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Functional redundancy in polychaete assemblages from a tropical Large Marine Ecosystem (LME)

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Abstract

Functional redundancy assumes a critical relevance nowadays due to the serious threats that affect marine life worldwide. We assessed and compared levels of functional redundancy in polychaete assemblages from the continental shelf and from estuarine environments along the South Brazil Shelf Large Marine Ecosystem (SBSLME). To quantify functional redundancy, we used functional originality (FOri) and functional uniqueness (FUni). We found 57 and 47 polychaete taxa distributed in 48 and 41 functional entities (i.e., a unique combination of trait values) in continental shelf and estuarine environments, respectively. Results suggest a low level of functional redundancy in both environments. However, FOri was higher in the estuarine environment, whereas FUni was higher in the continental shelf. As expected, estuarine polychaetes have fewer unique combinations of trait values, but these combinations are more original and adequate to the varying conditions imposed by estuarine environmental drivers.

Key words: benthic community, functional diversity, functional entity, continental shelf, estuarine environment, South Brazil Shelf Large Marine Ecosystem

Introduction

Polychaetes, a diverse group of marine worms, usually dominate the macrobenthic communities of coastal areas (Rouse & Pleijel 2001; Musco 2012; Dorgham *et al.* 2014). These annelids display a high functional trait plasticity, and putatively a high functional diversity (Martin & Bastida 2006; Otegui *et al.* 2016; van der Linden *et al.* 2017) with many supported functions or roles in benthic ecosystems. Polychaetes actively participate in relevant marine ecological processes, such as bioturbation, which contributes to aerating and remobilizig the sediment, nutrient cycling, secondary production, and energy flow (Faulwetter *et al.* 2014; Dolbeth *et al.* 2015; van der Linden *et al.* 2017; Wouters *et al.* 2018). For these reasons, polychaete assemblages have been commonly used as surrogates or proxies to understand the biodiversity of marine benthic communities as a whole.

Even a large amount of functional diversity can be vulnerable and lead to local extinction if, for instance, each function, expressed by a unique combination of traits, is supported by only a few or a single species. Conversely, when each function can be supported by many species, communities or assemblages display functional redundancy (Fonseca & Ganade 2001; Luck *et al.* 2013; Ricotta *et al.* 2016). The functional diversity of polychaete assemblages is well-documented (Otegui *et al.* 2016; van der Linden *et al.* 2017; Wouters *et al.* 2018), but little is known about their levels of functional redundancy. Functional redundancy assumes a critical relevance nowadays, considering that benthic communities are under serious threats worldwide, due to the growing degradation of the seafloor resulting from habitat loss, hydrodynamic alteration, pollution, and climate change (Danovaro *et al.* 2008; Defeo *et al.* 2009; Bernardino *et al.* 2016). Functional redundancy is anticipated to be higher in the tropics where many species are likely to share the same traits and play the same role. However, over-redundancy, i.e., the disproportional packing of species richness in some functional groups to the detriment of others, challenges this view. High species richness may or may not guarantee a concomitant

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high functional redundancy depending on the evaluated ecosystem or type of communities (Mouillot *et al.* 2014). Much remains to be discovered about the real level of functional redundancy especially in marine environments within tropical latitudes, where considerable large-scale changes have occurred without rigorous documentation (Jackson 2001; Feng *et al.* 2018).

Due to the increasing number of ecological studies addressing functional redundancy in the last decades, an array of measures has been proposed to quantify this property (Ricotta *et al.* 2016). Functional originality (FOri) and functional uniqueness (FUni) are two relevant facets of functional redundancy that have been overlooked, despite the valuable information they can provide. These indices characterize the position of a species in the functional space compared to other species of the pool (Buisson *et al.* 2013; Mouillot *et al.* 2013). In this paper we report levels of functional redundancy in polychaete assemblages of the continental shelf and estuarine environments in the South Brazil Shelf Large Marine Ecosystem (SBSLME). We have used a detailed dataset of taxa occurrences and functional traits to examine (1) the distribution of species across different "functional entities", i.e., a unique combination of trait values *sensu* Mouillot *et al.* (2014) in continental shelf and estuarine environments; and (2) the functional redundancy patterns (expressed by FOri and FUni) in the assemblages of these two environments. Continental shelves are stable environments that generally present more diverse communities than estuarine ones, where only extremely adapted species are able to cope with higher environmental variability. Thus, we hypothesize that functional redundancy will be lower in continental shelf than in estuarine environments as the environmental stressors operating in these latter systems can lead to high convergent evolution (i.e., many different species sharing similar functional traits). Functional originality and functional uniqueness, in turn, will be inversely related to functional redundancy and, therefore, we hypothesize that their values should be conversely lower in estuarine than in continental shelf environments.

Materials and Methods

Construction of taxonomic composition and functional traits matrices

We extracted occurrence data from NONATObase (Pagliosa *et al.* 2014), a database for polychaetes from the southwestern Atlantic Ocean. We considered all the soft-bottom records from continental shelf and estuarine environments of the South Brazil Shelf Large Marine Ecosystem (SBSLME). The SBSLME covers an area of about 565,500 km^2 and has a wide continental shelf, encompassing the Brazilian states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Ekau & Knoppers 2003). It represents the only coastal sector in Brazil with a subtropical to temperate climate (Mahiques *et al.* 2010). In total, presence/absence data from 1,234 sites from continental shelf and 347 sites from estuarine environments, ranging from ~22ºS to ~34ºS (i.e., the latitudinal extension of the SBSLME), were used to construct the matrices listing polychaete occurrences.

We used a functional categorization based on the morphological characteristics of polychaetes, modified from Otegui *et al.* (2016). This classification allows for a standardization of existing trait data into unique morphological characteristics, which eliminates the main subjectivities of the analytical process (Otegui *et al.* 2016). We selected a combination of nine categorical morphological traits composed by 27 attributes/categories (Table 1, Table S1). Information for polychaete families was obtained from Faulwetter *et al.* (2014), Jumars *et al.* (2015), and Otegui *et al.* (2016), as well as ad-hoc opinion of experts. The family level was previously recognized as capable of showing accurate and robust ecological patterns for polychaetes (Muniz & Pires-Vanin 2005; Aguado-Giménez *et al.* 2015). We followed a simple classification considering only the primary attribute for each characteristic (i.e., each family holds only one of the categories for the trait considered).

Measuring and analyzing functional redundancy

Following Mouillot *et al.* (2014), the total number of functional entities (FEs) was defined as unique combinations of the nine morphological traits. FEs were computed for each taxon (family) using the R function "species_to_FE" (described in the Supplement) and the number of FEs was reported for each environment. From this function, some metrics can be extracted for each assemblage, such as functional redundancy (i.e., the mean number of species per FE; Fonseca & Ganade 2001), functional over-redundancy (i.e., the percentage of species in excess for FEs containing more species than expected from functional redundancy; Mouillot *et al.* 2014), and functional vulnerability (i.e., the percentage of functional entities containing only one species; Bihn *et al.* 2010). The function also returns the presence data of the taxa in functional entities. In order to visualize similarities in FEs in continental shelf and estuarine environments, we used these data to perform a Principal Coordinates Analysis (PCoA; Laliberté & Legendre 2010) based on Jaccard's distance matrices (Jaccard 1912).

TABLE 1. Trait classification used in the trait matrix, according to Faulwetter *et al.* (2014), Jumars *et al.* (2015), Otegui *et al.* (2016), and ad hoc information from specialists.

Morphological trait	Category	ID	Description
Pharynx complexity	Absent	PH.ab	Pharynx is an auxiliary buccal organ used for feeding, which
	Ventral	PH.ve	also describes where the organism lives
	Axial muscular	PH.am	
	Axial non-muscular	PH.nm	
Jaws presence	Absent	JA.ab	Jaws are cuticular structures for resource capture, which also
	Present	JA.pr	assist in defense and show where the organism lives
Feeding structures	Absent	FS.ab	Peristomium appendices that assists in feeding by capturing
	A single structure (palp or tentacle)	FS.ss	resources, and also show where the organism lives
	A pair of structures	FS.ps	
	Multiple structures	FS.ms	
Sensory appendages	Absent	SA.ab	Head structures (e.g., antenna, sensorial palps, and cirrus)
	Only one structure	SA.os	used for defense and feeding
	Multiple structures	SA.ms	
Body appendages	Absent	BA.ab	Lateral organs, statocysts, dorsal organs, and parapodial cirri
	Present	BA.pr	used for defense and feeding
Chaetal (parapodia) pattern	All parapodial features absent	CP.ab	Parapodia are stout un-jointed lateral structures that bear the
	Parapodia uniramous simple	CP.us	chaetae, helping in locomotion and providing
	Parapodia uniramous with uncini or hook	CP.uh	support to the body
	Parapodia biramous simple	CP.bs	
	Parapodia biramous with uncini or hook	CP.bh	
Branchiae regionalization	Absent	BR.ab	Branchiae are located at the ends or along the body and are
	Regionalized	BR.re	responsible for gaseous exchanges that provide
	Non-regionalized	BR.nr	energy for locomotion and feeding
Body regionalization	Regionalized	BO.re	The body can be divided into thorax and abdomen or not be
	Non-regionalized	BO.nr	divided. Regionalized body provides better mobility
Body size	≤ 100 segments	SE.100	Body metameres can be little or very segmented. Body size
	≥ 101segments	SE.200	defines life strategies and the ecological niche

The many facets of functional diversity can be measured within a multidimensional space derived from the set of functional traits which were quantified (Villéger *et al.* 2008; Mouchet *et al.* 2010). Following Villéger *et al.* (2008) and Buisson *et al.* (2013), we constructed a multidimensional functional space using the 27 categories of functional traits. First, a functional distance matrix was computed for each pair of species using

Gower's distance (Gower 1966) that accepts any type of trait data, including categorical and ordinal measures. This distance matrix was then employed to carry out a PCoA (Laliberté & Legendre 2010), using the Cailliez correction to accommodate negative eigenvalues. The scores of the first three axes of the PCoA were kept to build the multidimensional functional space, which provides a clear picture of the relationships among species functional traits. All morphological traits were overlaid as vectors to discriminate the sources of the differences among species.

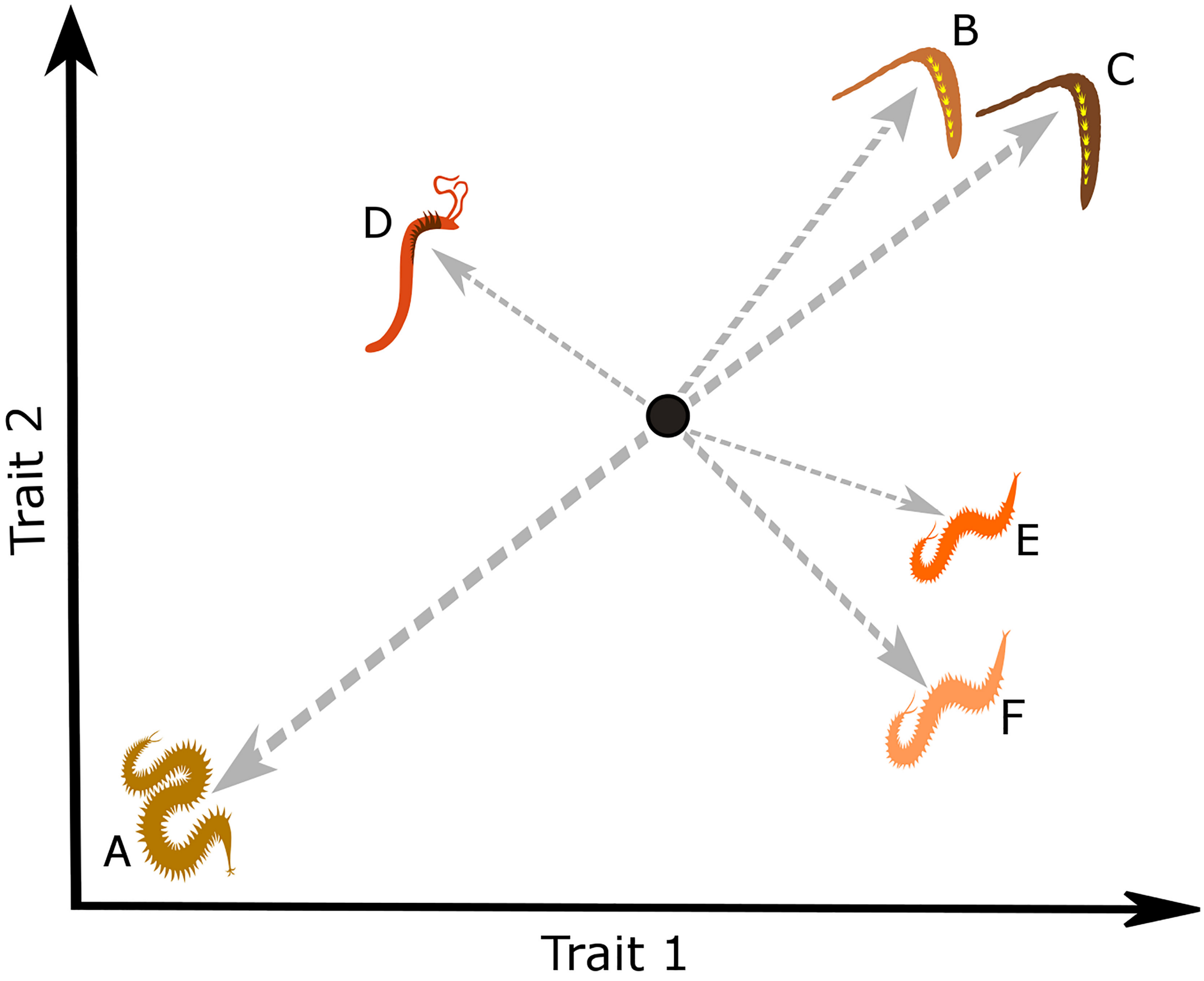

FIGURE 1. Possible patterns of functional originality and functional uniqueness in a polychaete assemblage. Six species (A-F) of polychaetes are plotted in a two-dimensional functional space. The black circle indicates the center of gravity of this hypothetical species pool. If the species is far from the center it is considered original, if close to the center it is not original. On the other hand, if the species is functionally different from the other species, it is unique. However, if close to another species in the functional space, it is functionally redundant. In the figure, species A is functionally original and unique; species B and C are original, but functionally redundant; species D is not original, but is unique; and species E and F are not original and are functionally redundant (adapted from Buisson *et al.* 2013).

To evaluate functional redundancy patterns in polychaetes assemblages of continental shelf and estuarine environments we used the functional originality (FOri) and functional uniqueness (FUni) indices (Buisson *et al.* 2013; Mouillot *et al.* 2013). Functional originality corresponds to the isolation degree of a species at the functional niche, in relation to the average rarity of its functional attributes (Pavoine *et al.* 2005; Mouillot *et al.* 2008, 2013). However, this measure does not consider that two species can share a unique combination of traits that is not present in the other species of the pool. Thus, functional uniqueness 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). In practice, high values of FOri means that the investigated species is functionally different from the theoretical average species (i.e., the center of the multidimensional functional space); and high values of FUni indicate that a species has a unique combination of traits compared to each species of the pool (i.e., low redundancy) (Fig. 1; Buisson *et al.* 2013; Maire *et al.* 2013). Using the species coordinates in the three-dimensional space defined by the PCoA and species occurrences matrix, the indices were estimated. FOri and FUni of a certain species were defined as the Euclidean distance to the average position of the species and the center of the functional space, and of its nearest neighbor in the species pool, respectively. Since FOri and FUni are not normally distributed, we used the Kruskal-Wallis nonparametric test (Kruskal & Wallis 1952) to test for significant differences in the values of the indices between continental shelf and estuarine environments.

All the calculations and analyzes were performed using the software R (R Core Team 2017). The procedures and required packages are detailed in the R script available as Supplement material.

Results

To classify the 57 and 47 polychaetes families of the regional pool of continental shelf and estuarine environments (Table S1), we identified respectively 48 and 41 functional entities based on unique combinations of nine categorical morphological traits (Fig. 2, Table S2). This high number of FEs in relation to the number of families – with at most three families per FE in both environments – indicate a low functional redundancy in continental shelf and estuarine environments. In addition, the observed values of FE metrics show the same low functional redundancy (Table 2).

TABLE 2. Metrics associated with the functional entities of the polychaetes assemblages of continental shelf and estuarine environments.

FE metrics	Continental shelf	Estuarine
Functional redundancy	1.19	1.15
Functional over-redundancy (%)	15	12
Functional vulnerability (%)	85	88

The PCoA ordinations showed differences in functional entities of continental shelf and estuarine environments (Fig. 3). The FEs of continental shelf are separated from each other, which means that the combinations of traits of these FEs are less similar than the combinations of FEs of the estuarine environments, where FEs are closer to each other.

Mean values of functional originality were higher than the mean values of functional uniqueness in both environments (Table 3). We observed differences in the functional redundancy patterns assessed by FOri and FUni indices between the two studied environments. Functional originality was higher in the polychaete assemblages of estuarine environments (Fig. 4a), whereas functional uniqueness showed higher values in the assemblages of continental shelf environments (Fig. 4b). The differences between continental shelf and estuarine environments were significant for both indices (Table 3).

TABLE 3. Results of Kruskal-Wallis comparing functional originality (FOri) and functional uniqueness (FUni) between continental shelf (n = 1,234) and estuarine (n = 347) environments. Mean values (SE) of each index are reported for each environment.

Index	Continental shelf	Estuarine	*KW-H*	df	P
FOri	0.624 (0.004)	0.67 (0.006)	71.85	1	< 0.001
FUni	0.35 (0.007)	0.286 (0.011)	25.07	1	< 0.001

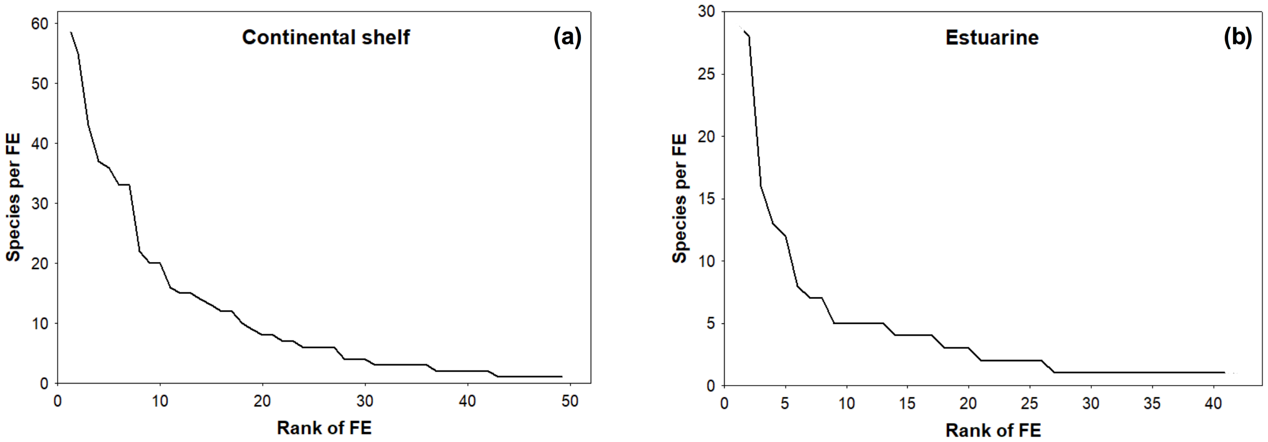

FIGURE 2. Distribution of polychaete species into functional entities displayed for continental shelf (a) and estuarine environments (b). For graphical convenience, we counted the total number of species per family, considering all the species of a family belonging to the same FE.

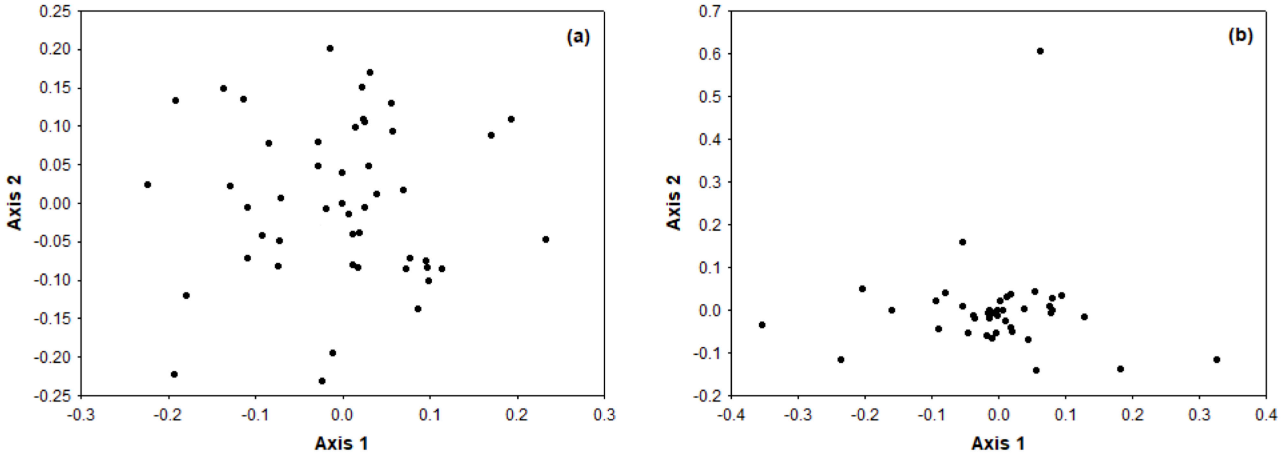

FIGURE 3. PCoA ordinations using Jaccard's distance matrices of 48 and 41 functional entities in continental shelf (a) and estuarine environments (b), respectively.

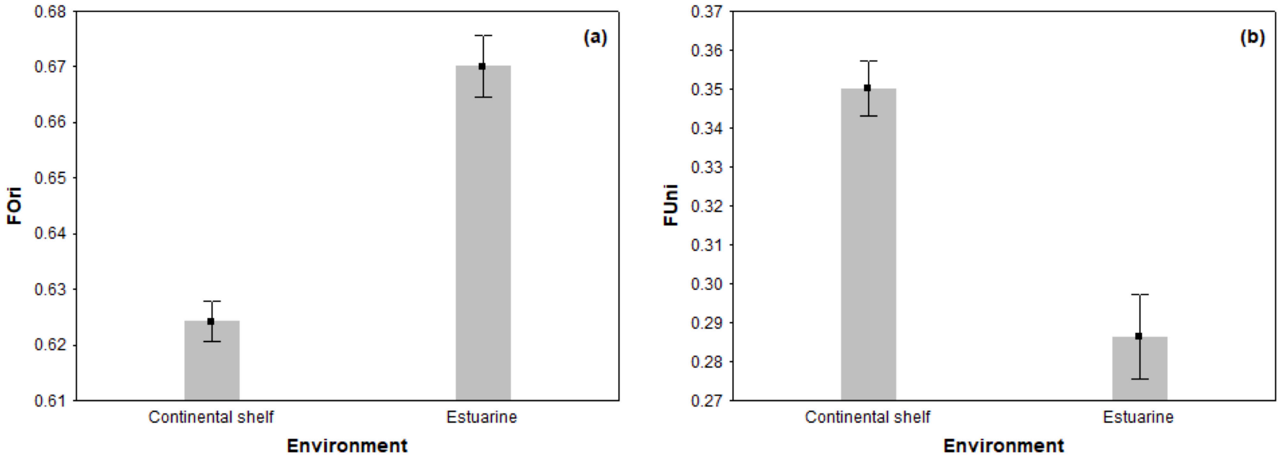

FIGURE 4. Mean values (SE) of (a) functional originality index (FOri) and (b) functional uniqueness index (FUni) in continental shelf and estuarine environments.

Discussion

In general, both estuarine and continental shelf polychaete assemblages along the South Brazil Shelf Large Marine Ecosystem were characterized by low functional redundancy. However, functional redundancy differed significantly between the two environments, as predicted. Higher redundancy (expressed by low functional uniqueness that is roughly the opposite of functional redundancy) was observed in estuarine environments. However, we also found higher values of functional originality in estuarine environments. These results only partially support our working hypothesis, since both indices were expected to exhibit lower values in estuarine environments.

The higher number of functional entities observed in continental shelf environments may result from sampling bias (1,234 sites *versus* 347 in estuarine environments), which can admittedly lead to an accumulation of information (Zuquim *et al.* 2007). In other words, the greater sampling effort may allow for more taxa to be found and thus, more functional entities to be registered. However, considering the number of families observed in each environment, a large number of functional entities were identified in both cases. According to Fonseca & Ganade (2001), communities in which species are distributed in a larger number of functional groups will exhibit less functional redundancy than communities whose species are distributed in a few functional groups. Following this reasoning, functional entities can be understood under the same context as the functional groups. In total, 48 and 41 FEs were identified based on the classification of 57 and 47 polychaetes families composing the assemblages of continental shelf and estuarine environments, respectively. Most of them (85% and 88%) were supported by only one family, which indicates a low functional redundancy (i.e., if there is only a single taxon for each functional entity).

The percentage of FEs with only one taxon is also understood as a measure of the functional vulnerability or, in the ecological sense, of the potential decrease in functional diversity after species loss (Bihn *et al.* 2010). In ecosystems with low functional redundancy, species loss is usually equivalent to function loss (Guillemot *et al.* 2011), and then high environmental vulnerability can be detected, as revealed here by the metrics derived from "species_to_FE" function. Although at lower taxonomic levels (e.g., genus and species) functional redundancy tends to increase because more taxa are identified, the number of unique combinations of traits we reported to polychaete families confirm that functional redundancy was satisfactorily assessed at this taxonomic level. However, we must also consider that we evaluate exclusively morphological aspects of a group presenting high plasticity in these characteristics, which guarantees reliability in the interpretation of results. Communities with considerable morphological variation between families display a greater phylogenetic representativeness and, consequently, an amplification of the occupied functional space (Gatz 1979). Therefore, our findings indicate that polychaete assemblages have low functional redundancy and high vulnerability of ecosystem functions to diversity loss in continental shelf and estuarine environments of the South Brazil Shelf Large Marine Ecosystem.

Low levels of functional redundancy were also reported by Magalhães & Barros (2011) for estuarine assemblages. Although these authors made assumptions about the functional redundancy, they were actually assessing other aspects of the functional structure. More recently, Kokarev *et al.* (2017) also observed low functional redundancy on macrobenthic communities on a high-Arctic shelf using as a measure the ratio between functional diversity and taxonomic diversity. To our knowledge, our study was the first to investigate the functional redundancy of a benthic assemblage having this as the main research objective, and through metrics closely linked to this purpose. On the other hand, the potential applicability of FUni and FOri has been neglected, since they have only been used together to evaluate fish assemblages in freshwater ecosystems (e.g., Buisson *et al.* 2013; Maire *et al.* 2013). Thus, broader comparison of our findings with other studies is difficult as measures of originality and uniqueness are currently scarce. In addition, both indices are estimated based on species pool so that caution is needed when extrapolating results outside the study context (Mouillot *et al.* 2008; Buisson *et al.* 2013).

In species-rich tropical systems, an increase in functional redundancy is expected, because if one species providing an essential ecosystem function goes extinct, there will probably be another similar species to occupy its place (Fonseca & Ganade 2001; Martins *et al.* 2012; Mouillot *et al.* 2014). When many species perform similar functions, functional redundancy ensures that ecosystem functioning continues to operate normally even if there is species loss (Fonseca & Ganade 2001). Recent studies reported high functional redundancy in tropical freshwater assemblages of fish (Casatti *et al.* 2015) and phytoplankton (Kruk *et al.* 2017). Conversely, some marine assemblages display little functional redundancy among species in both tropical and temperate ecosystems (e.g., Micheli & Halpern 2005; Guillemot *et al.* 2011; van der Linden *et al.* 2012; Magalhães & Barros 2011; Dolbeth *et al.* 2016; Kokarev *et al.* 2017). Our results and these previous studies suggest that a low redundancy in the majority of functions may broadly characterize marine assemblages. Thus, besides the specificities of the taxonomic group used as a study tool, the observed patterns can be, at least partially, explained by the historical and evolutionary factors that occur in the marine environments underlying a latitudinal gradient of diversity.

Estuarine systems display characteristics that set them apart from other coastal environments (Fonseca & Netto 2014) and make their biota appropriate for the study of functional aspects. Marked temporal and spatial variation in environmental variables are pronounced in estuaries, and changes in physical, chemical and biological properties result in environmental stress that may be related to low diversity when compared to other marine systems (Alves *et al.* 2006; Elliott & Whitfield 2011). Environmental stress can provide high convergent evolution (i.e., many different species sharing a large number of functional traits with each other), and so estuarine species generally play similar ecological roles, being also highly specialized to the environment (Magalhães & Barros 2011; Gerisch *et al.* 2012). The results of PCoAs highlighted this for polychaetes, since the combinations of FEs traits of the estuarine environments were more similar (i.e., with more grouped distribution in the ordination) than the combinations of the FEs traits of the continental shelf.

Similarly, functional uniqueness was used to evaluate the proximity of each polychaete family to its nearest neighbor in the functional space, comparing the unique traits combinations among taxa of the pool (Buisson *et al.* 2013). Thus, in addition to what was pointed out by the PCoAs ordinations, we observed low values of FUni in estuarine environments (i.e., less functional redundancy). The low values are a consequence of traits mainly shared among the families Nereididae, Capitellidae, and Spionidae. These families are frequent in regional estuaries, where they possibly perform equivalent estuarine functions, such as organic matter cycling, turbidity control, and sediment stability through bioturbation. In contrast, polychaete taxa of the continental shelf have a more exclusive combination of traits, and the most frequent families (e.g., Onuphidae, Spionidae, and Lumbrineridae) share few traits among themselves. Unlike estuaries, continental shelf environments are more stable (i.e., they do not undergo extreme variations in the environmental conditions, such as salinity and temperature), and potentially support a more diverse set of species and consequently, of functional traits.

On the other hand, estuarine polychaete assemblages were more original than the continental shelf ones. This means that although estuarine polychaetes are close to each other in the multidimensional functional space, they are far from the center of gravity (i.e., investigated taxa are functionally different from the theoretical average taxon). It has been proposed that the most specialized species are also the most functionally original (Mouillot *et al.* 2008; Devictor *et al.* 2010) and, as discussed earlier, estuarine species are fully specialized to the environment. Even if there is high functional redundancy, it is possible to find high functional originality, because the species have an original combination of traits appropriate to a narrow ecological niche within the particular environment in which they live (Buisson *et al.* 2013; Brandl *et al.* 2016). Thus, although estuarine polychaetes assemblages have fewer unique combinations of trait values, these combinations are more original and suitable to the varying conditions that are imposed on the environment.

Conclusions

Polychaete assemblages from the South Brazil Shelf Large Marine Ecosystem (SBSLME) were characterized by low functional redundancy, but significant variations were clearly associated with main habitat types. Higher levels of functional redundancy reported in estuaries indicate that the convergent evolution imposed by environmental stressors plays a primary role in the functional structuring of polychaete assemblages in these environments. This possibly masks any large-scale factor associated with latitudinal gradient in trait diversity (i.e., an expected high functional redundancy among species in tropical region), which also holds true for continental shelf environment. We recognize the potential limitations of our approach, especially with regard to the used taxonomic resolution, at family level. This study is the first to describe levels of functional redundancy in polychaete assemblages of distinct environments in the southwestern Atlantic. Future descriptive and experimental studies can take advantage of our results for a better understanding of functional redundancy patterns in tropical regions.

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TABLE S1. Morphological traits of polychaetes recorded in continental shelf and estuarine environments (PH.ab= absent; PH.ve= ventral; PH.am= axial muscular; PH.nm= axial non-muscular; JA.ab= absent; JA.pr= present; FS.ab= absent; FS.ss= a single structure; FS.ps= a pair of structures; FS.ms= multiple structures; SA.ab= absent; SA.os= only one structure; SA.ms= multiple structures; BA.ab= absent; BA.pr= present; CP.ab= all parapodial features absent; CP.us= parapodia uniramous simple; CP.uh= parapodia uniramous with uncini or hook; CP.bs= parapodia biramous simple; CP.bh= parapodia biramous with uncini or hook; BR.ab= absent; BR.re= regionalized; BR.nr= non-regionalized; BO.re= regionalized; BO.nr= non-regionalized; SE.100= ≤ 100 segments; SE.200= ≥ 101segments). *taxa exclusive of continental shelf environment; **taxa exclusive of estuarine environment.

Family	Morphological trait								
	Pharynx complexity	**Jaws presence**	**Feeding structures**	**Sensory appendages**	**Body appendages**	**Chaetal (parapodia) pattern**	**Branchiae regionalization**	**Body regionalization**	**Body size**
*Acoetidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.100
*Acrocirridae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.re	BO.nr	SE.200
Ampharetidae	PH.ve	JA.ab	FS.ms	SA.ab	BA.ab	CP.bh	BR.re	BO.re	SE.100
Amphinomidae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Aphroditidae	PH.am	JA.pr	FS.ps	SA.os	BA.pr	CP.bs	BR.re	BO.nr	SE.100
**Apistobranchidae	PH.am	JA.ab	FS.ps	SA.ab	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
*Arenicolidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bh	BR.re	BO.re	SE.100
Capitellidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.ab	BO.nr	SE.100
Chaetopteridae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bs	BR.ab	BO.re	SE.100
Chrysopetalidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.re	SE.100
Cirratulidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bh	BR.nr	BO.nr	SE.200
Cossuridae	PH.am	JA.ab	FS.ss	SA.ab	BA.ab	CP.bs	BR.re	BO.re	SE.100
*Ctenodrilidae	PH.ve	JA.ab	FS.ab	SA.ab	BA.ab	CP.ab	BR.ab	BO.nr	SE.100
*Dinophilidae	PH.ve	JA.ab	FS.ab	SA.ab	BA.ab	CP.ab	BR.ab	BO.nr	SE.100
Dorvilleidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Eulepethidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.re	BO.nr	SE.100
Eunicidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Euphrosinidae	PH.ve	JA.ab	FS.ab	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Fabriciidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
*Fauveliopsidae	PH.ab	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.re	BO.nr	SE.100

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TABLE S1. (Continued)

Family	Morphological trait								
	Pharynx complexity	**Jaws presence**	**Feeding structures**	**Sensory appendages**	**Body appendages**	**Chaetal (parapodia) pattern**	**Branchiae regionalization**	**Body regionalization**	**Body size**
Flabelligeridae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Glyceridae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Goniadidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Hesionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.100
**Histriobdellidae	PH.ve	JA.pr	FS.ps	SA.ms	BA.pr	CP.ab	BR.ab	BO.nr	SE.200
**Longosomatidae	PH.ve	JA.ab	FS.ps	BA.ab	BA.pr	CP.bh	BR.re	BO.re	SE.200
Lumbrineridae	PH.ve	JA.pr	FS.ab	SA.ab	BA.pr	CP.bh	BR.ab	BO.nr	SE.200
Magelonidae	PH.ve	JA.ab	FS.ps	SA.ab	BA.ab	CP.bh	BR.ab	BO.re	SE.200
Maldanidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.ab	BO.nr	SE.100
Nephtyidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
Nereididae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Oenonidae	PH.ve	JA.pr	FS.ab	SA.ab	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Onuphidae	PH.ve	JA.pr	FS.ms	SA.ms	BA.pr	CP.bh	BR.nr	BO.nr	SE.200
Opheliidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.pr	CP.bs	BR.nr	BO.re	SE.100
Orbiniidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.re	BO.nr	SE.100
Oweniidae	PH.ve	JA.ab	FS.ms	SA.os	BA.ab	CP.bh	BR.ab	BO.nr	SE.100
*Paralacydoniidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Paraonidae	PH.nm	JA.ab	FS.ab	SA.os	BA.pr	CP.bs	BR.re	BO.nr	SE.200
Pectinariidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.100
Pholoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Phyllodocidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Pilargidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.100
Poecilochaetidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Polygordiidae	PH.ve	JA.ab	FS.ps	SA.os	BA.ab	CP.ab	BR.ab	BO.nr	SE.200

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TABLE S1. (Continued)

Family	Morphological trait								
	Pharynx complexity	**Jaws presence**	**Feeding structures**	**Sensory appendages**	**Body appendages**	**Chaetal (parapodia) pattern**	**Branchiae regionalization**	**Body regionalization**	**Body size**
Polynoidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.100
Protodrilidae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.ab	BR.ab	BO.nr	SE.100
*Protodriloididae	PH.ve	JA.ab	FS.ps	SA.ab	BA.pr	CP.ab	BR.ab	BO.nr	SE.200
Sabellariidae	PH.ab	JA.ab	FS.ps	SA.os	BA.pr	CP.uh	BR.re	BO.re	SE.100
Sabellidae	PH.ab	JA.ab	FS.ms	SA.os	BA.pr	CP.uh	BR.re	BO.re	SE.100
Saccocirridae	PH.ve	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
*Scalibregmatidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.bs	BR.nr	BO.re	SE.200
Serpulidae	PH.ab	JA.ab	FS.ms	SA.os	BA.ab	CP.uh	BR.re	BO.re	SE.100
Sigalionidae	PH.am	JA.pr	FS.ps	SA.ms	BA.pr	CP.bs	BR.nr	BO.nr	SE.200
*Sphaerodoridae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Spionidae	PH.nm	JA.ab	FS.ps	SA.os	BA.pr	CP.uh	BR.nr	BO.nr	SE.100
Sternaspidae	PH.nm	JA.ab	FS.ab	SA.ab	BA.ab	CP.uh	BR.re	BO.nr	SE.100
Syllidae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.us	BR.ab	BO.nr	SE.200
Terebellidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200
*Tomopteridae	PH.am	JA.ab	FS.ps	SA.ms	BA.pr	CP.bs	BR.ab	BO.nr	SE.200
Trichobranchidae	PH.ve	JA.ab	FS.ms	SA.os	BA.pr	CP.bh	BR.re	BO.re	SE.200

TABLE S2. Functional entities (FEs) of the polychaetes families recorded in continental shelf and estuarine environments (the codes are found in Table 1 and Table S1).

Functional entities (i.e., unique combinations of the nine morphological traits evaluated)	**ID**	**Taxa with this traits combination**	**Families per FE**	
			Continental shelf	**Estuarine**
PHam_JApr_FSps_SAms_BApr_CPus_BRab_BOnr_ SE.100	FE1	Acoetidae, Polynoidae	2	1
PHvp_JAab_FSps_SAos_BAab_CPbs_BRre_BOnr_SE.200	FE2	Acrocirridae	1	0
PHvp_JAab_FSms_SAab_BAab_CPbo_BRre_BOre_SE.100	FE3	Ampharetidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE4	Amphinomidae	1	1
PHam_JApr_FSps_SAos_BApr_CPbs_BRre_BOnr_SE.100	FE5	Aphroditidae	1	0
PHnm_JAab_FSab_SAab_BAab_CPbo_BRre_BOre_SE.100	FE6	Arenicolidae	1	0
PHam_JAab_FSps_SAab_BApr_CPbs_BRnr_BOnr_SE.100	FE7	Apistobranchidae	0	1
PHnm_JAab_FSab_SAab_BAab_CPuo_BRab_BOnr_SE.100	FE8	Capitellidae	1	1
PHvp_JAab_FSps_SAab_BAab_CPbs_BRab_BOre_SE.100	FE9	Chaetopteridae	1	1
PHam_JAab_FSps_SAms_BApr_CPbs_BRab_BOre_SE.100	FE10	Chrysopetalidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPbo_BRnr_BOnr_SE.200	FE11	Cirratulidae	1	1
PHam_JAab_FSss_SAab_BAab_CPbs_BRre_BOre_SE.100	FE12	Cossuridae	1	1
PHvp_JAab_FSab_SAab_BAab_CPab_BRab_BOnr_SE.100	FE13	Ctenodrilidae, Dinophilidae	2	0
PHvp_JApr_FSps_SAms_BAab_CPbs_BRnr_BOre_SE.200	FE14	Dorvilleidae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRre_BOnr_SE.100	FE15	Eulepethidae	1	1
PHvp_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE16	Eunicidae	1	1
PHvp_JAab_FSab_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE17	Euphrosinidae	1	0
PHab_JAab_FSms_SAos_BAab_CPuo_BRre_BOre_SE.100	FE18	Fabriciidae, Serpulidae	2	2
PHab_JAab_FSab_SAab_BAab_CPbs_BRre_BOnr_SE.100	FE19	Fauveliopsidae	1	0
PHvp_JAab_FSps_SAos_BAab_CPbs_BRre_BOnr_SE.100	FE20	Flabelligeridae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.200	FE21	Glyceridae, Goniadidae, Nereididae	3	3
PHam_JApr_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.100	FE22	Hesionidae	1	1
PHvp_JApr_FSps_SAms_BApr_CPab_BRab_BOnr_SE.200	FE23	Histriobdellidae	0	1
PHvp_JAab_FSps_SAab_BApr_CPbo_BRre_BOre_SE.200	FE24	Longosomatidae	0	1
PHvp_JApr_FSab_SAab_BApr_CPbo_BRab_BOnr_SE.200	FE25	Lumbrineridae	1	1
PHvp_JAab_FSps_SAab_BAab_CPbo_BRab_BOre_SE.200	FE26	Magelonidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRab_BOnr_SE.100	FE27	Maldanidae	1	1
PHam_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.200	FE28	Nephtyidae, Sigalionidae	2	2
PHvp_JApr_FSab_SAab_BApr_CPbs_BRab_BOnr_SE.200	FE29	Oenonidae	1	1
PHvp_JApr_FSms_SAms_BApr_CPbo_BRnr_BOnr_SE.200	FE30	Onuphidae	1	1
PHnm_JAab_FSab_SAab_BApr_CPbs_BRnr_BOre_SE.100	FE31	Opheliidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRre_BOnr_SE.100	FE32	Orbiniidae	1	1
PHvp_JAab_FSms_SAos_BAab_CPbo_BRab_BOnr_SE.100	FE33	Oweniidae	1	1
PHam_JApr_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE34	Paralacydoniidae	1	0
PHnm_JAab_FSab_SAos_BApr_CPbs_BRre_BOnr_SE.200	FE35	Paraonidae	1	1
PHvp_JAab_FSms_SAos_BApr_CPbo_BRre_BOre_SE.100	FE36	Pectinariidae	1	1

...Continued on the next page

TABLE S2. (Continued)

Functional entities (i.e., unique combinations of the nine morphological traits evaluated)	ID	Taxa with this traits combination	Families per FE	
			Continental shelf	**Estuarine**
PHam_JApr_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.100	FE37	Pholoidae	1	1
PHam_JAab_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE38	Phyllodocidae, Sphaerodoridae, Syllidae	3	2
PHam_JAab_FSps_SAms_BApr_CPbs_BRnr_BOnr_SE.100	FE39	Pilargidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPbs_BRnr_BOre_SE.200	FE40	Poecilochaetidae	1	1
PHvp_JAab_FSps_SAos_BAab_CPab_BRab_BOnr_SE.200	FE41	Polygordiidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPab_BRab_BOnr_SE.100	FE42	Protodrilidae	1	1
PHvp_JAab_FSps_SAab_BApr_CPab_BRab_BOnr_SE.200	FE43	Protodriloididae	1	0
PHab_JAab_FSps_SAos_BApr_CPuo_BRre_BOre_SE.100	FE44	Sabellariidae	1	1
PHab_JAab_FSms_SAos_BApr_CPuo_BRre_BOre_SE.100	FE45	Sabellidae	1	1
PHvp_JAab_FSps_SAms_BApr_CPus_BRab_BOnr_SE.200	FE46	Saccocirridae	1	1
PHnm_JAab_FSab_SAab_BAab_CPbs_BRnr_BOre_SE.200	FE47	Scalibregmatidae	1	0
PHnm_JAab_FSps_SAos_BApr_CPuo_BRnr_BOnr_SE.100	FE48	Spionidae	1	1
PHnm_JAab_FSab_SAab_BAab_CPuo_BRre_BOnr_SE.100	FE49	Sternaspidae	1	1
PHvp_JAab_FSms_SAos_BApr_CPbo_BRre_BOre_SE.200	FE50	Terebellidae, Trichobranchidae	2	2
PHam_JAab_FSps_SAms_BApr_CPbs_BRab_BOnr_SE.200	FE51	Tomopteridae	1	0

SUPPLEMENT S1. R script: packages and procedures employed to measure and analyze the functional redundancy of polychaetes assemblages.

```
#### Attaching the necessary packages to run the functions and analyzes
library(FD)
library(vegan)
library(cluster)
library(ade4)
library(ape)
library(geometry)

#### Loading general data
spe<-read.table(“spe.txt”, sep=”;”, header=T, row.names=1) #species occurrences
traits<-read.table(“traits.txt”, sep=”;”, header=T, row.names=1) #species functional traits

#### species_to_fe function
species_to_FE<-function(x){
    if ( nrow(traits)<2 ) stop(“Error: ‘traits’ should have at least 2 rows”)
    if ( ncol(traits)<2 ) stop(“Error: ‘traits’ should have at least 2 columns”)
    for ( t in names(traits) )
    {
        if ( is.numeric(traits[,t]) ) stop( paste(“Error: trait ‘”,t,”’ is coded as ‘numeric’ “, sep=””) )
        if( sum(is.na((traits[,t])))>0 ) stop(paste(“Error: NA in trait ‘”,t,”’ “, sep=””))
    }
    traits_codes<-substr(names(traits),1,1)
    if ( length(unique(traits_codes))!=ncol(traits) ) {
```

```
        traits_codes<-substr(names(traits),1,2)
    if ( length(unique(traits_codes))!=ncol(traits) ) stop(«Error: 2 first letters of trait names should be unique «)
    }
    names(traits_codes)<-names(traits)
    for ( t in names(traits) )
    {
        mod_t<-unique(traits[,t])
        if ( length(unique(substr(mod_t,1,2)))!=length(mod_t) )  stop( paste(«Error: some levels of trait ‘»,t,»’ have the same 2 first letters», sep=»») )
    }
    FE<-paste( toupper(traits_codes[1]), tolower(substr(traits[,1], 1,2) ) ,sep=»») #defining FEs as unique combinations of trait values
    for (t in names(traits)[-1] )
    {
    FE<-paste( FE, paste( toupper(traits_codes[t]), tolower(substr(traits[,t], 1,2) ) ,sep=»») , sep=»_»)
    }
    names(FE)<-row.names(traits)
    FE_codes<-unique(FE) #codes of FE
    FE_sp_01<-matrix(0, length(FE_codes), nrow(traits), dimnames=list( FE_codes, row.names(traits) ) ) # matrix of species occurence in FE
    for (f in FE_codes)
    {
        FE_sp_01[f,names(which(FE==f))]<-1
    }
    FE_traits<-traits[apply(FE_sp_01, 1, function(x) {names(which(x==1))[1]} ), ] #trait values for FE
    row.names(FE_traits)<-row.names(FE_sp_01)
    res<-list( FE=FE, FE_codes=FE_codes, FE_sp_01=FE_sp_01, FE_traits=FE_traits) #results in a single list
    return(res)
} #end of function
```

PCoA with presence/absence data of families in functional entities

```
FEs<-read.table(“FEs.txt”, sep=”;”, header=T, row.names=1) #loading the presence/absence data of families in functional entities
jaccard.FEs<-vegdist(FEs,’jaccard’) #transforming the original data matrix into a Jaccard distance matrix
pcoa.FEs<-pcoa(jaccard.FEs)
summary(pcoa.FEs)
```

Multidimensional functional space on the basis of the species traits

```
traits.diss<-daisy(traits, metric = “gower”)
traits.pcoa<-pcoa(traits.diss, correction=”cailliez”)
traits1<-traits.pcoa$vectors[,1:3] #select the 3 first axis of the PCoA
```

Functional originality (FOri) and functional uniqueness (FUni) - according to Buisson *et al.* (2013), Maire *et al.* (2013), Mouillot *et al.* (2013)

```
T<-dim(traits1)[3] #T = number of axis
# definition of the vector for results, with species’ names as given in ‘spe’
N<-nrow(spe)
FOri<-rep(NA,N) ; names(FOri)<-row.names(spe)
FUni<-rep(NA,N) ; names(FUni)<-row.names(spe)
# scaling and centering of each trait according to all species values
```

```
traitsSC<-scale(traits1, center=TRUE, scale=TRUE)
# functional specialization of each species (distance to point 0,0 in the standardized functional space)
FOriS <- (apply(traits1, 1, function(x) {x%*%x} ) )^0.5
FOriS <- FOriS/max(FOriS)
# functional originality and functional uniqueness of each species (distance to point nearest neighbour in the standardized functional space)
dist_Uni = as.matrix(dist(traits1, method=”eucl”))
FUniS = vector()
for (j in 1:nrow(dist_Uni))
{
    FUniS[j] = min(dist_Uni[-j,j])
}
FUniS2=FUniS/(max(FUniS))
# computation of the two indices site by site
for (i in 1:nrow(spe)) ## a loop for all sites (row of the faunistic table)
{
    if (length(which(spe[i,]>0))>0) ## we exclude the site without species and give them a 0-value in the ‘else’ below
    {
        ## FOri
        # mean functional specialization in the communities
        FOri[i]<-as.numeric(spe[i,]/sum(spe[i,]))%*%as.numeric(FOriS)
        ## FUni
        # mean functional originality in the communities according to the full pool of species
        FUni[i] <- as.numeric(spe[i,]/sum(spe[i,]))%*%as.numeric(FUniS2)
    }
    else
    {
        FOri[i] <- 0
        FUni[i] <- 0
    }
} #end of function
# the value by species can be extracted from FOriS and FUniS2
func_species<-data.frame(SP=colnames(spe), SP_FOri=FOriS, SP_FUni=FUniS2)
print(func_species)
```

Kruskal-Wallis nonparametric test

```
fori_funi<-read.table(“fori_funi.txt”,header=T) #loading the data with the FOri and FUni values measured for each environment
kruskal1<-kruskal.test(FOri~environment, data=fori_funi)
kruskal2<-kruskal.test(FUni~environment, data=fori_funi)
```

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