fuzR: an R package providing biological trait data and utilities for marine benthic ecology

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Abstract

fuzR is an R-package that provides a global data base of biological trait data and utilities for marine benthic ecology. The data base includes 41 traits of 1893 macrozoobenthic species describing fitness components and ecosystem functions. The traits are organised in a fuzzy format that requires specific R functions to be easily handled. In this vignette, we show different applications of the package particularly beneficial to species community ecology.

```
library(knitr)
library(kableExtra)
opts_chunk$set(echo = TRUE)
```

S1 The fuzR package

The document provides guidelines to handle fuzzy trait data by mean of the package fuzR. Such data are organized at two levels: numerical scores are attributed to modalities, themselves nested within traits. The handling of those complex data is facilitated by specifically designed functions in fuzR. Also, the package hosts the MacroTraits data base intended to marine benthic ecology. The extraction and use of the data base are examplified through common practices in functional ecology. Besides, the package remains useful for any data set composed of fuzzy traits.

You can install the development version of fuzR like so:

```
#install.packages("remotes")
#remotes::install_github("https://raw.githubusercontent.com/obeauchard/fuzR")
library(fuzR)
```

S2 Data extraction and manipulation

Trait data are typically used in taxa x trait modalities matrices, either for specific purposes of community ecology or for other practical matters. In MacroTraits, the biological traits are organised in a long-format table that requires special attention before conversion into long format since modalities are nested within traits. Firstly, let’s visualise the trait long-format data frame:

```
data(MacroTraits)
print(head(MacroTraits$traits, 15))
```

```
##                  Species Trait.ID Modality.ID Score Reference.ID
## 1  Abarenicola pacifica        1           1     0         3291
## 2  Abarenicola pacifica        1           2     2         3291
## 3  Abarenicola pacifica        1           3     0         3291
## 4  Abarenicola pacifica        1           4     0         3291
## 5  Abarenicola pacifica        1           5     0         3291
## 6  Abarenicola pacifica        2           1     0         3291
## 7  Abarenicola pacifica        2           2     0         3291
## 8  Abarenicola pacifica        2           3     1         3291
## 9  Abarenicola pacifica        2           4     1         3291
## 10 Abarenicola pacifica        2           5     0         3291
## 11 Abarenicola pacifica        3           1     0         3291
## 12 Abarenicola pacifica        3           2     0         3291
## 13 Abarenicola pacifica        3           3     1         3291
## 14 Abarenicola pacifica        3           4     0         3291
## 15 Abarenicola pacifica        3           5     0         3291
```

The label data frame:

```r
print(head(MacroTraits$labels, 20))
```

```
##    Trait.ID Modality.ID             Trait                   Modality
## 1         1           1             Biome                      Polar
## 2         1           2             Biome                  Temperate
## 3         1           3             Biome                   Tropical
## 4         1           4             Biome                       Deep
## 5         1           5             Biome                      HV-CS
## 6         2           1          Salinity                Oligohaline
## 7         2           2          Salinity                 Mesohaline
## 8         2           3          Salinity                 Polyhaline
## 9         2           4          Salinity                   Euhaline
## 10        2           5          Salinity                Hyperhaline
## 11        3           1       Water depth              Extralittoral
## 12        3           2       Water depth              Supralittoral
## 13        3           3       Water depth              Mediolittoral
## 14        3           4       Water depth                      Shore
## 15        3           5       Water depth                      Shelf
## 16        3           6       Water depth                      Slope
## 17        3           7       Water depth                      Abyss
## 18        4           1 Sea floor affinity       Mainly hyperbenthic
## 19        4           2 Sea floor affinity Occasionally hyperbenthic
## 20        4           3 Sea floor affinity                Epibenthic
```

S2.1 Endo-substratum engineering

As a first example of data manipulation and ordination, we choose four traits related to endo-substratum engineering: endo-bioconstruction type, endo-bioconstruction depth, ventilation/pumping and sediment biomixing type, indexed 33, 34, 36 and 37, respectively. The command fuz.tab takes the data frames df and lab and returns a list of two objects: the species x trait modalities data frame (`$tab`) and the equivalent to the lab data frame as the rows of the corresponding selected traits (`$lab`).

```
print(unique(MacroTraits$labels[c(1, 3)]))
```

```
##     Trait.ID                           Trait
## 1          1                           Biome
## 6          2                        Salinity
## 11         3                     Water depth
## 18         4               Sea floor affinity
## 23         5                      Substratum
## 30         6        Substratum depth occupancy
## 36         7    Epi-bioconstruction occupancy
## 46         8                       Life span
## 54         9                 Age at maturity
## 60        10                      Voltinism
## 64        11                      Sexuality
## 68        12          Reproductive frequency
## 72        13                   Fertilisation
## 75        14                Annual fecundity
## 81        15                  Offspring type
## 84        16                  Offspring size
## 89        17            Offspring protection
## 94        18           Offspring development
## 99        19 Offspring benthic stage duration
## 105       20 Offspring pelagic stage duration
## 111       21         Offspring settlement size
## 117       22                 Body resistance
## 122       23                       Body mass
## 128       24                     Body length
## 134       25                        Motility
## 139       26                        Mobility
## 144       27                        Rafting
## 147       28            Degree of attachment
## 150       29                       Sociality
## 153       30          Epi-bioconstruction type
## 161       31    Epi-bioconstruction extension
## 167       32          Epi-bioconstruction size
## 174       33         Endo-bioconstruction type
## 182       34        Endo-bioconstruction depth
## 187       35        Endo-bioconstruction width
## 191       36               Ventilation/Pumping
## 195       37           Sediment biomixing type
## 200       38                      Bioerosion
## 204       39                 Biostabilisation
## 207       40                    Feeding type
## 213       41                  Foraging depth
```

```
w <- fuz.tab(data = MacroTraits$traits, lab = MacroTraits$labels,
             which.traits = c(37, 33, 34, 36))
indic <- w$lab$Trait.ID
```

The species x trait modalities data frame (`w$tab`) is linked to the label data frame by its column names: “T” for “trait” and “M” for “modality”. The vector `indic` enables an easier horizontal selection of traits as blocks of modality columns afterward. Below, the two first traits.

```r
print(head(w$tab)[indic %in% 1:2])
```

```
##                         T1.M1 T1.M2 T1.M3 T1.M4 T1.M5 T2.M1 T2.M2 T2.M3 T2.M4
## Abarenicola pacifica        0     0     1     0     0     0     0     0     0
## Abatus cordatus             0     1     0     0     0     1     0     0     0
## Abdopus aculeatus           1     0     0     0     0     1     0     0     0
## Abludomelita obtusata       0     1     0     0     0     1     0     0     0
## Abra alba                   0     1     0     0     0     1     0     0     0
## Abra nitida                 0     1     0     0     0     1     0     0     0
##                         T2.M5 T2.M6 T2.M7 T2.M8
## Abarenicola pacifica        0     1     0     0
## Abatus cordatus             0     0     0     0
## Abdopus aculeatus           0     0     0     0
## Abludomelita obtusata       0     0     0     0
## Abra alba                   0     0     0     0
## Abra nitida                 0     0     0     0
```

```r
print(w$lab[indic %in% 1:2,])
```

```
##    Column.name Trait.ID Modality.ID                     Trait
## 1        T1.M1        1           1   Sediment biomixing type
## 2        T1.M2        1           2   Sediment biomixing type
## 3        T1.M3        1           3   Sediment biomixing type
## 4        T1.M4        1           4   Sediment biomixing type
## 5        T1.M5        1           5   Sediment biomixing type
## 6        T2.M1        2           1 Endo-bioconstruction type
## 7        T2.M2        2           2 Endo-bioconstruction type
## 8        T2.M3        2           3 Endo-bioconstruction type
## 9        T2.M4        2           4 Endo-bioconstruction type
## 10       T2.M5        2           5 Endo-bioconstruction type
## 11       T2.M6        2           6 Endo-bioconstruction type
## 12       T2.M7        2           7 Endo-bioconstruction type
## 13       T2.M8        2           8 Endo-bioconstruction type
##              Modality
## 1                None
## 2           Diffusion
## 3    Upward conveying
## 4  Downward conveying
## 5        Regeneration
## 6     None/Surficial
## 7     Rugosities/Pit
## 8     Chimney/Funnel
## 9                Tube
## 10   IJ-shaped burrow
## 11   UY-shaped burrow
## 12    Branched burrow
## 13 Anastomosed burrow
```

Fuzzy coding followed by Fuzzy Correspondence Analysis (FCA) is a typical operation on such a data table (Chevenet et al. 1994). This enables the identification of trait correlations along multivariate axes as biological gradients. This can be done with the ade4 package (Chessel et al. 2004).

```r
library(ade4)
fuz <- prep.fuzzy.var(df = w$tab, col.blocks = table(indic))
fca <- dudi.fca(df = fuz, scannf = FALSE)
par(mfrow = c(2, 2), mar = rep(0.1, 4))
for(i in 1:max(w$lab$Trait.ID)){
  s.label(fca$li, cpoint = 0, clab = 0, cgrid = 1.5)
  points(fca$li, pch = 1, col = "grey60", cex = 1.5)
  sub <- paste(letters[i], ") ", unique(w$lab$Trait)[i], sep = "")
  s.distri(fca$li, fuz[indic == i], clab = 1, cstar = 0, cpoint = 0,
           lab = w$lab$Modality[indic == i], sub = sub,
           possub = "topleft", csub = 1.5, add.p = TRUE)
}
```

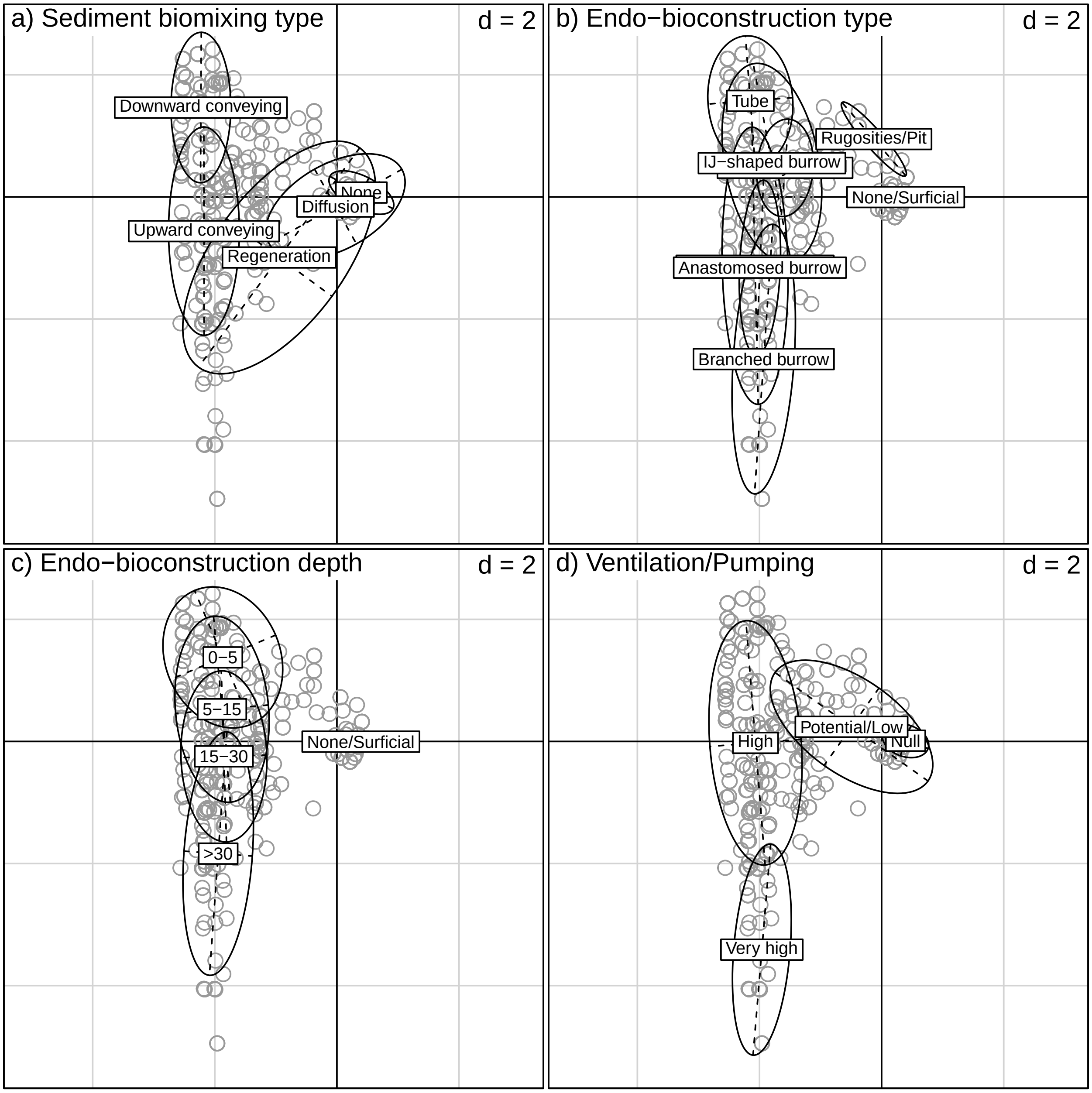

Figure S1. Endo-substratum engineering pattern. Grey dots are the 1893 species; due to identical trait profiles, many species have the same position. From (a) to (d), each panel represents the same species pattern, but grouped per modality of the specified trait. Trait modalities are positioned at the gravity centre of their respective species. The first axis (horizontal) opposes absence of engineering ability (a, “None”, right side of the axis) to burrowing species (left). The second axis (vertical) expresses the burrowing depth, associated to non-local transfer of sediment (a).

In Figure S1, the type of bioconstruction seems slightly specific to depth (Fig. S1b) and might be useful for some specific purposes. However, in bioturbation, fluxes of solutes through the sediment matrix (e.g., oxygen) depend on the type of burrow opening system toward the sediment-water interface whereby two or more openings enhance fluxes with less pressure against the burrow wall unlike a single one (“IJ-shaped”) induces greater effect on the surrounding sediment (Aller 1984, Meysman et al. 2005). Hence, a simplification is required here. The command `modif.trait` modifies a trait by merging its modalities according to a vector of new categories; new modality labels can also be created. The trait endo-bioconstruction type is modified according the criterion of burrow openness, respecting the previous order of the modalities. Note that the modality “Tube” is optional and does not characterise the burrow itself; tubes can have one or two openings towards the water column, so it is considered “None” in the new categorisation.

```
print(w$lab[-1][indic == 2,])
```

```
##    Trait.ID Modality.ID                     Trait           Modality
## 6         2           1 Endo-bioconstruction type     None/Surficial
## 7         2           2 Endo-bioconstruction type     Rugosities/Pit
## 8         2           3 Endo-bioconstruction type     Chimney/Funnel
## 9         2           4 Endo-bioconstruction type               Tube
## 10        2           5 Endo-bioconstruction type   IJ-shaped burrow
## 11        2           6 Endo-bioconstruction type   UY-shaped burrow
## 12        2           7 Endo-bioconstruction type    Branched burrow
## 13        2           8 Endo-bioconstruction type Anastomosed burrow
```

```
w <- fuz.modif(w$tab, w$lab, which.trait = 2,
               merge = c(1, 1, 3, 1, 3, 2, 3, 2),
               mod = c("None", "Open-ended", "Blind-ended"))
```

As previously, `w` is a list containing similar objects `w$tab` and `w$lab`, but accordingly modified. The new table can be processed by FCA again, within the same script for the graphical representation.

```
indic <- w$lab$Trait.ID
fuz <- prep.fuzzy.var(df = w$tab, col.blocks = table(indic))
fca <- dudi.fca(fuz, scan = FALSE)
par(mfrow = c(2, 2), mar = rep(0.1, 4))
for(i in 1:max(w$lab$Trait.ID)){
  s.label(fca$li, cpoint = 0, clab = 0, cgrid = 1.5)
  points(fca$li, pch = 1, col = "grey60", cex = 1.5)
  sub <- paste(letters[i], ") ", unique(w$lab$Trait)[i], sep = "")
  s.distri(fca$li, fuz[indic == i], clab = 1, cstar = 0, cpoint = 0,
           lab = w$lab$Modality[indic == i], sub = sub,
           possub = "topleft", csub = 1.5, add.p = TRUE)
}
```

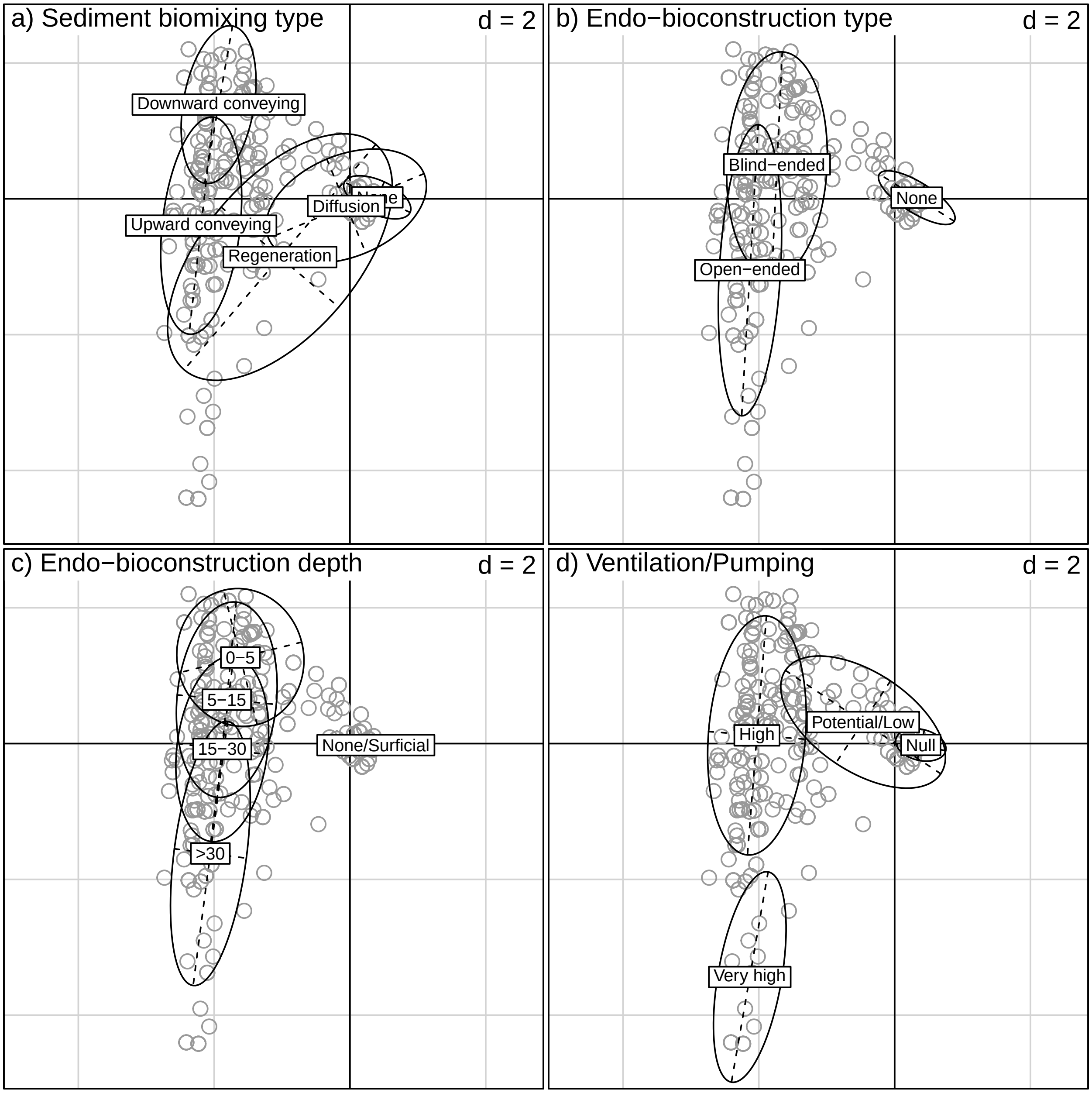

Figure S2. Endo-substratum engineering pattern after modification of the trait “Endo-bioconstruction type”. See Figure S1 for details.

S2.2 Visualisation of biological gradients

The use of multiple biological traits enable the identification of synthetic biological gradients. Sometimes, the graphical representation of a single gradient is justified either when only a single one is significant or some aspects deserve to be specifically visualised. This can be the case with trade-offs that involve coevolved traits. Typical trade-offs are found in reproductive strategies whereby energy allocation in offspring is balanced between quantity and size. For a given trait, the function `fuz.plot` distributes the modalities according to there positions along a predifined gradient as shown below.

```
#unique(MacroTraits$labels[c("Trait.ID", "Trait")])
w <- fuz.tab(which.traits = c(10, 14:18))
tab <- w$tab
lab <- w$lab
indic <- lab$Trait.ID
fuz <- prep.fuzzy.var(df = tab, col.blocks = table(indic))
fca <- dudi.fca(fuz, scannf = FALSE)
par(mfrow = c(3, 2), mar = c(4, 8, 3, 1))
for(i in 1:max(indic)){
  # Order trait modalities according to their respective first axis score
  x <- tab[indic == i][order(fca$co[,1][indic == i])]
  # Similarly for modality labels
  mod <- lab$Modality[indic == i][order(fca$co[,1][indic == i])]
  # Plotting execution
  fuz.plot(x = x, y = fca$li[,1], ylab = "", mod = mod)
  # Add trait label
  mtext(unique(lab$Trait)[i], cex = 1, adj = 0, line = 1)
}
```

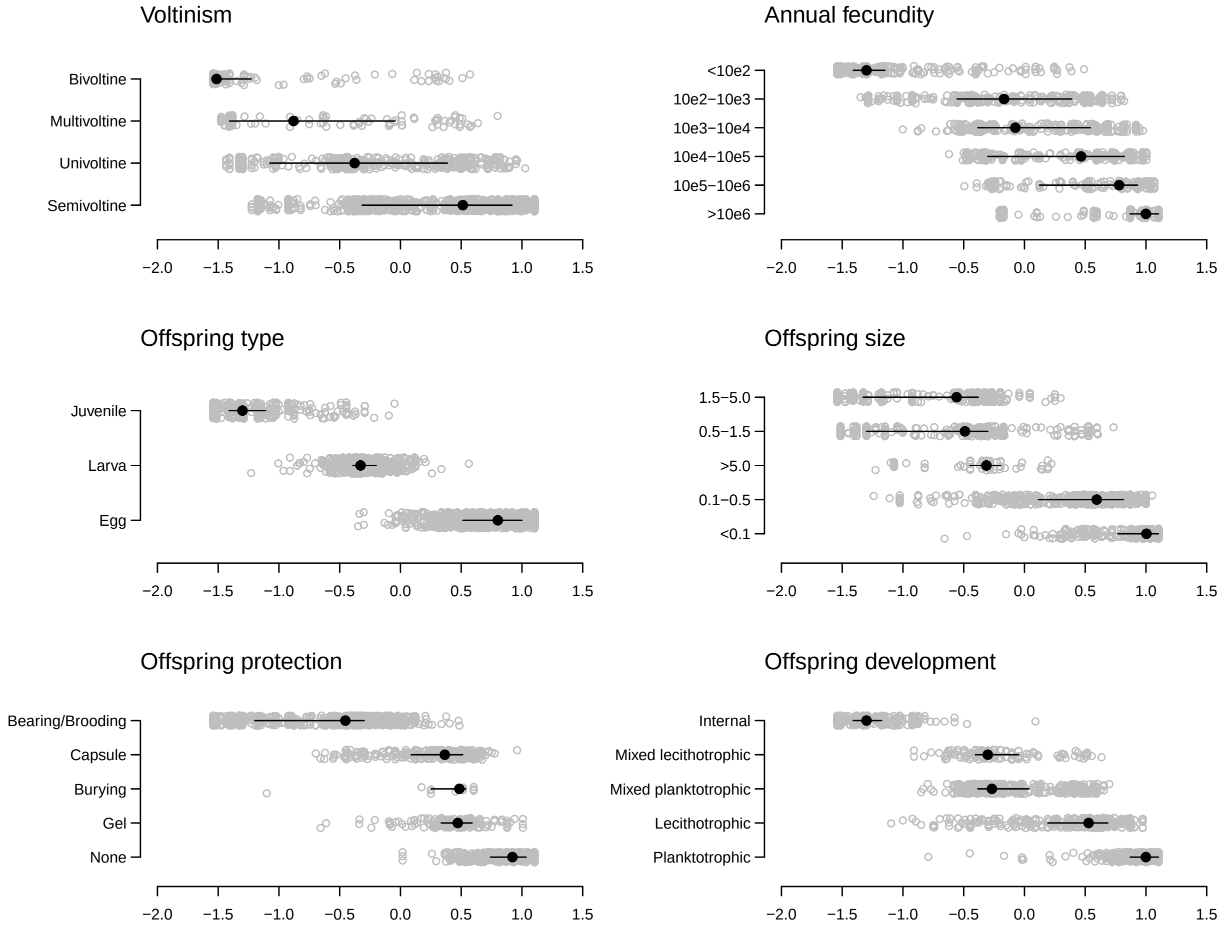

Figure S3. Reproductive and developmental trait modality distributions along the first axis of their Fuzzy Correspondence Analysis.

S3 Building indices incorporating several fuzzy traits

S3.1 Reproductive allocation

Energy allocation into reproduction or self-maintenance represents an important trade-off in life-history strategies (Stearns 1992). Reproductive allocation can be calculated as the ratio of reproductive output (product of fecundity by offspring size) by body mass (Clarke 1987). The function `fuz.comb` enables an easy combination of different fuzzy traits into a same formula. The argument `list.sco` is a list containing vectors of modality performance scores. Here, fecundity and body mass follow a log10 scale, so performance scores are attributed integers. As offspring size is coded according to more arbitrary intervals, median values are attributed. By default, traits are equally weighted by dividing performance scores by their maximum. For a species profile, a single value is obtained by summing the products of fuzzy scores (0 or 1) by the performance scores (ranging between 0 and 1), which is a weighted mean. Before being combined in the formula, each trait is rescaled between 0 and 1. By default, the formula is the cumulative product of the selected traits, but any change is possible by rewriting the formula with the desired operators between traits that are noted “x1”, “x2”,…, “xn” for n traits according to their order in the data frame `tab`.

```
#print(unique(MacroTraits$labels[c("Trait.ID", "Trait")]))
w <- fuz.tab(which.traits = c(14, 16, 23))
tab <- w$tab
lab <- w$lab
taxo <- MacroTraits$taxonomy
#identical(taxo$Species, rownames(tab))
print(lab[-1])
```

```
##    Trait.ID Modality.ID            Trait     Modality
## 1         1           1 Annual fecundity        <10e2
## 2         1           2 Annual fecundity    10e2-10e3
## 3         1           3 Annual fecundity    10e3-10e4
## 4         1           4 Annual fecundity    10e4-10e5
## 5         1           5 Annual fecundity    10e5-10e6
## 6         1           6 Annual fecundity        >10e6
## 7         2           1   Offspring size         <0.1
## 8         2           2   Offspring size      0.1-0.5
## 9         2           3   Offspring size      0.5-1.5
## 10        2           4   Offspring size      1.5-5.0
## 11        2           5   Offspring size         >5.0
## 12        3           1        Body mass       <0.001
## 13        3           2        Body mass  0.001-0.010
## 14        3           3        Body mass  0.010-0.100
## 15        3           4        Body mass  0.100-1.000
## 16        3           5        Body mass 1.000-10.000
## 17        3           6        Body mass      >10.000
```

```
sco.list <- list(1:6,
                 c(0.05, 0.3, 1, 3.25, 6),
                 1:6)
y <- fuz.comb(tab, lab, list.sco = sco.list,
              formula = "x1 * x2 / x3")
```

The resulting synthetic and continuous trait can be represented per clade. With the taxonomy in `MacroTraits$taxonomy`, we choose the orders containing a minimum of 30 species.

```r
w <- taxo["Order"]
x <- model.matrix(data = w, ~ 0 + Order)
x <- data.frame(x)
colnames(x) <- unique(sort(w[,1]))
colnames(x) <- gsub("[unassigned] ", "", colnames(x), fixed = TRUE)
rownames(x) <- taxo$Species
x <- x[apply(x, 2, sum) >= 30]
x <- x[apply(x, 1, sum) > 0,]
y <- y[names(y) %in% rownames(x)]
taxo <- taxo[taxo$Species %in% rownames(x),]
x <- x[order(tapply(y, taxo$Order, mean))]
#identical(rownames(x), names(y))
par(mar = c(5, 8, 1, 1))
ylab <- expression(paste("Reproductive allocation (",
                         bar(x) %+-% CI, ")", sep = ""))
fuz.plot(x, y, mean, "ci", ylim = c(0, 0.5),
         pch.p = "", ylab = ylab)
```

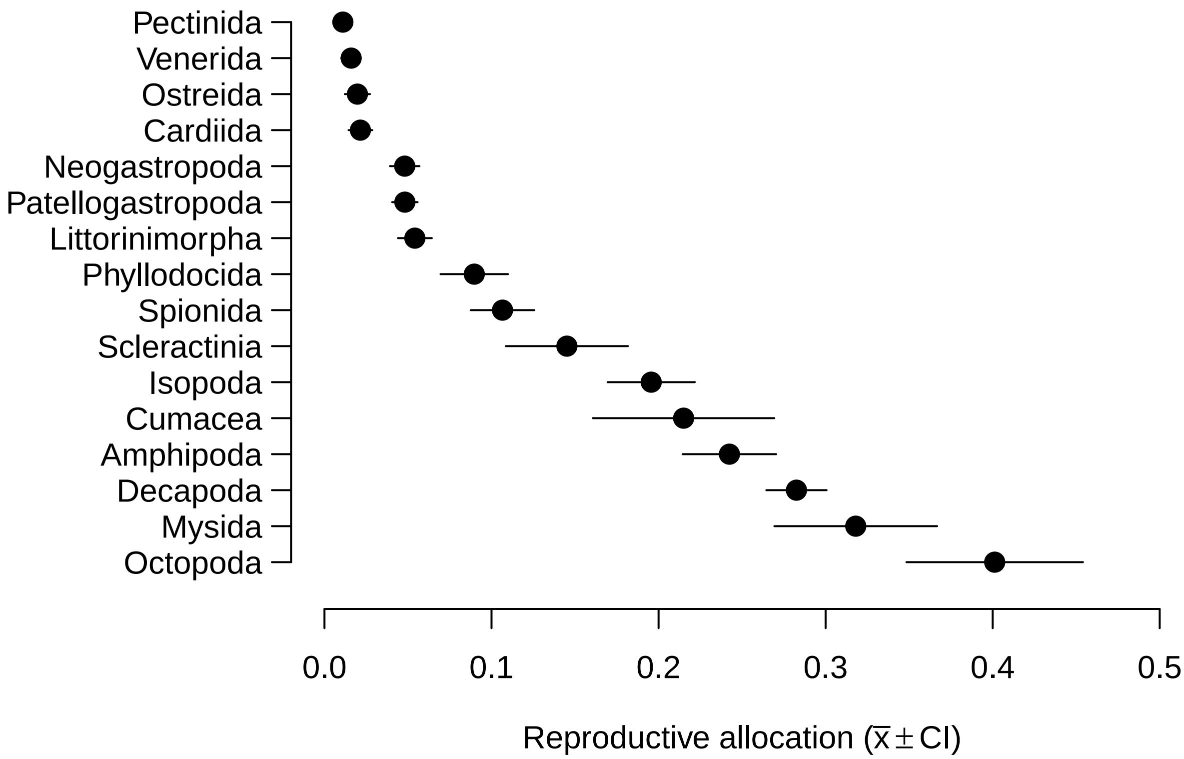

Figure S4. Reproductive allocation as the ratio of reproductive output over body mass within various orders. Each group comprises a minimum of 30 species.

In Figure S4, although reproductive allocation, as a dimensionless ratio, is a coarse approximation of the reality, the trend is quite consistent with general considerations (Bekeuma 1989, Giangrande et al. 1994, Marshall and Keough 2007, Kooijman and Augustine 2022). The gradient opposes high fecundity in sessile egg broadcasters (bivalves) to low fecundity in highly mobile internal or external incubators (Malacostraca and Cephalopoda). The formers are characterised by less efficient fertilisation and experience fewer reproductive successes that need to be compensated by longer reproductive life span while the latters, mostly semelparous, experience a high reproductive success immediately after maturing and that does not require multiple reproductive attempts. Interestingly, body size remains independent as underlined by the proximity between tiny crustaceans (e.g., amphipods, mysids) and comparably gigantic octopuses.

S3.2 Intrinsic rate of natural increase

Intrinsic rate of natural increase (r) is another important descriptor of adaptation to disturbance frequency (Stearns 1992). Its empirical assessment is irrealistic for many species as it requires the follow up of several generations, which can take several decades or centuries. Savage et al. (2004) provided evidence that inversed age at maturity (alpha) is proportional to r. Recently, Beauchard and Soetaert (2026), using measurement on short-lived species estimated r = 2.26 * 1/alpha. Similar to reproductive output, we can use the `fuz.comb` function to calculate r.

```
#print(unique(MacroTraits$labels[c("Trait.ID", "Trait")]))
w <- fuz.tab(which.traits = 9)
tab <- w$tab
lab <- w$lab
taxo <- MacroTraits$taxonomy
#identical(taxo$Species, rownames(tab))
print(lab)
```

```
##   Column.name Trait.ID Modality.ID           Trait Modality
## 1       T1.M1        1           1 Age at maturity      <6m
## 2       T1.M2        1           2 Age at maturity    6m-1y
## 3       T1.M3        1           3 Age at maturity     1-3y
## 4       T1.M4        1           4 Age at maturity     3-5y
## 5       T1.M5        1           5 Age at maturity     5-7y
## 6       T1.M6        1           6 Age at maturity      >7y
```

```
y <- fuz.comb(tab, lab,
              list.sco = list(c(0.25, 0.75, 1.5, 4, 6, 8)),
              formula = "2.26 / x1", sco.scale = FALSE, trait.scale = FALSE)
```

The variable can be represented with the same taxonomic partition as previously used (Fig. S5).

```
w <- taxo["Order"]
x <- model.matrix(data = w, ~ 0 + Order)
x <- data.frame(x)
colnames(x) <- unique(sort(w[,1]))
colnames(x) <- gsub("[unassigned] ", "", colnames(x), fixed = TRUE)
rownames(x) <- taxo$Species
x <- x[apply(x, 2, sum) >= 30]
x <- x[apply(x, 1, sum) > 0,]
y <- y[names(y) %in% rownames(x)]
taxo <- taxo[taxo$Species %in% rownames(x),]
x <- x[order(tapply(y, taxo$Order, mean))]
#identical(rownames(x), names(y))
par(mar = c(5, 8, 1, 1))
ylab <- expression(paste("Intrinsic rate of natural increase (",
                         bar(x) ~ year^-1 %+-% CI, ")", sep = ""))
fuz.plot(x, y, mean, "ci", ylim = c(0, 8),
         pch.p = "", ylab = ylab)
```

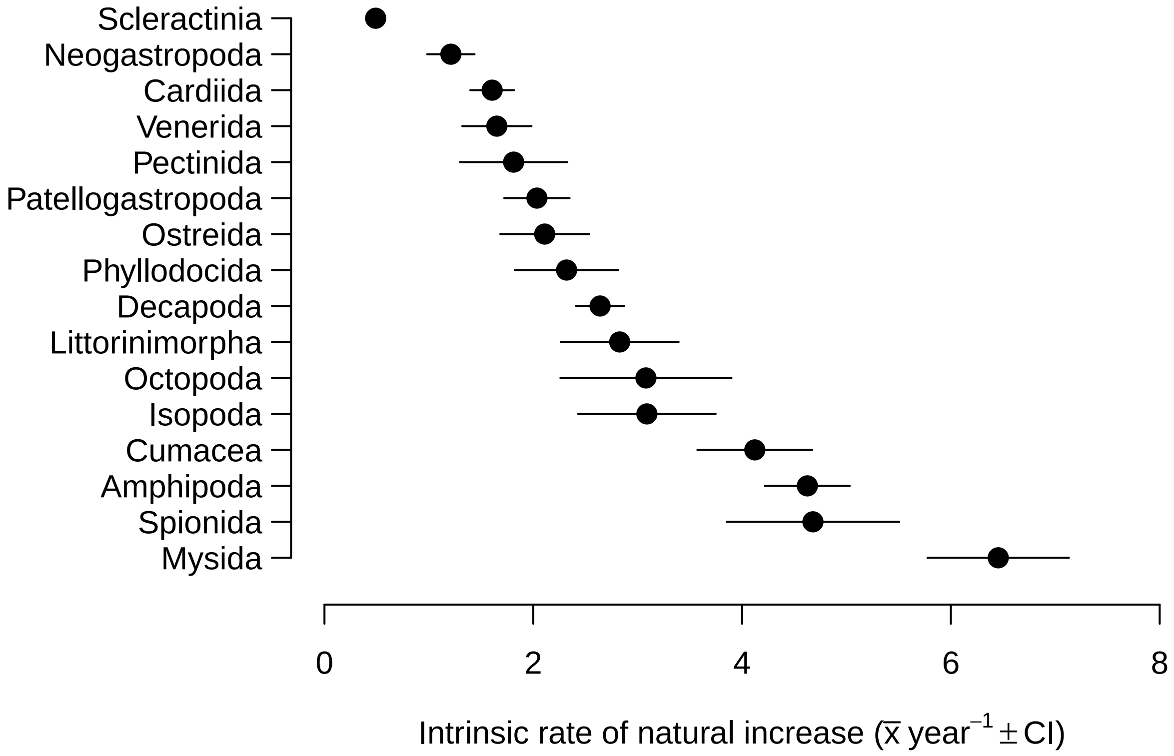

Figure S5. Intrinsic rate of natural increase in various orders. Each group comprises a minimum of 30 species.

S3.3 Conversion of a fuzzy trait into a continuous one

The function `fuz.comb`, in its simplest use, is the conversion of a fuzzy trait into a continuous one. Let's consider the example of age at maturity and life span. As these traits are conmtinuous, we fix `sco.scale = FALSE` and `trait.scale = FALSE` in order to keep the magnitude measured in years.

```
#Age at maturity
w <- fuz.tab(which.traits = 9)
tab <- w$tab
lab <- w$lab
#print(lab)
alpha <- fuz.comb(tab, lab,
                  list.sco = list(c(0.25, 0.75, 1.5, 4, 6, 8)),
                  sco.scale = FALSE, trait.scale = FALSE)
w <- fuz.tab(which.traits = 8)
tab <- w$tab
lab <- w$lab
#print(lab)
#Life span
Tmax <- fuz.comb(tab, lab,
                 list.sco = list(c(0.25, 0.75, 1.5, 6.5, 15, 35, 75, 125)),
                 sco.scale = FALSE, trait.scale = FALSE)
```

In general, these two traits are correlated (Charnov 1993); see Figure S6. On the figure, the dot size is proportional to the number of species.

```
cor.test(log(Tmax), log(alpha))
```

```
##
##  Pearson's product-moment correlation
##
## data:  log(Tmax) and log(alpha)
## t = 68.137, df = 1891, p-value < 2.2e-16
## alternative hypothesis: true correlation is not equal to 0
## 95 percent confidence interval:
##  0.8294019 0.8555185
## sample estimates:
##       cor
## 0.8429561
```

```
w <- as.data.frame(table(Tmax, alpha))
w <- w[w$Freq > 0,]
x <- as.numeric(as.character(w$Tmax))
y <- as.numeric(as.character(w$alpha))
par(mar = c(4, 5, 1, 1), cex.axis = 0.8)
plot(log(x), log(y), bty = "n", pch = 20, cex = log(w$Freq),
     xlim = log(c(0, 200)+1), ylim = log(c(0, 12)+1),
     xaxt = "n", yaxt = "n", xlab = "", ylab = "")
clip(0, 5, 0, 2.5)
abline(lm(log(alpha) ~ log(Tmax) - 1))
axis(side = 1, at = log(c(1, 3, 10, 40, 150)), lab = c(0, 3, 10, 40, 150))
axis(side = 2, at = log(c(1, 2, 4, 7, 10)), lab = c(0, 2, 4, 7, 10))
mtext(side = 1, "Life span (years)", line = 2.3, cex = 1)
mtext(side = 2, "Age at maturity (years)", line = 2.2, cex = 1)
```

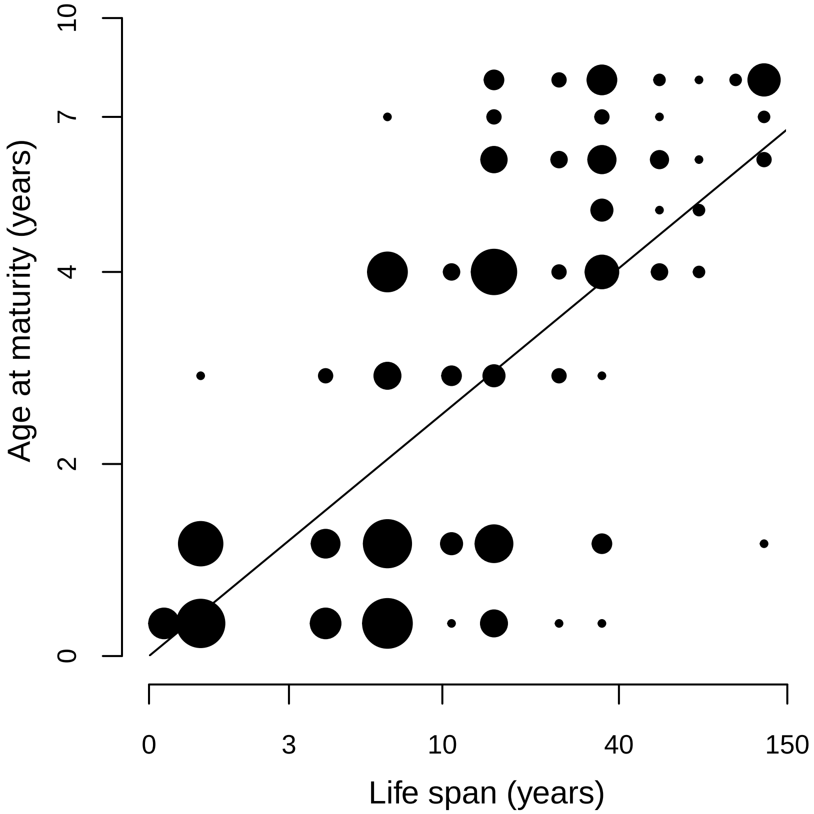

Figure S6. Relationship between life span and age at maturity after conversion from fuzzy to continuous format. Dot size proportional to number of species.

The reverse operation, the conversion of a continuous trait into a fuzzy one is also possible in fuzR. The function `fuz.conv` generates a series of binary variables from a continuous trait. The user is free to define interval boundaries. It is useful for technical purposes such as homogenising a data set, coping with outliers or circumventing problems of multivariate non-linearity. See `?fuz.conv`.

S3.3 Indices of ecosystem function

In the marine benthos, ecosystem functions represent also an important domain of trait index development. The mechanisms through which benthic species engineer the sea floor can be quantified by combining appropriate biological traits. Among engineering functions, bioturbation, the effects of animals that directly or indirectly impact biogeochemical transports through sediment matrices, includes biomixing as solid particle displacement or reworking, and bioirrigation as water transport (Kristensen et al. 2012). Biodeposition is the transfert of materials from the water column to the sea floor (pelagic-benthic coupling) (Gili and Coma 1998).

S3.3.1 Biomixing

Sediment biomixing has been subject to quantification with particular interest (Swift 1993, Solan et al. 2004, Queirós et al. 2013). The trait “Biomixing type” includes the four types of sediment displacements induced by the fauna (François et al. 1997): biodiffusion as random sediment particle displacements; upward and downward conveying as non-local and vertical transfers of particles (advection); regeneration as sudden upward displacement and later followed by sudden downward burrow collapse.

Solan et al. (2004) proposed an index called "bioturbation potential" (BP) that multiplies faunal abundance, mobility and a score of sediment reworking type (R) that combines biomixing type, motility and burying depth: 1 = epibenthos; 2 = surficial diffusor (1-2 cm); 3 = advector; 4 = deep diffusor; 5 = regenerator. R is considered to express the magnitude of sediment biomixing (also called "reworking"). Then, BP equals to the multiplication of observed faunal biomass, mobility and R.

Although this framework represents important advances and focus in current researches, it exhibits some limitations. (1) While R is purely categorical, an organism can differently rework the sediment; for instance, a large crab can induce substantial bioffusion when walking on the sediment and regeneration when burying; callianassid shrimps, considered as specifically biodiffusors (Queirós et al. 2013), are also and particularly upward conveyors as shown by important "volcano-shaped" mounds around the burrow opening (Rowden et al. 1998). (2) So far, the quantification of R has been limited to European waters by expert jugement (Queirós et al. 2013), without possible generalisation in faunas from other parts of the world through a universal and easily applicable formula beyond expert jugement. (3) Some inconsistencies in category attribution may occur among the taxa currently documented.

The MacroTraits data base provides an up-to-date fuzzy version of traits required to an equivalent of R, with detailed sediment depth distribution and mobility. In absence of field biomass, adult individual body mass at the species level is available; note that its log10 scale expressed through `sco.scale = 1:6` results in a similar effect than the square root of total community biomass in the formula from Solan et al. (2004). Here, we illustrate index computation for taxa typical of soft sediments (410 species).

```
#print(unique(MacroTraits$labels[c("Trait.ID", "Trait")]))
w <- fuz.tab(which.traits = c(5:6, 23, 26, 33, 36:37))
tab <- w$tab
lab <- w$lab
#Select soft-sediment species
print(lab[-1])
```

```
##    Trait.ID Modality.ID                     Trait          Modality
## 1         1           1                 Substratum     Mud-Sandy mud
## 2         1           2                 Substratum       Muddy sand
## 3         1           3                 Substratum             Sand
## 4         1           4                 Substratum     Mixed gravel
## 5         1           5                 Substratum           Gravel
## 6         1           6                 Substratum  Mixed soft-hard
## 7         1           7                 Substratum             Hard
## 8         2           1 Substratum depth occupancy                0
## 9         2           2 Substratum depth occupancy              0-5
## 10        2           3 Substratum depth occupancy             5-15
## 11        2           4 Substratum depth occupancy            15-30
## 12        2           5 Substratum depth occupancy              >30
## 13        2           6 Substratum depth occupancy      Crevice/Den
## 14        3           1                  Body mass           <0.001
## 15        3           2                  Body mass      0.001-0.010
## 16        3           3                  Body mass      0.010-0.100
## 17        3           4                  Body mass      0.100-1.000
## 18        3           5                  Body mass     1.000-10.000
## 19        3           6                  Body mass          >10.000
## 20        4           1                   Mobility         Immobile
## 21        4           2                   Mobility          Limited
```

```
## 22        4           3                   Mobility               Slow
## 23        4           4                   Mobility               Fast
## 24        4           5                   Mobility          Very fast
## 25        5           1  Endo-bioconstruction type     None/Surficial
## 26        5           2  Endo-bioconstruction type     Rugosities/Pit
## 27        5           3  Endo-bioconstruction type     Chimney/Funnel
## 28        5           4  Endo-bioconstruction type               Tube
## 29        5           5  Endo-bioconstruction type   IJ-shaped burrow
## 30        5           6  Endo-bioconstruction type   UY-shaped burrow
## 31        5           7  Endo-bioconstruction type    Branched burrow
## 32        5           8  Endo-bioconstruction type Anastomosed burrow
## 33        6           1        Ventilation/Pumping               Null
## 34        6           2        Ventilation/Pumping      Potential/Low
## 35        6           3        Ventilation/Pumping               High
## 36        6           4        Ventilation/Pumping          Very high
## 37        7           1    Sediment biomixing type               None
## 38        7           2    Sediment biomixing type          Diffusion
## 39        7           3    Sediment biomixing type   Upward conveying
## 40        7           4    Sediment biomixing type Downward conveying
## 41        7           5    Sediment biomixing type       Regeneration
```

```r
hard <- tab[lab$Modality %in% c("Mixed soft-hard", "Hard")]
hard <- apply(hard, 1, sum)
tab <- tab[hard == 0,]
taxo <- MacroTraits$taxonomy
taxo <- taxo[taxo$Species %in% rownames(tab),]
taxo <- unique(taxo[c("Phylum", "Family", "Species")])
#print(unique(taxo[1:2][order(taxo[,1], taxo[,2]),]))
taxo <- taxo[taxo$Family %in% c(#Annelids
                                "Arenicolidae", "Capitellidae", "Cirratulidae",
                                "Glyceridae", "Magelonidae", "Nephtyidae",
                                "Onuphidae", "Opheliidae", "Oweniidae",
                                "Spionidae", "Terebellidae",
                                #Arthropods
                                "Ampeliscidae", "Axiidae", "Bathyporeiidae",
                                "Bodotriidae", "Callianassidae", "Callichiridae",
                                "Cirolanidae", "Corophiidae", "Crangonidae",
                                "Diastylidae", "Diogenidae", "Gammaridae",
                                "Geryonidae", "Haustoriidae", "Hippidae",
                                "Idoteidae", "Lithodidae", "Mysidae",
                                "Nephropidae", "Ocypodidae", "Oregoniidae",
                                "Polybiidae", "Portunidae", "Sesarmidae",
                                "Upogebiidae", "Urothoidae", "Varunidae",
                                #Echinoderms
                                "Amphiuridae", "Asteriidae", "Brissidae",
                                "Holothuriidae", "Loveniidae", "Ophiuridae",
                                #Bivalves
                                "Cardiidae", "Donacidae", "Macridae", "Nuculidae",
                                "Mesodesmatidae", "Pectinidae", "Pharidae",
                                "Pinnidae", "Semelidae", "Solenidae",
                                "Tellinidae", "Veneridae", "Yoldiidae"),]
#Excluding, Paphies ventricosa, bivalve with disproportionate biomass
tab <- tab[rownames(tab) != "Paphies ventricosa",]
taxo <- taxo[taxo$Species != "Paphies ventricosa",]
```

```
taxo$tax <- paste(taxo$Phylum, taxo$Family, sep = " - ")
tab <- tab[rownames(tab) %in% taxo$Species,]
```

Let's calculate biomixing potential for each reworking mode by multiplying body mass, substratum depth occupancy and mobility. As the four reworking modes are calculated in a same way, their ranges can be compared (Figure S7).

```
#Data frame to store resulting indices
res <- data.frame(matrix(0, nrow(tab), 4))
colnames(res) <- lab$Modality[lab$Trait == "Sediment biomixing type"][-1]
rownames(res) <- rownames(tab)
for(i in 1:4){
  #Consider successively each biomixing type
  sco.biomix <- matrix(c(0, 1, 0, 0, 0,
                         0, 0, 1, 0, 0,
                         0, 0, 0, 1, 0,
                         0, 0, 0, 0, 1),
                       nr = 4, byrow = TRUE)
  #Performance scores of each trait
  list.sco <- list(c(1, 2.5, 10, 22.5, 30, 0),
                   c(1:6),
                   c(0:4),
                   sco.biomix[i,])
  #Combine the selected traits
  res[,i] <- fuz.comb(tab, lab, which.traits = c(2:4, 7),
                      list.sco = list.sco)
}
#Represent the non-null values of each index
par(mfrow = c(4, 1), mar = c(2, 3, 2, 1))
for(i in 1:4){
  w <- res[,i][res[,i] > 0]
  r <- range(pretty(c(min(res[res>0]), max(res))))
  hist(w, xlim = r, main = colnames(res)[i], breaks = seq(r[1], r[2], len = 20),
       freq = FALSE, col = 1, border = "white", ylim = c(0, 30))
}
```

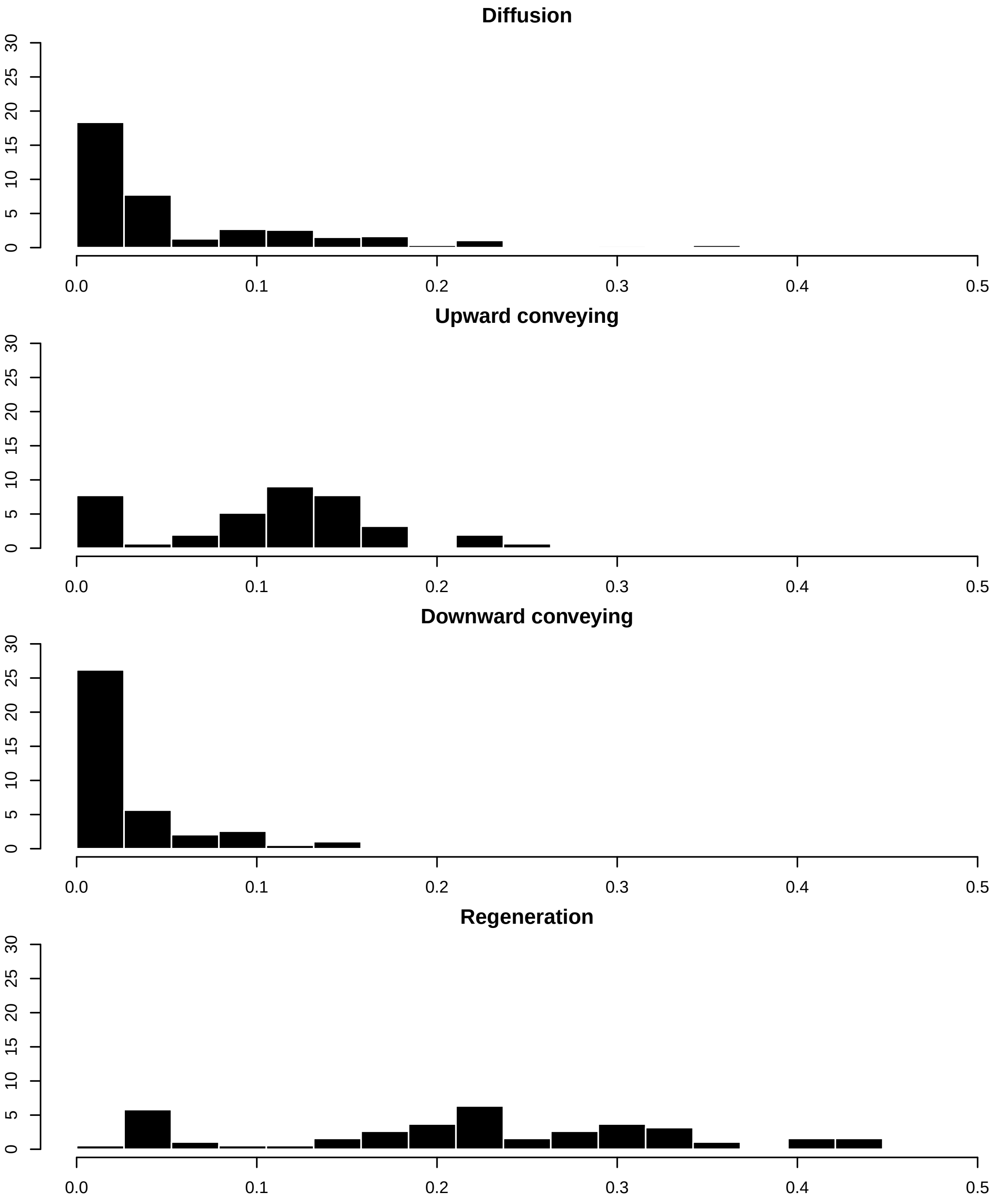

Figure S7. Distributions of the four sediment biomixing modes. The same 417 species are considered in each panel.

If the reworking magnitude of the burrowing fauna must be considered based on those three traits, then biomixing type is not discriminant of the magnitude, except, to a lesser extent, regeneration (Fig. S7). Hence, in case of biogeochemical or species community compositional justification, each biomixing type can be separately investigated. Otherwise, a single biomixing index can result in the product of the four scores.

```r
biomix <- fuz.comb(tab, lab, which.traits = c(2:4, 7),
                   list.sco = list(c(1, 2.5, 10, 22.5, 30, 0),
                                   c(1:6),
                                   c(0:4),
                                   c(0, 1, 1, 1, 1)))
x <- taxo["Family"]
x <- model.matrix(data = x, ~ 0 + Family)
x <- data.frame(x)
w <- taxo[order(taxo$Family),]
colnames(x) <- unique(w$tax)
w <- unique(w[c("Phylum", "Family")])
x <- x[order(w[,1], tapply(biomix, taxo$Family, mean))]
par(mar = c(3, 13, 1, 1))
fuz.plot(x, biomix)
```

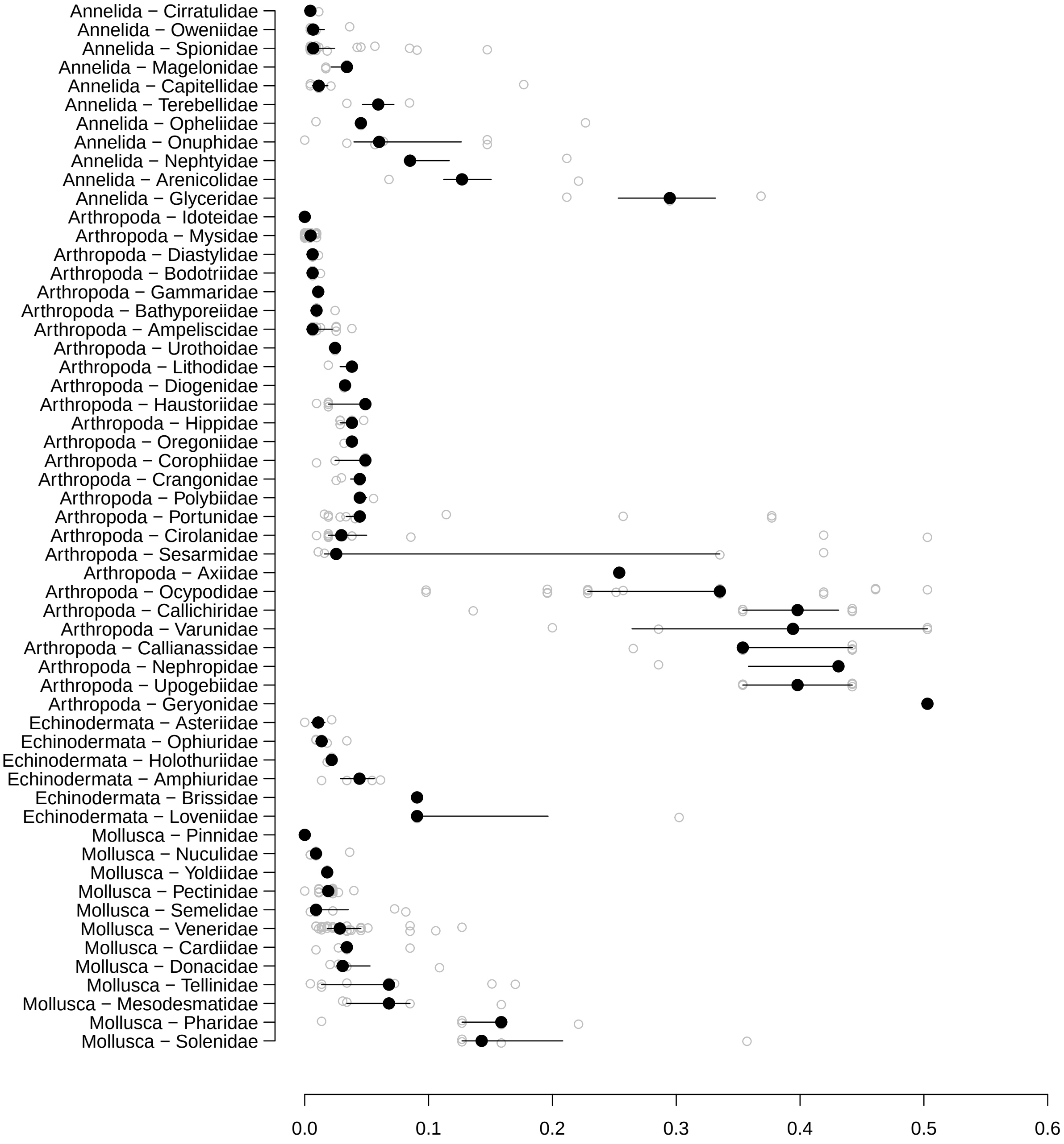

Figure S8. Total biomixing score per family as the product of the four individual biomixing types (biodiffusion, upward conveying, downward conveying and regeneration). Grey dots, species; black dot, mean; bars extend from 25th to 75th percentile.

In Figure S8, consistent variations from immobile or small taxa such as large pen shells (Pinnidae) or tiny crustacean (Idoteidae) to highly mobile and deep burrowing ones such as gerionid, fidler and magrove crabs (Ocypodidae, Varunidae), and mud shrimps (Callianassidae, Callichiridae, Upogebiidae). In between lies various combinations of trait performances. Rag worms (Nereidae), lug worms (Arenicolidae), brittle stars (Amphiuridae), urchins (Brissidae and Loveniidae) and razor clams (Pharidae, solenidae) are slowly mobile, but deep and sometimes massive burrowers. Small amphipods (Ampeliscidae) are very active and some of them deep burrowers (Corophiidae, Haustoridae, Urotheidae).

S3.3.2 Bioirrigation

Bioirrigation is a function of ventilation or pumping ability in buried organisms, burrow type and water injection depth (Kristensen et al. 2012). Here, the distinction bewteen “burying” and “burrowing” is crucial since the former state does not imply an endo-bioconstruction such as a burrow that can more easily transfer water. Then, the type of burrow is assumed to be determinant depending on its contact with the sediment surface: water should be more flushed through a system that starts and ends at the sediment-water interface (e.g., “U-shaped”) than a system that ends within the sediment matrix (single or multiple ends). However, the absence of permanent or semi-permanent burrow does not exclude significant sediment irrigation through local pore water transport induced by body movements (Aller 1982, Kristensen 1988, Berg et al. 2001, Volkenborn et al. 2012, Volkenborn et al. 2016). Such an ability is expressed by the modality “Potential/Low” from the trait “Ventilation/Pumping”. The modality “None” is especially attributed to strictly epibenthic species, and “High” and “Very high” when documented or assumed, in general in deep gallery builders (Lindroth 1941, Kristensen 1988). “Very high” is specifically attributed to buried suspension-feeders that likely ventilate more due to feeding requirements as evidenced in nereid worms and mud shrimps (Kristensen 1981, Christensen et al. 2000, Kristensen and Kostka 2005, Kristensen et al. 2012).

Wrede et al. (2018) provided a first empirical quantification and assessment of a bioirrigation index. Faunal biomass is multiplied by injection depth and feeding type whereby suspension feeding, carnivory, deposit feeding and sub-surface suspension feeding are attributed the scores 1, 2, 3 and 4, respectively. The MacroTraits data enable the calculation of such an index, with possible improvements. (1) As for biomixing, the fuzzy version of the data can provide more precise estimates. (2) The use of scored feeding types by Wrede et al. (2018) might be too arbitrary. Consistently, buried suspension-feeders are attributed the highest score. However, there is no justification to attribute different scores between depositivore, suspensivore and carnivore. Therefore, we propose a simpler index that includes burrow type, injection depth and ventilation ability, the most complex part of the mechanism being expressed by the trait “Ventilation/Pumping”.

Firstly, the trait “Endo-bioconstruction type”, that includes burrow type, is modified in order to only express the three modalities of interest. The modality “Tube” becomes “None”; by this way, a species that buids a IJ-shaped burrow with a tube is attributed a 1/0/1 profile (i.e., for None/Open-ended/Blind-ended). Then, the weighted-mean performance score will account for it as tubes reduce water exchanges between the burrow and the sediment matrix (up to 10-40 % of flux in free solution; Aller 1983).

```r
#print(lab)
w <- fuz.modif(tab, lab, which.trait = 5,
               merge = c(1, 1, 3, 1, 3, 2, 3, 2),
               mod = c("None", "Open-ended", "Blind-ended"))
tab <- w$tab
lab <- w$lab
print(lab[lab$Trait.ID == 5,])
```

```
##     Column.name Trait.ID Modality.ID                     Trait    Modality
## 110       T5.M1        5           1 Endo-bioconstruction type        None
## 25        T5.M2        5           2 Endo-bioconstruction type  Open-ended
## 31        T5.M3        5           3 Endo-bioconstruction type Blind-ended
```

Injection depth was expressed by substratum depth occupancy. Mobile species that build a burrow may not always occur at the maximum depth of the burrow, whereas they can inject water deeper. So, we fix `fun = c("max", rep("sum", 3))` whereby, for the first trait (depth occupancy), the score for maximum depth is selected while score for the three other traits remain a weighted mean as the sum of fuzzy and performance score products. Burrow type scoring is subject to debate. While Wrede et al. (2018) attributed highest score to blind-ended burrow, Renz et al. (2018) argued that open- or blind-ended type is not determinant as other factors may create context dependency. Here, we attribute highest score to blind-ended burrow since the induced increased pressure enhances radial advective exchanges with the surrounding sediment (Aller

1984, Meysman et al. 2005), effects being exacerbated over depth (Ziebis et al. 1996, Satoh and Okabe 2013).

```r
print(lab[-1])
```

```
##     Trait.ID Modality.ID                      Trait           Modality
## 1          1           1                 Substratum      Mud-Sandy mud
## 2          1           2                 Substratum         Muddy sand
## 3          1           3                 Substratum               Sand
## 4          1           4                 Substratum       Mixed gravel
## 5          1           5                 Substratum             Gravel
## 6          1           6                 Substratum    Mixed soft-hard
## 7          1           7                 Substratum               Hard
## 8          2           1 Substratum depth occupancy                  0
## 9          2           2 Substratum depth occupancy                0-5
## 10         2           3 Substratum depth occupancy               5-15
## 11         2           4 Substratum depth occupancy              15-30
## 12         2           5 Substratum depth occupancy                >30
## 13         2           6 Substratum depth occupancy        Crevice/Den
## 14         3           1                  Body mass             <0.001
## 15         3           2                  Body mass        0.001-0.010
## 16         3           3                  Body mass        0.010-0.100
## 17         3           4                  Body mass        0.100-1.000
## 18         3           5                  Body mass       1.000-10.000
## 19         3           6                  Body mass            >10.000
## 20         4           1                   Mobility           Immobile
## 21         4           2                   Mobility            Limited
## 22         4           3                   Mobility               Slow
## 23         4           4                   Mobility               Fast
## 24         4           5                   Mobility          Very fast
## 110        5           1  Endo-bioconstruction type               None
## 25         5           2  Endo-bioconstruction type         Open-ended
## 31         5           3  Endo-bioconstruction type        Blind-ended
## 33         6           1        Ventilation/Pumping               Null
## 34         6           2        Ventilation/Pumping      Potential/Low
## 35         6           3        Ventilation/Pumping               High
## 36         6           4        Ventilation/Pumping          Very high
## 37         7           1    Sediment biomixing type               None
## 38         7           2    Sediment biomixing type          Diffusion
## 39         7           3    Sediment biomixing type   Upward conveying
## 40         7           4    Sediment biomixing type Downward conveying
## 41         7           5    Sediment biomixing type       Regeneration
```

```r
bioirr <- fuz.comb(tab, lab, which.traits = c(2:3, 5, 6),
                   list.sco = list(c(0, 2.5, 10, 22.5, 30, 0),
                                   c(1:6),
                                   c(1:3),
                                   c(1:4)),
                   fun = c("max", rep("sum", 3)))
x <- taxo["Family"]
x <- model.matrix(data = x, ~ 0 + Family)
x <- data.frame(x)
w <- taxo[order(taxo$Family),]
```

```
colnames(x) <- unique(w$tax)
w <- unique(w[c("Phylum", "Family")])
x <- x[order(w[,1], tapply(bioirr, taxo$Family, mean))]
par(mar = c(3, 13, 1, 1))
fuz.plot(x, bioirr)
```

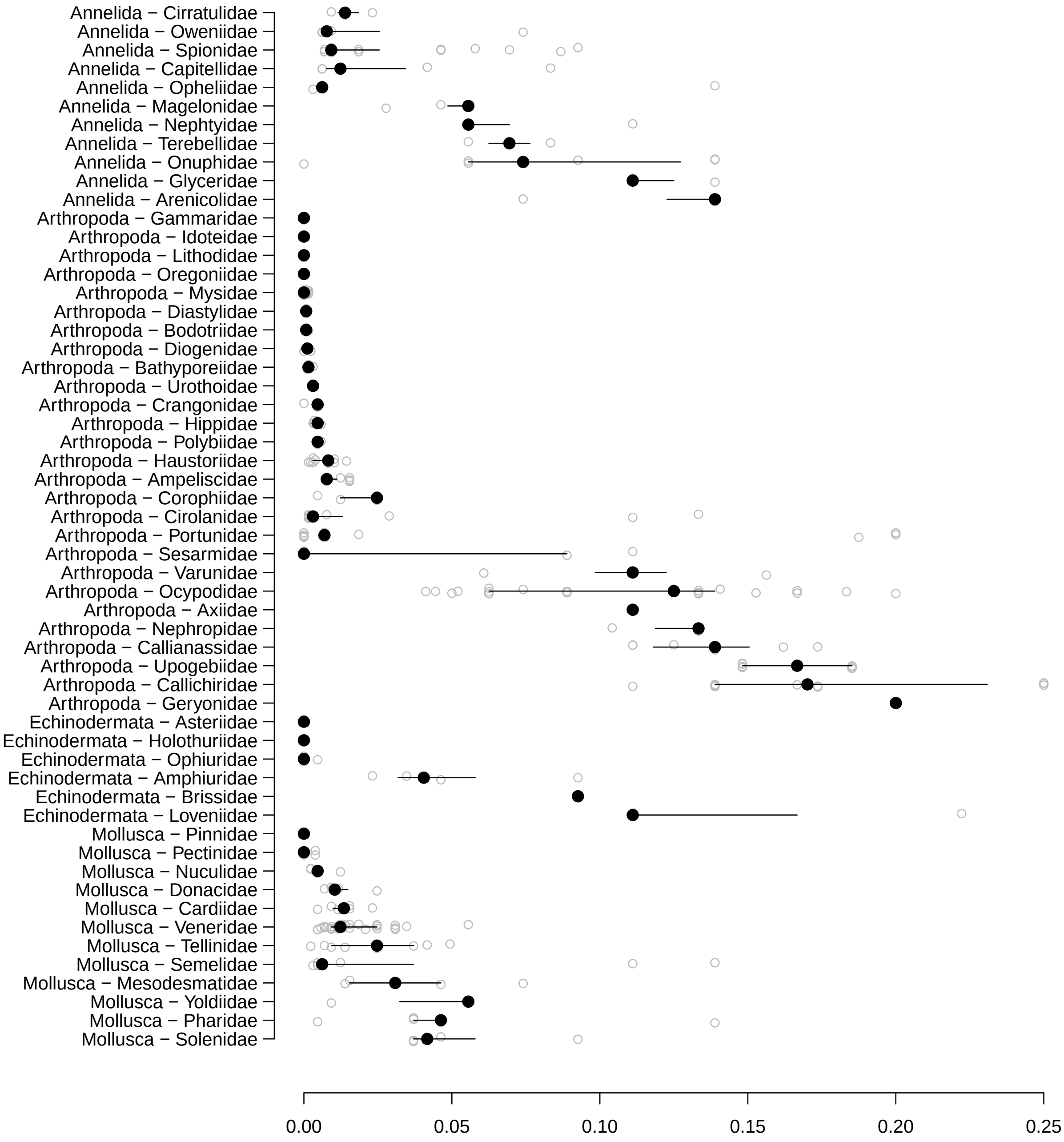

Figure S9. Total bioirrigation score per family. Grey dots, species; black dot, mean; bars extend from 25th to 75th percentile.

The figure returns a consistant image of current considerations, especially, as biomixing, the fact that only a few species among many produce disproportionate effects on the sediment (Solan et al. 2004). Two species, Chaetopterus variopedatus and Urechis caupo, with disproportionate scores (> 0.3 and > 0.5, respectively), were discarded for a better visualisation. Further improvements could include the mobility as several arthropods do not remain sedentary in their burrow, but continuously build new burrow systems (e.g., Callianassidae) while relic burrows can still ensure a minimum of passive irrigation (Aller 1984).

S3.3.3 Further considerations on ecosystem functions

It is important to keep in mind that a synthetic index as examplified above remains a trait as it is calculated at the species level. In related applications from the literature, values of individual taxa are usually aggregated to obtain community scores (i.e., community-weighted mean, "CWM"). However, Peres-Neto et al. (2017) pointed to critical issues with CWM when correlating CWM scores with other variables measured at the sample level. Technically, as CWM ignores within-community trait variations; experimentally, attributing random trait scores can yield substantial correlations, hence leading to excessively inflated type I error. Instead, the Fourth-corner or RLQ method must be considered for sound statistical validation (Dray et al. 2014, ter Braak et al. 2017). Regarding indices of benthic ecosystem functions, any trait combination should be validated by a significant relationship to empirical measurements (e.g., field or incubated core measurements of biomixing or bioirrigation). To our knowledge, there is no such valid approach in the field of benthic ecosystem functions (Queirós et al. 2015, Wrede et al. 2018). Therefore, the development of bioturbation indices is still an open research field. Further tests should proceed through an RLQ design: empirical measurements as table R (samples x measurement variable), faunal biomass as table L (samples x taxa) and trait index as table Q (taxa x index). Note that biomass used in our examples should not be part of tested indices as it should be replaced by experimental biomasses in table L.

S4 Extraction of bibliographical sources

The source documentation related to specified species and trait combinations can be obtained through the function `get.ref`. The function simply combines the selection of trait IDs and the vector of desired species after having specified the data, label and reference data frames. The result is a long-format data frame.

```r
sp <- c("Corophium volutator", "Lanice conchilega", "Macoma balthica")
w <- get.ref(sp = sp, which.traits = c(8, 9, 25, 40))
kable(w, caption = "Table S1. Example of output from the function get.ref().") %>%
      kable_styling(latex_options = "hold_position", font_size = 9) %>%
      column_spec(3, width = "9cm")
```

Table S1. Example of output from the function get.ref().

Species	Trait	Reference
Corophium volutator	Life span	Fish JD, Mills A (1979) The reproductive biology of Corophium volutator and C. arenarium (Crustacea: Amphipoda). Journal of the Marine Biological Association of the United Kingdom 59:355□368
Corophium volutator	Age at maturity	Smit MGD, Kater BJ, Jak RG, van den Heuvel-Greve MJ (2006) Translating bioassay results to field population responses using a Leslie-matrix model for the marine amphipod Corophium volutator. Ecological Modelling 196:515–526
Corophium volutator	Motility	Meadows PS, Reid A (1966) The behaviour of Corophiurn volutator (Crustacea: Amphipoda). Journal of Zoology 150:1966:387–399

Corophium volutator	Feeding type	Jensen KT, Kristensen LD (1990) A field experiment on competition between Corophium volutator (Pallas) and Corophium arenarium Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. Journal of Experimental Marine Biology and Ecology 137:1–24
Corophium volutator	Feeding type	Meadows PS, Reid A (1966) The behaviour of Corophiurn volutator (Crustacea: Amphipoda). Journal of Zoology 150:1966:387–399
Lanice conchilega	Life span	Rabaut M (2009) Lanice conchilega, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, Ghent, 354 p
Lanice conchilega	Age at maturity	Rabaut M (2009) Lanice conchilega, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, Ghent, 354 p
Lanice conchilega	Motility	Rabaut M (2009) Lanice conchilega, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, Ghent, 354 p
Lanice conchilega	Feeding type	Rabaut M (2009) Lanice conchilega, fisheries and marine conservation: towards an ecosystem approach to marine management. PhD thesis, Ghent University, Ghent, 354 p
Macoma balthica	Life span	Gilbert MA (1973) Growth rate, longevity and maximum size of Macoma balthica (L.). Biological Bulletin 145:119–126
Macoma balthica	Age at maturity	Lammens JJ (1967) Growth and reproduction in a tidal flat population of Macoma balthica (L.). Netherlands Journal of Sea Research 3:315–382
Macoma balthica	Motility	Brafield AE, Newell GE (1961) The behaviour of Macoma balthica (L.). Journal of the Marine Biological Association of the United Kingdom 41:81–87
Macoma balthica	Feeding type	Olafsson EB (1986) Density dependence in suspension-feeding and deposit-feeding populations of the bivalve Macoma balthica: a field experiment. The Journal of Animal Ecology 55:517–526

S5 Case study on life-history strategies in the North Sea

Most functions in fuzR are not specific of the MacroTraits data base. As an application example, we reproduce the analyses of Beauchard et al. (2022) on benthic data from the Dutch sector of the North Sea. The area is composed of two main habitats: deep and low hydrodynamics (“LD”), and shallow and high hydrodynamics (“HD”). Given those contrasting environmental conditions, the authors investigated the specificity of responsive trait combinations. A particular feature of these habitats is a similar number of taxa (152 and 167 for LD and HD, respectively) and a high number in common (129) that suggest the implication of the phenomenon of “spatial contingency” (Peres-Neto et al. 2012): two similar species pools can find different solutions in habitat occupancy under variable landscape heterogeneity. Indeed, variations in environment-trait relationships over the whole area and within each habitat were found to strongly differ. The higher environmental heterogeneity within HD induced more perceptible relationships and distinctions among life-history strategies.

S5.1 Data preparation

We use the MacroTraits data as an update of the original trait data (purely qualitative) to demonstrate the vality of their fuzzy version. `Beauchard2022` contains the original habitat descritors (`env`) and faunal distributions (`fau`) as organism individual densities.

```r
library(raster)
```

```
## Loading required package: sp
```

```r
data(MacroTraits)
data(Beauchard2022)
fau <- Beauchard2022$fau
env <- Beauchard2022$env
hab <- Beauchard2022$hab
geo <- Beauchard2022$geo
bat <- Beauchard2022$bat
```

We select most of the traits considered in the original publication and add voltinism and sexuality; motility is replaced by mobility, functionaly more expressive. Although many taxa are identified at the species level, several are identified only at the genus level. The function `fuz.avg` enables the averaging of trait modality scores at the desired taxonomic level based on an existing taxa x trait data frame and a corresponding taxa x taxonomic level data frame. Within the investigated taxocenosis, the genera Gammarus and Glycera are represented in MacroTraits by some European species, but also by some others that occur outside European waters. Therefore, the argument `restrict.clade` limits the averaging to specified species biogeographically relevant. From phylum to species, the argument `max.lev` is attributed a value between 1 (phylum) and 6 (species). We limit the averaging at the genus level (5).

```r
txn <- MacroTraits$taxonomy[8:13]
print(unique(MacroTraits$labels[c(1, 3)]))
```

```
##     Trait.ID                           Trait
## 1          1                           Biome
## 6          2                        Salinity
## 11         3                     Water depth
## 18         4               Sea floor affinity
## 23         5                      Substratum
## 30         6       Substratum depth occupancy
## 36         7    Epi-bioconstruction occupancy
## 46         8                       Life span
## 54         9                 Age at maturity
## 60        10                      Voltinism
## 64        11                       Sexuality
## 68        12          Reproductive frequency
## 72        13                   Fertilisation
## 75        14                 Annual fecundity
## 81        15                  Offspring type
## 84        16                  Offspring size
## 89        17            Offspring protection
## 94        18           Offspring development
## 99        19 Offspring benthic stage duration
## 105       20 Offspring pelagic stage duration
## 111       21        Offspring settlement size
## 117       22                 Body resistance
## 122       23                       Body mass
## 128       24                     Body length
## 134       25                        Motility
## 139       26                        Mobility
```

```
## 144       27                          Rafting
## 147       28             Degree of attachment
## 150       29                        Sociality
## 153       30         Epi-bioconstruction type
## 161       31    Epi-bioconstruction extension
## 167       32         Epi-bioconstruction size
## 174       33        Endo-bioconstruction type
## 182       34       Endo-bioconstruction depth
## 187       35       Endo-bioconstruction width
## 191       36              Ventilation/Pumping
## 195       37          Sediment biomixing type
## 200       38                       Bioerosion
## 204       39                 Biostabilisation
## 207       40                     Feeding type
## 213       41                   Foraging depth
```

```
w <- fuz.tab(which.traits = c(8:21, 23, 26, 6, 40))
rc <- list(c("Gammarus locusta"),
           c("Glycera alba", "Glycera tridactyla"))
w <- fuz.avg(txc = colnames(fau), tab = w$tab, lab = w$lab,
             txn = txn, max.lev = 5, restrict.clade = rc,
             round.sco = 0.3)
```

Some trait modalities are marginally represented and some of them can be discarded.

```
apply(w$tab, 2, sum)
```

```
##  T1.M1  T1.M2  T1.M3  T1.M4  T1.M5  T1.M6  T1.M7  T1.M8  T2.M1  T2.M2  T2.M3
##     34     97     97     75     24      6      1      2     56    186    120
##  T2.M4  T2.M5  T2.M6  T3.M1  T3.M2  T3.M3  T3.M4  T4.M1  T4.M2  T4.M3  T5.M1
##     32      3      2    163     88     30      2    240     12      8    211
##  T5.M2  T5.M3  T5.M4  T6.M1  T6.M2  T6.M3  T7.M1  T7.M2  T7.M3  T7.M4  T7.M5
##     71      4      5    111     39    110     77     62     56     53     18
##  T7.M6  T8.M1  T8.M2  T8.M3  T9.M1  T9.M2  T9.M3  T9.M4 T10.M1 T10.M2 T10.M3
##     18    140     41     80     60    106     46     58    107     22     15
## T10.M4 T11.M1 T11.M2 T11.M3 T11.M4 T11.M5 T12.M1 T12.M2 T12.M3 T12.M4 T12.M5
##    125     88     56     45     11     77    107     49     57     34     28
## T12.M6 T13.M1 T13.M2 T13.M3 T13.M4 T13.M5 T13.M6 T14.M1 T14.M2 T14.M3 T14.M4
##      7    111     36     67     65     17      2     90    102     83      3
## T14.M5 T15.M1 T15.M2 T15.M3 T15.M4 T15.M5 T15.M6 T16.M1 T16.M2 T16.M3 T16.M4
##      1    115     67     41     35     23      1     11     95    101    119
## T16.M5 T17.M1 T17.M2 T17.M3 T17.M4 T17.M5 T17.M6 T18.M1 T18.M2 T18.M3 T18.M4
##     15    132    189     85     28     11     27    142    102     15     84
## T18.M5
##      2
```

```
print(w$lab[-1])
```

```
##    Trait.ID Modality.ID                            Trait             Modality
## 1         1           1                        Life span                  <6m
## 2         1           2                        Life span                6m-1y
## 3         1           3                        Life span                 1-3y
```

```
## 4         1           4                        Life span                3-10y
## 5         1           5                        Life span               10-20y
## 6         1           6                        Life span               20-50y
## 7         1           7                        Life span              50-100y
## 8         1           8                        Life span                >100y
## 9         2           1                  Age at maturity                  <6m
## 10        2           2                  Age at maturity                6m-1y
## 11        2           3                  Age at maturity                 1-3y
## 12        2           4                  Age at maturity                 3-5y
## 13        2           5                  Age at maturity                 5-7y
## 14        2           6                  Age at maturity                  >7y
## 15        3           1                        Voltinism          Semivoltine
## 16        3           2                        Voltinism           Univoltine
## 17        3           3                        Voltinism            Bivoltine
## 18        3           4                        Voltinism         Multivoltine
## 19        4           1                        Sexuality          Gonochorism
## 20        4           2                        Sexuality             Homogamy
## 21        4           3                        Sexuality            Protandry
## 22        5           1           Reproductive frequency      Sexual seasonal
## 23        5           2           Reproductive frequency    Sexual continuous
## 24        5           3           Reproductive frequency     Asexual seasonal
## 25        5           4           Reproductive frequency   Asexual continuous
## 26        6           1                    Fertilisation         Broadcasting
## 27        6           2                    Fertilisation         Spermcasting
## 28        6           3                    Fertilisation              Pairing
## 29        7           1                 Annual fecundity                <10e2
## 30        7           2                 Annual fecundity            10e2-10e3
## 31        7           3                 Annual fecundity            10e3-10e4
## 32        7           4                 Annual fecundity            10e4-10e5
## 33        7           5                 Annual fecundity            10e5-10e6
## 34        7           6                 Annual fecundity                >10e6
## 35        8           1                   Offspring type                  Egg
## 36        8           2                   Offspring type                Larva
## 37        8           3                   Offspring type             Juvenile
## 38        9           1                   Offspring size                 <0.1
## 39        9           2                   Offspring size              0.1-0.5
## 40        9           3                   Offspring size              0.5-1.5
## 41        9           4                   Offspring size              1.5-5.0
## 42       10           1             Offspring protection                 None
## 43       10           2             Offspring protection                  Gel
## 44       10           3             Offspring protection              Capsule
## 45       10           4             Offspring protection     Bearing/Brooding
## 46       11           1            Offspring development       Planktotrophic
## 47       11           2            Offspring development       Lecithotrophic
## 48       11           3            Offspring development Mixed planktotrophic
## 49       11           4            Offspring development Mixed lecithotrophic
## 50       11           5            Offspring development             Internal
## 51       12           1 Offspring benthic stage duration                 Null
## 52       12           2 Offspring benthic stage duration                  <15
## 53       12           3 Offspring benthic stage duration                15-30
## 54       12           4 Offspring benthic stage duration                30-60
## 55       12           5 Offspring benthic stage duration               60-180
## 56       12           6 Offspring benthic stage duration                 >180
## 57       13           1 Offspring pelagic stage duration                 Null
```

```
## 58       13            2 Offspring pelagic stage duration                  <15
## 59       13            3 Offspring pelagic stage duration                15-30
## 60       13            4 Offspring pelagic stage duration                30-60
## 61       13            5 Offspring pelagic stage duration               60-180
## 62       13            6 Offspring pelagic stage duration                 >180
## 63       14            1        Offspring settlement size                 <0.5
## 64       14            2        Offspring settlement size              0.5-1.5
## 65       14            3        Offspring settlement size                1.5-5
## 66       14            4        Offspring settlement size                 5-10
## 67       14            5        Offspring settlement size                10-20
## 68       15            1                        Body mass               <0.001
## 69       15            2                        Body mass          0.001-0.010
## 70       15            3                        Body mass          0.010-0.100
## 71       15            4                        Body mass          0.100-1.000
## 72       15            5                        Body mass         1.000-10.000
## 73       15            6                        Body mass              >10.000
## 74       16            1                         Mobility             Immobile
## 75       16            2                         Mobility              Limited
## 76       16            3                         Mobility                 Slow
## 77       16            4                         Mobility                 Fast
## 78       16            5                         Mobility            Very fast
## 79       17            1       Substratum depth occupancy                    0
## 80       17            2       Substratum depth occupancy                  0-5
## 81       17            3       Substratum depth occupancy                 5-15
## 82       17            4       Substratum depth occupancy                15-30
## 83       17            5       Substratum depth occupancy                  >30
## 84       17            6       Substratum depth occupancy          Crevice/Den
## 85       18            1                     Feeding type                   De
## 86       18            2                     Feeding type                   Su
## 87       18            3                     Feeding type                 HeGr
## 88       18            4                     Feeding type                 CaSc
## 89       18            5                     Feeding type                   Sy
```

```r
w$tab <- w$tab[!w$lab$Modality %in%
                 c("Crevice/Den", "Asexual seasonal", "Asexual continuous", "Sy")]
w$lab <- w$lab[!w$lab$Modality %in%
                 c("Crevice/Den", "Asexual seasonal", "Asexual continuous", "Sy"),]
```

Some traits deserve to be simplified with a lower number of modalities. The function `fuz.modif` is used to this aim.

```r
print(w$lab[-1])
```

```
##    Trait.ID Modality.ID                            Trait             Modality
## 1         1           1                        Life span                  <6m
## 2         1           2                        Life span                6m-1y
## 3         1           3                        Life span                 1-3y
## 4         1           4                        Life span                3-10y
## 5         1           5                        Life span               10-20y
## 6         1           6                        Life span               20-50y
## 7         1           7                        Life span              50-100y
## 8         1           8                        Life span                >100y
## 9         2           1                  Age at maturity                  <6m
```

```
## 10        2           2                  Age at maturity                6m-1y
## 11        2           3                  Age at maturity                 1-3y
## 12        2           4                  Age at maturity                 3-5y
## 13        2           5                  Age at maturity                 5-7y
## 14        2           6                  Age at maturity                  >7y
## 15        3           1                        Voltinism          Semivoltine
## 16        3           2                        Voltinism           Univoltine
## 17        3           3                        Voltinism            Bivoltine
## 18        3           4                        Voltinism         Multivoltine
## 19        4           1                        Sexuality          Gonochorism
## 20        4           2                        Sexuality             Homogamy
## 21        4           3                        Sexuality            Protandry
## 22        5           1           Reproductive frequency      Sexual seasonal
## 23        5           2           Reproductive frequency    Sexual continuous
## 26        6           1                    Fertilisation         Broadcasting
## 27        6           2                    Fertilisation         Spermcasting
## 28        6           3                    Fertilisation              Pairing
## 29        7           1                 Annual fecundity                <10e2
## 30        7           2                 Annual fecundity            10e2-10e3
## 31        7           3                 Annual fecundity            10e3-10e4
## 32        7           4                 Annual fecundity            10e4-10e5
## 33        7           5                 Annual fecundity            10e5-10e6
## 34        7           6                 Annual fecundity                >10e6
## 35        8           1                   Offspring type                  Egg
## 36        8           2                   Offspring type                Larva
## 37        8           3                   Offspring type             Juvenile
## 38        9           1                   Offspring size                 <0.1
## 39        9           2                   Offspring size              0.1-0.5
## 40        9           3                   Offspring size              0.5-1.5
## 41        9           4                   Offspring size              1.5-5.0
## 42       10           1             Offspring protection                 None
## 43       10           2             Offspring protection                  Gel
## 44       10           3             Offspring protection              Capsule
## 45       10           4             Offspring protection     Bearing/Brooding
## 46       11           1            Offspring development       Planktotrophic
## 47       11           2            Offspring development       Lecithotrophic
## 48       11           3            Offspring development Mixed planktotrophic
## 49       11           4            Offspring development Mixed lecithotrophic
## 50       11           5            Offspring development             Internal
## 51       12           1 Offspring benthic stage duration                 Null
## 52       12           2 Offspring benthic stage duration                  <15
## 53       12           3 Offspring benthic stage duration                15-30
## 54       12           4 Offspring benthic stage duration                30-60
## 55       12           5 Offspring benthic stage duration               60-180
## 56       12           6 Offspring benthic stage duration                 >180
## 57       13           1 Offspring pelagic stage duration                 Null
## 58       13           2 Offspring pelagic stage duration                  <15
## 59       13           3 Offspring pelagic stage duration                15-30
## 60       13           4 Offspring pelagic stage duration                30-60
## 61       13           5 Offspring pelagic stage duration               60-180
## 62       13           6 Offspring pelagic stage duration                 >180
## 63       14           1        Offspring settlement size                 <0.5
## 64       14           2        Offspring settlement size              0.5-1.5
## 65       14           3        Offspring settlement size                1.5-5
```

```
## 66       14         4       Offspring settlement size           5-10
## 67       14         5       Offspring settlement size          10-20
## 68       15         1                       Body mass         <0.001
## 69       15         2                       Body mass    0.001-0.010
## 70       15         3                       Body mass    0.010-0.100
## 71       15         4                       Body mass    0.100-1.000
## 72       15         5                       Body mass   1.000-10.000
## 73       15         6                       Body mass        >10.000
## 74       16         1                        Mobility       Immobile
## 75       16         2                        Mobility        Limited
## 76       16         3                        Mobility           Slow
## 77       16         4                        Mobility           Fast
## 78       16         5                        Mobility      Very fast
## 79       17         1      Substratum depth occupancy              0
## 80       17         2      Substratum depth occupancy            0-5
## 81       17         3      Substratum depth occupancy           5-15
## 82       17         4      Substratum depth occupancy          15-30
## 83       17         5      Substratum depth occupancy            >30
## 85       18         1                    Feeding type             De
## 86       18         2                    Feeding type             Su
## 87       18         3                    Feeding type           HeGr
## 88       18         4                    Feeding type           CaSc
```

```r
w <- fuz.modif(w$tab, w$lab, which.trait = 1, merge = c(1:5, 5, 5, 5),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 1][1:4], ">10y"))
w <- fuz.modif(w$tab, w$lab, which.trait = 2, merge = c(1:4, 4, 4),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 2][1:3], ">3y"))
w <- fuz.modif(w$tab, w$lab, which.trait = 3, merge = c(1:3, 3),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 3][1:2], "Bi/Multivoltine"))
w <- fuz.modif(w$tab, w$lab, which.trait = 12, merge = c(1:3, 3, 3, 3),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 12][1:2], ">15"))
w <- fuz.modif(w$tab, w$lab, which.trait = 13, merge = c(1:3, 3, 3, 3),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 13][1:2], ">15"))
w <- fuz.modif(w$tab, w$lab, which.trait = 14, merge = c(1:3, 3, 3),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 14][1:2], ">1.5"))
w <- fuz.modif(w$tab, w$lab, which.trait = 15, merge = c(1:5, 5),
               mod = c(w$lab$Modality[w$lab$Trait.ID == 15][1:4], ">1.000"))
tabQ <- w$tab
labQ <- w$lab
indic <- labQ$Trait.ID
```

Some species with a wide geographic distribution have variable scores for life span and age at maturity. They must be adjusted to the local populations.

```r
tabQ[rownames(tabQ) == "Echinocardium cordatum",][indic == 2] <- c(0, 0, 0, 1)
tabQ[rownames(tabQ) == "Macoma balthica",][indic == 1] <- c(0, 0, 1, 1, 0)
```

S5.2 Whole area

The analyses are carried out with the ade4 package. As shown in Beauchard et al. (2022), presence-absence yields the best analytical output in this analysis. The environment-trait relationships are explored through the combination of RLQ ordination with the Fourth-corner testing procedure (Dray et al. 2014).

```r
library(ade4)
#Presence-absence faunal data (table L)
tabL <- data.frame(ifelse(fau == 0, 0, 1), check.names = FALSE)
tabL <- tabL[colnames(tabL) %in% rownames(tabQ)]
identical(colnames(tabL), rownames(tabQ))
```

```
## [1] TRUE
```

```r
#Faunal ordination
dudiL <- dudi.coa(tabL, scan = FALSE)
#Environmental ordination (table R)
dudiR <- dudi.hillsmith(env, row.w = dudiL$lw, scan = FALSE)
#Trait ordination (table Q)
fuz <- prep.fuzzy.var(df = tabQ, col.blocks = table(indic), row.w = dudiL$cw)
dudiQ <- dudi.fca(df = fuz, scannf = FALSE)
#RLQ ordination
rlq1 <- rlq(dudiR, dudiL, dudiQ, scannf = FALSE)
#RLQ pattern significance testing
print(randtest(rlq1, 9999))
```

```
## class: krandtest lightkrandtest
## Monte-Carlo tests
## Call: randtest.rlq(xtest = rlq1, nrepet = 9999)
##
## Number of tests:   2
##
## Adjustment method for multiple comparisons:   none
## Permutation number:   9999
##      Test        Obs   Std.Obs   Alter Pvalue
## 1 Model 2 0.03740827 36.990365 greater 0.0001
## 2 Model 4 0.03740827  2.666167 greater 0.0210
```

The test indicates that both R-L and L-Q relationships are significant ($p < 0.05$). The eigenvalue diagram displays a prominent first axis (Fig. S10). Therefore, the RLQ pattern can be considered unidimensional and only the first axis is interpreted.

```r
layout(matrix(1:3, nc = 3), width = c(2, 1.3, 2))
par(mar = c(3, 5, 1, 1), cex.lab = 2)
barplot(100*rlq1$eig/sum(rlq1$eig), col = 1, ylab = "% muldimensional variance")
x <- data.frame(model.matrix(data = data.frame(hab), ~ 0 + hab))
fuz.plot(x, y = rlq1$lR[,1], mod = c("HD", "LD"), cex.mod = 1.5,
         amount= 0.1, horiz = FALSE, ylab = "First RLQ axis",
         pch.mct = 21, pch.pt = 20, cex.mct = 2.5, cex.pt = 2,
         col.mct = "white", bg.mct = 1,
         col.pt = adjustcolor("dodgerblue4", 0.4), bar.lwd = 2)
par(mar = c(3, 1, 1, 1))
plot(geo, type = "n", xaxt = "n", yaxt = "n", bty = "n", xlab = "", ylab = "")
contour(bat, levels = seq(0, 80, by = 10), labcex = 1, add = TRUE)
s.value(geo, rlq1$lR[,1], cleg = 0, add.p = TRUE)
```

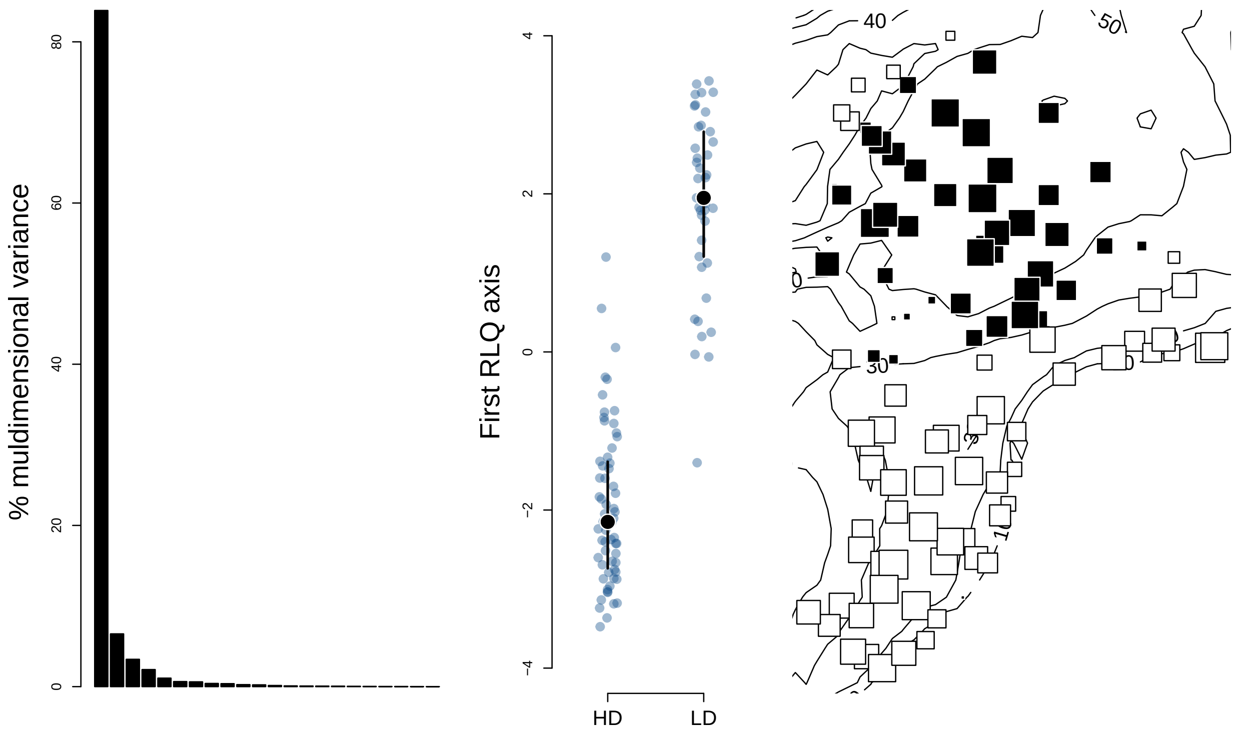

Figure S10. RLQ analysis of the whole area. Left panel, eigenvalue diagram showing a prominent first axis. Middle, sampling station first axis scores (blue dots) showing the distinction between hight and low dynamics habitats (HD and LD, respectively; black dot, median score; bars extend from 25th to 75th percentile). Right, sampling axis scores mapped over the area; black, positive scores; white, negative scores; square size proportional to deviation from 0. Contour lines, depth in meters.

The gradient is clearly spatialised, with low RLQ axis scores for the HD habitat, and high scores for LD, consistently with the habitat typology in Beauchard et al. (2022). This suggests that the two habitat are characterised by different trait compositions.

The ade4 function `fourthcorner2` tests the coinertia between blocks of variables: either qualitative R variable (as a block of dummy variables) with the RLQ axis species score `rlq1$lQ` or the RLQ axis station score `rlq1$lR` with a fuzzy trait (block of modality columns). The p-values of the habitat descriptor tests after correction for multiple testing (false discovery rate):

```r
pR <- as.numeric()
indicR <- c(rep(1:4, rep(5, 4)), rep(5, 4), 6:8)
for(i in 1:ncol(env)){
  pR[i] <- fourthcorner2(dudiR$tab[indicR == i], tabL,
                         rlq1$lQ[1], nrepet = 999)$trRLQ$pvalue
}
names(pR) <- colnames(env)
pR <- p.adjust(pR, method = "fdr")
print(round(pR, 3))
```

```
##   depth current    wave stratif   sedim      PP     POM     POC
##   0.001   0.001   0.001   0.001   0.001   0.001   0.001   0.001
```

The biological information is organised at two levels: the trait and, within the trait, the modalities. A first series of tests enables the identification of the traits with a significant relationship with the first RLQ axis.

Note that the number of random permutations is limited to 999 due to the long computation time; several tens of thousands must be executed for a correct test (e.g., 49999).

```
pQ <- as.numeric()
for(i in 1:max(indic)){
  pQ[i] <- fourthcorner2(rlq1$lR[1], tabL,
                         dudiQ$tab[indic == i], nrepet = 999)$trRLQ$pvalue
}
names(pQ) <- unique(labQ$Trait)
pQ <- p.adjust(pQ, method = "fdr")
print(round(pQ, 3))
```

```
##                        Life span                    Age at maturity
##                            0.112                              0.063
##                        Voltinism                          Sexuality
##                            0.234                              0.704
##           Reproductive frequency                      Fertilisation
##                            0.259                              0.438
##                  Annual fecundity                     Offspring type
##                            0.666                              0.234
##                   Offspring size               Offspring protection
##                            0.123                              0.288
##            Offspring development Offspring benthic stage duration
##                            0.320                              0.538
## Offspring pelagic stage duration        Offspring settlement size
##                            0.462                              0.054
##                        Body mass                           Mobility
##                            0.123                              0.090
##       Substratum depth occupancy                       Feeding type
##                            0.657                              0.112
```

Not a single trait is significant, although the overall RLQ pattern is highly significant. Note that a few traits lie at the limit of significance (< 0.100). This indicates that the significant part of the biology consists in covariances among modalities from a few traits as shown by the tests of the individual modality variables:

```
fc <- fourthcorner.rlq(rlq1, modeltype = 6, typetest = "Q.axes",
                       nrepet = 999, p.adjust.method.G = "fdr", p.adjust.method.D = "fdr")
plot(fc, stat = "D", col = c("white", "black", "dodgerblue3"))
```

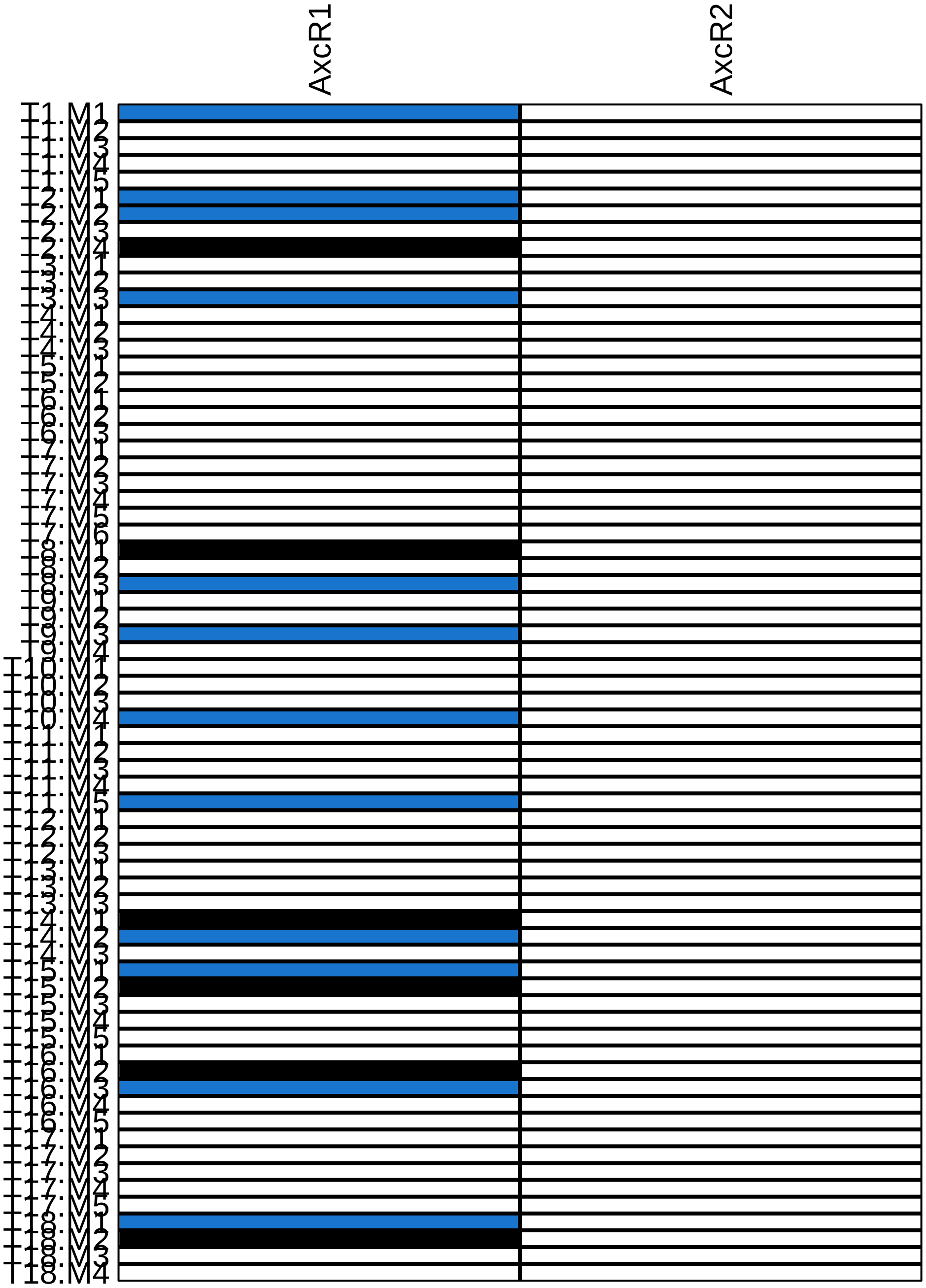

Figure S11. Significance tests of correlations between trait modalities and RLQ axes (right, first axis; left, second axis). White, not significant (p >= 0.05); blue, significant and positive correlation; black, significant and negative correlation.

As described in Beauchard et al. (2022), this first RLQ axis loosely opposes short-lived (Fig. S11, first blue cell) and early maturing species (second and third blue cells) to lately mature ones (first black cell, i.e., negatively correlated), suggesting also longer-lived ones, although long-lived modalities are not significant. This could simplistically interpreted as an r-K gradient, but this analysis expresses only a fragment of the biological pattern due to scale-dependent considerations as follows.

S5.3 Low dynamics

The RLQ pattern in the low dynamics habitat was not found significant (p-value around 0.3) due to the relative homogeneity of the deep and muddy area, which may not be selectively strong enough to generate variations in trait composition.

```
tabLL <- data.frame(ifelse(fau == 0, 0, 1)[hab == "LD",], check.names = FALSE)
tabLL <- tabLL[apply(tabLL, 2, sum) > 0]
tabQL <- tabQ[rownames(tabQ) %in% colnames(tabLL),]
tabLL <- tabLL[colnames(tabLL) %in% rownames(tabQL)]
identical(colnames(tabLL), rownames(tabQL))
```

```
## [1] TRUE
```

```
tabQL <- tabQL[apply(tabQ, 2, sum) > 0]
labQL <- labQ[labQ$Column.name %in% colnames(tabQL),]
indicL <- labQL$Trait.ID
tabRL <- env[hab == "LD",]
dudiLL <- dudi.coa(tabLL, scan = FALSE)
dudiRL <- dudi.hillsmith(tabRL, row.w = dudiLL$lw, scan = FALSE)
fuzL <- prep.fuzzy.var(df = tabQL, col.blocks = table(indicL), row.w = dudiLL$cw)
dudiQL <- dudi.fca(df = fuzL, scannf = FALSE)
rlqL <- rlq(dudiRL, dudiLL, dudiQL, scannf = FALSE)
print(randtest(rlqL, 9999))
```

```
## class: krandtest lightkrandtest
## Monte-Carlo tests
## Call: randtest.rlq(xtest = rlqL, nrepet = 9999)
##
## Number of tests:   2
##
## Adjustment method for multiple comparisons:   none
## Permutation number:   9999
##      Test        Obs   Std.Obs   Alter Pvalue
## 1 Model 2 0.00849578 6.3638804 greater 0.0002
## 2 Model 4 0.00849578 0.3810041 greater 0.3047
```

S5.4 High dynamics

Although this habitat is characterised by higher hydrodynamics and sediment granulometry on average, its highly heterogeneous geomorphology creates local changes in abiotic conditions whereby species communities endowed with variable trait combinations can locally shift over space. The test of the RLQ pattern is highly significant.

```
tabLH <- log(fau[hab == "HD",]+1)
tabLH <- tabLH[apply(tabLH, 2, sum) > 0]
tabQH <- tabQ[rownames(tabQ) %in% colnames(tabLH),]
tabLH <- tabLH[colnames(tabLH) %in% rownames(tabQH)]
identical(colnames(tabLH), rownames(tabQH))
```

```
## [1] TRUE
```

```r
tabQH <- tabQH[apply(tabQ, 2, sum) > 0]
labQH <- labQ[labQ$Column.name %in% colnames(tabQH),]
indicH <- labQH$Trait.ID
tabRH <- env[hab == "HD",]
dudiLH <- dudi.coa(tabLH, scan = FALSE)
dudiRH <- dudi.hillsmith(tabRH, row.w = dudiLH$lw, scan = FALSE)
fuzH <- prep.fuzzy.var(df = tabQH, col.blocks = table(indicH), row.w = dudiLH$cw)
dudiQH <- dudi.fca(df = fuzH, scannf = FALSE)
rlqH <- rlq(dudiRH, dudiLH, dudiQH, scannf = FALSE)
print(randtest(rlqH, 9999))
```

```
## class: krandtest lightkrandtest
## Monte-Carlo tests
## Call: randtest.rlq(xtest = rlqH, nrepet = 9999)
##
## Number of tests:   2
##
## Adjustment method for multiple comparisons:   none
## Permutation number:   9999
##      Test       Obs   Std.Obs   Alter Pvalue
## 1 Model 2 0.0238938 14.767110 greater 0.0001
## 2 Model 4 0.0238938  2.997401 greater 0.0097
```

The pattern is expressed along two axes; the trait data update may have been at the origin of a third axis compared to the original publication. We restrict the illustration to the two first ones.

```r
par(mfrow = c(1, 3), mar = c(1, 5, 1, 1), cex.lab = 2)
barplot(100*rlqH$eig/sum(rlqH$eig), col = 1, ylab = "% muldimensional variance")
par(mar = c(1, 1, 1, 1), cex.lab = 2)
#Axis directions changed to compare with Figure 5 of Beauchard et al. (2022)
df <- rlqH$lR
df[,2] <- -df[,2]
for(i in 1:2){
  plot(geo, type = "n", xaxt = "n", yaxt = "n", bty = "n", xlab = "", ylab = "")
  contour(bat, levels = seq(0, 80, by = 10), labcex = 1, add = TRUE)
  s.value(geo[hab == "HD",], df[,i], cleg = 0,
          sub = paste("RLQ axis", i, sep = " "), csub = 2.5,
          possub = "bottomright", add.p = TRUE)
}
```

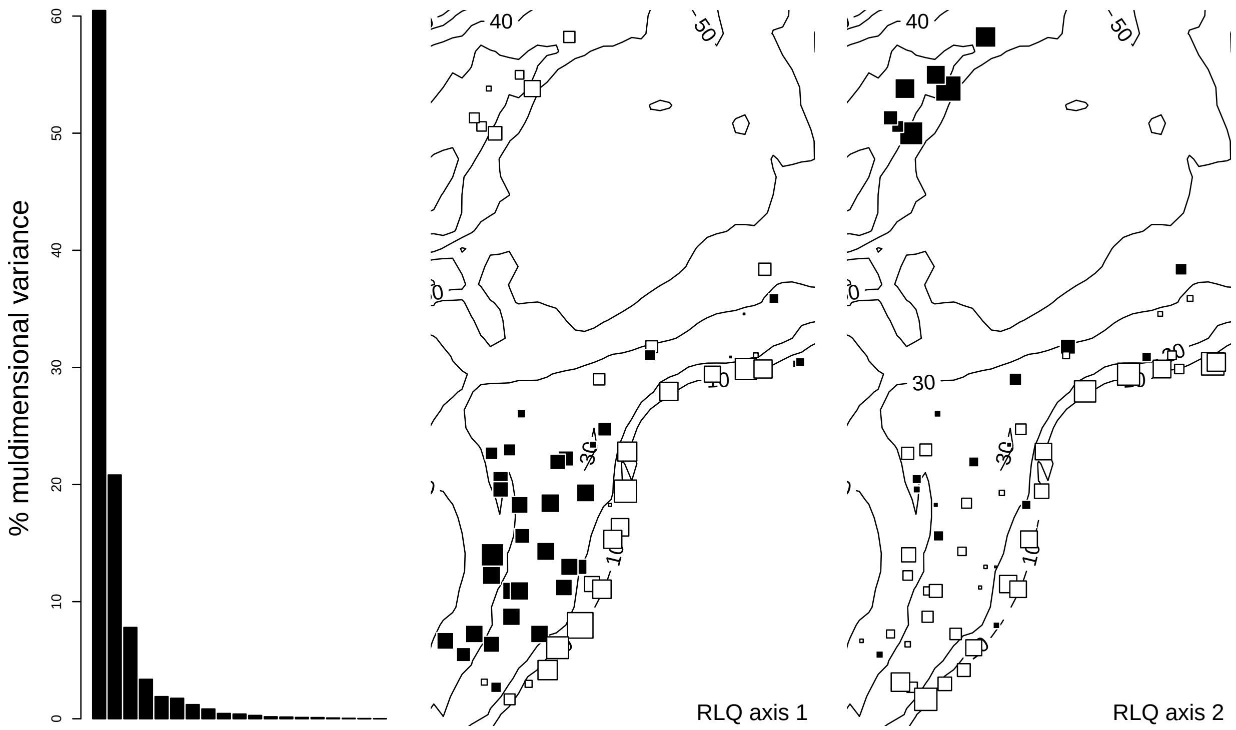

Figure S12. RLQ analysis of the high dynamics habitat. Left panel, eigenvalue diagram showing at least two axies that deserve interpretation. Middle and right, mapping of sampling station first and second axis scores, respectively. Black, positive scores; white, negative scores; square size proportional to deviation from 0. Contour lines, depth in meters.

Compared to the first analysis, the pattern here reveals shorter spatial wave lengths of variations in functional composition (Fig. S11). As perfectly continuous abiotic gradients at the shelf scale are rarely encountered, this suggests that trait pattern significance in marine benthic ecology may be spatially limited (see Fig. S11 middle and right panels; main variations of 50-100 km). Next to environmental variables (not shown), several entire traits are significant. As two axes can be interpreted, multivariate trait significance can be tested for each axis and the combination of the two.

```
w <- list(1, 2, 1:2)
pQH <- matrix(0, max(indicH), length(w))
rownames(pQH) <- unique(labQH$Trait)
colnames(pQH) <- c("Axis 1", "Axis 2", "Axes 1-2")
for(i in 1:length(w)){
  for(j in 1:max(indicH)){
    pQH[,i][j] <- fourthcorner2(rlqH$lR[w[[i]]], tabLH,
                              dudiQH$tab[indicH == j], nrepet = 999)$trRLQ$pvalue
  }
  p.adjust(pQH[,i], method = "fdr")
}
print(round(pQH, 3))
```

```
##                                  Axis 1 Axis 2 Axes 1-2
## Life span                         0.070  0.088    0.039
## Age at maturity                   0.182  0.028    0.039
## Voltinism                         0.038  0.943    0.111
## Sexuality                         0.298  0.920    0.578
```

```
## Reproductive frequency           0.223  0.806    0.458
## Fertilisation                    0.163  0.380    0.185
## Annual fecundity                 0.004  0.309    0.007
## Offspring type                   0.148  0.434    0.199
## Offspring size                   0.022  0.933    0.073
## Offspring protection             0.468  0.928    0.782
## Offspring development            0.229  0.497    0.346
## Offspring benthic stage duration  0.145  0.267    0.138
## Offspring pelagic stage duration  0.021  0.783    0.103
## Offspring settlement size        0.010  0.616    0.035
## Body mass                        0.153  0.018    0.015
## Mobility                         0.001  0.890    0.001
## Substratum depth occupancy       0.337  0.807    0.636
## Feeding type                     0.026  0.471    0.049
```

The abiotic heterogeneity of the HD habitat enables more easily the detection of the three existing life-history strategies (Fig. S13). (1) A-strategists, adversity-selected species, right side of the figure. Very small, stress resistant through high mobility on mobile sand with short life and early maturity, important reproductive allocation (low fecundity, release of large juveniles as adult miniatures after internal incubation). (2) r-selected species, bottom of the figure. Also short life and early maturity, but mixed development; disturbance resilient. (3) K-strategists, top-left corner; longer-lived species, some of them reaching maturity much later, infrequent reproductive sucesses, absence of parental cares, small and numerous offspring; many bivalves, with typical suspension feeding and planktotrophic development, and sometimes with large body mass; in general, vulnerable to disturbance.

```r
par(mfrow = c(5, 4), mar = rep(0.1, 4))
#Axis directions changed to compare with Figure 5 of Beauchard et al. (2022)
df <- rlqH$lQ
df[,2] <- -df[,2]
for(i in 1:max(indicH)){
  s.label(df, cpoint = 0, clab = 0)
  points(df, pch = 20, cex = 2,
         col = adjustcolor("dodgerblue4", 0.4))
  s.distri(df, fuzH[indicH == i], cstar = 0, cpoint = 0,
           lab = labQH$Modality[indicH == i], clab = 1.5,
           sub = unique(labQH$Trait)[i], possub = "topleft",
           csub = 2, add.p = TRUE)
}
```

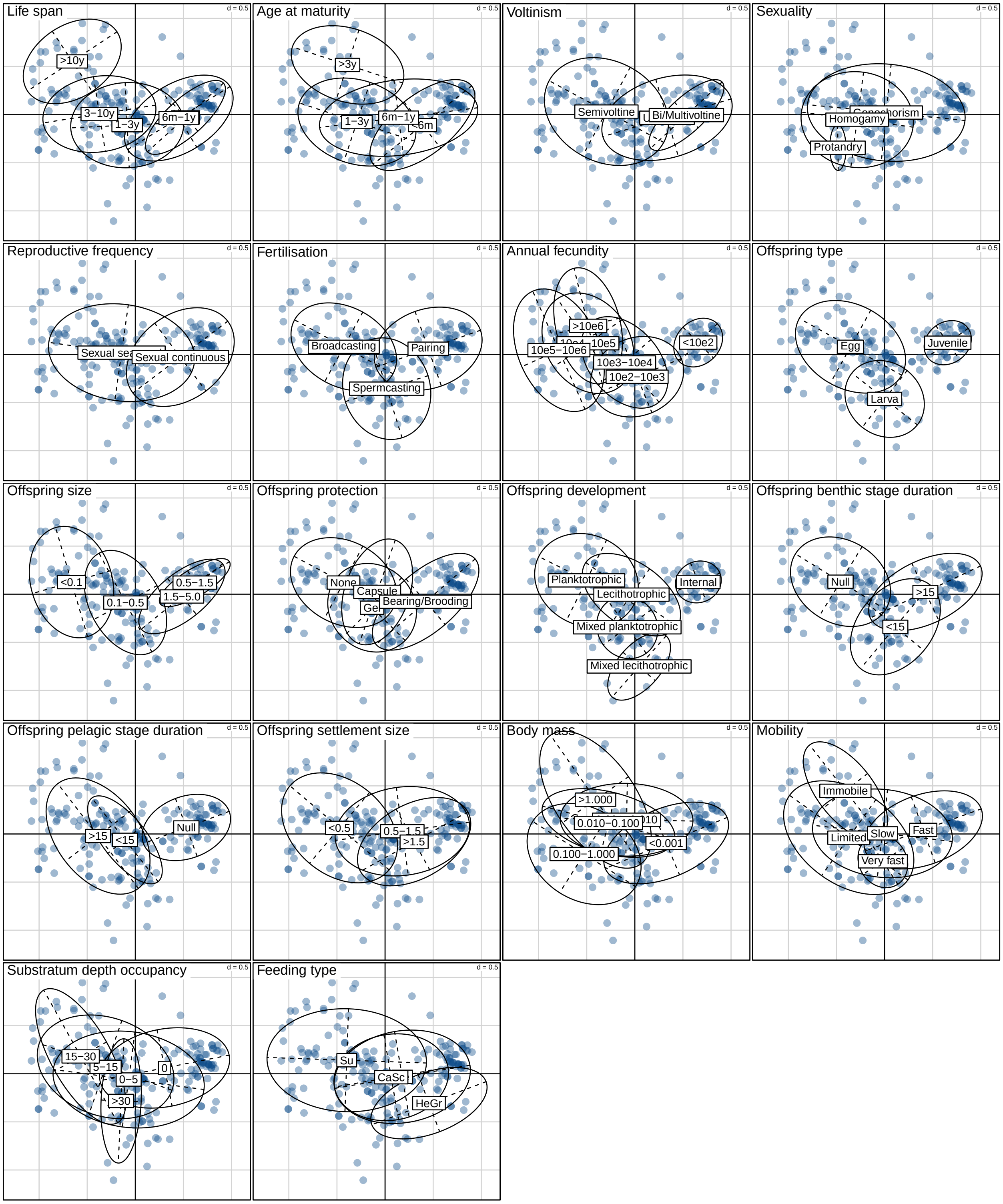

Figure S13. RLQ analysis of the hight dynamics habitat, trait representation along axis 1 (horizontal) and 2 (vertical). Each panel represents the same species pattern (blue dots) group by their respective modalities of the considered trait.

Conclusively, this illustrative case study validates the analytical relevance of the updated traits in the Macro-Traits data base. Besides, the provided R code can be useful in other case studies from a comparative perspective, especially regarding the concept of spatial contingency that remains insufficiently investigated in the marine benthos.

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