



Salt Marsh-Upland Ecotones in Central California: Vulnerability to Invasions and Anthropogenic Stressors

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Abstract Ecotones, zones of abrupt biological transition typically reflecting strong physical gradients, may be particularly sensitive to changes in environmental conditions. Our characterization of the ecotone between salt marshes and uplands in the Elkhorn Slough watershed in central California revealed that extent of appropriate habitat for native high marsh species endemic to this zone is extremely limited. The ecotone is highly invaded, with non-native upland weeds accounting for a significant proportion of cover. We investigated responses to two anthropogenic landscape management strategies, restriction of tidal exchange through water control structures and cattle grazing. Moderate tidal restriction resulting in muted tidal exchange dramatically decreased ecotone width, native marsh plant richness, and cover by native ecotone specialists. Even stronger tidal restriction resulting in very low tidal exchange led to a seaward shift of the ecotone into the area formerly occupied by mid-marsh vegetation; upland plants now occupy the former ecotone zone so net loss of wetland habitat has occurred. Cattle grazing led to a very substantial increase in bare ground, a significant decrease in native marsh plant richness and a significant increase in non-native plant cover. Thus, both of these management regimes can have significant negative impacts on rare salt marsh ecotone extent and biodiversity.

Keywords Disturbance · Grazing · Invasion · Transition zone · Water control structure

Introduction

Ecotones, the transitional areas between adjacent ecological systems, frequently host high biodiversity because they contain characteristics of both adjacent systems as well as distinctive microhabitats. They can intensify flows of water and nutrients and facilitate movement of organisms (Risser 1995). Ecotones tend to be narrow zones between two larger ecosystems. In temperate estuaries, there is typically a distinctive, diverse and narrow ecotone between the broader and more homogeneous salt marsh plain on the seaward side, and the adjacent upland habitat type on the landward side of the transition zone. The processes that generate diversity patterns in areas of biotic transition are vital for understanding not only the transition zones themselves, but also for understanding the fate of the ecosystems on either side of the boundary: ecotone dynamics can drive landscape change (Peters et al. 2006). We investigated the dynamics of the salt marsh-upland ecotone in coastal California, to identify factors that affect ecotone diversity, and that influence ecotone boundaries and thus landscape change.

The first goal of our investigation was to characterize landscape parameters and plant communities of the marsh-upland ecotone at Elkhorn Slough estuary, which hosts one of the most extensive salt marshes in California. The emphasis of our study was on “ecotone specialists,” native high marsh species that are limited almost entirely to the zone between the marsh plain and the uplands. As a part of our characterization of ecotone dynamics, we attempted to determine whether the ecotone was homogenous in terms of

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plant communities or whether there were gradient properties within this transition zone, such that seaward portions of the ecotone differed from landward portions. Such strong gradients are one feature that has been ascribed to ecotones between other habitat types (Risser 1995).

The second goal of our study was to examine how invaded the marsh-upland ecotone was by non-native plant species. Wetlands may have a propensity to become dominated by invasive species, because they function as “landscape sinks,” accumulating materials from both terrestrial and wetland disturbances (Zedler and Kercher 2004). Non-native plants have been reported as widespread in high salt marsh at sites in North America, Australia, Spain, and Portugal (Adam et al. 1988; SanLeon et al. 1999; Adam 2002; Campos et al. 2004; Grewell et al. 2007; Costa et al. 2009). The upland habitat adjacent to salt marshes at Elkhorn Slough typically consists of grasslands, although in some areas oak woodlands, willow-dominated riparian tracts, or cultivated fields abut the marsh. The grasslands as well as the understory of woodlands in this watershed are highly invaded by non-native terrestrial plants (Caffrey et al. 2002), thus our objective was to determine whether these non-native species also had invaded the marsh-upland ecotone, potentially posing a threat to native ecotone specialists.

The third goal of our study was to determine how ecotone boundaries and biodiversity responded to human alterations of landscape properties. Ecotones may be sensitive to environmental changes in general, and can be particularly vulnerable to anthropogenic alterations (Levin et al. 2001). Some alterations may decrease the extent of the ecotone, for instance by making the gradient between the adjacent ecosystems more steep, or by leading to loss of vegetation. In addition to wholesale loss of habitat through narrowing or loss of vegetation, alterations could lead to changes in species assemblages (Risser 1995). The marsh-upland ecotone could be affected by human activities originating in the dominant habitat type seaward of the ecotone (e.g., changes to wetland hydrology) and landward of it (e.g., changes to upland land use). To explore the response of ecotones to human alterations, we investigated dynamics of the salt marsh-upland ecotone subjected to two management strategies, one originating the wetland and one in the upland.

One common coastal management strategy is to restrict tidal flow using water control structures, which can include berms, dikes, tide gates, and culverts (Kennish 2002). Water control structures have typically been constructed in order to “reclaim” wetlands for human uses, to prevent flooding of adjacent lands, or to impound freshwater for waterfowl hunting or livestock use. They may also be used in the future to protect against marsh loss in the face of rapidly rising sea levels. In marshes without an adequate

sediment supply to keep pace with rising sea level, water control structures may create the relative elevations and sediment stability needed to protect marshes in danger of drowning (Adam 2002; French 2008). In Louisiana, where ground subsidence has already led to relative sea level rise, and where mineral sediments are insufficient, water level manipulation with control structures has been used and advocated to increase marsh plant expansion and growth (Sanzone and McElroy 1998). As sea level rise begins to threaten more salt marshes, coastal managers may increasingly consider the use of water control structures in an effort to protect estuarine habitats. Because hydrology is the driving force for salt marsh function (Callaway 2001), we expected that water control structures would affect marsh ecotone properties as well.

A second common management strategy in coastal habitats is cattle grazing. Salt marshes in Europe and North America have been used for livestock grazing for centuries (Adam 2002), and, in California, cattle grazing is frequently used not only for economic reasons, but also in an effort to reduce fuel loads, control invasive weeds, and to enhance species diversity in coastal habitats (Huntsinger et al. 2007). Grazing has been shown to alter species composition in European marshes (Andresen et al. 1990; Bos et al. 2002; Schröder et al. 2002), but its ability to promote species richness in Californian tidal marshes requires more research (Zedler 2000). Some authors have endorsed managed grazing as a tool for promoting biodiversity in California grasslands, although this recommendation is somewhat controversial (Huntsinger et al. 2007). We expected that grazing would affect plant richness and habitat extent of the ecotone.

We examined the response of the marsh-upland ecotone to water control structures and cattle grazing in terms of landscape features and plant communities. We employed both univariate statistical analyses of environmental parameters and community indices, and multivariate analyses of community composition to investigate ecotone response to these two disparate types of management regimes. Taken together, our characterization of the ecotone community, examination of invasions, and assessment of two management practices, allowed us to make recommendations for best management practices for conserving native biodiversity and extent of this rich coastal habitat.

Methods

Study System

We conducted this research in the salt marsh-upland ecotone of the Elkhorn Slough watershed in central California. The estuarine complex in this area is comprised

of multiple channels flanked by salt marsh; the largest channel is Elkhorn Slough, and smaller ones include Moro Cojo Slough, the Old Salinas River channel, and Bennett Slough. There is a single mouth to the sea for this estuarine network, near Moss Landing in the middle of the Monterey Bay. About 900 ha of estuarine habitat in the Elkhorn Slough watershed receive unrestricted tidal exchange (with the same tide range as the adjacent open coast, about 250 cm maximum); the remaining 500 ha have tidal exchange artificially restricted by water control structures (dikes, berms, culverts, tide gates).

In the estuarine habitats of the Elkhorn Slough area, intertidal marsh occurs above unvegetated intertidal mudflats. A single dominant plant, pickleweed (*Salicornia virginica*), accounts for almost all the cover in the low to mid marsh, or marsh plain (approximately mean high water to mean higher high water in areas open to full tidal exchange). Above mean higher high water, high marsh plants co-occur with pickleweed and also with upland

plants. This transition zone between a virtual monoculture of pickleweed and pure upland vegetation is the salt marsh-upland ecotone (Traut 2005a).

Sites and Management Treatments

We sampled the marsh-upland ecotone at 18 sites in the Elkhorn Slough watershed (Fig. 1; Appendix). We examined two types of management strategies, tidal restriction and cattle grazing, and compared these to control sites with full tidal exchange and no cattle. We separated tidally restricted sites into two categories *a priori*: muted vs. very low tidal exchange, because an earlier study at Elkhorn Slough used this classification and found significant differences between these categories (Ritter et al. 2008). This resulted in a total of four treatment categories. We used sites as replicates for each treatment. Despite this being a fairly large estuarine complex with many separate wetlands behind different water control structures or under

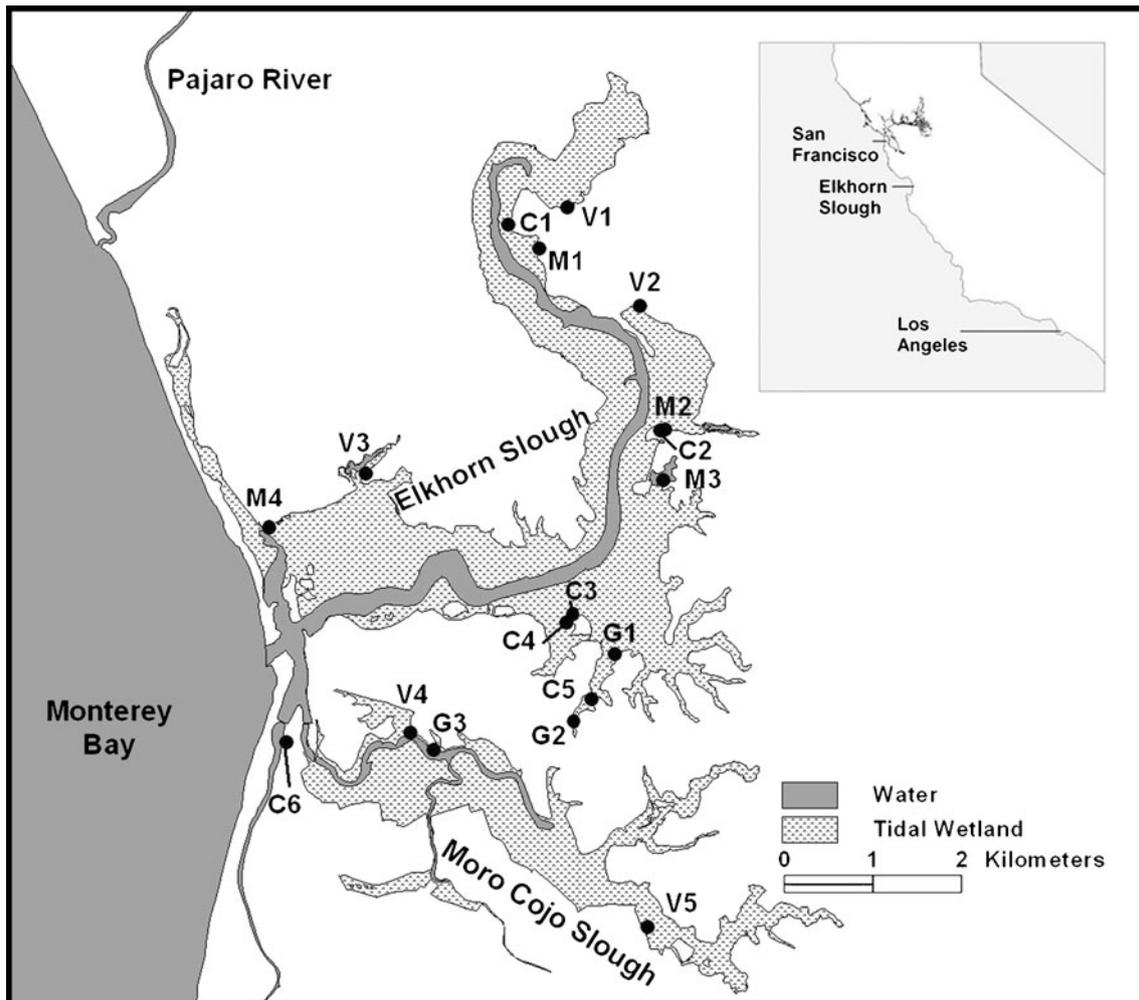


Fig. 1 Location of study sites. Six control sites are labeled C1-6; four sites with muted exchange are labeled M1-4; five sites with very low tidal exchange are labeled V1-5; three cattle grazed sites are labeled G1-3

different upland management, replication was necessarily limited and varied across treatments; we used all independent sites available under a particular management treatment.

Control Sites We used six sites as controls. These sites were subject to full tidal exchange and had not been grazed by cattle for at least five years. Previous research indicated that marsh plants in Elkhorn Slough recover quickly after the removal of cattle, resembling ungrazed sites within a year of livestock exclusion (Woolfolk 1999). We chose sites that were similar in location, slope and aspect to nearby sites of the other treatments. These sites typically had a fairly broad ecotone with dense vegetation (Fig. 2a).

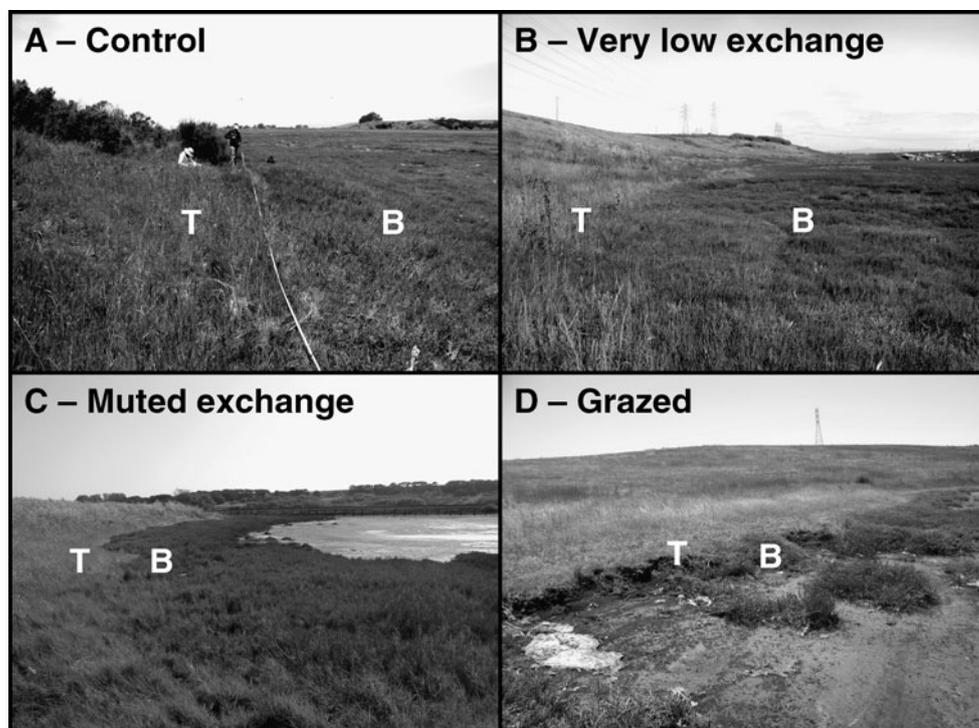
Muted Tidal Exchange We used four sites with regular, daily tidal exchange (tidal range between 10–50% of that of adjacent full tidal exchange sites). Each of these was an independent wetland with tidal exchange restricted through a separate water control structure. These sites had extensive standing water at all tide levels (Fig. 2c).

Very Low Tidal Exchange We used five sites with tidal exchange extremely limited by water control structures (0.5–5% of that of adjacent full tidal exchange sites). All of these are managed with the intent to entirely exclude tidal exchange, but receive limited tidal water through leaking water control structures and/or occasional flood events that overtop the water control structures. As with muted sites,

each was an independent wetland with tidal exchange restricted through a separate water control structure. These sites typically have narrow channels of permanent standing water flanked by extensive salt marshes (Fig. 2b).

Grazed Sites We used three sites grazed by cattle. These were three separate fenced properties where cattle had access to salt marsh as well as adjacent grasslands; more replication was desirable, but we did not find any other independent sites with cattle in the salt marsh. Two of these sites were subject to full tidal exchange, one had very low exchange. The grazed treatment thus potentially confounds the effects of tidal restriction (the very low exchange category) and cattle, but since the subsequent analyses showed no similarity in the effects of grazing and very low exchange (e.g., grazing decreased ecotone width while very low exchange had the reverse effect), including the very low exchange grazed site to increase replication was justified. Cattle densities on each property were estimated from various high resolution aerial photographs taken within 19 months of our field sampling. Densities ranged from 0.30–2.42 cattle/ha for these three sites, with an average of 1.23 cattle/ha. Any differences observed between the grazed and the control treatment may be due to grazing, trampling, nutrient enrichment, or other direct or indirect effects of cattle; our use of the term “grazed” as a name for this treatment does not refer to mechanisms of impact on ecotone plants, only to land use type (land grazed by cattle). These sites had conspicuously less vegetation than sites of the other treatments (Fig. 2d).

Fig. 2 Characteristic ecotones in different treatments. Note wide ecotone above broad marsh plain in Control and Very low exchange treatments. In Muted exchange, ecotone is narrow, above limited marsh that fringes a lagoon. In Grazed treatment, ecotone is narrow and there is substantial bare ground. In all photos, the landward side is to the left, the seaward side to the right. The approximate Top (T) of the ecotone (100% upland vegetation) and Bottom (B) (100% pickleweed) are indicated



Field Sampling Design

We sampled all sites between mid-April and early June 2005. Sampling occurred in this period because it is a temporal window in which many upland plants flower prior to senescing during the summer dry season, and marsh plants have begun growing after a winter dormant period. At each site, we ran a 100 m transect along the ecotone, parallel to the land-sea gradient. We began this transect at a haphazard representative location as close as possible to the spot where we accessed the site, but away from any visible disturbance caused by the access trail. We used a random number generator to locate three random points along this 100 m transect. If a point fell within 10 m of another, we rejected it and used the next random number.

At each of the random points, we set up a transect perpendicular to the land-sea gradient (and the 100 m transect). We located and marked the bottom, middle, and top of the ecotone along this transect, defined arbitrarily but repeatably as follows: Bottom—the most landward spot in the transect with 100% of the vegetative cover consisting of pickleweed; Middle—the most landward spot in the transect with a marsh plant measuring >20 cm in height; and Top—the most seaward spot with 100% of the vegetative cover consisting of upland plants. We measured the width of the ecotone from the bottom to the top.

We assessed relative abundance of plants in each transect by taking a point intercept every 50 cm from the top to the bottom. We kept track of whether the point fell into the seaward (bottom to middle) or landward (middle to top) part of the ecotone. Any plant that was touched by a 0.5 cm diameter rod was counted as present at the intercept; in most cases this was a single plant, but sometimes multiple plants were encountered. If no plants were touched by the rod, this was recorded as “bare ground.” After assessing the three transects perpendicular to the shoreline, we walked the entire length of the 100 m transect running along the ecotone parallel to the shoreline, and noted any additional plant species occurring within ecotone that had not been encountered during the transects assessments.

Plants were mostly identified in the field using regional field guides (Hickman 1993; Matthews 1998). Difficult specimens were collected and examined further in the laboratory. Some plants (lacking flowers or other diagnostic characteristics) were considered “unknowns,” and given descriptive labels to distinguish them from other identified species or unknowns.

Elevation

We used remote sensing to assess elevation and slope of the ecotone. We used high resolution aerial photographs taken by the California Department of Fish and Game on 4 April 2005, and georeferenced them using ArcView 3.2 and Image

Analysis to 2005 National Agriculture Imagery Program aerial photographs. For each site, we created a polygon 100 m in length (parallel to shore) with the width the same as the average width measured in the field, centered on what we interpreted in the aerials to be the boundary between characteristic marsh and upland vegetation. We then used Light Detection and Ranging (LiDAR) imagery to obtain elevations at approximately 1 m intervals along the 100 m landward and seaward edges of the ecotone polygon. On average, the vertical accuracy of the LiDAR data was 12 cm. We initially obtained these elevations in NAVD88; locally 0.0 m NAVD88 is equivalent to 0.015 m above MLLW (Mean Lower Low Water), so we subtracted 0.015 m from all values in order to express elevations relative to MLLW, which is how NOAA tide predictions reference coastal water levels. All the landward and all the seaward elevations were averaged for each site to obtain a single estimate of the elevation of the top and the bottom of the ecotone zone. We calculated the elevational gradient by subtracting the elevation of the bottom from the elevation at the top.

Plant Community Calculations

To determine relative abundance (percent cover) of bare ground, we used the point intercept data and calculated: $(\text{number of intercepts with only bare ground} / \text{total number of intercepts}) \times 100$. To determine relative abundance (percent cover) of each plant species, we used the point intercept data and calculated: $(\text{number of intercepts where plant occurred} / \text{total number of intercepts with vegetation}) \times 100$.

We determined which plant species that we had encountered in the field were closely associated with salt marshes, using habitat descriptions in the published literature (Macdonald 1977; Hickman 1993) as the basis for this determination. These species were then categorized as “marsh plants” and all other species were considered “upland plants”. We also determined which plant species were native to central California vs. non-native, using the same references. Unidentified species were omitted from these assessments but only accounted for between 1–4% cover on average in the four treatments.

Statistical Analysis

We averaged values across all 18 sites in order to provide an overall characterization of landscape parameters and plant community summary statistics. For all subsequent statistical analyses, we averaged the values for each parameter for the three transects per site, and used this single average value per site as the replicate for treatments for all analyses. All tests thus had limited power due to low sample size.

We employed one-way Analysis of Variance (ANOVA) to examine landscape and plant community summary

parameters. Visual inspection of frequency distributions revealed no major deviations from normality, although the low sample sizes did not allow the distributions to be well characterized. All parameters met standard tests for equal variances between treatments (O'Brien and Bartlett tests) except for percent cover of bare ground, which was $\log(x+1)$ transformed (and then satisfied these tests). No other parameters were transformed for analyses. We conducted one-way ANOVA to distinguish seaward and landward portions of the ecotone in terms of percent cover by upland vs. marsh species. We also conducted one-way ANOVA to test for differences among the four management regimes (control, muted tidal exchange, very low tidal exchange, grazed) for landscape and plant community summary parameters. Fisher's PSLD was used as a post-hoc statistical test for pair-wise differences between treatments.

We conducted several related multivariate analyses using the program Primer v. 6 (Clarke and Gorley 2006) to examine differences in plant communities in seaward vs. landward portions of the ecotone and under the four management regimes. We used the plant species percent cover data as described above, omitting all unknown species, averaged across the three transects per site. We supplemented these transect data with the additional species identified in the final walk-through of the ecotone at each site, assigning each of these species an arbitrary cover value of 0.1% to allow for their inclusion in the community analysis. We log-transformed the cover data to downweight the influence of the most abundant species. To graphically examine patterns of species composition across treatments, we first visualized dissimilarity sites of different treatments using non-metric multidimensional scaling (nMDS) plots based on Bray-Curtis resemblance matrices. Analysis of similarities (ANOSIM) was used to determine whether dissimilarity in community structure among sites in different treatments was statistically significant. We report the global R-statistic as well as that generated by ANOSIM for pairwise comparisons among treatments; R values close to 1 represent very different community composition among treatments while R values close to 0 represent very similar composition. Similarity percentages (SIMPER) were used to determine levels of dissimilarity within and among treatments, and to identify which species contributed the most to dissimilarities among treatments. Background on all these statistical techniques is provided by Clarke and Warwick (2001).

Results

Characterization of Ecotone Extent and Diversity

The synthesis of data from all 18 sites revealed that the amount of high marsh–upland ecotone habitat at Elkhorn

Slough was very limited. The average width of the ecotone was only 460 cm. Its vertical distribution relative to tidal datums was on average between 1.45 and 1.75 m above MLLW, thus a vertical elevational range of only about 30 cm.

By definition, “ecotone specialists” (native high marsh plants) were limited to this narrow ecotone zone in our transects (100% cover by pickleweed occurred seaward of the ecotone, and 100% cover by upland plants occurred landward of it). Nevertheless, on average across these 18 sites, ecotone specialists accounted for only 31% of plant cover in this narrow ecotone. Pickleweed accounted for 44%, while upland plant species comprised the remainder.

For all sites combined, we identified a total of 65 plant species in the Elkhorn Slough ecotone, of which six were ecotone specialists (Table 1). Native salt marsh richness averaged 4.2 species per transect. Only two ecotone specialists, salt grass (*Distichlis spicata*) and alkali heath (*Frankenia salina*) had >10% average percent cover in the ecotone. While we found 22 species of upland natives in the ecotone, few of these accounted for much cover on average (Table 1). The most common upland natives in the Elkhorn Slough ecotone were coyote brush (*Baccharis pilularis*), creeping wild rye (*Leymus triticoides*), stinging nettle (*Urtica dioica*), and unidentified rushes (*Juncus* spp.).

Even within the narrow ecotone zone lying between the mid-marsh and upland habitats, we found evidence for strong gradients in plant communities. Plant communities in seaward portions of the ecotone were significantly different from those in landward portions (ANOSIM $R=0.12$, $p=0.001$). A SIMPER analysis revealed that marsh plants were the top three contributors to dissimilarity between landward and seaward portions: pickleweed and alkali heath were more abundant in the seaward portions, while salt grass was more abundant in the landward portion. Not surprisingly, percent cover of salt marsh plants overall was greater in the seaward than landward portion (85 vs. 62%, ANOVA $p=0.008$), while percent cover of upland plants was lower in the seaward vs. landward portion (9 vs. 34%, ANOVA $p<0.0001$). Average Bray-Curtis similarity among sites in plant communities was greater for the seaward vs. landward portions (44 vs. 21% in SIMPER analysis). The greater dissimilarity between sites in landward plant communities was due to greater variability in upland species composition between sites.

Invasions by Non-Native Plants

In terms of salt marsh plants, two of nine species encountered at all sites combined were non-native (Table 1). One of these, sickle grass (*Parapholis incurva*), was moderately abundant. Nevertheless, non-native species only accounted for 3% of marsh plant abundance across all sites.

Table 1 Plants found in marsh-upland ecotone. Species are categorized as being tightly associated with salt marshes (“salt marsh” category) vs. not (“upland” category), and as native vs. non-native species; under these headings they are alphabetical by genus. Percent

cover is shown averaged per treatment; a “p” (for “present”) is shown for species detected but whose abundance in point counts was zero. To highlight the most abundant species, percent cover values >1.0 are shown in bold

| Category & Scientific name | Common name | Family | Control | Muted exchange | Very low exchange | Grazed |
|---|------------------------|---------------------|-------------|----------------|-------------------|-------------|
| Salt Marsh Natives (7 species) | | | | | | |
| <i>Salicornia virginica</i> | pickleweed | Chenopodiaceae | 34.4 | 64.7 | 46.2 | 24.4 |
| Marsh-upland ecotone specialists | | | | | | |
| <i>Atriplex triangularis</i> | spearscale | Chenopodiaceae | 0.4 | 4.2 | 0.2 | p |
| <i>Cuscuta salina</i> | salt marsh dodder | Cuscutaceae | 0.3 | 0 | p | p |
| <i>Distichlis spicata</i> | salt grass | Poaceae (Festuceae) | 17.8 | 0 | 21.1 | 19.2 |
| <i>Frankenia salina</i> | alkali heath | Frankeniaceae | 17.3 | 0 | 3.7 | 14.7 |
| <i>Jaumea carnosa</i> | fleshy jaumea | Asteraceae | 7.9 | 9.5 | 0.4 | 1.4 |
| <i>Spergularia marina</i> | salt marsh sand spurry | Caryophyllaceae | 0 | p | 0 | 0 |
| Salt Marsh Non-natives (2 species) | | | | | | |
| <i>Cotula coronopifolia</i> | brass buttons | Asteraceae | 0 | 0 | p | p |
| <i>Parapholis incurva</i> | sickle grass | Poaceae (Hordeae) | 1.9 | 0 | 0.4 | 11.1 |
| Upland Natives (22 species) | | | | | | |
| <i>Ambrosia chamissonis</i> | beach bur | Asteraceae | p | 0 | 0 | 0 |
| <i>Atriplex californica</i> | California saltbush | Chenopodiaceae | p | 0 | 0 | 0 |
| <i>Baccharis pilularis</i> | coyote brush | Asteraceae | p | 3.3 | 0.2 | 0 |
| <i>Camissonia ovata</i> | suncups | Onagraceae | p | 0 | 0 | 0 |
| <i>Carex sp.</i> | unidentified sedge | Cyperaceae | p | 0 | 0 | 0 |
| <i>Chlorogalum pomeridianum</i> | wavy-leaved soap plant | Liliaceae | p | 0 | 0 | 0 |
| <i>Claytonia perfoliata</i> | miner’s lettuce | Portulacaceae | 0 | 0 | p | 0 |
| <i>Galium aparine</i> | goose grass | Rubiaceae | 0 | 0 | 0.3 | 0 |
| <i>Grindelia latifolia</i> | coastal gum plant | Asteraceae | p | 0 | 0 | 0 |
| <i>Heliotropium curassavicum</i> | seaside heliotrope | Boraginaceae | p | 0 | 0 | 0 |
| <i>Hordeum brachyantherum</i> | meadow barley | Poaceae (Hordeae) | p | 0 | 0.2 | p |
| <i>Horkelia californica</i> | California horkelia | Rosaceae | p | 0 | 0 | 0 |
| <i>Juncus bufonius</i> | common toad rush | Juncaceae | 0 | 0 | p | 0 |
| <i>Juncus sp.</i> | unidentified rush | Juncaceae | 3.0 | 2.1 | 0.6 | 0 |
| <i>Leymus triticoides</i> | creeping wild rye | Poaceae (Hordeae) | 0.3 | p | 1.8 | 0 |
| <i>Pentagramma triangularis</i> | golden fern | Pteridaceae | 0 | 0 | p | 0 |
| <i>Perideridia kelloggii</i> | Kellogg’s yampah | Apiaceae | p | 0 | 0 | 0 |
| <i>Rubus ursinus</i> | California blackberry | Rosaceae | 0 | 0 | p | 0 |
| <i>Salix sp.</i> | unidentified willow | Salicaceae | 0 | 0 | p | 0 |
| <i>Sanicula crassicaulis</i> | gambleweed | Apiaceae | 0 | p | 0 | 0 |
| <i>Scirpus americanus</i> | three square | Cyperaceae | 0 | 0 | p | 0 |
| <i>Urtica dioica</i> | stinging nettle | Urticaceae | 0 | 0 | 2.1 | 0 |
| Upland Non-natives (34 species) | | | | | | |
| <i>Anagallis arvensis</i> | scarlet pimpernel | Primulaceae | p | p | p | p |
| <i>Anthemis cotula</i> | dog fennel | Asteraceae | 0 | 0 | p | 0 |
| <i>Anthriscus caucalis</i> | bur chervil | Apiaceae | 0 | 0 | 0.4 | 0 |
| <i>Avena barbata</i> | slender wild oat | Poaceae (Aveneae) | p | 0 | 0 | 0 |
| <i>Avena fatua</i> | wild oat | Poaceae (Aveneae) | 0.3 | 0 | 0 | 0 |
| <i>Brassica nigra/rapa</i> | black/field mustard | Brassicaceae | p | p | p | 0 |
| <i>Bromus diandrus</i> | ripgut grass | Poaceae (Festuceae) | 1.2 | p | p | 0 |
| <i>Bromus hordeaceus</i> | soft chess | Poaceae (Festuceae) | 0.3 | p | 2.3 | p |
| <i>Bromus japonicus</i> | Japanese brome | Poaceae (Festuceae) | 1.3 | 0 | 0 | 0 |

Table 1 (continued)

| Category & Scientific name | Common name | Family | Control | Muted exchange | Very low exchange | Grazed |
|--------------------------------------|------------------------------|-----------------------|------------|----------------|-------------------|-------------|
| <i>Carduus pycnocephalus</i> | Italian thistle | Asteraceae | 0 | p | 0.3 | 0 |
| <i>Carpobrotus edulis</i> | ice plant | Aizoaceae | 1.0 | 0 | 1.4 | 0 |
| <i>Cirsium vulgare</i> | bull thistle | Asteraceae | 0 | 0 | p | 0 |
| <i>Conium maculatum</i> | poison hemlock | Apiaceae | p | p | p | 0 |
| <i>Erodium moschatum</i> | white-stemmed filaree | Geraniaceae | 0 | p | p | 0 |
| <i>Geranium dissectum</i> | cut-leaved geranium | Geraniaceae | 0.3 | p | 0.4 | 0 |
| <i>Hordeum marinum</i> | Mediterranean barley | Poaceae (Hordeae) | p | p | 2.1 | 12.5 |
| <i>Lavatera cretica</i> | Cretan mallow | Malvaceae | 0 | p | 0 | 0 |
| <i>Lolium multiflorum</i> | Italian ryegrass | Poaceae (Hordeae) | 7.7 | 0 | 4.9 | 11.1 |
| <i>Lythrum hyssopifolia</i> | grass poly | Lythraceae | 0 | 0 | p | 0 |
| <i>Medicago polymorpha</i> | bur clover | Fabaceae | p | p | 0.2 | p |
| <i>Melilotus indicus</i> | Indian melilot | Fabaceae | 0.4 | p | 0 | p |
| <i>Picris echioides</i> | bristly oxtongue | Asteraceae | p | 0 | p | 0 |
| <i>Plantago coronopus</i> | cut-leaved plantain | Plantaginaceae | 0.9 | 0 | p | p |
| <i>Plantago lanceolata</i> | English plantain | Plantaginaceae | 1 | 0 | p | 0 |
| <i>Polypogon monspeliensis</i> | rabbitfoot grass | Poaceae (Agrostideae) | p | 4.6 | 2.7 | 0 |
| <i>Raphanus raphanistrum/sativus</i> | jointed charlock/wild radish | Brassicaceae | 0.3 | 7.4 | 0.2 | 0 |
| <i>Rumex acetosella</i> | sheep sorrel | Polygonaceae | p | 0 | 0.3 | 0 |
| <i>Rumex crispus</i> | curly dock | Polygonaceae | p | p | 0.4 | p |
| <i>Silybum marianum</i> | milk thistle | Asteraceae | 0 | p | p | 0 |
| <i>Sonchus asper/oleraceus</i> | prickly/common sowthistle | Asteraceae | p | p | 1.7 | p |
| <i>Spergularia ?bocconii</i> | Bocconi's sand spurry | Caryophyllaceae | p | 0 | 0 | 0 |
| <i>Tetragonia tetragonioides</i> | New Zealand spinach | Aizoaceae | p | p | 0 | 0 |
| <i>Vicia sativa</i> | spring vetch | Fabaceae | p | 0 | 0 | 0 |
| <i>Vulpia bromoides/myuros</i> | unidentified fescue | Poaceae (Festuceae) | 1.8 | p | 4.9 | 0 |

In terms of upland species, 34 of 56 species encountered were non-native. These non-native species jointly accounted for 83% of cover by upland plant species in the ecotone. The most abundant of these was Italian ryegrass (*Lolium multiflorum*). A variety of other non-native grasses were also moderately abundant, including ripgut (*Bromus diandrus*), soft chess (*B. hordeaceus*), Mediterranean barley (*Hordeum marinum*), rabbitfoot grass (*Polypogon monspeliensis*), and two similar fescues (*Vulpia bromoides*, *V. myuros*). Among forbs, ice plant (*Carpobrotus edulis*) and radish (*Raphanus raphanistrum/sativus*) were most abundant.

Effects of Management Strategies

Ecotone width was significantly affected by the treatments (Table 2); width was significantly narrower in the muted exchange vs. the control, and significantly wider in the very low exchange treatment (Fig. 2). We found little bare ground in the ecotone in all treatments except the grazed treatment, where it comprised 47% (on average), a significant difference (Table 2).

Elevation of the ecotone also showed significant differences across treatments (Table 2). The bottom of the ecotone at control sites averaged 164 cm above MLLW; this is approximately equivalent to Mean Higher High Water at sites at Elkhorn Slough with full tidal exchange. The bottom of the ecotone occurred at a significantly lower elevation in the very low exchange treatment (82 cm above MLLW). Likewise, the elevation of the top of the ecotone was significantly lower in the very low exchange treatment than the control. The elevation gradient between the top and bottom of the ecotone was significantly lower in the muted and grazed treatments than the control, where it averaged 38 cm.

Plant community composition as assessed by summary indices was also affected by the treatments. Richness of salt marsh natives per transect was significantly reduced in the muted and grazed treatments relative to the control (Table 2). Percent cover by ecotone specialists was significantly reduced in the muted treatment (Table 2). Percent cover by non-native plants was significantly greater in the grazed treatment (Table 2); in particular, cover by sickle grass was dramatically elevated in the grazed treatment (Table 1).

Table 2 Summary of univariate analyses of management regimes. Each parameter was analyzed using analysis of variance (ANOVA); P values <0.05 are bold. Average values are presented by treatment, with

superscripts to indicate statistical differences in post-hoc tests (Fisher's PSLD, $\alpha=0.05$); values that differed significantly from the control are underlined

| | ANOVA | Average values by treatment | | | |
|--|--------------|-----------------------------|-------------------------|------------------------|------------------------|
| | P value | Control | Muted exchange | Very low exchange | Grazed |
| ecotone width (cm) | 0.002 | 470 ^a | <u>113^b</u> | <u>898^c</u> | 171 ^{ab} |
| bare ground (percent) | 0.01 | 4 ^a | 6 ^a | 3 ^a | <u>47^b</u> |
| elevation of ecotone bottom (cm above MLLW) | 0.03 | 164 ^a | 194 ^a | <u>82^b</u> | 132 ^{ab} |
| elevation of ecotone top (cm above MLLW) | 0.04 | 202 ^a | 200 ^a | <u>131^b</u> | 144 ^{ab} |
| elevation gradient (cm between top and bottom) | 0.02 | 38 ^a | <u>6^b</u> | 50 ^a | <u>11^b</u> |
| marsh native richness (species/transect) | 0.01 | 4.8 ^a | <u>1.7^{bc}</u> | 3.6 ^{ac} | <u>2.7^c</u> |
| native ecotone specialist cover (%) | 0.16 | 44 ^a | <u>14^b</u> | 25 ^{ab} | 35 ^{ab} |
| non-native cover (%) | 0.09 | 17 ^a | 12 ^a | 23 ^{ab} | <u>35^b</u> |

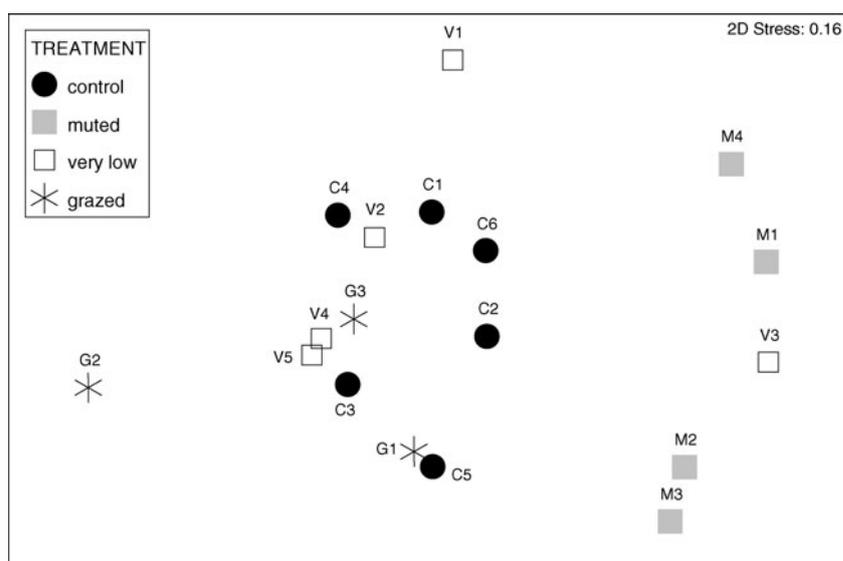
Analysis of similarities (ANOSIM) revealed that plant community structure was strongly affected by the management treatments (ANOSIM global $R=0.38$, $p=0.001$). This is illustrated graphically by a nMDS plot (Fig. 3). A pairwise ANOSIM test between control and muted treatments revealed highly significant differences ($R=0.80$, $p=0.005$), and a SIMPER analysis supported that these two treatments were more dissimilar than any of the other treatment pairs. The plant communities in very low tidal exchange and grazed treatments were not significantly different than the control in these analyses. The four species that contributed the most to dissimilarity between control and muted exchange sites in the SIMPER analysis were the ecotone specialists alkali heath, salt grass and fleshy jaumea, as well one non-native upland species, Italian ryegrass, all of which were more abundant in the control than muted exchange.

Discussion

Extremely Limited Habitat for Ecotone Specialists

Transition zones may harbor “ecotonal species” or “ecotone specialists” whose distribution is limited mostly or entirely to these narrow zones between two larger habitat types, but evidence for this is mixed for different systems (Lloyd et al. 2000; Walker et al. 2003). In California, the salt marsh-upland transition zone harbors much higher richness of marsh plants than the broad mid-marsh plain seaward of it, as well as providing habitat for ecotone specialists (James and Zedler 2000; Traut 2005a). Our study revealed that native marsh-upland ecotone specialists such as salt grass and alkali heath occur within an extremely narrow elevational band at Elkhorn Slough, and even within this zone they account for less than a

Fig. 3 Non-metric multidimensional scaling plot. Each point represents the plant community at a single site, illustrating dissimilarity in community composition between treatments, which is particularly pronounced between control and muted treatments



third of the plant cover. The estuary-wide distribution and abundance of these ecotone specialists is thus extremely limited. We also showed that plant community composition differs in the seaward vs. landward portions of the ecotone, so even within this very narrow zone there appears to be a gradient of physical conditions, which allows marsh plants to generally be more abundant in the seaward portion and upland plants in the landward portion. This is consistent with the concept of ecotones as zones of rapid directional spatial change (Lloyd et al. 2000).

Native salt marsh richness has been shown to contribute to recruitment of native species, canopy complexity, biomass, and nitrogen accumulation in California marshes (Zedler et al. 2001). So the paucity of appropriate habitat to support these species is of conservation concern. Furthermore, while the marsh-upland ecotone accounts for a tiny fraction of estuarine ecosystems, and even of vegetated intertidal habitats, it serves important functions in terms of nutrient cycling and animal use (Page 1995, Traut 2005a). The extremely limited extent of marsh-upland ecotone habitat and low estuary-wide abundance of ecotone specialists indicates that this zone should be an explicit target of conservation and restoration efforts at Elkhorn Slough, as has been suggested for other California estuaries (James and Zedler 2000).

Invasions of the High Marsh Ecotone

Ecotones may be particularly vulnerable to invasion by non-native species (Risser 1995), though evidence for this is mixed (Lloyd et al. 2000, Walker et al. 2003). We found that the marsh-upland ecotone at Elkhorn Slough was highly invaded, with upland non-natives particularly well represented in terms of both richness and cover. Given how limited the area of ecotone habitat is in the estuary, the occupation of a significant portion of the habitat by non-native species represents a serious threat to the ecotone specialists that are limited almost entirely to this zone. Moreover, in many parts of Elkhorn Slough, upland weeds such as ice plant, poison hemlock (*Conium maculatum*) and mustards (*Brassica* spp.), form virtual monocultures just above the ecotone. These were not captured in our surveys (which ended at the top of the ecotone, defined as the most seaward occurrence of 100% cover by upland plants). However, we suspect that these upland species may be occupying former ecotone habitat, having moved down from the upland into the wetland transition zone. This is supported by restoration projects at Elkhorn Slough (Woolfolk and Wasson, unpublished data), where removal of upland weeds landward of the ecotone has resulted in landward expansion by native high marsh plants. Several of the non-native species found in Elkhorn

Slough ecotones have been reported as invading other high marshes worldwide. Sickie grass and cut-leaved plantain (*Plantago coronopus*) are also common in Australian salt marshes (Adam et al. 1988), and brass button (*Cotula coronopifolia*) has become established in European marshes (Adam 2002; Costa et al. 2009), indicating that the patterns seen in California may extend far beyond the region.

Effects of Tidal Restriction with Water Control Structures

Ecotones may harbor particularly high diversity, because of representation from two adjacent plant communities, but because many of these plants may be near their physiological limits in the ecotone, they may also be particularly sensitive to perturbations (Risser 1995). Our investigation of the effects of management regimes revealed that the marsh-upland ecotone in coastal California displays such sensitivity to human perturbations.

We detected significant effects of tidal restriction on marsh-upland ecotone extent and biodiversity, both for the muted and the very low tidal exchange treatments, although patterns differed between these. While no other studies have focused on tidal restriction effects on the ecotone, investigations from other regions have demonstrated effects of tidal restriction on salt marsh vegetation composition and zonation (Roman et al. 1984; de Leeuw et al. 1994; Burdick et al. 1997; Sun et al. 2003), and in southern California and Baja California, tidal restriction has been shown to decrease marsh plant richness (Zedler et al. 2001; Ibarra-Obando et al. 2010).

Muted tidal exchange differed from the control in having a much narrower ecotone (113 vs. 470 cm on average). Tidal muting also greatly decreased the vertical elevational range (from 38 to 6 cm on average) of the ecotone. This decrease in ecotone width and elevational range appears to be the result of mean water level being higher in these ponded, lagoonal sites; while not significant, the elevation of the bottom of the ecotone was considerably higher at these vs. control sites. Muted tidal exchange also differed from the control in terms of much lower native marsh plant richness (1.7 vs. 4.8 species per transect on average), and cover by native ecotone specialists (14 vs. 44% on average). In particular, the absence of salt grass and alkali heath from all muted exchange sites is striking, since these species are at all of the control sites and most of the sites in other treatments. We suspect that at control sites, these ecotone specialists are limited to a very narrow zone where edaphic conditions permit them to displace both pickleweed and upland plants. These particular conditions appear to be absent from muted tidal exchange sites, perhaps because the elevational gradient between areas that are permanently submerged vs. never submerged is so abrupt. Extended and

unpredictable inundation or waterlogging is known to limit the occurrence of some plant species in the ecotone (Alexander and Dunton 2002), and distributions of high marsh species in San Francisco Bay, California have been shown to correlate well with a suite of environmental conditions including sediment salinity and elevation (Watson and Byrne 2009).

Very low tidal exchange resulted in a significant increase in ecotone width relative to the control. In areas with regular tidal inundation, one would expect ecotone width to decrease with tidal range. However, the natural hydrological cycles have been interrupted at these sites, and they have such low tidal ranges (0.5–5% of full exchange sites) that their marshes are virtually never inundated by tidal water; they are occasionally submerged when freshwater runoff floods the site during major storm events. This pattern of seasonal freshwater inundation paired with the dramatic reduction of tidal influence may lead to less pronounced soil salinity or moisture boundaries between the mid-marsh and the ecotone than in full tidal exchange, and has apparently resulted in seaward expansion of the ecotone to occupy former marsh plain. Such a seaward expansion is supported by the markedly decreased elevation of the ecotone top and bottom at very low exchange sites relative to control sites. Upland plants, especially various weedy non-natives (poison hemlock, mustards, thistles) now occupy the elevation at very low exchange sites where the ecotone community occurs at control sites. Moreover, these weedy upland plants continue to move down the elevational gradient at these very low exchange sites over time (Wasson and Woolfolk, unpublished long-term monitoring data). So while ecotone area has not decreased at very low exchange sites, there has been a net loss of wetland habitat, as the entire ecotone and marsh community has shifted seaward and upland plants have occupied former ecotone habitat.

Effects of Cattle Grazing

Cattle grazing also significantly affected ecotone extent and plant communities. Most striking was the dramatic increase in bare ground at grazed sites vs. all other treatments, likely due to the direct effects of foraging and trampling on this zone. The ecotone also spanned a significantly narrower elevational gradient (just 11 cm) relative to the control; the average elevation of the top was much lower in grazed sites, suggesting that cattle disturbance has truncated the landward portion of the ecotone. Sites with cattle had significantly lower marsh native species richness than control sites, and had significantly higher cover by non-native plants. Indeed, 100% of cover and richness by upland plants at grazed sites was comprised of non-native plants; of marsh plants, non-native sickle grass was highly abundant. Earlier studies of Elkhorn Slough salt marshes demonstrated that trampling at high

frequencies and intensities and grazing can decrease pickleweed abundance, lead to changes in community structure, promote invasions by introduced species, and contribute to loss of marsh habitat (Woolfolk 1999; Martone and Wasson 2008). At another central California estuary, Tomales Bay, marshes that had increased nutrients associated with cattle grazing had more cover by salt grass, but marsh plant diversity overall did not decrease (Traut 2005b). Increased nutrient concentrations and clipping of native vegetation has also been shown to increase spread of invasive common reed (*Phragmites australis*) into coastal marshes of the northwest Atlantic (Minchinton and Bertness 2003). Studies of northwestern Atlantic islands have shown effects similar to those we observed, with feral horses dramatically reducing vegetation cover especially in lower areas (Levin et al. 2002). In Europe, about three-quarters of remaining marshes are extensively grazed (Andresen et al. 1990), and in some areas this practice has been documented to date back for over 1000 years (Bos et al. 2002). Grazing in European marshes has been shown to change species composition and decrease canopy height, and has been demonstrated to shift vegetation zonation upward along the estuarine gradient, because low marsh species are small, rapidly colonizing annuals that are better able to tolerate grazing and move into higher marsh areas (Andresen et al. 1990; Schröder et al. 2002).

Cattle grazing is considered a management tool in European marshes and in coastal California grasslands. In Europe, grazing is used to increase marsh plant richness and to support vegetation favorable to migratory (hunted) geese (Bos et al. 2002). In central California coastal prairies, including in the Elkhorn Slough watershed, cattle grazing has been recommended to conserve native annual forb richness and cover (Hayes and Holl 2003). However, in Elkhorn Slough marshes, at cattle densities comparable to those in European systems and California grasslands, grazing did not appear to have beneficial effects, enhancing primarily non-native species. This may be due to the life histories and morphology of Elkhorn Slough's dominant ecotone plants. In European marshes, short grasses and annual species, including common salt marsh grass (*Puccinellia maritima*) and common glasswort (*Salicornia europaea*), benefit from sheep and cattle grazing, while a woody perennial sea purslane (*Atriplex portulacoides*) and a tall perennial grass (*Elymus athericus*) have been shown to be sensitive to grazing (Jensen 1985; Kiehl et al. 1996; Bos et al. 2002; Schröder et al. 2002). In coastal California grasslands, grazed areas have been found to have higher cover of annual grasses and forbs, but lower cover and species richness of native perennial forbs (Hayes and Holl 2003). Three out of the four most abundant ecotone species at control sites (pickleweed, alkali heath, fleshy jaumea) are perennial forbs or shrubs that appear to be very susceptible to damage by grazing. In contrast, salt grass is a short-

statured perennial grass, and its cover was highest at grazed sites in Elkhorn Slough. Likewise, a number of non-native annual grasses (sickle grass, Mediterranean barley, Italian ryegrass) were most abundant at grazed sites. In this habitat, grazing did not serve to increase total native plant cover or richness, instead creating bare space that was colonized in many cases by invasive grasses.

Recommendations for Management

The marsh-upland ecotone is very limited in extent in California and many other regions, but provides critical habitat for native plant species that are ecotone specialists, confined in their distribution almost entirely to this transition zone. We found the marsh-upland ecotone to be highly invaded, and recommend that coastal managers explore restoration strategies to control the abundance of the most common non-native upland weeds in the ecotone, and attempt to eradicate newly established non-native species before they become abundant. We also evaluated the response of the marsh-upland ecotone to tidal restriction with water control structures and cattle grazing, both common components of environmental management in coastal systems. We found that different management

regimes strongly affected habitat extent, species richness, and community composition in the salt marsh-upland ecotone. It is possible that lower intensities of grazing and more limited tidal restriction with water control structures would be compatible with ecotone diversity; experimental tests of ecotone response to very low levels of grazing and tidal restriction could be conducted. However, based on the results of this study examining moderate levels of grazing and significant restriction of tidal exchange, we recommend that both of these practices be avoided in Californian salt marsh ecosystems to conserve the endemic biodiversity, habitat extent, and associated ecological functions of this diverse yet very rare transition zone.

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Appendix

Summary of sites and treatments

| Site Name | Treatment | Abbreviation | Latitude | Longitude |
|---------------------|-------------------------|--------------|---------------|----------------|
| Azevedo Peninsula | Control | C1 | 36° 51' 3" N | 121° 45' 28" W |
| Coyote Marsh | Control | C2 | 36° 49' 46" N | 121° 44' 20" W |
| Yampah Marsh | Control | C3 | 36° 48' 38" N | 121° 45' 6" W |
| Hester's Marsh | Control | C4 | 36° 48' 35" N | 121° 45' 4" W |
| Finger Marsh | Control | C5 | 36° 48' 7" N | 121° 44' 53" W |
| Moss Landing Marsh | Control | C6 | 36° 47' 52" N | 121° 47' 12" W |
| Dolan Peninsula | Grazed | G1 | 36° 48' 23" N | 121° 44' 42" W |
| PG&E Marsh | Grazed | G2 | 36° 47' 59" N | 121° 45' 1" W |
| Moro Cojo Mid | Grazed | G3 | 36° 47' 49" N | 121° 46' 6" W |
| Azevedo North Pond | Muted tidal exchange | M1 | 36° 50' 54" N | 121° 45' 15" W |
| North Marsh | Muted tidal exchange | M2 | 36° 49' 46" N | 121° 44' 18" W |
| Whistle Stop Lagoon | Muted tidal exchange | M3 | 36° 49' 27" N | 121° 44' 19" W |
| Bennett Slough | Muted tidal exchange | M4 | 36° 49' 11" N | 121° 47' 19" W |
| Porter Marsh | Very low tidal exchange | V1 | 36° 51' 9" N | 121° 45' 1" W |
| Estrada Marsh | Very low tidal exchange | V2 | 36° 50' 32" N | 121° 44' 29" W |
| Struve Pond | Very low tidal exchange | V3 | 36° 49' 31" N | 121° 46' 35" W |
| Moro Cojo ESF | Very low tidal exchange | V4 | 36° 47' 55" N | 121° 46' 16" W |
| Moro Cojo Upper | Very low tidal exchange | V5 | 36° 46' 42" N | 121° 44' 29" W |

Abbreviations are used throughout the text and in figures

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