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 milions proteins from 5090 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.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 Revestarol has been performed and compared to a control composed by A549 lung cancer cells threated 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 )
```

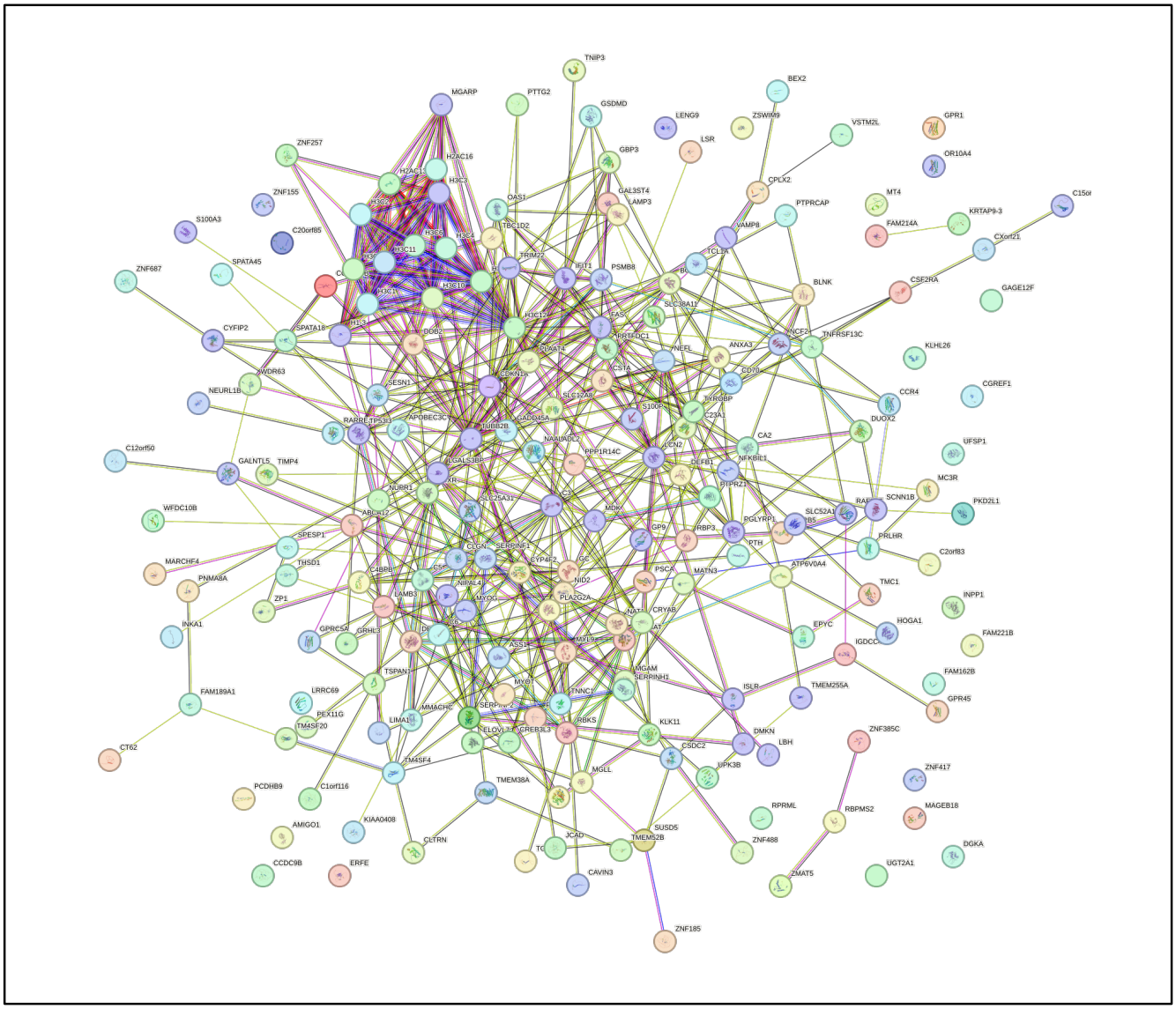
```
Warning:  we couldn't map to STRING 15% of your identifiers
```

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.

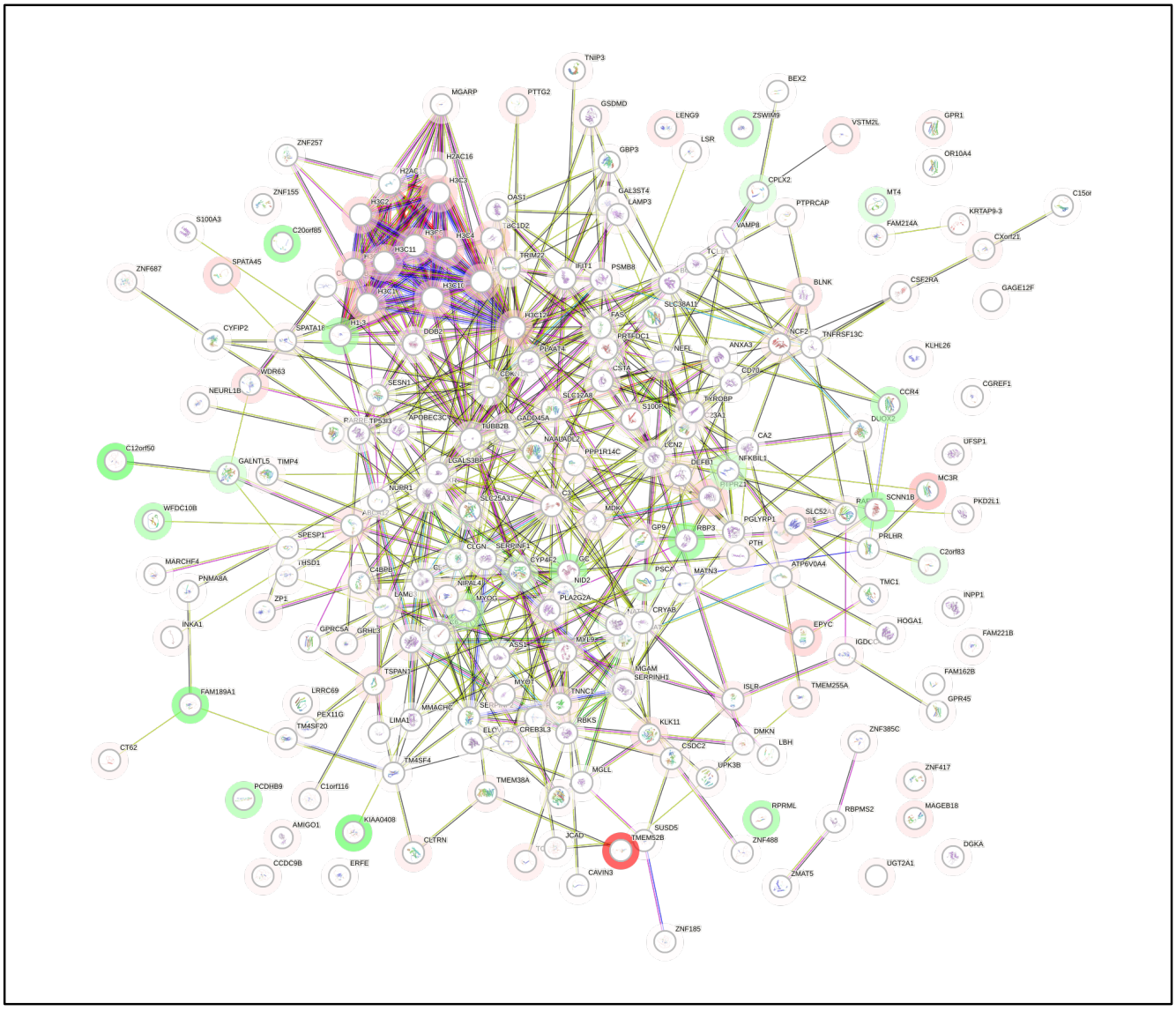
For example, this allows to color in green the genes that are down-regulated and in red the genes that are up-regulated. For this mechanism to work, we provide a function that posts the information on our web server.

```
> # filter by p-value and add a color column
> # (i.e. green down-regulated gened 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
5         9606
6         9606
7         9606
8         9606
9         9606
10        9606
11        9606
12        9606
13        9606
14        9606
15        9606
16        9606
17        9606
18        9606
19        9606
20        9606
```

9606.ENSP00000008938,9606.ENSP00000014914,9606.ENSP00000187762,9606.ENSP00000216286,9606.ENSP00000

PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C4BPB,C3,ISLR,SERPINF1,THSD1,TUBB2B,EPYC,LGALS3BP,C6,VAMP8,
PGLYRP1,GPRC5A,TMEM38
PGLYRP1,GPRC5A,TMEM38A,NID2,C5,RARRES1,C3,

	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

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19 9606.ENSP00000008938,9606.ENSP00000216286,9606.ENSP00000223642,9606.ENSP00000243611,9606.ENSP00000
20

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19 PGLYRP1,NID2,C5,C4BPB,C3,SERPINF1,THSD1,TUBB2B,LGALS3BP,C6,CSTA,ANXA3,ZP1,CA2,TIMP4,DEFB1,PSCA,SEP
20
                                    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
```

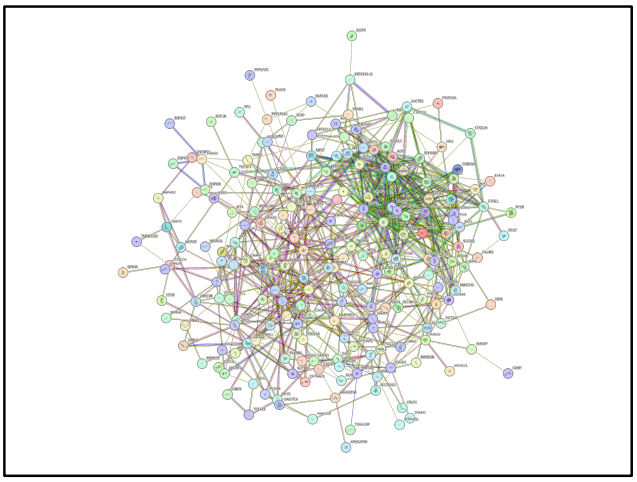
4 CLUSTERING

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

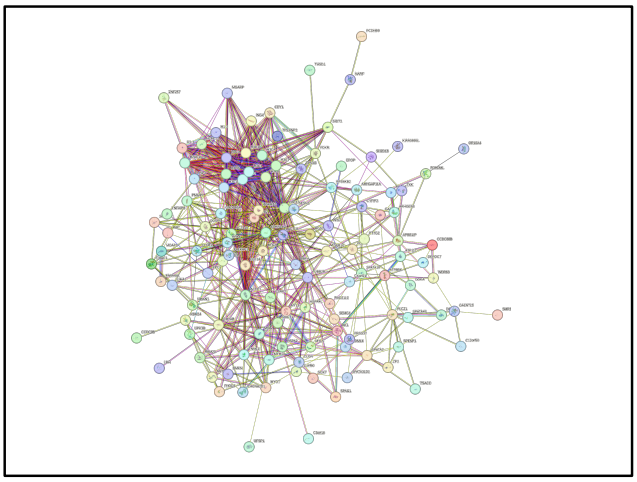
```
> # get clusters
> clustersList <- string_db$get_clusters(example1_mapped$STRING_id[1:600])

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

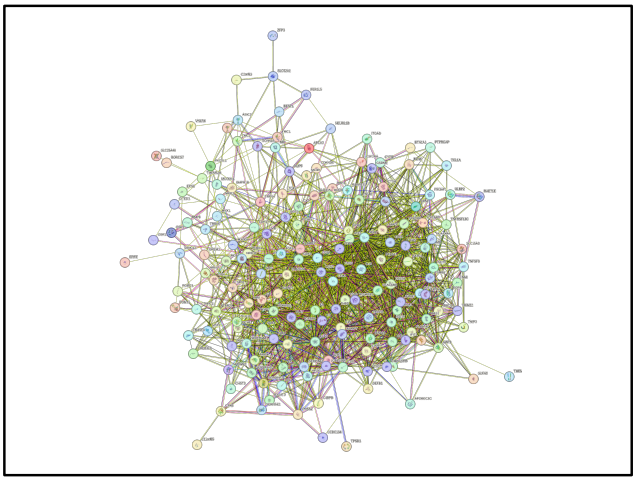
proteins: 204
interactions: 673
expected interactions: 238 (p−value: 0)



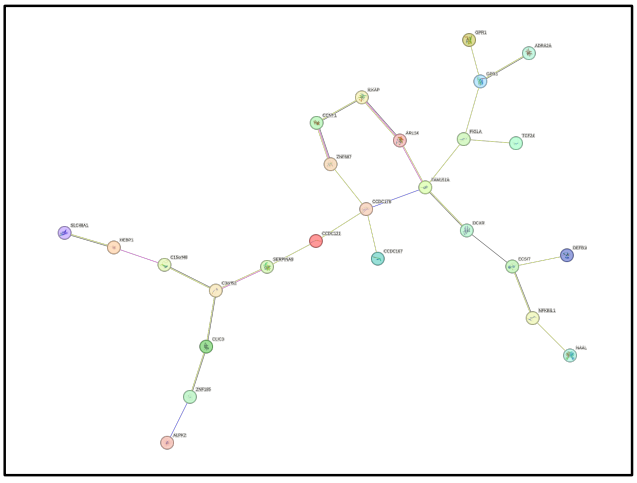
proteins: 121
interactions: 581
expected interactions: 165 (p−value: 0)



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"
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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 retrive 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_besthits(tp53)
```

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82	9606	9606.ENSP00000269305	37548	37548.ENSCAPP00000017521	600.1
83	9606	9606.ENSP00000269305	10141	10141.ENSCPOP00000029751	599.0
84	9606	9606.ENSP00000269305	10090	10090.ENSMUSP00000104298	598.2
85	9606	9606.ENSP00000269305	10036	10036.ENSMAUP00000025852	597.8
86	9606	9606.ENSP00000269305	1328070	1328070.ENSPSMP00000026875	595.5
87	9606	9606.ENSP00000269305	10103	10103.ENSMSIP00000031034	595.1
88	9606	9606.ENSP00000269305	10047	10047.ENSMUGP00000017526	593.6
89	9606	9606.ENSP00000269305	9785	9785.ENSLAFP00000006292	592.0
90	9606	9606.ENSP00000269305	9823	9823.ENSSSCP00000050664	591.7
91	9606	9606.ENSP00000269305	9978	9978.ENSOPRP00000005906	586.3
92	9606	9606.ENSP00000269305	246437	246437.L9KM90	574.3
93	9606	9606.ENSP00000269305	9813	9813.ENSPCAP00000011892	568.5
94	9606	9606.ENSP00000269305	10020	10020.ENSDORP00000023664	562.4
95	9606	9606.ENSP00000269305	59463	59463.ENSMLUP00000005861	559.3
96	9606	9606.ENSP00000269305	37293	37293.ENSANAP00000025592	547.4
97	9606	9606.ENSP00000269305	38626	38626.ENSPCIP00000039513	502.3
98	9606	9606.ENSP00000269305	29139	29139.ENSVURP00010004263	496.1

99	9606	9606.ENSP00000269305	9305	9305.ENSSHAP00000018268	486.1
100	9606	9606.ENSP00000269305	9365	9365.ENSEEUP00000013295	477.6
101	9606	9606.ENSP00000269305	9371	9371.ENSETEP00000007296	420.2
102	9606	9606.ENSP00000269305	132908	132908.ENSPVAP00000015400	415.6
103	9606	9606.ENSP00000269305	9545	9545.ENSMNEP00000030865	399.8
104	9606	9606.ENSP00000269305	56216	56216.A0A1A6GWM4	394.0
105	9606	9606.ENSP00000269305	7897	7897.ENSLACP00000015915	393.3
106	9606	9606.ENSP00000269305	8496	8496.A0A151MW63	373.6
107	9606	9606.ENSP00000269305	2587831	2587831.ENSTMTP00000028378	372.5
108	9606	9606.ENSP00000269305	9315	9315.ENSMEUP00000011978	371.7
109	9606	9606.ENSP00000269305	8478	8478.ENSCPBP00000031582	364.8
110	9606	9606.ENSP00000269305	113540	113540.ENSSFOP00015035795	361.3
111	9606	9606.ENSP00000269305	38654	38654.A0A3Q0FUE5	359.8
112	9606	9606.ENSP00000269305	38772	38772.ENSGAGP00000006237	359.8
113	9606	9606.ENSP00000269305	13735	13735.ENSPSIP00000014905	359.4
114	9606	9606.ENSP00000269305	106734	106734.ENSCABP00000018274	359.0
115	9606	9606.ENSP00000269305	7918	7918.ENSLOCP00000017063	359.0
116	9606	9606.ENSP00000269305	62062	62062.ENSHHUP00000013468	357.1
117	9606	9606.ENSP00000269305	1676925	1676925.ENSPKIP00000014805	357.1
118	9606	9606.ENSP00000269305	8032	8032.ENSSTUP00000101309	356.7
119	9606	9606.ENSP00000269305	75366	75366.ENSSGRP00000074183	356.3
120	9606	9606.ENSP00000269305	8030	8030.ENSSSAP00000057928	355.5
121	9606	9606.ENSP00000269305	307959	307959.ENSSRHP00000051429	353.2
122	9606	9606.ENSP00000269305	1608454	1608454.ENSSANP00000026698	352.8
123	9606	9606.ENSP00000269305	27687	27687.ENSECRP00000015713	351.7
124	9606	9606.ENSP00000269305	8005	8005.ENSEEEP00000033982	345.9
125	9606	9606.ENSP00000269305	8010	8010.ENSELUP00000026168	344.0
126	9606	9606.ENSP00000269305	7998	7998.ENSIPUP00000031919	343.6
127	9606	9606.ENSP00000269305	74533	74533.ENSPTIP00000024834	343.2
128	9606	9606.ENSP00000269305	96440	96440.ENSSMRP00000003871	340.9
129	9606	9606.ENSP00000269305	7955	7955.ENSDARP00000116736	340.9
130	9606	9606.ENSP00000269305	84645	84645.A0A498NKF5	340.1
131	9606	9606.ENSP00000269305	8364	8364.ENSXETP00000041856	339.7
132	9606	9606.ENSP00000269305	37347	37347.ENSTBEP00000010189	336.7
133	9606	9606.ENSP00000269305	299321	299321.ENSDCDP00000007017	332.0
134	9606	9606.ENSP00000269305	8469	8469.M7CJF0	330.9
135	9606	9606.ENSP00000269305	103695	103695.ENSPVIP00000017506	324.3
136	9606	9606.ENSP00000269305	623744	623744.A0A553PV69	319.7
137	9606	9606.ENSP00000269305	8508	8508.ENSSPUP00000018842	313.9
138	9606	9606.ENSP00000269305	2489341	2489341.ENSSHBP00005007544	313.2
139	9606	9606.ENSP00000269305	42514	42514.ENSPNAP00000014501	313.2
140	9606	9606.ENSP00000269305	61221	61221.ENSVKKP00000029045	310.8
141	9606	9606.ENSP00000269305	7994	7994.ENSAMXP00000021366	309.3
142	9606	9606.ENSP00000269305	7950	7950.ENSCHAP00000042143	305.1
143	9606	9606.ENSP00000269305	586833	586833.ENSMMDP00005051289	304.7
144	9606	9606.ENSP00000269305	8022	8022.A0A060XN97	304.3
145	9606	9606.ENSP00000269305	8081	8081.ENSPREP00000019676	293.5
146	9606	9606.ENSP00000269305	52904	52904.ENSSMAP00000015064	292.0
147	9606	9606.ENSP00000269305	47969	47969.ENSOABP00000003944	291.6
148	9606	9606.ENSP00000269305	181472	181472.ENSSFAP00005012771	291.6
149	9606	9606.ENSP00000269305	375764	375764.ENSSORP00005058467	291.6

150	9606	9606.ENSP00000269305	8153	8153.ENSHBUP00000022213	291.2
151	9606	9606.ENSP00000269305	8167	8167.A0A484CCM0	291.2
152	9606	9606.ENSP00000269305	215358	215358.ENSLCRP00005011976	290.8
153	9606	9606.ENSP00000269305	80972	80972.ENSAOCP00000001385	290.0
154	9606	9606.ENSP00000269305	161767	161767.ENSAPEP00000017927	290.0
155	9606	9606.ENSP00000269305	8083	8083.ENSXMAP00000028829	290.0
156	9606	9606.ENSP00000269305	37003	37003.ENSKMAP00000018969	289.7
157	9606	9606.ENSP00000269305	64176	64176.ENSPMRP00000017811	289.3
158	9606	9606.ENSP00000269305	441366	441366.ENSGWIP00000038103	288.9
159	9606	9606.ENSP00000269305	8128	8128.ENSONIP00000041809	287.7
160	9606	9606.ENSP00000269305	80966	80966.ENSAPOP00000027715	287.3
161	9606	9606.ENSP00000269305	31033	31033.ENSTRUP00000030644	287.0
162	9606	9606.ENSP00000269305	32473	32473.ENSXCOP00000002276	285.8
163	9606	9606.ENSP00000269305	48701	48701.ENSPMEP00000001243	285.4
164	9606	9606.ENSP00000269305	244447	244447.ENSCSEP00000003997	285.4
165	9606	9606.ENSP00000269305	8154	8154.ENSACLP00000007040	285.0
166	9606	9606.ENSP00000269305	8175	8175.ENSSAUP00010029879	285.0
167	9606	9606.ENSP00000269305	48698	48698.ENSPFOP00000007556	284.6
168	9606	9606.ENSP00000269305	56723	56723.ENSLBEP00000036857	284.6
169	9606	9606.ENSP00000269305	64144	64144.ENSATEP00000028323	284.3
170	9606	9606.ENSP00000269305	8187	8187.ENSLCAP00010016052	283.9
171	9606	9606.ENSP00000269305	210632	210632.ENSPRNP00000030862	283.5
172	9606	9606.ENSP00000269305	48699	48699.ENSPLAP00000022694	283.1
173	9606	9606.ENSP00000269305	61819	61819.ENSACIP00000020373	282.3
174	9606	9606.ENSP00000269305	144197	144197.ENSSPAP00000022019	282.3
175	9606	9606.ENSP00000269305	299123	299123.ENSLSDP00000017092	280.4
176	9606	9606.ENSP00000269305	56716	56716.ENSCGOP00000014430	279.6
177	9606	9606.ENSP00000269305	205130	205130.ENSMAMP00000005315	279.6
178	9606	9606.ENSP00000269305	137246	137246.A0A401SCC1	279.3
179	9606	9606.ENSP00000269305	99883	99883.ENSTNIP00000013035	278.1
180	9606	9606.ENSP00000269305	173247	173247.ENSENLP00000038795	277.3
181	9606	9606.ENSP00000269305	8078	8078.ENSFHEP00000026765	276.6
182	9606	9606.ENSP00000269305	41447	41447.ENSSDUP00000028226	276.6
183	9606	9606.ENSP00000269305	59729	59729.ENSTGUP00000021519	276.2
184	9606	9606.ENSP00000269305	28743	28743.ENSCVAP00000022398	276.2
185	9606	9606.ENSP00000269305	33528	33528.ENSGAFP00000008062	276.2
186	9606	9606.ENSP00000269305	43700	43700.ENSMALP00000000877	275.8
187	9606	9606.ENSP00000269305	47308	47308.ENSNMLP00000021935	275.8
188	9606	9606.ENSP00000269305	143630	143630.A0A402EXU8	275.4
189	9606	9606.ENSP00000269305	240159	240159.A0A4U5UJG8	275.4
190	9606	9606.ENSP00000269305	52670	52670.A0A2I4CET8	275.0
191	9606	9606.ENSP00000269305	69293	69293.ENSGACP00000018012	275.0
192	9606	9606.ENSP00000269305	106582	106582.ENSMZEP00005006261	274.6
193	9606	9606.ENSP00000269305	8049	8049.ENSGMOP00000000401	274.6
194	9606	9606.ENSP00000269305	303518	303518.ENSPNYP00000025442	274.2
195	9606	9606.ENSP00000269305	1841481	1841481.ENSSLDP00000032981	274.2
196	9606	9606.ENSP00000269305	158456	158456.ENSBSLP00000007319	273.9
197	9606	9606.ENSP00000269305	8355	8355.A0A1L8FGI1	273.9
198	9606	9606.ENSP00000269305	28377	28377.ENSACAP00000001746	273.9
199	9606	9606.ENSP00000269305	75743	75743.A0A401P193	273.5
200	9606	9606.ENSP00000269305	109280	109280.ENSHCOP00000022970	273.1

201	9606	9606.ENSP00000269305	8673	8673.ENSPTXP00000024136	273.1
202	9606	9606.ENSP00000269305	8090	8090.ENSORLP00000019616	272.7
203	9606	9606.ENSP00000269305	9089	9089.ENSCPIP00010009060	271.9
204	9606	9606.ENSP00000269305	30732	30732.ENSOMEP00000009309	271.9
205	9606	9606.ENSP00000269305	59894	59894.ENSFALP00000010031	271.6
206	9606	9606.ENSP00000269305	156563	156563.ENSCCEP00000019692	271.6
207	9606	9606.ENSP00000269305	12930	12930.A0A0Q3T504	271.6
208	9606	9606.ENSP00000269305	333673	333673.A0A3M0IUV8	271.2
209	9606	9606.ENSP00000269305	8996	8996.ENSNMEP00000004526	271.2
210	9606	9606.ENSP00000269305	9157	9157.ENSPMJP00000017734	271.2
211	9606	9606.ENSP00000269305	44394	44394.ENSZALP00000002887	270.8
212	9606	9606.ENSP00000269305	9135	9135.ENSSCAP00000001137	270.8
213	9606	9606.ENSP00000269305	93934	93934.ENSCJPP00005010805	270.4
214	9606	9606.ENSP00000269305	409849	409849.ENSPMGP00000017230	270.4
215	9606	9606.ENSP00000269305	9031	9031.ENSGALP00000001485	270.4
216	9606	9606.ENSP00000269305	9049	9049.ENSPSTP00000007061	270.4
217	9606	9606.ENSP00000269305	9054	9054.ENSPCLP00000024156	270.4
218	9606	9606.ENSP00000269305	13146	13146.ENSMUNP00000017973	270.4
219	9606	9606.ENSP00000269305	372326	372326.A0A1V4KNI0	270.0
220	9606	9606.ENSP00000269305	13616	13616.ENSMODP00000018831	270.0
221	9606	9606.ENSP00000269305	94827	94827.A0A099ZQ65	269.6
222	9606	9606.ENSP00000269305	44316	44316.ENSEGOP00005018987	269.2
223	9606	9606.ENSP00000269305	55661	55661.A0A091G407	269.2
224	9606	9606.ENSP00000269305	94237	94237.ENSMMOP00000018694	269.2
225	9606	9606.ENSP00000269305	128390	128390.A0A091UUY0	269.2
226	9606	9606.ENSP00000269305	441894	441894.ENSSCUP00000005331	269.2
227	9606	9606.ENSP00000269305	7868	7868.ENSCMIP00000007753	269.2
228	9606	9606.ENSP00000269305	9238	9238.A0A093R114	269.2
229	9606	9606.ENSP00000269305	55544	55544.A0A4D9E5P9	268.9
230	9606	9606.ENSP00000269305	85066	85066.A0A091EA06	268.9
231	9606	9606.ENSP00000269305	198806	198806.ENSCPUP00000025340	268.9
232	9606	9606.ENSP00000269305	308060	308060.ENSARWP00000009421	268.9
233	9606	9606.ENSP00000269305	425635	425635.ENSCPGP00000026631	268.9
234	9606	9606.ENSP00000269305	8502	8502.ENSCPRP00005017750	268.9
235	9606	9606.ENSP00000269305	8790	8790.ENSDNVP00000009001	268.9
236	9606	9606.ENSP00000269305	8823	8823.ENSAHAP00000009000	268.9
237	9606	9606.ENSP00000269305	8824	8824.ENSAOWP00000012514	268.9
238	9606	9606.ENSP00000269305	9244	9244.A0A091HZ84	268.9
239	9606	9606.ENSP00000269305	30464	30464.ENSNPEP00000010833	268.9
240	9606	9606.ENSP00000269305	40217	40217.ENSJHYP00000001101	268.9
241	9606	9606.ENSP00000269305	50402	50402.A0A0A0AU13	268.5
242	9606	9606.ENSP00000269305	118200	118200.A0A093GLW0	268.5
243	9606	9606.ENSP00000269305	132585	132585.ENSABRP00000009434	268.5
244	9606	9606.ENSP00000269305	194338	194338.ENSACUP00000017269	268.5
245	9606	9606.ENSP00000269305	211598	211598.ENSANIP00000006686	268.5
246	9606	9606.ENSP00000269305	241587	241587.ENSACOP00000010351	268.5
247	9606	9606.ENSP00000269305	8840	8840.ENSAPLP00000032186	268.5
248	9606	9606.ENSP00000269305	8845	8845.ENSACDP00005018035	268.5
249	9606	9606.ENSP00000269305	8932	8932.A0A2I0LU30	268.5
250	9606	9606.ENSP00000269305	30419	30419.A0A091VW97	268.5
251	9606	9606.ENSP00000269305	223781	223781.ENSACCP00020004462	268.1

252	9606	9606.ENSP00000269305	328815	328815.ENSMVIP00005001759	268.1
253	9606	9606.ENSP00000269305	9233	9233.A0A087R7Z2	268.1
254	9606	9606.ENSP00000269305	9258	9258.ENSOANP00000021753	268.1
255	9606	9606.ENSP00000269305	321398	321398.ENSLCOP00000004510	267.7
256	9606	9606.ENSP00000269305	10029	10029.G3GT84	266.9
257	9606	9606.ENSP00000269305	8663	8663.ENSNSUP00000003328	264.6
258	9606	9606.ENSP00000269305	7757	7757.ENSPMAP00000010479	258.1
259	9606	9606.ENSP00000269305	32507	32507.ENSNBRP00000026855	257.7
260	9606	9606.ENSP00000269305	9009	9009.A0A226MN96	255.4
261	9606	9606.ENSP00000269305	7764	7764.ENSEBUP00000013202	251.9
262	9606	9606.ENSP00000269305	9358	9358.ENSCHOP00000009300	241.9
263	9606	9606.ENSP00000269305	7739	7739.C3XPU2	230.3
264	9606	9606.ENSP00000269305	9014	9014.A0A226P7S4	224.2
265	9606	9606.ENSP00000269305	283909	283909.R7UHV7	209.1
266	9606	9606.ENSP00000269305	6573	6573.A0A210QTK4	203.4
267	9606	9606.ENSP00000269305	7719	7719.ENSCINP00000003956	200.7
268	9606	9606.ENSP00000269305	37653	37653.A0A0L8G262	198.7
269	9606	9606.ENSP00000269305	225164	225164.V4A869	194.5
270	9606	9606.ENSP00000269305	6526	6526.A0A2C9K4K6	193.7
271	9606	9606.ENSP00000269305	7574	7574.A0A1S3IK29	192.2
272	9606	9606.ENSP00000269305	188477	188477.A0A433U4Z3	190.7
273	9606	9606.ENSP00000269305	51511	51511.ENSCSAVP00000016940	185.7
274	9606	9606.ENSP00000269305	10195	10195.A0A3M7Q6B9	184.5
275	9606	9606.ENSP00000269305	7668	7668.W4XZV7	175.3
276	9606	9606.ENSP00000269305	10228	10228.B3RZS6	162.2
277	9606	9606.ENSP00000269305	46731	46731.A0A3M6T6Q0	161.8
278	9606	9606.ENSP00000269305	287889	287889.A0A369SDE5	161.8
279	9606	9606.ENSP00000269305	407821	407821.A0A087U4M0	159.5
280	9606	9606.ENSP00000269305	50429	50429.A0A2B4RUK1	158.7
281	9606	9606.ENSP00000269305	6832	6832.A0A553NYY4	153.3
282	9606	9606.ENSP00000269305	307972	307972.A0A2G8L3N1	150.6
283	9606	9606.ENSP00000269305	418985	418985.A0A1V9Y190	149.8
284	9606	9606.ENSP00000269305	7070	7070.D7EJV6	144.1
285	9606	9606.ENSP00000269305	45351	45351.A7S162	142.9
286	9606	9606.ENSP00000269305	30538	30538.ENSVPAP00000011479	137.5
287	9606	9606.ENSP00000269305	6669	6669.E9FW11	135.2
288	9606	9606.ENSP00000269305	6945	6945.B7QF52	134.0
289	9606	9606.ENSP00000269305	6973	6973.A0A2P8XLZ2	134.0
290	9606	9606.ENSP00000269305	400727	400727.A0A2T7PT95	131.0
291	9606	9606.ENSP00000269305	35525	35525.A0A0P5UBN4	127.1
292	9606	9606.ENSP00000269305	126957	126957.T1INQ8	124.4
293	9606	9606.ENSP00000269305	7029	7029.J9JP39	123.2
294	9606	9606.ENSP00000269305	121224	121224.E0V916	122.5
295	9606	9606.ENSP00000269305	224129	224129.A0A1W4XBP0	121.7
296	9606	9606.ENSP00000269305	136037	136037.A0A067QKS2	120.9
297	9606	9606.ENSP00000269305	1661398	1661398.A0A482VJ27	120.9
298	9606	9606.ENSP00000269305	6412	6412.T1EZJ4	120.2
299	9606	9606.ENSP00000269305	121845	121845.A0A3Q0IPE1	113.6
300	9606	9606.ENSP00000269305	543379	543379.A0A232FJ48	112.8
301	9606	9606.ENSP00000269305	195883	195883.A0A482XMX2	110.2
302	9606	9606.ENSP00000269305	7425	7425.K7IV69	109.8

303	9606	9606.ENSP00000269305	597456	597456.A0A0L7RJB6	108.6
304	9606	9606.ENSP00000269305	67767	67767.A0A0J7L4T2	107.8
305	9606	9606.ENSP00000269305	81824	81824.A9UZX3	106.7
306	9606	9606.ENSP00000269305	568069	568069.A0A1J1HKW3	105.5
307	9606	9606.ENSP00000269305	166423	166423.A0A0N1IU42	105.1
308	9606	9606.ENSP00000269305	178035	178035.A0A154PH19	105.1
309	9606	9606.ENSP00000269305	94128	94128.A0A2A3EPF3	104.8
310	9606	9606.ENSP00000269305	7460	7460.A0A088AGC6	104.4
311	9606	9606.ENSP00000269305	268475	268475.A0A0V1H034	103.6
312	9606	9606.ENSP00000269305	6337	6337.A0A0V0XWZ0	103.6
313	9606	9606.ENSP00000269305	105785	105785.A0A2J7RT65	103.2
314	9606	9606.ENSP00000269305	268474	268474.A0A0V1MEE0	102.4
315	9606	9606.ENSP00000269305	13347	13347.A0A444TIG8	102.1
316	9606	9606.ENSP00000269305	13249	13249.T1HHW8	101.3
317	9606	9606.ENSP00000269305	70415	70415.A0A5S6Q6J5	100.5
318	9606	9606.ENSP00000269305	990121	990121.A0A0V0ZFM8	96.3
319	9606	9606.ENSP00000269305	45882	45882.A0A0V1D8F8	95.5
320	9606	9606.ENSP00000269305	92179	92179.A0A0V0WQ02	95.5
321	9606	9606.ENSP00000269305	144512	144512.A0A0V0U5U4	95.5
322	9606	9606.ENSP00000269305	667725	667725.A0A0L0G1F4	95.5
323	9606	9606.ENSP00000269305	6335	6335.A0A0V1LDC9	95.5
324	9606	9606.ENSP00000269305	610380	610380.E2B2V4	95.1
325	9606	9606.ENSP00000269305	104421	104421.E2APG2	94.7
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329	9606	9606.ENSP00000269305	181606	181606.A0A0V0V4L8	93.6
330	9606	9606.ENSP00000269305	92180	92180.A0A0V1P3X2	93.2
331	9606	9606.ENSP00000269305	77166	77166.N6UG92	92.8
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336	9606	9606.ENSP00000269305	6334	6334.A0A0V1B7T2	89.7
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368	9606	9606.ENSP00000269305	34720	34720.A0A195FHS0	78.6
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372	9606	9606.ENSP00000269305	520822	520822.A0A195B173	77.8
373	9606	9606.ENSP00000269305	471704	471704.A0A195DK69	77.4
374	9606	9606.ENSP00000269305	12957	12957.A0A158ND95	77.4
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394	9606	9606.ENSP00000269305	6290	6290.A0A0N4W3M7	66.2
395	9606	9606.ENSP00000269305	7168	7168.A0A182N4N0	65.9
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402	9606	9606.ENSP00000269305	1518534	1518534.A0A182LFH4	65.1
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405  9606  9606.ENSP00000269305   30066            30066.A0A182V190   63.9
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417  9606  9606.ENSP00000269305  387005           387005.A0A183HOZ1   57.0
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420  9606  9606.ENSP00000269305   70667            70667.A0A183STT5   56.6
421  9606  9606.ENSP00000269305    7370             7370.A0A1I8N839   56.6
422  9606  9606.ENSP00000269305   35570            35570.A0A1I8QBH4   56.6
423  9606  9606.ENSP00000269305    7091                 7091.E9JEI4   56.2
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425  9606  9606.ENSP00000269305    7240                 7240.B4R1C4   54.3
426  9606  9606.ENSP00000269305   34690            34690.A0A182UJE7   53.5
427  9606  9606.ENSP00000269305    7375             7375.A0A0L0CLI5   53.1
428  9606  9606.ENSP00000269305    7266             7266.A0A3B0JRN9   52.0
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430  9606  9606.ENSP00000269305  947166           947166.A0A1D1VBG3   51.6
431  9606  9606.ENSP00000269305    7244                 7244.B4MB49   51.2
432  9606  9606.ENSP00000269305   54126                54126.H3FK89   50.8
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... 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.ENSP00000269305 X10090 X10090.ENSMUSP00000104298 X598.2
1  9606  9606.ENSP00000278616  10090  10090.ENSMUSP00000156344 5328.8
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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