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Can conservation biologists rely on established community structure rules to manage novel systems? . . . Not in salt marshes

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Abstract. We experimentally examined plant zonation in a previously unstudied Chilean salt marsh system to test the generality of mechanisms generating zonation of plants across intertidal stress gradients. Vertical zonation in this system is striking. The low-lying clonal succulent, *Sarcocornia fruticosa*, dominates the daily flooded low marsh, while intermediate elevations are dominated by the much taller *Spartina densiflora*. Irregularly flooded higher elevations are dominated by *Schoenoplectus californicus*, with the small forb, *Selliera radicans*, found associated with *Schoenoplectus* at its base. Transplant studies of all four species into each zone both with and without competition revealed the mechanisms driving these striking patterns in plant segregation.

In the regularly flooded low marsh, *Sarcocornia* and *Spartina* grow in the zone that they normally dominate and are displaced when reciprocally transplanted between zones with neighbors, but without neighbors they grow well in each other's zone. Thus, interspecific competition alone generates low marsh zonation as in some mediterranean marshes, but differently than most of the Californian marshes where physical stress is the dominant factor. In contrast, mechanisms generating high marsh patterns are similar to New England marshes. *Schoenoplectus* dies when transplanted to lower elevations with or without neighbors and thus is limited from the low marsh by physical stress, while *Selliera* grows best associated with *Schoenoplectus,* which shades and ameliorates potentially limiting desiccation stress.

These results reveal that mechanisms driving community organization across environmental stress gradients, while generally similar among systems, cannot be directly extrapolated to unstudied systems. This finding has important implications for ecosystem conservation because it suggests that the mechanistic understanding of pattern generation necessary to manage and restore specific communities in novel habitats cannot rely exclusively on results from similar systems, and it identifies a critical role for experimental ecology in the management and conservation of natural systems and the services they provide.

Key words: Chile; competition; physical stress; plant zonation; salt marshes; Sarcocornia fruticosa; Schoenoplectus californicus; Selliera radicans; Spartina densiflora.

INTRODUCTION

One of the basic goals of ecology is to understand the processes that generate the distribution of organisms in natural communities. To elucidate mechanisms responsible for generating organism distribution and abundance patterns, ecologists have long been attracted to studying the distribution of organisms across physical gradients. The zonation of organisms along steep physical gradients is often striking, making describing patterns and testing their causation relatively straightforward. While early work on zonation patterns was descriptive (Stephenson and Stephenson 1949, Whitaker 1975), experimental studies have identified the physical and biological mechanisms that generate zonation patterns (Connell 1961, Paine 1966, Bertness and Ellison 1987). Mechanistic studies of the causes of zonation patterns can lead to simple assembly rules for natural communities and an understanding of pattern generation in natural assemblages. On rocky shores, for example, the upper borders of most species with a marine ancestry are set by harsh physical conditions, while biological processes such as interspecific competition (Connell 1961) and predation (Paine 1974) set lower borders.

Appreciation of the physical and biotic processes responsible for the distribution of organisms across environmental gradients was initially a question of interest for the conceptual development of ecology (e.g., Whitaker 1975), but has become critical for the conservation and restoration of natural ecosystems. For example, work in New England has revealed that the elevation zonation of plants across salt marsh landscapes is driven by nutrient competition and that when nutrients are experimentally added, nutrient competition is relaxed and competition for light becomes the main

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determinant of plant zonation pattern (Levine et al. 1998, Emery et al. 2001). This mechanistic understanding of New England marsh plant zonation led to: (1) specific predictions of how shoreline development and eutrophication would impact marsh vegetation patterns, (2) the discovery that shoreline development and eutrophication were already strongly impacting new England salt marsh vegetation patterns, and (3) simple, but effective marsh conservation strategies to abate this eutrophication threat (Silliman and Bertness 2002, Bertness et al. 2004). Without a mechanistic understanding of the processes that generate pattern in natural communities, ecologists are generally unable to confidently predict how human impacts will affect communities and detect whether or not they are occurring. Managers are then left to rely on educated guess work to form the basis of conservation decisions and actions.

An important question for both ecologists and conservation biologists is whether the mechanisms generating spatial patterns in communities can be generalized among community types. If mechanisms generating pattern can be generalized, ecology can become a rigorous predictive science that can contribute to and inform conservation biology in the management and restoration of natural systems. If the mechanisms generating structure in different natural communities are idiosyncratic and cannot be generalized among communities, ecology cannot contribute as much to conservation biology and the management and restoration of natural systems. Our best chance to begin to understand community organization well enough to generalize the results of experimental studies and extrapolate assembly rules to unstudied systems is in well-studied, simple systems like rocky intertidal or salt marsh systems.

Salt marshes are ecologically important systems that develop on wave-protected shorelines in temperate zone habitats worldwide. They are biogenic ecosystems that are built, engineered, and maintained by the halophytic plants that colonize shorelines and accrete and stabilize sediment. Salt marshes are a common intertidal ecosystem on soft sediment shorelines in both North America and Europe, and play a particularly important role in the ecology of nearshore ecosystems as nursery grounds for fish and invertebrates and are important for the functioning of coastal systems as buffers from erosion and storm damage and biochemical filters of terrestrial runoff entering shallow water systems. Salt marshes are of considerable conservation concern because historically they have been ditched, drained, and filled for mosquito control and shoreline development (Bromberg and Bertness 2005).

The vertical zonation of halophytic plants across salt marsh landscapes is often striking and has long attracted the attention of ecologists (Clements et al. 1926). Salt marshes are physically stressful habitats for vascular plants. The waterlogged soils in salt marshes can be anoxic, limiting the distribution of plants that do not have structural or metabolic mechanisms of dealing with anoxic conditions (Mendelssohn et al. 1981). Salt marsh soils can also be highly saline, limiting plants that do not have mechanisms to deal with the osmotic stress of hypersaline soils (Pennings and Callaway 1992). Salt marsh communities are also commonly saturated with plants so that space is limiting, often leading to interspecific plant competition playing a leading role in the segregation of plant species across salt marsh landscapes. The mechanisms generating vertical plant zonation in salt marshes have been studied in a variety of systems. In New England (Bertness 1991*a*, *b*, Ewanchuk and Bertness 2003), Georgia (Pennings et al. 2005), and England (Castellanos et al. 1994, Castillo et al. 2000), experimental studies have found that in general the lower intertidal distribution of plant species is set by physical stress, while the upper intertidal distribution of plant species is set by interspecific plant competition. The physical stress generating this pattern is waterlogged anoxic soils, which increases with decreasing marsh elevation and increased regular tidal inundation. At higher elevations, salt accumulation driven by evaporative water loss from surface sediments exposed to solar radiation and wind can also limit the distribution of salt-sensitive plants. This leads to positive interactions between high marsh plants driven by neighbors shading marsh soil and reducing soil salinities (Bertness and Hacker 1994).

Experimental studies in the mediterranean salt marshes of California reveal different mechanisms underlying plant community organization. In these lower latitude marshes, increased physical stress due to hypersaline soils limits the success of the plants that dominate lower intertidal elevations at higher elevations, while increased physical stress due to soil anoxia at lower elevations limits the success of the plants that dominate higher elevations at lower elevations (Pennings and Callaway 1992). All of the dominant plant species in these California salt marsh systems, however, are capable of living across a wide range of marsh elevations, leading to fuzzy elevational zonation borders (see Zedler et al. 1999 for discussion and review) and interspecific competition potentially setting both the lower elevation limit of high marsh species and the high elevation limit of low marsh species (Pennings and Callaway 1992). The positive interspecific plant interactions driven by soil salinity amelioration found in New England salt marshes also occur in California marshes (Pennings et al. 2003). Brazilian salt marshes have also been studied and do not show strong plant zonation because tidal inundation is unpredictable and driven by wind rather that tides leading to a diffuse elevation gradient in physical stress and intense crab herbivory, which leads to space not being limiting (Costa et al. 2003). Thus, studies to date have suggested that marsh systems in different climates and tidal regimes have variable assembly rules and will require different management and conservation strategies. In this paper we test the generality of these results

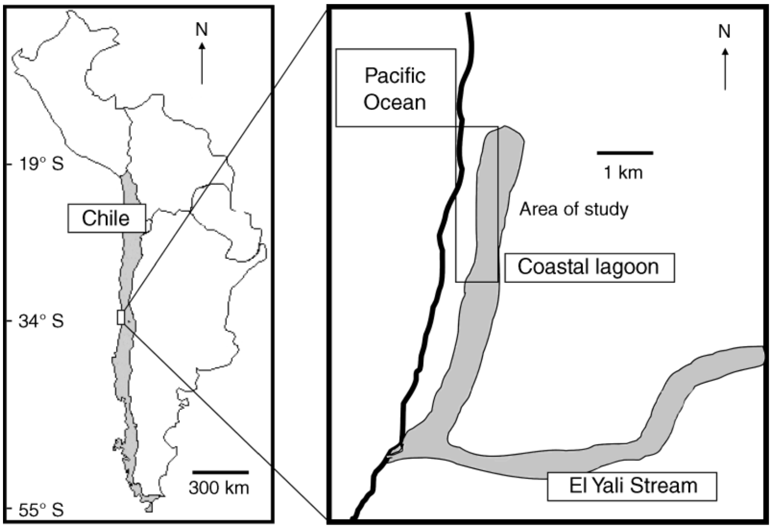

FIG. 1. Map showing the study site in the coastal region of central Chile.

by examining a previously unstudied marsh system on the Pacific coast of South America.

On most of the Pacific coast of southern South America the steep topography (rocky shores with cliffs 40–200 m high) restricts the presence of salt marshes to the mouths of rivers and bays (West 1981, Bujalesky et al. 2001). Because of the absence of rain in the desert areas of southern Perú and northern Chile (6° S to 28° S), some of the rivers that reach the sea have sand barriers blocking direct entry into the ocean that open only occasionally. High evaporation induces hypersaline conditions in the surrounding deltaic soils. Low intertidal habitats in these environments are dominated by *Sarcocornia* and by *Distichlis spicata* and occasionally *Schoenoplectus californicus* at higher elevations (San Martin et al. 2001, Arana and Salinas 2003). Below 28° S rainfall increases and *Spartina densiflora* abundance increases, whereas *Sarcocornia fruticosa* decreases (Ramírez and Añazco 1982, San Martin et al. 1992, Hauenstein et al. 2002). Less saline marshes tend to be occupied by *Juncus acutus*, *Typha angustifolia*, and the South African invader *Cotula coronopifolia* (San Martin et al. 1992, 2001). As in Brazilian salt marshes, water level fluctuations in most Chilean salt marshes do not depend primarily on tides, but on wind and storms. Unlike salt marshes on the Atlantic coast of South America, marine invertebrates are practically absent in Chilean salt marshes (J. M. Fariña, *personal observation*). Chilean salt marshes have been described in the literature (Ramírez and Añazco 1982), but to date no experimental studies have examined the mechanisms generating plant zonation in these systems.

In this paper we experimentally examine plant zonation in a central Chilean salt marsh system, a system weakly affected by tidal fluctuations and lacking obvious marine consumers. Because Chilean marshes have not been previously studied, we used them to test the generality of previous salt marsh zonation studies as well as to develop the mechanistic understanding of Chilean salt marshes necessary for their management and conservation. Based on previous work in Californian marshes with a similar mediterranean climate, we hypothesized that the mechanisms driving marsh zonation in central Chile would be similar to what had previously been found in California.

METHODS

Study site

The study was carried out at the "La Albufera" lagoon (94 ha), a brackish coastal lagoon in the "El Yali" National Reserve (33°50′ S, 71°38′ W). The study site is in the mediterranean region of Chile (Fig. 1) and has warm (11.9–20.1°C), dry summers (7.2–34.0 mm of precipitation) and cold (6.6–8.9°C), rainy (173.9–255.3 mm of precipitation) winters. The rainy season usually occurs from May to September, but the rest of the year experiences drought or near drought conditions (Di Castri and Hayek 1976). Mean annual rainfall during the last decade was 371 mm with a range of 127–852 mm, while mean annual temperature was 13.2°C (Di Castri and Hayek 1976, Vilina et al. 2002). Nearly 25% of Chilean bird species have been recorded at El Yali, and since 1996 the wetland has been declared a Ramsar site (under the Convention on Wetlands of International Importance especially as Waterfowl habitat; *available online*).[5] High interannual variation in precipitation at the site is due to the periodic occurrence of El Niño-Southern Oscillation (ENSO) events, which increase rainfall, modifying ocean salinity and the local biota (Vilina and Cofre 2000, Vilina et al. 2002).

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[5] ⟨http://www.ramsar.org/key_sitelist.htm⟩

Descriptive data

Plant zonation around the lagoon is conspicuously structured by three species: *Schoenoplectus californicus* var. *spoliatus*, *Spartina densiflora*, and *Sarcocornia fruticosa*. The bullrush *Schoenoplectus californicus* dominates the terrestrial border of the marsh (high marsh), an area flooded only during storm events. *Sarcocornia fruticosa* dominates the regularly (two or three times per week) flooded low zone, while *Spartina densiflora* dominates intermediate elevations, which are only flooded after heavy rains and storm events. A fourth species, the swamp weed *Selliera radicans*, is abundant on the seaward border of the high marsh, where *S. densiflora* and *S. californicus* meet, occurring mostly under the shade of these species. Because plant zonation is quite homogeneous around the lagoon and correlates with the flooding regime, the aerial extent of each specific zone was determined following the spatial representation of the flooding events assessed by a previous hydrological study of the site (Galdames 2006). We quantified plant zonation at the site by placing a transect line perpendicular to the lagoon from the low to the high marsh. The transect was placed in the same area where a previous hydraulic study (Galdames 2006) had taken place, and we used this previous study to determine the aerial extent of the marsh vegetation zones based on a strong relationship between flooding and plant zones. Along the transect line, at three random dates between 2003 and 2006, plant cover was quantified at 54 permanent quadrats (1 m^2 each) placed at 1-m intervals. A distance of 180 m from the lagoon to the high marsh was covered, and survey results were generated by pooling data from the quadrats every 10 m (nine groups of five quadrats).

Edaphic data

To characterize soil physical characters the following edaphic physical variables were quantified at four random dates within each zone (low, mid, and high) from July 2003 to July 2004: substrate redox was measured (three replicates per zone) with a redox electrode inserted directly into the substrate (Howes et al. 1981). Pore water salinity was measured (four replicates per zone) with a refractometer ($\pm 1\%$) using pore water collected in pore water sample tubes (Bertness and Ellison 1987). Substrate drainage was measured (three replicates per zone) with percolation tubes (Bertness 1985).

Redox measurements were taken with an untreated platinum disk fixed to the end of a reinforced glass tube with resin epoxy, connected to an Orion specific ion meter. The reference electrode was an Orion double junction Ag/AgCl (reference potential +242 mV). The platinum electrodes were inserted 10 cm into the surface and allowed to equilibrate for 15 minutes before recording. The electrodes were standardized with ZoBell's solution (0.003 mol/L potassium ferricyanide, 0.003 mol/L potassium ferrocyanide, and 0.1 mol/L potassium chlorine) with a Eh value of +430 mV at 25°C (Howes et al. 1981). Percolation rate measurements were made using an open-ended calibrated plastic cylinder (3 cm internal diameter × 30 cm long) firmly placed in the sediment (without compacting sediment inside or outside the cylinder) and filled with seawater. The volume of water draining into the substrate was then recorded at 10-minute intervals for one hour. All percolation tubes were placed on bare sediment devoid of grass shoots. For the same period of study, temperature on the marsh surface in both natural bare and plant-shaded areas in each zone was recorded, every 30 minutes, using temperature dataloggers (Onset Computer Corporation, Pocasset, Massachusetts, USA). Soil moisture content was assessed gravimetrically in the high, mid, and low marsh zones in June and September of 2004. For each zone, six samples of the first 15 cm of soil were taken to the laboratory, initially weighed, dried for 48 hours at 80°C until a constant mass was reached, and then reweighed. Water content was calculated as the difference between wet and dried soil samples. Edaphic data, i.e., redox, salinity, drainage, and soil humidity, from all dates were pooled and analyzed by one-way analysis of variance using marsh zone as main factor with three levels (low, mid, and high). For ground temperature the data were analyzed by a two-way analysis of variance considering zone and shading as factors with three and two levels, respectively. After each analysis a post hoc Tukey's hsd test was used to evaluate significant differences between levels. For all the statistical analyses, normality of the data was checked by graphical procedures and homogeneity of variances, and independence of the data was verified using Levene's and Durbin-Watson tests, respectively (Wilkinson et al. 1996). When appropriate (i.e., for salinity, drainage, and soil moisture), the data were log-transformed. In every case, results are reported using the original (i.e., non-transformed) variables.

Transplant experiments

To assess the performance of S. *californicus*, *S. densiflora*, *S. fruticosa*, and *S. radicans* out of their zones, with and without interspecific competition (neighbors) and with increased soil saturation conditions, in June of 2003, complete reciprocal transplants were established across all zones (see Bertness and Ellison 1987). Large (30 × 30 × 30 cm, length × width × depth) blocks of substrate + plants were excavated from monospecific stands of the three species and planted in identically sized holes in the three marsh zones (low, mid, and high). To assay performance with competition, blocks were transplanted into large (>100 m^2) natural patches of *S. fruticosa*, *S. densiflora*, and *S. californicus*, at low, mid, and high zones, respectively. To assay the performance without competitors, blocks were transplanted into artificially generated bare patches of 1.75 × 1.75 m in the three zones (*S. fruticosa*, *S. densiflora*, and *S. californicus*). Additionally, to assay plant perfor-

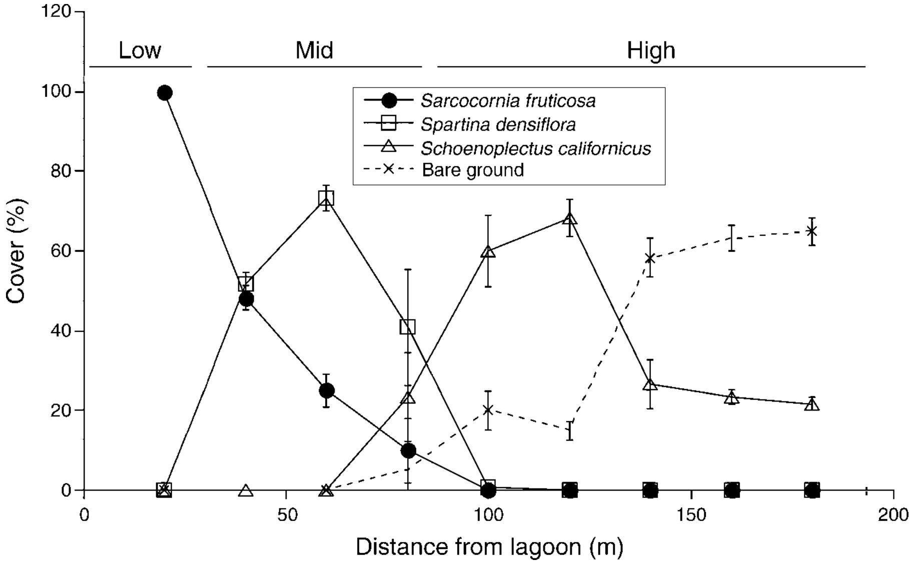

FIG. 2. Plant zonation pattern around the coastal lagoon showing variation in percent cover of the dominant species in relation to the low, mid, and high marsh zones.

mance without neighbors without the decreased soil humidity and increased soil salinity that accompanies plant removal in salt marshes (Bertness and Yeh 1994), blocks were also transplanted into artificial bare patches (1 × 1 m) covered by vinyl garden tarp to prevent regrowth of cleared plants and prevent salt buildup and soil drying. The use of tarps effectively prevents salt buildup due to evaporation (which was evident in the artificial bare patches after the first month of the experiment), but also inhibits the possible accumulation of salt in the upper soil layers as a consequence of the upward movement of saline water due to suction by plant roots. Tarp shading accurately mimics the natural shading of the canopy and leads to soil salinity and moisture levels similar to that found under natural canopies, in contrast to unvegetated bare areas that have higher salinities and lower moisture (Bertness 1991*a*, Bertness and Yeh 1994). In both bare and tarp-covered patches, neighbors were removed weekly by weeding. Each transplant treatment was replicated 12 times with all replicates separated by at least 2 m. Transplants were maintained for two growing seasons (June 2003–September 2004) and harvested for biomass at the end of the second year. Results for each transplant species were analyzed by two-way analysis of variance with marsh zone and treatment as main factors, with three levels (low, mid, and high and matrix, bare, and sheet). After each analysis, a post hoc Tukey's hsd test was used to evaluate significant differences between levels. Normality of the data was checked by graphical procedures and homogeneity of variances and independence of the data were verified using Levene's and Durbin-Watson tests, respectively (Wilkinson et al. 1996). When appropriate, the biomass data were log-transformed, and results are reported using the original (i.e., non-transformed) variables.

RESULTS

Transect surveys confirmed the striking plant zonation at El Yali marsh (Fig. 2). From the lagoon toward the terrestrial border, *S. fruticosa* dominates the first 20 m and, from 30 to 40 m, it is gradually replaced by *S. densiflora*. From 50 to 60 m, *S. densiflora* dominates and is then replaced by S. *californicus*, which dominates between 100 and 120 m. At the highest level of the marsh and the beginning of the sand dune ecosystem (~140 m from the lagoon), *S. californicus* appears at reduced cover and bare ground dominates.

Edaphic data

Most of the measured physical variables showed statistically significant differences between marsh zones (Table 1). From low to high marsh both substrate redox (Fig. 3A) and pore water salinity (Fig. 3B) increased sharply. Following a similar trend, substrate drainage showed a significant increase from low to the highest marsh (Fig. 3C). Mean ground temperature increased significantly from the low to the high marsh (Fig. 3D). Air temperature was always lower under plants in all three zones; however, the differences between bare and shaded patches were highest in the high marsh (Fig. 3D). Soil water content was highest in the low marsh and decreased significantly in the high marsh (Fig. 3E).

Transplant experiments

Sarcocornia fruticosa, the low zone dominant, showed a significant decrease in biomass from the low to the high zone (Table 2, Fig. 4A). However, within each zone, its biomass was significantly highest in tarp-

TABLE 1. Summary of ANOVA test for each physical variable measured on the different marsh zones in El Yali National Reserve, Chile.

Effect	df	MS	*F*	*P*
Redox				
Zone	2, 45	247 673	11.99	0.0003
Salinity				
Zone	2, 21	23.23	4315.7	2.2×10^{-16}
Drainage				
Zone	2, 33	16.53	302.59	2.2×10^{-16}
Temperature				
Zone	2, 16 518	329	6.61	0.00134
Shading	1, 16 518	14 674	295.02	2.2×10^{-16}
Zone × shading	2, 16 518	2949	29.64	1.4×10^{-13}
Soil humidity				
Zone	2, 15	0.3377	41.13	8.1×10^{-7}

covered treatments followed by no-neighbor treatments. Lowest biomasses were recorded for this species in with-neighbor treatments.

Spartina densiflora, the mid-zone dominant, showed the same trend as *S. fruticosa*, significantly decreasing from low to high zones (Table 2, Fig. 4B). Within the low and high zones, the highest biomasses were recorded in increased-humidity, tarp-covered treatments, followed by no-neighbor treatments and then by the with-neighbor treatments. In the mid zone, the highest biomass was recorded in the increased-humidity treatment, but with-neighbor and no-neighbor treatments showed no differences in *Spartina* biomass.

Transplants of the high zone dominant, *S. californicus* practically disappeared in the low zone regardless of treatment (Table 2, Fig. 4C). In the mid zone there were significantly lower values in the tarp-covered treatment, while in the high zone a significant reduction was observed in no-neighbor treatments.

Selliera radicans, the plant living under *S. densiflora* and *S. californicus* on the border between mid and high zones, practically disappeared in all the treatments in the low zone (Table 2, Fig. 4D). In the mid zones, the significantly highest biomasses were recorded in the tarp-covered, increased-humidity treatments, followed by the with-neighbor treatments. The no-neighbor and with-neighbor treatments of mid and high zones, respectively, showed similarly reduced biomass.

DISCUSSION

Our experiments show that interspecific biological interactions are largely responsible for the vertical zonation of salt marsh plant communities on the coast of Chile. At lower elevations, interspecific plant competition leads to plant species segregation, while at higher

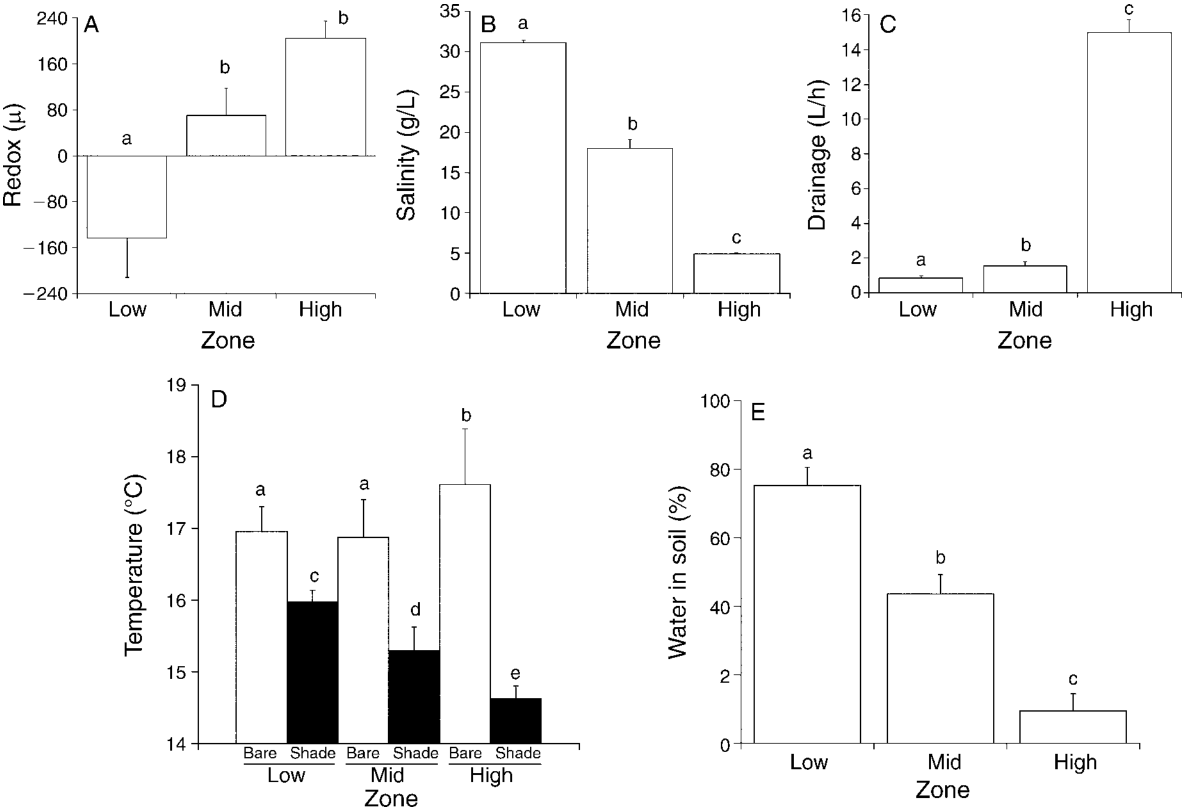

FIG. 3. Edaphic condition variation among marsh zones: (A) redox, (B) salinity, (C) drainage, (D) temperature, and (E) soil moisture. Significant differences ($P < 0.005$) are denoted by letters (a, b, or c), and each bar represents the mean and SE.

TABLE 2. Summary of ANOVA tests for the results of transplant experiments.

Species	SS	df	MS	*F*	*P*
Sarcocornia fruticosa					
Zone	19 394	2	9697	55.72	2.2×10^{-16}
Treatment	9114	2	4557	26.19	7.4×10^{-10}
Zone × treatment	3363	4	840	4.83	0.001
Error	17 229	99	174		
Spartina densiflora					
Zone	6710	2	3355	44.2	1.9×10^{-14}
Treatment	3256	2	1628	21.4	1.8×10^{-8}
Zone × treatment	3368	4	842	11.1	1.8×10^{-7}
Error	7518	99	76		
Schoenoplectus californicus					
Zone	4153	2	2076	50.4	7.8×10^{-16}
Treatment	95	2	47	1.2	0.03194
Zone × treatment	546	4	136	3.3	0.01358
Error	4076	99	41		
Selliera radicans					
Zone	104	2	52	21.11	2.3×10^{-8}
Treatment	17	2	8	3.5	0.033977
Zone × treatment	37	4	9	3.8	0.006376
Error	244	99	2		

elevations, interspecific plant facilitation leads to plant species associations. These patterns reveal that these systems, while similar to previously studied systems, have their own unique organization, likely due to differences in plant phylogeny, and point to the important role experimental ecology has in understanding and managing novel systems.

Chilean salt marsh zonation

All previous studies of Chilean salt marsh plant communities have been descriptive and have correlated the zonation and distribution of halophytic plants across marsh landscapes (Montero 1969, Donoso 1974, Dollenz 1977, 1979, Pisano 1977) with variation in edaphic factors such as soil oxygen, salinity, and nutrient levels (e.g., Schwaar 1978, Palma et al. 1987, Ramirez et al. 1988). The assumption that the correlation between marsh plant distributions and edaphic factors is causal was once also widely believed to be the case in North American and European salt marshes as well (e.g., Nixon 1982, Teal 1986). Experimental work in these systems (Vince and Snow 1984, Bertness and Ellison 1987, Pennings and Callaway 1992), however, led to the realization that biological factors played a major role in

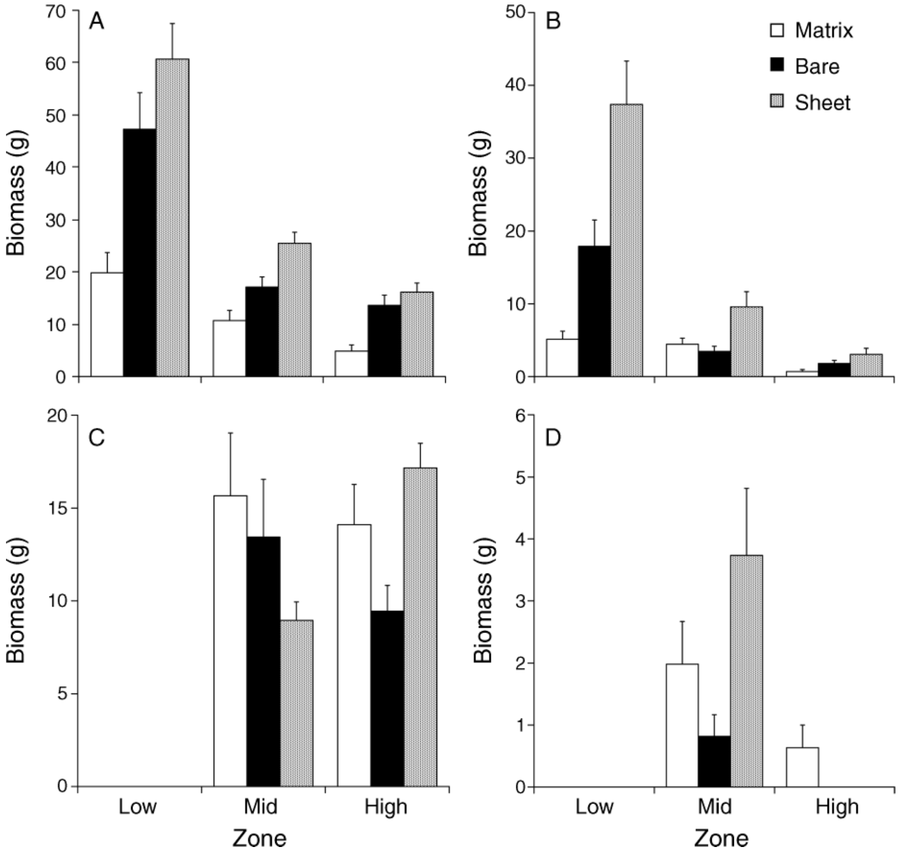

FIG. 4. Final biomass of the transplants of (A) *Sarcocornia fruticosa*, (B) *Spartina densiflora*, (C) *Schoenoplectus californicus*, and (D) *Seliera radicans* to low, mid, and high marsh areas under the different treatments: with neighbors (matrix), no neighbors (bare), and with increased humidity conditions (sheet) (each bar represents the mean and SE).

generating plant zonation in these salt marsh systems. The experimental results in this paper reveal that biological forces are also largely responsible for the plant zonation in Chilean salt marshes.

Chilean salt marshes are scarce, have restricted geographical distributions, and are not broadly known (West 1981). San Martin et al. (1992) described plant zonation in Chilean salt marshes and found patterns similar to those at El Yali and in good agreement with our description of edaphic conditions and vegetation in the low, middle, and high marsh zones. In contrast to previous studies in these systems that attributed plant zonation to spatial variation in edaphic conditions or human perturbations (associated with agricultural or livestock activities), however, our experimental results reveal that plant competition and facilitation are critical drivers of spatial patterning in these communities.

Schoenoplectus californicus dominates the highest Chilean marsh zone, but our transplant experiments show that both *S. densiflora* and *S. fruticosa*, that dominate lower elevations, could live under the physical conditions in the highest zone in the absence of neighbors. When *S. californicus* neighbors were present, however, both *S. fruticosa* and *S. densiflora* transplants did not survive in the highest marsh zone, demonstrating that *S. californicus* domination of the high zone is due to competition. Interspecific plant competition is also a strong driver of plant zonation at lower elevations in these marshes. *Spartina densiflora* dominates the middle marsh zone, but our transplant experiments reveal that *S. fruticosa* is able to live under the physical conditions of this zone in the absence of neighbors but is competitively eliminated when neighbors are present. Experimental transplants also demonstrate that *Sarcocornia fruticosa* dominates the low marsh by competitively excluding *S. densiflora* to higher elevations. While our results reveal that interspecific competition plays a major role in generating elevational zonation in this system, they also show that interspecific facilitation is critical in generating plant distributions in the high marsh. *Selliera radicans*, the numerically dominant forb in the system, lives in the high marsh only in association with interspecific neighbors due to habitat amelioration. Given that the most conspicuous differences in temperature between bare and shade patches were detected at high marsh zones, reduced desiccation and lower temperatures occurring between plants of *S. californicus* may allow the persistence of *S. radicans* at marsh higher elevations.

Our results reveal that the processes driving the zonation of Chilean salt marshes have similarities to both previously studied temperate zone and mediterranean salt marshes. Like the mediterranean marshes of California (Pennings and Callaway 1992), both *Sarcocornia fruticosa* and *Spartina densiflora*, that can dominate low and middle marsh elevations, respectively, are capable of living at all marsh elevations and can be competitively restricted to their respective zones. In contrast, like the northern temperate marshes of New England (Bertness and Ellison 1987), *Schoenoplectus californicus* is limited from low marsh elevations by physical stress, but competitively displaces the other zonal dominants (*Sarcocornia fruticosa* and *Spartina densiflora*) from the high marsh. In common with both north temperate and mediterranean marshes (Pennings and Callaway 1992, Bertness and Hacker 1994), the amelioration of potentially limiting physical stress at higher marsh elevations facilitates the presence of forbs in the high marsh associated with the zonal dominants. It is widely recognized that zonation patterns and their generating mechanisms vary widely in some regions. For example, some Californian marshes lack plants in their lower zone, in particular there is no *Spartina* sp. at lower zones, but in other Californian marshes, the Chilean marsh grass, *S. densiflora* has invaded and dominates mid-marsh elevations, as we have found in Chilean marsh. In this sense, the organization of Chilean marshes is a hybrid of mechanisms driving patterns in mediterranean and north temperate marshes, and the processes generating zonation in Chilean marshes could thus not have been predicted a priori based on previous studies.

From a historical South American perspective, the previous literature on Chilean and South American salt marshes (Dollenz 1979, Bujalesky et al. 2001, Hauenstein et al. 2002) suggests that physical forces determine species range limits in salt marshes and that biological interactions are unimportant. While our work was restricted to a single study site, it clearly demonstrates that, like well-studied Chilean rocky intertidal shores (Castilla 2000, Navarrete and Castilla 2003), marsh communities are also characterized by strong biological interactions determining species range limits and primary production. These results open a new perspective to develop future studies in the region and across the continent.

Salt marsh conservation message

One of the important questions in conservation biology is whether or not ecology can be a predictive science that can guide ecosystem management and conservation. If experimental ecology can successfully predict how unstudied systems are structured and will respond to disturbances, ecological theory can generally inform conservation biology. If, on the other hand, experimental ecology cannot predict how novel systems are structured and will respond to perturbations, ecological theory cannot be used to guide general conservation strategies.

Salt marshes are particularly valuable systems to explore the role of ecology in ecosystem conservation. Salt marshes are critically valuable coastal ecosystems because they provide important ecological and societal services, including serving as nursery grounds for marine species (Boesch and Turner 1984), coastal buffers from erosion and storm damage (Frey and Basan 1985), and chemical filters of terrestrial runoff (Todd and Todd 1994). They are also a serious conservation concern because humans have overexploited salt marshes since the beginning of human history (Lotze et al. 2006). Salt marshes are also relatively simple, low species diversity systems that are conducive to manipulative field experiments to elucidate the mechanisms driving the distribution and abundance of organisms and primary production patterns across marsh landscapes. As a result of the importance of salt marshes and their value as simple experimental systems, salt marshes could be an ideal model system for using an experimentally derived mechanistic understanding of salt marshes to predict the processes responsible for patterns generation in unstudied systems.

Our results, however, reveal that in spite of considerable previous research on salt marshes, the structure and dynamics of Chilean marsh systems could not be perfectly predicted from previous research. The structure and organization of Chilean marshes had striking similarities to both the cold temperate salt marshes of New England and the mediterranean marshes of California, but their structure and organization is a hybrid of that found in other systems. Thus, while experimental work in other systems can provide guidance for understanding novel systems and general "rules of thumb" for designing conservation strategies in unstudied systems, the organization and structure of novel systems can be too idiosyncratic to be entirely predicted from previous studies. This points to a clear and important role for experimental community ecology in management and conservation of novel systems. For successful conservation of coastal plant systems, managers should thus rely on an experimental understanding of community structure in their local systems and take caution when extrapolating from geographically distant, but well-understood communities.

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