

# 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 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](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
```

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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 Revestarol has been performed and compared to a control composed by A549 lung cancer cells threatened 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.

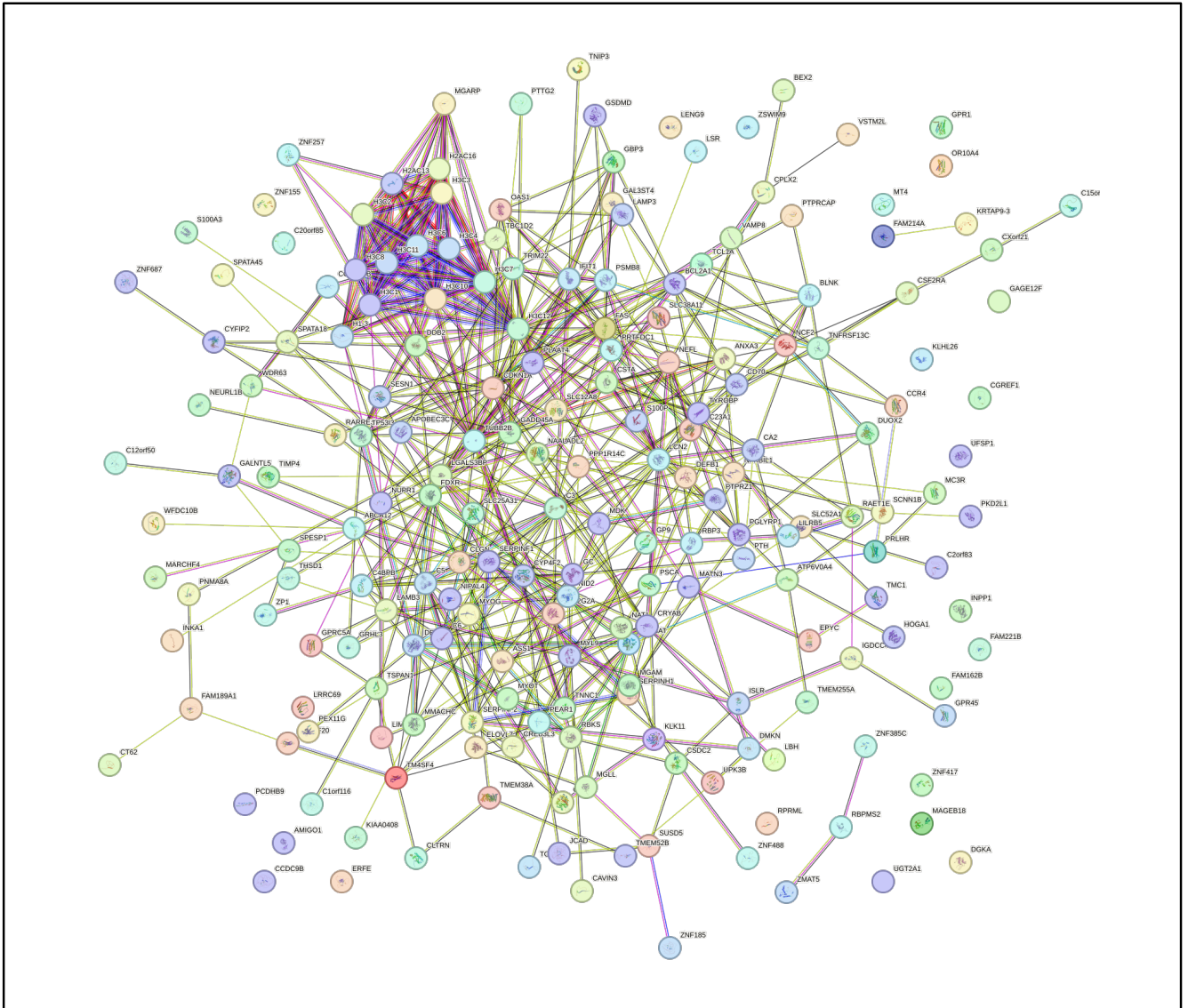
Finally, we extract the most significant 200 genes and we produce an image of the STRING network for those. The image shows clearly the genes and how they are possibly functionally related. On the top of the plot, we insert a pvalue that represents the probability that you can expect such an equal or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

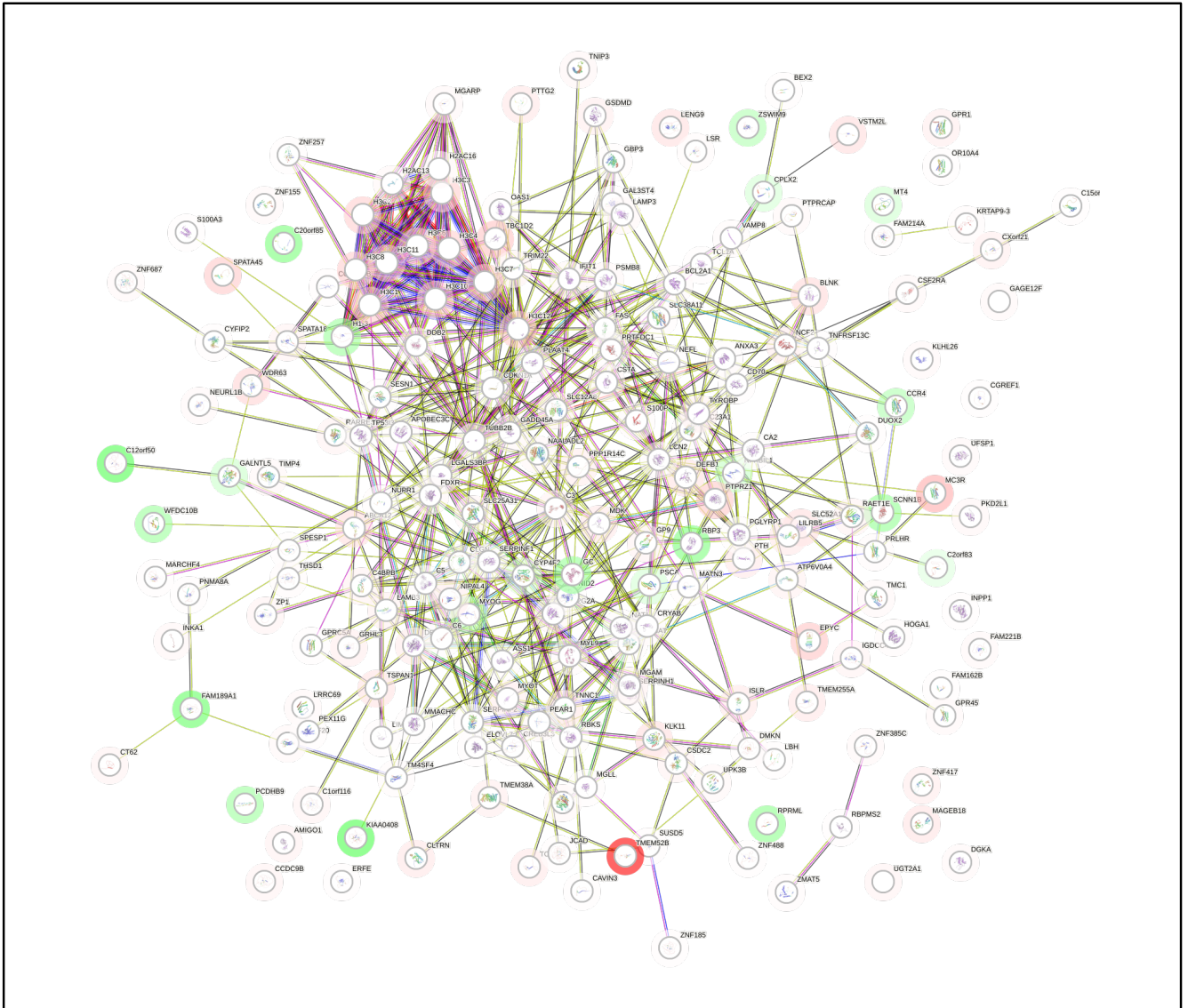
For example, this allows to color in green the genes that are down-regulated and in red the genes that are up-regulated. For this mechanism to work, we provide a function that posts the information on our web server.

```
> # 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 )
```

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			
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17 9606.ENSP00000008938,9606.ENSP00000014914,9606.ENSP00000187762,9606.ENSP00000216286,9606.ENSP0000000000000000  
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17 PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C4BPB,C3,ISLR,SERPINF1,THSD1,TUBB2B,EPYC,LGALS3BP,C6,VAMP8,  
18 PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C4BPB,C3,ISLR,SERPINF1,THSD1,TUBB2B,EPYC,LGALS3BP,C6,VAMP8,  
19 PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C3,ISLR,SERPINF1,THSD1,TUBB2B,EPYC,LGALS3BP,C6,VAMP8,  
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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18  
19 PGLYRP1, NID2, C5, C4BPB, C3, SERPINF1, THSD1, TUBB2B, LGALS3BP, C6, CSTA, ANXA3, ZP1, CA2, TIMP4, DEFB1, PSCA, SER

		description
1	Nucleotide-excision	repair complex
2		Golgi membrane
3		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.

```

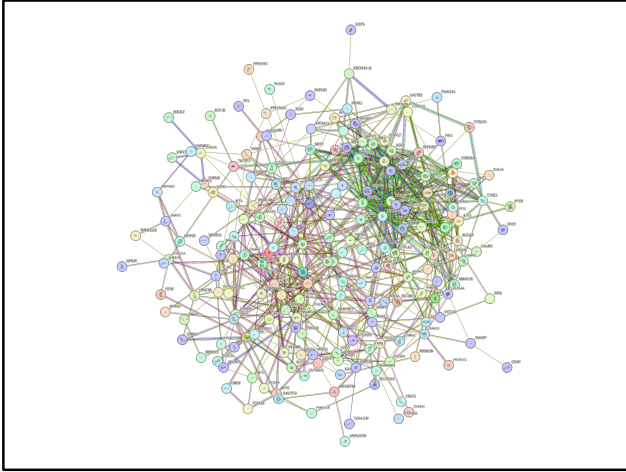
> # get clusters
> clustersList <- string_db$get_clusters(example1_mapped$STRING_id[1:600])

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

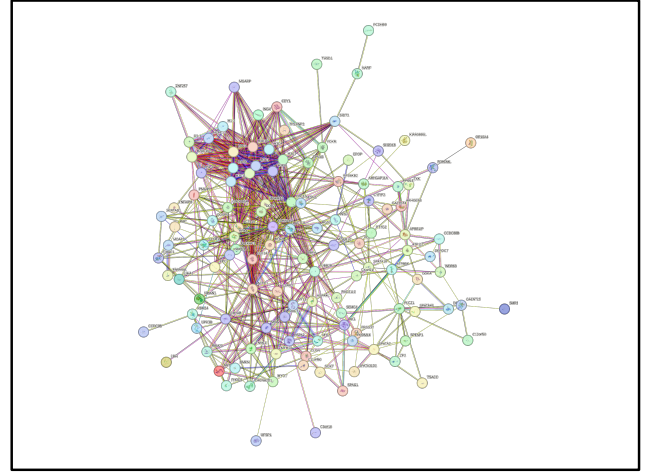
```



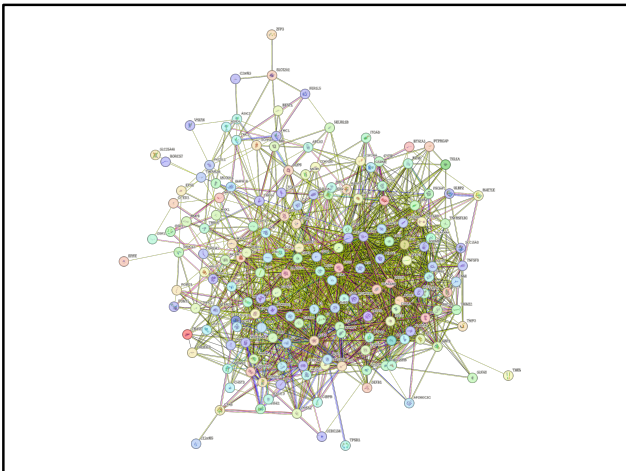
proteins: 204  
interactions: 673  
expected interactions: 238 (p-value: 0)



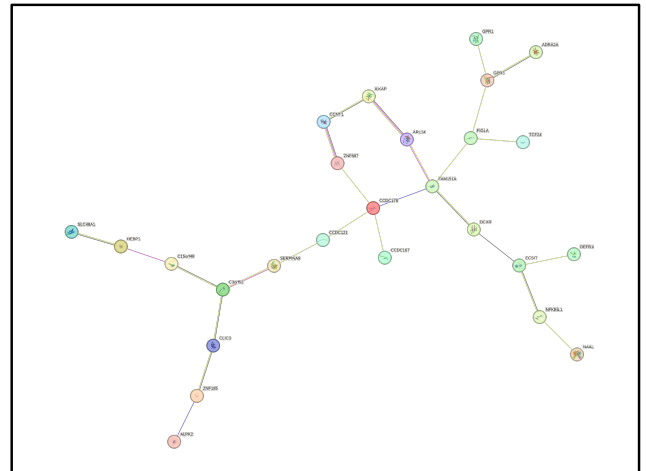
proteins: 121  
interactions: 581  
expected interactions: 165 (p-value: 0)



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"  
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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\_besthits" 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
1	9606	9606.ENSPO0000269305	9598	9598.ENSPTRP00000014836	815.8
2	9606	9606.ENSPO0000269305	9606	9606.ENSPO0000269305	815.8
3	9606	9606.ENSPO0000269305	9601	9601.ENSPPYP00000008923	799.3
4	9606	9606.ENSPO0000269305	61621	61621.ENS RBIP00000028632	786.6
5	9606	9606.ENSPO0000269305	61622	61622.ENSRR0P00000026843	786.6
6	9606	9606.ENSPO0000269305	591936	591936.ENSPT0P00000010553	785.8
7	9606	9606.ENSPO0000269305	60711	60711.ENS CSAP00000007551	785.0
8	9606	9606.ENSPO0000269305	9541	9541.ENS MFAP00000038526	783.9
9	9606	9606.ENSPO0000269305	9544	9544.ENS MMUP00000011334	783.9
10	9606	9606.ENSPO0000269305	9565	9565.ENS TGEP00000031378	783.1
11	9606	9606.ENSPO0000269305	9531	9531.ENS CATP00000032045	738.8
12	9606	9606.ENSPO0000269305	9568	9568.ENS MLEP00000037099	738.4
13	9606	9606.ENSPO0000269305	9555	9555.ENS PANP00000033477	737.3
14	9606	9606.ENSPO0000269305	336983	336983.ENS CANP00000028904	735.7
15	9606	9606.ENSPO0000269305	9516	9516.ENS CCAP00000029525	729.6
16	9606	9606.ENSPO0000269305	1868482	1868482.ENS TSYP00000023752	707.6
17	9606	9606.ENSPO0000269305	379532	379532.ENS PCOP00000031758	704.1
18	9606	9606.ENSPO0000269305	61853	61853.ENS NLEP00000011861	702.6
19	9606	9606.ENSPO0000269305	9994	9994.ENS MMMP00000022491	699.1
20	9606	9606.ENSPO0000269305	43179	43179.ENS STOP00000019678	697.2
21	9606	9606.ENSPO0000269305	9999	9999.ENS UPAP00010019485	696.4
22	9606	9606.ENSPO0000269305	99837	99837.ENS SDAP00000002829	696.0
23	9606	9606.ENSPO0000269305	9986	9986.ENS OCUP00000000989	683.7
24	9606	9606.ENSPO0000269305	9483	9483.ENS CJAP00000066800	682.6
25	9606	9606.ENSPO0000269305	30608	30608.ENS MICP00000039812	681.8
26	9606	9606.ENSPO0000269305	1026970	1026970.ENS NGAP00000007306	679.9
27	9606	9606.ENSPO0000269305	9755	9755.ENS PCTP000005020186	676.8
28	9606	9606.ENSPO0000269305	9749	9749.Q8SPZ3	676.4
29	9606	9606.ENSPO0000269305	118797	118797.A0A340XCN5	674.9
30	9606	9606.ENSPO0000269305	1706337	1706337.A0A341BQX3	671.4
31	9606	9606.ENSPO0000269305	9593	9593.ENS GGOP00000030954	671.4
32	9606	9606.ENSPO0000269305	310752	310752.A0A383YUA7	669.8
33	9606	9606.ENSPO0000269305	9739	9739.ENS TTRP00000009721	668.3
34	9606	9606.ENSPO0000269305	10181	10181.G5B5D6	662.1
35	9606	9606.ENSPO0000269305	9838	9838.ENS CDRP000005013165	656.8
36	9606	9606.ENSPO0000269305	39432	39432.ENS SBOP00000008181	656.4
37	9606	9606.ENSPO0000269305	30611	30611.ENS OGAP00000015106	655.6
38	9606	9606.ENSPO0000269305	34839	34839.ENS CLAP00000010404	655.6
39	9606	9606.ENSPO0000269305	9796	9796.ENS ECAP00000032751	655.2
40	9606	9606.ENSPO0000269305	83772	83772.ENS EASP000005028399	653.7
41	9606	9606.ENSPO0000269305	51154	51154.ENS CWAP00000005800	652.9
42	9606	9606.ENSPO0000269305	230844	230844.ENS PEMP00000010300	651.7
43	9606	9606.ENSPO0000269305	68415	68415.ENS MMSP00000026578	640.6
44	9606	9606.ENSPO0000269305	9646	9646.ENS AMEP00000017825	640.2
45	9606	9606.ENSPO0000269305	885580	885580.ENS FDAP00000011613	636.3
46	9606	9606.ENSPO0000269305	9643	9643.ENS UAMP00000000913	635.6
47	9606	9606.ENSPO0000269305	116960	116960.A0A3Q7Y5W2	634.4

48	9606	9606.ENSPO0000269305	29073	29073.ENSUMAP00000023207	634.4
49	9606	9606.ENSPO0000269305	286419	286419.ENSCAFP00020009510	634.0
50	9606	9606.ENSPO0000269305	9708	9708.AOA2U3VT95	634.0
51	9606	9606.ENSPO0000269305	9361	9361.ENSDNOP00000004075	633.6
52	9606	9606.ENSPO0000269305	9615	9615.ENSCAFP000000064590	633.3
53	9606	9606.ENSPO0000269305	9691	9691.ENSPPRP000000022844	633.3
54	9606	9606.ENSPO0000269305	59479	59479.ENSRFEP00010016808	631.7
55	9606	9606.ENSPO0000269305	9627	9627.ENSVVUP000000039187	631.7
56	9606	9606.ENSPO0000269305	9713	9713.AOA2U3Y5G3	630.9
57	9606	9606.ENSPO0000269305	29088	29088.AOA2Y9HEV7	629.8
58	9606	9606.ENSPO0000269305	10160	10160.ENSDERP000000024162	624.8
59	9606	9606.ENSPO0000269305	72004	72004.ENSBMUP000000028863	622.9
60	9606	9606.ENSPO0000269305	30521	30521.ENSBGRP000000021669	622.9
61	9606	9606.ENSPO0000269305	43346	43346.ENSBFBP000000018891	622.9
62	9606	9606.ENSPO0000269305	79684	79684.ENSMOCP000000023219	621.3
63	9606	9606.ENSPO0000269305	391180	391180.AOA2Y9L4Q2	620.5
64	9606	9606.ENSPO0000269305	9913	9913.ENSBTAP000000001420	620.2
65	9606	9606.ENSPO0000269305	452646	452646.ENSNVIP000000005141	619.4
66	9606	9606.ENSPO0000269305	9925	9925.ENSCHIP000000030141	618.2
67	9606	9606.ENSPO0000269305	9669	9669.ENSMUPP000000008945	617.8
68	9606	9606.ENSPO0000269305	30522	30522.AOA4W2I2P0	617.5
69	9606	9606.ENSPO0000269305	42254	42254.ENSSARP000000005616	617.1
70	9606	9606.ENSPO0000269305	51337	51337.ENSJAP000000008090	616.7
71	9606	9606.ENSPO0000269305	9940	9940.ENSARP000000016707	616.7
72	9606	9606.ENSPO0000269305	37032	37032.ENSSSUP000005028514	616.7
73	9606	9606.ENSPO0000269305	61383	61383.ENSLCNP000005018106	615.5
74	9606	9606.ENSPO0000269305	127582	127582.AOA2Y9R5B9	613.6
75	9606	9606.ENSPO0000269305	9685	9685.ENFCAP000000045749	612.1
76	9606	9606.ENSPO0000269305	10089	10089.MGP_CAROLIEiJ_P0027554	606.3
77	9606	9606.ENSPO0000269305	51338	51338.ENSCCNP000000017223	604.7
78	9606	9606.ENSPO0000269305	10096	10096.MGP_SPRETEiJ_P0028933	603.6
79	9606	9606.ENSPO0000269305	10093	10093.MGP_PahariEiJ_P0034306	601.3
80	9606	9606.ENSPO0000269305	9402	9402.L5JZ91	600.1
81	9606	9606.ENSPO0000269305	10116	10116.ENSRNOP000000074031	600.1
82	9606	9606.ENSPO0000269305	37548	37548.ENSCAPP000000017521	600.1
83	9606	9606.ENSPO0000269305	10141	10141.ENSCPOP000000029751	599.0
84	9606	9606.ENSPO0000269305	10090	10090.ENSMUSP000000104298	598.2
85	9606	9606.ENSPO0000269305	10036	10036.ENSMAP000000025852	597.8
86	9606	9606.ENSPO0000269305	1328070	1328070.ENSPSMP000000026875	595.5
87	9606	9606.ENSPO0000269305	10103	10103.ENSMSIP000000031034	595.1
88	9606	9606.ENSPO0000269305	10047	10047.ENSMUGP000000017526	593.6
89	9606	9606.ENSPO0000269305	9785	9785.ENSLAFP000000006292	592.0
90	9606	9606.ENSPO0000269305	9823	9823.ENSSSCP000000050664	591.7
91	9606	9606.ENSPO0000269305	9978	9978.ENSOPRP000000005906	586.3
92	9606	9606.ENSPO0000269305	246437	246437.L9KM90	574.3
93	9606	9606.ENSPO0000269305	9813	9813.ENSPCAP000000011892	568.5
94	9606	9606.ENSPO0000269305	10020	10020.ENSDORP000000023664	562.4
95	9606	9606.ENSPO0000269305	59463	59463.ENSMUP000000005861	559.3
96	9606	9606.ENSPO0000269305	37293	37293.ENSANAP000000025592	547.4
97	9606	9606.ENSPO0000269305	38626	38626.ENSPCIP000000039513	502.3
98	9606	9606.ENSPO0000269305	29139	29139.ENSVURP00010004263	496.1

99	9606	9606.ENSPO0000269305	9305	9305.ENSSHAP00000018268	486.1
100	9606	9606.ENSPO0000269305	9365	9365.ENSEEUP00000013295	477.6
101	9606	9606.ENSPO0000269305	9371	9371.ENSETEP00000007296	420.2
102	9606	9606.ENSPO0000269305	132908	132908.ENSPVAP00000015400	415.6
103	9606	9606.ENSPO0000269305	9545	9545.ENSMNEP00000030865	399.8
104	9606	9606.ENSPO0000269305	56216	56216.AOA1A6GWM4	394.0
105	9606	9606.ENSPO0000269305	7897	7897.ENSLACP00000015915	393.3
106	9606	9606.ENSPO0000269305	8496	8496.AOA151MW63	373.6
107	9606	9606.ENSPO0000269305	2587831	2587831.ENSTMTTP00000028378	372.5
108	9606	9606.ENSPO0000269305	9315	9315.ENSMEEP00000011978	371.7
109	9606	9606.ENSPO0000269305	8478	8478.ENSCBP000000031582	364.8
110	9606	9606.ENSPO0000269305	113540	113540.ENSSFOP00015035795	361.3
111	9606	9606.ENSPO0000269305	38654	38654.AOA3Q0FUE5	359.8
112	9606	9606.ENSPO0000269305	38772	38772.ENSGAGP00000006237	359.8
113	9606	9606.ENSPO0000269305	13735	13735.ENSPSIP00000014905	359.4
114	9606	9606.ENSPO0000269305	106734	106734.ENSCABP00000018274	359.0
115	9606	9606.ENSPO0000269305	7918	7918.ENSLACP00000017063	359.0
116	9606	9606.ENSPO0000269305	62062	62062.ENSHHUP00000013468	357.1
117	9606	9606.ENSPO0000269305	1676925	1676925.ENSPKIP00000014805	357.1
118	9606	9606.ENSPO0000269305	8032	8032.ENSTTUP00000101309	356.7
119	9606	9606.ENSPO0000269305	75366	75366.ENSSGRP00000074183	356.3
120	9606	9606.ENSPO0000269305	8030	8030.ENSSSAP00000057928	355.5
121	9606	9606.ENSPO0000269305	307959	307959.ENSSRHP00000051429	353.2
122	9606	9606.ENSPO0000269305	1608454	1608454.ENSSANP00000026698	352.8
123	9606	9606.ENSPO0000269305	27687	27687.ENSECRP00000015713	351.7
124	9606	9606.ENSPO0000269305	8005	8005.ENSEEEP00000033982	345.9
125	9606	9606.ENSPO0000269305	8010	8010.ENSELUP00000026168	344.0
126	9606	9606.ENSPO0000269305	7998	7998.ENSIPUP00000031919	343.6
127	9606	9606.ENSPO0000269305	74533	74533.ENSPTIP00000024834	343.2
128	9606	9606.ENSPO0000269305	96440	96440.ENSSMRP00000003871	340.9
129	9606	9606.ENSPO0000269305	7955	7955.ENSDARP00000116736	340.9
130	9606	9606.ENSPO0000269305	84645	84645.AOA498NKF5	340.1
131	9606	9606.ENSPO0000269305	8364	8364.ENSXETP00000041856	339.7
132	9606	9606.ENSPO0000269305	37347	37347.ENSTBEP00000010189	336.7
133	9606	9606.ENSPO0000269305	299321	299321.ENSDCDP00000007017	332.0
134	9606	9606.ENSPO0000269305	8469	8469.M7CJF0	330.9
135	9606	9606.ENSPO0000269305	103695	103695.ENSPVIP00000017506	324.3
136	9606	9606.ENSPO0000269305	623744	623744.AOA553PV69	319.7
137	9606	9606.ENSPO0000269305	8508	8508.ENSSPUP00000018842	313.9
138	9606	9606.ENSPO0000269305	2489341	2489341.ENSSHBP00005007544	313.2
139	9606	9606.ENSPO0000269305	42514	42514.ENSPNAP00000014501	313.2
140	9606	9606.ENSPO0000269305	61221	61221.ENSVKKP00000029045	310.8
141	9606	9606.ENSPO0000269305	7994	7994.ENSAMXP00000021366	309.3
142	9606	9606.ENSPO0000269305	7950	7950.ENSCHAP00000042143	305.1
143	9606	9606.ENSPO0000269305	586833	586833.ENSMMDP00005051289	304.7
144	9606	9606.ENSPO0000269305	8022	8022.AOA060XN97	304.3
145	9606	9606.ENSPO0000269305	8081	8081.ENSPREP00000019676	293.5
146	9606	9606.ENSPO0000269305	52904	52904.ENSSMAP00000015064	292.0
147	9606	9606.ENSPO0000269305	47969	47969.ENSOABP00000003944	291.6
148	9606	9606.ENSPO0000269305	181472	181472.ENSSFAP00005012771	291.6
149	9606	9606.ENSPO0000269305	375764	375764.ENSSORP00005058467	291.6

150	9606	9606.ENSPO0000269305	8153	8153.ENSHBUP00000022213	291.2
151	9606	9606.ENSPO0000269305	8167	8167.AOA484CCMO	291.2
152	9606	9606.ENSPO0000269305	215358	215358.ENSLCRP00005011976	290.8
153	9606	9606.ENSPO0000269305	80972	80972.ENSAOCP00000001385	290.0
154	9606	9606.ENSPO0000269305	161767	161767.ENSAPEP00000017927	290.0
155	9606	9606.ENSPO0000269305	8083	8083.ENSXMAP000000028829	290.0
156	9606	9606.ENSPO0000269305	37003	37003.ENSXMAP00000018969	289.7
157	9606	9606.ENSPO0000269305	64176	64176.ENSXMRP00000017811	289.3
158	9606	9606.ENSPO0000269305	441366	441366.ENSGWIP000000038103	288.9
159	9606	9606.ENSPO0000269305	8128	8128.ENSONIP000000041809	287.7
160	9606	9606.ENSPO0000269305	80966	80966.ENSAPOP000000027715	287.3
161	9606	9606.ENSPO0000269305	31033	31033.ENSTRUP000000030644	287.0
162	9606	9606.ENSPO0000269305	32473	32473.ENSXCOP00000002276	285.8
163	9606	9606.ENSPO0000269305	48701	48701.ENSXMEP00000001243	285.4
164	9606	9606.ENSPO0000269305	244447	244447.ENSXSEP000000003997	285.4
165	9606	9606.ENSPO0000269305	8154	8154.ENSACLP000000007040	285.0
166	9606	9606.ENSPO0000269305	8175	8175.ENSXSAUP00010029879	285.0
167	9606	9606.ENSPO0000269305	48698	48698.ENSXPOP000000007556	284.6
168	9606	9606.ENSPO0000269305	56723	56723.ENSLBEP000000036857	284.6
169	9606	9606.ENSPO0000269305	64144	64144.ENSATEP000000028323	284.3
170	9606	9606.ENSPO0000269305	8187	8187.ENSLCAP00010016052	283.9
171	9606	9606.ENSPO0000269305	210632	210632.ENSXPRNP000000030862	283.5
172	9606	9606.ENSPO0000269305	48699	48699.ENSXPLAP000000022694	283.1
173	9606	9606.ENSPO0000269305	61819	61819.ENSXACIP000000020373	282.3
174	9606	9606.ENSPO0000269305	144197	144197.ENSXPAP000000022019	282.3
175	9606	9606.ENSPO0000269305	299123	299123.ENSLSDP000000017092	280.4
176	9606	9606.ENSPO0000269305	56716	56716.ENSXGOP000000014430	279.6
177	9606	9606.ENSPO0000269305	205130	205130.ENSXMAMP000000005315	279.6
178	9606	9606.ENSPO0000269305	137246	137246.AOA401SCC1	279.3
179	9606	9606.ENSPO0000269305	99883	99883.ENSTNIP000000013035	278.1
180	9606	9606.ENSPO0000269305	173247	173247.ENSENLP000000038795	277.3
181	9606	9606.ENSPO0000269305	8078	8078.ENSXFEP000000026765	276.6
182	9606	9606.ENSPO0000269305	41447	41447.ENSXDUP000000028226	276.6
183	9606	9606.ENSPO0000269305	59729	59729.ENSXGUP000000021519	276.2
184	9606	9606.ENSPO0000269305	28743	28743.ENSXVAP000000022398	276.2
185	9606	9606.ENSPO0000269305	33528	33528.ENSXGAFP000000008062	276.2
186	9606	9606.ENSPO0000269305	43700	43700.ENSXMALP000000000877	275.8
187	9606	9606.ENSPO0000269305	47308	47308.ENSXNMLP000000021935	275.8
188	9606	9606.ENSPO0000269305	143630	143630.AOA402EXU8	275.4
189	9606	9606.ENSPO0000269305	240159	240159.AOA4U5UJG8	275.4
190	9606	9606.ENSPO0000269305	52670	52670.AOA2I4CET8	275.0
191	9606	9606.ENSPO0000269305	69293	69293.ENSXGACP000000018012	275.0
192	9606	9606.ENSPO0000269305	106582	106582.ENSXMZEP00005006261	274.6
193	9606	9606.ENSPO0000269305	8049	8049.ENSXGMP000000000401	274.6
194	9606	9606.ENSPO0000269305	303518	303518.ENSXPYYP000000025442	274.2
195	9606	9606.ENSPO0000269305	1841481	1841481.ENSXSLDP000000032981	274.2
196	9606	9606.ENSPO0000269305	158456	158456.ENSXBSLP000000007319	273.9
197	9606	9606.ENSPO0000269305	8355	8355.AOA1L8FGI1	273.9
198	9606	9606.ENSPO0000269305	28377	28377.ENSXACAP000000001746	273.9
199	9606	9606.ENSPO0000269305	75743	75743.AOA401P193	273.5
200	9606	9606.ENSPO0000269305	109280	109280.ENSXCOP000000022970	273.1



201	9606	9606.ENSPO0000269305	8673	8673.ENSPTXP00000024136	273.1
202	9606	9606.ENSPO0000269305	8090	8090.ENSORLP00000019616	272.7
203	9606	9606.ENSPO0000269305	9089	9089.ENSCHIP00010009060	271.9
204	9606	9606.ENSPO0000269305	30732	30732.ENSOMEPO00000009309	271.9
205	9606	9606.ENSPO0000269305	59894	59894.ENSFALP00000010031	271.6
206	9606	9606.ENSPO0000269305	156563	156563.ENSCEP00000019692	271.6
207	9606	9606.ENSPO0000269305	12930	12930.AOA0Q3T504	271.6
208	9606	9606.ENSPO0000269305	333673	333673.AOA3M0IUV8	271.2
209	9606	9606.ENSPO0000269305	8996	8996.ENSNMEP00000004526	271.2
210	9606	9606.ENSPO0000269305	9157	9157.ENSMPJP00000017734	271.2
211	9606	9606.ENSPO0000269305	44394	44394.ENSZALP00000002887	270.8
212	9606	9606.ENSPO0000269305	9135	9135.ENSZCAP00000001137	270.8
213	9606	9606.ENSPO0000269305	93934	93934.ENSZJPP00005010805	270.4
214	9606	9606.ENSPO0000269305	409849	409849.ENSMPGP00000017230	270.4
215	9606	9606.ENSPO0000269305	9031	9031.ENSZGALP00000001485	270.4
216	9606	9606.ENSPO0000269305	9049	9049.ENSZSTP00000007061	270.4
217	9606	9606.ENSPO0000269305	9054	9054.ENSZCLP000000024156	270.4
218	9606	9606.ENSPO0000269305	13146	13146.ENSZMUNP00000017973	270.4
219	9606	9606.ENSPO0000269305	372326	372326.AOA1V4KNI0	270.0
220	9606	9606.ENSPO0000269305	13616	13616.ENSZMDP000000018831	270.0
221	9606	9606.ENSPO0000269305	94827	94827.AOA099ZQ65	269.6
222	9606	9606.ENSPO0000269305	44316	44316.ENSZGOP00005018987	269.2
223	9606	9606.ENSPO0000269305	55661	55661.AOA091G407	269.2
224	9606	9606.ENSPO0000269305	94237	94237.ENSZMOP00000018694	269.2
225	9606	9606.ENSPO0000269305	128390	128390.AOA091UUY0	269.2
226	9606	9606.ENSPO0000269305	441894	441894.ENSZCUP00000005331	269.2
227	9606	9606.ENSPO0000269305	7868	7868.ENSZMIP00000007753	269.2
228	9606	9606.ENSPO0000269305	9238	9238.AOA093R114	269.2
229	9606	9606.ENSPO0000269305	55544	55544.AOA4D9E5P9	268.9
230	9606	9606.ENSPO0000269305	85066	85066.AOA091EA06	268.9
231	9606	9606.ENSPO0000269305	198806	198806.ENSZPUP000000025340	268.9
232	9606	9606.ENSPO0000269305	308060	308060.ENSZARWP00000009421	268.9
233	9606	9606.ENSPO0000269305	425635	425635.ENSZCPGP000000026631	268.9
234	9606	9606.ENSPO0000269305	8502	8502.ENSZPRP00005017750	268.9
235	9606	9606.ENSPO0000269305	8790	8790.ENSZDVP00000009001	268.9
236	9606	9606.ENSPO0000269305	8823	8823.ENSZAHAP00000009000	268.9
237	9606	9606.ENSPO0000269305	8824	8824.ENSZOWP00000012514	268.9
238	9606	9606.ENSPO0000269305	9244	9244.AOA091HZ84	268.9
239	9606	9606.ENSPO0000269305	30464	30464.ENSZNEP00000010833	268.9
240	9606	9606.ENSPO0000269305	40217	40217.ENSZJHYP00000001101	268.9
241	9606	9606.ENSPO0000269305	50402	50402.AOA0A0AU13	268.5
242	9606	9606.ENSPO0000269305	118200	118200.AOA093GLW0	268.5
243	9606	9606.ENSPO0000269305	132585	132585.ENSZABRP00000009434	268.5
244	9606	9606.ENSPO0000269305	194338	194338.ENSZACUP00000017269	268.5
245	9606	9606.ENSPO0000269305	211598	211598.ENSZANIP00000006686	268.5
246	9606	9606.ENSPO0000269305	241587	241587.ENSZACOP00000010351	268.5
247	9606	9606.ENSPO0000269305	8840	8840.ENSZAPLP000000032186	268.5
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432	9606	9606.ENSPO0000269305	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.ENSPO0000278616 X10090 X10090.ENSMUSP00000156344 X5328.8
1 9606 9606.ENSPO0000269305 10090 10090.ENSMUSP00000104298 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