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## Evaluating Monoculture Versus Polyculture Planting Regimes in a Newly-Restored Southern California Salt Marsh

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*Abstract.*—Salt marsh plants are a key source of primary productivity, ameliorate harsh abiotic conditions, and provide habitat structure to many organisms. As a consequence, rapid re-establishment of plant cover following restoration can speed the recovery of degraded ecosystems. Despite demonstrated positive relationships between plant biodiversity and ecosystem functions, many salt marsh restoration plans still incorporate single-species plantings under the belief that this approach will lead to faster increases in plant cover (a typical management goal). In this study, we evaluated post-restoration recovery of a non-vegetated high marsh berm in Brookhurst Marsh, Huntington Beach, CA, with two active planting strategies: monoculture plots of the competitive dominant *Sarcocornia pacifica* (pickleweed) versus polyculture plots of pickleweed and eight other common salt marsh plant species. Although monocultures did increase in total percent plant cover faster than polycultures, both treatments had reached 80–100% cover after one year, easily exceeding the permit-mandated goal of 20–40% cover in that time. The effects of increasing plant cover on abiotic parameters (e.g., % light reaching the ground, soil temperature, and soil salinity) were comparable between the two treatments and provided physical conditions sufficient to support similar macroinvertebrate communities. In contrast, plant species richness and canopy complexity were significantly higher in polyculture versus monoculture plots by the end of the experiment. Mean plant height was lower in polyculture plots, but maximum plant height (which can influence habitat use by perching birds) did not differ by treatment. Our data suggest that polyculture plots performed as well as, or better than, *S. pacifica* alone with respect to multiple indicators of ecosystem function. Active planting of high-diversity plots should therefore be seriously considered as a restoration tool to achieve common management goals in southern California salt marshes.

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Coastal wetlands provide a variety of key ecosystem functions that include food web support, nutrient cycling, sediment stabilization, and nursery habitat for many ecological and economically important species (Mitsch and Gosselink 1993; Minello et al. 2003). Nevertheless, during the past century loss of coastal wetlands and their associated services has been extensive; in California, less than 10% of historical distributions remain intact (Dahl 1990; MacDonald et al. 1990). To offset such habitat loss, wetland managers and conservation groups have increasingly turned to restoration and mitigation as potential solutions (Zedler 2000). In southern California, nearly every major embayment has one or more wetland restoration programs completed, in progress, or planned (Zedler 1996; SCWRP 2001). The success of such activities will depend upon how well we

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understand the ecological processes that control salt marsh community organization and function (Montalvo et al. 1997; Pennings and Bertness 2001) and the degree to which we incorporate such knowledge into restoration planning.

Current theory and empirical evidence suggest that post-restoration salt marsh succession is highly contingent on the overall amount of plant cover within a given system (Palmer et al. 1997; Levin and Talley 2002). As percent cover and density of vegetation increase, shading by the plant canopy ameliorates harsh abiotic conditions such as high soil temperatures, salinities, and degree of compaction, all factors that influence the development of local invertebrate communities (Bertness et al. 1992; Nomann and Pennings 1998; Bortolus et al. 2002; Whitcraft and Levin 2007). Fish and other free-swimming organisms are more likely to recolonize vegetated rather than non-vegetated areas (Williams and Desmond 2001) as plants provide food and a refuge from predation (Vince et al. 1976; Rozas and Odum 1988; Irlandi and Crawford 1996). Birds also benefit from increased plant cover in marshes; for example, in southern California the state-listed endangered Belding's Savannah Sparrow (*Passerculus sandwichensis beldingi*) uses several marsh plant species for nesting habitat (Powell, 1993). For these reasons, establishing high plant cover is perceived to be an important restoration target for coastal wetland projects (Streever et al. 2000; O'Brien and Zedler 2006).

To achieve this management goal, restoration plans can incorporate either passive or active re-vegetation strategies. Passive restoration assumes that natural recruitment of plants will occur after suitable habitat is created or restored. Although this method requires minimal investment of resources, it can take a long time for plants to become established if local source populations are absent or propagules exhibit low dispersal capabilities (Bakker et al. 1997). In contrast, active restoration (the method chosen for this study) involves the planting of native vegetation in specific areas at specific relative densities, with the expectation that the resulting plant community will be similar to some desired endpoint (Parsons and Zedler 1997; Sullivan 2001).

Implementing an active restoration strategy requires that planners identify in advance which plant species to include in the project. A common approach is to use only a few (or even a single) species, typically introduced in monoculture plots (Gilbert and Anderson 1998). Often the most common and easily established species are chosen, in the belief that this approach will lead to faster increases in plant cover (Sullivan 2001). The downside of using local dominants in an active restoration is that less competitive species may never become established, resulting in a permanent state of reduced species diversity relative to natural marshes. There is ample evidence that plant species richness, relative abundances, and identity can have significant effects on ecosystem function in coastal wetlands (Callaway et al. 2003; Armitage et al. 2006; Diggory and Parker 2011; Doherty et al. 2011). High species richness potentially increases the resilience of the plant community and decreases the likelihood that a single extreme environmental event will wipe out all plant populations at once, as certain species have differential success in response to varying environmental stresses (e.g., high salinity, drought, long-term inundation) (Zedler and Nordby 1986). Species-rich canopies may also reach taller heights and exhibit more discrete layers than monocultures, even when both exhibit comparable percent cover (Keer and Zedler 2002). Determining the most effective and efficient active restoration methods is necessary if we are to successfully evaluate alternative restoration proposals and policies (Streever et al. 2000; Callaway et al. 2003; Zedler 2005).

The Huntington Beach Wetlands complex is an approximately 200-acre remnant of a 2900-acre wetland area that once existed at the mouth of the Santa Ana River in

Huntington Beach, California. This area consists of restored salt marsh and coastal dune habitat and is bisected by roadways into several distinct sections, including Brookhurst Marsh where this study takes place. The marsh is hydraulically linked to the Pacific Ocean by a flood control channel running along its northeastern border. Historically, the natural tidal creeks in the marsh were diked and filled for the purpose of oil and gas exploration, isolating the area from surface tidal exchange for over 70 years (Dage and Reardon 2004). Full tidal flow was restored to the 67-acre marsh in 2009. In this study, we evaluate post-restoration recovery of plant cover and associated indicators of ecosystem function on a high marsh berm in Brookhurst Marsh with two active planting strategies: monoculture plots of the competitive dominant *Sarcocornia pacifica* (pickleweed) versus polyculture plots of *S. pacifica* and eight other common salt marsh plant species. We were particularly interested in whether the different treatments could reach a permit-mandated goal of 20–40% plant cover within one year of planting. The specific aim was to provide suitable nesting habitat (dense, complex canopies) for the state-listed endangered Belding's Savannah Sparrow. We also hypothesized that treatment-specific differences in plant community structure and plant traits would lead to changes in abiotic conditions, invertebrate species richness and abundances, and plant community structure over time.

## Materials and Methods

### *Experimental Design and Planting*

All work was done on an unvegetated high marsh berm in Brookhurst Marsh, Huntington Beach, CA (33° 39' N, 117° 59' W). Full tidal influence was restored to the marsh in June 2009; initial sampling and planting was done in September 2009. To test the effects of monoculture versus polyculture plantings on post-restoration recovery of ecosystem functions, we established a series of plots with either 1 or 9 plant species. *Sarcocornia pacifica* was chosen as the focal species in our monoculture plots because the site restoration plan included it as the primary species to be used in re-vegetating the other berms in the marsh. In addition to *S. pacifica*, polyculture plots included eight additional plant species common in southern California: *Arthrocnemum subterminale* (glasswort), *Batis maritima* (saltwort), *Cressa truxillensis* (alkali weed), *Distichlis spicata* (saltgrass), *Frankenia salina* (alkali heath), *Isocoma menziesii* (goldenbush), *Jaumea carnosa* (salty susan), and *Monanthochloe littoralis* (shoregrass). These species were chosen based on their ability to survive and grow in this habitat and their general use by multiple organisms within the marsh (Powell 1993; Sullivan 2001).

Paired plots ( $n = 10$  per treatment group) were spaced 2 m apart in a randomized block design at a single tidal elevation (~1.5m above Mean High Water). Each 2 × 2 m plot was tilled and planted with eighty-one seedlings (~7.5 cm tall) supplied by the Tree of Life Nursery, San Juan Capistrano, CA, and the Huntington Beach Wetlands Conservancy Nursery, Huntington Beach, CA. Seedlings were planted in a 9 × 9 grid with 20-cm spacing between plants (Callaway et al. 2003) and 15 g of slow-release fertilizer (Osmocote®; 19-6-12) in each hole (Broome 1990). Whereas monoculture plots (designated S) each had 81 *S. pacifica* seedlings initially, polyculture plots (S+) were comprised of 9 *S. pacifica*, 9 *A. subterminale*, 12 *B. maritima*, 9 *C. truxillensis*, 3 *D. spicata*, 9 *F. salina*, 9 *I. menziesii*, 12 *J. carnosa*, and 9 *M. littoralis* seedlings. Composition of the polyculture plots was determined by the relative abundances of the different species in nearby natural systems (authors' personal observations) and the availability of seedlings. The location of individuals within each plot was randomized. Plots were

watered with fresh water twice daily for one year via an automated sprinkler system, after which the irrigation was shut off.

### *Sampling*

Starting in September 2009, changes in total plant cover were monitored monthly until March 2011 (18 months after planting), with the exception of April–June 2010 when the marsh was closed due to bird nesting activity. Plant cover was estimated for the entire plot using the Daubenmire method with classifications of 0–20%, 20–40%, 40–60%, 60–80%, and 80–100% cover (Daubenmire 1959). Abiotic conditions in experimental plots were sampled in September 2009, February 2010, May 2010, October 2010, and March 2011. On each sampling date at a randomly selected point in each plot, incoming solar radiation ( $\text{W}/\text{m}^2$ ) was recorded with a LI-COR 250A light meter and pyranometer; three readings above and below the plant canopy yielded a mean percent light reaching the ground. Soil temperature in the top 2 cm was measured with a digital thermometer and probe and porewater salinity was measured with the paste method on a single sediment core (Richards 1954).

Plant community composition and attributes were measured at the end of the experiment. Plant cover by species (% species cover) was estimated using the same method as total plant cover and species richness as the number of plant species per plot. Canopy complexity was estimated as the mean number of discrete canopy layers intersecting a vertical meter stick placed at the center of each plot and four additional points located halfway between the center and each corner (after Sullivan 2001). Mean plant height was calculated from individuals measured at the same five points, and maximum plant height was measured on the single tallest individual in each plot.

Macroinvertebrate groups were sampled in several different ways in September 2009, February 2010, October 2010, and March 2011. Mobile ground-dwelling fauna were sampled with a pitfall trap (50-mL centrifuge tube containing 8% formalin) buried near the center of each plot and collected after 24 h. Benthic infauna were sampled with a sediment core (18.1  $\text{cm}^2$ , 2 cm deep) collected at a random point within each plot. Samples were preserved in 8% formalin and washed through a 300- $\mu\text{m}$  sieve. Canopy insect communities were sampled only in October 2010 and March 2011 using a leaf blower modified to vacuum air. The plant canopy in each plot was vacuumed for 30 seconds; samples were frozen until processing. In all cases, organisms were identified to the lowest possible taxonomic group and total abundance, species richness, and relative species abundances recorded. The combination of these three different sampling methods provides a relatively robust measurement of overall macroinvertebrate community composition (Topping and Sunderland, 1992).

### *Data Analysis*

Treatment-specific differences in percent cover over time were evaluated with a Wilcoxon signed-rank test, with sampling date and treatment as nominal predictors and percent cover as the ordinal response variable. Mean percent cover at the end of the experiment (based on mid-class values) was compared with a general linear model that included block as a random nuisance factor and treatment as a fixed main effect. Plant attributes (species richness, canopy complexity, and mean and maximum height) were tested with the same model. Abiotic factors (light, temperature, and salinity) and macroinvertebrate abundances and species richness (pitfalls, infauna, and canopy insects) were tested with a general linear model that included block as a random nuisance factor,

sampling date and treatment as fixed main effects, and their interaction. Visual inspection of model residuals was done for every analysis. Where variances showed significant heterogeneity or departures from normality were detected, data were transformed with a  $\ln(x + 1)$  function (Sokal and Rohlf 2011). Tukey's HSD post hoc tests were used to identify differences among appropriate means when the main test was statistically significant at the  $\alpha = 0.05$  level. All univariate statistical analyses were done with Minitab 16 software (Minitab, Inc., State College, PA).

Hypotheses about multivariate differences in macroinvertebrate community structure as a function of sampling date and treatment were tested with rank-based two-way analysis of similarity (ANOSIM; 9999 random permutations). Abundance data were transformed with a  $\sqrt{x}$  function prior to analysis to increase the relative contribution of rarer species to Bray-Curtis similarity coefficients (Clarke 1993). Non-metric multidimensional scaling (MDS) ordinations were used to visualize variation in macroinvertebrate assemblages (Field et al. 1982). All multivariate statistical analyses were done with PRIMER v6 software (PRIMER-E, Ltd., Plymouth, UK).

### Results

Total plant cover increased through time, with monocultures initially increasing faster than polycultures (Wilcoxon signed-rank test;  $N = 11$ ,  $W = 66$ ,  $P = 0.004$ ); however, by the end of the experiment both treatment groups had reached 80–100% cover, and there was no significant difference between them (Table 1A; Fig. 1). The increase in plant cover in experimental plots was associated with significant decreases in % light reaching the ground, soil temperature, and soil salinity (Table 1F-H; Fig. 2). There was no evidence that effects of plant cover on abiotic conditions differed between treatments (all  $P > 0.05$ ).

By the end of the experiment, the species composition of plots that were initially monocultures of *S. pacifica* was essentially unchanged, with plant cover comprised almost exclusively of pickleweed (Fig. 3). In contrast, although the % contribution of *S. pacifica* to plot totals typically increased from the initial value, polyculture plots were otherwise characterized by a relatively even mix of many plant species (Fig. 3). There was substantial variation among polyculture plots with respect to final species composition, such that spatial variation in plant community structure was greater than it might appear from just looking at pooled data. Treatment-specific differences in plant community structure resulted in significant differences in plant attributes as well. Plant species richness and canopy complexity were significantly higher in polyculture versus monoculture plots by the end of the experiment and mean plant height was lower; maximum plant height did not differ by treatment (Table 1B-E; Fig. 4).

The observed increase in plant cover over time and associated changes in abiotic conditions were accompanied by significant increases in the abundances and richness of mobile ground-dwelling fauna, benthic infauna, and canopy insects (Table 1I-N; Fig. 5). There was no evidence of treatment effects or interactions between treatment and sampling date (all  $P > 0.05$ ). Similarly, multivariate analyses of macroinvertebrate community structure demonstrated significant differences among sampling dates (ANOSIM; pitfalls:  $R = 0.44$ ,  $P = 0.001$ ; infauna:  $R = 0.07$ ,  $P = 0.004$ ; canopy insects:  $R = 0.70$ ,  $P = 0.001$ ), but no difference between monoculture versus polyculture plots (pitfalls:  $R = -0.02$ ,  $P = 0.681$ ; infauna:  $R = -0.04$ ,  $P = 0.990$ ; canopy insects:  $R = -0.01$ ,  $P = 0.563$ ). These conclusions are supported by MDS plots that show overlapping macroinvertebrate assemblages between treatments but clear differences among assemblages across sampling dates (Fig. 6).

Table 1. Tests of multiple response variables (A–N) in experimental monoculture versus 9-species polyculture plots over time (see text for details of experimental design). Bolded *P* values are significant at the 0.05 level.

Plant attributes										
		(A) % cover			(B) Plant richness			(C) Canopy complexity		
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<b>Block</b>	9	97.8	0.79	0.637	1.3	2.03	0.152	0.3	2.11	0.141
<b>Treatment</b>	1	80.0	0.64	0.443	115.2	178.76	<b>&lt;0.001</b>	2.4	16.07	<b>0.003</b>
<b>Residual</b>	9	124.4			0.6			0.1		
	df	(D) Mean height			(E) Maximum height					
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>			
<b>Block</b>	9	105.5	1.61	0.257	214.4	0.81	0.625			
<b>Treatment</b>	1	612.5	9.33	<b>0.016</b>	0.5	0.00	0.966			
<b>Residual</b>	9	65.6			265.9					
Abiotic factors										
		(F) % light			(G) Soil temperature			(H) Soil salinity		
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<b>Block</b>	9	662.9	2.17	0.032	23.9	3.17	0.003	774.9	2.14	0.036
<b>Date</b>	4	17242.2	56.56	<b>&lt;0.001</b>	1461.9	193.99	<b>&lt;0.001</b>	11198.3	30.89	<b>&lt;0.001</b>
<b>Treatment</b>	1	83.4	0.27	0.602	27.0	3.59	0.062	52.2	0.14	0.705
<b>Date x Trt</b>	4	629.0	2.06	0.093	7.1	0.94	0.445	132.9	0.37	0.832
<b>Residual</b>	81	304.9			7.5			362.5		
Macroinvertebrates										
		(I) Pitfalls abundance			(J) Infauna abundance			(K) Insect abundance		
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<b>Block</b>	9	2.3	2.64	0.012	0.9	1.01	0.444	0.6	1.91	0.096
<b>Date</b>	3	26.8	31.14	<b>&lt;0.001</b>	5.0	5.74	<b>0.002</b>	25.4	86.17	<b>&lt;0.001</b>
<b>Treatment</b>	1	3.4	3.93	0.052	0.2	0.18	0.675	1.1	3.84	0.061
<b>Date x Trt</b>	3	0.9	1.09	0.360	0.1	0.15	0.929	0.0	0.01	0.930
<b>Residual</b>	63	0.9			0.9			0.3		
	df	(L) Pitfalls richness			(M) Infauna richness			(N) Insect richness		
	df	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>	MS	<i>F</i>	<i>P</i>
<b>Block</b>	9	1.8	1.50	0.169	1.3	0.90	0.528	29.5	3.36	0.007
<b>Date</b>	3	26.3	21.87	<b>&lt;0.001</b>	7.4	5.15	<b>0.003</b>	1478.3	168.05	<b>&lt;0.001</b>
<b>Treatment</b>	1	0.5	0.37	0.543	0.3	0.22	0.644	3.3	0.37	0.548
<b>Date x Trt</b>	3	0.2	0.15	0.928	0.1	0.08	0.972	0.0	0.00	0.985
<b>Residual</b>	63	1.20			1.45			8.80		

Notes: df = degrees of freedom, MS = mean square, *F* = *F* ratio, *P* = *P* value.

### Discussion

Our data suggest that polyculture plots performed as well as, or better than, *S. pacifica* alone with respect to multiple indicators of ecosystem structure and function. Although monocultures did increase in total percent plant cover faster than polycultures, both treatments had reached 80–100% cover after one year, easily exceeding the permit-mandated target of 20–40% cover in that time. As the polycultures eventually achieved

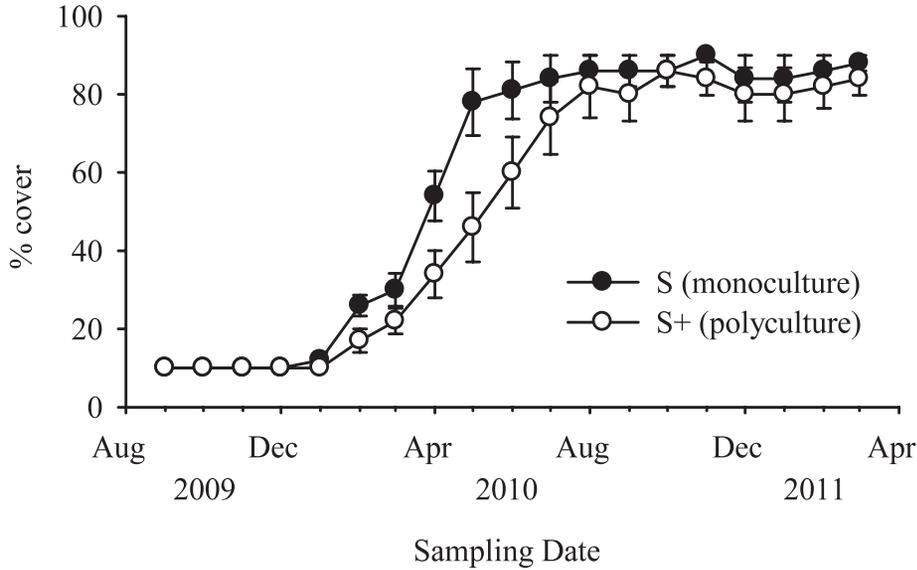


Fig. 1. Mean  $\pm$  SE percent plant cover over time in experimental plots as a function of original plant species diversity (S, monoculture (*black circles*); S+, 9-species polyculture (*white circles*)).

equivalent percent cover to monoculture plantings of the local competitive dominant, our data address landowner concerns that high plant species diversity and high percent cover are incompatible management goals.

The effects of increasing plant cover on abiotic parameters (e.g., % light reaching the ground, soil temperature, and soil salinity) were comparable between the two treatments, resulting in the rapid amelioration of harsh environmental conditions present on the berm prior to planting. This pattern is consistent with restoration trajectories observed in other vegetated marsh ecosystems (Nomann and Pennings 1998; Bortolus et al. 2002; Whitcraft and Levin 2007). Habitat amelioration such as shading and decreased soil evaporation due to the presence of neighbors has been shown to have positive effects in polycultures relative to monocultures, where mortality is often higher due to increased intra-specific competition among individuals (Callaway 1995; Hacker and Bertness 1996; Callaway and Pugnaire 2007). Nevertheless, we found few mortality differences between treatments. This discrepancy is likely because we used only a single high-performing species in monoculture. Presumably, if we had instead assessed many different species, each in monoculture, the average performance of plants in monocultures would be lower than the average in polycultures (Callaway et al. 2003; Stachowicz et al. 2007).

Although previous research has evaluated relationships between plant species diversity and attributes such as percent cover, height, and canopy complexity (Keer and Zedler 2002; Doherty et al. 2011), our study also addressed the concurrent development of macroinvertebrate communities which few studies have experimentally investigated. Within 12–18 months post-restoration, monoculture and polyculture plots provided physical conditions and food resources sufficient to support similar assemblages of macroinvertebrates. At the end of the experiment in March 2011 (six months after regular watering was stopped), the plants in many of the plots were noticeably drier than on previous sampling dates (e.g., *S. pacifica* exhibited redder tips or had turned brown in some plots). This change may explain observed decreases in some components of the

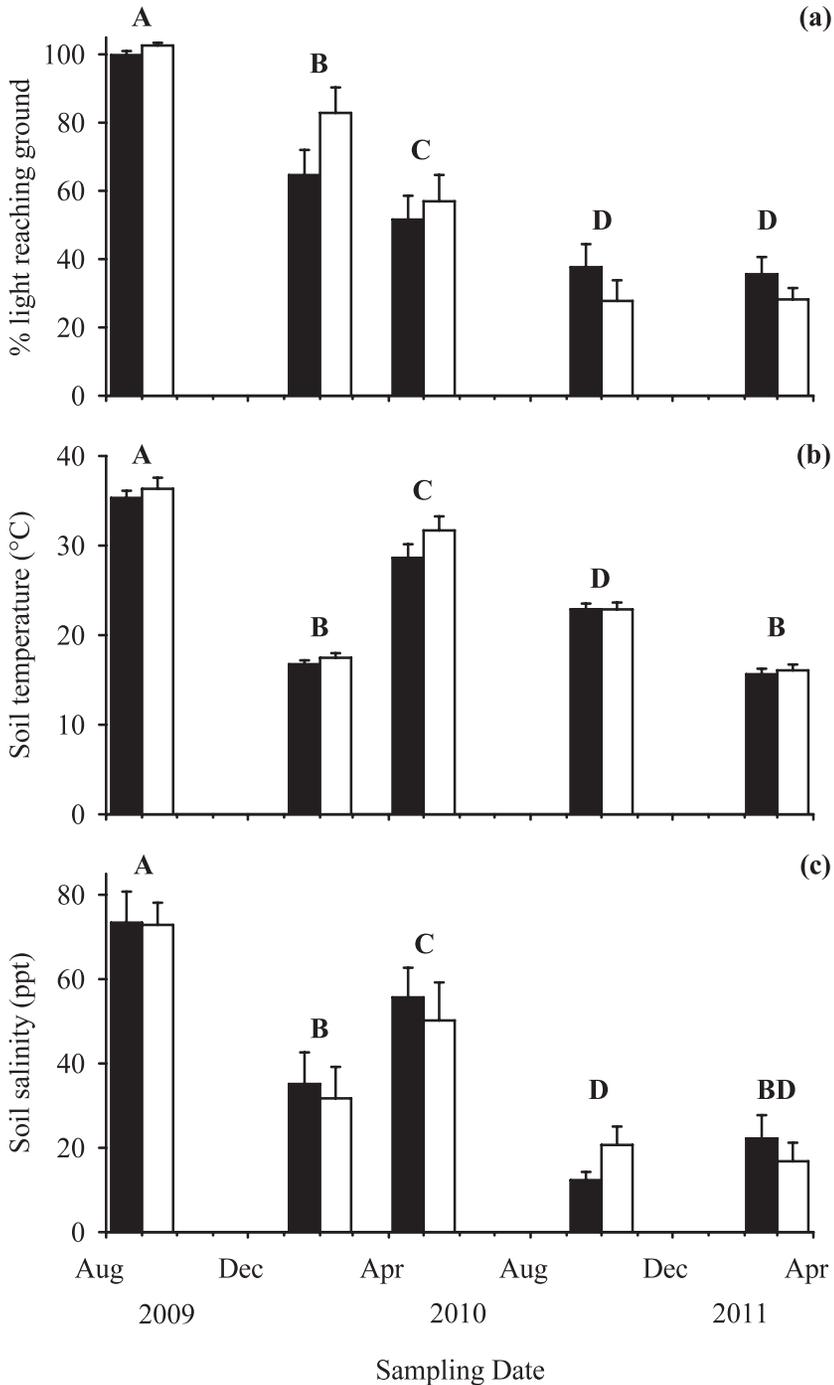


Fig. 2. Mean  $\pm$  SE abiotic conditions over time in experimental plots as a function of original plant species diversity (S, monoculture (black bars); S+, 9-species polyculture (white bars)): % light reaching the ground (a), soil temperature (b), and soil salinity (c). Plots were sampled in September 2009, February 2010, May 2010, October 2010, and March 2011. Different letters indicate statistically significant differences among sampling dates at the  $\alpha = 0.05$  level with Tukey's HSD test. There were no significant differences among treatments (all  $P > 0.05$ ).

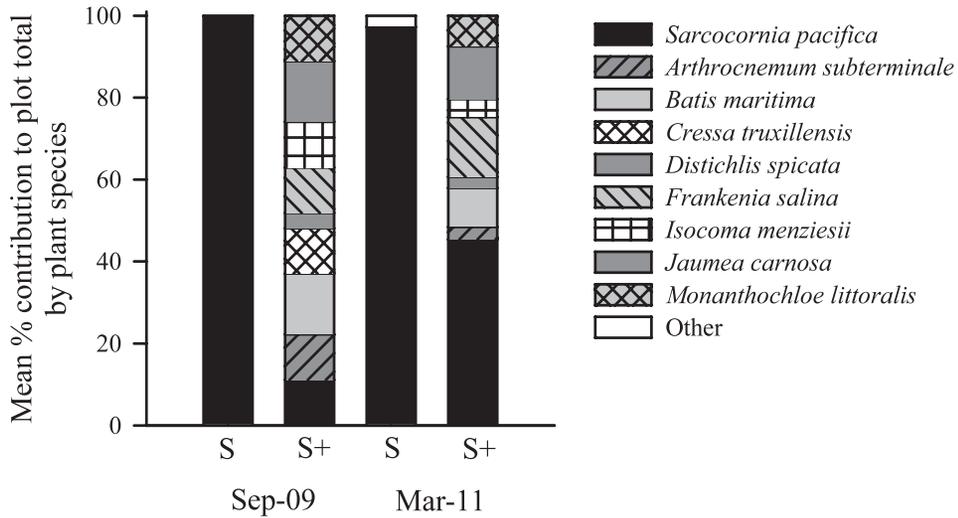


Fig. 3. Mean percent contribution to plot total by plant species in September 2009 (number of individuals) and March 2011 (percent cover) as a function of original plant species diversity (S, monoculture; S+, 9-species polyculture). The 'Other' category refers to plant species not originally planted and includes plant of both native and non-native status.

macroinvertebrate communities relative to October 2010. This research can facilitate understanding of the sequential consequences of changing salt marsh plant cover for higher trophic levels, including rapid development of trophic support for fish and birds and contribution of primary production from the marsh to secondary production in deeper water (Minello et al. 2003).

There were no substantive changes in species composition within treatment plots over the course of the experiment. Plots that were initially monocultures of *S. pacifica* had plant cover comprised almost exclusively of pickleweed 18 months later. Other studies have shown that dense stands of perennial dominants can suppress recruitment of less competitive species, hindering development of a diverse salt marsh plant assemblage (Bertness et al. 1992; Zedler and West 2008). In contrast, mean plant species richness in this study remained high in polyculture plots. Persistent differences in plant species diversity resulted in characteristic differences in canopy complexity and mean (but not maximum) plant height in monocultures versus polycultures. Keer and Zedler (2002) reported similar patterns in both an observational field study and manipulative experiments in the field and greenhouse. The physical arrangement of vegetation is an important determinant of the degree to which plants provide important functions to other species. For example, canopy complexity is correlated with bird species diversity (MacArthur and MacArthur 1961; Karr and Roth 1971), predator foraging efficiency (Crowder and Cooper 1982), and local retention of plant propagules (Peterson and Bell 2012). Plant canopy height can determine the suitability of restored habitat for use by nesting birds (Zedler 1993).

Current theory suggests that communities with many species that perform a given function in a similar way but have different sensitivities to abiotic conditions will exhibit greater temporal stability of ecosystem properties (Hooper et al. 2005). In addition to influencing resistance to environmental perturbations, species diversity has been linked to a variety of ecosystem properties that include primary productivity (Hacker and Bertness 1994; Tilman et al. 1997), nutrient accumulation rates (Sullivan et al. 2007), community

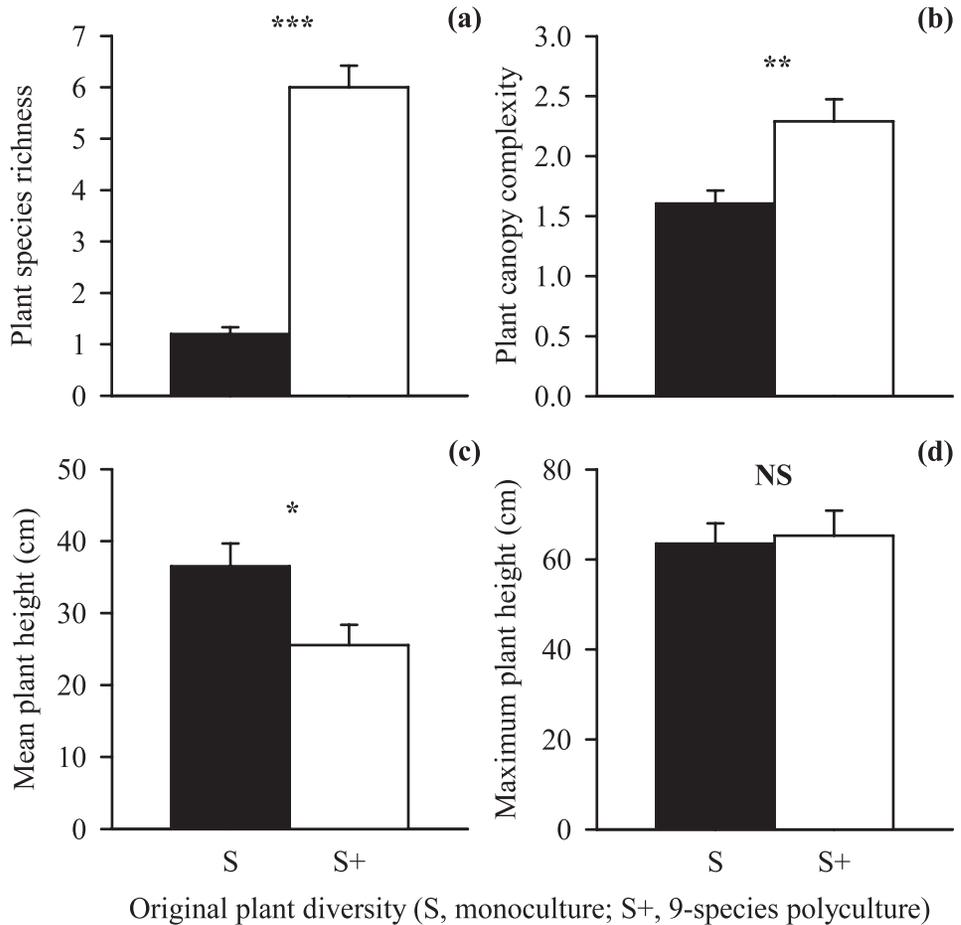


Fig. 4. Mean  $\pm$  SE plant traits in experimental plots in March 2011 as a function of original plant species diversity (S, monoculture (black bars); S+, 9-species polyculture (white bars)): species richness (a), canopy complexity (b), mean plant height (c), and maximum plant height (d). Statistically significant differences among treatment groups are indicated as: \*\*\* ( $P < 0.001$ ), \*\* ( $P < 0.01$ ); \* ( $P < 0.05$ ), or NS (not significant).

invasibility (Stachowicz et al. 1999; Naeem et al. 2000), and habitat provision. Many of these relationships are likely mediated by the functional traits of the species involved, both “response traits” that determine how a species responds to a change in environmental conditions and “effect traits” that determine how that species affects ecosystem properties (Hooper et al. 2005; Bonin and Zedler 2008; Funk et al. 2008). Using habitat provision as a relevant example in this study, the state-listed endangered Belding’s Savannah Sparrow uses tall, dense vegetation in the high marsh zone for nesting, perching during territory defense, and as a supplemental food source (Massey 1979; Zembal 1986; Powell and Collier 1998). Although *S. pacifica* is their preferred habitat, they will also nest in *D. spicata*, *F. salina*, and *B. maritima* (Powell 1993). So-called functional redundancy should lead to compensation among species, as some will do better when others do worse in response to environmental variability, due to different tolerances or competitive release. The marsh plant species used by Belding’s Savannah

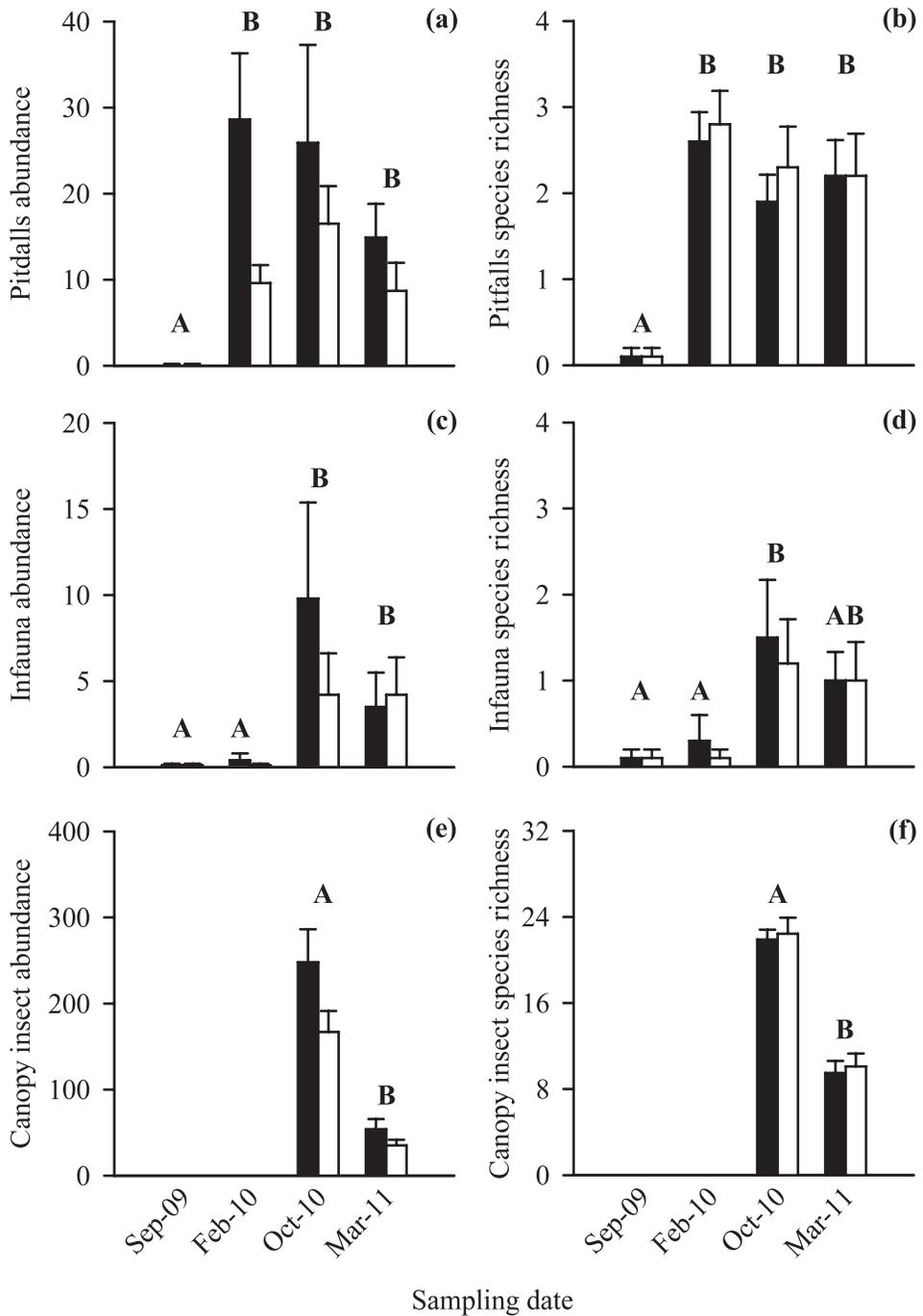


Fig. 5. Mean  $\pm$  SE invertebrate abundances (a, c, e) and species richness (b, d, f) over time in experimental plots as a function of original plant species diversity (S, monoculture (*black bars*); S+, 9-species polyculture (*white bars*)): pitfalls (a, b), infauna (c, d), and canopy insects (e, f). Different letters indicate statistically significant differences among sampling dates at the  $\alpha = 0.05$  level with Tukey's HSD test. There were no significant effects of treatment or interactions (all  $P > 0.05$ ).

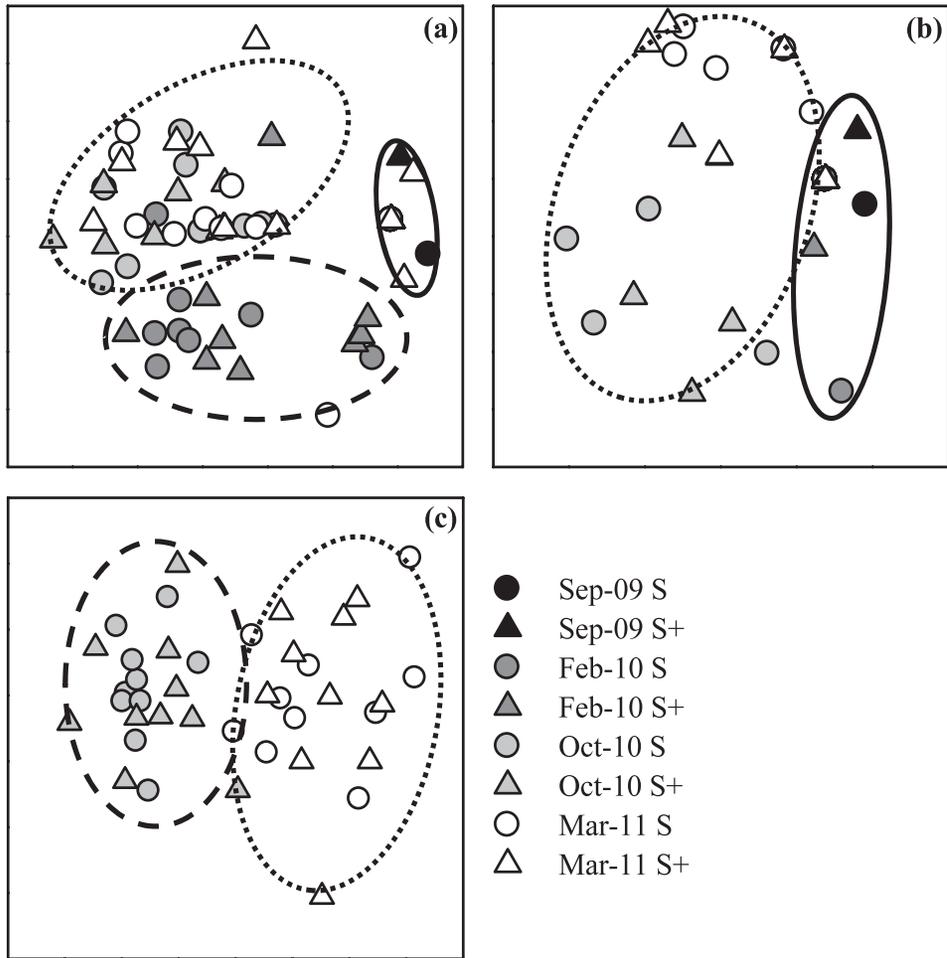


Fig. 6. Two-dimensional nMDS ordination plots of invertebrate community structure over time in experimental plots as a function of original plant species diversity (S, monoculture (*circles*); S+, 9-species polyculture (*triangles*)): pitfalls (a), infauna (b), and canopy insects (c). Ellipses drawn on graphs illustrate groups that were statistically significantly different at the  $\alpha = 0.05$  level with ANOSIM tests.

Sparrows have been shown to respond differently to varying environmental stresses (e.g., high salinity, drought, or long-term inundation; Zedler and Nordby 1986), such that plantings with all species present should provide habitat for birds across a wider range of conditions than plantings limited to just *S. pacifica*.

In general, increasing species diversity is expected to result in increasing functional trait diversity, although the strength and shape of the relationship between taxonomic and functional diversity are poorly known for most systems (Hooper et al. 2005; Micheli and Halpern 2005). Diverse ecosystems that have multiple species performing similar roles should be relatively insensitive to species loss (at least initially) due to redundancy. Inherently low diversity systems like southern California salt marshes, however, may be much more vulnerable to the loss of even a few species. Inclusion of functional diversity and redundancy in restoration projects should therefore increase resilience to future climate change, facilitating the adaptation of local salt marshes to predicted alterations in

temperature and precipitation levels. As a consequence, maximizing plant species diversity should be a key restoration goal to promote long-term persistence of critical ecosystem processes. More studies involving active restoration would help to determine the best plant species to utilize in a planting palette and thus aid in establishing planting protocols. Based on our results, active planting of high-diversity plots should be considered as a restoration tool to achieve management goals and speed functional recovery in southern California salt marshes.

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