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Diatoms as tools for inferring ecotone boundaries in a coastal freshwater wetland threatened by saltwater intrusion

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ABSTRACT

Species sorting mechanisms often control community assembly patterns across environmentally heterogeneous landscapes, particularly within microbial communities that respond quickly to environmental variability and are not dispersal-limited on intermediate time scales. In this study, we describe the spatial and seasonal patterns of two key environmental drivers, porewater (PW) conductivity and total phosphorus (TP), in the southern Everglades, FL., USA where saltwater intrusion, caused by rising sea level and hydrologic management, are transforming the natural environmental gradients of this ecological stressor and limiting nutrient. We surveyed diatom assemblages along transects capturing PW conductivity and TP gradients and searched for spatial boundaries in diatom assemblages along each transect. We also determined diatom assemblage thresholds to PW conductivity and TP, and identified significant indicator taxa with either negative (declining) or positive (increasing) relationships to each driver and their individual thresholds. We demonstrate that the southern Everglades exhibits spatially-structured gradients of conductivity and P that are oriented in two dimensions (i.e., with distance from the coast and from west to east) and are often, but not always, positively correlated. Our results show that these gradients drive spatial patterns of compositional similarity among our sampling sites. We found the location of greatest dissimilarity in diatom assemblages for each transect coincided with the upper boundary of the "white zone" – the visible ecotone between freshwater and coastal marshes. We did not detect seasonal differences in the position of the diatom-inferred ecotone as expected, nor did we detect significant differences in PW conductivity or TP between wet and dry seasons. Diatom assemblages were highly sensitive to both PW conductivity, with freshwater indicator assemblages declining above 2 $mS\,cm^{-1}$ and becoming replaced by a brackish water assemblage at around 20 $mS\,cm^{-1}$, and periphyton TP, with thresholds at 82 and 285 $\mu g\,g^{-1}$ for negatively- and positively responding taxa, respectively. Our study highlights that small increases in PW conductivity and TP are sufficient to cause shifts in the diatom assemblages of the Everglades. As saltwater continues to encroach into this area, compositional changes in this important primary producer assemblage are expected to cascade through the ecosystem and influence the food web. The diatom indicator taxa and assemblage thresholds presented here offer a sensitive tool that should continue to be developed and applied to management strategies for saltwater intrusion while its effects can still be mitigated.

1. Introduction

The patterns and mechanisms of community assembly are central to ecological theory and have practical applications in employing indicator species to detect and predict environmental change. Environmental gradients are often the strongest structuring force behind community assembly due to species sorting (i.e., environmental filtering), one of the four paradigms of metacommunity theory (along with neutral theory, mass effects, and patch dynamics; Leibold et al. 2004). Although these four mechanisms of metacommunity structure are not mutually exclusive, species sorting is considered to have the strongest influence on community assembly in heterogeneous environments and over spatial scales favoring intermediate dispersal (Heino and Soininen 2005; Heino et al., 2015, Leibold et al. 2004, Chase and Myers 2011). Species-sorting along spatially-structured environmental gradients often produce landscape-scale habitat zonation patterns that may include ecotones – transitional areas between adjacent habitat types that are characterized by rapid species turnover and the presence of species that are at their distributional limits (Walker et al. 2003; Peters et al., 2006; Attrill and Rundle 2002). These characteristics suggest that community response to environmental variability will likely be observed in ecotones first, making them

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potentially valuable gauges of changing climatic conditions (Wasson et al. 2013).

The Florida Everglades is a coastal, freshwater wetland characterized by a spatially-structured gradient of increasing salinity and phosphorus (P) from the inland freshwater marshes to the coast. An ecotone is present between the fresh and brackish water wetlands that, in some regions of the ecosystem, is clearly visible from the air and remote imagery as a "white zone". This zone is characterized by sparse vegetation, dominated by "dwarf" red mangroves (*Rhizophera mangle*), sawgrass (*Cladium jamaicense*), and spikerush (*Eleocharis* spp.), and light-colored marl soil that is responsible for the appearance of this area as a white band in aerial and satellite imagery (Egler 1952, Ross et al. 2000, Davis et al. 2005). The width and location of this "white zone" ecotone have changed markedly over decadal timescales in response to saltwater intrusion caused by rising sea levels and reduced freshwater flows from upstream (Ross et al. 2000, Davis et al. 2005). Ross et al. (2000) documented the interior migration of the "white zone" by 1.46 km using a series of aerial photographs from 1940 to 1994 and noted that areas where the "white zone" migrated the furthest were those most deprived of freshwater (i.e., southeastern region). Another study estimated the rate of ecotone transgression elsewhere in the coastal Everglades at 3.1 m/yr. over the last 70 years using fossil mollusks (Gaiser et al. 2006a).

The effects of saltwater intrusion in the Everglades is exacerbated by the flat, karstic geology of the landscape which creates extraordinary susceptibility to changing freshwater and marine supplies (Ross et al. 2000, Wanless and Vlaswinkel, 2005). Marine water intrusion not only elevates salinities in the interior marshes (Davis et al. 2005, Saha et al. 2011) but can also increase P availability (Price et al., 2006, Briceno et al., 2014). The Florida Everglades is a naturally P-limited system described as "upside down" because it receives most of this limiting nutrient from the sea rather than from land like most estuaries (Childers et al. 2006, Price et al. 2006). In the absence of freshwater restoration, saltwater intrusion continues to cause transgression of the coastal ecotone into the oligotrophic freshwater marshes by modifying environmental conditions to favor coastal communities (Jiang et al. 2012, Troxler et al. 2014). The effects of changes in the freshwater-marine balance are expected to be most pronounced at the ecotone, particularly in areas that are most disconnected from upstream freshwater flow where there is less freshwater to hold back intruding marine water. Therefore, the ecotone is an important area to focus research that will inform best management practices with regards to saltwater intrusion for the southern Everglades.

The characteristic, calcareous periphyton mats of the Everglades, and particularly their diatom assemblages, provide an ideal community to study the patterns and mechanisms of community assembly along environmental gradients with ecotones. Understanding these pattern and mechanisms can be incorporated into tools for predicting changes in coastal gradients due to climate change and water management decisions. Periphyton mats are composed of diatoms, cyanobacteria, and chlorophytes embedded in a matrix of mucilage and interstitial calcium carbonate ($CaCO_3$) in which bacteria, fungi, and detritus are also incorporated (Hagerthey et al. 2011). The structure and distribution of these mats across the Everglades landscape is being altered through a combination of elevated salinity and P associated with saltwater intrusion. When exposed to elevated P 5 μg L^{-1} above background (~5–10 μg L^{-1}), periphyton biomass decreases and community composition shifts from endemic to weedy taxa that do not form cohesive $CaCO_3$ mats (McCormick and O'Dell, 1996, Gaiser et al., 2006a,b). Changes in solute concentration caused by elevated salinity disturb algal cell physiology and trigger community composition shifts from freshwater to salt-tolerant species that do not form cohesive-calcareous mats (Ross et al., 2002; Gaiser et al. 2004; Frankovich et al. 2006, Wachnicka et al. 2011). Periphyton has been shown to respond more quickly and predictably to these changes in hydrology and water quality than other wetland plant communities because of the environmental specificity and short generation rates of resident taxa (Gaiser 2009). For instance, periphytic diatoms can predict 67% of the variance in periphyton TP in northern Taylor Slough (Gaiser et al., 2006a,b) and 75% of water column TP in coastal Everglades wetlands (Wachnicka et al. 2010); 97% of salinity in coastal wetlands (Wachnicka et al. 2010); and 63% of hydroperiod variance in the Greater Everglades (Lee et al. 2013). Accordingly, periphytic diatoms are used to monitor these variables in assessment studies of those regions (Gaiser et al. 2011) and represent an enormous untapped potential for tracking the advancement (or retreat) of P-rich marine supplies into freshwater marshes and the associated inland migration of the ecotone.

Understanding the organization of periphytic diatom assemblages along the freshwater-ecotone-coastal gradient in the southern Everglades and the mechanisms shaping those patterns is necessary to develop diatom indicators that can be used to document and predict rates of ecotone movement driven by saltwater intrusion and changing freshwater inflows. Diatom-based autecological indices are a trusted and popular tool in ecological assessments given the short generation rates, sensitivity to environmental fluctuations, and relative ease of diatom identification compared to other algae (Stevenson et al. 1999). They also are sentinels of changes in ecosystem properties including dependent food web structure and function (Trexler et al. 2015). Although the freshwater and coastal algal communities of the Everglades have been described in several studies (Wachnicka et al. 2010, La Hée and Gaiser, 2012), the ecotone community remains less well understood and is an integral part in the development of diatom-based indicators of coastal transgression.

The goals of this study were to describe 1) the spatial and seasonal patterns of the predominant abiotic drivers of community structure - salinity and TP - in the southeastern Everglades, and 2) the ways in which these drivers shape community assembly of mat-dwelling diatoms. We hypothesized that the southern Everglades exhibits spatially-structured gradients of salinity and TP that reflect differences in hydrological connectedness between fresh and marine water sources in western and eastern portions of the southern Everglades. We expected that periphytic diatom assemblages would be strongly controlled through species-sorting by these gradients in ways that would allow us to detect spatial boundaries and environmental thresholds. Seasonal differences in freshwater inputs from upstream were expected to result in ecotone boundaries occurring further inland during the dry season when freshwater flows are reduced, thus allowing marine water to intrude further inland. These patterns were predicted to be most pronounced in the eastern portions of the study region which are more deprived of upstream freshwater input.

2. Methods

2.1. Field and laboratory methods

Patterns of environmental variation and diatom community structure along the freshwater-marine gradient of Everglades National Park, FL., USA were examined by sampling along a series of transects extending from oligotrophic, freshwater marshes through the ecotone and down to the northern edge of the fringing mangrove forests. Seven transects spanning the west-east extent of the southeast Everglades, from the Main Park Road in the west to the Model Lands in the east, were sampled once in the dry season (May) and once in the wet season (November) of 2014 and 2015 (Fig. 1). Transect sites were set 1 km apart and, although the number of points differed among transects due to sampling constraints, were sufficient to capture the conductivity-P gradient.

We haphazardly selected three replicate points at each site for microbial mat collection and environmental measurements. At each of the 3 replicate points, surface (SW) and porewater (PW) conductivity (mS cm^{-1}) were measured with a YSI 30 Pro meter (Yellow Springs Inc.,