

STRINGdb Package Vignette

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1 INTRODUCTION

STRING (<https://www.string-db.org>) is a database of known and predicted protein-protein interactions. The interactions include direct (physical) and indirect (functional) associations. The database contains information from numerous sources, including experimental repositories, computational prediction methods and public text collections. Each interaction is associated with a combined confidence score that integrates the various evidences. We currently cover over 24 millions proteins from 5090 organisms.

As you will learn in this guide, the STRING database can be useful to add meaning to list of genes (e.g. the best hits coming out from a screen or the most differentially expressed genes coming out from a Microarray/RNAseq experiment.)

We provide the STRINGdb R package in order to facilitate our users in accessing the STRING database from R. In this guide we explain, with examples, most of the package's features and functionalities.

In the STRINGdb R package we use the new ReferenceClasses of R (search for "ReferenceClasses" in the R documentation.). Besides we make use of the iGraph package (<http://igraph.sourceforge.net>) as a data structure to represent our protein-protein interaction network.

To begin, you should first know the NCBI taxonomy identifiers of the organism on which you have performed the experiment (e.g. 9606 for Human, 10090 for mouse). If you don't know that, you can search the NCBI Taxonomy (<http://www.ncbi.nlm.nih.gov/taxonomy>) or start looking at our species table (that you can also use to verify that your organism is represented in the STRING database). Hence, if your species is not Human (i.e. our default species), you can find it and their taxonomy identifiers on STRING webpage under the 'organisms' section (https://string-db.org/cgi/input.pl?input_page_active_form=org) or download the full list in the download section of STRING website.

```
> library(STRINGdb)
> string_db <- STRINGdb$new( version="12.0", species=9606,
+                               score_threshold=200, network_type="full", input_directory="")
```

As it has been shown in the above commands, you start instantiating the STRINGdb reference class. In the constructor of the class you can also define the STRING version to be used and a threshold for the combined scores of the interactions, such that any interaction below that threshold is not loaded in the object (by default the score threshold is set to 400).

You can also specify the network type "functional" for full functional STRING network or "physical" for physical subnetwork, which link only the proteins which share a physical complex.

Besides, if you specify a local directory to the parameter input-directory, the database files will be downloaded into this directory and most of the methods can be used off-line. Otherwise, the database files will be saved and cached in a temporary directory that will be cleaned automatically when the R session is closed.

For a better understanding of the package two other commands can be useful:

```
> STRINGdb$methods()          # To list all the methods available.  
  
[1] ".objectPackage"           ".objectParent"  
[3] "add_diff_exp_color"       "add_proteins_description"  
[5] "benchmark_ppi"           "benchmark_ppi_pathway_view"  
[7] "callSuper"                "copy"  
[9] "enrichment_heatmap"       "export"  
[11] "field"                   "getClass"  
[13] "getRefClass"             "get_aliases"  
[15] "get_annotations"         "get_bioc_graph"  
[17] "get_clusters"            "get_enrichment"  
[19] "get_graph"                "get_homologs"  
[21] "get_homologs_besthits"   "get_homology_graph"  
[23] "get_interactions"        "get_link"  
[25] "get_neighbors"           "get_paralogs"  
[27] "get_pathways_benchmarking_blackList" "get_png"  
[29] "get_ppi_enrichment"       "get_ppi_enrichment_full"  
[31] "get_proteins"             "get_pubmed"  
[33] "get_pubmed_interaction"  "get_subnetwork"  
[35] "get_summary"              "get_term_proteins"  
[37] "import"                  "initFields"  
[39] "initialize"               "load"  
[41] "load_all"                 "map"  
[43] "mp"                      "plot_network"  
[45] "plot_ppi_enrichment"      "post_payload"  
[47] "ppi_enrichment"           "remove_homologous_interactions"  
[49] "set_background"           "show"  
[51] "show#envRefClass"         "trace"  
[53] "untrace"                  "usingMethods"  
  
> STRINGdb$help("get_graph")      # To visualize their documentation.  
  
Call:  
$get_graph()
```

Description:

Return an igraph object with the entire STRING network.

We invite the user to use the functions of the iGraph package to conveniently search/analyze the network.

References:

Csardi G, Nepusz T: The igraph software package for complex network research, InterJournal, Complex Systems 1695. 2006.
<http://igraph.sf.net>

See Also:

In order to simplify the most common tasks, we do also provide convenient functions that wrap some iGraph functions.

```
get_interactions(string_ids)    # returns the interactions in between the input proteins  
get_neighbors(string_ids)       # Get the neighborhoods of a protein (or of a vector of proteins).  
get_subnetwork(string_ids)      # returns a subgraph from the given input proteins
```

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For all the methods that we are going to explain below, you can always use the help function in order to get additional information/parameters with respect to those explained in this guide.

As an example, we use the analyzed data of a microarray study taken from GEO (Gene Expression Omnibus, GSE9008). This study investigates the activity of Resveratrol, a natural phytoestrogen found in red wine and a variety of plants, in A549 lung cancer cells. Microarray gene expression profiling after 48 hours exposure to Resveratrol has been performed and compared to a control composed by A549 lung cancer cells treated only with ethanol. This data is already analyzed for differential expression using the limma package: the genes are sorted by fdr corrected pvalues and the log fold change of the differential expression is also reported in the table.

```
> data(diff_exp_example1)  
> head(diff_exp_example1)
```

	pvalue	logFC	gene
1	0.0001018	3.333461	VSTM2L
2	0.0001392	3.822383	TBC1D2
3	0.0001720	3.306056	LENG9
4	0.0001739	3.024605	TMEM27
5	0.0001990	3.854414	LOC100506014
6	0.0002393	3.082052	TSPAN1

As a first step, we map the gene names to the STRING database identifiers using the "map" method. In this particular example, we map from gene HUGO names, but our mapping function supports several other common identifiers (e.g. Entrez GeneID, ENSEMBL proteins, RefSeq transcripts ... etc.).

The map function adds an additional column with STRING identifiers to the dataframe that is passed as first parameter.

```
> example1_mapped <- string_db$map( diff_exp_example1, "gene", removeUnmappedRows = TRUE )
```

```
Warning: we couldn't map to STRING 15% of your identifiers
```

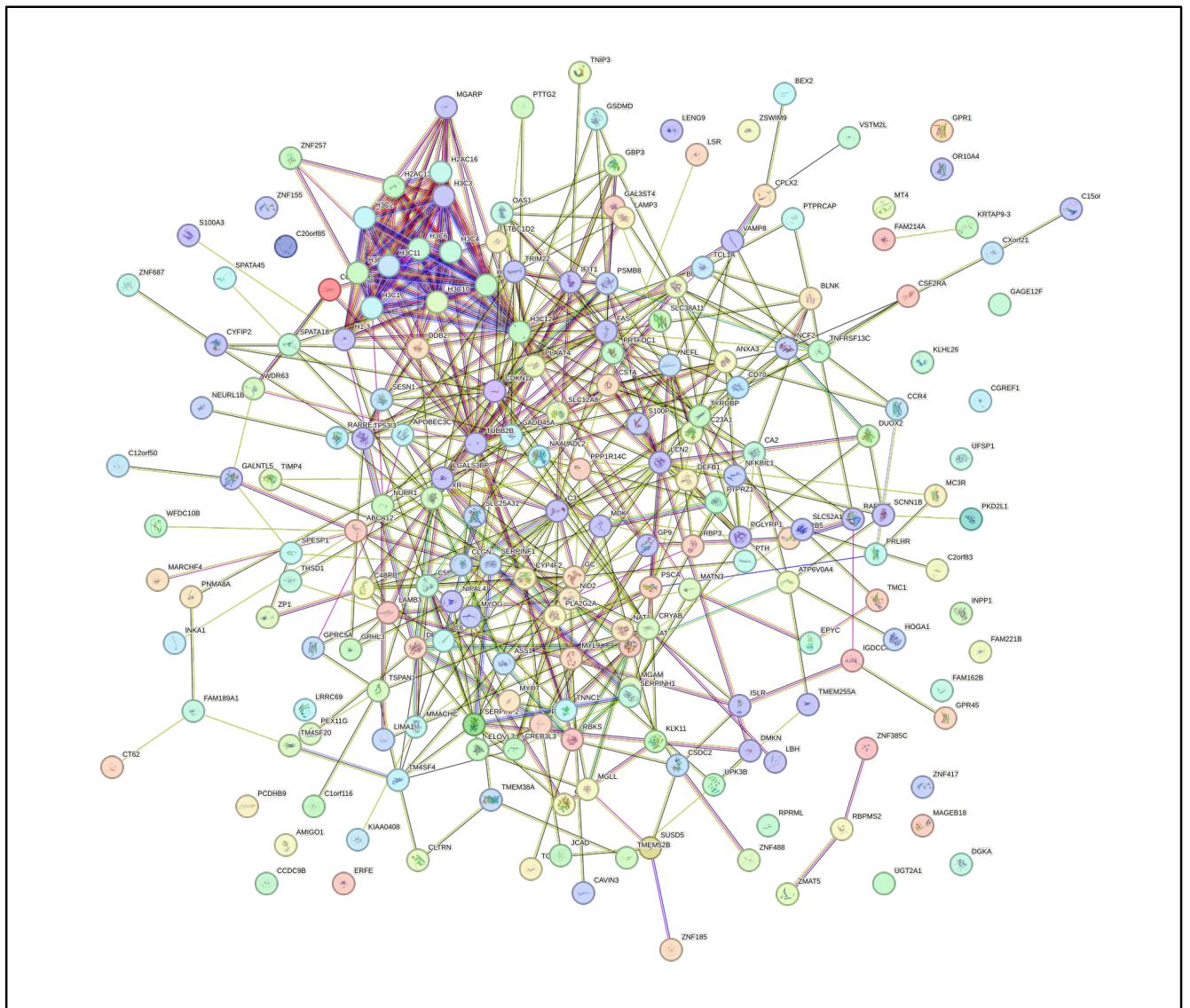
As you may have noticed, the previous command prints a warning showing the number of genes that we failed to map. In this particular example, we cannot map all the probes of the microarray that refer to position of the chromosome that are not assigned to a real gene (i.e. all the LOC genes). If we remove all these LOC genes before the mapping we obtain a much lower percentage of unmapped genes (i.e. < 6 %).

If you set to FALSE the "removeUnmappedRows" parameter, than the rows which corresponds to unmapped genes are left and you can manually inspect them.

Finally, we extract the most significant 200 genes and we produce an image of the STRING network for those. The image shows clearly the genes and how they are possibly functionally related. On the top of the plot, we insert a pvalue that represents the probability that you can expect such an equal or greater number of interactions by chance.

```
> hits <- example1_mapped$STRING_id[1:200]  
> string_db$plot_network( hits )
```

proteins: 200
 interactions: 546
 expected interactions: 333 (p-value: 0)



2 PAYLOAD MECHANISM

This R library provides the ability to interact with the STRING payload mechanism. The payload appears as an additional colored "halo" around the bubbles.

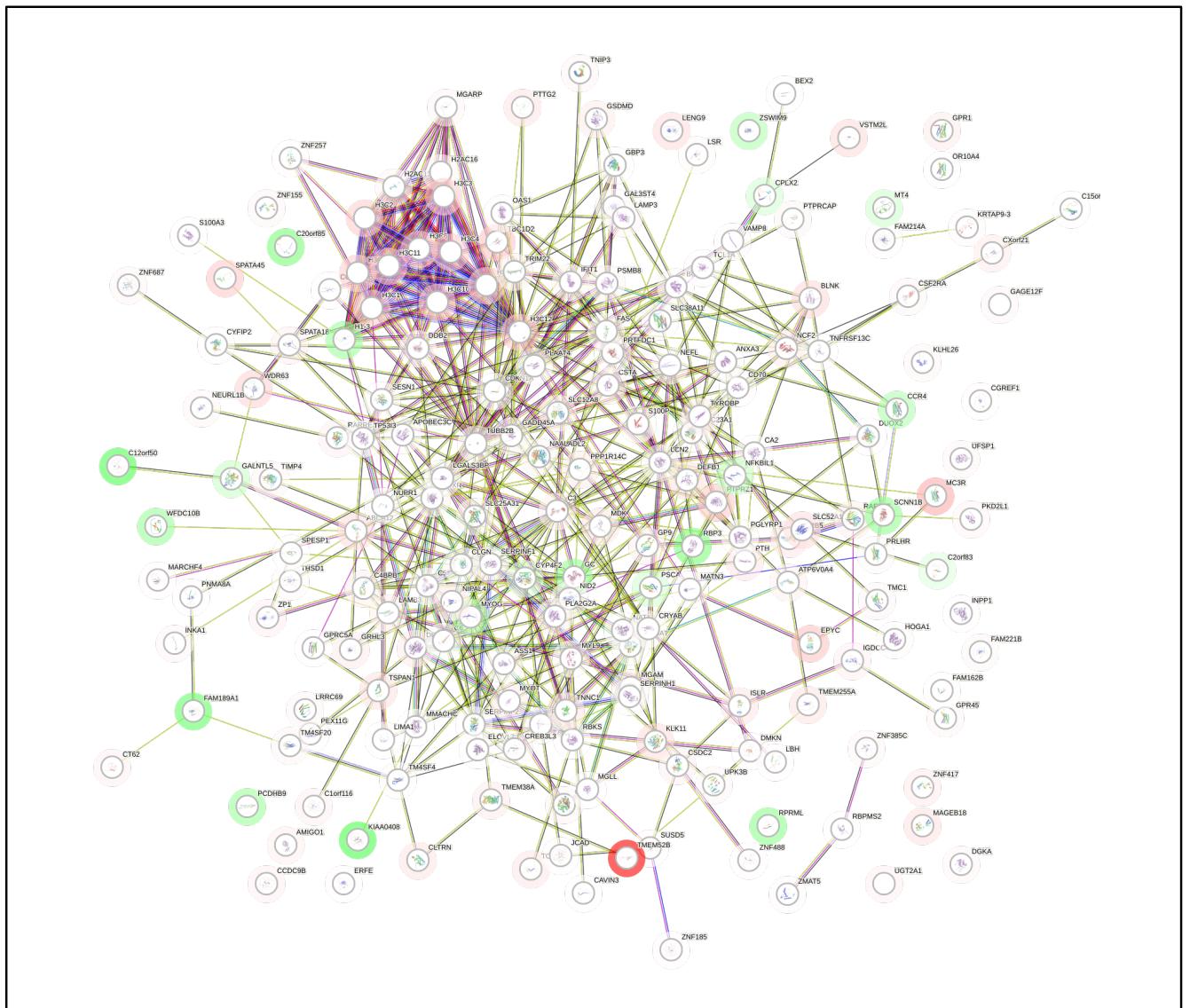
For example, this allows to color in green the genes that are down-regulated and in red the genes that are up-regulated. For this mechanism to work, we provide a function that posts the information on our web server.

```
> # filter by p-value and add a color column
> # (i.e. green down-regulated genes and red for up-regulated genes)
> example1_mapped_pval05 <- string_db$add_diff_exp_color( subset(example1_mapped, pvalue<0.05),
+                                         logFcColStr="logFC" )

> # post payload information to the STRING server
> payload_id <- string_db$post_payload( example1_mapped_pval05$STRING_id,
+                                         colors=example1_mapped_pval05$color )

> # display a STRING network png with the "halo"
> string_db$plot_network( hits, payload_id=payload_id )
```

proteins: 200
interactions: 546
expected interactions: 333 (p-value: 0)



3 ENRICHMENT

We provide a method to compute the enrichment in Gene Ontology (Process, Function and Component), KEGG and Reactome pathways, PubMed publications, UniProt Keywords, and PFAM/INTERPRO/SMART domains for your set of proteins all in one simple call. The enrichment itself is computed using an hypergeometric test and the FDR is calculated using Benjamini-Hochberg procedure.

```
> enrichment <- string_db$get_enrichment( hits )
> head(enrichment, n=20)
```

	category	term	number_of_genes	number_of_genes_in_background
1	COMPARTMENTS	GOCC:0000786	10	94
2	COMPARTMENTS	GOCC:0032993	12	198
3	COMPARTMENTS	GOCC:0005576	42	2079
4	COMPARTMENTS	GOCC:0043230	17	524
5	Process	GO:0006335	10	32
6	Process	GO:0006334	11	124
7	Process	GO:0006952	35	1394
8	Process	GO:0040029	10	123
9	Process	GO:0032200	10	129
10	Process	GO:0009607	32	1375
11	Process	GO:0051707	31	1328
12	Process	GO:0006955	30	1321
13	Component	GO:0000786	13	133
14	Component	GO:0070062	51	2096
15	Component	GO:1903561	52	2120
16	Component	GO:0032993	15	226
17	Component	GO:0005576	76	4175
18	Component	GO:0005615	63	3247
19	Component	GO:0031982	65	3957
20	Component	GO:0000228	10	244
	ncbiTaxonId			
1	9606			
2	9606			
3	9606			
4	9606			
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17 9606.ENSP00000008938,9606.ENSP0000014914,9606.ENSP00000187762,9606.ENSP00000216286,9606.ENSP00000
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17 PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C4BPB,C3,ISLR,SERPINF1,THSD1,TUBB2B,EPYC,LGALS3BP,C6,VAMP8,
18
19
20
    p_value      fdr          description
1  9.65e-08  2.20e-04          Nucleosome
2  1.50e-06  1.70e-03  protein-DNA complex
3  1.28e-05  7.30e-03  Extracellular region
4  3.51e-05  1.61e-02  Extracellular organelle
5  9.34e-12  1.46e-07  DNA replication-dependent chromatin assembly
6  1.21e-07  6.30e-04  Nucleosome assembly
7  7.80e-07  3.10e-03  Defense response
8  9.70e-07  3.10e-03  Regulation of gene expression, epigenetic

```

9	1.45e-06	3.80e-03	Telomere organization
10	1.15e-05	2.01e-02	Response to biotic stimulus
11	1.52e-05	2.38e-02	Response to other organism
12	3.51e-05	4.29e-02	Immune response
13	2.84e-09	3.30e-06	Nucleosome
14	3.19e-09	3.30e-06	Extracellular exosome
15	1.61e-09	3.30e-06	Extracellular vesicle
16	2.30e-08	7.84e-06	protein-DNA complex
17	5.34e-08	1.56e-05	Extracellular region
18	1.46e-07	3.74e-05	Extracellular space
19	2.77e-05	5.70e-03	Vesicle
20	2.60e-04	4.83e-02	Nuclear chromosome

If you have performed your experiment on a predefined set of proteins, it is important to run the enrichment statistics using that set as a background (otherwise you would get a wrong p-value!). Hence, before to launch the method above, you may want to set the background:

```
> backgroundV <- example1_mapped$STRING_id[1:2000] # as an example, we use the first 2000 genes
> string_db$set_background(backgroundV)
```

You can also set the background when you instantiate the STRINGdb object:

```
> string_db <- STRINGdb$new( score_threshold=200, backgroundV = backgroundV )
```

If you just want to know terms are assigned to your set of proteins (and not necessary enriched) you can use "get_annotations" method. This method will output all the terms from most of the categories (the exceptions are KEGG terms due to licensing issues and PubMed due to the size of the output) that are associated with your set of proteins.

```
> annotations <- string_db$get_annotations( hits )
> head(annotations, n=20)
```

	category	term_id	number_of_genes	ratio_in_set	species
1	COMPARTMENTS	GOCC:0000109	1	0.005	9606
2	COMPARTMENTS	GOCC:0000139	1	0.005	9606
3	COMPARTMENTS	GOCC:0000151	2	0.010	9606
4	COMPARTMENTS	GOCC:0000152	1	0.005	9606
5	COMPARTMENTS	GOCC:0000228	10	0.050	9606
6	COMPARTMENTS	GOCC:0000307	1	0.005	9606
7	COMPARTMENTS	GOCC:0000323	6	0.030	9606
8	COMPARTMENTS	GOCC:0000417	2	0.010	9606
9	COMPARTMENTS	GOCC:0000502	1	0.005	9606
10	COMPARTMENTS	GOCC:0000785	11	0.055	9606
11	COMPARTMENTS	GOCC:0000786	10	0.050	9606
12	COMPARTMENTS	GOCC:0000791	1	0.005	9606
13	COMPARTMENTS	GOCC:0001533	1	0.005	9606
14	COMPARTMENTS	GOCC:0001650	1	0.005	9606
15	COMPARTMENTS	GOCC:0001669	1	0.005	9606

16 COMPARTMENTS GOCC:0001725 2 0.010 9606
17 COMPARTMENTS GOCC:0001726 2 0.010 9606
18 COMPARTMENTS GOCC:0002133 1 0.005 9606
19 COMPARTMENTS GOCC:0005576 42 0.210 9606
20 COMPARTMENTS GOCC:0005577 1 0.005 9606

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19 9606.ENSP00000008938,9606.ENSP00000216286,9606.ENSP00000223642,9606.ENSP00000243611,9606.ENSP00000

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19 PGLYRP1,NID2,C5,C4BPB,C3,SERPINF1,THSD1,TUBB2B,LGALS3BP,C6,CSTA,ANXA3,ZP1,CA2,TIMP4,DEFB1,PSCA,SE

20

description
Nucleotide-excision repair complex
Golgi membrane
Ubiquitin ligase complex

```

4          Nuclear ubiquitin ligase complex
5          Nuclear chromosome
6 Cyclin-dependent protein kinase holoenzyme complex
7          Lytic vacuole
8          HIR complex
9          Proteasome complex
10         Chromatin
11         Nucleosome
12         Euchromatin
13         Cornified envelope
14         Fibrillar center
15         Acrosomal vesicle
16         Stress fiber
17         Ruffle
18         Polycystin complex
19         Extracellular region
20         Fibrinogen complex

```

4 CLUSTERING

The iGraph package provides several clustering/community algorithms: "fastgreedy", "walktrap", "spinglass", "edge.betweenness". We encapsulate this in an easy-to-use function that returns the clusters in a list.

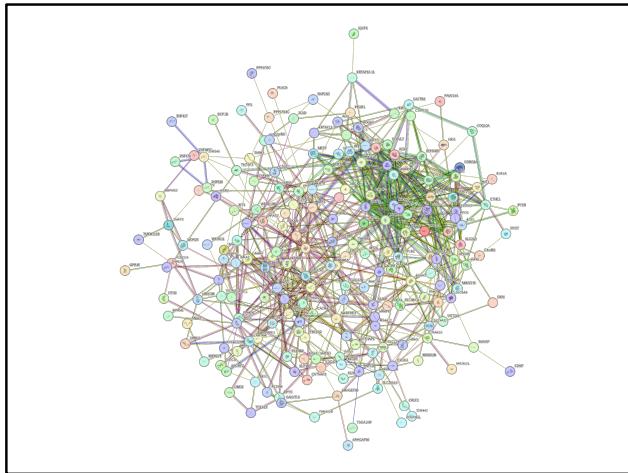
```

> # get clusters
> clustersList <- string_db$get_clusters(example1_mapped$STRING_id[1:600])

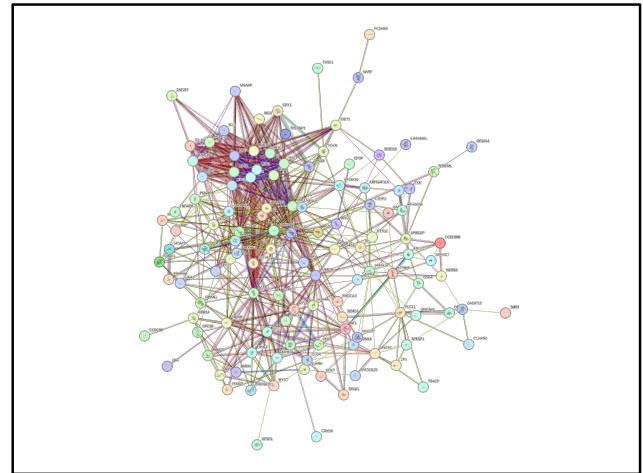
> # plot first 4 clusters
> par(mfrow=c(2,2))
> for(i in seq(1:4)){
+   string_db$plot_network(clustersList[[i]])
+ }

```

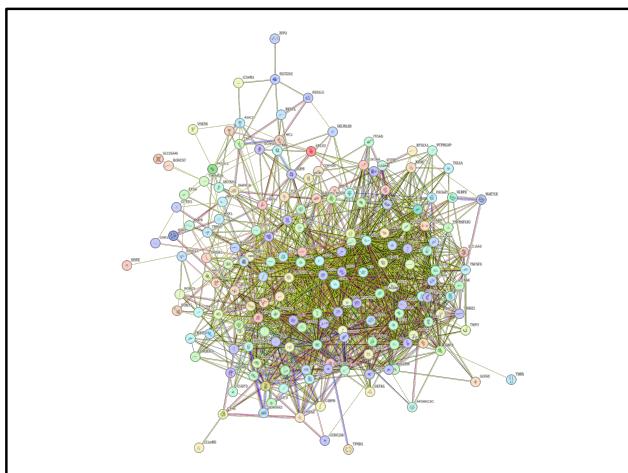
proteins: 204
interactions: 673
expected interactions: 238 (p-value: 0)



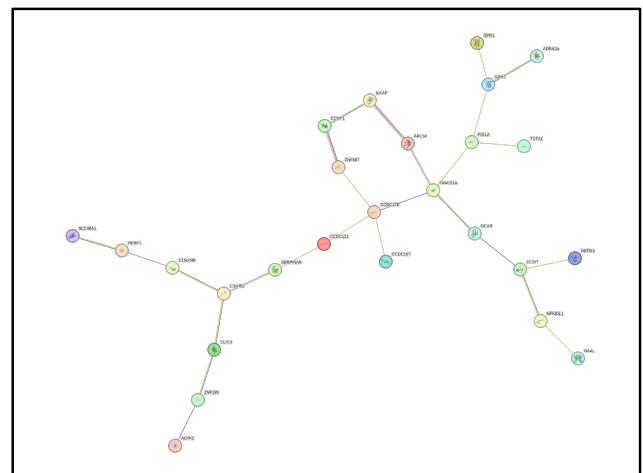
proteins: 121
interactions: 581
expected interactions: 165 (p-value: 0)



proteins: 173
interactions: 1576
expected interactions: 469 (p-value: 0)



proteins: 26
interactions: 26
expected interactions: 2 (p-value: 0)



5 ADDITIONAL PROTEIN INFORMATION

You can get a table that contains all the proteins that are present in our database of the species of interest. The protein table also include the preferred name, the size and a short description of each protein.

```
> string_proteins <- string_db$get_proteins()
```

In the following section we will show how to query STRING with R on some specific proteins. In the examples, we will use the famous tumor proteins TP53 and ATM .

First we need to get the STRING identifier of those proteins, using our mp method:

```
> tp53 = string_db$mp( "tp53" )
> atm = string_db$mp( "atm" )
```

The mp method (i.e. map proteins) is an alternative to our map method, to be used when you need to map only one or few proteins.

It takes in input a vector of protein aliases and returns a vector with the STRING identifiers of those proteins.

Using the following method, you can see the proteins that interact with one or more of your proteins:

```
> string_db$get_neighbors( c(tp53, atm) )

[1] "9606.ENSP00000001008" "9606.ENSP00000003084" "9606.ENSP00000003302"
[4] "9606.ENSP00000004531" "9606.ENSP00000004982" "9606.ENSP00000005178"
[7] "9606.ENSP00000005257" "9606.ENSP00000005260" "9606.ENSP00000005340"
[10] "9606.ENSP00000006015" "9606.ENSP00000006053" "9606.ENSP00000008527"
[13] "9606.ENSP00000009530" "9606.ENSP00000011619" "9606.ENSP00000011653"
[16] "9606.ENSP00000013807" "9606.ENSP00000014914" "9606.ENSP00000020945"
[19] "9606.ENSP00000025008" "9606.ENSP00000027335" "9606.ENSP00000037243"
[22] "9606.ENSP00000039007" "9606.ENSP00000044462" "9606.ENSP00000052754"
[25] "9606.ENSP00000053243" "9606.ENSP00000053867" "9606.ENSP00000055077"
[28] "9606.ENSP00000056233" "9606.ENSP00000072644" "9606.ENSP00000075120"
[31] "9606.ENSP00000078429" "9606.ENSP00000080059" "9606.ENSP00000085219"
[34] "9606.ENSP00000155840" "9606.ENSP00000155926" "9606.ENSP00000156084"
[37] "9606.ENSP00000156626" "9606.ENSP00000157812" "9606.ENSP00000159060"
[40] "9606.ENSP00000159111" "9606.ENSP00000160382" "9606.ENSP00000160827"
[43] "9606.ENSP00000161559" "9606.ENSP00000161863" "9606.ENSP00000162749"
[46] "9606.ENSP00000164139" "9606.ENSP00000164227" "9606.ENSP00000166345"
[49] "9606.ENSP00000167586" "9606.ENSP00000167588" "9606.ENSP00000168148"
[52] "9606.ENSP00000168712" "9606.ENSP00000170447" "9606.ENSP00000171887"
[55] "9606.ENSP00000172229" "9606.ENSP00000173229" "9606.ENSP00000174618"
[58] "9606.ENSP00000177694" "9606.ENSP00000178638" "9606.ENSP00000178640"
[61] "9606.ENSP00000179259" "9606.ENSP00000180166" "9606.ENSP00000181796"
[64] "9606.ENSP00000181839" "9606.ENSP00000184956" "9606.ENSP00000188790"
[67] "9606.ENSP00000198767" "9606.ENSP00000199280" "9606.ENSP00000199764"
[70] "9606.ENSP00000200181" "9606.ENSP00000200453" "9606.ENSP00000200676"
```

[73] "9606.ENSP00000201031" "9606.ENSP00000201979" "9606.ENSP00000202017"
[76] "9606.ENSP00000202556" "9606.ENSP00000202967" "9606.ENSP00000203407"
[79] "9606.ENSP00000203629" "9606.ENSP00000203630" "9606.ENSP00000203664"
[82] "9606.ENSP00000204517" "9606.ENSP00000204961" "9606.ENSP00000205143"
[85] "9606.ENSP00000205636" "9606.ENSP00000205948" "9606.ENSP00000206513"
[88] "9606.ENSP00000206765" "9606.ENSP00000209668" "9606.ENSP00000209728"
[91] "9606.ENSP00000209875" "9606.ENSP00000210313" "9606.ENSP00000210444"
[94] "9606.ENSP00000211287" "9606.ENSP00000211998" "9606.ENSP00000212015"
[97] "9606.ENSP00000212355" "9606.ENSP00000214869" "9606.ENSP00000215057"
[100] "9606.ENSP00000215071" "9606.ENSP00000215530" "9606.ENSP00000215567"
[103] "9606.ENSP00000215574" "9606.ENSP00000215631" "9606.ENSP00000215659"
[106] "9606.ENSP00000215743" "9606.ENSP00000215754" "9606.ENSP00000215781"
[109] "9606.ENSP00000215793" "9606.ENSP00000215794" "9606.ENSP00000215829"
[112] "9606.ENSP00000215832" "9606.ENSP00000215882" "9606.ENSP00000215909"
[115] "9606.ENSP00000216037" "9606.ENSP00000216039" "9606.ENSP00000216044"
[118] "9606.ENSP00000216099" "9606.ENSP00000216115" "9606.ENSP00000216117"
[121] "9606.ENSP00000216122" "9606.ENSP00000216133" "9606.ENSP00000216139"
[124] "9606.ENSP00000216160" "9606.ENSP00000216181" "9606.ENSP00000216185"
[127] "9606.ENSP00000216211" "9606.ENSP00000216218" "9606.ENSP00000216223"
[130] "9606.ENSP00000216225" "9606.ENSP00000216254" "9606.ENSP00000216271"
[133] "9606.ENSP00000216274" "9606.ENSP00000216277" "9606.ENSP00000216297"
[136] "9606.ENSP00000216330" "9606.ENSP00000216336" "9606.ENSP00000216341"
[139] "9606.ENSP00000216373" "9606.ENSP00000216392" "9606.ENSP00000216420"
[142] "9606.ENSP00000216446" "9606.ENSP00000216455" "9606.ENSP00000216479"
[145] "9606.ENSP00000216489" "9606.ENSP00000216492" "9606.ENSP00000216629"
[148] "9606.ENSP00000216639" "9606.ENSP00000216714" "9606.ENSP00000216727"
[151] "9606.ENSP00000216733" "9606.ENSP00000216780" "9606.ENSP00000216797"
[154] "9606.ENSP00000216802" "9606.ENSP00000216807" "9606.ENSP00000216862"
[157] "9606.ENSP00000216911" "9606.ENSP00000216962" "9606.ENSP00000216968"
[160] "9606.ENSP00000217026" "9606.ENSP00000217086" "9606.ENSP00000217109"
[163] "9606.ENSP00000217169" "9606.ENSP00000217182" "9606.ENSP00000217244"
[166] "9606.ENSP00000217246" "9606.ENSP00000217386" "9606.ENSP00000217426"
[169] "9606.ENSP00000217515" "9606.ENSP00000217740" "9606.ENSP00000217958"
[172] "9606.ENSP00000217961" "9606.ENSP00000217971" "9606.ENSP00000218089"
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It is also possible to retrieve the interactions that connect certain input proteins between each other. Using the "get_interactions" method we can clearly see that TP53 and ATM interact with each other with a good evidence/score.

```
> string_db$get_interactions( c(tp53, atm) )

      from          to combined_score
1 9606.ENSP00000269305 9606.ENSP00000278616      999
2 9606.ENSP00000269305 9606.ENSP00000278616      999
```

STRING provides a way to get homologous proteins: in our database we store ALL-AGAINST-ALL alignments within all 5090 organisms. You can retrieve all of the paralogs of the protein using "get_paralogs" method.

```
> # Get all homologs of TP53 in human.
> string_db$get_paralogs(tp53)

[1] X9606          X9606.ENSP00000269305  X9606.1
[4] X9606.ENSP00000269305.1 X815.8
<0 rows> (or 0-length row.names)
```

STRING also stores best hits (as measured by bitscore) between the proteins from different species. "get_homologs_bestscores" lets you retrieve these homologs.

```
> # get the best hits of the following protein in all the STRING species
> string_db$get_homologs_besthits(tp53)
```

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3	9606	9606.ENSP00000269305	9601	9601.ENS PPYP00000008923	799.3
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339	9606	9606. ENSP00000269305	46835	46835. AOA504YVH4	87.4
340	9606	9606. ENSP00000269305	6183	6183. AOA3Q0KN56	87.4
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344	9606	9606. ENSP00000269305	6186	6186. AOA183JFI6	85.9
345	9606	9606. ENSP00000269305	60517	60517. AOA158R7U3	85.1
346	9606	9606. ENSP00000269305	1147741	1147741. AOA0R3RXLO	85.1
347	9606	9606. ENSP00000269305	6184	6184. AOA430QT47	84.7
348	9606	9606. ENSP00000269305	102285	102285. AOA0R3TMT8	84.3
349	9606	9606. ENSP00000269305	300112	300112. AOA4S2JFH1	84.3
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355	9606	9606. ENSP00000269305	6185	6185. AOA095C5C5	83.2
356	9606	9606. ENSP00000269305	6210	6210. W6U916	82.8
357	9606	9606. ENSP00000269305	7160	7160. AOA182GIF0	82.8
358	9606	9606. ENSP00000269305	7159	7159. Q171M1	81.6
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360	9606	9606. ENSP00000269305	6293	6293. AOA1I8EB15	80.9
361	9606	9606. ENSP00000269305	6205	6205. AOA0R3WQW6	80.5
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366	9606	9606. ENSP00000269305	103372	103372. F4X756	79.0
367	9606	9606. ENSP00000269305	2015173	2015173. AOA026WHR3	79.0
368	9606	9606. ENSP00000269305	34720	34720. AOA195FHS0	78.6
369	9606	9606. ENSP00000269305	37001	37001. AOA1A9W1P0	78.6
370	9606	9606. ENSP00000269305	66420	66420. AOA0N1PE05	77.8
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373	9606	9606. ENSP00000269305	471704	471704. AOA195DK69	77.4
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378	9606	9606. ENSP00000269305	400682	400682. AOA1X7UD97	75.1
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382	9606	9606. ENSP00000269305	76193	76193. AOA0N0PC7	72.0
383	9606	9606. ENSP00000269305	7395	7395. AOA1A9UZU7	72.0
384	9606	9606. ENSP00000269305	62324	62324. AOA182RCW2	70.5
385	9606	9606. ENSP00000269305	199890	199890. AOA182PA25	70.5
386	9606	9606. ENSP00000269305	158441	158441. AOA226DFT1	70.1
387	9606	9606. ENSP00000269305	69004	69004. AOA3F2YX69	69.3
388	9606	9606. ENSP00000269305	43151	43151. W5JCA5	68.9
389	9606	9606. ENSP00000269305	7167	7167. AOA182FR67	68.6
390	9606	9606. ENSP00000269305	334426	334426. AOA0R3Q2A0	67.0
391	9606	9606. ENSP00000269305	7102	7102. AOA2A4JNC2	67.0
392	9606	9606. ENSP00000269305	139723	139723. AOA182M5Y6	66.6
393	9606	9606. ENSP00000269305	6313	6313. AOA0K0DP08	66.6
394	9606	9606. ENSP00000269305	6290	6290. AOA0N4W3M7	66.2
395	9606	9606. ENSP00000269305	7168	7168. AOA182N4N0	65.9
396	9606	9606. ENSP00000269305	41427	41427. AOA182J735	65.9
397	9606	9606. ENSP00000269305	51031	51031. W2SWL6	65.5
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399	9606	9606. ENSP00000269305	48709	48709. AOA1D2NAH9	65.1
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401	9606	9606. ENSP00000269305	7260	7260. B4N9F0	65.1
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403	9606	9606. ENSP00000269305	74873	74873. AOA084W6W1	63.9
404	9606	9606. ENSP00000269305	112268	112268. AOA182VY33	63.9

405	9606	9606.ESNP00000269305	30066		30066.AOA182V190	63.9
406	9606	9606.ESNP00000269305	34691		34691.AOA182XID1	63.9
407	9606	9606.ESNP00000269305	42157		42157.AOA182ELX1	63.9
408	9606	9606.ESNP00000269305	46245		46245.AOA0R3NKT4	63.2
409	9606	9606.ESNP00000269305	29170		29170.AOA368F8M2	63.2
410	9606	9606.ESNP00000269305	318479		318479.AOA0N4UDB8	62.8
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414	9606	9606.ESNP00000269305	7217		7217.AOAOP8XYV2	59.3
415	9606	9606.ESNP00000269305	7227		7227.FBpp0083753	58.5
416	9606	9606.ESNP00000269305	7232		7232.AOA484BSX2	58.5
417	9606	9606.ESNP00000269305	387005		387005.AOA183H0Z1	57.0
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419	9606	9606.ESNP00000269305	7238		7238.B4HFA1	57.0
420	9606	9606.ESNP00000269305	70667		70667.AOA183STT5	56.6
421	9606	9606.ESNP00000269305	7370		7370.AOA1I8N839	56.6
422	9606	9606.ESNP00000269305	35570		35570.AOA1I8QBH4	56.6
423	9606	9606.ESNP00000269305	7091		7091.E9JEI4	56.2
424	9606	9606.ESNP00000269305	27835		27835.AOA0N4YQF9	55.1
425	9606	9606.ESNP00000269305	7240		7240.B4R1C4	54.3
426	9606	9606.ESNP00000269305	34690		34690.AOA182UJE7	53.5
427	9606	9606.ESNP00000269305	7375		7375.AOA0LOCLI5	53.1
428	9606	9606.ESNP00000269305	7266		7266.AOA3B0JRN9	52.0
429	9606	9606.ESNP00000269305	30019		30019.AOA0M3QXK1	52.0
430	9606	9606.ESNP00000269305	947166		947166.AOA1D1VBG3	51.6
431	9606	9606.ESNP00000269305	7244		7244.B4MB49	51.2
432	9606	9606.ESNP00000269305	54126		54126.H3FK89	50.8

... or you can specify the species of interest (i.e. all the blast hits):

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> # get the homologs of the following two proteins in the mouse (i.e. species_id=10090)
> string_db$get_homologs_besthits(c(tp53, atm), target_species_id=10090)

X9606 X9606.ESNP00000269305 X10090 X10090.ESNMUSP00000104298 X598.2
1 9606 9606.ESNP00000278616 10090 10090.ESNMUSP00000156344 5328.8
```

6 CITATION

Please cite:

Szklarczyk D, Kirsch R, Koutrouli M, Nastou K, Mehryary F, Hachilif R, Annika GL, Fang T, Doncheva NT, Pyysalo S, Bork P, Jensen LJ, von Mering C. 'The STRING database in 2023: protein-protein association networks and functional enrichment analyses for any sequenced genome of interest.' Nucleic Acids Res. 2023 Jan 6;51(D1):D638-646