Natural and Restored Tidal Marsh Communities

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CONTENTS
Natural and Restored Tidal Marshes
   Natural Marshes
   Restored Marshes
Ecological Considerations in Tidal Marsh Restoration
Ecosystem Engineers
Assembly Rules and Alternate States
Diversity and Ecosystem Function
Disturbance and Diversity
Complexity and Diversity
Habitat and Population Connectivity
Scale and Context Dependency
Synthesis and Future Directions

Ecological restoration, the process of assisting recovery of an ecosystem that has been degraded, damaged, or destroyed (Society for Ecological Restoration 2002), can encompass a variety of activities in tidal marsh settings, including engineering the hydrology, grading to achieve appropriate elevations, and establishing desired plant and animal species. In San Francisco Estuary, most tidal marsh restoration efforts have focused on reestablishment of hydrological function to lands formerly diked for solar salt production or agriculture (Philip Williams and Associates and Faber 2004). Breaching these levees is the obvious first step in restoring tidal marsh function, as tidal flows are necessary to many of the physical, chemical, and biological processes within a salt marsh ecosystem. In addition, many diked lands have subsided to elevations too low to support tidal marsh vegetation. These former marshes lose elevation for reasons that include decomposition of organic matter during drying, compaction, and groundwater removal. In heavily subsided sites, dredged materials (typically from harbors) may be used in order to raise marsh elevations (e.g., at the former Hamilton Air Force Base). While remnant channels (Figure 17.1 A) can sometimes form the basis of new tidal systems, land use and dredged material often necessitate that new channels be excavated. Additionally, hydrological enhancements such as interior berms have been used at some restoration sites in order to direct channel formation or to reduce wind wave generation across unvegetated flats (e.g., at Sonoma Baylands).

This focus on engineering solutions to restoration of the Estuary’s tidal marshes over the last three decades made sense, considering the importance of physical factors, such as flow and elevation, to marsh development and persistence. But this emphasis, along with the large scale of many of the restoration projects and the lack of funding or resources put toward monitoring, has led to the assumption (or hope) that if the primary physical requirements are achieved and enough time is allowed, the diversity and function of native species will follow (Philip Williams and Associates and Faber 2004). And, in fact, many marshes have fully vegetated and support
native fauna. However, a number of these sites do not support the full suite of desired species, even several to many decades after tidal breaching.

With scores of tidal marsh restoration projects in progress or in the planning stages in the Bay area currently (see San Francisco Estuary Institute’s Wetland Portal, http://www .californiawetlands.net/tracker/ba), ranging from less than an acre to the multiple projects within the 15,000-acre South Bay Salt Pond Restoration Project (http://www.southbayrestoration.org/ index.html), we propose that greater attention to ecological aspects of restoration is needed, including more consideration of species composition, roles of species or assemblages, and biotic feedbacks to restoration site development. Further, we should continue to revisit older restoration sites in order to evaluate performance and determine whether we can improve ecological function.

We begin by describing natural and restored tidal marshes in San Francisco Estuary and reviewing similarities and differences. We then discuss ecological concepts and studies that apply

FIGURE 17.1. (A) Former ancient marsh channels still visible in a diked salt evaporation pond. (B) Rare plants *Muilla maritima*, *Castilleja ambigu* ssp. *ambigua*, and *Lasthenia glabrata* (left to right) at Whittell Marsh. (C) Newly establishing vegetation at Cooley Landing. (D) Nearly monotypic *Sarcocornia pacifica* stands on the low-complexity plains of Cogswell Marsh. Photos, Whitney Thornton; aerial images, property of California Coastal Conservancy’s Invasive Spartina Project.
to restoration of tidal marshes in the Estuary and that deserve consideration at both existing and upcoming restoration sites. Finally, we conclude by recommending actions and further study needed to better understand how particular species and interactions among species might be utilized at restoration sites to influence marsh characteristics and functioning.

NATURAL AND RESTORED TIDAL MARSHES

Natural Marshes

Generally speaking, marshes that develop naturally over long periods of time (upwards to 1,000 or more years) tend to slowly accumulate fine sediments over the marsh plain. Additionally, they build organic matter that upon decomposition remineralizes to provide plant-available nitrogen. Complexity in naturally formed marshes can be quite high. An ancient marsh typically has sinuous channels that meander through the marsh plain, with slightly higher elevations along channels due to localized sediment deposition. Pools that hold water after tides recede form as channels redirect over time, and microtopographical features form through various processes. Transitions to upland are gradual, having formed through submergence of terrestrial landforms and fluvial deposition. Settling of fine suspended sediments across much of the marsh plain contrasts with zones of distinctly coarser sediments derived from terrestrial sources and wave deposition.

In San Francisco Estuary, there are few tidal marshes that can be considered completely “natural,” in that most have been subjected to some human impacts, such as increased nutrient loading from up-estuary or upslope, reductions in acreage through filling, changes to hydrology from levees and roads, and invasive species. Still, some ancient remnant marshes contain many of the features described above, despite human modification. The tidal marsh at China Camp State Park (near San Rafael; see location on Figure 17.2) has been altered by mosquito ditching and a road bisecting the marsh; however, it includes a complex channel system and great connectivity to the mudflats and subtidal zone, in addition to being located in a nearby pristine, undeveloped watershed. Whittell Marsh, along the north Richmond Shoreline, is the site of historic explosives testing and some alterations to hydrology, yet there are sandy beaches adjacent to the marsh, coarse textured sediments within the marsh, many brackish and saline pools, and gently sloped transitions to upland. While the ancient Heerdt Marsh in Corte Madera Ecological Reserve has lost acreage and upland connectivity, this remnant contains microtopographical features across the marsh plain; meandering, branching channels; and extensive shoreline edge grading into mudflat and subtidal areas.

The features lending complexity to remnant ancient marshes and connectivity to adjacent habitats may increase species richness, and some of the rarest plants in the Estuary’s tidal marshes are found mostly or only in these sites (Table 17.1). For example, one of the only naturally occurring populations of *Castilleja ambigua* ssp. *ambigua* (owl’s clover) in the San Francisco Estuary is found in Whittell Marsh (Baye et al. 2000). This marsh also supports other seasonal wetland species now rarely found in tidal marshes, such as *Lasthenia glabrata* (goldfields) and *Muilla maritima* (common muilla) (Figure 17.1B). The endangered *Chloropyron molle* ssp. *molle* (formerly *Cordylanthus mollis* ssp. *mollis*, soft bird’s beak) is found in its largest numbers in old relict tidal marshes of Suisun Marsh (Grewell et al. 2003); this species can also be found at Whittell Marsh, and its threatened congener *Chloropyron maritimum* ssp. *palustre* (Point Reyes bird’s beak) at both Whittell and Heerdt Marshes. The formerly common Suisun thistle (*Cirsium hydrophilum* var. *hydrophilum*) is only known to occur today in three remnant marshes in the Suisun Marsh complex (U.S. Fish and Wildlife Service 2009). In addition to these very rare species, uncommon species in the Estuary are often best represented in the prehistoric remnant marshes (Table 17.1), for example, *Limonium californicum* (sea lavender), *Triglochin concinna* (arrowgrass), *T. maritima* (large arrowgrass), *Plantago maritima* (plantain), *Ambrosia psilostachya* (western ragweed), *Juncus articus* ssp. *balticus* (wire rush), *Leymus triticoides* (creeping wild rye), and *Carex praegracilis* (field sedge).

However, marsh age is only one factor that contributes to plant species composition and diversity. Other factors may include salinity patterns, substrate, wave energy, topographic diversity, hydrologic connectivity, sedimentation, invasive species presence, and erosion (Goals Project 1999).
FIGURE 17.2. Locations of San Francisco Estuary marshes listed in Table 17.1. Imagery from the California Coastal Conservancy’s Invasive Spartina Project.
Case Study of San Francisquito Creek Marshes

In 1857, the U.S. Coast Survey mapped San Francisquito Creek and its tidal marshes near East Palo Alto. At this time, tidal marsh habitat covered 1,142 acres. Significant modification to marshlands occurred during 1900–1920; diked bayland replaced tidal marsh, which in 1920 only covered 428 acres (Hermstad et al. 2009). However, these remnant tidal marshes were still relatively diverse. In 1926, Cooper described the salt marshes of San Francisquito Creek as dominated by pickleweed (Sarcocornia pacifica), but both salt grass (Distichlis spicata) and arrowgrass (Triglochin concinna) appeared in certain areas as monotypic stands. Other species in the marsh included large arrowgrass (T. maritima), sea lavender (Limonium californicum), plantain (Plantago maritima), gumplant (Grindelia stricta), jaumea (Jaumea carnosa), and alkali heath (Frankenia salina). In the late 1920s, San Francisquito Creek was rerouted, and over the next three decades additional marshes were filled. By the 1960s, only 270 acres of tidal marsh remained. In 1954, Hinde described the vegetation of San Francisquito Creek: T. concinna was still plentiful, but T. maritima and P. maritima were no longer described as present. Restoration has restored tidal action to 352 acres of the watershed; however, these species have not returned. Further, the once-common T. concinna has not been observed at these marshes in multiple recent surveys (authors’ personal observation).

In fact, many species still present in the North Bay and once common in the South Bay are now absent on the peninsula side of the South Bay. For example, in his 1961 catalog of flora, Thomas noted that Chlo- rropyron maritimum ssp. palustre (Point Reyes bird’s beak) was found in salt marshes in San Francisco, Redwood City, Palo Alto, and Alviso. C. maritimum is no longer found in these marshes in any abundance, and this trend is mirrored by P. maritima and T. concinna (authors’ personal observation).

Habitat fragmentation might be another factor in vegetative diversity. For example, some species are no longer found on the peninsula side of the South Bay (see box). These species are much more common to North Bay marshes, perhaps partly due to the conservation of a greater number and acreage of remnant tidal marshes and a much lower occurrence of invasion by hybrid cordgrass (Spartina alterniflora × foliosa) than in the South Bay (see Invasive Spartina Project, http://www.spartina.org/maps_findings.htm).

Restored Marshes

While restoration of tidal marsh vegetation can be through secondary succession (e.g., where terrestrial vegetation is present in baylands prior to breaching levees), many restoration marshes in their early stages are defined by open, unvegetated space (Figure 17.1C). A lack of vegetation in tidally inundated flats with long exposure times on neap tides can lead to harsh physical conditions. Salt accumulation can result from high rates of evaporation of tidal waters not ameliorated by shading vegetation. Studies in a number of other regions have found that open space initiated by wrack (dead plant material accumulated on the marsh) or geese grazing can become quite saline and thus limiting to a number of tidal marsh plants (e.g., Iacobelli and Jeffrey 1991; Bertness et al. 1992). In Mission Bay in San Diego, experimentally cleared marsh plant communities resulted in increased salinities and temperatures, an increase in diatoms, and a large shift in the invertebrate community (Whitcraft and Levin 2007). At an 8 ha newly graded restoration marsh at Tijuana Estuary (south of San Diego), salinities over 100 parts per thousand (ppt) developed following construction delays to planting and contributed to low plant survivorship (9%), although warm temperatures across the large area of the dark-colored sediment, sedimentation, and microbial blooms were also implicated (Zedler et al. 2003).

Nutrient availability can also influence development of plant communities at newly restored sites. Nitrogen, the primary limiting nutrient for salt and brackish marsh vegetation (Valiela and Teal 1974; Boyer et al. 2001; Crain 2007), has been shown to increase plant growth in both nitrogen-depleted coarse dredged material and nitrogen-replete fine-grained marsh sediments when added in fertilization experiments (Boyer and Zedler 1998; Boyer et al. 2001; Tyler et al. 2007). Further, nitrogen supply can influence plant competitive dynamics; for example,
<table>
<thead>
<tr>
<th>Marsh</th>
<th>Date</th>
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<tr>
<td></td>
<td></td>
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</tr>
<tr>
<td>Heerdt</td>
<td>1995</td>
<td>p</td>
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<tr>
<td>Laumeister</td>
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<tr>
<td>Arrowhead</td>
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<td>Whale's Tail</td>
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<td>Ideal</td>
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<tr>
<td></td>
<td>1976</td>
<td>p</td>
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<tr>
<td>Marta's</td>
<td>1998</td>
<td>p</td>
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<tr>
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<td>1999</td>
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<tr>
<td>Heron's Head</td>
<td>1977</td>
<td>p</td>
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<td>p</td>
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<tr>
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<td>1982</td>
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<td>1983</td>
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<tr>
<td>LaRiviere</td>
<td>1997</td>
<td>p</td>
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<tr>
<td>Cooley Landing</td>
<td>2000</td>
<td>p</td>
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<tr>
<td>Faber Tract</td>
<td>1971</td>
<td>p</td>
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</table>

p = present, r = rare or not integrated into marsh, a = absent, + = known to have been planted, − = known population removed.

* = Spartina foliosa presence uncertain due to large Spartina alterniflora × S. foliosa infestation

Date is year marsh restoration was initiated (intentional or not).
<table>
<thead>
<tr>
<th>Plant Species Present in Selected Prehistoric Remnant, Historic-Era, and Younger Marshes</th>
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<tbody>
<tr>
<td><strong>Date</strong> is year marsh restoration was initiated (intentional or not).</td>
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<tr>
<td><strong>Location</strong></td>
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<tr>
<td>Cooley Landing</td>
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<td>Seal Slough</td>
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<td>Oro Loma Landing</td>
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<td>Robert's MLK</td>
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<td>Heron's Head</td>
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<td>Crissy Field</td>
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<td>Marta's Whale's Tail</td>
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<td>Laumeister</td>
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<td>Upper Newark</td>
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<td>Heerdt</td>
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<td>Whittell</td>
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<td>Spartina foliosa</td>
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<td>Spartina alterniflora</td>
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<td>Juncus arcticus</td>
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<td>Juncus balticus</td>
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<td>Leymus triticoides</td>
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<td>Lasthenia glabrata</td>
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<td>Lasthenia sp.</td>
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<td>Chloropyron maritimum</td>
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<td>Chloropyron ssp.</td>
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<td>Chloropyron molle</td>
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<td>Castilleja ambigua</td>
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<tr>
<td>Nonnative vegetation</td>
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<tr>
<td>Spartina alterniflora</td>
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<tr>
<td>Spartina foliosa</td>
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<tr>
<td>Lepidium latifolium</td>
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<tr>
<td>Salsola soda</td>
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<tr>
<td>Limonium ramosissimum</td>
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<tr>
<td>Puccinellia maritima</td>
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Spartina foliosa responded positively to nitrogen addition only in the absence of Sarcocornia pacifica (Covin and Zedler 1988) or the annual pickleweed Salicornia bigelovii (Boyer and Zedler 1999) in Southern California marshes. While sediment nitrogen concentrations in San Francisco Bay marshes are low (0.1%) in sandy areas near Alameda and San Leandro (Tyler et al. 2007), most marshes were formed by deposition of nutrient-rich bay muds; thus, plants that recruit quickly and exploit nutrients most effectively may dominate new restoration sites. Higher nutrient availability in open patches can benefit Distichlis spicata in New England marshes (Valiela and Teal 1974; Levine et al. 1998), and this species was also favored in a local greenhouse experiment when brackish conditions were combined with supplemental nitrogen (Ryan and Boyer 2012). In more saline conditions, species that are better able to convert excess nitrogen into biomass than others, for example, Sarcocornia pacifica in comparison with Distichlis spicata and Jaumea carnosa (Ryan and Boyer 2012), may benefit most from nutrients available at restoration sites. Open canopies can also lead to greater light penetration, resulting in algal blooms that can supply nitrogen to tidal marsh plants (Boyer and Fong 2005a), again potentially benefitting those best suited to uptake and rapid growth and spread.

The open space of newly established restoration marshes presents an opportunity for the best dispersing and colonizing species. Sarcocornia pacifica can overwhelmingly dominate recruitment to restored California tidal marshes even when there are other species in adjacent natural marshes to supply seed (Armitage et al. 2006; Morzaria-Luna and Zedler 2007). Allison (1995) found that experimentally disturbed patches (from sediment burial) of salt marsh at Bolinas Lagoon (north of San Francisco Bay) did not benefit less common species; Distichlis spicata and Sarcocornia pacifica recruited well, but Frankenia salina and Jaumea carnosa did not. Notably, establishment from seed was infrequent even for the more common species; vegetative growth into disturbed patches was the primary recruitment mode (Allison 1995). Patches experimentally made in a Sarcocornia pacifica–dominated salt marsh in Southern California did not recruit rarer species, suggesting a lack of a persistent seed bank or delivery of seeds to these areas (Vivian-Smith 2001). Diggory and Parker (2011) found that while composition of the seed rain was similar at natural and restored marshes in the Napa River marsh complex (San Pablo Bay), species richness was significantly lower at the restored sites.

Open space also presents opportunity for invasive species to establish. San Francisco Bay invaders such as hybrid Spartina alterniflora × foliosa and Lepidium latifolium have established over many hundreds of acres in the Estuary, including at a number of restored sites. Scientists at the California Coastal Conservancy’s Invasive Spartina Project have strongly advocated that Spartina hybrids be controlled because of the threat of their invasion in upcoming restoration projects (P. Olofson, personal communication). Newly detected invaders such as Puccinellia maritima (seaside alkiegrass) and Limonium ramosissimum (Algerian sea lavender) also potentially pose threats (authors’ personal observation; Hubbard and Page 1997; Archbald 2011). Sometimes these invaders show signs of having responded to the opening of new habitat; for example, L. ramosissimum distribution at Sanchez Marsh in San Mateo closely mirrors the site’s restoration footprint (Figure 17.3). A past nursery offering in the Bay Area, this species may have benefitted from open space and low competition at a time when a ready seed supply was available from the adjacent suburban landscape.

There are several physical differences apparent in many restored marshes compared with natural marsh remnants in the Estuary, and these are likely to influence the quality or quantity of particular habitats and thus the species composition at restored sites. Topography in restored sites is often less complex than in natural sites. While some restoration projects at appropriate marsh elevations can take advantage of former channel networks retained while diked (Figure 17.1A), others that are graded or supplemented with dredged materials can have lower complexity (e.g., Muzzi, Robert’s Landing, and Cogswell Marshes; see Figure 17.1D). In addition, gradual slopes leading from the marsh into the adjacent upland are frequently missing from restoration sites, perhaps in an effort to maximize restored marsh acreage, permit public access, or reduce construction costs. Steep inland berms (e.g., at Sonoma Baylands, San Pablo Bay), while often deemed necessary for flood control, reduce the area available to high marsh plant species, the high tide refuges needed by species such as the
California clapper rail and the salt marsh harvest mouse, and the coarser terrestrial sediment supplied from upland sources.

In an effort to evaluate the degree to which restored marsh communities resemble those of prehistoric marsh remnants, we have assembled species lists for 21 tidal marshes from San Pablo Bay through the South Bay regions of the Estuary (Table 17.1; Figure 17.2). Some of the earliest restoration sites “self-restored” after levee failures in the early 1900s, while others were actively restored beginning in the 1970s; many others have followed (see San Francisco Estuary Institute’s Wetland Portal, http://www.californiawetlands.net/tracker/ba, for a comprehensive list). In our survey, ancient remnant marshes had an average of 14 and a maximum of 19 native plant species present (out of the 20 included in our evaluation). For the most part, active planting was not conducted at restored sites; planting is noted in Table 17.1 when this information was available from reports or personal communications. With the exception of Crissy Field, where many of the 14 species currently present were planted, the remaining 15 restored marshes we evaluated averaged only 9 native species, and some had as few as 7 or 8 (with several of those species rare despite being common regionally). We also detected a general pattern of lower species richness in the South Bay compared with the Central and San Pablo Bays. Interestingly, older historic-era restored marshes were not necessarily more diverse than those restored in the late twentieth century; with the exception of Bothin Marsh on Richardson Bay (15 native species), other early- to mid-twentieth-century marshes had relatively low species richness (8–9 native species) despite marsh development for periods of >80 years. Ecotone transition species such as *Leymus triticoides*, *Ambrosia psilostachya*, and *Carex praegracilis*...
were mostly encountered at prehistoric remnant marshes with gradual slopes to adjacent uplands.

Restored tidal marshes we evaluated are strongly dominated by pickleweed, *Sarcocornia pacifica* (Table 17.1), and follow a pattern of lower plant species richness or lower abundance of less common species than remnant natural marshes within the same region of the Estuary. When Cogswell Marsh (Figure 17.1D) was restored to tidal action in 1980, it rapidly became vegetated by *Sarcocornia pacifica* and hybrid *Spartina*. While the hybrid *Spartina* has been greatly reduced, much of this large marsh complex is a dense monoculture of *S. pacifica*. *Grindelia stricta* is a recent colonizer, but this may be because seeds were broadcast over the marsh plain. This marsh does not have the structural complexity of the more naturally developed marshes south of it within the Don Edwards San Francisco Bay National Wildlife Refuge. Seal Slough, restored in the 1980s, also lacks the plant diversity of ancient marsh remnants in the region (such as Laumeister Marsh), and it too was heavily invaded by hybrid *Spartina* and currently is composed almost entirely of *S. pacifica*. While native species such as *D. spicata* and *F. salina* do occur at this site, they are not found interspersed in middle marsh zones but, rather, are restricted to landward edges. Large populations of the non-native *Limonium ramosissimum* and *Puccinellia maritima* can also be found at this site. Exactly why these restored marshes lack the less common native species found at ancient marshes could be related to multiple factors, including an inadequate supply of viable seeds, interspecific competition, or unsuitable abiotic conditions (see below). It is clear that for some sites, it may not just be a matter of time, as many decades have passed without these species establishing and producing a complex matrix of vegetative structure. This is not to say that restoration marshes never recruit rarer species; for example, *Chloropyron maritimum* ssp. *palustre* was recently found in a young restoration site, LaRiviere Marsh in Newark (Alfaro 2010).

Notably, restored marshes in very close proximity to prehistoric remnants tend to be almost as diverse. For example, LaRiviere Marsh is near the ancient remnant at Upper Newark Slough and was found to be similar in species richness. The prehistoric Heerdt Marsh had 13 native species, and nearby restored Muzzi Marsh had almost as many (10). Muzzi Marsh has the best long-term record of vegetation patterns of any restored marsh in the Estuary, and these data clearly show the evolution of greater species richness over the 35 years since construction (Philip Williams and Associates and Faber 2004). However, the recruitment or establishment of some species remains elusive despite the close proximity of a seed source.

Another important consideration in marsh restoration in the Central and South Bays is the decreased presence of a formerly abundant species, *Spartina foliosa* (Table 17.1). Hybridization with *S. alterniflora* has led to reduction of native *S. foliosa* throughout much of this region. After hybrid *Spartina* removal, it may be necessary to restore *S. foliosa* to these marshes. However, little *S. foliosa* restoration has occurred in the San Francisco Bay since the 1970s and 1980s (Williams and Faber 2001). After this time, it was observed that *S. foliosa* tended to naturally colonize restoration sites, and planting efforts stopped. However, this approach may have to be reevaluated in light of genetically polluted seed stock in the South Bay. Further, some species such as *Grindelia stricta* have been excluded or weakened by hybrid *Spartina* invasion at higher elevations, and plant stress may increase vulnerability to nontarget effects of herbicides used to control the invader (W. J. Thornton, personal observation). Active restoration may be necessary to ensure inclusion of these species in new restoration sites, as well as to restore plant communities in natural marshes where herbicide was or continues to be used to control hybrid *Spartina*.

**ECOLOGICAL CONSIDERATIONS IN TIDAL MARSH RESTORATION**

We have pointed out a number of differences in natural and restored marshes, both in their physical conditions and in the plant communities they support. But does species composition matter in tidal marshes? How do physical features of marshes influence the identity and richness of species present? How do feedbacks from initially recruiting biota and starting abiotic features of marshes influence marsh structure and function? How can we use restoration sites to learn about how best to conduct restoration? Here we review concepts and studies from the ecological literature pertinent to restoration of San Francisco Estuary tidal marshes.
ECOSYSTEM ENGINEERS

Species that play large roles in altering physical habitats or processes are often called ecosystem engineers or habitat modifiers. These include species that affect environmental conditions or available resources simply through their presence (this group is also known as autogenic engineers or foundation species) and those that modify habitats or change the state of materials through their actions (the allogenic engineers) (Dayton 1972; Jones et al. 1997; Bruno and Bertness 2001). By definition, wetlands contain plants adapted to survive periods of inundation by water, and these plants form the habitat required by many other species. In addition, certain plants and animals in tidal marshes perform important roles through their actions, such as stabilizing sediments and changing physicochemical conditions of soils.

Plant species that provide tall canopies (50 cm above mean high water) benefit the endangered California clapper rail by aiding nest concealment and preventing tidal inundation (U.S. Fish and Wildlife Service 2009). Species used for nest construction include Spartina spp., Sarcocornia pacifica, Grindelia stricta, Distichlis spicata, Scirpus spp. (bulrushes), Typha (cattails), and Jaumea carnosa (U.S. Fish and Wildlife Service 2009). Song sparrows will use most marsh plants for nests but prefer S. pacifica, G. stricta, and sedge species. These birds are territorial and use tall vegetation such as G. stricta as perches. The shrub Suada california, though extremely rare currently (reintroduced to several sites after extirpation in San Francisco Estuary; see Baye 2006), likely provides perches in the high marsh, as documented for congeners Suada vera in France (Geslin et al. 2002) and Suada esteroa in Southern California (Zedler et al. 2001). Sarcocornia pacifica is essential to the survival of the salt marsh harvest mouse and supports greatest abundances in tall, dense stands of this plant (U.S. Fish and Wildlife Service 2009). A partial food web analysis noted 11 species of invertebrates that use Frankenia salina (Maffei 2000).

Cordgrass species (Spartina), with their clonal growth through dense rhizomes, are well known for their ability to hold sediments in place and reduce erosion of shorelines. Spartina alterniflora in its native habitat in Florida and the Chesapeake Bay can produce a 71%–92% reduction in wave height over 20–30 m, with a 92%–100% reduction in wave energy (Knutson et al. 1982), and its effects on flow reduction and substrate stabilization benefit a number of other marsh species (Bruno 2000). Locally, both the native Spartina foliosa and the Spartina hybrids (S. alterniflora × foliosa) are likely to perform this function. Experimental transplants of S. foliosa sods in San Francisco Bay in the 1970s resulted in stabilization of sediments with up to 7 km of wave fetch (Newcombe et al. 1979). As hybrid Spartina is removed from the Estuary, this function of the native Spartina may be especially important to consider. Other clonal plants that grow densely along channels and shorelines in more brackish areas (e.g., alkali bulrush, Bolboschoenus maritimus) are likely to perform this function as well. Salt marsh forbs in England have been found to reduce wave height by 54% over 180 m, with a 79% reduction in wave energy (Moeller et al. 1996). In addition, both cordgrass and pickleweed lead to increased sediment shear strength, a measure of the degree of erosibility (Pestrong 1965).

Species that ameliorate harsh physical conditions can have important effects on tidal marsh community composition. For example, in New England, the black rush Juncus gerardi shades soil surfaces and reduces salinities, permitting the marsh elder Iva frutescens to extend its range from terrestrial borders down to midmarsh elevations (Bertness and Hacker 1994). Studies in the same region showed that recovery of saline bare patches produced by wrack can depend on less common species that are able to colonize and reduce salinities, Distichlis spicata and Salicornia europaea (Bertness et al. 1992). At a Tijuana Estuary restoration site, Jaumea carnosa enhanced survivorship when plants were planted closely (five individuals of different species with 10 cm spacing) compared with greater spacing (90 cm); the mechanism may have been reduced salinity, structural support, or other benefits (O’Brien and Zedler 2006). Some species are able to concentrate nitrogen in their tissues; for example, in a greenhouse experiment in San Diego, Triglochin concinna had ~30% higher tissue nitrogen than most other species, including three found in San Francisco Estuary: Sarcocornia pacifica, Frankenia salina, and Jaumea carnosa (Sullivan et al. 2007). Similarly, in a greenhouse experiment using plants from Mugu Lagoon (Ventura County), Frankenia salina had a tissue nitrogen concen-
tration more than 50% greater than did *Jaumea carnosa* and *Distichlis spicata*, whether or not soils were nitrogen enriched from algal amendments (Boyer et al. in review). In the San Diego study, biomass declined in assemblages that included *T. concinna*, suggesting that nitrogen concentration by *T. concinna* could reduce dominance of more common species and enhance species richness (Sullivan et al. 2007). It is also possible that species that concentrate nitrogen later release it, benefiting other species that differ in timing of nitrogen demand (Morzaria-Luna 2005).

The best-studied plant invaders in San Francisco Bay tidal marshes, *Spartina alterniflora* × *foliosa* hybrids and *Lepidium latifolium*, produce a number of engineering effects. Hybrid *Spartina* produces taller stems and greater biomass over a larger tidal range than the native *S. foliosa* and also supports significantly lower densities of infaunal invertebrates and shifts trophic relationships (Brusati and Grosholz 2006; Levin et al. 2006). Stands of *L. latifolium* in multiple tidal marshes ranging in salinity have soils with lower moisture, organic matter, and carbon-to-nitrogen ratios and higher pH than adjacent areas of *Sarcocornia pacifica* with similar elevation and distance from channels, and they also differ in canopy characteristics that may influence insect and bird communities (Reynolds and Boyer 2010). A number of invaders outcompete natives for space, which could be particularly detrimental when the natives are rare species, for example, *L. latifolium* versus the very rare *Chloropyron molle* ssp. *molle* and *Cirsium hydrophilum* var. *hydrophilum* in Suisun marshes (Grewell et al. 2003). Dramatic effects of invasion are not limited to plants; the isopod *Sphaeroma quoyanum* has invaded restored and natural marsh channels in great abundance in some areas and may lead to channel slumping and loss of channel-edge habitat (Talley et al. 2001).

**ASSEMBLY RULES AND ALTERNATE STATES**

The sequence of species arrival and establishment can determine the order or identity of later arrivals and influence species composition. These so-called assembly rules and priority effects have received much attention in the ecological literature, recently in relation to restoration ecology (Temperton et al. 2004). A few experiments in California tidal marsh restoration sites have considered these ideas by planting species combinations and observing whether the starting assemblage influenced the community that established over time. At Mugu Lagoon (Ventura County), Armitage et al. (2006) found that only with diverse plantings were any species except *Sarcocornia pacifica* (which recruited from seed) present after 2 years at a salt marsh restoration site. Similarly, plots in Tijuana Estuary had less-common species present only where planted, even when evaluated 10 years later (O’Brien and Zedler 2006). A related concept, that there can be alternate community states (Lewontin 1969), has been applied to restoration sites that might persist with a particular assemblage due to feedbacks that help to maintain its characteristics (see review by Suding et al. 2004). Restoration sites can lack desired features even after long periods of time because of many factors, including sequence of recruitment, lack of connectivity to rarer species pools, and non-native species invasions, while established conditions and species reinforce their persistence through positive feedbacks. That *Sarcocornia pacifica* overwhelmingly dominates restored marshes in San Francisco Estuary may be reinforced by its resistance to colonization by other species (Bonin and Zedler 2008) and its increase in dominance during periods of high salinity, as shown in historic pollen patterns (Goman et al. 2008) and in short-term salt addition experiments (Ryan and Boyer 2012). Invaders to the Estuary’s tidal marshes may reinforce their persistence and spread through positive feedbacks such as sediment accretion and pollen swamping (*Spartina* hybrids: Sloop et al. 2005; Neira et al. 2006) and salinity and moisture reduction (*Lepidium latifolium*: Reynolds and Boyer 2010). Invasive species may have legacy effects of altered sediment conditions after they are removed that further reduce potential to restore native species, for example, thick root mats after removal of aboveground tissues of *Spartina* hybrids and negative effects of thatch on germination of other species (authors’ personal observations and unpublished data). On the other hand, relative rarity of the less common tidal marsh species (e.g., *Limonium californicum*, *Triglochin* ssp.) and especially the very rare species (e.g., *Chloropyron* species, *Castilleja ambigua* ssp. *ambigua*, and the recently reintroduced *Suaeda californica*) means few seeds and little possibility of arriving at most restoration sites, thus reinforcing their absence.
DIVERSITY AND ECOSYSTEM FUNCTION

Concerns over losses of native species worldwide have motivated over a decade of study of biodiversity effects on community properties and ecosystem processes (e.g., Tilman et al. 1997; Hooper et al. 2005). Meta-analyses across hundreds of experiments have found that species richness commonly has a positive effect on productivity or other measures of plant community function (Balvanera et al. 2006; Cardinale et al. 2006), and theory and experimental evidence indicate that species richness can lead to increased community stability (Cottingham et al. 2001; Loreau et al. 2003; Boyer et al. 2009). Species with different functional roles or responses to disturbance (i.e., “response diversity”) can help to provide insurance of community persistence (Naeem 1998; Yachi and Loreau 1999; Elmqvist et al. 2003). Wetland plants have been shown to differ in the types and magnitude of functions, thus maximizing richness may maximize the range of functions of a plant assemblage even if richness does not increase plant productivity (Engelhardt and Richie 2002). In Southern California, manipulative studies of species richness showed a positive relationship with canopy complexity (Keer and Zedler 2002) and biomass production and nutrient retention (Callaway et al. 2003); further, higher richness maximized different attributes of structure and function (Sullivan et al. 2007). In addition, higher richness at the level of primary producers has been shown to increase the abundance, richness, and stability of assemblages at higher trophic levels (e.g., Haddad et al. 2011). In Tomales Bay, Traut (2005) found that higher species richness in the high marsh also supported greater numbers of spider species. Genetic variability within a species can also provide important ecosystem functions, including increased resilience to disturbance (e.g., Hughes and Stachowicz 2004), and may be important to establishing species in restoration sites that present novel conditions (Lesica and Allendorf 1999).

DISTURBANCE AND DIVERSITY

Disturbance of intermediate size or magnitude may be necessary in many communities to maintain species diversity (Sousa 2001; Shea et al. 2004). In tidal marshes, plants that senesce in the late fall or winter produce masses of dead material that accumulate as wrack. These patches, which can be >10 cm thick and many meters across, tend to deposit along higher elevations where they are pushed on the highest tides or become trapped by taller vegetation (Bertness and Yeh 1994; authors’ personal observation). In San Francisco Estuary marshes, this wrack is often composed of cordgrass, and in recent years it has been largely composed of invasive hybrid cordgrass. Areas of light wrack accumulation may have a positive effect on underlying vegetation (perhaps through nutrient or moisture subsidies or by limiting salt accumulation) (Pennings and Richards 1998), while thicker mats that stay in place for periods of months kill the vegetation beneath them, creating bare patches (Bertness and Ellison 1987; Valiela and Rietsma 1995). Such bare patches permit recruitment of less common species, for example, Distichlis spicata and Salicornia europaea in New England studies (Bertness et al. 1992) and D. spicata and Jaumea carnosa on an otherwise pickleweed-dominated plain at China Camp State Park (authors’ personal observation). Large debris can also create bare patches in the vegetation, leading to recruitment of less common species (e.g., at northern Petaluma Marsh), and while today this can be wood from old boats and pier pilings, it is likely that native oaks and redwoods served this purpose before the region’s watersheds became largely deforested (P. Baye, personal communication). The native parasitic vine Cuscuta salina (Dodder) has been shown to perform a similar function in a marsh at Bodega Bay by reducing biomass and fecundity of its primary host there, Plantago maritima, with a strong indirect positive effect on the growth and fitness of the rare Chloropyron maritimum ssp. palustre and an overall increase in species diversity (Grewell 2008). In Southern California, Pennings and Callaway (1996) found preferential parasitism by C. salina on the dominant Sarcocornia pacifica and evidence that C. salina–induced declines in S. pacifica led to increased species richness. Seeds of C. salina appear to move with the wrack, leading to infections of Sarcocornia pacifica along areas of wrack accumulation from the previous winter; at China Camp State Park, mats of wrack combined with C. salina infection may be the cause of large areas of S. pacifica dieback in some years (authors’ personal observation). In our survey of
tional marshes, 5 out of 16 restored marshes had little or no C. salina, and this may contribute to the rarity or absence of several other species at these sites (Table 17.1). Notably, a congener in more brackish areas of the Estuary, Cuscuta sub-inclusa, was found to reduce biomass and fitness of the invasive Lepidium latifolium and thus likely also influences species composition (Benner 2005).

COMPLEXITY AND DIVERSITY

Complexity of physical features can lead to increased species richness by providing more physical space or resources, thus creating a greater number of niches (e.g., MacArthur 1970). As mentioned previously, the greater complexity of sediment textures, creek networks, pools, and microtopographical features in many of the Estuary’s historic marsh remnants and known from historic records may encourage a greater number of species by supporting a wide range of habitat requirements. Marshes that have deposits of coarse sediments, due to connections to fluvial sources or overwash of barrier beaches of sand or shell, can provide conditions most suitable to some of the rarer or even locally extirpated species known to be more common historically (e.g., Chloropyron maritimum ssp. palustre, Castilleja ambiguus ssp. ambiguus, Suaeda californica: Baye et al. 2000). Channels, creeks, and pools are associated with greater plant species richness than adjacent plains (Zedler et al. 1999; Sanderson et al. 2001). Microtopographical variation across marsh surfaces can be very important to plant species richness across wetlands (Vivian-Smith 1997; Morzaria-Luna et al. 2004), and we have described above how patches in the dominant vegetation can benefit some less common species. In addition, there are wildlife benefits to this heterogeneity. The presence of both creeks and pools has been shown to maximize habitat for fish species in a Southern California restoration study (Larkin et al. 2008). The abundance of California clapper rails is positively correlated with channel density or the total length of channel per unit area of marshland (Evans and Collins 1992; Collins et al. 1994; Garcia 1995; Foin et al. 1997). Keldsen (1997) found that these rails prefer locations with a greater number of tidal creeks, Grindelia shrubs, and higher elevations (U.S. Fish and Wildlife Service 2009). Attention to topographic features has been increasing in some very recent and planned restoration projects in San Pablo Bay, with side-cast channel edge berms and mounds being added to increase complexity (e.g., Bahia, Napa salt ponds, Sears Point).

HABITAT AND POPULATION CONNECTIVITY

It is possible that patterns in species diversity observed in natural remnant and restored marshes are at least partly related to the degree to which source populations are able to contribute propagules to nearby sites. We have noted that the adjacent ancient Heerdt Marsh and restored Muzzi Marsh do not exhibit the same species richness. Despite their close proximity, it is likely that dispersal limits the seed supply to Muzzi, perhaps because of the mostly diked shoreline edge that may impede distribution of seeds. In other cases, species that were once common may no longer be present within a large region of the Estuary (see box), thus the chances of propagules of these species arriving passively at restoration sites within the region are low. Species that are not common or dominant pioneers are likely to require active introduction to these sites if inclusion of the full suite of natural marsh species is desired. Historic records and remnant marshes can provide guidance as to what species might be actively restored in the Estuary’s tidal marshes (see Baye et al. 2000 for a comprehensive review of historic occurrences), and evaluation of the habitat needs of these species (e.g., Grewell et al. 2003; Baye 2006) can help determine whether restoration sites currently have been, or could be, modified to provide the conditions needed to support and maintain populations of these species.

SCALE AND CONTEXT DEPENDENCY

New restoration sites provide an opportunity to test our ideas of how species interact with each other and their environments (Bradshaw 1987; Palmer 2009) and to test hypotheses pertinent to the establishment of species and functions in restored systems (e.g., Callaway et al. 2003; Boyer and Fong 2005b; Armitage et al. 2006). Logistical constraints often dictate that experiments be conducted at small scales, for example, plots of 4 m² or less and greenhouse pots that simulate field conditions. However, one of the most valu-
able questions ecologists can answer is, how do patterns observed at the small plot or pot size scale up to much larger areas? Large-scale restoration experiments can present their own suite of problems but still provide important lessons (see Zedler et al. 2003, Wallace et al. 2005, and Larkin et al. 2008 for a Southern California example). There are many upcoming, large restoration projects in San Francisco Estuary that could permit evaluation of ecological interactions and restoration methodologies in replicated experimental plots at a more realistic landscape scale over which many natural functions occur.

In addition, the specific environmental context at any particular location can influence the types and magnitudes of patterns we observe. This means that it is possible that restoration designs and procedures may work differently at sites that differ in environmental conditions, such as sediment supply or large-scale hydrological patterns (e.g., the South Bay, with minimal fluvial inputs and high residence time, functions like a separate lagoonal system: Nichols et al. 1986). It also means that we could use multiple restoration sites to test the importance of context dependency on ecological functions as well as restoration methodologies.

SYNTHESIS AND FUTURE DIRECTIONS

While restoration of tidal marshes has been underway for many decades in the San Francisco Estuary, there has been limited development of biotic and abiotic complexity relative to remnant natural marshes or historic records. Related studies in other regions point to important ecological relationships that warrant consideration as numerous restoration projects move forward. However, the unique suite of species and the setting in a large and urbanized estuary, with no comparable systems on the West Coast or elsewhere, require that we evaluate local patterns and processes. We have identified the need for the following:

- Investigate ways to maximize plant species richness, as this may increase canopy complexity, the suite of functions represented by the species pool, and perhaps processes such as primary production and enhancement of richness or production at higher trophic levels.
- Conserve extant populations of rare and uncommon species to provide propagules for restoration sites and conserve genetic diversity.
- Determine limitations and experiment with methods to promote increased abundance of rare species and the number of locations where they occur. Use historic information and current conditions to prioritize these locations.
- Actively introduce uncommon species, as dispersal limitation of these species or rapid recruitment of more common species and space preemption may limit the ability of rarer species to establish on their own. Experimentally test effects of introduction order with an eye to enhancing native species richness and decreasing potential for invasion.
- Further evaluate the role of physical heterogeneity, including small differences in sediment elevation and sediment texture, on species composition. Experiment with ways to include these features in restoration sites.
- Experiment with disturbance (e.g., creation of patches) and ways to enhance natural disturbance processes (e.g., by connecting tidal wetlands to adjacent creeks) in order to provide spatial refuge for rarer species.
- Provide gradual slopes to adjacent upland wherever possible to promote ecotone transition species.
- Carefully monitor for invaders, as they can displace natives and alter conditions with positive feedbacks to their own persistence and spread. Pay particular attention to newly recognized invaders that may pose threats, such as Limonium ramosissimum and Puccinellia maritima.
- Follow removal of invaders and creation of patches in dominant native vegetation with seeding or transplanting to encourage establishment of desired native species. Place renewed attention on restoration of the formerly abundant Spartina foliosa because of alterations of sediment conditions and genetically polluted seed sources following hybrid Spartina invasion.
• Capitalize on the large scale of restoration projects to evaluate small-scale patterns revealed in experiments.

• Use concurrent restoration projects in different locations to test context dependency of ecological and methodological patterns and inform future restoration activities.

• Apply lessons from experiments, pilot studies, and unexpected results to improve ecological function of new projects as well as former restoration sites.

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248

CONSERVATION AND RESTORATION


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