



A framework for investigating general patterns of benthic β -diversity along estuaries



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ABSTRACT

The description of major patterns in beta (β) diversity is important in order to understand changes in community composition and/or richness at different spatial and temporal scales, and can interrogate processes driving species distribution and community dynamics. Human impacts have pushed many estuarine systems far from their historical baseline of rich, diverse, and productive ecosystems. Despite the ecological and social importance of estuaries, there has not yet been an attempt to investigate patterns of β -diversity and its partitioning along estuarine systems of different continents. We aimed to evaluate if benthic assemblages would show higher turnover than nestedness in tropical than in temperate systems, if well-known impacted estuaries would show greater nestedness than less polluted systems, and to propose a conceptual framework for studying benthic macrofauna beta diversity along estuaries. We analyzed subtidal benthic macrofaunal data from estuaries in Brazil, USA and France. We estimated alpha (α), beta (β) and gamma (γ) diversity for each sampling time in each system, investigated patterns of β -diversity as multivariate dispersion and the partitioning (nestedness and replacement) of β -diversity along each estuary. There was a decrease in the α -diversity along marine to freshwater conditions at most of the estuaries and sampling dates. Beta diversity as multivariate dispersion showed high variability. Most of the estuaries showed a greater proportion of the β -diversity driven by replacement than nestedness. We suggest a conceptual framework for estuaries where relatively pristine estuaries would have their β -diversity mostly driven by replacement while impacted estuaries subjected to several anthropogenic stressors would show total nestedness or total replacement, depending on the stress.

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1. Introduction

Biological diversity can be understood as composed by alpha, gamma and beta diversity. Alpha (α) diversity is the diversity on a relatively small scale (e.g. sites, plots, quadrats), gamma (γ) diversity is that of the whole ecosystem or region of interest (mostly measured by pooling observations) and beta (β) diversity is the variation in species composition among sites in the area of interest (Legendre et al., 2005). Since Whittaker (1960), an increasing number of ecological studies have focused on spatial and temporal variability of beta diversity (hereafter called β -diversity), especially

in recent decades (Anderson et al., 2011). The description of major patterns in β -diversity at multiple scales is important in order to understand how changes in community composition or species richness at local scales are connected to larger spatial and temporal scales (Soininen, 2010); understanding the processes by which β -diversity is created and maintained is necessary to properly manage natural ecosystems (Legendre et al., 2005).

It is relatively well accepted that at the global scale, diversity generally increases from high latitudes to the tropics, for several taxonomic groups and ecosystems (e.g. Rex et al., 2000), and there is a claim that it is not necessary to continue documenting the obvious but to look for real explanatory variables (e.g. Hawkins and Diniz-Filho, 2004). Regarding β -diversity, it seems that latitudinal gradients in turnover (i.e. β -diversity) are scale dependent in space and time (Soininen, 2010). Nevertheless, β -diversity can be controlled by historical, evolutionary and other biogeographical

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processes and also related to an organism's physiology (Soininen et al., 2007).

There are several papers dealing with conceptual and methodological aspects of β -diversity and recent discussion regarding the most appropriate approach to investigate it (e.g. Tuomisto, 2010; Anderson et al., 2011). However, it is well accepted that interrogation of β -diversity as variation (sensu Anderson et al., 2006) can provide insights into β -diversity patterns and processes driving species distribution and community structural differences (Bevilacqua et al., 2012).

Despite the wide acceptance of the ecological and social importance of estuaries worldwide, there are very few studies that have investigated patterns of β -diversity along estuarine systems. For instance, Giberto et al. (2007), studied the benthic assemblages in Rio da Plata and suggested that β -diversity was affected strongly by changes in salinity and that these assemblages were 'discrete' with higher species turnover in boundaries between different salinity zones. In the Baltic Sea, subtidal benthic macroinfaunal β -diversity was negatively related to species dispersivity and salinity was found to be the overriding factor at the regional scale (Josefson and Göke, 2013). The Baltic Sea was the origin of one of the oldest paradigms in estuarine ecology, the Remane's Artenminimum zone (see Whitfield et al., 2012). This paradigm states that between salinities of 5 and 8 the relative number of "true brackish water species" reaches a maximum while species richness of organisms of freshwater or marine origin decreases to minimum, and then, mostly due to marine species, the richness increases again towards marine waters. However, some studies have challenged this pattern, especially in systems with marked temporal salinity fluctuations (e.g. Barros et al., 2012). Attrill (2002) suggested another model in which higher diversities are expected in estuarine zones with less variation in salinity. However, this latter model does not consider potential evolutionary physiological barriers, for instance it is almost intuitive to expect that fewer species are adapted to survive in places that vary from fresh to saline waters (i.e. 0–5) than at places with 30–35 variation, although both have the same absolute salinity variation range (i.e. 5). Thus, it seems clear that there are no widely accepted diversity or richness model (essentially alpha diversity) for the benthic estuarine fauna. Furthermore, there has been no attempt to evaluate whether β -diversity along estuaries in different biogeographical regions show similar patterns.

Baselga (2012, 2010) derived an additive partitioning of β -diversity that provides the two separate components of spatial turnover and nestedness underlying the total amount of β . Where species exhibit a high degree of specificity along a gradient, such as benthic invertebrates in estuarine systems, and occur as specialists that are adapted to local conditions, dissimilarities will arise due to species turnover (Gutiérrez-Cánovas et al., 2013). In contrast, sites that share a higher percentage of species, because taxa occurring at poorer sites are stress-tolerant generalists (i.e. species that cover almost the whole stress gradient), are places where richness gradients are a consequence of communities being reduced to nested subsets of those at richer sites; in those cases, β -diversity is more likely to arise from nestedness. Thus, it is expected that more pristine estuarine systems will present a higher turnover (species replacement) than impacted systems but this expectation has not yet been evaluated. It has also been suggested that the relative portion of β -diversity due to nestedness is higher in areas where the effects of glaciation are stronger (Dobrovolski et al., 2012), thus it is also expected that temperate estuaries will generally show less turnover than tropical estuaries.

Human impacts have pushed many estuarine systems far from their historical baseline of rich, diverse, and productive ecosystems (Lotze et al., 2006) and studies on estuarine benthic assemblages looking at a variety of β -diversity metrics can identify early stress

(De Juan et al., 2013). Protecting biodiversity is a goal of fundamental importance and can support efforts to safeguard the intrinsic capacity of ecosystems for self-renewal, adaptive dynamics, and supporting humanity now and for generations to come (Naeem et al., 2012).

The present study is the first to describe patterns of β -diversity in tropical and temperate estuaries on different continents. We aimed not only to describe general α -, β - and γ -diversity patterns in different estuaries, but (i) to evaluate whether benthic macrofaunal assemblages would show higher turnover than nestedness in tropical (Northeast Brazil) than in temperate (Central Western US and Southwest France) estuarine systems; (ii) to evaluate whether impacted estuaries would show greater nestedness than less polluted systems, and (iii) to propose a framework for studying benthic macrofaunal beta diversity along estuaries.

2. Material and methods

2.1. Field and laboratory procedures

2.1.1. Brazil

The estuarine portion of the three main tributaries of Baía de Todos os Santos (BTS) and two minor estuarine systems were sampled in this study. Macrozoobenthic assemblages from 8 to 11 subtidal stations in each estuary were sampled on different occasions (Fig. 1). The Subaé estuary was sampled in June 2004, March 2006 and April 2011; Paraguaçu in May and December 2005 and in June 2011, Jaguaripe in May 2006, August 2007 and July 2010, and Mataripe and São Paulo estuaries were both sampled in January and September 2010. Six (Paraguaçu) or eight (all the others) replicates were collected at each sampling station. The lower numbered stations (i.e. 1) were most seaward and generally deepest while higher numbered stations (e.g. 10) were furthest inland and shallowest. In Paraguaçu Estuary six replicate samples were collected at each station using a 0.05 m² van Veen grab (see details in Barros et al., 2008). In the other systems (Jaguaripe, Subaé, Mataripe and São Paulo) eight replicate samples were collected, by divers using a manual 0.008 m² corer. Core sampling was not suitable in the Paraguaçu River due to large depth at some stations and also due to very strong currents and zero visibility. All macrofaunal samples were sieved through a 0.5 mm mesh in the field and preserved in 70% alcohol until sorting in the laboratory.

Subaé Estuary is a well-known impacted system, more specifically for high levels of inorganic contamination in the upper estuary and São Paulo and Mataripe are near several chemical and petrochemical industries (Hatje and Barros, 2012).

2.1.2. United States

In Elkhorn Slough, benthic assemblages were sampled with a 0.008 m² corer to a sediment depth of 10–12 cm and a single core was taken from each of 18 stations (Fig. 1) between April and September 2003. Samples were washed through a 0.5 mm screen. Screen residues were exposed to magnesium chloride for about one hour to relax animals and were then preserved in a solution of buffered 10% formalin for 48–72 h. Residues were transferred to 80% ethyl alcohol and stained with rose bengal. Invertebrates were sorted from the screen residues under dissecting microscopes, identified and counted (see details in Oliver et al., 2007).

A Young-modified van Veen grab (0.1 m²) was used to collect one sample at each station in San Francisco Bay from 2008 to 2012. The number of sampled stations varied between 27 (2008, 2009, 2010 and 2012, as shown in Fig. 1) and 32 (2011). Samples were collected at 27 or 32 sites during each sediment cruise at 20 randomly allocated sites and 7 historic sites (with 5 additional random sites in 2011), following a stratified, random sampling

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