

Declining Biodiversity: Why Species Matter and How Their Functions Might Be Restored in Californian Tidal Marshes

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Species diversity is being lost in habitats that are increasingly diminished by development, fragmentation, and urban runoff; the sensitive species drop out and a few aggressive ones persist, at the expense of others. Alarmed by declining biodiversity, many conservationists and researchers are asking what happens to ecosystem functioning if we lose species, how diverse communities can be restored, which (if any) particular species are critical for performing ecosystem services, and which functions are most critical to ecosystem sustainability. In southern California, 90% of the coastal wetland area has been destroyed, and remaining wetlands continue to be damaged; even the region's protected reserves are threatened by highway and utility-expansion projects. The fate of biodiversity in these diminished wetlands serves to warn other regions of the need for continual assessment of the status and function of both common and rare species, as well as the need for experimental tests of their importance—before they are lost.

This article synthesizes data for tidal marshes of the Californian biogeographic region, which stretches from Point Conception near Santa Barbara south to Bahía San Quintín in Baja California. We focus on the broad marsh plain, which is dominated by eight species of halophytes (salt-tolerant plants; Figure 1). From regional censuses, we document the recent loss of short-lived species from several wetlands. From eyewitness accounts of tidal-exclusion events at Estero de Punta Banda and Tijuana Estuary, we link species loss to the interruption of tidal influence. And from experimental plantings of marsh halophytes in a bare restoration site, we document the difficulty of restoring plant diversity, demonstrate

BIODIVERSITY WAS DECLINING BEFORE OUR EYES, BUT IT TOOK REGIONAL CENSUSES TO RECOGNIZE THE PROBLEM, LONG-TERM MONITORING TO IDENTIFY THE CAUSES, AND EXPERIMENTAL PLANTINGS TO SHOW WHY THE LOSS OF SPECIES MATTERS AND WHICH RESTORATION STRATEGIES MIGHT REESTABLISH SPECIES

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what each species potentially contributes to ecosystem functioning, and develop recommendations for restoring biodiversity. Our experimental tests of the relationship of species richness to ecosystem functioning at Tijuana Estuary contribute to the debate about whether ecosystem functioning is influenced more by the presence of many species or by the presence of one or two high-performance species. We evaluate the contribution of multiple and individual species and show that individual species can match the performance of six-species assemblages (sextets), but no single species excels in all functions. Our experimentation with increasing levels of biodiversity in an actual restoration site (a bare marsh plain) provided results of immediate use to biodiversity enhancement projects while simultaneously vegetating the site.

Does diversity matter in restoration?

Questions about species number, species identity, and specific functions are especially relevant to the restoration of ecosystems. When confronted with a bare restoration site, one begins by asking if planting is necessary and, if so, of which and how many species. The answers may well depend on the restoration target—what level of diversity and function is desired and when? The goal of many restoration projects is to match the structural and functional attributes of regional reference ecosystems as quickly as possible. Thus, any planting practice that speeds the development of species-rich vegetation is of interest, as are vegetation attributes that support more animal species and confer greater resilience to the system.

The role of species richness has been explored in several diversity experiments by planting randomly drawn assemblages of herbaceous plants and evaluating a range of functional attributes, most notably biomass accumulation. In general, increasing numbers of plant species lead to increases in productivity (Naeem et al. 1994, 1995, 1996), nutrient retention (Ewel et al. 1991), resiliency (Tilman and Downing 1994), reliability (Johnson et al. 1996, Naeem and Li 1997), and decreases in invasibility of other species (Tilman 1997, Symstad 2000). In a series of diversity experiments conducted in eight European countries, Hector and colleagues (1999) reported that a 50% decline in species richness reduced aboveground biomass by 10%–20%. A recent review of the diversity literature confirmed that many functions increase in concert with a rise in the number of plant species, although there was little support for a continually increasing, linear relationship between species diversity and function (Schwartz et al. 2000). In addition, diversity effects reach across trophic levels; mycorrhizal diversity affects plant diversity (van der Heijden et al. 1998), and insect diversity is related to plant diversity (Knops et al. 1999), although weakly in one case (Siemann et al. 1998).

Although a variety of functions respond positively to greater diversity, it remains unclear whether the response is due to the number of species or the chance inclusion of an outstanding stress-tolerator, colonizer, competitor, or other “superplant.” To restore habitat most effectively, managers need to know how many and which species to plant so that the veg-

etation will perform multiple functions, such as persistence, canopy development, and retention of carbon and nutrients. If the target community has only one species, for example, *Spartina alterniflora* monotypes along the Atlantic Coast, then restoration is greatly simplified. If the reference system includes many species, a subset of plantings might suffice for accelerating the development of vegetation. To simplify choices, some researchers classify species into functional groups based on life span (annual versus perennial), growth form (succulent or nonsucculent, upright or trailing, grass or forb), or presence of nitrogen-fixing symbionts. Experiments with species drawn randomly from functional groups have uncovered effects on productivity, nutrient availability, and other functions (Ewel et al. 1991, Chapin et al. 1992, Silver et al. 1996, Hooper and Vitousek 1997, Huston et al. 2000). Thus, introducing one or more representatives of a functional group to a restoration site might suffice for providing critical ecosystem functions—for example, nitrogen-fixers to accelerate nitrogen accumulation (Crocker and Major 1955, Vitousek and Reiners 1975) or highly productive species to increase overall grassland productivity (Symstad et al. 1998). Restoration efforts could then be streamlined by limiting initial plantings to a few key members of the target community. In southern California salt marshes, however, functional groups have proven elusive (Sullivan and Zedler 1999).

Californian salt marshes

The Californian salt marsh (Figure 1) is a useful model system for testing the effect of diversity on ecosystem function for several reasons:

- It includes a small number of species (eight dominate the marsh plain).



Figure 1. Salt marsh vegetation at Bahía San Quintín, Baja California Norte, Mexico.

- It has naturally occurring assemblages that range from one to many species.
- It includes various growth forms (Table 1).
- The plants are readily grown from seed, and all become reproductive in their first or second year.

As recommended by Vitousek and Hooper (1993 p. 14), we “manipulate diversity as an experimental treatment and emphasize the range of diversity from one to ten species.” Concern about experimentation with “immature vegetation” (Huston et al. 2000) is not an issue for restoration sites, because the establishment of vegetation on newly graded substrate always involves immature plants, and any approaches that can accelerate the maturation process are immediately useful to ecological restoration. In other words, we seek ways to increase the rate of biomass accumulation and the development of complex canopies in sites with coarse soils and limited nutrients, especially nitrogen (N). We ask whether planting is necessary and, if so, how many and which species need to be planted to accelerate the development of complex canopies and the accumulation of soil N.

The Californian tidal marsh (Figure 2) has a fringe of *Spartina foliosa*, a broad marsh plain, and a high marsh transition to upland. Tides inundate *S. foliosa* twice daily and

the marsh plain at least once daily, with water depth varying by season. Tidal amplitudes are narrowest and marsh plain inundation least frequent in March and April, about the time vegetation begins to grow exponentially (Winfield 1980). The marsh plain is riddled with tidal creeks and spans a ~30-cm elevation range at our Bahía San Quintín reference system (Zedler et al. 1999) and a ~20-cm range at Tijuana Estuary (approximately 60–80 cm NGVD [National Geodetic Vertical Datum]; Figures 2, 3; Zedler et al. 1992). Marshes in Mexico’s Bahía San Quintín have large tidal channels with uninterrupted seawater flows (Figure 3).

The regular influence of tides is punctuated by river flooding and sea storms over the long term. Annual rainfall averages only 25 cm in San Diego, and river flows are correspondingly low; however, high interannual variation leads to catastrophic flooding. Wetlands with large watersheds or with disturbed lands (agricultural fields, urbanization) upstream are subject to major inflows of sediments; for example, Mugu Lagoon lost 40% of its low-tide volume during two flooding–sedimentation events (Onuf 1987). Such extreme sedimentation episodes are attributable to disturbance of vegetation and soils upstream of the estuaries. Tijuana Estuary has a large watershed, but the Tijuana River did not flood from 1944 to 1977. Since then, however, flows exceeded 70 cubic meters per second during the winters of 1978, 1980, 1983, 1986, 1988, 1993, 1995, and 1997. In addition, a major sea storm overwashed the dunes during the 1983 El Niño event, filling tidal channels with sand and reducing tidal inflows (Zedler et al. 1992). The estuary mouth subsequently closed, in April 1984.

Marshes north of the US–Mexico border are still numerous (Figure 4), but their loss of area and habitat quality has caused many wetland-dependent species to become threatened with extinction—for example, an endangered hemiparasitic annual plant known as salt marsh bird’s-beak (*Cordylanthus maritimus* ssp. *maritimus*), the wandering skipper (*Panoquina errans*), five species of tiger beetle (*Cicindella* spp.), the light-footed clapper rail (*Rallus longirostris levipes*), and the Belding’s Savannah sparrow (*Passerculus sandwichensis beldingi*). These rare species and several more abundant wading birds and waterfowl species are highly valued by the public. But these charismatic species are not the only victims of habitat loss and degradation. The marsh plain halophytes, although not very showy (Table 1), are still at risk.

Table 1. Life history and growth forms of eight halophytes common to the marsh plain of Californian coastal wetlands. Illustrations (by Donovan McIntire) show relative proportions of biomass above and below ground, as well as rooting depths, based on greenhouse experiments. Regional distributions are for 23 wetlands within the region (Table 2); fewer occurrences indicate sensitivity to tidal closure. Recent declines (Table 2) were recorded from selected wetlands (mostly San Diego County). Recruitment data (H=high, M=medium, L=low) are from Table 3. Species codes are Sv, *Salicornia virginica*; Fs, *Frankenia salina*; Jc, *Jaumea carnosa*; Lc, *Limonium californicum*; Se, *Suaeda esteroa*; Tc, *Triglochin concinna*; Sb, *Salicornia bigelovii*; Bm, *Batis maritima*.

		Sv	Fs	Jc	Lc	Se	Tc	Sb	Bm
Regional distribution		23	22	22	11	8	8	7	7
Recent declines/losses			1		2	6		3	
Life span	Annual							X	
	Perennial	Short-lived				X			
		Long-lived	X	X	X	X			
	Ephemeral shoots					X			
Growth form	Succulent	X		X		X	X	X	X
	Broad-leaved		X		X				
	Upright	X	X			X	X	X	
	Trailing			X					X
	Rosette				X				
Recruitment capability		H	L	L	L	M	L	H	L

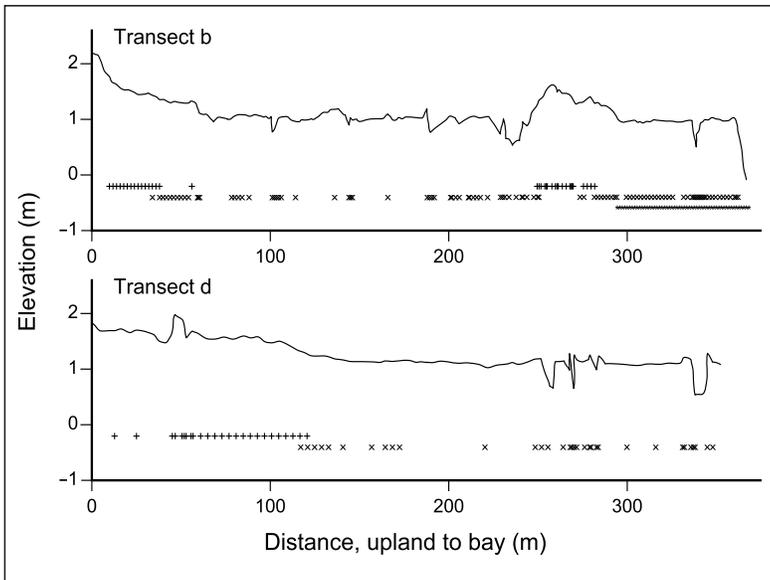


Figure 2. Topographic profile of Volcano Marsh at Bahía San Quintín. Transects extend from the upland (left) to the bay (right), crossing tidal creeks and channels, as well as hummocks formed by ancient lava deposits. Elevations are relative to the lowest occurrence of *Spartina foliosa* (Zedler et al. 1999). Occurrences of three species are given: + is a high-marsh indicator, *Salicornia subterminalis*; X is *S. virginica*; and the third row of symbols under transect b is cordgrass, *S. foliosa*.

Spatial and temporal patterns of halophyte diversity on the marsh plain.

At Bahía San Quintín, the marsh plain supports nine species that are both common and abundant (Zedler et al. 1999). The species include the eight species that dominated the marsh plain of Tijuana Estuary

before 1984 (Zedler et al. 1992). The latter, 1000-ha site is San Diego County’s largest tidal wetland and a National Estuarine Research Reserve.

Southern California marshes differ in their biodiversity. Historical records of eight halophyte distributions in 23 coastal salt marshes (Table 2) show that only three species are very widespread (Sv, Fs, Jc; species codes are in Table 1). Of these, *Salicornia virginica* has broad ecological tolerance (as indicated by its elevation range; Figure 2) and is dominant in most of the region’s wetlands (Zedler 1982, Barbour and Major 1988), including nontidal systems (Zedler et al. 1980). Lc is more restricted than Sv, Fs, and Jc, while the remaining four species are regionally restricted in their distribution, especially the two short-lived species (Sb and Se). The eight species’ regional occurrences indicate that species richness is greatest in wetlands with long histories of good tidal flow and lowest in wetlands that have been closed to tidal flow for one or more lengthy periods. For example, Los Peñasquitos Lagoon was closed for 5 years in the 1950s (Carpelan 1969); it lacks three of the eight marsh plain species. San Elijo Lagoon (Figure 5) is usually closed to tidal action, and it lacks five of the marsh plain halophytes. In each of these wetlands, tidal flows are constrained by both a railroad bridge and, at the tidal inlet, a coastal highway.

The spatial pattern of fewer species in wetlands with impaired tidal flow suggests that mouth closure has reduced biodiversity. Two lines of evidence support this cause-and-effect relationship. First, a 1998 resurvey of San Diego County’s tidal marshes documented the loss of species at sites with impaired tidal flows. Species Se was lost at four sites and nearly lost at two additional sites, Lc was lost at two sites, and Sb was lost at one site and nearly lost at Tijuana Estuary (Table 2). Second, the species declines were witnessed during two 1984 tidal closure episodes, one at Estero de Punta Banda in Baja California, following the permanent diking of a large marsh area (Ibarra-Obando and Poumian-Tapia 1991), and one at Tijuana Estuary during a temporary (8-month) closure (Zedler et al. 1992). At Estero de Punta Banda, monthly sampling documented that Sb and Se persisted only 13 months after a large portion of the salt marsh was diked. At Tijuana Estuary, the mouth closed in April 1984 after the 1983 El Niño storm filled the tidal channels. After closure, there was no rainfall

Table 2. Occurrence of eight marsh-plain halophytes in southern California coastal wetlands. Species are ranked according to the number of sites in which they occur; wetlands are in order of the number of species they support. Data in boxes represent changes in the status of a species at a site, determined by G. Sullivan’s 1998 census (# = now rare; 0 = now absent).

Sp.	Mugu Lagoon	Anaheim Bay	Upper Newport Bay	Mission Bay Reserve	Sweetwater Marsh	Tijuana Estuary	Bolsa Chica Wetland	Santa Margarita Wetland	Carpinteria Marsh	Goleta Slough	Los Peñasquitos Lagoon	Batiquitos Lagoon	Agua Hedionda Lagoon	Ballona Wetland	San Elijo Lagoon	Deveraux Lagoon	Santa Clara R. Estuary	Las Flores Marsh	McGrath Marsh	Malibu Lake	San Mateo Lagoon	San Mateo Marsh	Rank
Sv	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	1
Fs	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	0	X	X	X	X	2
Jc	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	3
Lc	X	X	X	X	X	X	0	X	X	X	X	0											4
Se	X	X	X	X	X	#	X	0	#	0	0		0										5
Tc	X	X	X	X	X	X		X	X														6
Sb	X	X	X	X	X	#	X	0															7
Bm	X	X	X	X	X	X	X																8

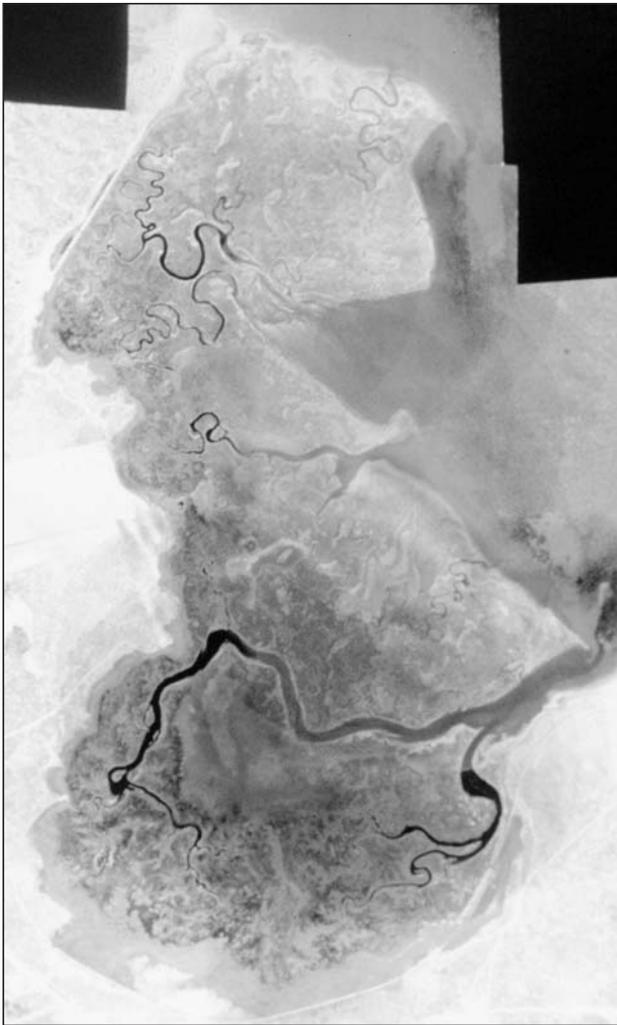


Figure 3. A remotely sensed image of Volcano Marsh, showing tidal channels. Mosaic compiled by Bruce Nyden, Pacific Estuarine Research Lab, San Diego State University.

in an unusually dry growing season. Channel salinities rose to about 60 parts per thousand (ppt), and soil salinities rose to an average of 104 ppt (Zedler et al. 1992). Species Sb and Se were virtually extirpated and did not recover from the 8-month nontidal catastrophe (Table 2).

The pattern of Sb and Se loss with reduced tidal influence is consistent across the region, in both space and time and at both Estero de Punta Banda and Tijuana Estuary. The pattern is also obvious from monitoring small-scale (0.25 m²) quadrats (Figure 6). Prior to tidal closure, the marsh plain of Tijuana Estuary supported a mean of 4.5 species; during closure the mean dropped below 2.0. Little recovery was evident in subsequent years, despite the return of tidal influence. Our May 1999 data from Bahía San Quintín had a mean of 4.7 species per 0.25-m² quadrat ($n = 224$). We conclude that biodiversity has declined at Punta Banda and Tijuana estuaries as a result of interrupted tidal influence.

Testing species' roles in ecosystem function

Given the 90% loss of wetland habitat in southern California, restoration is a high priority. Early attempts sought only to provide vegetation cover. It was common to plant just one or two easily grown species (*S. foliosa* in low elevations, Sv on the marsh plain; Zedler 2001). We hypothesize that ecosystem functioning might be impaired if too few species are restored. No one knows how many are needed for the system to develop at maximum speed or to achieve desired levels of ecosystem functions, such as the development and maintenance of natural community composition, the development of appropriate canopy structure, and the accumulation of organic matter and nitrogen. These span the range of indicators that Noss (1990) recommends for monitoring biodiversity. The assessment of just one function, such as net primary productivity above ground (or its surrogate structural attribute, biomass at the end of the growing season), is not likely to serve ecosystem managers or settle international debates about the importance of diversity to ecosystem functioning. Hence, we tested the effects of species-rich plantings on the development of multiple functions that are critical in restoration sites.

In 1997 we established a large field experiment at Tijuana Estuary to test the effects of species richness on three specific response variables:

1. Recruitment: Which species need to be planted and which readily establish and spread?
2. Canopy complexity: Which grow taller and produce more layers, as might be needed by insects and birds?
3. Belowground biomass and N accumulation. Which plots store the most N in roots and rhizomes?

Our experimental site was a graded marsh plain that had room for 87 2 × 2-m plots, distributed among five blocks, along an excavated tidal channel (Figure 7). Our experimental conditions included single-species plots of each of the eight species of the nearby reference marsh, plus randomly chosen six- and three-species assemblages, which roughly correspond to small-scale richness levels before and after tidal closure at Tijuana Estuary (Figure 6). Several of our experimental assemblages occurred in Tijuana Estuary in 1974 and Bahía San Quintín in 1999, but random draws missed the most common trio (Bm, Sv, Sb) and sextet (Bm, Sv, Sb, Fs, Jc, Se) from Tijuana Estuary's 0.25-m² plots. Hence, we added one plot with Bm, Sv, Sb and one with Bm, Sv, Sb, Fs, Jc, Se. The 87 field experimental plots were planted in April 1997 and replanted and weeded as needed that summer to maintain planting treatments and compensate for early mortality. The assemblages planted resulted in similar numbers of plants introduced within the experimental site. Thus, differential starting densities were not of concern in comparing recruitment. Assemblage composition was maintained during 1998 by removing

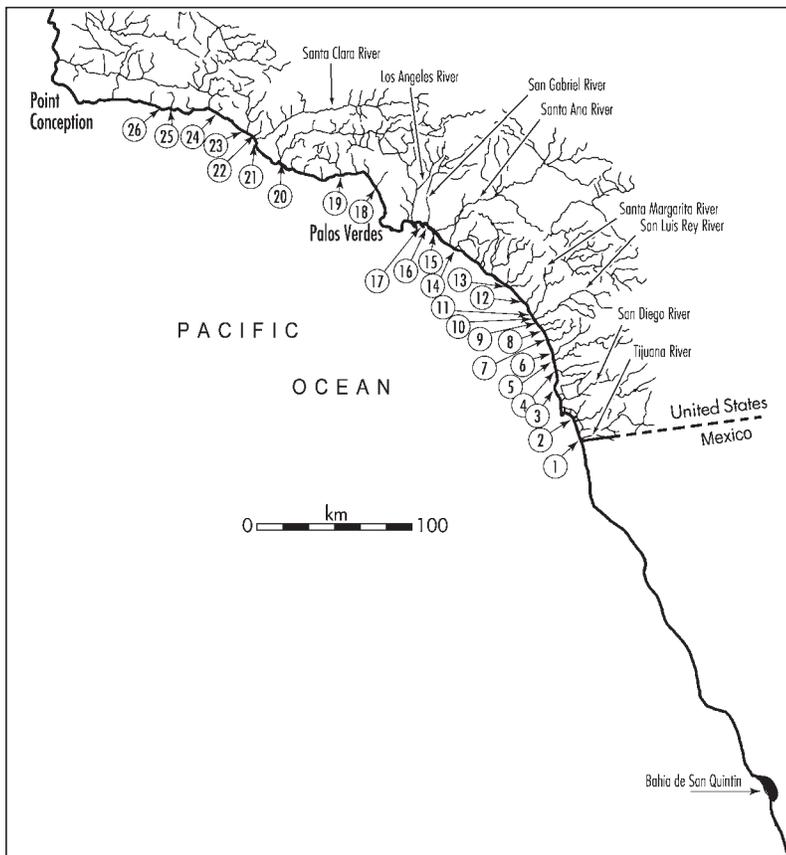


Figure 4. Coastal wetlands of southern California. 1, Tijuana Estuary; 2, Sweetwater Marsh; 3, Mission Bay Reserve; 4, Los Peñasquitos Lagoon; 5, San Dieguito Lagoon; 6, San Elijo Lagoon; 7, Batiqitos Lagoon; 8, Agua Hedionda Lagoon; 9, Buena Vista Lagoon (brackish wetland); 10, San Luis Rey River Mouth; 11, Santa Margarita Estuary; 12, Las Flores Marsh; 13, San Mateo Marsh; 14, Upper Newport Bay; 15, Bolsa Chica Wetland; 16, Anaheim Bay; 17, Los Cerritos Marsh (mostly filled and developed); 18, Ballona Wetland; 19, Malibu Lagoon; 20, Mugu Lagoon; 21, McGrath Lake; 22, Santa Clara River Estuary; 23, Ventura River (brackish); 24, Carpinteria Marsh; 25, Goleta Slough; 26, Deveraux Lagoon.

seedlings of other species; thereafter, recruits were allowed to persist.

Seedlings were censused by Roberto Lindig-Cisneros (2001); canopy architecture was documented by Keer and Zedler (forthcoming), and biomass and N accumulation were assessed by J. Callaway. Because we were most concerned about the increasing ability of the site to retain N, we assessed biomass and N accumulation in midwinter, after most plants had slowed growth. Furthermore, because we wanted to minimize destructive sampling, we removed small root cores in year 2 and root and shoot samples at the end of year 3. Both biomass components were analyzed for above- and belowground N content.

We complemented the field study with an experiment in the greenhouse, where we were able to compare individual assemblages. We replicated all 15 randomly drawn trios and sex-

tets 8-fold, all solos 16-fold, and the common trio and sextet 16-fold for a total of 400 microcosms. Planting treatments were maintained in the pots through vegetative growth and seedling recruitment, but assemblage composition did not change. All but 80 pots were grown for 2 years and assessed for canopy attributes and harvested for biomass and N content above and below ground.

The importance of diversity to restoration

Results from the field and greenhouse experiments support the general hypothesis that diversity matters in restoration sites. Our plantings with six species enhanced recruitment, made canopies more complex, increased biomass, and increased N accumulation.

Recruitment. Only three species (Sv, Sb, and Se) recruited readily (Table 3). Of these, only one (Sv) is widely distributed (Table 2) and available to disperse into restoration sites. It germinates in seawater and produces abundant seedlings in both natural and restored wetlands, including our unplanted plots; it does not need to be planted to restoration sites if a seed source exists nearby. The other two abundant recruiters, Sb and Se, are the marsh plain’s only short-lived species. Personal observation revealed that Se recruitment potential was much lower than that of Sb, reflecting its lower density in regional wetlands and differences in seedling mortality within this experiment. The fact that both recruited readily in the bare restoration site and poorly in the salt marsh where it occurred historically is evidence that the Tijuana Estuary marsh plain no longer provides suitable habitat for these species. The remaining five species did not readily colonize either our planted or unplanted plots. Their inability to recruit may be at-

Table 3. Seedling recruitment of eight marsh-plain species into experimental plots. Data are for the 1998 growing season. Note that the number of plants introduced to the site as seedlings in April 1997 (column 2) was similar, but only three species recruited extensively. Species codes are in Table 1.

Code	Number planted	Number of recruits
Sv	840	17,703
Sb	735	15,978
Se	795	1,668
Tc	810	73
Jc	840	33
Bm	720	26
Lc	795	24
Fs	765	2

tributable to small seed supply, poor germination, or unsuitable conditions for establishment.

Canopy architecture.

Keer and Zedler (forthcoming) found that all plots rapidly achieved high cover but that canopy height and layering were slow to develop. Cover is a poor measure of canopy complexity; it does not differentiate species or species-richness treatments. Maximum heights were greatest for trios and sextets, reaching about 60 cm by year 3. Sv grew the tallest in the first 18 months of study, followed by Sb and Se. Layering (the number of times a vertical rod encounters plant parts as it is lowered through the canopy) was greater for trios and sextets, both of which achieved three layers within 18 months. The effects of individual species were likely to be seen early in the development of the plots; Fs and Se had six and five layers, respectively, with Jc at four layers. Layering is hypothesized to enhance habitat for both arthropods and birds. These canopies are far from fully developed; reference marshes with monotypic Sv averaged 45 cm tall with seven layers, and areas with multiple species were 55 cm tall and had 13 layers (Keer and Zedler forthcoming).

Biomass and N accumulation. In the field plots, above-ground biomass averaged under 300 g per m² for solos and over 400 g per m² for sextets. Belowground biomass also increased with species richness and over time—means doubled between years 2 and 3 (to 500g per m² for sextets). The rapid increase in belowground biomass is highly desirable for bare restoration sites. To determine whether N crops increased, we measured biomass and tissue N concentrations. The resulting estimates of accumulated N showed a higher crop for sextets than for unplanted and solo plots. The rapid accumulation of N is beneficial for restoration sites that have coarse soil and where N is the limiting factor (a common problem in created and restored wetlands; Langis et al. 1991, Boyer and Zedler 1996, 1998, Zedler and Callaway 1999, 2000, Boyer et al. 2000). Our greenhouse experiment revealed similar patterns in a more benign environment (that is, one with warmer temperatures). Total biomass was higher for sextets, because belowground biomass increased with species richness. As in the field, N crops tracked biomass, with greater total N accumulation and greater belowground accumulation at year 2. A species composition effect—namely, the chance inclusion of high biomass producers in the randomly drawn assemblage—is indicated, because Jc, Fs, and Lc solos all accumulated more N than the mean for sextets, and Sv and Bm



Figure 5. San Elijo Lagoon, San Diego County, California.

solos both accumulated as much as the trios. Although Tc, Se, and Sb solos all had below-average N crops, Sb and Tc accumulated the most N per unit biomass.

These findings were used to design the planting of the 8-ha “Friendship Marsh,” a \$3 million project that aims to support rare species of plants and animals (Figure 8). Located in the south arm of Tijuana Estuary, this site was opened to tidal flushing in February 2000 after floodborne sediments (1–2 m) were excavated and the historical marsh plain uncovered. Because Sv dominates the nearby wetlands and readily establishes on its own, it was not introduced as seeds or plants. Instead, we planted five species for which we had abundant seedlings (Fs, Jc, Bm, Lc, and Se) to help provide the functions mentioned above—namely, recruitment, complex canopies, and biomass and N accumulation. The protocol of not planting Sv (to slow time to dominance) and adding multispecies clusters (to accelerate the development of species-rich

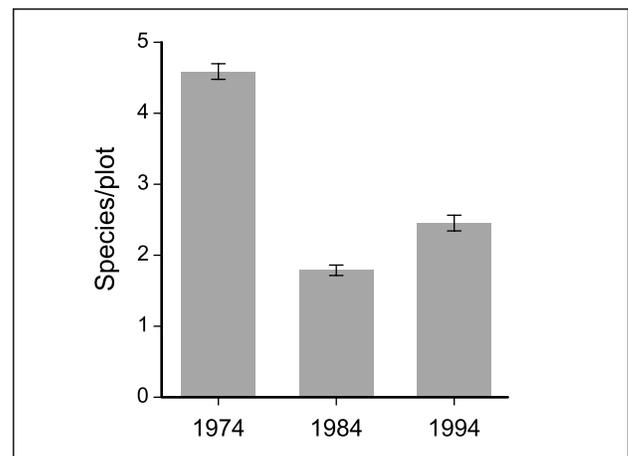


Figure 6. Historical patterns of species richness at Tijuana Estuary; data (means and standard errors) are from 0.25-m² circular plots.



Figure 7. Adaptive restoration exemplified by the experimental planting of 87 2-by-2-meter plots with 0, 1, 3, and 6 species in a newly excavated marsh plain at Tijuana Estuary. Photograph taken in June 1997, 2 months after planting greenhouse-grown seedlings (90 per plot).

canopies) is new to the region. Previous marsh plain restoration efforts have focused on planting Sv.

Although the field and greenhouse experiments taught us that species-rich plots promote recruitment, develop more complex canopies, and accumulate more biomass and N, the performance of sextets could be attributable to the combined performance of the six species or to the chance inclusion of a single high-performance species (a species composition effect). Data from the replicated assemblages in the greenhouse allowed us to evaluate these alternatives. In the microcosms, species composition was stable over time (whereas recruitment increased richness of solo plots in the field). We compared the eight species and found that Jc produced the most shoot biomass, Fs the most root biomass, and Sv the most total biomass, while Tc had the highest root:shoot biomass. But their rankings changed when ash-free biomass

was considered, because Sv had the most ash per plant and Sb the most ash per unit biomass. For ash-free biomass, Jc was highest for shoots, Fs for roots, and Jc for total, with Tc still having the highest root:shoot ratio. The N concentration of shoots was highest for Sb; for roots, it was highest for Tc. Jc had the highest crop of N in its shoots and Fs the highest root N crop, while Jc had the highest total N crop. Height was greatest for Se, and layering was greatest for Fs. Interestingly, the region's "superplant," Sv, achieved its first place overall ranking not by excelling in multiple attributes but by scoring second or third in most attributes. It scored highest only in total biomass, but it achieved high biomass by accumulating a large volume of salts in its tissues, in addition to accumulating considerable carbon.

This meta-analysis supports both alternatives: Species composition effects (Symstad et al. 1998) were indicated for every attribute considered (there is at least one species that can match the performance of the average sextet), but it is not the same species for all response variables (that is, all species are needed to achieve high levels of all functions). Furthermore, each species excelled in at least one attribute. Thus, we conclude that diversity matters a great deal, and the only way to ensure that multiple functions are provided is to plant and sustain all species. Retaining diversity results in less risk that functions will be eliminated. The planting of species-rich assemblages in restoration sites would help ensure that more functions are restored.

There is support for the suggestion that attributes measured in the greenhouse translate into performance in the field: The species that performed best in the greenhouse are most widespread geographically. Overall, the eight species ranked in virtually the same order as in their distributional ranking (that is, the number of southern California wetlands in which they occur; Table 1). The top three performers in the greenhouse were Sv, Jc, and Fs, and they all occur in 22 or 23 wetlands. Lc ranked fourth in greenhouse performance and fourth in regional distribution, occurring in 13 wetlands in the historical record and in 11 wetlands in 1998. The others ranked fifth through eighth in performance; they are the most restricted in their distributions, now occurring in only six to eight sites. Jc, Fs, and Sv are all highly productive, long-lived perennials that reproduce vegetatively and form monotypic patches (Zedler et al. 1980, Ferren 1985). It is not surprising that they persist in wetlands that experience closure to tidal influence.

What functions were lost when short-lived species dropped out of Tijuana Estuary?

Sb and Se are short-lived halophytes that do not reproduce vegetatively. Their roles in the ecosystem are arguably unique from these perspectives alone. Their annual recruitment of seedlings following winter rainfall adds seasonality to the canopy and soil, perhaps changing food availability both above and below ground. Regrettably, these functions have not been quantified.

As our field data document, Sv, Sb, and Se are all good recruiters, capable of filling canopy openings with seedlings and rapidly revegetating bare sites. However, the 1998 recruitment data (Lindig-Cisneros 2001) show that Sb and Se produced seedlings earlier than Sv. In early April 1998, there were 2,199 Sb and 220 Se seedlings but only 89 Sv seedlings. In our experimental design, we pulled seedlings of invading species to retain assemblage composition in 1997–1998, so there was ample opportunity for Sv seedlings to recruit later. In early May 1998, there were 9,261 Sv seedlings but only 842 Sb and 50 Se; recruitment then declined for all species over the late May and July sampling dates, despite the fact that seedlings were being pulled and space remained available for establishment. We infer from these results that Sb and Se have important roles in filling gaps; that is, space opened late in the year is filled by Sb and Se the following winter and spring.

Both Sb and Se are capable of rapid height growth, as demonstrated in the greenhouse. Se might be the first species to provide perch sites for the endangered Belding's Savannah sparrow, which defends its nesting territories by singing while perching on the tallest plants (Powell 1993). The vertical structure afforded by Se differs from that of Sv in having a more horizontal branching angle and more layers, attributes that may increase its attraction of small birds. It is not uncommon to see sparrows perching on tall branches of Se in the field, whether the plants are alive or dead. We conclude that the loss of Sb and Se could impair the community's ability to recover from disturbance and to support an endangered bird. These functions are not entirely eliminated by the demise of Sb and Se, but the ecosystem's functional potential might not be realized in their absence.

Is the loss of species reversible?

Tijuana Estuary's current salt marsh community is certainly different from that prior to 1984, when an open canopy supported thousands of Sb seedlings per square meter and Se was common throughout the tidal marsh. Today, these species persist in a tiny fraction of the area they occupied historically. As short-lived species, both Sb (annual) and Se (lives only a few years)



Figure 8. An 8-ha marsh plain excavation at Tijuana Estuary. Because of the large size of this site, plantings emphasized species that would not likely recruit on their own.

depend on recruitment for their persistence, while all of the other marsh plain species reproduce vegetatively. Seedlings were young when Tijuana Estuary became nontidal in April 1984, and one likely cause of their mortality was the drying of surface soil and rise in salinity to an average of greater than 100 ppt (Figure 9). Moderate hypersalinity (40–45 ppt) is typical for marsh plain soils, but extreme hypersalinity is more characteristic of higher elevations with less frequent tidal inundation (Noe and Zedler 2001). Sb and Se can germinate in seawater, but higher salinities reduce germination rates (Zedler and Beare 1986). Had their seed banks persisted through the

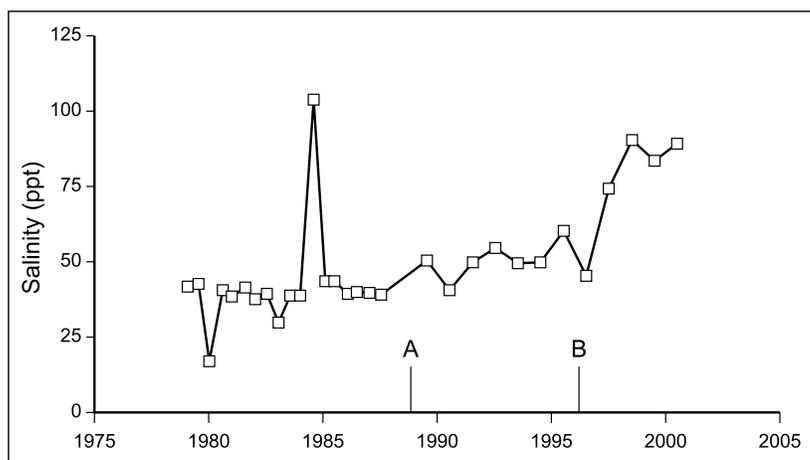


Figure 9. Soil salinity at Tijuana Estuary (data from the Pacific Estuarine Research Lab). Means before A on the x-axis include *Spartina* marsh and the marsh plain; means after A are marsh plain only. Means before B are for interstitial soil water; after B are for soil pastes (adding deionized water underestimates interstitial salinity).

period of tidal closure, Sb and Se should have germinated in 1985; they did not.

A recent reintroduction experiment by Vivian-Smith and Zedler (2001) indicated that neither species retains a marsh plain seed bank at Tijuana Estuary. Vivian-Smith added 2000 seeds of each species in 1998; Sb produced 272 seedlings and Se produced 2, with seedlings establishing only where seeds were added. Also, the current Sv-dominated canopy reduced recruitment, with Sb seedling density twice as high where the canopy was removed (Table 4). Hence, we learned that a lack of seeds and shading by Sv restricted recovery of the Sb population. And because H. N. Morzaria-Luna (University of Wisconsin-Madison, unpublished data) could not locate either species during her search in 2001, we suspect that changes in both the physical and biological conditions of this marsh further inhibit recovery. We explore each of these in turn.

Irreversible physical changes. According to recent information, both elevation and soil salinities have changed in the 16 years since tidal closure. A study of marsh accretion rates (Weis et al. forthcoming) using cesium-137 (¹³⁷Cs, a globally dispersed radioisotope) suggests that since 1984 (the year when Sb and Se declined) the marsh plain elevation has risen 13 cm, based on two soil cores. At three additional locations, benchmarks placed on the marsh plain in the 1970s by the US Army Corps of Engineers were relocated; there we have measured an average of 6 cm accretion since 1984 (Morzaria-Luna, unpublished data). Further sedimentation data from Tijuana Estuary corroborate this rapid rise in elevation. Cahoon and colleagues (1996) measured 2.0–8.5 (mean 5.9) cm accretion in the *S. foliosa* marsh between 1992 and 1993, and in a nearby tidal pond (lower elevation). Ward (2000) found 4–12.7 (mean 8.8) cm of sediment accretion from 1997 to 1998. The marsh plain elevation has risen because of sedimentation, and the recent record of flooding provides an explanation.

Tijuana Estuary has a large watershed with highly erodable soils and major slope failures that are visible both north and south of the US–Mexico border. The 1993 floodwaters cut an entirely new river channel just inland of the estuary. The huge volume of sediment that was mobilized could have contributed to a rise in elevation on the marsh plain. Increased soil salinities (now averaging 60 ppt; Figure 9) cor-

roborate a shift toward a higher, and hence drier, marsh plain. For intertidal species that are sensitive to 5–10-cm differences in elevation, the accretion rates and associated salinities documented at Tijuana Estuary would seem to be fatal. Persistent hypersaline conditions would reduce Sb and Se establishment, drier conditions would favor Sv, and denser canopies of Sv would reduce the persistence of seedlings.

If rising elevation and increasing salinity prevent reestablishment of Sb and Se, then reversing these changes would require a massive sediment removal effort—the marsh plain would have to be bulldozed to lower the elevation by 6–13 cm or more. Such a disruption to the vegetation would not be allowed by resource managers, because the plant canopy is used by light-footed clapper rails for cover and Belding’s Savannah sparrows for nesting.

There is an alternative. Although these recent physical changes are not reversible, it is possible to excavate sediments and restore areas where sediment loads have shifted topography well out of the tidal range. Exactly this procedure is planned for up to 200 ha of former tidal wetlands in the southern arm of the estuary (Entrix et al. 1991). The removal of sediments in the south arm can conceivably compensate for some of the accretion that is occurring in the estuary and in the region. Attempts are also being made to control the flow of sediments upstream.

Irreversible biological changes. When the full complement of species is present, the community presumably has maximum biocomplexity—that is, a variety of interspecific interactions and feedback mechanisms. Its biodiversity would lead to biocomplexity. It is possible that the marsh’s biocomplexity helped sustain its biodiversity. If some interactions facilitated rare species and others kept dominants from out-competing subordinates, then more species would persist. In that event, losing some species would make the community less able to support all the naturally occurring species, both plant and animal. Where dense canopy cover reduces seedling recruitment, any species that reduces overall biomass above-ground could reduce shading and enhance recruitment and species richness. The greenhouse experiments with replicated assemblages suggest such a species effect.

We explored effects of selected species by comparing microcosms with and without such a species. We found three species (Sv, Fs, and Jc) that tended to increase whole-pot biomass (a typical effect of productive species) and one (Tc) that tended to decrease whole-pot biomass (an unusual effect). Assemblages with Tc had lower shoot biomass than assemblages without it. Tc produces little biomass when grown alone; it is short, with an unimpressive canopy. Although low in biomass, Tc accumulates a disproportionate concentration of N, twice that for Sv. In the microcosms, total ash-free biomass values for Tc and Sv were significantly negatively correlated ($r = -0.43$, $p < .01$, $n = 72$ sextets). Despite its small size, Tc seems capable of reducing the biomass of Sv. Field data from Bahía San Quintín also suggest a negative relationship between Tc and Sv cover ($r = -0.133$, $p = .05$, $n = 224$). We conclude that Tc has some mechanism for reduc-

Table 4. Experimental attempt to reestablish Sb and Se at Tijuana Estuary in 1998 (unpublished data collected by Gabrielle Vivian-Smith, Pacific Estuarine Research Lab). Species codes are Sb, *Salicornia bigelovii*; Se, *Suaeda esteroa*. The “seeds added” treatment had 2000 seeds added per species. “Recruitment” is the total number of seedlings found.

Treatment	Recruitment
No seeds added	0 Sb, 0 Se
Seeds added, canopy left intact	92 Sb, 0 Se
Seeds added, canopy cleared	180 Sb, 2 Se

ing the aboveground biomass of other species, and where shoot biomass is reduced, canopies are more open and recruitment should be facilitated.

Any of three mechanisms could lead to reduction of whole-pot biomass by Tc: (1) direct competition for N, which reduces other species' growth; (2) allelopathy (negative chemical effects); or (3) indirect interactions that favor other species, which in turn reduce Sv biomass. In support of direct competition, Tc sequesters a large mass of N because it has the highest concentration of N in its roots. In the field, long-lived clones of Tc could tie up substantial stores of N. In support of indirect interaction, Tc's phenology and life history are highly complementary to that of Sb. Tc

has an open canopy (the fewest layers of all species), which most likely facilitates Sb germination; Tc's canopy declines in May, when Sb grows rapidly. Sb reaches peak biomass, fruits, and dies in fall. The N in Sb tissues would then be released about the time that Tc resumes aboveground growth. The potential exists for complementary N use.

The post hoc evaluation of assemblages with Tc suggested a biocomplexity model in which Tc facilitates the co-occurrence of Sb (Table 5). Like a keystone species, Tc might be preventing overdominance by Sv, Fs, or Jc. It could thus be a key to biodiversity support in the Californian salt marsh (Table 5). It is widespread at San Quintín Bay (greater than 70% frequency in 0.25-m² quadrats). Its absence in many California salt marshes could be part of the reason Sv is so often dominant. Ibarra-Obando and Poumian-Tapia (unpublished data) recorded large differences in Tc cover where tidal flushing was eliminated at Estero de Punta Banda (46% versus less than 10% cover in 1984 and 71% versus less than 3% in 1985 for areas with and without tidal flushing, respectively, and occurrences of 73% versus 15% ± tidal flushing). The potential for low-biomass species to open Sv canopies is not unprecedented. *Cuscuta salina* sometimes facilitates recruitment on the marsh plain (Pennings and Callaway 1996), but this obligate parasite is not amenable to experimental plantings. We conclude that Tc, Sb, and Se are all highly sensitive to tidal interruption and suggest that establishing Tc in restoration sites could promote establishment and persistence of Sb and Se. Had it not been for the random drawing of species combinations, we would not have tested assemblages with and without Tc, because this small and often inconspicuous species is a winter–spring ephemeral that displays little evidence of its rich store of N. Hence, we disagree with

Table 5. Schematic, based on greenhouse experimentation, showing low species richness where *Triglochin concinna* (Tc) is absent (and the presence of only the more productive and aggressive competitors (Fs, Jc), versus a more species-rich system where Tc is present. Tc might reduce aboveground biomass and cover of the perennial *Salicornia virginica* (Sv) in the field, thereby allowing some of the less competitive species to coexist with Sv, Fs, and Jc. Reduced biomass would make more light available for the annual *S. bigelovii* (Sb) to recruit from seed. Plants illustrated by Donovan McIntire.

		
	+ Tc	– Tc
Biomass	low	high
Light penetration	high	low
Seedling recruitment	Sb, Se, Sv	minimal
Species richness	high	low

Huston and colleagues (2000), who argue that randomly drawn assemblages lack relevance.

The biodiversity debate revisited

Biodiversity and function are positively related in the salt marsh; that is, all of the species appear to be needed to provide all of the functions. Our comparison of species richness levels and single-species treatments contributes quantitative data on multiple functions, showing that different species perform different functions best (Sullivan and Zedler 1999). Furthermore, our biocomplexity model suggests that a small but N-rich species might keep a highly productive species in check, thereby allowing other species to coexist. Ecosystem disruptions, such as tidal closure, can be catastrophic by eliminating species, but a more elusive response might also occur, if the loss of a keystone species simultaneously removes the mechanism for sustaining diversity. The loss of biodiversity might mean the loss of biocomplexity, which in turn means loss of the ability to sustain biodiversity. If Tc has a keystone role in biodiversity maintenance, then its loss during tidal closure would have lasting effects on the entire assemblage. These biologically complex interactions are now under experimental study, and long-term follow-up of the immature vegetation in our experimental plots will help test this model.

Conclusions

The Californian salt marsh plain is a model system for exploring the importance of diversity to restoration. Species-rich plantings enhanced the restoration site by increasing recruitment of native species, canopy complexity, biomass, and N accumulation.

Once lost, diversity might not be easily restored because of changes in the environment or disruption of critical species interactions. The hypothesis emerged that biocomplexity (in this case, species interaction) sustains biodiversity (persistence of all species), when experiments showed that a low biomass species (Tc) reduces the growth of high-biomass species (especially Sv). Mechanisms that might explain this surprising outcome include N sequestering, allelopathy, and phenology that facilitates growth of an annual plant (Sb).

Experiments with young vegetation and randomly drawn assemblages are highly relevant in the restoration context. Restoration sites offer outstanding opportunities to advance both the science and practice of restoration.

Recommendations for restoration

In general:

- Do not ignore uncommon, inconspicuous species in planning the restoration of vegetation. Even if dominant species are easy to propagate, they might not fulfill all essential functions or achieve any one desired goal. They might also impair the establishment of desirable species that contribute functions that are less conspicuous.
- Plant species that recruit poorly.
- Employ measures of canopies that evaluate complexity (such as height and layering), not just plant cover.
- Incorporate more physical complexity into restoration sites and foster biological interactions (via mixed-species plantings) to sustain biological diversity.
- Use restoration sites to test further the ability of topographic variability and interspecific interactions to enhance the persistence of species-rich assemblages. The design of restoration sites as experiments can simultaneously vegetate the site and improve knowledge.

For Californian salt marshes:

- Sow seeds of Sb and Se and plant seedlings of Bm, Tc, Lc, Fs, and Jc. Allow Sv to recruit from seed on its own so it will not immediately dominate the site.
- Introduce plants as multispecies assemblages to accelerate development of biomass (Fs, Jc), N accumulation (Tc), height (Se), layering (Fs, Se), shade (Lc), seedling density (Sb), and vegetative spread (Bm). Test the effect of planting Tc first, and then introducing short-lived species (Sb, Se).
- Track the outcomes by monitoring plantings in late spring (to evaluate Tc establishment and growth) and late fall (to assess other species' performance), and by monitoring recruitment by volunteers (Sv) as well as planted species.

Acknowledgments

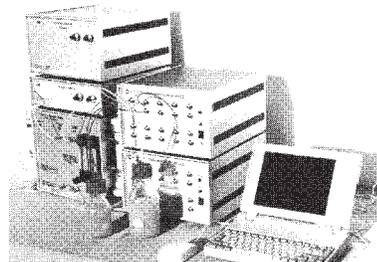
We thank the National Science Foundation (DEB 96-19875) and Earth Island Institute for support of this research. Georgeann Keer and Roberto Lindig-Cisneros conducted studies of canopy architecture and seedling recruitment, respectively, providing results that greatly improved our understanding of species richness and species composition effects. The research could not have been completed without help from our colleagues and staff at the Pacific Estuarine Research Laboratory at San Diego State University, who helped grow, transplant, and maintain thousands of seedlings for the field and greenhouse experiments.

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