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Flood regime as a driver of the distribution of mangrove and salt marsh species in a subtropical estuary

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ABSTRACT

Tidal patterns of the subtropical Paranaguá Estuarine Complex, in southern Brazil, are strongly affected by episodic cold fronts and by the coastal geometry and bottom topography, resulting in high temporal variability and marked gradients in flood regime. We delimit tolerance ranges of submersion and exposure for representative plant and animal species from local mangroves and salt marshes, through a quantitative analysis of flooding patterns in three estuarine sectors. Our results are consistent with flood regime being the leading factor on how species are distributed over the intertidal flats of the PEC. Subleading factors might be related to salinity, sediment composition and nutrient flow.

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1. Introduction

Distribution patterns of mangrove plants and animals are directly affected by the hydroperiod (or flood regime), which is characterized by the frequency, duration and depth of flooding. The hydroperiod is determined by the tidal regime, which contributes to the regular supply of "new" water, facilitates the flow of nutrients, particulate matter, debris, residues and sediments (Costa et al., 2003; Furukawa et al., 1997). The alternating conditions of submersion and emersion influence competition between plants (Crain et al., 2004), predation of propagules, and seedling establishment and survival (Patterson et al., 1997). Inundation by seawater also affects salinity, temperature, desiccation stress and soil variables such as the redox potential, pH and availability of oxygen and nutrients (Cohen et al., 2004).

There is consistent evidence that in temperate regions, the distribution of coastal plant species is regulated by the annual variation in water level. In temperate regions with predictable climatic conditions and small tide range, standard annual submersion levels are equally predictable (Adam, 1990). On the other hand, in tropical and subtropical regions, the climate is strongly influenced by the occurrence of episodic cold fronts that, in turn, can affect the tidal regime and decrease the predictability of submergence rates. The unpredictability or the high temporal variability of tides may complicate the determination of upper limits on the expected distribution of species (Costa et al., 2003), particularly in intertidal mangroves and salt marshes. Exposure times are also important, since they may vary between locations with the same tidal range and affect the biota, which present varying tolerances to desiccation (Long and Manson, 1983).

Although a number of papers discuss the science of mangrove hydrology (Furukawa et al., 1997; Kjerfve, 1990; see also the review in Mazda et al., 2007), their focus has been on tidal and freshwater flows within the forests, and not on the critical periods of inundation and emersion that govern the health of the forest (Lewis III, 2009). There is scant and often conflicting information on how critical periods of inundation and emersion may regulate the actual distribution of mangrove trees (see, for instance, Cardona-Olarte et al., 2006; Delgado et al., 2001; He et al., 2007; Krauss et al., 2006; Lewis III, 2009). The conclusions in the literature also depend on whether the studies were performed under controlled laboratory conditions or in field studies. In the former it is possible to adjust the hydroperiod while keeping other variables constant. The observed responses of mangrove species, however, generally differ from those observed *in situ*, given the influence of other uncontrolled factors such as salinity and nutrient levels (Krauss et al., 2006).

With respect to the relationship between hydroperiods and the distribution of fauna, most of the studies available use indirect measurements for determining flooding patterns, such as the distance from the shore (*e.g.* Hattori, 2006) and the elevation of Bostrychietum algae (*sensu* Post, 1936). It is not consensus, however, that the elevation of Bostrychietum algae is determined by a fixed tide level, partly because there are other interfering factors relevant to Bostrychietum algae

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elevation, such as variations in salinity, solar radiation, water temperature, nutrient content and desiccation (Peña et al., 1999; Yokoya et al., 1999). These environmental variations may influence patterns of horizontal and vertical distribution of macroalgae, modifying the structure of communities along the estuarine environment (Cunha and Costa, 2002).

Elevation is used as a quantitative parameter in characterizing the abiotic gradient in tidal systems for plants and sessile animals that tolerate stressful conditions (Crooks et al., 2002). The frequency and duration of flooding are usually calculated from the relation between the surface elevation and the official tide gauges (Leendertse et al., 1997) or tide forecast values (Davy et al., 1991). However, tide amplitudes differ between sites, being consistently higher than the estimated values (Bockelmann et al., 2002). Therefore, calculations of frequency and duration of flooding using official tide templates do not always show accurate correlations with surface elevation, because of nonlinear components of the tide (meteorological tide), related to the passages of cold fronts and strong winds, that are not factored into the equation (Silvestri and Marani, 2005).

The submersion rate of a mangrove or salt marsh decreases with increasing elevation (Silvestri and Marani, 2005). The curves of submersion, in which the elevation is plotted against the annual number of flooding hours, are sigmoidal, which may suggest the existence of critical tidal levels (CTL) (Lobban and Harrison, 1994). CTLs are capable of influencing biological variables, such as density and distribution of plants and animals (Chen et al., 2006; He et al., 2007). The submersion curves vary greatly from location to location and it is unclear whether their biological relevance can be disentangled from other factors. For instance, Long and Mason (1983) suggest that salt marshes begin to colonize intertidal flats above Mean High Water Neaps. Guiss (1995), however, found that salt marshes at Laranjeiras Bay (in the N–S axis of the PEC) occur below Mean Sea Level. To complicate the picture, the tide range increases towards the inner parts of the PEC (Marone et al., 2005), but it is unknown whether that leads to a corresponding increase in flood regimes.

The main goal of this study is to evaluate the role of the hydroperiod in determining distribution patterns of plants and animals across gradients of tidal energy at the Paranaguá Estuarine Complex, in the south of Brazil. In order to accomplish this goal, we have collected data spanning a two year period (2008–2009) from three tide gauges located at different sectors of the estuary, and mapped it into measurements of local water levels at chosen study sites. With this data we were able to characterize in detail, for the first time, the tidal patterns at different sectors of the PEC, quantifying the distribution of tidal amplitudes and how they affect submersion/exposure patterns of mangrove areas. We evaluated not only annual hour averages of inundation at a given elevation, but also the frequency and duration of submersion and exposure periods. We incorporated in our study additional variables such as the mean duration of submersion and exposure periods at a given elevation, how often a mangrove stretch remains submerged/exposed for periods longer than a given number of hours or days, as well as the frequency of extreme events, such as excessively long periods of desiccation, that albeit infrequent, have a strong impact on the biota. Differently from (annual) flooding averages, such variables retain important information on the hydroperiod that we believe are relevant for the distribution of mangrove species. To the best of our knowledge, no analogous study on these specific variables has been previously carried out in the literature (see however alternative variables in related studies, Lewis III, 2009; Krauss et al., 2006; Knight et al., 2008; Foti et al., 2012; Crase et al., 2013). We hope our results will motivate the use of such variables.

We selected a few representative species to be studied. Of the dominant vegetation at the PEC intertidal flats, we determined the range of occurrence of salt marsh (*Spartina alterniflora*), red mangroves (*Rhizophora mangle*), white mangroves (*Laguncularia racemosa*) and black mangroves (*Avicennia schaueriana*) along the different chosen sites. Among benthic species of economic interest, we measured the occurrence of crabs (*Ucides cordatus* — Linnaeus, 1763), oysters (*Crassostrea* spp. — Sacco, 1897) and mussels (*Mytella guyanensis* — Lamarck, 1819) (Blankensteyn et al., 1997; Miranda, 2004). We also determined the range of occurrence of mangrove associated algae (Bostrychietum).

The geometry of the PEC, combined with meteorological conditions and freshwater input, lead to substantial temporal and spatial variations in tidal amplitude and phase across different sectors of the PEC (Marone & Camargo, 1994; Marone et al., 2005). The PEC also has marked gradients in salinity, sediment composition and nutrient availability (Marone et al., 2005; Mizerkowski et al., 2012). Since those factors could, in principle, be major drivers of mangrove distribution in the PEC, it is not evident whether mangroves and salt marshes at different sectors are subject to different rates of submersion and exposure. For this reason, it is important to quantify flooding patterns across different mangrove sectors of the PEC. That can help disentangle the effects of the hydroperiod from other variables that affect biota, and at least to some degree help distinguish dominant from subdominant drivers of biota distribution.

2. Methods

2.1. Study area

The Paranaguá Estuarine Complex (PEC) (25°20′ S–25°35′ S/48°20′ W–48°45′ W), with an open water area of 552 km^2, is among the largest estuaries in Brazil and is of great economical as well as ecological importance to the entire southern region of the country. The PEC is considered a semi-closed estuarine system, divided into two main axes, which are defined by well-marked salinity gradients and environmental energy. The east–west axis is formed by the Antonina Bay and by the Paranaguá Bay itself, with an approximate length of 50 km and a maximum width of 7 km. The north–south axis is formed by the bays of Guaraquecaba and Laranjeiras, with an approximate length of 30 km and a maximum width of 13 km (Lana et al., 2001). A map of the PEC is shown in Fig. 1,

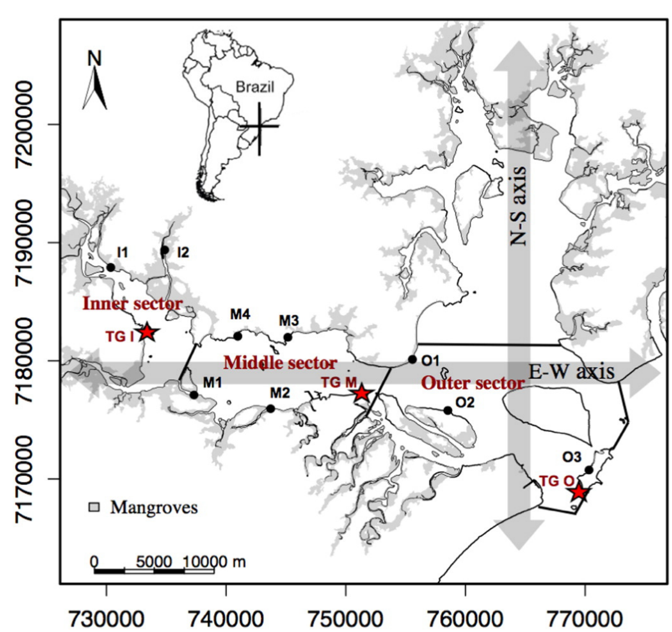

Fig. 1. Map of the Paranaguá Estuarine Complex, indicating the east–west and north–south axes, the inner, middle and outer sectors, the location of the chosen study sites, and the location of the three tide gauges.

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