

# Resource competition model predicts zonation and increasing nutrient use efficiency along a wetland salinity gradient

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**Abstract.** A trade-off between competitive ability and stress tolerance has been hypothesized and empirically supported to explain the zonation of species across stress gradients for a number of systems. Since stress often reduces plant productivity, one might expect a pattern of decreasing productivity across the zones of the stress gradient. However, this pattern is often not observed in coastal wetlands that show patterns of zonation along a salinity gradient. To address the potentially complex relationship between stress, zonation, and productivity in coastal wetlands, we developed a model of plant biomass as a function of resource competition and salinity stress. Analysis of the model confirms the conventional wisdom that a trade-off between competitive ability and stress tolerance is a necessary condition for zonation. It also suggests that a negative relationship between salinity and production can be overcome if (1) the supply of the limiting resource increases with greater salinity stress or (2) nutrient use efficiency increases with increasing salinity. We fit the equilibrium solution of the dynamic model to data from Louisiana coastal wetlands to test its ability to explain patterns of production across the landscape gradient and derive predictions that could be tested with independent data. We found support for a number of the model predictions, including patterns of decreasing competitive ability and increasing nutrient use efficiency across a gradient from freshwater to saline wetlands. In addition to providing a quantitative framework to support the mechanistic hypotheses of zonation, these results suggest that this simple model is a useful platform to further build upon, simulate and test mechanistic hypotheses of more complex patterns and phenomena in coastal wetlands.

**Key words:** coastal wetland; productivity; resource competition; resource use efficiency; salinity; stress; zonation.

## INTRODUCTION

Coastal wetlands, especially salt marshes, have been extensively studied as a model system to understand the combined effects of competition and stress on patterns of zonation (Barbour 1978, Bertness and Ellison 1987, Pennings and Callaway 1992, Emery et al. 2001, Greiner La Peyre et al. 2001, Pennings et al. 2005). These studies support the idea that coastal wetlands are often nitrogen limited (Mendelsohn 1979, Mendelsohn and Morris 2000) and that zonation results from a tradeoff between competitive ability and stress tolerance.

Mostly independent of the zonation studies, there has been a long history of studying the patterns of productivity in relation to abiotic factors in coastal wetlands (Miller and Egler 1950, Teal 1962, Linthurst and Seneca 1980, Howes et al. 1981, Cooper 1982, King et al. 1982). These patterns of productivity are important for a number of reasons that range from the fact that coastal wetlands are among the most productive habitat types in the world (Schelske and Odum 1962), to the important role above-

and belowground productivity plays for the stability and sustainability of these systems (Morris et al. 2002, Deegan et al. 2012). In coastal wetlands, plant production stimulates elevation gain through contributions to vertical accretion, i.e., mineral and organic matter accumulation (French 2006) and subsurface expansion in the root zone (McKee et al. 2007). Furthermore, primary production is stimulated at higher elevations (Stagg and Mendelsohn 2010) creating a feedback loop that sustains coastal wetlands during periods of sea-level rise. However, disturbance to hydrological regime or vegetation could disrupt the feedback loop resulting in habitat loss (Kirwan and Murray 2007). Thus, sea-level rise and other climate drivers that cause changes in plant community composition and primary production could have significant impacts on wetland sustainability. It is therefore important to understand the relationship between patterns of zonation and patterns of productivity in these systems.

If, as is generally suggested, patterns of zonation in these systems are strongly related to increasing stress associated with salinity and flooding, the question becomes, what is the relationship between stress and productivity? There are few general hypotheses about the form of this relationship. The most prominent is Grime's CSR model (1977, 1979), which posits that, as environmental stress increases, plant species with high

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resource capture rates and the potential for rapid growth should give way to species with slow growth rates and lower resource demand. Thus, this mechanism predicts a negative relationship between stress and productivity. However, this relationship has not been found in studies of New England salt marsh (Bertness and Ellison 1987, Bertness 1991, Emery et al. 2001) or along the gradient of freshwater to saline coastal marshes in southern Louisiana (Stagg et al. 2017; Appendix S1: Fig. S1).

Resource competition theory (Tilman 1982) has been considered an alternative to Grime's models to explain zonation along a stress gradient (Grace 1990, Emery et al. 2001). However, the predicted relationship between stress, zonation, and productivity for resource competition theory is unclear. In resource competition models, changes in species dominance along a gradient is a result of changes in the relative ability of the species to compete for resources (i.e., reduce resources to lowest concentration). In single resource models, the parameters controlling how stress affects the relative ability of a species to reduce resources are at least partially independent of the parameters that determine how efficiently they produce biomass. Quantitatively, the outcome is determined by the relationship of demographic variables given by the functional form of the specific model. Specifically, the relationship between stress, zonation, and production will depend on which demographic parameters are affected by stress and how they relate to both production of biomass and the ability to reduce resources. For this reason, resource competition models, in general, do not inform the relationship between stress, zonation, and production, but they can be used to develop specific models that can address these questions.

In this paper, we develop a simple dynamic model of plant growth as a function of resource competition and abiotic stress that can be used to understand the relationship between stress, productivity, and zonation. We use this model to show that a trade-off between competitive ability and stress tolerance can result in the community zonation patterns observed along salinity gradients in coastal marshes. We then compare the patterns of productivity across the salinity gradient predicted by the model to data from Louisiana coastal wetlands. Where there are differences between model-predicted and actual patterns, we use the model as a framework to develop hypothesized relationships among model parameters that can lead to observed patterns. Finally, we test the model-informed hypotheses using data from field studies.

## MODEL AND METHODS

### *Single-species model*

We consider a very simple model of a plant species growing on a single resource  $R$ . We assume that the rate of change in biomass,  $n$ , over time,  $t$ , of a plant species is proportional to the concentration of a limiting resource,  $R$ , and decrease at a constant per capita rate,  $m$ , i.e.

$$\frac{dn}{dt} = n(t)(bR(t) - m) \quad (1)$$

where  $b$  is the resource-dependent per capita production rate. Salinity negatively impacts marsh plant production by disrupting the uptake of resources and diverting critical resources away from biomass production. Increasing salinity decreases ammonium uptake efficiency in *Spartina alterniflora* through competitive ion inhibition (Bradley and Morris 1992). Moreover, salinity tolerance in marsh plants is partly due to the production of nitrogen-based osmoregulatory compounds (Cavaleri and Huang 1981, Naidoo et al. 1992), which leads to an increase in critical nitrogen requirements with increasing salinity (Bradley and Morris 1992, Mendelssohn and Morris 2000). Thus, considering  $R$  to be the concentration of the available nitrogen, we let the concentration of  $R$  available for growth depend linearly on salinity  $S$  and the amount of resource currently in plant tissues

$$R(t) = R_0 - \gamma S - \alpha n(t). \quad (2)$$

In Eq. 2,  $R_0$  is the pool of potential resource,  $\gamma$  is a species-specific effect of salinity on resource availability (i.e., the inverse of tolerance to salinity) and  $\alpha$  is the species-specific tissue concentration of the resource. This simple treatment of resource dynamics (i.e., as a closed system) should be a reasonable approximation where the magnitude of local resource cycling is large compared to the magnitude gain and loss of resources from outside the system.

Substituting Eq. 2 into Eq. 1 and solving for equilibrium gives two potential stable points,  $\hat{n} = 0$  and  $\hat{n} = (bR_0 - bS\gamma - m)/(b\alpha)$ . The effect of salinity on the equilibrium biomass can be demonstrated by plotting  $dn/dt$  as a function of  $n$  for different values of  $S$  (Fig. 1). Where the line in Fig. 1 is above the zero, the biomass is increasing, where below, it is decreasing. As such, equilibrium points occur where the curve crosses the zero (the open and solid points). The stability of the equilibrium points can also be read from this graph. Where the curve crosses with a positive slope (e.g., open point Fig. 1) the equilibrium is unstable. Where the curve crosses the  $x$ -axis with a negative slope, the equilibrium point is stable. Fig. 1 shows that at low salinity (small values of  $S$ ), the non-zero equilibrium is stable, but as salinity increases, biomass declines toward zero equilibrium. As salinity is increased further, the zero equilibrium becomes stable, which equates to the level of salinity that is outside the tolerance of the species (i.e., the species is locally extinct).

Plotting the value of the stable equilibrium as a function of salinity shows the salinity threshold for that species (Fig. 2, solid line). This threshold, the value of  $S$  at which  $\hat{n} = 0$  becomes stable,  $\hat{S}$ , can be found analytically by taking the derivative of Eq. 1 with respect to  $n$ , setting it to zero, substituting  $n = 0$  and solving for  $S$ . This gives

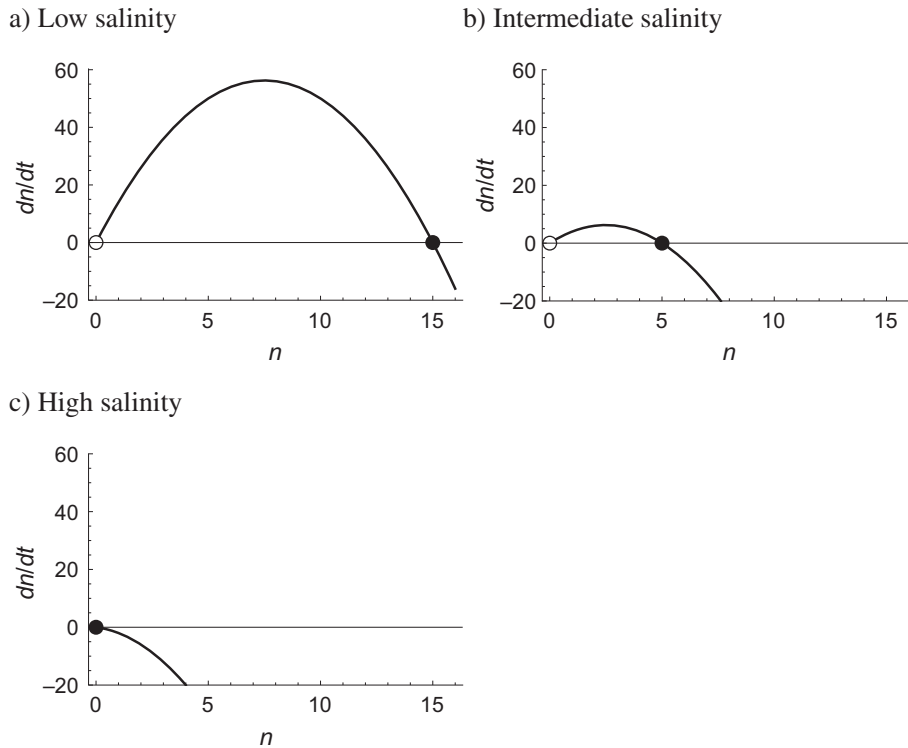


FIG. 1. Example of how the stability of equilibria of Eq. 1 change with salinity,  $S$ , where  $dn/dt$  is the rate of change in biomass,  $n$ , over time,  $t$ , of a plant species. Stable equilibria are indicated by solid points, unstable by open points. (a) At low salinity, there are two equilibria: a stable point at  $\hat{n} > 0$  and an unstable point at  $\hat{n} = 0$ . (b) As salinity is increased, the positive, stable equilibrium point moves toward the point at zero. (c) As salinity is increased further, the equilibria points collide and the point at  $\hat{n} = 0$  becomes stable. In this example,  $b = 10$ ,  $R_0 = 2$ ,  $m = 1$ ,  $\alpha = 0.1$ ,  $\gamma = 0.2$ , and  $S = 2, 7, 10$  for panels a, b, and c, respectively.

$$\hat{S} = \frac{1}{\gamma} \left( R_0 - \frac{m}{b} \right). \tag{3}$$

The expression  $m/b$  is the concentration of resources left behind by the population at equilibrium in the absence of salinity stress (i.e.,  $R^*$  sensu Tilman 1982). Other, equally valid, interpretations of  $R^*$  are the

minimum resource concentration at which a population can survive, and, in a multi-species context,  $R^*$  is a measure of competitive ability. Specifically, in the absence of additional mechanisms or factors (such as stress), the species with the lowest  $R^*$  will competitively displace all others. Thus, Eq. 3 can be interpreted as the difference between the potential pool of resource,  $R_0$  and the amount left behind at equilibrium,  $R^*$ , scaled by the inverse of its sensitivity to salinity  $\gamma$ . The scaling by  $1/\gamma$  indicates that as the effect of salinity on nutrient availability  $\gamma$  declines, the species' salinity threshold,  $\hat{S}$ , increases. Note that assuming a more complex functional relationship between growth rate and resource concentration results in the expression for  $R^*$  being a complex combination of model parameters, but otherwise does not affect the analysis presented above.

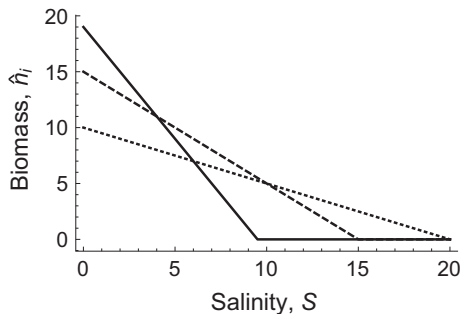


FIG. 2. Single species equilibrium biomass as a function of salinity for three species exhibiting a tradeoff between competitive ability and sensitivity to salinity. Salinity thresholds for changes in species dominance are found where lines cross. Parameter values are  $R_0 = 2$ ,  $m_1 = m_2 = m_3 = 1$ ,  $\alpha_1 = \alpha_2 = \alpha_3 = 0.1$ ,  $b_1 = 10$ ,  $b_2 = 2$ ,  $b_3 = 1$ ,  $\gamma_1 = 0.2$ ,  $\gamma_2 = 0.1$ ,  $\gamma_3 = 0.05$ .

*Multiple-species model and zonation*

The model described in Eqs. 1 and 2 can be extended to include multiple species competing for a single resource in multiple sites. This allows us to examine thresholds for changes in species dominance (zonation) along salinity gradients. Generalizing this model to multiple species and explicitly adding space gives

$$\frac{dn_{i,x}}{dt} = n_{i,x}(t)(b_i R_{i,x}(t) - m_i) \tag{4}$$

$$R_{i,x}(t) = R_{0,x} - \gamma_i S_x - \sum_{i=1}^N \alpha_i n_{i,x}(t) \tag{5}$$

where  $n_{i,x}$  is the biomass of species  $i = \{1..N\}$  at site  $x$ . Notice that the major difference between this system and a single-species system is that the pool of available resource  $R_x$  at a site  $x$ , is now a function of the sum of the biomass of all species present at the site. This model does not include a mechanism for dispersal between sites.

For a given site and  $N$  species, this system gives  $N + 1$  sets of equilibrium values, one where each species  $j \in i$  has an equilibrium equal to

$$\hat{n}_{i=j,x} = \frac{b_j R_{0,x} - b_j S_x \gamma_j - m_j}{b_j \alpha_j} \tag{6}$$

while all others are zero,  $\hat{n}_{i \neq j,x} = 0$ , and one where all the biomass of all species is zero  $\forall i : \hat{n}_{i,x} = 0$ . Thus, this model states that, in a given site, there will either be no biomass, or a monoculture. Given that there is some biomass, the species that will be dominant at the site depends on salinity of the site. For any subset of two species, we calculate the threshold level of salinity at which dominance switches between species. Mathematically, this is represented by the salinity at which the non-zero equilibrium for one species switches from stable to unstable, and the non-zero equilibrium of another switches from unstable to stable. This threshold is calculated by substituting the desired set of equilibria into the Jacobian matrix of the system and solving for the value of  $S$  where the dominant eigenvalue of the Jacobian matrix is equal to zero. For example, for two species,  $i = \{j, k\}$  this gives

$$\hat{S}_{j,k} = \frac{b_j m_k - b_k m_j}{b_j b_k (\gamma_j - \gamma_k)} \tag{7}$$

Substituting  $R_i^* = m_i/b_i$  in Eq. 7, gives the more interpretable result

$$\hat{S}_{j,k} = \frac{R_k^* - R_j^*}{\gamma_j - \gamma_k} \tag{8}$$

which states that the salinity threshold for a change from one species to another is a function of the ratio between the difference in their competitive abilities (i.e.,  $R_i^*$ ) and the difference of their sensitivity to salinity  $\gamma_i$ . Because only non-negative values of  $\hat{S}$  are reasonable, in order to observe a change in dominance from one species  $i = j$  to another  $i = k$  along an increasing salinity gradient (i.e., zonation),  $R_k^* > R_j^*$  and  $\gamma_j > \gamma_k$ . That is, there must be a trade-off between competitive ability and tolerance of salinity such that species that are better resource competitors (i.e., species with the lowest  $R_i^*$  is the best competitor) are more sensitive to salinity (i.e., higher  $\gamma_i$ ).

Fig. 2 presents a three-species example that fulfills these requirements. It shows the equilibrium biomass of each species in monoculture as a function of salinity. In this example, because we have assumed that the nutrient efficiency and mortality rate are equal for all species (i.e.,  $\alpha_i = \alpha$  and  $m_i = m$ ), the salinity thresholds for species transitions are the values of  $S$  at which their biomass lines intersect (i.e.,  $\hat{n}_j = \hat{n}_k$ ) and the dominant species is the one with the highest biomass at the given salinity.

*Productivity along the salinity gradient*

Fig. 3a presents the results of simulating Eq. 4 for three species with the parameters presented in Fig. 2 for 300 sites in which values of  $R_{0,x}$  and  $S_x$  were selected randomly from uniform distributions. All species were present in all sites at equal abundance at the beginning of the simulations and they were run until equilibrium was achieved ( $t = 1 \times 10^5$ ). The simulations confirm the analytical results for patterns of species dominance and thresholds values of  $S$ .

Fig. 3a displays a pattern of negative relationships between biomass and salinity both within zones (i.e.,  $(d\hat{n}_i)/dS < 0$ ) and across zones (i.e.,  $E(\hat{n}_3) < E(\hat{n}_2) < E(\hat{n}_1)$ ). The general relationship between biomass and salinity within a zone can be found by taking the derivative of equilibrium biomass with respect to salinity

$$\frac{d\hat{n}_{i,x}}{dS_x} = -\frac{\gamma_i}{\alpha_i} + c_1 \frac{dR_{0,x}}{dS_x} - c_2 \frac{d\alpha_i}{dS_x} - c_1 \left( \frac{dR_i^*}{dS_x} + S_x \frac{d\gamma_i}{dS_x} \right), \tag{9}$$

where  $c_1 = 1/\alpha_i$  and  $c_2 = (R_i^* + S_x \gamma_i - R_{0,x})/\alpha_i^2$  are positive constants. Assuming no salinity-driven plasticity within species (i.e.,  $d\alpha_i/dS_x = 0$ ,  $dR_i^*/dS_x = 0$ , and  $d\gamma_i/dS_x = 0$ ), Eq. 9 this to be simplified to

$$\frac{d\hat{n}_{i,x}}{dS_x} = \frac{1}{\alpha_i} \left( -\gamma_i + \frac{dR_{0,x}}{dS_x} \right). \tag{10}$$

Eq. 10 indicates that in the absence of a within-zone resource gradient (i.e.,  $dR_{0,x}/dS_x = 0$ ), the relationship between salinity and biomass will be negative with slope  $-\gamma_i/\alpha_i$ . However, the negative relationship between biomass and salinity could be counteracted if variation in within-zone potential resource pools  $R_0$  and salinity  $S$  is positively associated (i.e.,  $dR_{0,x}/dS_x > 0$ ). This could occur, for example, if nitrogen mineralization rates, and thus nitrogen availability, tended to increase with salinity.

The relationship between biomass and salinity among zones is more complicated because the change in species across zones is discontinuous. To simplify it to allow intuitive argument, we will consider the case of two species  $i = j, k$  such that  $R_j^* < R_k^*$  and  $\gamma_j > \gamma_k$  in adjacent sites  $x = \{1, 2\}$  at salinities very near the salinity threshold  $\hat{S}_{j,k}$ . Specifically, the salinity in site  $x = 1$  is slightly lower than the threshold,  $S_1 = \hat{S}_{j,k} - \epsilon$  and that of site  $x = 2$  is slightly higher than the threshold,  $S_2 = \hat{S}_{j,k} + \epsilon$ , where  $\epsilon$  is small relative to  $\hat{S}_{j,k}$ . Substituting into Eq. 6 and simplifying gives

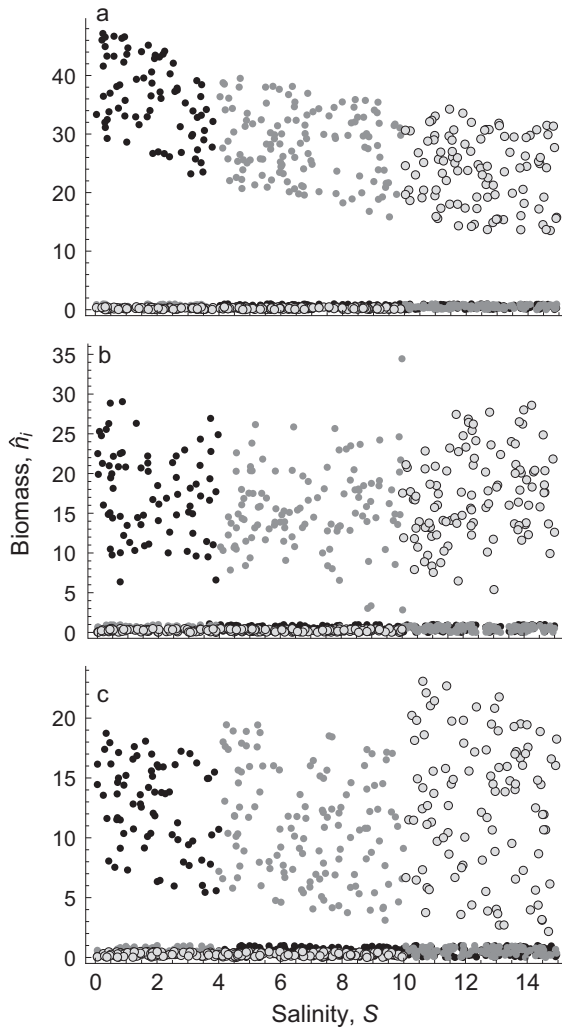


FIG. 3. Simulations of Eq. 4 demonstrating factors that could counteract the otherwise expected negative relationship between salinity and biomass for three species shown in 300 sites with (a) randomly chosen values for  $R_{0,x}$  and  $S_x$ . Panels b and c demonstrate that (b) resource pools that are positively correlated with salinity or (c) nutrient efficiency that is correlated with salinity tolerance could counteract the otherwise expected negative relationship between salinity and biomass seen in panel a. Notice that panel c shows a negative relationship within species, but no relationship for the overall pattern. For the simulations in panel a,  $m_1 = m_2 = m_3 = 1$ ,  $\alpha_1 = \alpha_2 = \alpha_3 = 0.1$ ,  $b_1 = 10$ ,  $b_2 = 2$ ,  $b_3 = 1$ ,  $\gamma_1 = 0.2$ ,  $\gamma_2 = 0.1$ ,  $\gamma_3 = 0.05$ ,  $R_{0,x} \sim U(3, 5)$  and  $S_x \sim U(0, 15)$ . In (b)  $S_x \sim U(0, 15)$ ,  $R_{0,x} = 2 + S_x/9 + \varepsilon$ ,  $\varepsilon \sim N(0, 0.5)$ . For the simulations in panel c,  $\alpha_1 = 0.25$ ,  $\alpha_2 = 0.2$ ,  $\alpha_3 = 0.15$ ,  $R_{0,x} \sim U(3, 5)$  and  $S_x \sim U(0, 15)$ , all others are the same as in panel a.

$$\hat{n}_{j,1} = \frac{R_{0,1} - \mu + \gamma_j \varepsilon}{\alpha_j}, \hat{n}_{k,1} = 0 \quad (11)$$

$$\hat{n}_{j,2} = 0, \hat{n}_{k,2} = \frac{R_{0,2} - \mu - \gamma_k \varepsilon}{\alpha_k} \quad (12)$$

where  $\mu = -R_j^* - \gamma_j \hat{S}_{j,k}$ . Comparing Eqs. 11 and 12 shows that, as with the within-zone pattern, if all else is equal (i.e.,

$R_{0,1} = R_{0,2}$  and  $\alpha_j = \alpha_k$ ), the relationship between biomass and salinity is negative (i.e.,  $\hat{n}_{j,1} > \hat{n}_{k,2}$ ). However, this pattern can be counteracted if resource pools increase along the gradient,  $R_{0,1} < R_{0,2}$ , or if nutrient use efficiency increases across the species along the gradient  $\alpha_k < \alpha_j$ .

Fig. 3b, c show simulation results for the biomass-salinity relationship in cases where the potential nutrient pool  $R_{0,x}$  is positively correlated with  $S_x$  (Fig. 3b) and where the nutrient efficiency of species increases along with its tolerance to salinity (Fig. 3c). Both confirm the analysis we have described. In the next sections, we treat these as model-informed hypotheses to explain the lack of an overall decrease in biomass along the salinity gradient in Louisiana coastal wetlands and we describe tests of each using resource pool (e.g., total nitrogen) data and nutrient efficiency (e.g., tissue concentration) data.

#### Connections between dynamic model, statistical model, and data

In this section, we use the equilibrium solution from the analytical model described above to inform the specification of statistical models that were tested with data from production, soil, and tissue data from along a landscape salinity gradient of Louisiana coastal wetlands. The equilibrium solution of the analytical model indicates that biomass is a linear function of the salinity and the pool of potential resources at the site,  $R_{0,x}$ . In addition, because there are community shifts along the observed salinity gradient, a separate intercept ( $\beta_{0,i}$ ) and slope associated with salinity ( $\beta_{2,i}S$ ) should be fitted for each wetland type  $i$  (i.e., a salinity by wetland type interaction). This results in a model

$$\hat{n}_{\text{obs},i} = \beta_{0,i} + \beta_1 R_0 + \beta_{2,i} S. \quad (13)$$

Eq. 13 is equivalent to the equilibrium biomass given in Eq. 6, and can thus be rewritten in terms of the parameters of the dynamic model:  $\beta_{0,i} = -1/\alpha R_i^*$ ,  $\beta_1 = 1/\alpha$  and  $\beta_{2,i} = -\gamma_i/\alpha$ . Since the intercept  $\beta_{0,i}$  represents the biomass when the  $R_0 = 0$  and a necessary condition for positive biomass is  $R > R^* > 0$  and  $\alpha > 0$ ,  $\beta_{0,i}$  should be negative for all wetland types. If upon fitting it is found that  $\beta_{0,i} > 0$ , it suggests that the plants in the field had an additional source of nitrogen that is not captured by the measurement of soil total nitrogen.

In the case where nutrient use efficiency, represented by  $\alpha$ , varies among wetland types, the parameter  $\beta_1$ , will also vary among wetland types (i.e.,  $\beta_{1,i}$ ), and the appropriate model should include a resource by wetland type interaction

$$\hat{n}_{\text{obs},i} = \beta_{0,i} + \beta_{1,i} R_0 + \beta_{2,i} S. \quad (14)$$

Thus, given the model described in Eqs. 4 and 5, comparing the two statistical models described here (i.e., with vs. without resource by wetland type interaction) can be used as a test of the hypothesis that nutrient use



efficiency ( $\alpha$ ) changes across the wetland types along the salinity gradient.

To fit this model to the data, we used aboveground biomass as an estimate  $\hat{n}_{\text{obs},i}$ , where  $i$  indicates the wetland type,  $i = \{\text{Fresh, Intermediate, Brackish, Saline}\}$  and soil total nitrogen is used as an estimate of  $R_0$ . Ideally, our measure of  $R_0$  would be a measure of total nitrogen that is independent of biomass. While we did not have such a measure, we did have measurements of soil total nitrogen and porewater total nitrogen, which we chose to be a measure of the total potential resource pool ( $R_0$ ) and a measure of the equilibrium resource concentration ( $R_i^*$ ), respectively.

#### Tests of model predictions

The model described in Eqs. 4 and 5 can be used to generate predictions of two different types. One type are predictions the model makes about the phenomena of interest (e.g., the pattern of productivity along the salinity gradient) given that the model is a good approximation of the actual system. The other type of predictions are those that do not necessarily relate directly to the phenomena of interest, but are more general side-products of the model's assumptions. These can be tested to address whether or not the model is an adequate approximation of the actual system. In the following sections, we describe predictions of each type and discuss the data and methods we used to test them.

*Productivity along the salinity gradient.*—Eqs. 10–15 predicts that if all else is equal, biomass will be negatively correlated with salinity. However, if this is not the case, then the model predicts that  $R_{0,x}$  is positively correlated to  $S_x$ , the nutrient use efficiency increases (i.e.,  $\alpha_i$  decreases) across the gradient, or both. We tested the relationship between biomass and salinity with Pearson correlation of total aboveground biomass and salinity. Likewise, we used Pearson correlation of soil total nitrogen and salinity to test for a relationship between  $R_{0,x}$  and  $S_x$ .

To test the predicted relationship that nutrient use efficiency decreases across the gradient, we fit tissue nitrogen concentration as a function of wetland type. Pairwise tests were done with the `pairwise.t.test()` function using Holm  $P$  value adjustment on the R platform (R Core Team 2016).

*General model predictions.*—There are a number of conditions specified by the dynamic model that can be tested with the data to inform whether the patterns in the data support the existence of the mechanisms described by the dynamic model. Specifically, (1) Equilibrium biomass  $\hat{n}_{i,x}$  is negatively related to salinity  $S_x$  within wetland types  $i$ . (2) Equilibrium biomass  $\hat{n}_{i,x}$  is positively related to  $R_{0,x}$ . (3)  $\beta_{0,i}$  should be negative for all wetland types along the gradient. (4) Equilibrium resource concentration  $R_i^*$  is predicted to be independent of equilibrium biomass,  $\hat{n}_{i,x}$  (Eq. 3). Finally, analysis of the dynamic model shows

two necessary conditions for zonation: (5) equilibrium resource concentration should increase across the salinity gradient, such that  $R_1^* < R_2^* < \dots < R_n^*$  and (6) sensitivity to salinity should decrease across wetland types along the salinity gradient,  $\gamma_1 > \gamma_2 > \dots > \gamma_n$ .

Predictions 1–3 were tested by fitting Eq. 14 to data collected along the landscape salinity gradient in Louisiana. Prediction 1 states that the parameters  $\beta_{2,i}$  of Eq. 14 are negative and the salinity by wetland type interaction is significant. Likewise, prediction 2 states that the parameters  $\beta_{1,i}$  of Eq. 14 are positive. As suggested above, statistical significance of the soil total nitrogen by wetland type interaction term indicates variation in nutrient use efficiency across the gradient. Prediction 3 states that the fitted intercept  $\beta_{0,i}$  should be less than zero.

To test predictions 4 and 5, we fit a linear model of the concentration of porewater total nitrogen as function of wetland type and aboveground biomass of the form

$$R_{\text{obs},i} = \beta_{\text{pw},0,i} + \beta_{\text{pw},1}n_{\text{obs},i} \quad (15)$$

where  $i$  indicates the wetland type,  $i = \{\text{Fresh, Intermediate, Brackish, Saline}\}$ , and  $\beta_{\text{pw},0,i}$  is a porewater based estimate of  $R_i^*$  (i.e., independent of that in Eq. 13). Thus, prediction 4 states that  $\beta_{\text{pw},1}$  is not significantly different from zero and prediction 5 states that  $\beta_{\text{pw},0,\text{Fresh}} < \beta_{\text{pw},0,\text{Intermediate}} < \beta_{\text{pw},0,\text{Brackish}} < \beta_{\text{pw},0,\text{Saline}}$ .

We were unable to test prediction 6, that sensitivities to salinity decrease with wetland type along the salinity gradient because we lacked independent data on measures of sensitivity to salinity.

#### Empirical methods

The data used to test the relationships between community zonation, stress, and productivity were originally presented in Stagg et al. (2017). Total aboveground biomass (live + dead), plant tissue nitrogen concentrations, and soil and porewater nitrogen concentrations were measured in four wetland types (i.e., zones) along a gradient of increasing salinity. The wetland types were defined by salinity zone (Cowardin et al. 1979, Odum 1984) and dominant plant species (Visser et al. 2002). Fresh sites (0–0.5 ppt) were dominated by *Panicum hemitomon* and *Typha latifolia*, intermediate sites (0.5–5 ppt) were dominated by *Sagittaria lancifolia* and *Schoenoplectus americanus*, brackish sites (5–18 ppt) were dominated by *Spartina patens* and *Schoenoplectus americanus*, and saline sites (>18 ppt) were dominated by *Spartina alterniflora* and *Juncus roemerianus*.

Aboveground plant biomass was harvested once per season (i.e., spring, summer, etc.) over two years (2012–2014). To measure plant tissue nitrogen concentrations, live and dead aboveground leaves and stems were oven dried to 60°C, ground, digested using a wet ashing technique, and analyzed by colorimetry (Plank 1992). Soil cores (30 cm) and porewater samples (15 cm) were taken at the end of the growing season in October 2012 and

2013. To measure soil total nitrogen, homogenized soil samples were oven dried at 60°C, pulverized, and analyzed by gas chromatography using a combustion analyzer (Keeney and Nelson 1982). To measure porewater total nitrogen, an aliquot of the porewater sample was digested using persulfate digestion and analyzed by colorimetry (D'Elia et al. 1977).

## RESULTS

### *Productivity along the salinity gradient*

There was no overall correlation between aboveground biomass and salinity ( $r(229) = -0.03$ ,  $P = 0.611$ ). Accordingly, the model (Eqs. 9–12) predicts a positive correlation between  $R_0$  and salinity, a trend of increasing nutrient use efficiency (decreasing  $\alpha_i$ ) across the wetland types along the salinity gradient, or both. The former was not supported by data; the correlation between soil total nitrogen, our estimate of  $R_0$ , and salinity was negative ( $r(229) = -0.207$ ,  $P = 0.002$ ). Thus, the model predicts that the lack of a negative correlation between aboveground biomass is due to increasing nutrient use efficiency across the salinity gradient. This prediction was supported by two lines of evidence. First, fitting Eq. 14, which included a wetland type by soil total nitrogen interaction, resulted in a better model compared to the fit of Eq. 13, which did not ( $\Delta\text{AIC} = 8.82$ ). This suggests the existence of variation in nutrient use efficiency across wetland types.

Second, analysis of tissue nitrogen content supported the existence of increasing nutrient use efficiency across the salinity gradient. Fitting tissue nitrogen content as a function of wetland type resulted in a much better model than a “null” model that included a single intercept ( $\Delta\text{AIC} = 15.98$ ). The estimates (i.e., independent measures of nutrient use efficiency) follow a very similar pattern to those predicted by the model; plants from fresh and intermediate wetland types are similar to one another and have higher tissue nitrogen content (i.e., lower nutrient use efficiency) than those in brackish and saline wetlands (Fig. 4).

### *General model predictions*

Fitting Eq. 14 to the data resulted in a much better model fit compared to an intercept-only model ( $R^2 = 0.387$ ,  $\Delta\text{AIC} = 89.25$ ). The ANOVA table from fitting Eq. 14 is shown in Table 1, parameter estimates

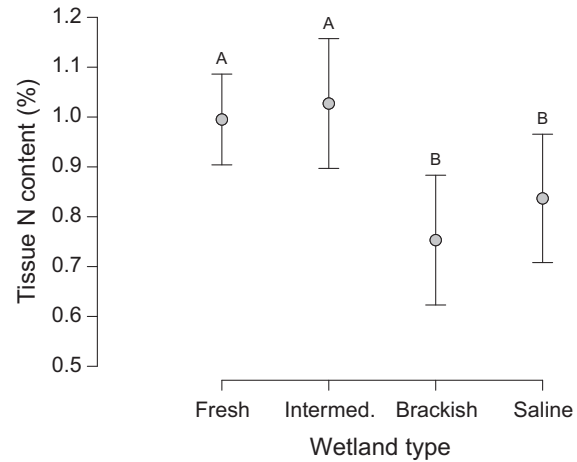


FIG. 4. Tissue nitrogen content across wetland types. Estimates with the same letters were not significantly different from one another.

TABLE 1. Model ANOVA resulting from fit of Eq. 12.

	df	SS	MS	F	P
Wetland type	3	1485090	495030	13.47	<0.01
Soil total N	1	506521	506521	13.78	<0.01
Salinity	1	240749	240749	6.55	0.01
Wetland type × Soil total N	3	471619	157206	4.28	<0.01
Wetland type × Salinity	3	2098396	699465	19.03	<0.01
Residuals	219	8050997	36763		

are shown Table 2 and the fitted relationships between biomass and salinity are shown in Fig. 5.

*Prediction 1.*—The estimates of the effect of salinity on biomass were negative for three of the four wetland types: Fresh, Brackish, and Saline. However, uncertainty in the estimates was large (Table 2). The salinity by wetland type interaction was significant, indicating variation in sensitivity to salinity among wetland types (Table 1).

*Prediction 2.*—The estimates of the effect of soil total nitrogen on biomass were positive. As with the salinity estimates, the uncertainty in the estimates was large (Table 2). The soil total nitrogen by wetland type interaction was significant, indicating variation in nutrient use

TABLE 2. Estimates from fitting aboveground biomass to Eq. 12.

	Fresh	Intermediate	Brackish	Saline
Intercept ( $\beta_0$ )	439.72 (69.43)	159.64 (56.62)	690.95 (77.24)	761.09 (95.60)
Soil total N ( $\beta_1$ )	3,971.72 (2,697.40)	5,045.10 (4,341.83)	23,786.75 (5,387.42)	9,866.41 (7,092.23)
Salinity ( $\beta_2$ )	-263.97 (175.58)	107.70 (176.46)	-32.79 (175.95)	-31.46 (175.76)

Note: Standard errors of the estimates are in parentheses.

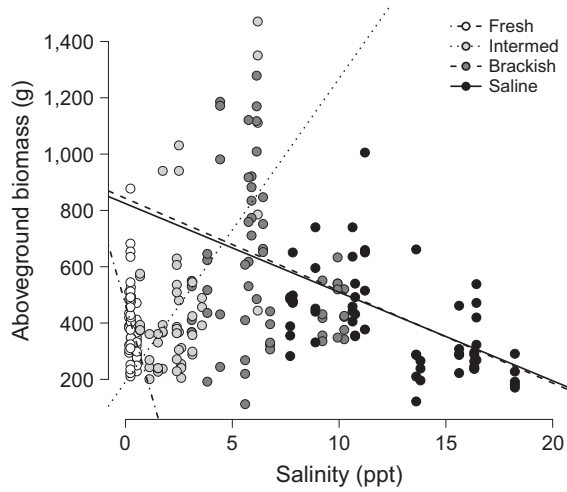


FIG. 5. Aboveground biomass as a function of salinity across four wetland types. Lines show fit of Eq. 12.

efficiency among wetland types (Table 1), as discussed in the previous section.

*Prediction 3.*—The estimates of the intercepts of the model were positive for all wetland types, opposite of what was predicted by the model (Table 2). This result is an indication that soil total nitrogen was an imperfect measurement of the true amount of nitrogen available to the plants.

*Predictions 4 and 5.*—The estimated coefficients resulting from fitting Eq. 14 are given in Table 3. As predicted by the resource competition model (prediction 4), we found that the effect of biomass on the concentration of porewater nitrogen was not significantly different from zero. We also found that the estimates of equilibrium resource concentration,  $R_i^*$ , as measured by porewater total nitrogen, increases across wetland types over the salinity gradient (prediction 5).

DISCUSSION

We developed a simple model of resource competition along a salinity gradient to explore both the phenomenon of community zonation and patterns of aboveground

TABLE 3. Estimates resulting from model of porewater total nitrogen ( $\mu\text{mol/L}$ ) as a function of wetland type and aboveground biomass.

	Estimate	SE	<i>t</i>	<i>P</i>
$\beta_{\text{Fresh}}$	142.67	23.97	5.95	<0.01
$\beta_{\text{Intermediate}}$	209.65	25.75	2.60	<0.01
$\beta_{\text{Brackish}}$	362.88	26.53	8.30	<0.01
$\beta_{\text{Saline}}$	370.15	25.28	9.00	<0.01
Biomass	-0.017	0.0403	-0.427	0.670

productivity along the gradient. Analysis of the model shows that a necessary condition for community zonation to occur along the gradient is a trade-off between competitive ability (as defined by  $R^*$ ) and sensitivity to salinity stress ( $\gamma$ ). Such a trade-off has been suggested and observed in many empirical studies of coastal wetlands (Bertness and Ellison 1987, Bertness 1991, Greiner La Peyre et al. 2001, Crain et al. 2004, Pennings et al. 2005) as well as in other systems (Connell 1961, Lubchenco 1980), but until now, not derived quantitatively from first principles. In addition, this model predicts that the concentration of salinity that marks the transition zone between two communities can be calculated as the ratio between the difference in the competitive abilities,  $R^*$ , and the difference in sensitivities,  $\gamma$  (Eq. 8). With respect to production, the model predicts that, all else being equal, biomass will decline across the gradient, as predicted by Grime (1979). However, this trend can be counteracted if either resource supply increases over the salinity gradient, or if nutrient use efficiency increases (i.e.,  $\alpha$  decreases) over the salinity gradient.

We used multiple lines of evidence to judge how well the dynamic resource competition model explained the data from Louisiana coastal marshes. The overall fit of the theory-derived model was much better than the null model, suggesting that the dynamic model captured some drivers of variation in aboveground biomass over the salinity gradient. Moreover, some of the specific predictions of the model were supported, such as the independence of porewater total nitrogen and biomass within wetland types (prediction 4), the increasing trend in porewater total nitrogen across the gradient (prediction 5), and the general positive relationship between soil total nitrogen and aboveground biomass (prediction 2). Support for prediction 5 suggests a pattern of decreasing competitive ability for nitrogen along the salinity gradient, an important aspect of the hypothesized mechanism of zonation implied by the dynamic model. Support for prediction 4, which is a common feature of resource competition models, suggests that the simple, single resource modeling approach we used is a useful approximation of these coastal wetland systems. This is notable, because, while the usefulness of the  $R^*$  approach has been well-documented in aquatic systems (e.g., Tilman 1982), it has been challenged in terrestrial systems (Craine 2005). Our results suggest that coastal wetlands, which share features with each of these systems, may function as an intermediate case.

Some patterns in the data were noisy or at odds with predictions of the model. For example, prediction 1 suggests that the parameter estimates associated with the affect of salinity on biomass should be negative. This was true for only three of the four wetland types, and the uncertainty around the estimates was large.

It is likely that the mismatch between the model predictions and data was driven by the fact that aboveground biomass in the intermediate marshes increased with salinity. This possibility cannot be explained by the



current model and the mechanisms that inspired it. As a result, the parameter estimate of  $\beta_{1,Intermediate}$  was positive. This implies that the sensitivity to salinity stress,  $\gamma_{Intermediate}$ , was negative, which is not biologically realistic in the context of the competition model. There are a few possibilities that could explain the observed pattern. The fact that the intercepts resulting from fitting Eq. 12 were positive, the opposite of prediction 3, suggests that our measurement of soil total nitrogen were biased such that they underrepresented the potential pool of soil nitrogen. If the unaccounted fraction of the resource pool (i.e., the degree of bias) increased along the salinity gradient, it would cause error in the model fit and the possible erroneously negative estimate of  $\gamma$ . Another possibility is that, within wetland types, nutrient use efficiency,  $1/\alpha_i$  is an increasing function of salinity. This pattern was reported by Linthurst and Seneca (1981), who found that as salinity increased, nutrient tissue concentrations of *Spartina alterniflora* declined as production increased, indicating greater nutrient use efficiency with increased stress. Once a reasonable functional form of that relationship is specified, it could be added to the model and the results quantitatively compared to the current model. Finally, there are many other known drivers of biomass in coastal marshes in addition to nitrogen and salinity. Including additional drivers of aboveground biomass such as consumers (He and Silliman 2015) or human disturbance (e.g., Valiela et al. 2016) not currently included in the model would likely reduce uncertainty in the model estimates.

Simple models are best judged by their ability to make useful predictions. We used Eq. 12 to derive model-predicted estimates of nutrient use efficiency for each wetland type. While there was a large amount of uncertainty in the estimates themselves, variation in nutrient use efficiency was predicted by two other lines of evidence from the model. First, we compared the fits of Eqs. 13 and 14 to data. These models differ only by the addition of a  $R_0$  by wetland type interaction, which allows for nutrient use efficiency to vary over wetland type. We found that Eq. 14 fit the data better (i.e., the soil total nitrogen by wetland type interaction was statistically significant), suggesting variation in nutrient use efficiency among wetland types. Second, the pattern of nutrient use efficiency predicted by the model follows well the pattern of the actual tissue nutrient content; that tissue nutrient content of plants from fresh and intermediate wetlands are higher than those from brackish and saline wetlands. Taken together, we conclude that the model predicted a pattern in tissue nutrient content that was verified by independent data, and accords well with what has been reported in other systems. For example, patterns of increasing nutrient use efficiency with increasing nutrient stress have been also been reported among freshwater marsh plants (Shaver and Melillo 1984) and forest trees (Hebert and Fownes 1999).

Using our results to evaluate the predictions of Grime's CSR model, we find mixed support. We found

that (1) a trade-off between competitive ability and stress tolerance was a necessary condition for zonation, (2) a pattern of increasing nutrient use efficiency with increasing stress tolerance, and (3) increasing stress can be associated with reduced productivity along the stress gradient, as predicted by Grime (1979). However, we found that relationship among zonation, stress and productivity is more nuanced. For example, the second and third predictions of the CSR model listed above tend to work against one another. A pattern of decreasing productivity across zones can be counteracted by increasing nutrient use efficiency, and/or increasing resource availability along the gradient. We also found that the measure of competitive ability that is most relevant to producing these patterns is not the rate of resource uptake ( $b_i$  in our model) but the ability to reduce resources to the lowest concentration at equilibrium. This trait is related to resource uptake rate, but is also a function of other traits as well ( $m_i$ , for example). Thus, we find support for the CSR model's predictions under certain conditions, but more adaptable models will provide the capacity for more robust and useful predictions and a better basis for interpreting vegetation patterns in coastal marshes.

#### CONCLUSION

In this paper, we presented a model of resource competition that included the effects of salinity stress based on physiological mechanisms. This model allowed us to evaluate the relationship between competition, stress, zonation, and production. Our results demonstrate how adding a physiological mechanism related to abiotic stress to a resource competition model can be used to derive the necessary conditions for the development of zonation along a salinity gradient. Fitting this model to data from Louisiana coastal wetlands allowed us to generate predictions about patterns of resource concentration and nutrient use efficiency across the landscape salinity gradient that were supported by independent data. The work presented here could be expanded along multiple fronts. We will explore the effects of adding factors known to affect aboveground biomass and more complex functional forms for model parameters with the goal of accounting for the uncertainty in estimated model parameters. Further, this model could be used to evaluate empirical claims about the relative roles of competition and stress change along the gradient, explore the effects of climate change on marsh zonation, and interpret the results of competition experiments conducted in coastal marshes.

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#### SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.2131/supinfo>

#### DATA AVAILABILITY

The supporting data presented in this paper have been publicly archived at [sciencebase.gov](https://sciencebase.gov): C. L. Stagg, D. R. Schoolmaster, S. C. Piazza, G. Snedden, G. D. Steyer, C. J. Fischennich, R. W. McComas. Primary production across a coastal wetland landscape in Louisiana, USA (2012–2014). U.S. Geological Survey (2017), <https://doi.org/10.5066/F7G44NFJ>.