

Biogeography of salt marsh plant zonation on the Pacific coast of South America

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Abstract

Aim: The aim of this study was to investigate the biogeography of plant zonation in salt marshes on the Pacific coast of South America; to examine whether salt marsh plant zonation varies with latitude; and to explore the relative importance of climatic, tidal, edaphic and disturbance factors in explaining large-scale variation in salt marsh plant community structure.

Location: A 2,000-km latitudinal gradient on the Pacific coast in Chile, with a climate shift from hyper-arid at low to hyper-humid at high latitudes.

Methods: Plant zonation was quantified in field surveys of ten marshes. Climate, tidal regimes, edaphic factors and disturbances (tsunami and rainfall floods) were determined. We used multivariate analyses to explore their relative importance in explaining large-scale variation in salt marsh plant community structure.

Results: Across latitude, marshes were dominated by distinct plant communities in different climate regions, especially at the extreme dry and wet latitudes. Intertidal plant species zonation was present in hyper-arid and semi-arid climates, but not in arid, humid and hyper-humid climates. Latitudinal variation in low-marsh plant communities (regularly flooded at high tide) was largely a function of precipitation, while at high marshes (never flooded at high tide) latitudinal variation was explained with precipitation, temperature, tidal cycles, soil salinity and disturbances.

Main conclusions: Salt marshes on the Pacific coast of South America belong to Dry Coast and Temperate biogeographic types. Salt marsh plant zonation varies across latitude, and is explained by climatic, tidal, edaphic and disturbance factors. These patterns appear to be mechanistically explained by extrapolating experimentally generated community assembly models and have implications for predicting responses to climate change.

KEYWORDS

Chile, climate and latitudinal gradients, community assembly, disturbance, South America, species zonation

1 | INTRODUCTION

Understanding the environmental predictors of large-scale patterns in natural communities is central to biogeography and macroecology (Cox & Moore, 2010; Gaston & Blackburn, 2000). While species ranges across climate and latitudinal gradients and their determinants

are a major focus of current studies, it is important to understand how local species distribution patterns vary geographically (Lee & Chun, 2016). Local species distribution patterns are striking in many ecosystems, such as plant zonation along tidal gradients in coastal wetlands (Crain, Silliman, Bertness, & Bertness, 2004; Cui, He, & An, 2011), sessile species zonation along wave exposure gradients on



rocky shores (Harley & Helmut, 2003), and tree zonation along elevational gradients (McCain & Grytnes, 2010; Ohsawa, 1995). These local species distribution patterns are likely to vary geographically as a function of climate, environmental history and large-scale terrestrial/oceanographic processes (Gaston, 2000). On the Pacific coast of North America, for example, the upper intertidal distribution of mussels (Mislán, Helmut, & Wetthey, 2014) and snails (Kuo & Sanford, 2009) is regulated by different environmental factors in different geographic regions. How species distribution patterns in other ecosystems vary geographically is poorly understood.

Coastal wetlands, such as salt marshes and mangroves, have long been a model system for studying plant distributions along intertidal gradients, due to their striking plant zonation along steep environmental stress gradients (Clements, Weaver, & Hanson, 1926). Studies from New England (Bertness, 1991a, 1991b) reveal that plant zonation in salt marshes are a result of interactions between physical stress and plant species interactions. Along marsh elevation gradients, physical stresses, such as sediment anoxia and salinity, decrease with increasing elevation. The lower limits of plants are thought to be determined by physical stress, while the upper limits of plants are determined by interspecific plant competition. This simple community assembly model has been tested in California (Pennings & Callaway, 1992), Spain (Castellanos, Figueroa, & Davy, 1994; Castillo, Fernandez-Baco, Castellanos, & Davy, 2000), Brazil (Costa, Marangoni, & Azevedo, 2003), China (He, Cui, Bertness, & An, 2012; He et al., 2009), Argentina (Alberti et al., 2010; Idaszkin & Bortolus, 2011; Idaszkin, Bortolus, & Bouza, 2011, 2014), and Chile (Farina, Silliman & Bertness, 2009).

An emerging hypothesis from these studies is that geographic variation in the mechanisms underlying salt marsh plant zonation is driven by variation in climate (Bertness & Pennings, 2000; Cui et al., 2011), tidal regime (Kunza & Pennings, 2008), and species adaptation (Sanford & Bertness, 2009). For example, low-latitude salt marshes may have steeper soil salinity and moisture gradients, with hotter climates leading to increased soil salinity at high-marsh elevations due to evaporative salt accumulation (Pennings, Selig, Houser, & Bertness, 2003). Elevation gradients in soil salinity and moisture are typically less pronounced in colder high-latitude marshes (Bertness & Pennings, 2000). This difference in environmental stress gradients could underlie variation in the determinant of the upper limits of plants between low- and high-latitude salt marshes (Cui et al., 2011; Pennings et al., 2003). Our current understanding of geographic variation in marsh plant zonation, however, is largely based on studies from single sites. Studies comparing marsh plant zonation across a latitudinal climate gradient are scarce.

In this study, we examine patterns and environmental predictors of plant zonation in salt marshes across a 2,000-km latitudinal gradient on the Pacific coast of Chile. Across this gradient, climate shifts from hyper-arid at low latitudes to hyper-humid at high latitudes (Amigo & Ramirez, 1998). In northern Chile, high evaporation and the lack of rain leave salt marshes dry and saline. In central Chile, rainfall is almost 300 mm/year, and coastal salt marshes have lower soil salinity. In southern Chile, precipitation is almost 2,000 mm/year, and the marshes are commonly wet and with low salinities (Fariña &

Camaño, 2012; Ramirez & Añazco, 1982). This continental climate gradient provides an opportunity to examine how plant zonation patterns vary geographically.

We quantified geographical variation in salt marsh plant zonation across this latitudinal gradient and key environmental factors. We hypothesized that: (1) marshes along this gradient are dominated by different plant species as climate varies; and (2) plant zonation is most conspicuous in low-latitude dry marshes with strong salinity gradients and weakens with increasing latitude in colder marshes where climate-driven salinity stress gradients are less pronounced. We used field surveys to quantify plant distribution patterns at ten marshes, and multivariate analyses to examine the relative importance of climatic, tidal, edaphic and disturbance factors in explaining large-scale variation in salt marsh plant community structure.

2 | MATERIALS AND METHODS

2.1 | Study sites

We worked at ten marshes (Figure 1, Table 1), which are among the main salt marshes in Chile that have not been severely modified by urbanization and agricultural activities. The Chilean coast is supported by a narrow oceanic platform that limits salt marshes to the mouths of rivers. These marsh sites' climate regions (hyper-arid, arid, semi-arid, humid and hyper-humid) were defined by Santibañez, Roa, and Santibañez (2006) using the ratio between annual precipitation-potential evapotranspiration (Pp/PET) and the number of degree-days (Thom, 1966), which also corresponded with regional characteristic vegetational formations (Luebert & Pliscoff, 2006).

Based on 5 years of field experience and interviews with fishermen, the sites can be characterized as follow: The two northernmost, hyper-arid sites—Salinas and Carrizal—are in coastal lagoons on the coast of the Atacama Desert. The Salinas salt marsh has been separated from the sea by a sand barrier for at least 10 years, while the Carrizal salt marsh is partially connected with the sea only during the high spring tides and storms (generally twice a year). The salt marshes at El Litre and Pachingo are in the bay of Tongoy, have an arid climate, and are hydrologically connected to the sea, while the Limari salt marsh is located at the mouth of the Limari River and is permanently connected to the sea. The Pullally salt marsh is in a semi-arid climate at the confluence of Pullally and La Ligua Rivers, while the El Yali salt marsh is located around a coastal lagoon. Both marshes are connected to the sea during high tides. In more humid climates, the Carampangue salt marsh is associated with the Carampangue River, and is permanently connected to the sea. In the hyper-humid climate region, the Putemum and Huiladad marshes are located on the protected coastline of Chiloe Island and face some of the largest tides in Chile.

2.2 | Plant and soil data

Field sampling was conducted in the spring of 2014 (during the growing season, September–December). To quantify plant zonation

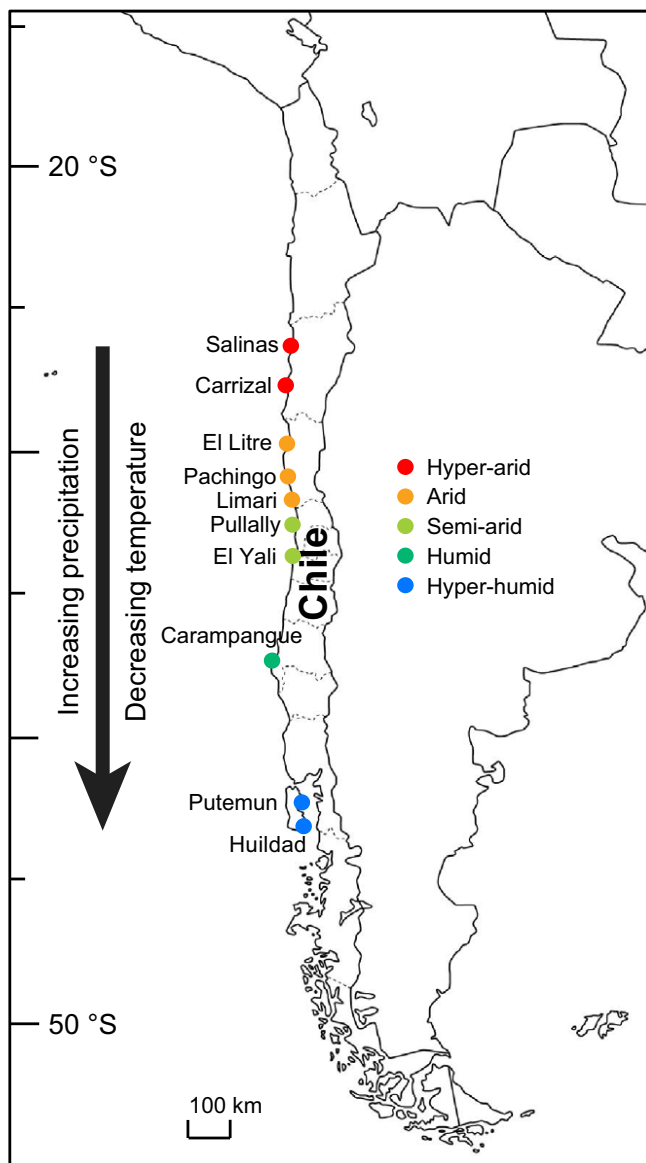


FIGURE 1 Salt marsh study sites on the Pacific coast of South America in Chile. Different colours indicate different climatological regions, as defined in Santibañez et al. (2006)

along representative elevation profiles at each of the 10 study sites, we positioned five transects perpendicular to the shoreline in areas selected based on a preliminary inspection of topography and vegetation across the entire study site. Transects were separated by 6 m and were 28 to 36 m long, with about half of each transect was in low, and half in high-marsh zones, respectively. Low marsh was normally inundated during high tides (between mean low tide levels and mean high tide levels), and high marsh was above the mean level of high tides (between mean high tides and mean high spring tides). Mean elevations of the low and high marshes at each site relative to mean sea level were determined by topographic measurements and are given in Table S1 in Appendix S1. One m^2 quadrats were placed at 2-m intervals along each transect. The number of quadrats surveyed in low and high saltmarsh zones were: Salinas (low:15 and high:20), Carrizal (low:15 and high:20), El Litre (low:40 and high:35),

Pachingo (low:15 and high:20), Limari (low:15 and high:20), Pullally (low:15 and high: 20), El Yali (low:20 and high:25), Carampangue (low:15 and high:20), Putemun (low: 15 and high:20) and Huiladad (low: 15 and high:20). In these terms, differences in the number of quadrats between low and high marshes were <1 per transect. Then, we estimated the percent cover of each plant species and bare area by subdividing the quadrat into 100, 10×10 cm cells and recording their presence in each cell. Data from the five quadrants at the same distance from the shore at each site were averaged for analysis.

To quantify soil water and organic matter content, we randomly took six samples of the first 15 cm of soil from the low and high-marsh zones, respectively, at each study site. To avoid the effect of seawater inundation, soil samples were taken during the lowest spring tides. Soil water content was assessed gravimetrically by weighing, drying (for 48 hr at 80°C), and then reweighing each sample. Soil water content was estimated as the percent difference between initial and final weight of the soil sample. Soil organic content was estimated with the loss on ignition (LOI) method which estimates the percent difference in weight between dried samples before and after being ignited in a muffle furnace at 500°C for 16 hr (Ghabbour, Davies, Cuozzo, & Miller, 2014; Storer, 1984). In the same zones (high and low), we measured salinity (six replicates per zone/site) with a refractometer using pore water collected in pore water sample tubes.

2.3 | Climate, estuarine morphology, and disturbance data

In addition to soil factors that often vary greatly at small local scales, we also considered three groups of site-scale variables, including climate, estuarine morphological and disturbance factors. Four climate variables (annual mean temperature, coefficient of temperature variation, annual precipitation and coefficient of precipitation variation), two estuarine morphological variables (presence of sand barriers blocking tides and number of days flooded by tides), and two disturbance variables (tsunami and rainfall floods) were considered to explore their relationships with vegetation patterns across sites.

For climate variables, monthly mean temperature and total precipitation data in 2014 were obtained from the National Agricultural Service (<http://agromet.inia.cl/estaciones.php>). Coefficients of variation in temperature and precipitation were estimated as the percent standard deviation over time (months in a year) relative to the monthly mean. For estuarine morphological variables, presence of sand barriers was coded as a binomial variable. For tidal frequency, we defined a tide level for each site that corresponds with a complete tidal flood of each site. The number of days flooded by tides/year/site between 2010 and 2015 were estimated with tidal data from the Oceanographic Office of the Chilean Navy (<http://www.snamchile.cl>). For disturbance variables, presence of tsunami impacts was coded as a binomial variable. Tsunamigenic earthquakes happen every few years in Chile and can delete marsh vegetation where they hit (Fariña & Camaño, 2012). The tsunami associated with the big earthquake of February 27 of 2010 effectively hit 700 km the central Chilean coast, affecting three of our 10 study sites (ie,

TABLE 1 Summary data for the study sites. Temperature and precipitation data are from 2014 when field sampling was conducted. Tidal frequency is number of days flooded/year. Number of rainfall floods are those reported from 2010 to 2014

Site	Geographic coordinates	Annual mean temperature (°C)	Annual precipitation (mm)	Tidal frequency (days)	Presence of sand barrier	Rainfall floods	Tsunami
Salinas	27°17'S, 70°56'W	17.41	44.9	0	Full	4	
Carrizal	28°05'S, 71°08'W	14.08	45.4	3.17	Partial	4	
El Litre	30°17'S, 71°32'W	14.68	34.2	3.5	Partial	4	
Pachingo	30°18'S, 71°34'W	14.40	71.3	3.5	Partial	4	
Limari	30°43'S, 71°41'W	13.58	88.3	8.5	Partial	3	
Pullally	32°24'S, 71°24'W	13.83	100.1	8.5	Partial	1	2010
El Yali	33°45'S, 71°43'W	13.41	397.7	8.5	Partial	1	2010
Carampangue	37°14'S, 73°18'W	12.53	834.2	14.17	Partial	1	2010
Putemun	42°25'S, 75°25'W	9.90	1511.5	358.5	None	0	
Huillard	43°03'S, 73°37'W	9.68	1553.9	358.5	None	0	

Pullally, El Yali and Carampangue). From 2010 to 2014, the three study sites were in a recovery process, while none of the other sites were hit by tsunamis in the previous 5 years. To examine if differences in marsh plants between these three sites and the other sites can be explained by this difference in vegetation succession history, we included a binomial variable indicating the occurrence of the tsunami in our analysis (see the ordination analysis below). In addition, extreme rainfall in Chile often causes floods and landslides that disturb marshes at estuaries adjacent to mountains. We estimated the total number of rainfall floods that occurred at each study site by screening rainfall disaster reports of the National Agricultural Service (<http://agromet.inia.cl/estaciones.php>). Note that site-scale, rather than zone-scale, climate and disturbance data were used in our analysis, since climate and disturbance are factors operating at larger scales relative to soil factors.

2.4 | Statistical analysis

To explore latitudinal variations in environmental factors, we analysed the relationships of climatic and soil variables with latitude, using linear models. Differences in the three soil variables among marsh sites and elevation zones were analysed with nested ANOVAs with Marsh Zone nested in Site. Normality of the data was checked graphically, and homogeneity of variance and independence of the data were verified using Levene's and Durbin-Watson tests, respectively (Wilkinson, Blank, & Gruber, 1996). Data were log- (salinity) or arcsine-transformed (soil water content and soil organic content) prior to the ANOVAs.

To examine similarity in species composition among the study sites, we initially analysed differences in the cover of each dominant plant species (*Distichlis spicata* (L.) Greene, *Sarcocornia fruticosa* (L.) Scott, and *Spartina densiflora* Brongn.) among the study sites using one-way ANOVA followed by *post hoc* Tukey's HSD test. Plant cover data were arcsine-transformed. To a priori group study sites pooled into biogeographic regions (Saintilan, 2009), we conducted a cluster analysis of the study sites (mean % plant species cover data/site), using Euclidean distance and standardized average linkage. We

considered the grouping results of this cluster analysis to analyse zonation patterns.

Plant community composition and environmental factors were analysed with canonical correspondence analysis (CCA; Legendre & Legendre, 2012). Although understanding the biogeography of plant zonation in terms of physiological competences is desirable, multivariate statistics that explore species-environment correlations are often a useful tool to obtain a first-step understanding of large-scale species patterns and their potential environmental drivers (eg, Drenovsky, Steenwerth, Jackson, & Scow, 2010; Hamer & Parris, 2011; Hoeninghaus, Winemiller, & Birnbaum, 2007). The environmental metrics in our analysis included 11 environmental factors: soil (soil salinity, water content and organic matter content), climatic (annual mean temperature, coefficient of temperature variation, annual precipitation and coefficient of precipitation variation), tidal (number of days flooded and presence of sand barriers), and disturbance (tsunami and floods caused by extreme rainfall) variables. We included both site- and zone-scale environmental data, and it is common in ordination analyses to include environmental factors operating at different spatial scales (eg, Drenovsky et al., 2010; Hamer & Parris, 2011; Hoeninghaus et al., 2007). The plant species metrics included percent cover data of five plant species, as well as those of bare soil (considered as a unique species). Upper and lower elevations of each site were included separately in different rows in the environmental factor and plant species metrics. We determined the best-performing CCA model using the *step* function in the R 'vegan' package (Oksanen et al., 2017). The *step* function determines the best-performing model by adding or removing each environmental factor individually from the initial model and comparing the resulting model to the initial model based on the Akaike information criterion (AIC). Analysis using the smallest model (with no environmental variables included) and the largest model (with all of the 11 environmental variables included) as the initial models, respectively, yielded the same best-performing model. Significance of each of the environmental variables and each of the CCA components was tested using permutation tests (1,000 steps). We repeated this analysis considering only low-marsh data and only high-marsh data, respectively.

Data analysis was conducted with JMP 8.0.2, and the cluster analysis and the CCA with the “vegan” package in R 3.3 (R Core Team, 2017).

3 | RESULTS

3.1 | Geographical patterns in environmental factors

Along the latitudinal gradient, precipitation increased ($R^2 = 0.97$, $p < .0001$) and mean temperature decreased ($R^2 = 0.92$, $p < .0001$) with increasing latitude. Similarly, coefficients of precipitation and temperature variation showed latitudinal trends, with generally more variable temperature ($R^2 = 0.61$, $p = .0124$) and less variable precipitation ($R^2 = 0.85$, $p = .0003$) at higher latitudes. For soil variables, salinity strongly decreased with increasing latitude ($R^2 = 0.33$, $p = .0075$), from nearly 30 ppt in the most northern marsh (Salinas) to ~0.5 ppt in the most southern sites Putemun and Huilad (Figure S1a in Appendix S2). In contrast, soil moisture increased with increasing latitude ($R^2 = 0.73$, $p = .0001$), from 4.8% at the high zone of the Salinas marsh (the most northern site) to almost 80% in the most southern marshes in Putemun and Huilad (Figure S1b in Appendix S2). No pattern in soil organic matter content was detected ($R^2 = 0.13$, $p = .1222$).

Soil factors were also affected by site X zone interactions. Soil salinity was higher at high than at low marshes at the two most northern sites (Salinas and Carrizal), but was similar between low and high marshes at all other sites (Figure S1a in Appendix S2, Table S2 in Appendix S1). Soil moisture was often lower at high than at low marshes in sites north of El Yali, but was similar at southern sites (Figure S1b in Appendix S2, Table S2 in Appendix S1). Soil

organic matter content was higher in high than low marshes at one northern site (Salinas) and two southern sites (Carampangue and Putemun), but was not significantly different among zones at other sites (Figure S1c in Appendix S2, Table S2 in Appendix S1).

3.2 | Geographical patterns in plant communities

Sites differed in the cover of the three dominant marsh plants *Distichlis spicata* ($F_{9,430} = 69.13$, $p < .0001$), *Sarcocornia fruticosa* ($F_{9,430} = 87.53$, $p < .0001$) and *Spartina densiflora* ($F_{9,430} = 359.32$, $p < .0001$) (Figure 2). *Distichlis spicata* and *S. densiflora* were almost entirely restricted to the northern and southern sites, respectively, and the abundance of *S. fruticosa* was highest at central latitudes and decreased at higher or lower latitudes (Figure 2). Only two other plants (*Cotula coronopifolia* (L.), and *Frankenia salina* (Molina) I.M. Johnst) that were recorded in these marshes occurred in low cover only in one (*Cotula coronopifolia* in Pullally) or two sites (*Frankenia salina* in Pullally and El Litre). Plant cover was generally over 80%, with minimal bare sediment, except for Carrizal and Pachingo.

Plant zonation varied geographically, loosely falling into four groupings. In the two northern, hyper-arid sites, low marshes are dominated by *S. fruticosa* that was gradually replaced by *D. spicata* in high marshes (Figure 3a,b). In the arid climates (El Litre, Pachingo and Limari), *S. fruticosa* dominated almost the entire marsh, without conspicuous zonation of plant species (Figure 3c–e). In the semi-arid climates (Pullally and El Yali), *S. fruticosa* dominated the low marsh and was replaced by *S. densiflora* in the high marsh, though this pattern was less obvious in Pullally than in El Yali (Figure 3f,g). In humid and hyper-humid climates (Carampangue, Putemun and Hildad), marshes were dominated primarily by *S. densiflora* with a low cover of *S. fruticosa* in the low marsh and weak plant zonation. These four

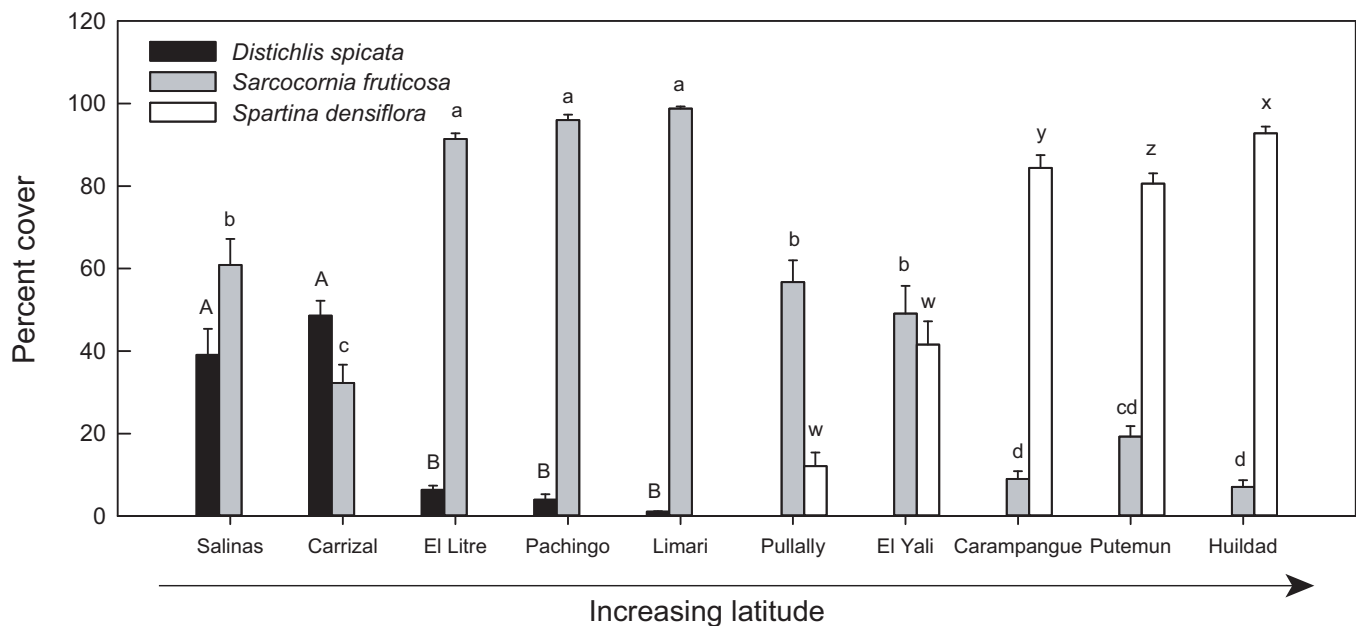


FIGURE 2 Geographic distributions of salt marsh plants across latitude along the Pacific coast of Chile. Shown are means (and SE) of percent cover of the three dominant plant species. Within each species, bars sharing a letter are not significantly different from one another ($p > .05$)

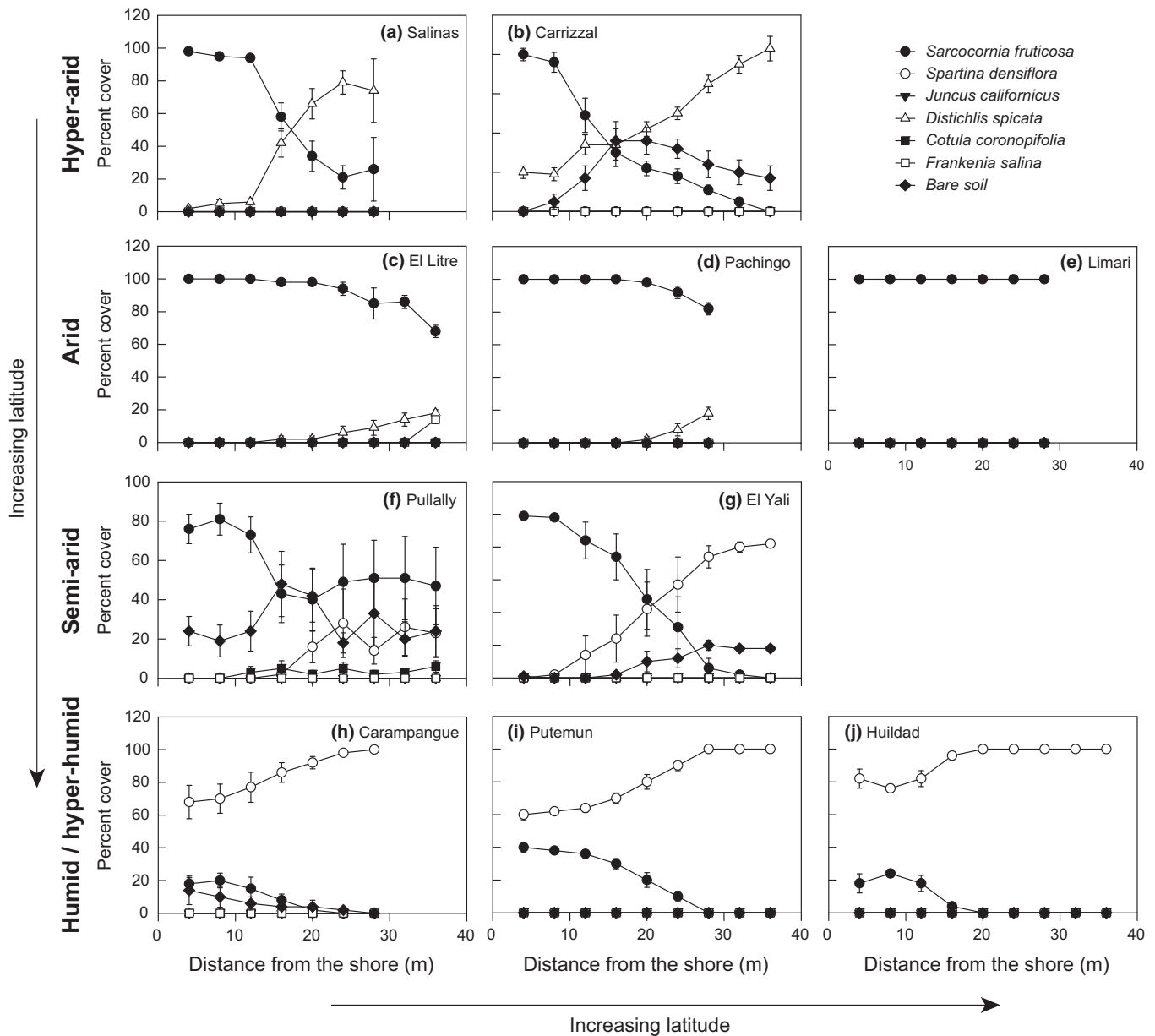


FIGURE 3 Geographic variation in site-scale salt marsh zonation across latitude along the Pacific coast of Chile. Data are means and SE

community groupings were evident in a cluster analysis (Figure S2 in Appendix S2).

3.3 | Variation in marsh plant distributions as a function of environmental factors

The best-fitting CCA model included nine of the 11 environmental factors explaining plant community composition across sites. Six were significant (precipitation, temperature, tidal frequency, soil salinity, tsunami and flood disturbance) (Table S4 in Appendix S1). The CCA model explained 87% of the plant community variability. The first four of the five CCA components were significant (at the level of $p < .05$), though the first three accounted for 93% of the explainable variance (Table S3 in Appendix S1). In the CCA biplots (Figure 4), all the environmental variables except soil

salinity and tsunami were primarily correlated with the primary CCA component, soil salinity with the secondary CCA component, and tsunami disturbance with the third CCA component. Thus, variation in plant communities across sites was primarily explained by precipitation, temperature, tidal frequency and flood disturbance, and to a much lesser extent by soil salinity and tsunami disturbance. Marshes dominated by *S. densiflora* and *F. salina* were most strongly associated with high precipitation and high tidal frequency, those dominated by *S. fruticosa*, *C. coronopifolia* and bare soil were associated with high temperature and frequent/recent disturbance from rainfall floods, and those dominated by *D. spicata* and *C. coronopifolia* were associated with high soil salinity and tsunami disturbance, respectively.

Environmental predictors of plant communities differed between low and high marshes. For the low marsh CCA, only the first CCA

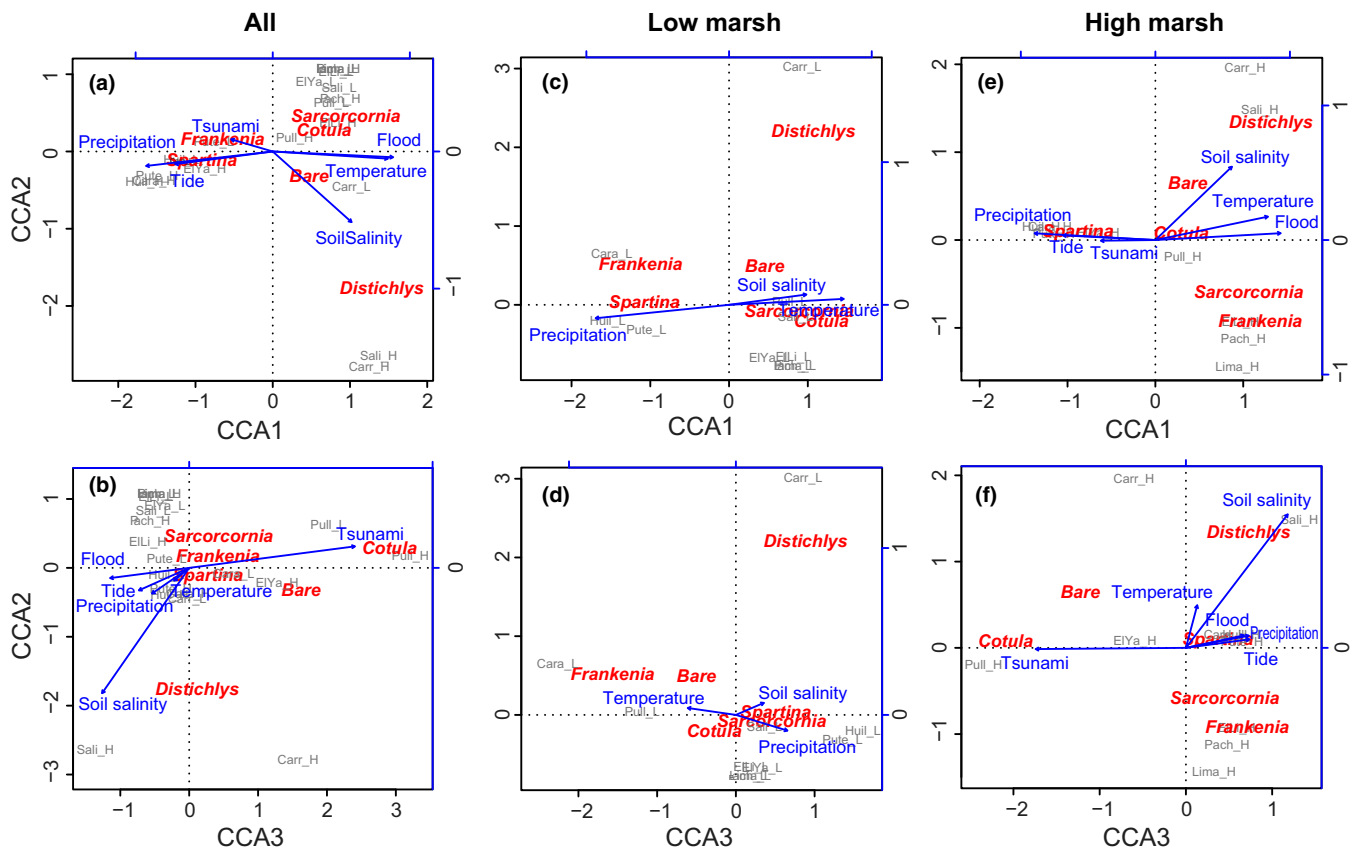


FIGURE 4 Canonical correspondence analysis (CCA) of salt marsh plant communities and environmental predictors along the Pacific coast of Chile. (a), (b) All, (c), (d) low marsh only, and (e), (f) high marsh only. Sites are shown with the first four characters of their name, and low and high zones are indicated with “L” and “H”, respectively. Also, given in each plot are the genus names of plant species. Note that all CCA components shown here are statistically significant ($p < .05$), except the second and third CCA components in (c) and (d), which were marginally significant (see statistics in Table S3 in Appendix S1)

component was highly significant (Table S3 in Appendix S1), and only the effect of precipitation was significant in the CCA model (though the effects of temperature and soil salinity were marginally significant; see Table S4 in Appendix S1). Low marshes dominated by *S. densiflora* were associated with high precipitation, while those dominated by *S. fruticosa* were associated with low precipitation. For the high-marsh CCA, the first three CCA components were all highly significant (Table S3 in Appendix S1), and the effects of precipitation, temperature, tidal frequency, soil salinity, tsunami and flood disturbance were all significant (Table S4 in Appendix S1). High marshes dominated by *S. densiflora* were associated with high precipitation, low temperature, high tidal frequency, and low flood disturbance, those dominated by *D. spicata* were associated with high salinity (Figure 4e), and marshes with the presence of *C. coronopifolia* and bare soils were associated with tsunami disturbance (Figure 4f).

4 | DISCUSSION

Distinct plant communities in different climate regions dominate marshes on the Pacific coast of South America. Plant zonation is present in dry low-latitude marshes. At central latitudes that are

transitional between dry and wet marshes, plant zonation can also be present. Our results suggest that geographic variation in plant zonation can be explained by differences in the environmental predictors between low and high marshes. While variation in low-marsh plant communities was primarily a function of precipitation, those in high marshes were jointly explained by precipitation, temperature, tidal frequency, soil salinity and disturbances. These correlative findings along with previous site-specific experimental studies help explain why plant distribution patterns vary across climate gradients, and have important implications for predicting how climate change will impact salt marsh plant communities.

From a biogeographic perspective, our study fills the knowledge gap of salt marsh flora on the Pacific coast of South America, which have not been previously studied (Adam, 1990; Chapman, 1960; Isacch et al., 2006). General patterns of plants species composition and diversity of Chilean salt marshes have been described (Fariña & Camaño, 2012; Ramirez & Añazco, 1982), but to date no studies have examined geographic variation in zonation or the mechanisms generating the zonation. Our study shows conspicuous shifts in dominant plant species with latitude. Although *Sarcocornia fruticosa* is present across the entire latitudinal gradient, it dominates arid marshes at low latitudes rather than humid marshes at high latitudes.

Distichlis spicata is restricted to dry marshes at low latitudes and *Spartina densiflora* is limited to wet marshes at high latitudes. The dry marshes dominated by *S. fruticosa* and *D. spicata* and those dominated by *S. densiflora* may correspond to, respectively, the Dry Coast and Temperate types in Adam (1990) biogeographic classification of salt marshes globally. While salt marshes on the Pacific and Atlantic coasts of South America share the South American cordgrass *S. densiflora*, our finding of the Dry Coast marshes differs from a previous study which suggests that salt marshes on the Atlantic coast of South America are primarily Temperate (Bortolus, 2006; Isacch et al., 2006).

Our results also suggest that the Dry Coast salt marshes on the Pacific coast of South America are associated with low precipitation, high temperature and high soil salinity. Shifts from Dry Coast marshes at low latitudes to Temperate marshes at high latitudes are also present in Australia (Saintilan, 2009). Dry Coast salt marshes in Australia are also believed to be driven by low precipitation, high temperature, and elevated soil salinity (Saintilan, 2009). Precipitation is also a major predictor of salt marsh plant community composition on the Atlantic coast of South America (Isacch et al., 2006). It should be noted that in our study, marshes dominated by *Distichlis spicata* are associated with high temperature, which likely acts more as an indicator of heat and aridity stress, instead of solar energy and cold stress. Although solar energy and cold stress have been thought to be a main driver of biogeographic variation in salt marsh flora (Adam, 1990; Chapman, 1960) and of biome shifts between mangroves and salt marshes (Cavanaugh et al., 2013; Gabler et al., 2017), biogeographical studies that quantitatively investigate shifts between temperate, boreal, and Arctic coastal marshes are still lacking, especially from the northern hemisphere, but are needed to further our understanding with impending biome shifts with climate change.

Our study provides a biogeographic perspective of plant zonation in coastal wetlands. This is the first study to test whether plant zonation along environmental gradients varies geographically, and to test whether this variation is correlated with environmental variation. Plant zonation in salt marshes and mangroves have been widely reported and assumed to be ubiquitous in coastal wetlands. Our results show that plant zonation in Chilean salt marshes is most conspicuous in hyper-arid low latitudes and is less conspicuous in arid, humid, and hyper-humid high latitudes. Plant zonation is also evident in marshes at middle latitudes in semi-arid intermediate climates. In these climate ecotones, overlapping plant species from dry to wet climate marshes may lead to species sorting along environmental gradients, resulting in species zonation patterns.

Latitudinal variation in plant zonation in Chilean salt marshes can be explained by differences in environmental processes controlling plant species composition between low and high-marsh areas. Climatic variables like annual precipitation and mean temperature are among the most important predictors of low-marsh plant community composition across latitude. *Spartina densiflora* and *Sarcocornia fruticosa* are associated with high and low precipitation, respectively. Although climatic variables including precipitation and temperature remain strong predictors of plant community composition in the high

marsh, they do not explain geographic variation alone. The dominance of *Distichlis spicata* in high marshes in hyper-arid climates, for example, is more strongly related with variation in soil salinity than in climate. Consistently, *D. spicata* is the most common salt-tolerant colonizer of bare, high-salinity marsh areas in New England (Bertness & Ellison, 1987; Bertness, Wanchuk, & Silliman, 2002). Disturbances, such as tsunamis and floods that frequently occur in Chile, may also be important (Fariña & Camaño, 2012). *Cotula coronopifolia*, for example, is found to be associated with tsunamis disturbance, and also colonizes gaps in tall perennial vegetation (Costa, Neto, Arsénio, & Capelo, 2009). Thus, while the latitudinal gradient we examined encompassed a broad range of climates, climate is not the only predictor of geographic variation in salt marsh plant zonation, and other factors such as disturbance can play a role in mediating how salt marsh plant zonation varies geographically.

Mechanistically, latitudinal variation in plant zonation can be inferred by extrapolating experimentally validated community assembly models. In hyper-arid low latitudes, for example, segregation between *S. fruticosa* and *D. spicata* zones is likely a result of high-marsh salinity stress restricting *S. fruticosa* and providing *D. spicata* a refugia habitat (see Bertness, Cough, & Shumway, 1992; Bertness & Ellison, 1987). In arid higher latitudes, lowered high-marsh salinity stress due to increased precipitation allows *S. fruticosa* to occupy the entire marsh. This results in the displacement of *D. spicata* from the high marsh. In semi-arid central latitudes, salinity stress decreased further with increased precipitation and decreased temperature, allowing the competitively dominant *S. densiflora* to displace *S. fruticosa* in the high marsh (Farina, Silliman, & Bertness, 2009). In humid and hyper-humid high latitudes with high precipitation and low temperature, low salinity stress across the entire marsh leads to the cordgrass *S. densiflora* displacing *S. fruticosa* in both the low and high marsh. Replicated experiments across latitude would be needed to further our understanding of these mechanisms (see Alexander, Diez, Hart, & Levine, 2016). In addition, it should be noted that consumer pressure can also vary across latitude in coastal wetlands (Alberti et al., 2007; He & Silliman, 2015, 2016) and can mediate plant zonation in salt marshes (He, Altieri, & Cui, 2015). In salt marshes on the Pacific coast of Chile, conspicuous herbivorous animals are rare (most salt marsh animals are coleoptera, amphipods and isopods eating debris; Figueroa, Suárez, Andreu, Ruiz, & Vidal-abarca, 2009), except livestock that were present at three of the salt marsh sites we examined (ie, Pullally, Carampangue, and Putemun). Our field sampling at these sites avoided areas with intense livestock grazing (by locating transects in areas where livestock access was limited by tidal creeks).

This study fills a knowledge gap and contributes to understanding of the biogeography of salt marsh vegetation on the Pacific coast of South America. It also highlights how understanding local plant distributions can be enhanced with a biogeographic perspective. Incorporating a biogeographic perspective into elucidating local ecological patterns can advance understanding of community and ecosystem dynamics across local, regional, and global scales, and can be a powerful approach to predicting community responses to predicted global climate change.



5 | CONCLUSIONS

Salt marshes on the Pacific coast of South America belong to Dry Coast and Temperate biogeographic types. Salt marsh plant zonation varies across latitude, and is explained by climatic, tidal, edaphic and disturbance factors. These patterns appear to be mechanistically explained by extrapolating experimentally generated community assembly models and have implications for predicting responses to climate change.

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DATA ACCESSIBILITY

Data on vegetation analysis and environmental variables are available on: <https://github.com/konguitos/Biogeography-of-plant-zonation-Journal-of-Biogeography-2017/issues/1>.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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