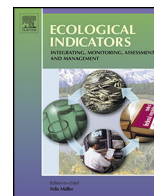




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The performance of trait-based indices in an estuarine environment

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ABSTRACT

The performance of several indices of benthic functioning, based on the traits of estuarine macro-invertebrates, was tested in the lower Mondego estuary (Portugal), whose two arms exhibit different disturbance levels related to hydromorphology. The results showed that some indices responded clearly to this type of disturbance and others not so well. We argue that the community-weighted mean trait values (CWM) in combination with the newly developed SR-FRED index provided the best overall picture of how the benthic communities might have been affected by hydromorphological disturbance. This study also showed that certain indices should be used with caution when dealing with communities with few and dominant species, such as in estuarine environments.

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1. Introduction

Traditionally, species–environment relationships have often been studied using taxonomic-based indices (e.g. richness, diversity and abundance of species) (Tilman, 2001; Vandewalle et al., 2010). These indices may accurately describe spatial and temporal differences in the composition and structure between species communities. However, they do not capture the causal mechanisms underlying species–environment relationships (Statzner and Bêche, 2010; Mouillot et al., 2013a; Stuart-Smith et al., 2013; Verberk et al., 2013). Trait-based indices are based upon the richness, diversity and abundance of species ‘traits’ (morphological, physiological and life-history characteristics of species), and offer a useful alternative approach, since a species’ ability to deal with environmental disturbance is at least partly prompted by its traits (e.g. Dolédec et al., 1996; Townsend et al., 1997; Statzner and Bêche, 2010; Mouillot et al., 2013a). The concept behind this approach is based upon Southwood’s ‘habitat templet theory’ (1977), which states that the habitat provides the template upon which evolution forges species traits. When disturbance increases, only species with

specific combinations of traits suitable for survival pass through the environmental filter.

Since the 1990s, the number of studies using trait-based indices to investigate the effects of environmental disturbance on different species communities has been steadily increasing (Statzner and Bêche, 2010; Vandewalle et al., 2010; Verberk et al., 2013). Many of these studies have shown that species traits are, to some extent, predictably affected by disturbance (e.g. Statzner and Bêche, 2010; Vandewalle et al., 2010; Stuart-Smith et al., 2013). The functional structure of communities (the traits displayed by the species in a community) have often been described quantitatively by calculating two trait-based indices: (a) the dominant trait-categories in a community, which can be measured by calculating the community-weighted mean trait values (CWM) and/or (b) functional diversity (FD) (Petchey and Gaston, 2006; De Bello et al., 2010; Vandewalle et al., 2010). FD has been defined as the extent of trait differences among species in a community (Petchey and Gaston, 2006), and can be further partitioned into three components: (1) functional richness, i.e. the number of species traits in a community; (2) functional evenness, i.e. the distribution of traits in a community weighted by the relative abundance of species; and (3) functional divergence, i.e. the degree of dissimilarity among traits weighted by the relative abundance of species (Mason et al., 2005; Villéger et al., 2008). Each component provides independent information on the trait structure, and a separate index is required to quantify each

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component (Mouchet et al., 2010; Mason et al., 2013). To date, there are about a dozen trait-based indices, most of which measure one component of FD, while only a few integrate more components. Existing trait-based indices and the methods to calculate them are constantly being upgraded and new indices, or forms of computing them, have been developed (e.g. Villéger et al., 2008; Laliberté and Legendre, 2010; Mouchet et al., 2010; Schleuter et al., 2010; Mason et al., 2013; Mouillot et al., 2013a). Most of these studies used theoretical models as surrogates for biological communities along a hypothetical stress gradient, and their general conclusion is that many of the tested FD indices are complementary, each one illustrating its own unique information of community functioning. Mouchet et al. (2010) and Mason et al. (2013) recommended that any study examining changes in assembly processes along disturbance gradients should employ several complementary FD indices. As with taxonomic-based indices, trait-based indices also have their pitfalls (e.g. Petchey and Gaston, 2006; Verberk et al., 2013). For example, indices that take abundance into account (e.g. Rao's quadratic entropy) measure the amount of trait dissimilarity between two random individuals in a community (Botta-Dukát, 2005) and by so doing, might give a differential weight to the traits of the dominant species (Petchey and Gaston, 2006). This could provide a distorted picture of functioning in environments where a few species are naturally dominant, as in estuaries. One possible solution when addressing this issue is to measure the amount of trait 'dissimilarity' between 'species' in a community, instead of measuring it between two random 'individuals'. One way of doing so is by measuring the amount of 'functional redundancy' (FRED) among species in a community, i.e. the relationship between species diversity (SD) and FD (*sensu* Rosenfeld, 2002; Sasaki et al., 2009). FRED is defined as how much a community is saturated by species with similar trait-categories (Petchey and Gaston, 2006) and can range from being non-existent, when all species display different trait-categories (FD = SD), to maximum, when all species share the same trait-categories (i.e. they are functionally identical: FD = 0) (De Bello et al., 2007).

As such, FRED has the potential to be used as an indicator of disturbance (Micheli and Halpern, 2005; Sasaki et al., 2009). The concept behind it goes back to the 'habitat templet theory' (Southwood, 1977). FRED is expected to increase (to a certain extent) with increasing disturbance due to the environmental filtering of traits, i.e. rare species with rare trait-categories unsuitable for survival are the first to be filtered out, being substituted by species with less dissimilar trait-categories that can cope with the increase in disturbance. In coastal and marine benthic communities, FRED has been used rather as an indicator of 'ecosystem resilience' (e.g. Van der Linden et al., 2012; Törnroos and Bonsdorff, 2012; Darr et al., 2013; Dolbeth et al., 2013; Rodil et al., 2013), assuming that FRED acts as a natural 'buffer' against the loss of function in the event that species are lost: the higher FRED is, the greater the probability that at least some of these species will survive changes in the environment and maintain ecosystem functioning (Díaz and Cabido, 2001; Loreau et al., 2001). These two seemingly contrasting concepts, as an indicator of disturbance or as an indicator of resilience, make FRED difficult to interpret. More so, because FRED can increase or decrease regardless of the number of species in the community (see also Sasaki et al., 2009), and here we argue that this relationship between FRED and species richness (SR) is important when investigating the effects of disturbance on species communities. Based on this relationship, we developed a new index, the SR-FRED index.

The aim of this study was to test the performance of the SR-FRED index in an estuarine environment, alongside nine other indices, seven of which were based on species traits. As descriptors we used subtidal benthic invertebrate communities from the Mondego estuary, Portugal. The lower estuary consists of a north

and a south arm, each with different hydromorphological features, causing differences in the hydrodynamics and benthic community composition between both arms (Teixeira et al., 2009; Veríssimo et al., 2013b). The indices were tested according to the hypothesis that the benthic communities in the north arm are more disturbed, mainly due to the stronger hydrodynamic conditions, than the south arm communities. Thus, we expected to find a higher proportion of traits able to cope with that disturbance for the north arm communities, lower values of taxonomic and functional diversity indices, and lower values of the SR-FRED index.

2. Methods

2.1. Study site

The study was conducted in the lower Mondego estuary which is located on the west central Atlantic coast of Portugal (40°08'N, 8°50'E). The downstream part of the estuary consists of two arms with dissimilar hydromorphological features: the north and the south arms (Fig. 1).

The north arm has been subjected to several physical interventions over the last few decades, such as river embankment (canalisation) and the construction of the Figueira da Foz harbour, as it is the estuary's main shipping channel. As a result, the north arm is deeper (4–8 m during high tide), handles most of the Mondego river's freshwater discharge, and the combination with fast tidal penetration of seawater results in strong hydrodynamic conditions, i.e. current velocities, turbidity and tidal salinity changes (Teixeira et al., 2008; Veríssimo et al., 2013a). The daily intensity of these conditions is further amplified by seasonal and annual changes in rainfall. The hydrological conditions in the north arm's downstream areas do not change much, i.e. water depth, bottom salinity (30–35) and sediment characteristics (mostly medium-sized sand with low organic matter content (Teixeira et al., 2008). Dredging activities take place only in the most downstream area of the north arm maintain an optimum depth for shipping activities (Ceia et al., 2011).

The morphology of the south arm was less changed, with most of its area (75%) being covered by intertidal mudflats, including seagrass and salt marsh areas. Between the end of the 1980s and 1998, eutrophication was a major threat to the ecological quality in the south arm. During this period, the riverhead connection with the north arm completely silted up, resulting in high water residence time, followed by eutrophication symptoms, which led to several negative impacts on the seagrass and benthic communities in the south arm's upstream stations (Patrício et al., 2009; Dolbeth et al., 2011). In 1998, limited communication between the two arms was re-established which led to a reduction in the water residence time and a general improvement in the ecological quality in the south arm (e.g. Grilo et al., 2010; Dolbeth et al., 2011). In 2006, the riverhead connection was completely restored, resulting in a further reduction of the water residence time (Veríssimo et al., 2013a). Still, most of the river's freshwater discharge flows through the north arm and, as a result, the hydrodynamic conditions are weaker in the south arm.

2.1.1. Disturbance in the benthic communities

Previous studies have pointed out that the benthic communities in the north arm are less diverse than those in the south arm (e.g. Teixeira et al., 2008, 2009; Veríssimo et al., 2013b) and the main causes are the strong hydrodynamic conditions in this arm, making it difficult for species to settle. The communities in the south arm are faced with milder hydrodynamic conditions, and the higher habitat heterogeneity of this arm allows the settlement of different species and higher species diversity compared to the north

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