

# Trait-based approaches to address animal-soft sediment relationships in marine ecosystem: a mini review

Barbara C. G. Gimenez<sup>1\*</sup>, Joao B. Gusmao<sup>2</sup>, Danielle Katharine Petsch<sup>3</sup>,  
Felipe Jacob Fernandes<sup>4</sup>, Paulo C. Lana<sup>1†</sup>

<sup>1</sup> Universidade Federal do Paraná – Lab of Benthic Ecology, Center for Marine Studies – (Av. Beira-Mar, s/n – Pontal do Paraná – 83255-976 – PR – Brazil)

<sup>2</sup> Faculty of Science and Engineering, Åbo Akademi University – Dep. of Environmental and Marine Biology (Tuomiokirkontori 3 – Turku 20500 – Finland)

<sup>3</sup> Universidade Estadual de São Paulo – Departamento de Biologia, Letras e Ciências (Av. Dom Antônio, 2100 – 19806-900 – Assis – SP – Brazil)

<sup>4</sup> Universidade Federal de Rio Grande – Instituto de Oceanografia (Av. Itália, km 8 – 96203-900 – Rio Grande – RS – Brazil)

† *In memoriam*

\* Corresponding author: [barbaracggimenez@gmail.com](mailto:barbaracggimenez@gmail.com)

## ABSTRACT

Trait-based approaches have gained prominence in assessing the relationships between benthic diversity, habitat structure, and functioning in marine ecosystems. We reviewed the popular trait-based approaches currently used to evaluate the connections between macrobenthic communities and marine soft sediments. We examined techniques mainly based on response traits (i.e., that reflect animal responses to the environment), including benthic quality indices, metrics of community functional diversity, and biological trait analysis (BTA). We also discussed approaches focused on effect traits (i.e., reflecting the impact of animals on the environment). These approaches also use functional diversity indices and BTA, but specific indices such as community bioturbation potential (BPC) and community bioirrigation potential (BIPc) enable a more direct assessment of the impacts of macrobenthic communities on soft sediment habitats. We highlight the advantages and limitations of these techniques and discuss the need for standardized protocols and improved data collection methods. Despite their limitations, trait-based techniques are valuable tools for marine ecologists because they are closely related to ecosystem functioning and can be used for investigating many hypotheses of animal-sediment relationships in marine ecosystems.

**Keywords:** Functional diversity, Functional traits, Macrobenthic function, Biological traits, Multivariate analyses, Ecological Indices

## INTRODUCTION

Macrobenthic species play a critical role in the functioning of marine systems. Benthos macrofauna (including polychaetes, bivalves,

and mollusks from soft-sediments) participate in many marine ecological processes, such as benthic-pelagic coupling (i.e., the exchange of energy and mass between the water column and the sediment), bioturbation, and nutrient cycling (Griffiths et al., 2017; van der Linden et al., 2017; Wouters et al., 2018). Consequently, trait-based approaches have become valuable tools in marine benthic ecological research over the last few years, focusing on the functional characteristics

Submitted: 30-Aug-2023

Approved: 10-Sep-2024

Associate Editor: Karen Diele



© 2024 The authors. This is an open access article distributed under the terms of the Creative Commons license.

of macrofauna. Biological traits are measurable attributes that can be observed and measured at the individual level and influence an organism's performance, fitness, and ecological interactions within ecosystems (Violle et al., 2007; Lavorel et al., 2008). These traits reflect a species' life history, adaptations to environmental conditions, and ability to modify its habitat via biological activities (Verberk et al., 2013; Wang et al., 2022).

In total, two key categories of biological traits are commonly used in trait-based ecology, namely effect traits and response traits (e.g., Naeem and Wright, 2003; Suding et al., 2008; Piccini et al., 2018). Effect traits are frequently referred to as functional traits (Naeem and Wright, 2003), although many authors use the term 'functional trait' in a broader sense. These traits directly or indirectly influence ecosystem properties, determining the impacts of organisms on ecosystem processes and their roles in ecosystem functioning (Naeem and Wright, 2003; Piccini et al., 2018). In marine soft sediment habitats, effect traits include morphological and behavioral attributes that can disrupt and change the physical and biogeochemical structure of the sediment (Reise, 2002; Widdows and Brinsley, 2002; Bremner et al., 2006a). On the other hand, response traits determine an organism's ability to adapt and respond to environmental changes (Naeem and Wright, 2003). These traits are closely associated with species' fitness and survival under different environmental conditions. Response traits enable species to persist, thrive, and adapt to changing conditions, as well as withstand environmental stressors and colonize new habitats (Díaz et al., 2013).

The study of the relationship between macrobenthic traits and the characteristics of soft sediment habitats has a long history in the marine ecological literature. Classic studies such as "The Diet of Worms" by Fauchald and Jumars (1979) and the conceptual models of macrobenthic succession proposed by Pearson and Rosenberg (1978) have laid the groundwork for studies addressing how macrobenthic communities respond to gradients in sediment properties and how they can change those properties by their activity. In recent decades, the combination of advanced statistical techniques

(e.g., multivariate ordinations) and the availability of online trait databases (e.g., Biotic and Polytraits) has led to a significant increase in publications addressing animal-sediment relationships in marine ecosystems using a trait-based approach. Some of these methodologies were explicitly designed for marine soft benthos, such as AMBI Index (Borja et al., 2000) and bioturbation potential (Solan et al., 2004; Birchenough et al., 2012). Other analytical tools, such as the estimation of functional diversity indices (e.g., functional and dispersal diversity) and Biological Trait Analysis (BTA; Bremner et al., 2003), have shown not only a wide range of applications across different ecosystems and taxonomic groups but also the capacity of assessing changes in macrobenthic trait structure in soft benthos.

## LITERATURE SEARCH

We conducted a literature search to identify the most frequently used trait-based methods for investigating animal-sediment relationships in marine benthos, highlighting their advantages, limitations, and key challenges. The search process involved the following steps:

**Keyword search:** The initial search was conducted using the following keywords: "trait-based approaches," "benthic diversity," "habitat structure," "ecosystem functioning," "macrobenthic communities," "marine soft sediments," "response traits," "benthic quality indices," "community functional diversity metrics," "biological trait analysis (BTA)," "effect traits," "functional diversity indices," "bioturbation potential," "bioirrigation potential," "animal-sediment relationships," and "marine ecosystems" in scientific databases like Web of Science, Google Scholar, and Scopus.

**Inclusion criteria:** To be considered for the review, articles had to meet the following criteria: (a) Focus on trait-based approaches for assessing animal-sediment relationships in marine benthic ecosystems; (b) Provide a detailed description of the methods used; (c) Discuss the advantages, limitations, and challenges associated with the employed methods; (d) Be published in peer-reviewed journals.

**Screening and selection:** The titles and abstracts of the retrieved articles were screened

to identify those that met the inclusion criteria. Full-text articles were then obtained and further assessed for eligibility.

**Data extraction:** Key information was extracted from the selected articles, including the trait-based methods used, their advantages and limitations, and the challenges associated with their application in assessing animal-sediment relationships.

**Synthesis:** The extracted data was synthesized to identify the most frequently employed trait-based

methods, their main features, and the common challenges faced when using these approaches in marine benthic ecosystems.

The literature search resulted in the inclusion of articles that met the specified criteria. These articles were published from 1978 to 2023 and covered various trait-based methods used to evaluate animal-sediment relationships across various marine benthic ecosystems worldwide. Table 1 shows a summary of the reviewed methods.

**Table 1.** Summary of the most widely used methods for evaluating marine macrobenthic function in coastal environments, with some recent practical applications.

Method	Original reference(s)	Main advantages	Main limitations	Practical applications evaluating marine microbenthic function	Quantifies (the effect of/on) what?
<b>Biotic indices</b>					
AMBI index	Borja et al., 2000	- Very useful for coastal management - Facilitates the interpretation of grossly raw ecological data	- Loss of information in deriving a single index to describe environmental condition	Feebarania et al., 2016 Lopes et al., 2017	Natural and anthropogenic stress
BENTIX	Simboura and Zenetos, 2002	- Can be statistically related to a range of physical, chemical, and biological measures	- Application is often restricted to specific systems	Brauko et al., 2015	Sediment contamination
TRIX	Wollenweider et al., 1998		- Efficiency is limited to a geographical context	Asha et al., 2016	Sewage contamination Eutrophication
<b>Bioturbation potential index (BPc)</b>	Solan et al., 2004 Birchenough et al., 2012	- Good indicator of benthic faunal function on sediment reworking - Can also be used as an indicator of environmental quality, and for the management of marine ecosystems	- Not account for intraspecific variability in trait values, intra- and inter-specific interactions, the actual contribution of species/individuals to the bioturbation process, and the effect of feeding behavior and vertical distribution that are important for the bioturbation process	Gogina et al., 2017 Wrede et al., 2017	Ecosystem functioning expressed by bioturbation Biogeochemical processes
<b>Functional groups</b>	Wilson, 1999 Blondel, 2003	- Simple applicability - Enables the quantification of a given ecological process accurately  - Very useful in a descriptive context, besides its capacity to address ecosystem functioning and assembly mechanisms	- Affected by the abundance of numerically dominant species that hinders the detection of subtle patterns  - Difficulties in comparing the results from different studies due to the lack of standardized protocols to classify species into functional groups	Alexandridis et al., 2017 Murray et al., 2017 Rius et al., 2018	Assembly mechanisms Environmental impacts Metabolic fluxes
<b>Functional diversity indices</b>		- Reflect the various functional facets of communities or ecosystem functioning - Describe aspects of community structure that are not detectable by the conventional indices of taxonomic diversity - Can be statistically related or modeled with environmental variables	- Usage is often restricted to comparative situations - The results can be abstract and difficult to interpret - Indices reflecting the same functional facet may provide opposite results due to differences in the nature of the estimations		

continued

Method	Original reference(s)	Main advantages	Main limitations	Practical applications evaluating marine macrobenthic function	Quantifies (the effect of/on) what?
<i>Univariate metrics</i> CWM	Garnier et al., 2004	- Useful in analyses of the relationship between a specific functional trait and certain ecosystem function - Provides relevant information on the capacity of the species to modulate an ecosystem process - Identifies dominant traits that may be linked to specific functions within the community (CWM)	- Restricted use, as most ecosystem properties are dependent on multiple types of functional traits - Often considered unattractive measures and replaced by an equivalent multivariate measure	van der Linden et al., 2016a Weigel et al., 2016	Effluents Functional identity
<i>Multivariate metrics</i> FD	Petchey and Gaston, 2002	- Focus on different functional attributes of the community	- Highly influenced by the methodological decisions	Törnroos et al., 2015	Reductions in richness
RaoQ	Champely and Chessel, 2002	- Can express in a simple way an ecological pattern	and availability of trait information	Darr et al., 2014 Dimitriadis and Koutsoubas, 2011	Salinity gradient Aquaculture
FAD	Botta-Dukát, 2005	- Enables direct comparison between studied communities	- The results can only be interpreted in the context of a specific work and can hardly be compared across studies	Dolbeth et al., 2015	Secondary production
FRic, FEve, FDiv, and FDis	Schmera et al., 2009 Schleuter et al., 2010 Villéger et al., 2008 Laliberte and Legendre, 2010				
<b>Biological traits analysis (BTA)</b>	Statzner et al., 1994 Bremner et al., 2003	- Gathers information on a range of functional traits exhibited by the whole species pool - Allows objective comparisons among similar environments	- The outcome is affected by the traits chosen to perform the analysis - The gaps in the knowledge of species traits can lead to less robust results	Gusmao et al., 2016 Dauvin et al., 2017 Pitacco et al., 2018	Sewage discharges Human pressures Climate changes
RLQ/ fourth-corner	Dolédec et al., 1996 Legendre et al., 1997	- Provides an informative picture of how traits change across samples or environmental gradients	- Does not describe potential functions nor identifies dominant traits	Piló et al., 2016 Wouters et al., 2018	Metal contamination Latitudinal gradient and regional drivers

## ASSESSING CHANGES IN MACROBENTHIC TRAIT STRUCTURE: METHODS FOCUSING ON RESPONSE TRAITS

Methods focused on response traits play a crucial role in assessing changes in macrobenthic structure, mainly regarding the composition and diversity of biological traits within a community. These methods are particularly valuable for understanding variations in trait structure alongside gradients in sediment properties. The underlying principle is that species' traits reflect their adaptations to environmental conditions,

and environmental gradients provide a range of habitats that can either support or hinder species establishment based on their traits. Analytical tools based on response traits are particularly useful when studying macrobenthic structure changes resulting from stress conditions, including natural and human disturbances.

Several analytical techniques can examine the relationship between changes in macrobenthic trait structure and environmental variation. A straightforward method involves grouping species into feeding guilds based on their feeding traits and

functional groups encompassing multiple trait types. Additionally, specific indices can be employed to assess various aspects of community trait structure, such as biotic indices of benthic quality, which rely on life history, stress tolerance, and other relevant traits, as well as functional diversity indices. Another valuable tool is biological traits analysis (BTA), which employs multivariate techniques, particularly multivariate ordinations, to characterize the variability of trait attributes across different samples and environmental gradients (Juan et al., 2022). These approaches offer valuable insights into the intricate relationship between macrobenthic trait structure and environmental changes.

### **GUILDS AND FUNCTIONAL GROUPS**

An old and commonly used method in functional ecology is classifying species into groups based on specific traits, known as guilds or functional groups (Wilson, 1999; Blondel, 2003). While the terms guild and functional group are sometimes used interchangeably, they hold distinct meanings. Guilds refer to resource-sharing mechanisms in competitive contexts, whereas functional groups relate to how species process resources to provide ecosystem functions (Blondel, 2003). However, both concepts are applied in a similar way in ecological research.

Guilds and functional groups represent subsets of species within a community that share a particular trait. For instance, all macrobenthic species that feed on sediment deposits are classified as “detritivores” (Tilman, 2001; Norling et al., 2007). The classification can be performed arbitrarily based on ecologists’ objectives and assumptions or via statistical algorithms such as cluster analysis (Pla et al., 2012; Bolam and Eggleton, 2014). Once species are grouped into functional groups, ecologists can analyze the trait structure, evaluate changes along environmental gradients, estimate diversity indices, and investigate correlations with ecological factors, like the analyses used for taxonomic data.

While classifying species into functional groups offers a straightforward approach, it shows certain limitations that warrant consideration. Firstly, the variation in functional group abundances across gradients may be influenced by numerically

dominant species, making it challenging to detect subtle variation patterns (e.g., Gusmao-Junior and Lana, 2015). Secondly, the assumption that all members of a functional group are functionally identical. Finally, the absence of standardized protocols for classification hinders the comparison of results across different studies. To address these limitations, researchers should carefully select traits and consider the ecological context and statistical methods when classifying species into functional groups.

### **BIOTIC INDICES FOR ENVIRONMENTAL STATUS**

Biotic indices serve as valuable metrics to assess the impact of natural and human induced changes on benthic soft-bottom communities. These indices consolidate diverse information on species composition into a single value that effectively characterizes the environmental condition of a benthic ecosystem (Borja et al., 2000; Salas et al., 2006; Basatnia et al., 2015). Although environmental quality indices have not been developed to address changes in benthic trait structure, they are fundamentally derived from the life history traits of macrobenthic species (Bonada et al., 2006). Thus, biotic indices can be considered as estimates based on specific aspects of community structure, enabling the evaluation of ecosystem quality. They operate on the assumption that communities reflect their environment and the biotic interactions therein, accounting for the varying responses and tolerance levels of organisms towards different habitat structures and pollution (i.e., different combinations of response traits). Salas et al. (2006) classified benthic quality indices into five primary groups:

**Indicator species-based indices:** These indices rely on the presence or absence of specific indicator species (e.g., AMBI Index, BENTIX; Borja et al., 2000; Shi et al., 2022).

**Ecological strategy-based indices:** These indices focus on the life history traits of organisms (e.g., index of r/K strategies, Polychaeta/Amphipoda Index; Gesteira and Dauvin, 2000; De Boer et al., 2001).

**Specific diversity-based indices:** These indices employ measures such as Shannon, Margalef, and Simpson diversities (Magurran, 2011).

**Biomass or abundance-based indicators:** These indicators consider the biomass or abundance of species (e.g., abundance-biomass curves, *sensu* Pearson and Rosenberg, 1978).

**Integrative indicators:** These indicators incorporate multiple sources of information regarding benthic assemblages and their environment, synthesizing the data into a single value (e.g., IBI-Index, TRIX; Weisberg et al., 1997; Wollenweider et al., 1998).

Although estimating a single index may result in some loss of information concerning the condition of an entire community or ecosystem, these assessment tools are highly valuable for marine management. Using a single index simplifies the complexity of macrobenthic data, which otherwise consists of multiple data frames describing species abundances and their corresponding trait scores. This univariate metric can be statistically correlated with many physical, chemical, and biological measures, facilitating the interpretation of ecological data for both specialists and non-specialists engaged in ecosystem management and conservation. Nevertheless, it is essential to exercise caution when applying or extrapolating indices beyond their specific geographical context, as the efficacy of an index is inherently limited to the characteristics of the studied area, considering the high complexity and diversity of benthic assemblages (Dolédec et al., 1999; Borja et al., 2000; Statzner et al., 2001; Salas et al., 2006).

## FUNCTIONAL DIVERSITY INDICES

Functional diversity encompasses the vital aspects of biodiversity that impact ecosystem properties and processes (Tilman, 2001; Violle et al., 2007). Despite the growing body of research on functional diversity, a clear consensus regarding its conceptual definitions remains elusive (Petchey and Gaston, 2006; Laureto et al., 2015; Schmera et al., 2017). To measure functional diversity, it is necessary to quantify the diversity of species traits including behavioral, morphological, or physiological characteristics that impact ecosystem functioning (Tilman, 2001; Violle et al., 2007, 2012).

Quantifying the range of species trait values within a community represents one of the earliest

and simplest approaches to assessing functional diversity (Swenson, 2014). These quantifications are then synthesized into an index based on continuous values of one or more traits, which may or may not be weighted by species abundances. Ideally, a functional diversity index should provide insights into community structure that are not captured by conventional taxonomic diversity indices (Villéger et al., 2008).

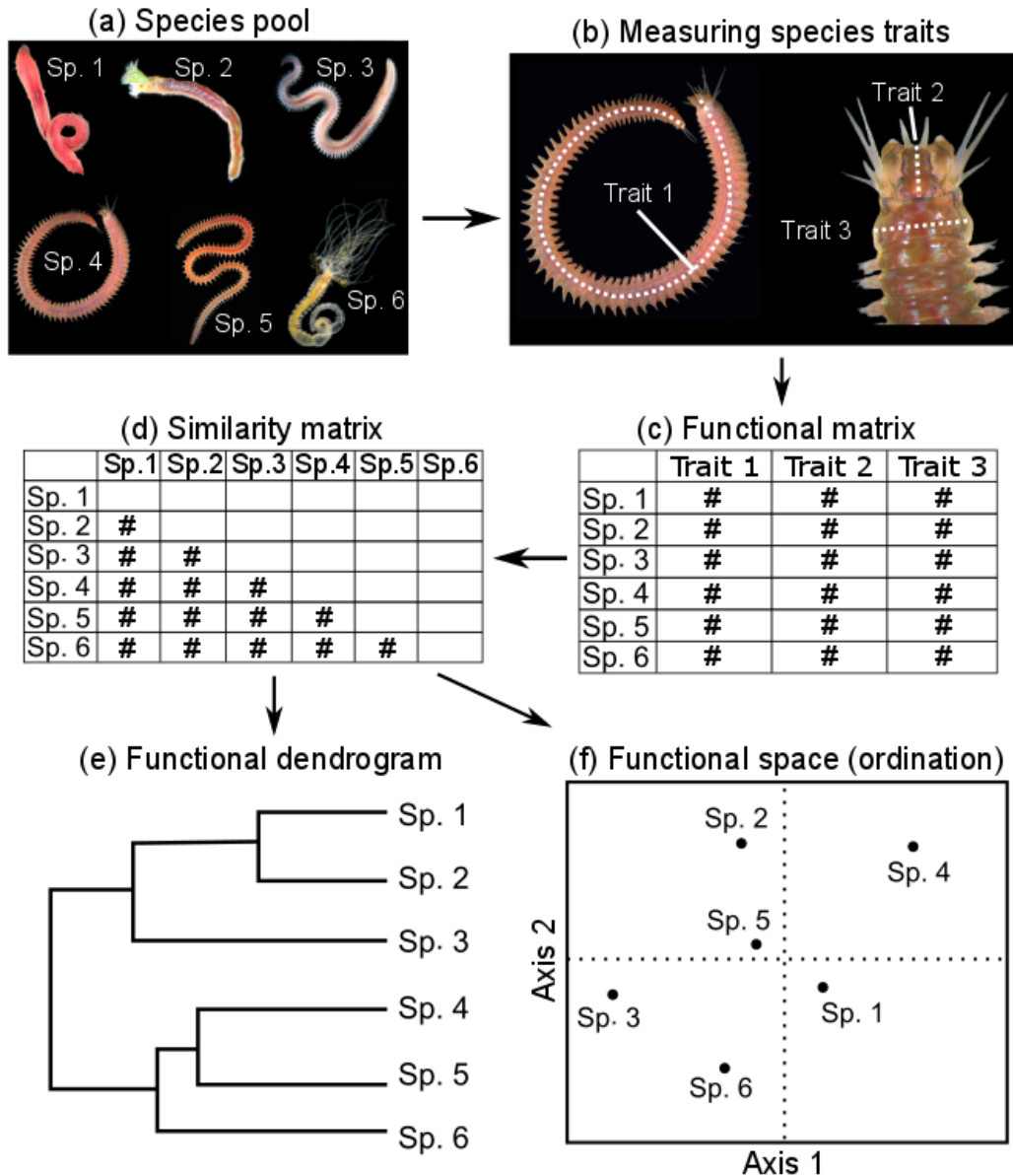
A commonly employed univariate index in functional ecology is the community-weighted mean (CWM) trait value (Garnier et al., 2004). The CWM indicates the expected functional value of a trait within a given community, estimated by averaging the trait values weighted by the relative abundances of each species (Garnier et al., 2007; Pla et al., 2012). This metric enables the identification of dominant trait categories in a community, considering the influence of the most abundant species on ecosystem processes (Ricotta and Moretti, 2011). Although the index is typically used to analyze individual traits independently, it is possible to construct a trait composition matrix at the community level (abundance-weighted trait values per sample) via the CWM. This matrix can then be utilized in ordination or gradient analyses (e.g., Gimenez and Higtuti, 2017) to aid understand trait composition and its impact on ecosystem dynamics.

A range of univariate indices enable the quantification of functional diversity and provide insights into various aspects of community trait structure. These indices include functional range (FRR; Mason et al., 2005), univariate functional richness (FRIS; Schleuter et al., 2010), functional regularity (FRO; Mouillot et al., 2005), and univariate functional divergence (FDvar; Mason et al., 2003). When studying the relationship between specific functional traits and the environment, these indices prove valuable in elucidating community responses along environmental gradients (Schleuter et al., 2010).

Recognizing that the capacity of species to influence ecosystem properties often relies on multiple functional traits, ecologists have developed multivariate indices to estimate community functional diversity (Pla et al., 2012). The first group of these metrics is based on dendrograms, which illustrate the similarities between species traits

within a community. To estimate a dendrogram-based index, a similarity matrix (Figure 1a-d) is constructed based on the functional traits of the species present in the community (Figure 1e). One of the most widely used dendrogram-based indices is functional diversity (FD) proposed by

Petchey and Gaston (2002). FD estimates the total length of the dendrogram branches. Note the choice of distance measure (e.g., Euclidean, Bray-Curtis) and the grouping method employed to construct the dendrogram can significantly impact the results (Petchey and Gaston, 2002).



**Figure 1.** Logical sequence for the construction of a dendrogram or a functional space representing the species' similarities regarding their functional traits: six species are part of the assemblage (a) and have three traits measured (b): body length (trait 1), prostome length (trait 2), and peristome width (trait 3). Then, the mean values of each trait measured for each species are organized in a functional matrix (c). Subsequently, a similarity matrix relating species according to their trait values is constructed based on a chosen distance measure (d). Finally, one can represent species trait similarities by using cluster analysis to construct a functional dendrogram (e) or a multivariate ordination to represent the functional trait space of the assemblage (f).

Numerous variants of FD have been proposed, some incorporating information on species' relative abundances, such as weighted functional diversity (wFD; Pla et al., 2012), or accounting for intraspecific trait variability, such as intraspecific functional diversity (iFD; Cianciaruso et al., 2009). Additionally, specific routines for dendrogram construction, like generalized functional diversity (GFD; Mouchet et al., 2008), have been developed to further enhance the analysis of functional diversity. Another group of multivariate indices focuses on the functional space of communities, which refers to a hypervolume of functional trait values describing the trait space occupied by species within a community (Villéger et al., 2008). To construct the functional space, a similarity matrix based on species' functional trait values is generated (Figure 1f). While the Euclidean distance is commonly used, the choice of similarity index depends on the type of trait data, whether continuous (e.g., size), categorical (e.g., type of embryo development: direct or indirect), or a combination of both (Laliberté and Legendre, 2010). The distribution of species within this multidimensional functional space can be visualized via ordination techniques such as principal component analysis (PCA) or principal coordinate analysis (PCoA), in which multiple traits are summarized on each axis (Figure 1f).

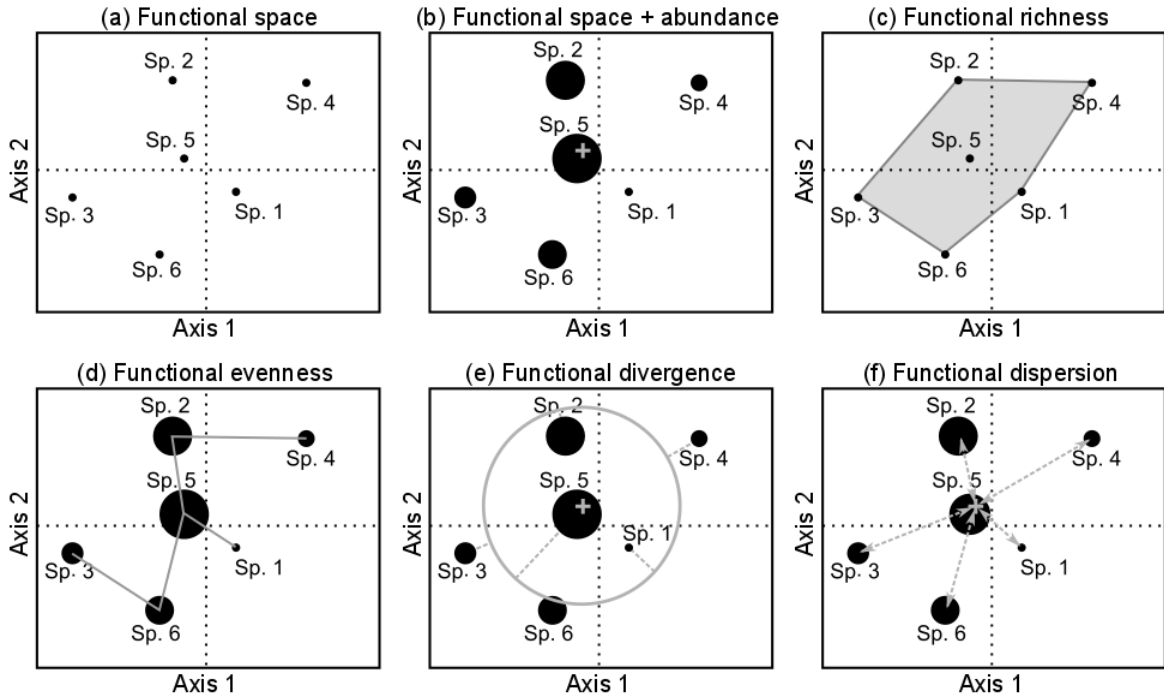
Rao's quadratic entropy (RaoQ) is an index based on the functional trait space that quantifies functional differences between pairs of species while considering their relative abundances. This metric, derived from Rao's quadratic entropy theory (Rao, 1982), represents a generalized form of the classic Simpson diversity index (Champely and Chessel, 2002; Botta-Dukát, 2005). RaoQ is widely used to measure functional dissimilarity, a key component of functional diversity that captures the dispersion and abundance of species within the functional space (Laliberté and Legendre, 2010; Gerisch et al., 2012). It is a robust tool for quantifying functional diversity in various environments, including marine benthos (e.g., Darr et al., 2014; Gusmao et al., 2016; van der Linden et al., 2012). Additionally, there are alternatives to decompose this index into components of  $\alpha$ ,  $\beta$ , and  $\gamma$  diversity (Ricotta and Szeidl, 2009; Villéger et al., 2012, 2013; Arnan et al., 2016).

The functional diversity attribute (FDA) represents a group of functional diversity metrics estimated based on the Euclidean distance in the functional trait space (Schmera et al., 2009; Schleuter et al., 2010). This group includes indices such as FAD1, FAD2, and MFAD. FAD1 quantifies different combinations of functional attributes present in a community. FAD2 estimates the sum of distances between pairs of species within the functional trait space. MFAD extends FAD2 by incorporating species abundance into the estimations (Schmera et al., 2009). Although these indices have been widely employed (Schmera et al., 2009; Bihn et al., 2010; Dimitriadis and Koutsoubas, 2011), they are correlated with species richness, limiting their interpretability (Mouchet et al., 2010; Pavoine and Bonsall, 2011).

Villéger et al. (2008) proposed three multivariate indices that capture various aspects of functional diversity: functional richness (FRic), functional evenness (FEve), and functional divergence (FDiv). These indices assess various dimensions of the functional space represented by a (dis)similarity matrix of trait values across species within a community (Villéger et al., 2008). FRic measures the total volume of the convex hull that encloses all species within the functional trait space (Figure 2c). Changes in FRic values indicate the appearance or disappearance of species with extreme or unique functional traits (i.e., located at the vertices of the convex hull). FEve estimates the degree of regularity in the distribution of species abundances across the trait space by measuring the branches of the shortest minimum spanning tree, weighted by species abundance, that connects all species within the functional trait space (Figure 2d). Alterations in FEve are associated with disproportional increases or decreases in abundance within specific regions of the functional space. FDiv estimates how species diverge from the average distance to the gravity center of the functional trait space, considering species abundance (Figure 2e). Variations in FDiv relate to changes in the abundances of species with extreme or intermediate trait values (i.e., located at the periphery or center of the functional trait space). Laliberté and Legendre (2010) proposed a fourth index, functional dispersion (FDis), which estimates the multivariate dispersion of species within the

functional trait space and can also incorporate species abundances into the estimation (Figure 2f). FDis is closely related to the RaoQ index and is sensitive to increases or decreases in species with intermediate (center of the functional space) or extreme trait values (periphery of the functional

space). For example, Kindeberg et al. (2022) explored functional diversity (FD), functional richness (FRic), and functional evenness (FEve) of macrofaunal communities in eelgrass meadows and adjacent bare habitats across contrasting environments in Southern Sweden.



**Figure 2.** Representation of the functional diversity components in a multidimensional space, as proposed by Laliberté and Legendre (2010) and adapted from Mouillot et al. (2013). Points represent the position of species in the functional space (defined by the first two axes of an ordination analysis). The size of black circles is proportional to the relative abundance of the species. (a) Distribution of species in the functional space (abundances not accounted); (b) representation of relative abundance in the functional space; (c) functional richness (FRic), in which the gray polygon represents the convex hull volume; (d) functional evenness (FEve); (e) functional divergence (FDiv), in which the gray circle corresponds to the average distance of the center of gravity in the functional space (gray cross); and (f) functional dispersion (FDis), in which the arrows depict the distance of each species to the centroid of the ordination.

Other indices can complement the metrics proposed by Villéger et al. (2008), such as functional specialization (FSpe), which quantifies the relative position of species within the functional trait space, and functional originality (FOri), which represents the relative isolation of species within the functional trait space (Mouchet et al., 2010; Mason et al., 2013; Mouillot et al., 2013). Gimenez and Lana (2020) used the functional originality (FOri) and functional uniqueness (FUni) indices (Buisson et al. 2013; Mouillot et al. 2013) to evaluate functional redundancy patterns in polychaetes assemblages of continental shelf and estuarine environments.

FOri does not consider that two species can share a unique combination of traits that is not present in the other species of the pool and FUni, in turn, describes this additional facet of the biological identity of species, representing approximately the opposite of functional redundancy (Buisson et al. 2013; Mori et al. 2016).

Finally, functional diversity of marine benthos can also be estimated at the beta scale (e.g., Bevilacqua and Terlizzi, 2020; Nasi et al., 2023). Functional beta diversity refers to the species traits dissimilarity among communities, and its decrease due to some human cause may indicate

functional homogenization (Petsch, 2016). For example, Nasi et al. (2023) used functional beta diversity to investigate the response of the soft-bottom macrofaunal community due to a wastewater treatment. Functional beta diversity can be estimated using different metrics, such as a dissimilarity index based on trait composition or the overlap of communities in a multidimensional functional space (Villéger et al., 2013).

## BIOLOGICAL TRAIT ANALYSIS (BTA)

BTA is a widely used approach for evaluating changes in the trait structure of marine benthic communities (see Juan et al., 2022 for a complete review of BTA in benthic marine ecology). Initially developed for freshwater systems, BTA (Bremner et al., 2003) employs a multivariate method (Chevenet et al., 1994; Statzner et al., 1994; Dolédec et al., 1996) to examine the distribution of trait categories within a community. By incorporating information on species abundances and biological traits across samples or experimental units (Bremner et al., 2006a), BTA offers insights into trait distribution patterns along environmental gradients and the relationship between individual traits and environmental factors (Bremner et al., 2006a).

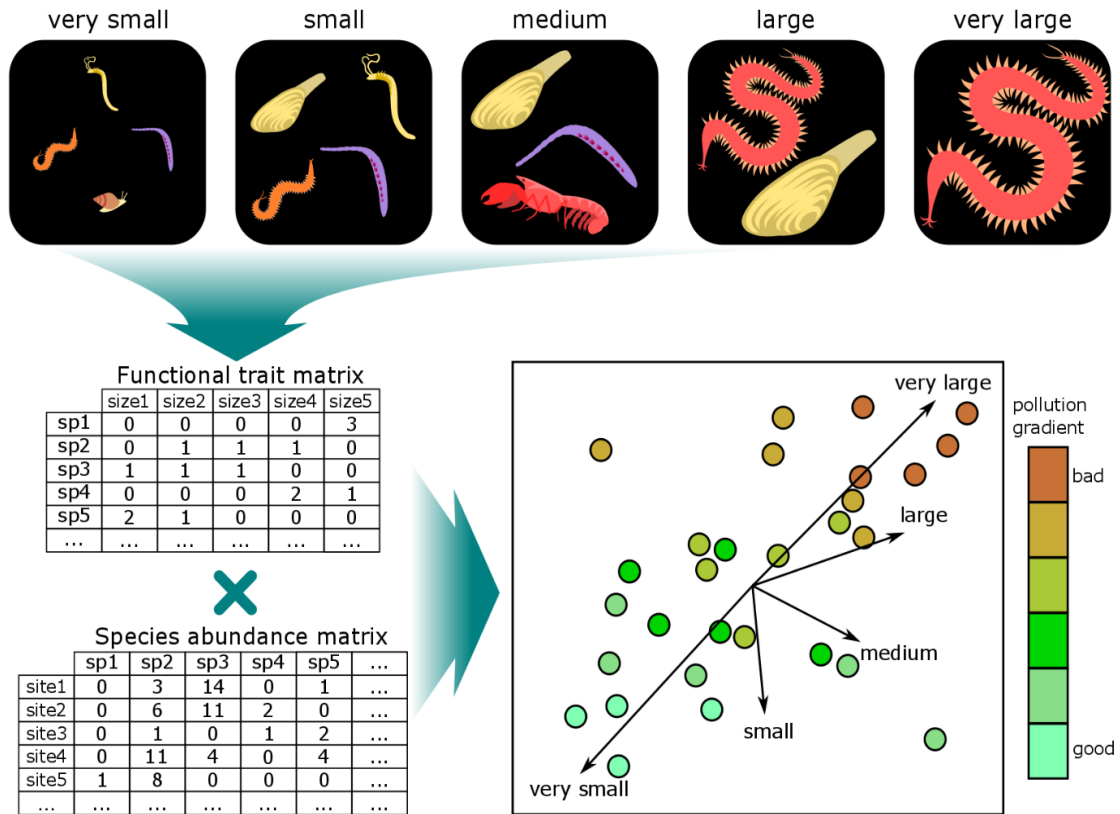
The application of BTA in marine systems has gained significant traction (e.g., Bremner et al., 2003, 2006a, 2006b; Schratzberger et al., 2007; Cesar and Frid, 2009; Paganelli et al., 2012; van der Linden et al., 2012; Rigolet et al., 2014; van Son et al., 2013; Juan et al., 2022). For instance, Gusmao et al. (2022) described notable changes in the trait structure of macroinvertebrates along with sediment gradients in the Wadden Sea, varying from communities dominated by small body size, deposit-feeding, and short life span in muddy sediments to a community characterized by large to medium body size, suspension-feeding, and long-life span in sandy sediments. BTA employs multivariate ordinations to describe variation patterns in the distribution of functional traits (Bremner et al., 2006a, Beauchard et al., 2017). There are two common methods for performing BTA, including fuzzy correspondence analysis (FCA) and coinertia analysis (CIA) (Chevene et al., 1994; Dolédec and Chessel,

1994). These analyses involve two matrices: a species abundance (or incidence) per sample matrix and a functional trait matrix (Figure 3). The functional trait matrix is constructed using a fuzzy coding procedure based on a score rank system, typically ranging from 0 to 3, representing the species' association with different categories of a functional trait (Chevene et al., 1994). For example, considering the functional trait “feeding mode,” an herbivorous species would receive a score of 3 for the category “herbivore” and 0 for other categories, while an omnivorous species would score 1.5 for both “herbivore” and “carnivore” categories. These matrices are then multiplied to generate a third matrix, representing trait frequencies weighted by species abundance in each sample (see Gayraud et al., 2003 for details). Correspondence analysis conducted on this “trait per sample” matrix can illustrate changes in trait composition along environmental gradients (Figure 3). It is important to note that the selection of traits for BTA can impact the analysis results and introduce bias in their interpretation. Bremner et al. (2006b) suggest that BTA becomes more informative when using as many traits as possible, whereas Mlambo (2014) emphasizes the careful consideration of traits, as some may introduce noise into the analysis. It should be noted that the biological traits of most macrobenthic species may lack precision or be unavailable.

Other multivariate techniques that incorporate environmental variables in BTAs include RLQ (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997). RLQ analysis combines the sites-by-environment (or R) matrix, species-by-sites (or L) matrix, and species-by-traits (or Q) matrix to construct the “fourth-corner” (traits-by-environment) matrix. While RLQ analysis provides a useful graphical summary, fourth-corner analysis tests the significance of the relationship between traits and environmental variables (Dray et al., 2014). These tools, when used together, can yield impressive results in assessing the trait structure of marine macrobenthic communities (e.g., Piló et al., 2016; Wouters et al., 2018). Despite their potential, RLQ and fourth-corner analysis are not yet widely used, and several challenges hinder

their application. Here, we discuss the reasons for this limited adoption and the computational

challenges that can be addressed to improve the significance of these relationships:



**Figure 3.** Diagram depicting the steps to perform a biological trait analysis (BTA) based on the functional trait relative adult size. The trait shows five categories (attributes), varying from very small to very large. Fuzzy scores are assigned to each species depending on their association degree to each trait category. By weighing the trait frequencies by the species' abundances in each sampling site, it is possible to represent the variation trends in trait composition across environmental gradients. In the above example, larger species are associated with polluted sites.

Other multivariate techniques that incorporate environmental variables in BTAs include RLQ (Dolédec et al., 1996) and fourth-corner analyses (Legendre et al., 1997). RLQ analysis combines the sites-by-environment (or R) matrix, species-by-sites (or L) matrix, and species-by-traits (or Q) matrix to construct the “fourth-corner” (traits-by-environment) matrix. While RLQ analysis provides a useful graphical summary, fourth-corner analysis tests the significance of the relationship between traits and environmental variables (Dray et al., 2014). These tools, when used together, can yield impressive results in assessing the trait structure of marine macrobenthic communities (e.g., Piló et al., 2016; Wouters et al., 2018). Despite their potential, RLQ and fourth-corner analysis are not

yet widely used, and several challenges hinder their application. Here, we discuss the reasons for this limited adoption and the computational challenges that can be addressed to improve the significance of these relationships:

**Limited Adoption:**

**Complexity:** The fourth-corner analysis and RLQ methods involve complex statistical models and require a good understanding of the underlying ecological concepts and statistical techniques. This can be a barrier for researchers without a strong background in these areas (Dray et al., 2014; Sarker et al., 2021).

**Computational Requirements:** These methods often involve computationally intensive procedures, such as permutation tests and Markov

Chain Monte Carlo (MCMC) simulations, which can be time-consuming and require significant computational resources (Sarker et al., 2021).

**Interpretation Challenges:** The results of these methods can be difficult to interpret, especially for researchers without a strong understanding of the underlying statistical models and ecological concepts (Dray et al., 2014).

**Computational Challenges:**

**Computational Power:** The fourth-corner analysis and RLQ methods require significant computational power, particularly when dealing with large datasets or complex models. This can challenge researchers with limited access to computational resources (Sarker et al., 2021).

**Model Selection:** Selecting the best model from a set of competing models can be challenging, especially when dealing with complex models and multiple environmental variables. This can be addressed by using model selection criteria such as the Deviance Information Criterion (DIC) (Sarker et al., 2021).

**Convergence Issues:** Ensuring the convergence of MCMC chains is crucial for obtaining reliable results. This can be challenging, especially when dealing with complex models or large datasets. Techniques such as the Gelman-Rubin statistic can be used to monitor convergence (Sarker et al., 2021).

**Resolving Challenges:**

**Improved Computational Power:** Advances in computational power and the development of more efficient algorithms can help alleviate the computational challenges associated with these methods.

**Simplified Model Selection:** Developing simpler and more interpretable models can help reduce the complexity of model selection and improve the adoption of these methods.

**Collaboration and Training:** Collaboration between ecologists and statisticians can help improve the adoption of these methods by providing training and support for researchers.

By addressing these challenges and improving the accessibility and interpretability of the fourth-corner analysis and RLQ methods, researchers can better understand the complex relationships between environment, traits, and species,

ultimately leading to more accurate predictions and better management of ecosystems.

## ASSESSING MACROBENTHIC FUNCTION: METHODS FOCUSING ON EFFECT TRAITS

Macrobenthic species are widely recognized for their pivotal role in the functioning of marine ecosystems by promoting the exchange of energy and mass between the water column and the sediment via bioturbation of the sediment (benthic-pelagic coupling; Griffiths et al., 2017; van der Linden et al., 2017; Wouters et al., 2018). The disturbance caused by macrobenthic organisms in the sediment matrix can alter the vertical structure of sediment layers and modify particle distribution and stability (Kristensen et al., 2012). These small-scale disturbances, mediated by bioturbators, are crucial in maintaining a mosaic of patches across various successional stages, promoting local heterogeneity and increasing beta diversity (Thrush and Dayton, 2002; Natálio et al., 2017). Bioturbation also leads to biogeochemical changes, aeration, and stimulation of aerobic microbial activity (Lohrer et al., 2004; Mermillod-Blondin, 2011). These changes in sediment redox conditions impact the cycling of nitrogen, sulfur, and organic carbon compounds in marine systems (Mermillod-Blondin, 2011).

Several techniques and approaches are available to assess the relationships between benthic trait structure and the functioning of benthic ecosystems, particularly regarding the composition, prevalence, and diversity of effect traits and their influence on biogeochemical processes in sedimentary systems. Many methods focusing on response traits can also address this problem. For instance, estimating functional diversity indices based on effect traits can reflect the variety of ways in which species in a community can impact the sediment matrix (Gusmao et al., 2016). However, certain functional diversity metrics are particularly useful when dealing with effect traits since they provide insights into the functional vulnerability of a habitat, which refers to the likelihood of losing specific animal-mediated processes due to local extinction. These

metrics are multivariate measures that emphasize the relationship between functional diversity and species richness, enabling the inference of functional redundancy in communities (Mayfield et al., 2010). Functional redundancy (FR; Fonseca and Ganade, 2001), functional vulnerability (FV; Bihn et al., 2010), and functional over-redundancy (FOR; Mouillot et al., 2014) are some commonly employed metrics to describe patterns of functional redundancy (Brandl et al., 2016; Micheli et al., 2014; Mouillot et al., 2014). These metrics can be used to estimate the vulnerability of ecosystem functions to disturbances since the functional redundancy of communities is directly related to resilience (Luck et al., 2013). Therefore, a community with high functional redundancy (i.e., species sharing similar traits) is less likely to lose specific functions driven by species extinction (Loreau, 2004; Mouillot et al., 2014). More recently, Violle et al. (2017) introduced metrics for estimating functional rarity that integrate the concepts of functional distinctiveness and taxonomic scarcity observed at the local scale, as well as functional uniqueness and taxonomic restrictedness at the regional scale. These metrics describe the functional equivalence of a species within the community and the relative abundance/extent of occurrence of a species in the community or the regional pool, respectively.

The application of BTA (Biological Trait Analysis), focusing on effect traits, enables the direct visualization and correlation between specific traits related to bioturbation, such as body size, burrowing capacity, and bioturbation behavior, as well as gradients in sediment texture and biogeochemistry. This approach enables the visualization of gradients in bioturbation capacity or potential to the environmental parameters they are likely to impact. Moreover, some specific metrics estimate the potential capacity of the macrobenthic community to impact the sediment matrix based on bioturbation-related traits (see below).

### **COMMUNITY'S BIOTURBATION POTENTIAL AND BIOIRRIGATION POTENTIAL**

Bioturbation, a crucial ecosystem function performed by benthic species in marine environments, is quantified using the bioturbation

potential index (BPc). Developed exclusively for soft-sediment benthos, the BPc considers average body size, mobility, and mode of sediment reworking as influential functional traits. It incorporates species abundance and biomass, enabling estimation for both individual species and entire communities (Birchenough et al., 2012). However, limitations exist, such as the lack of consideration for intraspecific variability and species interactions, hindering the accuracy of the BPc as a measure of real bioturbation capacity (Alves et al., 2017; Gogina et al., 2017).

In addition to the BPc, the community bioirrigation potential (BIPc) index focuses on quantifying the potential for solute exchange at the sediment-water interface (Renz et al., 2018). Bioirrigation, crucial for nutrient cycling and organic matter regeneration, is challenging to assess due to complex species interactions and the lack of direct measurement methods. The BIPc index overcomes these challenges by incorporating functional traits related to pore water and solute exchange, using a biomass- and abundance-weighted scoring system (Renz et al., 2018). It considers traits such as feeding type, burrow morphology, and burrowing depth, providing a mechanistic approach to quantifying bioirrigation potential for the entire benthic community (Renz et al., 2018). However, further research is needed to refine the BIPc index and address potential limitations associated with intraspecific variability and other important traits influencing the bioirrigation process (Gogina et al., 2017).

### **LIMITATIONS AND CAVEATS**

Many challenges should be considered before using trait-based approaches to assess the macrobenthic function in marine systems. Challenges and limitations mainly include scarcity and lack of standardization of trait data, lack of empirical studies testing the effect of specific traits on ecosystem processes, lack of standardized methods in analyzing trait data, and the frequently overlooked effect of intraspecific variation of trait attributes.

### **AVAILABILITY AND QUALITY OF TRAIT DATA**

Recent efforts have managed to organize trait information for specific taxonomic groups. One

example is the collaborative database Polytraits (Faulwetter et al., 2014), which compiles trait information of polychaetes species. Recent reviews have synthesized information on specific functional traits relevant to sediment processes, such as that by Queirós et al. (2013), which addressed the bioturbation behavior of European benthic species. There are also efforts to compile trait information of specific geographical regions, such as the Marine Macrofauna Genus Trait Handbook (Marine Ecological Surveys Ltd., 2008), which focused on benthic organisms occurring in British waters. Other bases compile more general data, namely, WoRMS (Costello et al., 2015), which includes trait information for all marine species globally, and BIOTIC (MarLIN, 2006), which provides biological trait information for individual benthic species. Such efforts, however, are still far from the extensive and standardized databases already available for other animals (e.g., FishBase; Froese and Pauly, 2014) and for freshwater organisms (e.g., freshwater ecology info database; Schmidt-Kloiber and Hering, 2015). Such unified and standardized databases are necessary for the broad application of trait-based approaches to assess benthic systems.

Detailed information on species traits is scarce or missing for most benthic organisms, especially in the case of poorly known taxonomic groups and overlooked geographic locations (Raunkiaeran shortfall of biodiversity; Hortal et al. 2015). This is mainly driven by the analytical costs of measuring traits of numerous but rare or inconspicuous species that thrive in the soft-bottom benthos, which can strongly impact the methodological decisions concerning a trait-based analysis. When reliable information is missing, a common practice is data extrapolation from the phylogenetic nearest neighbor species (i.e., assuming the similarity between species). However, despite the level of kinship, close species may display different behaviors and life modes, as is the case for polychaetes species of the genus *Nereis*.

### **LACK OF STANDARDIZATION TO DESCRIBE SPECIES TRAITS**

Another limitation is the lack of standardization to describe species traits and their associated

attributes (Verberk et al., 2013). Different studies that address similar traits frequently diverge on how to describe or measure trait attributes. Trait body size is a good example of such cross-study incongruence. Although some studies consider average weight or body mass as a proxy for body size (e.g., van der Linden et al., 2017), anatomical measures are also often used to describe species' body size (e.g., van der Linden et al., 2012; Rigolet et al., 2014; Gusmao et al., 2016; van der Linden et al., 2016). For instance, body size is described using shell length and height for bivalves (Berke et al., 2014) but using body length for annelid worms (Wouters et al., 2018). An ecologist may compile such anatomic-based trait measures of bivalves and worms to analyze the size structure of the entire benthic community. In that case, the values used for body size cannot be converted at the same proportion to represent organism biomass, biasing the trait structure of a benthic community. To minimize these discrepancies, van der Linden et al. (2017) considered body mass to categorize polychaetes and mollusks as very small, small, medium, and large. They considered distinct weight intervals for each taxon, considering the differences across species.

To reduce the limitations in the standardization of available data, Costello et al. (2015) developed a broader vocabulary and a classification of traits, prioritizing those that should be adopted for the marine species already included in the WoRMS database. To avoid issues related to cross-taxon-trait differences, one could focus on particularly abundant and diverse taxonomic groups. For example, Otegui et al. (2016) proposed a new BTA approach for the functional categorization of polychaetes assemblages based only on morphological traits. Since polychaete morphology enables the comparison of both taxonomical and functional approaches, despite not necessarily focused on functional traits, this technique also enables the standardization of existing trait data on unique morphological attributes, reducing the subjectivities of the analytical process (Otegui et al., 2016). However, most rare species are not yet coded, which can be problematic when addressing metrics such as functional richness.

## LACK OF EMPIRICISM LINKING TRAITS TO PROCESSES

Most studies on functional diversity do not justify their trait choices when addressing the function of species. In general, ecologists assume the potential effect of certain traits on a specific ecosystem process and intuitively include them in their analyses. For instance, a researcher interested in assessing the effects of macrobenthic communities on biogeochemical processes can choose traits that reflect the bioturbation potential, such as body size, type of bioturbation behavior, and mobility through the sediment (e.g., Bolam and Eggleton, 2014). However, studies that addressed the relationship of such morpho-behavioral traits with sediment properties are often restricted to an insufficient number of species (e.g., Michaud et al., 2005; Mermillod-Blondin, 2011), and there is no evidence that multiple species with similar traits would necessarily display the same bioturbation potential. Additionally, highly bioturbating species are determinants of nutrient cycling in muddy substrates, but they lose importance as sediment grain size increases (Mermillod-Blondin and Rosenberg, 2006; Mermillod-Blondin, 2011). These arguments highlight the importance of considering contexts where a trait is appropriate to address the effects of functional diversity in the environment (or vice versa). Considering the lack of information on the functional relevance of used traits, we stress the urgent need for empirical studies on the relationship between functional traits and specific ecosystem properties and processes.

## OVERLOOKED EFFECTS OF INTRASPECIFIC VARIATION

Since traits are often collected at the species level, interspecific variability is assumed to be higher than intraspecific variability (Kichenin et al., 2013). The capacity of organisms to change ecosystem properties and the intensity with which they interact with other organisms vary throughout their life (Díaz et al., 2013; Wong and Candolin, 2015). Excluding the obvious functional differences between pelagic larvae and settled adults, benthic organisms can present marked changes in their functional role depending on their development stage. These changes are mainly

related to body size (Linse et al., 2006; Eklöf et al., 2017) and diet (Bolnick et al., 2011), thus having direct implications for local food webs (Layman et al., 2005; Gravel et al., 2016). Different benthic species can also present behavioral changes during certain life stages. For instance, many species of fiddler crabs build sediment structures around their burrows when they become adults (Christy, 1982), changing the microtopography of their sedimentary environment. Trait expression of some species can also vary markedly, depending on their location or environmental context (Vaughn, 2010), such as the onuphid worm *Diopatra cuprea*, whose role as an ecosystem engineer changes along a latitudinal gradient (Berke, 2012). Intraspecific variations are determinant to increase the resilience of populations and communities to disturbances since they can alter species trait rankings along environmental gradients or in extreme situations (e.g., limited resource availability), enabling species persistence even under adverse conditions (Cianciaruso et al., 2009; Jung et al., 2010; Bolnick et al., 2011; Burton et al., 2017). Such examples indicate that intraspecific trait variation can impact species roles and introduce bias in studies that use trait identities or diversity to assess ecological function. In these cases, multivariate indices may not represent the best way to approach the functional ecology, and univariate metrics should be used instead (Bolnick et al., 2011; Violle et al., 2012). However, measuring trait attributes at the individual level is not a logistically viable procedure for most studies.

## LACK OF STANDARDIZED PROTOCOLS AND METHODOLOGIES

Although the general interest in trait-based approaches has increased, their application to assess marine benthic assemblages still lacks standardized protocols. Recent studies highlighted that some functional diversity metrics are highly affected by choices taken prior and during calculation (Lefcheck et al., 2015; Maire et al., 2015; Zhu et al., 2017a, 2017b). For instance, multivariate indices can be impacted by the number and type of traits chosen for the study, availability of detailed information on species' traits, distance measure used to construct the functional trait space

or dendrogram, type of measure used to quantify species' abundances (e.g. density, biomass, or coverage), and corrections or transformations that can be used when estimating the indices (Leps et al., 2006; Mouchet et al., 2010; Maire et al., 2015; Zhu et al., 2017a).

Indeed, there is no standardized methodology for selecting the most appropriate functional traits for a study (Bolam and Eggleton, 2014). Still, iterative selection or even hypothesis testing in combination with biological reasoning (Statzner and Bêche, 2010) could possibly reduce the noise of redundant or irrelevant trait information that could impact the results. All these biased sources indicate a more significant problem ahead. Considering the high degree of subjectivity in the estimation of functional diversity indices (especially those based on multivariate techniques), most of the results derived from such indices can only be interpreted considering the choices made by the ecologists and can hardly be compared across studies. Thus, unless benthic ecologists standardize trait choices and make their analytical protocols more objective, other trait-based approaches would represent a better choice to assess the potential function of benthic assemblages. In this context, BTA tends to be less prone to bias since it does not reduce the entire trait structure of assemblage in an index but describes merely how trait attributes vary across different samples or gradients. Similarly, all the information found in the BTA can be found when estimating the CWM, but CWM also indicates the dominant traits in the community, something that BTA performs less well. In turn, these dominant traits can be used to quantify the rate of ecosystem processes (Vandewalle et al., 2010).

## CONCLUSION

Although various methods have been proposed in recent decades to assess the relationship between species traits and ecosystem functioning, no technique can be universally applied. Different methods have their strengths and limitations, which depend on the aims of the study and the hypotheses to be evaluated. Major challenges that hinder the development of trait-based approaches as an objective way to assess assemblage function, including lack

of trait information, unstandardized terminology, and protocols. Among the most recent methods, multivariate indices have frequently been used in different types of environments, even though methodological decisions and the availability of trait information highly impacted such metrics. Thus, the results derived from such multivariate metrics can only be interpreted in the context of a specific study and can hardly be compared across studies. Conversely, BTA appears to be an alternative to assess the functional diversity of marine benthic assemblages since it enables more objective comparisons among similar environments. Such analyses facilitate the assessment of potential ecological functions of benthic assemblages since they provide a clear picture of how trait attributes change across samples or environmental gradients. BTA may not describe potential functions as a specific metric such as BPC, but it can still be highly useful to explore changes in assemblage structure. CWM has also been shown to be helpful since it perceives the shifts in the mean trait values, detecting dominant traits that may be linked to specific functions within the community. Even though there is much to be established and evaluated before widely applying trait-based approaches to assess macrobenthic function, the use of BTA, together with classical analysis (i.e., those that have been extensively used in studies of functional ecology, as the functional diversity indices) represents a more informative approach than using species' diversity solely to describe community structure and functioning.

## ACKNOWLEDGMENTS

First, we would like to thank Dr. Paulo Lana, whose dedicated involvement from the initial drafts to the final version of this manuscript showcases his unwavering commitment to the field of benthic ecology; it will stand as a lasting testament to his scientific legacy. We would like to thank the Federal University of Paraná (UFPR), the Center for Marine Studies (CEM), and the Post-Graduate Program in Coastal and Oceanic Systems (PGSISCO) for the logistic support. The first author thanks the Coordination for Improvement of Higher Education Personnel (CAPES) for the PhD scholarship. We are grateful to the anonymous reviewers

who provided comments and suggestions that significantly improved this manuscript.

## AUTHORS CONTRIBUTIONS

B.C.G.G., J.B.G.: Conceptualization; Methodology; Formal Analysis; Investigation; Writing – original draft; Writing – review & editing.

D.K.P., F.J.F.: Writing – review & editing.

P.C.L.: Conceptualization; Supervision; Resources; Project Administration; Writing – review & editing.

## REFERENCES

- Alves, R. M. S., Colen, C. V., Vincx, M., Vanaverbeke, J., De Smet, B., Guarini, J.-C., Rabaut, M. & Bouma, T. J. 2017. A case study on the growth of *Lanice conchilega* (Pallas, 1766) aggregations and their ecosystem engineering impact on sedimentary processes. *Journal of Experimental Marine Biology and Ecology*, 489, 15–23.
- Arnan, X., Cerdá X. & Retana, J. 2016. Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography*, 40(3), 448–457.
- Basatnia, N., Hosseini, S.A., Ghorbani, R. & Muniz, P. 2015. Performance comparison of biotic indices measuring the ecological status base on soft-bottom macroinvertebrates: a study along the shallow Gomishan lagoon (Southeast Caspian Sea). *Brazilian Journal of Oceanography*, 63(4), 363–378.
- Beauchard, O., Verissimo, H., Queirós, A. M. & Herman, P. M. J. 2017. The use of multiple biological traits in marine community ecology and its potential in ecological indicator development. *Ecological Indicators*, 76, 81–96.
- Bevilacqua, S. & Terlizzi, A. 2020. Nestedness and turnover unveil inverse spatial patterns of compositional and functional  $\beta$ -diversity at varying depth in marine benthos. *Diversity and Distributions*, 26(6), 649–778.
- Berke, S. K. 2012. Biogeographic variability in ecosystem engineering: patterns in the abundance and behavior of the tube-building polychaete *Diopatra cuprea*. *Marine Ecology Progress Series*, 447, 1–13.
- Berke, S. K., Jablonski, D., Krug, A. Z. & Valentine, J. W. 2014. Origination and immigration drive latitudinal gradients in marine functional diversity. *PLoS One*, 9, e101494.
- Bihn, J. H., Gebauer, G. & Brandl, R. 2010. Loss of functional diversity of ant assemblages in secondary tropical forests. *Ecology*, 91, 782–792.
- Birchough, S. N. R., Parker, R. E., McManus, E. & Barry, J. 2012. Combining bioturbation and redox metrics: Potential tools for assessing seabed function. *Ecological Indicators*, 12(1), 8–16.
- Blondel, J. 2003. Guilds or functional groups: does it matter? *Oikos*, 100(2), 223–231.
- Bolam, S. G. & Eggleton, J. D. 2014. Macrofaunal production and biological traits: Spatial relationships along the UK continental shelf. *Journal of Sea Research*, 88, 47–58.
- Bolnick, D.I., Amarasekare, P., Araújo, M.S., Bürger, R., Levine, J.M., Novak, M., Rudolf, V.H.W., Schreiber, S.J., Urban, M.C. & Vasseur, D. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution*, 26(4), 183–192.
- Bonada, N., Prat, N., Resh, V. H. & Statzner, B. 2006. Development in aquatic insect biomonitoring: A Comparative Analysis of Recent Approaches. *Annual Review of Entomology*, 51, 495–523.
- Borja, A., Franco, J. & Pérez, V. 2000. A marine biotic index to establish the ecological quality of soft-bottom benthos within European estuarine and coastal environments. *Marine Pollution Bulletin*, 40(12), 1100–1114.
- Botta-Dukát, Z. 2005. Rao's quadratic entropy as a measure of functional diversity based multiple traits. *Journal of Vegetation Science*, 16(5), 533–540.
- Brandl, S. J., Emslie, M. J., Ceccarelli, D. M. & Richards, Z. T. 2016. Habitat degradation increases functional originality in highly diverse coral reef fish assemblages. *Ecosphere*, 7(11), e01557.
- Bremner, J., Rogers, S. & Frid, C. 2003. Assessing functional diversity in marine benthic ecosystems: a comparison of approaches. *Marine Ecology Progress Series*, 254, 11–25.
- Bremner, J., Rogers, S. I. & Frid, C. L. J. 2006a. Methods for describing ecological functioning of marine benthic assemblages using biological traits analysis (BTA). *Ecological Indicators*, 6(3), 609–622.
- Bremner, J., Rogers, S. I. & Frid, C. L. J. 2006b. Matching biological traits to environmental conditions in marine benthic ecosystems. *Journal of Marine Systems*, 60(3–4), 302–316.
- Buisson, L., Grenouillet, G., Villéger, S., Canal, J. & Laffaille, P. 2013. Toward a loss of functional diversity in stream fish assemblages under climate change. *Global Change Biology*, 19(2), 387–400.
- Burton, J. I., Perakis, S. S., McKenzie, S. C., Lawrence, C. E. & Puettmann, K. J. 2017. Intraspecific variability and reaction norms of forest understorey plant species traits. *Functional Ecology*, 31(10), 1881–1893.
- Cesar, C. P. & Frid, C. L. J. 2009. Effects of experimental small-scale cockle (*Cerastoderma edule* L.) fishing on ecosystem function. *Marine Ecology*, 30(s1), 123–137.
- Champely, S. & Chessel, D. 2002. Measuring biological diversity using Euclidean metrics. *Environmental and Ecological Statistics*, 9, 167–177.
- Chevène, F., Dolédec, S. & Chessel, D. 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31(3), 295–309.
- Christy, J. H. 1982. Burrow structure and use in the sand fiddler crab, *Uca pugilator* (Bosc). *Animal Behaviour*, 30(3), 687–694.
- Cianciaruso, M. V., Batalha, M. A., Gaston, K. J. & Petchey, O.L. 2009. Including intraspecific variability in functional diversity. *Ecology*, 90(1), 81–89.
- Costello, M. J., Claus, S., Dekeyser, S., Vandepitte, L., Tuama, E. O., Lear, D. & Tyler-Walters, H. 2015. Biological and ecological traits of marine species. *PeerJ*, 3, e1201, 167–177.
- Darr, A., Gogina, M. & Zettler, M. L. 2014. Functional changes in benthic communities along a salinity gradient— a western Baltic case study. *Journal of Sea Research*, 85, 315–324.

- De Boer, W. F., Daniels, P. & Essink, K. 2001. *Towards ecological quality objectives for North Sea benthic communities*. Haren, National Institute for Coastal and Marine Management (RIKZ).
- Díaz, S., Andy, P., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P. & Pearse, W. D. 2013. Functional traits, the phylogeny of function, and ecosystem service vulnerability. *Ecology and Evolution*, 3(9), 2958–2975.
- Dimitriadis C. & Koutsoubas, D. 2011. Functional diversity and species turnover of benthic invertebrates along a local environmental gradient induced by an aquaculture unit: the contribution of species dispersal ability and rarity. *Hydrobiologia*, 670, 307–315.
- Dolédéc, S., Bernhard, S. & Bournard, M. 1999. Species traits for future biomonitoring across ecoregions: patterns along a human-impacted river. *Freshwater Biology*, 42, 737–758.
- Dolédéc, S. & Chessel, D., 1994. Co-inertia analysis: an alternative method for studying species–environment relationships. *Freshwater Biology*, 31, 277–294.
- Dolédéc, S., Chessel, D., Ter Braak, C. J. F., Champely, S., 1996. Matching species traits to environmental variables: A new three-table ordination method. *Environmental and Ecological Statistics*, 3, 143–166.
- Dray, S., Choler, P., Dolédéc, S., Peres-Neto, P. R., Thuiller, W., Pavoine, S. & ter Braak, C. J. 2014. Combining the fourth-corner and the RLQ methods for assessing trait responses to environmental variation. *Ecology*, 95, 14–21.
- Eklöf, J., Austin, A., Bergström, U., Donadi, S., Eriksson, B.D.H.K., Hansen, J. & Sundblad, G. 2017. Size matters: relationships between body size and body mass of common coastal, aquatic invertebrates in the Baltic Sea. *PeerJ*, 5, e2906.
- Fauchald, K. & Jumars, P. A. 1979. The diet of worms: A study of polychaete feeding guilds. *Oceanography and Marine Biology*, 17, 193–284.
- Faulwetter, S., Markantonatou, V., Pavlouidi, C., Papageorgiou, N., Keklikoglou, K., Chatziniolaou, E., Pafilis, E., Chatzigeorgiou, G., Vasileiadou, K., Dailianis, T., Fanini, L., Koulouri, P. & Arvanitidis, C. 2014. Polytraits: A database on biological traits of marine polychaetes. *Biodiversity Data Journal*, 2, e1024.
- Fonseca, C. R. & Ganade, G., 2001. Species functional redundancy, random extinctions and the stability of ecosystems. *Journal of Ecology*, 89(1), 118–125.
- Froese, R. & Pauly, D. (Eds.). 2017. *FishBase*. World Wide Web electronic publication. www.fishbase.org. Version (10/2017).
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630–2637.
- Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J., Eriksson, O., Fortunel, C., Freitas, H., Golodets, C., Grigulis, K., Jouany, C., Kazakou, E., Kigel, J., Kleyer, M., Lehsten, V., Lepš, J., Meier, T., Pakeman, R., Papadimitriou, M., Papanastasis, V.P., Quedsted, H., Quétiér, F., Robson, M., Roumet, C., Rusch, G., Skarpe, C., Sternberg, M., Theau, J.P., Thébault, A., Vile, D. & Zarovali, M. P. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: A standardized methodology and lessons from an application to 11 European sites. *Annals of Botany*, 99(5), 967–985.
- Gayraud, S., Statzner, B., Bady, P., Haybachp, A., Schöll, F., Usseglio-Polatera, P. & Bacchi, M. 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biology*, 48, 2045–2064.
- Gerisch, M., Agostinelli, V., Henle, K. & Dziock, F. 2012. More species, but all do the same: contrasting effects of flood disturbance on ground beetle functional and species diversity. *Oikos*, 121, 508–515.
- Gesteira, J. L. G. & Dauvin, J.-C., 2000. Amphipods are good bioindicators of the impact of oil spills on soft-bottom macrobenthic communities. *Marine Pollution Bulletin*, 40, 1017–1027.
- Gimenez, B. C. G. & Higuti, J. 2017. Land use effects on the functional structure of aquatic insect communities in Neotropical streams. *Inland Waters*, 3, 305–313.
- Gimenez, B. C. G. & Lana, P. 2020. Functional redundancy in polychaete assemblages from a tropical Large Marine Ecosystem (LME). *Zoosymposia*, 19, 72–90.
- Gogina, M., Morys, C., Forster, S., Gräwe, U., Friedland, R. & Zettler, M. L. 2017. Towards benthic ecosystem functioning maps: Quantifying bioturbation potential in the German part of the Baltic Sea. *Ecological Indicators*, 73, 574–588.
- Gravel, D., Albouy, C. & Thuiller, W. 2016. The meaning of functional trait composition of food webs for ecosystem functioning. *Philosophical Transactions of The Royal Society B*, 371, 20150268.
- Griffiths, J.R., Kadin, M., Nascimento, F.J.A., Tamelander, T., Törnroos, A., Bonaglia, S., Bonsdorff, E., Brüchert, V., Gårdmark, A., Järnström, M., Kotta, J., Lindegren, M., Nordström, M. C., Norkko, A., Olsson, J., Weigel, B., Žydelis, R., Blenckner, T., Niiranen, S. & Winder, M. 2017. The importance of benthic-pelagic coupling for marine ecosystem functioning in a changing world. *Global Change Biology*, 23(6), 2179–2196.
- Gusmao-Junior, J. B. L. & Lana, P.C., 2015. Spatial variability of the infauna adjacent to intertidal rocky shores in a subtropical estuary. *Hydrobiologia*, 743, 53–64.
- Gusmao, J. B., Brauko, K. M., Eriksson, B. K. & Lana, P. C. 2016. Functional diversity of macrobenthic assemblages decreases in response to sewage discharges. *Ecological Indicators*, 66, 65–75.
- Gusmao, J. B., Thielgtes, D. W., Dekker, R., Govers, L. L., Meijer, K. J. & Eriksson, B. K. 2022. Comparing taxonomic and functional trait diversity in marine macrozoobenthos along sediment texture gradients. *Ecological Indicators*, 145, 109718.
- Hortal, J., de Bello, F., Diniz-Filho, J. A. F., Lewinsohn, T. M., Lobo, J. M. & Ladle, R. J. 2015. Seven shortfalls that beset large-scale knowledge of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 46, 523–549.
- Juan, S., Bremner, J., Hewitt, J., Törnroos, A., Mangano, M.C., Thrush, S. & Hinz, H. 2022. Biological traits

- approaches in benthic marine ecology: Dead ends and new paths. *Ecology and Evolution*, 12(6), e9001.
- Jung, V., Violle, C., Mondy, C., Hoffmann, L. & Müller, S. 2010. Intraspecific variability and trait-based community assembly. *Journal of Ecology*, 98(5), 1134–1140.
- Kichenin, E., Wardle, D. A., Peltzer, D. A., Morse, C. W. & Freschet, G. T. 2013. Contrasting effects of plant inter-and intraspecific variation on community-level trait measures along an environmental gradient. *Functional Ecology*, 27(5), 1254–1261.
- Kindeberg, T., Severinsson, J., Carlsson, P., 2022. Eelgrass meadows harbor more macrofaunal species but bare sediments can be as functionally diverse. *Journal of Experimental Marine Biology and Ecology*, 554, 151777.
- Kristensen, E., Penha-Lopes, G., Delefosse, M., Valdemarsen, T., Quintana, C. O. & Banta, G. T. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series*, 446, 285–302.
- Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology*, 91, 299–305.
- Laureto, L. M. O., Cianciaruso, M. V. & Samia, D. S. M. 2015. Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, 13(2), 112–116.
- Lavorel, S., Grigulis, K., McIntyre, S., Williams, N. S. G., Garden, D., Dorrrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. 2008. Assessing functional diversity in the field – methodology matters! *Functional Ecology*, 22(1), 134–147.
- Layman, C. A., Winemiller, K. O., Arrington, A. & Jepsen, D. B. 2005. Body size and trophic position in a diverse tropical food web. *Ecology*, 86, 2530–2535.
- Lefcheck, J. S., Bastazini, V. A. G. & Griffin, J. N. 2015. Choosing and using multiple traits in functional diversity research. *Environmental Conservation*, 42, 104–107.
- Legendre, P., Galzin, R. & Harmelin-Vivien, M. L. 1997. Relating behavior to habitat: solutions to the fourth-corner problem. *Ecology*, 78, 547–562.
- Leps, J., Bello, F., Lavorel, S. & Berman, S. 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, 78, 481–501.
- Linse, K., Barnes, D. K. A. & Enderlein, P. 2006. Body size and growth of benthic invertebrates along an Antarctic latitudinal gradient. *Deep Sea Research Part II, Topical Studies in Oceanography*, 53(8-10), 921–931.
- Lohrer, A. M., Thrush, S. F. & Gibbs M. M. 2004. Bioturbators enhance ecosystem function through complex biogeochemical interactions. *Nature*, 431, 1092–1095.
- Loreau, M. 2004. Does functional redundancy exist? *Oikos*, 104, 606–611.
- Luck, G.W., Carter, A. & Smallbone, L. 2013. Changes in bird functional diversity across multiple land uses: Interpretations of functional redundancy depend on functional group identity. *PLoS One*, 8, e63671.
- Magurran, A. E., 2011. *Medindo a Diversidade Biológica*. Curitiba, Editora UFPR.
- Maire, E., Grenouillet, G., Brosse, S. & Villéger, S. 2015. How many dimensions are needed to accurately assess functional diversity? A pragmatic approach for assessing the quality of functional spaces. *Global Ecology and Biogeography*, 24(6), 728–740.
- Marine Ecological Surveys Ltd. 2008. *Marine Macrofauna Genus Trait Handbook*. Monmouth Place, Marine Ecological Surveys Ltd.
- MarLIN, 2006. *BIOTIC - Biological Traits Information Catalogue*. Marine Life Information Network, Marine Biological Association of the United Kingdom. Available from: [www.marlin.ac.uk/biotic](http://www.marlin.ac.uk/biotic). Access date: 2024 oct. 7.
- Mason, N.W.H., Bello, F., Mouillot, D., Pavoine, S. & Dray, S. 2013. A guide for using functional diversity indices to reveal changes in assembly processes along ecological gradients. *Journal of Vegetation Science*, 24(5), 794–806.
- Mason, N. W. H., MacGillivray, K., Steel, J. B. & Wilson, J. B. 2003. An index of functional diversity. *Journal of Vegetation Science*, 14, 571–578.
- Mason, N. W. H., Mouillot, D., Lee, W. G. & Wilson, J. B. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos*, 111, 112–118.
- Mayfield, M. M., Bonser, S. P., Morgan, J. W., Aubin, I., McNamara, S. & Vesk, P. A. 2010. What does species richness tell us about functional trait diversity? Predictions and evidence for responses of species and functional trait diversity to land-use change. *Global Ecology and Biogeography*, 19(4), 423–431.
- Mermillod-Blondin, F. 2011. The functional significance of bioturbation and biodeposition on biogeochemical processes at the water–sediment interface in freshwater and marine ecosystems. *Journal of the North American Benthological Society*, 30, 770–778.
- Mermillod-Blondin, F. & Rosenberg, R. 2006. Ecosystem engineering: the impact of bioturbation on biogeochemical processes in marine and freshwater benthic habitats. *Aquatic Sciences*, 68, 434–442.
- Michaud, E., Desrosiers, G., Mermillod-Blondin, F., Sundby, B. & Stora, G. 2005. The functional group approach to bioturbation: The effects of biodiffusers and gallery-diffusers of the *Macoma balthica* community on sediment oxygen uptake. *Journal of Experimental Marine Biology and Ecology*, 326(1), 77–88.
- Micheli, F., Mumby, P. J., Brumbaugh, D.R., Broad, K., Dahlgren, C. P., Harborne, A. R., Holmes, K. E., Kappel, C. V., Litvin, S. Y. & Sanchirico, J. N. 2014. High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. *Biological Conservation*, 171, 186–194.
- Mlambo, M. C. 2014. Not all traits are 'functional': insights from taxonomy and biodiversity-ecosystem functioning research. *Biodiversity and Conservation*, 23, 781–790.
- Mori, A.S., Isbell, F., Fujii, S., Makoto, K., Matsuoka, S. & Osono, T. 2016. Low multifunctional redundancy of soil fungal diversity at multiple scales. *Ecology Letters*, 19(3), 249–259.
- Mouchet, M., Guilhaumon, F., Villéger, S., Mason, N. W. H., Tomasini, J.-A. & Mouillot, D. 2008. Towards a consensus for calculating dendrogram-based functional diversity indices. *Oikos*, 117(5), 794–800.

- Mouchet, M. A., Villéger, S., Mason, N.W.H., Moullot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Functional Ecology*, 24, 867–876.
- Moullot, D., Graham, N. A. J., Villéger, S., Mason, N. W. & Bellwood, D. R. 2013. A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, 28(3), 167–177.
- Moullot, D., Mason, W. H. N., Dumay, O. & Wilson, J. B. 2005. Functional regularity: a neglected aspect of functional diversity. *Oecologia*, 142, 353–359.
- Moullot, D., Villéger, S., Parravicini, V., Kulbicki, M., Arias-Gonzalez, J. E., Bender, M., Chabanet, P., Floeter, S. R., Friedlander, A., Vigliola, L. & Bellwood, D. R. 2014. Functional over-redundancy and high functional vulnerability in global fish faunas on tropical reefs. *Proceedings of the National Academy of Sciences*, 111(38), 13757–13762.
- Naeem, S. & Wright, J. P. 2003. Disentangling biodiversity effects on ecosystem functioning: deriving solutions to a seemingly insurmountable problem. *Ecology Letters*, 6(6), 567–579.
- Nasi, F., Vesal, S. E., Relitti, F., Bazzaro, M., Teixidó, N., Auriemma, R. & Cibic, T. 2023. Taxonomic and functional macrofaunal diversity along a gradient of sewage contamination: A three-year study. *Environmental Pollution*, 323, 121022.
- Natálio, L. F., Pardo, J. C. F., Machado, G. B. O., Fortuna, M. D., Gallo, D. G. & Costa, T. M. 2017. Potential effect of fiddler crabs on organic matter distribution: A combined laboratory and field experimental approach. *Estuarine, Coastal and Shelf Science*, 184, 158–165.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A. & Bonsdorff, E. 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Marine Ecology Progress Series*, 332, 11–23.
- Otegui, M. B. P., Brauko, K. M. & Pagliosa, P. R. 2016. Matching ecological functioning with polychaete morphology: consistency patterns along sedimentary habitats. *Journal of Sea Research*, 114, 13–21.
- Paganelli, D., Marchini, A. & Occhipinti-Ambrogí, A. 2012. Functional structure of marine benthic assemblages using Biological Traits Analysis (BTA): A study along the Emilia-Romagna coastline (Italy, North-West Adriatic Sea). *Estuarine, Coastal and Shelf Science*, 96, 245–256.
- Pavoine, S. & Bonsall, M. B. 2011. Measuring biodiversity to explain community assembly: a unified approach. *Biological Reviews*, 86(4), 792–812.
- Pearson, T. H. & Rosenberg, R. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology*, 16, 229–311.
- Petchey, O. L. & Gaston, K. J., 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters*, 5(3), 402–411.
- Petchey, O. L. & Gaston, K. J. 2006. Functional diversity: back to basics and looking forward. *Ecology Letters*, 9(6), 741–758.
- Petsch, D. K. 2016. Causes and consequences of biotic homogenization in freshwater ecosystems. *International Review of Hydrobiology*, 101(3-4), 113–122.
- Piccini, I., Nervo, B., Forshage, M., Celi, L., Palestini, C., Rolando, A. & Roslin, T. 2018. Dung beetles as drivers of ecosystem multifunctionality: are response and effect traits interwoven? *Science of The Total Environment*, 616, 1440–1448.
- Piló, D., Ben-Hamadou, R., Pereira, F., Carriço, A., Pereira, P., Corzo, A., Gaspar, M. B. & Carvalho, S. 2016. How functional traits of estuarine macrobenthic assemblages respond to metal contamination? *Ecological Indicators*, 71, 645–659.
- Pla, L., Casanoves, F. & Di-Rienzo, J. 2012. *Quantifying Functional Biodiversity*. Springer, Berlin.
- Queirós, A.M., Birchenough, S.N.R., Bremner, J., Godbold, J.A., Parker, R.E., Romero-Ramirez, A., Reiss, H., Solan, M. Somerfield, P.J., Van Colen, C., Van Hoey, G. & Widdicombe, S. 2013. A bioturbation classification of European marine infaunal invertebrates. *Ecology and Evolution*, 3(11), 3958–3985.
- Rao, R. C. 1982. Diversity and dissimilarity coefficients: A unified approach. *Theoretical Population Biology*, 43(1), 24–43.
- Reise, K. 2002. Sediment mediated species interactions in coastal waters. *Journal of Sea Research*, 48(2), 127–141.
- Renz, J. R., Powilleit, M., Gogina, M., Zettler, M. L., Morys, C. & Forster, S. 2018. Community bioirrigation potential (BIPc), an index to quantify the potential for solute exchange at the sediment-water interface. *Marine Environmental Research*, 141, 214–224.
- Ricotta, C. & Moretti, M. 2011. CWM and Rao's quadratic diversity: a unified framework for functional ecology. *Oecologia*, 167, 181–188.
- Ricotta, C. & Szeidl, L. 2009. Diversity partitioning of Rao's quadratic entropy. *Theoretical Population Biology*, 76(4), 299–302.
- Rigolet, C., Dubois, S. F. & Thiébaud, E. 2014. Benthic control freaks: Effects of the tubicolous amphipod *Haploops nirae* on the specific diversity and functional structure of benthic communities. *Journal of Sea Research*, 85, 413–427.
- Salas, F., Marcos, C., Neto, J. M., Patrício, J., Pérez-Ruzafa, A. & Marques, J. C. 2006. User-friendly guide for using benthic ecological indicators in coastal and marine quality assessment. *Ocean & Coastal Management*, 49 (5-6), 308–331.
- Sarker, S. K., Reeve, R. & Matthiopoulos, J. 2021. Solving the fourth-corner problem: forecasting ecosystem primary production from spatial multispecies trait-based models. *Ecological Monograph*, 91(3), e01454.
- Schleuter, D., Daufresne, M., Massol, F. & Argillier, C. 2010. A user's guide to functional diversity indices. *Ecological Monographs*, 80(3), 469–484.
- Schmera, D., Erős, T. & Podani, J. 2009. A measure for assessing functional diversity in ecological communities. *Aquatic Ecology*, 43, 157–167.
- Schmera, D., Heino, J., Podani, J., Erős, T. & Dolédec, S. 2017. Functional diversity: a review methodology and

- current knowledge in freshwater macroinvertebrate research. *Hydrobiologia*, 787, 27–44.
- Schmidt-Kloiber, A. & Hering, D. 2015. www.freshwaterecology.info – An online tool that unifies, standardises and codifies more than 20,000 European freshwater organisms and their ecological preferences. *Ecological Indicators*, 53, 271–282.
- Schratzberger, M., Warr, K. & Rogers, S. I. 2007. Functional diversity of nematode communities in the southwestern North Sea. *Marine Environmental Research*, 63(4), 368–389.
- Solan, M., Cardinale, B. J., Downing, A. L., Engelhardt, K. A. M., Ruesink, J. L. & Srivastava, D. S. 2004. Extinction and ecosystem function in the marine benthos. *Science*, 306(5699), 1177–1180.
- Statzner, B. & Bêche, L. A. 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshwater Biology*, 55(s1), 80–119.
- Statzner, B., Bis, B., Dolédec, S. & Usseglio-Polatera, U. 2001. Perspectives for biomonitoring at large spatial scales: a unified measure for the functional composition of invertebrate communities in European running waters. *Basic and Applied Ecology*, 2(1), 73–85.
- Statzner, B., Resh, V. H. & Roux, L. A. 1994. The synthesis of long term ecological research in the context of concurrently developed ecological theory: design of research strategy for the Upper Rhone River and its floodplain. *Freshwater Biology*, 31, 253–263.
- Suding, K., Lavorel, S., Chapin, F., Cornelissen, J., Díaz, S., Garnier, E., Goldberg, D., Hooper, D., Jackson, S. T. & Navas, M. 2008. Scaling environmental change through the community-level: a trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5), 1125–1140.
- Swenson, N. G. 2014. *Functional and Phylogenetic Ecology in R*. New York, Springer.
- Thrush, S. F. & Dayton, P. K. 2002. Disturbance to marine benthic habitats by trawling and dredging: Implications for marine biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 33, 449–473.
- Tilman, D. 2001. Functional diversity. In: Levin, S.A. (Ed.). *Encyclopedia of Biodiversity* (pp. 109–120). San Diego: Academic Press.
- van der Linden, P., Marchini, A., Dolbeth, M., Patrício, J., Veríssimo, H. & Marques, J. C., 2016. The performance of trait-based indices in an estuarine environment. *Ecological Indicators*, 61, 378–389.
- van der Linden, P., Marchini, A., Smith, C. J., Dolbeth, M., Simone, L. R. L., Marques, J. C., Molozzi, J., Medeiros, C. R. & Patrício, J., 2017. Functional changes in polychaete and mollusc communities in two tropical estuaries. *Estuarine, Coastal and Shelf Science*, 187, 62–73.
- van der Linden, P., Patrício, J., Marchini, A., Cid, N., Neto, J. M. & Marques, J. C., 2012. A biological trait approach to assess the functional composition of subtidal benthic communities in an estuarine ecosystem. *Ecological Indicators*, 20, 121–133.
- Vandewalle, M., de Bello, F., Berg, M. P., Bolger, T., Dolédec, S., Dubs, F., Feld, C. K., Harrington, R., Harrison, P. A., Lavorel, S., da Silva, P. M., Moretti, M., Niemelä, J., Santos, P., Sattler, T., Sousa, J. P., Sykes, M. T., Vanbergen, A. J. & Woodcock, B. A. 2010. Functional traits as indicators of biodiversity response to land use changes across ecosystems and organisms. *Biodiversity and Conservation*, 19, 2921–2947.
- van Son, T.J., Oug, E., Halvorsen, R. & Melsom, F. 2013. Gradients in traits composition and their relation to environmental complex-gradients and structuring processes: a study of marine sediment species communities. *The Open Marine Biology Journal*, 7, 14–27.
- Vaughn, C. C. 2010. Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. *BioScience*, 60(1), 25–35.
- Verberk, W. C. E. P., van Noordwijk, C. G. E. & Hildrew, A. G. 2013. Delivering on a promise: integrating species traits to transform descriptive community ecology into a predictive science. *Freshwater Science*, 32(2), 531–547.
- Villéger, S., Grenouillet, G. & Brosse, S. 2013. Decomposing functional  $\beta$ -diversity reveals that low functional  $\beta$ -diversity is driven by low functional turnover in European fish assemblages. *Global Ecology and Biogeography*, 22(6), 671–681.
- Villéger, S., Mason, N. W. H. & Mouillot, D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology*, 89, 2290–2301.
- Villéger, S., Miranda, J. R., Hernandez, D. F. & Mouillot, D. 2012. Low functional  $\beta$ -diversity despite high taxonomic  $\beta$ -diversity among tropical estuarine fish communities. *PLoS One*, 7, e40679.
- Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. & Messier, J. 2012. The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, 27(4), 244–252.
- Violle, C., Navas, M-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. 2007. Let the concept of trait be functional! *Oikos*, 116, 882–892.
- Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N. J. B., Cadotte, M. W., Livingstone, S. W. & Mouillot, D. 2017. Functional rarity: The ecology of outliers. *Trends in Ecology & Evolution*, 32(5), 356–367.
- Wang, H., Wang, R., Harrison, S. P. & Prentice, I. C. 2022. Leaf morphological traits as adaptations to multiple climate gradients. *Journal of Ecology*, 110(6), 1344–1355.
- Weisberg, S. B., Ranasinghe, J. A., Dauer, D. M., Schaffner, L. C., Díaz, R. J. & Frithsen, J. B. 1997. An estuarine benthic index of biotic integrity (B-IBI) for the Chesapeake Bay. *Estuaries and Coasts*, 20, 149–158.
- Widdows, J. & Brinsley, M. 2002. Impact of biotic and abiotic processes on sediment dynamics and the consequences to the structure and functioning of the intertidal zone. *Journal of Sea Research*, 48(2), 143–156.
- Wilson, J. B. 1999. Guilds, functional types and ecological groups. *Oikos*, 86, 507–522.
- Wollenweider, R. A., Giovanardi, F., Montanari, G. & Rinaldi, A. 1998. Characterisation of the trophic conditions of marine coastal waters with special reference to the NW Adriatic Sea: proposal for a trophic scale, turbidity and generalised water quality index. *Environmetrics*, 9(3), 329–357.
- Wong, B. M. B. & Candolin, U. 2015. Behavioral responses to changing environments. *Behavioral Ecology*, 26(3), 665–673.

Wouters, J. M., Gusmao, J. B., Mattos, G. & Lana, P. 2018. Polychaete functional diversity in shallow habitats: Shelter from the storm. *Journal of Sea Research*, 135, 18–30.

Zhu, L., Fu, B., Zju, H., Wang, C., Jiao, L. & Zhou, J. 2017a. Trait choice profoundly affected the ecological

conclusions drawn from functional diversity measures. *Nature*, 7, 3643.

Zhu, L., Lefcheck, J. S. & Fu, B. 2017b. Is the use of unconstrained ordination appropriate for understanding plant ecological strategies and ecosystem functioning? *PeerJ Preprints*, 5, e2631v2.