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

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ABSTRACT

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

1. Introduction

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

Our understanding of drivers of ecotone dynamics has expanded rapidly in recent years. Any exogenous factor that increases growth or establishment of halophytic species will favor the ecotone boundary moving upland (Brinson et al., 1995; Jiang et al., 2012a; Saha et al., 2011). Among them,

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salinity intrusion and tidal inundation are two prominent environmental factors among several controlling the formation and boundary shift of coastal ecotones. For example, the upslope movement of the freshwater forest–salt marsh ecotone in North Inlet estuary, SC, under rising sea level (3.4 mm/yr) can be explained by combinations of soil salinization and tidal inundation (Gardner et al., 1992). Wasson et al. (2013) examined the migration of salt marsh–upland boundaries at Elkhorn Slough in California. They examined the correlation of tidal inundation, water level, precipitation, and boundary plant species with ecotone boundary movement at undiked sites and found that only tidal inundation showed patterns consistent with boundary movement. Other factors, such as elevation, water level, soil nutrients, and water channel are often correlated with salinity and inundation due to the characteristics of coastal habitat (Noe and Zedler, 2001; Rogers et al., 2006; Traut, 2005; Ungar, 1998). Salinity is a major driver in mangrove estuaries, where mangrove forest encroaches on hardwood hammocks or freshwater wetlands (Jiang et al., 2012a; Ross et al., 2000; Sternberg et al., 2007). In a reversal of the usual trend towards increasing salinity, in some intertidal zones, decreasing salinity of hypersaline saltpans during wet years can facilitate mangrove invasion of saltmarsh (Bertness, 2007; Eslami-Andargoli et al., 2009). Factors not related to salinity are also important. For example, increasing winter temperature because of global climate change has also resulted in pole-ward migration of mangroves, replacing some salt marsh habitat (Cavanaugh et al., 2014). Altered nutrient cycling may also explain dieback of tidally influenced freshwater-forested wetlands along the southern Atlantic coast of the USA (Brinson et al., 1985; Cormier et al., 2013; Krauss 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 can maintain a relatively warm local land surface during winter freezes, countering the effect of freezing temperatures that impede mangrove establishment in salt marsh habitat (cf. D'Odorico et al., 2013).

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

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

2. Drivers of coastal ecotone

Based on the causes of community sharpness, ecotones can be distinguished as *environmental*, caused by a sharp environmental change; *switch*, caused by a positive feedback between species and environment; or *anthropogenic*, caused directly by human activities (Lloyd et al., 2000; Walker et al., 2003). Here we review and discuss the relative contribution of external (*environmental* and *anthropogenic*) factors and internal feedbacks (*switch*) in combination to affect coastal ecotones (Fig. 1). Indeed, several examples of driver-feedback interactions exist along wetland ecotones that underscore the complexities required for predictive modeling of ecotone shifts. We detail the three specific types of coastal ecotones that are dramatically affected by environmental changes worldwide.

2.1. Mangrove forest–salt marsh ecotone

Mangroves are encroaching on salt marsh habitats globally (Saintilan et al., 2014), a temporal transition often linked to increases in global temperature minima (Cavanaugh et al., 2014; Osland et al., 2013; Sherrod and McMillan, 1985), sea-level rise (Egler, 1952; Krauss et al., 2011; Ross et al., 2000; Saha et al., 2011), short-term drought cycles (Rogers et al., 2006), seedling dispersal (Friess et al., 2012; Sengupta et al., 2005), or management-altered tidal regime shifts (Ross et al., 2000; Saintilan and Williams, 1999). Many of these driving variables are likely interactive; e.g.,