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Functional diversity: a study on the Bay of Biscay nursery habitats

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Abstract. Grouping species according to their biological (i.e. morphological, behavioural, and physiological) traits represents a decisive step in assessing the functional diversity of a community. As functional diversity represents a good measure of ecosystem resilience and resistance, it is thought that groups of functional traits may thus be use to develop indicators to assess community responses to natural and human perturbations. The present study aims at (i) testing the use of groups of functional traits as an alternative to the taxonomic-based approach to develop indicators of nursery states, and (ii) assessing the relationship between species and functional diversity to measure the functional redundancy in nursery fish communities. Groups of functional traits were determined at six coastal nurseries located in the Bay of Biscay. This was done using a methodological framework based on a three-matrix approach (species*sites, species*traits, sites*environment) allowing direct assessment of the relationship between groups of functional traits and the environment. Functional diversity was estimated using a recently developed continuous index. Analyses conducted on data collected yearly between 2000 and 2003 indicated differences in the number and composition of functional groups of traits across the nurseries. Nurseries showing higher number of functional traits were not the ones with higher measures of functional diversity. These results, together with the ones from the redundancy analyses, suggest that locally complex interactions between species identity and functional roles govern the nurseries of Bay of Biscay. Complementary analyses are however needed to advance our understanding and to investigate whether the observed differences in functional diversity among the nurseries may be anthropogenic or due to natural variability.

Key words: Anthropogenic pressures, Bay of Biscay, dendrogram-based approach, environmental variability, coastal nurseries, fish community, fourth-corner method, functional diversity.

INTRODUCTION

Coastal and estuarine environments are among the most productive ecosystems in the aquatic environment (Costanza et al. 1997). They provide many services to the human population (food, recreational areas, …) and they play an important role as nursery habitats for many commercial fish species and invertebrates. Several studies have noticed indirect evidences that habitat conditions (quality and quantity) prevailing in coastal nurseries are affecting the size of some fish populations (Pihl et al. 2005). With increasing uses of the coastal, littoral and adjacent terrestrial zones, nursery habitats are now facing increasing degradations (habitat fragmentation and chemical/organic pollutions) which represent threats to sustainability and productivity of marine ecosystems.

Following the "niche filtering hypothesis" (Hutchinson, 1957), the biological traits of organisms evolve in response to the properties of the habitats they use. Habitats act indeed as templates or filters on which evolution forges phenotypic attributes (Southwood, 1977, 1988). Grouping species according to their biological (i.e. morphological, behavioral, and physiological) traits represents a critical step in assessing the functional diversity of a community. As functional diversity represents a good measure of ecosystem resilience and resistance, groups of functional traits and related measures based on functional traits may be use to understand the ecosystem functioning and to develop indicators to assess community responses to natural and human perturbations.

Closely related to functional diversity is the concept of functional redundancy. The latter implies that the disappearance of one or more species does not affect the ecosystem process because species represent "redundant information" with respect to that process. Redundancy can be thought as a desirable property of ecological communities because it guaranties that specific (and may be essential) ecosystem functions will be maintain in the case of species removal from that ecosystem. This could be particularly important in coastal ecosystems in which (as stated above) communities are under multiple pressures (natural and anthropogenic) and in which the probability of loosing vulnerable species and hence essential ecosystem functions is likely high. In such ecosystems, functional redundancy may indeed favour long-term resilience (Diaz and Cabito 2001).

Using a newly developed methodological framework, the present study aims at (i) testing the use of functional traits as an alternative to the taxonomic-based approach to eventually develop indicators of nurseries states, and (ii) assessing the relationship between species and functional diversity to measure the functional redundancy in nursery communities.

MATERIALS AND METHODS

Study area and sampling procedure

Ifremer has been carrying out a number of dedicated coastal nursery surveys along the shore of the Bay of Biscay since the 80's. The present study focuses on the surveys that have been conducted from 2000 to 2003 on six nursery grounds located along the French coast of the Bay of Biscay (Figure 1). These nursery grounds have been described and classified by Gilliers et al (2006) into open shallow muddy estuarine areas under the direct influence of freshwater inflows (Vilaine, Loire, and Gironde) and semi-enclosed sheltered muddy marsh areas with shellfish-farming, little affected by rivers (Bay of Bourgneuf, Pertuis Antioche, Pertuis Breton).

The nursery-dedicated surveys were carried out from the end of August to the end of October. Early studies have found that this period coincides with the end of the growth phase of juvenile flatfish and that it was a suitable period for their collection, providing consistent estimates for notably 0+ fish age group (Dorel et al. 1991). The surveys were conducted using a stratified sampling design according to depth and sediment type. They were carried out in depths ranging from 5 to 25 m using a 2.9 m wide and 0.5 m high beam trawl with a 20-mm stretched mesh net in the cod-end. Each haul were conducted on homogeneous sediment and depth and lasted 20 min covering a mean area of 4500 to 5000 m^2. All the species caught were counted and total weight of the haul was recorded.

Nursery ground communities

The term 'community', commonly used throughout this paper, is defined as a collection of organisms found at a specific place and time and "it is formalized by a sample unit which arbitrarily bounds and sorts variation in species composition in space and time" (McCune et al. 2002). Owing to the benthic selectivity of the sampling gear only the species occurring in more than 5% of the sampling sites and displaying a relative density ≥ 5% of the total density were kept. However, as this paper aimed at describing the nursery communities based on functional traits of species, access to valuable and specific species information was prioritised and thus a selection on the species according to the availability of this information was done. At the end, 38 species (nearly 35% of the species caught in each haul) were included in the statistical analyses (Table 1).

Methodological framework

A methodological framework using different statistical methods was developed to estimate the functional diversity across the nursery grounds in the Bay of Biscay. The present section aimed at presenting this framework (Figure 2).

Choosing functional traits

The first step is the choice of functional traits. As recently stated by Petchey and Gaston (2006) only relevant traits should be included in the analysis. The relevance of the traits was assessed according to their known relationships with environmental conditions and/or anthropogenic perturbations prevailing in the study area.

Fourth-corner method

As previously mentioned in the introduction, communities may be viewed as being shaped by the « niche filtering hypothesis » which states that coexisting species are sharing similar traits (i.e. biological/ecological traits) because environmental conditions act as a filter allowing only specific traits to survive (Mouillot et al 2005). The fourth-corner method was used in that context prior to the calculation of the functional diversity. It allowed to assess the environmental variables that significantly contribute to the variability of the functional traits composition on each nursery ground. It was thought to present an indirect way of accounting for the abundance of the species, as the evenness of the species community is not involved in the calculation of the functional diversity index used in the present study (dendrogram-based index).

As the fourth-corner method is fully explained in Legendre et al. (1997) and in Dray and Legendre (Submitted), only a brief description of the method is provided in here. The fourth-corner method was used to test the hypothesis that functional traits were associated with the environmental conditions found in the nursery grounds. The method requires multiple data taking the form of three input matrices (**A**, **B** and **C**) and computes species functional traits-environment correlations in a fourth matrix (**D**; Figure 3). The first matrix (**A**: $k \times m$) contains the abundance (or density) of the k species at the m sampling sites (38 species and 521 sampling sites). The second matrix (**B**: $k \times n$) describes n functional traits of the same k species. Data in that matrix was composed of 32 functional traits classified in seven categories (Table 2). Functional traits were compiled using values mainly from the literature (Tillin et al. 2006, Nagelkerken and van der Velde 2004, Laptikhovsky et al. 2002, Raya et al. 1999, Elliott and Dewailly 1995, Knippers and Dapper 1984) and were completed with information found on Fishbase (Froese and Pauly 2006) and on the Marine Life Information Network (http://www.marlin.ac.uk). The third matrix **C** ($p \times m$) contained information about the p environmental variables that were significantly associated with the m sampling sites. The sampling sites were characterized by four environmental variables (sediment, depth, salinity, and temperature) at each site. The fourth-corner or matrix **D** ($p \times n$) contains the results obtained after conducting the analysis. The matrix **D** is composed of correlations of the n functional traits crossed with the p environmental variables. Analyses were conducted using a modified version of the fourth-corner method (Dray and Legendre, Submitted) implemented in a program written by S. Dray in the R language (Team, 2005). A global statistic, was calculated from matrix **D**; it was computed as the trace of ($\mathbf{D}^t\mathbf{D}$) matrix **D**. It estimated the overall link between all traits and all environmental variables. This statistic, which represents the total variability of the species traits explained by the environmental variables, was computed and tested for significance. Six analyses, one per nursery ground, were conducted. It is noteworthy to mentioned that global statistic in the six nursery grounds was significant.

Development of a new species-traits matrix

The correlations obtained in individual cells (d_{ij}) of the **D** matrices were tested using 999 permutations, thereby producing *P*-values. Holm's procedure (Holm, 1979) for adjustment of probabilities in multiple simultaneous tests was applied. Only the correlations that remained significant at the 0.05 level after adjustment were kept for the development of the new species-traits matrix. The functional traits that were significantly correlated with one of the environmental variables in a specific nursery ground were included in the new matrix of that nursery ground. This means that from the 32 traits comprised in the original species-traits matrix (**B**) some of them (the non-significant traits) were deleted from that matrix and a new 'reduce' matrix of species-traits was compiled. This procedure was repeated on the six nursery grounds thus giving six new species-traits matrices.

Functional Diversity

The functional diversity (FD) was estimated using a dendrogram-based approach (Petchey and Gaston 2002). Gower's dissimilarity coefficient was used on the standardised species-traits matrix to estimate the distance among the functional traits. This coefficient has been chosen because it can handle mixed variable types (quantitative, categorical, and binary) and missing values (Podani and Schmera 2006, Legendre and Legendre, 1998). A dendrogram was produced by hierarchical clustering using Unweight Pair Group Method with Arithmetic mean (UPGMA) method. The latter method was chosen after estimating the correlations between the original distances (Gower's species-traits matrix) and the cophenetic distances at each nursery grounds. Results showed that UPGMA effectively preserved the dissimilarity structure from the distance species-traits matrix (average Pearson's correlations: 0.75 ± 0.4). The functional diversity which corresponds to the total branch lengths of the dendrogram was afterward estimated using the formula described by Petchey and Gaston (2002). Statistical analyses were done using the R language (Team, 2005) and the codes for assessing the total branch length of a dendrogram were provided by O. Petchey (http://owensplace.wetpaint.com/).

RESULTS AND DISCUSSION

Species functional traits and environmental variables

Results from the fourth-corner analyses indicated that the nursery communities of the Bay of Biscay displayed different number and composition of functional traits-environment relationships. In decreasing order, the Loire (n=22), the Pertuis Antioche (n =17), the Pertuis Breton (n =14), the Gironde (n =12), the Bay of Bourgneuf (n =10) and the Vilaine (n =9) showed great differences in the number of significant functional traits (n). The nurseries showed however some similarities in the composition of the significant functional traits. This was the case of the Bay of Vilaine and the Pertuis Antioche which functional traits were mostly represented by bentho-demersal species eating invertebrates. Similarities were also found for the Bay of Bourgneuf and the Gironde in which the traits from both nurseries were characterized by marine migrant species with their eggs either attached/deposed in vegetation or guarded by one of the parents. As for the Pertuis Breton and the Loire, they were both represented by different functional traits. The former was characterized by viviparous and detritic species with long life-span (over 20 years) whereas the second was represented by carnivorous, marine juvenile migrants with maximum size ranging between 21 and 40 cm.

Functional diversity and functional redundancy

By "selecting" the functional traits that significantly structured the nursery communities, the fourth-corner method allowed situations in which the number of functional traits differed between nursery grounds. As individual traits are equally weighted by Gower's coefficient, they receive the same weight in calculating total branch lengths, one could hypothesise that different number of traits would modify the tree typology (and may be the tree length) which in turn would affect the values of the functional diversity. Results in the present study support in part this assumption as different values of the functional diversity index were found between some nurseries (Figure 4). The nurseries displaying greater measures of functional diversity were however not the same as the ones showing higher number of species traits. For instance, the Bay of Bourgneuf which displayed the higher index of functional diversity (FD = 7.51) was the second nursery having the least number of significant traits (*n*=10). The functional diversity index was on the other hand correlated with the number of functional categories of traits, suggesting that these nurseries may likely operate more efficiently and display greater resilience to disturbances (Micheli and Harpen 2005).

Assessment of the relationship between the functional diversity and the Shannon's diversity calculated in the six nurseries did not show any linear trends (Figure 5), i.e. the nurseries having the lower FD were not the ones having the lower taxonomic diversity (Shannon's index). It indicated however that some nurseries have high functional and taxonomic diversity (Bourgneuf and Loire) suggesting that the communities may be more 'redundant' than for instance the Gironde.

Results from the present study showed that the functional diversity index assessed using the newly developed methodological framework likely informed on the interactions between species composition and functional roles in the coastal nurseries of the Bay of Biscay. Complementary analyses are however needed to advance our understanding and to investigate whether the observed differences in FD among the nurseries may be anthropogenic or due to natural variability. Forthcoming developments should include the increase of the number of species and functional traits, therefore compiling new information from the literature, the comparison of different measures of functional diversity, and the development of a function to compare the FD estimates among the six nursery sectors using permutation tests. The method also remains to be tested across years to verify its effectiveness in assessing the temporal evolution of the FD within single nursery grounds.

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Tables

Table 1 List of species included in the statistical analyses.

Species	Code	Phylum	Family
Abra alba	ABRAALB	*Mollusca*	*Semilidae*
Alloteuthis	ALLO	*Mollusca*	*Loliginidae*
Arnoglossus laterna	ARNOLAT	*Chordata*	*Bothidae*
Asterias rubens	ASTIRUB	*Echinodermata*	*Asterias*
Buccinum undatum	BUCCUND	*Mollusca*	*Buccinidae*
Buglossidium luteum	BUGLLUT	*Chordata*	*Soleidae*
Callionymus lyra	CALMLYR	*Chordata*	*Callionymidae*
Chelidonichthys gurnardus	CHELGUR	*Chordata*	*Triglidae*
Chelidonichthys lucernus	CHELLUC	*Chordata*	*Triglidae*
Crangon crangon	CRAGCRA	*Arthropoda*	*Crangonidae*
Dicentrarchus labrax	DICELAB	*Chordata*	*Moronidae*
Dicologlossa cuneata	DICOCUN	*Chordata*	*Soleidae*
Gobius niger	GOBINIG	*Chordata*	*Gobiidae*
Hippocampus hippocampus	HIPPHIP	*Chordata*	*Syngnathidae*
Liocarcinus holsatus	LIOCHOL	*Arthropoda*	*Portunidae*
Loligo vulgaris	LOLIVUL	*Mollusca*	*Loliginidae*
Merlangius merlangus	MERNMER	*Chordata*	*Gadidae*
Merluccius merluccius	MERLMER	*Chordata*	*Merlucciidae*
Mullus surmuletus	MULLSUR	*Chordata*	*Mullidae*
Nassarius reticulatus	NASSRET	*Mollusca*	*Nassaridae*
Necora puber	NECOPUB	*Arthropoda*	*Portunidae*
Nucula	NUCU	*Mollusca*	*Nuculidae*
Ophiura albida	OPHUALB	*Echinodermata*	*Ophiolepidae*
Ophiura ophiura	OPHUOPH	*Echinodermata*	*Ophiolepidae*
Ostrea edulis	OSTAEDU	*Mollusca*	*Ostreidae*
Pagurus bernhardus	PAGUBER	*Arthropoda*	*Paguridae*
Palaemon serratus	PALOSER	*Arthropoda*	*Palaemonidae*
Pectinaria koreni	PECRKOR	*Annelida*	*Pectinariidae*
Philine aperta	PHILAPE	*Mollusca*	*Philinidae*
Platichthys flesus	PLATFLE	*Chordata*	*Pleuronectidae*
Pleuronectes platessa	PLEUPLA	*Chordata*	*Pleuronectidae*
Pomatoschistus minutus	POMOMIN	*Chordata*	*Gobiidae*
Raja clavata	RAJACLA	*Chordata*	*Rajidae*
Sepia officinalis	SEPIOFF	*Mollusca*	*Sepiidae*
Solea solea	SOLESOL	*Chordata*	*Soleidae*
Spondyliosoma cantharus	SPONCAN	*Chordata*	*Sparidae*
Trachurus trachurus	TRACTRA	*Chordata*	*Carangidae*
Trisopterus luscus	TRISLUS	*Chordata*	*Gadidae*

TABLE 2 List of species functional traits included in the analyses. Numbers in brackets indicate the class of the trait.

Category	Functional trait	Code
Feeding guild	Plankton	PS
	Invertebrates (molluscs, crustaceans)	IS
	Fishes	FS
	Plants	VS
	Detritus/substratum	DS
	Invertebrate and Fish	IF
	Carnivorous	CS
	Partly herbivorous and carnivorous	HC
	Omnivorous	OV
Reproductive guild	Viviparous (giving birth to a free living progeny)	V
	Ovoviviparous (giving birth to living organisms first enclosed in eggs)	W
	Oviparous (producing a certain quantity of eggs)	O
	Pelagic eggs	Op
	Eggs guarded by parents	Ob
	Eggs deposited in vegetation or attached	Ov
	Eggs protected in a shed, pouch or case	Os
Vertical distribution	Pelagic (water column)	P
	Demersal (above substrate)	D
	Benthic (on or in substrate)	B
Substrate preference	Sandy bottom (sand exclusively)	S
	Soft bottom (sand, mud, fine gravel)	F
	Rough bottom (rock, stone, pebble)	R
	Mixed or various (no apparent preferences)	M
	Vegetation (seaweeds)	Veg
Life-history strategy	Maximum size (maximum fork length/diameter/ mantle (cm))	MZ*
	Maximum age in years	YR*
Commercial	Commercial interest	COM
Ecological guild	Marine migrant (appears irregularly in the estuary)	MA
	Coastal	CO
	Marine seasonal migrant	MS
	Marine juvenile migrant (marine adults using estuary as nursery grounds)	MJ
	Estuarine resident (entire life in the estuary)	ER
	Diadromous species (catadromous or anadromous)	CA
	Freshwater migrant (freshwater species transit by the estuary)	FW

FIGURES

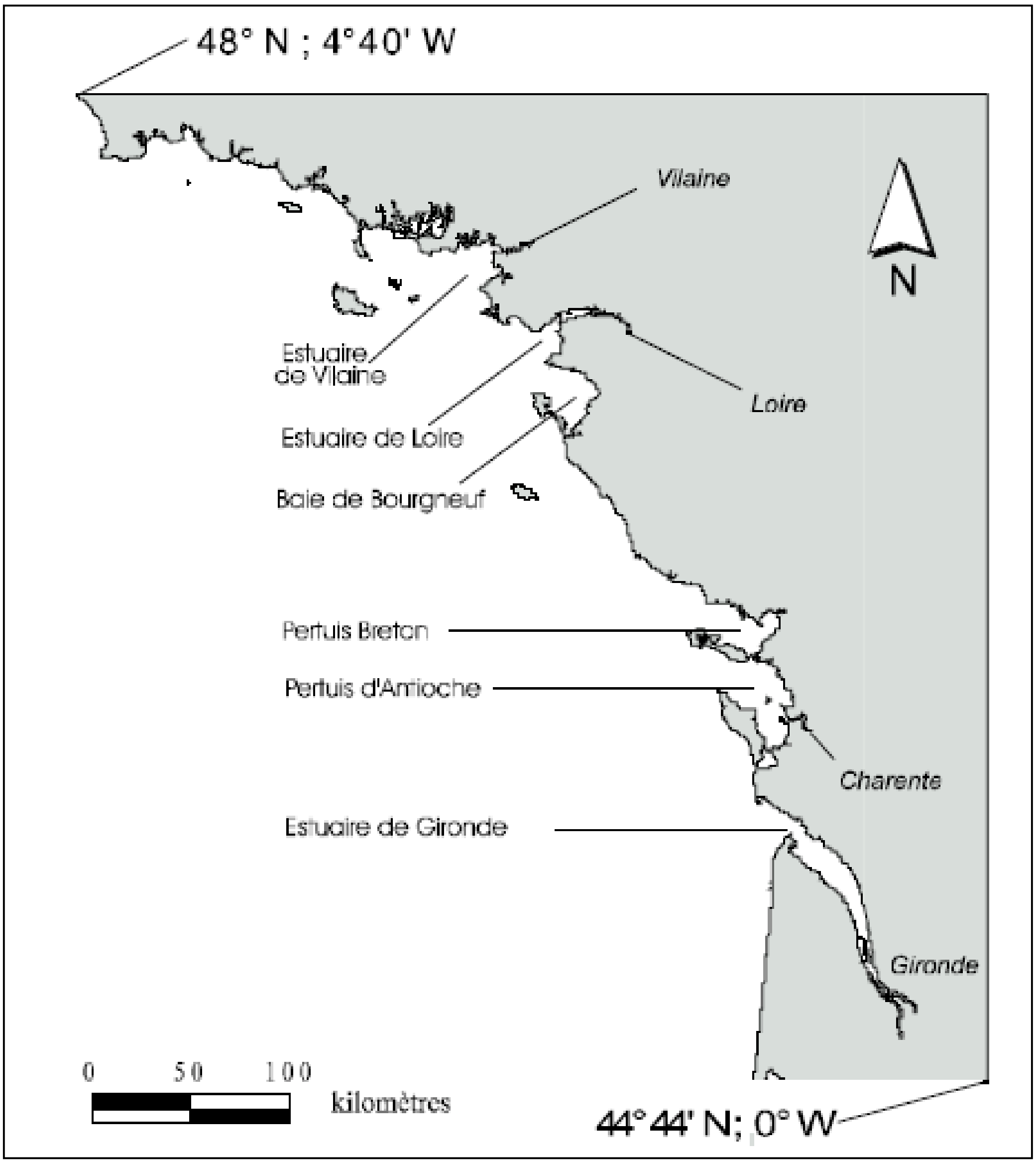

FIGURE 1 Map of the six nursery grounds along the coast of the Bay of Biscay (France). It was modified from Le Pape (2005).

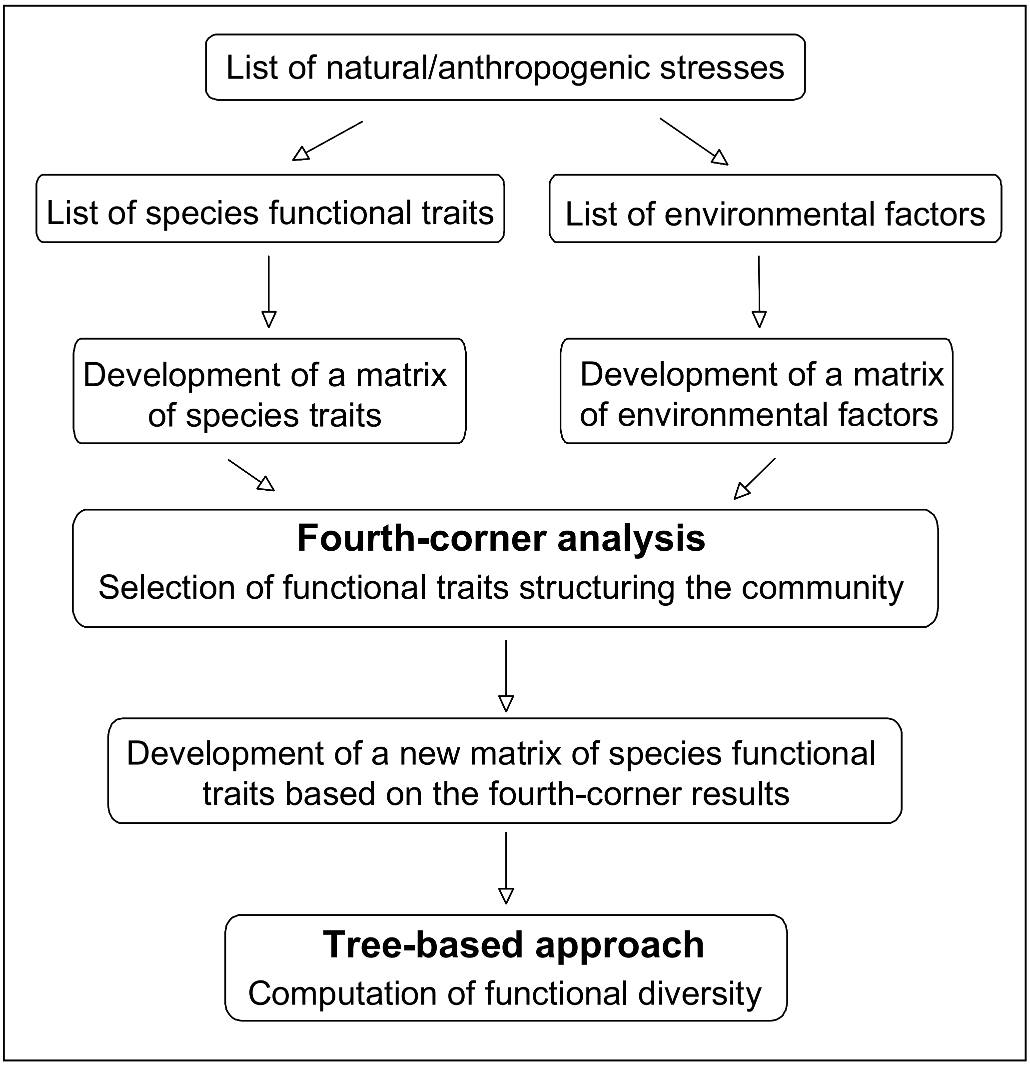

FIGURE 2 Summary of the statistical approach used in the present study. Each steps is fully detailed in the Material and methods section.

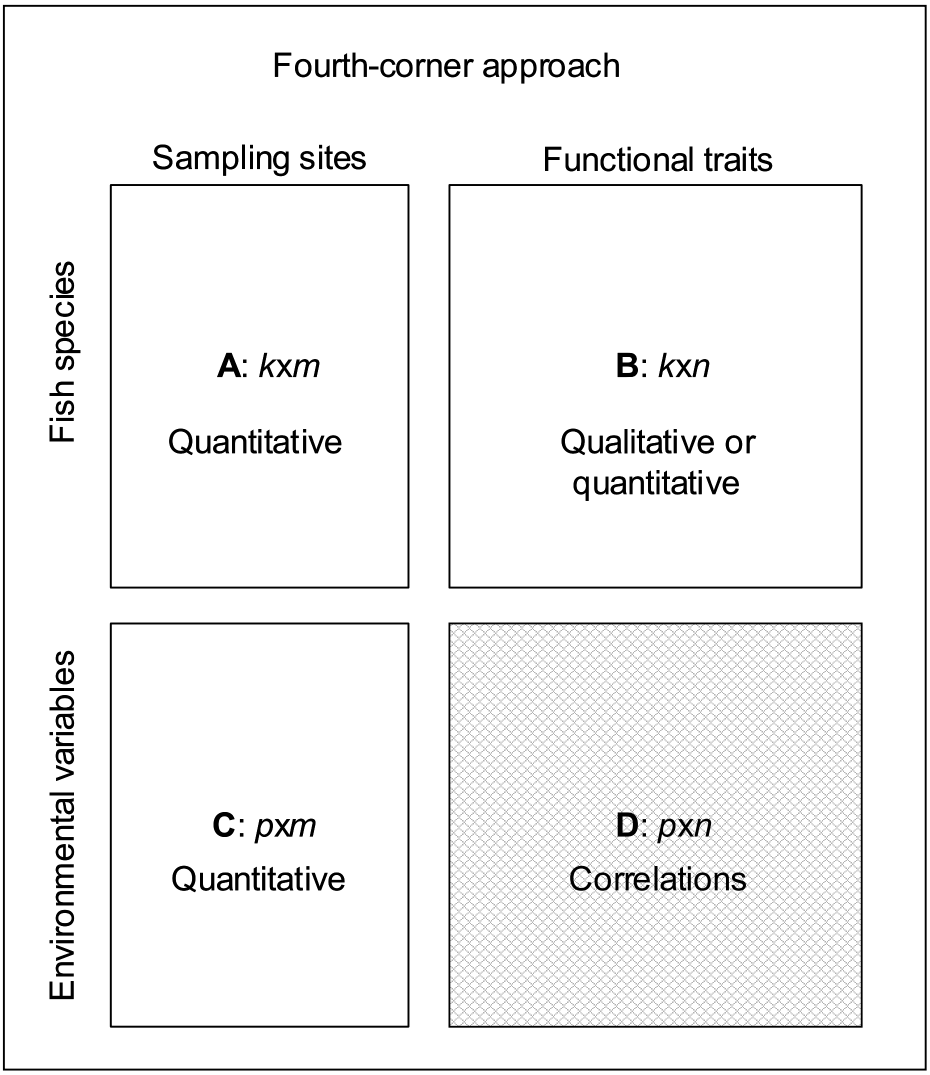

FIGURE 3 Schematic illustration of the fourth-corner statistical analysis used in the present study.

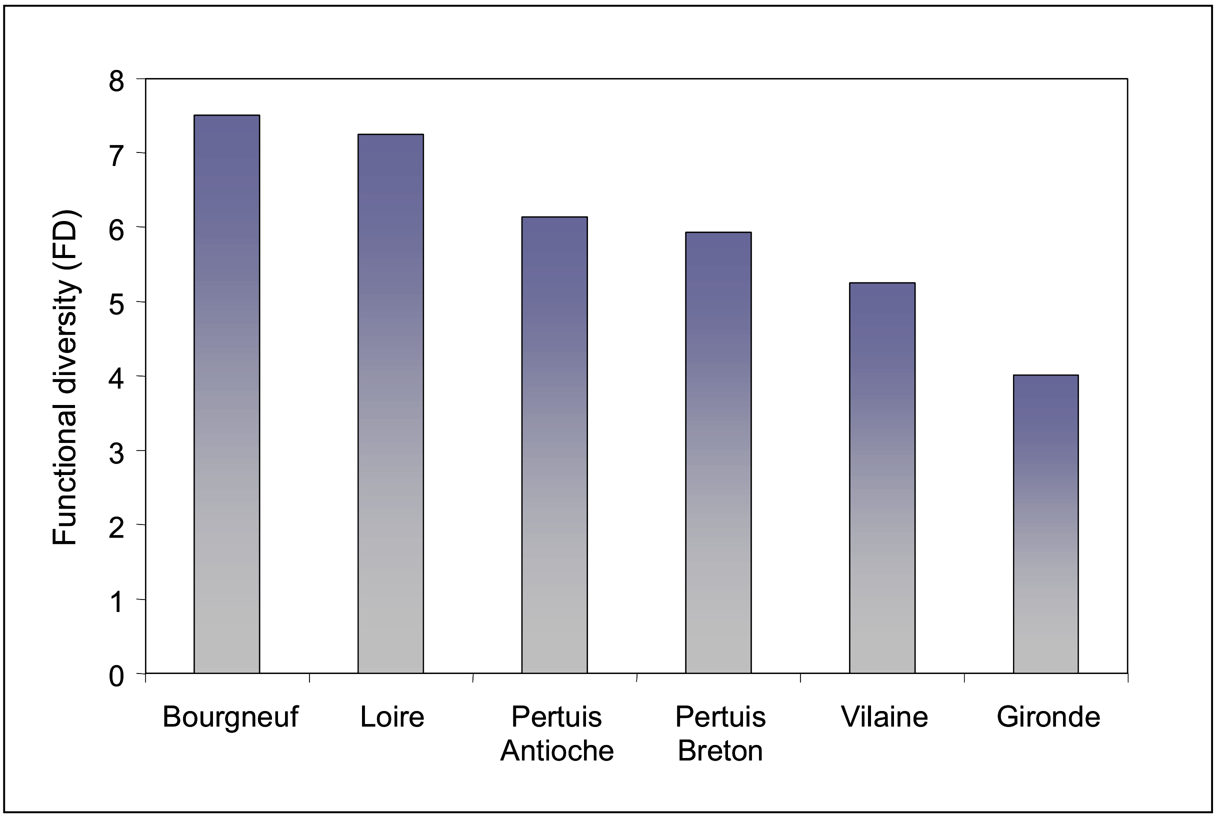

FIGURE 4 Decreasing functional diversity index (FD) in the six nurseries along the coast of the Bay of Biscay.

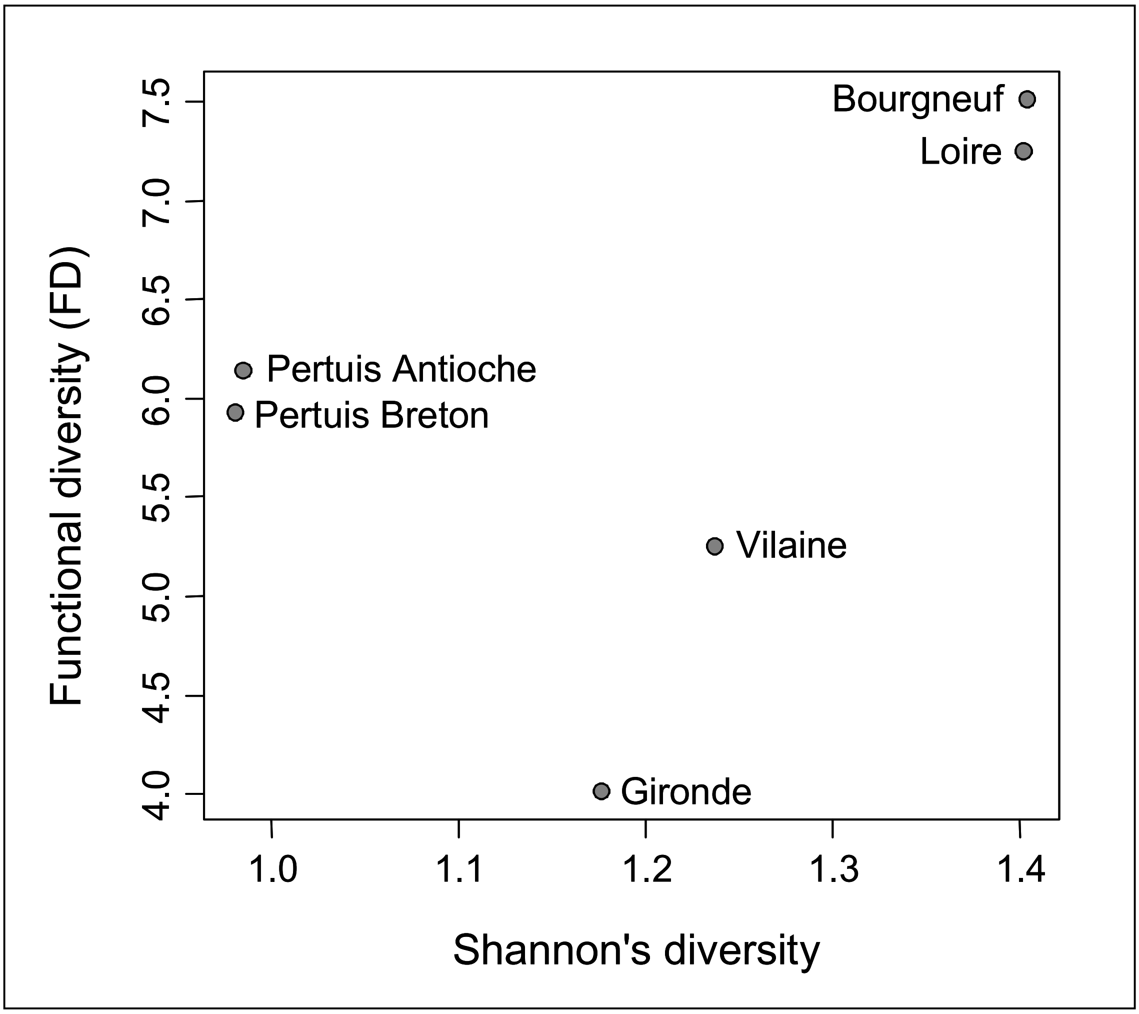

FIGURE 5 Functional redundancy in the six nurseries estimated by the relationship between the functional diversity index (FD) and Shannon's diversity index.