spread to dune, grassland, and scrub communities along the coast (D'Antonio 1993). Individual plants can increase in

diameter by more than 0.5 m per year (D'Antonio 1993), and branches form roots at the nodes, allowing plants to form thick mats as they age (Bossard et al. 2000). At our study site, iceplant comprised approximately 25 % cover (S. M. Magnoli and J. H. Cushman, unpublished data), and was present for at least 50 years (J. Sones, personal communication). While the majority of the iceplant patches at our site fit the morphology of *Carpobrotus edulis*, hybrids between this species and *C. chilense* also occur in the area (Vilà and D'Antonio 1998).

Dominant native species at this site include two shrub species, *Ericameria ericoides* and *Lupinus chamissonis,* which represent 20 and 15 % cover, respectively (Cushman et al. 2010). In addition to iceplant, dominant exotic species in this system are primarily annual forbs and grasses. *Bromus diandrus* (Poaceae), an annual exotic grass, is especially prevalent at the site and has become common in many habitats across California since its introduction in the sixteenth century (Hoopes and Hall 2002).

Characteristics of invaded and uninvaded plant communities

To compare the characteristics of iceplant-invaded and uninvaded communities, we sampled 31 iceplant patches paired with 31 adjacent areas of uninvaded dune vegetation. We selected the iceplant patches at random throughout a 500 × 20 m south-facing slope of the study area. We determined the size of each selected iceplant patch by measuring its maximum diameter and the diameter perpendicular to the midpoint of this measurement. As uninvaded paired controls, we randomly selected an uninvaded area of at least 1 m², 1 m away from the edge of each iceplant patch. In April 2010, we sampled the entire plant community within a 20 × 30 cm quadrat placed in the center of each of the 31 iceplant patches and adjacent uninvaded areas. We used this relatively small sampling area because most plants in the system are small-statured. We counted the number of individuals and visually estimated percent cover for each non-iceplant species rooted in the quadrats. With these abundance and cover data, we grouped species by geographic origin (native or exotic), life history (annual or perennial), and life form (forb or grass). This resulted in eight possible groups: native and exotic annual forbs, native and exotic perennial forbs, native and exotic perennial grasses, and native and exotic annual grasses. Four of these groups—native perennial grasses, exotic perennial forbs, exotic perennial grasses, and native annual grasses— were either absent from our sampling areas or extremely uncommon, so we excluded them from our analyses. This left us with four groups: native annual forbs (18 species), exotic annual forbs (11 species), native perennial forbs (seven species), and exotic annual grasses (three species).

Iceplant-removal experiment

To determine the response of the community to iceplant removal, we established an iceplant-removal experiment in January 2010. We haphazardly selected 40 discrete iceplant patches (separate from those used in the previously described comparative study) ranging from 1 to 38 m² in size and distributed across a 250 × 20 m section of our study area. We divided each of the 40 patches into four equally-sized quarters, and randomly assigned each to one of the following treatment levels: iceplant removed, iceplant and litter removed, iceplant and associated soil disturbed but left intact (a procedural control), and unmanipulated (control). We removed living aboveground material by pulling and clipping. The sandy soil made it easy to pull most of the iceplant from the soil with minimal disturbance. In areas where iceplant was too deeply rooted to pull without causing substantial soil disturbance, we cut branches at ground-level with clippers. We removed litter by gently raking it from the patch and relocated it to areas at least 20 m away from the study area. As a procedural control, we uprooted iceplant with a pitchfork to mimic the soil and root disturbance caused by iceplant removal. After uprooting the iceplant, we put it back in place, where it re-rooted and continued to grow.

In April 2010 and 2011, we sampled the plant community using a 0.2 m² quadrat placed in the center of each patch quarter. To minimize edge effects, we placed quadrats 10 cm from the two inside edges of each quarter and at least 10 cm from the outer edge. In each quadrat, we visually estimated percent cover and counted the abundance of all non-iceplant species. In the second year of the study, in April 2011, we also harvested all non-iceplant aboveground biomass from each quadrat, sorted the material to species, dried it at 60 ºC for 48 h and weighed the biomass. For the abundance, percent cover and biomass data, we pooled species into the same four groups described previously in the comparative study (native and exotic annual forbs, native perennial forbs, and exotic annual grasses).

Potential mechanisms of iceplant effects

We established a second experiment in November 2010 to assess whether iceplant affected another exotic plant, *Bromus diandrus*, via above- or belowground mechanisms. We chose *Bromus* because it was present in all of the iceplant patches in our removal experiment and is abundant throughout the dune site. Using *Bromus* also allowed us to test whether removing one invader facilitates increases in another invader. We randomly selected 20 of the 40 iceplant-removal patches described previously, each paired with an adjacent uninvaded area <1 m away. Within each block, we established four treatment levels: (1)

iceplant-invaded areas (to test for above- and belowground effects); (2) areas where iceplant had been removed in January 2010 (to test for belowground effects); (3) areas where iceplant branches were placed on top of uninvaded soil in November 2010 (to test for aboveground effects); and (4) uninvaded areas.

Within all treatment levels in each block, we used thin wire stakes to secure five 5 cm diameter plastic rings to the soil, and planted one *Bromus* seed within each ring. Prior to planting, we removed any other plants growing within the rings. We planted seeds at depths of 1 cm so that they were buried in the sand but their awns were still exposed. We recorded the emergence date and tracked the survival of seedlings until May 2011, counted the number of spikelets produced by each plant that survived to peak flowering, and then harvested the aboveground biomass of all plants. We dried this *Bromus* biomass at 60 °C for 48 h and then weighed it.

Statistical analyses

Unless otherwise noted, we conducted all statistical analyses using the general linear model procedure in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA). We transformed data when needed to correct for non-normal distributions or unequal variances. To analyze data on percent cover, abundance, and species richness from invaded and uninvaded patches, we conducted three multivariate analysis of variances (MANOVAs), with invasion status (iceplant-invaded, iceplant-uninvaded) and block (invaded–uninvaded pair 1–31) as grouping factors. We included block to account for spatial variation in the landscape, and treated it as a random effect. As response variables, the first MANOVA used the arcsine square root of percent cover of the four plant groupings (native and exotic annual forbs, native perennial forbs, and exotic annual grasses). The second and third MANOVAs used the natural log of abundance and species richness of these same plant groupings. For MANOVAs with significant invasion status main effects, we proceeded with protected ANOVAs using each of the four plant groupings as response variables. This method addresses possible correlations between multiple dependent variables (Scheiner 2001).

We used three repeated-measures MANCOVAs to analyze data on percent cover, abundance, and species richness from the iceplant-removal experiment, with iceplant treatment (iceplant removed, iceplant + litter removed, procedural control, control) as the grouping factor, patch size as a covariate, and year (2010, 2011) as the repeated measure. As response variables, the three MANCOVAs used the arcsine square root of percent cover and the natural log of abundance and species richness of the four plant groupings. We evaluated terms containing year using Pillai's trace,

which is robust to violations of assumptions (Scheiner 2001). We used a MANCOVA to analyze data on aboveground plant biomass (g/m^2) from 2011, with iceplant treatment as the grouping factor, patch size as a covariate, and the natural log of the biomass of the four plant groups as response variables. In all cases, we again followed MANCOVAs with significant iceplant treatment terms with ANCOVAs, using each of the four plant groups as response variables. For models with significant iceplant treatment terms, we performed Tukey–Kramer HSD multiple comparison tests ($\alpha = 0.05$) to compare means.

We used four linear mixed models to analyze the effects of iceplant on *Bromus* performance (percent germination, percent survival, average biomass per plant, and average number of spikelets per plant), with iceplant treatment (iceplant removed, added, present or absent) and patch (1–20) as the grouping factors. As before, we treated patch as a random effect.

Results

Characteristics of invaded and uninvaded plant communities

Our comparative study revealed that community composition differed between iceplant-invaded and -uninvaded areas. MANOVAs indicated that the four plant groupings considered collectively differed significantly in percent cover ($F_{4,26} = 10.78$, $p < 0.0001$), abundance ($F_{4,26} = 12.42$, $p < 0.0001$), and species richness ($F_{4,26} = 12.73$, $p < 0.0001$) between iceplant-invaded and -uninvaded patches. Subsequent ANOVAs showed that the cover of native annual forbs was significantly lower in invaded areas (Table 1; Fig. 1), while abundance and species richness did not differ between invaded and uninvaded areas (Table 1; Fig. 1). The cover, abundance, and species richness of exotic annual forbs did not differ between invaded and uninvaded areas, whereas cover, abundance,

Table 1 Results from a series of "protected" repeated-measures ANOVAs evaluating the effect of iceplant invasion status on the percent cover, abundance, and species richness of different plant groupings

Plant group	df	% Cover	Abundance	Species richness
Native annual forbs	1, 29	4.28*	1.11	0.88
Exotic annual forbs	1, 29	0.83	0.04	0.77
Native perennial forbs	13, 29	26.40**	24.45**	28.87**
Exotic annual grasses	1, 29	15.01**	22.37**	21.58**

F statistics are presented with significance levels indicated as follows: * *P* < 0.05, ** *P* < 0.01
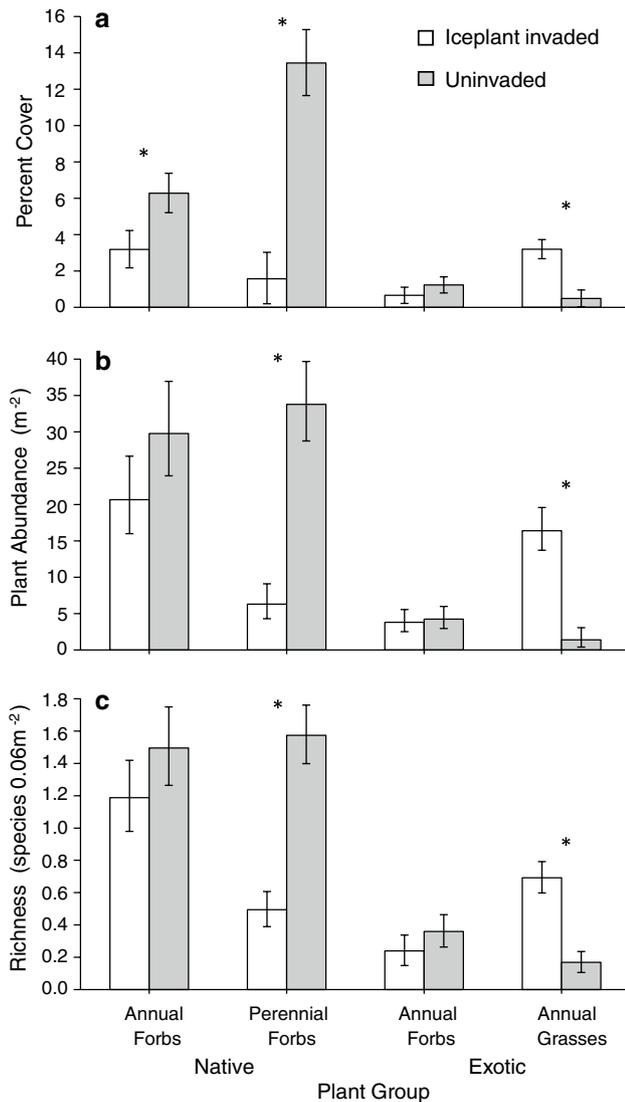
Fig. 1 Least square means (±1 SE) for **a** percent cover, **b** plant abundance (m^{-2}), and **c** richness (species 0.06 m^{-2}) of four plant groups as a function of iceplant invasion status (iceplant-invaded, iceplant-uninvaded). *Asterisks* denote significant differences between invasion statuses

and richness were significantly lower for native perennial forbs in iceplant-invaded areas (Table 1; Fig. 1). The opposite pattern was detected for exotic annual grasses, where cover, abundance, and species richness were all significantly higher in iceplant-invaded areas (Table 1; Fig. 1).

Iceplant-removal experiment

MANCOVAs indicated that our iceplant-removal treatment had a significant overall effect on percent cover ($F_{12,453} = 5.42$, $p < 0.0001$), abundance ($F_{12,453} = 5.68$, $p < 0.0001$), species richness ($F_{12,453} = 5.32$, $p < 0.0001$), and aboveground biomass ($F_{12,453} = 5.85$, $p < 0.0001$) of

the four plant groups considered collectively. Subsequent ANCOVAs showed that cover, abundance, species richness, and biomass of native annual forbs, native perennial forbs, and exotic annual forbs all increased with removal of iceplant (Table 2; Figs. 2, 3). Multiple comparisons tests indicated that, in all cases, iceplant removal and iceplant + litter removal were not significantly different from each other but both were significantly different than the two controls. In addition, the effects of iceplant removal on the cover, abundance, and species richness of native and exotic annual forbs increased significantly a year after treatments were applied (Table 2). A significant treatment × patch size interaction indicated that native perennial forb abundance and biomass decreased with increasing patch size in the removal treatments (Table 2). In contrast to the other groups, iceplant removal had no effect on the cover, abundance, richness, or biomass of exotic annual grasses (Table 2; Figs. 2, 3).

Potential mechanisms of iceplant effects

Our *Bromus* experiment revealed that percent seedling emergence for this exotic annual grass was significantly affected by the iceplant treatment ($F_{3,57} = 5.34$, $p = 0.0026$). A multiple comparison test showed that removed areas (belowground effects of iceplant) and invaded areas (above- and belowground effects of iceplant) did not differ in percent emergence, but that both had significantly lower emergence than uninvaded and iceplant-added areas (aboveground effects of iceplant), which did not differ from each other (Fig. 4a). Of the seedlings that emerged, there was a trend for the iceplant treatment to have an effect on aboveground biomass per plant ($F_{3,37} = 2.53$, $p = 0.0720$), with biomass being highest in uninvaded patches (Fig. 4c). In contrast, there was no effect of the iceplant treatment on percent survival ($F_{3,49} = 0.89$, $p = 0.45$; Fig. 4b) or spikelet production ($F_{3,37} = 2.02$, $p = 0.13$; Fig. 4d).

Discussion

Using a comparative study and two field experiments, we found strong differences in plant community composition between uninvaded areas and those invaded by a South African succulent in a coastal dune in northern California. Importantly, invader removal did not necessarily reverse all of these effects, at least in the timeframe of our experiment. We found that native plants were less abundant in iceplant-invaded areas, while some exotic species (namely annual grasses) were more abundant in iceplant-invaded areas. In general, both native groups and exotic forbs increased in abundance and cover following iceplant removal, but

Table 2 Results from a series of "protected" repeated-measures ANCOVAs evaluating the impact of iceplant removal treatment (IT), patch size (PS), and year (Y) on the percent cover, abundance, species richness, and biomass of different plant groupings

Plant group/variable	df	IT	IT × PS	IT × Y	IT × PS × Y
a) Native annual forbs					
% Cover	3, 152	5.58**	2.02	4.03**	3.01*
Abundance	3, 152	5.94**	1.45	6.02**	4.27**
Species richness	3, 152	7.74**	1.37	8.50**	3.23*
Biomass	3, 152	11.91**	2.17	–	–
b) Exotic annual forbs					
% Cover	3, 152	16.79**	0.63	7.03**	1.72
Abundance	3, 152	19.14**	1.59	14.31**	2.39
Species richness	3, 152	21.16**	1.35	11.47**	1.44
Biomass	3, 152	26.91**	1.57	–	–
c) Native perennial forbs					
% Cover	3, 152	8.97**	0.80	0.78	5.46**
Abundance	3, 152	8.01**	3.34*	0.75	2.87*
Species richness	3, 152	7.76**	2.20	1.52	0.39
Biomass	3, 152	9.17**	2.97*	–	–
d) Exotic annual grasses					
% Cover	3, 152	0.21	0.53	0.17	0.07
Abundance	3, 152	0.43	0.50	1.84	0.87
Species richness	3, 152	0.05	0.50	0.87	0.75
Biomass	3, 152	0.18	0.73	–	–

F statistics are presented with significance levels indicated as follows: * $P < 0.05$, ** $P < 0.01$. *F* statistics for patch size and year main effects are omitted

exotic annual grasses did not respond to removal. When we explored the effects of iceplant on the exotic annual grass *Bromus diandrus*, we found that, despite the positive association between iceplant invasion and *Bromus* abundance, iceplant negatively affected *Bromus* individuals.

Numerous studies have previously assessed various factors that influence the performance of iceplant and evaluated its effects on invaded environments. Some of these have examined the indirect effects of iceplant on native plants via pollinators (Moragues and Traveset 2005) and soil properties (Vilà et al. 2006; Conser and Connor 2009). Others have explored factors that influence the growth and invasion success of iceplant (D'Antonio 1993; D'Antonio et al. 1993; Traveset et al. 2008), or its seed production and dispersal (D'Antonio 1990b). D'Antonio and Mahall (1991) documented that iceplant had negative effects on two native shrubs via competition for water. Surprisingly, we know of only a few studies that have examined the effects of iceplant on entire plant communities (Vilà et al. 2006; Maltez-Mouro et al. 2009; Andreu et al. 2010). Consistent with the results of our comparative study, these studies have found predominantly negative associations between iceplant invasion and native plant richness and diversity. For example, Maltez-Mouro et al. (2009) found a weak negative association between iceplant invasion and the diversity of native perennial and biannual species in Portuguese coastal dunes. On eight islands in the Mediterranean basin, Vilà et al. (2006) found stronger associations, with 36 % lower native species richness in iceplant-invaded

areas than in uninvaded areas. Their study also showed that the effects of iceplant were island dependent, but that annual species were consistently negatively associated with iceplant invasion, possibly due to decreased seed germination in thick iceplant mats. Similarly, our comparative study revealed that iceplant-invaded areas had reduced cover of native annual forbs and reduced cover, abundance, and richness of native perennial forbs. The similar findings of these studies suggest that iceplant has consistently negative effects on native plants in geographically widespread regions. However, we also found that iceplant-invaded areas had greater cover, abundance and species richness of exotic annual grasses than uninvaded areas. These contrasting results emphasize the utility of analyzing responses of plant groups that differ in life history, life form, and geographic origin.

Our removal experiment provided insight into how iceplant can affect the community. We found that iceplant removal increased the cover, abundance, richness, and biomass of native annual and perennial forbs. This makes sense in light of our comparative study results, which showed a negative association between these groups and iceplant invasion. In addition, we found that native perennial forb abundance and biomass in the removal treatments decreased with increasing iceplant patch size. It is likely that perennial forbs were present in sites prior to iceplant invasion, so those located in small iceplant patches were likely competing with iceplant for less time, meaning that they recovered more quickly after iceplant removal than
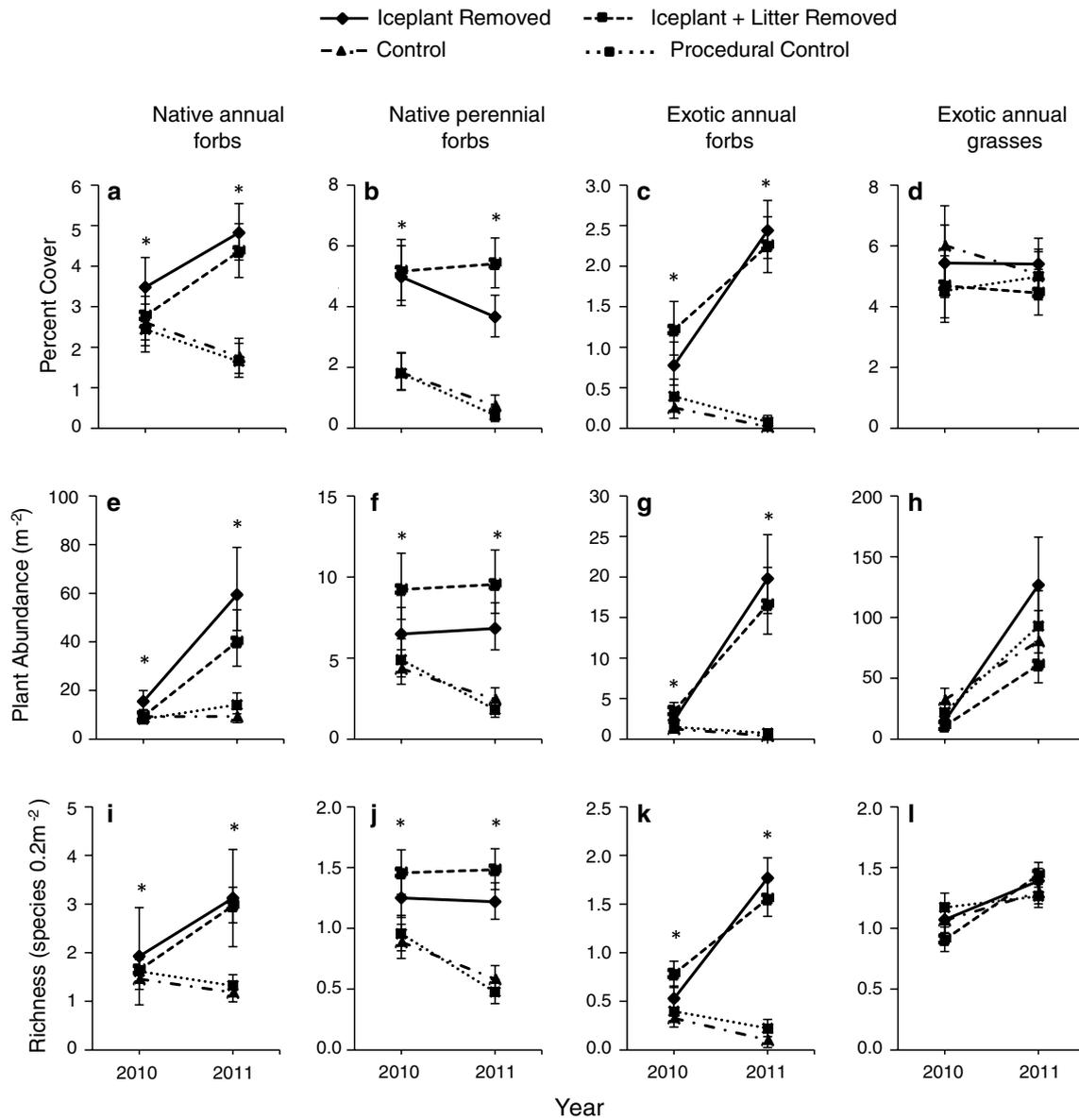
Fig. 2 Least square mean (±1 SE) percent cover, plant abundance (m^{-2}), and richness (species 0.2 m^{-1}) as functions of iceplant treatment (iceplant removed, iceplant + litter removed, procedural control, control), and year (2010, 2011) for **a**, **e**, **i** native annual forbs, **b**, **f**, **j** native perennial forbs, **c**, **g**, **k** exotic annual forbs, and **d**, **h**, **l** exotic annual grasses. *Asterisks* denote significant differences between treatment levels within years

those in larger, older iceplant patches. It is possible that we did not see a patch size effect on the other plant groups because they are all annuals. For exotic annual forbs, the effects of experimental removal were in opposition to those of the comparative study. Specifically, iceplant removal increased the cover, abundance and species richness of exotic annual forbs, whereas the comparative study did not detect differences in these variables. Such results are similar to those of Andreu et al. (2010), who found that iceplant removal in coastal dunes in southern Spain increased the cover of annual plant species, as well as other studies

showing that the removal of a dominant invader can sometimes benefit exotics as well as natives (e.g., Alvarez and Cushman 2002; Erskine Ogden and Rejmanek 2005). It is possible that the observed increases in exotic forb cover and abundance following iceplant removal are transient effects that will gradually diminish as the community moves back towards an uninvaded state. On the other hand, this increase in exotic forbs could potentially persist, making restoration of iceplant invaded areas more difficult.

Our study produced a set of seemingly contradictory results on the effect of iceplant on exotic annual grasses:
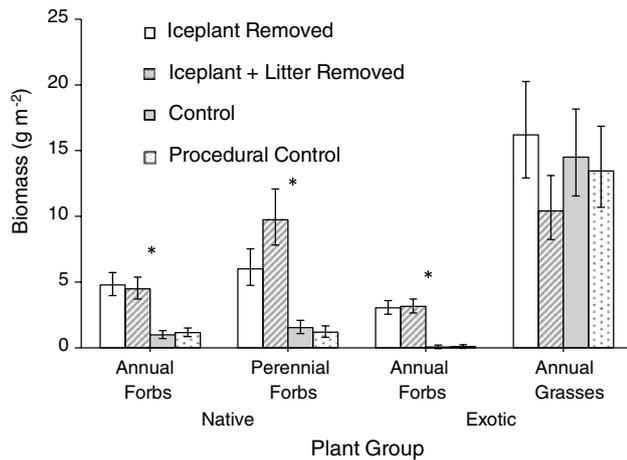
Fig. 3 Least square mean (±1 SE) aboveground biomass (g m^{-2}) of four plant groupings as a function of iceplant treatment (iceplant removed, iceplant + litter removed, control, procedural control). *Asterisks* denote significant differences between treatment levels

this group was more abundant where iceplant had invaded, yet iceplant removal did not lead to a decrease in this group's abundance. Moreover, we found negative effects of iceplant on the dominant exotic annual grass, *Bromus diandrus*. These results suggest that either iceplant and *Bromus* both favor similar microsites within the dune habitat, or iceplant invasion favors grasses such as *Bromus* in the long term despite the fact that iceplant directly reduces *Bromus* growth. Given these explanations, we suggest three possible hypotheses to explain why annual exotic grasses, especially *Bromus*, did not respond to iceplant removal in the manner predicted: (1) iceplant and *Bromus* favor similar sites, so iceplant removal should have no effect on *Bromus*; (2) the lack of response is short term, and as abundances of other species increase in removal plots, annual grass abundance will eventually decrease; or (3) iceplant acts as a seed trap that accumulates grass seeds. The first hypothesis is plausible if iceplant germinates more favorably in certain microsites that *Bromus* also favors and stays restricted to those sites as it grows. However, given the fast, clonal growth of iceplant, a patch might not remain restricted to these sites as it grows. In support of the third hypothesis, previous studies of seed banks in windy environments have found that vegetated microsites and shrubs have higher seed numbers and better seed retention than adjacent unvegetated areas (Aguiar and Sala 1997; Li 2008). Our study site experienced frequent high winds, and the dense mats of iceplant, surrounded by mostly bare sand where seeds are highly mobile, likely caught and retained seeds. Seeds of annual grasses could accumulate underneath iceplant, leading to increases in percent cover and abundance in the comparative study, despite the fact that *Bromus* individuals germinated and

grew best outside of iceplant. Removal may not have reduced this effect if there was a large seed bank of these species. Distinguishing between this and the two other hypotheses suggested above would require new experiments or long-term observations of the plant community after removal.

Our results provide insight into the potential mechanisms of iceplant influence on other species. The results of our *Bromus* experiment suggest that iceplant can affect this species by both above- and belowground means. We found that *Bromus* biomass was lower in areas with aboveground influence of iceplant than in areas with neither above- nor belowground influence, suggesting that *Bromus* competes with iceplant for light. The fact that biomass was also lower in areas with only belowground iceplant influence suggests that iceplant also influences *Bromus* by belowground means. We found that *Bromus* had significantly lower percent germination in areas with belowground iceplant influence than in areas without this influence. These results allow us to reject the hypothesis that iceplant invasion directly facilitates the invasion of *Bromus*—in contrast to the effects of iceplant on another exotic grass in a similar system (Cushman et al. 2011). Similarly, Conser and Connor (2009) found that a rare annual dune forb grew better in uninvaded soils than in iceplant-influenced soils. They hypothesized that an observed reduction in pH and increase in organic matter content had a negative effect on other plants. Increased organic matter is likely due to iceplant litter, the decomposition of which can lower soil pH, calcium, and nitrogen (Conser and Connor 2009), which could have negative effects on other plants. Vilà et al. (2006) also found significantly higher organic carbon content and lower soil pH in iceplant-invaded versus uninvaded soils. In contrast, we found no difference in soil pH between iceplant-influenced and -uninvaded soils at our dune site (Magnoli 2011). This suggests that the negative belowground effects of iceplant on *Bromus* in our study system were due to factors other than changes in soil pH.

Our removal experiment also showed that, for the most part, there were no differences in plant responses between iceplant-removed areas and areas where iceplant and litter were removed, suggesting that litter cover may not have large residual effects in this system. This could be because average litter cover and depth in our system were relatively low (42 % and <5 cm, respectively) compared to other areas where iceplant can form mats of live and dead material up to 40 cm deep (D'Antonio 1990a, b). Our results indicate that the arduous task of removing litter during restoration efforts may not be necessary when litter buildup is low.

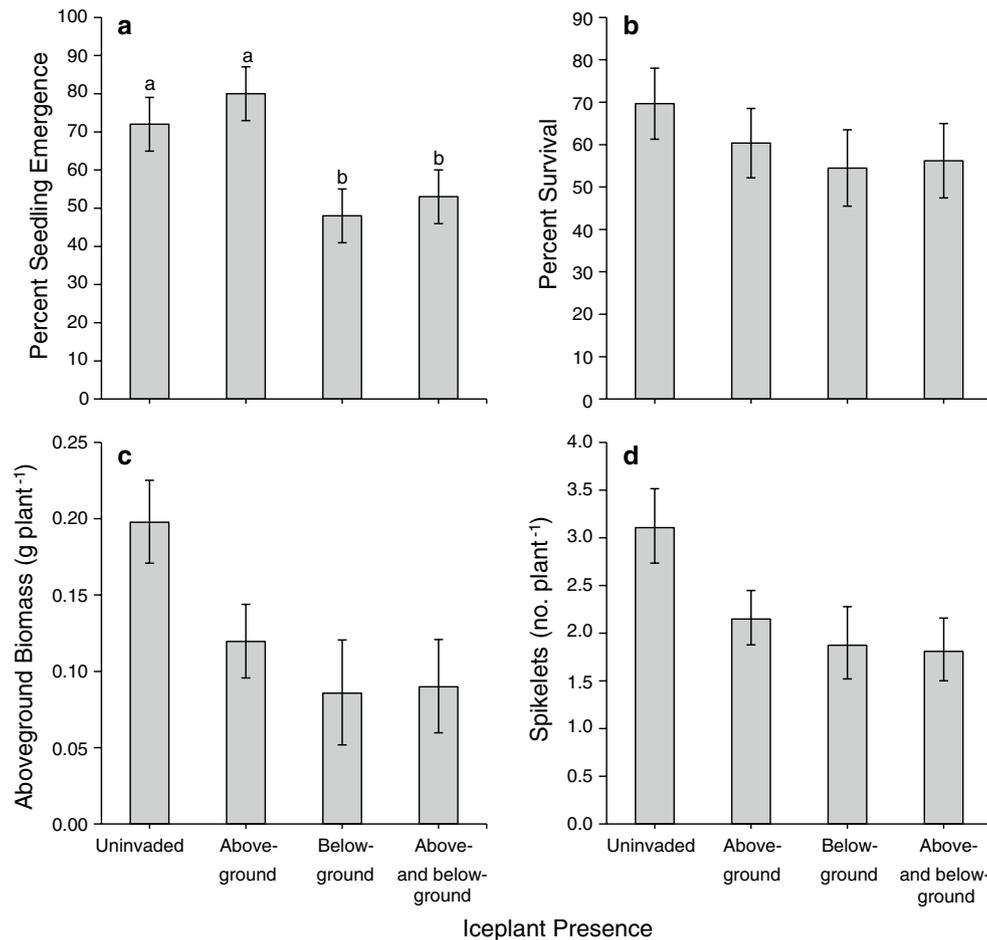Given the increasingly global nature of biological invasions, determining the effects of exotic species on the

Fig. 4 Least square mean (±1 SE) of **a** percent seedling emergence, **b** percent survival, **c** aboveground biomass (g plant^{-1}), and **d** spikelets (no. plant^{-1}) of *Bromus diandrus* as a function of iceplant treatment (uninvaded, added, removed, present)

communities they invade is critically important. Studies that quantify both invader effects and the responses to invader removal are especially useful in that they can reveal whether an invader has influences on the community that persist even after its eradication. This is not only relevant for restoration purposes, but can also give insight into the mechanisms of invader effects. Because many of the world's most diverse areas are already heavily invaded, we argue that we must move beyond asking only what the effects of historic plant invasions have been to conducting studies that address whether restoration practices, such as invasive plant removal, will produce desired results for conservation and resource management. Surprising results, such as some of those obtained in our study, may change the course of conservation and restoration strategies in invaded areas.

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