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PERSPECTIVES

Climatic Controls on the Distribution of Foundation Plant Species in Coastal Wetlands of the Conterminous United States: Knowledge Gaps and Emerging Research Needs

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Abstract

Foundation plant species play a critical role in coastal wetlands, often modifying abiotic conditions that are too stressful for most organisms and providing the primary habitat features that support entire ecological communities. Here, we consider the influence of climatic drivers on the distribution of foundation plant species within coastal wetlands of the conterminous USA. Using region-level syntheses, we identified 24 dominant foundation plant species within 12 biogeographic regions, and we categorized species and biogeographic regions into four groups: graminoids, mangroves, succulents, and unvegetated. Literature searches were used to characterize the level of research directed at each of the 24 species. Most coastal wetlands research has been focused on a subset of foundation species, with about 45% of publications directed at just one grass species—*Spartina alterniflora*. An additional 14 and 8% have been directed, respectively, at two mangrove species—*Rhizophora mangle* and *Avicennia germinans*. At the national scale, winter temperature extremes govern the distribution of mangrove forests relative to salt marsh graminoids, and arid conditions can produce hypersaline conditions that increase the dominance of succulent plants, algal mats, and unvegetated tidal flats (i.e., salt flats, salt pans) relative to graminoid and mangrove plants. Collectively, our analyses illustrate the diversity of foundation plant species in the conterminous USA and begin to elucidate the influence of climatic drivers on their distribution. However, our results also highlight critical knowledge gaps and identify emerging research needs for assessing climate change impacts. Given the importance of plant-mediated processes in coastal wetland ecosystems, there is a pressing need in many biogeographic regions for additional species- and functional group-specific research that can be used to better anticipate coastal wetland responses to rising sea levels and changing temperature and precipitation regimes.

Keywords Coastal wetland · Foundation species · Plant functional group · Salt marsh · Mangrove forest · United States

Introduction

We live in a rapidly changing world where the redistribution and loss of foundation species is increasingly affecting the structure and functioning of ecosystems (Ellison et al. 2005; Pecl et al. 2017). A foundation species is an organism that modulates ecosystem processes and builds the primary habitat features that support entire ecological communities (sensu Dayton 1972; Ellison 2019). Foundation plant species play an especially critical role in ecosystems that are governed by physiologically challenging abiotic conditions, like those found in deserts, intertidal rocky shores, and coastal wetlands (Bertness and Callaway 1994; Bruno et al. 2003; Maestre et al. 2009). In these severe conditions that are too stressful for many organisms, foundation plant species define and structure

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entire ecosystems, which provide valuable ecosystem goods and services to society (Millennium Ecosystem Assessment 2005; Barbier et al. 2011; Costanza et al. 2014). However, many foundation plant species are vulnerable to climate change (Vergés et al. 2014; Thomson et al. 2015; Lovelock et al. 2017), and ecologists and natural resource managers are increasingly challenged to better understand and anticipate the effects of changing temperature and precipitation regimes on the future distribution and persistence of foundation species and the ecosystems that they support. In this communication, we examine the influence of climatic drivers on foundation plant species in coastal wetlands of the conterminous United States.

Climate greatly influences the distribution, abundance, and diversity of plant communities in all ecosystems (Holdridge 1967; Whittaker 1970; Archibold 2012). However, the influence of climate has historically not been included in vulnerability assessments for coastal wetland foundation plant species (Osland et al. 2016; Gabler et al. 2017). Stressful salinity and inundation regimes limit the number of plant species that can survive in coastal wetlands (Mitsch and Gosselink 2007); hence, a small number of halophytic and flood-tolerant plants play a disproportionately important role in intertidal saline environments (Bertness and Ellison 1987; Mendelssohn and Morris 2000; Bruno and Bertness 2001; Lovelock et al. 2016). Salt marsh grasses and mangrove trees are well-known and visually-striking coastal wetland foundation species that have received much attention in the scientific literature due to their ability to dictate wetland ecosystem functions and create the primary habitat features that support coastal wetland ecological communities (Odum et al. 1982; Gosselink 1984; Visser et al. 1998). However, coastal wetland foundation species also include less-studied succulent plants and other kinds of graminoid plants (i.e., sedges and rushes, in addition to grasses) (Dunton et al. 2001; Saintilan 2009; Battaglia et al. 2012; Callaway et al. 2012; Fariña et al. 2018; Janousek et al. 2019). Moreover, where hypersaline conditions are too stressful for vascular plants, coastal wetlands can be dominated by algal mats and unvegetated tidal flats (i.e., salt flats, salt pannes, salt pans, salt barrens, sabkhas, salinas) (Zedler 1982; Ridd et al. 1988; Withers 2002), which are coastal wetland types that have not received much attention in the literature.

Given the role of plant-mediated responses to climate change and rising sea levels for coastal wetland stability and adaptation in the coming century (Morris et al. 2002; McKee 2011; Kirwan and Megonigal 2013), there is a pressing need to advance understanding of the ecology, biogeography, and adaptive capacity of coastal wetland foundation plant species across bioregions. In the 1980s, the U.S. Fish and Wildlife Service funded a series of biological reports, often referred to as the "community profile" reports, which provided ecological descriptions of coastal wetlands in different parts of the USA (e.g., Nixon 1982; Odum et al. 1982; Zedler 1982; Josselyn 1983; Seliskar and Gallagher 1983; Gosselink 1984; Stout 1984; Teal 1986; Wiegert and Freeman 1990). Building from these detailed and increasingly valuable reports, several book chapters and journal articles have described the coastal wetland plant communities present in certain regions of the USA (e.g., Visser et al. 1998; Roman et al. 2000; Visser et al. 2000; Baldwin et al. 2012; Battaglia et al. 2012; Callaway et al. 2012; Pennings et al. 2012; Wigand and Roman 2012). However, all these assessments have been conducted at regional scales, and to our knowledge, there has not been a national-scale synthesis of the biogeography of foundation plant species in coastal wetlands of the conterminous United States. Most regional-scale analyses have tended to encompass a single plant functional group (e.g., mangrove forest or graminoid-dominated marsh or succulent-dominated marsh), and there is a need for holistic analyses that span functional groups and ecosystem types. For example, in the southeastern United States, several recent studies have identified ecological thresholds using a mixture of data from different kinds of coastal wetland ecosystems (e.g., Osland et al. 2016; Feher et al. 2017; Gabler et al. 2017). Those studies have demonstrated the value of holistic analyses that include data from mangrove forests, salt marshes, and unvegetated tidal flats together, as opposed to more traditional analyses that have evaluated the ecological influence of climate using data from just one ecosystem type (e.g., just mangrove forests or just salt marshes). Data from mangrove forests and salt marshes have been used together to identify temperature thresholds governing mangrove dominance relative to salt marsh graminoids (Osland et al. 2013), and data from vegetated wetlands (e.g., salt marshes, mangrove forests) and unvegetated tidal flats have been combined to identify precipitation thresholds for plant coverage in coastal wetlands (Longley 1994; Montagna et al. 2007; Osland et al. 2014; Gabler et al. 2017; Duke et al. 2019). However, these kinds of cross-group synthetic analyses have not been conducted at the national scale for the entire conterminous United States.

Here, we examine climatic controls on the distribution of foundation plant species in coastal wetlands of the conterminous United States. First, we identified dominant foundation plant species within biogeographic regions and categorized species and biogeographic regions into the following four groups: graminoids, mangroves, succulents, and unvegetated tidal flats. Next, we evaluated the influence of climatic drivers to the distribution of these groups. Finally, literature database searches were conducted to characterize the level of research directed at each of the identified foundation species. Our analyses illustrate the diversity of foundation plant species in the conterminous USA and begin to quantify the influence of climatic drivers on their distribution. However, our efforts also highlight critical knowledge gaps and identify emerging research needs for assessing climate change impacts.

Identifying Biogeographic Regions and Foundation Plant Species

Our study area included the three coastlines of the conterminous United States (i.e., the Pacific Ocean, Atlantic Ocean, and Gulf of Mexico coasts). Throughout the communication, we use the term coastal wetland to refer to tidal saline wetlands (i.e., mangrove forests, graminoid-dominated marshes, succulent-dominated marshes, and unvegetated tidal flats). Our analyses do not include tidal freshwater wetlands, which are far more diverse and varied than tidal saline wetlands (Odum et al. 1984; Conner et al. 2007; Mitsch and Gosselink 2007). We used literature descriptions of coastal wetland plant communities to identify 12 discrete biogeographic regions (Fig. 1a), which we define as areas where coastal wetland plant communities are typically dominated by a common set of foundation species. Along the Pacific coast, we identified two regions: California and Pacific Northwest (Callaway et al. 2012; Janousek et al. 2019). The succulent plant-dominated marshes of San Francisco Bay were assigned to the California region (Janousek et al. 2019). The north Atlantic coast was divided into the following two regions: Northern New England and Southern New England/Mid-Atlantic (Roman et al. 2000; Wigand and Roman 2012). Chesapeake Bay was assigned its own region: Chesapeake (Baldwin et al. 2012). Graminoid-dominated areas south of Chesapeake Bay were assigned to the South Atlantic region (Dame et al. 2000; Pennings et al. 2012). Mangrove-dominated areas in Florida were assigned to the South Florida region (Odum et al. 1982). In addition to the South Florida region, the Gulf of Mexico was assigned five more regions, listed in counter-clockwise order: Northeast Gulf of Mexico (Battaglia et al. 2012), Mississippi River Delta (Visser et al. 1998), Chenier Plain of Louisiana/Texas (Visser et al. 2000; Johnson et al. 2013; Gabler et al. 2017), Central Texas (Dunton et al. 2001; Rasser et al. 2013; Gabler et al. 2017), and South Texas (Tunnell and Judd 2002; Withers 2002; Gabler et al. 2017). Within each of the 12 biogeographic regions, we used the sources noted in parentheses to develop a list of the most common foundation plant species (Table 1). We assigned each species and region to one of the following plant groups: mangrove, graminoid, succulent, or unvegetated. The mangrove group includes freeze-sensitive tidal saline wetland trees and shrubs (Tomlinson 1986; Duke et al. 1998). The graminoid group includes herbaceous plants with grass-like morphologies (e.g., long, linear culms and leaf

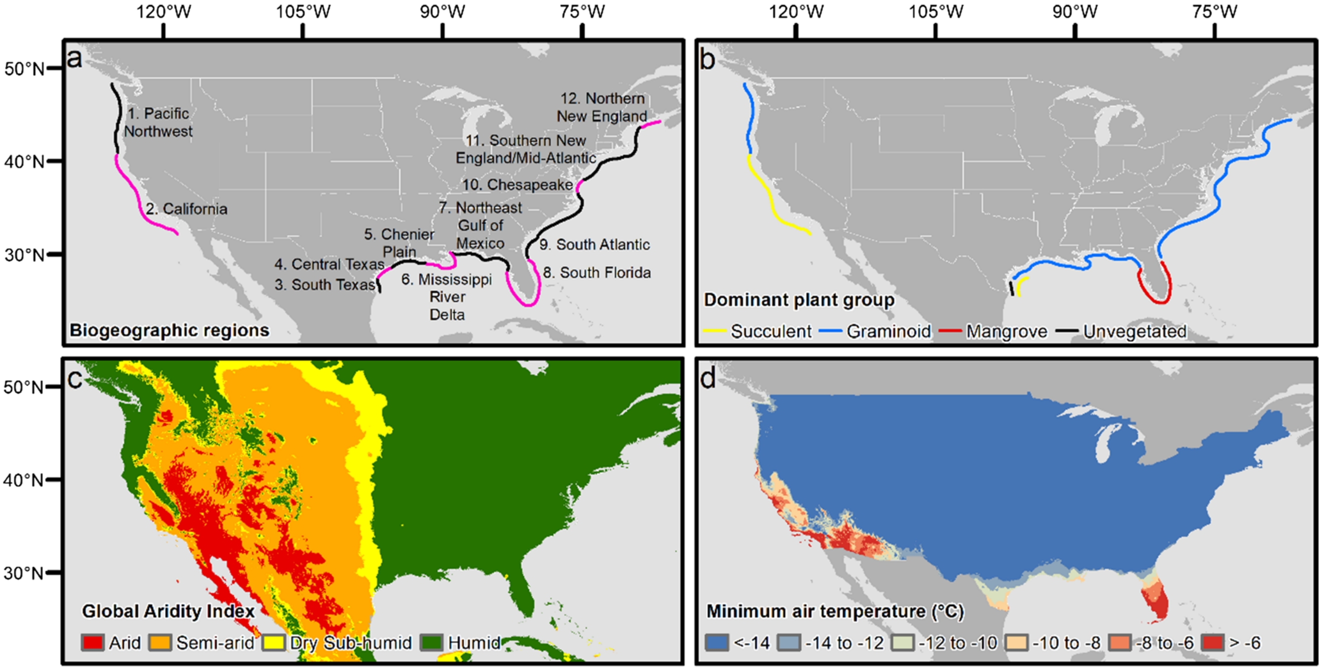


Fig. 1 Maps of the conterminous United States identifying the 12 assigned biogeographic regions (**a**) and the distribution of dominant plant groups in coastal wetlands (**b**) in relation to the Global Aridity Index (**c**) and winter temperature extremes (**d**). Within each biogeographic region, coastal wetland plant communities are generally dominated by a common set of foundation plant species. In panel **b**, blue indicates graminoid dominance, red indicates mangrove dominance, yellow indicates succulent plant dominance, and black indicates primarily unvegetated wetlands (e.g., salt flats, salt pans) often dominated by algal mats. Whereas winter temperature extremes govern the transitions from mangrove to graminoid dominance (see red to blue transitions in panel **b**, which occurs in Florida), aridity and salinity tend to govern the transitions from graminoid to succulent dominance and the absence of vegetation (see transitions from blue to yellow or blue to black in panel **b**, which occur in Texas and California). The Global Aridity Index represents the ratio of precipitation to potential evapotranspiration

Table 1 Dominant foundation plant species within each of the 12 coastal wetland biogeographic regions of the conterminous United States. Code represents the species' assigned four-letter abbreviation code. # indicates the number of biogeographic regions in which the species is included as a dominant species. Group represents the species' plant group (G = graminoid; M = mangrove; S = succulent). Dominance within a region is denoted with an X. The biogeographic region numbers, names, and locations are shown in Fig. 1 a

				Biogeographic region											
Species	Code	#	Group	1	2	3	4	5	6	7	8	9	10	11	12
Agrostis gigantea	AgGi	1	G												X
Avicennia germinans	AvGe	4	M			X	X		X		X				
Batis maritima	BaMa	2	S			X	X								
Borrichia frutescens	BoFr	1	S				X								
Carex paleacea	CaPa	1	G												X
Deschampsia cespitosa	DeCe	1	G	X											
Distichlis spicata	DiSp	7	G	X	X			X	X	X			X	X	
Festuca rubra	FeRu	1	G												X
Frankenia salina	FrSa	1	S		X										
Jaumea carnosa	JaCa	1	S	X											
Juncus arcticus	JuAr	1	G												X
Juncus gerardii	JuGe	2	G											X	X
Juncus roemerianus	JuRo	4	G						X	X		X	X		
Laguncularia racemosa	LaRa	1	M								X				
Monanthochloe littoralis	MoLi	2	S			X	X								
Rhizophora mangle	RhMa	1	M								X				
Salicornia depressa	SaDe	2	S			X	X								
Sarcocornia pacifica	SaPa	2	S	X	X										
Schoenoplectus americanus	ScAm	3	G					X	X				X		
Spartina alterniflora	SpAl	7	G					X	X	X		X	X	X	X
Spartina cynosuroides	SpCy	2	G									X	X		
Spartina foliosa	SpFo	1	G		X										
Spartina patens	SpPa	6	G					X	X	X			X	X	X
Triglochin maritima	TrMa	1	G	X											

blades). Coastal wetland graminoids are often in the grass, sedge, or rush families (Poaceae, Cyperaceae, and Juncaceae, respectively). The succulent group includes halophytic plants that have fleshy, water-storing leaves and/or stems, which help regulate internal salt concentrations to reduce osmotic stress (Ogburn and Edwards 2010). Prime examples of succulent salt marsh species include *Salicornia depressa*, *Sarcocornia pacifica*, and *Batis maritima*. We used the dominant plant group within each region's species list to assign one of the four group categories to each biogeographic region.

In total, we identified 24 foundation plant species across the 12 biogeographic regions including 14 graminoid, 3 mangrove, and 7 succulent species (Table 1). There were 12 species that appeared as dominant species in more than one biogeographic region and 12 species that appeared as dominant in only one region (Table 1). The species that were dominant in the greatest number of biogeographic regions included *Spartina alterniflora*, *Distichlis spicata*, *Spartina patens*, *Avicennia germinans*, *Juncus roemerianus*, and *Schoenoplectus americanus* (Table 1).

Climatic Controls on Dominant Plant Groups

We used maps and a two-dimensional niche-space representation to illustrate the distribution of dominant plant groups relative to two ecologically relevant climatic drivers—temperature and aridity (Osland et al. 2016, 2017; Gabler et al. 2017). For the conterminous United States, we created maps that illustrate plant group dominance (Fig. 1b) relative to aridity (Fig. 1c) and minimum air temperature (Fig. 1d). We determined the minimum and maximum values of aridity and minimum temperature for each region, which we used to illustrate the position of the biogeographic regions in climatic space (Fig. 2). For temperature data, we used gridded minimum daily temperature data produced by the PRISM Climate Group at Oregon State University (prism.oregonstate.edu) (Daly et al. 2008). For the 30-year period extending from 1981 to 2010, we obtained the coldest individual daily temperature (i.e., the absolute minimum daily temperature). Minimum temperature was selected as a variable due to its demonstrated influence on the distribution of mangrove forests relative to graminoid salt marshes (Osland et al. 2013, 2019; Cavanaugh et al. 2014, 2019). For aridity data, we used gridded Global Aridity Index data from a global data set produced by Zomer et al. (2006). The Global Aridity Index values represent the ratio between mean annual precipitation and potential evapotranspiration. Aridity was selected as a variable because highly arid climates can lead to hypersaline conditions, which can increase the dominance of succulent plants, algal mats, and unvegetated areas (i.e., salt flats, salt pannes, salt pans, salt barrens) relative to graminoid and mangrove plants (Osland et al. 2014, 2018a Gabler et al. 2017). To quantify the climatic space of biogeographic regions as well as the distribution of cells across climatic gradients, we created a study grid of 2.5-arcmin cells (~ 5 km cell size near the equator) for the coastal conterminous United States. We assigned a biogeographic region to each cell and we used 2010 Coastal Change Analysis Program data (C-CAP; https://coast.noaa.gov/digitalcoast/tools/lca.html) to identify cells containing tidal saline wetlands (i.e., cells containing any of the three C-CAP estuarine wetland categories). We used the previously described temperature and aridity data to determine cell-specific climatic conditions.

Our analyses show that temperature and aridity regimes greatly influence the distribution of dominant plant groups (Figs. 2 and 3, S1). In general, graminoid species are more dominant in humid temperate climates (e.g., the Pacific Northwest, the northern Atlantic, much of the southern Atlantic, and much of the northern Gulf of Mexico coasts). Mangrove species are more dominant in humid tropical and subtropical climates (e.g., south Florida). Succulent species and algal mats are more dominant in arid and semi-arid climates (e.g., the southern and central coasts of Texas and

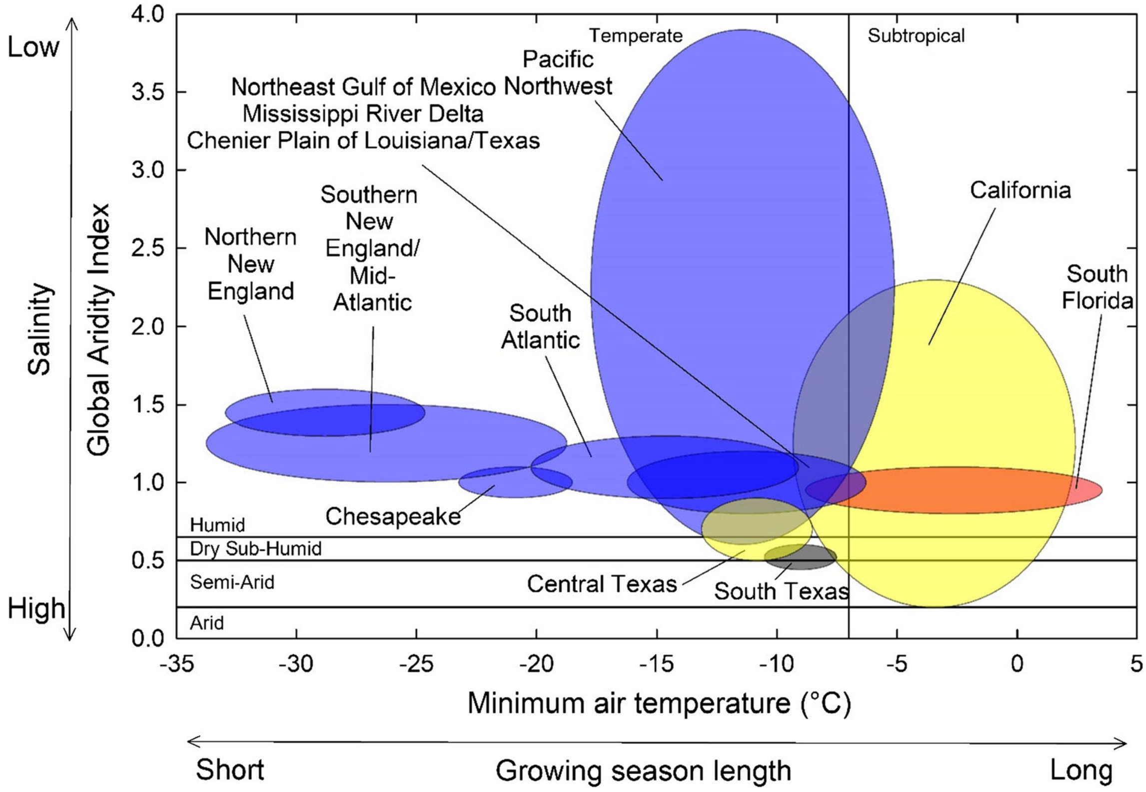
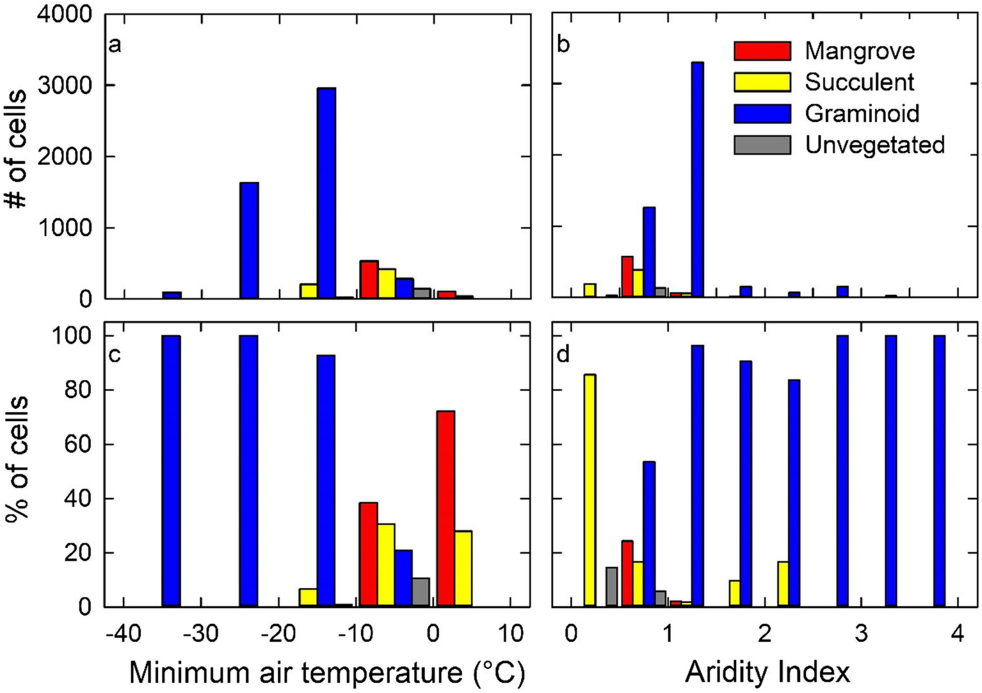


Fig. 2 The generalized position of the 12 coastal wetland biogeographic regions in a climatic space defined by winter temperature extremes (x axis) and the Global Aridity Index (y axis). Colors are used to depict the dominant plant group within each region as follows: blue = graminoid; red = mangrove; yellow = succulent; and gray = unvegetated. The horizontal lines are Global Aridity Index categories as defined by Zomer et al. 2006. Note that arid and semi-arid climates are represented by low Global Aridity Index values (i.e., less than 0.2 and between 0.2 and 0.5, respectively). The vertical line is the winter temperature extreme theshold (− 7 °C) that hinders mangrove dominance as determined by Osland et al. (2013). Along the x axis, growing season length is positively correlated with mean annual temperature and minimum air temperature (Feher et al. 2017). Along the y axis, the Global Aridity Index is negatively correlated with precipitation and salinity (Osland et al. 2014, 2018b)

Fig. 3 Histograms of the number of cells (**a**, **b**) and the percentage of cells (**c**, **d**) containing tidal saline wetlands in the mangrove, succulent, graminoid, or unvegetated categories in relation to minimum air temperature (**a**, **c**) and the Global Aridity Index (**b**, **d**)



California). While Fig. 2 uses ovals to coarsely depict the position of biogeographic regions in climatic space, Fig. S1 displays the climatic position of cell-based data for each of the 12 regions. In addition to illustrating the influence of climate on the distribution of plant groups, our analysis of the distribution of cells across climatic gradients (Fig. 3) provides an initial assessment of the relative abundance of these plant groups. While ~ 77% of cells were dominated by graminoid plants, 10% of cells were dominated by mangroves, 10% of cells were dominated by succulent plants, and ~ 3% of cells were unvegetated (Fig. 3).

Characterizing the Level of Species-Specific Research

To elucidate the level of research directed at each of the 24 foundation species, we conducted literature database searches within Web of Science (https://webofknowledge.com). The searches were conducted on 2 August 2019 using the Web of Science Core Collection for the period extending from 1985 to present. Initially, we conducted a general species-specific search for publications that included the following terms: TOPIC: ("species name" OR "species synonym[s]"). For each of the 24 species, we determined the official species names and synonyms using the USDA PLANTS Database (https://plants.usda.gov). Next, we conducted searches to characterize the level of research directed at three specific topics: (1) sea-level rise; (2) climate change, specifically warming and changing temperature regimes; and (3) climate change, specifically drought and changing precipitation regimes. We searched for publications that included the species name as a topic as well as one of the following terms: (1) TOPIC: ("sea-level rise" OR "sea level rise"); (2) TOPIC: ("warming" OR "temperature") AND ("climate change"); and (3) TOPIC: ("drought" OR "precipitation") AND ("climate change"). In Web of Science, the use of the topic field produces a search of the following fields within a record: title, abstract, author keywords, and keywords plus®, which are index terms that augment traditional keyword or title retrieval. Note that our search was designed to quantify the amount of research directed towards each of the 24 species regardless of study location; hence, the search was not restricted to studies conducted solely within the USA. Moreover, the search does not distinguish between native and non-native species and does not capture studies that do not include species names within the targeted search record fields. Thus, ecological studies focused on plant communities, rather than species, may not be included in these search results if the dominant species names were not mentioned in targeted search fields.

The literature review shows that most coastal wetland research has focused on a small number of foundation species (Table 2; Fig. 4). *Spartina alterniflora* is the most extensively studied foundation species and has been included in 2875 publications, which represents about 45% of the total number of publications (Table 2). In addition to being one of the most common native species along the Gulf of

Table 2 The number of publications focusing on each of the 24 dominant foundation plant species. General indicates the number of total found publications on that species. Sea-level rise indicates the number of found publications on that species that include "sea-level rise" or "sea level rise" as topical phrases. Warming indicates the number of found publications on that species that include "climate change" and "warming" or "temperature" as topical phrases. Drought indicates the number of found publications on that species that include "climate change" and "drought" or "precipitation" as topical phrases. The numbers in parentheses represent the corresponding percentages of the total number of found publications in the corresponding category

	No. of publications			
Species	General	Sea-level rise	Warming	Drought
Agrostis gigantea	18 (< 1)	1 (< 1)	0 (0)	0 (0)
Avicennia germinans	512 (8)	55 (9)	34 (23)	10 (16)
Batis maritima	38 (< 1)	4 (< 1)	1 (< 1)	0 (0)
Borrichia frutescens	54 (< 1)	4 (< 1)	0 (0)	0 (0)
Carex paleacea	4 (< 1)	0 (0)	0 (0)	0 (0)
Deschampsia cespitosa	10 (< 1)	1 (< 1)	1 (< 1)	0 (0)
Distichlis spicata	238 (4)	18 (3)	5 (3)	1 (2)
Festuca rubra	35 (< 1)	3 (< 1)	0 (0)	0 (0)
Frankenia salina	14 (< 1)	0 (0)	0 (0)	0 (0)
Jaumea carnosa	16 (< 1)	2 (< 1)	0 (0)	0 (0)
Juncus arcticus	48 (< 1)	2 (< 1)	1 (< 1)	0 (0)
Juncus gerardii	29 (< 1)	3 (< 1)	0 (0)	0 (0)
Juncus roemerianus	198 (3)	23 (4)	2 (1)	2 (3)
Laguncularia racemosa	347 (5)	18 (3)	9 (6)	1 (2)
Monanthochloe littoralis	7 (< 1)	1 (< 1)	0 (0)	0 (0)
Rhizophora mangle	902 (14)	60 (10)	21 (14)	10 (16)
Salicornia depressa	393 (6)	21 (3)	2 (1)	2 (3)
Sarcocornia pacifica	27 (< 1)	10 (2)	1 (< 1)	1 (2)
Schoenoplectus americanus	156 (2)	14 (2)	3 (2)	2 (3)
Spartina alterniflora	2875 (45)	279 (47)	55 (38)	29 (47)
Spartina cynosuroides	20 (< 1)	4 (< 1)	0 (0)	0 (0)
Spartina foliosa	119 (2)	20 (3)	0 (0)	1 (2)
Spartina patens	359 (6)	55 (10)	11 (8)	3 (5)
Triglochin maritima	35 (< 1)	3 (< 1)	0 (0)	0 (0)

Mexico and Atlantic coasts of the USA, *S. alterniflora* is also an invasive non-native species in other parts of the world including China, Europe, and the Pacific coast of North America (Strong and Ayres 2013). Thus, some of the *S. alterniflora*-focused studies were conducted outside of its native range. *Rhizophora mangle* and *A. germinans* are the second and third most studied species, respectively (Table 2; Fig. 4).

Of the 24 species, there were 6 and 12 species in fewer than 20 and 40 publications, respectively (Table 2). Within investigations of sea-level rise, there were 13 foundation species with fewer than 10 publications each. Within investigations of climate change, specifically the effects of warming and changing temperature regimes, there were just four foundation species (i.e., *S. alterniflora*, *A. germinans*, *R. mangle*, and *S. patens*) with more than 10 publications. Within investigations of climate change, specifically the effects of drought and changing precipitation regimes, *S. alterniflora*, *A. germinans*, and *R. mangle* were the only foundation species included in 10 or more publications. Across each category, *S. alterniflora* was the foundation species found in the greatest number of publications.

Knowledge Gaps and Emerging Research Needs for Evaluating Climate Change Effects

Climate greatly influences the distribution, abundance, and diversity of coastal wetland ecosystems (Woodroffe and Grindrod 1991; Saenger 2002; Saintilan 2009; Feher et al. 2017). Temperature and rainfall regimes greatly influence the dominance of plant functional groups (Osland et al. 2013, 2014; Gabler et al. 2017). Rainfall and aridity gradients influence the coverage (Longley 1994; Osland et al. 2014; Duke et al. 2019), composition (Gabler et al. 2017), height (Méndez-Alonzo et al. 2008; Feher et al. 2017; Simard et al. 2019), and productivity (Osland et al. 2018b) of coastal wetland plant communities. Algal mats, unvegetated tidal flats (i.e., salt flats, salt pannes, salt pans, salt barrens), and succulent plants are more dominant under hypersaline conditions, which often develop in response to low rainfall and high aridity (Fosberg 1961; Zedler 1982; Dunton et al. 2001; Gabler et al. 2017). In arid and semi-arid estuaries, human actions that lead to freshwater diversions, reductions in tidal exchange, and altered biophysical processes can also lead to increases in the dominance of salt stress-tolerant succulent plant

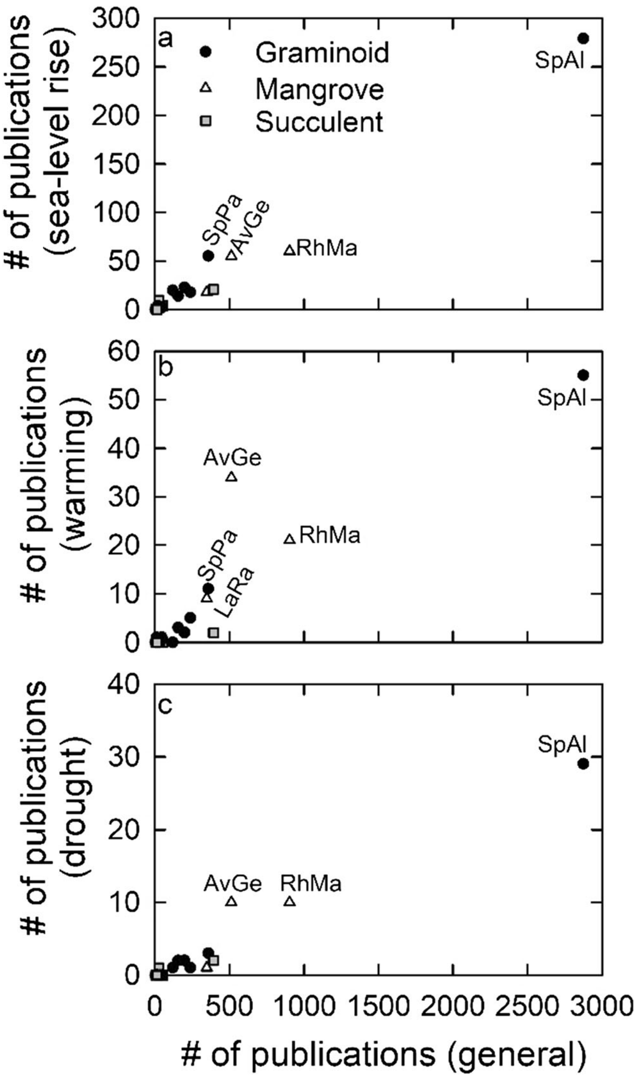


Fig. 4 The number of found publications on foundation plant species within different topical areas. The *x* axis indicates the number of total publications on that species. Along the *y* axes: **a** sea-level rise indicates the number of publications on that species that include the topical phrases "sea-level rise" or "sea level rise"; **b** warming indicates the number of publications on that species that include the topical phrases "climate change" and "warming" or "temperature"; and **c** drought indicates the number of publications on that species that include the topical phrases "climate change" and "drought" or "precipitation." Species abbreviation codes are defined in Table 1 and provided here for the most commonly studied species

communities (Zedler et al. 1986, 2001; Alexander and Dunton 2002; Ibarra-Obando et al. 2010; Montagna et al. 2017). The southern and central coasts of California and Texas are the only regions of the conterminous United States that are currently dry enough to support extensive hypersaline areas that develop into succulent-dominated salt marshes or unvegetated areas that lack vascular plants. However, climate change is expected to produce hotter, longer growing seasons and an increase in the frequency and duration of extreme precipitation events (i.e., drought and flooding) (USGCRP 2017). Moreover, coastal development and increasing human water demands are expected to decrease the amount of freshwater that is delivered to estuaries (Longley 1994; Alber 2002; Montagna et al. 2013). Collectively, these climate and land use changes indicate that hypersaline conditions are likely to become more common, and unvegetated tidal flats and succulent-dominated salt marshes may become more abundant in parts of the USA, especially in Texas and California.

Humid temperate climates typically support coastal wetlands that are dominated by graminoid plants, as is the case for the many regions in the northern Gulf of Mexico, the Pacific Northwest, and along the southern and northern Atlantic coast. Mangroves are sensitive to freezing temperatures and are replaced by graminoid salt marsh plants where winter air temperature extremes are too cold (Lugo and Patterson-Zucca 1977; Ross et al. 2009; Pickens et al. 2019). Hence, winter air temperature extremes govern the dominance of mangrove forests relative to graminoids (Cavanaugh et al. 2014; Gabler et al. 2017; Osland et al. 2018a), and South Florida is the only region of the conterminous United States that currently supports mature mangrove forests. However, in response to warming winter temperature extremes due to climate change (USGCRP 2017), mangrove forests are expected to expand northward at the expense of graminoid-dominated salt marshes in parts of Texas, Louisiana, and Florida (Osland et al. 2013; Cavanaugh et al. 2014).

Our analyses indicate that the air temperature and precipitation regimes in parts of California and the Pacific Northwest may be capable of supporting mangrove forests—note the position of these two biogeographic regions in Fig. 2 relative to the mangrove-marsh threshold. However, we expect the lack of mangroves along these coasts is potentially caused by dispersal limitation due to a combination of southbound ocean currents, cold ocean water temperatures, and lack of suitable estuarine habitat beyond the northern range limit of mangroves in Mexico (Osland et al. 2017; Cavanaugh et al. 2018; Van der Stocken et al. 2019). In other words, we expect that along the Pacific coast of the USA mangrove propagules are not able to disperse to and become established in climatically suitable estuaries beyond their current northern range limit; however, this topic has been understudied for this region. This hypothesis is supported by the establishment, reproduction, and persistence of *Avicennia marina*—an introduced mangrove species from the South Pacific—in Mission Bay (San Diego, CA), which is beyond the current northern range limit of mangrove forests on the Pacific coast of North America (Fourqurean et al. 2010; Cavanaugh et al. 2018).

The central and southern portion of California (i.e., the coastal reach south of San Francisco Bay) are areas that are consistent with our aridity-based hypotheses due to the dominance of succulent plants in these arid and hypersaline salt marshes. However, the northern portion of California (i.e., the coastal reach between San Francisco Bay and

Humboldt Bay) is an area that does not fit neatly within our aridity-based hypotheses. Given the higher annual rainfall in this area, our climate-based hypotheses indicate that wetlands should be dominated by graminoid plants or mangrove forests. However, succulent plants dominate the salt marshes in this region (Takekawa et al. 2013), and this unexpected result deserves additional consideration. One potential explanation may be associated with the annual distribution of rainfall—most of the rainfall in this region occurs during the winter, and the dry, hot summer conditions may lead to hypersaline conditions that favor succulent dominance. Hence, a more refined aridity variable may be needed to account for the timing of freshwater inputs, and additional work is needed to better characterize the influence of climate on the shift from graminoid to succulent plant dominance in the salt marshes near the Pacific Northwest-California transition.

To simplify, we focused on just two climatic variables that have been shown to be critically important for governing the distribution of different coastal wetland plant groups (Osland et al. 2016; Gabler et al. 2017). However, we acknowledge that this oversimplification is both a strength and weakness of our analyses. We recognize that the ecological influence of climate is more nuanced, and there is a need for additional analyses that examine the influence of the many different aspects of climate not included here, especially in areas with geographical knowledge gaps. Growing degree days, mean winter temperatures, and maximum summer temperatures are variables that have been used to explain and forecast the productivity of *S. alterniflora* (Kirwan et al. 2009) and may also explain the distribution of certain graminoid species along the northern and central Atlantic and Pacific coasts. For instance, the northern range limit of *J. roemerianus*, which occurs in the Mid-Atlantic region (Eleuterius 1976), can likely be explained by one of these additional winter temperature metrics. With regard to precipitation and aridity, salinity is often the more direct driver of vegetation changes. So, there is a need to advance understanding of the linkages between changes in freshwater inputs and the development of hypersaline conditions. For example, the timing of rainfall in California's Mediterranean climate is predominantly in the winter, which contrasts with the more continuous precipitation inputs in South Texas. In an early communication, Fosberg (1961) presented hypotheses regarding the influence of seasonal precipitation patterns on salinity regimes and the formation of unvegetated tidal flats (see also Duke et al. 2019). Since that communication nearly six decades ago, the influence of seasonal differences in the quantity and timing of precipitation has not been fully investigated.

The interactive effects of temperature, evapotranspiration, and tidal inundation on salinity greatly influence coastal wetland plant communities (Lovelock et al. 2017). Moreover, coastal wetlands are governed by many non-climatic factors, and there is a need to advance understanding of interactions between climatic variables and these other abiotic factors. For example, inundation and salinity regimes are two abiotic factors that play a critical role in coastal wetlands, and there is a need for more studies that examine the influence of climate on inundation and salinity regimes across elevation and vegetation zonation gradients (Gabler et al. 2017; Fariña et al. 2018).

Despite the diversity of coastal wetland foundation species in the conterminous United States, our literature searches indicate that there are many foundation species that have received little scientific attention. Most coastal wetlands research has been focused on a subset of foundation species with about 45% of publications directed at just one species—*S. alterniflora*. For contrast, only 3% of publications have been directed at *J. roemerianus*, which is an abundant species in salt marshes along the northern Gulf of Mexico and South Atlantic coasts (Eleuterius 1976). Only 4% of publications have been directed at *D. spicata*, which is a species that is common in 7 of the 12 bioregions. Unfortunately, region- and national-scale coastal wetland geospatial data do not currently distinguish between foundation plant species; hence, we currently cannot quantify the amount of area covered by each of the 24 foundation species. National-scale data regarding the distribution, structure, and coverage of the 24 foundation plant species identified in this communication would better equip scientists to document, understand, and anticipate the effects of climate change on coastal wetlands.

Coastal wetland biogeomorphic responses to climate change and sea-level rise are expected to be greatly influenced by plant-mediated processes. For example, coastal wetland vertical adaptation to sea-level rise is influenced by feedbacks between inundation, sedimentation, and plant growth (Morris et al. 2002; Kirwan and Murray 2007). The limited evidence available suggests that species identity can have a very strong influence on those feedbacks (Cherry et al. 2009; Kirwan and Guntenspergen 2012; Janousek et al. 2016). Coastal wetland landward migration in response to sea-level rise and saltwater intrusion is influenced by traits that affect plant dispersal, establishment, and competition for resources (Peterson and Bell 2012; Langston et al. 2017). Similarly, ecosystem recovery following disturbance is greatly influenced by species-specific regeneration traits (Jones et al. 2016). Plant physiology governs persistence during drought as well as plant community transformations that occur following drought-induced vegetation dieback (McKee et al. 2004; Duke et al. 2017; Lovelock et al. 2017). The stability of coastal wetlands is influenced by soil organic matter formation, which is greatly influenced by plant productivity and the cascading effects of precipitation on freshwater availability and salinity (Osland et al. 2018b). All of these examples highlight the importance of plant species, plant traits, and life histories to fully understand climate change effects. Given the diversity and climate sensitivity of foundation plant species in the conterminous

United States, there is clearly a need for additional species- and functional group-specific research to better understand and anticipate coastal wetland responses to rising sea levels and changing temperature and precipitation regimes.

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