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Distribution and Invasion Potential of *Limonium ramosissimum* subsp. *provinciale* in San Francisco Estuary Salt Marshes

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ABSTRACT

Non-native sea lavenders (*Limonium* spp.) are invasive in salt marshes of southern California and were first documented in the San Francisco Estuary (the estuary) in 2007. In this study, we mapped distributions of *L. ramosissimum* subsp. *provinciale* (LIRA) and *L. duriusculum* within the estuary and investigated how the invasion potential of the more common species, LIRA, varies with elevation and edaphic conditions. We contacted colleagues and conducted field searches to find and then map sea lavender populations. In addition, we measured LIRA's elevational range at three salt marshes. Across this range we measured (1) soil properties: salinity, moisture, bulk density, and texture; and (2) indicators of invasion potential: LIRA size, seed production, percent cover, spread (over 1 year), recruitment, and competition with native halophytes (over 6 months). We found LIRA in 15,144 m^2 of upper salt marsh habitat in central and south San Francisco bays and *L. duriusculum* in 511 m^2 in Richardson and San Pablo bays. LIRA was distributed from mean high water (MHW) to 0.42 m above mean higher high water (MHHW). In both spring and summer, soil moisture and salinity were lowest at higher elevations within LIRA's range, which corresponded with greater rosette size, inflorescence and seed production (up to 17,400 seeds per plant), percent cover, and recruitment. LIRA cover increased on average by 11% in 1 year across marshes and elevations. Cover of the native halophytes *Salicornia pacifica*, *Jaumea carnosa*, and *Distichlis spicata* declined significantly at all elevations if LIRA were present in plots (over a 6-month, fall–winter period). Results suggest LIRA's invasion potential is highest above MHHW where salinity and moisture are lower, but that LIRA competes with native plants from MHW to above MHHW. We recommend removal efforts with emphasis on the salt marsh-terrestrial ecotone where LIRA seed output is highest.

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INTRODUCTION

Invasive plants can be harmful to native species and ecosystem functions (Vitousek et al. 1997; D'Antonio et al. 2004), making early identification, assessment, and response to new plant invasions important for ecosystem management (Chornesky and Randall 2003; Ielmini and Ramos 2003). In the San Francisco Estuary (hereafter, the estuary) tidal marshes, invasive plants have spread aggressively (e.g., *Spartina alterniflora* × *foliosa* and *Lepidium latifolium*), displacing native species and their associated functions (Goals Project 1999; Levin et al. 2006; Boyer and Burdick 2010). As new non-native plant species establish, it is important to understand their ecology and potential for spread so that resources may be prioritized toward controlling species that pose the greatest threat. To this end, land managers and scientists recommend describing the current spatial extent of introduced species and evaluating how invasion potential is influenced by abiotic environmental factors that vary across landscapes (Grossinger et al. 1998; Byers et al. 2002; Robison 2009).

A single *Limonium* (sea lavender) species, *L. californicum* (marsh rosemary) is native to the estuary and is found in salt and brackish upper marsh habitats throughout most of coastal California (Baldwin et al. 2012). The *Limonium* genus, however, is cosmopolitan and includes a number of low growing, rosette-forming, perennial halophytic forbs native to sea-lavender steppe communities in western Mediterranean coastal salt marshes, maritime cliffs, and saline dunal depressions (Devillers–Terschuren and Devillers–Terschuren 2001). Several of these, including *L. ramosissimum* (Algerian sea lavender), *L. duriusculum* (no common name) and *L. binervosum* (rock sea lavender) have invaded estuarine wetlands on the West Coast of North America from Santa Barbara County south into Baja California (Barbour et al. 2007; COCH c2007). These species were likely introduced through the horticultural trade (Hubbard and Page 1997), and *L. ramosissimum* and *L. duriusculum* are highly invasive in salt marsh habitats in central and southern California (Hubbard and Page 1997; 2012 email from J. Sayers to G. Archbald, unreferenced, see "Notes").

Recently, *Limonium ramosissimum* subsp. *provinciale*[1] (hereafter LIRA) and *L. duriusculum* (hereafter LIDU) have been observed above and below the high tide line in estuary marshes (Baye 2008) (Figure 1). In spring of 2007, LIDU was discovered growing in dense patches in Strawberry Marsh, (Marin County, CA) in Richardson Bay (K. Boyer, pers. obs., 2007; email from A. Ryan to G. Archbald, unreferenced, see "Notes"). Later in 2007, LIRA was found growing densely at Sanchez Creek Marsh (San Mateo County, CA) and in multiple neighboring marshes, raising concern that both species could be widespread in the estuary. LIRA has simple, oblanceolate–spathulate leaves (80 to 100 mm × 15 to 20 mm, L×W) that form a basal rosette and annually produces branching inflorescences (30 to 50 cm) opening into flowered spikelets with purple corollas. LIDU has oblanceolate-spathulate, obtuse to truncate leaves (30 to 40 mm × 5 to 9 mm) and inflorescences similar to LIRA (Tutin 1964). LIRA and LIDU may have been mistaken for *L. californicum* in the estuary and thereby overlooked for a decade or more. In fact, LIRA was accidentally planted during at least one marsh restoration project in San Francisco in the 2000s (2010 in-person conversation between P. Baye and K. Boyer, unreferenced, see "Notes") and seeded at several restored marshes in the South San Francisco Bay region of the estuary (2012 email from D. Thomson to G. Archbald, unreferenced, see "Notes"). These events emphasize

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[1] In spite of comprehensive treatment of the genus *Limonium* by Tutin et al. (1964), Erben (1993), and Arrigoni and Diana (1993), taxonomic and nomenclatural issues in the genus remain unresolved. This is, in part, because there are many species of *Limonium* with similar morphological traits, and it is difficult to access European herbaria specimens for comparison with species found in California. Botanical samples from Sanchez Creek Marsh (Burlingame, CA) and Seal Slough (Foster City, CA) study sites were examined by D. Kelch, California Departure of Food and Agriculture, and submitted to California herbaria under the name *L. ramosissimum* subsp. *provinciale*; however, these specimens also keyed well to *L. binervosum* (2012a email from D. Kelch to G. Archbald, unreferenced, see "Notes"). While the name *L. ramosissimum* subsp. *provinciale* is accepted in the *Flora Europaea* (Tutin et al. 2001) and the United States Department of Agriculture Plants Database (USDA [mod 2014]), the Jepson Flora Project (c2014) considers *L. ramosissimum* subsp. *provinciale* unresolved and it may be synonymous with *L. ramosissimum*.

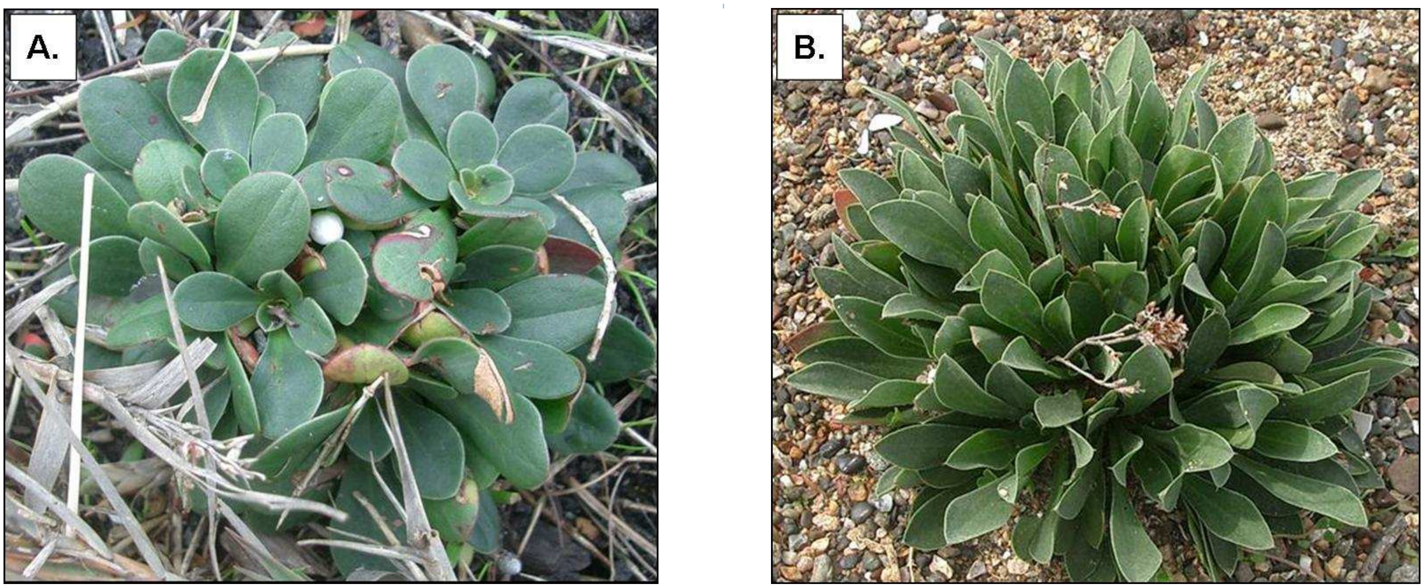

Figure 1 Invasive sea lavender in San Francisco Estuary marshes: (A.) *Limonium duriusculum*, (B.) *Limonium ramosissimum* subsp. *provinciale*. Photos by G. Archbald.

estuary (2012 email from D. Thomson to G. Archbald, unreferenced, see "Notes"). These events emphasize the need to document and increase awareness of *Limonium* species in estuary marshes.

LIRA and LIDU may threaten plant and vertebrate diversity in high salt marsh and marsh–terrestrial ecotone habitats (hereafter, the transition zone). Both habitats have been severely reduced from human activities in estuary tidal marshes (Collins and Grossinger 2004), yet still support high species richness relative to the marsh plain. Historically, these habitats contained a suite of plant species that are now rare and subject to conservation and restoration measures, including *Chloropyron maritimum* subsp. *palustre* (Point Reyes bird's beak), *Suaeda californica* (California sea-blight), *Elymus triticoides* (creeping wild rye), *Ambrosia psilostachya* (western ragweed), and *Carex praegracilis* (field sedge) (Josselyn 1983; Baye et al. 2000; Boyer and Thornton 2012). In addition, upper marsh habitats are important for endangered vertebrates, including *Rallus longirostris obsoletus* (California clapper rail) and *Reithrodontomys raviventris* (salt marsh harvest mouse), which rely on canopies of *Grindelia stricta* (gumplant), *Salicornia pacifica* (perennial pickleweed), and *Distichlis spicata* (saltgrass) either for nesting or refuge from predators, particularly during extreme high tide events (Josselyn 1983; SFBBO [cited 2013]). If LIRA or LIDU replace these native plants, the resulting vegetation structure dominated by short basal rosettes is unlikely to provide effective cover from predators.

Concern about the possible effects of invasive *Limonium* in the estuary has prompted research to detect it via remote sensing (Archbald 2010a), studies to understand how anthropogenic changes influence its spread (Cleave 2012), and removal efforts (e.g., by the Bay Area Early Detection Network, Richardson Bay Audubon Center and Sanctuary, and San Francisco State University classes). Decisions on how and where to manage this invasion require an understanding of the patterns of abundance and distribution of introduced sea lavenders within and among estuary marshes.

Both abiotic conditions and competition are important factors that structure salt marsh plant species assemblages, and both likely influence the potential for invasion by introduced *Limonium* species. Driven

Hedel 1976; Zedler 1982), variation in physical stress associated with salinity and moisture strongly influences species distributions in salt marshes (Chapman 1934; Hinde 1954; Bertness and Ellison 1987; Kuhn and Zedler 1997; Cantero et al. 1998; Crowl et al. 2008). Where abiotic stress is high (e.g., via hypersalinity, anaerobic conditions or extreme desiccation), plant species able to tolerate harsh environmental conditions succeed. But where abiotic stress is low (e.g., conditions of low salinity or moderate moisture), marsh halophytes often grow taller, and/or produce more seed (Seliskar 1985; Schile et al. 2011; Ryan and Boyer 2012) and interspecific competition may become a more important factor structuring marsh communities (Pennings and Callaway 1992; Crain et al. 2004).

In the estuary, our preliminary observations of introduced sea lavenders suggest they grow most vigorously at higher elevations in the upper high marsh and into the transition zone, which could result from a reduction in moisture, salinity, or other stressors. Previous studies in the region have found salinity to decline with elevation through the transition zone. For example, in San Pablo Bay (northern estuary), Mahall and Park (1976) found that maximum salinity occurred just above MHW (which corresponded in their study within the pickleweed plain) and decreased landward, regardless of season. Similarly, Traut (2005) found soil salinity decreased from the pickleweed dominated mid-marsh through the transition zone in Pt. Reyes National Seashore (50 km N of the estuary).

The effects of soil conditions on introduced sea lavenders in the estuary have not been evaluated, but another study found *Limonium vulgare* was inhibited by high inundation and salinity (Boorman 1971). Further, in Carpinteria Salt Marsh (near Santa Barbara, California) LIDU[2] was found to grow from the upper edge of the marsh plain, dominated by *S. pacifica* to the upper reach of tides (0.8 to 1.4 m above mean sea level [msl]) (Hubbard and Page 1997). In that warm, dry region, hypersalinity develops in summer with increasing elevation (Callaway et al. 1990), and LIDU grew largest, had the highest cover (up to 75%), and outcompeted native perennial halophytes in the lower portion of its range where soil moisture and salinity were more moderate (Hubbard and Page 1997). We predicted a similar improvement in introduced *Limonium* performance in the estuary with more favorable salinity and moisture conditions, although our preliminary observations and the studies of salinity in our region mentioned above suggested we might find a reverse in the elevational pattern found for LIDU in southern California.

In this study, we investigated LIRA and LIDU's distribution, and how the invasion potential of LIRA, which we determined to be the more abundant species, varies with abiotic factors in the estuary. Our objectives were to:

1. Document LIRA and LIDU populations in estuary marshes, because mapping is an important tool for invasive species management (Lass and Callihan 1993) and provides a baseline for detecting population increases (Webster and Cardina 1997);
2. Measure LIRA's elevational range relative to tides at three marshes to better understand the plant's distribution within and among marshes;
3. Characterize edaphic characteristics (salinity, moisture, texture, and bulk density) across LIRA's elevational range to identify conditions that may influence LIRA's spread; and
4. Across LIRA's elevational range, measure indicators of its invasion success—rosette size, inflorescence height, seed production, percent cover, recruitment, spread over 1 year, and spread versus native plants during fall–winter (a time when Hubbard and Page [1997] found LIDU spreads at

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[2] Hubbard and Page (2007) tentatively identified the invasive sea lavender in Carpinteria salt marsh as *L. ramosissimum*, but the plant was later identified as *L. duriusculum* (2012b email from D. Kelch to G. Archbald, unreferenced, see "Notes").

the expense of native plants)—and relate these findings to soil properties.

MATERIALS AND METHODS

Distribution and Abundance of LIRA and LIDU

We located non-native sea lavender populations in the estuary using field searches and outreach (e.g., querying colleagues). Beginning in 2007 through 2010, we searched marshes and shoreline within a few kilometers of known populations, repeating this process when occurrences of LIRA and LIDU were found or reported through 2010. Mapping weeds via landscape searches leverages knowledge of local experts but may miss locations considered unlikely to be invaded (Barnett et al. 2007). To augment our approach, in 2010, a spatially explicit species distribution model (SDM) was developed and used to identify LIRA habitat in south San Francisco Bay (South Bay). We used the model to guide 18 days of boat and ground searches, leading to the identification of additional LIRA populations (Archbald 2010b). We did not generate a SDM for LIDU because initial searches and outreach found it to be considerably less widespread.

Once identified, we mapped populations at the patch scale using a handheld Trimble GeoXH Global Positioning System (GPS) (sub-meter accuracy). We mapped only one LIDU population (at Strawberry Marsh in Richardson Bay), otherwise relying on colleagues for LIDU population locations. We defined patches as one or more sea lavender plants separated by at least one meter and visually estimated LIRA percent cover in each patch to the nearest 5%. During mapping, we noticed that larger patches appeared to have higher LIRA percent cover than smaller patches, so we evaluated the relationship between individual patch sizes and LIRA percent cover using regression analysis. We noted marsh substrate and plant communities where invasive sea lavenders were present and investigated the history of invaded marshes using the San Francisco Estuary Institute's Wetland Tracker website (SFEI 2010).

Study Sites

We monitored and measured soil properties and indicators of LIRA success across LIRA's elevational range between March 2008 and June 2009 at Sanchez Marsh (hereafter Sanchez), Coyote Point Marina (hereafter Coyote), and Seal Slough (hereafter Seal)—three marshes in the southwest estuary (Figure 2). Sanchez (37.5878° N, –122.3537° W) is a saline to seasonally brackish remnant tidal marsh. In 1987, a compensatory mitigation project restored tides to 1.3 ha of former wetlands at Sanchez by grading filled marsh back to tidal elevations along the southern edge of the marsh

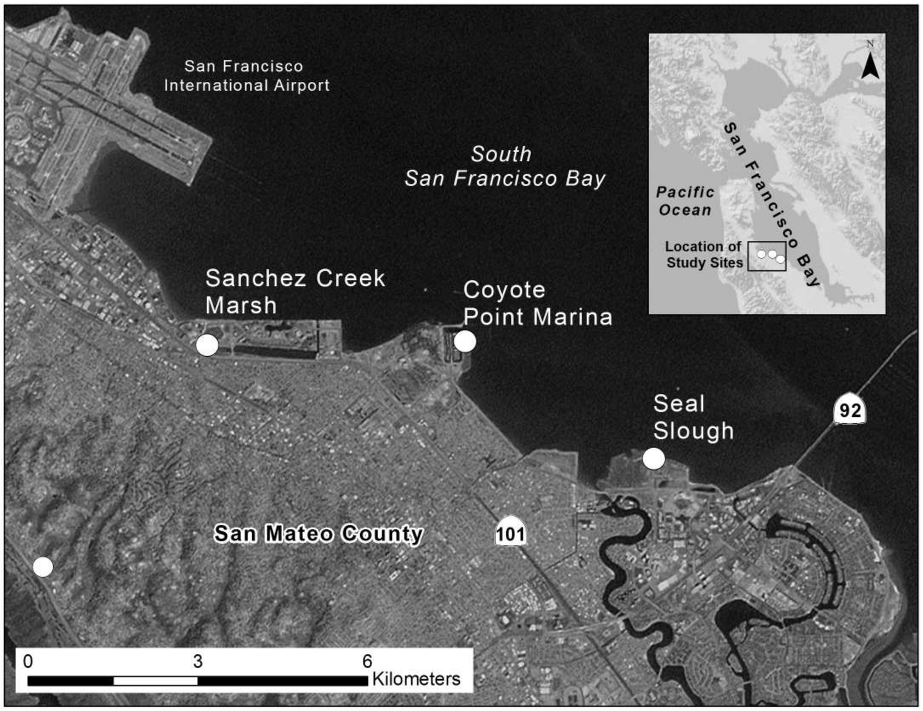

Figure 2 Mensurative studies were carried out at three marshes on the west side of south San Francisco Bay, California: Sanchez Creek Marsh in Burlingame, Coyote Point Marina in San Mateo, and Seal Slough in Foster City

(SFEI 2010). Other alterations at Sanchez include earthwork associated with installation of electrical towers in the marsh and storm drains, which empty into the high marsh. Coyote (37.5901° N, –122.3148° W) is a 2-km-long remnant tidal marsh that extends along the bayward edge of the breakwall levee on the east side of Coyote Point Marina. The marsh substrate along the levee slope has an abundance of chert and concrete cobbles. Seal, located at the mouth of Seal Slough (37.5736° N, –122.2851° W), has been altered via a major re-routing of the slough's historic path to the estuary (SFEI 2010). Our study site was located in the southern end of the marsh, a portion of the marsh that is exposed to high wind wave energy evidenced during the study period by migrating oyster shell berms and by active marsh erosion with the accumulation of large areas of wrack.

Elevational Range of LIRA Relative to Tides

We measured the estimated ten highest and lowest occurrences of LIRA using a Leica GX1230 Real Time Kinetic (RTK) GPS (estimated post-correction vertical accuracy 10-mm root mean square error) (Leica Geosystems 2013) at Sanchez, Coyote, and Seal in June of 2010. We displayed LIRA's vertical range (in NAVD88) as boxplots relative to tidal datums [mean high water (MHW) and mean higher high water (MHHW)] and 100-year flood elevations (USACE 1984) using the R statistical package. Tidal datums have been used to describe the distribution of marsh vegetation in the estuary (Hinde 1954; Atwater et al. 1979; Takekawa et al. 2012), and the 100-year flood elevation shows the approximate upper reach of tidal inundation. We obtained tidal datum values referenced to mean lower low water (MLLW) from 16 surrounding National Ocean Service (NOS) water level stations from the *http://www.noaa.gov* website (NOAA CO–OPS 2010), and point locations of 100-year flood elevation data (in NAVD88) from the Pacific Institute website (PI 2011). We converted MLLW referenced tidal datums to NAVD88 using the "Benchmarks" page at *http://www.tidesandcurrents.noaa.gov*, when conversions were available (NOAA CO–OPS 2010); otherwise, we used a conversion table developed by NOS for the South Bay (Foxgrover et al. 2005). We interpolated the tidal datum and flood elevation point data, then extracted values from the output rasters at the study sites using ArcGIS 9.1 (Archbald 2010c).

Study Design

At Sanchez, Coyote, and Seal, in March 2008, we established 30 randomly located 1-m^2 sampling plots (90 plots total) equally divided between vegetated

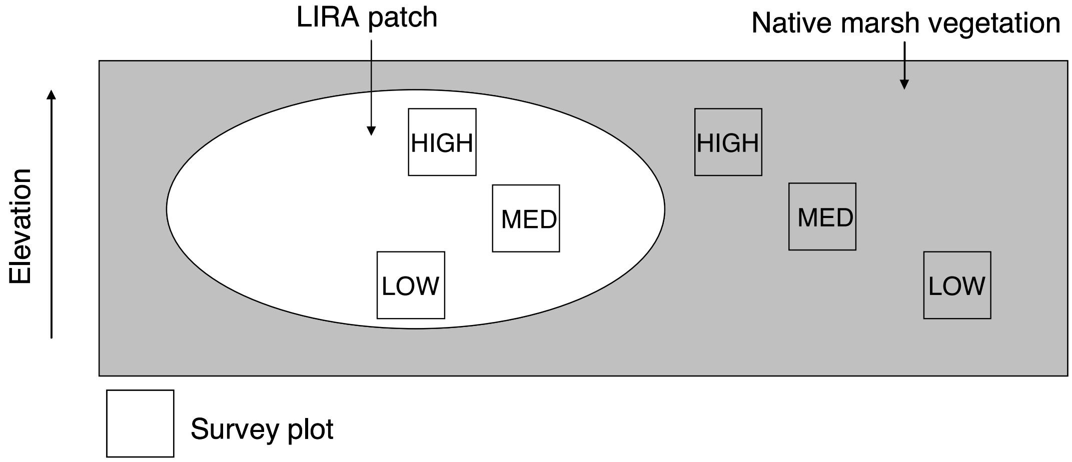

Figure 3 Survey plots ($n = 5$) were established at Sanchez Creek Marsh, Coyote Point Marina, and Seal Slough study sites to measure indicators of invasion success and soil properties in and out of LIRA patches across LIRA's elevational range

marsh in and out of LIRA patches, and stratified across high, medium, and low elevations relative to the vertical range of the invader ($n = 5$) (Figure 3). We set the elevation of plot positions using a Topcon laser level to ensure that elevations of plots in and out of LIRA patches were comparable within marshes (see Appendix A, Figure A-1) and then surveyed plot positions relative to the NAVD88 geodetic datum with a Leica GX1230 RTK GPS.

Soil Properties

We collected one soil core (10-cm depth, 4-cm diameter) per plot in LIRA patches (45 plots total) to measure salinity and moisture during low tides in March 2008. We collected one soil core in and out of LIRA patches (90 plots total) in September 2008 to measure salinity, moisture, texture, and bulk density. Nearby, rainfall was 19.8, 5.2 and 0.1 cm in January, February, and March of 2008, respectively, then negligible through September 2008 (San Francisco International Airport data; ~16 km from all study sites). In the lab, we weighed cores wet and dry to determine percent moisture and bulk density (g cm^{-3}), measured relative soil salinity using saturated soil pastes and a refractometer (Richards 1954) and measured soil texture using the hydrometer method (Bouyoucos 1962).

Indicators of Invasion Success

During peak LIRA flowering (July 2008) we measured the height and diameter of the ten largest LIRA rosettes per plot and the height and number of inflorescences per rosette. At Coyote, in August 2008, we collected one representative inflorescence from all LIRA plots and counted seeds per inflorescence to derive seeds per plant at each elevation. We measured LIRA percent cover in all invaded plots in March 2008 and March 2009 by placing a 1-m^2 quadrat subdivided into 100 cells over each plot and recording presence or absence of LIRA in every other cell. To quantify recruitment, we measured in March 2009 percent cover of LIRA in plots that had no LIRA in March 2008. Finally, we measured the percent cover of plant species in all plots (45 with and 45 without LIRA) in August 2008 and March 2009 to test spread of LIRA versus native plants. This period spans the late-winter period, a time when the invasive sea lavender, LIDU, has been found to grow while native marsh plants senesce (Hubbard and Page 1997).

Statistical Analysis

At Sanchez and Coyote, the LIRA distribution divided into low, medium, and high study plots was similarly situated relative to tides, but LIRA at Seal was distributed over a narrower vertical range and situated 0.1 to 0.2 m higher (Figure A-1). Therefore, when testing the effect of LIRA and/or elevation on soil properties and invasion success measurements, we assessed Seal separately. We used IBM SPSS Statistics 20 to perform statistical analyses.

Patterns by Marsh, Elevation, and Season in LIRA Patches. We tested how soil salinity and moisture in LIRA plots varied with two time points in spring and summer (March 2008 versus September 2009) and elevation using 2-way repeated measures MANOVA for Sanchez and Coyote and 1-way repeated measures MANOVA for Seal. Data were transformed to meet the assumptions of the statistical tests.

In and Out of LIRA Patches. We evaluated how soil salinity, moisture, texture, and bulk density differed between plots established in and out of LIRA patches. Test assumptions were met when we used separate 3-way ANOVAs at Sanchez and Coyote and 2-way ANOVAs at Seal. Percent sand was used as the indicator of texture in statistical analysis. We used mean texture measurements (percent sand, silt, and clay) to describe soil types in and out of LIRA patches at each marsh (USDA [cited 2013]).

Morphometric Response to Elevation. We tested the response of LIRA rosette height, rosette width, number of inflorescences, and percent cover of LIRA (March 2008) to elevation and marsh (at Sanchez and Coyote) using 2-way MANOVA (inflorescence height was excluded to limit dependent variables to

$n-1$ and is displayed graphically only). Dependent variables were transformed to meet parametric test assumptions. We tested the same dependent variables (transformed) using a 1-way MANOVA at Seal. Because seeds were counted at Coyote only, we tested the effect of elevation group on number of seeds per inflorescence using 1-way ANOVA.

Spread. We measured change in percent cover of LIRA in those plots that were not buried or eroded between March 2008 and March 2009 and that did not have 100% cover at the start of the survey. Thirty-one plots met these criteria: 7 from Sanchez, 15 from Coyote, and 9 from Seal. MANOVA was precluded due to violation of the assumption of homogeneity of variance-covariance matrices, so one-way ANOVAs were used to test the effect of elevation on spread rate within each marsh individually.

Recruitment. We included in our analysis the 36 plots that had zero LIRA in March 2008 and that were not lost to erosion or burial through March 2009. Change in percent cover of LIRA could not be transformed adequately, so recruitment was converted to count data with a Poisson distribution by assuming each observation of LIRA from percent cover data (2% cover) equals one seedling, then a Poisson log-linear model was used to test for an effect of elevation and marsh on establishment (Quinn and Keough 2003).

Competition. We tested how percent cover of three native plants that commonly co-occurr with LIRA, *S. pacifica*, *Jaumea carnosa* (*jaumea*), and *D. spicata* changed with marsh, elevation, and presence versus absence of LIRA over a 6-month period (August 2008 to March 2009) using 3-way MANOVA. We excluded Seal from this analysis because nearly half the plots were lost to burial, erosion, and wrack during this time period. Dependent variables were multimodal; hence, we used a rank transformation, the suggested approach when no non-parametric alternative exists for the test (Conover 1998).

RESULTS

Distribution and Abundance of LIRA and LIDU

From 2007 to the end of 2010, 20 populations of LIRA and 5 populations of LIDU were found, totaling 15,655 m^2 (~1.6 hectares) of invaded upper salt marsh habitat (Table 1, Figure 4). LIRA was found in far greater abundance (30:1 by area) with populations ranging in size from a single plant to 4,357 m^2, while LIDU populations ranged in size from a few plants to about 300 m^2. Populations of LIRA were primarily found in the South Bay region of the estuary with small populations in the Central Bay. In contrast, populations of LIDU were mainly in Richardson Bay, though one was identified as far north as San Pablo Bay (Table 1, Figure 4).

The largest populations of LIRA were found in habitats with a history of disturbance to the marsh substrate and vegetation. For example, at Sanchez (the largest population), LIRA primarily occupied a portion of the marsh that had been graded for restoration (SFEI 2010; see Appendix A, Figure A-2), as well as in other clearly disturbed locations including at the base of power towers, along constructed earthen berms, in bare patches, and near the base of a drainage outflow pipe strewn with debris. The large LIRA populations at San Francisco International Airport (3,858 m^2), Coyote (2,301 m^2), and Oyster Point Marina (1,596 m^2) were all in upper salt marsh areas at the filled margins of the estuary. Marsh substrates at these sites appeared to be a mix of coarse and fine-grained sediments and larger debris (e.g., concrete rubble, cobbles). LIRA was also found growing on cobble-dominated substrate at Ideal Marsh (317 m^2). At Greco Island and Bird Island, individual colonizing LIRA plants were found on (apparently) native sediments near the high tide/wrack line in areas of low native plant cover. LIRA occurrences were also mapped in naturally occurring sandy and coarse grain substrates, including oyster shell hash berms at Beach Park (20 m^2), and above the high tide line at a small beach north of Coyote Point Marina (North Coyote Point) (449 m^2) (Table 1, Figure 4).

The vast majority (538 out of 558) of LIRA patches were under 200 m^2, and these patches had 27% cover on average. In contrast, patches larger than 200 m^2 had 70% cover on average. Both average and maximum LIRA patch cover were generally higher in larger populations (Table 1), and LIRA cover increased logarithmically with patch size ($R^2 = 0.32$, $P < 0.0001$, Figure A-3).

Elevational Range of LIRA Relative to Tides

LIRA at Sanchez and Coyote had nearly identical elevational ranges, while at Seal, LIRA was absent from

Table 1 *Limonium ramosissimum* subsp. *provinciale* and *Limonium duriusculum* mapping statistics

Location (north to south)	Latitude	Longitude	Year mapped	Average patch cover (%) ± 1 S.E.	Maximum patch cover (%)	No. of patches	Area (m^2)
Limonium ramosissimum subsp. *provinciale*							
Corte Madera	37.9396	-122.5060	2010	5 ± 0	5	1	1
Albany Bulb	37.8889	-122.3100	2009	28 ± 10	45	3	32
Sausalito	37.8750	-122.5080	2010	5 ± 0	5	1	1
Pier 94	37.7460	-122.3760	2008	5 ± 0	5	2	2
Yosemite Slough	37.7220	-122.3830	2008	7 ± 2	15	5	5
Candlestick Point State Park	37.7091	-122.3790	2008	5 ± 0	5	2	2
Oyster Point Marina	37.6626	-122.3750	2008	32 ± 5	8	28	1596
San Francisco Intl. Airport	37.6104	-122.3740	2008	37 ± 3	90	58	3858
Whale’s Tail	37.6008	-122.1460	2010	13 ± 3	50	17	38
Coyote Point Marina	37.5893	-122.3150	2010	25 ± 2	80	83	2301
Sanchez Creek Marsh	37.5888	-122.3560	2010	43 ± 2	95	154	4357
North Coyote Point	37.5877	-122.3340	2008	15 ± 0	15	1	449
Seal Slough	37.5745	-122.2850	2010	18 ± 2	80	111	519
Beach Park	37.5629	-122.2490	2010	29 ± 6	75	12	20
Bird Island	37.5517	-122.2430	2010	5 ± 0	5	1	1
Ideal Marsh	37.5358	-122.1140	2010	16 ± 3	80	42	317
Greco Island	37.5214	-122.2020	2010	5 ± 0	5	1	1
Plummer Creek Marsh	37.5131	-122.0533	2010	—	—	—	500[a]
Outside Pond R1	37.5041	-122.1480	2010	11 ± 4	40	9	12
Coyote Creek Lagoon	37.4770	-121.9530	2010	32 ± 5	80	28	1132
Totals						558	15,144
Limonium duriusculum							
Guadalcanal	38.1181	-122.2889	2010	--	--	--	5
Greenbrae Boardwalk	37.9427	-122.5136	2010	--	--	--	8
Strawberry Marsh	37.8890	-122.5126	2008	--	--	--	178
Seminary Drive #1	37.8880	-122.5104	2010	--	--	--	300
Seminary Drive #2	37.8858	-122.5106	2010	--	--	--	20
Total							511

a. Extent estimated from aerial imagery following site visit by W. Thornton.

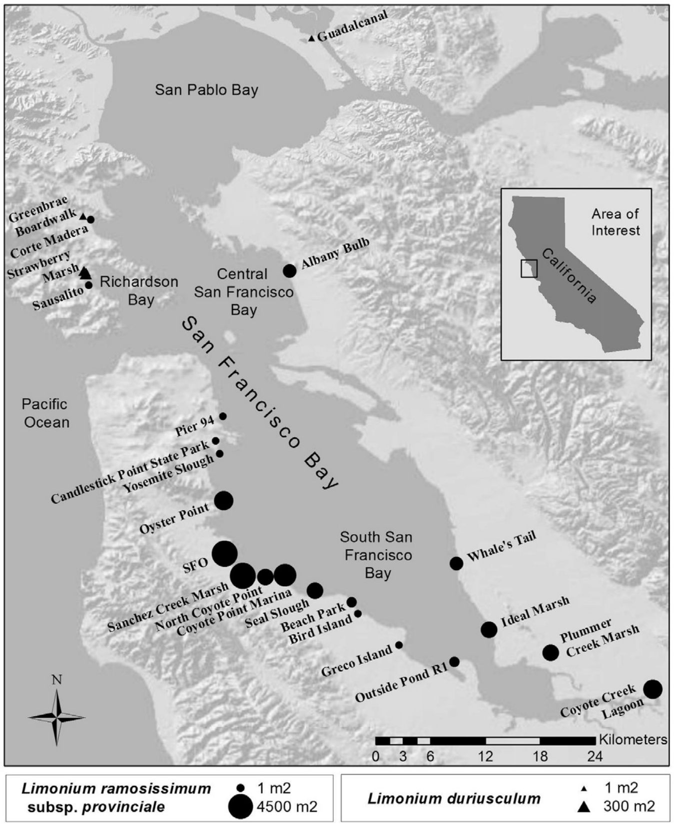

Figure 4 Relative size and location of populations of *L. ramosissimum* subsp. *provinciale* and *L. duriusculum* mapped in the San Francisco Estuary from 2008 through 2010. Strawberry Marsh includes Seminary Drive #1 and Seminary Drive #2 (see Table 1).

lower elevations. LIRA's elevation range was 1.77 to 2.51 m NAVD88 at Sanchez and Coyote and 2.05 to 2.43 m NAVD88 at Seal. Relative to tidal datums, LIRA ranged from 0.09 m below MHW to 0.42 m above MHHW at Sanchez and Coyote. At Seal, plants extended from 0.02 m below MHHW to 0.36 m above MHHW (Figure 5).

Marsh Plant Community Invaded

At Sanchez and Coyote, native species *J. carnosa*, *S. pacifica*, and *D. spicata* were common across LIRA's vertical range (Table 2). A native halophyte indicative of the high marsh, *Frankenia salina* (alkali heath) was most abundant (18.8% cover) in low elevations of LIRA's range. The native sea lavender, *L. californicum*, occurred across LIRA's range. At Coyote, *G. stricta* commonly co-occurred with LIRA at the invader's medium and high elevations (8.8% and 15.6% cover, respectively). At LIRA's highest elevations, species less tolerant of salinity and inundation were present, including *Plantago coronopus* (buckhorn plantain), *Avena fatua* (common wild oat), *Foeniculum vulgare* (fennel), and *Lolium multiflorum* (Italian rye grass). At Seal, at LIRA's medium and high elevations, an alkali grass (*Puccinellia* sp.) was commonly found.

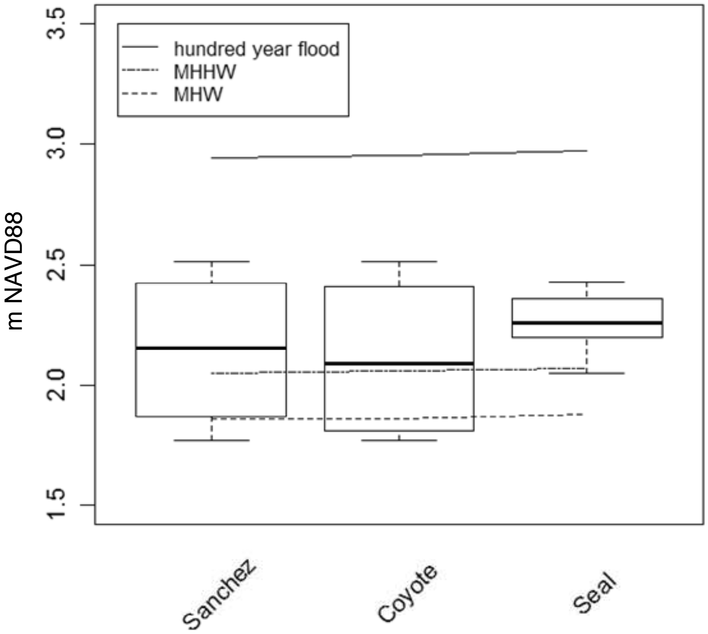

Figure 5 Vertical range (m NAVD88) of LIRA at study sites relative to tidal datums measured with RTK GPS in 2008. Box plots show the median, first, and third quartile of elevation measurements; whiskers show the range.

Soil Properties

Patterns by Marsh, Elevation, and Season in LIRA Patches. In March 2008, soil salinity within each marsh was highest at the low end of LIRA's eleva-

Table 2 Average percent cover of species, wrack, and bare ground in survey plots in and out of *Limonium ramosissimum* subsp. *provinciale* (LIRA) patches in September 2008

	Average Percent Cover								
	Sanchez Creek Marsh			Coyote Point Marina			Seal Slough		
Species	Elevation								
IN LIRA PATCHES	Low	Med	High	Low	Med	High	Low	Med	High
Atriplex prostrata[a]			0.8%						
Avena fatua[a,b]			5.2%			4.0%			
Cuscuta pacifica[c]				0.4%	4.8%				
Distichlis spicata[c]	57.6%	56.0%	46.0%	14.8%	39.2%	2.8%	0.8%	0.0%	18.4%
Foeniculum vulgare[a,b]						2.2%			
Frankenia salina[c]	18.8%	1.2%				1.2%		0.5%	
Grindelia stricta[c]		0.4%		0.8%	8.8%	15.6%			
Jaumea carnosa[c]	92.0%	74.8%	56.0%	89.6%	65.6%	12.4%	38.8%		0.4%
Limonium californicum[c]	8.4%	5.2%	0.4%	4.8%	3.2%		7.2%	10.0%	0.8%
Limonium ramosissimum subsp. *provinciale*[a]	58.8%	99.2%	97.2%	66.8%	90.0%	90.4%	54.0%	26.0%	43.2%
Lolium multiflorum[a,b]			5.6%						
Plantago coronopus[a,b]		1.2%	3.6%			0.4%			
Puccinellia sp.[d]	5.6%	14.4%	10.8%	8.8%	3.6%	22.8%	42.4%	39.5%	33.6%
Salicornia pacifica[c]	68.8%	16.4%	17.2%	67.2%	47.2%	45.6%	49.2%	33.0%	26.0%
Salsola soda[a]							0.4%		
Trifolium sp.[b,d]									
Bare Ground							2.8%	20.0%	23.6%
Wrack								73.8%	39.0%
OUT OF LIRA PATCHES									
Atriplex prostrata[a]						0.8%			
Cuscuta pacifica[c]		2.0%		1.2%	27.2%	0.8%			
Distichlis spicata[c]	65.6%	79.6%	39.2%	41.6%	36.0%	73.6%	1.0%	2.0%	23.5%
Frankenia salina[c]			0.8%						
Grindelia stricta[c]		13.2%	3.6%	9.6%	14.0%	26.0%			7.5%
Jaumea carnosa[c]	99.6%	98.0%	43.2%	71.6%	43.2%	3.2%	3.5%	1.0%	
Limonium californicum[c]				2.0%				6.0%	2.5%
Limonium ramosissimum subsp. *provinciale*[a]	4.4%	0.4%	1.6%	3.2%		1.6%	0.5%		0.5%
Plantago coronopus[a]									4.0%
Puccinellia sp.[d]					18.8%		20.0%	88.0%	25.0%
Salicornia pacifica[c]	67.2%	65.2%	75.6%	93.6%	90.4%	81.6%	97.5%	75.0%	58.5%
Salsola sola[a]		9.6%				0.8%			
Spartina sp.[d]				7.2%					
Trifolium sp.[b,d]			5.2%						
Triglochin maritima[c]			8.4%						
Bare Ground							2.0%	2.0%	21.5%
Wrack							23.8%	68.8%	33.8%

a. Non-native plant.
b. Typically associated with upland habitats.
c. Native halophyte.
d. Native/non-native status not identified.

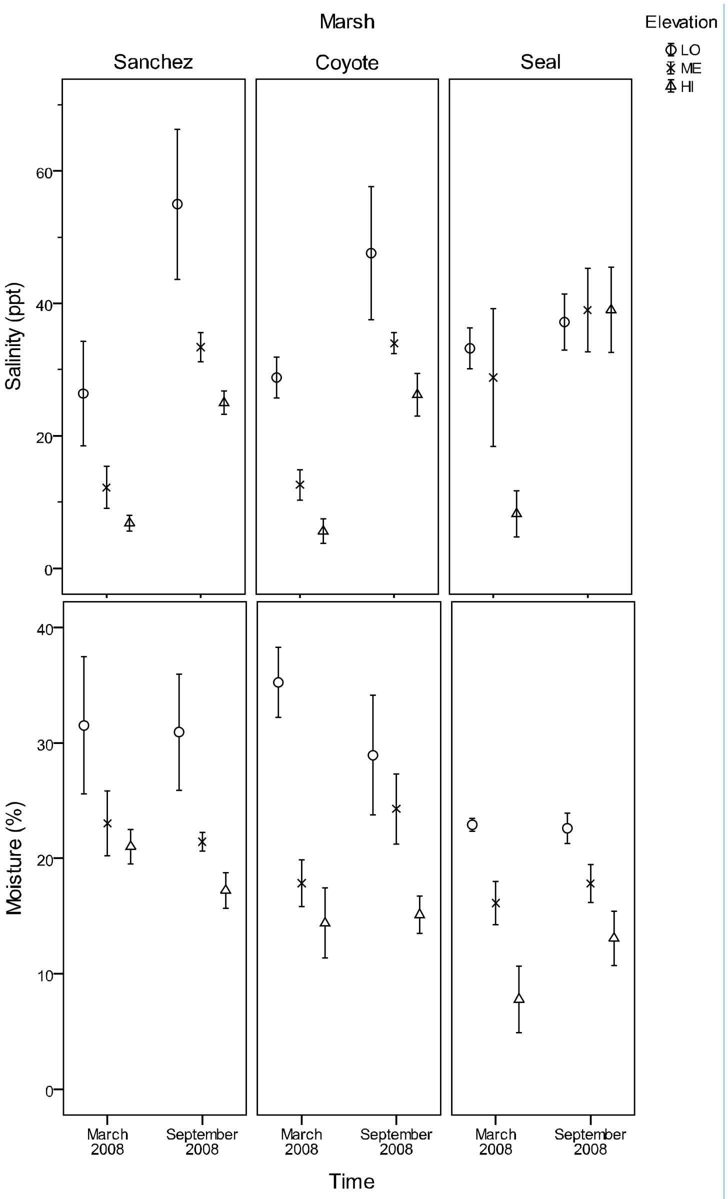

Figure 6 Seasonal variation (March and September 2008) in soil salinity (ppt) and moisture (%) within LIRA patches at Sanchez, Coyote, and Seal marshes across LIRA's elevational range. Error bars represent ±1 S.E.

tional range and decreased with elevation (Figure 6; Appendix B, Tables B-1, B-2). Average salinity at low elevations at Sanchez and Coyote was ~28 ppt, 57% lower at mid-elevations (~12 ppt) and another 50% lower (~6 ppt) at high elevations of LIRA distribution. Soil salinity at Seal also decreased from low to high elevations (Figure 6, Tables B-1, B-2). Soil percent moisture decreased from about 33% to 18% from low to high elevations at both Sanchez and Coyote. Soil moisture at Seal also decreased with elevation but was lower overall than at the other marshes (Figure 6, Tables B-1, B-2).

In September 2008, soil salinities were higher across marshes compared to March measures (significant effect of time on salinity, Tables B-1, B-2), as high as 55 ppt at low elevations and 26 ppt at high elevations (Figure 6). The inverse relationship of salinity and elevation still held at Sanchez and Coyote; however, at Seal, salinities were similar with elevation (~38 ppt) unlike in March (time × elevation effect on salinity, Table B-1). Patterns in moisture in September 2008 were comparable to those in March (Figure 6, Tables B-1, B-2).

In and Out of LIRA Patches. At Sanchez and Coyote in September 2008, soil bulk density was significantly higher ($P=0.025$) and moisture was significantly lower ($P=0.035$) in versus out of LIRA patches. Salinity and percent sand did not differ with LIRA presence. At Seal, none of the four measured soil properties differed significantly in and out of LIRA patches (Figure 7). Assessing texture averaged across elevations, soils were sandy loam at Sanchez, Coyote, and Seal, regardless of LIRA presence.

Both in and out of LIRA patches in September 2008, salinity and moisture decreased significantly with elevation ($P<0.0001$ for both, no interaction with LIRA presence) but neither bulk density nor percent sand showed an elevation effect (Figure 7). Between Sanchez and Coyote, bulk density and percent sand differed ($P=0.020$ and $P=0.004$, respectively), with bulk density higher and percent sand lower at Sanchez. At Seal, soil moisture declined ($P<0.0001$) and percent sand increased ($P=0.001$) with elevation,

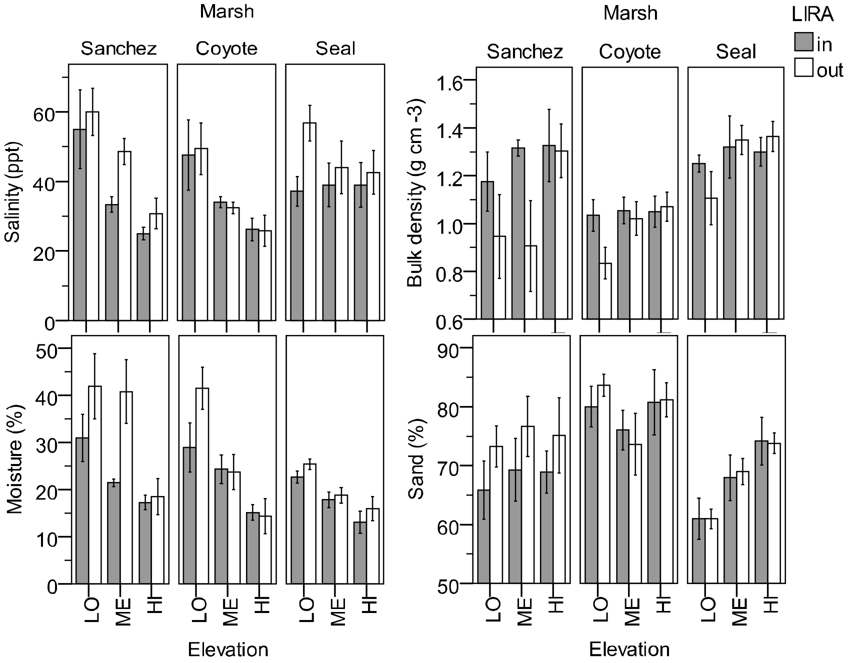

Figure 7 Soil properties relative to elevation (See Figure 4), marsh, and in versus out of LIRA patches from cores collected in September 2008. Error bars represent ±1 S.E.

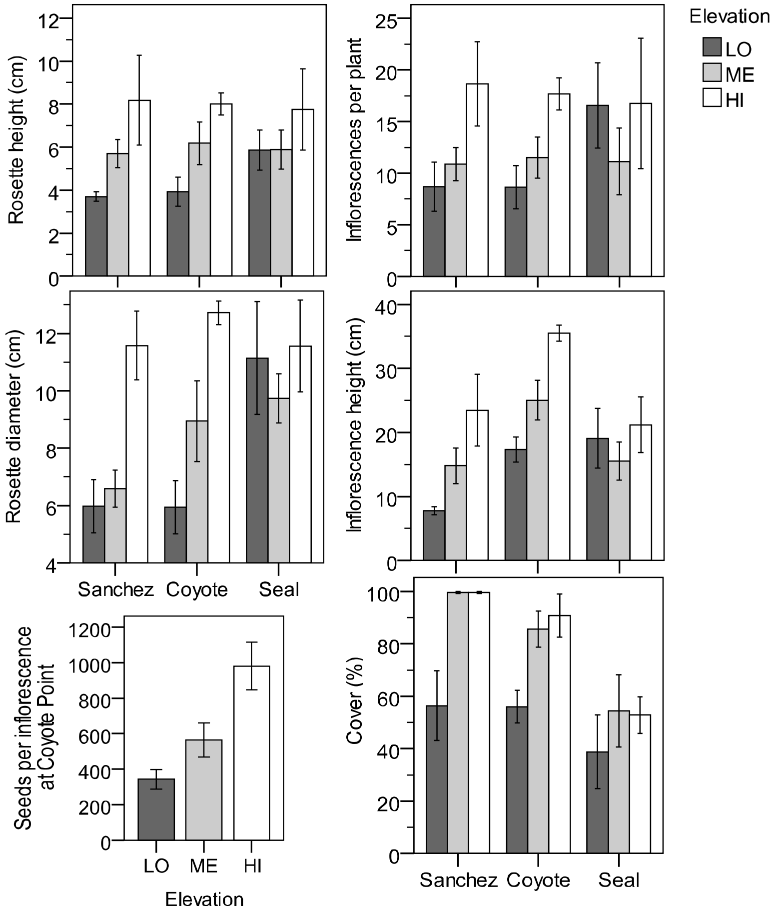

Figure 8 Comparison of LIRA size (July 2008), inflorescence production (July 2008), seed production (August 2008), and percent cover (March 2008) with elevation at the three study marshes. Seeds per inflorescence measured at Coyote only. Error bars represent ±1 S.E.

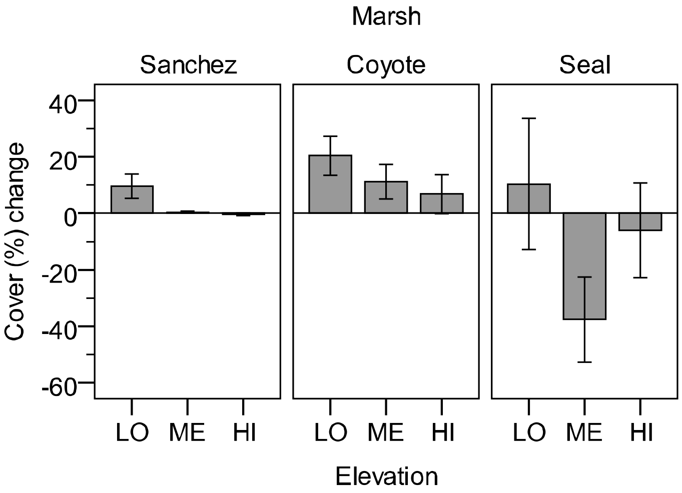

Figure 9 Change in percent cover of LIRA within plots in LIRA patches, by elevation, at the three study marshes over 1 year (March 2008 to 2009). Figure includes plots lost to burial and erosion, and plots that began with 100% cover. Error bars represent ±1 S.E.

but soil salinity and bulk density were similar across elevations (Figure 7).

Indicators of Invasion Success

Morphometric Response to Elevation. Rosette height, diameter, number of inflorescences per plant, and percent cover of LIRA increased significantly with elevation at Sanchez and Coyote (Figure 8, $P=0.0002$; no effect of marsh or interaction). By contrast, there was no multivariate effect of elevation on morphometric response variables at Seal ($P=0.483$). Rosette height increased from low to high elevation at Sanchez and Coyote, from ~ 3.8 to 8.0 cm; the increase was more moderate at Seal, where rosette heights ranged from 5.9 to 7.7 cm. Rosette diameter also increased with elevation from ~6 to 12 cm at Sanchez and Coyote with a more muted range of 11.1 to 11.6 cm at Seal. Number of inflorescences, too, increased with elevation at Sanchez and Coyote, from 8.7 to ~18 inflorescences per plant; however, there was no difference at Seal from low to high elevation (~17 inflorescences throughout). Cover of LIRA at Sanchez and Coyote was ~56% at low and 95% at high elevations: at Seal, LIRA ranged in cover from 39% to 53% with increasing elevation. Inflorescence height was not assessed statistically but showed similar patterns (Figure 8). Seeds per inflorescence, evaluated only at Coyote, increased from ~375 to nearly 1000 from low to high elevation (Figure 8, $P=0.002$).

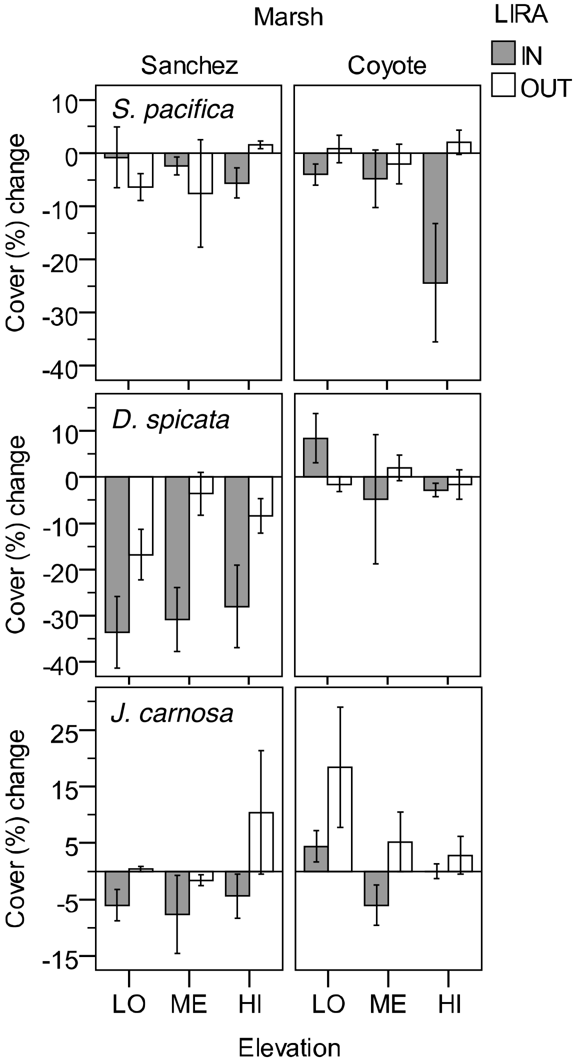

Figure 10 Change in percent cover in native plants (*S. pacifica, J. carnosa,* and *D. spicata*) in plots in and out of LIRA patches across elevations at Sanchez and Coyote from August 2008 to March 2009. Seal data were excluded because nearly half the plots were lost to burial, erosion, and wrack. Error bars represent ±1 S.E.

Spread. Between March 2008 and March 2009, deposition of *Spartina* (cordgrass) wrack and wind-wave erosion caused near total loss of vegetation in some plots at Seal: some plots at Sanchez initially had 100% cover, precluding measurement of further increase. Change in cover of LIRA was highly variable if all those plots were included in calculations (Figure 9). Excluding those plots, percent cover of LIRA tended to increase (on average by 11.0%) across marsh and elevation treatments. Increases in percent cover ranged from 7.7% at Sanchez, to 9.1% at Seal, to 13.6% at Coyote. No difference in LIRA spread as a function of elevation was found at any marsh based on 1-way ANOVAs (all $P > 0.38$).

Recruitment. One or more LIRA seedlings recruited between August 2008 and March 2009 in 27.8% of the plots assessed at Coyote, Sanchez, and Seal. Plots were colonized more frequently by LIRA at high (36.4%) than medium (33.3%) or low elevations (15.4%). Elevation significantly affected the number of plots colonized by LIRA ($\chi^2 = 6.427$, df = 2, $P = 0.040$), but there was no difference in seedling recruitment among marshes ($\chi^2 = 2.350$, df = 2, $P = 0.303$).

Competition. From August 2008 to March 2009, all three native halophytes lost significantly more cover in LIRA patches than occurred in surrounding vegetation (Figure 10, MANOVA effect of LIRA presence, $P = 0.001$) and this effect was consistent among marshes and elevations (no interactions). Negative effects of LIRA presence were most pronounced in the case of *D. spicata* at Sanchez (Figure 10), with a mean 21% decline in cover. Overall, there was a greater decline in native plant cover at Sanchez than at Coyote (Table B-3).

DISCUSSION

Although the presence of introduced *Limonium* species in the estuary was only first recognized in 2007, we documented widespread occurrence in our survey from 2008 to 2010, with 25 populations covering ~1.6 hectares of high marsh and transition zone habitat. LIRA, by far the most common species, had populations concentrated in and around Sanchez, near the San Francisco International Airport. LIRA's abundance in this region and prodigious seed production suggest that propagule pressure, a strong driver of species invasions (Simberloff 2009), is likely highest along the west side of the south estuary. Both LIRA and LIDU populations were generally located ~2 to 8 km from other invaded marshes, suggesting invasion potential may be highest in this range. However, LIRA populations were also identified ~18 km from known seed sources and a single LIDU population was found ~30 km from other populations. Therefore, LIRA and LIDU are also either capable of dispersing across long distances, or multiple introductions of each species have occurred. As we know of two cases of accidental planting or seeding at restoration sites (see Introduction), human-mediated dispersal may have played a role in the distributions we documented.

Habitats Susceptible to Invasion

LIRA and LIDU have primarily established in human- and naturally-disturbed upper salt marsh habitats. Disturbance often increases resources such as space, light, and nutrients (Davis et al. 2000), creating opportunities for colonization (Horvitz et al. 1998; Shea and Chesson 2002; Renz et al. 2012). Many non-native plants gain a foothold in disturbed sites and then invade adjacent undisturbed habitat (Hobbs and Huenneke 1992), a scenario that seems possible for LIRA but that has not been observed to date. Our finding of lower soil moisture and higher bulk density in LIRA-invaded areas suggests that LIRA may be particularly well suited to, or contribute to, these conditions.

LIRA's elevational range across Sanchez, Coyote, and Seal (1.77 to 2.51 m NAVD88, or 0.75 to 1.49 m above MSL) corresponds with the high marsh (0.7 to 1.0 m MSL) and upland transition zone (> 1.0 m MSL) in estuary tidal marshes (Takekawa et al. 2012). At the low end of its range, LIRA occurred with *S. pacifica*, *J. carnosa*, *D. spicata*, *F. salina*, and *L. californicum*, species indicative of the high marsh (Atwater and Hedel 1976; Josselyn 1983; Takekawa et al. 2012). At the upper end of its range, LIRA was found with both native high marsh halophytes and with upland species (e.g., *F. vulgare*, *A. fatua*, and *Trifolium* spp.) typical of the transition zone (Wasson and Woolfolk 2011). Importantly, these findings indicate LIRA can tolerate inundation conditions coincident with mature tidal salt marsh plains, which stabilize near MHHW, and occur in younger pickleweed-dominated marshes, which are typically a few decimeters lower (near MHW; Atwater and Hedel 1976). Further, invasion of the transition zone may lead to a loss of species that contribute to high species richness there, including rare species such as *Chloropyron maritimum* subsp. *palustre* and *Suaeda californica*, which we have observed growing among LIDU and LIRA patches, respectively.

LIRA was found across a soil salinity gradient that decreased from the high marsh into the transition zone, a salinity pattern consistent with findings in the estuary (Mahall and Park 1976; St. Omer 2004), at Pt. Reyes National Seashore (Traut 2005), in Elkhorn Slough (Harvey et al. 1978; Byrd and Kelley 2006), and in cooler climates (Oregon: Seliskar 1985), but contrasting with patterns in southern California marshes where soil is hypersaline during summer months through the transition zone up to maximum high water (Callaway et al. 1990). Soil moisture, too, decreased with elevation across LIRA's vertical range. Declining moisture across this vertical range is well established, but our soil moisture values were lower than similar studies. Traut (2005) found moisture decreased from 40% to 15% from mid-marsh into upland soils in June and July. St. Omer (2004) found little variation in moisture seasonally in the high marsh, but moisture ranged from 47% to 62%. Texture was not reported for either study, but it is possible that moisture values were lower at our study sites because of: (1) high sand content in the soils in our study, which leads to lower water-holding capacity (Brady and Weil 1999), and (2) lack of adjacent upland with a concurrent water table. Together, these findings support a conceptual model of LIRA as a species that can establish in both dry, sandy soils as well as moist, seasonally hypersaline soils.

Indicators of Invasion Success

Across our study sites, LIRA size and reproductive output noticeably increased above MHHW, particularly in the transition zone where soil moisture and salinity were lowest. Below MHHW, higher salinity and inundation likely limit the size and reproductive output of LIRA. This fits with prior studies of *Limonium* species (e.g., Boorman 1971) and with upper salt marsh species in general (e.g., Cooper 1982; Seliskar 1985; Schile et al. 2011; Ryan and Boyer 2012). Since LIRA grows largest in low stress conditions, we suspect it may compete most aggressively within the transition zone.

Seed output for LIRA at Coyote was orders of magnitude higher than LIDU seed output reported by Hubbard and Page (1997), which ranged from 360 to 11,400 seeds per square meter at Carpinteria Salt Marsh in Santa Barbara. At Coyote, we found LIRA seed output ranged from about 3,000 to about 17,400 seeds <u>per plant</u>, depending on elevation. Assuming seed production at Sanchez and Seal is on par, we estimate LIRA seed output typically ranges from about 36,000 to 130,000 seeds per square meter at low versus high elevations, respectively. This difference alone may explain why LIRA is more widespread than LIDU in the estuary. In the highly invaded marshes near Sanchez, we observed carpet-like growth of hundreds of LIRA seedlings in and around LIRA patches. Furthermore, LIRA cover was consistently high in large patches (mean of 70% cover in patches over 200 m^2). These observations suggest that, once established in suitable habitat, infilling of space between LIRA plants is likely aided by intense, local propagule pressure within marshes.

Over one year, LIRA's rate of spread (11%) was consistent with average invasive plant spread rates across western wildlands (Asher and Dewey 2005). LIRA recruitment was greatest at high elevations, suggesting seeds are more frequently distributed by tidal action to higher elevations, germinate and establish more readily at higher elevations, or both. No difference in recruitment was found between marsh sites, which was unexpected since Sanchez and Coyote have considerably larger populations (and hence seed production) than Seal. These findings suggest that seed from adjacent populations may contribute significantly to recruitment at Seal.

We found native plant cover rebounded less after winter senescence in LIRA patches. In Carpinteria Salt Marsh, Hubbard and Page (1997) found LIDU was associated with decreased native plant cover over the course of 1 year, and attributed this to LIDU's ability to grow when most native plants senesce. In our study at Sanchez and Coyote, *S. pacifica*, *J. carnosa*, and *D. spicata* cover was lower over 6 months with LIRA present. We hypothesize that LIRA may draw down nutrients and/or physically expand during winter, thereby reducing resources available to other plants emerging from winter senescence. A longer study period that includes summer months is needed to verify LIRA's effect on native plant cover.

Transition zone habitats provide important high tide refuge for endangered vertebrates, and this function depends, in part, on the physical structure of the plants in the transition zone. Salt marsh harvest mice, for example, require an overhead canopy for protection from predators (Fisler 1965; Shellhammer 1989). LIRA rosettes, however, form dense, low-growing (~3 to 10 cm tall) patches that likely provide poor refuge from predators. Dense LIRA cover too, by virtue of physically covering marsh substrate, may impede seedling establishment of high marsh plants such as *G. stricta* that provide essential nesting habitat and high tide refuge for the endangered California clapper rail (Evens 2010).

CONCLUSION

LIRA and LIDU appear well suited to invade disturbed, sandy loam soils in upper salt marsh habitats in the estuary. LIRA growth and reproductive output are greatest in the transition zone where soil moisture and salinity are lower, but the invader can also establish, spread, and compete with native plants in the high marsh above MHW. LIRA competes with native high marsh and transition zone species important as high tide refugia for endangered native vertebrates. Combined with the many locations of introduced *Limonium* we documented, this suggests upper salt marsh habitats in the estuary are at risk of invasion, with consequences for native special status species conservation, and leads us to strongly recommend localized and regionally-coordinated control efforts. Managers should regularly monitor marshes located fewer than 8 km from known invasion sites to identify and prevent spread between marshes and should initiate removal efforts in the transition zone in invaded marshes. Further, the recent mis-identification and accidental introduction of invasive sea lavenders to restoration sites in San Francisco and in the South Bay suggest that outreach and improved awareness are necessary to avoid further human-mediated spread. Finally, genetic studies are needed to help resolve the possibility of multiple introductions as well as the potential for hybridization (Palacios et al. 2000) among the established sea lavender species in estuary marshes.

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