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Where do you draw the line? Determining the transition thresholds between estuarine salt marshes and terrestrial vegetation

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ABSTRACT

The aim of this study was to determine if abiotic thresholds are responsible for maintaining the salt marsh–terrestrial vegetation boundary. In eight estuaries along the South African coast, sediment and groundwater characteristics were measured in quadrats spanning the salt marsh, ecotone and terrestrial habitats. The cover of salt marsh vegetation showed no obvious limitation to any of the recorded environmental variables. This supports Purer's hypothesis that the upper boundary of estuaries is limited by competition. In contrast, terrestrial vegetation cover declined with increasing sediment electrical conductivity (threshold ~20–30 mS/cm), groundwater electrical conductivity (threshold ~60–80 mS/cm), and groundwater salinity (threshold ~20–40 ppt) and sediment moisture content (threshold ~20–25%). These variables were strongly correlated, and may be operating synergistically or a subset of these may be responsible for restricting terrestrial vegetation from occurring in the salt marsh. In the absence of landuse changes at the salt marsh–terrestrial boundary, salt marshes are unlikely to be unaffected by rising sea-levels as a landward migration will not be constrained by abiotic factors.

1. Introduction

Coastal salt marshes are intertidal wetlands consisting of salt-tolerant flowering plants in the form of low growing shrubs, herbs and grasses (Adam, 1990; Pennings et al., 2005). Coastal salt marshes differ from inland salt marshes mostly because the latter do not have frequent tidal inundation and the chemistry of the dominant salts is derived from geological sources (Eallonardo and Leopold, 2014; Seaman et al., 1991). This study and references herein refer to coastal salt marshes, which we differentiate from non-halophytic terrestrial vegetation. Salt marshes are distributed throughout artic and temperate regions but are generally displaced by mangrove forests in the subtropics and tropics (Adam, 1990; Saintilan, 2009). The distribution of species within in a salt marsh has been ascribed to biotic factors such as competition (Pennings and Callaway, 1992) and abiotic factors such as sediment salt and moisture content (Bertness and Ellison, 1987; Noe and Zedler, 2000). Cui et al. (2011) suggested that it is also these environmental variables that separate salt marsh and terrestrial vegetation. Here we looked at the environmental correlates along the salt marsh terrestrial transition within the South African context.

The borders between the salt marsh and adjacent terrestrial (or upland) habitat tend to be very distinctive and narrow (Wasson and Woolfolk, 2011). Purer (1942) studied salt marshes in San Diego County, California where she observed a gradual change from salt marsh plants to the less salt tolerant terrestrial or upland vegetation which was Chaparral, the climax vegetation for this region. Baye (2012) found that in Californian salt marshes the salt marsh–terrestrial boundary forms narrow bands that support distinctive and regionally uncommon plant assemblages. The shape and composition of the salt marsh–terrestrial boundary has been attributed to changes in elevation, inundation and salinity based on ecophysiology (James and Zedler, 2000) and species composition (Traut, 2005).

Within the salt marsh, extreme environmental variables that influence the distribution of species operate synergistically (Adams et al., 1992; Pennings and Callaway, 1992). The most important abiotic factors or stressors that delimit both the small and large scale distributions of coastal and inland salt marshes are salinity and water availability (Gray and Scott, 1967; Sánchez et al., 1998). These abiotic variables also tend to vary seasonally and over shorter time scales (e.g., after major floods and rainfall events). Therefore when investigating the distribution of salt marsh species the variability of abiotic factors also need to be considered. For example Bornman et al. (2002) recorded lower sediment electrical conductivity, groundwater electrical conductivity and depth to groundwater during the high rainfall season (winter) for the Olifants Estuary, South Africa. Similar changes, as a result of seasonal flooding, were found by Minello et al. (2012). The zonation patterns of salt marshes are well studied (González-Alcaraz et al., 2014; Kim, 2014; Weilhoefer et al., 2013); however studies focussing on the salt marsh–terrestrial boundaries are rare.

The few studies available mostly investigated the species composition across the boundaries without describing abiotic variables (Baye, 2012; Wasson and Woolfolk, 2011; Wasson et al., 2013). Where abiotic variables have been investigated only a subset of species (James and

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Zedler, 2000) or abiotic variables are reported (Cui et al., 2011). It is important that a number of abiotic variables across different terrestrial habitats are investigated, to be used in delineation for conservation and management. Studies that investigated the salt marsh–terrestrial boundary also focussed on sediment moisture content and sediment salinity as primary drivers (Cui et al., 2011). However within the salt marsh studies have shown that sediment redox potential (Naidoo and Mundree, 1993), pH (Eallonardo and Leopold, 2014), particle size (Traut, 2005), groundwater characteristics such as depth, electrical conductivity and salinity (Bornman et al., 2008) are important abiotic variables in structuring salt marsh zonation. Sediment organic content has been shown to be less important (Richards et al., 2005) in salt marshes, however we have included this because the study spans various terrestrial spheres. In this study a wide array of abiotic variables (sediment moisture content, organic content, particle size, electrical conductivity, Redox potential, pH, depth to water table, groundwater salinity and electrical conductivity) were investigated across the salt marsh–terrestrial boundary, and also includes different estuary types, terrestrial biomes and bioregions.

This broad range of abiotic variables is particularly important in the South African context where salt marshes border a wide range of terrestrial biomes (Mucina et al., 2006) and are distributed across different bioregions (cool and warm temperate) and estuary types (Whitfield, 1992). Each of these contains unique plants and animals that show different responses with changes in physiochemical characteristics. Richards et al. (2005) explained that these factors are important because salinity has been shown to affect plants, and that sediment water content and redox potential are correlated. Redox potential is correlated with the amount of oxygen available in sediment which is difficult to measure, and nutrient availability is correlated with sediment organic content. Bornman et al. (2008) showed that groundwater is a source of moisture for floodplain and supratidal salt marsh vegetation along the west coast of South Africa. It is expected that both salt marsh and terrestrial vegetation have an ecological threshold of occurrence across these abiotic variables. An ecological threshold is a point or zone at which vegetation cover changes from one type to another (Radford and Bennett, 2004). Vegetation cover is the abundance of all species measured within a 1 m × 1 m plot. The focus of this study was on temperate (cool and warm temperate) salt marshes and consequently mangrove forests that occur in the subtropical zone were not included. Our aim was to determine the abiotic correlates across the salt marsh and terrestrial vegetation transition and to identify abiotic thresholds. We found clear environmental correlates and thresholds for terrestrial vegetation but none for salt marsh vegetation.

2. Materials and methods

The salt marsh–terrestrial boundary was divided into different vegetation zones: salt marsh, ecotone and terrestrial. The salt marsh was further split into two zones: intertidal salt marsh and supratidal salt marsh. Intertidal salt marsh occurs below mean high water spring mark (~0.5–1.5 masl) and supratidal salt marsh above 1.5 masl. Species characteristic of intertidal salt marshes were *Sarcocornia tegetaria*, *Triglochin striata* and *Spartina maritima*. The species *Sarcocornia pillansii* is common in the supratidal zone and large stands can occur in estuaries (e.g. in the Olifants Estuary). Salt marshes consist of salt-tolerant flowering plants in the form of low growing shrubs, herbs and grasses. Across transects the tallest salt marsh plant was *S. pillansii* that can reach a height of 150 cm. In the terrestrial vegetation, the tallest vegetation was forest followed by subtropical thicket. Succulent karoo and fynbos vegetation were the shortest. An area with an overlap of salt marsh and terrestrial species was visually designated as the ecotone zone; the terrestrial or upland zone was identified based on a physiognomy that was obviously different from that of the salt marsh. Terrestrial vegetation mostly occur greater than 2.5 masl.

Each zone was sampled along a transect that spanned the gradient from the intertidal salt marsh into the terrestrial vegetation; transects were always situated further than 20 m apart (locations of transects are presented in Appendix B, Table B1). Within each zone per transect, species cover abundance was quantified using replicate quadrats ($n = 2$, size $= 1$ m^2). Not all zones were present along specific transects or within certain estuaries (e.g. the intertidal salt marsh was absent in the upper reaches of the Olifants Estuary and completely absent in the Gouritz Estuary). The abundance of all species within each zone was converted to percentage of salt marsh or terrestrial cover.

Each vegetation quadrat had a paired environmental sample that was collected nearby (within a metre) in the same zone; the environmental sample consisted of two replicate surface (0–15 cm) sediment samples and one hand augered hole. The augered hole was used to determine the depth to groundwater and groundwater salinity and electrical conductivity. The abiotic variables are listed in Table 1; all sediment variables were averaged between the two replicate sediment samples. The temporarily open/closed estuaries were the Verlorenvlei (transects = 6; n = 20 across all zones) and the Kabeljous (transects = 4; n = 12) estuaries. The permanently open estuaries were the Olifants (transects = 6; n = 22), Berg (transects = 6; n = 22), Uilkraals (transects = 3; n = 9), Goukou (transects = 5; n = 25), Gouritz (transects = 5; n = 23), and Keurbooms (transects = 5; n = 32) estuaries (Fig. 1).

This sample of estuaries can be considered representative of the temperate salt marsh types in South Africa (Adams et al., 1999). Terrestrial and salt marsh vegetation classification followed Mucina et al. (2006). Sampling was conducted during summer in November 2012 (Goukou, Gouritz, Keurbooms and Kabeljous estuaries) and winter in July 2013 (Olifants, Verlorenvlei, Berg and Uilkraals estuaries). The estuaries were sampled before any major rainfall events. Table C1 (Supplementary material) shows the rainfall of estuaries ten days before and on the day of sampling. All estuaries were sampled at low tide.

The data were analysed by plotting the habitat cover of salt marsh and terrestrial vegetation against each environmental variable; each variable was binned and the percentage salt marsh and terrestrial cover summed within each bin range. Principal component analysis (PCA) was performed using the environmental variables as input parameters; the percentage of terrestrial or salt marsh vegetation

Table 1
Environmental variables measured across the salt marsh terrestrial boundary.

Parameter	Methods	Reference
Sediment moisture content (%)	Drying of sediment	Black (1965)
Sediment organic content (%)	Ashing of sediment	Briggs (1977)
Sediment particle size (%)	Hydrometer method	Black (1965)
Sediment electrical conductivity (mS/cm)	Filtrate of a saturated paste, YSI 30 m/10 ft multimeter	Barnard (1990)
Sediment redox potential (mV)	5 g of sediment in 100 ml distilled water. Metrohm oxidation–reduction potential platinum electrode attached to a pH/redox metre	Black (1965)
Sediment pH	5 g of sediment in 100 ml distilled water. pH probe glass electrode (Mettler Toledo InLab 407)	Black (1965)
Depth to water table (cm)	Boreholes hand augered	Bornman et al. (2008)
Groundwater salinity (ppt) and electrical conductivity	YSI 30 m/10 ft multimeter	Bornman et al. (2008)
Elevation (m)	Real time kinetic (RTK) surveys were done using a Trimble RTK base receiver and 4400 rover (L1 and L2 channels) with a vertical accuracy of 9 mm and 1 ppm and the 5 m contour	