Perennial Pepperweed (*Lepidium latifolium*): Properties of Invaded Tidal Marshes

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Lepidium latifolium (perennial pepperweed) is recognized as a threat to wetland habitats throughout much of the western United States, but its role in tidal marshes has not been explored. Over three seasons in three regions of San Francisco Estuary (Suisun, San Pablo, and South San Francisco bays), we characterized locations in tidal marshes where monotypic stands of *L. latifolium* are replacing the native *Sarcocornia pacifica* (pickleweed). Soils within *L. latifolium* stands had significantly lower moisture, salinity, organic matter, and carbon : nitrogen (C : N) and higher pH than in adjacent *S. pacifica* stands at similar elevation and distance from channels. In addition, *L. latifolium* canopies were 2 to 3 times taller, thus increasing light reaching soils, and tended to support different insect/spider assemblages (sampled only at the Suisun site). Patterns were generally consistent across the three sites, although less pronounced for some measures at the South Bay site. Overall, these data suggest that *L. latifolium* invasion of tidal marshes is leading to modification of both structural and functional properties, several of which might further facilitate spread of the invader; however, additional study is needed to determine cause vs. effect for several soil characteristics.

Nomenclature: Perennial pepperweed, *Lepidium latifolium* Linnaeus, *Sarcocornia pacifica* (Standl.) A. J. Scott.

Key words: Invasive species, pickleweed, San Francisco Bay, *Sarcocornia*, soils, wetlands.

Wetland ecosystems are the downstream recipients of physical and chemical inputs from the surrounding watershed as well as propagules carried by water and sediment, and thus are especially vulnerable to species introductions (Tyler et al. 2007; Zedler and Kercher 2004). Coastal wetlands, particularly in estuaries with extensive urbanization, farming, commercial shipping, or small boat usage, are particularly vulnerable to arrival and establishment of nonnative species (Holland et al. 2004). Several successful plant invasions in tidal marsh systems illustrate the range of alterations that can result. For example, a nonnative genotype of *Phragmites australis* (Cav.) Trin. ex Steud has transformed marshes on the U.S. east coast by

altering biogeochemistry, reducing microtopography, replacing native plant species, and reducing habitat value for several bird species (Benoit and Askins 1999; Chambers et al. 1999; Saltonstall 2002). Invasion of Tijuana River Estuary in southern California by *Tamarix* sp. (salt cedar) has led to changes in food web structure (Whitcraft et al. 2008). Several cordgrass species successfully have invaded tidal marshes, with dramatic effects. In the United Kingdom, the invasion of *Spartina anglica* C. E. Hubbard (Common Cordgrass), a hybrid between *Spartina maritima* (M. A. Curtis) Fern (small cordgrass) and *Spartina alterniflora* Loisel (smooth cordgrass) has led to decreased bird abundance (Goss-Custard and Moser 1988). In San Francisco Estuary, California, the introduction of *Spartina alterniflora*, and subsequent hybridization with the native *Spartina foliosa* Trin. (California cordgrass) has led to rapid spread of the hybrids over unvegetated mudflats as well as higher marsh elevations (Ayres et al. 2004), resulting in major changes in sediment physicochemical properties, community structure, and trophic dynamics (Brusati and Grosholz 2006; Levin et al. 2006; Neira et al. 2006).

In the San Francisco region, an estuary-wide effort began in 2005 to control *Spartina* hybrids (Grijalva et al. 2008); meanwhile, the spread of another invader in tidal marshes has gone relatively unnoticed. *Lepidium latifolium* Lin-

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Interpretive Summary

Until recently, pepperweed has been considered a nuisance in farm areas as well as fresh and brackish wetlands. This study documents large, near monospecific stands of this invasive weed in salt marshes with summer soil salinities well above 32 ppt. In addition, we observe differences in soil moisture, salinity, pH, organic matter, and nitrogen content between *Lepidium* dominated areas and adjacent areas dominated by the native *Sarcocornia pacifica*. A limited study also shows differences in insect and spider communities. These data indicate that the change in tidal marsh vegetation from *Sarcocornia pacifica* to *Lepidium latifolium* brings about community level and potentially ecosystem level changes. *Lepidium* is not easy or inexpensive to control (see Spenst 2006); therefore, careful monitoring and early removal (before stands have become well established) is essential.

naeus, commonly known as perennial pepperweed or tall white top, is a broad-leaved forb now found in all nine counties surrounding the San Francisco Estuary. Native to Eurasia, it was probably introduced to California in a shipment of sugar beet seeds in the 1930s (Robbins et al. 1951) and subsequently has invaded agricultural lands, grasslands, riparian areas, and coastal and inland marshes (Grossinger et al. 1998; Renz 2002; Young et al. 1995, 1997). Its prolific seed production and spread by creeping roots and detached root fragments provide multiple modes of recruitment both within and among wetlands (Trumbo 1994). The California Invasive Plant Council lists *Lepidium latifolium* as a severe threat in terms of impact, distribution, and invasiveness (Cal–IPC 2008). Although previously considered a wetland threat only in freshwater systems (Grossinger et al. 1998), land managers around the San Francisco Estuary now recognize this invader as an impediment to tidal marsh conservation (e.g., *Lepidium* Science and Management Workshop, October 2008, convened by the San Francisco Bay National Estuarine Research Reserve). *L. latifolium* can form dense and even monotypic patches in tidal marshes in all regions of the estuary, replacing the dominant native species (L. K. Reynolds and K. E. Boyer, personal observation). It is often found near channels (Andrew and Ustin, 2009) where plant species richness can be highest, and co-occurs with rare endemic species; e.g., *Cordylanthus mollis* ssp. *mollis* A. Gray (soft bird's beak) and *Cirsium hydrophilum* var. *hydrophilum* (Greene) Jeps. (Suisun thistle), excluding them or leading to a reduction in their cover or heights (Fiedler et al. 2007; Grewell et al. 2003).

For a number of successful invaders, modifications of soil properties are a particular concern, because changes can remain long after removal of the invader, perhaps creating positive feedbacks that further facilitate invasion and impede restoration of native species and functions (Byers et al. 2006; Suding et al. 2004). In seasonally flooded wetlands of intermountain eastern California, *L. latifolium* has been shown to increase the concentrations of carbon, nitrogen, phosphorus, sodium, and other elements in the soils relative to the tall wheatgrass [*Elytrigia elongata* (Host) Nevsk (Tall Wheatgrass)] it is replacing, with some elements concentrating in the upper horizons (Blank and Young 1997a, 2002, 2004). The effects of *L. latifolium* invasion on biogeochemical properties of soils in tidal marshes have not been explored.

The objective of this study was to evaluate differences in tidal marsh habitats where *L. latifolium* has established, and to do so over multiple regions of the San Francisco Estuary over several seasons. We focused on locations where the invader has established large (> 20 m diameter) nearly monotypic patches, where adjacent vegetation at similar elevations is composed of the California tidal marsh dominant, *Sarcocornia pacifica* (Standley) A. J. Scott (pickleweed). This permitted us to identify differences that could be attributed with a high degree of confidence to *L. latifolium* presence and to predict changes that are likely to occur across marsh landscapes as the invasion proceeds.

Materials and Methods

We selected three tidal marshes with large infestations of *Lepidium latifolium* to represent different regions of the estuary with different salinities and rainfall patterns: Rush Ranch, located in Suisun Bay; Petaluma Marsh, on the Petaluma River on San Pablo Bay; and South Bay, at Don Edwards National Wildlife Refuge, in south San Francisco Bay (Figures 1 and 2). At each of these sites, three stations were chosen, each consisting of adjacent patches of *Lepidium latifolium* and *Sarcocornia pacifica* (hereafter called by generic names). At each station, six 2 m by 2 m (6.6 ft by 6.6 ft) plots were established, three in *Lepidium*, and three in *Sarcocornia*. Within each station, all plots had similar elevations (within 3 cm [1.2 inches]; Topcon laser level), and if there was a nearby creek or channel, each plot was placed equidistant from its edge. All stations were inundated by the higher tides of each tidal cycle. The 54 plots were sampled three times (July 2004, November 2004, and March 2005). On each date, plant cover was estimated using a 1 by 1 m quadrat grid with 25 points. The percentage of points occupied by a plant species was used as an estimate of total plant cover. Canopy height was measured at five equally spaced points on the grid, then averaged. If the *Lepidium* canopy was bent over, as was common in summer, additional measures of plant heights were made with plants held erect. In July and March, light conditions above the canopy and at the soil surface were measured (LI-COR spherical PAR sensor[1]; 3 replicate measures pooled for each plot) so that the proportion of light blocked by the plants could be estimated.
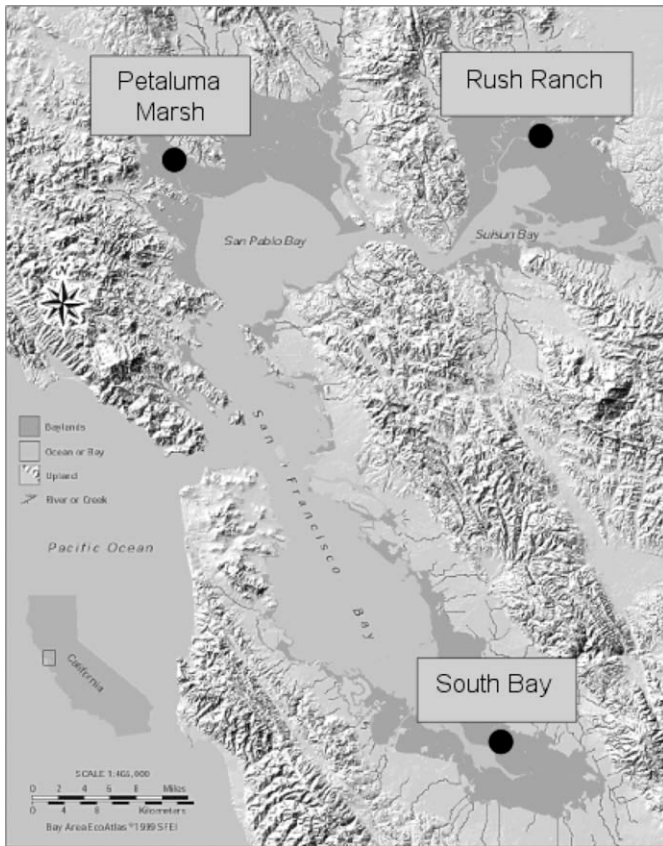
Figure 1. Location of study sites at Rush Ranch (a National Estuarine Research Reserve Site owned by the Solano Land Trust; UTM coordinates N 585123, W 4228227), Petaluma Marsh (owned by the California Department of Fish and Game; N 539347, W 4228006), and South Bay (Don Edwards San Francisco Bay National Wildlife Refuge; N 588489; W 4148518). Map adapted from Bay Area EcoAtlas (San Francisco Estuary Institute 1999).

Figure 2. Monthly (left) and annual ("A," right) averages for rain gauges (site in parentheses) near each of the study sites. The study period (dark bars) ranged from July 2004 to June 2005. Averages (white bars) for Rush Ranch were from data collected from 1950 to 2000, for Petaluma Marsh from 1931 to 2000, and for South Bay from 1948 to 2000. Data for the study period were from http://www.weatherundergound.com/history. Data for the monthly averages are from http://ggweather.com/climate.

At each plot, two soil cores (5-cm-diam) were collected, sectioned into 0 to 2 cm and 2 to 6 cm depths, and pooled by depth. These are depths that are important to seed germination and to rooting of both recruiting and established plants, respectively. Soils were weighed wet and dry (50 C oven) to determine percent moisture, then ground with a mortar and pestle to pass through a 2 mm sieve. We prepared saturated soil pastes for measures of relative pH (Oakton Acorn Series pH meter[2]) and salinity (parts per thousand [ppt] with a Leica refractometer[3]), and measured organic matter by loss on ignition (percent based on combustion in a 500 C muffle furnace[4] for 5 h). The 2- to 6-cm-deep samples collected in July 2004 and March 2005 were passed through a 1 mm sieve and analyzed for carbon (C) and nitrogen (N) using an elemental analyzer at the Marine Science Institute Analytical Lab at the University of California, Santa Barbara.

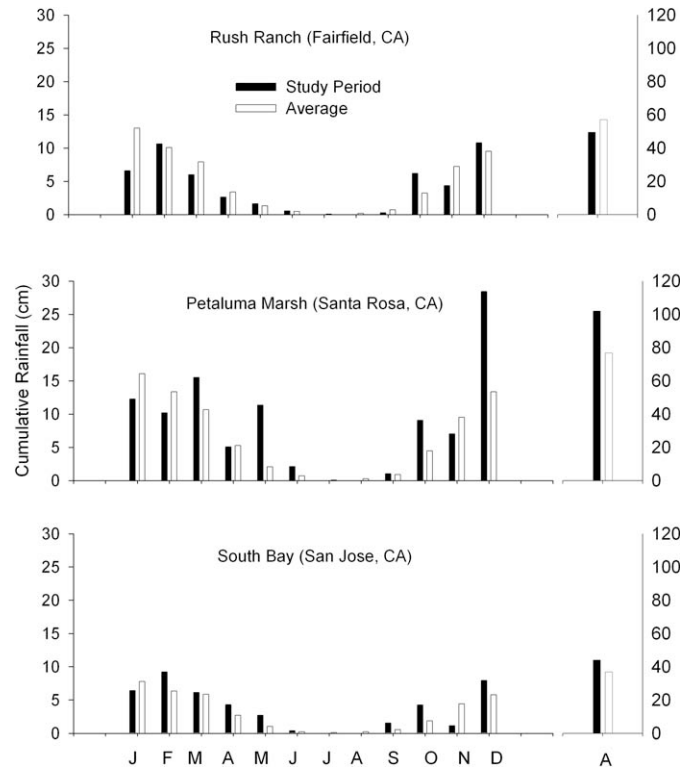In July 2005, at each of the three sampling stations at Rush Ranch, we conducted a limited sampling of insects and spiders via sweep net along five transects through each vegetation type (10 sweeps along each 5 m transect). Samples were preserved in 90% isopropyl alcohol, counted, and identified to family.

Percent cover, canopy height, and the proportion of light blocked by the vegetation were analyzed using repeated measures ANOVA of power-transformed data (factors: site, species). Statistical comparisons of species richness were not conducted due to the manner by which stands of *Lepidium* (densest, purest available) and *Sarcornia* (adjacent to selected *Lepidium*) were chosen for study. Soil data were analyzed using repeated measures ANOVA (factors: site, species, soil depth); salinity, pH, and C : N data were transformed (salinity and pH were power transformed, C : N was sine transformed) to meet the assumption of homogeneity of variances. Total insect/spider density and the number of families present in each sample were square root transformed and analyzed using one-factor ANOVA (factor: vegetation species). All ANOVAs were conducted with Proc Mixed in SAS.[5]
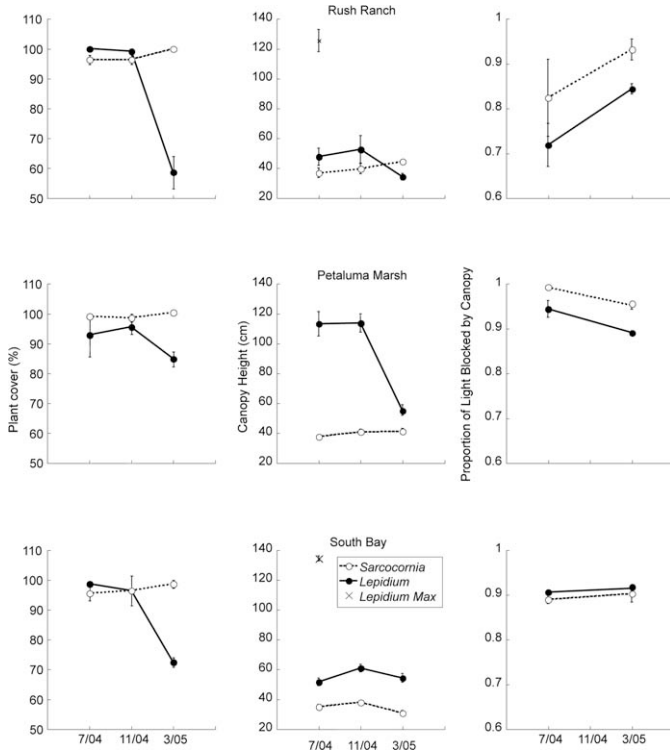
Figure 3. Percent cover (left), canopy height (center), and proportion of light blocked by canopies (right) in *Lepidium latifolium*- and *Sarcocornia pacifica*-dominated plots at the three study sites across three seasons. "*Lepidium* max" values represent height when held erect. Bars represent ± 1 SE; *n* = 3 stations at each study site.

Results

In all study sites, percent cover was similarly high for both *Sarcocornia* and *Lepidium* (> 90%) in their respective plots during the summer and fall sampling periods (Figure 3). However, percent cover differed between species in spring, because *Lepidium* senesces each fall and new shoots were still relatively small in March, whereas *Sarcocornia* plots maintained high cover throughout the year (Table 1, significant date by species interaction). *Lepidium* plots had a grand mean of 1.2 ± 0.1 (SE) species present, with *Sarcocornia* the primary species co-occurring with the invader. The nearby *Sarcocornia* plots had an average of 2.6 ± 0.2 species; *Jaumea carnosa* A. Gray (marsh jaumea), *Distichlis spicata* (L.) Greene (saltgrass) *Triglochin maritima* L. (seaside arrowgrass) and *Frankenia salina* (Molina) I. M. Johnston (alkali heath) co-occurred with *Sarcocornia*.

Lepidium canopy height was generally 2 to 3 times greater than that of *Sarcocornia* (Figure 3). This difference was least pronounced in the early spring, when foliage of *Lepidium* only had recently emerged (Figure 3, Table 1, interaction between date and species). Canopy height differences were greatest in summer and fall at Petaluma Marsh, where *Lepidium* remained erect (> 110 cm tall), unlike at the other two sites where *Lepidium* plants were as tall (> 120 cm) but bent over in summer and fall (50 to 60 cm canopy height; Figure 3). Despite being shorter, the *Sarcocornia* canopy blocked significantly more light from the soil surface than the *Lepidium* canopy, except at the South Bay site, where light penetration was similar through canopies of both species (Figure 3, Table 1, species by site interaction).

Several seasonal patterns in soil characteristics were evident across sites and vegetation types. Percent moisture was lowest in summer at all sites, higher in fall, and highest in spring (Figure 4, Table 2), reflecting rainfall patterns (Figure 2). Porewater salinity was two- to five-fold higher in summer (reaching up to 50 ppt) than in spring (~10 ppt), and intermediate in fall (Figure 3, Table 2). pH was higher on average in spring, whereas %N, and C : N were relatively constant over time (Figures 4 and 5, Table 2).

Table 1. Results of repeated measures ANOVA on plant measures by species (*Sarcocornia* or *Lepidium*) and site (the three marshes, Rush Ranch, Petaluma Marsh, and South Bay).

	Cover			Canopy height			Light blocked		
	N df	D[1] df	P	N df	D df	P	N df	D df	P
date	2	96	**< 0.0001[2]**	2	96	**< 0.0001**	1	48	0.1
species	1	48	**< 0.0001**	1	48	**< 0.0001**	1	48	**0.0002**
site	2	48	**0.05**	2	48	**< 0.0001**	2	48	**0.0003**
date · species	2	96	**< 0.0001**	2	96	**0.006**	1	48	0.9
date · site	4	96	**0.0003**	4	96	0.5	2	48	**0.008**
species · site	2	48	0.17	2	48	**0.0003**	2	48	**< 0.0001**
date · species · site	4	96	**0.003**	4	96	**< 0.0001**	2	48	**0.04**

[1] Abbreviation: N df, numerator degrees of freedom; D, denominator.

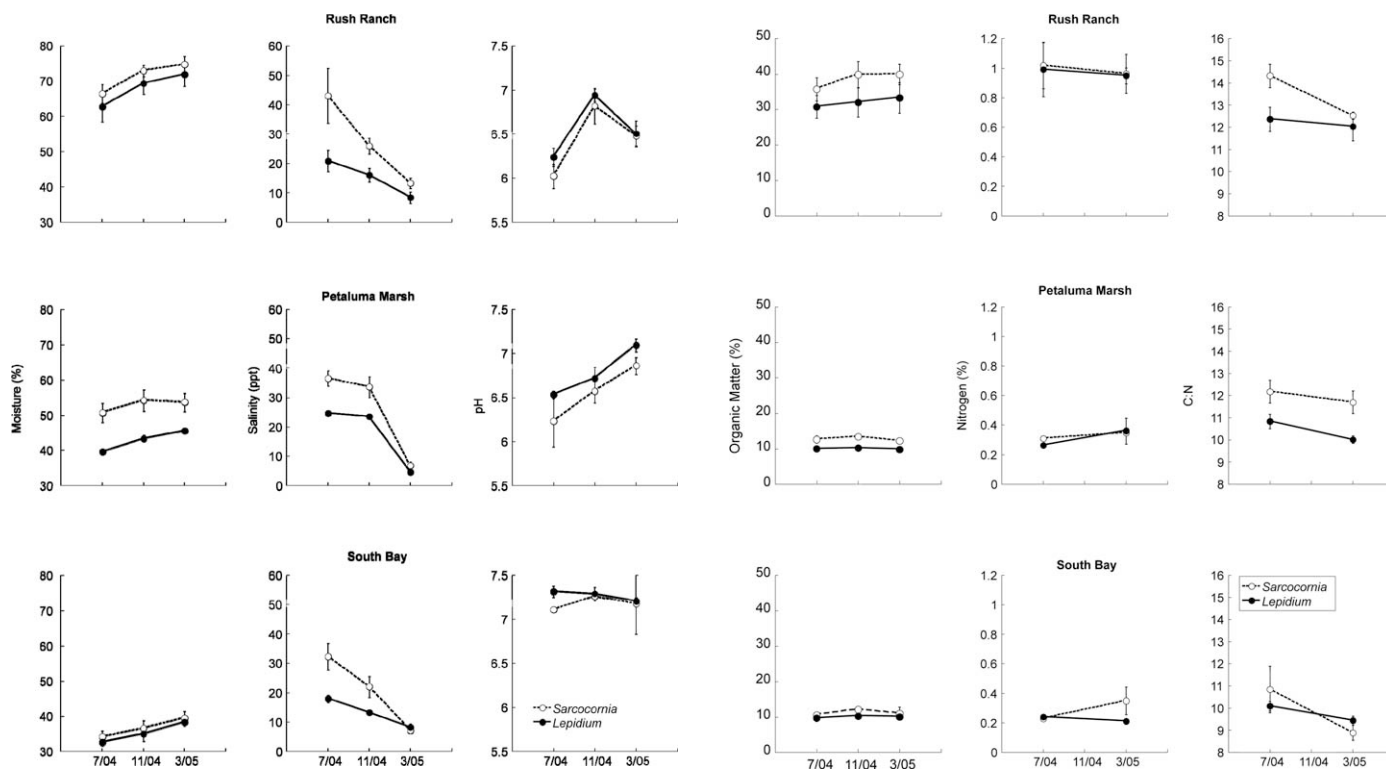[2] Bold values are significant at P < 0.05.

Figure 4. Soil moisture (left), salinity (center), and pH (right) of *Lepidium latifolium-* and *Sarcocornia pacifica*-dominated plots at the three study sites across three seasons. Data are from the 2 to 6 cm depth. Bars represent ± 1 SE; *n* = 3 stations at each study site.

Figure 5. Soil organic matter (left), nitrogen (center), and carbon : nitrogen (right) in *Lepidium latifolium-* and *Sarcocornia pacifica*-dominated plots at the three study sites across three seasons. Data are from the 2 to 6 cm depth. Bars represent ± 1 SE; *n* = 3 stations at each study site.

Table 2. Results of repeated measures ANOVA on soil measures by species (*Sarcocornia* or *Lepidium*) and site (the three marshes, Rush Ranch, Petaluma Marsh, and South Bay). Soil depth (0 to 2 cm vs. 2 to 6 cm) was an additional factor for all soil measures except for C : N (measured in 2 to 6 cm depth only). The degrees of freedom are the same for all analyses.

	N df	D[1] df	Moisture P	Soil salinity P	pH P	Organic matter P	C : N P
date	2	192	**< 0.0001[2]**	**< 0.0001**	**< 0.0001**	**0.0005**	0.5
species	1	96	**< 0.0001**	**< 0.0001**	**0.01**	**< 0.0001**	**< 0.0001**
depth	1	96	**0.04**	0.5	0.3	**< 0.0001**	—
site	2	96	**< 0.0001**	**0.02**	**< 0.0001**	**< 0.0001**	**0.003**
date · species	2	192	**0.06**	**< 0.0001**	**0.03**	0.2	0.1
date · depth	2	192	**< 0.0001**	**< 0.0001**	0.3	0.1	—
date · site	4	192	**0.004**	**< 0.0001**	**< 0.0001**	**0.002**	**0.002**
species · depth	1	96	0.5	0.5	0.5	0.1	—
species · site	2	96	**0.003**	**0.007**	0.5	**0.01**	0.2
depth · site	2	96	**0.05**	0.3	**0.03**	**< 0.0001**	—
date · species · depth	2	192	0.6	0.8	0.7	0.4	—
date · species · site	2	96	0.1	**0.0003**	0.2	0.7	0.2
date · depth · site	4	192	**0.03**	0.6	0.08	0.7	—
species · depth · site	4	192	0.5	0.5	0.7	0.5	—
date · species · site · depth	4	192	0.6	1.0	0.8	0.5	—

[1] Abbreviation: N df, numerator degrees of freedom; D, denominator.

[2] P values. Bold values are significant at P < 0.05.

Regardless of dominant species, the three marsh sites differed significantly in all measured soil characteristics (Figures 4 and 5, Table 2). Rush Ranch had the highest soil moisture, approximately twice that of the South Bay site, with Petaluma Marsh intermediate. Rush Ranch and South Bay had higher salinity on average across seasons and species, than did Petaluma Marsh. pH tended to be higher at South Bay than at the other sites. Rush Ranch soils had > 3 times more organic matter and N than the other two marshes. C : N also tended to be higher at Rush Ranch (Figure 5, Table 2).

Soil characteristics in *Lepidium* stands differed in a number of ways from those of *Sarcocornia* stands. Soils beneath *Lepidium* had significantly lower percent moisture at both Rush Ranch and Petaluma Marsh, although this effect was less pronounced at the South Bay site (Figure 4, Table 2, species by site interaction). Salinity was 35 to 60% lower in *Lepidium* soils than in *Sarcocornia* soils in July, 30 to 40% lower in November, and similar in March, when all soils had salinities of ~10 ppt or lower (Figure 4, Table 2, species by date interaction). Soil pH was significantly higher in *Lepidium* stands; again, the difference between species was smaller in March (Figure 4, Table 2, species by date interaction). The soils in *Lepidium* plots tended to have lower organic matter concentrations than those in *Sarcocornia* plots, especially at Rush Ranch (Figure 5, Table 2, species by site interaction). Soil C : N was lower in *Lepidium* plots than in *Sarcocornia* plots (Figure 5, Table 2). The nitrogen content of the soils varied little by vegetation type; therefore the lower C : N in *Lepidium* soils was driven by lower C content as opposed to higher N (Figure 5).

There was a significant effect of depth on soil percent moisture, with the shallow (0 to 2 cm) depths wetter than deeper (2 to 6 cm) depths for both species (Table 2). Organic matter concentration was higher overall at the soil surface (Table 2). Soil salinity was similar with depth except in July (Table 2, date by depth interaction), when salinity was elevated in *Sarcocornia* surface soils at the South Bay site (Figure 6, Table 2).

In July at Rush Ranch, there was a nonsignificant trend of greater total insect and spider density in *Lepidium* stands than in *Sarcocornia* stands (Figure 7; F = 4.3, P = 0.1). There were significantly more families represented in *Lepidium* samples (6.6 families per sample) than *Sarcocornia* samples (4.3 families per samples) (F = 11.2, P = 0.02). Three orders of insects were found only in *Lepidium* stands: Hymenoptera, Neuroptera, and Psocoptera. Within the Hemiptera, Diptera, Coleoptera, and Araneae, some families tended to have greater density in *Lepidium* and others in *Sarcocornia* (Figure 7).

Discussion

Although *Lepidium latifolium* is an acknowledged threat to freshwater wetlands in the western United States
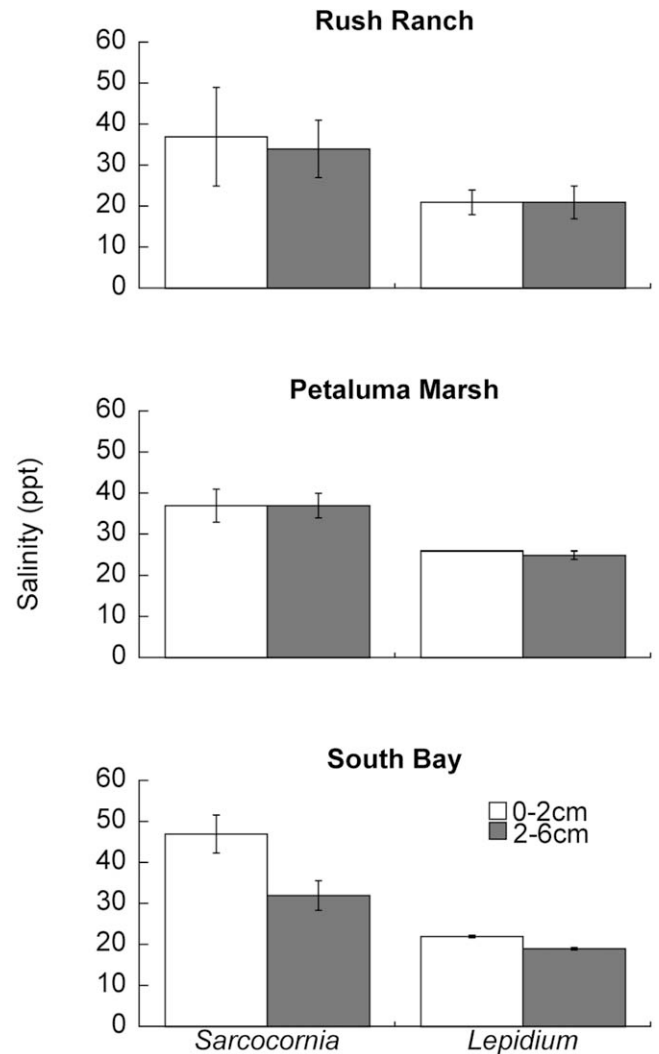

Figure 6. Soil salinity in *Lepidium latifolium*- and *Sarcocornia pacifica*-dominated plots at the three study sites in July 2004. Bars represent ± 1 SE; *n* = 3 stations at each study site.

(Grossinger et al. 1998; Renz 2002; Young et al. 1995, 1997), managers have been slow to recognize its potential for invading and altering more saline tidal marsh habitats. Sampling a variety of characteristics of tidal marshes within three regions of the San Francisco Estuary where *Lepidium* has created large, near-monotypic stands permitted us to document differences that are or might be resulting from *Lepidium* presence. Many soil properties differed in *Lepidium* stands, as well as canopy architecture, light penetration, and perhaps the insect/spider assemblage (as suggested by limited sampling at one site), compared to nearby *Sarcocornia pacifica* stands at similar elevations and distance from channels. These data suggest that *Lepidium* invasion of tidal marshes within San Francisco Estuary leads to differences in several physical characteristics, and could influence functions such as biogeochemical cycling and food web support.
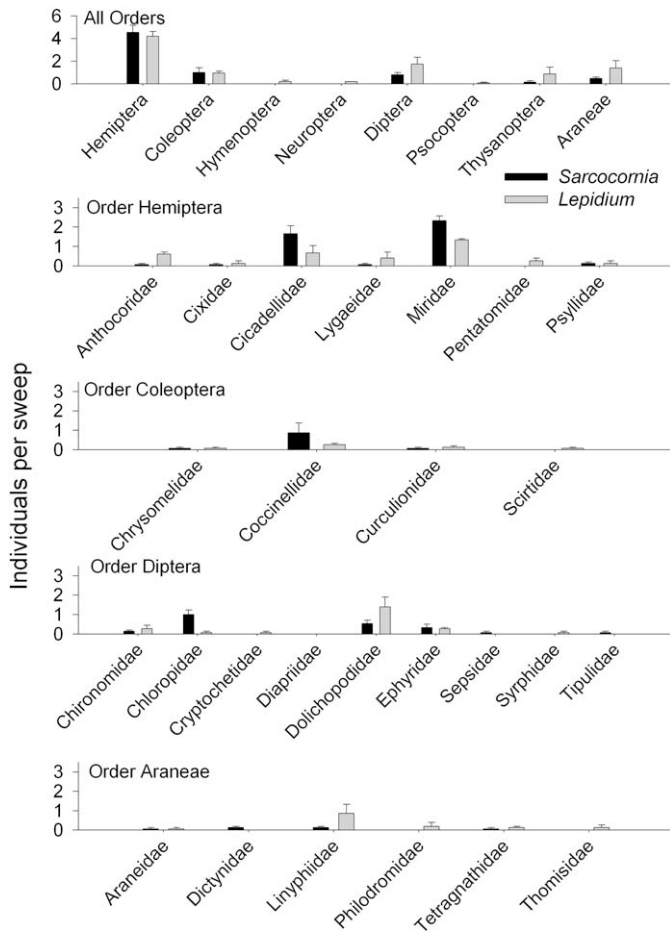
Figure 7. Insect and spider assemblage in *Lepidium latifolium*- and *Sarcocornia pacifica*-dominated plots at Rush Ranch, July 2005. The most common orders, Hemiptera (true bugs), Coleoptera (beetles), Diptera (flies), and Araneae (spiders) are shown identified to family. Data are means from five sweep net transects (10 sweeps each) at each of three patches in each vegetation type; bars represent ± SE.

The difference in phenology between *Sarcocornia* and *Lepidium* might partly explain the manner by which *Lepidium* is invading tidal marshes. *Lepidium* uses stored carbohydrates in its creeping roots for rapid shoot development in the spring (Blank and Young 1997b). Foliage emerges in January or early February and the plant flowers and reaches maximum cover and biomass by May in the tidal marshes we have studied. In contrast, *Sarcocornia* begins to develop new succulent tips on persistent woody branches in March and does not flower or reach peak biomass until fall (Boyer et al. 2001; Efloras 2009, Zouhar 2004; L. K. Reynolds and K. E. Boyer personal observation). Although *Lepidium* seeds do not germinate well in saline environments (Spenst 2006), winter rains present a low salinity window in tidal marshes during which *Lepidium* germinates and emerges from overwintering rootstock (Figures 2 and 3). Hence, it is plausible that *Lepidium* capitalizes on both reduced salinities and reduced competition with the native tidal marsh dominant during the late winter and early spring months.

Because experimental plots in this study were at similar elevation and similar distance from channels, one would expect that soil properties would be quite similar. However, many significant differences in soil characteristics were documented between adjacent *Sarcocornia* and *Lepidium* stands. It is likely that *Lepidium* plays a role in initiating or maintaining the differences we observed. *Sarcocornia* is relatively short, with highly reduced leaves (essentially photosynthetic stems), whereas *Lepidium* is a much taller (Figure 3) broad-leaved plant with high photosynthetic surface area. Hence, *Lepidium* is likely to have higher transpiration rates leading to substantially greater translocation of water from the soil to the atmosphere, a hypothesis supported by our measures of lower soil moisture in *Lepidium* stands. *Lepidium* shows reduced growth in saturated soils (Blank et al. 2002); therefore, if it is modifying its environment by drying the soil, positive feedback might lead to further spread of the invader. In addition, evapotranspiration can bring dissolved salts to the surface, as observed in *Lepidium*-invaded native hay fields (Blank and Young 1997a). However, in our study, hypersaline conditions developed within *Sarcocornia* stands (soil salinities 2 to 19 ppt higher than full strength seawater) in summer, whereas *Lepidium* soils were 9 to 15 ppt below seawater salinity. If *Lepidium* is able to remove dissolved salts from the soil column, there is again potential for positive feedback, because this invader might enhance its own spread by reducing soil salinities. Our data suggest this feedback would be most prevalent at all sites during the summer; salinities during the spring germination period were usually similar among *Lepidium*- and *Sarcocornia*-dominated areas. There also was relatively lower soil organic matter in *Lepidium* plots. Senescence of *Lepidium* aboveground tissues results in a large amount of detritus each year; however, either this material decomposes more slowly than *Sarcocornia* detritus or it is washed away by tides before it decomposes, because it appears to contribute little to soils (Figure 5). These results were remarkably consistent at three tidal marshes in different parts of the estuary with different background soil characteristics and rainfall patterns. Because *Lepidium* is forming near-monocultures in all these sites, all with differences in soil properties compared to adjacent areas, these differences likely are due to *Lepidium* presence and, therefore, similar changes are expected in other invaded marshes under a range of conditions. An important next step would be manipulative experiments to quantify the degree to which *Lepidium* is responsible for modifying or maintaining the differences we have documented in this

field survey and to predict the type and magnitude of changes expected under different soil and climate scenarios.

Although *Lepidium* often first establishes in tidal marshes along well-drained channel edges (personal observation), our observations and study of large stands (> 20 m) of *Lepidium* on the otherwise *Sarcocornia*-dominated marsh plain suggest the invader is able to use clonal integration to spread into more stressful areas farther from channels (Pennings and Callaway 2000). Further, if *Lepidium* is able to alter soil characteristics to its own advantage, this might facilitate persistence and further spread into less suitable areas, including those with greater waterlogging and higher summer soil salinities. This phenomenon could result in a lag effect in which the rate of *Lepidium* spread is initially low in saturated saline areas, but increases over time as harsh soil conditions are ameliorated.

Our insect and spider sampling was limited to one marsh at one time using one method; however, our data are suggestive of a shift in both total insect/spider densities, numbers of taxa, and community composition. *Lepidium* has prolific and showy flowers in comparison to *Sarcocornia* and might attract pollinators. Furthermore, the height of the *Lepidium* canopy is much greater than that of *Sarcocornia*, even when bent over (as it was in the summer and fall at two of our sites), thus providing a greater canopy volume for habitat and predation refuge. In addition, *Lepidium* woody thatch covers the soil surface, creating an additional habitat feature. Changes to insect density and composition could propagate up the food web. This hypothesis is supported in that some bird species preferentially nest in *Lepidium* (Spautz and Nur 2004); however, further study is needed to understand such potential functional linkages.

This study documents large stands of the invasive *Lepidium latifolium* in relatively saline areas of tidal marshes despite the understanding that it is taller, more dense, and produces more viable seeds in areas of lower salinity (Leininger and Foin 2009). The abundance of *Lepidium* reproductive material (both seed and roots) in marshes in all reaches of the estuary and its early growing season advantage over marsh natives suggest that both existing marshes and proposed restoration sites could be at risk of invasion. Because *Lepidium* occurs in all tidal marsh restoration sites in the San Pablo Bay region of San Francisco Estuary (G. Block, U.S. Fish and Wildlife Service, personal communication) and in close proximity to a number of large upcoming tidal marsh restoration projects (e.g., South Bay Salt Ponds in south San Francisco Bay and the Sears Point and Hamilton Restoration projects in San Pablo Bay (EDAW et al. 2007; Wetlands and Water Resources 2007), it is important that managers recognize the potential for this species to invade and influence structure and function of restored tidal marsh communities.

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