1 **Defining the next generation modeling of coastal ecotone dynamics**
2 **in response to global change**

3 Jiang Jiang^{1*}, Donald L. DeAngelis², Su-Yean Teh³, Ken W. Krauss⁴, Hongqing Wang⁴,
4 Haidong Li⁵, Thomas J. Smith III⁶, Hock-Lye Koh⁷

5
6 ¹Department of Ecology and Evolutionary Biology, University of Tennessee, 569
7 Dabney Hall, Knoxville, TN 37996, USA.

8 ²U.S. Geological Survey, Department of Biology, University of Miami, Coral Gables, FL
9 33124, USA.

10 ³School of Mathematical Sciences, Universiti Sains Malaysia, Penang 11800,
11 Malaysia.

12 ⁴U.S. Geological Survey, National Wetlands Research Center, 700 Cajundome Blvd,
13 Lafayette, LA 70506, USA.

14 ⁵Nanjing Institute of Environmental Sciences, Ministry of Environmental Protection,
15 Nanjing 210042, China.

16 ⁶U.S. Geological Survey, Southeast Ecological Science Center, 600 Fourth Street
17 South, St. Petersburg, FL 33701, USA.

18 ⁷Office of the DVC for Research & Postgraduate Studies, UCSI University, Kuala
19 Lumpur 56000, Malaysia.

20

21 * To whom correspondence should be addressed. E-mail: ecologyjiang@gmail.com

1 **Abstract**

2 Coastal ecosystems are especially vulnerable to global change; e.g., sea level rise
3 (SLR) and extreme events. Over the past century, global change has resulted in salt-
4 tolerant (halophytic) plant species migrating into upland salt-intolerant
5 (glycophytic) dominated habitats along major rivers and large wetland expanses
6 along the coast. While habitat transitions can be abrupt, modeling the specific
7 drivers of abrupt change between halophytic and glycophytic vegetation is not a
8 simple task. Correlative studies, which dominate the literature, are unlikely to
9 establish ultimate causation for habitat shifts, and do not generate strong predictive
10 capacity for coastal land managers and climate change adaptation exercises. In this
11 paper, we first review possible drivers of ecotone shifts for coastal wetlands, our
12 understanding of which has expanded rapidly in recent years. Any exogenous factor
13 that increases growth or establishment of halophytic species will favor the ecotone
14 boundary moving upslope. However, internal feedbacks between vegetation and the
15 environment, through which vegetation modifies the local microhabitat (e.g., by
16 changing salinity or surface elevation), can either help the system become resilient
17 to future changes or strengthen ecotone migration. Following this idea, we review a
18 succession of models that have provided progressively better insight into the
19 relative importance of internal positive feedbacks versus external environmental
20 factors. We end with developing a theoretical model to show that both abrupt
21 environmental gradients and internal positive feedbacks can generate the sharp
22 ecotonal boundaries that we commonly see, and we demonstrate that the responses
23 to gradual global change (e.g., SLR) can be quite diverse.

1 **Keywords:** Coastal habitat, Vegetation change, Ecotone migration, Sea level rise,
2 Feedback

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4 **1. Introduction**

5 Coastal ecotones are typically distinctive and narrow between salt-tolerant
6 (halophytic) plant species, i.e., mangroves and salt marsh, on the seaward side, and
7 adjacent upslope salt-intolerant (glycophytic) species, i.e., freshwater marsh,
8 hardwood hammocks, and freshwater tidal forest, on the landward side of the
9 transition zone. Transition zones often parallel shorelines or major river corridors
10 and lie at the forefront of sea level rise (SLR). Saltwater intrusion is often a
11 consequence of SLR and can be punctuated by storm surges, droughts, and
12 anthropogenic landscape modifications (Cormier et al., 2013; Salinas et al., 1986).
13 Thus, shifts in salinity from a number of sources – acute and chronic – increase the
14 extent of halophyte-dominated plant communities in coastal ecosystems. Over the
15 past century, the positions of coastal ecotones have migrated inland in many areas
16 resulting from various causes, ranging from warmer temperatures and SLR, to salt
17 intrusion and human activities (Brinson et al., 1995; Krauss et al., 2011; McKee and
18 Rooth, 2008; Osland et al., 2013; Ross et al., 2000).

19 Our understanding of drivers of ecotone dynamics has expanded rapidly in
20 recent years. Any exogenous factor that increases growth or establishment of
21 halophytic species will favor the ecotone boundary moving upland (Brinson et al.,
22 1995; Jiang et al., 2012a; Saha et al., 2011). Among them, salinity intrusion and tidal
23 inundation are two prominent environmental factors among several controlling the

1 formation and boundary shift of coastal ecotones. For example, the upslope
2 movement of the freshwater forest – salt marsh ecotone in North Inlet estuary, SC,
3 under rising sea level (3.4 mm/yr) can be explained by combinations of soil
4 salinization and tidal inundation (Gardner et al., 1992). Wasson et al. (2013)
5 examined the migration of salt marsh–upland boundaries at Elkhorn Slough in
6 California. They examined the correlation of tidal inundation, water level,
7 precipitation, and boundary plant species with ecotone boundary movement at
8 undiked sites and found that only tidal inundation showed patterns consistent with
9 boundary movement. Other factors, such as elevation, water level, soil nutrients, and
10 water channel are often correlated with salinity and inundation due to the
11 characteristics of coastal habitat (Noe and Zedler, 2001; Rogers et al., 2006; Traut,
12 2005; Ungar, 1998). Salinity is a major driver in mangrove estuaries, where
13 mangrove forest encroaches on hardwood hammocks or freshwater wetlands (Jiang
14 et al., 2012a; Ross et al., 2000; Sternberg et al., 2007). In a reversal of the usual trend
15 towards increasing salinity, in some intertidal zones, decreasing salinity of
16 hypersaline saltpans during wet years can facilitate mangrove invasion of saltmarsh
17 (Bertness, 2007; Eslami-Andargoli et al., 2009). Factors not related to salinity are
18 also important. For example, increasing winter temperature because of global
19 climate change has also resulted in pole-ward migration of mangroves, replacing
20 some salt marsh habitat (Cavanaugh et al., 2014). Altered nutrient cycling may also
21 explain dieback of tidally influenced freshwater-forested wetlands along the
22 southern Atlantic coast of the USA (Brinson et al., 1985; Cormier et al., 2013; Krauss
23 et al., 2009).

Exogenous environmental conditions influence the way halophytic and glycophytic plant species are distributed along elevation gradients increasing inland. However, vegetation does not simply respond passively to exogenous influences, but may alter its environment, through creating positive feedbacks that shape the local environment. These positive feedbacks can generate sharp gradients between vegetation types, through the so-called 'switch mechanism'. This switch mechanism was first described to explain the forest/mire ecotone (Agnew et al., 1993; Wilson and Agnew, 1992), and is well studied in the forest/savanna system (Staver et al., 2011), alpine treeline (Wiegand et al., 2006), and sand dunes (Adema and Grootjans, 2003). What is characteristic of the ecotones formed by this switch mechanism is that the exogenous environmental conditions change smoothly, while the positive feedbacks of the vegetation on the environment create much of the sharpness of the ecotone, but its exact location is not determined uniquely, and it may depend on initial conditions. This can be a source of uncertainty in predictive models (Pearson et al., 2006; Refsgaard et al., 2006). A few recent studies hypothesized that self-reinforcing feedback between vegetation and environmental conditions can create alternative stable states in coastal zones. For example, various marsh macrophytes increase soil accretion rates and thus alter local elevation and flooding frequency (Marani et al., 2013; Morris, 2006), which favor discrete, narrow elevation bounds of marsh zonation (Silvestri et al., 2005). In mangrove estuaries, the ability to affect local soil salinity is another mechanism that forms a switch type of ecotone between mangroves and freshwater plants (Jiang et al., 2014b; Sternberg et al., 2007). In mangrove forest-salt marsh transitions, the canopy of mangroves

1 can maintain a relatively warm local land surface during winter freezes, countering
2 the effect of freezing temperatures that impede mangrove establishment in salt
3 marsh habitat (c.f. D'Odorico et al., 2013).

4 Developing models that describe changes within individual ecotones, but
5 with application to multiple transitions, is a challenge, especially in relation to
6 forecasting responses to SLR, storm surges, and unpredictable anthropogenic
7 landscape changes. Simple models that focus on a change in a single condition
8 without considering feedbacks will not accurately describe ecotone dynamics.
9 Synthesizing the ecosystem drivers from across a range of transitional wetland
10 environments is urgently needed if we are to understand how ecotones form, how
11 they change through time, and the processes and feedback mechanisms that govern
12 changes in the location of ecotones and community assembly in response to future
13 changes in climate and other environmental drivers. A large body of modeling work
14 has been implemented and has improved our understanding of coastal habitat
15 changes in response to SLR (e.g., Di Nitto et al., 2014; Doyle et al., 2010; March and
16 Smith, 2012; Schile et al., 2014). Many models have captured physical feedbacks of
17 vegetation on sediment dynamics (e.g. Morris et al., 2002; Rogers et al., 2012; Yang
18 et al., 2014). By including sediment accretion, these models forecast a maintenance
19 of resilience of coastal vegetation in response to a slow rate of SLR. However, these
20 models' predictions are based on correlative studies between vegetation
21 distribution and elevation, inundation, water level and other abiotic factors. Models
22 can predict saltmarsh or mangrove movement inland, as well as mangrove
23 encroachment on saltmarsh, based on elevation. As sea level rises, models can

1 describe upslope forest losing ground to halophytic vegetation, but due to the
2 common ignoring of competition and a range of positive feedback mechanisms,
3 current models may under- or over-estimate ecotone migration.

4 In this paper, we provide a novel framework of the ways that wetland
5 ecotones can shift, including internal feedbacks, in order to establish a basis for
6 future predictions about coastal ecotone dynamics, as well as a mechanistic
7 synthesis of lower-level processes underlying patterns of ecotone formation and
8 responses to global changes that are incorporated into models. We further review
9 the succession of models that gave us progressively better insight into the relative
10 importance of internal positive feedbacks versus external environmental factors.
11 We developed a cellular automata model to investigate how different mechanisms
12 contribute to patterns of coastal ecotone differently and how the ecotone position
13 responds to gradual climate change. We suggest next generation models in coastal
14 ecotone dynamics to take into account internal positive feedbacks.

16 **2. Drivers of coastal ecotone**

17 Based on the causes of community sharpness, ecotones can be distinguished as
18 *environmental*, caused by a sharp environmental change; *switch*, caused by a
19 positive feedback between species and environment; or *anthropogenic*, caused
20 directly by human activities (Lloyd et al., 2000; Walker et al., 2003). Here we review
21 and discuss the relative contribution of external (*environmental* and *anthropogenic*)
22 factors and internal feedbacks (*switch*) in combination to affect coastal ecotones
23 (Fig. 1). Indeed, several examples of driver-feedback interactions exist along

1 wetland ecotones that underscore the complexities required for predictive modeling
2 of ecotone shifts. We detail the three specific types of coastal ecotones that are
3 dramatically affected by environmental changes worldwide.

4 **2.1 Mangrove forest - salt marsh ecotone**

5 Mangroves are encroaching on salt marsh habitats globally (Saintilan et al.,
6 2014), a temporal transition often linked to increases in global temperature minima
7 (Cavanaugh et al., 2014; Osland et al., 2013; Sherrod and McMillan, 1985), sea-level
8 rise (Egler, 1952; Krauss et al., 2011; Ross et al., 2000; Saha et al., 2011), short-term
9 drought cycles (Rogers et al., 2006), seedling dispersal (Friess et al., 2012; Sengupta
10 et al., 2005), or management-altered tidal regime shifts (Ross et al., 2000; Saintilan
11 and Williams, 1999). Many of these driving variables are likely interactive; e.g.,
12 increased winter temperatures would release mangroves from freeze-induced
13 growth constraints such that they can establish landward in response to rising sea-
14 levels. *Avicennia germinans* mangrove forests have been shown to use less water
15 than adjacent *Spartina alterniflora* marsh during the early portion of the growing
16 season in coastal Louisiana (Krauss et al., 2014a), thus establishing a potential
17 interplay between warming temperatures, which allow for mangrove colonization,
18 and drought, which would be less detrimental to mangroves because they have
19 lower physiological water demand than salt marsh.

20 Mangrove forests located at low-temperature transitions with grass can
21 warm understory environments by reflecting thermal energy back to the soil
22 surface to reduce seedling mortality during extreme cold events (D'Odorico et al.,
23 2013). For example, seedlings from mangroves in temperate Florida, USA, limited

1 freeze damage better in the understory versus open marsh environments because
2 the forest provides warmer microsites, greater protection from strong north winds,
3 and reduced incidence of frost (Lugo and Patterson-Zucca, 1977; Stevens et al.,
4 2006). The warming effect is evident when air temperatures (at 0.5 m) within the
5 marsh and mangrove understory are compared (Fig. 2a). For one site in Louisiana,
6 USA, minimum marsh temperatures were approximately 2 °C lower during a two-
7 day cold spell than in the understory of stunted mangroves (K.L. McKee and W.C.
8 Vervaeke, unpubl.). This protection from canopy forest provides a potential
9 feedback by ensuring more favorable understory conditions along mangrove
10 transitions to salt marsh during the winter. Potentially as important is the greater
11 degree of warming over the day in marsh environments immediately following low
12 temperature periods; the mangrove understory provides a better buffer to extreme
13 temperature fluctuations, both low and high (Fig. 2b).

14 Mangrove encroachment of saltmarsh habitat may also be affected by
15 facilitation or competition of species interactions. On one hand, the facilitation by
16 herbaceous plants can improve mangrove forest restoration after disturbance
17 (Zhang and Shao, 2013). Grass can trap mangrove propagules, provide structure,
18 and even ameliorate soil temperatures (McKee et al., 2007b). On the other hand,
19 grass tends to be better than trees at competing for water and nutrients in upper
20 soil layers, due to their higher root density (McKee and Rooth, 2008). Facilitation is
21 anticipated to extend mangrove species distribution and realized niche, while
22 competition will help maintain distinct plant zonation in the coastal zones. The

1 relative contribution of facilitation and competition to the ecotone movement or
2 stability of ecotone is still poorly understood.

3 **2.2 Mangrove forest – upland vegetation ecotone**

4 The coastal mangroves – hardwood hammocks, mangroves- buttonwood, and
5 mangroves- freshwater marsh ecotones are mainly determined by salinity pattern.

6 Mangroves can tolerate high salinities in the rhizosphere, and more generally the
7 vadose zone or unsaturated zone of the soil, through salt exclusion, salt secretion
8 and salt accumulation (Tomlinson, 1994). Freshwater plants cannot survive outside
9 of their physiological salt tolerance range, while mangroves can grow in freshwater
10 as well as saltwater, but do not occur in strictly freshwater environments due to
11 superior competition from freshwater plant species (Krauss et al., 2008; Sternberg
12 and Swart, 1987). Global changes such as warming and SLR have caused coastal
13 vegetation to move towards higher latitudes or inland. Mangroves in the Ten
14 Thousand Islands region of Florida, USA, have shifted inland with SLR and landscape
15 modifications that have vectored tides and created new seedling dispersal corridors
16 (Krauss et al., 2011); mangroves occupied a 5403 ha area in 1927, but had expanded
17 inland while holding ground at the seaward edge to incorporate 7281 ha by 2005, a
18 35% increase. Other factors, such as changes in fire frequency, may also be affecting
19 the ecotones between some of these bands (Smith III et al., 2013).

20 The salt tolerance mechanisms in mangroves allow them to transpire during
21 periods of higher salinity, even though mangroves often have conservative water
22 use (Becker et al., 1997; Krauss et al., 2014a). A meta-analysis demonstrated that
23 transpiration reduction in response to salinity increase is greater in less salt-

1 tolerant plants (Jiang et al., 2014b). Yet, even low transpiration of mangroves under
2 high salinity conditions can lead to vadose zone salinity increases (Passioura et al.,
3 1992). Lower transpiration within gaps in mangrove canopy may lead to lower
4 salinity than surrounding forest. Unfortunately, the very few existing data do not
5 show differences in soil porewater salinity between gap and canopy (Ewel et al.,
6 1998), probably due to variation of precipitation, gap size, gap age and density of
7 seedling in the gap. In an Australian river delta mangrove forest, Fass et al. (2007)
8 found that chloride concentration was almost three times that of ocean water. In
9 contrast to the mangroves, freshwater plants can reduce transpiration largely to
10 maintain low salinity at expense of lower photosynthesis. The result of different
11 species exerting different feedbacks on soil salinity may affect the patterns of both
12 salinity and vegetation.

14 **2.3 Tidal freshwater forest – salt marsh ecotone**

15 Tidal freshwater forested wetlands, which often occur along coastal reaches
16 along major rivers, have been in the process of transitioning temporally from
17 forested wetland to marsh at the ecotone boundaries, and this change seems to be
18 associated with mean porewater salinity of 2 psu or greater (Hackney et al., 2007).
19 This threshold value for conversion is quite consistent and has been verified along
20 the lower Cape Fear River (NC), Waccamaw River (SC), Savannah River (GA), and
21 expanses of swamp forests in Louisiana. In these settings, oligohaline marsh grasses
22 encroach into degraded, salt-impacted wetland forests (dominated by *Taxodium*
23 *distichum*) as progressive degradation in canopy structure allows for greater

1 amounts of light penetration to the understory (Krauss et al., 2009). Interestingly,
2 this temporal change from forest to marsh follows salinity tightly across broad tidal
3 ranges (0.3-2.1 m); the greater the salinity relative to the threshold (2 psu), the
4 faster the rate of change from forest to marsh. The primary driver of change is not
5 the mean salinity concentration of 2 psu per se, but rather, the fluctuation around
6 this concentration associated with regional drought cycles. During the low rainfall
7 years of 2006 and 2007, monthly salinity concentrations fluctuated from 1.9 to 6.8
8 psu for a site transitioning from forested wetland to marsh along the lower
9 Savannah River in Georgia, USA (Krauss and Whitbeck, 2012). If ≤ 2 psu were held
10 constant, habitat shifts might be avoided.

11 This temporal transition associated with sea-level rise and saltwater
12 intrusion may display yet a different feedback than described in other ecotones.
13 Tree species diversity is fairly high under freshwater conditions, but trees gradually
14 die out over time with small, annual increments in salinity. Trees that do survive,
15 mostly *T. distichum*, undergo considerable morphological and physiological re-
16 structuring to accommodate increased salinity (Krauss and Duberstein, 2010). In
17 this situation the salinity stress on trees fosters their gradual senescence, along with
18 greater availability of labile detritus, and altered productivity (Cormier et al., 2013),
19 which gives rise to greater rates of nitrogen mineralization from soils as they
20 transition to marsh (Noe et al., 2013), thus establishing a possible feedback that may
21 facilitate marsh encroachment due to greater bioavailable nitrogen in the
22 porewater. In a South Carolina watershed, baldcypress also reduced water uptake
23 by more than 75% as a response to short-term salinity stress along a very similar

transition to marsh (Krauss and Duberstein, 2010), affecting the local water cycle as well.

3. Mechanistic models

3.1 Succession of models

Simple correlative studies are unlikely to establish ultimate causation and predict coastal ecotone response to global change accurately. It is important to develop a mechanistic understanding of ecotone dynamics. A prominent mechanism is habitat-specific sedimentation rate. This can be taken into account to determine how the wetland ecosystems themselves affect soil surface elevation change such that local elevation is able to track SLR better. Several models and empirical assessments indicate that, as SLR increases, tidal wetlands can increase sediment accretion and/or surface elevation change through various feedback mechanisms (Kirwan and Murray, 2007; McKee et al., 2007a; Morris et al., 2002). Indeed, tidal wetlands can respond to SLR through a host of feedbacks that can facilitate vertical accretion of sediments in response to hydroperiod, forest processes, and root structural traits. They can stimulate soil organic matter production through root growth and retention of surface litter; they can reduce root, leaf, and wood decomposition; and they can promote benthic mat formation to consolidate soils (reviewed by Krauss et al., 2014b), or some combination of these mechanisms. Many of these drivers can be quantified and incorporated into models (Kirwan et al., 2012; Morris et al., 2002), as their relative influence is determined across each specific ecotone. Soil surface elevation can also be affected by drivers that are more difficult

1 to predict, such as acute storm deposition of sediments on the soil surface (Whelan
2 et al., 2009) or storm damage-induced peat collapse (Cahoon et al., 2003) and
3 subsidence caused by human activities (Syvitski et al., 2009). Even increased CO₂ in
4 the atmosphere may affect the balance of surface elevation change by affecting
5 growth differently between adjacent wetland communities (Cherry et al., 2009;
6 Langley et al., 2009). Many of these factors can be included as feedbacks in models,
7 including individual-based models.

8 Other positive feedbacks reviewed in this article have generally not been
9 incorporated in landscape models of coastal ecotones, although growing theoretical
10 work suggests that model predictions might be different if the switch mechanisms
11 are taken into account. By including the positive feedback between vegetation and
12 vadose zone salinity through transpiration regulation, Sternberg et al. (2007) was
13 able to explain sharp boundaries observed in the mangrove- hardwood hammock
14 ecotone. The boundaries are resilient to small disturbance but could change
15 catastrophically if a tipping point is passed due to either gradual change or a large
16 disturbance. For example, if the abiotic disturbance is large enough in area and
17 magnitude (e.g., severe hurricane or high storm surge event), the resilience of the
18 inundated hardwood hammock vegetation may be overcome and, if the disturbance
19 is accompanied by high input of mangrove propagules, a large area could be pushed
20 over a tipping point such that they gradually shift to mangroves (e.g. Jiang et al.,
21 2014a; 2012b; Teh et al., 2008). Furthermore, because of the spatial variations in
22 the condition of the physical environment and the biological difference among
23 ecotone plant species at regional, landscape, and local scales, the spatial and

1 temporal patterns of coastal ecotone migration will not be uniform, and may be
2 influenced by other factors. For example, Smith III et al. (2013) found that in the
3 coastal Everglades in southern Florida the greatest mangrove-marsh ecotone
4 movement occurred in the area with the largest number of fires.

5 Due to the different formation mechanisms, responses of coastal ecotones to
6 gradual global change may vary. In a system where positive feedbacks play a major
7 role, a regime shift could occur over a certain area in response to a gradual change
8 of external factors when passing a tipping point. Here we briefly present an
9 example, using a pattern-oriented approach, in which model patterns of ecotone
10 dynamics emerge from lower-level plant fitness and environmental gradients to
11 demonstrate that different mechanisms generate different patterns in response to
12 climate change. We develop a modeling framework to simulate two types of plants
13 distributed along an environmental gradient.

14 **3.2 Model description**

15 The model description follows the widely employed Overview, Design concepts and
16 Details (ODD) protocol for describing individual-based models proposed by Grimm
17 et al (2006), although our model is a cellular model rather than individual-based.

18 *Overview:* We used a spatially explicit simulation model to investigate how
19 different mechanisms contribute to patterns of coastal ecotone differently and how
20 the ecotone position responds to gradual climate change. Our model is a general
21 theoretical study that includes species-environmental feedbacks in coastal ecotone
22 dynamics (Jiang and DeAngelis, 2013), and is not designed for particular coastal
23 species or specific locations. Individual trees or a cohort of grasses compete for

1 space in the landscape and establishment is a fitness-driven lottery process (Hurtt
2 and Pacala, 1995).

3 *Design concepts:* We based our model on that of Jiang and DeAngelis (2013)
4 and applied it to study different types of ecotone in response to gradual
5 environmental change. The model incorporates major elements required for
6 investigation of ecotone formation: a spatially explicit environmental gradient,
7 environment-mediated competition for space, species modification of the
8 microenvironment, and stochastic demography. The combination of these elements
9 allows one to observe ecotone dynamics that emerge from the interplay of
10 exogenous environmental gradient and internal positive feedbacks.

11 We did not model any specific exogenous environmental factor reviewed in
12 “*Drivers of coastal ecotone*”, because the dominant drivers are often different for
13 different ecotone systems. Here a general environmental gradient represents a
14 combination of niche gradients, of which plant species differ in fitness. By allowing
15 plant species to alter the environmental conditions of the occupied grid cell, we can
16 turn on the switch mechanism. We assume that there are seedling banks of each
17 species in the landscape waiting for favorable conditions, so we do not model
18 explicit dispersal processes.

19 *Entities, state variables and scales:* There are two types of entities: halophytic
20 and glycophytic individual trees or clumped cohorts of grasses. These differ in niche
21 optima along the environmental gradient. If the model is applied to marsh species, a
22 cohort of grasses is taken to be roughly the size of an adult tree canopy. For
23 convenience, we aggregate individual grass (or sedge, etc.) stems as super-

1 individuals in this model. Two states of life history are considered: seeds and adult
2 plants. A two-dimensional 100 x 100 grid cell represents the landscape, with each
3 grid cell being the size of a tree canopy and occupied by one individual. Each grid
4 cell has an environmental state, with potential values between 0 and 1. The values
5 determine plant fitness in recruiting from the seedling state to adult state, and these
6 can be changed by focal and neighboring trees when the switch mechanism is on.
7 For convenience, we assume grid cells at the seaward side have lower
8 environmental values, while those at the inland side have higher values. The edges
9 of the landscape are cut off at the two ends of the environmental gradient, but are
10 wrapped-around in the direction perpendicular to the gradient to avoid edge effects.

11 *Process overview and scheduling:* The total number of adult individuals in the
12 landscape always equals the number of cells. At each time step, one individual is
13 selected at random to die and instantaneously be replaced by another plant recruit
14 from the seedling bank according to the fitness function of both species. The
15 environmental state of each grid cell is either static or a function of species-
16 environment feedback, and depends on whether the switch mechanism is off or on.
17 At the end of a time step, the location and identity of surviving adults and
18 environmental values are passed to the next time step.

19 *Initialization and input data:* Simulations began with randomly assigned
20 individuals, with equal probability for both species, for a given site on the landscape.
21 Halophytic and glyophytic species differed only in their optimal environmental
22 state. The landscape was composed of a user-defined baseline state environment,
23 which could be either smooth or sharp along one spatial direction. No input data

1 were required when the simulation was to find steady state spatial distribution of
2 both species. But when the model was used to investigate ecotone migration in
3 response to global change, the baseline state of the environment was forced to
4 change at a constant gradual rate.

5 *Submodel:* When an adult died, one seedling from the seedling bank in each
6 grid cell was chosen to recruit based on the relative fitness. The recruitment
7 probability R_s of species s was

$$R_s = \frac{F_s}{\sum_{k=1}^S F_k}$$

8 where the total number of species $S = 2$ in our study. The fitness function (F_s) of
9 species s was calculated from a Gaussian function, with optimal environmental state
10 (niche optimum) at μ_s and a fundamental niche breadth (b_s)

$$F_s = -\frac{(E_{i,j} - \mu_s)^2}{2b_s^2}$$

11 where $E_{i,j}$ is the current state of environment at location $[i, j]$. We assumed $\mu_1 = 0.25$
12 and $\mu_2 = 0.75$ for halophytic and glycophytic species, respectively, in a standardized
13 environmental gradient varies from 0 to 1.0 (saline to fresh). Niche breadth b_s was
14 set to 0.15 for both species.

15 The switch mechanism was built on the species' ability to alter the abiotic
16 local environment state. By positive feedback, a species tends to change
17 environmental condition towards its niche optimum. Without positive feedback, the
18 environment returns to its original baseline state $E_{i,j}^0$. We defined a relative strength
19 ($\alpha=0.5$) of species-environment feedback to the recovery rate of the environment to
20 its baseline state (Jiang and DeAngelis, 2013), so that

$$E_{i,j} = \frac{1}{N} \sum \alpha \mu_s + (1 - \alpha) E_{i,j}^0$$

1 where $N=9$ is number of neighboring cells and the focal cell. Plants in each of the 9
 2 cells have potential to modify the middle focal cell towards its niche optimum,
 3 through neighborhood affects. We averaged these niche optima to account for total
 4 species-environment feedback.

5 Two sets of baseline environments were studied, representing smooth and
 6 sharp environmental change long a spatial direction. In the case of a smoothly
 7 changing environment, the environmental state ($E_{i,j}^{smooth}$) increased from 0 at
 8 seaward cells to 1.0 at inland cells. In the case of a sharp environment, the smooth
 9 baseline state is *logit* transformed

$$E_{i,j}^{sharp} = \frac{e^{c(E_{i,j}^{smooth}-d)}}{1 + e^{c(E_{i,j}^{smooth}-d)}}$$

10 where parameter c determines how sharply the environment changes along the
 11 spatial dimension, and parameter d is the location of the breakpoint.

12 Global change was simulated after vegetation distribution reached a steady
 13 state. We ran each simulation 500 000 generations to reach steady state, and ran an
 14 additional 100 000 generations in response to global change. In the case of a smooth
 15 environment (Fig. 4 top left), we assumed that the state value of each cell decreased
 16 gradually at a rate of 0.5 over the 100 000 generations, representing global change
 17 favor halophytic plants. To avoid negative environmental values, we set a lower
 18 limit of 0 to each cell. In case of sharp environment (Fig. 4 top right), we assumed
 19 the breakpoint position moved gradually towards higher end of environment, at
 20 rate of 0.5 over the 100 000 generations.

1 *Sharpness index and breakpoint analysis:* We calculated the sharpness index
2 for a snapshot at steady state from each single simulation. The sharpness was based
3 on entropy of mixing, where higher entropy corresponding to lower sharpness
4 (Jiang et al., 2012a),

$$Sharpness = \omega(1 - \frac{W}{W_{max}})$$

5 where W is the entropy of the system and is calculated by $W = -\sum_{i=1}^{100} p_i \ln(p_i)$. We
6 counted the total number of cells for each plant type. Then, along the direction of the
7 environmental gradient, we calculated p_i the fraction of cells of one vegetation type
8 with respect to the total number of cells of that type. Entropy reaches a maximum
9 (E_{max}), if species are evenly distributed along the gradient, with probability of 0.01.
10 The sharpness is normalized by ω , which corresponds to each vegetation type
11 occupying half of the landscape, and being evenly distributed among their region. In
12 this case, sharpness is 1.0.

13 In the global change simulations, boundaries move along the environmental
14 gradient. We determined the boundary position by breakpoint analysis (R package:
15 changepoint). The basic idea of the method is to calculate the maximum likelihood
16 of all possible change point locations.

17 **3.3 Model outputs**

18 The positive feedbacks in each system presented in this paper have a general
19 feature: different types of vegetation modify environmental conditions away from
20 baseline values to favor themselves. Also, the drivers of abiotic factors result in
21 ecological niche along the environmental gradient. We use contrasting model

1 structures to represent different mechanisms. By tuning parameter values, we can
2 generate sharp boundaries between the two vegetation types for different model
3 structures (Fig. 3), with different combinations of exogenous environmental change
4 and positive feedback reinforcement. Without a contribution from the positive
5 feedback in smoothly (we use ‘smooth’ to refer to spatial variation, and ‘gradual’ to
6 refer to temporal variation) varying environments (Fig 3A), the sharpness index is
7 lower than when there is also a *switch* ecotone (Fig 3B). In some cases, we cannot
8 easily say which mechanism, whether the exogenous environmental factors or the
9 positive feedback between the vegetation and abiotic conditions, contributes more
10 to the sharpness of ecotone from this theoretical simulation. Some of the current
11 simulations show that the sharpness of *environmental* ecotone is probably the major
12 factor, and the *switch* mechanism merely strengthens the sharpness of the ecotone
13 formed by the exogenous factors (Fig 3C, 3D). The parameters that control the
14 sharpness of each type of ecotone formation (exogenous factors or positive feedback
15 switch) are different, and need to be calibrated from the real system. However,
16 these two types of ecotone creators differ significantly in response to gradual
17 changes of environment. Figure 4 plots the position of the boundary as a function of
18 an index of global climate change. Without positive feedback, the boundary position
19 in both a smoothly and a sharply changing environment responds to environmental
20 change linearly (Fig. 4A, 4C). But when the *switch* mechanism is present, the
21 boundary position may be relatively stable through long periods of gradual
22 environmental change, and then change abruptly when certain threshold levels of
23 change are reached, showing an overall slower response (Fig. 4B). In the final case,

Fig. 4D, it seems that the sharp spatial environment is the overwhelming effect, and the positive feedback does not produce enough resilience to cause a lagged effect.

No response data exist for future global change scenarios. If an ecotone model does not explicitly take into account possible positive feedbacks in the system, and is calibrated based on correlative studies between ecotone response and global change, the model predictions could overestimate the initial ecotone migration, because positive feedbacks result in resilience that delays the migration of the ecotone. But if the data calibrations are based on slow response of boundary position due to resilience, the model could underestimate ecotone migration, because after some threshold, the ecotone can respond rapidly or even change catastrophically. Resolution of model scale may affect the results. Normally, large-scale data are associated with coarse resolution, which may result in stronger environmental driven patterns. At coarse resolution, spatial changes of environmental condition might be abrupt because the entire ecotone zone might be represented by only one grid in some global models. Further studies on ecotone migration simulating different scales and resolutions are needed.

4. Conclusions

In this review we have shown that positive feedbacks have been documented across mangrove-upland, marsh-upland and mangrove-marsh transitional communities. In the mangrove forest–upland vegetation ecotone, different transpiration regimes of halophytic and glycophytic plants in response to enhanced salinities lead to differential ability of influencing vadose zone salinity, which feeds

1 back to vegetation water uptake and growth rate. Replacement of upslope habitats
2 by salt marsh is largely reported to be due to increasing inundation, which is
3 reinforced by a feedback by which the marsh can adjust flooding frequency to favor
4 itself. Temporal transition from upstream freshwater forest to marsh might also be
5 due to increasing nitrogen mineralization rate after marsh encroachment. The
6 mangrove- salt marsh boundaries are mainly controlled by canopy – temperature
7 feedbacks, where mangrove seedlings can survive from winter freezes under the
8 canopy of adult trees.

9 Although the specific feedbacks are different in each transition, all habitat
10 transitions they have a common feature that each vegetation type is able to modify
11 microsite abiotic conditions to favor itself. Our model demonstrates that prediction
12 of vegetation change is quite different when taking into account the positive
13 feedback. We suggest that the next generation of ecotone models to include these
14 internal feedbacks.

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1 **Figure Captions**

2 **Fig. 1.** A schematic diagram shows the combination effects of external
3 environmental and anthropogenic factors and internal feedbacks between plant
4 species and soil environments.

5 **Fig. 2.** (A) Temperatures in the understory of black mangrove (*Avicennia*
6 *germinans*) versus marsh (*Spartina alterniflora*) communities in Port Fourchon,
7 Louisiana, during a 2008 cold spell. Means ($\pm$ 1 SE) represent observations from
8 three replicate mangrove and marsh sites each. (B) Differences are partitioned by
9 high temperature versus low temperature extremes over the six days to facilitate
10 comparisons. (K.L. McKee and W.C. Vervaeke, unpubl.)

11 **Fig. 3.** Sharpness index from model simulations, and a snapshot of the spatial
12 pattern for case (A) Null model: no positive feedback is involved in a smooth
13 environment. (B) Switch ecotone: caused by positive feedback between vegetation
14 and environment, in which the underlying environment is smooth. (C)
15 Environmental ecotone: caused purely by sharp environmental changes. (D) A
16 combination of switch mechanism and sharp environmental change. Error bars are
17 standard deviation from 20 replicates.

18 **Fig. 4.** Boundary positions in 4 types of ecotone (same as Fig. 3) in response to
19 gradual global change (bottom panels). Boundary position is quantified as location
20 of breakpoint from left to right on the simulated landscape. Initial boundary
21 positions are at middle of landscape (0.5), and move towards locations where
22 environmental values are high (1.0) in response to global change. The global change
23 axis indicates temporal changes of environmental values shown in top panels, e.g.

- 1 changing from the solid line the dash line. 20 replicated simulations (gray) were
- 2 used to determine mean positions (black). .

1

2 Fig. 1.

B

High temp. (°C)	a. Marsh	b. Mangrove	<i>Diff (a-b)</i>
Jan 30	17.59	14.81	2.78
Jan 31	24.59	22.91	1.68
Feb 1	19.35	14.07	5.28
Feb 2	26.27	21.86	4.41
Feb 3	26.83	24.74	2.09
Feb 4	29.42	26.09	3.33
Low temp. (°C)	a. Marsh	b. Mangrove	<i>Diff (a-b)</i>
Feb 1	9.99	11.86	-1.87
Feb 2	3.64	5.87	-2.23

1

2 Fig. 2.

1

2 Fig. 3.

A

B

C

D

Fig. 4.