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Towards a theory of ecotone resilience: Coastal vegetation on a salinity gradient

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ABSTRACT

Ecotones represent locations where vegetation change is likely to occur as a result of climate and other environmental changes. Using a model of an ecotone vulnerable to such future changes, we estimated the resilience of the ecotone to disturbances. The specific ecotone is that between two different vegetation types, salinity-tolerant and salinity-intolerant, along a gradient in groundwater salinity. In the case studied, each vegetation type, through soil feedback loops, promoted local soil salinity levels that favor itself in competition with the other type. Bifurcation analysis was used to study the system of equations for the two vegetation types and soil salinity. Alternative stable equilibria, one for salinity-tolerant and one for salinity intolerant vegetation, were shown to exist over a region of the groundwater salinity gradient, bounded by two bifurcation points. This region was shown to depend sensitively on parameters such as the rate of upward infiltration of salinity from groundwater into the soil due to evaporation. We showed also that increasing diffusion rates of vegetation can lead to shrinkage of the range between the two bifurcation points. Sharp ecotones are typical of salt-tolerant vegetation (mangroves) near the coastline and salt-intolerant vegetation inland, even though the underlying elevation and groundwater salinity change very gradually. A disturbance such as an input of salinity to the soil from a storm surge could upset this stable boundary, leading to a regime shift of salinity-tolerant vegetation inland. We showed, however, that, for our model as least, a simple pulse disturbance would not be sufficient; the salinity would have to be held at a high level, as a 'press', for some time. The approach used here should be generalizable to study the resilience of a variety of ecotones to disturbances.

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1. Introduction

Ecological resilience and regime shifts have been major topics in the study of ecosystem dynamics during the past two decades (Briske et al., 2010; Scheffer et al., 2001). These concepts are particularly important to the study of ecotones, or zones over which there is a rapid transition between adjacent types of vegetation. Ecotones are zones where changes in vegetation type are likely to occur when environmental conditions change. Ecotones usually occur along externally imposed environmental gradients, that is, changes in edaphic characteristics or climatic variables, such as temperature or precipitation. In some cases, these environmental gradients are strong enough that they determine a boundary that rigidly separates the vegetation types, such as that occurring at the shore of a lake. In other cases the gradients are weak enough, or the vegetation types are plastic enough in their tolerances, that there is a large potential range of

overlap between the vegetation types. In such cases, the ecotone might occur as a gradual change from dominance of one vegetation type to the other. However, situations also exist where even relatively weak environmental gradients are characterized by ecotones so sharp that they almost resemble edges. These can result from what has been termed a positive feedback 'switch', in which each vegetation type alters the local environment through positive feedback in a way that favors itself (Lloyd et al., 2000; Wilson and Agnew, 1992), such that it excludes the other type.

When different vegetation types can each potentially occupy the same sites along some region of a gradient, and also exhibit this switch behavior, then alternative stable states, or bistability, can exist in this region. Alternative stable states and their mechanisms have been identified for some ecotones that have been studied in detail. Among these are grass–tree ecotones (e.g., Accatino et al. (2010), Boughton et al. (2006), Sternberg (2001), Vilà et al. (2001)), alpine tree lines (e.g., Bekker (2005), Malanson (1997), Nishimura and Kohyama (2002), Wiegand et al. (2006)), tropical alpine tree-lines (Bader et al., 2008; Martin et al., 2010) rush–mangrove ecotones (Walker et al., 2003), Sphagnum bog–vascular plant ecotones (Ehrenfeld et al., 2005; Hotes et al., 2010), forest–mire ecotones (Agnew et al., 1993), ecotones between different vegetation

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successional stages in a calcareous dune slack (Adema and Grootjans, 2003), sclerophyllous shrub–forest ecotones (Odion et al., 2010), and ecotones around allelopathic plants (Gentle and Duggin, 1997). These systems all involve a switch mechanism (*sensu* (Wilson and Agnew, 1992)) of some sort, in which vegetation types alter the environment to favor themselves and exclude other types.

Some of the mechanisms that maintain ecotones act continuously in time, but others are episodic. Fire is an episodic mechanism that favors pyrogenic vegetation such as grass over forest in such ecotones as Mediterranean Basin woodlands (Vilà et al., 2001), higher elevation pines over lower elevation cloud forest in tropical mountains (Martin et al., 2010), and sclerophyllous shrub vegetation over forest in mountains such as the Klamath Mountains of California (Odion et al., 2010). In the absence of fire, the non-pyrogenic vegetation is superior to the pyrogenic vegetation is superior (e.g., forest shades out grass), so the ecotone could move shift in favor of the former during intervals between fires, but occasional fire events will burn back the young growth of non-pyrogenic vegetation, setting back the ecotone. The forest–mire ecotone is an example of continuous mechanism of enforcement of a sharp ecotone. Tree seedlings cannot establish in the mire, but they can establish on fallen tree boles, maintaining the boundary (Agnew et al., 1993). In both of these examples, the vegetation types show this switch mechanism.

In all of the examples there are zones along the environmental gradient where the fundamental conditions are such that either of two alternative vegetation types could exist. The ecotone merely represents the current position of the sharp boundary within this area of overlap, influenced by the positive feedbacks of each vegetation type favoring itself and excluding the other. Because this overlap area is a zone of bistability, it is possible that either changing environmental conditions or disturbances could lead to regime shifts, that is, sudden, spatially extensive changes in favor of one of the vegetation types that shifts the position of the ecotone. The reason that regime shifts can be sudden and extensive stems from the positive feedbacks that maintain the ecotone between the two vegetation types. Because of these self-reinforcing positive feedbacks, the ecotone resists change until the change in the environment is great enough to overcome the feedbacks. That is termed ‘resilience’. But once the resilience of the self-reinforcing feedbacks is overcome, feedbacks operate to promote change to the alternative vegetation type. Two types of environmental change can trigger regime shift (e.g., Beisner et al. (2003); Briske et al. (2008)). One is gradual change in some environmental variable that eventually reaches a threshold past which the shift occurs (e.g., Carpenter et al. (1999), Folke et al. (2004), Petersen et al. (2008), Scheffer et al. (2001)). The second type of change is a large disturbance that pushes the system beyond the threshold, such that it cannot return to the original vegetation state, but moves to the alternative state (e.g., May (1977), Stringham et al. (2003)). If the disturbance is not so large that it pushes the system outside its domain of ecological resilience, the ecosystem can return to its original state following a disturbance (Holling, 1973).

Areas on which gradients are slight may be vulnerable to regime shifts covering large areas, The Everglades in southern Florida, which is very flat in elevation, is one such place, and thus is of special concern with respect to the potential effects of climate change. Regime shifts from one stable state to an alternative stable state due to disturbance have been hypothesized to be possible in both the coastal margin and freshwater marshes of the Everglades (D’Odorico et al., 2011; Larsen and Harvey, 2010; Sternberg et al., 2007).

Because ecotones are places along which regime shifts are most likely to occur, ways of estimating the resilience of these ecotones are needed (Briske et al., 2008). This paper examines an ecotone in the coastal Everglades that has been the object of recent study

(Sternberg et al., 2007; Teh et al., 2008), the case of competition between salt-tolerant (halophytic) mangroves and salt-intolerant (glycophytic) hardwood hammock or freshwater marsh vegetation types that can coexist in coastal areas, such as the southern coast of Florida. We use this as a specific case of an ecotone that is vulnerable to a regime shift. We analyze a model of this system and estimate the resilience of the system against the most likely cause of regime shift, a storm surge. Although the model is applied to the specific case of an ecotone between halophytic and glycophytic vegetation, it is generic in nature.

Empirical research shows that mangrove and hardwood hammock vegetation types are spatially separated by sharp ecotones, such that salt-tolerant mangroves line the coastal areas, and salt-intolerant species, hardwood hammocks or freshwater marsh, occupy slightly higher elevations where salinity is lower (Ross et al., 1992). The soil salinity level decreases sharply across the boundary from salt-tolerant to salt-intolerant vegetation. The differences in elevation may be so slight that it is not clear why the sharp ecotones exist precisely where they do. This led Sternberg et al. (2007) to propose that feedback effects of the two vegetation types on local soil salinity maintain the sharp ecotone, which has been studied through simulation modeling by Jiang et al. (2012). The ecohydrology of the salt-tolerant vegetation (mangroves) promotes high local soil salinity by maintaining high transpiration even when soil salinity is high, while the salt-intolerant vegetation tends to promote low levels of local soil salinity, by decreasing transpiration when soil salinity is high (Lin and Sternberg, 1992; Passioura et al., 1992; Volkmar et al., 1998). But it has also been suggested that a sufficiently large pulse of salinity, due to a storm surge, could cause a regime shift, moving the location of the ecotone inland from the coast (Teh et al., 2008).

Our objective was to build a model of an appropriate degree of complexity to not only capture the mechanisms in the mangrove–hammock ecotone, but to also allow analysis. Models built by theoretical ecologists to describe regime shifts can, for convenience, be classified into three general categories of increasing complexity: (1) systems with a single variable (e.g., a species population) with multiple equilibria (May, 1977), (2) systems with two or more variables (e.g., competing species populations) interacting through positive feedback loops (Accatino et al., 2010; Churkina and Svirezhev, 1995; Genkai-Kato and Carpenter, 2005; Gilad et al., 2007), but still analytically tractable, and (3) large network simulation models, which can only be studied numerically (Shannon et al., 2004). Systems of two competing vegetation types, each of which tends to create a local environment (e.g., abiotic conditions) favorable to itself, can often be described with models that fall into the second category, that is, they are simple enough that some mathematical analysis is possible. Such systems can be described fairly simply in terms of feedback loops between each vegetation type and its local environment. We take this approach to consider the case in which the one vegetation type can create changes in the local environmental conditions that inhibit the other vegetation type, while the other vegetation type is a better competitor in the absence of those high levels of the inhibitor. Together, these mechanisms maintain a stable spatial boundary or ecotone between the vegetation types. We hypothesize, however, that a sufficiently strong external disturbance, by influencing the inhibitor concentration over parts of the spatial domain of the competing species, might cause a regime shift involving the two vegetation types, in which one vegetation type expands in space at the expense of the other. The inhibitor in our case is salinity and storm surges are such disturbances, as they can push large volumes of sea water far inland, carrying salinity far up the usual gradient from marine to freshwater conditions (Krauss et al., 2009).

Theoretical studies have shown that spatial heterogeneity may weaken the tendency for large-scale catastrophic regime shifts

in ecosystems if local environmental characteristics vary along a smooth gradient (van Nes and Scheffer, 2005). This is a situation that applies to our case of coastal vegetation, as groundwater salinity, which plays a role in soil salinity dynamics, decreases gradually as the distance inland from the coastline increases. Here, we first examine the dynamics of two competing coastal plant species, along with the inhibitor, salinity, which is explicitly considered as a variable. Second, we extend the model to the case in which there is a slight gradient in an environmental condition, specifically groundwater salinity along one dimension, in order to investigate the effect of the gradient on potential large-scale regime shifts. We calculate the resilience of the ecotone, that is, the characteristics of the disturbance needed to cause a large spatial shift in the ecotone.

2. Materials and methods

We consider a very simple model in order to obtain results that are easily comprehended in an analytic framework and that can be compared with analogous models of competing vegetation types. Our model combines two-species Lotka–Volterra (LV) competition with the effects of a growth inhibitor, salinity. The model equations for the competing vegetation types are,

$$\frac{dN_1}{dt} = N_1 (\rho_1 f(S) - \alpha_{11} N_1 - \alpha_{12} N_2) \quad (1)$$

$$\frac{dN_2}{dt} = N_2 (\rho_2 h(S) - \alpha_{21} N_1 - \alpha_{22} N_2) \quad (2)$$

where N_1 and N_2 are the biomasses (kg/m^2) of salt-intolerant and salt-tolerant species, respectively. All parameters are positive: ρ_i is the intrinsic growth rate for species i , α_{ij} is the competition coefficient of species j on species i , and $f(S)$ and $h(S)$ are growth rate reduction functions for salt-intolerant (SI) (i.e., freshwater) species and salt-tolerant (ST) (halophytic) species, respectively, as a function of the salinity level in the soil, S . It is well known that in the traditional LV competition model, coexistence occurs only if both

$$\frac{\alpha_{21}}{\alpha_{11}} < \frac{\rho_2 h(S)}{\rho_1 f(S)} \quad \text{and} \quad (3a)$$

$$\frac{\alpha_{12}}{\alpha_{22}} < \frac{\rho_1 f(S)}{\rho_2 h(S)} \quad (3b)$$

hold. It is also clear that S affects this relationship. The salinity inhibits growth of the SI species more than the ST species, so $f(S) < h(S)$ for all values of $S > 0$. When salinity increases above about 2 ppt, $f(S)$ decreases dramatically, while $h(S)$ shows little decline within salinity levels below about 30 ppt (Sternberg et al., 2007). For mathematical convenience, we assume $h(S) = 1$, and $f(S) = \mu/(\mu + S)$, μ is half attenuation coefficient; $f(S) = 0.5$, when $S = \mu$. For a list of the parameters and their values, estimated to be consistent with conditions of a coastal Florida ecosystem, see Table 1.

Salt-intolerant species are usually superior competitors to salt-tolerant species under low salinity conditions (Kenkel et al., 1991). We assumed SI species can outcompete the ST species under low salinity circumstances (i.e., $\alpha_{21} > \alpha_{12}$). When salinity is very low, $f(S)$ approaches its maximum, 1.0, and criterion (3a) is the one that is likely to be violated. This implies that species 1 (SI) has a relatively strong effect on species 2 (ST) and species 2 has a relatively weak effect on species 1, allowing species 1 to exclude species 2. At high salinity, the situation is reversed due to the decreased growth rate of species 1, i.e., $f(S)$ approaches 0, in which case species 2 outcompetes species 1, so that criterion (3b) is more likely to be violated, allowing species 2 to exclude species 1. Because the zero-growth isoclines of N_1 and N_2 can intersect when salinity is at intermediate levels, a positive equilibrium can feasibly

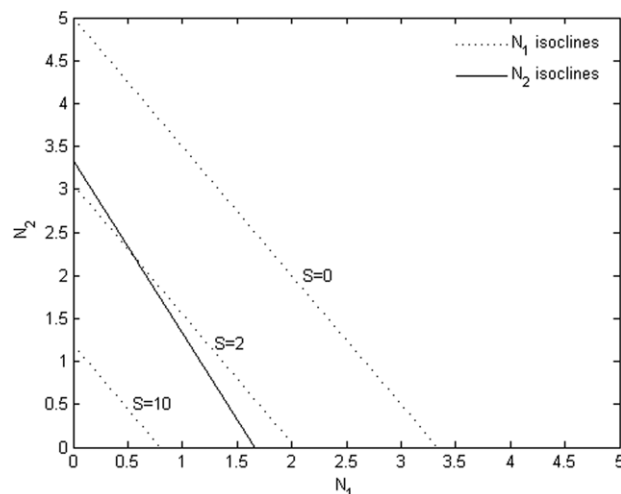


Fig. 1. Zero-growth isoclines of N_1 (dash line) at condition of $S = 0, 2$ and 10 , respectively, and N_2 (solid line).

exist, with coexistence of the two species. Under conditions in which the product of interspecific competition coefficients is larger than the product of intraspecific competition coefficients in Eq. (3) (or $\alpha_{12}\alpha_{21} > \alpha_{11}\alpha_{22}$), however, both criteria (3a) and (3b) are violated, that is, the equilibrium point is unstable, and one of the two species will go to extinction, depending on initial population densities. We made this assumption in our model. Fig. 1 shows the zero-growth isoclines of the two species. Coexistence is impossible at all three salinity levels shown in the figure. These conditions are consistent with the positive feedback switch mechanism for sharp ecotone formation.

We make soil salinity, S , a variable and introduce an equation to describe the dynamics of salinity. Soil salinity is assumed to be positively affected by salt-tolerant species, following the fact that salt-tolerant plants continuously transpire, even under highly saline circumstances, tending to cause infiltration of salt from saline groundwater (Passioura et al., 1992; Sternberg et al., 2007). We describe salinity dynamics by the following equation,

$$\frac{dS}{dt} = \beta_0 g + \frac{\beta_1 N_2}{k + N_2} g - \varepsilon S. \quad (4)$$

Here g is the groundwater salinity and β_0 is the coefficient that describes the rate at which salinity infiltrates upwards into the soil from saline groundwater through capillary action, replacing soil water that is lost through evaporation. The second term in (4) describes the increase in soil salinity due to the same infiltration process, except that the loss of water from the soil is through evapotranspiration of the salt-tolerant mangroves (for simplicity we ignore the smaller evapotranspiration from the SI species, which does not change our results qualitatively). The final term describes the loss of salinity from the soil, where ε is the washout rate of salinity due to precipitation or other freshwater input. This model form Eqs. (1), (2) and (4) resembles some other ecotone models, such as that of Accatino et al. (2010), who use the variable tree biomass, grass biomass, and soil moisture to model savanna dynamics as functions of precipitation and fire frequency.

To extend the model to spatial dynamics along a one-dimensional gradient, we assume that the densities of both vegetation types can vary spatially as distance, z , inland from the coast increases. We assume also that groundwater salinity, $g(z)$, decreases monotonically from the coastline, and we add diffusion terms to all equations.

$$\frac{\partial N_1}{\partial t} = N_1 (\rho_1 f(S) - \alpha_{11} N_1 - \alpha_{12} N_2) + D_1 \frac{\partial^2 N_1}{\partial z^2} \quad (5)$$

Table 1
Parameter values in mathematical model.

Parameter	Definition	Value used	Units
ρ_i	Intrinsic growth rate of species i	0.1	year ⁻¹
α_{ij}	Competition coefficient of species j to species i	$\alpha_{11} = \alpha_{22} = 0.03$ $\alpha_{12} = 0.02$ $\alpha_{21} = 0.06$	kg m ⁻² year ⁻¹
β_0	Salinity increase coefficient by groundwater salinity	0.3	year ⁻¹
β_1	Salinity increase coefficient by ST species, N_2	1.0	year ⁻¹
μ	Half attenuation coefficient	3.14	ppt
k	Monod coefficient	1.2	kg
ε	Salinity washout rate by precipitation	1.5	year ⁻¹
g	Groundwater salinity	0~20	ppt
D_1, D_2, D_s	Diffusion coefficients	Can be varied	m ² /year

$$\frac{\partial N_2}{\partial t} = N_2 (\rho_2 h(S) - \alpha_{21} N_1 - \alpha_{22} N_2) + D_2 \frac{\partial^2 N_2}{\partial z^2} \quad (6)$$

$$\frac{\partial S}{\partial t} = \beta_0 g(z) + \frac{\beta_1 N_2}{k + N_2} g(z) - \varepsilon S + D_s \frac{\partial^2 S}{\partial z^2}. \quad (7)$$

The diffusion terms assume that both vegetation types can spread horizontally due to vegetation growth and propagule dispersal and that salinity can also diffuse horizontally. D_1 , D_2 and D_s are diffusion rates of species 1, species 2 and salinity, respectively.

The above model is studied using a combination of mathematical and numerical analyses. First we study the equilibrium spatial vegetation patterns that emerge in this model, and then we study the effects of external disturbances on this pattern.

3. Results

3.1. Groundwater salinity g as a bifurcation parameter

We first study the system of Eqs. (5)–(7), without diffusion, by using the groundwater salinity value, g , as a bifurcation parameter. Eqs. (1), (2) and (4) imply the existence of a positive feedback loop, that is, species 2 has positive effect on soil salinity, while increasing soil salinity inhibits species 1, which benefits species 2 by reducing its direct competition effects. Bifurcation analysis shows that an unstable positive equilibrium occurs over a certain range of groundwater salinity values, g , that is, between the bifurcation points, $g_1^* < g < g_2^*$ (Fig. 2). Other equilibria include an unstable trivial equilibrium E_0 ($N_1 = 0, N_2 = 0, S > 0$), and two boundary equilibria, E_1 ($N_1 = \frac{\rho_1 f(S)}{\alpha_{11}}, N_2 = 0, S > 0$) and E_2 ($N_1 = 0, N_2 = \frac{\rho_2}{\alpha_{22}}, S > 0$). These two boundary equilibria represent two alternative steady states, both of which are stable over the range $g_1^* < g < g_2^*$ (Fig. 2, Appendix A). Outside of this range, only one of these equilibrium points is stable.

Solutions for the values of g_1^* and g_2^* for this system is presented in Appendix A, and the values are shown below:

$$g_1^* = \frac{\varepsilon \mu \left(\frac{\rho_1 \alpha_{22}}{\rho_2 \alpha_{12}} - 1 \right) (k \alpha_{22} + \rho_2)}{k \beta_0 \alpha_{22} + (\beta_0 + \beta_1) \rho_2},$$

$$g_2^* = \frac{\varepsilon \mu \left(\frac{\rho_1 \alpha_{21}}{\rho_2 \alpha_{11}} - 1 \right)}{\beta_0}.$$

The interval (g_1^*, g_2^*) represents the spatial zone along the gradient in which a regime shift from one vegetation type to the other could be caused by a sufficiently large external stress or disturbance. The size of the interval, $\Delta g = g_2^* - g_1^*$, is sensitive to β_0 , the coefficient related to the effect of groundwater salinity on soil salinity through upward capillary movement due to evaporation (Fig. 3). When β_0 is small, the increase in soil salinity due to direct salinity infiltration from groundwater into the soil due to evaporation is likely to be negligible compared with the

effect on infiltration due to vegetative evapotranspiration, which makes upward movement of saline groundwater sensitive to the type of vegetation; therefore, g_1^* changes very little with changes in β_0 . However, g_2^* is sensitive to changes in β_0 . In the range of small β_0 , decreasing β_0 causes a rapid increase in g_2^* , so the zone where regime shifts could occur becomes large. In contrast, if the groundwater salinity coefficient, β_0 , is relatively large (i.e., larger than the effect of evapotranspiration), g_1^* , along with g_2^* , decreases with increasing values of β_0 , so the size interval between them, $\Delta g = g_2^* - g_1^*$, shrinks to relatively small values.

3.2. Spatial boundary formation under a groundwater salinity gradient

From the bifurcation analysis above, we know that two alternative stable states exist over a range of groundwater salinities, $g_1^* < g < g_2^*$. It can be shown that, along a gradient of groundwater salinities, when there is no diffusion, there is the possibility of a discontinuous transition from complete dominance by one species to complete dominance by the other at any point along the gradient, with the location depending on the initial biomasses of each species.

When horizontal spatial diffusion of the three variables is non-zero but small, a stationary solution of the system exists, and it still shows a sharp transition from one species to another species along the gradient (this is a result similar to that of Levin (1974); see our Appendix A). In the following we ignored horizontal diffusion of salinity, because measurements of salinity diffusion in relevant soils (Hollins et al., 2000; Passioura et al., 1992) showed it to be small ($D_s < 0.0003$ m²/day). As a result, vertical movements of salinity due to evapotranspiration are much faster than horizontal diffusion. We also studied the sensitivity of our simulations to somewhat larger values of the salinity diffusion rate and found that they do not change the position of the sharp transition (results not shown). However, when we increased the non-zero diffusion coefficients of vegetation, D_1 and D_2 , we found that the interval over which there are two alternative equilibria is no longer the same as the original interval without diffusion, (g_1^*, g_2^*), but it shrinks as the diffusion coefficient of vegetation increases in size. We were not able to derive expressions for the new bifurcation points, g_1 and g_2 , as analytic functions of the D_1 and D_2 . Instead, extensive numerical evaluations were used to determine the behavior of the bifurcation points in response to a gradual increase of D_1 and D_2 . To calculate these, the diffusion coefficients were incremented together stepwise from zero. After each increment of the diffusion rates, the model was initialized with a large value of one vegetation type and a small amount of the other type, and then simulated to determine the attractors of the new trajectory. Each set of simulations was stopped when a bifurcation point was detected. Fig. 4 shows the bifurcation points as a function of the diffusion coefficients. Only diffusion coefficients less than 0.015

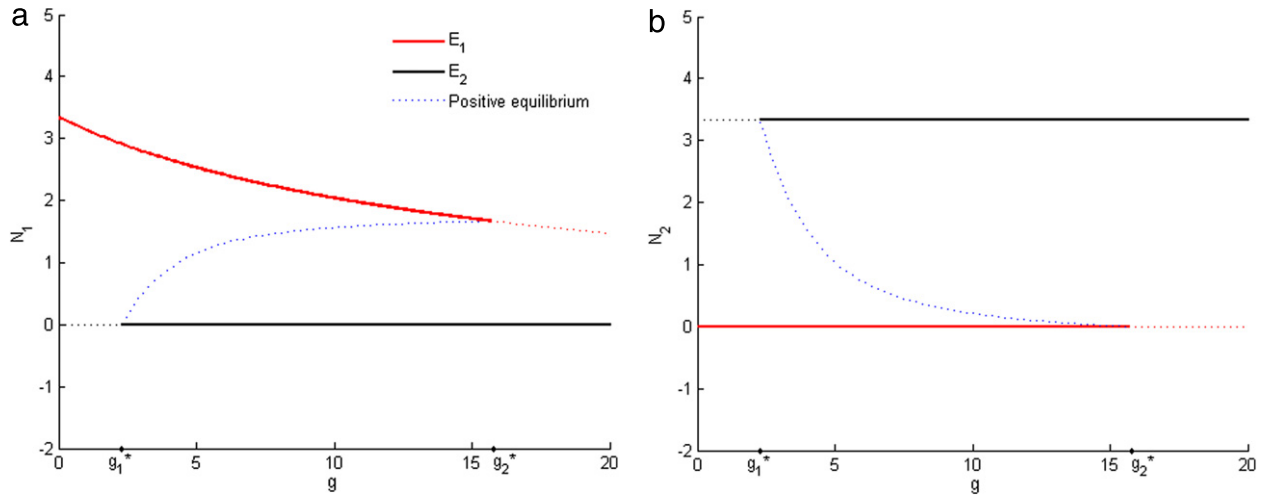


Fig. 2. Bifurcation diagram showing the values of N_1 and N_2 at the stable equilibria E_1 (red), E_2 (black) (solid lines) and at the unstable equilibrium (dashed blue line) as groundwater salinity, g , is varied. The top panel shows the value of N_1 at E_1 decreasing from a maximum value as g is increased from zero and disappearing at $g = g_2^*$. It also shows N_1 at E_1 remaining at zero as g is decreased from very large values, and disappearing at $g = g_1^*$. In the overlap region between the stable equilibria for N_1 , there is an unstable equilibrium denoted by the dashed line. The lower panel shows the analogous pattern for N_2 .

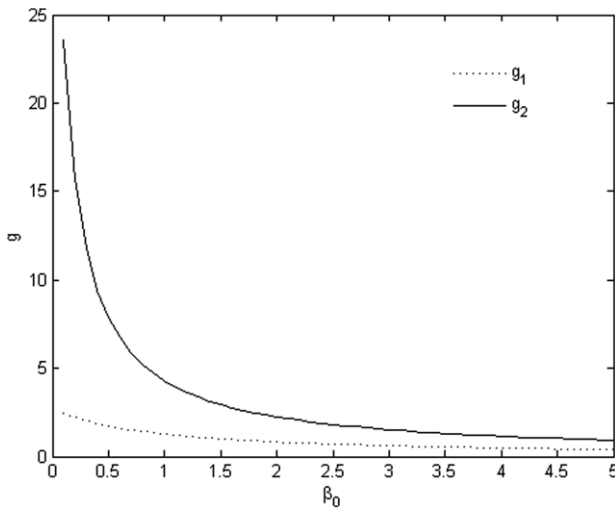


Fig. 3. Changes of g_1^* and g_2^* as functions of the coefficient, β_0 , for the rate of upward capillary movement.

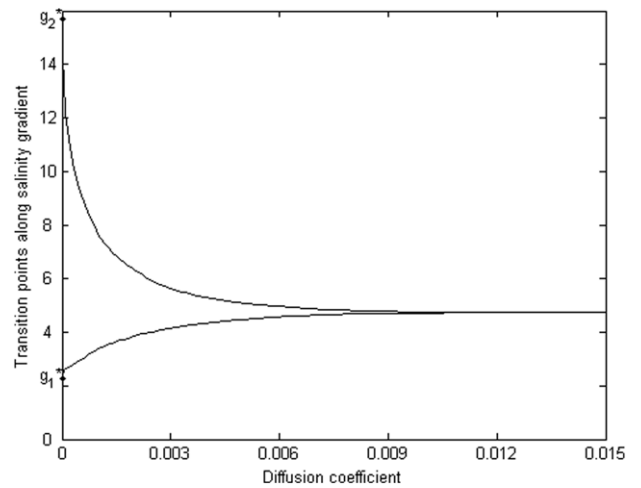


Fig. 4. Bifurcation points vary with diffusion coefficients of the vegetation. It is assumed that $D_1 = D_2$, and that they change together. g_1^* and g_2^* are the bifurcation points when diffusion coefficients equal zero.

were used, because higher diffusion rates led to mixing of the species and a very diffuse boundary, such that no bifurcation point could be detected. As the diffusion rates increase, the bifurcation points converge on each other.

3.3. Simulating the effects of size and duration of a salinity disturbance on potential regime shifts

Case 1: without diffusion

Regime shifts may occur at any point on the range from g_1^* to g_2^* , over which each of the two boundary equilibria, E_1 and E_2 , has its own basin of attraction. Any disturbances that cause N_1 and N_2 to cross over the separatrix from one basin of attraction to the other one will result in a regime shift. We numerically studied many different initial points to identify the basin to which each belongs, enabling us to construct the boundary between basins. First, we investigated the uniform system without diffusion. Fig. 5 shows the basin boundary, or separatrix, for the special case of $g = 5.0$ ppt. For the parameter values listed in Table 1, the

initial biomasses of N_1 and N_2 determine that trajectories stay within the basin of attraction of either E_1 or E_2 (Fig. 5a). The initial salinities have virtually no influence on the basin of attraction. Even a very high initial value of salinity would not shift the domain of attraction from E_1 to E_2 , because the salinity dynamics are much faster than vegetation dynamics, and salinity tends to wash out of the soil before it appreciably affects the biomasses of SI vegetation. Only if we slow down the speed of the salinity dynamics relative to the vegetation dynamics is the basin location of the initial point sensitive to initial salinity (for example, see Fig. 5b, in which salinity dynamics are slowed down 20-fold). The basins for the equilibria E_1 and E_2 are located on opposite sides of the boundary.

Ecological resilience here is defined to embody the range of disturbance magnitudes that cannot push the system from one basin of attraction into another basin. For example, we investigated whether pulses of salinity, with the vegetation densities unperturbed, would result in a regime shift, if the vegetation state was initially near E_1 (SI dominant). It can be

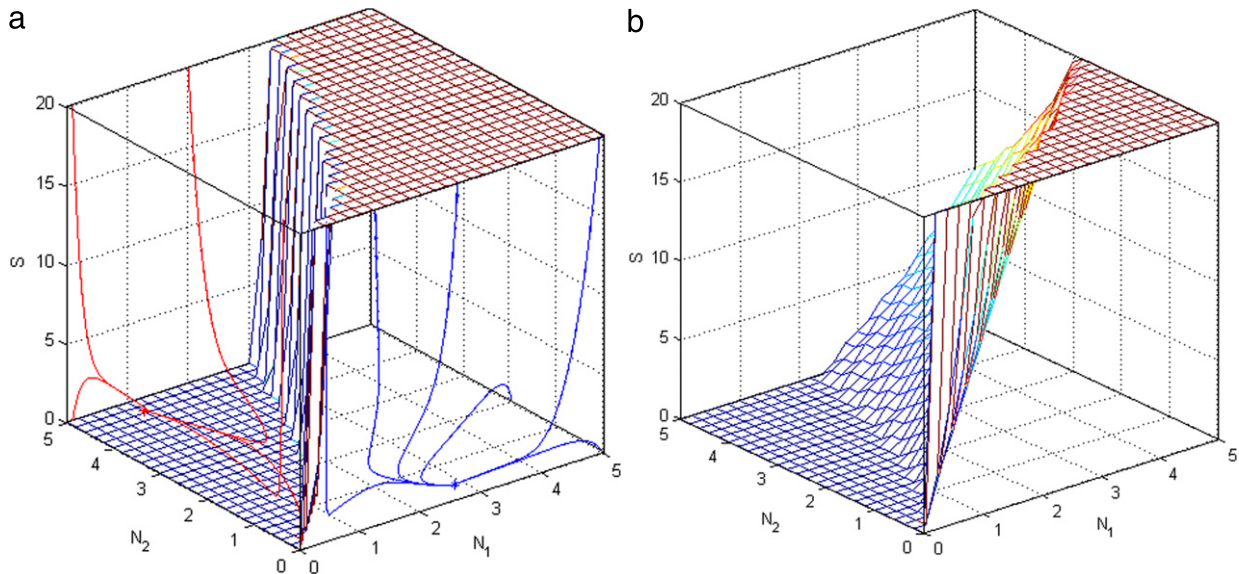


Fig. 5. Basins of attraction separated by a boundary between E_1 and E_2 for $g = 5.0$ based on (a) parameter values from Table 1, and (b) the case in which salinity dynamics are slowed by 20-fold. Red lines with arrows show the trajectories of different initial points that go to E_2 , blue lines with arrows show the trajectories of different initial points that go towards E_1 .

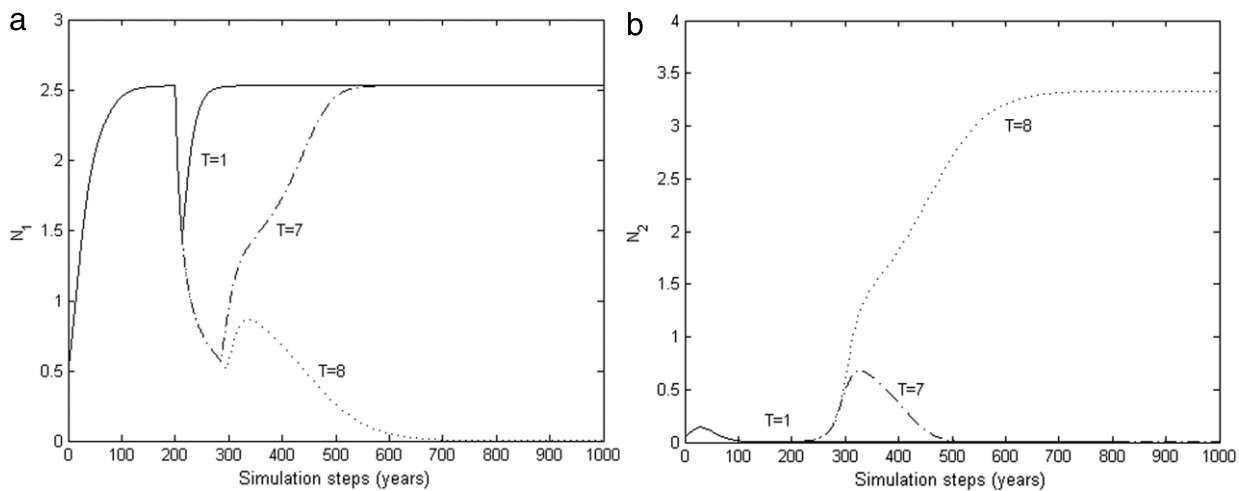


Fig. 6. Numerical evaluation of (a) N_1 and (b) N_2 , $g = 5.0$. The disturbance starts at year 200, and the durations are $T = 1, 7$ and 8 years, respectively.

shown, with reference to Fig. 5a (in which $g = 5.0$ ppt), that a salinity pulse of 20 ppt, without any accompanying change in N_1 and N_2 , except for a tiny increment in N_2 away from zero (i.e., initially, $N_1 = 2.53, N_2 = 0.01$), will result in trajectories that always remain within the initial basin of attraction of E_1 . As g increases, the basin of E_1 will decrease in size. As long as $g < g_2$, however, an instantaneous pulse of salinity alone will not push the system into the basin of E_2 . But if the salinity pulse is turned into a ‘press’, that is, if it is held at about 20 ppt for a sufficiently long period, this can result in a regime shift (Fig. 6). When salinity S is held at a high level, N_1 starts to decline dramatically, while N_2 stays close to zero for some time due to its low initial value. When S is held to 20 ppt for enough time (8 years, in this case), the trajectory moves from the basin of attraction of E_1 to the basin of attraction of E_2 , and then approaches E_2 , even though the press on S had been released ($T = 8$ years in Fig. 6). For shorter press durations, the system will still go back to E_1 , after the press on S is released, allowing it to follow the dynamics prescribed by Eq. (4) ($T = 7$ years in Fig. 6). Thus, a critical disturbance duration, T , is needed for a regime shift to occur, when the disturbance involves only changing salinity.

3.4. Simulating the effects of size and duration of a salinity disturbance on potential regime shifts

Case 2: with diffusion

Next we investigated the critical disturbance duration, T , when a groundwater salinity gradient, $g(z)$, was included, for a few different levels of the vegetation diffusion rate. The disturbance was set at $S = 20$ ppt for a duration of T years. We used simulations to determine the value of T needed for a regime shift, by incrementing the duration over which S was held at 20 ppt from 0 to larger values of time. After each increment of disturbance duration (T) by 0.1, the simulation was run for initial conditions of N_1 set at equilibrium values along the salinity gradient, and $N_2 = 0.01, S = 20$, and then run until there was no detectable movement from the new stable state for at least 1000 years. The spatial gradient of salinity along a transect inland from the coast was modeled on a one-dimensional spatial grid of discrete spatial cells in which the groundwater salinity, $g(z_i)$, jumped by 0.01 increments of ppt from 0 to 20 ppt over the length of the transect. The critical disturbance duration, T , needed for a vegetation shift to occur was recorded for each point along the salinity gradient.

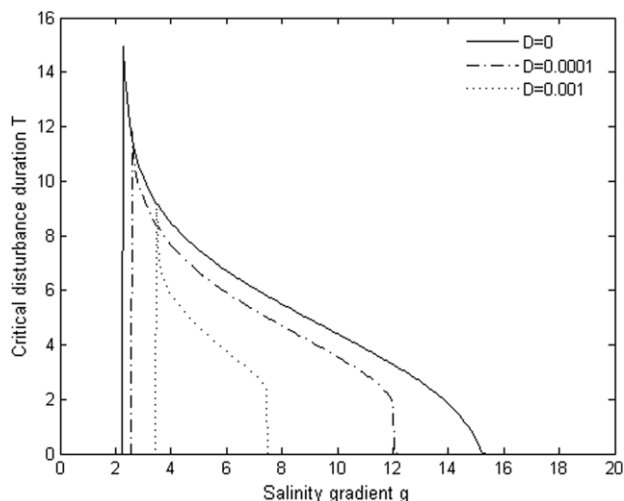


Fig. 7. Simulation outputs of critical disturbance duration against salinity gradient at different diffusion rate levels. Note that the two bifurcation points converge as D increases. For convenience, we assumed the same diffusion rates for both vegetation types.

Fig. 7 shows that the critical disturbance duration varies with position along the salinity gradient, for different values of the diffusion coefficients. It also shows, as in Fig. 4, that the distance between the bifurcation points (g_1, g_2) shrinks from the original bifurcation points without diffusion (g_1^*, g_2^*), as the diffusion increases. Outside of the relevant range of bifurcation points, (g_1, g_2) for a given set of diffusion coefficients, only one boundary equilibrium is stable, so a regime shift is impossible. Also, a regime shift occurs only when disturbance duration lies above the relevant critical curve in Fig. 7. The areas below the curves are domains where ecological resilience is effective in resisting a regime shift, such that the system will always return to its original state after withdrawal of the disturbance. The value of critical disturbance duration, T , declines as groundwater salinity g increases, equivalent to regime shifts from N_1 to N_2 (E_1 to E_2) being more likely to occur at high groundwater salinity levels. With diffusion, the critical value declines sharply as g approaches g_2 , where resilience of E_1 decreases to zero. We expect T to approach infinity when g approaches g_1 from above, because a regime shift is impossible when $g < g_1$. There was a limit to what we could demonstrate numerically, because the finite (0.01) size of our salinity grid scale did not allow us to let g approach g_1 indefinitely. As diffusion rate increases, potential regime shift zone shrinks, as indicated in Fig. 4. Overall critical disturbance duration, T , also decreases with diffusion rate.

Fig. 7 also implies that each patch along the groundwater salinity gradient between the bifurcation points shifts to an alternative stable state at a different value of the disturbance duration. Therefore, the response of the ecosystem to disturbances along the whole gradient might be patchy rather than involving the whole gradient simultaneously. We further find that the response is not straightforwardly linear. In the case of vegetation diffusion between patches, as disturbance duration gradually increases, the ecosystem as a whole does not change until it reaches a critical value; patches close to g_2^* begin to shift first, and for the shift to occur at lower values of g , more time is required (Fig. 7).

4. Discussion

This research studied the ecotone between two vegetation types along an environmental gradient. The vegetation types can occur as alternative stable states along part of the gradient on either side of the ecotone. The specific system that we studied, the

ecotone between halophytic and glycophytic vegetation along a groundwater salinity gradient, is highly vulnerable to disturbances, such salinity pulses from storm surge overwash, so it was important to estimate the resilience of the ecotone to disturbances of various magnitudes and durations. We believe this sort of estimation of resilience of an ecotone to a disturbance is relatively novel.

Analogous to other ecotones sharpened by positive feedback switches (e.g., Wilson and Agnew (1992)), in the ecotone considered here each vegetation type promotes local soil salinity levels that favor itself in competition with the other type. We found that, because of these positive feedbacks, there is a range of values of groundwater salinity bounded by two bifurcation points, $g_1^* < g < g_2^*$, for which two alternative equilibria exist. This range was shown to depend sensitively on parameters such as β_0 , the rate at which evaporation from soil can cause upward infiltration of salinity from groundwater into the soil. We showed also that increasing diffusion rates of vegetation can lead to shrinkage of the range between the two bifurcation points. The usual pattern of vegetation caused by these interactions is a sharp ecotone between salt-tolerant vegetation (mangroves) near the coastline and salt-intolerant vegetation inland, although the underlying elevation and groundwater salinity may change only slightly along the ecotone. A disturbance such as an input of salinity from a storm surge could upset this stable boundary, leading to a regime shift of salt-tolerant vegetation inland. We showed, however, that, for the parameters of our model as least, a simple pulse disturbance is not sufficient; the salinity has to be held at high levels for some time. However, our model probably overestimates the critical disturbance duration needed for the regime shift. This is because we assumed groundwater salinity as a gradient was not increased by the assumed storm surge overwash disturbance, although hydrologic models indicate that groundwater salinity may be increased for years after such a disturbance (personal communication, Eric Swain, US Geological Survey). In addition, direct mortality of SI vegetation and increasing floating dispersal of mangrove propagules due to storm surge were not considered, both of which could increase the likelihood of a regime shift.

Our model considered competition of vegetation types along a gradient in which each vegetation type could modify its local environmental conditions, where the conditions are factors that act as inhibitors of one of the species (salinity in our case, but low temperature, drought, fire, soil pH, allelopathy, etc., in others). This includes a large class of situations. But it should be noted that there is another class of models, structurally similar, that considers competition for a resource (e.g., nutrient) whose rate of input has a spatial gradient. The situation that is analogous to ours is the case in which one species is more efficient and can suppress resource concentration lower than the second species can survive. If the second species is a better competitor for another resource, light, then a stable boundary could occur with the second species occupying the part of the gradient with a higher rate of resource input. Therefore, we expect connections to exist between our study and studies of resource competition along gradients (see, e.g., Grover (1997)).

The Lotka–Volterra competition equations have long provided insights about the possibility of coexistence of two species. The LV equations demonstrated, in particular, that the coexistence of two stable states is impossible when strength of interspecific competition is stronger than strength of intraspecific competition. Our analyses were also based on this special case of LV competition. Research has indicated that interspecific competition plays an important role in halophytic species distribution, and it suggests that halophytic species are usually excluded from areas of low salinity by competitive exclusion, although they do well in monocultures (Kenkel et al., 1991; La Peyre et al., 2001; Silander and Antonovics, 1982).

Two alternative non-coexistence stable states indicate a discontinuous transition from one species to another species can occur as a consequence of a continuous change in the value of some parameter. Our results indicate that an ecotone would be formed with a distinct boundary line if groundwater salinity has a spatial gradient. Yamamura (1976) confirmed this property of LV competition equations with mathematical proof. In a non-mathematical context, Shugart et al. (1980) simulated beech-yellow poplar transition along a temperature gradient using an individual-based model. More recently, ecotone models, such as treeline models (Bader et al., 2008; Malanson et al., 2001; Wiegand et al., 2006), have simulated complex positive feedback along smooth environmental gradients, in which competition is included. In all cases, two competitors form a simple positive feedback loop, which can explain many of sharp species boundaries (DeAngelis, 1986).

The rates of diffusion that we consider in this model do not lead to mixing of individuals of the two vegetation types. Instead, in our case there were still sharp boundaries. This is not too surprising, first because positive feedback, which is explicitly connected by salinity dynamics, is strong enough to overcome small diffusional mixing effects. Second, our model simulates gradients instead of homogeneous space, and the gradient narrows the ecotone width. Fagan et al. (1999) suggested that sharp edges can be described by stipulating either zero flux (Neumann boundary) or mortality on a boundary (Dirichlet boundary). The boundary between the two vegetation types in our model corresponds to Dirichlet conditions, because propagules of each species encounter high mortality rates if they happen to land on the other side of the boundary. Mangrove propagules are outcompeted when their neighbors are mostly glycophytic types, and the glycophytic propagules are not able to survive, given the high salinity of the soil in the zone dominated by mangroves. This corresponds to our mechanism of positive feedback that overcomes diffusion near boundary and increases mortality outside the boundary. Reaction–diffusion systems are classical examples where positive feedback interacts with diffusion to form patterns (Koch and Meinhardt, 1994).

Our results are consistent with theoretical studies showing that spatial heterogeneity may weaken the tendency for large-scale catastrophic regime shifts, either if dispersion is unimportant or if local environmental characteristics vary along a smooth gradient (van Nes and Scheffer, 2005). If dispersion between patches is negligible, each patch along a gradient shifts to alternative stable state at different values of overall disturbance duration. Therefore, the response of the ecosystem as a whole is gradual.

These findings all have implications for possible changes in the vegetation of low-lying coastal regions, such as southern Florida, where rising sea level is leading to greater vulnerability of coastal vegetation to storm surges from hurricanes. While the model results here are hypothetical, changes towards salinity-tolerant vegetation have been noted in experimental studies on salinity inundation (Baldwin and Mendelssohn, 1998). Also, observations of coastal areas of Louisiana following hurricanes Katrina and Rita in 2005, which created storm surges affecting the coastal areas of Louisiana, have identified changes towards more salinity-tolerant vegetation (Steyer et al., 2010). Therefore, modeling is needed to anticipate future changes.

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Appendix. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.tpb.2012.02.007>.

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