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# A relação de atributos funcionais de comunidades macrobentônicas de marismas com diferentes escalas espaciais de variações ambientais

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"A relação de atributos funcionais de comunidades macrobentônicas de marismas com diferentes escalas espaciais de variações ambientais"

Por

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Dissertação julgada e aprovada em sua forma final pelos membros titulares da Banca Examinadora (008/PPGECO/2017) do Programa de Pós-Graduação em Ecologia - UFSC.

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Florianópolis, 20 de junho de 2017.

Aos meus pais e à minha filha.

## Agradecimentos

Se a ecologia é movida por padrões e estes estão diretamente ligados a escalas espaciais este trabalho seguiu a mesma linha. Escalas espaciais locais e regionais são as responsáveis por este trabalho.

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"Em biologia nada tem sentido, exceto a luz da evolução"
**Dobzhansky**

**Resumo**

A composição dos atributos funcionais de espécies é geralmente é investigada em apenas uma parte do espectro da variação espaço-temporal e espaço-ambiente. Como consequência disso, o estudo da variação de atributos é dividido em diferentes disciplinas. Identificar quais escalas refletem a maior parte da variação em atributos funcionais e como diferentes atributos devem ser relacionados com diferentes escalas espaciais pode ajudar a concentrar esforços de pesquisa em padrões e processos em escalas ecologicamente mais importantes. As variáveis ambientais deste estudo foram divididas em dois grupos de acordo com a relação mais próxima com uma escala espacial, neste caso, pequena ou macro-escala. Para analisar se diferentes tipos de atributos funcionais da macrofauna bentônica estão relacionados com diferentes escalas espaciais ecológicas (macro e pequena escala), dividimos os oito atributos selecionados em dois grupos, quatro atributos funcionais internos e quatro atributos funcionais externos. Todos os atributos foram subdivididos em categorias. A partição da variância foi utilizada para testar a porcentagem das variáveis ambientais de macro e de pequena escala na explicação de padrões de atributos funcionais internos e externos. Os resultados tiveram uma resposta diferente nas duas escalas espaciais analisadas. Os atributos funcionais internos mostraram uma estreita relação com a macro escala e apresentaram baixa afinidade com a pequena escala. Por outro lado, os atributos funcionais externos não tiveram qualquer afinidade com uma escala específica. Quando considerado os dois tipos de atributos, internos e externos, e as duas escalas de observação, macro e pequena escalas, houve um aumento na explicação do modelo de atributos funcionais, com a mais alta taxa de explicação compartilhada entre as escalas espaciais. A divisão dos atributos em dois grupos com maior e menor afinidade com a biologia do organismo ou com a ação do organismo em seu habitat circundante e espécies associadas é uma tentativa de identificar melhor sua funcionalidade. As análises mostram que a maior parte da variação ocorre entre escalas espaciais. Nossos resultados demonstram que a hierarquia, bem como os tipos e os números de atributos são importantes e, dependendo das escolhas feitas neste ponto, o trabalho pode tomar rumos distintos.



**Palavras-chave**: **marismas, macroescala, pequena escala, atributos funcionais, comunidades bênticas.**

**Abstract**

Species traits composition and abundances are typically accessed over only a part of the spectrum of spatio-temporal and spatio-environment variation. As a consequence of this the study of traits variation is portioned across disciplines. Identifying which scales reflect most of the variation in traits and how different traits should be related with different spatial scale can help focus research efforts on patterns and processes at scales that are ecologically most important, for that we must be aware of different traits definitions and also consider other important factors involved when choosing functional traits, considering that these responses vary spatially in each particular case. To put this approach into practice, traits must be collected at the appropriate scale. In this study the environmental variables were divided into two groups according to the closer relation with a spatial scale, small or macro-scale in this case. To analyse if different types of traits are related with different ecological spatial scales (macro and small scale) we split traits into two groups, inwardly traits and outwardly traits. Eight functional traits, four for each group were selected to the analysis of the benthic macrofaunal community. All traits were further sub-divided into several categories. The variation partitioning was used to test the likelihood of macro and small-scale environmental variables in explaining patterns in inwardly and outwardly functional traits. The response in each group of functional traits varied according to the spatial scale in which the traits were inserted. Inwardly traits showed a closer relation with the macro scale and presented a low affinity with the small scale. On the other hand, outwardly traits did not have any affinity to a specific scale. When we considered together both types of traits, inwardly and outwardly, and the two spatial scales of observation, macro and small scales, there was an increased in the model explanation of functional traits and with the highest explanation shared between scales. The division of the traits into two groups with higher (inwardly) and lower (outwardly) affinity to the organism biology or to the action of the organism in their surrounding habitat and associated species is an attempt to better identify their functionality and their assembly rules. The analyses show that most of the variation occurs between space scales. Our results demonstrate that the hierarchy, as well as the types and numbers of traits matters and depending on the choices made at this point, work can follow different paths.

**Key words: salthmarshes, macro-scale, small-scale, functional traits, benthic communities**

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## Introdução Geral

A busca por padrões gerais associando atributos de espécies a condições ambientais, são questões atuais que ainda afligem ecólogos de comunidade (Grime 1979; Southwood 1988). Uma alternativa para explicar a  não-existência de padrão pode estar relacionada ao fato de que os processos ecológicos estão vinculados com base na escala espacial que eles operam (Huston, 1999).  O uso de atributos funcionais tem ajudado a entender melhor esses padrões e regras. Recentemente Mcgill (2006) sugeriu que a esperança para o surgimento de regras gerais para ecologia de comunidades seria com base na utilização de atributos funcionais.

Na sua definição mais simples, os atributos eram proxies do desempenho do organismo (Darwin 1859). Atualmente, sua definição é muito mais complexa e pode ser descrita como aqueles que definem as espécies em termos de seus papéis ecológicos, como eles interagem com o meio ambiente e com outras espécies ou ainda como qualquer atributo organizacional relacionado ao desempenho individual que pode afetar direta ou indiretamente uma ou mais propriedades ou processos do ecossistema (Violle et al 2007; MIambo 2014). No entanto, nos últimos anos o número de artigos que utilizam o termo atributos para diferentes propostas identificou um enorme mal-entendido em demonstrar tantos de aspectos diferentes de uma comunidade (Viole et. al 2007). Existe atualmente uma grande mistura no uso não apenas do termo atributo por si só, mas também nos conceitos fundamentais a que se refere. (Viole 2007). Uma grande variedade de atributos funcionais estão potencialmente disponíveis para descrever o funcionamento ecológico, mas podem não ser igualmente úteis. Alguns atributos estão intimamente ligados a funções específicas, enquanto outros servem apenas como indicadores indiretos (Lavorel & Garnier 2002).

A abordagem baseada em atributos rapidamente se tornou uma alternativa na ecologia, especialmente em comparação com outros métodos, como a taxonomia, porque oferece uma maneira generalizável de descrever e comparar estratégias ecológicas (Lavorel & Garnier 2002, McGill et al., 2006). Muitas técnicas foram acessadas para medir a diversidade funcional. Uma delas, a análise de atributos biológicos (BTAs), considera uma variedade de atributos biológicos expressa pelos organismos para acessar o funcionamento que varia entre as comuniades. Os BTAs podem fornecer informações sobre uma maior variedade de

funções ecológicas comparado a outras técnicas e revelaram relações muito diferentes entre as assembléias (Bremner 2008). O tipo de atributo escolhindo nas análises tem o potencial de afetar a forma como as assembléias bentônicas são vistas, de modo que o número e o tipo de atributo funcional escolhidos para os BTAs não devem ser uma decisão arbitrária. O desenvolvimento do BTA deve, portanto, incluir também uma avaliação de quais características fornecem a descrição mais útil do funcionamento ecológico para que a seleção seja otimizada (Bremner et al., 2006).
Uma grande variedade de características estão potencialmente disponíveis para descrever o funcionamento ecológico, mas podem não ser igualmente úteis. A seleção de atributos é geralmente limitada pela quantidade de informações disponíveis (Gayraud et al., 2003). Porém sabe-se que atributos funcionais podem descrever diferentes aspectos do funcionamento ecológico, sendo alguns ligados a funções particulares, enquanto outros servem apenas como indicadores indiretos (Lavorel e Garnier 2002).

Marismas são sistemas dinâmicos, habitats intertidal amplamente distribuídos, respondendo às mudanças nas condições ambientais (Adam 2002). Juntamente com mangues e áreas úmidas são ambientes muito sensíveis e produtivos, que conectam a terra ao mar (Saintilan & Williams 1999; Schaeffer-Novelli et al. 2002; Stevens et al. 2006), podem ser definidas como áreas vegetadas por ervas, gramas ou arbustos baixos, margeadas por corpos de água salina e sujeitas a inundações periódicas resultantes das flutuações nos níveis do mar adjacente. São frequentes em regiões temperadas, sendo ecossistemas de transição entre o ambiente marinho e terrestre, do qual são diretamente dependentes (Adam 1990). Eles estão sujeitos a ampla variação nos fatores ambientais (Nybakken e Bertness 2005). Alguns dos principais atributos ecológicos de marismas, são citados por (Alongi 1998): abrigo e alimentação para várias espécies marinhas e estuarinas (principalmente formas juvenis); cordão de proteção contra processos erosivos provocados pelas marés, tempestades e inundações, favorecendo a proteção da costa; formam verdadeiros filtros biológicos para nutrientes, poluentes e alguns patógenos resultantes das atividades antropogênicas.

As relações diretas e indiretas entre a fauna bentônica e áreas de marismas, como o papel da vegetação em assentamento, refúgio, alimentação, ciclagem de nutrientes e dispersão de sementes, foram bem estabelecidas (Daiber, 1977). Porém, sabe-se também que os invertebrados bentônicos estão fortemente envolvidos na manutenção de processos ecológicos e a investigação dos atributos funcionais desses organismos pode nos fornecer melhores informações sobre o funcionamento do sistema (Bremner, 2006).

O funcionamento do ecossistema é feito por vários filtros ambientais em uma hierarquia de escalas, que, ao selecionar indivíduos com respostas apropriadas, resultam em assembléias com composição de diferentes atributos (Lavorel & Garnier 2002).A variação dos atributos pode ser observada em todas as escalas espaciotemporais. Identificar em quais escalas estão os atributos que apresentam a maior parte das variações, pode ajudar a evidenciar a investigação sobre os padrões e processos em escala espaço –temporais que são ecologicamente mais importantes (McGill 2010).

Assim como atributos funcionais podem indicar a forma como um indivíduo se relaciona e responde ao seu ambiente, seu estudo oferece uma abordagem eficaz para abordar questões ecológicas. Nossa idéia é identificar uma abordagem mais apropriada para conectar os atributos de macroinvertebrados bentônicos a outros fatores importantes que determinam suas características funcionais, como escalas espaciais e sua capacidade de expressar mudanças nas comunidades e como a variação de um determinado atributo varia conforme a escala ecológica que se encontra inserido. Identificar quais escalas refletem a maior parte da variação nos traços também pode ajudar a concentrar esforços de pesquisa em padrões e processos em escalas espaciotemporais que são ecologicamente mais importantes (McGill, 2010).

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# Capítulo Único

*The relationship of functional attributes from the macrobenthic communities of saltmarshes with different spatial scales of environmental variations*

**Abstract**

Species traits composition and abundances are typically accessed over only a part of the spectrum of spatio-temporal and spatio-environment variation. As a consequence of this the study of traits variation is portioned across disciplines. Identifying which scales reflect most of the variation in traits and how different traits should be related with different spatial scale can help focus research efforts on patterns and processes at scales that are ecologically most important, for that we must be aware of different traits definitions and also consider other important factors involved when choosing functional traits, considering that these responses vary spatially in each particular case. To put this approach into practice, traits must be collected at the appropriate scale. In this study the environmental variables were divided into two groups according to the closer relation with a spatial scale, small or macro-scale in this case. To analyse if different types of traits are related with different ecological spatial scales (macro and small scale) we split traits into two groups, inwardly traits and outwardly traits. Eight functional traits, four for each group were selected to the analysis of the benthic macrofaunal community. All traits were further sub-divided into several categories. The variation partitioning was used to test the likelihood of macro and small-scale environmental variables in explaining patterns in inwardly and outwardly functional traits. The response in each group of functional traits varied according to the spatial scale in which the traits were inserted. Inwardly traits showed a closer relation with the macro scale and presented a low affinity with the small scale. On the other hand, outwardly traits did not have any affinity to a specific scale. When we considered together both types of traits, inwardly and outwardly, and the two spatial scales of observation, macro and small scales, there was an increased in the model explanation of functional traits and with the highest explanation shared between scales. The division of the traits into two groups with higher (inwardly) and lower (outwardly) affinity to the organism biology or to the action of the organism in their surrounding habitat and associated species is an attempt to better identify their functionality and their assembly rules. The analyses show that most of the variation occurs between space scales. Our results demonstrate that the hierarchy, as well as the types and numbers of traits matters and depending on the choices made at this point, work can follow different paths.

**Key words: salthmarshes, macro-scale, small-scale, functional traits, benthic communities**

## Introduction

The recent perception that ecology is scale dependent has helped to solve seemingly conflicting key issue (Wiens 1989; Levin 1992). For instance, the distribution and abundance of species is driven by multiple environmental and spatial filters working in a hierarchy of scales (Leibold et al. 2004; McGill et al. 2010). In a local perspective, organisms in a community tend to be more similar in their ecological requirements, while species coexistence may be restricted by their trait similarity (MacArthur & Levins 1967). Under a broader spatial scale, all those puzzled processes can lead to a multitude of organism traits within a metacommunity. Notwithstanding, species traits composition and abundances are typically accessed over only a part of the spectrum of spatiotemporal and spatio-environment variation and as a consequence of this, the study of traits variation is portioned across disciplines (Messier et al. 2010) leaving large gaps of knowledge incomplete. Identifying which scales reflect most of the variation in traits can help focus research efforts on patterns and processes at scales that are ecologically more suitable (McGill 2008).

In the past few years the numbers of researches using the term trait for different proposes have identified a huge misunderstanding in demonstrating such different aspects from a community. A wide variety of traits are potentially available for describing ecological functioning, but they may not all be equally useful. Some traits are intimately linked to particular functions, whereas others serve only as indirect indicators (Lavorel & Garnier 2002). There is not an unique way of classifying traits or even one classification that can be used in a general way for most different species (Hooper et al. 2005). Greatly because of that, the concept of trait has been used in studies ranging from the level of organisms to ecosystems (Violle et al. 2007), and not only on organism level. Thus, the more studies involving the use of traits appear in recent years, the greater and more evident is the need for an understanding of the meaning of their use and if or in what way functional traits differ from each other. An alternative to explain these general varying significance of traits may be related to the fact that ecological processes are linked based on the spatial scale that they operate (Ricklefs et al. 1993, Huston 1999). Thus, depending if we are dealing with intrinsic or extrinsic organismal traits (i.e., from individual to ecosystem) we could infer the traits being functional in different spatial scales. That means that different levels of spatial scales can be used as proxy of different types of traits.

Here, the attributes that are straight related to individual's natural characteristics, more specifically, the attributes with relation to something that can be measured and seen directly in the individual (e.g., morphology) will be called inwardly traits. On the other side, attributes that express characteristics relate to an action of those individuals, that means, attributes outside the individual characteristics, such as something they produce in the environment or in the place where they live (e.g., bioturbation) will be called outwardly traits. Our idea is to identify an appropriate approach to connect intrinsic and extrinsic benthic macroinvertebrates functional traits to different environment-spatial scales in saltmarsh meadows.

Saltmarshes meadows habitat of benthic macroinvertebrates are well known and studied (Kneib 1984, Levin et al. 1998, Pagliosa & Lana 2005). However, there are still few studies in these wetlands that focus on the functional response and traits differences among their inhabiting organisms (Boutin & Keddy 1993; Pennings et al. 1998) and these studies do not include the investigation of benthic communities at different spatial scale. Benthic invertebrate assemblage and distribution are direct linked by the physico-chemical environment over a range of scales (Hall et al. 1994; Huttunen et al. 2014). They are heavily involved in the maintenance of ecological processes and the investigation and selection of the best traits that characterize function and life history from these organisms can help to provide and support information of the ecosystem functioning.

Understanding how different traits should be related with different spatial scale can be one key point to start a research on traits variability and significance. Based on that we believed that general rules can be created on how variation in a given trait changes across ecological scale. However, for that, we must be aware of different traits definitions and also consider other important factors involved when choosing attributes, considering that these responses vary spatially in each particular case. To put this approach into practice, traits must be collected at the appropriate scale (Lavorel et al. 2008; Baraloto et al. 2010). In this study, we hypothesize that different traits must be analyzed considering the spatial scale at which they are inserted. Based on that, we believed that **inwardly traits** will be more connected with environment variables of macro scale (i.e. climatic and oceanographic), considering that these traits are inherent to the organism and will not undergo changes with minor variation. The opposite will be observed with the **outwardly traits**, that will be more related to environmental variables of small scales (i.e., sediment), given that changes in the sediment can cause variations in the attributes involved.

## Material and Methods

*Sampling design and sample processing at different ecological scales*

Samplings were conducted at austral summer, between December 2012 and February 2013, along an environmental gradient of ~40 degrees of latitude in four regions in the Southwestern Atlantic Coast (from 0 to 40° S latitude) (Fig.1). The regions were spaced between 1000−1500 km each other were established assuring to their major differences in climate and oceanographic characteristics. The climate varied from tropical to temperate, with average annual temperature and precipitation ranging from 27 to 13.8 °C and from 2,770 to 848 mm, respectively. The tides ranged from microtidal to macrotidal. Within each region two different saltmarsh locations spaced ~100 km were selected. The saltmarshes bed was similar in extension, wide, and cord-grass composition. Locations around 40° S latitude were mainly colonized by the *Sarcocornia*, while monospecific beds of *Spartina alterniflora* were found in other regions and specific locations. The mainly differences among locations were related to sediment features. To access the benthic macrofaunal community in each spatial scale of the study, two sites spaced ~10 m from each other with three replicates each were randodomly sampled using cores of 15 cm diameter and 4 cm height were randomly taken for each combination of location and region. Macrofaunal samples were sieved in a 500 µm, fixed 10% formalin buffered with seawater. Organisms were identified under stereomicroscope, counted, and preserved in 70% alcohol.

The sediment parameters were analyzed by particle size distribution and organic matter content. The sand fractions were assessed by dry sieving using meshes between −1.5 and 4.0 Phi, and fine fractions were separated via wet sieving mesh of 0.062 mm and subsequent pipetting at 20°C (Suguio 1973). The organic content was determined by weight loss on ignition at 550°C for 2 hours. Sediment variables used in the analysis included organic matter content, mean grain size (phy), and the percentage of fine sand, medium silt, fine silt, very fine silt, and clay.

The geographical position of each combination of location and region was used to extract the climatic and oceanographic data from different databases. The mean annual precipitation (mm) data was extracted from the WorldClim database (Hijmans et al. 2005). The available climate data were interpolated into climate surfaces for global land areas at a spatial resolution of 0.008 degree, from the 1950–2000 periods. The WorldClim database has a higher spatial resolution, was derived from more weather stations, and used a more accurate global elevation data set than previously available surfaces. Sea surface temperature (minimum, °C), phosphate (mean, μmol/l), pH (mean), photosynthetically available radiation (mean, Einstein/m²/day), dissolved oxygen (mean, ml/l) were extracted from Bio-Oracle database (Tyberghein et al. 2012). Bio-Oracle is a compilation of global coverage data presenting relevant aspects from the marine environment in a resolution of 0.083 degrees. A global tidal range (≈ MHWS - MLWS) was calculated using the tidal atlas of finite element solutions FES2012 (Carrère et al. 2012). On a grid of 0.062 degree resolution the highest values of the sum of the two major tidal constituents (i.e., semidiurnal amplitude M2 + S2 or diurnal amplitude K1 + O1) were chosen. The final amplitude values were doubled to take the tidal range output (cm). Validations showed a best fit of FES2012 in coast and shelf regions compared with previous models of the global ocean tides. These improvements in coastal regions came from the use of a finer resolution, more accurate bathymetry, and the specific selection of assimilated data in these regions (i.e., altimeter measurements from Topex/Poseidon and European remote-sensing satellite/ERS crossover points, plus the harmonic analysis of tide gauge time series). The whole process of analysis and choice of variables, as well as the standardization of the data were run in R software using the packages “raster” and “vegan” (R Development Core Team).

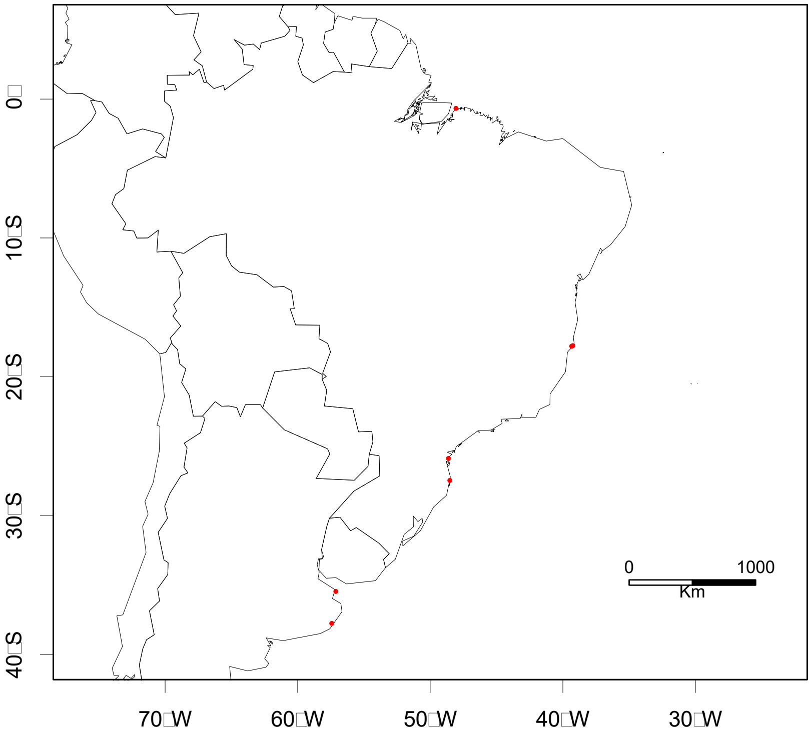


**Figure 1-** Sampled localities in Southwestern Atlantic Coast. Red circles indicate the location in each studied region.

*Traits assignment*

To analyse if different types of traits are related with different ecological scales we split the traits into two groups, inwardly biological traits and outwardly biological traits. Inwardly biological traits here are defined as the traits that are inherent to the organism, as the level of the individual only, measurable in the organism, connected directly to the life history of the organism. Outwardly biological traits consist in the ones related to something the organism perform in the environment, it implies information that overcomes the simple morphology of individuals and can be expressed at the community level. Eight biological traits, four in each group, were selected for the analysis of the benthic macrofaunal community (Table 1). All traits were further sub-divided into several categories. The categories allow each trait to show a better significance response of the organism to that classification, thus representing the wide range of possible variations in each category. Fuzzy coding with a scoring range from 0-3, was used to code individual taxa for the degree to which they exhibited the different categories of each trait. No affinity for a determined trait was coded 0, 1 means no affinity with some exceptions, 2 means affinity with some exceptions, and 3 means complete affinity. Fuzzy code allows taxa to exhibit categories of a variable to different degrees. This ordination method uses eigenvalues to express differences between samples, based on the traits exhibited by species, weighted by their abundance (Chevenet et al. 1994). Information for the selected traits were obtained from different sources, such as online databases Polytraits (Faulwetter et al. 2014) and BIOTIC (MarLIN 2006) and specific literature.

Table 1- Inwardly traits and categories used to describe functional diversity.

| Trait | Category |
|---|---|
| **Body design** | Soft |
| | Soft protected |
| | Hard exoskeleton |
| | Hard shell |
| **Feeding mode** | Deposit feeders |
| | Filter |
| | Opportunist/Scavenger |
| | Predator |
| **Longevity** | 0-2 |
| | 2-5 |
| | >5 |
| **Body size** | <5 |
| | 5_10 |
| | 10_40 |
| | 40_80 |
| | >160 |

Table 2 - Outwardly traits and categories used to describe functional diversity.

| Trait | Category |
|---|---|
| **Living habitat** | Tube dweller<br>Permanent burrow<br>Crevice dweller<br>Free living |
| **Living location** | Infaunal<br>Epifaunal |
| **Sediment reworking** | Epifauna<br>Superficial modifiers<br>Upward and downward conveyors<br>Biodifusor |
| **Mobility** | None<br>Low<br>Medium<br>High |

***Data analysis***

To verify the relationships between traits and spatial scales we first ascertained what environmental variables are already characteristic of a macroscale and which are distinguishing a small-scale. For that, crossed analyses of variances were performed for each environmental variable. The factor "macroscale" was fixed with the levels corresponding to the four regions sampled along the south western Atlantic coast, and the factor "small-scale" was fixed with levels being the two locations sampled in each region. The two sites with three samples within each combination of location and regions provided the replicates. The interaction between factors was used to show how independent or dependent the effects of one factor are relative to the effects of another factor (Underwood 1997). Additionally, the components of variation were used to estimate the proportion of the total variance that occurs at each factor (ecological scale), their interaction, and for the residuals by restricted maximum likelihood estimation (Pinheiro & Bates 1996). The significance of a factor describes how likely the patterns explained by the factor are simply due to random chance. Conversely, determination of the magnitude of the effect for individual factors based on components of variation is not probabilistic, but rather is an estimate of the variance in a response variable that can be explained by the factor (Graham et al. 2001; Commito et al. 2006). Data were previously assessed for homogeneity of variances with the Cochran test and squared-root transformed whenever necessary. The climatic and oceanographic data were standardized. For the ANOVAs, we used the GAD package (Sandrini-Neto & Camargo 2012).

After stablishing the environmental variables according to their potentiality to express spatial patterns, we grouped them into macroscale or small-scale variables to model the macrofaunal traits also grouped into inwardly or outwardly types. Thus, for each group of traits, we performed three canonical analyses of principal coordinates (CAP), modelling trait type against all environmental variables, with only macroscale variables, and only small-scale variables. We first used a double stopping criterion as forward selection procedure of explanatory variables in order to avoid type I error and overestimate the quantity of variation explained by the environmental variables (Blanchet et al. 2008). CAP was also chosen by the fact that it allows constrained ordination to be done on the basis of any distance or dissimilarity method.

For each model we estimated the percentage of variation ($R^2_{adj}$) referred to the explanatory variables (Peres-Neto et al. 2006). Then, the variation partitioning was used to test the likelihood of macro and small-scale environmental variables in explaining patterns in inwardly and outwardly biological traits. These procedures allow the division of the variation to be explained by small scale effects, by regional scale effects, by effects shared between the local and regional scales, and also by residual or unexplained effects by any of the scales in the matrix of traits (Fig. 2). The total percentage of the variation ($R^2_{adj}$) explained by the model using all environmental variables was partitioned into unique and common contributions of the sets of predictors (Borcard et al. 1992; Peres-Neto et al. 2006). Partition variation has been widely used in the ecology of metacommunities and its use allows a deeper analysis of the importance of spatial scales for understanding biological processes that structure a community locally and regionally (Da Silva & Hernandez 2014).

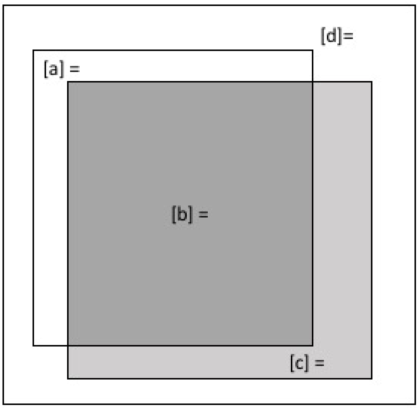


Fig 2. Schematic representation of variation partitioning Venn diagrams. Fraction (a) represents the portion explained by regional variables, fraction (b) is the intersection of the macro and small scale, (c) portion explained by local scale and (d) portion not explain (Adapted from Bocard et al. 1992).

## Results

Variance analyzes confirmed the abiotic pattern we assumed. In this way, the macro variables, sea surface temperature, phosphate, Ph, photosynthetically available radiation, dissolved oxygen, precipitation and tide presented a value of significance related to the macroscale, and none of them were significant at small variables, not even for the interaction between the two scales. The same happened with the variables selected locally, organic matter, medium silt, fine silt, very fine silt, clay, fine sand and grain size, which presented significance values for the small scale, but also in half of the parameters, the value of significance was also presented for the intersection between the two scales. The high explanatory power presented by the selected variables and the scale to which they were inserted (all components of variation > 50%) confirm that the significance test and show us that these environmental variables are linked to a certain spatial scale, outlining a pattern.

**Table 3. Hierarchical analysis of variance (ANOVA) and components of variation (CV) of regional variables.**

| Source | ANOVA | | | | C.V(%) |
|---|---|---|---|---|---|
| | **Df** | **MS** | **F.VALUE** | **P. VALUE** | |
| **Sstmin** | | | | | |
| Regional | 3 | 371.9411 | 198.9297 | **0.0005** | **90,866** |
| Local | 1 | 0.6723 | 0.3595 | 0.5909 | 0 |
| Interaction | 3 | 1.8697 | 2,97E+28 | **<0,0001** | 9,134 |
| residuals | 16 | 6,30E-29 | | | 0 |
| **Phosphate** | | | | | |
| Regional | 3 | 0.4202 | 445.1257 | **0.0001** | **93,711** |
| Local | 1 | 1,44E-05 | 0.0152 | 0.9094 | 0 |
| Interaction | 3 | 0.0009 | 3,42E+29 | **<0,0001** | 6,289 |
| residuals | 16 | 2,76E-33 | | | 0 |
| **Ph** | | | | | |
| Regional | 3 | 1.4767 | 10828.7763 | **<0,0001** | **98,659** |
| Local | 1 | 3,04E-05 | 0.2227 | 0.6691 | 0 |
| Interaction | 3 | 0.0001 | 8,44E+25 | **<0,0001** | 1,341 |
| residuals | 16 | 1,61E-30 | | | 0 |
| **Parmean** | | | | | |
| Regional | 3 | 59.1287 | 12.3325 | **0.0340** | **70,418** |
| Local | 1 | 2.9190 | 0.6088 | 0.4921 | 0 |
| Interaction | 3 | 4.7945 | 7,65E+30 | **<0,0001** | 29,582 |
| residuals | 16 | 6,27E-31 | | | 0 |
| **Dissolv. oxi** | | | | | |
| Regional | 3 | 1.4909 | 221.8378 | **0.0005** | **91,31** |
| Local | 1 | 0.0002 | 0.0321 | 0.8691 | 0 |
| Interaction | 3 | 0.0067 | 1,65E+27 | **<0,0001** | 8,69 |
| residuals | 16 | **<0,0001** | | | 0 |

| | | | | | |
|---|---|---|---|---|---|
| **Precipitation** | | | | | |
| Regional | 3 | 1699407.375 | 79.6857 | **0.0023** | **86,249** |
| Local | 1 | 21063.3749 | 0.9876 | 0.3935 | 0 |
| Interaction | 3 | 21326.375 | 1,85E+43 | **<0,0001** | 13,751 |
| residuals | 16 | **<0,0001** | | | 0 |
| **Tide** | | | | | |
| Regional | 3 | 150933.4810 | 135.8249 | **0.0010** | **89,143** |
| Local | 1 | 955.9089 | 0.8602 | 0.4220 | 0 |
| Interaction | 3 | 1111.2355 | 4,79E+28 | **<0,0001** | 10,857 |
| residuals | 16 | **<0,0001** | | | 0 |

**In bold P<0.05, Df= degrees of freedom, MS= mean square.**

**Table 4. Hierarchical nested analysis of variance (ANOVA) and components of variation (CV) of local abiotic variables.**

| Source | ANOVA | | | | C.V(%) |
|---|---|---|---|---|---|
| | Df | MS | F.VALUE | P. VALUE | |
| **Organic matter** | | | | | |
| Regional | 3 | 0.1471 | 1.4547 | 0.3827 | 13.212 |
| Local | 1 | 13.066 | 12.9220. | **0.0368** | 47.832 |
| Interaction | 3 | 0.1011 | 15.5935 | 5,22E+09 | 26.803 |
| residuals | 16 | 0.0064 | | | 12.153 |
| **Medium silt** | | | | | |
| Regional | 3 | 35.8798 | 1.3444 | 0.4067 | 10.245 |
| Local | 1 | 541.9833 | 20.3093 | **0.0204** | 54.237 |
| Interaction | 3 | 26.6864 | 13.1515 | **0.0001** | 23.728 |
| residuals | 16 | 2.0291 | | | 11.79 |
| **Fine silt** | | | | | |
| Regional | 3 | 28.5568 | 3.1579 | 0.1850 | 17.554 |
| Local | 1 | 326.9930 | 36.1599 | **0.0092** | 50.105 |
| Interaction | 3 | 9.0429 | 2.1417 | 0.1350 | 12.339 |
| residuals | 16 | 4.2222 | | | 20.002 |
| **Very fine silt** | | | | | |
| Regional | 3 | 10.9467 | 3.9826 | 0.1430 | 16.564 |
| Local | 1 | 210.0616 | 76.4240 | **0.0031** | 58.898 |
| Interaction | 3 | 2.7486 | 3.07605 | 0.0575 | 11.143 |
| residuals | 16 | 0.8935 | | | 13.395 |
| **Clay** | | | | | |
| Regional | 3 | 0.0935 | 0.7281 | 0.5997 | 0 |
| Local | 1 | 3.2482 | 25.2817 | **0.0151** | 61.756 |
| Interaction | 3 | 0.1284 | 8.7835 | **0.0011** | 23.595 |
| residuals | 16 | 0.0146 | | | 14.649 |

| | | | | | |
|---|---|---|---|---|---|
| **Fine sand** | | | | | |
| Regional | 3 | 5.5500 | 2.5135 | 0.2344 | 13.336 |
| Local | 1 | 142.4587 | 64.5186 | **0.0040** | 61.09 |
| Interaction | 3 | 2.2080 | 5.0146 | **0.0122** | 13.717 |
| residuals | 16 | 0.4403 | | | 11.857 |
| **Grain size** | | | | | |
| Regional | 3 | 1.0256 | 0.9911 | 0.5028 | 0 |
| Local | 1 | 36.6474 | 35.41542 | **0.0094** | 66.037 |
| Interaction | 3 | 1.0347 | 9.4687 | **0.0007** | 21.291 |
| residuals | 16 | 0.1092 | | | 12.672 |

**In bold P<0.05, Df= degrees of freedom, MS= mean square.**

In the canonical analyses of principal coordinates (CAP), when we considered inwardly traits and regional variables (Fig.5), the cumulative percentage of variance explained by the first two canonical axes accounted for 67% (59% and 8% respectively for the first and the second axis). The variables selected by the analyses were: tide, phosphate, precipitation, photosynthetically available radiation and pH. The second CAP (Fig.6), considered inwardly traits and local environmental variables, the cumulative percentage of variance explained by the first two canonical axes accounted for 30% (27% and 3% for the first and second axis respectively). The variables selected were: clay and type of grain.

The third CAP (Fig.7), considered the outwardly traits and regional variables, the cumulative percentage of variance explained by the first two canonical axes accounted for 55% and 6% respectively and variables selected were: tide and phosphate. The fourth and last CAP (Fig.8), considered the outwardly traits and local variables, the cumulative percentage of variance explained by the first two canonical axes accounted for 49% (46% and 3% respectively). The variables selected were: type of grain, clay and medium silt.

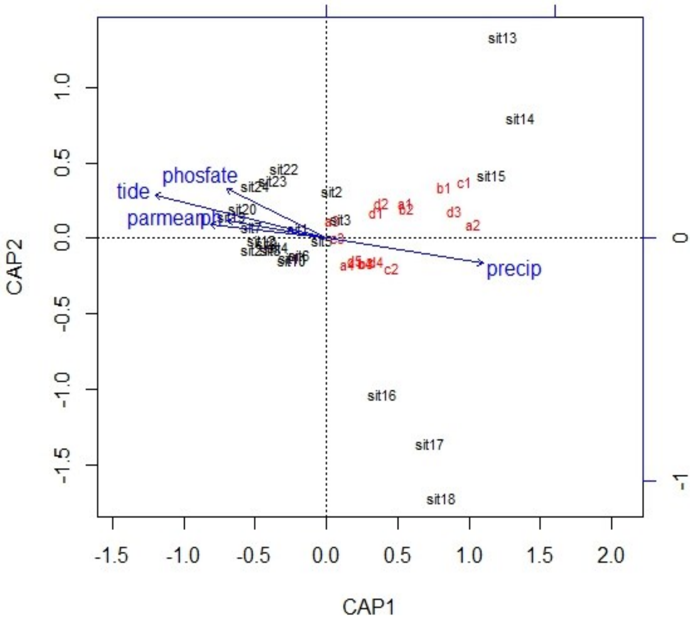


**Fig 3. Constrained Analysis of Principal Coordinates (CAP). Relationship among Inwardly traits (red) and selected macroscale environmental variables (blue arrows), site location (black). The arrows indicate the direction of the increase for the studied variables. The angles between variables reflect their correlations. The angles between variables reflect their correlations (angles of 90° indicate no correlation, angles near 0° indicate high positive correlation and angles near 180° indicate high negative correlation).**

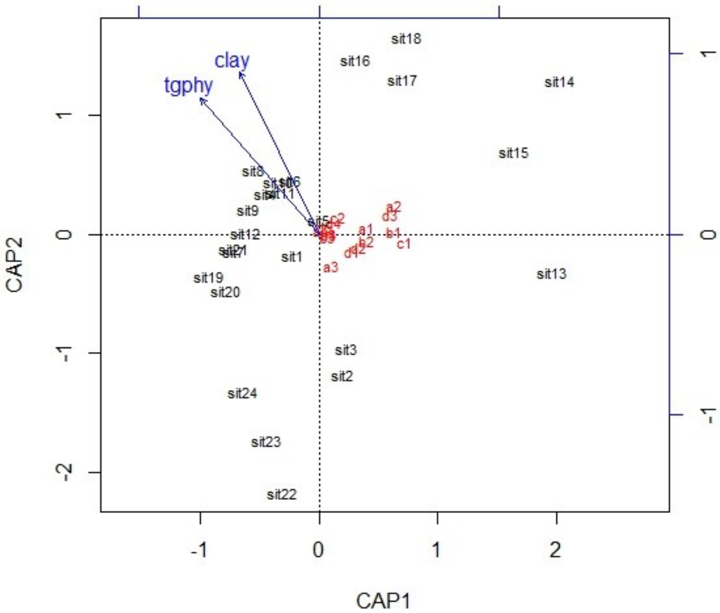


**Fig. 4. Constrained Analysis of Principal Coordinates (CAP). Relationship among Inwardly traits (red) and selected local environmental variables (blue arrows), site location (black). The arrows indicate the direction of the increase for the studied. The angles between variables reflect their correlations. The angles between variables reflect their correlations (angles of 90° indicate no correlation, angles near 0° indicate high positive correlation and angles near 180° indicate high negative correlation).**

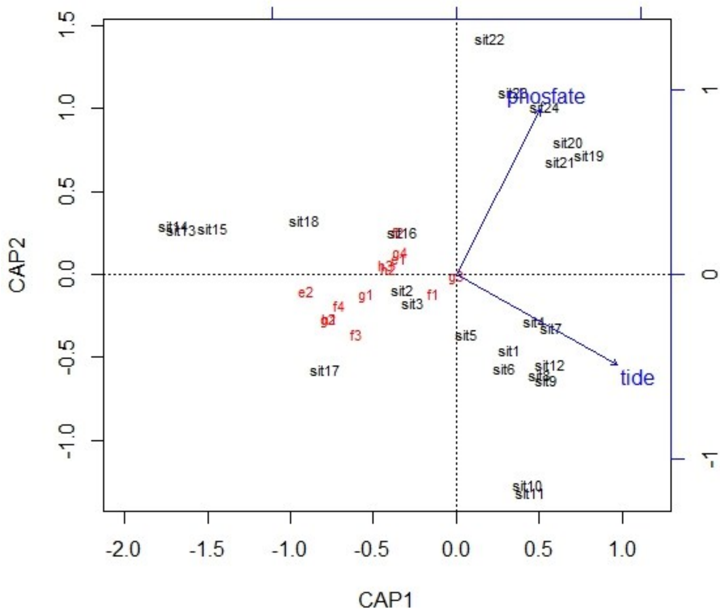


**Fig. 5. Constrained Analysis of Principal Coordinates (CAP). Relationship among Outwardly traits (red) and selected macro-scale environmental variables (blue arrows), site location (black). The arrows indicate the direction of the increase for the studied variables. The angles between variables reflect their correlations. The angles between variables reflect their correlations (angles of 90° indicate no correlation, angles near 0° indicate high positive correlation and angles near 180° indicate high negative correlation).**

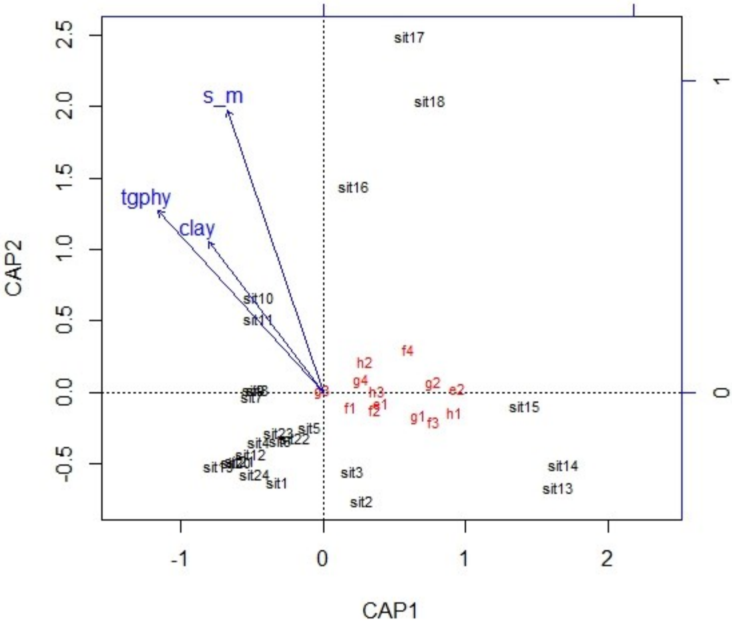


**Fig.6. Constrained Analysis of Principal Coordinates (CAP). Relationship among Outwardly traits (red) and selected small-scale environmental variables (blue arrows), site location (black). The arrows indicate the direction of the increase for the studied variables. The angles between variables reflect their correlations. The angles between variables reflect their correlations (angles of 90° indicate no correlation, angles near 0° indicate high positive correlation and angles near 180° indicate high negative correlation).**

Results on variation partitioning based on the functional traits of inwardly or outwardly traits had a different response at each spatial scale. The inwardly traits presented a very strong relation with the macroscale (Fig.9), explaining 47% of the influence in the traits. The interaction between small and macroscale concentrated 21% of the variation of traits data, small scale explained less than 1,5% and 30% wasn't explained by any of the spatial scales. On the other hand, the outwardly traits presented a closer relationship with the variables from small scale 19%, 15% was the relation with the macroscale variables, 25% was explained by local and regional variables together and 40% wasn't explained by any of the environmental variables. That means that the portion where the two scales act together has a greater influence than just the small scale.

When all traits were analyzed together, with no subdivision, the regional scale concentrated 17% of the traits explanation, the local scale only 4%, 56% were explained by the two scales combined and 26% wasn´t explained by any of the scales.

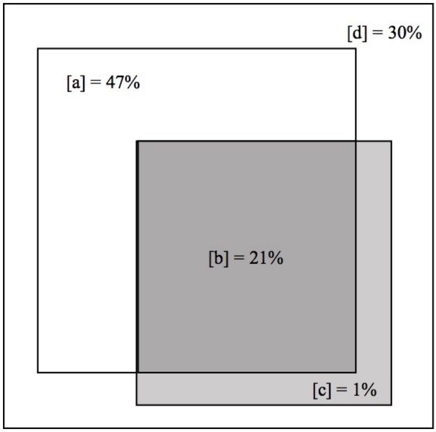


**Fig.7.** Venn diagram variation partitioning, representing the contribution of spatial scales environmental variables for the inwardly traits, [a] macroscale variables, fraction [b] represents the shared variation between the macro and small scale, [c] represents the contribution of small scales variables and [d] represent the percentage of the residual variation left unexplained by the canonical model

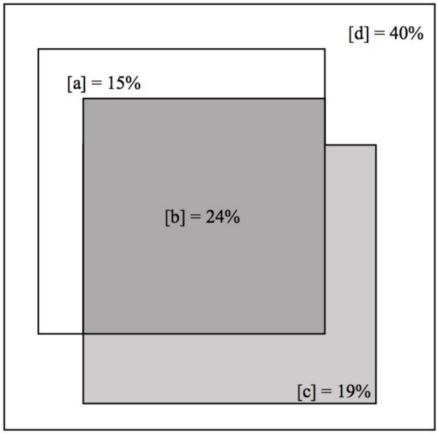


**Fig.8.** Venn diagram variation partitioning, representing the contribution of spatial scales environmental variables for the outwardly traits, [a] macroscale variables, fraction [b] represents the shared variation between the macro and small scale, [c] represents the contribution of small scales variables and [d] represent the percentage of the residual variation left unexplained by the canonical model

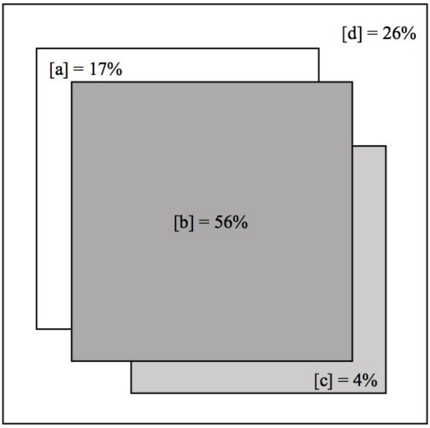


**Fig.9**.Venn diagram variation partitioning, representing the contribution of spatial scales environmental variables for the all traits, [a] macroscale variables, fraction [b] represents the shared variation between the macro and small scale, [c] represents the contribution of small scales variables and [d] represent the percentage of the residual variation left unexplained by the canonical model.

## Discussion

We demonstrated that functional traits are related to different spatial scale and represent an initial attempt to list functional attributes according to a given spatial scale. This would further facilitate the choice of traits in accordance with the object of studies. The division of traits into two groups with higher and lower affinity to the organism biology or to the action of the organism on their surrounding habitat and associated species is an attempt to better separate their functionality and their assembly rules. Inwardly and outwardly traits were influenced in different proportions by macro and small scales and this could be rooted in differences of the traits conception used. Biological traits, the defining characters of life organization, are usually traits of life-history and are seen as characteristics of an organism that are shaped by evolutionary forces to achieve reproductive success (Sterns 2000). This natural selection is measured in populations by the changes it induces in phenotypic characteristics and is expressed as the relationship between trait and fitness (Arnold 1983). Then, if we see the classical trait-based approach in a perspective of spatial scales and coexistence, we could say that species in a community tend to be more similar in their ecological requirements due to macroscale filtering processes, which may lead to trait convergence (Pillar et al. 2009; Pillar & Duarte 2010). The opposite perspective asserts that processes of small scale are acting by limiting similarities (MacArthur and Levins 1967) and causing divergence due to chance in shaping trait variation. The base experiment to those questions came from the perspective of traits being hierarchically arranged with respect to one another (Marks 2007) and with respect to the environment (Laughlin 2014). In a broad view, the variation in organismal level traits, on top hierarchy, could be most closely related to processes acting on macroscale. On the other hand, up-scaling organismal traits variations, on bottom hierarchy, are expected to be more closely related to small scale processes.

Here, inwardly traits showed a close relation with the macro scale and presented low affinity with the small scale. On the other hand, outwardly traits did not have any affinity to a specific scale. When we considered together both types of traits, inwardly and outwardly, and the two scales of observation, macro and small scales, there was an increased in the models explanation of functional traits and with the highest explanation shared between scales. Those results could elucidate two different conclusions:

i- the hierarchy of traits matters. The top hierarchy traits should be moulded by evolutionary forces and are easily recognized using environmental variables of macroscale. On the other hand, the bottom hierarchy traits should be closer related to biological interaction and resource partitioning to allow coexistence (MacArthur and Levins 1967), or this environment works as a habitat templet where evolution forges characteristic species traits (Southwood 1977; Townsend & Hildrew 1994; Townsend et al. 1997). It is necessary to realize that biological interaction are usually pointed as a major force modelling bottom hierarchy trait related to processes that occurs at small spatial scales, but plays an important role even at the large scale (Gotelli et al. 2010, McGill 2010).

In a first attempt we could say that the non-affinity to scales of the up-scaling organismal (outwardly) traits could indicate the lower influence of environment. Nevertheless, environmental variables of small scale are not so easily observed and have a confounding effect with large scale variables. It is more plausible to understand that this lack of affinity can demonstrate that the use of outwardly traits in species level are not of good help to elucidate functional ecology, regardless the scale of study. Then, bottom hierarchy traits need a better refinement resolution than species level to be worked in. These are particularly well debated and practised by evolutionary ecologists that are using individual trait-based approach (Lavorel et al. 2008; Carlucci et al. 2012) instead of using species trait-based approach, that in benthic ecology are usually called "biological traits analysis" (Bremner et al. 2003, Pacheco et al. 2011). On the other hand, many studies sampling in a small scale where there is a great environmental variation (i.e., along gradients of energy and salinity in estuaries; along depth gradients in shelfs; between polluted *vs* preserved sites) have successfully used inwardly as well as outwardly traits (Pacheco et al. 2011; Van der Linden et al., 2012, 2016). These could mean that species level traits are better used as trait-response indicators of environmental situation (van der Linden, 2016a,b) than when fitting in an evolutionary perspective of an trait-effect on the ecosystem (McGill 2010 & Messier et al. 2016).

ii- the spatial scales of study are a paramount to understand the functional traits meaning. In complex systems such as estuarine saltmarshes, a reliable way to be sure that observed differences are indeed associated with the scale claimed is to demonstrate that differences at smaller scales are not as large (Morrisey et al., 1992). Here, we were able to show scale differences in functional traits when assessing each scale separated, and also that environmental small scale contributed little to traits spatial distribution (three of four lowest values of importance considering all Models). When all traits (inwardly and outwardly) were contrasted the shared effect of scales appeared in high standards. Two not excluding factors could produce these pattern of response. One is related with the explicit incorporation of the spatial variation in sampling design, and other with the number of traits used. In the first one, determining precision of estimates and maximising power to detect changes helps to avoid the confounding effect between scales (Underwood and Chapman, 2013). We applied a hierarchical sampling design and were able to show scale differences in functional traits when assessing each scale separated.

The selection of traits types as well as traits numbers can be a critical point. Whilst some authors defend that, the inclusion of many traits as possible would provide a more informative picture of ecosystem functioning (Usseglio-Polatera et al. 2000; Bremner et al. 2006) and most studies using traits rely on this statement (Bremner et al.2006, Bremner 2008, Jones et al 2009, Pacheco et al. 2011). With this idea, studies with only few biological traits risk to produce an erroneous view of the functioning of the system, Conversely, a limited number of traits could resembling all functionality incorporated by a great number of traits (Bremner et al. 2006a). However, some studies point that just some key traits are enough to describe the functionality of the assemblage (Jones et al. 2009, Gusmão et al 2016). What we observed was that when many traits are used, often very similar traits are been analysed (e.g., movement method and mobility; living habit and life habitat; skeletal thickness and fragility) and these might cause a wrong evaluation of a determined group of traits, inferring a bigger importance than it actually has. It's hard to decide which traits should be retained and which discarded, certain types of trait may be more appropriate than other in some circumstances. And in fact, more important than the number of traits selected, is the identity of the traits themselves (Bremner 2008). In that way, selected traits based on the investigation hypothesis, and the exclusion of traits that behave in the same way as others, could improve functional analysis. Different types of trait may produce different pictures of functioning in assemblages (Bremner et al., 2006b) and the performance of environment-trait models depends on the traits analysed, because some can be more accurately modelled than others (Pöyry et al., 2008). Depending on the functional traits selected, different traits may present different variations of their categories. In this way, we could say that will never be possible to treat each factor equally or to study each variable and all the interactions simultaneously (McGill 2006). So that means that there will not be a single index that will described the whole ecosystem functioning (Giller et al., 2004). Then, analysis of traits and their interpretation will depend directly on the selected traits.

By analysing just spatial scales, we are living on the side, others factors that can contribute to distinguish differences between functional attributes, like, biological interactions, intraspecific trait variation and even other scales, like temporal and a more refined spatial scale. However, the fact that most of variation was explained by spatial scale suggests that there might be general trends in ecological functioning across benthic communities that are better revealed using functional traits linked with a scale.

Recognizing that patterns in ecology are scale dependent is a main idea that should be considered in macroecology studies (Gotelli et al. 2010, McGill 2010). Our analyses show that most of the variation occurs across space scales. One approach to better understand this variation between communities and space is to identify traits that better fit in that determined scale. Which of these factors are most important? It is becoming increasingly evident that the response will depend on the scale being analyzed.

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## Conclusão Geral

Atributos funcionais estão relacionados com diferentes escalas espaciais. A divisão dos atributos em dois grupos, um com características mais relacionadas a biologia do indivíduo e outro mais relacionado a ação do organismo no seu habitat e ainda a análise em uma pequena escala e uma macro escala é uma tentativa de identificar sua funcionalidade e seus padrões nas assembleias. Os dois grupos de atributos funcionais foram influenciados pelas escalas espaciais em diferentes proporções. Sendo que os atributos internos mostraram uma forte relação com a macro-escala. Já os atributos externos não se mostraram ligados a nenhuma das duas escalas em particular. Quando todos atributos funcionais foram analisados juntos uma houve um aumento na explicação nos modelos de traços funcionais e com a mais alta explicação compartilhada entre escalas.

O número e tipo de atributos funcionais que irão ser analisados também é de suma importância, tendo em vista que, dependendo da escolha de diferentes tipos de atributos funcionais pode produzir diferentes imagens do funcionamento de assembleias.

Reconhecer que padrões ecológicos são dependentes de escalas é fundamental para que se consiga fazer uma análise mais aprofundada e correta em estudos futuros. Nossas analises mostram que variações ocorrem entre escalas espaciais. Uma maneira de compreender essas variações entre comunidades e espaço é identificando quais são os atributos funcionais que melhor se encaixam em uma determinada escala.

## Appendices

**Table 1-** Region and local where the samples were collected and the geographic localization.

| Region | Local | Latitude | Longitude |
|---|---|---|---|
| **Pará** | **São Caetano de Odivelas** | -0,666725 | 48,060217 |
| | **Mocooca** | -0,691625 | 48.021.444 |
| **Bahia** | **Encalhado das marés** | -17,791461 | -39,326381 |
| | **Porto Fímbria** | -17,754772 | -39,2425 |
| **PR/SC** | **Guaratuba** | -25,870506 | -48,630728 |
| | **Ratones** | -27,451736 | -48,523658 |
| **ARG** | **Argentina ponto 01** | -35,445753 | -57,127272 |
| | **Argentina ponto 03** | -37,74735 | -57,435722 |

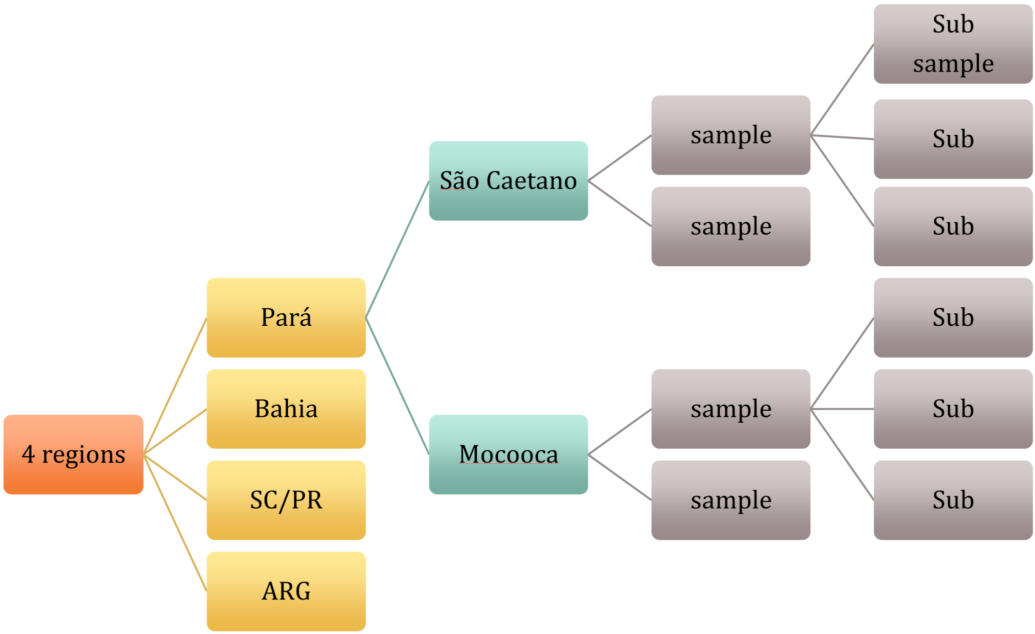


**Fig 1.** Schematic representation of the hieraquical sample design.

**Table 2**. Table with total abundance of individuals found in the four sampling regions.

| Group | Total |
|---|---|
| **Annelida** | |
| Capitellidae | 1624 |
| Nereididae | 1538 |
| Ampharetidae | 635 |
| Spionidae | 1509 |
| Goniadidae | 9 |
| Glyceridae | 20 |
| Sabellidae | 1 |
| Eunicidae | 4 |
| Magelonidae | 1 |
| Nephtyidae | 17 |
| Syllidae | 156 |
| Pillargidae | 14 |
| Orbiniidae | 20 |
| Phyllodocidae | 5 |
| Lumbrineridae | 40 |
| Fabriciidae | 559 |
| Owenidae | 1 |
| Oligochaeta | 627 |
| Hirudinea | 2 |
| **Crustacea** | |
| Tanaididae | 295 |
| Ostracoda | 215 |
| Amphipoda | 25 |
| Ocypodidae | 72 |
| Grapsidae | 12 |
| Sphaeromatidae | 47 |
| Kalliapseudidae | 31 |
| **Insecta** | |
| Tipulidae | 31 |
| Chironomidae | 17 |
| Muscidae | 8 |
| Hemiptera | 3 |
| **Mollusca** | |
| Neritidae | 1 |
| Mactridae | 14 |
| Veneridae | 39 |
| Myidea | 25 |
| Mitilidae | 35 |
| Cochliopidae | 180 |
| Solecurtidae | 5 |
| Tellinidae | 14 |
| Nemertea | 3 |
| Platyhelminthes | 7 |
| Sipuncula | 3 |
| Edwardsiidae | 18 |

**Table 3.** Categories of traits and the value given to each sub categories.

| Group | a1 | a2 | a3 | a4 | b1 | b2 | b3 | b4 | c1 | c2 | c3 | d1 | d2 | d3 | d4 | d5 | e1 | e2 | f1 | f2 | f3 | f4 | g1 | g2 | g3 | g4 | h1 | h2 | h3 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Capitellidae | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Nereididae | 0 | 3 | 0 | 0 | 1 | 2 | 3 | 3 | 3 | 3 | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 3 | 0 | 2 | 1 |
| Ampharetidae | 0 | 3 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Spionidae | 0 | 3 | 0 | 0 | 3 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 2 | 1 | 3 | 3 | 0 | 0 | 3 | 0 | 0 |
| Gonididae | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 2 |
| Glyceridae | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 2 |
| Sabellidae | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 2 | 2 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| Eunicidae | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 2 | 0 | 1 | 0 | 1 | 2 |
| Magelonidae | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Nephitidae | 3 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 2 | 0 | 0 | 3 |
| Syllidae | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 3 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| Pillargidae | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 |
| Orbinidae | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| Phyllodocidae | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 2 | 0 | 2 | 0 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 |
| Lumbrineridae | 3 | 0 | 0 | 0 | 1 | 0 | 1 | 3 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 1 | 2 |
| Fabriciidae | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| Owenidae | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 |
| Oligochaeta | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 3 |
| Tanaidae | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 |
| Ostracoda | 0 | 0 | 3 | 0 | 2 | 2 | 1 | 1 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 1 | 2 |

| | | | | | | | | | | | | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Amphipoda | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 2 | 0 | 0 | 1 | 0 | 1 | 2 |
| Ocypodidae | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 |
| Grapsidae | 0 | 0 | 3 | 0 | 2 | 1 | 1 | 1 | 3 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 |
| Shapaeromatidae | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| Kalliapseudidae | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 1 | 3 | 0 | 0 | 1 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 1 | 2 |
| Tipulidae | 0 | 0 | 3 | 0 | 2 | 0 | 0 | 1 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| Quironomidae | 0 | 0 | 3 | 0 | 0 | 2 | 0 | 2 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 |
| Muscidae | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| Hemiptera | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 |
| Neritidae | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 |
| Mactridae | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Veneridae | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 1 | 0 | 2 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Myidea | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Mytilidae | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 3 | 3 | 0 | 1 | 2 | 1 | 2 | 0 | 0 | 1 | 2 | 0 | 0 | 3 | 0 | 0 |
| Cochliopidae | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 3 | 1 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Solecurtidae | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Tellinidae | 0 | 0 | 0 | 3 | 3 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Nemertina | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 2 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 3 | 0 | 0 |
| Platelminte | 3 | 0 | 0 | 0 | 0 | 0 | 1 | 2 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |
| Sipuncula | 3 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 | 1 | 2 |
| Hirudinea | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 | 0 | 0 | 3 | 0 | 0 | 2 | 1 | 0 | 3 | 0 | 0 | 0 | 0 | 0 | 3 | 3 | 0 | 0 |
| Edwardsiidae | 0 | 3 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 3 | 0 | 3 | 0 | 0 | 0 | 3 | 0 | 0 | 3 | 0 | 0 |