Estuarine, Coastal and Shelf Science 118 (2013) 11–23

Contents lists available at SciVerse ScienceDirect

Estuarine, Coastal and Shelf Science

journal homepage: www.elsevier.com/locate/ecss

Predictive occurrence models for coastal wetland plant communities: Delineating hydrologic response surfaces with multinomial logistic regression

Gregg A. Snedden*, Gregory D. Steyer

U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd, Lafayette, LA 70506, United States

ARTICLE INFO

Article history:
Received 18 May 2012
Accepted 7 December 2012
Available online 22 December 2012

Keywords:
wetlands
ecological zonation
hydrology
vegetation cover
community composition

ABSTRACT

Understanding plant community zonation along estuarine stress gradients is critical for effective conservation and restoration of coastal wetland ecosystems. We related the presence of plant community types to estuarine hydrology at 173 sites across coastal Louisiana. Percent relative cover by species was assessed at each site near the end of the growing season in 2008, and hourly water level and salinity were recorded at each site Oct 2007–Sep 2008. Nine plant community types were delineated with *k*-means clustering, and indicator species were identified for each of the community types with indicator species analysis. An inverse relation between salinity and species diversity was observed. Canonical correspondence analysis (CCA) effectively segregated the sites across ordination space by community type, and indicated that salinity and tidal amplitude were both important drivers of vegetation composition. Multinomial logistic regression (MLR) and Akaike's Information Criterion (AIC) were used to predict the probability of occurrence of the nine vegetation communities as a function of salinity and tidal amplitude, and probability surfaces obtained from the MLR model corroborated the CCA results. The weighted kappa statistic, calculated from the confusion matrix of predicted versus actual community types, was 0.7 and indicated good agreement between observed community types and model predictions. Our results suggest that models based on a few key hydrologic variables can be valuable tools for predicting vegetation community development when restoring and managing coastal wetlands.

Published by Elsevier Ltd.

1. Introduction

Plant community zonation in coastal marshes is strongly dictated by spatial gradients in salinity and inundation frequency and duration (Mitsch and Gosselink, 1986; Bertness and Ellison, 1987; Mendelssohn and McKee, 1987; Howard, 1995). Salinity advection and dispersion processes determine the estuarine salinity gradient and are largely governed by a location's connectivity to the coastal ocean and proximity of that location to runoff sources (Miranda et al., 1998, 2005), while inundation regimes are determined to a large extent by the vertical positioning of the marsh surface within the tidal frame. The width of this tidal frame is primarily dictated by average water depth and the degree to which friction attenuates the tidal wave as it progresses inland from the coastal ocean (Officer, 1976; Snedden et al., 2007). These variables interact to create a broad array of hydrologic conditions that support a mosaic of wetland plant species assemblages that transition across subtle changes in salinity or hydroperiod.

Eustatic sea-level rise (ESLR; an increase in sea level resulting from a change in ocean volume), currently estimated to exceed 3 mm yr^{-1} (IPCC, 2007; Ablain et al., 2009), is a critical problem in coastal regions today. This crisis is greatly exacerbated in subsiding deltas worldwide, where subsidence contributes to a relative sea-level rise (RSLR; an apparent change in local sea level due to the additive effects of ESLR and subsidence) that far exceeds ESLR alone. Relative sea-level rise effectively reduces the elevation of the marsh surface within the tidal frame, which can alter hydroperiod and increase estuarine salinity (Hilton et al., 2008).

In coastal Louisiana, rates of RSLR on the order of 10 mm yr^{-1} have been observed (Coleman et al., 1998) and these rates are sufficient to more than double the average depth of the shallow subestuaries of the Mississippi River deltaic plain over the next century (current average depth = 0.7 m, Swenson et al., 2006). Because the saltwater intrusion length of an idealized estuary is proportional to the square of its average depth (Savenije, 1993), saltwater intrusion lengths may exhibit a fourfold increase by 2100,

---

* Corresponding author.
E-mail addresses: gsnedden@usgs.gov, sneddeng@usgs.gov (G.A. Snedden).

0272-7714/$ – see front matter Published by Elsevier Ltd.
http://dx.doi.org/10.1016/j.ecss.2012.12.002

and may effect vegetation community shifts similar to those observed after periods of elevated salinities associated with severe drought (Visser et al., 2002; Forbes and Dunton, 2006), and ultimately result in a widespread landward encroachment of saline marsh community types into regions that are currently occupied by fresh and oligohaline communities (Boesch et al., 1994).

In addition to impacts of RSLR, which are expected to continue and strengthen in the future, many of Louisiana's coastal restoration alternatives aim to alter hydrology through a variety of methods including restoring connectivity of the wetland landscape to the Mississippi River. As such, there is a need to anticipate the impacts that RSLR and future restoration efforts may have on many aspects of coastal ecosystem structure and function, including the distribution of plant community types across the coastal zone. The distribution of these community types is important, as biodiversity (Callaway et al., 2007), resilience to disturbance (Gunderson, 2000), and trophic structure (Weinstein et al., 2000; Wissel and Fry, 2005; Alfaro, 2006) are all at least partially dependent upon the type of wetland ecosystem present.

Many laboratory studies have investigated the performance of common wetland plant species as it relates to variations in salinity and hydroperiod (Pezeshki et al., 1987a, 1987b; Pezeshki and DeLaune, 1993; Ewing et al., 1995; Spaulding and Hester, 2007). While these studies shed light on the physiological tolerances of these species to common hydrologic stressors under specified conditions, they have limited utility in predicting species presence or abundance in field settings. For example, niche overlap for plants growing naturally with contraspecifics can be greatly reduced compared to the same species grown in monoculture (Silvertown et al., 1999). Furthermore, Greiner-LaPeyre et al. (2001) found that competition becomes a strong factor for species abundance when abiotic stress is low. Thus, for many applications it may be of more use to examine the response of species assemblages to hydrologic variability using field-derived abundance and hydrologic data, rather than relying on mesocosm studies that examine only single-species assemblages.

This study utilizes a robust dataset of hydrologic and plant species composition measurements obtained at 173 sites throughout the Louisiana coastal zone to quantify the realized hydrologic niches of commonly occurring species assemblages. The objectives of this study are to 1) classify sites into distinct vegetation communities, 2) identify indicator species of these communities, 3) identify which hydrologic variables determine community structure, and 4) develop a probabilistic model to predict the presence/absence of various vegetation community types from observed hydrologic variables.

2. Methods

2.1. Data collection and processing

All data utilized in this study were obtained from 173 sites selected from the Coastwide Reference Monitoring System (Fig. 1; CRMS; www.lacoast.gov/crms), a statewide coastal monitoring network of randomly selected sites distributed across coastal Louisiana. Emergent marsh vegetation percent cover data were collected between August 1 and September 30, 2008, utilizing a modified Braun-Blanquet design (Braun-Blanquet, 1932, 1964; Fig. 2). Each site consisted of ten 2 m × 2 m vegetation cover plots along a 280-m transect. In each vegetation plot, percent cover of each plant species was visually estimated, and cover values for all ten plots were then averaged to obtain average cover values for each species at each site. For each site, average cover of each species was then divided by the total cover to obtain relative cover values (the sum of relative covers at each site was 100 percent). Plant species nomenclature followed the USDA PLANTS Database (U. S. Department of Agriculture, 2010).

From October 1, 2007 to September 30, 2008, hourly salinity (in Practical Salinity Units) and water level data were collected within 150 m of the vegetation transect at each of the 173 sites. It was assumed that no appreciable salinity or water level gradient (surface slope) existed across this 150-m distance and that these data reflected hydrologic conditions experienced by the plant communities along the vegetation transect at each site. Short gaps (<15 days) were filled by linear interpolation. Datasets from all sites were missing less than 750 (out of a possible 8784) hourly readings and no contiguous data gaps exceeded 15 days. At each site, the average marsh surface elevation was obtained by randomly surveying 20–40 points (each point separated from other points by 6–12 m), and taking an average of all of those points. Marsh elevations and water level recorders were surveyed to a common datum, allowing for the measurement of inundation periods, and

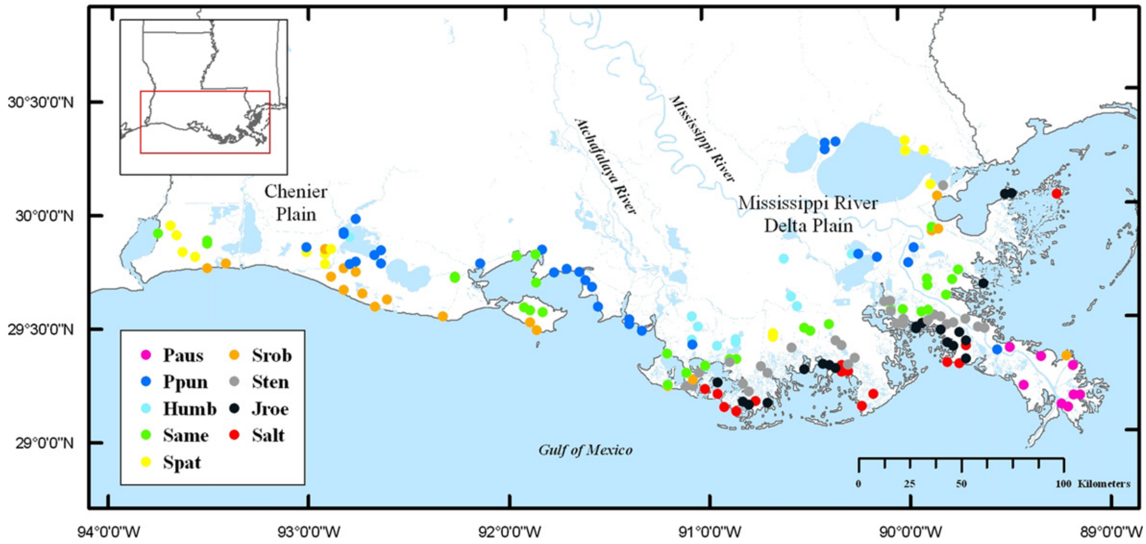

Fig. 1. Location of 173 sampling locations where vegetation cover, salinity, and water level data were collected. Color indicates vegetation community type to which each site was classified, based on *k*-means clustering of vegetation cover data. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

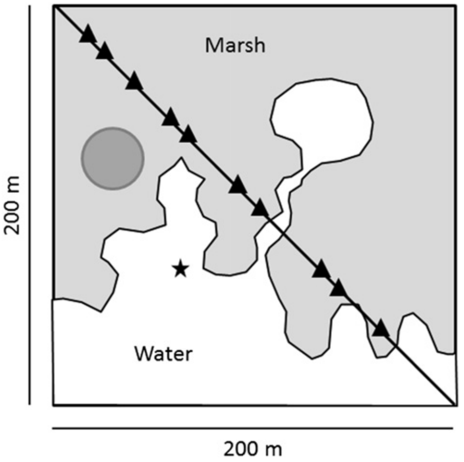

Fig. 2. Representation of a typical Coastwide Reference Monitoring System (CRMS) site, showing the 280-m vegetation transect (diagonal line), ten 2 m × 2 m vegetation plots (triangles), water level/salinity recorder (star), and marsh elevation survey area (shaded circle).

calculations of mean annual salinity, the upper 95th percentile salinity (used to convey the prevalence of brief, episodic high salinity events that may not be well-reflected in the mean value), percent time flooded, and diurnal tidal amplitude were made from each time series record. Tidal amplitudes were obtained by taking the sum the amplitudes of the O_1 (lunar diurnal, 25.82-h period) and K_1 (luni-solar diurnal, 23.93-h period) tidal constituents (the largest contributors to the astronomical tidal signal on the Louisiana coast; Snedden and Swenson, 2012), which were estimated for each station with harmonic analysis (Emery and Thompson, 2001). Because marsh elevations were not obtained specifically at each of the vegetation plots and salinity and water level data were assumed to be representative of conditions along the entire vegetation transect, hydrologic gradients within sites could not be detected and this study focuses on variation between sites.

2.2. Data analysis

Sites were assigned to vegetation community types by applying the *k*-means clustering method (Hair et al., 1992; Legendre and Legendre, 1998) to the vegetation site-by-species matrix. This approach uses a least-squares clustering method that partitions *n* observations into *k* clusters in which each observation is a member of the cluster with the nearest mean. Unlike other classification methods, *k*-means clustering is robust to differences in within-group sample sizes and to differences in abundances across species; both of these circumstances were prevalent in the vegetation data collected in this study. Because it does not assume that a single, strong gradient dominates the data matrix, it is capable of identifying secondary gradients that may exist. The Calinski–Harabasz (C–H) criterion (Calinski and Harabasz, 1974) was used to determine the optimum number of clusters to use. C–H is a pseudo-*F*-statistic that is based on the ratio of the mean square for the given partition to the mean square of the residuals. The number of clusters that provides the highest C–H value is taken as the optimum solution.

Indicator species were identified for each community type by calculating the indicator value index (IV; Dufrene and Legendre, 1997) for each species *j* in group *m*. This method uses categories (i.e., community types) defined *a priori*, and determines the degree to which the species in question can indicate the presence of a particular category, based on the species' specificity and fidelity to the category in question. Specificity (concentration of abundance to a specific category) is assessed by determining the relative abundance RAm_j of species *j* in category *m*, computed as the mean abundance of species *j* in group *m*, divided by the sum of mean abundances of species *j* across all categories. Fidelity is assessed by computing the relative frequency RF_{mj} of species *j* in category *m*, defined as the proportion of sites in category *m* that contain species *j*. The indicator value IV is then calculated as

$$\mathrm{IV}_{mj} = 100\left(RA_{mj} \times RF_{mj}\right) \quad (1)$$

and it identifies indicator taxa whose inter-group variability exceeds the variability that would be expected by chance. The indicator value varies from 0 to 100, attaining its maximum value when all individuals of species *j* occur at all sites assigned to group *m*, and are not found at any sites that are not assigned to group *m*. This method thus selects indicator species based on both high specificity for and high fidelity to a specific group. After computing indicator values, a Monte Carlo significance test of observed maximum indicator values for a given species was applied with 1000 permutations.

Detrended correspondence analysis (DCA; Hill and Gauch, 1980) of log-transformed species relative covers was used to assess the beta diversity in community composition along the ordination axes. The gradient lengths of the 2 axes were 5.5 and 4.6 standard deviation units, respectively, indicating that a unimodal species response model was most appropriate for constrained ordination (Jongman et al., 1995; Leps and Smilauer, 2003). Canonical correspondence analysis (CCA) was performed on the log-transformed site-by-species matrix using CANOCO (ter Braak and Smilauer, 2002). To primarily focus on responses by common species to hydrologic variation, species that were not present in at least 5% of all samples were excluded from analyses. CCA is a particularly robust method of constrained ordination when species show a unimodal (humped) relationship to environmental variability and zero values in many samples (Leps and Smilauer, 2003). Because of the large beta diversity along the ordination axes, Hill's scaling of scores with a focus on species was used so that distances between species were generalized Mahalanobis distances, and distances between samples represented species turnover across the sites (beta diversity). A Monte Carlo simulation with 499 iterations was used to test for significant relationships between the environmental variables and vegetation variation. Additionally, a partial CCA was run for each environmental variable, using the remaining variables as covariables, to partition the vegetation variability attributable to independent additive effects of each environmental variable (Legendre and Legendre, 1998). Canonical coefficients defined the ordination axes as linear combinations of plant species, and intraset correlations were used to examine the relationships between ordination axes and each environmental variable. Diversity at each site was calculated with Shannon's Index of Diversity (H') based on the natural logarithm of relative cover values.

Multiple multinomial logistic regression (MLR; Hosmer and Lemeshow, 2000) was used to model the probability of occurrence for each community type as a function of each environmental variable that was determined to be significant by the CCA. MLR is an extension of binary logistic regression that may be applied when the response variable has more than two categories. The response variable has *k* categories (i.e., community types) and MLR models will generate $k - 1$ equations where each equation compares the probability of occurrence of one of the $k - 1$ categories (P_k) to the probability of occurrence of the *k*th category, which serves as a baseline category. If there are *z* explanatory variables ($x_1, x_2, \ldots, x_z$) and *k* response categories ($A, B, \ldots, K$), the model is written as

$$\begin{aligned}\ln\left(\frac{P_B}{P_A}\right) &= \alpha_B + \beta_{1B}x_1 + \beta_{2B}x_2 + \ldots + \beta_{zB}x_z \\ &\vdots \\ \ln\left(\frac{P_K}{P_A}\right) &= \alpha_K + \beta_{1K}x_1 + \beta_{2K}x_2 + \ldots + \beta_{zK}x_z\end{aligned} \tag{2}$$

Here *A* serves as the baseline category. Each equation models the probability of an observation belonging to a particular category divided by the probability that it belongs to the baseline category. Because the model is constrained such that $\sum P_k = 1$, the probabilities can be solved as

$$\begin{aligned}P_A &= \frac{1}{1 + e^{\alpha_B+\beta_{1B}x_1+\beta_{2B}x_2+\ldots+\beta_{zB}x_z} + \ldots + e^{\alpha_K+\beta_{1K}x_1+\beta_{2K}x_2+\ldots+\beta_{zK}x_z}} \\ P_B &= \frac{e^{\alpha_B+\beta_{1B}x_1+\beta_{2B}x_2+\ldots+\beta_{zB}x_z}}{1 + e^{\alpha_B+\beta_{1B}x_1+\beta_{2B}x_2+\ldots+\beta_{zB}x_z} + \ldots + e^{\alpha_K+\beta_{1K}x_1+\beta_{2K}x_2+\ldots+\beta_{zK}x_z}} \\ &\vdots \\ P_K &= \frac{e^{\alpha_K+\beta_{1K}x_1+\beta_{2K}x_2+\ldots+\beta_{zK}x_z}}{1 + e^{\alpha_B+\beta_{1B}x_1+\beta_{2B}x_2+\ldots+\beta_{zB}x_z} + \ldots + e^{\alpha_K+\beta_{1K}x_1+\beta_{2K}x_2+\ldots+\beta_{zK}x_z}}\end{aligned} \tag{3}$$

Thus, MLR allows for the estimation of the probability of occurrence of each category as a function of the environmental variables in question. Quadratic terms were included in MLR models to account for nonlinearity. The Wald statistic (Hosmer and Lemeshow, 2000) was used to evaluate the significance of independent variables, and Akaike's Information Criterion (AIC; Akaike, 1974) was used to select the best model from a set of candidate models. The AIC is a likelihood statistic with a degrees-of-freedom adjustment, and this approach aims to select the most parsimonious model by balancing the overall fit (likelihood) of the model with the number of effects (degrees of freedom) included in the model. Computations of AIC were bias-corrected for small sample sizes (AIC_c) because in some models the ratio of sample size to number of parameters was less than 40 (Hurvich and Tsai, 1989). We also calculated Akaike weights (w_i) for each model, which can be interpreted as approximate probabilities that the model in question is, in fact, the best model in the candidate set (Anderson et al., 2000). Competing models were identified as models with $w_i \geq 10\%$ of the highest ranking model. This information-theoretic approach to model selection is superior to traditional hypothesis testing in that it allows for simultaneous comparison of more than two models, it balances precision and bias when selecting the best model, and it does not require that data be obtained from a formally designed experiment (Burnham and Anderson, 1998).

Once the best model was selected, the predictive accuracy of the model was assessed by calculating the weighted Cohen's kappa coefficient (κ; Cohen, 1968; Naesset, 1996) from the confusion matrix obtained through leave-one-out cross-validation (Fielding and Bell, 1997), where the community type predicted by the model was defined as the type with the highest modeled probability. The weighted version of κ is useful when a large number of simulated outcome classes with varying pairwise dissimilarities are evaluated and hence the magnitude of possible classification errors can vary (Guisan and Zimmermann, 2000). Weightings for each cell in the confusion matrix were obtained from the normalized distance matrix between cluster centroids obtained from the *k*-means clustering. This approach thus penalizes community type misclassifications that were very different from actual community types more severely than misclassifications to community types with relatively similar species compositions. Values of κ can range from -1 to 1, with $\kappa < 0$ indicating no predictive ability, $0 < \kappa < 0.4$ indicating poor predictive ability, $0.4 < \kappa < 0.75$ indicating good agreement, and $\kappa > 0.75$ indicating excellent agreement (Landis and Koch, 1977; Fielding and Bell, 1997; Araujo et al., 2005; Fielding, 2007; Puls et al., 2012).

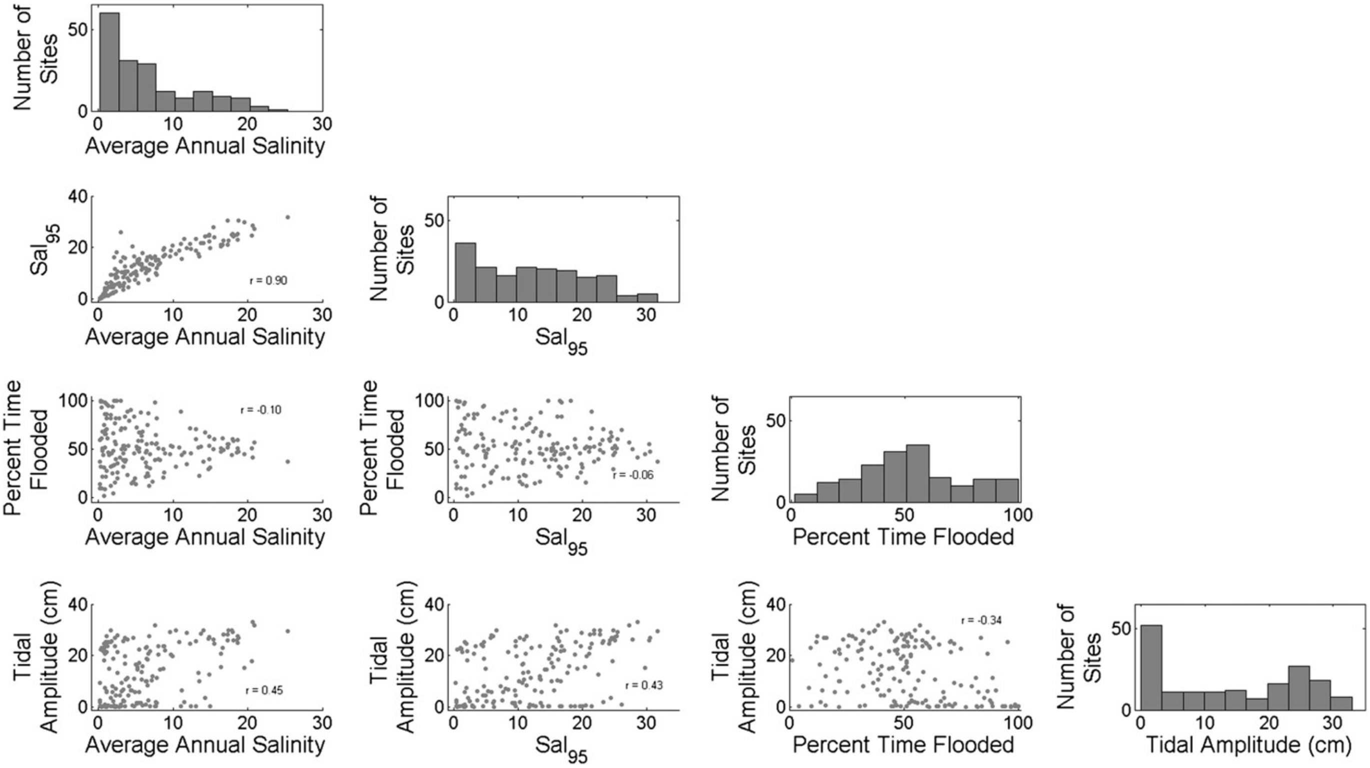

Fig. 3. (Diagonals) Histograms of environmental variables collected at 173 sites in the study area. (Off-diagonals) Scatter plots of pairs of environmental variables, along with correlation coefficients (r).

3. Results

3.1. Environmental variation

Average annual salinity (0.2–25.3, mean = 6.5, S.D. = 5.9), 95th percentile salinity (sal_{95}; 0.3–31.6, mean = 12.1, S.D. = 8.3), percent time flooded (1.4–100, mean = 52.2, S.D. = 23.6) and tidal amplitude (0–32.9 cm, mean = 13.7, S.D. = 10.8) were highly variable among sites, indicating the presence of strong spatial gradients in hydrology across the Louisiana coast (Fig. 3). Histograms of the environmental variables show a bias of sites with high flood durations and low salinities. Because the CRMS monitoring network consists of randomly selected sites across Louisiana's coastal zone, this bias is a reflection of the spatial variability of these variables across the landscape. Average annual salinity and sal_{95} were highly correlated ($r = 0.90$), and thus excluded from subsequent analysis to avoid issues related to multicollinearity. None of the remaining pairs of environmental variables were strongly correlated ($|r| < 0.5$ for all other variable combinations).

3.2. Community classification and indicator species

The most compact set obtained by *k*-means clustering was composed of nine communities (C–H criterion = 34.16). Indicator species and values, along with relative abundances and relative frequencies for each community are given in Table 1. The nine community types will hereafter be referred by first letter of the genus name and first three letters of the specific name of their most important indicator species. *Phragmites australis* (*Paus*) communities ($n = 8$; IV = 96.1; Table 1) were primarily located near the mouth of the Mississippi River (Fig. 1), and relative cover at these sites was dominated by *Phragmites australis* (Table 2). *Phragmites australis* occurred at nearly all *Paus* sites, and was rarely present at

Table 1
Indicator species for community types, indicator values (IV), relative abundance (RA) and relative frequency (RF) by community type for the 49 species included in the analysis. Blank cells for % RA/% RF indicate values of 0 for % RA and % RF. IVs in bold indicate species was a significant indicator of its community type for $\alpha = 0.01$.

Group	Species	IV	% RA/% RF by community								
			Paus	*Ppun*	*Humb*	*Same*	*Spat*	*Srob*	*Sten*	*Jroe*	*Salt*
Paus	*Phragmites australis*	**96.1**	**96/100**	1/14			0/7	3/16			
	Alternanthera philoroxoides	**34.2**	**46/75**	32/86	16/73	3/13	2/14	1/11			
	Panicum repens	**32.8**	**87/38**	10/7	1/9	1/3					
Ppun	*Polygonum punctatum*	**54.3**	2/25	**58/93**	26/82	10/33		4/5	0/4		
	Ipomoea sagittata	**39.4**		**57/69**	5/45	19/50	12/29	1/16	5/11		
	Cicuta maculata	**27.1**		**98/28**	2/9						
	Vigna luteola	**24.1**	20/38	**33/72**	5/45	33/57	1/7	8/21	1/11		
	Cyperus odoratus	21.3		69/31		20/30	1/7	11/21			
	Echinochloa walteri	20.9		61/34		11/13	8/14	21/16			
	Cladium mariscus	**19.1**		**69/28**		1/3	30/21				
	Zizaniopsis miliacea	**18.3**	10/25	**59/31**	31/18						
	Colocasia esculenta	15.5	48/25	45/34	7/18	0/3					
	Schoenoplectus californicus	14.1		51/28		2/7	47/21				
	Typha domingensis	13.5	11/13	56/24			33/14				
	Eleocharis quadrangulata	10.3		100/10							
	Eleocharis cellulosa	9.3	14/13	45/21	16/18	22/10	1/7	1/5			
	Schoenoplectus pungens	6.0	8/13	87/7				5/5			
	Mikania scandens	5.8	34/13	28/21	18/18		7/14	13/11			
	Panicum dichotomiflorum	5.4		52/10		48/10					
	Eleocharis rostellata	2.6		77/3		23/3					
Humb	*Hydrocotyle umbellata*	**89.5**		10/38	**89/100**	0/3					
	Panicum hemitomon	**78.9**		13/28	**87/91**						
	Thelypteris palustris	**69.0**		5/10	**95/73**						
	Morella cerifera	**54.5**			**100/55**						
	Leersia hexandra	**51.7**		29/38	**71/73**						
	Ludwigia grandiflora	**38.8**		29/14	**71/55**						
	Sacciolepsis striata	**35.6**		36/41	**56/64**		1/7	7/11			
	Sagittaria lancifolia	**32.1**	0/25	35/76	**50/64**	6/13	5/21	3/11	0/4		
	Sagittaria latifolia	16.5		40/17	60/27						
Same	*Schoenoplectus americanus*	**56.1**	10/13	4/34	3/18	**60/93**		18/26	4/18		
	Lythrum lineare	**46.9**		16/24		**61/77**	6/29	6/16	11/21		
	Eleocharis parvula	17.5				88/20		3/11	1/4	9/5	
	Baccharis halimifolia	16.0		12/14	11/27	69/23	3/14	5/5	0/4		
	Amaranthus australis	11.5	1/13	30/34	1/9	43/27	1/7	15/26	9/14		
Spat	*Spartina patens*	**34.1**	1/25	4/55		22/97	**34/100**	21/95	17/100	0/5	0/7
	Typha latifolia	**28.6**		3/7	12/9		**80/36**	5/11			
	Bacopa monnieri	11.0		23/14	14/36	8/23	51/21	4/21	0/4		
	Paspalum vaginatum	10.3		14/3		20/13	48/21	18/5			
	Leptochloa fusca	6.7		6/3			94/7				
Srob	*Schoenoplectus robustus*	**77.7**		7/10		4/27	5/14	**78/100**	6/14		
	Distichlis spicata	**49.9**	2/13	0/7		14/60	1/14	**50/100**	30/79		3/21
	Batis maritima	15.7		0/3		0/3		75/21	0/4		24/7
	Iva frutescens	11.6		18/14		31/30	8/21	28/42	15/11		
Sten	*Symphyotrichum tenuifolium*	15.1		38/31		16/43	3/7	12/21	30/50	1/5	
	Spartina cynosuroides	9.7		20/17		12/10		1/5	68/14		
Jroe	*Juncus roemerianus*	**65.6**		0/7		9/37	4/14		22/39	**66/100**	
Salt	*Spartina alterniflora*	**43.2**	1/25	0/3		0/20		2/42	17/100	37/100	**43/100**
	Avicennia germinans	21.4							0/4		100/21
	Salicornia depressa	6.1							15/4		85/7

Table 2
Mean % relative cover of the seven most abundant species for each community type. Bold indicates species was a significant indicator ($\alpha = 0.01$) for the group in question. Asterisk indicates species' highest indicator value was for group in question.

Paus		Ppun		Humb		Same		Spat	
_Phragmites australis_*	**66**	_Sagittaria lancifolia_	9	**_Panicum hemitomon_***	**16**	_Spartina patens_	45	**_Spartina patens_***	**70**
_A. philoxeroides_*	**8**	**_Vigna luteola_***	**9**	**_Sagittaria lancifolia_***	**13**	**_Schoen. americanus_***	**13**	**_Typha latifolia_***	**7**
Vigna luteola	5	_Spartina patens_	9	**_Eleocharis_***	**10**	_Vigna luteola_	9	_Leptichloa fusca_*	4
_Panicum repens_*	**4**	**_Polygonum punctatum_***	**8**	**_Leersia hexandra_***	**8**	_Distichlis spicata_	7	_Paspalum vaginatum_*	4
Colocasia esculenta	4	_A. philoxeroides_	6	**_Thelypteris palustris_***	**7**	**_Lythrum lineare_***	**6**	_Bacopa monnieri_*	3
Spartina patens	3	_Colocasia esculenta_*	4	**_Hydrocotyle umbellata_***	**7**	_Juncus roemerianus_	3	_Schoen. californicus_	2
Spartina alterniflora	2	_Leersia hexandra_	3	**_Morella cerifera_**	**4**	_Baccharis halimfolia_*	2	_Typha domingensis_	2

Srob		Sten		Jroe		Salt	
Spartina patens	43	_Spartina alterniflora_	36	_Spartina alterniflora_	79	**_Spartina alterniflora_***	**92**
_Distichlis spicata_*	**24**	_Spartina patens_	34	**_Juncus roemerianus_***	**19**	_Avicennia germinans_*	3
_Schoen robustus_*	**9**	_Distichlis spicata_	15	_Spartina patens_	1	_Salicornia depressa_*	2
Spartina alterniflora	4	_Juncus roemerianus_	7	_Batis maritime_	<1	_Distichlis spicata_	1
Schoen. americanus	4	_Spartina cynosuroides_*	2	_Avicennia germinans_	<1	_Batis maritime_	1
Vgina luteola	2	_Symphyotrichum ten._*	2	_Distichlis spicata_	<1	_Spartina patens_	<1
Phragmites australis	2	_Lythrum lineare_	1	_Eleocharis parvula_	<1		

sites not classified as *Paus*. Other species present included *Alternanthera philoxeroides* and *Vigna luteola*.

Polygonum punctatum (Ppun) communities ($n = 29$; IV = 54.3; Table 1) were most prevalent along the coastal regions of the western delta plain (Fig. 1) that are under strong influence of Atchafalaya River inflows. *Polygonum punctatum* was present at 93% of *Ppun* sites. *Sagittaria lancifolia*, *Vigna luteola*, *Spartina patens*, and *P. punctatum* co-dominated the vegetation assemblages at these sites (Table 2).

Hydrocotyle umbellata (*Humb*) communities ($n = 11$; IV = 89.5; Table 1) were mainly located at the most inland regions of the central delta plain (Fig. 1). *Panicum hemitomon* (IV = 78.9) was also a strong indicator for this community, and both of these species were present at nearly all of *Humb*, and absent from nearly all other sites. Co-dominant species at *Humb* sites included *P. hemitomon* and *Sagittaria lancifolia* (Table 2).

Spartina alterniflora (*Salt*) communities ($n = 14$, IV = 43.2; Table 1) were mainly situated along the shores of major bays along the delta plain (Fig. 1). Vegetation assemblages at these sites consisted almost entirely of *Spartina alterniflora* (Table 1). Though *Spartina alterniflora* was also the strongest indicator for this community type, and was present at all *Salt* locations, it exhibited a low specificity to *Salt* communities (i.e., it was commonly present at sites classified as other communities; Table 1), which greatly diminished the species' IV.

Juncus roemerianus (*Jroe*) communities ($n = 20$, IV = 65.6; Table 1) were situated along the seaward end of the delta plain, just inland from *Salt* sites (Fig. 1). Like *Salt* communities, these sites were dominated by *Spartina alterniflora*, but average cover at these sites also consisted of nearly 20% *J. roemerianus* (Table 2). Thus, the presence of *J. roemerianus* distinguished *Jroe* sites from *Salt* sites.

Symphyotrichum tenuifolium (*Sten*) sites ($n = 28$; IV = 15.1; Table 1) were situated just inland from *Jroe* sites (Fig. 1). These sites were co-dominated by *Spartina alterniflora* and *Spartina patens*, and *Distichlis spicata* was also present in substantial quantities (Table 2). Because dominant species of this group were also dominant in other groups, *Sten* communities did not have strong indicator species. *Symphyotrichum tenuifolium* and *Spartina cynosuroides*, neither of which demonstrated high specificity nor fidelity to *Sten* sites, were the strongest indicators for this community, though neither were statistically significant.

Schoenoplectus americanus (*Same*) sites ($n = 30$; IV = 56.1; Table 1) were concentrated in a band across the delta plain just inland from *Sten* sites, and were also prevalent along the bays on the western portion of the delta plain (Fig. 1). These sites were dominated by *Spartina patens*, and *Schoenoplectus americanus* was almost always present (Table 2). This species showed specificity (60% of all *Schoenoplectus americanus* relative cover occurred at *Same* sites) and fidelity (93% of all *Same* sites contained *Schoenoplectus americanus*) to *Same* sites, and its presence distinguished *Same* communities from other *Spartina patens*-dominated communities.

Schoenoplectus robustus (*Srob*) sites ($n = 19$; IV = 77.7; Table 1) were primarily situated along the coastal reaches of the Chenier Plain in southwest Louisiana (Fig. 1). Like *Same* communities, these sites were dominated by *Spartina patens* (Table 2). However, *Srob* sites could be distinguished from other *Spartina patens*-dominated sites by the presence of *Schoenoplectus robustus* and *Distichlis spicata* (*IV* = 49.9), both which demonstrated high specificity and fidelity to *Srob* communities.

Spartina patens (*Spat*) sites ($n = 14$; IV = 34.1; Table 1) were primarily situated across the Chenier plain at locations inland from *Srob* sites (Fig. 1). These sites were strongly dominated by *Spartina patens*, which on average comprised 70% of the relative cover at these sites (Table 2). Though *Spartina patens* was the strongest indicator for *Spat* sites, its IV was low due to the lack of specificity of this species for *Spat* sites.

3.3. Ordination and species diversity

The first two canonical axes could account for over 90% of the species–environmental relation. Though the combined sum of the canonical eigenvalues comprised only 16.8% of the total inertia in the dataset, this outcome is to be expected to some degree because constrained ordinations such as CCA extract only the variance in species distributions that can be attributed to specific environmental relationships. This low explained variance is also typical of noisy data sets with many zero values (ter Braak, 1986; Jongman et al., 1995). Partial CCA showed that of the 16.8% variance explained by the full CCA model, 9.2%, 5.2%, and 0.9% could be attributable to the pure effects of salinity, tidal amplitude, and percent time flooded, respectively. Another 1.5% could be attributed to interactions between the variables.

Eigenvalues (Table 3) and the intraset correlations (Table 4) of hydrologic variables with the first two ordination axes indicated a strong primary gradient (axis 1) related to average annual salinity and a secondary, nearly orthogonal gradient that was associated with diurnal tidal amplitude. Percent time flooded was not strongly correlated with either of the first two canonical axes. Community types identified by *k*-means clustering are indicated in

Table 3
Summary statistics table for CCA ordination presented.

CCA axis	1	2	3	4
Eigenvalues	0.559	0.191	0.074	0.482
Species-environmental correlations	0.895	0.712	0.562	0.000
Cumulative percentage variance				
Of species data	11.4	15.3	16.8	26.6
Of species-environmental relation	67.9	91.0	100.0	0.0

the ordination diagram of site scores and environmental variables (Fig. 4a), and though some overlap exists, these community types each show a tendency to occupy specific regions of the ordination space. In the ordination diagram, the vector length of a given environmental variable on the CCA plot indicates the degree of correlation between that variable and species distribution. Thus, the first canonical axis distinguishes high salinity sites (*Srob*, *Jroe*, and *Salt*) on the right side of the ordination diagram from lower salinity sites (*Paus*, *Ppun*, and *Humb*) on the left. The second axis largely distinguishes sites with high tidal amplitudes (*Paus*, *Jroe*, and *Salt*) near the lower portion of the ordination diagram from sites with lower amplitudes (*Humb*, *Spat*, and *Srob*) near the top. Sites situated near the center of the diagram either showed intermediate values of tidal amplitude and salinity or showed little variation associated with those variables.

Associations between hydrologic variables and significant indicator species are shown in Fig. 4b. Species associated with higher salinities included *Schoenoplectus robustus*, *Distichlis spicata*, *Juncus roemerianus*, and *Spartina alterniflora*, while those associated with lower salinities included *Hydrocotyle umbellata*, *Panicum hemitomon*, *Polygonum punctatum* and *Ipomoea sagittata*. Concerning tidal amplitude, species associated with higher tidal amplitudes included *Alternanthera philoxeroides*, *Panicum repens*, *J. roemerianus*, and *Spartina alterniflora*, while those associated with lower amplitudes included *P. hemitomon*, *Schoenoplectus robustus*, and *Spartina patens*.

Species diversity varied widely across community types and was greatest in *Ppun* and *Humb* communities (Fig. 5a). Diversity was intermediate for *Paus*, *Same*, *Spat*, *Srob and Sten* communities, and very low for *Jroe* and *Salt* communities. Diversity was inversely correlated with salinity (Fig. 5b; $r^2 = 0.47$, $p < 0.001$).

3.4. Multiple multinomial logistic regression

Because percent time flooded comprised less than 1% of the total inertia in the 173 samples (compared with 9.2% and 5.2% for salinity and tidal amplitude, respectively), the candidate set of MLR models was restricted to those that only included the effects of salinity and/or tidal amplitude. Fifteen combinations of linear and quadratic terms of salinity and tidal amplitude were included in the candidate set, and all models in the set were highly significant (Table 5). The minimum AIC$_c$ score was obtained for the model that included a linear term for salinity and linear and quadratic terms for tidal amplitude (model 1), and was therefore accepted as the best model of community type as a function of salinity and tidal amplitude. Akaike weights indicated that none of the remaining candidate models could be considered competing models.

Table 4
Canonical coefficients and intraset correlations of environmental variables with the first two axes of the CCA.

Variables	Canonical coefficients		Intraset correlations	
	Axis 1	Axis 2	Axis 1	Axis 2
Salinity	1.35	0.61	0.97	0.21
Tide range	0.37	−0.52	0.53	−0.77
% Time inundated	0.01	−1.28	−0.18	−0.01

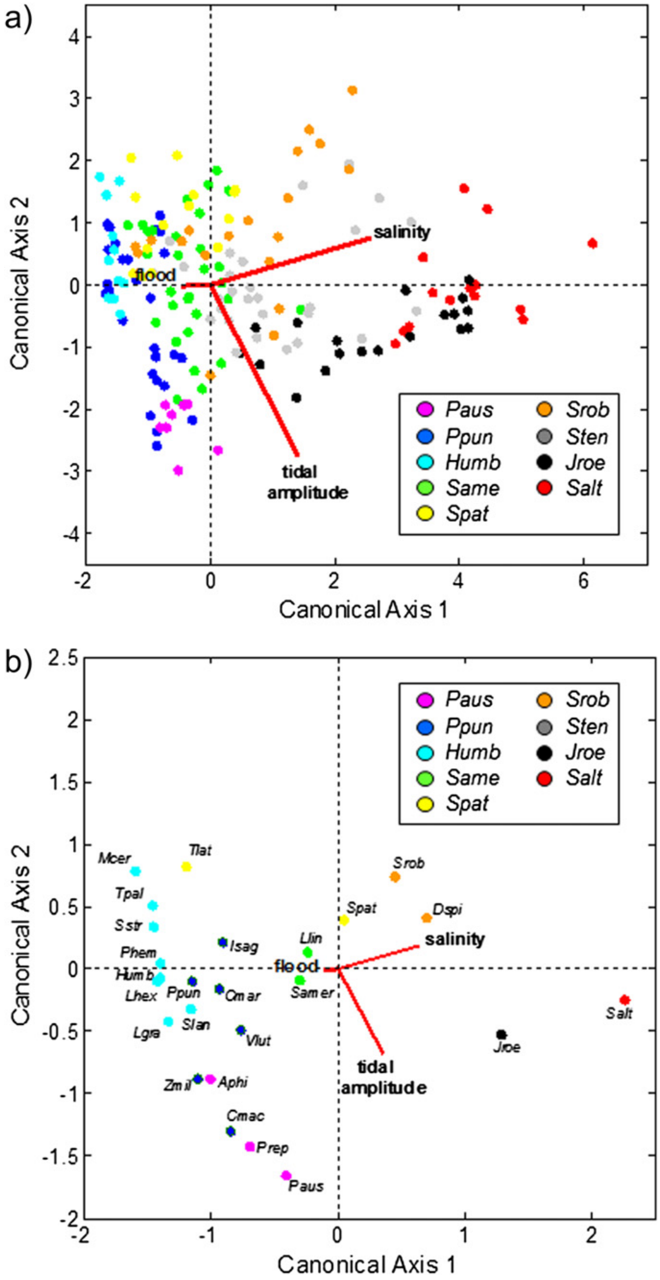

Fig. 4. Plot of sample scores (a) and centroids for significant indicator species (b) on the first two canonical axes for the canonical correspondence analysis of vegetation cover in the 173 samples. Arrows indicate direction of increasing value for environmental variables. Color indicates community type to which samples were classified (upper panel) or community type best indicated by species (lower panel). Species codes are first letter of genus and first three letters of specific name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Model 1 was used to estimate the probability of occurrence for each community type as a function of salinity and tidal amplitude (Table 6; Fig. 6). In a general sense, the model corroborates the CCA results. Community types most likely to occur at sites with low salinity include *Paus*, *Ppun*, *Humb*, and *Same*. These sites contain high abundances of *Phragmites australis*, *Sagittaria lancifolia*, *Polygonum punctatum*, *Panicum hemitomon*, *Spartina patens*, and

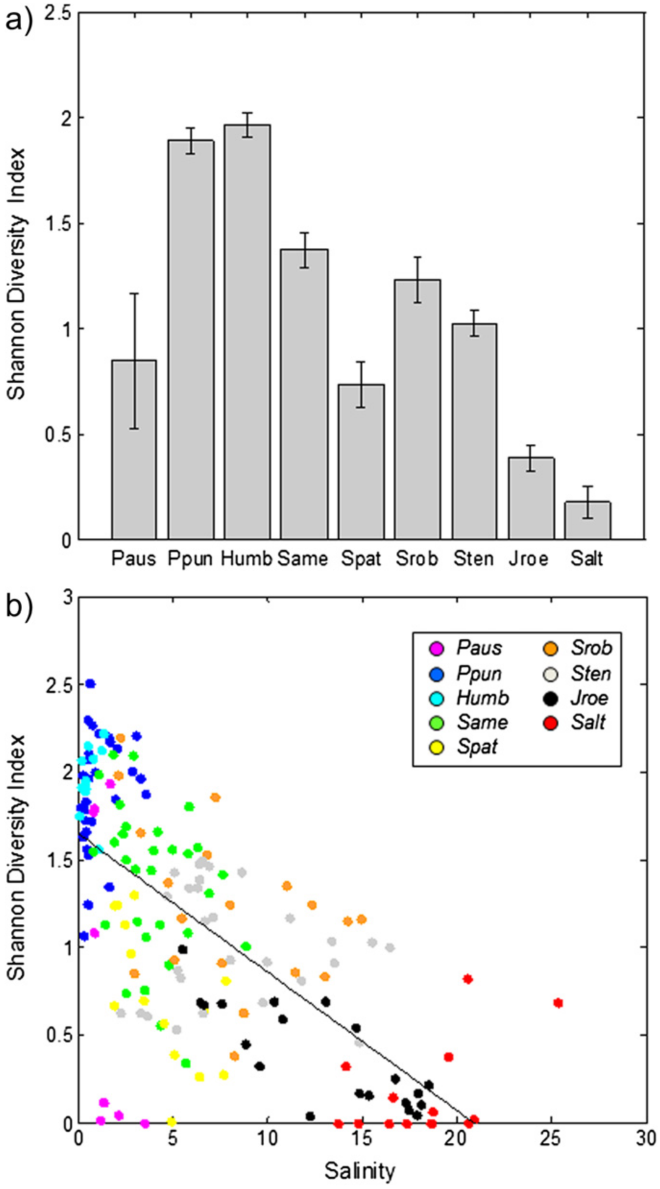

Fig. 5. Mean Shannon diversity indices with standard errors for the nine community types (a) and regression of Shannon diversity indices against average annual salinity for the 173 samples (b).

Table 5
Model variables (T = tide, S = salinity), number of estimated variables (k), log likelihood ($-2\ln L$), model probabilities (p, from Wald statistic), Akaike's Information Criteria corrected for small sample size (AIC_c), and Akaike weights (w_i) for the 10 best models in the candidate set.

Model	Effects	k	-2 (ln$L$)	p	AIC_c	w_i
1	$S + T + T^2$	32	345.59	<0.0001	410.20	0.96
2	$S^2 + T + T^2$	32	352.71	<0.0001	417.32	0.03
3	$S + T$	24	372.05	<0.0001	420.48	0.01
4	$S + S^2 + T + T^2$	40	340.89	<0.0001	421.72	<0.01
5	$S^2 + T$	24	378.95	<0.0001	427.39	<0.01
6	$S + T^2$	24	381.64	<0.0001	430.07	<0.01
7	$S + S^2 + T^2$	32	369.44	<0.0001	434.06	<0.01
8	$S^2 + T^2$	24	387.99	<0.0001	436.43	<0.01
9	$S + S^2 + T^2$	32	379.27	<0.0001	443.89	<0.01
10	S	16	468.85	<0.0001	501.13	<0.01

Table 6
Estimated regression coefficients for the best MLR model. Coefficients were not obtained for *Salt* communities because *Salt* was used as the reference category.

Community type	Intercept	S	T	T^2
Paus	−67.63	−1.78	6.85	−0.14
Ppun	28.43	−2.95	−1.13	0.02
Humb	28.34	−4.06	−0.02	−0.15
Same	23.89	−1.23	−0.89	0.02
Spat	24.28	−1.14	−1.12	0.01
Srob	21.95	−0.76	−1.14	0.02
Sten	17.57	−0.66	−0.47	0.01
Jroe	−1.91	−0.44	0.63	−0.01

Schoenoplectus americanus (Table 2). *Srob*, *Sten*, *Jroe*, and *Salt* communities, which are dominated by species such as *Spartina patens*, *Distichlis spicata*, *Schoenoplectus robustus*, *Juncus roemerianus*, and *Spartina alterniflora*, are expected to be found at high salinity sites. *Humb*, *Spat*, and *Srob* communities are most likely to be found at sites with low tidal amplitudes, while higher amplitudes are predicted to be occupied by *Paus*, *Jroe*, and *Salt* communities. The model predicts *Ppun* and *Same* communities to be found across a broad range of tidal amplitudes. The range and mean value of the predictor variables for each community type (Table 7) reflect the general patterns obtained with the MLR model.

Overall correct classification rate of the model was 60.7%, which far exceeds the chance accuracy rate of 12.9%, calculated as the sum of the squared proportions of each community type in the dataset (Hand et al., 2001). The weighted Cohen's kappa value, obtained from the confusion matrix (Table 8) and weightings obtained from the normalized distance matrix between community types (Table 9), was 0.70 and indicates good agreement between observed and model-predicted community types (Fielding and Bell, 1997). When classification errors occurred, they tended to occur between community types with relatively low pairwise distances, indicating misclassification to ecologically-similar community types. Regarding specific community types, the model prediction accuracies ranged from below 40% for *Srob* communities to greater than 70% for *Paus*, *Ppun*, *Sten*, and *Salt* communities (Table 8).

4. Discussion

The various aspects of wetland hydrology act to influence coastal wetland vegetation zonation in complex and interacting ways. Anticipating and modeling the manner in which hydrologic variability governs plant zonation is important, as rates of productivity (Callaway et al., 2012), sediment accretion (Becket, 2009), and carbon sequestration (Odum, 1988) are all strongly related to the type of vegetation community present. Though landscape habitat change models have been developed to forecast vegetation community composition response to hydrologic variability in coastal Louisiana (Reyes et al., 2000; Visser et al., 2003), they resolve communities to no more than four types, whereas upwards of 15 community types have been delineated (Visser et al., 1998, 2000). Additionally, these models have relied on arbitrary salinity ranges based on either expert opinion or limited data related to only the single most dominant species in each community type to determine which community is present at a given location. Community occurrence probabilities as a function of hydrology obtained with the multinomial logistic regression approach here take into account all species comprising each community type, and can be readily incorporated into existing landscape habitat change models, increasing their resolution in terms of community type and making their predictions probabilistic in nature. Incorporating these empirically-determined occurrence probabilities into these models would increase their

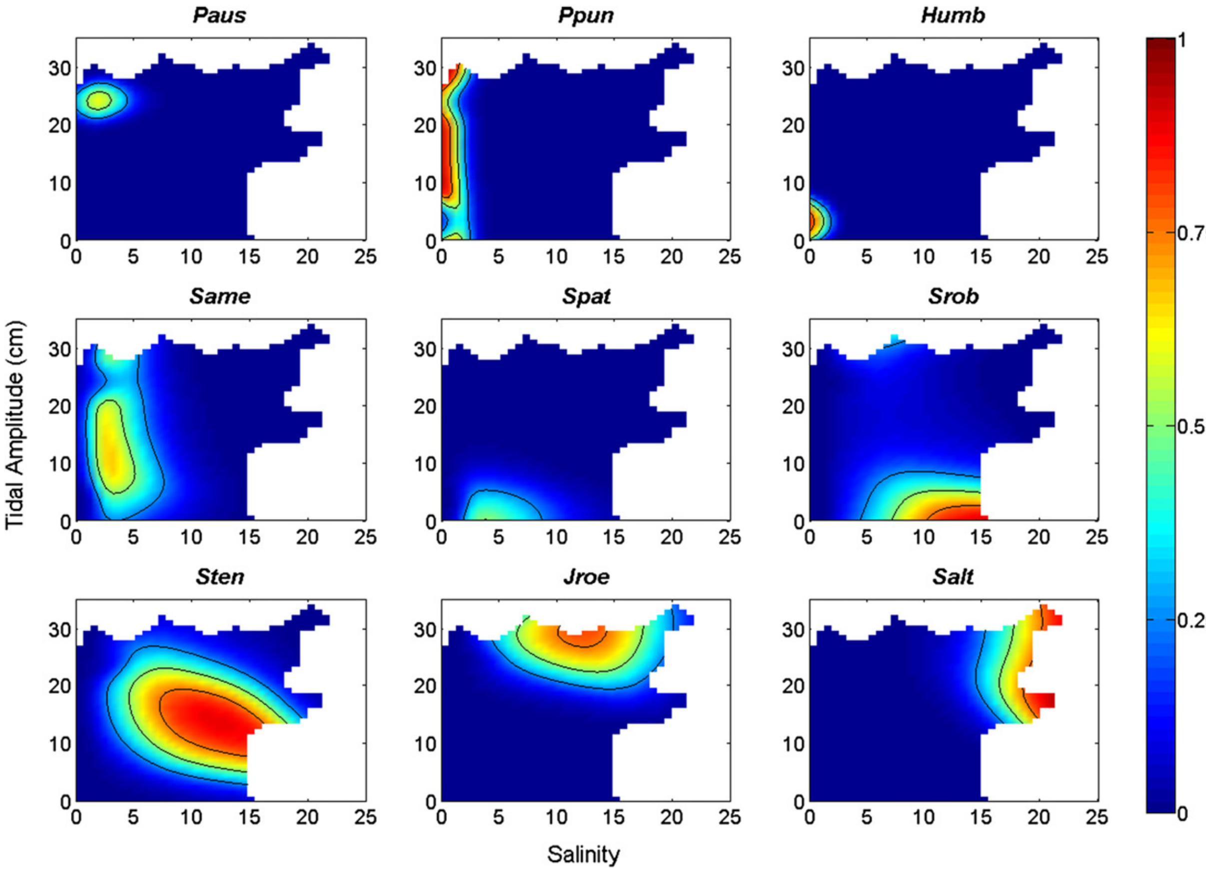

Fig. 6. Probability surfaces as a function of salinity and tidal amplitude for the nine community types identified by *k*-means clustering. The white region outside the bounds of the probability surface represents salinity and tidal amplitude combinations that did not exist in the dataset.

rigor and enhance their ability to predict landscape changes to continued hydrologic alterations such as river diversions, levee construction and sea-level rise that are occurring in coastal wetlands throughout the world.

The vegetation communities delineated by *k*-means clustering in this study correspond in a general sense with classifications obtained from previous studies on the Mississippi River Delta Plain (southeastern Louisiana; Visser et al., 1998) and Chenier Plain (southwestern Louisiana; Visser et al., 2000, Fig. 7). For example, the community types delineated in this study effectively subdivided the polyhaline oystergrass community described by Visser et al. (1998, 2000) into communities containing only *Spartina alterniflora* (*Salt*), those dominated by *S. alterniflora* that also included *Juncus roemerianus* (*Jroe*), and those where *S. alterniflora* was co-dominant with *Distichlis spicata* and *Spartina patens* (*Sten*). *Humb* sites, which were dominated by *Panicum hemitomon* and *Sagittaria lancifolia*, were mainly classified as fresh bulltongue and fresh maidencane communities by Visser et al. (1998, 2000).

Table 7
Mean values (range in parentheses) for average annual salinity, percent time flooded, and tidal amplitude for each of the nine community types identified.

Community type	Average annual salinity	Percent time flooded	Tidal amplitude (cm)
Paus	1.5 (0.8–3.5)	68.6 (46.1–95.5)	24.3 (20.7–26.8)
Ppun	1.2 (0.2–3.6)	57.3 (1.4–100.0)	10.4 (0.3–29.9)
Humb	1.0 (0.2–3.3)	61.7 (9.6–98.5)	1.8 (0.1–6.1)
Same	4.0 (0.2–8.8)	44.9 (8.6–90.4)	11.3 (0.3–27.7)
Spat	4.3 (1.9–7.8)	55.4 (4.3–100.0)	2.2 (0.0–10.1)
Srob	7.8 (2.1–14.9)	55.2 (12.2–98.5)	7.0 (0.1–27.4)
Sten	8.2 (2.3–16.4)	44.8 (16.1–81.7)	16.4 (6.7–28.9)
Jroe	12.8 (3.5–18.5)	50.8 (29.1–72.0)	26.5 (19.8–31.7)
Salt	18.3 (13.7–20.9)	49.7 (37.1–61.5)	25.9 (15.2–32.9)

Indicator species analysis was generally effective at identifying species indicative of the nine community types delineated by *k*-means clustering. Scores for *Spartina patens* and *Spartina alterniflora* were relatively low for their respective groups because although these species were often present in high abundances, they were commonly present in multiple community types (i.e., the fidelity of these species to a particular community was low). Nevertheless, *S. patens* and *S. alterniflora* could effectively indicate their respective communities when taking into account the absence of other indicator species with higher *IV* scores. Only *Sten* communities lacked any significant indicator species, which may reflect that these communities result from overlap between *Spat*, *Jroe*, and *Salt* communities.

Salinity clearly had the strongest association with the zonation of vegetation assemblages across a spatial gradient from sites situated near freshwater inputs, provided either by upland runoff or discharge from the Mississippi and Atchafalaya Rivers, to sites hydrologically isolated from these inputs. The strength of salinity relative to other factors was reflected by its high intraset correlation with the first canonical axis (Table 4), and also by its relatively high proportion of variance explained compared to the other hydrologic variables. The overriding importance of salinity in regulating community composition across an estuarine gradient observed in this study is in agreement with several previous studies (Adams, 1963; Phleger, 1971; Cooper, 1982; Ewing, 1983; Odum, 1988; Latham et al., 1994).

Table 8
Leave-one-out cross-validation confusion matrix for predicting community type. Bold cells in table diagonals indicate correct classifications.

Actual	Predicted									Total	Proportion correct
	Paus	*Ppun*	*Humb*	*Same*	*Spat*	*Srob*	*Sten*	*Jroe*	*Salt*		
Paus	**6**	1		1						8	0.75
Ppun	1	**21**	2	3	2					29	0.72
Humb		5	**6**							11	0.55
Same		4		**16**	3	3	3	1		30	0.53
Spat		3		1	**6**	3	1			14	0.43
Srob	1	2		1	3	**7**	4	1		19	0.37
Sten				5			**20**	3		28	0.71
Jroe							4	**12**	4	20	0.60
Salt								3	**11**	14	0.79

Vegetation assemblages were further differentiated by tidal amplitude, which produced a vector in ordination space orthogonal to that of salinity (Fig. 4). For example, whereas *Ppun* and *Humb* communities were both found where salinities were low, *Humb* communities showed a strong tendency toward low tidal amplitude. Similarly, though *Jroe* and *Srob* occupied similar positions along the salinity gradient in ordination space, they were strongly separated along the tidal amplitude gradient. Casanova and Brock (2000) observed that duration of individual inundation events, rather than total time inundated, correlated best with segregation of communities. In the wetlands of the northern Gulf of Mexico, sites with high tidal amplitudes typically exhibit many punctuated inundation events whereas those with low tidal amplitudes usually exhibit fewer inundation events of greater duration driven by non-astronomical phenomena such as meteorological or fluvial forcing. Edaphic factors such as porewater salinity (Lara and Cohen, 2006), redox potential (Armstrong et al., 1985; Pezeshki, 2001), pH (Gambrell et al., 1991) and nutrient availability (Odum et al., 1979), all of which can influence vegetation zonation (Bockelmann et al., 2002), are largely dependent on the lengths of wetting and drying events on the marsh surface and the frequency at which water exchanges between the marsh surface and surrounding waters occur.

The orthogonal nature of the salinity and tidal amplitude vectors suggest that the variables were uncorrelated with each other (Leps and Smilauer, 2003) and together the salinity and tidal amplitude gradients effectively partition the sites into four distinct hydrologic regimes, and these regimes were reflected in their spatial distribution with regard to hydrographic features across the Louisiana coast. First, sites with high tidal amplitudes and high salinities are situated along the coastal ocean away from fluvial inputs. These sites are concentrated along the lower reaches of interdistributary basins along the deltaic plain (Fig. 8), while the upper reaches of these distributary basins consist of sites with reduced salinity and tidal amplitude. Sites with high tidal amplitude and low salinities were concentrated around the mouths of the Mississippi and Atchafalaya Rivers, while sites with elevated salinities and minimal tidal amplitudes were found primarily in the managed marshes situated far from freshwater inputs on the Chenier plain in southwest Louisiana.

This study did not identify percent time flooded as being an important factor that governs plant species composition. This finding is contrary to several studies that have shown transitions in species composition from *Spartina alterniflora* to *Juncus* spp. along increasing elevation gradients in saline marshes (Eleuterius and Eleuterius, 1979; Niering and Warren, 1980; Latham et al., 1994; Pennings et al., 2005). Transitions in species composition along elevation gradients have also been observed in tidal fresh marshes (Simpson et al., 1983; Latham et al., 1994), although patterns of zonation may be less distinct than those observed in saline marshes (Hoover, 1984; Odum et al., 1984). The absence of a flooding effect observed in this study may result from the discrepancy in scales at which marsh elevation and vegetation composition were assessed. Protocols for the CRMS monitoring program are such that marsh elevation for each site was assessed within a 15-m radius of a central point at each of the 173 sites, whereas vegetation at each site was assessed at 10 plots along a 280-m transect and subsequently averaged (Fig. 2). At some sites, gradients in vegetation species composition along the lengths of the transects were

Table 9
Normalized distance matrix between cluster centroids for the nine community types delineated by *k*-means clustering. Dashes in table diagonals indicate zero distance.

	Paus	*Ppun*	*Humb*	*Same*	*Spat*	*Srob*	*Sten*	*Jroe*	*Salt*
Paus	–	0.56	0.60	0.66	0.79	0.67	0.69	0.83	0.97
Ppun	0.56	–	0.21	0.34	0.53	0.38	0.42	0.65	0.83
Hum	0.60	0.21	–	0.45	0.63	0.47	0.49	0.67	0.84
Same	0.66	0.34	0.45	–	0.27	0.20	0.35	0.73	0.90
Spat	0.79	0.53	0.63	0.27	–	0.32	0.45	0.85	1.00
Srob	0.67	0.38	0.47	0.20	0.32	–	0.31	0.72	0.88
Sten	0.69	0.42	0.49	0.35	0.45	0.31	–	0.44	0.59
Jroe	0.83	0.65	0.67	0.73	0.85	0.72	0.44	–	0.27
Salt	0.97	0.83	0.84	0.90	1.00	0.88	0.59	0.27	–

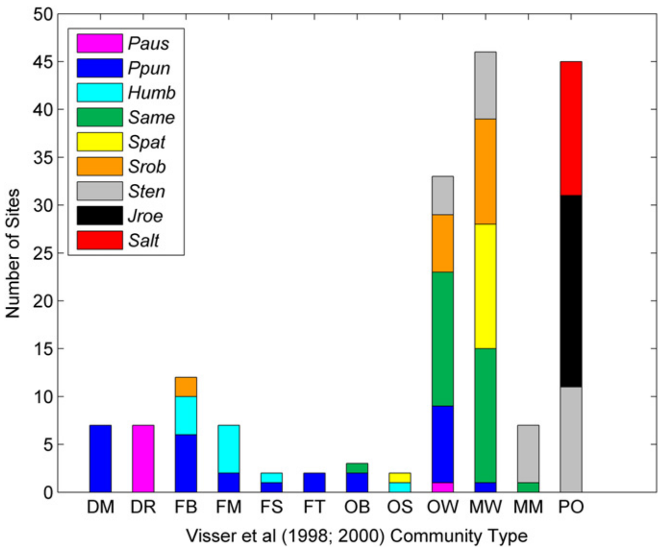

Fig. 7. Correspondence of nine community types identified in this study with classifications previously established by Visser et al. (1998, 2000), which include deltaic mixture (DM), deltaic Roseau cane (DR), fresh bulltongue (FB), fresh maidencane (FM), fresh spikerush (FS), fresh Typha (FT), oligohaline bulltongue (OB), oligohaline spikerush (OS), oligohaline wiregrass (OW), mesohaline wiregrass (MW), mesohaline mixture (MM), and polyhaline oystergrass (PO).

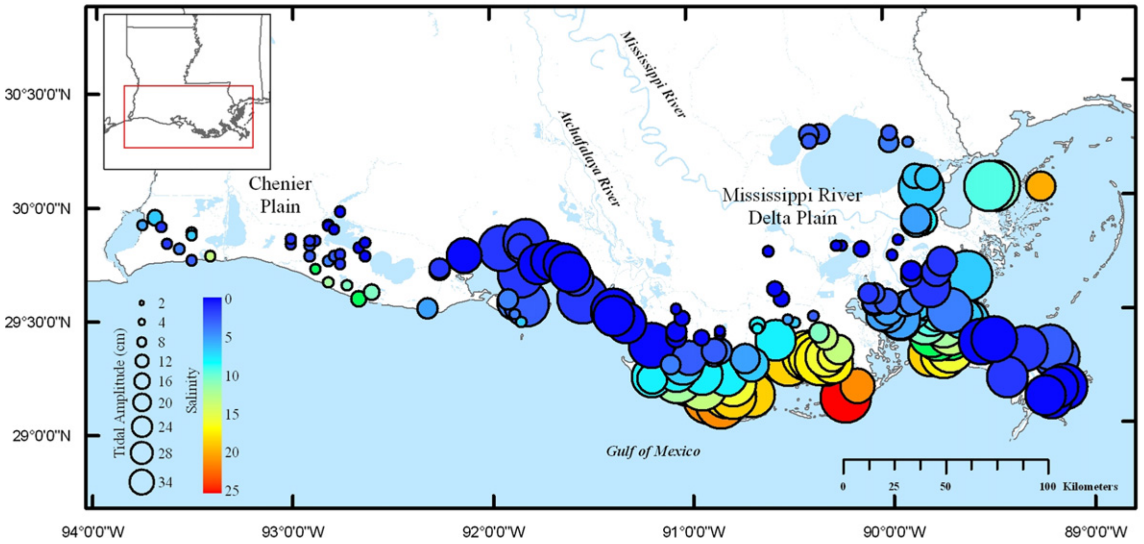

Fig. 8. Average annual salinity and tidal amplitude for the 173 sites included in the study.

observed, and the possibility that these composition gradients may have existed in response to subtle changes in elevation along the transects needs to be further examined.

The inverse relationship between salinity and species diversity observed in this study, combined with the patterns of zonation we observed along the estuarine salinity gradient, corroborate findings from others studies which suggest that although salinity tolerance may regulate the downstream distributional limits of estuarine vegetation species (or community types, in this case), it may not govern the upstream limits. Wilson et al. (1996) observed correlation between the salinity tolerances of nine vegetation species assessed through greenhouse experiments and their downstream distributional limits, but not with their upstream limits, and suggested that other factors such as competition are the important factors regulating community structure in fresh and intermediate marshes. This hypothesis is supported by findings from transplant studies, in which freshwater vegetation species transplanted to saline settings with or without neighboring salt marsh vegetation present experienced increased mortality in both cases, while salt marsh vegetation transplanted to fresh settings experienced increased mortality only in the presence of neighboring fresh marsh vegetation (Crain et al., 2004; Engels and Jensen, 2010). Wieski et al. (2010) suggest that salinity acts as an evolutionary filter in the downstream direction by preventing fresh species from adapting to harsh saline conditions, while acting as an ecological filter in the opposite direction by competitively excluding salt tolerant species even though they should perform better in low salinity regimes where their osmoregulatory energy expenditures would be reduced. Thus, models that predict estuarine marsh vegetation community structure and productivity based on edaphic factors should include not only the impacts of physiological tolerance, but also interspecific competitive interactions.

The weighted Cohen's kappa coefficient (0.70) obtained from the confusion matrix indicated good agreement between actual and model-predicted vegetation communities (Landis and Koch, 1977). The broad range in correct classification rate across community types (0.37–0.79; Table 8) tended to reflect the degree to which the species composition of a particular community type was distinct from those of other community types, as indicated by the pairwise distance matrix between cluster centroids (Table 9). For example, *Salt* communities generally exhibited relatively high pairwise distances to other communities and, as such, were rarely classified as other communities. In contrast, *Srob* communities exhibited a correct classification rate of only 0.37, and when the model misclassified *Srob* sites, it tended to classify them as community types which exhibited relatively low pairwise distances from *Srob* communities. In other words, assuming pairwise distances between community types reflect their ecological dissimilarity (Jongman et al., 1995), misclassifications were generally restricted to ecologically similar community types.

Brief, extreme events which may not be strongly reflected by the annual mean may in some cases be able to strongly influence productivity, and ultimately species composition. McKee and Mendelssohn (1989) observed that sudden salinity increases to 15 were lethal to *Sagittaria lancifolia*, *Panicum hemitomon* and *Leersia oryzoides*. Pezeshki et al. (1987b) reported diminished gas exchange of *P. hemitomon* within one day of exposure to salinities of 5, and tissue death after four days of exposure to 10. Net photosynthesis in *Spartina patens* was reduced 43% within 24 h following rapid exposure to ambient salinities in excess of 22 (Pezeshki et al., 1987c). Though sal_{95}, used as a metric for the importance of episodic salinity pulses, was not included in the MLR model, it was excluded on the basis of its high correlation with average annual salinity ($r = 0.90$; Fig. 3), another predictor variable already included in the model.

Increases in salinity and tidal amplitude in coastal wetlands are expected outcomes of continued sea level rise, and the model presented here helps to illustrate what kinds of vegetation community shifts can be anticipated. For example, an increase in the prevalence of *Salt* and *Jroe* communities could be expected as they are associated with high salinities and tidal amplitudes. *Humb* communities, which are dominated by *Panicum hemitomon* and found in regions with very low values for both salinity and tidal amplitude, would likely become far less prevalent and be replaced by either *Same*, *Srob*, or *Sten* communities. Many of the sites classified as *Humb* are either fully or seasonally floating *P. hemitomon* stands (Sasser et al., 1995, 1996) located in regions of the deltaic plain that have been abandoned by the Mississippi River where very high rates of peat accretion (>0.75 cm yr^{-1}) now control soil accretion (DeLaune, 1986; Nyman et al., 2006). Facing rising sea levels, restoration efforts in tidal freshwater marshes receiving little or no fluvial sediment delivery may be most effective if they aim to sustain communities such as *Humb* where organic accretion processes dominate (Turner et al., 2004). Enhancing the rigor of landscape change simulation models with empirically-derived parameters obtained from field studies that relate vegetation community types to hydrology is critical for effective restoration planning.

Acknowledgments

This study was funded in part by the U.S. Geological Survey and the National Aeronautics and Space Administration under the solicitation “Earth Science for Decision Making: Gulf of Mexico Region”, and in cooperation with the Coastal Wetlands Planning, Protection and Restoration Act, Coastwide Reference Monitoring Program. Megan LaPeyre, Guerry Holm, James Grace and four anonymous reviewers provided valuable comments on a previous version of this manuscript. Any use of trade, product, or firm names is for descriptive purposes and does not imply endorsement by the U.S. Government.

References

Ablain, M.A., Cazenave, A., Valladeau, G., Guinehut, S., 2009. A new assessment of the error budget of global mean sea level rage estimated by satellite altimetry over 1993–2008. Ocean Science 5, 193–201.

Adams, D.A., 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44, 445–455.

Akaike, H., 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 19, 716–723.

Alfaro, A.C., 2006. Benthic macro-invertebrate community composition within a mangrove/seagrass estuary in northern New Zealand. Estuarine, Coastal and Shelf Science 66, 97–110.

Anderson, D.R., Burnham, K.P., Thompson, W.L., 2000. Null hypothesis testing: problems, prevalence, and an alternative. Journal of Wildlife Management 64, 912–923.

Araujo, M.B., Pearson, R.G., Thuillers, W., Erhard, M., 2005. Validation of species-climate impact models under climate change. Global Change Biology 11, 1504–1513.

Armstrong, W., Wright, E.J., Lythe, S., Gaynard, T.J., 1985. Plant zonation and the effects of the spring-neap tidal cycle on soil aeration in a Humber salt marsh. Journal of Ecology 73, 323–339.

Beckett, L.H.M., 2009. Marsh elevation and accretion dynamics along estuarine salinity gradients: observational and experimental studies. M.S. thesis, University of Maryland, p. 78.

Bertness, M.D., Ellison, A.M., 1987. Determinants of pattern in a New England salt marsh community. Ecological Monographs 57, 129–147.

Boesch, D.F., Josselyn, M.N., Mehta, A.J., Morris, J.T., Nuttle, W.K., Simenstad, C.A., Swift, D.J.P., 1994. Scientific assessment of coastal wetland loss, restoration and management in Louisiana. Journal of Coastal Research Special Issue 20, 1–103.

ter Braak, C.J.F., 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. Ecology 67, 1167–1179.

ter Braak, C.J.F., Smilauer, P., 2002. CANOCO Reference Manual and CanoDraw for Windows User’s Guide: Software for Canonical Community Ordination (Version 4.5). Microcomputer Power, Ithaca, NY, p. 500.

Bockelmann, A.-C., Bakker, J.P., Neuhaus, R., Lage, J., 2002. The relation between vegetation zonation, elevation and inundation frequency in the Wadden Sea salt marsh. Aquatic Botany 73, 211–221.

Braun-Blanquet, J., 1932. Plant Sociology (Transl. Fuller, G.D. and Conrad, H.S.). McGraw-Hill, New York, p. 539.

Braun-Blanquet, J., 1964. Pflanzensociologie: Grundzuge der Vegetation-skunde. Springer-Verlag, Vienna, p. 865.

Burnham, K.P., Anderson, D.R., 1998. Model Selection and Multimodel Inference: a Practical Information-theoretic Approach. Springer, New York, p. 488.

Calinski, T., Harabasz, J., 1974. A dendrite method for cluster analysis. Communications in statistics. Theory and Applications 3, 1–27.

Callaway, J.C., Bordge, A.B., Diefenderfer, H.L., Parker, V.T., Rybczyk, J.M., Thom, R.M., 2012. Pacific coast tidal wetlands. In: Batzer, D.P., Baldwin, A.H. (Eds.), Wetland Habitats of North America: Ecology and Conservation Concerns. University of California Press, Berkely, USA, p. 389.

Callaway, R.M., Parker, V.T., Vasey, M.C., Schile, L.M., 2007. Emerging issues for the restoration of tidal marsh ecosystems in the context of predicted climate change. Madrono 54, 234–248.

Casanova, M.T., Brock, M.A., 2000. How do depth, duration and frequency of flooding influence the establishment of wetland plant communities? Plant Ecology 147, 237–250.

Cohen, J., 1968. Weighted Kappa: nominal scale agreement with provision for scaled disagreement or partial credit. Psychological Bulletin 70, 213–220.

Coleman, J.M., Roberts, H.H., Stone, G.W., 1998. The Mississippi River delta: an overview. Journal of Coastal Research 3, 698–716.

Cooper, A., 1982. The effects of salinity and waterlogging on the growth and cation uptake of salt marsh plants. New Phytologist 90, 263–275.

Crain, C.M., Sillman, B.R., Bertness, S.L., Bertness, M.D., 2004. Physical and biotic drivers of plant distribution across estuarine salinity gradients. Ecology 85, 2539–2549.

DeLaune, R.D., Smith, C.J., Sarafyan, M.N., 1986. Nitrogen cycling in a freshwater marsh of Panicum hemitomon on the deltaic plain of the Mississippi River. Journal of Ecology 74, 249–256.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological. Monographs 67, 345–366.

Eleuterius, L.N., Eleuterius, C.K., 1979. Tide levels and salt marsh zonation. Bulletin of Marine Science 29, 394–400.

Emery, W.J., Thompson, R.E., 2001. Data Analysis Methods in Physical Oceanography. Elsevier, Amsterdam, p. 638.

Engels, J.G., Jensen, K., 2010. Role of biotic interactions and physical factors in determining the distribution of marsh species along an estuarine salinity gradient. Oikos 119, 679–685.

Ewing, K., 1983. Environmental controls in Pacific Northwest intertidal marsh plant communities. Canadian Journal of Botany 61, 1105–1116.

Ewing, K., McKee, K., Mendelssohn, I., Hester, M., 1995. A comparison of indicators of sublethal salinity stress in the salt marsh grass, Spartina patens (Ait.) Muhl. Aquatic Botany 52, 59–74.

Fielding, A.H., 2007. Cluster and Classification Techniques for the Biosciences. Cambridge University Press, Cambridge, p. 258.

Fielding, A.H., Bell, J.F., 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24, 38–49.

Forbes, M.G., Dunton, K.H., 2006. Response of a subtropical estuarine marsh to local climatic change in the southwestern Gulf of Mexico. Estuaries and Coasts 29, 1242–1254.

Gambrell, R.P., DeLaune, R.D., Patrick, W.H., 1991. Redox processes in soils following oxygen depletion. In: Hook, D.D., Crawford, R.M.M. (Eds.), Plant Life in Anaerobic Environments. Ann Arbor Science, Ann Arbor, Michigan, USA, pp. 375–423.

Greiner La Peyre, M.K., Grace, J.B., Hahn, E., Mendelssohn, I.A., 2001. The importance of competition in regulating species abundance along a salinity gradient. Ecology 82, 62–79.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. Ecological Modelling 135, 147–186.

Gunderson, L.H., 2000. Ecological resilience – in theory and application. Annual Review of Ecology and Systematics 31, 425–439.

Hair, J.F., Anderson, R.E., Tatham, R.L., Black, W.C., 1992. Multivariate Data Analysis. Macmillan Publishing Company, New York, p. 544.

Hand, D.J., Mannila, H., Smyth, P., 2001. Principles of Data Mining. MIT Press, Cambridge, MA, p. 578.

Hill, M.O., Gauch, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42, 47–58.

Hilton, T.W., Najjar, R.G., Zhong, L., Li, M., 2008. Is there a signal of sea-level rise in Chesapeake Bay salinity? Journal of Geophysical Research 113, C09002.

Hoover, J.K., 1984. Spatial and temporal niche relationships in a tidal freshwater macrophyte community. M.S. thesis, University of Virginia-Charlottesville, p. 85.

Hosmer, D.W., Lemeshow, S., 2000. Applied Logistic Regression. Wiley-Interscience, New York, p. 392.

Howard, R.J., 1995. Increased salinity and water depth as constraints on growth of freshwater plants. Ph.D. thesis, Louisiana State University, Baton Rouge.

Hurvich, C.M., Tsai, C.L., 1989. Regression and time series model selection in small samples. Biometrika 76, 297–307.

IPCC, 2007. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis, Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, p. 996.

Jongman, R.H.G., ter Braak, C.J.F., Van Tongeren, O.F.R., 1995. Data Analysis in Community and Landscape Ecology. Cambridge University Press, New York, p. 299.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. Biometrics 33, 159–174.

Latham, P.J., Pearlstine, L.G., Kitchens, W.M., 1994. Species association changes across a gradient of freshwater, oligohaline, and mesohaline tidal marshes along the lower Savannah River. Wetlands 14, 174–183.

Lara, R.J., Cohen, M.C.L., 2006. Sediment porewater salinity, inundation frequency and mangrove vegetation height in Bragança, North Brazil: an ecohydrology-based empirical model. Wetlands Ecology and Management 14, 349–358.

Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier, Amsterdam, p. 853.

Leps, L., Smilauer, P., 2003. Multivariate Analysis of Ecological Data using CANOCO. Cambridge University Press, New York, p. 269.

McKee, K.L., Mendelssohn, I.A., 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. Aquatic Botany 34, 301–316.

Mendelssohn, I.A., McKee, K.L., 1987. Experimental field and greenhouse verification of the influence of saltwater intrusion and submerging on marsh deterioration: mechanisms of action. In: Turner, R.E., Cahoon, D.R. (Eds.), Causes of Wetland Loss in the Coastal Central Gulf of Mexico, vol. II. Technical narrative (OCS Study/MMS 87-120, Final report).

Miranda, L.B., Castro, B.M., Kjerfve, B.J., 1998. Circulation and mixing due to tidal forcing in the Bertioga Channel, Sao Paulo, Brazil. Estuaries 21, 204–214.

Miranda, L.B., Bergamo, A.L., Castro, B.M., 2005. Interactions of river discharge and tidal modulation in a tropical estuary, NE Brazil. Ocean Dynamics 55, 430–440.

Mitsch, W.J., Gosselink, J.G., 1986. Wetlands. Van Norstrand Reinhold Company, New York, NY, USA, p. 539.

Naesset, E., 1996. Use of the weighted Kappa coefficient in classification error assessment of thematic maps. International Journal of Geographic Information Systems 10, 591–604.

Niering, W.A., Warren, R.S., 1980. Vegetation patterns and processes in New England salt marshes. Bioscience 30, 301–307.

Nyman, J.A., Walters, R.J., Delaune, R.D., Patrick, W.H., 2006. Marsh vertical accretion via vegetative growth. Estuarine, Coastal and Shelf Science 69, 370–380.

Odum, E.P., Finn, J.T., Franz, E.H., 1979. Perturbation theory and the subsidy-stress gradient. BioScience 29, 349–352.

Odum, W.E., 1988. Comparative ecology of tidal freshwater and salt marshes. Annual Review of Ecological Systems 19, 147–176.

Odum, W.E., Smith, T.J., Hoover, J.K., McIvor, C.C., 1984. The Ecology of Tidal Freshwater Marshes of the United States East Coast: a Community Profile, US Fish and Wildlife Service FWS/OBS-83/17, p. 177.

Officer, C.B., 1976. Physical Oceanography of Estuaries (and Associated Coastal Waters). John Wiley & Sons, p. 465.

Pennings, S.C., Grant, M.B., Bertness, M.D., 2005. Plant zonation in low-latitude salt marshes: disentangling the roles of flooding, salinity, and competition. Journal of Ecology 93, 159–167.

Pezeshki, S.R., 2001. Wetland plant responses to soil flooding. Environmental and Experimental Botany 46, 299–312.

Pezeshki, S.R., DeLaune, R.D., 1993. Effects of soil hypoxia and salinity on gas exchange and growth of Spartina patens. Marine Ecology Progress Series 96, 75–81.

Pezeshki, S.R., DeLaune, R.D., Patrick, W.D., 1987a. Effects of flooding and salinity on photosynthesis of *Sagittaria lancifolia*. Marine Ecology Progress Series 41, 87–91.

Pezeshki, S.R., DeLaune, R.D., Patrick, W.D., 1987b. Response of the freshwater marsh species, *Panicum hemitomon* Schult, to increased salinity. Freshwater Biology 17, 195–200.

Pezeshki, S.R., DeLaune, R.D., Patrick, W.D., 1987c. Response of Spartina patens to increasing levels of salinity in rapidly subsiding marshes of the Mississippi River Deltaic Plain. Estuarine, Coastal and Shelf Science 24, 389–399.

Phleger, C.F., 1971. Effect of salinity on growth of a salt marsh grass. Ecology 52, 908–911.

Puls, W., van Bernem, K.-H., Eppel, D., Kapitza, H., Pleskachevsky, A., Riethmuller, R., Vaessen, B., 2012. Prediction of benthic community structure from environmental variables in a soft-sediment tidal basin (North Sea). Helgoland Marine Research 66, 345–361.

Reyes, E., White, M.L., Martin, J.F., Kemp, G.P., Day, J.W., Aravamuthan, V., 2000. Landscape modeling of coastal habitat change in the Mississippi Delta. Ecology 81, 2331–2349.

Savenije, H., 1993. Predictive model for salt intrusion in estuaries. Journal of Hydrology 148, 203–218.

Sasser, C.E., Gosselink, J.G., Swenson, E.M., Evers, D.E., 1995. Hydrologic, vegetation, and substrate characteristics of floating marshes in sediment-rich wetlands of the Mississippi River delta plain, Louisiana, USA. Wetlands Ecology 3, 171–187.

Sasser, C.E., Gosselink, J.G., Swenson, E.M., Swarzenski, C.M., Liebowitz, N.C., 1996. Vegetation, substrate and hydrology in floating marshes in the Mississippi River delta plain wetlands, USA. Vegetatio 122, 129–146.

Silvertown, J., Dodd, M.E., Gowing, D.J.G., Mountford, J.O., 1999. Hydrologically defined niches reveal a basis species richness in plant communities. Nature 400, 61–63.

Simpson, R.L., Good, R.E., Leck, M.A., Whigham, D.F., 1983. The ecology of freshwater wetlands. Bioscience 33, 255–259.

Snedden, G.A., Cable, J.E., Wiseman, W.J., 2007. Subtidal sea level variability in a shallow Mississippi River deltaic estuary, Louisiana. Estuaries and Coasts 30, 802–812.

Snedden, G.A., Swenson, E.M., 2012. Hydrologic Index Development and Application to Selected Coastwide Reference Monitoring System Sites and Coastal Wetlands Planning, Protection and Restoration Act Projects, U.S. Geological Survey Open-File Report 2012–1122, p. 25.

Spaulding, E.A., Hester, M.W., 2007. Interactive effects of hydrology and salinity on oligohaline plant species productivity: implications of relative sea-level rise. Estuaries and Coasts 30, 214–225.

Swenson, E.M., Cable, J.E., Fry, B., Justic, D., Das, A., Snedden, G.A., Swarzenski, C., 2006. Estuarine flushing times influenced by freshwater diversions, pp 403–412. In: Singh, V.P., Xu, Y.J. (Eds.), Coastal Hydrology and Processes. Water Resources Publications, Highlands Ranch, CO.

Turner, R.E., Swenson, E.M., Milan, C.S., Lee, J.M., Oswalt, T.A., 2004. Below-ground biomass in healthy and impared salt marshes. Ecological Research 19, 29–35.

U. S. Department of Agriculture, National Resource Conservation Service, 2010. The PLANTS Database. 24 September 2010). National Plant Data Center, Baton Rouge, LA. http://plants.usda.gov.

Visser, J.M., Sasser, C.E., Chabreck, R.H., Linscombe, R.G., 1998. Marsh vegetation types of the Mississippi River deltaic plain. Estuaries 21, 818–828.

Visser, J.M., Sasser, C.E., Linscombe, R.G., Chabreck, R.H., 2000. Marsh vegetation types of the Chenier Plain, Louisiana, USA. Estuaries 23, 318–327.

Visser, J.M., Sasser, C.E., Chabreck, R.H., Linscombe, R.G., 2002. The impact of a severe drought on the vegetation of a subtropical estuary. Estuaries 25, 1184–1195.

Visser, J.M., Steyer, G.D., Shaffer, G.P., Höppner, S.S., Hester, M.W., Reyes, E., Keddy, P., Mendelssohn, I.A., Sasser, C.E., Swarzenski, C., 2003. Habitat switching module, chapter 9. Final Report to. In: Twilley, R.R. (Ed.), Coastal Louisiana Ecosystem Assessment and Restoration (CLEAR) Model of Louisiana Coastal Area (LCA) Comprehensive Ecosystem Restoration Plan. Tasks 1–8, vol. I. Department of Natural Resources, Coastal Restoration Division, Baton Rouge, LA., p. 319. Contract No. 2511-02-24.

Weinstein, M.P., Litvin, S.Y., Bosley, K.L., Fuller, C.M., Wainright, S.C., 2000. The role of tidal salt marsh as an energy source for marine transient and resident finfishes: a stable isotope approach. Transactions of the American Fisheries Society 129, 797–810.

Wieski, K., Guo, H., Craft, C.B., Pennings, S.C., 2010. Ecosystem functions of tidal fresh, brackish, and salt marshes on the Georgia Coast. Estuaries and Coasts 33, 161–169.

Wilson, J.B., King, W.M., Sykes, M.T., Partridge, T.R., 1996. Vegetation zonation as related to the salt tolerance of species of brackish riverbanks. Canadian Journal of Botany 74, 1079–1085.

Wissel, B., Fry, B., 2005. Tracing Mississippi River influences in estuarine food webs of coastal Louisiana. Oecologia 144, 659–683.