



Contributions of Perennial Pepperweed (*Lepidium latifolium*) Invasion to Rarity of the Endangered Suisun Thistle (*Cirsium hydrophilum* var. *hydrophilum*)

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Abstract

Invasive species exert disproportionate impacts in wetlands and pose particular challenges for rare species persisting at small spatial scales. In the urbanized San Francisco Estuary (SFE), which contains 90% of California's remaining coastal wetlands, invasive and rare species often co-occur. One narrow endemic taxon, the federally listed Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*) is restricted to two or three locations where the invasive perennial pepperweed (*Lepidium latifolium*) has an increasing presence. Perennial pepperweed has invaded salt, brackish, and freshwater wetlands around the SFE, leading to high management concern. In this study, we investigated how perennial pepperweed may contribute to further rarity of the Suisun thistle, by conducting a removal experiment and surveying soil-plant relationships. Removing pepperweed led to a doubling of native species relative cover and an increase in native species richness by an average of one species per plot, positive effects on Suisun thistle cover, number, and reproductive output, and shifts in soil properties. Combined with survey data inside and outside of pepperweed stands, we conclude that pepperweed competes with Suisun thistle via competition for space, nutrients, and light, interferes with the Suisun thistle's reproductive success, and alters brackish marsh soil physicochemical characteristics to further favor pepperweed. We recommend local control of pepperweed to prevent further loss of Suisun thistle. Further, the wide range of mechanisms by which this invasion may proceed if unchecked should be considered in other settings where rare or uncommon species are at risk from invaders.

Keywords Brackish marsh · Invasive species · Perennial pepperweed · Rare plant · San Francisco Estuary · Suisun thistle

Introduction

Invasive plants are known to impact a variety of ecosystem functions (Vila et al. 2011), but these effects are not evenly distributed among ecosystems. Wetlands, which comprise 6% of the earth's land mass, host 24% of the most invasive plant species (Zedler and Kercher 2004). These wetland

invaders compete with native species and modify physical and biological environments through increased sediment trapping and altered nutrient dynamics, food webs, and water cycling (Zavaleta 2000; Blank and Young 2002; Able et al. 2003; Windham and Meyerson 2003; Zedler and Kercher 2004; Burkle et al. 2012; Wigginton et al. 2014; Robison et al. 2021).

In addition to their disproportionate presence in wetland systems, the effect of invasive plants on native plant species richness is more pronounced at smaller compared to larger spatial scales (Gaertner et al. 2009; Powell et al. 2011, 2013), perhaps due to the increased importance of competition and other ecological interactions at this level (Huston 1999). This presents a particular challenge for rare species confined to specific habitat types and/or small geographic ranges, as they are already susceptible to extirpation from environmental stochasticity, genetic bottlenecks, and minimum density effects (Shaffer 1981; Frankham 2005).

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Invasive plants vary widely in the mechanisms by which they impact rare species; past work has documented impacts from competition, decreased recruitment, facilitating increased predation, and reproductive interference. For example, direct competition from invasive *Coronilla varia* and *Festuca arundinacea* reduced seedling establishment and growth of the endangered *Solidago shortii* in a grassland system (Walck et al. 1999). Similarly, invasive annual grasses reduced seedling recruitment of the endangered *Oenothera deltoides* ssp. *howellii*, mainly due to a thick thatch layer and reduced soil disturbance associated with the grasses (Thomson 2005a). In coastal dunes, seed predation by *Peromyscus maniculatus* mice on the endangered *Lupinus tidestromii* increased to highly detrimental levels with proximity to invasive *Ammophila arenaria*, which provided habitat and cover for the mice (Dangremond et al. 2010). Invaders can also interfere with reproduction of rare species through competition for pollination; for example, the presence of pollen from the invasive *Lythrum salicaria* reduced seed set in its rare congener, *Lythrum alatum* (Brown and Mitchell 2001).

The highly urbanized nature of the San Francisco Estuary (SFE) has led to widespread invasion of non-native species, and some native species with inherently limited distributions have become increasingly rare. Because the SFE has retained at most only 18% of its historic coastal wetlands (Brophy et al. 2019), managers aim to restrict invasive species and enhance survival of rare species, towards the larger goals of restoring wetland function and biodiversity (U.S. Fish and Wildlife Service 2013; Goals Project 2015). One invader of particular interest, in part due to its rapid spread into habitats with sensitive species, is perennial pepperweed, *Lepidium latifolium* (hereafter, *Lepidium*; Schoenig et al. 2003; Fiedler et al. 2007; Hogle et al. 2007; Reynolds and Boyer 2010).

Native to Eurasia, *Lepidium* is the fifth most common weed in California. It has been a longtime nuisance in the Western United States, invading floodplains, rangelands, riparian areas, crop fields, and tidal marshes (Miller et al. 1986; Renz 2000; Schoenig et al. 2003). More recently, *Lepidium* has become highly invasive in several marshes throughout New England (Orth et al. 2006; Connolly and Hale 2016) and is invasive in Canada (Francis and Warwick 2007) and Mexico (Roldán et al. 2009). *Lepidium* plants live for several years, reproducing both by seeds and from root fragments. It tolerates a range of salinity and inundation regimes and in tidal marshes is found most dense at the transition zone and in the marsh plain (Grossinger et al. 1998; Whitcraft et al. 2011). It is insect-pollinated, with small but abundant and fragrant flowers. Dense monotypes establish quickly, with a thick litter layer inhibiting growth of other species (Young et al. 1995; Renz and Blank 2004). *Lepidium* may alter soil properties by increasing elemental cycling and reducing soil salinity (Blank and Young 2002; Renz and

Blank 2004; Reynolds and Boyer 2010). Management has been particularly challenging in SFE wetlands, as mechanical control and herbicides are often impractical or prohibited (Spent 2006; Hogle et al. 2007; Boyer and Burdick 2010).

In Suisun Marsh (northeast SFE), *Lepidium* co-occurs with a number of rare species, including the endemic federally listed endangered Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*, hereafter, *Cirsium*; Goals Project 2000; Whitcraft et al. 2011; USFWS 2013). A biennial plant reproducing by seed, *Cirsium*, grows in intact brackish tidal marsh plain, along borders of channels and creeks, where average inundation time is 12.5% in a 24-h period, with a minimum of 6% and maximum of 24% (USFWS 2013; Graham-Bruno et al. 2023). It is likely pollinated by bees (USFWS 2013). In 1892, the botanist Greene described *Cirsium* as “very common in the brackish marshes of Suisun Bay, California, where it grows within reach of tide water” (Greene 1892). Wetland diking and reclamation through the 1930s destroyed much of *Cirsium*’s original habitat, and it is now restricted to two or three populations in fragments of intact tidal marsh, the largest of which is at Rush Ranch, Suisun City (Whitcraft et al. 2011; USFWS 2013). *Lepidium* started invading Rush Ranch in the 1990s, with dense infestations developing in the mid-2000s (Whitcraft et al. 2011). A census of the Rush Ranch *Cirsium* population in 2003 found that *Lepidium* was *Cirsium*’s third most common plant associate, present among 85% of subpopulations (Fiedler et al. 2007). Due to this high degree of habitat overlap, there is a concern that *Lepidium* may be increasing rarity in *Cirsium* through direct competition or other mechanisms (USFWS 2013). Additionally, there is a growing interest in understanding how *Lepidium* alters abiotic and biotic properties and interactions within ecosystems (Reynolds and Boyer 2010; Whitcraft et al. 2011; USFWS 2013; Wigginton et al. 2014; Wigginton et al. 2022).

To address the question of how *Lepidium* affects *Cirsium* and its brackish marsh ecosystem, we conducted a *Lepidium* removal experiment at a small spatial scale and monitored the response of *Cirsium*, other plant species, and soil properties over two growing seasons. To further quantify habitat and plant-soil relationships for *Lepidium* and *Cirsium*, we surveyed soil properties and plant characteristics in additional unmanipulated survey sites over two growing seasons, also at a small spatial scale of our study marsh.

We hypothesized that the invasion of *Lepidium* into *Cirsium* habitat presents a further challenge for a narrow endemic species already experiencing limitations at several life history stages, e.g., seed set, seed predation, and seed dispersal (Schneider and Boyer 2021; Graham-Bruno et al. 2023). Specifically, we expected that *Cirsium* abundance and reproductive output would increase following experimental *Lepidium* removal, as it would no longer face competition for light and nutrients from the invader. Alternatively, given

that *Cirsium* was rare before *Lepidium* invasion, competition with native dominant species recruiting following *Lepidium* removal could be similar to effects of *Lepidium*, and *Cirsium* might not benefit.

At unmanipulated survey sites, we expected soil salinity, moisture, and organic matter to be lower beneath *Lepidium* than *Cirsium* growing in the absence of *Lepidium*, as has been demonstrated for soils beneath the invader compared to soils beneath pickleweed (*Salicornia pacifica*) (Reynolds and Boyer 2010). A change in these and other soil properties in removal plots would suggest that *Lepidium* modifies them, perhaps in addition to colonizing areas that already have these characteristics.

Methods and Materials

Study Site

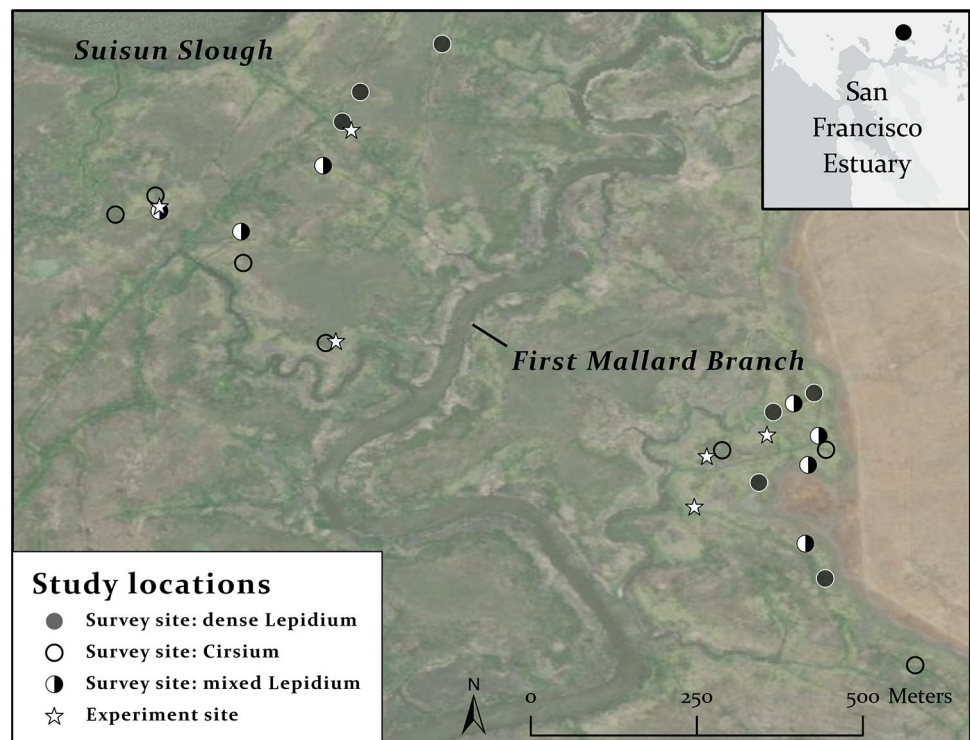
Rush Ranch in Suisun Marsh (38° 12' 31.7" N, 122° 1' 31.9" W) contains 425 ha of brackish tidal marsh within a 2000 ha preserve that is part of the National Estuarine Research Reserve System (Fig. 1). Like the surrounding Suisun Marsh, Rush Ranch is invaded by *Lepidium*; uniquely, however, it retains relatively large areas of undiked, intact tidal marsh and is home to several rare, threatened, and endangered species, including the California black rail (*Lateralus jamaicensis coturniculus*), California Ridgway's rail (*Rallus obsoletus obsoletus*), salt marsh harvest mouse

(*Reithrodontomys raviventris*), soft bird's beak (*Chloropyron molle* ssp. *molle*), Suisun Marsh aster (*Symphotrichum lentum*), and *Cirsium* (Goals Project 1999; Whitcraft et al. 2011). This study took place in the mid marsh zone within the First Mallard Branch area, which contains several sub-populations of *Cirsium* and is highly invaded by *Lepidium*.

Lepidium Removal Experiment

One pair of removal and control plots was established in March 2011 at each of six sites, with > 2 m between plots (Fig. 1). Sites were chosen where *Cirsium* rosettes were growing within dense *Lepidium* stands. In all plots, *Lepidium* was the dominant species present; percent cover of leaves (basal rosettes remaining green year-round) ranged from 19 to 52%, and percent cover of either dead stems or horizontal thatch exceeded 55% (Table S1, Online Resource 1). *Cirsium* rosettes (2–3) were present in each plot with an average cover of 4.8% (Table S1). Orthometric heights (elevation relative to a tidal datum) of the soil surfaces of all plots were within a range of 6 cm, and paired plots within a site had similar elevations (1–4 cm, Leica Real-Time Kinematic Global Positioning System, accurate to ± 2 cm). Control and removal treatments were randomly assigned; treatment areas were 4 m², centered on a 1 m² study plot. In removal treatment areas, *Lepidium* was clipped to remove aboveground biomass; dead stems and thatch were also removed. Resprouts and seedlings of *Lepidium* (but not thatch) were removed monthly throughout the experiment.

Fig. 1 Map of experimental plots and survey sites at Rush Ranch. Inset map shows location of study area within the San Francisco Estuary



In September 2012, light levels (photosynthetically active radiation, PAR) at the soil surface were measured using a spherical quantum sensor (LI-COR LI-193, Lincoln, NE) and compared for each pair of removal and control plots.

Plant cover was assessed on a quarterly basis over two growing seasons using a 1-m² quadrat grid with 25 sampling points. At each sampling point, a fiberglass rod was placed perpendicular to the ground, and plant species with green tissue touching the rod were recorded. Species present in the plot but not sampled by any of the points were recorded and used to determine species richness. Number of *Cirsium* plants was also recorded, and thatch depth was measured at four randomly chosen locations within each plot.

In August 2012, inflorescences per plant on all flowering *Cirsium* individuals were counted. In both August 2011 and 2012, three inflorescences in each plot that were past flowering but had not yet developed seeds were covered in a cloth bag with drawstrings (dimensions 6.5 cm × 8 cm) for later collection to determine seed set, seed predation by the beetle *Lasioderma haemorrhoidale* (family Anobiidae) observed during preliminary field visits, and seed germination levels in the lab (2012 only) (Surlles and Kok 1978). Inflorescences were randomly chosen whenever possible, though some plots had three or fewer inflorescences that met our criteria, in which case inflorescences closest to the plot were used, including some outside of the treatment area. Maximum height of the tallest individual in each plot was also recorded.

Soil samples were collected quarterly for two growing seasons using a PVC corer (diameter = 4 cm, depth = 10 cm) just inside the 1 m² plots. In the lab, soil moisture was determined gravimetrically. Soils were ground with a mortar, pestle, and mechanical grinder (Cuisinart Grind Central Coffee Grinder) to pass through a 2-mm sieve; salinity was determined using saturated soil pastes and a Leica refractometer (Reichert Analytical Instruments, Depew, NY) and percent organic matter determined by loss on ignition (500 °C for 3 h, Isotemp Programmable Muffle Furnace Model 650-126, Fisher Scientific, Pittsburgh, PA). A subset of samples 1 year apart representing spring conditions (March 2011 and March 2012) was analyzed for phosphorus and extractable cations (A and L Western Agricultural Labs, Modesto, CA; Bray and Kurtz 1945) and for carbon and nitrogen content (Costech ECS4010, Costech Analytical Technologies Inc., Valencia, CA).

Statistical Analyses

Statistical analyses were conducted in R Studio Version 1.1.453 (R Studio 2016, PBC, Boston, MA). Relative percent cover of native species in each plot was calculated by summing cover values for all native species and dividing by the sum of cover values for all species. This procedure was

repeated for non-native species other than *Lepidium*. Species richness was compared over time using a repeated measures ANOVA with month, treatment, and month*treatment as factors. Because percent cover values could not be adequately transformed to meet the assumption of normality, separate *t*-tests or Wilcoxon rank sum tests for treatment effects were conducted within each month.

A permutational multivariate analysis of variance (PERMANOVA) using distance matrices (*adonis* function, *vegan* package, Oksanen et al. 2018) was used to assess effects of *Lepidium* removal, stratified by site, on plant community composition during the summer of the second growing season. Mean thatch depth was compared between removal and control plots within each month using a *t*-test or Wilcoxon rank sum test.

Effect of *Lepidium* removal on *Cirsium* percent cover, number, mean seed set per inflorescence, and mean maximum height was examined by calculating effect size using Hedges' *g* (analogous to Cohen's *d* but for unequal or small sample sizes) at the end of the experiment (August and September 2012, depending on the variable). Effect sizes were also calculated to compare mean inflorescences per plant (per plot), mean seeds germinated per inflorescence (per plot), and mean number of larvae of the seed predator *L. haemorrhoidale* per inflorescence (per plot for August 2012 data).

Repeated measures ANOVAs were used to test for treatment and site effects on soil organic matter and salinity over time. Because soil moisture data could not be transformed to meet assumptions of normality, separate two sample *t*-tests or Wilcoxon rank sum tests were used to test for treatment effect within each sampling month.

A principal component analysis (PCA) was conducted on the nine measured variables (soil salinity, moisture, organic matter, carbon, nitrogen, phosphorus and extractable cations Na⁺, K⁺, Mg²⁺, and Ca²⁺) from cores from before the experimental treatment (March 2011) and 1 year later (March 2012). One observation was omitted due to lack of sufficient sample for phosphorus and cation analyses. Scores from principal components with Eigenvalues > 1 were then used in a two-way repeated measures ANOVA to test for year and treatment effects. Principal component 2 (PC2) scores could not be adequately transformed to meet normality assumptions; separate Welch two-sample *t*-tests were conducted for overall year effect and within-year treatment effects.

Unmanipulated Survey Sites

In April 2011, soil survey sites were established in unmanipulated areas that included dense *Lepidium* stands, mixed stands of *Lepidium* and other species, and *Cirsium* (*n* = 7 for each vegetation type, Fig. 1). For *Lepidium*, sites

were chosen using a random compass direction and distance; the first *Lepidium* encountered after walking the specified distance was classified as either dense (monotypic in April, with other species present later in the season) or mixed (other species present in April). For *Cirsium*, upon reaching known locations, sites were chosen by walking in a random compass direction, and soil was sampled beneath the first individual encountered. *Lepidium* was not present in these *Cirsium* sites.

At each survey site, two 5-cm diameter soil cores were taken to a depth of 6 cm and divided into 0–2 cm and 2–6 cm fractions to examine potential differences between surface and deeper soils as documented in previous *Lepidium* research (Reynolds and Boyer 2010). Cores were taken quarterly through July 2012 and were analyzed for moisture, salinity, and organic matter, as described above. A subset of soils from the peak growing season (samples from July 2011, 2–6 cm) was also analyzed for carbon, nitrogen, and phosphorus, as described above.

In August 2011 and 2012, plant measurements were taken at survey sites. At *Cirsium* sites, a 0.25-m² quadrat was positioned haphazardly, ensuring that at least one flowering *Cirsium* was contained therein. Maximum canopy height, total number of stems, and number of stems per individual were recorded, and stem length was measured for up to five randomly chosen stems. A leaf was collected from the non-flowering thistle closest to the sampling point, as leaves on reproducing thistles had already started to senesce.

At *Lepidium* sites (both dense and mixed stands), the 0.25-m² quadrat was placed randomly, while ensuring that *Lepidium* plants originated within. Maximum canopy height, approximate area covered by flowers, total stem number, and number of stems per plant of three randomly chosen individuals were recorded. Stem length was measured for five randomly chosen stems, and a leaf sample was taken.

Leaf samples were rinsed in deionized water, dried at 50 °C overnight, and ground using a mortar and pestle. Carbon and nitrogen content were determined using an elemental analyzer (Costech ECS4010, Costech Analytical Technologies Inc., Valencia CA); subsamples were sent to the UC Davis Analytical Laboratory for phosphorus analysis (extractable or acid digestion method).

For soil properties that were measured quarterly (salinity, moisture, and organic matter), repeated measures ANOVAs were conducted with month, treatment, month*treatment, and depth as fixed effects. We also calculated and analyzed the difference in soil moisture between the surface (0–2 cm) and deeper (2–6 cm) samples. When data could not be adequately transformed to meet assumptions of normality and homogeneity of variances, separate one-way ANOVAs or Kruskal–Wallis tests were conducted within each month at each depth. Measurements taken only once (leaf and soil

% P, % N, % C, C:N, and N:P) were tested using one-way ANOVAs by treatment.

To examine the relationship between soil properties and plant characteristics for each species, a PCA was conducted on soil measurements taken beneath each species in July 2011. Linear regression models were run for species-specific plant measurements taken in August 2011 versus principal components that encompassed over 80% of the variation (PC1 and PC2 for *Cirsium* soils, and PC1, PC2, and PC3 for *Lepidium* soils).

Results

Response of Plant Community to *Lepidium* Removal

Revegetation of removal plots was rapid, with only 1.3% (95% CI = $\pm 2.7\%$) bare ground observed at the first quarterly sampling. Monthly clipping of *Lepidium* was effective in controlling the invader (Fig. 2a); though *Lepidium* resprouted vigorously in removal plots during the first month following removal, in subsequent months during the first growing season little to no removal was required. During the spring of the second growing season (April 2012), an average of 13 vegetative resprouts was present per 4-m² treatment area. In September 2012, light levels at the soil surface varied between 1.8 $\mu\text{mol s}^{-1} \text{m}^{-2}$ in the most vegetated control plot to 61 μmol in the least vegetated removal plot and were on average 2.02 times greater in removal plots than in paired control plots (95% CI ± 0.46), i.e., light levels were between 1.56 and 2.48 times greater in removal plots.

By the second growing season of the experiment, *Lepidium* removal significantly increased cover of native species ($p < 0.01$ for effect of treatment in September 2011, March 2012, June 2012, and September 2012, Fig. 2b). Total species richness was significantly higher in removal compared to control plots ($F_{1,79} = 23.00$, $p < 0.0001$; treatment by time interaction not significant). Initially, this effect was due to an increase in non-native species at the first quarterly re-sampling (June 2011). In subsequent sampling, both native and non-native species were encouraged by *Lepidium* removal, with non-natives (primarily annuals and senescing perennials) less consistently enhanced in fall (Fig. 2b–e).

Aside from *Cirsium*, which is a biennial species, the most abundant species in experimental plots were all perennials. In order of decreasing total cover values over all months, these were *Lepidium*; *Schoenoplectus americanus* (chairmaker's bulrush), a dominant, native brackish marsh species; *Potentilla anserina* ssp. *pacifica* (Pacific silverweed), a native herb; *Cirsium*; *Epilobium ciliatum* ssp. *ciliatum* (willow herb), a native herb; *Grindelia stricta* (marsh gumplant), a native shrub; and *Juncus balticus*,

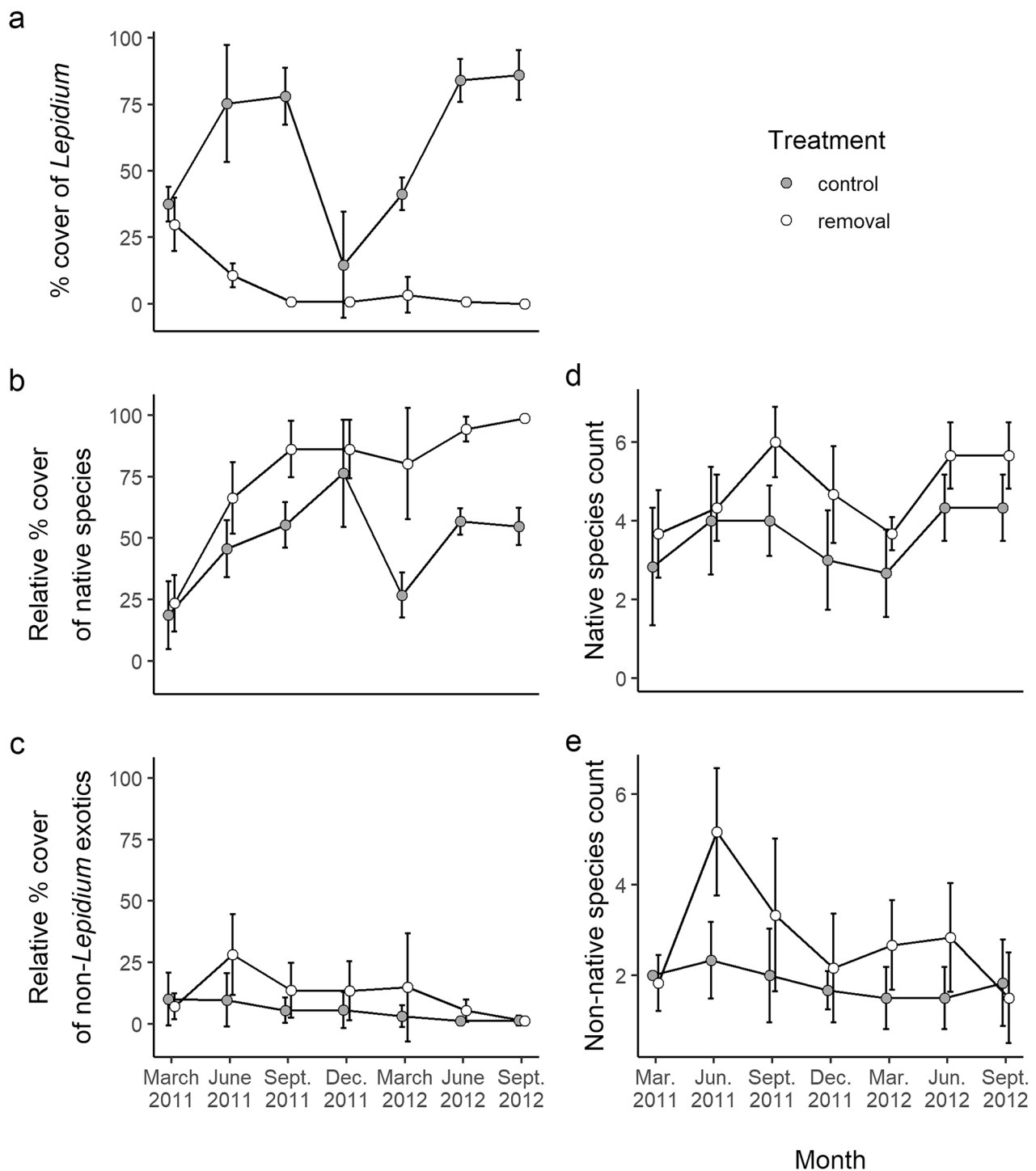


Fig. 2 **a** Percent cover of live *Lepidium* over time in removal compared to control (no removal) plots. Relative cover of **b** native species and **c** non-native species besides *Lepidium*, and species richness of

d native and **e** non-native species in removal and control plots over time. Error bars indicate 95% confidence intervals

(Baltic rush), a widespread native rush at this site. Figure S1 (Online Resource 1) shows cover of some of these species over time in removal versus control plots. Notably, some non-native species, including the annual *Atriplex prostrata*

(fat hen), annual or biennial *Apium graveolens* (wild celery), and annual or perennial *Helminthotheca echioides* (bristly ox-tongue), showed trends towards higher mean cover in removal plots during the first growing season, but not in

the second. The first season was during a wet year, and the second season was much drier, with 75% of average rainfall in the region (National Weather Service 2022), and was the first of several years of drought (California Department of Water Resources 2021). The one removal plot with high cover of a non-native species (*Helminthotheca echioides*, bristly ox-tongue) in the first year also had the highest *Cirsium* cover and number of individuals by the end of the experiment.

The PERMANOVA showed a significant effect of *Lepidium* removal on plant species composition in June 2012 ($F_{1,11}=0.99$, $p=0.03$). Relative to control plots, species with the largest responses to *Lepidium* removal were the natives *Schoenoplectus americanus*, *Epilobium ciliatum* ssp. *ciliatum*, *Juncus balticus*, and *Cirsium* (Table S2, Online Resource 1).

Lepidium thatch did not build up in removal plots, and litter layer depth was significantly greater in control plots than removal plots ($p<0.05$ in all months following initial *Lepidium* removal treatment; Table S3, Online Resource 1).

Response of *Cirsium* to *Lepidium* Removal

By September 2012, only one control plot contained *Cirsium*, compared to four removal plots (Fig. 3a). Removal showed a high effect size on percent cover of *Cirsium* (removal plot mean = 22.33, SD = 29.66, $n=6$; control plot mean = 0.67, SD = 1.63, $n=6$; Hedges' $g=1.00$, 95% CI = -0.20, 2.20, Fig. 3b) and a high effect size on number of *Cirsium* (removal plot mean = 3.50, SD = 4.93, $n=6$; control plot mean = 0.17, SD = 0.41, $n=6$; Hedges' $g=0.88$, 95% CI = -0.31, 2.06, Fig. 3c), though confidence intervals were large on the effect sizes (Cohen 1988). Recruitment of *Cirsium* was very high at one removal plot in particular, which contained 13 individuals at the end of the experiment.

Annual Measurements of Reproductive *Cirsium* Plants

In 2012, removal showed a medium effect size on viable seed production per plant (removal plot mean = 124.78, SD = 113.68, $n=4$; control plot mean = 51.79, SD = 28.07, $n=3$; Hedges' $g=0.68$, 95% CI = -0.80, 2.35, Fig. 3d) and a large effect size on number of *L. haemorrhoidale* larvae per seedhead (removal plot mean = 1.22, SD = 1.67, $n=6$; control plot mean = 3.17, SD = 1.45, $n=4$; Hedges' $g=1.10$, 95% CI = -0.20, 2.59, Fig. 3e). Removal showed a medium effect size on mean seed set per inflorescence during 2012 (removal plot mean = 25.0, SD = 21.8, $n=6$; control plot mean = 12.7, SD = 8.13, $n=4$; Hedges' $g=0.62$, 95% CI = -0.64, 1.98, Fig. 3f). Removal showed a low effect size on mean maximum height of *Cirsium*

(removal plot mean = 115.10, SD = 20.61, $n=5$; control plot mean = 120.92, SD = 7.32, $n=3$; Hedges' $g=0.29$, 95% CI = -1.73, 1.75, Fig. 3g.)

Effect of *Lepidium* Removal on Soil Properties

There was no treatment effect on soil salinity, moisture, or organic content. The PCA on nine soil variables (Fig. 4) resulted in three factors with Eigenvalues > 1. PC1 explained 37% of the variance in soil variables and was highly negatively correlated with Na^+ cations ($R^2=0.73$, $p<0.0001$), moisture ($R^2=0.61$, $p<0.0001$), and salinity ($R^2=0.60$, $p<0.0001$). Strong interannual differences in these soil conditions are indicated by significantly higher PC1 scores in March 2011 than March 2012 ($F_{1,15}=4.80$, $p=0.04$). There was no *Lepidium* removal effect on PC1.

PC2 explained 32% of the variance in soil variables and was positively correlated with K^+ cations ($R^2=0.76$, $p<0.0001$) and Mg^{2+} cations ($R^2=0.57$, $p<0.0001$) and negatively correlated with organic matter ($R^2=0.45$, $p=0.0005$) and moisture ($R^2=0.23$, $p=0.02$). Scores for PC2 were significantly higher in control plots than removal plots in 2012 ($t=2.3417$, $\text{df}=8.701$, $p=0.04$); thus, removal of *Lepidium* was associated with lower K^+ and Mg^+ and higher organic matter and moisture. PC2 scores were higher in 2012 than in 2011 across all treatments (Wilcoxon rank sum test, $W=25$, $p=0.01$).

PC3 explained 15% of the variance in soil variables and was mainly correlated with phosphorus ($R^2=0.65$, $p<0.0001$). PC3 values were significantly higher in 2011 than 2012 ($F_{1,18}=5.75$, $p=0.03$) and showed no treatment effect.

Unmanipulated Survey Sites

In unmanipulated survey sites, soil salinity in the deeper section only (2–6 cm) was affected by month ($F_{5,89}=43.00$; $p<0.0001$), and there was a trend of a treatment effect, with salinity tending to be lowest beneath dense *Lepidium*, and higher beneath both *Cirsium* and mixed *Lepidium* ($F_{2,17}=2.69$, $p=0.10$, Fig. 5a). Soil organic content (0–2 cm depth only) differed significantly by treatment in July 2011 (mixed *Lepidium* > dense *Lepidium*, $F_{2,18}=4.15$, $p=0.03$) and July 2012 (mixed *Lepidium* > *Cirsium*, $F_{2,18}=4.23$, $p=0.03$) (Fig. 5b). Soil moisture was not significantly different by month or treatment. The difference between soil moisture at 0–2 cm and 2–6 cm tended to be lower beneath *Cirsium* and higher beneath *Lepidium*, most notably in July 2011 ($F_{2,17}=2.73$, $p=0.09$) and January 2012 (Kruskal–Wallis $\chi^2=5.276$, $\text{df}=2$, $p=0.07$) (Fig. 5c).

Leaf %P, %N, and %C were all significantly higher in *Lepidium* than in *Cirsium* and did not differ significantly between *Lepidium* stand types (Table 1). Plant C:N was

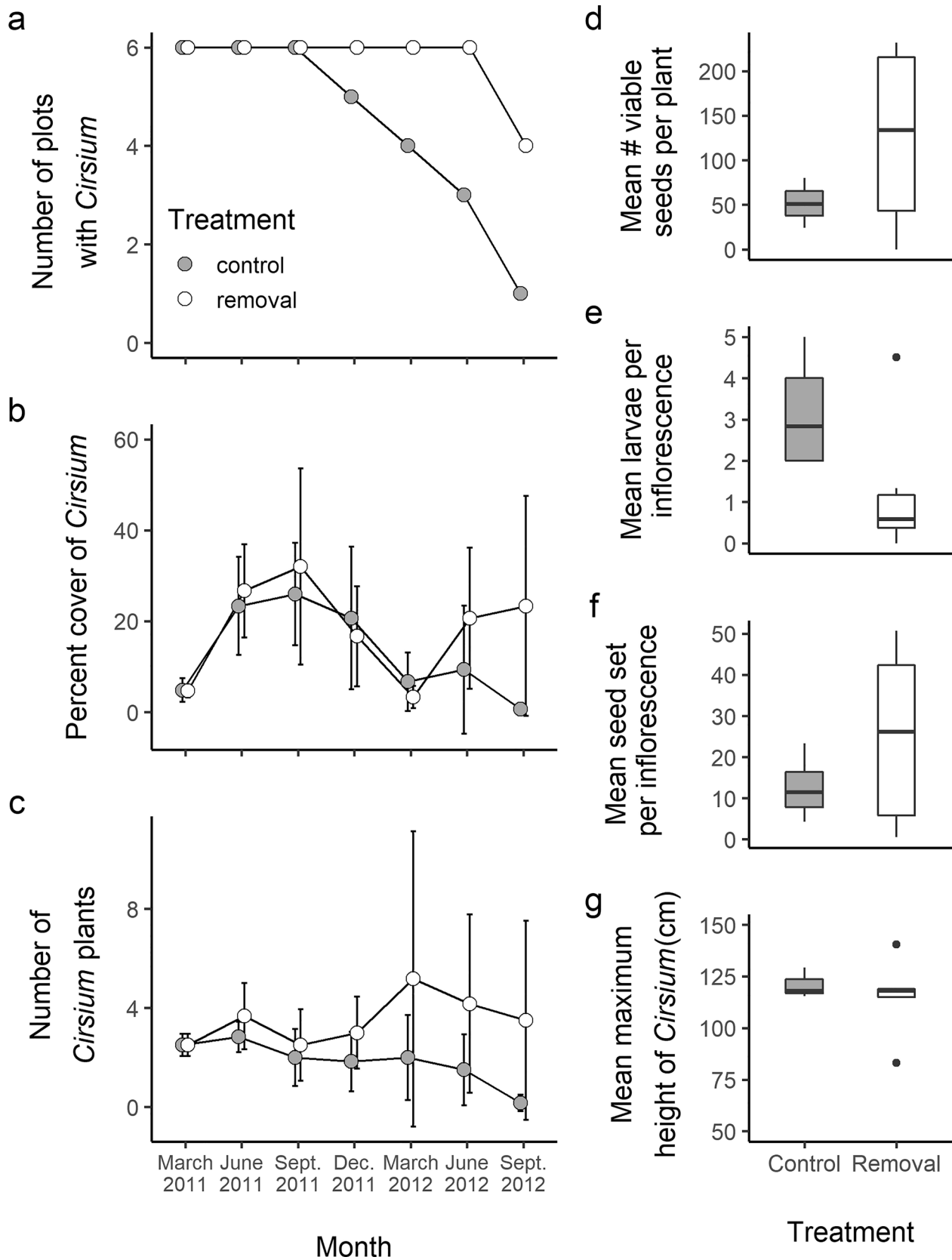
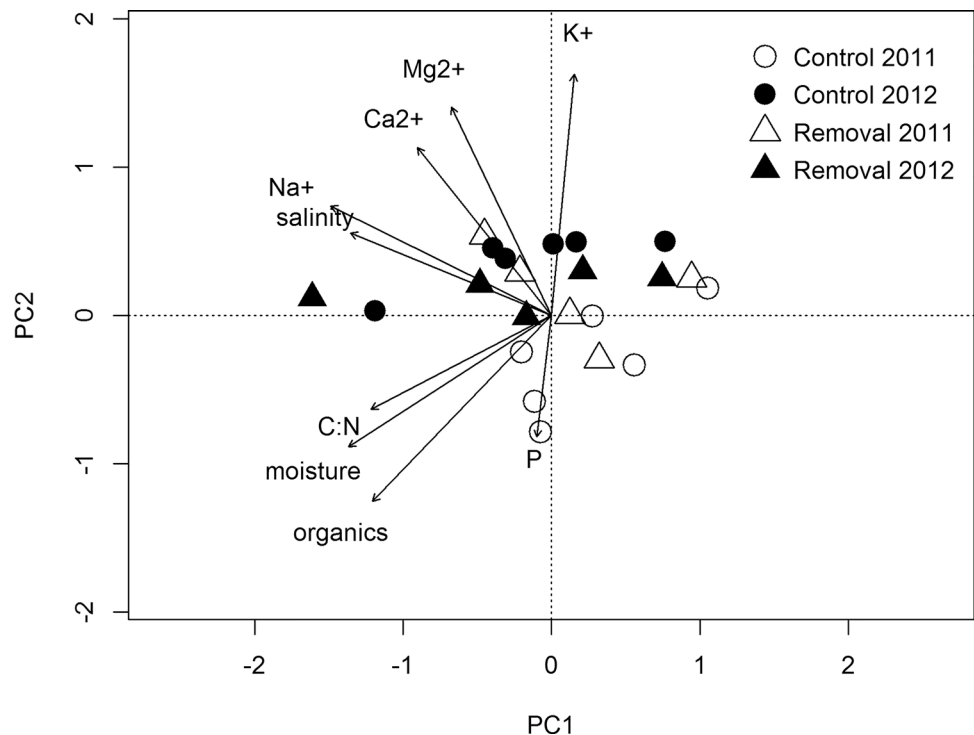


Fig. 3 *Cirsium* in removal and control plots over time. **a** Proportion of control plots containing Suisun thistle, **b** mean percent cover, **c** mean number of plants, **d** mean viable seeds per plant (Aug. 2012), **e**

mean *Lasioderma haemorrhoidale* larvae per seedhead (Aug. 2012), **f** mean seed set per inflorescence (Aug. 2012), and **g** mean maximum height (Aug. 2012). Error bars indicate 95% confidence intervals

Fig. 4 Principal component analysis on pepperweed removal experiment soil characteristics from March 2011 and March 2012



significantly higher in *Cirsium* than in *Lepidium*, due to relatively lower %N in *Cirsium*. Plant N:P was not significantly different between *Cirsium* and *Lepidium*. Soil from beneath *Cirsium* and *Lepidium* did not contain significantly different %P, %N, %C, C:N, or N:P (Table 1).

PC1 explained 71% of the variance in soil properties beneath *Cirsium* and was most highly correlated with soil moisture (2–6 cm depth), %C, organic content (both depth segments), and %N (Table S4, Online Resource 1). Mean number of inflorescences per plant was significantly positively correlated with PC1 ($R^2=0.63$, $p=0.04$), as was mean number of stems per plant ($R^2=0.68$, $p=0.03$) (Fig. S2, Online Resource 1). PC2 explained 14% of the variance in soil properties and was not significantly correlated with any plant measurements. None of the *Lepidium* plant characteristics we measured in unmanipulated plots were significantly correlated with PC1 or PC2 scores for *Lepidium* soil properties. A summary of plant measurements is given in Table S5 (Online Resource 1).

Discussion

Both theoretical models and empirical research indicate that invasive species impacts on species richness are greater at small spatial scales (Gaertner et al. 2009; Powell et al. 2011, 2013) and that invasive species present critical additional stress to rare species (Walck et al. 1999; Brown and Mitchell 2001; Thomson 2005a, b; Dangremond

et al. 2010; Combs et al. 2011). At the small spatial scale of our study, we also found evidence suggesting that *Lepidium* has a variety of effects on *Cirsium*, including competition for space, nutrients, and light, alteration of soil physicochemical characteristics, and interference with reproductive success, which taken together may be driving this endangered species along a path towards extinction (per Gilbert and Levine 2013; Downey and Richardson 2016). Though our results are specific to our study system, *Lepidium* impacts a variety of wetland habitats across different countries, and the interactions between invasive and rare species are of global relevance. We hope that this approach will inform research and management discussions in other places and systems.

Response of Plant Community to *Lepidium* Removal

Removal plots revegetated rapidly, with an increase in native species cover and overall species richness, indicating that the marsh contains a diversity of native propagules. The species that colonized removal plots generally reflected the vegetation composition adjacent to the plots, which varied across the study area. Although increased native cover and overall species richness was consistent with our hypothesis, native species also persisted in control plots, despite the presence of *Lepidium*. These areas of the marsh may be too frequently inundated for *Lepidium* to establish monotypic stands as it does in higher elevation zones (i.e., the marsh-terrestrial ecotone and levees).

Fig. 5 Soil properties beneath mixed *Lepidium*, dense *Lepidium*, and *Cirsium*. **a** Soil salinity at 2–6 cm, **b** soil organic matter at 0–2 cm, and **c** difference in soil moisture between 0–2 cm and 2–6 cm. Error bars indicate 95% confidence intervals

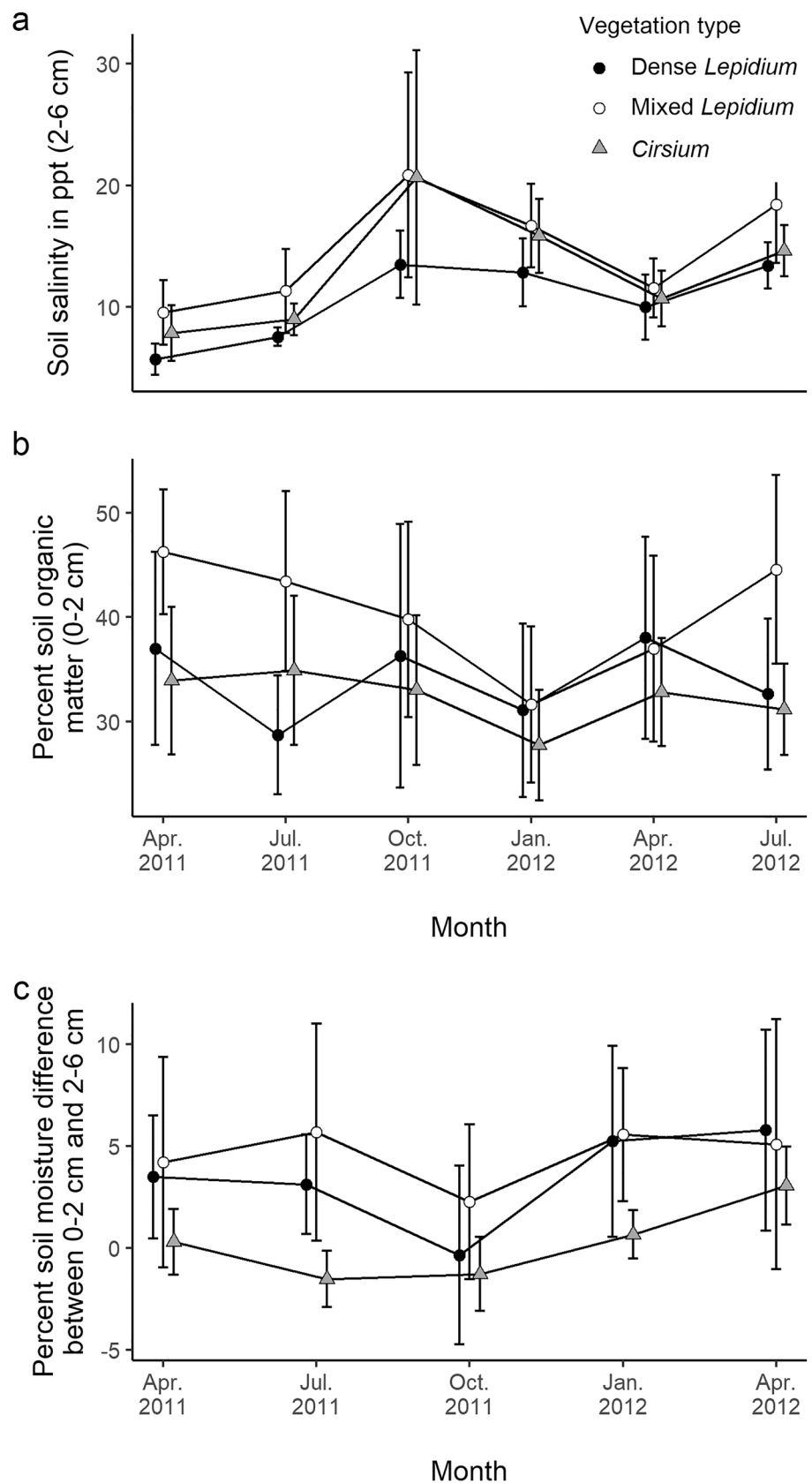


Table 1 Mean and standard deviations of leaf and soil concentrations of % C, % N, and % P, and ratios of C:N and N:P for *Cirsium* and *Lepidium* (mixed and dense stand data combined), summer 2011.

Asterisks denote variables that differed significantly by species at $p < 0.05$. Format is mean $\pm$ standard deviation

Leaf					
Species	C*	N*	P*	C:N*	N:P
<i>Cirsium</i>	38.20 $\pm$ 3.58	1.32 $\pm$ 0.42	0.14 $\pm$ 0.02	30.60 $\pm$ 9.41	9.11 $\pm$ 2.44
<i>Lepidium</i>	44.80 $\pm$ 1.86	3.48 $\pm$ 0.97	0.42 $\pm$ 0.18	13.36 $\pm$ 3.41	8.37 $\pm$ 1.61
Soil					
Species	C	N	P	C:N	N:P
<i>Cirsium</i>	15.11 $\pm$ 3.61	1.23 $\pm$ 0.16	15.01 $\pm$ 8.06	11.73 $\pm$ 1.98	95.18 $\pm$ 41.67
<i>Lepidium</i>	14.14 $\pm$ 5.32	1.21 $\pm$ 0.33	11.35 $\pm$ 4.24	11.08 $\pm$ 1.00	114.97 $\pm$ 40.75

Although some non-native species besides *Lepidium* were present in experimental plots, their abundance decreased during the drier second year; thus, removing *Lepidium* using this method did not facilitate establishment of other invasive plants. As mentioned above, the one removal plot with high cover of a non-native species (*Helminthotheca echinoides*, bristly ox-tongue) in the first year also had the highest *Cirsium* cover and number of individuals by the end of the experiment.

Response of *Cirsium*

By the end of the *Lepidium* removal experiment, *Cirsium* was present in one control plot and four removal plots. *Cirsium* number and cover showed positive effects of *Lepidium* removal over time in removal plots, which was concordant with our hypothesis. *Cirsium* may have been released from direct competition with *Lepidium* for light and nutrients. Because native vegetation and associated litter allow more light to reach the soil surface than *Lepidium* and its thatch, *Cirsium* seeds may have had increased chances of germination and survival. As we found higher levels of %N and %P in *Lepidium* leaves than *Cirsium* leaves in survey sites, removing *Lepidium* likely left more nutrients for uptake by other species. As noted above, *Cirsium* inflorescences per plant and stems per plant were significantly positively correlated PC1 (which was highly correlated with %N) at unmanipulated survey sites. Interspecific competition combined with limited reproductive output in *Cirsium* (Schneider and Boyer 2021) probably explains why we did not see a larger increase in *Cirsium* with *Lepidium* removal.

Lepidium removal may have had a positive effect on *Cirsium*'s production of viable seeds per plant because they had more resources available to them. Additionally, while *Lepidium* blooms are vast, showy, and fragrant, dominant native species are either wind pollinated (*Schoenoplectus americanus* and *Juncus balticus*, for instance) or do not form large, dense blooms (e.g., *Epilobium ciliatum* ssp. *ciliatum*). Thus, *Cirsium* may have a greater chance of

attracting pollinators when not growing directly with *Lepidium*. Alternatively, we may not have observed significant differences in seed set because all plots were surrounded by dense *Lepidium*; i.e., the matrix environment with respect to pollinators was fairly similar.

Notably, there were significant differences in *Cirsium* reproductive output between plants in experimental plots (removal and control plots combined) and those growing outside of dense *Lepidium* blooms measured in a separate study (Schneider and Boyer 2021). Seed set in experimental plots was 19.7 seeds per inflorescence (95% CI $\pm$ 4.5) compared to 33.7 seeds outside of the experiment (95% CI $\pm$ 4.7). There were 1.5 *L. haemorrhoidale* larvae per seedhead (95% CI $\pm$ 0.6) in experimental plots compared to 0.4 larvae per seedhead (95% CI $\pm$ 0.2) outside of the experiment. Finally, 17.4% of all seeds collected from the removal experiment germinated, compared to 34.2% of seeds collected from other areas. Vast *Lepidium* blooms may attract generalist pollinators, decreasing their visits to *Cirsium* plants, which could lead to reduced seed set in the latter. *Lepidium* may also provide suitable habitat for *L. haemorrhoidale*, or there may be other environmental variables affecting seed set, seed viability, and seed predation that correlate with *Lepidium* presence.

Effects of *Lepidium* on Soil Properties: Combined Evidence from Removal Experiment and Survey Sites

In addition to direct competition and interference with reproductive success, experimental and survey data point to a positive feedback loop in which *Lepidium* modifies soil properties towards conditions conducive to its growth (Reynolds and Boyer 2010). This feedback loop may increase rarity in *Cirsium* by magnifying the impacts of *Lepidium* discussed above and may impact the brackish marsh ecosystem as a whole through larger scale shifts in soil properties. Such ecosystem modifications have been demonstrated by other tidal marsh invaders such as non-native genotypes of *Phragmites*

australis on the East Coast (Windham and Ehrenfeld 2003) and hybrid *Spartina* (*Spartheina alterniflora* × *Spartina foliosa*) (Levin et al. 2006).

The largest responses of soil properties to *Lepidium* removal were decreases in K^+ and Mg^{2+} . Notably, PC2 scores were lower in *Lepidium* removal plots than in controls after 1 year of treatment and higher in 2012 than in 2011, as were overall levels of salinity and Na^+ in 2012. That K^+ and Mg^{2+} were lower in removal plots, while at the same time salinity, Na^+ , K^+ , and Mg^{2+} were higher overall in 2012 than 2011, suggests that *Lepidium* differentially affects those cations. In another study, *Lepidium* was found to have higher levels of K^+ and Mg^{2+} in its tissues than wheatgrass (*Elytrigia elongata*), so perhaps removing *Lepidium* led to a decrease of these cations in the soil (Blank and Young 2002). *Lepidium* may also be actively modifying its soil environment. Blank and Young (2002) followed *Lepidium*'s invasion of a grassland over time and documented that *Lepidium* increased Mg^{2+} , K^+ , and Ca^{2+} in soils, possibly by preferentially binding these cations to the soil complex in place of Na^+ to meet its higher requirements for these nutrients. The Na^+ may then leach down in the soil when it becomes inundated (Renz and Blank 2004), possibly explaining why lower Na^+ was observed beneath *Lepidium* in that study. Sodium cations, however, were not higher in removal than control plots, so perhaps anions or other factors contributing to salinity were at work in this study. Consistently higher mean salinity beneath mixed stands compared to dense *Lepidium* provides further evidence that *Lepidium* may be lowering soil salinity. Reynolds and Boyer (2010) also found lower salinity in dense *Lepidium* compared to *Salicornia pacifica*. Since 2012 was the first year of a prolonged drought (California Department of Water Resources 2021), it is possible that overall higher salinity levels in 2012 due to low rainfall may have made it difficult to detect changes in salinity resulting from *Lepidium*.

If *Lepidium* is indeed reducing soil salinity, this could put *Cirsium* and other native brackish marsh species at a disadvantage, as salinity tolerance can come with the tradeoff of reduced competitive ability (Bertness 1992; Pennings and Bertness 2001). Furthermore, brackish marsh plant community composition shifts during periods of higher and lower rainfall, with more saline periods favoring *Cirsium* (USFWS 2013). Additional implications could exist if certain native species have unusual requirements for specific cations.

Another notable soil response to *Lepidium* removal was an increase in organic matter. That *Lepidium* presence apparently leads to decreased soil organic matter is consistent with a study by Reynolds and Boyer (2010) who found lower organic matter beneath *Lepidium* than beneath *S. pacifica*. Indeed, organic matter tended to be higher in mixed than dense *Lepidium* stands. *Lepidium*'s persistent thatch layer may retard decomposition and increase conditions favorable for its growth.

Organic matter tended to be lower beneath *Cirsium* than at *Lepidium* sites. This is not surprising, as many congeners of *Cirsium* grow on poor soils, and its conspecific variety, *Cirsium hydrophilum* var. *vaseyi* (Mt. Tamalpais thistle) is restricted to serpentine soils, which have very low organic matter. Thus, in the absence of other impacts from *Lepidium* such as competition for nutrients and light, low organic matter does not appear to limit *Cirsium*. However, *Lepidium*'s reduction of soil organic matter has larger implications for the marsh, as organic matter accumulation is critical to marsh accretion in the face of sea level rise (Morris et al. 2002).

A few lines of evidence combine to suggest that *Lepidium* is decreasing soil moisture. Soil moisture in the *Lepidium* removal experiment was negatively correlated with PC2, which was higher in control plots than in removal plots. Additionally, the difference in soil moisture between 0–2 cm and 2–6 cm layers was greater in some months beneath *Lepidium* than *Cirsium*, suggesting that *Lepidium* is drying out deeper soil through evapotranspiration via roots. This may negatively affect *Cirsium*; as noted above, in the unmanipulated survey plots, both *Cirsium* inflorescences per plant and stems per plant were significantly positively correlated with PC1, which was most highly correlated with soil moisture (2–6 cm depth). Reynolds and Boyer (2010) found lower moisture beneath *Lepidium* stands compared to pickleweed stands at the same elevation and distance from channels. They suggested that evapotranspiration is greater from *Lepidium* than pickleweed due to its larger stature and non-succulent tissues. Many species present in the *Lepidium* removal experiment (such as *Cirsium*, *Grindelia stricta*, and *Schoenoplectus americanus*), by contrast, form tall canopies and have non-succulent tissues, which may explain why the soil moisture response was not greater in *Lepidium* removal plots.

Management Implications

By demonstrating how *Lepidium* affects *Cirsium* and its habitat, this study leads to a key management recommendation, to remove *Lepidium* in the vicinity of *Cirsium*, as the effects of *Lepidium* are reversible. Though labor intensive, the monthly reclipping method used in this study is effective and alleviates concerns about herbicides use and machinery in the vicinity of sensitive species. It could be carried out, potentially on a less frequent basis targeted to the spring and summer growing season, by staff or volunteers trained in discerning *Lepidium* leaves on early-season rosettes from those of other species. The timeframe for recovery would be expected to be at least two growing seasons, as some areas may initially experience an increase in other non-native species as seen in this experiment.

Treatment areas could be larger than in this study (4 m²) to minimize edge effects from *Lepidium* reseeding and could be combined with direct reseeding of *Cirsium* to increase chances of its persistence in these locations. Removal would ideally begin in early spring, before *Lepidium* resprouts vigorously. Areas in which *Lepidium* is less dense or just beginning to invade should be prioritized to prevent the development of dense infestations. Control efforts may also have increased effectiveness if timed to drought years; *Lepidium* has been shown to have lower stand density, seed production, and seed viability at high salinity sites (Leininger and Foin 2009), and recent work documented reduced vigor in *Lepidium* throughout the San Francisco Estuary due to salinity stress during the extreme drought of 2012–2016 (Kelso et al. 2020; Wigginton et al. 2020). In addition to increasing the presence of *Cirsium*, removal of *Lepidium* will also increase cover of other native species and prevent further shifts in soil properties demonstrated in this study such as decreases in organic matter, soil moisture, and soil salinity.

Conclusions

In this study, we examined whether invasive *Lepidium* is increasing rarity in the endangered *Cirsium*. Using a removal experiment and a survey of soil properties and plant characteristics in unmanipulated plots, we found evidence suggesting that *Lepidium* negatively affects *Cirsium* through several mechanisms, including competition for nutrients and light, changes to soil physicochemical characteristics, and interference with reproductive output and recruitment. As a narrow endemic species within an urbanized and altered estuary, additional impacts from *Lepidium* may be pushing *Cirsium* towards dangerously low population numbers. Other rare plants in Suisun Marsh and the larger San Francisco Estuary such as *Chloropyron molle* ssp. *molle* (soft bird's beak) and *Symphyotrichum lentum* (Suisun Marsh aster) may be similarly disproportionately impacted by *Lepidium* due to their small population sizes, habitat requirements, and/or life history limitations. The approach and results from this study can inform research and management in other wetland systems experiencing invasion from *Lepidium* or other ecosystem engineer-type invasive plants.

Effects of *Lepidium* documented in this study are, of course, occurring within a larger ecosystem context. Not only *Cirsium*, but also other plant species along with their pollinators, consumers, and decomposers are facing new abiotic conditions and biotic interactions, particularly with respect to altered soil physiochemical processes created by the invader. As in this study, quantifying and elucidating the mechanisms at work will help identify appropriate management actions, as well as strengthen our empirical understanding of invasive species effects.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-024-01326-x>.

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