

Package ‘doubletrouble’

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Title Identification and classification of duplicated genes

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Description doubletrouble aims to identify duplicated genes from whole-genome protein sequences and classify them based on their modes of duplication. The duplication modes are i. segmental duplication (SD); ii. tandem duplication (TD); iii. proximal duplication (PD); iv. transposed duplication (TRD) and; v. dispersed duplication (DD). Transposon-derived duplicates (TRD) can be further subdivided into rTRD (retrotransposon-derived duplication) and dTRD (DNA transposon-derived duplication). If users want a simpler classification scheme, duplicates can also be classified into SD- and SSD-derived (small-scale duplication) gene pairs. Besides classifying gene pairs, users can also classify genes, so that each gene is assigned a unique mode of duplication. Users can also calculate substitution rates per substitution site (i.e., Ka and Ks) from duplicate pairs, find peaks in Ks distributions with Gaussian Mixture Models (GMMs), and classify gene pairs into age groups based on Ks peaks.

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URL <https://github.com/almeidasilvaf/doubletrouble>

BugReports <https://support.bioconductor.org/t/doubletrouble>

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cds_scerevisiae	<i>Coding sequences (CDS) of S. cerevisiae</i>
-----------------	--

Description

Data were obtained from Ensembl Fungi, and only CDS of primary transcripts were included.

Usage

```
data(cds_scerevisiae)
```

Format

A DNASTringSet object with CDS of S. cerevisiae.

Examples

```
data(cds_scerevisiae)
```

classify_genes	<i>Classify genes into unique modes of duplication</i>
----------------	--

Description

Classify genes into unique modes of duplication

Usage

```
classify_genes(gene_pairs_list = NULL)
```

Arguments

gene_pairs_list

List of classified gene pairs as returned by `classify_gene_pairs()`.

Details

If a gene is present in pairs with different duplication modes, the gene is classified into a unique mode of duplication following the order of priority indicated in the levels of the factor **type**.

For scheme "binary", the order is SD > SSD. For scheme "standard", the order is SD > TD > PD > DD. For scheme "extended", the order is SD > TD > PD > TRD > DD. For scheme "full", the order is SD > TD > PD > rTRD > dTRD > DD.

Value

A list of 2-column data frames with variables **gene** and **type** representing gene ID and duplication type, respectively.

Examples

```

data(scerevisiae_kaks)

cols <- c("dup1", "dup2", "type")
gene_pairs_list <- list(Scerevisiae = scerevisiae_kaks[, cols])

class_genes <- classify_genes(gene_pairs_list)

```

classify_gene_pairs *Classify duplicate gene pairs based on their modes of duplication*

Description

Classify duplicate gene pairs based on their modes of duplication

Usage

```

classify_gene_pairs(
  annotation = NULL,
  blast_list = NULL,
  scheme = "standard",
  blast_inter = NULL,
  intron_counts,
  evalue = 1e-10,
  anchors = 5,
  max_gaps = 25,
  proximal_max = 10,
  collinearity_dir = NULL
)

```

Arguments

annotation	A processed GRangesList or CompressedGRangesList object as returned by <code>syntenet::process_input()</code> .
blast_list	A list of data frames containing BLAST tabular output for intraspecies comparisons. Each list element corresponds to the BLAST output for a given species, and names of list elements must match the names of list elements in annotation . BLASTp, DIAMOND or similar programs must be run on processed sequence data as returned by <code>process_input()</code> .
scheme	Character indicating which classification scheme to use. One of "binary", "standard", "extended", or "full". See details below for information on what each scheme means. Default: "standard".
blast_inter	(Only valid if <code>scheme == "extended" or "full"</code>). A list of data frames containing BLAST tabular output for the comparison between target species and outgroups. Names of list elements must match the names of list elements in <code>annotation</code> . BLASTp, DIAMOND or similar programs must be run on processed sequence data as returned by <code>process_input()</code> .

intron_counts	(Only valid if scheme == "full"). A list of 2-column data frames with the number of introns per gene as returned by <code>get_intron_counts()</code> . Names of list elements must match names of annotation .
evaluate	Numeric scalar indicating the E-value threshold. Default: 1e-10.
anchors	Numeric indicating the minimum required number of genes to call a syntenic block, as in <code>syntenet::infer_syntenet</code> . Default: 5.
max_gaps	Numeric indicating the number of upstream and downstream genes to search for anchors, as in <code>syntenet::infer_syntenet</code> . Default: 25.
proximal_max	Numeric scalar with the maximum distance (in number of genes) between two genes to consider them as proximal duplicates. Default: 10.
collinearity_dir	Character indicating the path to the directory where <code>.collinearity</code> files will be stored. If NULL, files will be stored in a subdirectory of <code>tempdir()</code> . Default: NULL.

Details

The classification schemes increase in complexity (number of classes) in the order 'binary', 'standard', 'extended', and 'full'.

For classification scheme "binary", duplicates are classified into one of 'SD' (segmental duplications) or 'SSD' (small-scale duplications).

For classification scheme "standard" (default), duplicates are classified into 'SD' (segmental duplication), 'TD' (tandem duplication), 'PD' (proximal duplication), and 'DD' (dispersed duplication).

For classification scheme "extended", duplicates are classified into 'SD' (segmental duplication), 'TD' (tandem duplication), 'PD' (proximal duplication), 'TRD' (transposon-derived duplication), and 'DD' (dispersed duplication).

Finally, for classification scheme "full", duplicates are classified into 'SD' (segmental duplication), 'TD' (tandem duplication), 'PD' (proximal duplication), 'rTRD' (retrotransposon-derived duplication), 'dTRD' (DNA transposon-derived duplication), and 'DD' (dispersed duplication).

Value

A list of 3-column data frames of duplicated gene pairs (columns 1 and 2), and their modes of duplication (column 3).

Examples

```
# Load example data
data(diamond_intra)
data(diamond_inter)
data(yeast_annot)
data(yeast_seq)

# Get processed annotation data
annotation <- syntenet::process_input(yeast_seq, yeast_annot)$annotation

# Get list of intron counts
```

```
txdb_list <- lapply(yeast_annot, GenomicFeatures::makeTxDbFromGRanges)
intron_counts <- lapply(txdb_list, get_intron_counts)

# Classify duplicates - full scheme
dup_class <- classify_gene_pairs(
  annotation = annotation,
  blast_list = diamond_intra,
  scheme = "full",
  blast_inter = diamond_inter,
  intron_counts = intron_counts
)

# Check number of gene pairs per class
table(dup_class$Scerevisiae$type)
```

diamond_inter	<i>Interspecies DIAMOND output for yeast species</i>
---------------	--

Description

This list contains a similarity search of *S. cerevisiae* against *C. glabrata*, and it was obtained with `run_diamond()`.

Usage

```
data(diamond_inter)
```

Format

A list of data frames (length 1) containing the output of a DIAMOND search of *S. cerevisiae* against *C. glabrata* (outgroup).

Examples

```
data(diamond_inter)
```

diamond_intra	<i>Intraspecies DIAMOND output for S. cerevisiae</i>
---------------	--

Description

List obtained with `run_diamond()`.

Usage

```
data(diamond_intra)
```

Format

A list of data frames (length 1) containing the whole paranome of *S. cerevisiae* resulting from intragenome similarity searches.

Examples

```
data(diamond_intra)
```

find_ks_peaks	<i>Find peaks in a Ks distribution with Gaussian Mixture Models</i>
---------------	---

Description

Find peaks in a Ks distribution with Gaussian Mixture Models

Usage

```
find_ks_peaks(ks, npeaks = 2, min_ks = 0.01, max_ks = 4, verbose = FALSE)
```

Arguments

ks	A numeric vector of Ks values.
npeaks	Numeric scalar indicating the number of peaks in the Ks distribution. If you don't know how many peaks there are, you can include a range of values, and the number of peaks that produces the lowest BIC (Bayesian Information Criterion) will be selected as the optimal. Default: 2.
min_ks	Numeric scalar with the minimum Ks value. Removing very small Ks values is generally used to avoid the incorporation of allelic and/or splice variants and to prevent the fitting of a component to infinity. Default: 0.01.
max_ks	Numeric scalar indicating the maximum Ks value. Removing very large Ks values is usually performed to account for Ks saturation. Default: 4.
verbose	Logical indicating if messages should be printed on screen. Default: FALSE.

Value

A list with the following elements:

mean Numeric with the estimated means.

sd Numeric with the estimated standard deviations.

lambda Numeric with the estimated mixture weights.

ks Numeric vector of filtered Ks distribution based on arguments passed to min_ks and max_ks.

Examples

```

data(scerevisiae_kaks)
ks <- scerevisiae_kaks$Ks

# Find 2 peaks in Ks distribution
peaks <- find_ks_peaks(ks, npeaks = 2)

# From 2 to 4 peaks, verbose = TRUE to show BIC values
peaks <- find_ks_peaks(ks, npeaks = c(2, 3, 4), verbose = TRUE)

```

get_anchors_list *Get a list of anchor pairs for each species*

Description

Get a list of anchor pairs for each species

Usage

```

get_anchors_list(
  blast_list = NULL,
  annotation = NULL,
  evalue = 1e-10,
  anchors = 5,
  max_gaps = 25,
  collinearity_dir = NULL
)

```

Arguments

blast_list	A list of data frames containing BLAST tabular output for intraspecies comparisons. Each list element corresponds to the BLAST output for a given species, and names of list elements must match the names of list elements in annotation. BLASTp, DIAMOND or similar programs must be run on processed sequence data as returned by process_input().
annotation	A processed GRangesList or CompressedGRangesList object as returned by syntenet::process_input().
evalue	Numeric scalar indicating the E-value threshold. Default: 1e-10.
anchors	Numeric indicating the minimum required number of genes to call a syntenic block, as in syntenet::infer_syntenet. Default: 5.
max_gaps	Numeric indicating the number of upstream and downstream genes to search for anchors, as in syntenet::infer_syntenet. Default: 25.
collinearity_dir	Character indicating the path to the directory where .collinearity files will be stored. If NULL, files will be stored in a subdirectory of tempdir(). Default: NULL.

Value

A list of data frames representing intraspecies anchor pairs.

Examples

```
data(diamond_intra)
data(yeast_annot)
data(yeast_seq)
blast_list <- diamond_intra

# Get processed annotation for S. cerevisiae
annotation <- syntenet::process_input(yeast_seq, yeast_annot)$annotation

# Get list of intraspecies anchor pairs
anchorpairs <- get_anchors_list(blast_list, annotation)
```

get_intron_counts	<i>Get a data frame of intron counts per gene</i>
-------------------	---

Description

Get a data frame of intron counts per gene

Usage

```
get_intron_counts(txdb)
```

Arguments

txdb A txdb object with transcript annotations. See details below for examples on how to create txdb objects from different kinds of input.

Details

The family of functions `makeTxDbFrom*` from the **GenomicFeatures** package can be used to create txdb objects from a variety of input data types. You can create txdb objects from e.g., GRanges objects (`makeTxDbFromGRanges()`), GFF files (`makeTxDbFromGFF()`), an Ensembl database (`makeTxDbFromEnsembl`), and a Biomart database (`makeTxDbFromBiomart`).

Value

A data frame with intron counts per gene, with variables:

gene Character with gene IDs.

introns Numeric with number of introns per gene.

Examples

```

data(yeast_annot)

# Create txdb object from GRanges
txdb <- GenomicFeatures::makeTxDbFromGRanges(yeast_annot[[1]])

# Get intron counts
intron_counts <- get_intron_counts(txdb)

```

```

get_segmental          Classify gene pairs derived from segmental duplications

```

Description

Classify gene pairs derived from segmental duplications

Usage

```
get_segmental(anchor_pairs = NULL, pairs = NULL)
```

Arguments

anchor_pairs A 2-column data frame with anchor pairs in columns 1 and 2.

pairs A 2-column data frame with all duplicate pairs. This is equivalent to the first 2 columns of the tabular output of BLAST-like programs.

Value

A 3-column data frame with the variables:

dup1 Character, duplicated gene 1

dup2 Character, duplicated gene 2

type Factor indicating duplication types, with levels "SD" (segmental duplication) or "DD" (dispersed duplication).

Examples

```

data(diamond_intra)
data(yeast_annot)
data(yeast_seq)
blast_list <- diamond_intra

# Get processed annotation for S. cerevisiae
annotation <- syntenet::process_input(yeast_seq, yeast_annot)$annotation[1]

# Get list of intraspecies anchor pairs
anchor_pairs <- get_anchors_list(blast_list, annotation)
anchor_pairs <- anchor_pairs[[1]][, c(1, 2)]

```

```
# Get duplicate pairs from DIAMOND output
duplicates <- diamond_intra[[1]][, c(1, 2)]
dups <- get_segmental(anchor_pairs, duplicates)
```

```
get_tandem_proximal    Classify gene pairs derived from tandem and proximal duplications
```

Description

Classify gene pairs derived from tandem and proximal duplications

Usage

```
get_tandem_proximal(pairs = NULL, annotation_granges = NULL, proximal_max = 10)
```

Arguments

pairs A 3-column data frame with columns **dup1**, **dup2**, and **type** indicating duplicated gene 1, duplicated gene 2, and the mode of duplication associated with the pair. This data frame is returned by `get_segmental()`.

annotation_granges A processed GRanges object as in each element of the list returned by `syntenet::process_input()`.

proximal_max Numeric scalar with the maximum distance (in number of genes) between two genes to consider them as proximal duplicates. Default: 10.

Value

A 3-column data frame with the variables:

dup1 Character, duplicated gene 1.

dup2 Character, duplicated gene 2.

type Factor of duplication types, with levels "SD" (segmental duplication), "TD" (tandem duplication), "PD" (proximal duplication), and "DD" (dispersed duplication).

Examples

```
data(yeast_annot)
data(yeast_seq)
data(scerevisiae_kaks)

# Get processed annotation for S. cerevisiae
pdata <- annotation <- syntenet::process_input(yeast_seq, yeast_annot)
annot <- pdata$annotation[[1]]

# Get duplicated pairs
pairs <- scerevisiae_kaks[, c("dup1", "dup2", "type")]
pairs$dup1 <- paste0("Sce_", pairs$dup1)
```

```

pairs$dup2 <- paste0("Sce_", pairs$dup2)

# Get tandem and proximal duplicates
td_pd_pairs <- get_tandem_proximal(pairs, annot)

```

<code>get_transposed</code>	<i>Classify gene pairs originating from transposon-derived duplications</i>
-----------------------------	---

Description

Classify gene pairs originating from transposon-derived duplications

Usage

```

get_transposed(
  pairs,
  blast_inter,
  annotation,
  evalue = 1e-10,
  anchors = 5,
  max_gaps = 25,
  collinearity_dir = NULL
)

```

Arguments

<code>pairs</code>	A 3-column data frame with columns dup1 , dup2 , and type indicating duplicated gene 1, duplicated gene 2, and the mode of duplication associated with the pair. This data frame is returned by <code>get_tandem_proximal()</code> .
<code>blast_inter</code>	A list of data frames of length 1 containing BLAST tabular output for the comparison between the target species and an outgroup. Names of list elements must match the names of list elements in <code>annotation</code> . BLASTp, DIAMOND or similar programs must be run on processed sequence data as returned by <code>syntenet::process_input()</code> .
<code>annotation</code>	A processed <code>GRangesList</code> or <code>CompressedGRangesList</code> object as returned by <code>syntenet::process_input()</code> .
<code>evalue</code>	Numeric scalar indicating the E-value threshold. Default: 1e-10.
<code>anchors</code>	Numeric indicating the minimum required number of genes to call a syntenic block, as in <code>syntenet::infer_syntenet</code> . Default: 5.
<code>max_gaps</code>	Numeric indicating the number of upstream and downstream genes to search for anchors, as in <code>syntenet::infer_syntenet</code> . Default: 25.
<code>collinearity_dir</code>	Character indicating the path to the directory where <code>.collinearity</code> files will be stored. If <code>NULL</code> , files will be stored in a subdirectory of <code>tempdir()</code> . Default: <code>NULL</code> .

Value

A 3-column data frame with the following variables:

dup1 Character, duplicated gene 1.

dup2 Character, duplicated gene 2.

type Factor of duplication types, with levels "SD" (segmental duplication), "TD" (tandem duplication), "PD" (proximal duplication), "TRD" (transposon-derived duplication), and "DD" (dispersed duplication).

Examples

```
data(diamond_inter)
data(diamond_intra)
data(yeast_seq)
data(yeast_annot)
data(scerevisiae_kaks)

# Get processed annotation
pdata <- syntenet::process_input(yeast_seq, yeast_annot)
annotation <- pdata$annotation

# Get duplicated pairs
pairs <- scerevisiae_kaks[, c("dup1", "dup2", "type")]
pairs$dup1 <- paste0("Sce_", pairs$dup1)
pairs$dup2 <- paste0("Sce_", pairs$dup2)

# Classify pairs
trd <- get_transposed(pairs, diamond_inter, annotation)
```

get_transposed_classes

Classify TRD genes as derived from either DNA transposons or retrotransposons

Description

Classify TRD genes as derived from either DNA transposons or retrotransposons

Usage

```
get_transposed_classes(pairs, intron_counts)
```

Arguments

pairs A 3-column data frame with columns **dup1**, **dup2**, and **type** indicating duplicated gene 1, duplicated gene 2, and the mode of duplication associated with the pair. This data frame is returned by `get_transposed()`.

intron_counts A 2-column data frame with columns **gene** and **introns** indicating the number of introns for each gene, as returned by `get_intron_counts`.

Value

A 3-column data frame with the following variables:

dup1 Character, duplicated gene 1.

dup2 Character, duplicated gene 2.

type Factor of duplication types, with levels "SD" (segmental duplication), "TD" (tandem duplication), "PD" (proximal duplication), "dTRD" (DNA transposon-derived duplication), "rTRD" (retrotransposon-derived duplication), and "DD" (dispersed duplication).

Examples

```
data(diamond_inter)
data(diamond_intra)
data(yeast_seq)
data(yeast_annot)
data(scerevisiae_kaks)

# Get processed annotation
pdata <- syntenet::process_input(yeast_seq, yeast_annot)
annotation <- pdata$annotation

# Get duplicated pairs
pairs <- scerevisiae_kaks[, c("dup1", "dup2", "type")]
pairs$dup1 <- paste0("Sce_", pairs$dup1)
pairs$dup2 <- paste0("Sce_", pairs$dup2)

# Classify pairs
trd <- get_transposed(pairs, diamond_inter, annotation)

# Create txdb object from GRanges
txdb <- GenomicFeatures::makeTxDbFromGRanges(yeast_annot[[1]])

# Get intron counts
intron_counts <- get_intron_counts(txdb)

# Get TRD classes
trd_classes <- get_transposed_classes(trd, intron_counts)
```

gmax_ks

Duplicate pairs and Ks values for Glycine max

Description

This data set was obtained with `classify_gene_pairs()` followed by `pairs2kaks()`.

Usage

```
data(gmax_ks)
```

Format

A data frame with the following variables:

dup1 Character, duplicated gene 1.

dup2 Character, duplicated gene 2.

Ks Numeric, Ks values.

Examples

```
data(gmax_ks)
```

pairs2kaks

Calculate Ka, Ks, and Ka/Ks from duplicate gene pairs

Description

Calculate Ka, Ks, and Ka/Ks from duplicate gene pairs

Usage

```
pairs2kaks(gene_pairs_list, cds, model = "MYN", threads = 1)
```

Arguments

gene_pairs_list	List of data frames containing duplicated gene pairs as returned by <code>classify_gene_pairs()</code> .
cds	List of DNASTringSet objects containing the coding sequences of each gene.
model	Character scalar indicating which codon model to use. Possible values are "Li", "NG86", "NG", "LWL", "LPB", "MLWL", "MLPB", "GY", "YN", "MYN", "MS", "MA", "GNG", "GLWL", "GLPB", "GMLWL", "GMLPB", "GYN", and "GMYN". Default: "MYN".
threads	Numeric scalar indicating the number of threads to use. Default: 1.

Value

A list of data frames containing gene pairs and their Ka, Ks, and Ka/Ks values.

Examples

```
data(diamond_intra)
data(diamond_inter)
data(yeast_annot)
data(yeast_seq)
data(cds_scerevisiae)
blast_list <- diamond_intra
blast_inter <- diamond_inter
```

```

pdata <- syntenet::process_input(yeast_seq, yeast_annot)
annot <- pdata$annotation["Scerevisiae"]

# Binary classification scheme
gene_pairs_list <- classify_gene_pairs(annot, blast_list)
gene_pairs_list <- list(
  Scerevisiae = gene_pairs_list[[1]][seq(1, 5, by = 1), ]
)

cds <- list(Scerevisiae = cds_scerevisiae)

kaks <- pairs2kaks(gene_pairs_list, cds)

```

plot_ks_peaks

Plot histogram of Ks distribution with peaks

Description

Plot histogram of Ks distribution with peaks

Usage

```
plot_ks_peaks(peaks = NULL, binwidth = 0.05)
```

Arguments

peaks	A list with elements mean , sd , lambda , and ks , as returned by the function <code>fins_ks_peaks()</code> .
binwidth	Numeric scalar with binwidth for the histogram. Default: 0.05.

Value

A ggplot object with a histogram and lines for each Ks peak.

Examples

```

data(scerevisiae_kaks)
ks <- scerevisiae_kaks$Ks

# Find 2 peaks in Ks distribution
peaks <- find_ks_peaks(ks, npeaks = 2)

# Plot
plot_ks_peaks(peaks, binwidth = 0.05)

```

scerevisiae_kaks *Duplicate pairs and Ka, Ks, and Ka/Ks values for S. cerevisiae*

Description

This data set was obtained with `classify_gene_pairs()` followed by `pairs2kaks()`.

Usage

```
data(scerevisiae_kaks)
```

Format

A data frame with the following variables:

dup1 Character, duplicated gene 1.

dup2 Character, duplicated gene 2.

Ka Numeric, Ka values.

Ks Numeric, Ks values.

Ka_Ks Numeric, Ka/Ks values.

type Character, mode of duplication

Examples

```
data(scerevisiae_kaks)
```

split_pairs_by_peak *Split gene pairs based on their Ks peaks*

Description

The purpose of this function is to classify gene pairs by age when there are 2+ Ks peaks. This way, newer gene pairs are found within a certain number of standard deviations from the highest peak, and older genes are found close within smaller peaks.

Usage

```
split_pairs_by_peak(ks_df, peaks, nsd = 2, binwidth = 0.05)
```

Arguments

ks_df	A 3-column data frame with gene pairs in columns 1 and 2, and Ks values for the gene pair in column 3.
peaks	A list with mean, standard deviation, and amplitude of Ks peaks as generated by <code>find_ks_peaks</code> .
nsd	Numeric with the number of standard deviations to consider for each peak.
binwidth	Numeric scalar with binwidth for the histogram. Default: 0.05.

Value

A list with the following elements:

pairs A 4-column data frame with the variables **dup1** (character), **dup2** (character), **ks** (numeric), and **peak** (numeric), representing duplicate gene pair, Ks values, and peak ID, respectively.

plot A ggplot object with Ks peaks as returned by `plot_ks_peaks`, but with dashed red lines indicating boundaries for each peak.

Examples

```
data(scerevisiae_kaks)

# Create a data frame of duplicate pairs and Ks values
ks_df <- scerevisiae_kaks[, c("dup1", "dup2", "Ks")]

# Create list of peaks
peaks <- find_ks_peaks(ks_df$Ks, npeaks = 2)

# Split pairs
spairs <- split_pairs_by_peak(ks_df, peaks)
```

yeast_annot

Genome annotation of the yeast species S. cerevisiae and C. glabrata

Description

Data obtained from Ensembl Fungi. Only annotation data protein-coding genes (with associated mRNA, exons, CDS, etc) are included.

Usage

```
data(yeast_annot)
```

Format

A `CompressedGRangesList` containing the elements **Scerevisiae** and **Cglabrata**.

Examples

```
data(yeast_annot)
```

`yeast_seq`*Protein sequences of the yeast species *S. cerevisiae* and *C. glabrata**

Description

Data obtained from Ensembl Fungi. Only translated sequences of primary transcripts were included.

Usage

```
data(yeast_seq)
```

Format

A list of AAStringSet objects with the elements **Scerevisiae** and **Cglabrata**.

Examples

```
data(yeast_seq)
```

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