LETTER

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Architecture of the human interactome defines protein communities and disease networks

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ORFeome-------Proteome--------Interactome

- the proteome can be viewed as constellations of interacting protein modules organized into signal transduction networks, molecular machines, and organelles

- our knowledge of proteome architecture is fragmentary, as is our conception of how protein interconnectivity is influenced by genetic and cellular variation

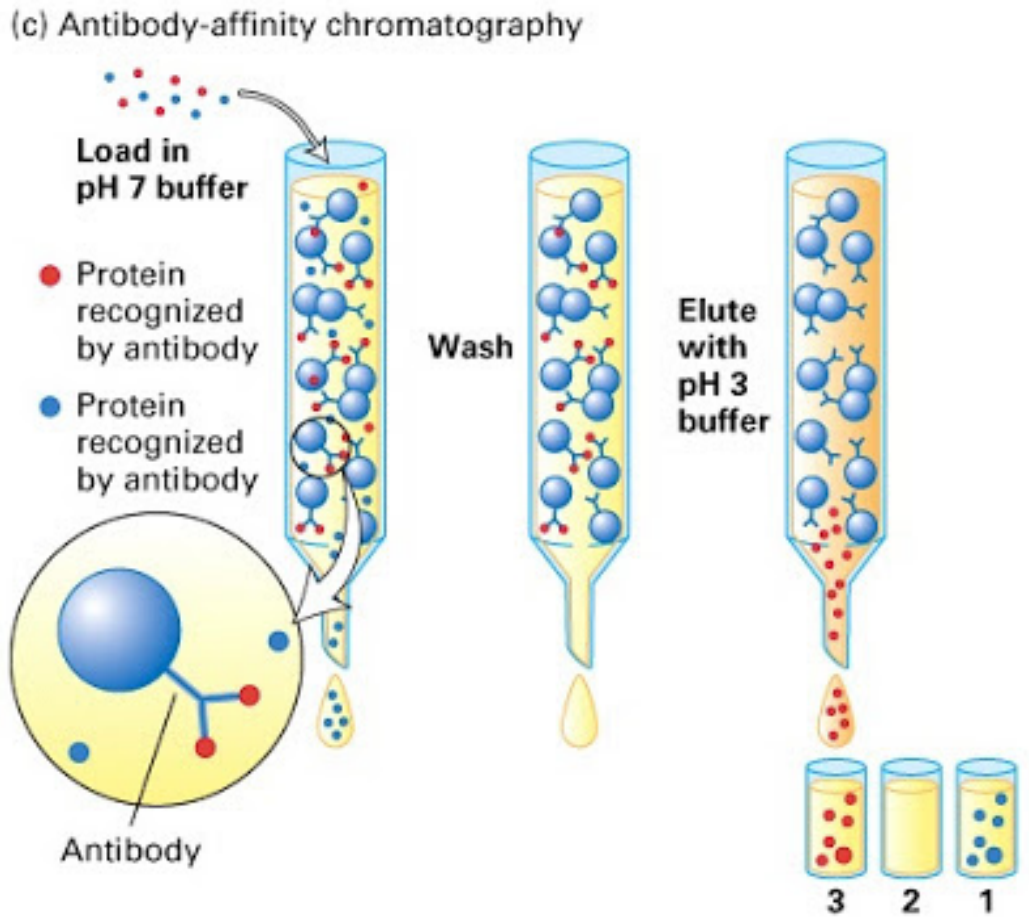
Challenges….

- Myriad genes, isoforms, and modification states encoded by the human genome
- Low abundance of many proteins, which limits detection
- Many transient interactions that complicate signaling network mapping
- Prevalence of membrane proteins, which often requires specialized methods for purification ….
- …..
- …..

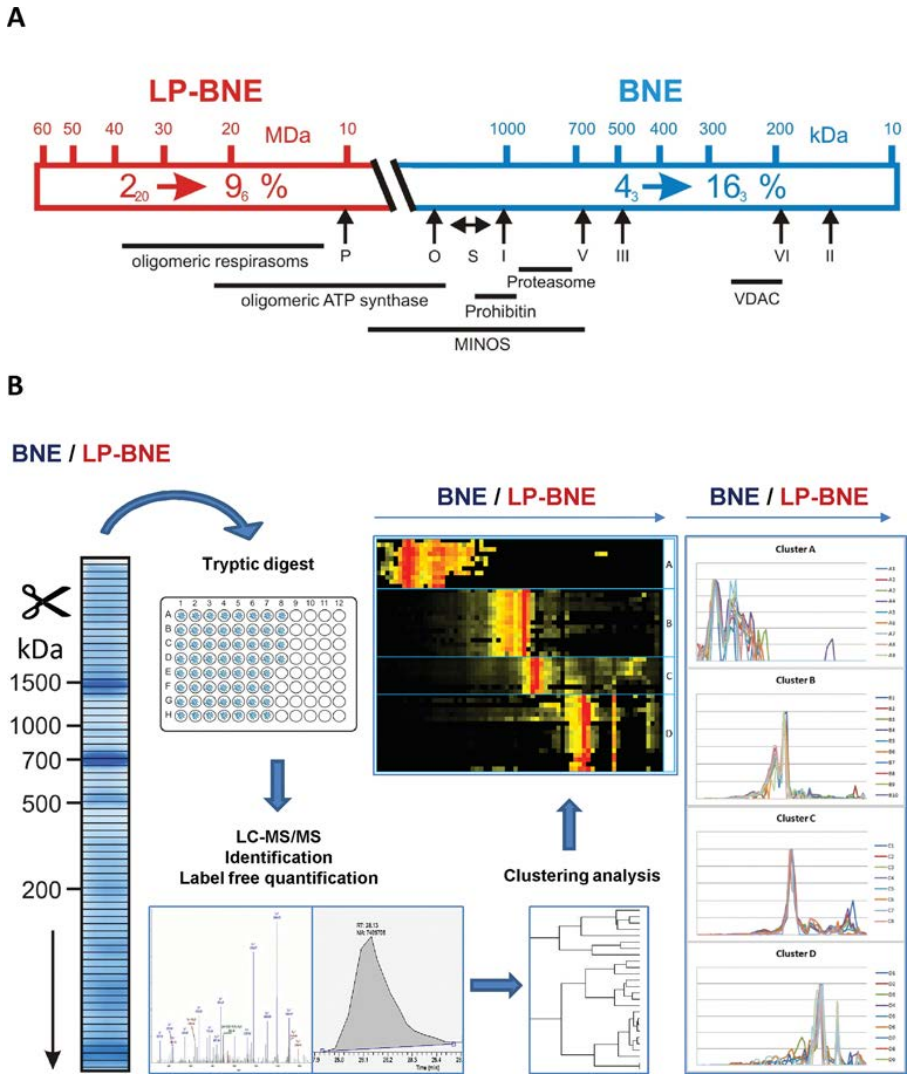
Main strategies to study mammalian proteome structure

- Biochemical experiments reveal stable macromolecular complexes
- Affinity purification of tagged protein followed by MS (AP-MS)
- Immunoprecipitation followed by MS (IP-MS)
- Protein correlation profiling (Blue native electrophoresis +/- IP) followed by MS
- Yeast 2Hybrid analysis
- Database archive protein interaction from literature (context dependant)

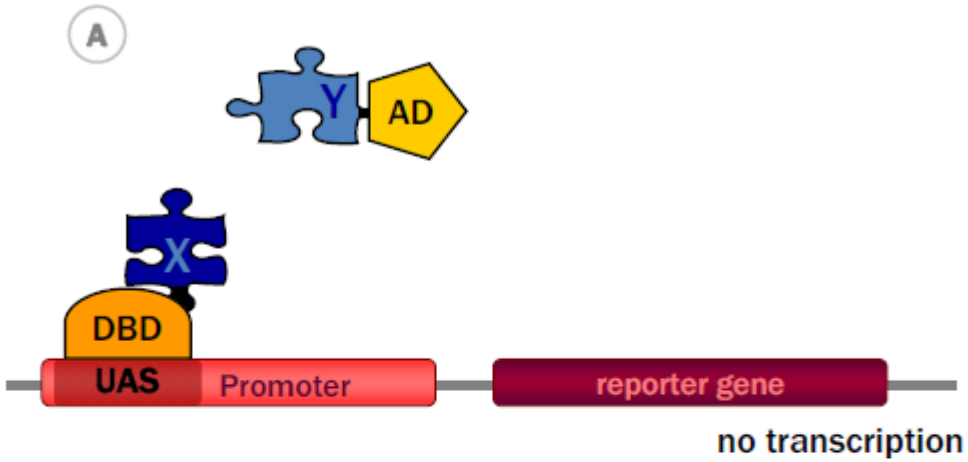
Example of affinity purification-targeted

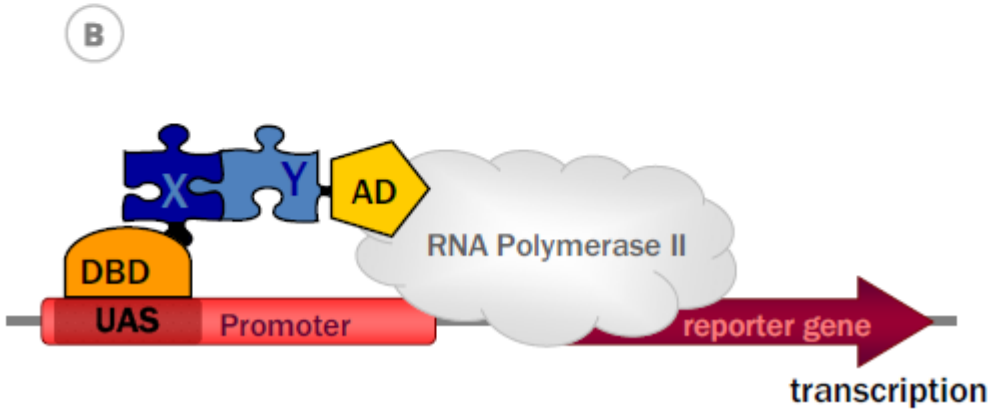


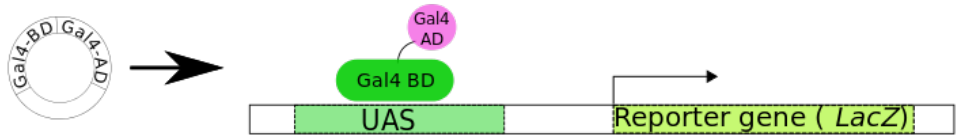
Protein correlation profiling---Non targeted



Y2H system

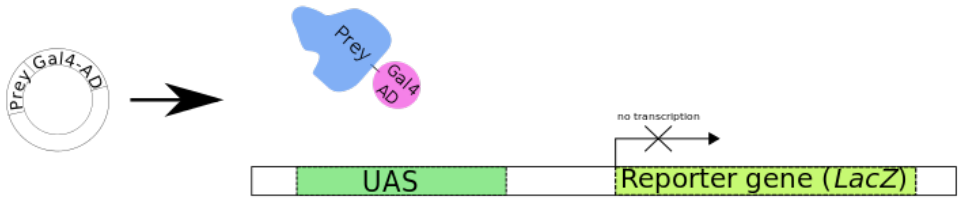




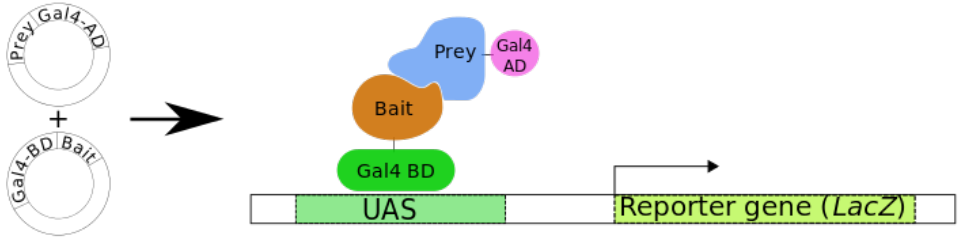


A. Regular transcription of the reporter gene

B. One fusion protein only (Gal4-BD + Bait) - no transcription



C. One fusion protein only (Gal4-AD + Prey) - no transcription



D. Two fusion proteins with interacting Bait and Prey

Databases

- **MINT: a Molecular INTeraction database (italian)**
- **GeneMania**
- **BioGRID**
- **STRING (Swiss)**
- **BioPixie**
- **IntAct**
- **CORUM**
- .
- .

BioPlex 1.0 --------- BioPlex 2.0

The BioPlex Network: A Systematic Exploration of the Human Interactome

Edward L. Huttlin,[1] Lily Ting,[1] Raphael J. Bruckner,[1] Fana Gebreab,[1] Melanie P. Gygi,[1] John Szpyt,[1] Stanley Tam,[1] Gabriela Zarraga,[1] Greg Colby,[1] Kurt Baltier,[1] Rui Dong,[2] Virginia Guarani,[1] Laura Pontano Vaites,[1] Alban Ordureau,[1] Ramin Rad,[1] Brian K. Erickson,[1] Martin Wühr,[1] Joel Chick,[1] Bo Zhai,[1] Deepak Kolippakkam,[1] Julian Mintseris,[1] Robert A. Obar,[1,3] Tim Harris,[3] Spyros Artavanis-Tsakonas,[1,3] Mathew E. Sowa,[1] Pietro De Camilli,[2] Joao A. Paulo,[1] J. Wade Harper,[1,*] and Steven P. Gygi[1,*]

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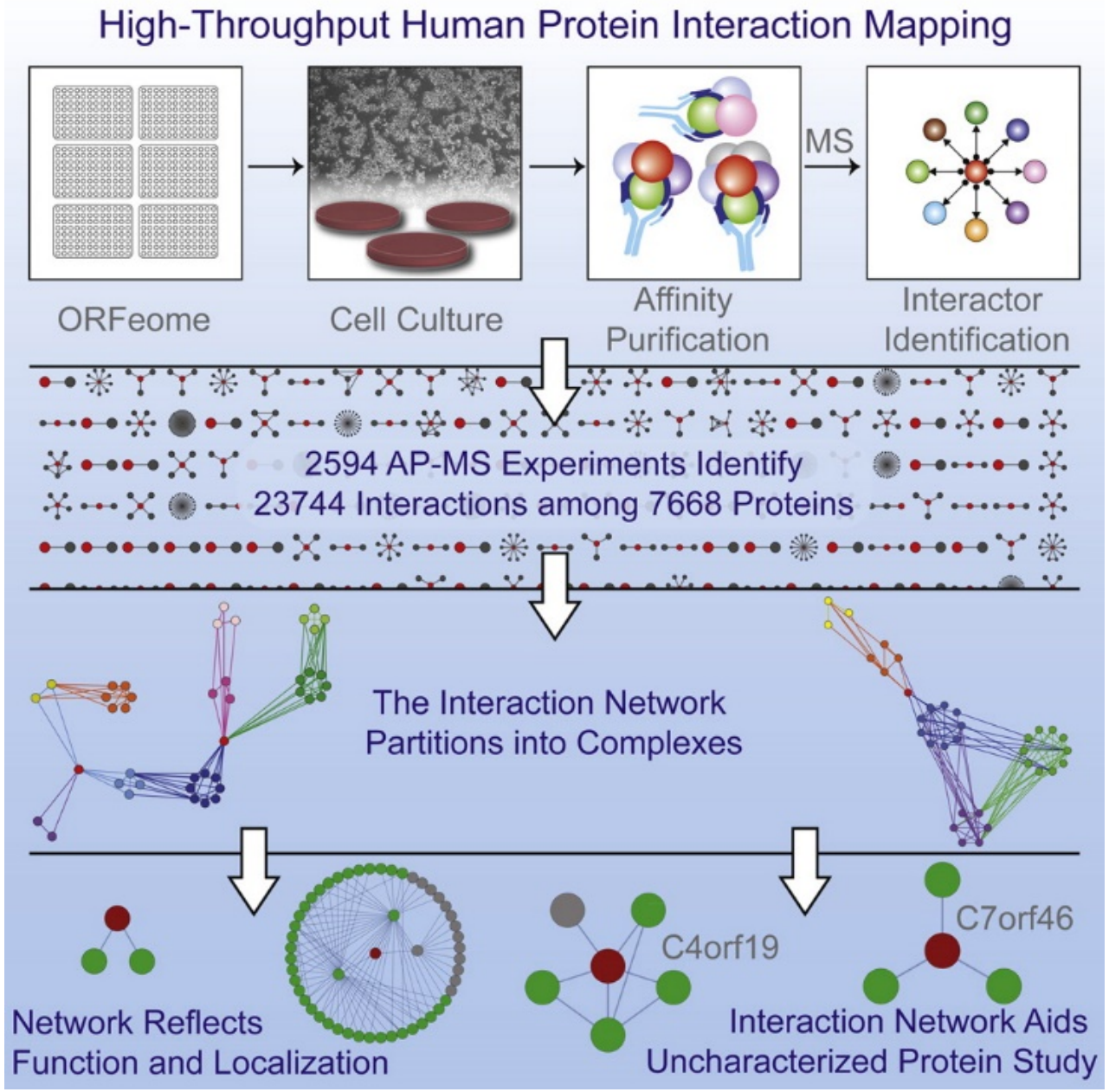
Cell


High-Throughput Human Protein Interaction Mapping
MS
ORFeome
Cell Culture
Affinity Purification
Interactor Identification
2594 AP-MS Experiments Identify
23744 Interactions among 7668 Proteins
The Interaction Network Partitions into Complexes
C4orf19
C7orf46
Network Reflects Function and Localization
Interaction Network Aids Uncharacterized Protein Study

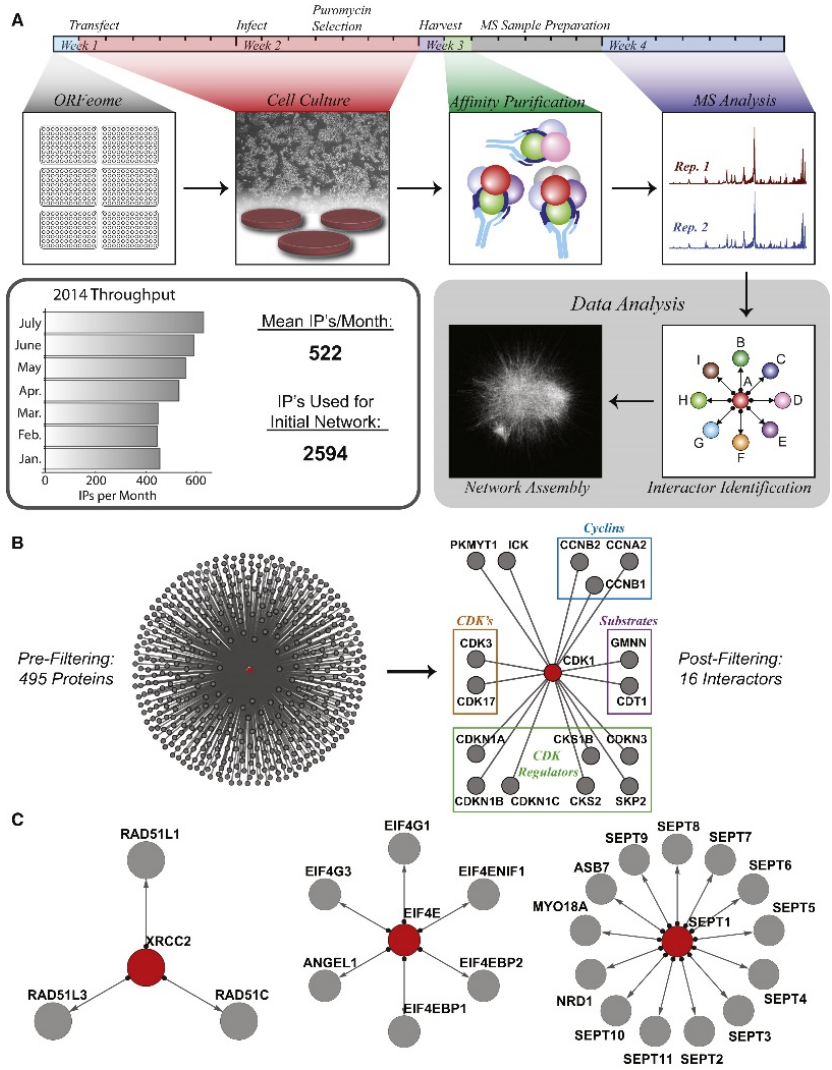
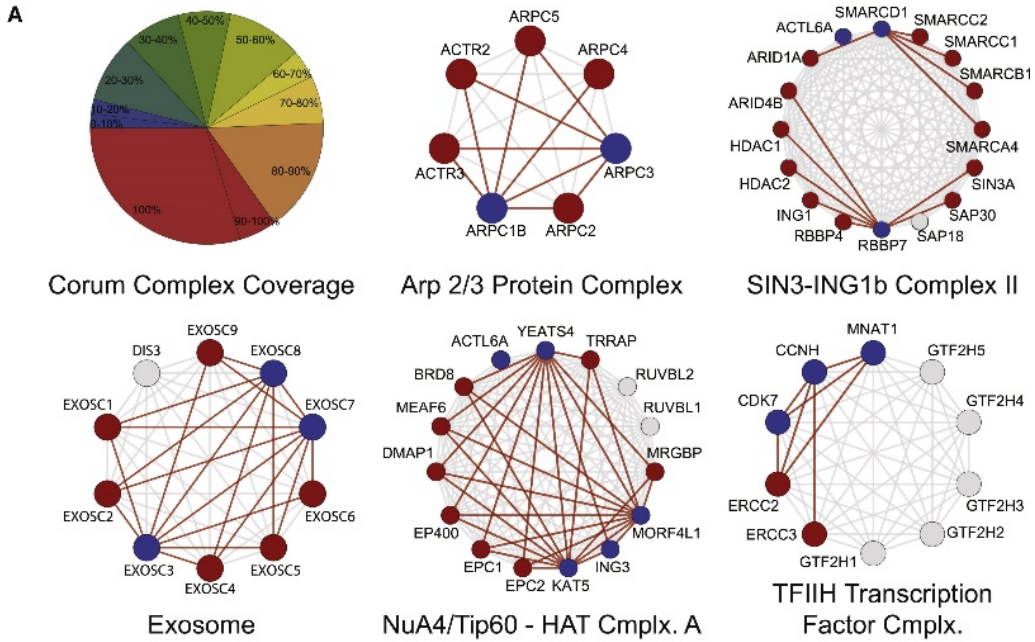


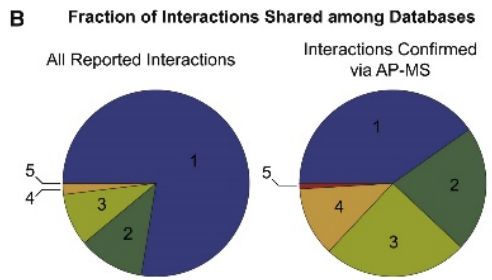
Figure 1. High-Throughput Interaction Mapping via AP-MS

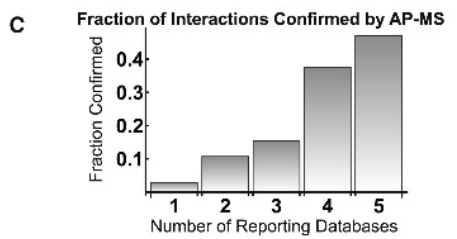
(A) AP-MS platform: (1) a lentiviral library of 13,000 FLAG-HA-tagged ORFs was constructed from the Human ORFEOME; (2) 293T cells were infected and expanded under puromycin selection; (3) baits and preys were immuno-purified; (4) tryptic digests were analyzed in technical duplicate by LC-MS; (5) proteins were identified and specific interactors found; (6) and interactions were assembled to model the human interactome. Up to 600 AP-MS experiments may be completed per month.

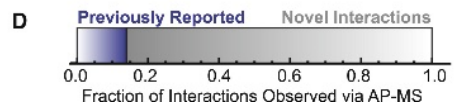
(B) *CompPASS-Plus* extracts 16 interactors for bait CDK1 from a background of nearly 500 proteins.

(C) Interaction maps for baits XRCC2, EIF4E, and SEPT1 (red). Nearly all interactions have been previously described. Interactors were identified from backgrounds of 487, 778, and 749 proteins, respectively.









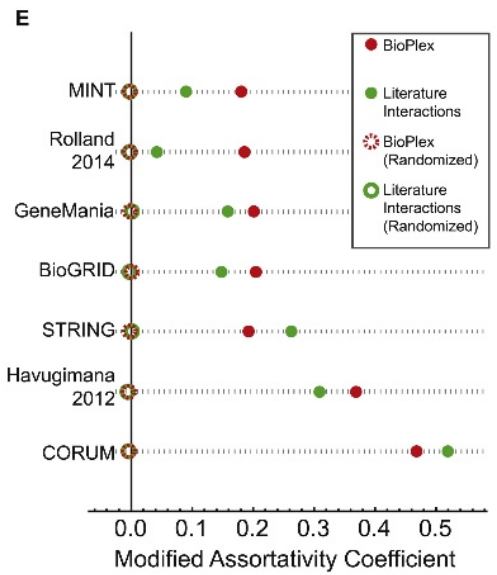


Figure 3. Evaluation of AP-MS Protein Interactions

(A) AP-MS interactions superimposed onto CORUM complexes. The pie chart depicts the fraction of complexes achieving the indicated coverage in BioPlex. Only complexes containing two or more baits were considered. Five representative CORUM complexes: baits are colored blue, whereas preys are red and proteins not observed by AP-MS are gray. Interactions among CORUM complex members are gray, whereas interactions confirmed by AP-MS are red.

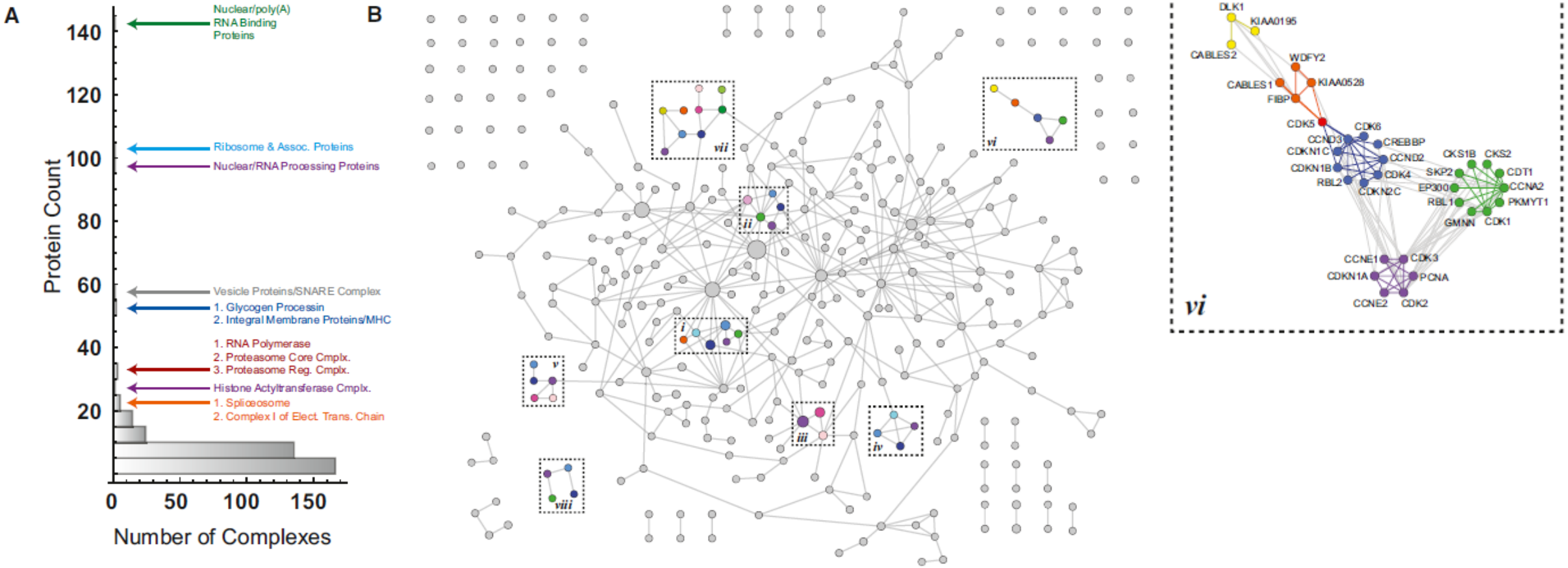
(B) Physical protein interactions reported in BioGrid, CORUM, GeneMania, STRING, and MINT were merged. Left: overlap among databases. Right: overlap among databases for interactions confirmed by AP-MS.

(C) Fraction of database interactions confirmed by AP-MS as a function of the number of supporting database reports. The composite interaction database was filtered to include only interactions connecting one of 2,594 baits with proteins observed as baits or preys in the interaction network.

(D) 86% of AP-MS interactions have not been reported in the databases listed above.

(E) Pairwise comparisons of BioPlex with published interaction networks were performed, using graph assortativity to quantify preferential interaction in cases of shared localization among proteins detected in both networks. Literature datasets included BioGRID, CORUM, GeneMania, STRING, and MINT, as well as interactions recently reported via yeast-two-hybrid (Rolland et al., 2014) and LC-MS correlation profiling (Havugimana et al., 2012). Each analysis was repeated with randomized localizations as a control.

Protein “communities” 356



BioPlex 2.0: more proteins, more interactions

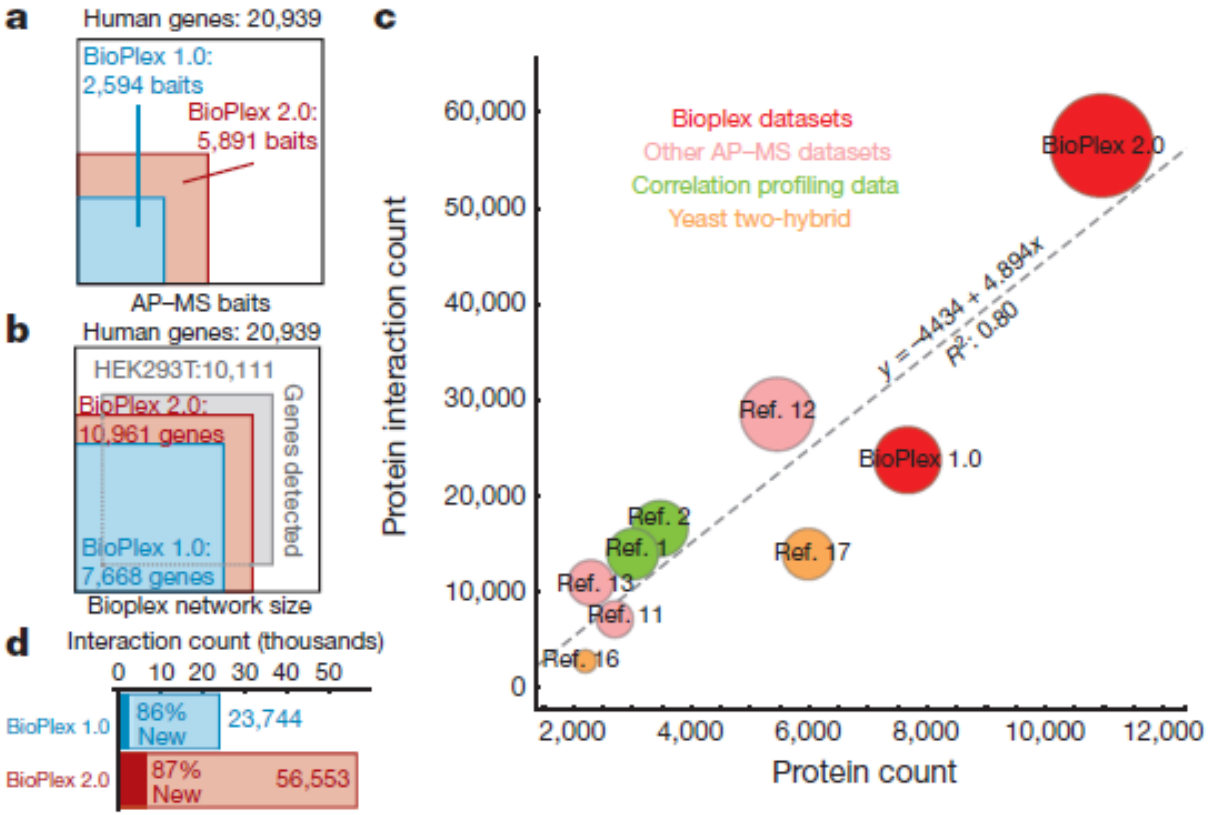


Figure 1 | BioPlex 2.0 substantially increases depth and breadth of interactome coverage. a, Bait proteins targeted for AP–MS analysis. b, Protein-coding genes included in BioPlex 2.0 as baits or preys. c, The BioPlex 2.0 network substantially exceeds previous experimentally derived interaction networks with respect to protein and interaction counts. Circle area is proportional to interaction counts, while shading denotes the experimental strategy used for interaction mapping. d, BioPlex 2.0 doubles the numbers of interactions revealed in BioPlex 1.0.

Better coverage vs. BioPlex 1.0

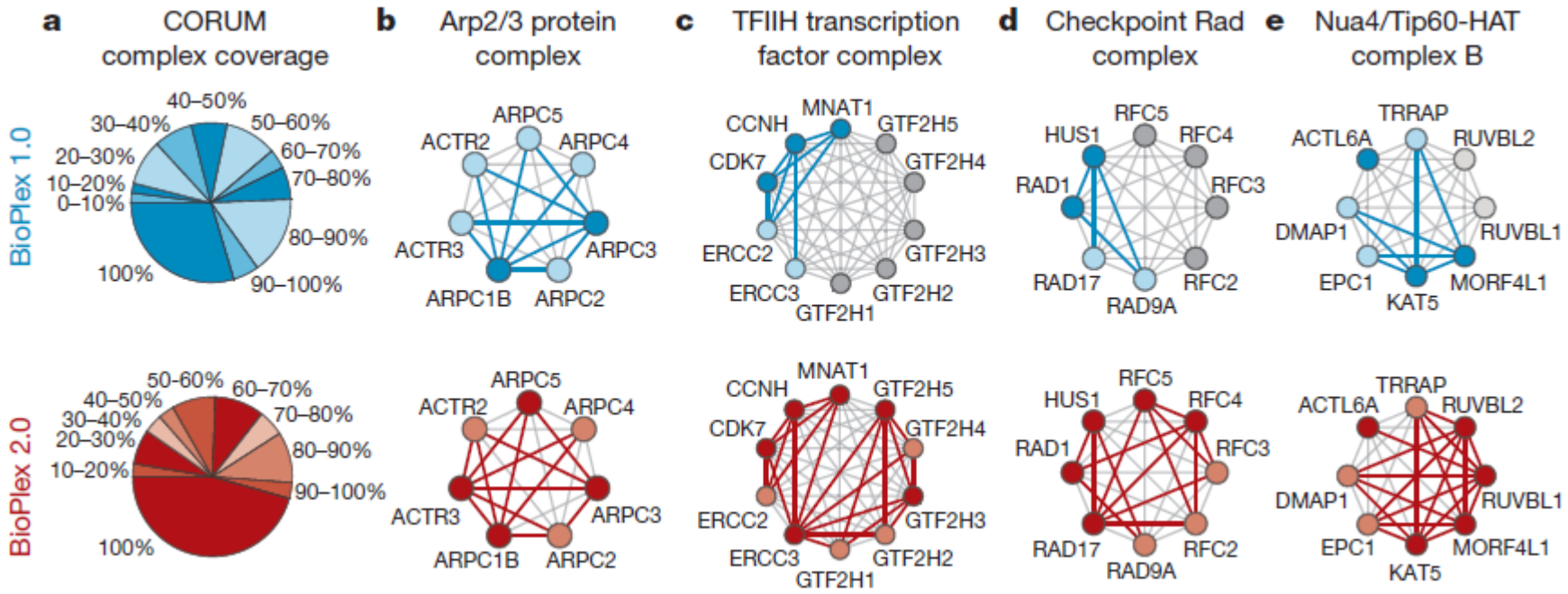


Figure 2 | BioPlex 2.0 maps protein complexes with increased resolution. **a**, Agreement among BioPlex networks and CORUM complexes. Pie charts indicate the fraction of CORUM complexes that attained the indicated protein coverage. Compared with BioPlex 1.0 (blue), BioPlex 2.0 (red) provides substantially improved coverage. **b–e**, Network coverage achieved by BioPlex 1.0 (blue) and BioPlex 2.0 (red) for selected CORUM complexes. Dark and light shades depict bait and prey proteins, respectively, while grey proteins were not observed in the network. Red and blue edges represent detected protein interactions.

BioPlex 2.0 Protein Communities

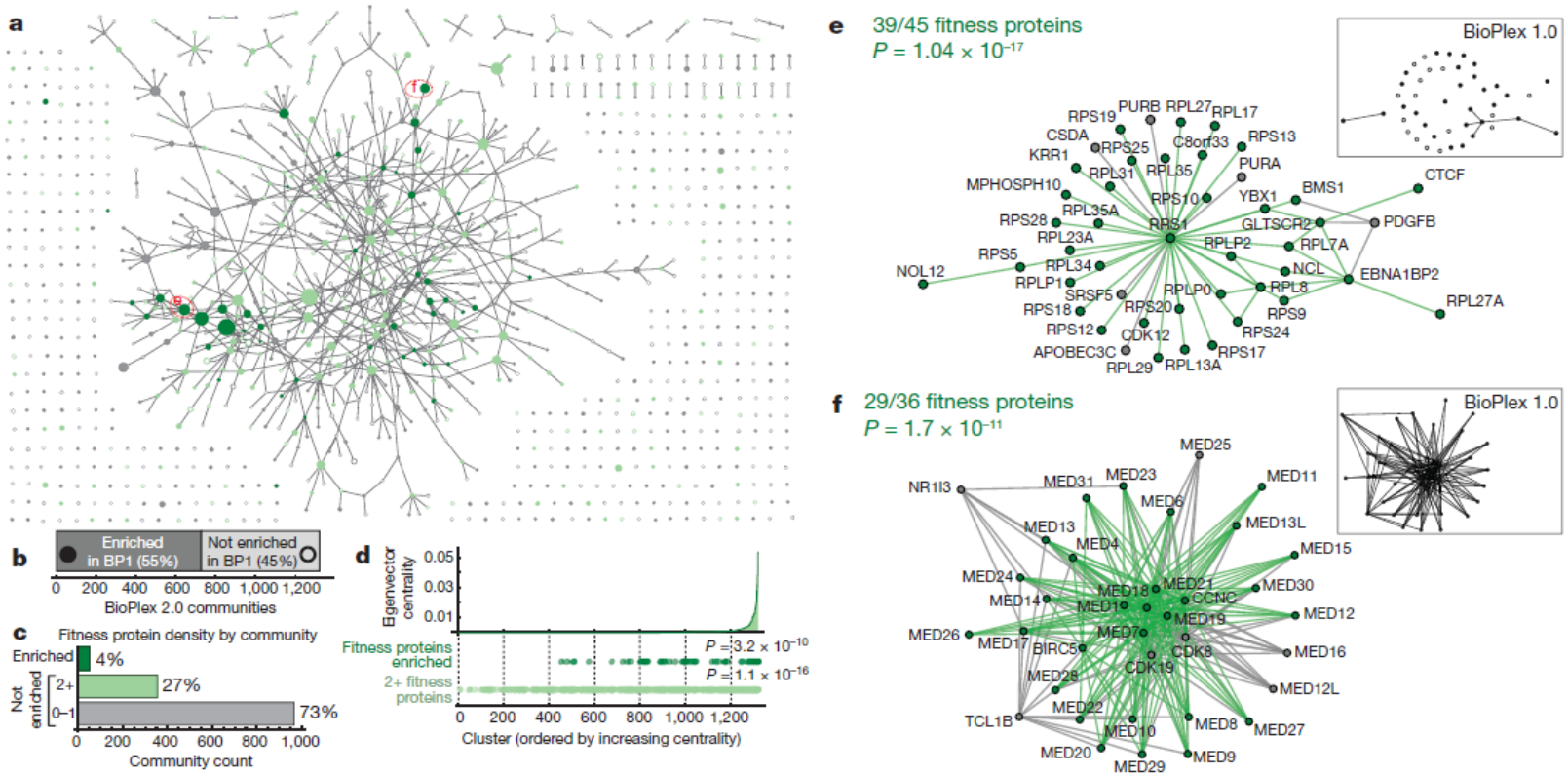


Figure 3 | BioPlex communities subdivide the interaction network according to functional properties and fitness effects. a, Network of communities revealed through MCL clustering of the BioPlex 2.0 network. Nodes represent distinct communities and are scaled to reflect the numbers of proteins in each (3–76 proteins). Nodes are connected by edges when proteins within the respective communities interact with unusually high frequency (see Methods). Filled nodes depict communities that were also found to be interconnected by unusual numbers of interactions in BioPlex 1.0; open circles represent communities of proteins that exhibited only background numbers of interactions in BioPlex 1.0. Communities containing two or more proteins associated with increased cellular fitness are highlighted in light green; communities that are enriched with cellular fitness proteins (1% false discovery rate (FDR)) are highlighted in dark green. Communities circled and marked with red letters 'e' and 'f' refer to those selected in **e** and **f**. **b**, Mapping BioPlex 2.0 communities onto BioPlex 1.0 reveals lower connectivity, with 45% of complexes showing no significant enrichment of interactions above background levels (binomial test; Benjamini–Hochberg-adjusted $P < 0.05$). **c**, Relative fractions of 1,320 communities that contain specified numbers of fitness proteins. **d**, When BioPlex 2.0 clusters are ranked according to their eigenvector centrality within the BioPlex 2.0 community network (**a**), clusters that contain multiple fitness proteins (light green) or are enriched for fitness proteins (dark green) tend to have higher centralities (Kolmogorov–Smirnov test). **e**, **f**, Selected BioPlex 2.0 communities highlighting proteins associated with cellular fitness (green). Inset maps depict the same communities as observed in BioPlex 1.0. Filled nodes indicate proteins that were in BioPlex 1.0, while black edges indicate interactions that were visible. In contrast, open circles indicate proteins that were not found in BioPlex 1.0.

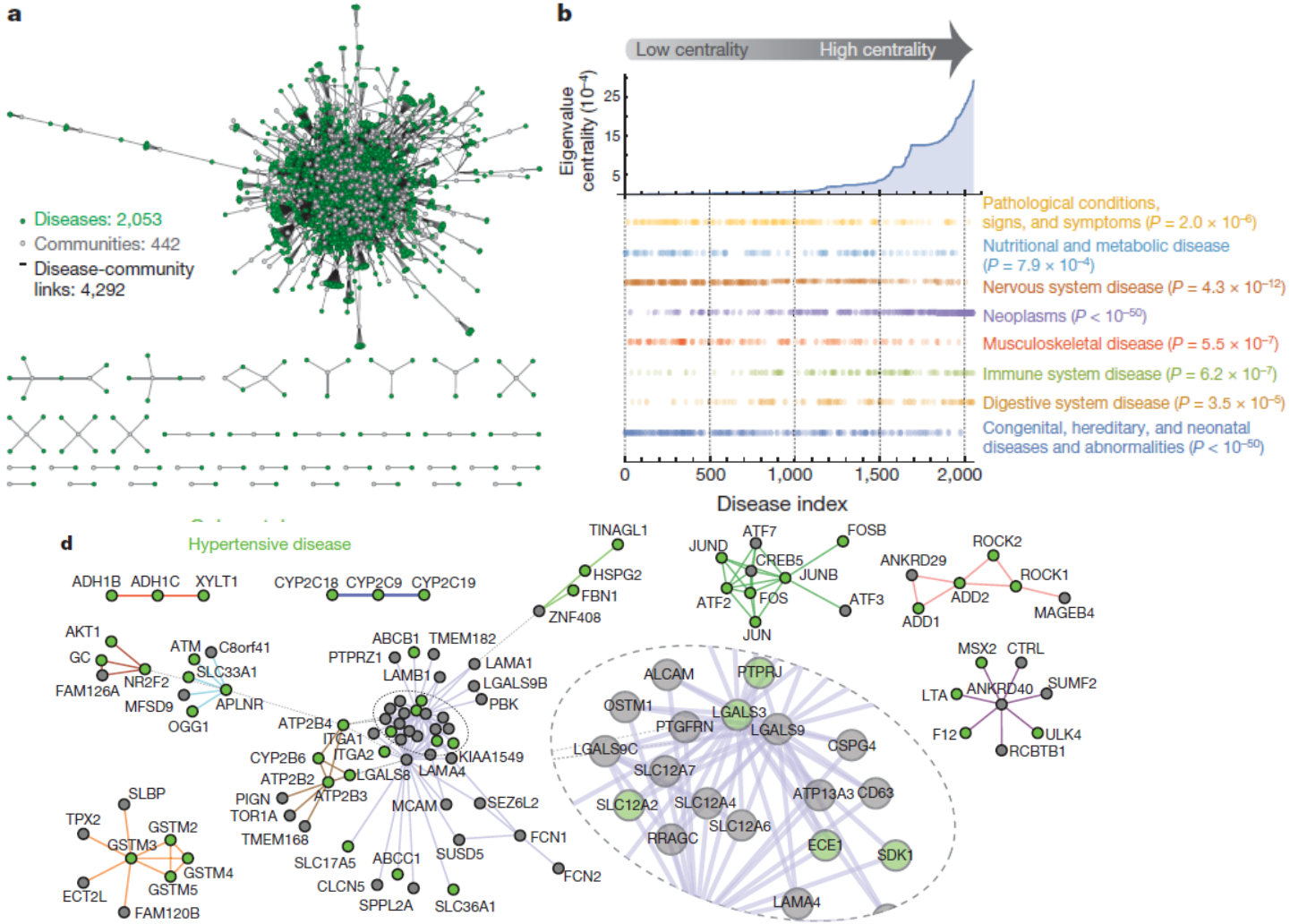
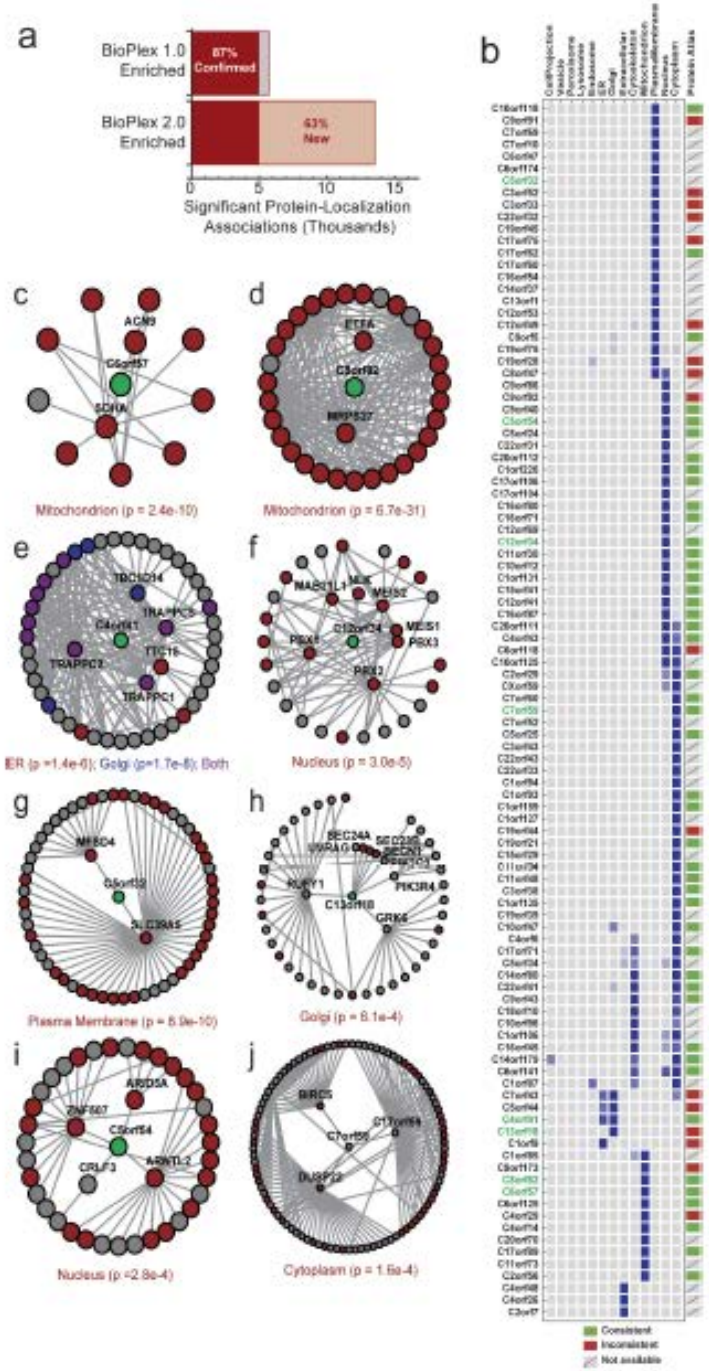
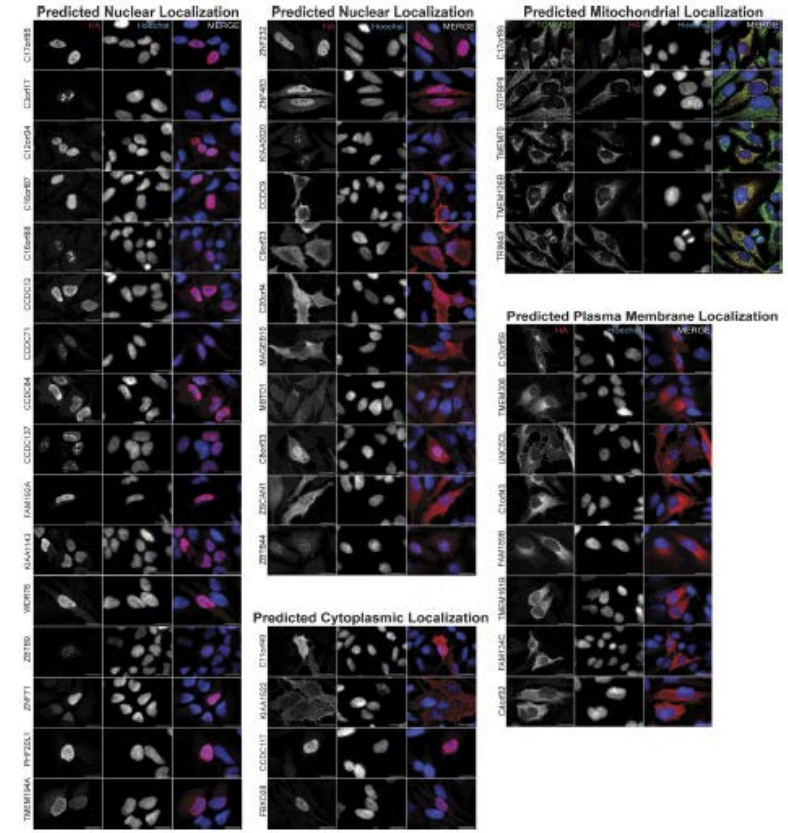


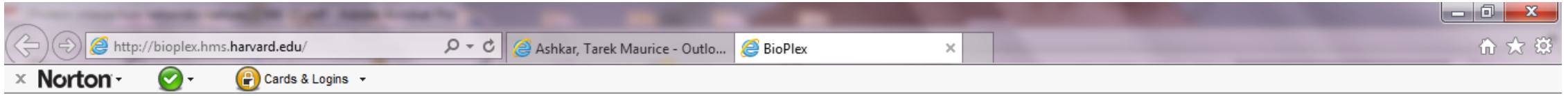
Figure 4 | Integration of BioPlex 2.0 and the DisGeNET network associates protein complexes with disease processes. **a**, Network of associations among protein interaction communities and disease conditions (see Methods). The network depicts 4,292 associations between 442 protein complexes (grey) and 2,053 disease states (green). **b**, Ranking of 2,053 disease states on the basis of eigenvalue centrality in the disease–complex network (**a**). Scatter plots below highlight disease classes that are non-randomly distributed (Kolmogorov–Smirnov test; Benjamini–Hochberg $P < 0.01$). **c**, **d**, Sub-networks associated with selected disease states: colorectal cancer (BRAF complex: $P < 0.05$) and hypertensive disease. Nodes associated with the indicated disease are highlighted in green, while other complex members are grey; thick, multi-coloured edges connect proteins belonging to individual communities revealed through MCL clustering; thin, dashed, grey edges connect proteins among adjacent communities.



Extended Data Figure 3 | BioPlex 2.0 enables subcellular localization prediction for additional uncharacterized proteins. **a**, Increased interaction density expands subcellular localization predictions from BioPlex 2.0. **b**, Subcellular localization predictions for a selection of uncharacterized human proteins for which no confident prediction could be made in BioPlex 1.0. Where possible, the figure indicates whether predicted localization is consistent with the Human Protein Atlas[21]. **c**–**j**, Sub-networks highlighting primary and secondary neighbours for selected uncharacterized human proteins whose subcellular localization can be predicted using the BioPlex network. Nodes are coloured according to subcellular localization data provided by UniProt. *P* values were calculated by Fisher's exact test as described in Methods with multiple testing correction. Localizations depicted in **c**, **e**, **g**, and **i** are consistent with recent characterization as listed in UniProt; The localization given in **d** is consistent with MitoCarta 2.0 (ref. 41).



Extended Data Figure 4 | Validation of subcellular localization predictions using anti-HA immunofluorescence. The indicated bait proteins fused at their C terminus with an HA tag were expressed after transient infection of lentiviruses at low multiplicity of infection; after 2 days, cells were fixed and subjected to anti-HA-based immunofluorescence (red). Nuclei were stained with Hoechst. For baits with predicted mitochondrial localization, cells were co-stained with anti-TOMM20 antibodies (green). Z-series optical sections were acquired via spinning disk confocal microscopy; maximum intensity projections are shown. Scale bar, 20 μm.



BioPlex

The BioPlex (biophysical interactions of ORFeome-based complexes) network is the result of creating thousands of cell lines with each expressing a tagged version of a protein from the ORFeome collection. Immunopurification of the tagged protein and detection of associated proteins by mass spectrometry are the building blocks of the network. The overarching project goal is to determine protein interactions for every member of the collection. A first paper in *Cell* reports the first ~2,500 experiments (~23,000 interactions). Our current release with more than 5,000 human proteins as baits (~50,000 interactions) is also now available.

Read more

HARVARD MEDICAL SCHOOL

Department of Cell Biology

A Gygi & Harper Lab Collaboration

Funding:

- Biogen
- NHGRI: U41 HG006673

Huttlin EL, Ting L, Bruckner RJ, Gebreab F, Gygi MP, Szpyt J, Tam S, Zarraga G, Colby G, Baltier K, Dong R, Guarani V, Vaites LP, Ordureau A, Rad R, Erickson BK, Wühr M, Chick J, Zhai B, Kolippakkam D, Mintseris J, Obar RA, Harris T, Artavanis-Tsakonas S, Sowa ME, De Camilli P, Paulo JA, Harper JW, Gygi SP. (2015) The BioPlex Network: A Systematic Exploration of the Human Interactome. Cell 162:425-440.

Databases

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- **IntAct**
- **CORUM**
- .
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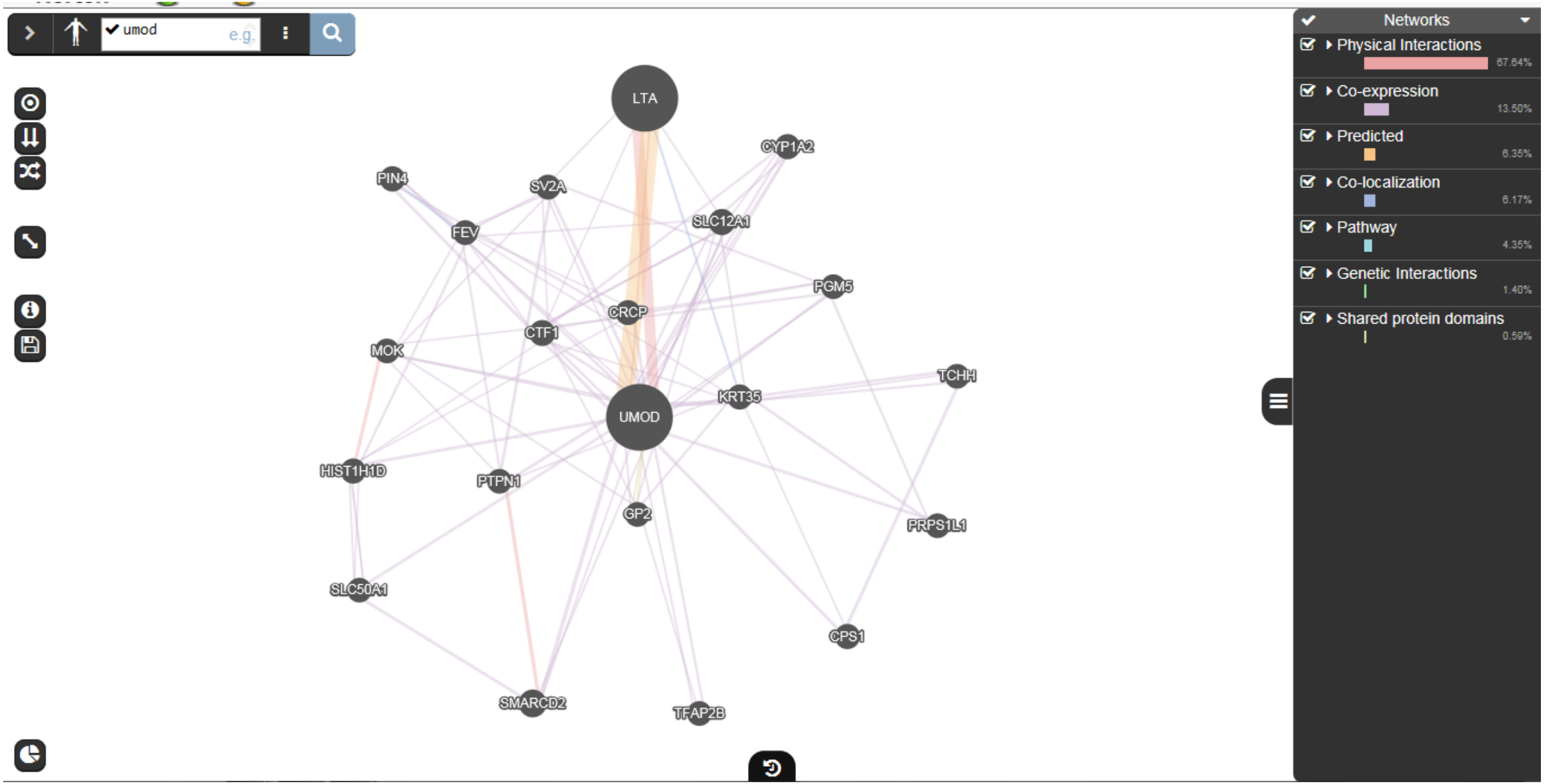
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e.g.
LTA
CYP1A2
PIN4
SV2A
SLC12A1
FEV
PGM5
CRCP
CTF1
MOK
TCHH
KRT35
UMOD
HIST1H1D
PTPN1
GP2
PRPS1L1
SLC50A1
CPS1
SMARCD2
TFAP2B
Networks
Physical Interactions
67.64%
Co-expression
13.50%
Predicted
6.35%
Co-localization
6.17%
Pathway
4.35%
Genetic Interactions
1.40%
Shared protein domains
0.59%

Result Summary

Gene / Identifier Search

umod

All Organisms

GO

UMOD

Homo sapiens

ADMCKD2, FJHN, HNFJ, HNFJ1, MCKD2, THGP, THP

uromodulin

GO Process (5) | GO Function (1) | GO Component (7)

EXTERNAL DATABASE LINKOUTS

OMIM | VEGA | HGNC | Entrez Gene | RefSeq | UniprotKB | Ensembl | HPRD

Download 1 Published Interactions For This Protein

Stats & Options

Current Statistics **Publication:** 1

High Throughput		Low Throughput
0 (0%)	1 Physical Interaction	1 (100%)
0 (0%)	0 Genetic Interactions	0 (100%)

Search Filters Customize how your results are displayed...

No Filter: Show All Associations

Switch View: Interactors (1) | Interactions (1) | Network

Displaying **1** total unique interactors

Sort By: [Evidence] [Alphabetical]

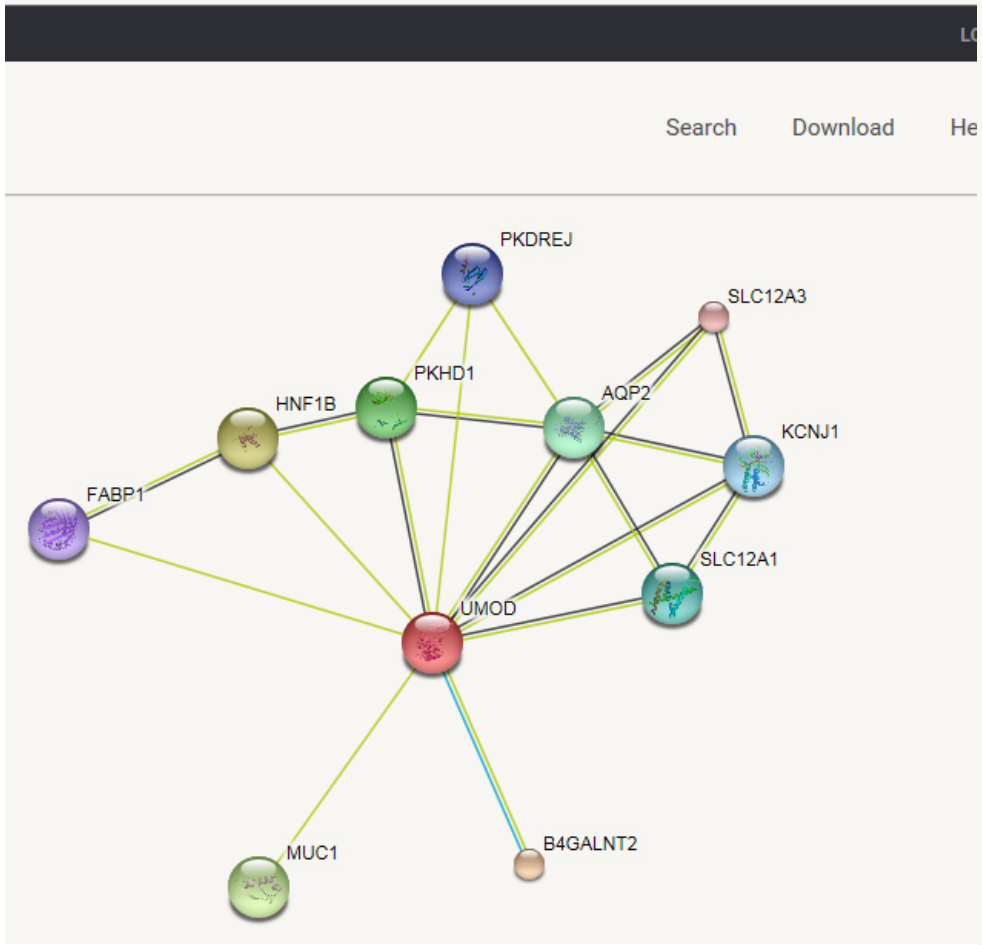
LTA | DAMA-25N12.13-004, LT, TNFB, TNFSF1

lymphotoxin alpha

1 [details]

Experimental Evidence Code	Role	Dataset	Throughput	Curated By	Notes
Reconstituted Complex ⊞	BAIT	Fukushima K (1993)	Low	BioGRID	-

STRING



Nodes:

Network nodes represent proteins

splice isoforms or post-translational modifications are collapsed, i.e. each node represents all the proteins produced by a single, protein-coding gene locus.

Node Size

small nodes: protein of unknown 3D structure

large nodes: some 3D structure is known or predicted

Node Color

colored nodes: query proteins and first shell of interactors

white nodes: second shell of interactors

Edges:

Edges represent protein-protein associations

associations are meant to be specific and meaningful, i.e. proteins jointly contribute to a shared function; this does not necessarily mean they are physically binding each other.

Known Interactions

from curated databases

experimentally determined

Predicted Interactions

gene neighborhood

gene fusions

gene co-occurrence

Others

textmining

co-expression

protein homology

Your Input:

UMOD	*Uromodulin; Uromodulin- Functions in biogenesis and organization of the apical membrane of epithelial cells of the thick ascending limb of Henle's loop (TALH), where it promotes formation of complex filamentous gel-like structure that may play a role in the water barrier permeability (Probable). May serve as a receptor for binding and endocytosis of cytokines (IL-1, IL-2) and TNF (PubMed-3498215). Facilitates neutrophil migration across renal epithelia (PubMed-20798515) (640 aa)*								

Predicted Functional Partners:

		Neighborhood	*Gene Fusion*	*Cooccurence*	*Coexpression*	*Experiments*	*Databases*	*Textmining*	*[Homology]*	**Score**
B4GALNT2	*beta-1,4-N-acetyl-galactosaminyl transferase 2; Involved in the synthesis of the Sd(a) antigen (Sia- alpha2,3-[GalNAc-beta1,...*						●	●		0.917
HNF1B	*HNF1 homeobox B; Transcription factor, probably binds to the inverted palindrome 5'-GTTAATNATTAAC-3' (557 aa)*						●			0.723
MUC1	*Mucin 1, cell surface associated; The alpha subunit has cell adhesive properties. Can act both as an adhesion and an anti-a...*						●			0.703
PKHD1	*Polycystic kidney and hepatic disease 1 (autosomal recessive); May be required for correct bipolar cell division through the...*				●		●			0.663
AQP2	*Aquaporin 2 (collecting duct); Forms a water-specific channel that provides the plasma membranes of renal collecting duct...*				●		●			0.620
SLC12A1	*Solute carrier family 12 (sodium/potassium/chloride transporters), member 1; Electrically silent transporter system. Mediat...*				●		●			0.551
KCNJ1	*Potassium inwardly-rectifying channel, subfamily J, member 1; In the kidney, probably plays a major role in potassium hom...*				●		●			0.495
PKDREJ	*Polycystic kidney disease (polycystin) and REJ homolog (sperm receptor for egg jelly homolog, sea urchin); May have a cen...*						●			0.491
FABP1	*Fatty acid binding protein 1, liver; Plays a role in lipoprotein-mediated cholesterol uptake in hepatocytes (PubMed-2573285...*						●			0.487
SLC12A3	*Solute carrier family 12 (sodium/chloride transporters), member 3; Key mediator of sodium and chloride reabsorption in thi...*				●		●			0.480

Your Current Organism:

Network Stats

number of nodes:	11	expected number of edges:	10
number of edges:	20	PPI enrichment p-value:	0.00428
average node degree:	3.64	*your network has significantly more interactions than expected (what does that mean?)*	
avg. local clustering coefficient:	0.811		

Functional enrichments in your network

Note: some enrichments may be expected here (why?)

Biological Process (GO)

pathway ID	*pathway description*	*count in gene set*	*false discovery rate*
GO:0007588	excretion	4	0.00011
GO:0001822	kidney development	5	0.000503
GO:0072001	renal system development	5	0.000503
GO:0001655	urogenital system development	5	0.00069

Molecular Function (GO)

pathway ID	*pathway description*	*count in gene set*	*false discovery rate*
GO:0015377	cation:chloride symporter activity	2	0.0101
GO:0022892	substrate-specific transporter activity	6	0.0101
GO:0022891	substrate-specific transmembrane transporter activity	5	0.0279

Cellular Component (GO)

pathway ID	*pathway description*	*count in gene set*	*false discovery rate*
GO:0045177	apical part of cell	7	1.33e-07
GO:0016324	apical plasma membrane	6	1.39e-06
GO:0044459	plasma membrane part	7	0.00989
GO:0070062	extracellular exosome	7	0.02
GO:0098805	whole membrane	6	0.02

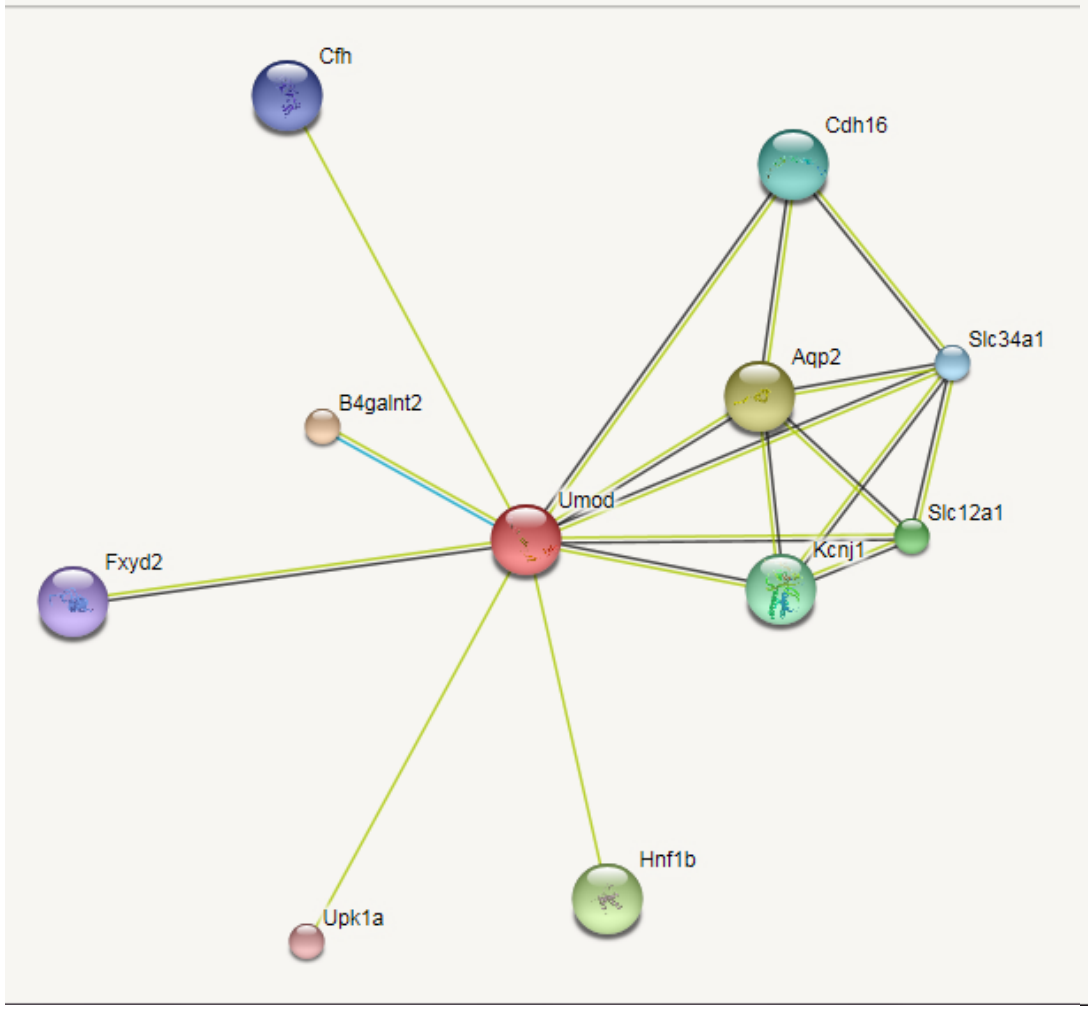
(more ...)

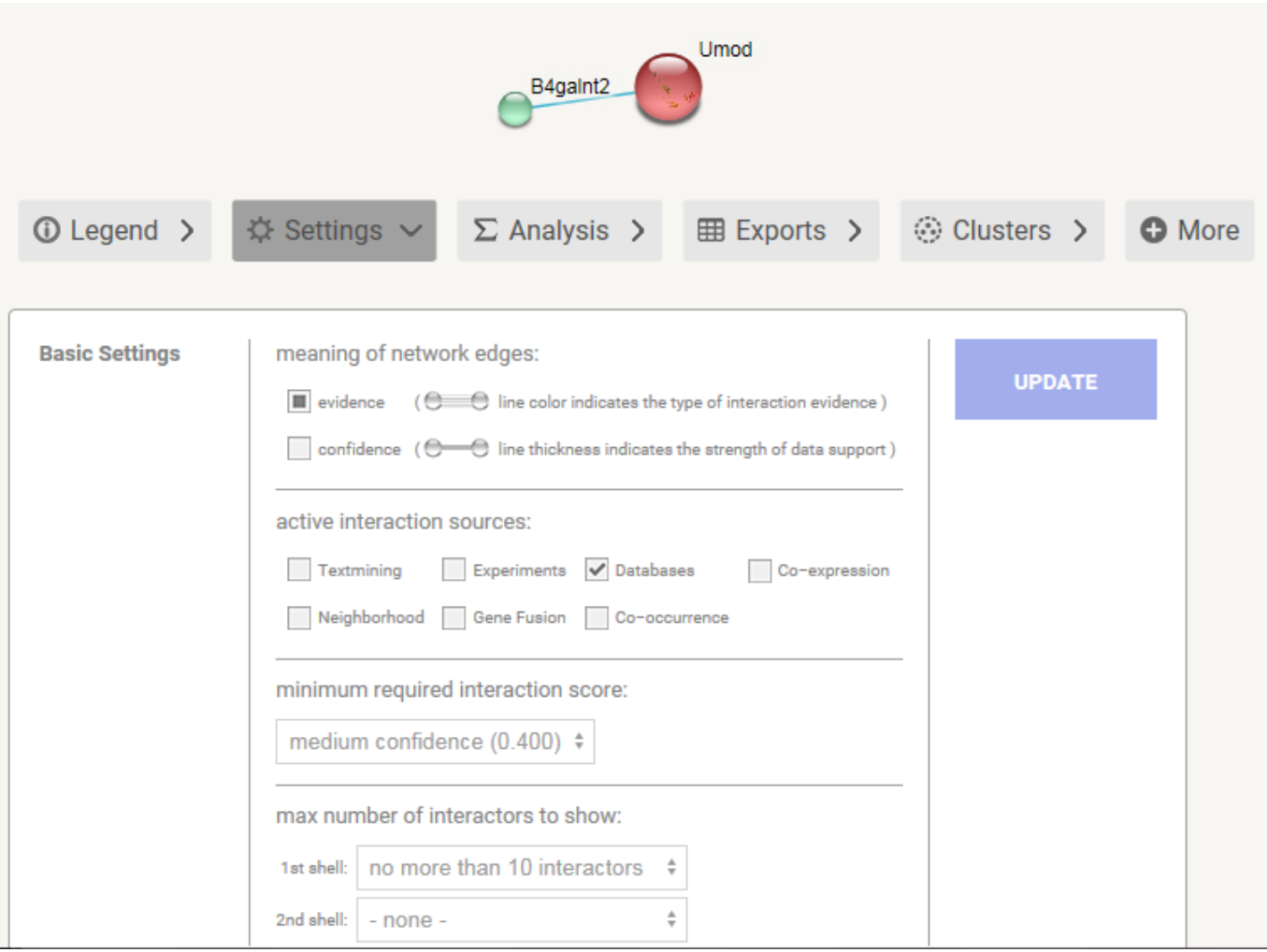
Statistical background

For the above enrichment analysis, the following statistical background is assumed: Whole Genome

UPDATE

STRING- Mouse UMOD





IMP

Gene View

In Homo sapiens, analyze the gene, UMOD × Go

UMOD

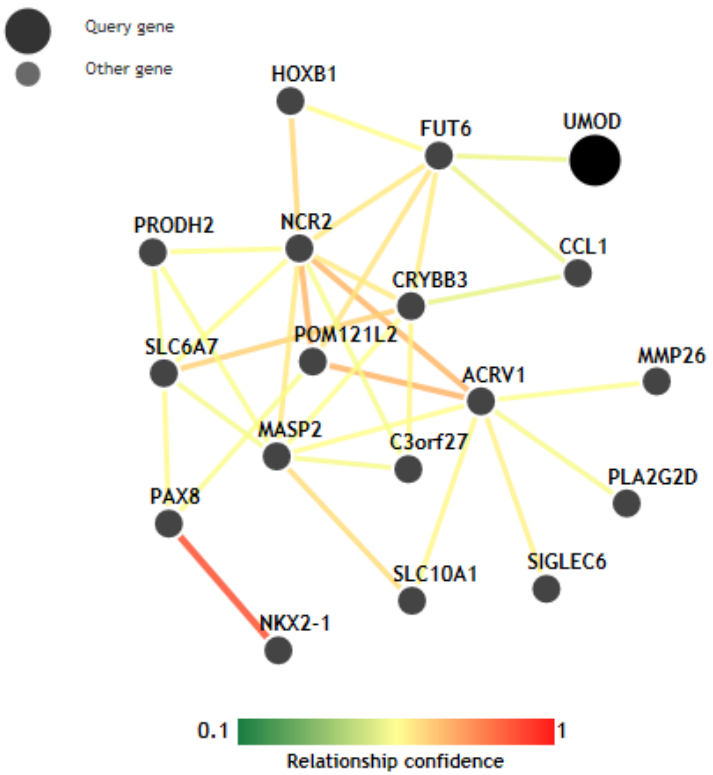
Homo sapiens

uromodulin

28 known processes

(Aliases: HNFJ,MCKD2,THGP,HNFJ1,FJHN,THP,ADMCKD2)

MIM: 191845 Entrez: 7369 HPRD: 11771 HGNC: 12559 Ensembl: ENSG00000169344 UniProtKB: P07911



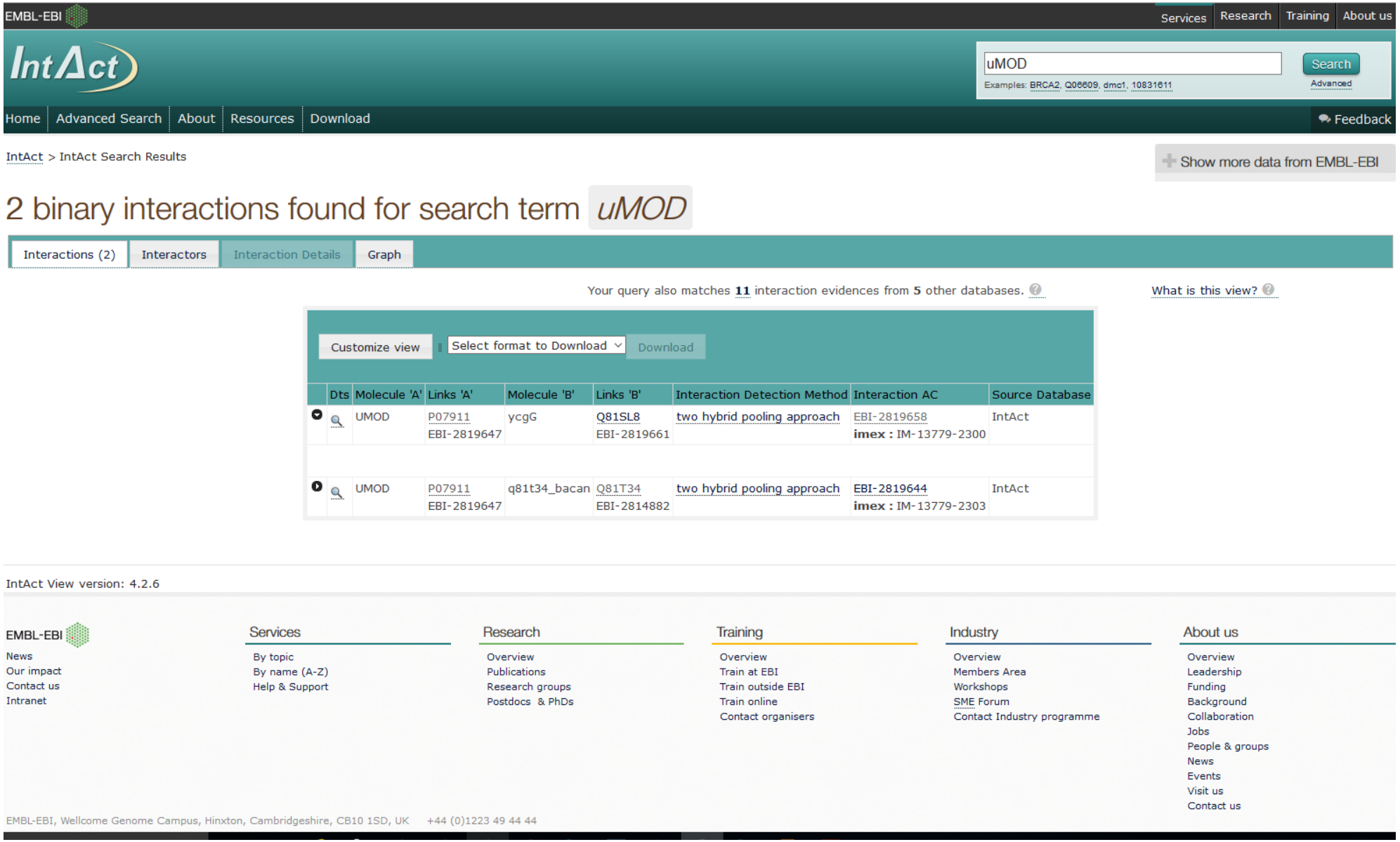
Process Predictions | Disease Predictions | FUT6/UMOD

Evidence for gene pair FUT6 and UMOD

Dataset	Title or Summary	Description	Weight
GSEA C2 CGP	Chemical and genetic perturbations		0.0945
Jaspar	Co-occurence of transcription factor binding sites		0.0052
GDS4085	Estrogen receptor-positive and -negative breast cancer tumors	Analysis of primary breast carcinoma tumors from estrogen receptor positive or negative (ER+/-) patients. ER+ tumors tend to metastasize to the bone while ER- tumors tend to induce visceral metastasis. Results provide insight into molecular basis of different metastatic phenotypes in breast	0.0045

Network Filters

Minimum relationship confidence: 0.51


EMBL-EBI
Services
Research
Training
About us
IntAct
uMOD
Search
Examples: BRCA2, Q06609, dmc1, 10831611
Advanced
Home
Advanced Search
About
Resources
Download
Feedback
IntAct > IntAct Search Results
Show more data from EMBL-EBI
2 binary interactions found for search term uMOD
Interactions (2)
Interactors
Interaction Details
Graph
Your query also matches 11 interaction evidences from 5 other databases.
What is this view?
Customize view
Select format to Download
Download
Dts
Molecule 'A'
Links 'A'
Molecule 'B'
Links 'B'
Interaction Detection Method
Interaction AC
Source Database
UMOD
P07911
EBI-2819647
ycgG
Q81SL8
EBI-2819661
two hybrid pooling approach
EBI-2819658
imex : IM-13779-2300
IntAct
UMOD
P07911
EBI-2819647
q81t34_bacan
Q81T34
EBI-2814882
two hybrid pooling approach
EBI-2819644
imex : IM-13779-2303
IntAct
IntAct View version: 4.2.6
EMBL-EBI
News
Our impact
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Intranet
Services
By topic
By name (A-Z)
Help & Support
Research
Overview
Publications
Research groups
Postdocs & PhDs
Training
Overview
Train at EBI
Train outside EBI
Train online
Contact organisers
Industry
Overview
Members Area
Workshops
SME Forum
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About us
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EMBL-EBI, Wellcome Genome Campus, Hinxton, Cambridgeshire, CB10 1SD, UK +44 (0)1223 49 44 44

Interaction

Accession: EBI-2819658

Description: -

Name: q81sl8-umod

Type: physical association

Links

Find similar interactions

Cross References:

Database	Identifier	Secondary identifier	Qualifier
psi-mi	MI:0469	-	imex source
imex	IM-13779-2300	-	imex-primary

Annotations:

Topic	Text
figure legend	Table S1

Interaction Confidences:

Type	Value
author score	1

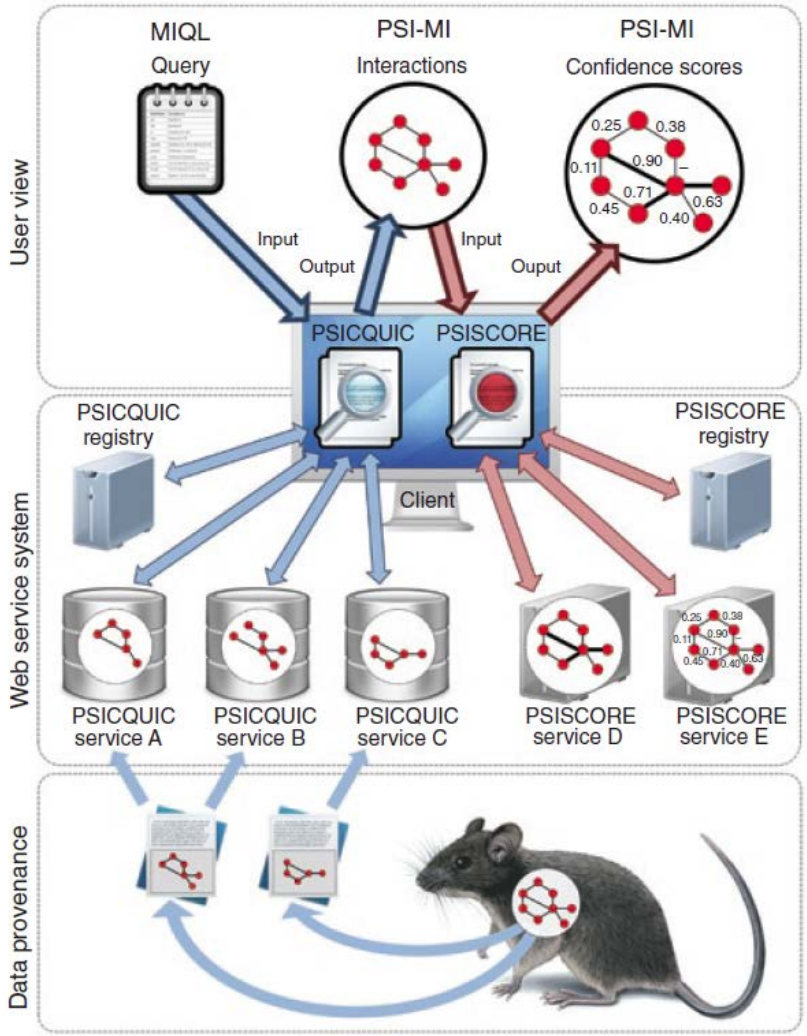
Participants (2)

Legend: A Annotation and Cross Reference | P Experimental Parameter | S Stoichiometry | F Experimental Feature | C Participant Confidence

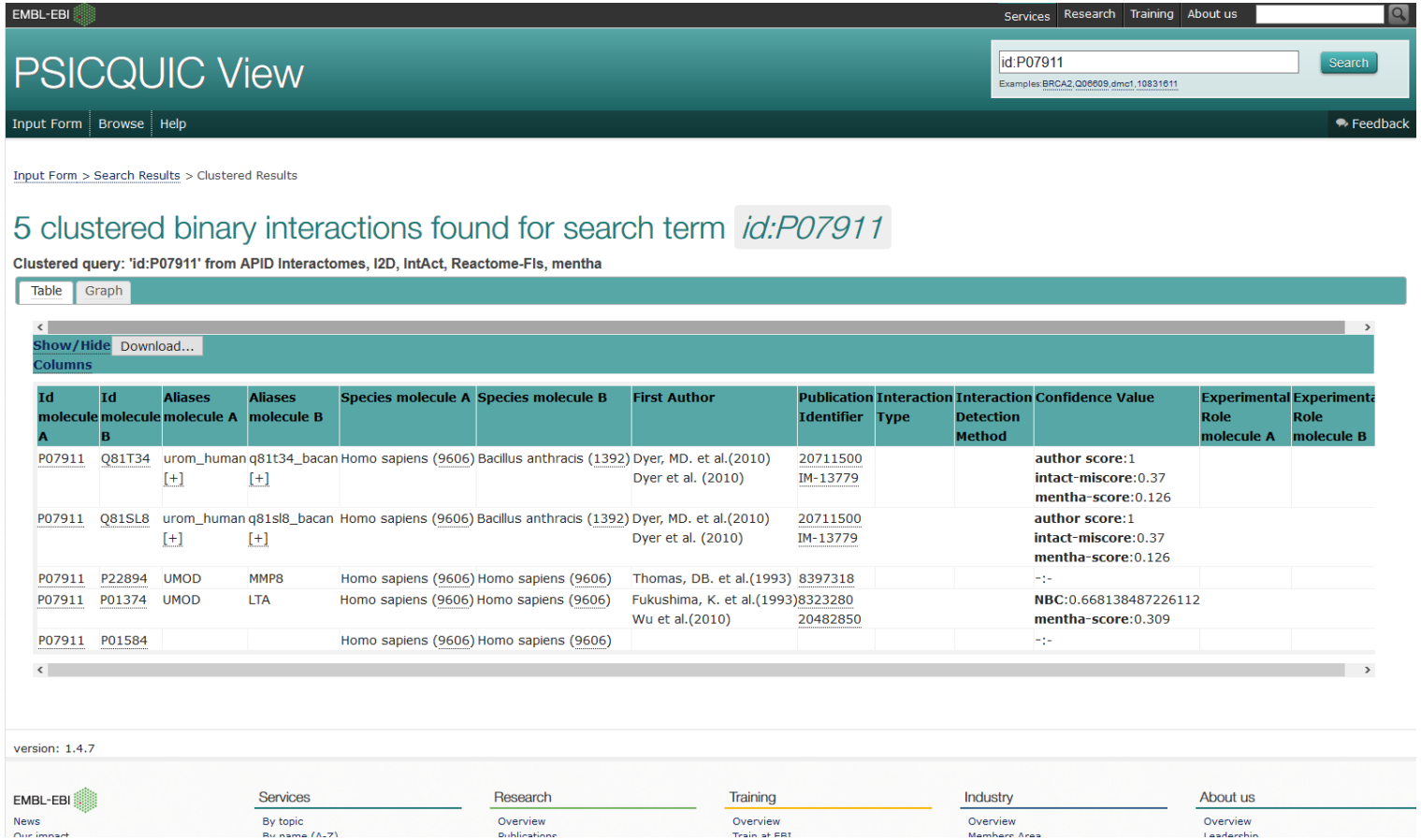
#	Name	Links	Primary Identifier	Aliases	Description	Species	Expression system	Experimental role	Biological role	Interactor type	More...
1	EBI-2819661	UniProt	Q81SL8	ycgG BASH2_04220 BVB96_08510 [+1]		Bacillus anthracis	-	bait	unspecified role	protein	A P S F C
2	EBI-2819647	UniProt	P07911	UMOD Tamm-Horsfall urinary glycoprotein	Uromodulin	Homo sapiens	-	prey	unspecified role	protein	A P S F C

IntAct View version: 4.2.6

Proteomics Standards Initiative Common Query Interface (PSICQUIC)



PSICQUIC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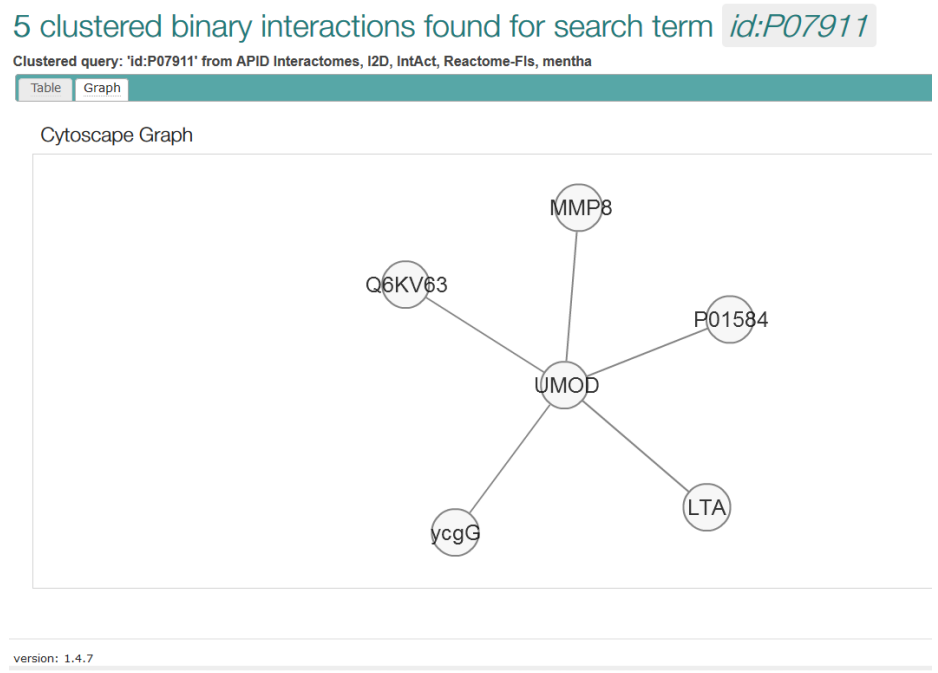
About us
PSICQUIC View
id:P07911
Search
Examples:BRCA2,Q06609,dmc1,10831611
Input Form
Browse
Help
Feedback
Input Form > Search Results > Clustered Results
5 clustered binary interactions found for search term id:P07911
Clustered query: 'id:P07911' from APID Interactomes, I2D, IntAct, Reactome-FIs, mentha
Table
Graph
Show/Hide
Download...
Columns
Id molecule A
Id molecule B
Aliases molecule A
Aliases molecule B
Species molecule A
Species molecule B
First Author
Publication Identifier
Interaction Type
Interaction Detection Method
Confidence Value
Experimental Role molecule A
Experimental Role molecule B
P07911 Q81T34 urom_human [+] q81t34_bacan [+] Homo sapiens (9606) Bacillus anthracis (1392) Dyer, MD. et al.(2010) Dyer et al. (2010) 20711500 IM-13779 author score:1 intact-miscore:0.37 mentha-score:0.126
P07911 Q81SL8 urom_human [+] q81sl8_bacan [+] Homo sapiens (9606) Bacillus anthracis (1392) Dyer, MD. et al.(2010) Dyer et al. (2010) 20711500 IM-13779 author score:1 intact-miscore:0.37 mentha-score:0.126
P07911 P22894 UMOD MMP8 Homo sapiens (9606) Homo sapiens (9606) Thomas, DB. et al.(1993) 8397318 -:-
P07911 P01374 UMOD LTA Homo sapiens (9606) Homo sapiens (9606) Fukushima, K. et al.(1993) 8323280 Wu et al.(2010) 20482850 NBC:0.668138487226112 mentha-score:0.309
P07911 P01584 Homo sapiens (9606) Homo sapiens (9606) -:-
version: 1.4.7
EMBL-EBI
Services
Research
Training
Industry
About us
News
By topic
Overview
Overview
Overview


5 clustered binary interactions found for search term id:P07911
Clustered query: 'id:P07911' from APID Interactomes, I2D, IntAct, Reactome-FIs, mentha
Table
Graph
Cytoscape Graph
MMP8
Q6KV63
P01584
UMOD
LTA
ycgG
version: 1.4.7