

STRINGdb Package Vignette

Andrea Franceschini

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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 60 millions proteins from more than 12000 organisms.

As you will learn in this guide, the STRING database can be usefull 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?input_page_active_form=organ) 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", link_data='combined_only', in
```

To use the STRINGdb package, start by creating an instance of the STRINGdb reference class. In the class constructor, you can specify the STRING version and set a threshold for the combined interaction scores. Any interactions with scores below this threshold will not be loaded into the object (the default threshold is 400).

You can also choose the 'network_type': "functional" for the full functional STRING network, or "physical" for the physical subnetwork that links only proteins within the same physical complex. STRING will automatically download additional data like protein name tables and link data as needed. By default, only combined scores are downloaded, but you can obtain more detailed information by setting the 'link_data' parameter: "combined_only" (default), "detailed" for scores separated by evidence channel, or "full" to further separate confidence score into direct and orthology-transferred. If you specify a local directory via the 'input_directory' parameter, database files will be downloaded there so most methods can function offline. Otherwise, files will be cached in a temporary directory and automatically deleted when the R session ends.

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
```

Author(s):

Andrea Franceschini

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 *p*values 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. $< 6\%$).

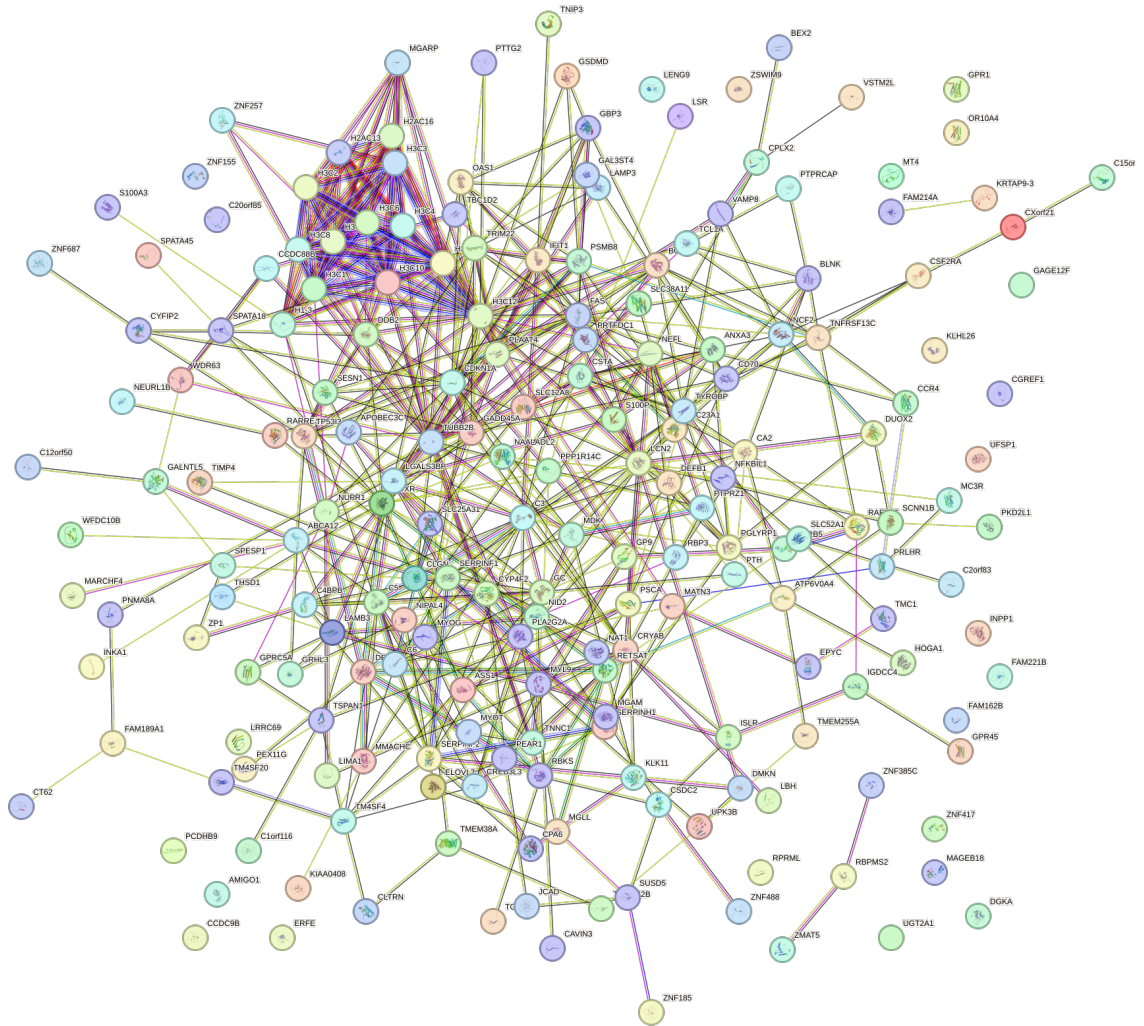
If you set to FALSE the "removeUnmappedRows" parameter, than the rows which corresponds to unmapped genes are left and you can manually inspect them.

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 )
```


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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	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

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

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", "springlass", "edge.betweenness". We encapsulate this in an easy-to-use function that returns the clusters in a list.

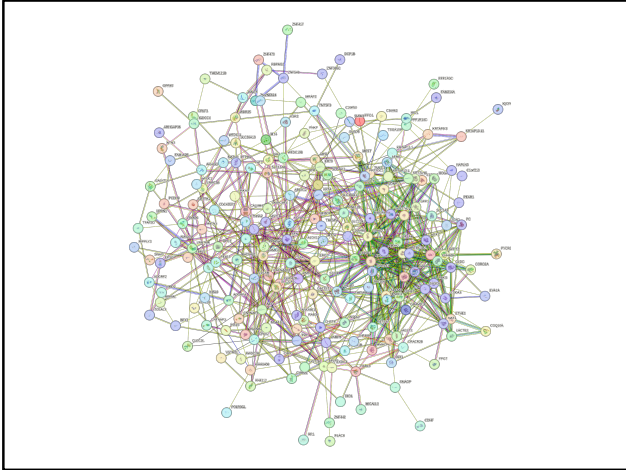
```

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

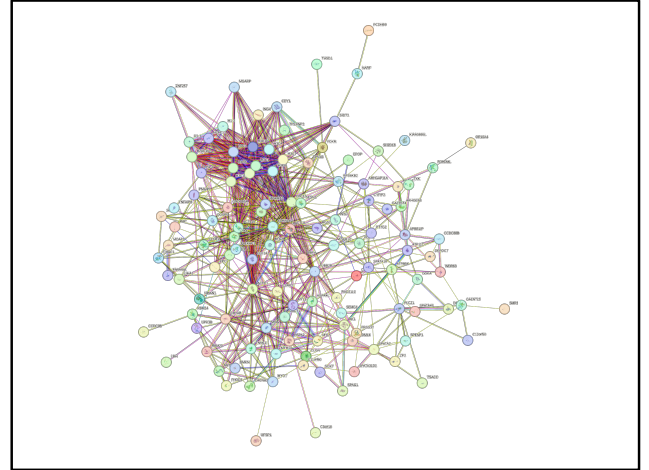
> # plot first 4 clusters
> par(mfrow=c(2,2))
> for(i in seq(1:4)){
+   string_db$plot_network(clustersList[[i]])
+ }

```

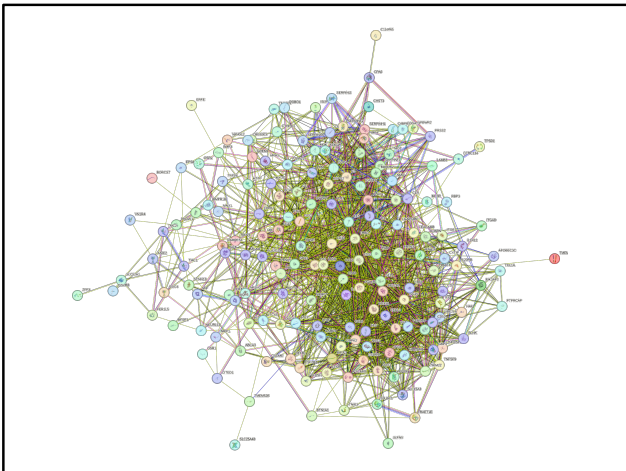

proteins: 203
interactions: 668
expected interactions: 236 (p-value: 0)



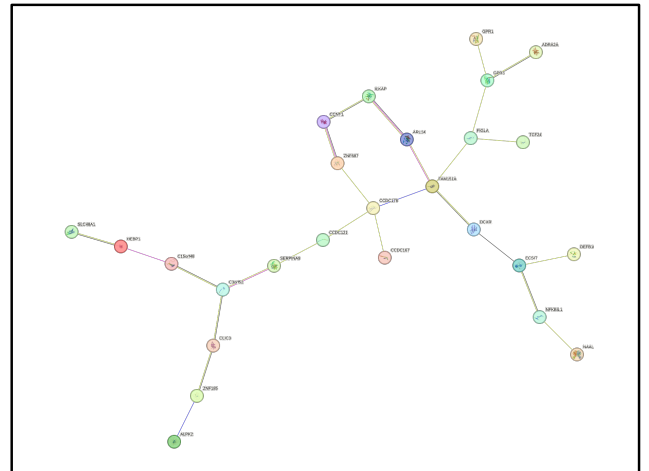
proteins: 121
interactions: 581
expected interactions: 165 (p-value: 0)



proteins: 174
interactions: 1583
expected interactions: 473 (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"
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 [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"
 [175] "9606. ENSP00000218348" "9606. ENSP00000218388" "9606. ENSP00000218548"
 [178] "9606. ENSP00000218758" "9606. ENSP00000219022" "9606. ENSP00000219066"
 [181] "9606. ENSP00000219069" "9606. ENSP00000219070" "9606. ENSP00000219097"
 [184] "9606. ENSP00000219162" "9606. ENSP00000219204" "9606. ENSP00000219235"
 [187] "9606. ENSP00000219240" "9606. ENSP00000219244" "9606. ENSP00000219252"
 [190] "9606. ENSP00000219313" "9606. ENSP00000219334" "9606. ENSP00000219345"
 [193] "9606. ENSP00000219431" "9606. ENSP00000219476" "9606. ENSP00000219479"
 [196] "9606. ENSP00000219548" "9606. ENSP00000219596" "9606. ENSP00000219660"
 [199] "9606. ENSP00000219746" "9606. ENSP00000219782" "9606. ENSP00000219789"
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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_bests" lets you retrieve these homologs.

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

	X9606	X9606.ENSPO0000269305	X9597	X9597.ENSPPAP00000011040	X815.8
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103	9606	9606.ENSPO00000269305	9545	9545.ENSMNEP000000030865	399.8
104	9606	9606.ENSPO00000269305	56216	56216.A0A1A6GWM4	394.0
105	9606	9606.ENSPO00000269305	7897	7897.ENSLACP000000015915	393.3
106	9606	9606.ENSPO00000269305	8496	8496.A0A151MW63	373.6
107	9606	9606.ENSPO00000269305	2587831	2587831.ENSTMTTP000000028378	372.5
108	9606	9606.ENSPO00000269305	9315	9315.ENSMEUP000000011978	371.7
109	9606	9606.ENSPO00000269305	8478	8478.ENSCLBP000000031582	364.8
110	9606	9606.ENSPO00000269305	113540	113540.ENSSFOP00015035795	361.3
111	9606	9606.ENSPO00000269305	38654	38654.A0A3Q0FUE5	359.8
112	9606	9606.ENSPO00000269305	38772	38772.ENSAGAP000000006237	359.8
113	9606	9606.ENSPO00000269305	13735	13735.ENSPSIP000000014905	359.4
114	9606	9606.ENSPO00000269305	106734	106734.ENSCLBP000000018274	359.0
115	9606	9606.ENSPO00000269305	7918	7918.ENSLACP000000017063	359.0
116	9606	9606.ENSPO00000269305	62062	62062.ENSHHUP000000013468	357.1
117	9606	9606.ENSPO00000269305	1676925	1676925.ENSPKIP000000014805	357.1
118	9606	9606.ENSPO00000269305	8032	8032.ENSTTUP0000000101309	356.7
119	9606	9606.ENSPO00000269305	75366	75366.ENSSGRP000000074183	356.3
120	9606	9606.ENSPO00000269305	8030	8030.ENSSSAP000000057928	355.5
121	9606	9606.ENSPO00000269305	307959	307959.ENSSRHP000000051429	353.2
122	9606	9606.ENSPO00000269305	1608454	1608454.ENSSANP000000026698	352.8
123	9606	9606.ENSPO00000269305	27687	27687.ENSECRP000000015713	351.7
124	9606	9606.ENSPO00000269305	8005	8005.ENSEEEP000000033982	345.9
125	9606	9606.ENSPO00000269305	8010	8010.ENSELUP000000026168	344.0
126	9606	9606.ENSPO00000269305	7998	7998.ENSIPUP000000031919	343.6
127	9606	9606.ENSPO00000269305	74533	74533.ENSPTIP000000024834	343.2
128	9606	9606.ENSPO00000269305	96440	96440.ENSSMRP000000003871	340.9
129	9606	9606.ENSPO00000269305	7955	7955.ENSDARP0000000116736	340.9
130	9606	9606.ENSPO00000269305	84645	84645.A0A498NKF5	340.1
131	9606	9606.ENSPO00000269305	8364	8364.ENSXETP000000041856	339.7
132	9606	9606.ENSPO00000269305	37347	37347.ENSTBEP000000010189	336.7
133	9606	9606.ENSPO00000269305	299321	299321.ENSDCDP000000007017	332.0
134	9606	9606.ENSPO00000269305	8469	8469.M7CJF0	330.9
135	9606	9606.ENSPO00000269305	103695	103695.ENSVPVP000000017506	324.3
136	9606	9606.ENSPO00000269305	623744	623744.A0A553PV69	319.7
137	9606	9606.ENSPO00000269305	8508	8508.ENSSPUP000000018842	313.9
138	9606	9606.ENSPO00000269305	2489341	2489341.ENSSHBP000005007544	313.2
139	9606	9606.ENSPO00000269305	42514	42514.ENSPNAP000000014501	313.2
140	9606	9606.ENSPO00000269305	61221	61221.ENSVKKP000000029045	310.8
141	9606	9606.ENSPO00000269305	7994	7994.ENSAMXP000000021366	309.3
142	9606	9606.ENSPO00000269305	7950	7950.ENSCHAP000000042143	305.1
143	9606	9606.ENSPO00000269305	586833	586833.ENSMMDP000005051289	304.7
144	9606	9606.ENSPO00000269305	8022	8022.A0A060XN97	304.3
145	9606	9606.ENSPO00000269305	8081	8081.ENSPREP000000019676	293.5
146	9606	9606.ENSPO00000269305	52904	52904.ENSSMAP000000015064	292.0
147	9606	9606.ENSPO00000269305	47969	47969.ENSQABP000000003944	291.6
148	9606	9606.ENSPO00000269305	181472	181472.ENSSFAP000005012771	291.6
149	9606	9606.ENSPO00000269305	375764	375764.ENSSORP000005058467	291.6

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151	9606	9606.ENSPO00000269305	8167	8167.A0A484CCMO	291.2
152	9606	9606.ENSPO00000269305	215358	215358.ENSLCRP000005011976	290.8
153	9606	9606.ENSPO00000269305	80972	80972.ENSACOP00000001385	290.0
154	9606	9606.ENSPO00000269305	161767	161767.ENSAPEP00000017927	290.0
155	9606	9606.ENSPO00000269305	8083	8083.ENSXMAP000000028829	290.0
156	9606	9606.ENSPO00000269305	37003	37003.ENSXMAP000000018969	289.7
157	9606	9606.ENSPO00000269305	64176	64176.ENSXMAP000000017811	289.3
158	9606	9606.ENSPO00000269305	441366	441366.ENSXWIP000000038103	288.9
159	9606	9606.ENSPO00000269305	8128	8128.ENSXNIP000000041809	287.7
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161	9606	9606.ENSPO00000269305	31033	31033.ENSXTRUP000000030644	287.0
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163	9606	9606.ENSPO00000269305	48701	48701.ENSXMEP00000001243	285.4
164	9606	9606.ENSPO00000269305	244447	244447.ENSXSEP000000003997	285.4
165	9606	9606.ENSPO00000269305	8154	8154.ENSXCLP000000007040	285.0
166	9606	9606.ENSPO00000269305	8175	8175.ENSXAUP00010029879	285.0
167	9606	9606.ENSPO00000269305	48698	48698.ENSXPFP000000007556	284.6
168	9606	9606.ENSPO00000269305	56723	56723.ENSXBEP000000036857	284.6
169	9606	9606.ENSPO00000269305	64144	64144.ENSATEP000000028323	284.3
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171	9606	9606.ENSPO00000269305	210632	210632.ENSXPRNP000000030862	283.5
172	9606	9606.ENSPO00000269305	48699	48699.ENSXLAP000000022694	283.1
173	9606	9606.ENSPO00000269305	61819	61819.ENSXCIP000000020373	282.3
174	9606	9606.ENSPO00000269305	144197	144197.ENSXPAP000000022019	282.3
175	9606	9606.ENSPO00000269305	299123	299123.ENSXSDP000000017092	280.4
176	9606	9606.ENSPO00000269305	56716	56716.ENSXGFP000000014430	279.6
177	9606	9606.ENSPO00000269305	205130	205130.ENSXMAMP000000005315	279.6
178	9606	9606.ENSPO00000269305	137246	137246.A0A401SCC1	279.3
179	9606	9606.ENSPO00000269305	99883	99883.ENSXNIP000000013035	278.1
180	9606	9606.ENSPO00000269305	173247	173247.ENSXNLP000000038795	277.3
181	9606	9606.ENSPO00000269305	8078	8078.ENSXFEP000000026765	276.6
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183	9606	9606.ENSPO00000269305	59729	59729.ENSXGUP000000021519	276.2
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187	9606	9606.ENSPO00000269305	47308	47308.ENSXNMLP000000021935	275.8
188	9606	9606.ENSPO00000269305	143630	143630.A0A402EXU8	275.4
189	9606	9606.ENSPO00000269305	240159	240159.A0A4U5UJG8	275.4
190	9606	9606.ENSPO00000269305	52670	52670.A0A2I4CET8	275.0
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194	9606	9606.ENSPO00000269305	303518	303518.ENSXPYP000000025442	274.2
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196	9606	9606.ENSPO00000269305	158456	158456.ENSXSLP000000007319	273.9
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199	9606	9606.ENSPO00000269305	75743	75743.A0A401P193	273.5
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203	9606	9606.ENSPO00000269305	9089	9089.ENSCHIP000010009060	271.9
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205	9606	9606.ENSPO00000269305	59894	59894.ENSFALP000000010031	271.6
206	9606	9606.ENSPO00000269305	156563	156563.ENSCEP000000019692	271.6
207	9606	9606.ENSPO00000269305	12930	12930.A0A0Q3T504	271.6
208	9606	9606.ENSPO00000269305	333673	333673.A0A3M0IU8	271.2
209	9606	9606.ENSPO00000269305	8996	8996.ENSNMEP000000004526	271.2
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266	9606	9606. ENSP00000269305	6573	6573. A0A210QTK4	203.4
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274	9606	9606. ENSP00000269305	10195	10195. A0A3M7Q6B9	184.5
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328	9606	9606. ENSP00000269305	946362	946362.F2U8Q9	94.4
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346	9606	9606. ENSP00000269305	1147741	1147741.A0A0R3RXLO	85.1
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356	9606	9606. ENSP00000269305	6210	6210. W6U916	82.8
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358	9606	9606. ENSP00000269305	7159	7159. Q171M1	81.6
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361	9606	9606. ENSP00000269305	6205	6205. AOA0R3WQW6	80.5
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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
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372	9606	9606. ENSP00000269305	520822	520822. AOA195B173	77.8
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379	9606	9606. ENSP00000269305	201502	201502. AOA1A9YB05	74.7
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386	9606	9606. ENSP00000269305	158441	158441. AOA226DFT1	70.1
387	9606	9606. ENSP00000269305	69004	69004. AOA3F2YX69	69.3
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389	9606	9606. ENSP00000269305	7167	7167. AOA182FR67	68.6
390	9606	9606. ENSP00000269305	334426	334426. AOA0R3Q2A0	67.0
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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
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401	9606	9606. ENSP00000269305	7260	7260. B4N9F0	65.1
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405	9606	9606.ENSPO00000269305	30066	30066.A0A182V190	63.9
406	9606	9606.ENSPO00000269305	34691	34691.A0A182XID1	63.9
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408	9606	9606.ENSPO00000269305	46245	46245.A0A0R3NKT4	63.2
409	9606	9606.ENSPO00000269305	29170	29170.A0A368F8M2	63.2
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420	9606	9606.ENSPO00000269305	70667	70667.A0A183STT5	56.6
421	9606	9606.ENSPO00000269305	7370	7370.A0A1I8N839	56.6
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425	9606	9606.ENSPO00000269305	7240	7240.B4R1C4	54.3
426	9606	9606.ENSPO00000269305	34690	34690.A0A182UJE7	53.5
427	9606	9606.ENSPO00000269305	7375	7375.A0A0LOCLI5	53.1
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430	9606	9606.ENSPO00000269305	947166	947166.A0A1D1VBG3	51.6
431	9606	9606.ENSPO00000269305	7244	7244.B4MB49	51.2
432	9606	9606.ENSPO00000269305	54126	54126.H3FK89	50.8

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

```
> # 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.ENSPO00000278616 X10090 X10090.ENSMUSP000000156344 X5328.8
1 9606 9606.ENSPO00000269305 10090 10090.ENSMUSP000000104298 598.2
```

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