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Original Research Article

Ecotone formation induced by the effects of tidal flooding: A conceptual model of the mud flat-coastal wetland ecosystem

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ABSTRACT

The boundary between mud flat and coastal wetland ecosystems is highly productive and a haven of considerable biodiversity. It is also embedded in a highly dynamic environment and can be easily destabilised by environmental changes, invasive species, and human activity. Thus, understanding the processes which govern the formation of this ecotone is important both for conservation and economic reasons. In this study we introduce a simple conceptual model for this joint ecosystem, which demonstrates that the interaction between tidal flooding and habitat elevation is able to produce an ecotone with similar characteristics to that observed in empirical studies. In particular, the transition from mud flat to vegetated state is locally abrupt, occurring at a critical threshold elevation, but, on broader spatial scales can occur over a range of elevations determined by the variability in high tide water levels. Additionally, the model shows the potential for regime shifts, resulting from periods of unusual weather or the invasion of a fast growing, or flood resistant, species.

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1. Introduction

The transition between intertidal mud flat and coastal wetland ecosystems is of great ecological and economic importance. These habitats are found around the world, with salt marshes forming in temperate regions, e.g. the German Wadden Sea and New England coast, and mangrove swamps forming in subtropical regions, e.g. Florida and south east China, but, regardless of climate, are characterised by the highly productive communities of benthic invertebrates and plants that they support (Alongi, 1990; Barnes et al., 1997; Erftemeijer and Lewis, 1999; Zedler and Kercher, 2005). While these basal communities may be relatively homogenous (less so in subtropical environments), the biomass produced supports a wide range of higher organisms and thus these habitats as a whole represent a haven of biodiversity (Erftemeijer and Lewis, 1999; Zedler and Kercher, 2005). In addition to their ecological importance, many of the species in these communities are harvested, producing significant economic yields (Barbier et al., 1997) and the transition to a vegetated state protects the coastline from erosion, a significant problem in sub-tropical communities (Thampanya et al., 2006). These transitional ecosystems are threatened by a variety of factors and, despite their importance, are in decline globally (Zedler and Kercher, 2005). For example, human harvesting activities often damage the wetland community leading to a regime shift to mud flats (Thampanya et al., 2006). On the other hand, invasive grasses (such as *Spartina* species) can rapidly convert mud flats to vegetated meadows (Hacker et al., 2001; Zhang et al., 2012). The loss of either community naturally reduces biodiversity and productivity of the joint ecosystem, and thus understanding the population dynamics underlying this transition is important for both conservation and economic reasons.

Transition zones where one community gives way to another, also referred to as ecotones, have been studied extensively, see (Cadenasso et al., 2003; Strayer et al., 2003; Yarrow and Marín, 2007) and the references contained therein. Naturally occurring ecotones often form in the presence of an environmental gradient, such as temperature (Shugart et al., 1980) or salinity (Jiang et al., 2012; Basset et al., 2013), which induces a transition between similar communities, e.g. grassland or forest succession, with different tolerances to that gradient, e.g. see Walker et al. (2003). Alternatively, periodic disturbances, such as storms (Dollar and Tribble, 1993) or fires (Hoffmann et al., 2012), can allow species to coexist in a long term transitional community which would otherwise be dominated by one species type, e.g. savanna ecosystems (Hoffmann et al., 2012). We note that the transition in

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wetland communities, from mangrove swamp to coastal wetland, results, in part, from a combination of these factors, as decreasing temperatures with latitude increase the frequency of winter freezes, a disturbance that mangroves are less able to tolerate (Guo et al., 2013; Saintilan et al., 2014).

Mathematical modelling has been used successfully in a variety of frameworks to describe features of ecotone formation (or more generally pattern formation) (Shugart, 1990; Gilad et al., 2004; Kondo and Miura, 2010; Gastner et al., 2011). In general, boundary formation in these models is a consequence of the interactions between species or a species and its environment. A particular focus of this research has been the important role of ecosystem engineers, that is species which significantly modify their habitats, in this process. For example, Jiang and DeAngelis (2013) show that an abrupt ecotone forms between species that have opposed engineering effects; in their case, halophytic mangroves and glycophytic hardwood hammocks compete to influence soil salinity. These engineering effects also create the potential for regime shifts in response to severe system disturbances, e.g. tropical storms, which create an opportunity for mangroves to invade hardwood hammock habitat. The role of more moderate disturbances in maintaining transitional communities has also been explored, for example in savanna ecosystems see (Thonicke et al., 2001; Hanan et al., 2008; Scheiter and Higgins, 2009).

However, even when incorporating such moderate disturbances, the systems considered in most studies are relatively stable compared to that of the mud flat to coastal wetland ecotone. This habitat is subject to daily tidal flooding, which causes a variety of effects, including soil erosion and sedimentation, fluctuations in salinity and, of course, direct changes in the populations of the two communities (Mahall and Park, 1976; Balke et al., 2014). The result is a highly dynamic environment which is known to have significant effects on the biodiversity and functioning of this ecosystem (Brose and Hillebrand, 2016; Fischer et al., 2016) and which, furthermore, can reasonably be expected to influence ecotone formation.

In addition to these interesting ecological effects however, the complexity of this environment represents a considerable source of uncertainty to be addressed in any model seeking to describe this system. In particular, a mechanistic approach, e.g. (Thonicke et al., 2001; Scheiter and Higgins, 2009), must determine an appropriate mathematical description for each of the many processes that make up the system behaviour. The parameters for each of these descriptions must then be determined by experimental data, which may not be available. Moreover, the more closely a model describes a particular set of environmental conditions, the greater the risk that the insights it provides are unique to that setting and that general phenomena cannot be readily identified or explained. On the other hand, a conceptual approach, e.g. (Holling, 1966; Hanan et al., 2008), represents the underlying physical processes only abstractly, and thus ignores these uncertainties, but cannot claim to represent a particular physical system. Instead, such models can be used to connect aspects of (abstract) processes to particular phenomena.

These considerations are, of course, inherent to any mathematical model and debate over which approach to use, and under what circumstances, is ongoing (Evans et al., 2013). We mention them here to provide some context regarding our modelling approach in this study. In particular, in contrast to existing models of the mud flat and coastal wetland ecosystem which are primarily mechanistic, e.g. (van de Koppel et al., 2001; Marani et al., 2010), we develop a minimal conceptual model in order to explore the key mechanisms producing and defining this ecotone. We assume that each of these habitat types, mud flat and coastal wetland, is characterised by a particular community, one benthic and the other terrestrial, which are affected differently by tidal flooding. We then model the dynamics of these communities as species competing for a common resource, which we regard as space, with the terrestrial "species" being assumed to act as an ecosystem engineer. The underlying dynamics of these populations is given by a simple system of differential equations. The tidal flooding process is modelled as a series of discrete stochastic events, representing differences in the high tide water level in relation to a fixed habitat elevation, which may negatively affect one or other of the populations. Using this model we seek to determine: (1) under what circumstances an ecotone can form and (2) how the spatial characteristics of that ecotone are affected by model parameters. In particular, we note that the mud flat to coastal wetland ecotone is known to occur over a relatively narrow range of elevations in a given habitat (Balke et al., 2014), however on a broader spatial scale, the position of this switch can vary significantly (Simenstad et al., 1997). Thus, we investigate how these characteristics can be reproduced in the model framework described.

2. Model

We describe the combined mud flat and coastal wetland ecosystem, and its environment, using a simple conceptual model consisting of two components. A series of sketches, providing an overview of this model, can be found in Fig. 1. The first sketch, Fig. 1 top, is a cross-section through the ecosystem, showing the benthic b and vegetative v communities dominating at low and high elevations h, respectively. The water level at high tide η, which determines how much of the habitat is flooded, varies on a daily basis. The underlying structure of the model is presented in a schematic diagram, Fig. 1 bottom left. The two communities

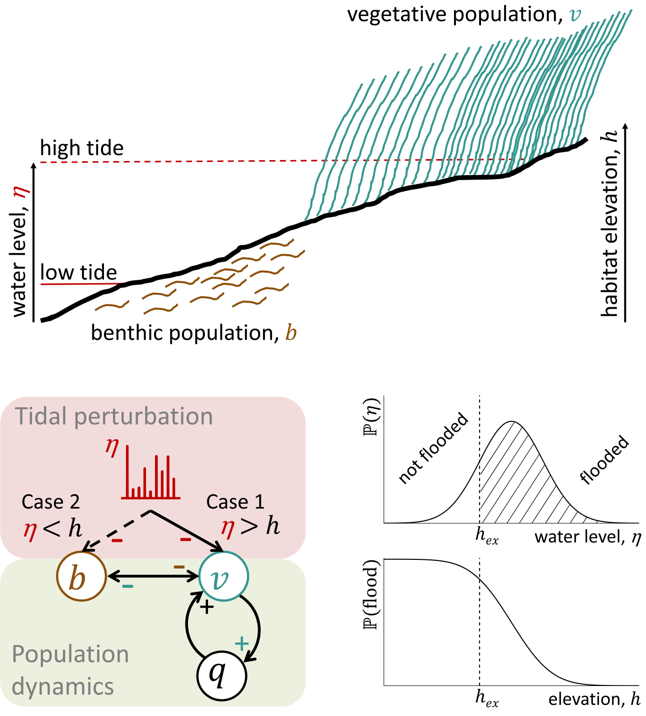

Fig. 1. Top: Sketch of the transition from mud flat to coastal wetland. The vegetative and benthic populations, v and b respectively, compete for space on an elevation gradient, h. The water level at high tide η varies. Bottom left: Schematic diagram of the model components showing the qualitative interactions between populations, habitat quality q and the tide. Further details can be found in the text. Bottom right: The probability of a particular high tide water level $\mathbb{P}(\eta)$ (top) and the corresponding probability that a habitat at a given elevation h will be flooded $\mathbb{P}(\text{flood})$ (bottom).

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