

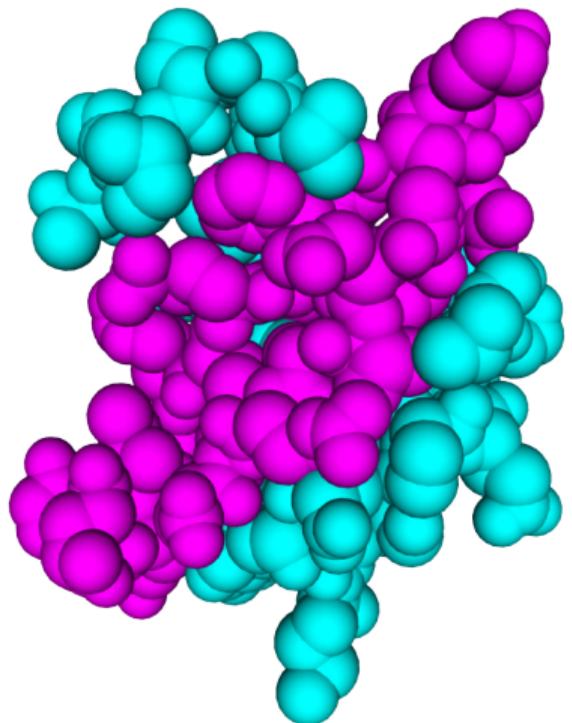
# Using and predicting structural heterogeneity of Voronoi tessellation-based contacts

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2025-07-15





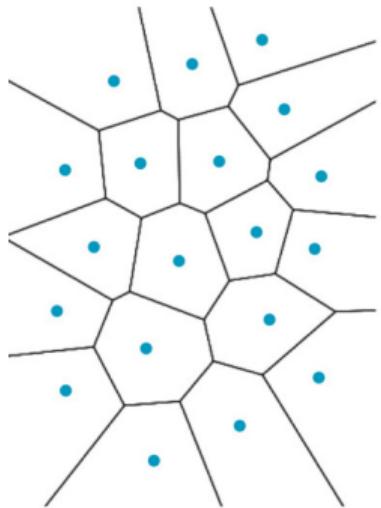
Common problems:

- ▶ analyzing how different parts in a molecule interact
- ▶ selecting the best model of a multimeric complex

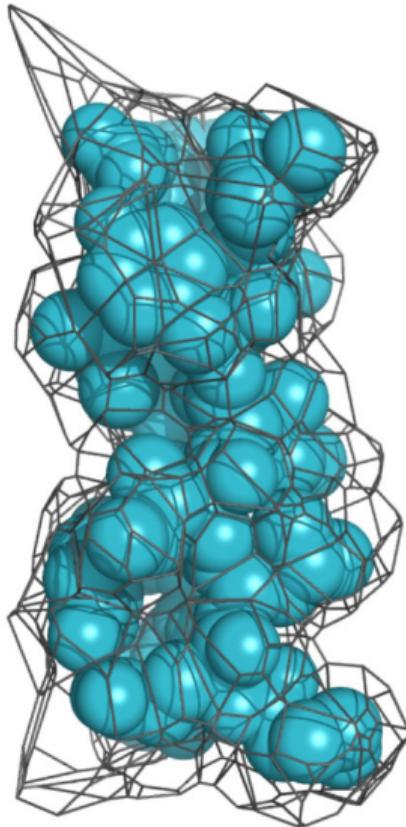
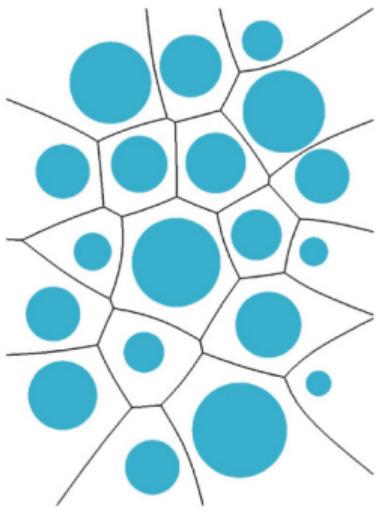
Describing interactions in molecular conformations using the  
Voronoi tessellation

# Voronoi diagram of points and balls

"Classic" Voronoi diagram  
of points

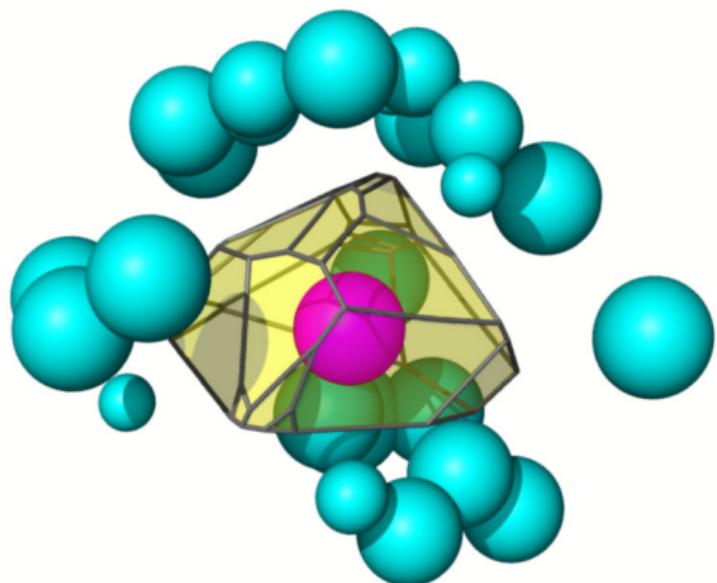


Voronoi diagram  
of balls

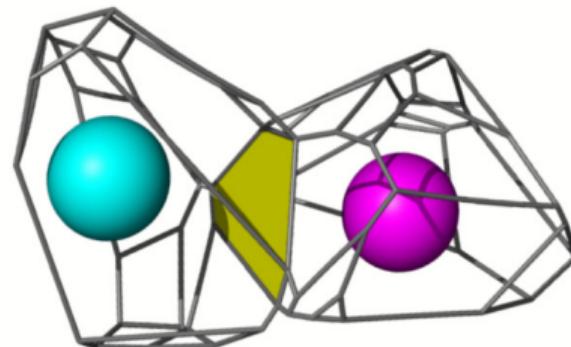


## Voronoi tessellation-based analysis of structures

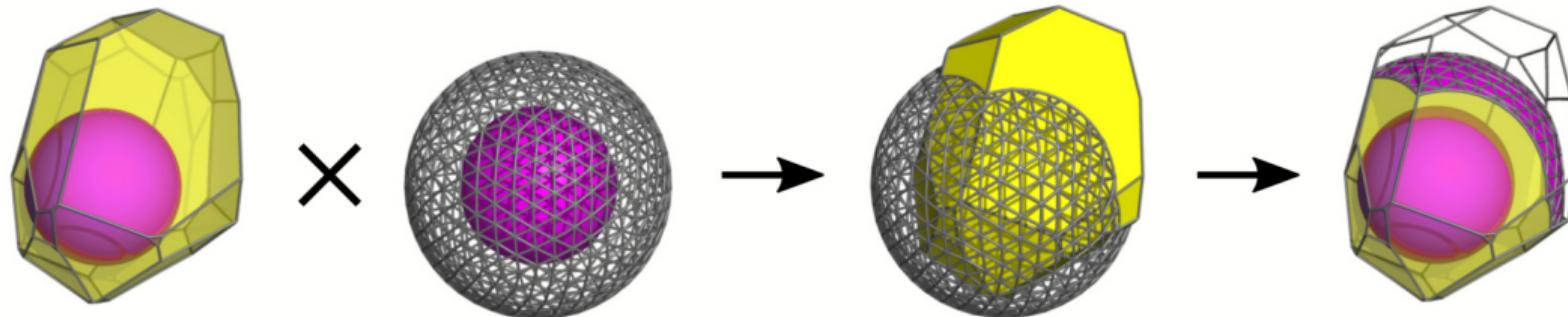
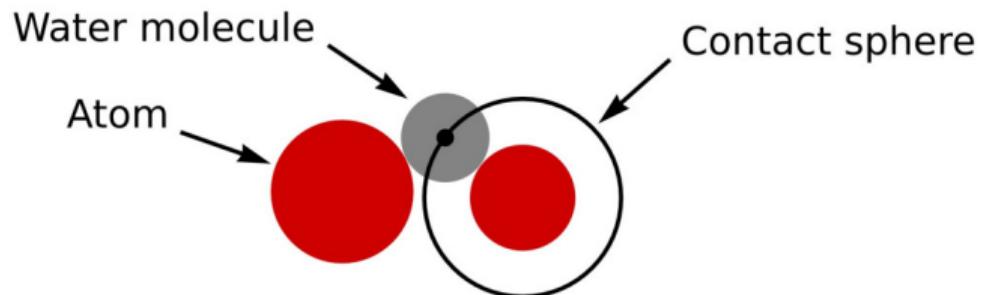
Voronoi cell of an atom surrounded by its neighbors



Atom-atom contact surface defined as the face shared by two adjacent Voronoi cells.

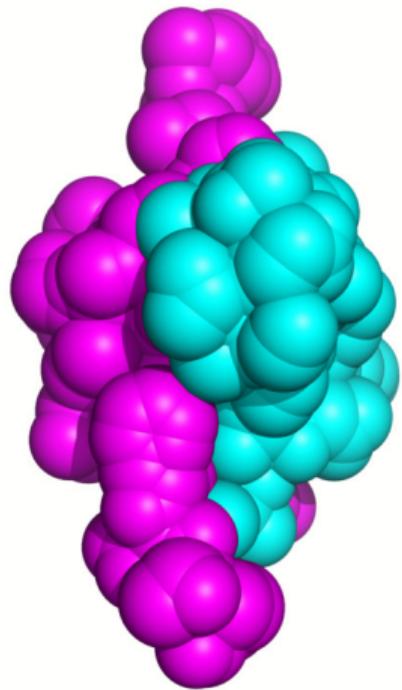


## Constrained contacts

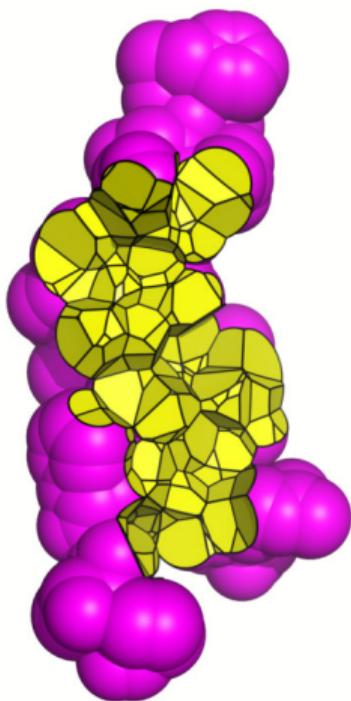


## Inter-chain contacts

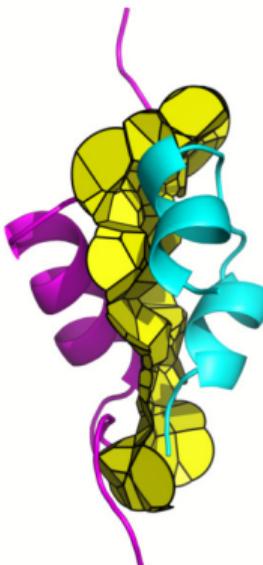
Solvent-accessible surface  
of an insulin heterodimer  
PDB:4UNG colored by subunit



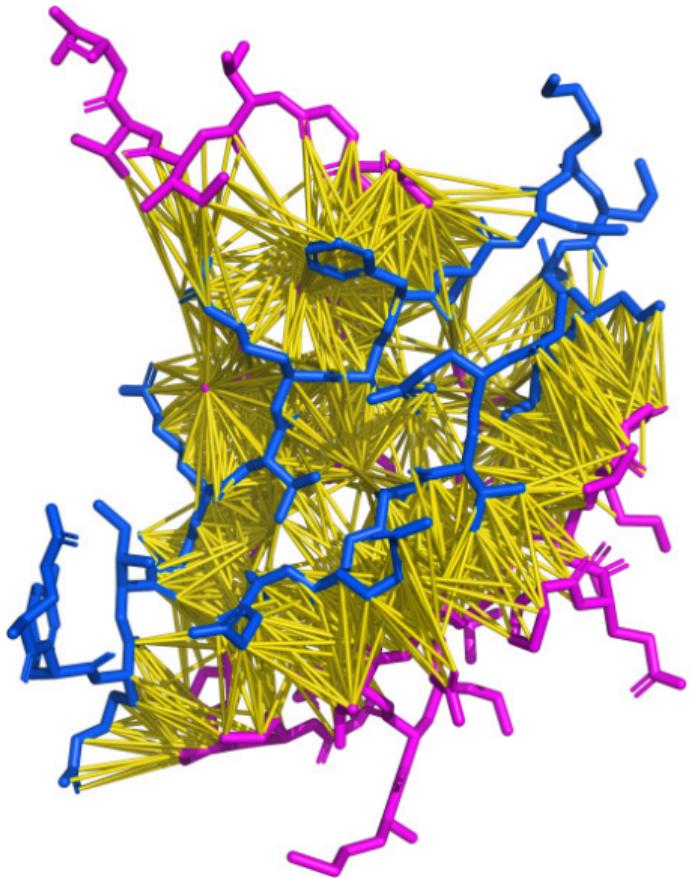
The intersubunit interface  
shown together with the  
SAS of one subunit



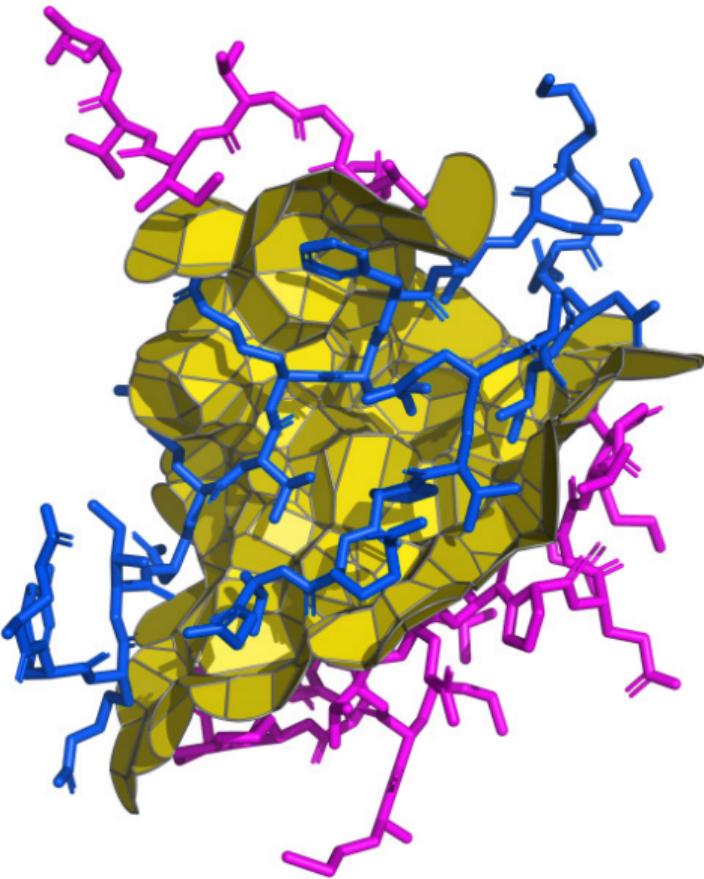
The intersubunit interface  
shown together with  
both subunits represented  
as cartoons



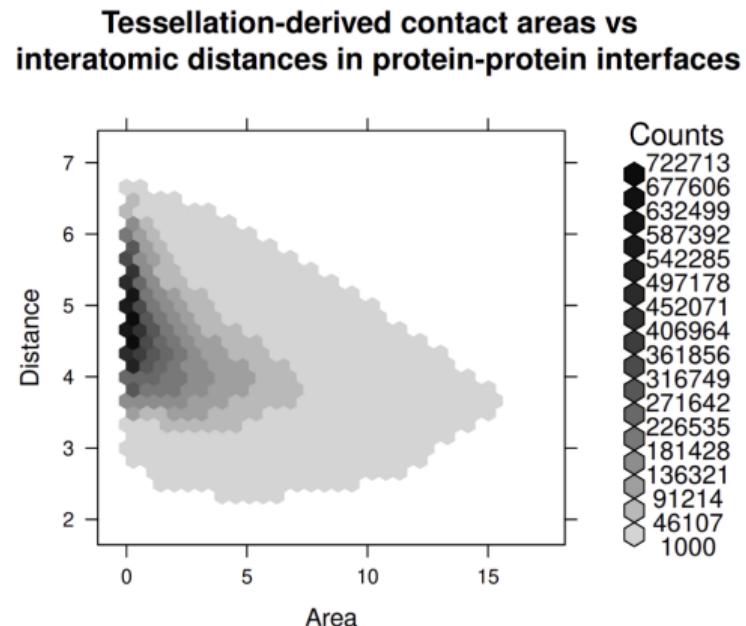
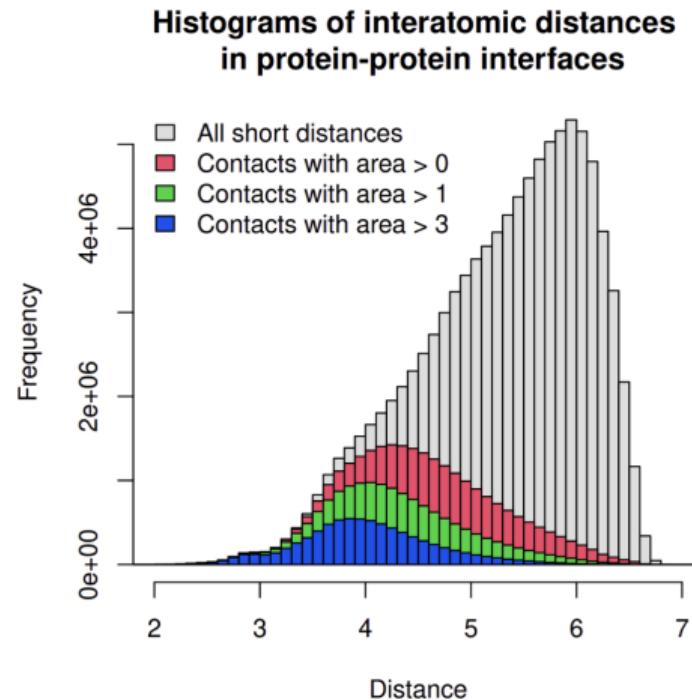
## Inter-chain contact areas vs distances



VS



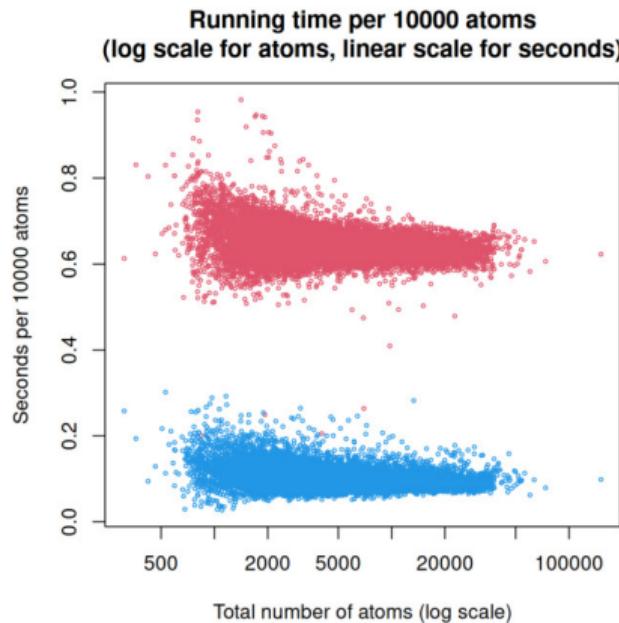
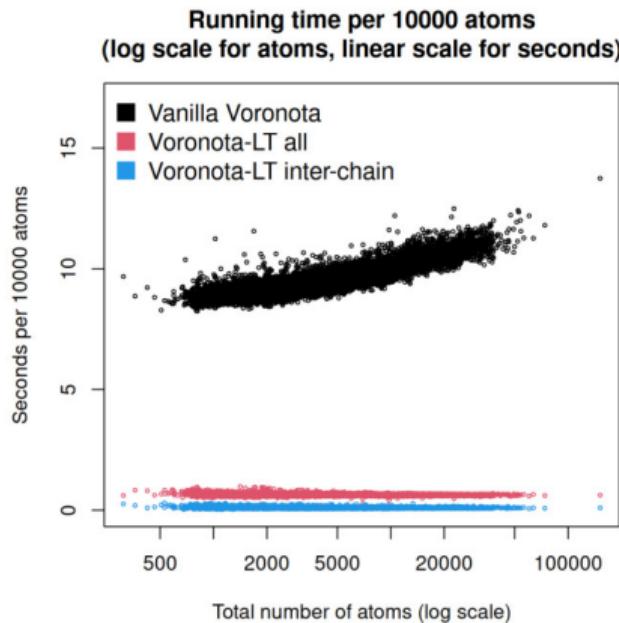
# Inter-chain contact areas vs distances, PDB-based statistics



$$\text{corr}(\text{area}, \text{distance}) \approx -0.43$$

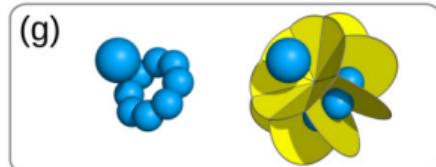
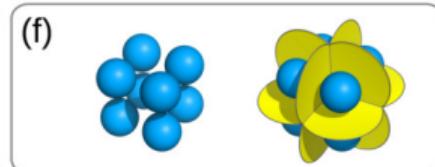
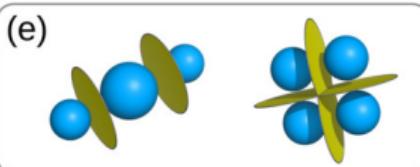
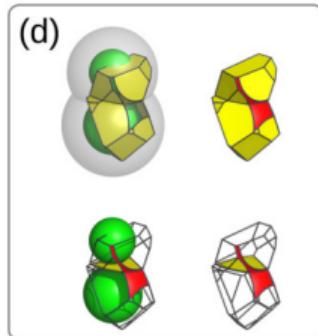
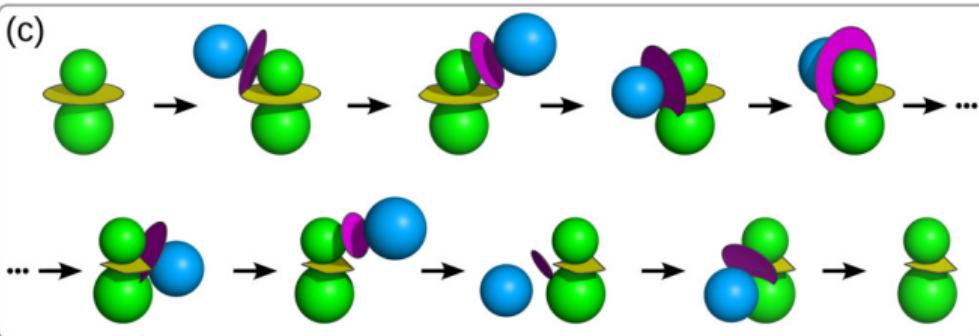
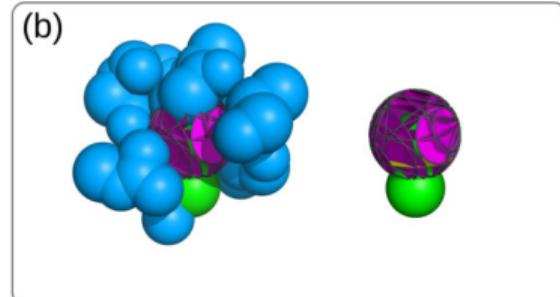
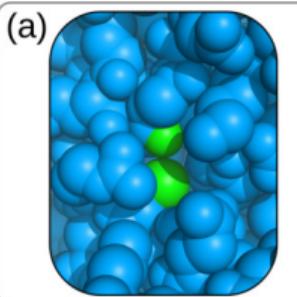
# Voronota-LT

Voronota-LT is a new fast software for constructing tessellation-derived atomic contact areas and volumes. It is significantly faster than its predecessor, Voronota:



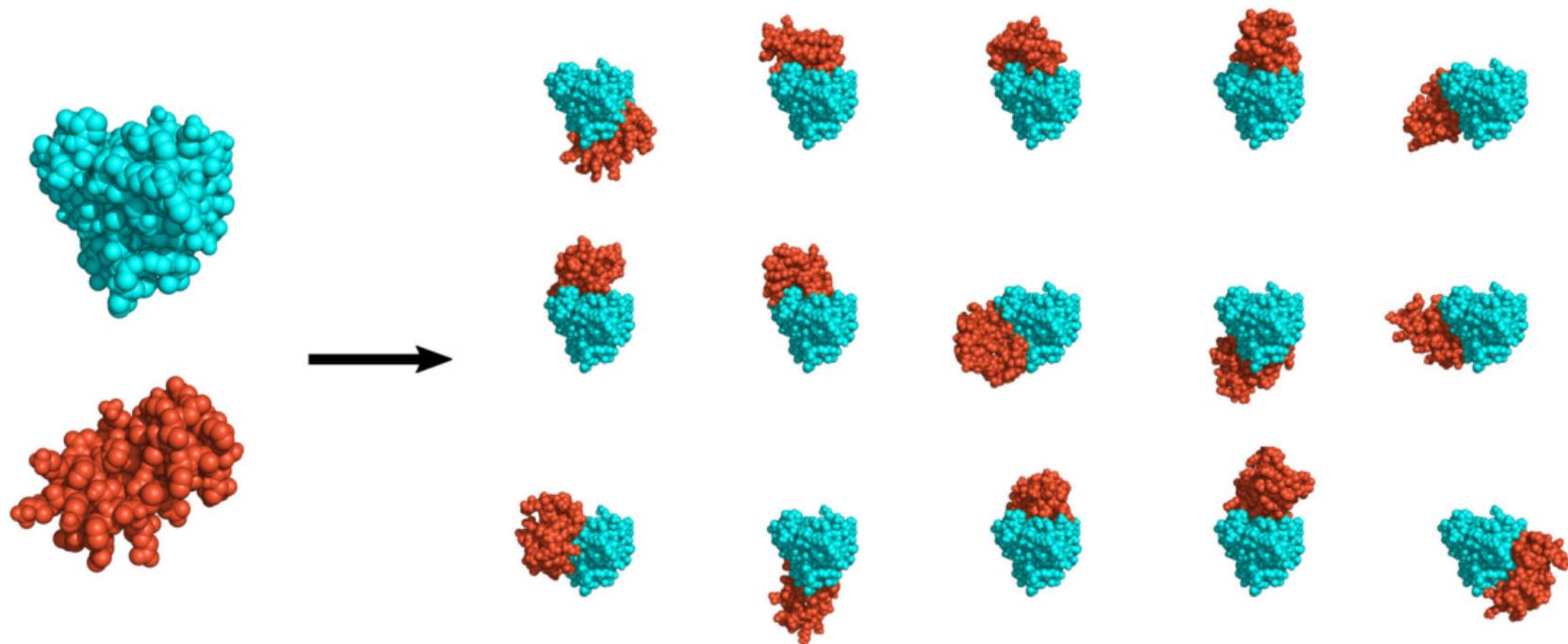
Olechnovic and Grudinin. *Voronota-LT: efficient, flexible and solvent-aware tessellation-based analysis of atomic interactions*. JCC (2025)

# Voronota-LT

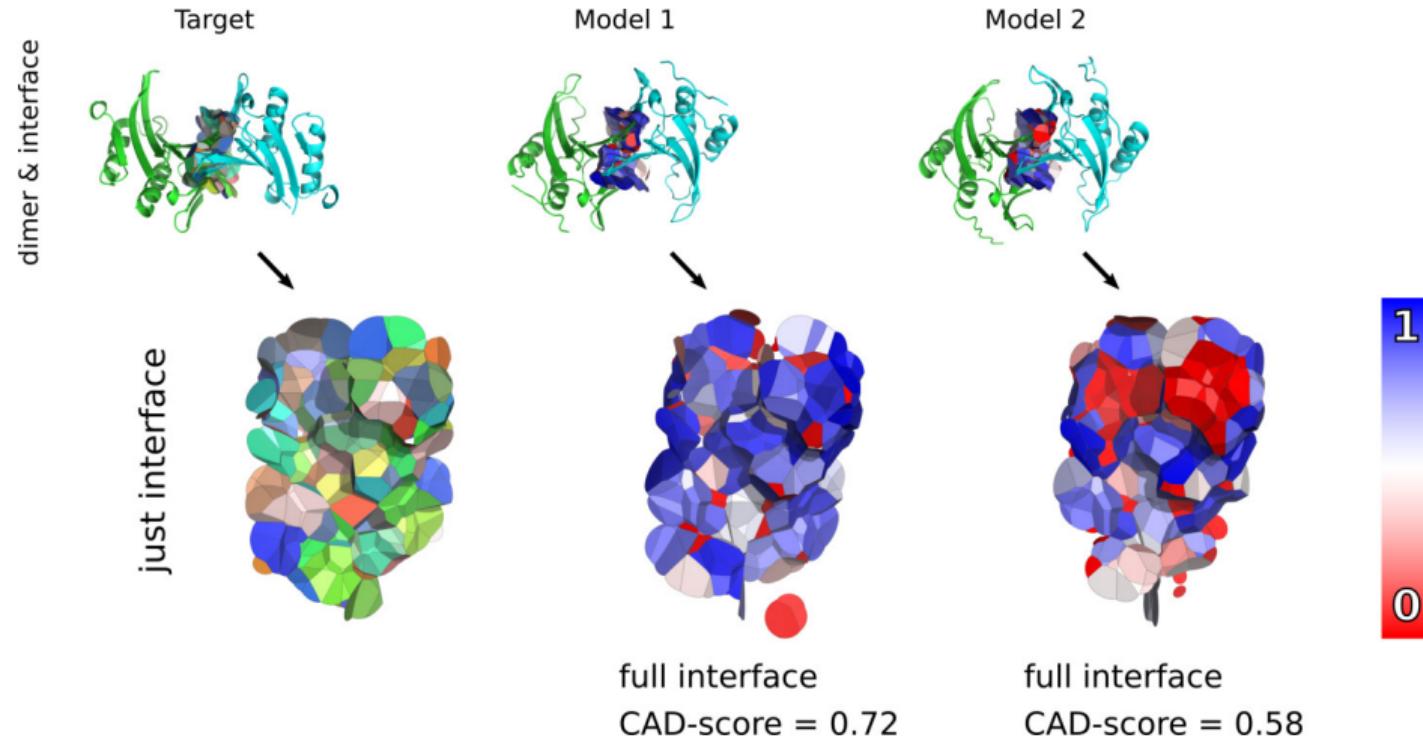


Some applications of tessellation-based description of interactions

Same chains can have differently modelled interfaces

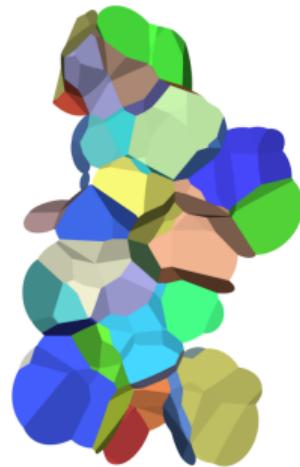


# Comparing interfaces using CAD-score (Contact Area Difference score)



Olechnovic and Venclovas. *Contact Area-Based Structural Analysis of Proteins and Their Complexes Using CAD-Score*. Methods in Molecular Biology (2020)

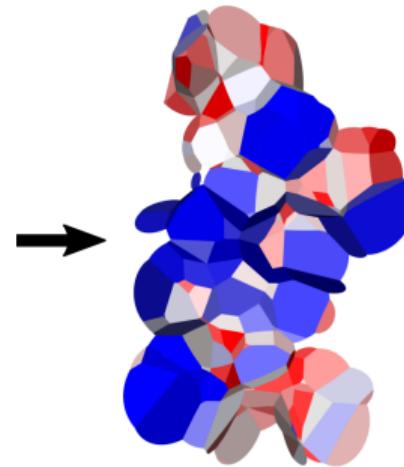
# Evaluating interfaces with an area-based potential (e.g. VoroMQA)



Interface  
contact areas

$$\begin{aligned} E(a_i, a_j, c_k) &= \log \frac{P_{\text{exp}}(a_i, a_j, c_k)}{P_{\text{obs}}(a_i, a_j, c_k)} = \\ &= \log \frac{F_{\text{exp}}(\text{area}(a_i), \text{area}(a_j), \text{area}(c_k))}{F_{\text{obs}}(\text{area}(a_i, a_j, c_k))} \\ E_n(\Omega_\phi) &= \frac{\sum_{\omega \in \Omega_\phi} E(\text{type}_\omega) \cdot \text{area}_\omega}{\sum_{\omega \in \Omega_\phi} \text{area}_\omega} \end{aligned}$$

Statistical potential  
for contact areas



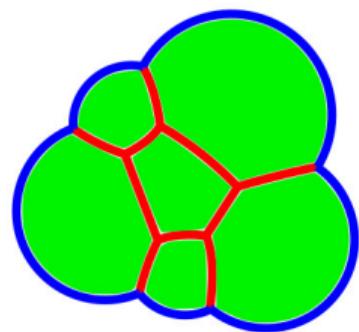
Interface  
pseudo-energy



Olechnovic and Venclovas. *VoroMQA: Assessment of protein structure quality using interatomic contact areas*. Proteins (2017)

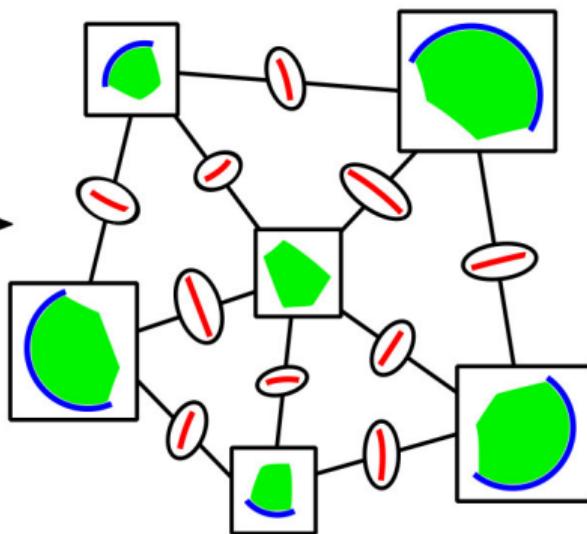
# Input interface graph for a graph neural network (e.g. VorolF-GNN)

## Tessellation-derived interface contacts



Contact surface  
Contact-solvent border  
Inter-contact border

## Interface graph



Graph **node** attributes  
(15 values)

Contact surface area

Contact-solvent  
border length

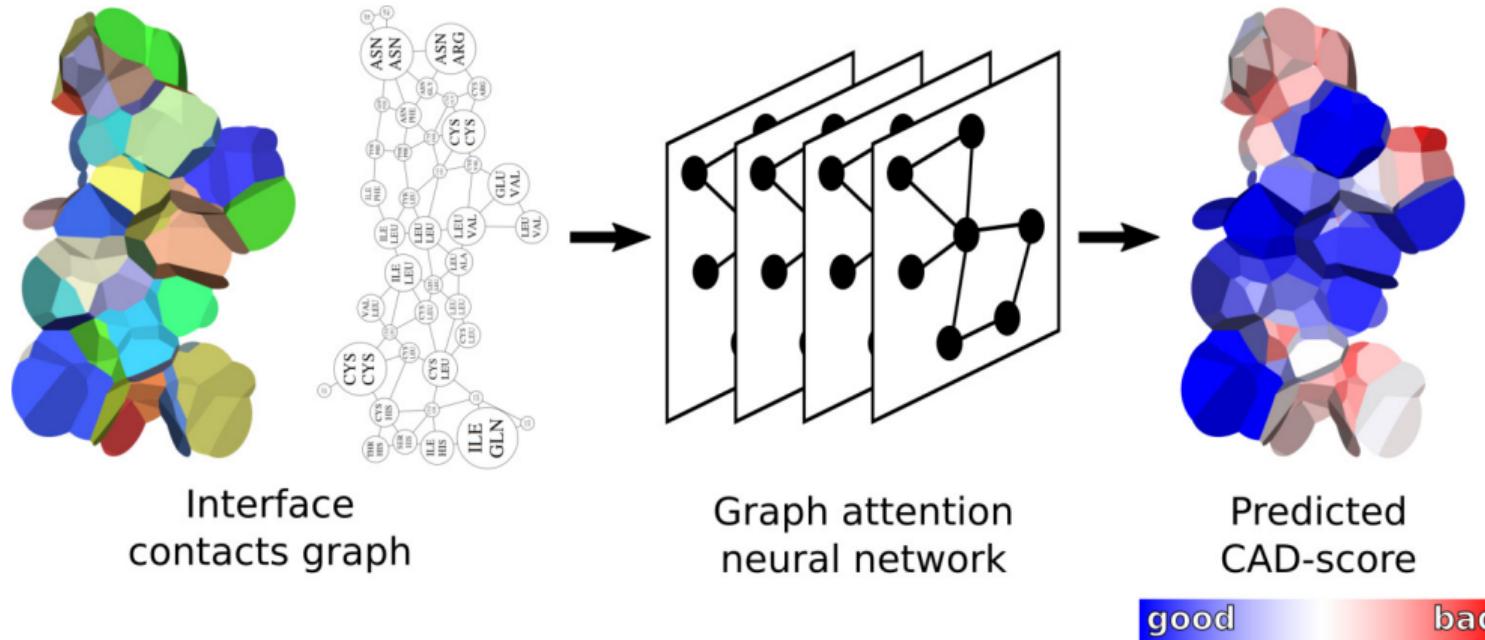
Sum of inter-contact  
border lengths

Contact type-dependent  
descriptors (12 values)

Graph **edge** attribute  
(1 value)

Inter-contact  
border length

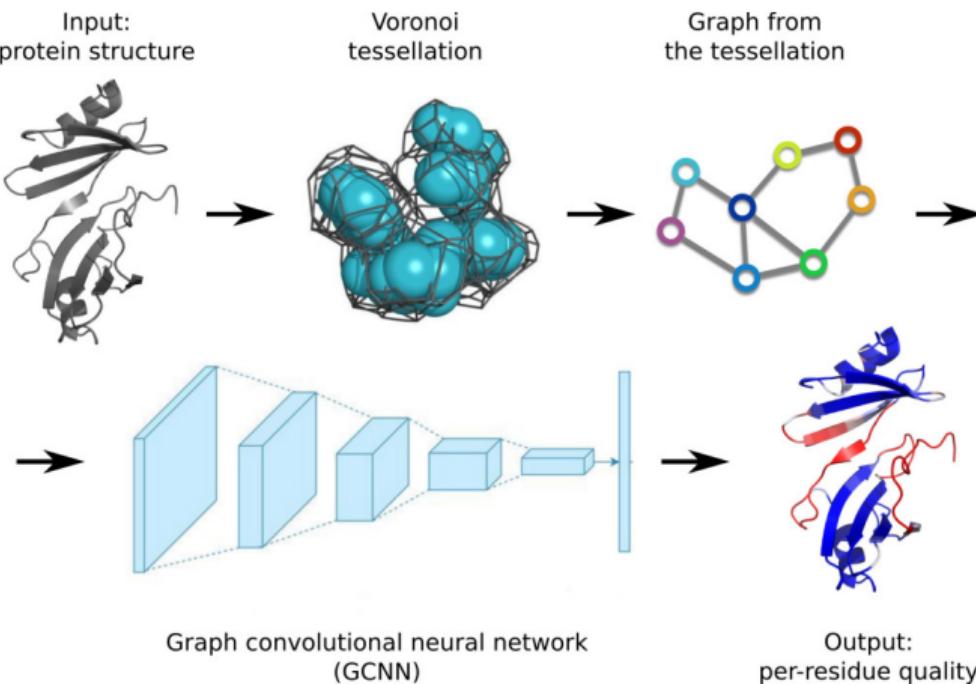
# Evaluating interfaces with a graph neural network (e.g. VoroIF-GNN)



Olechnovic and Venclovas. *VoroIF-GNN: Voronoi tessellation-derived protein-protein interface assessment using a graph neural network*. Proteins (2023)

# Remembering VoroCNN

Igashov I, Olechnovič K, Kadukova M, Venclavas Č, Grudinin S. *VoroCNN: Deep convolutional neural network built on 3D Voronoi tessellation of protein structures*. Bioinformatics (2021)



# Selecting complex models using VorolF-jury (a.k.a. FTDMP)

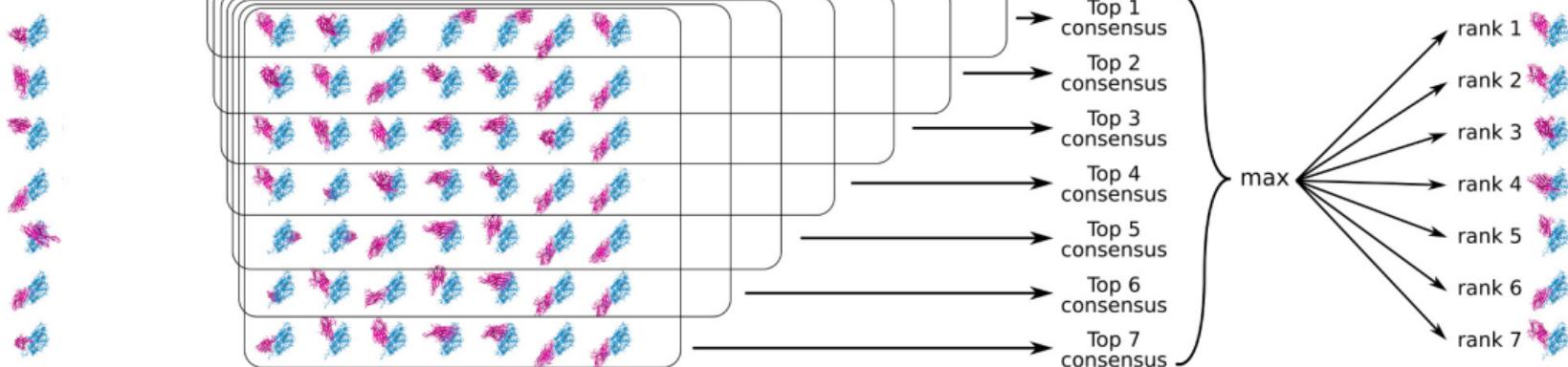
Collect all  
models from  
all sources  
(AlphaFold2,  
docking, TBM)

Score and rank using different methods

VorolF-GNN  
res. VorolF-GNN  
VorOMQA-energy  
V-select 2018  
V-select 2020  
VorOMQA-dark  
VorOMQA-light

Compute interface  
CAD-score consensus  
scores for supersets  
of top models

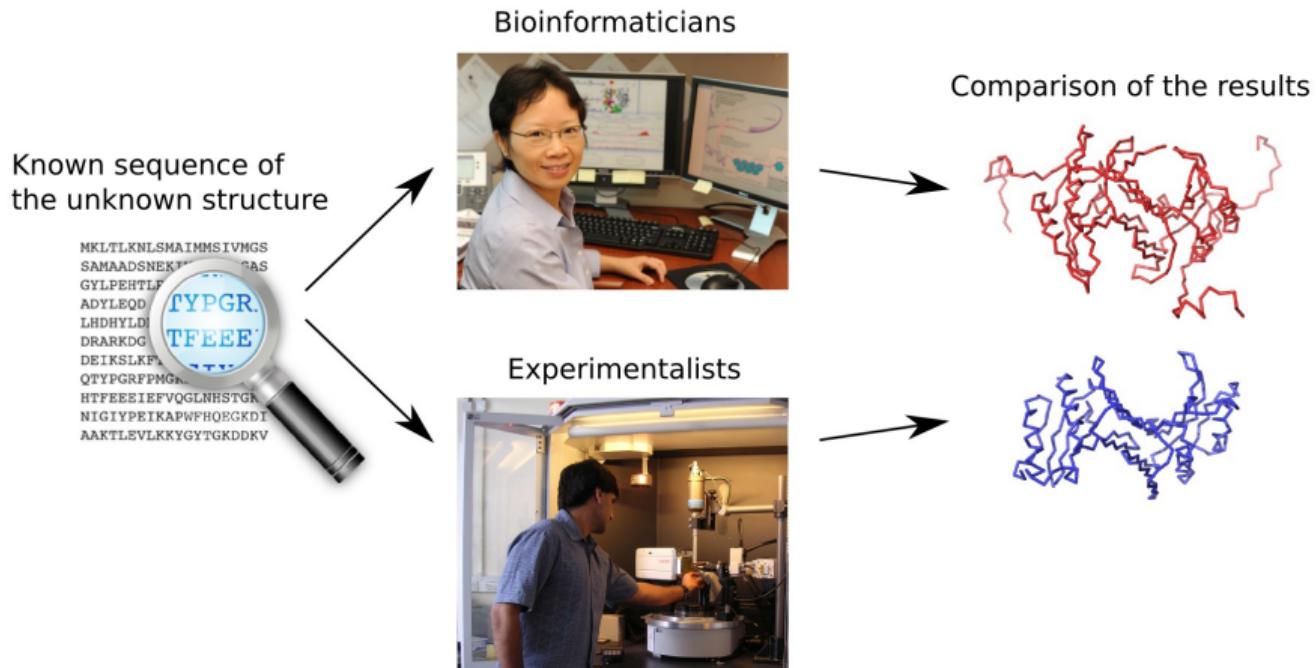
Calculate max achieved  
"Top X" consensus for  
every model and use it  
for the final ranking



VorolF-jury was the best-performing multimeric model selector in 2022 CASP and CAPRI double-blind challenges.

# CASP and CAPRI double-blind challenges

The main way to test new methods in structural bioinformatics are the community-wide double-blind testing experiments — CASP and CAPRI.



# Our results in CASP and CAPRI challenges over the years

CASP (Critical Assessment of Techniques for Protein Structure Prediction) and CAPRI (Critical Assessment of Predicted Interactions) are worldwide experiments focused on the blind testing of methods for protein structural bioinformatics.

After  
AF2

- 2024** Top performance (ranked 1st in the CAPRI assessment of scoring groups) in the CASP16-CAPRI scoring experiment. Group “Olechnovic”.
- 2024** Contributed to the top performance (ranked 1st) in modeling structures of protein complexes in the CAPRI experiment rounds 47–55. Group “Venclovas”, members: Dapkūnas J, Olechnovič K, Venclovas Č.
- 2022** Contributed to one of the top performances in modeling structures of protein complexes in CASP15 and CASP15-CAPRI experiments (ranked 2nd in CASP, ranked 1st in CAPRI). Group “Venclovas”, members: Olechnovič K, Valančauskas L, Dapkūnas J, Venclovas Č.
- 2022** One of the top performances in EMA (estimation of model accuracy) in CASP15 experiment (and ranked 1st in CASP15-CAPRI scoring experiment). Groups “Venclovas” and “VoroIF”.
- 2020** Contributed to one of the top performances in modeling structures of protein complexes in CASP14 and CASP14-CAPRI experiments (ranked 2nd in CASP, ranked 1st in CAPRI jointly with two other groups). Group “Venclovas”, members: Olechnovič K, Dapkūnas J, Venclovas Č.
- 2019** Contributed to one of the top performances (ranked 3rd) in modeling structures of protein complexes in the CAPRI experiment rounds 38–45. Group “Venclovas”, members: Dapkūnas J, Kairys V, Olechnovič K, Venclovas Č.
- 2018** Contributed to the best results (ranked 1st) in modeling structures of protein complexes in CASP13 and CASP13-CAPRI experiments. Group “Venclovas”, members: Dapkūnas J, Olechnovič K, Venclovas Č.
- 2018** One of the top performances in EMA (estimation of model accuracy) in CASP13 experiment (ranked 1st in prediction of unreliable regions). Groups “VoroMQA-A” and “VoroMQA-B”.
- 2016** Contributed to the best results (ranked 1st) in modeling structures of protein complexes in CASP12-CAPRI experiment. Group “Venclovas”, members: Dapkūnas J, Olechnovič K, Venclovas Č.
- 2016** One of the top performances in protein structure prediction in CASP12 experiment. Group “VoroMQA-select”.

Before  
AF2

# CASP and CAPRI team



CASP15 Team

**Justas Dapkūnas  
Lukas Valančauskas  
Česlovas Venclovas**

[bioinformatics.lt](http://bioinformatics.lt)

Rytis Dičiūnas  
Kęstutis Timinskas  
Albertas Timinskas  
Darius Kazlauskas  
Mindaugas Margelevičius  
Visvaldas Kairys



Life Sciences  
Center



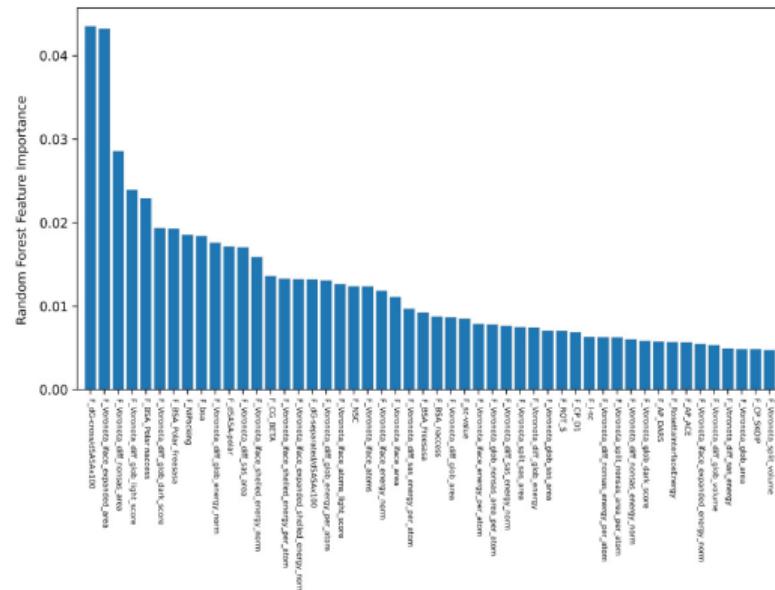
Institute of  
Biotechnology

Funding: Research Council of Lithuania

# Discriminating Physiological from Non-Physiological Interfaces

- ▶ Discriminating physiological from non-physiological interfaces in structures of protein complexes: A community-wide study. Schweke H et al. *Proteomics*. 2023 Jun 27.

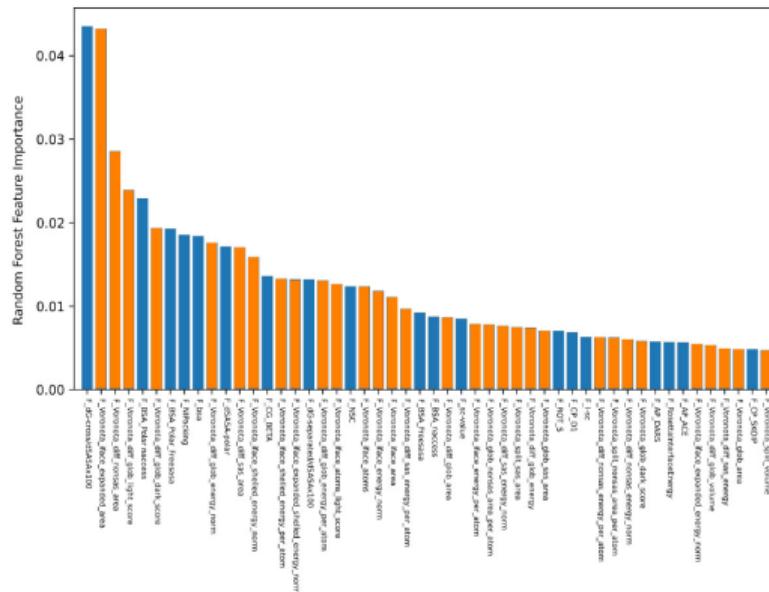
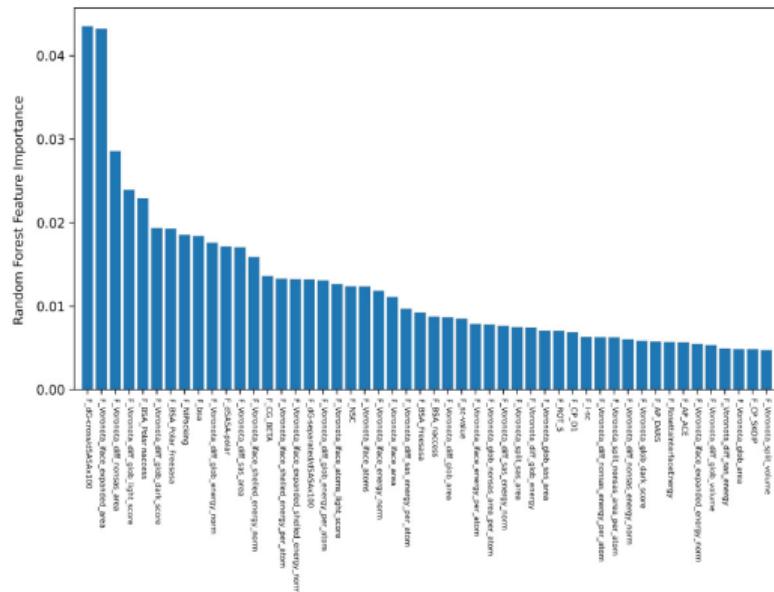
## Top 50 useful features:



## Discriminating Physiological from Non-Physiological Interfaces

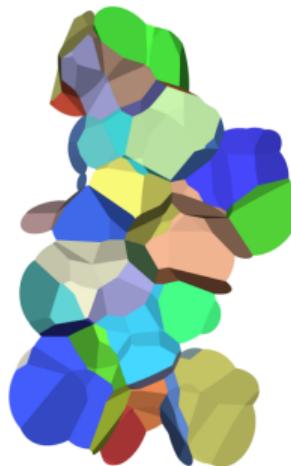
- ▶ Discriminating physiological from non-physiological interfaces in structures of protein complexes: A community-wide study. Schweke H et al. *Proteomics*. 2023 Jun 27.

## Top 50 useful features:



## Area-based potential may still be used for testing new ideas

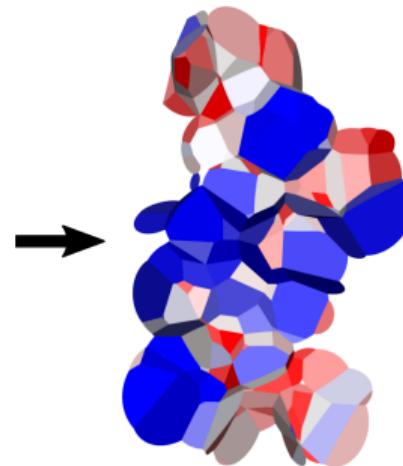
Area-based pairwise interaction potential alone is not the best scoring method, but it may still serve as simple a tool to explore benefits of newer data and descriptors.



Interface  
contact areas

$$\begin{aligned} E(a_i, a_j, c_k) &= \log \frac{P_{\text{exp}}(a_i, a_j, c_k)}{P_{\text{obs}}(a_i, a_j, c_k)} = \\ &= \log \frac{F_{\text{exp}}(\text{area}(a_i), \text{area}(a_j), \text{area}(c_k))}{F_{\text{obs}}(\text{area}(a_i, a_j, c_k))} \\ E_n(\Omega_\phi) &= \frac{\sum_{\omega \in \Omega_\phi} E(\text{type}_\omega) \cdot \text{area}_\omega}{\sum_{\omega \in \Omega_\phi} \text{area}_\omega} \end{aligned}$$

Statistical potential  
for contact areas

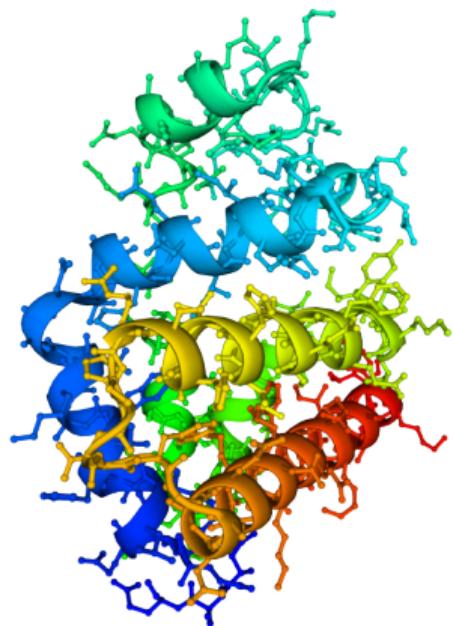


Interface  
pseudo-energy

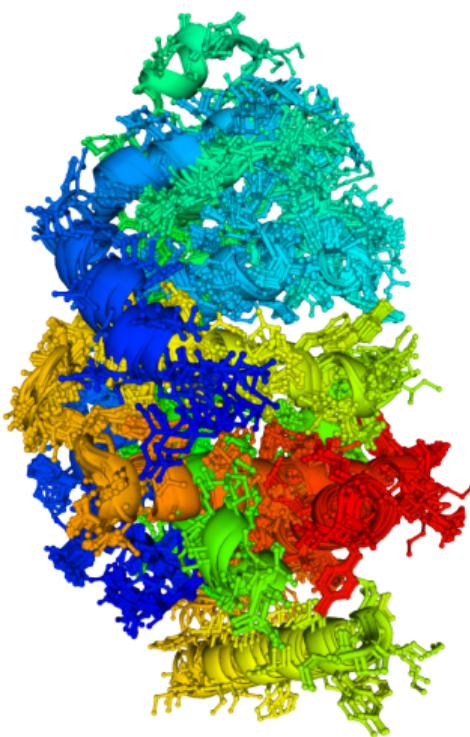


Deriving and using statistics of contact areas from ensembles  
of conformations

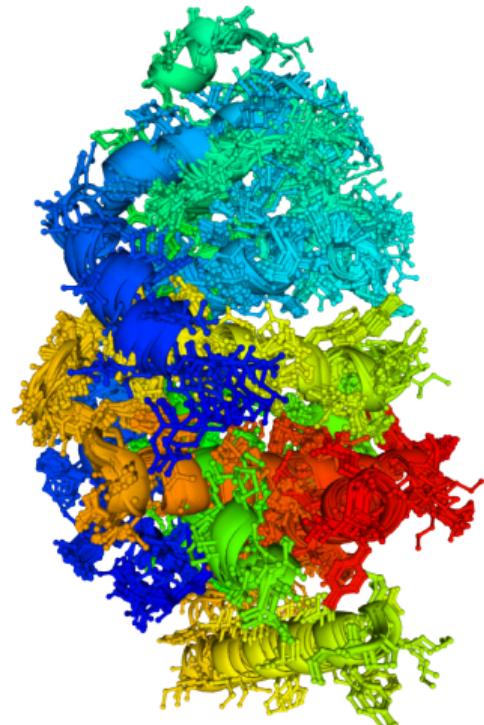
a single conformation



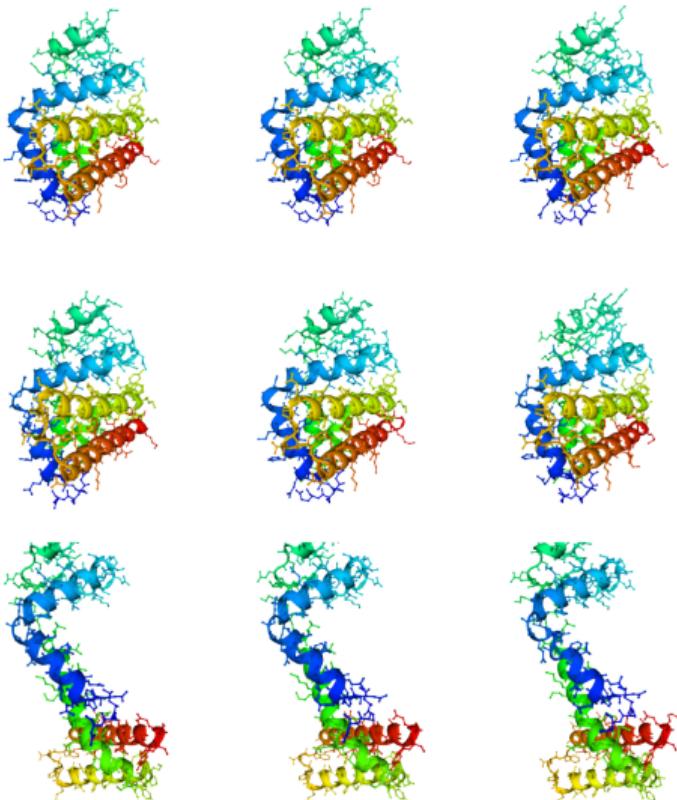
an ensemble of conformations



an ensemble of conformations



the same ensemble of conformations



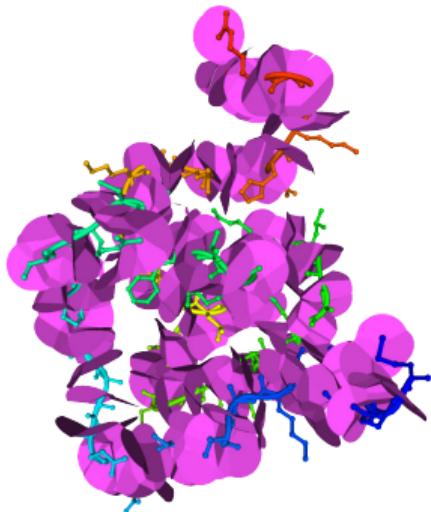
## A dataset of ensembles of conformations from PDB

- ▶ Collected from the **Protein Data Bank** (PDB), <https://www.wwpdb.org/>.
- ▶ Ensembles formed by clustering chain sequences using **90%** identity.
- ▶ We used all **38'807** ensembles that were available.
- ▶ Ensembles have very different numbers of chains:
  - ▶ the largest ensemble contains **1413** chains
  - ▶ **9989** ensembles contain **only two** chains.

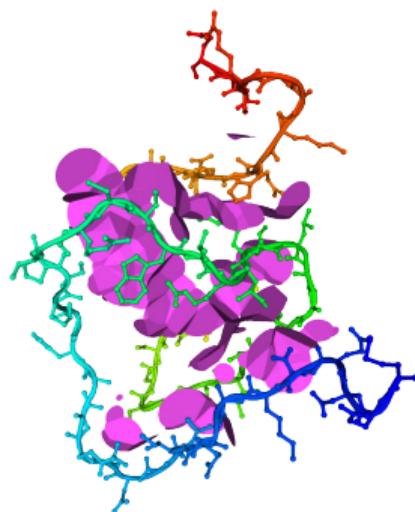
## Contacts from a single conformation

A contact type is a tuple (*first atom type, second atom type, contact category*) =  $(a_1, a_2, c)$ .

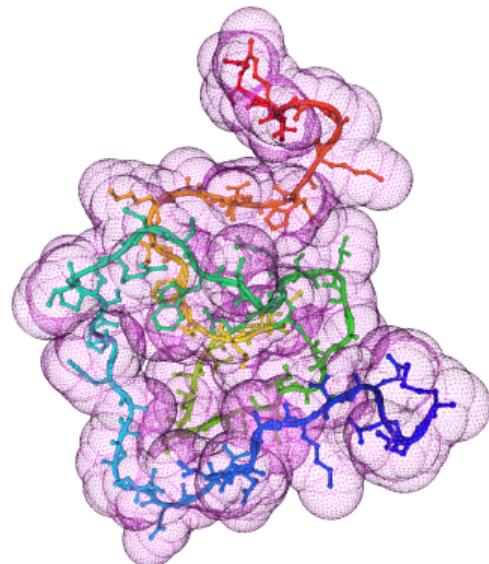
sequence separation  $\leq 5$



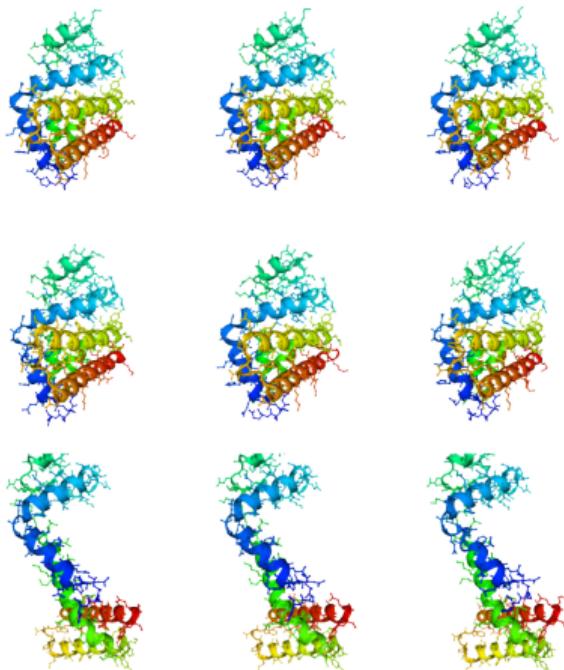
sequence separation  $> 5$



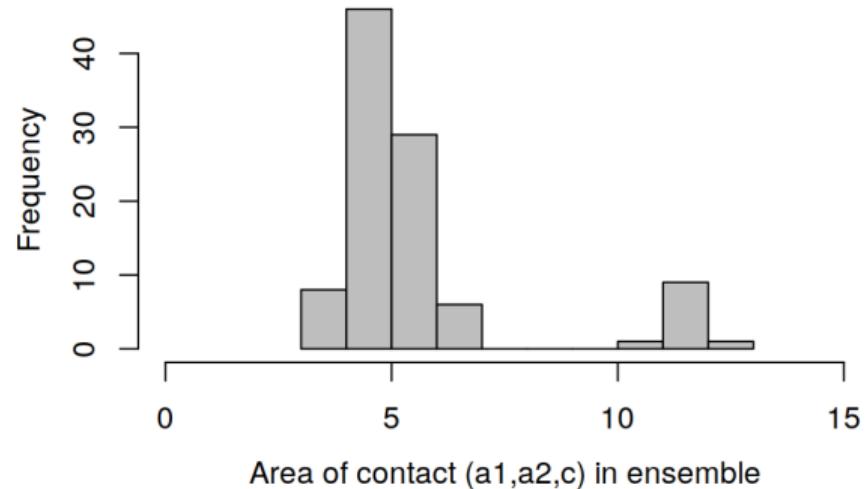
solvent-accessible surface



An ensemble



Distribution of areas of some contact in the ensemble



We summarize a contact type  $t = (a_1, a_2, c)$  area distribution in a PDB ensemble with:

- ▶  $v^t = \min(\text{observed } t \text{ areas})$
- ▶  $u^t = \max(\text{observed } t \text{ areas})$

## Areas of contact types from a multiple ensembles of conformations

$v^t$  and  $u^t$  values are areas, therefore we can sum them.

For a contact type  $t = (a_1, a_2, c)$  we sum the relevant  $v^t$  and  $u^t$  values from all the available ensembles  $G$  to get  $V^t$  and  $U^t$  sums:

$$V^t = \sum_{g \in G} v^t(g) \quad (1)$$

$$U^t = \sum_{g \in G} u^t(g) \quad (2)$$

We do it for every contact type  $t$  from the set of all possible contact types  $T$ .

## Observed probabilities of areas of contact types

Observed probability estimate of contact area unit of type  $t = (a_1, a_2, c)$  to occur:

$$P_{\text{obs}}^t(\text{occur}) = \frac{V^t + U^t}{\sum_{s \in T} (V^s + U^s)} \quad (3)$$

Observed conditional probability estimate of contact area unit to persist:

$$P_{\text{obs}}^t(\text{persist|occur}) = \frac{2V^t}{V^t + U^t} \quad (4)$$

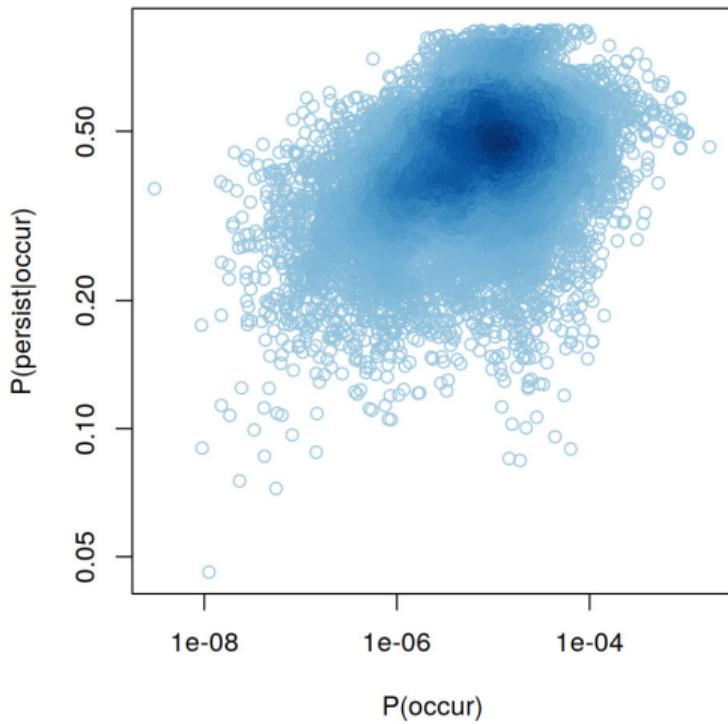
Observed probability estimate of contact area unit to occur and persist:

$$P_{\text{obs}}^t(\text{occur and persist}) = P_{\text{obs}}^t(\text{occur}) \cdot P_{\text{obs}}^t(\text{persist|occur}) \quad (5)$$

# Low correlation between occurrence and persistence probabilities

$$\text{corr}(P_{\text{obs}}(\text{occur}), P_{\text{obs}}(\text{persist|occur})) = 0.11$$

Observed  $P(\text{occur})$  vs  $P(\text{persist|occur})$ ,  
logarithmic scale



## Expected probabilities of areas of contact types

Expected probability estimate of contact area unit of type  $t = (a_1, a_2, c)$  to occur (modeling the situation where there are no atom type-dependent or contact category-dependent effects):

$$P_{\text{exp}}^{t=(a_1, a_2, c)}(\text{occur}) \sim P_{\text{obs}}^{(a_1, *, *)}(\text{occur}) \cdot P_{\text{obs}}^{(*, a_2, *)}(\text{occur}) \cdot P_{\text{obs}}^{(*, *, c)}(\text{occur}). \quad (6)$$

Expected conditional probability estimate of contact area unit to persist:

$$P_{\text{exp}}^t(\text{persist}|\text{occur}) = \frac{2 \cdot \sum_{s \in T} V^s}{\sum_{s \in T} (V^s + U^s)} \quad (7)$$

Expected probability estimate of contact area unit to occur and persist:

$$P_{\text{exp}}^t(\text{occur and persist}) = P_{\text{exp}}^t(\text{occur}) \cdot P_{\text{exp}}^t(\text{persist}|\text{occur}) \quad (8)$$

## Using pseudo-energy to score inter-chain interfaces

Pseudo-energy coefficient for a contact area unit of type  $t = (a_1, a_2, c)$ :

$$\begin{aligned} E_{\alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta}^t &= \alpha_1 \cdot \log P_{\text{obs}}^t(\text{occur}) + \alpha_2 \cdot \log P_{\text{exp}}^t(\text{occur}) + \\ &+ \alpha_3 \cdot \log P_{\text{obs}}^t(\text{persist|occur}) + \alpha_4 \cdot \log P_{\text{exp}}^t(\text{persist|occur}) + \beta \end{aligned} \quad (9)$$

A total pseudo-energy score for a set of contacts  $K$  is:

$$S_{\alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta}(K) = \sum_{k \in K} \text{area}(k) \cdot E_{\alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta}^{\text{type}(k)} \quad (10)$$

We optimize the weights  $(\alpha_1, \alpha_2, \alpha_3, \alpha_4, \beta)$  for the task of selecting best-modelled interfaces.

## A dataset of correct and incorrect interfaces

- ▶ A non-redundant set of 1549 native heterodimers, selected using PPI3D and downloaded from PDB.
- ▶ Each native structure (target) was redocked and a set of models of varying quality was selected (about 15-20 models for a target), for example:

ID	x	y	z	a1	a2	a3	CAD-score	binding_site_CAD-score
1E50_2250	-7	27	4	45	153	90	0.74375	0.87635
1E50_32	-13	25	2	18	153	90	0.63728	0.75543
1E50_2735	-7	28	1	72	162	120	0.53173	0.68644
1E50_15946	-16	26	-2	45	162	120	0.38075	0.55364
1E50_10393	-16	28	5	0	153	90	0.24134	0.47034
1E50_3759	7	29	7	351	117	40	0.13939	0.51889
1E50_17192	24	22	8	315	63	0	0.0386	0.42122
1E50_15006	-13	27	13	342	18	0	0	0.40432
1E50_5533	28	-13	20	0	45	204	0	0.30295
1E50_14280	27	-22	-22	180	126	60	0	0.20266
1E50_532	34	4	-18	207	54	100	0	0.10126
1E50_20368	1	-39	10	324	117	80	0	0.00119
1E50_9297	37	5	-22	261	54	80	0	0

## 5-fold cross-validation results of selection performance

Correct selection rate = (number of good cases) / (number of all cases = 1549)

A "good case" is when: 1) the native structural model has lower total pseudo-energy than all the predictions; 2) the most accurate prediction has lower total pseudo-energy than all the other predictions.

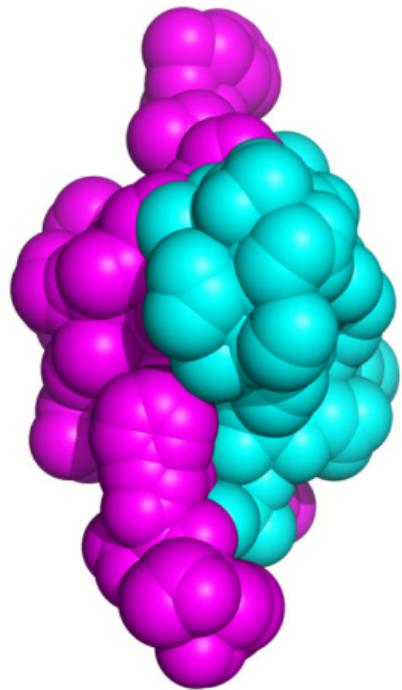
Method	Components	Correct selection rate	
		mean	std. deviation
Ideal selector		1	0
Random		0.04	0.017
Total area		0.05	0.016
Simple pseudo-energy	$P(\text{occur})$	0.53	0.039
	$P(\text{persist} \text{occur})$	0.56	0.035
	$P(\text{occur}) \cdot P(\text{persist} \text{occur})$	0.63	0.030

Progress: from **0.53** to **0.63**

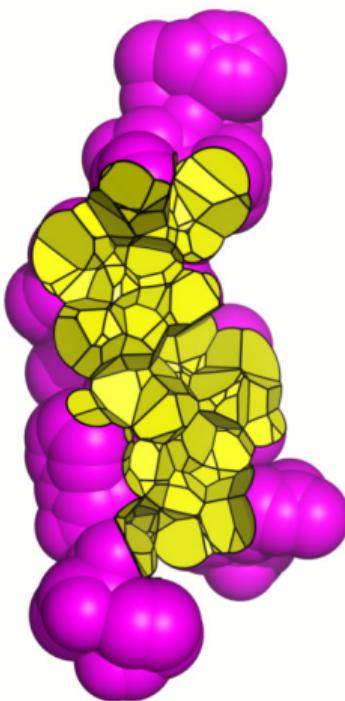
Extending geometry of contacts

## Inter-chain contacts

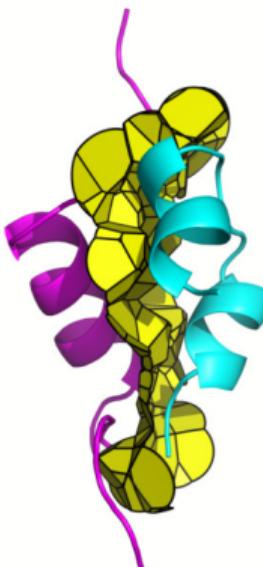
Solvent-accessible surface  
of an insulin heterodimer  
PDB:4UNG colored by subunit



The intersubunit interface  
shown together with the  
SAS of one subunit

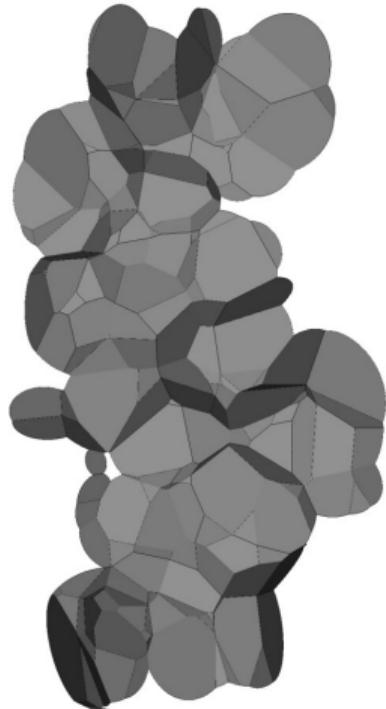


The intersubunit interface  
shown together with  
both subunits represented  
as cartoons

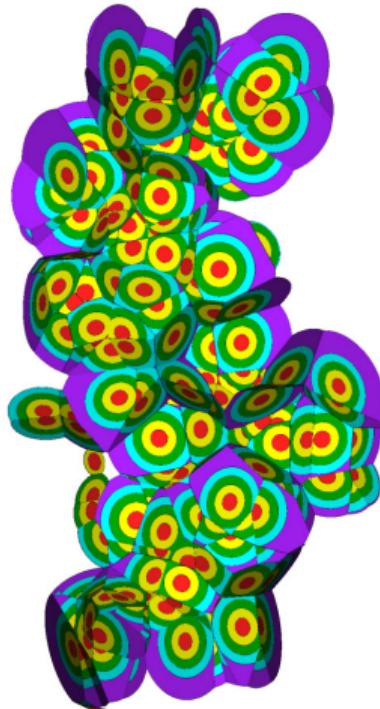


## Introducing contact layers

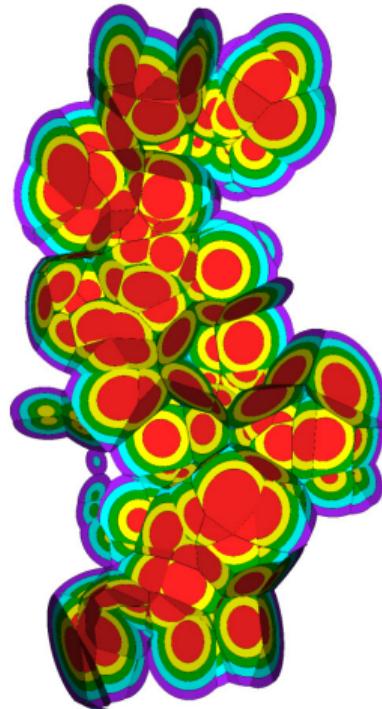
Simple contacts



Contact layers v1

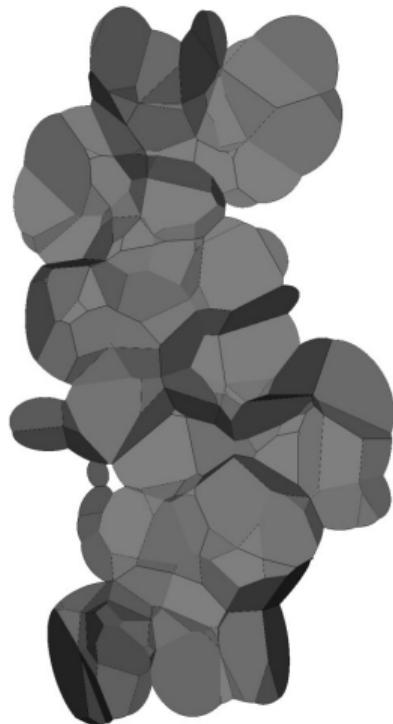


Contact layers v2

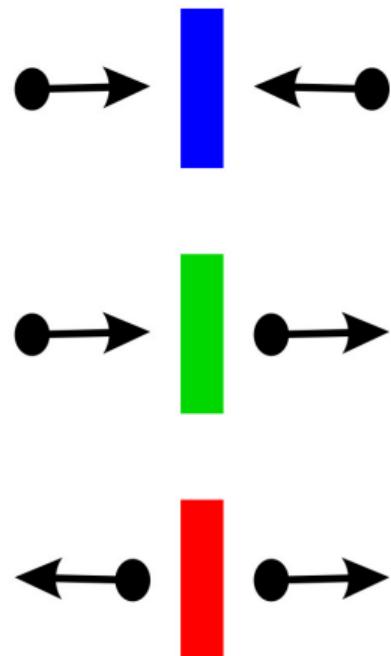
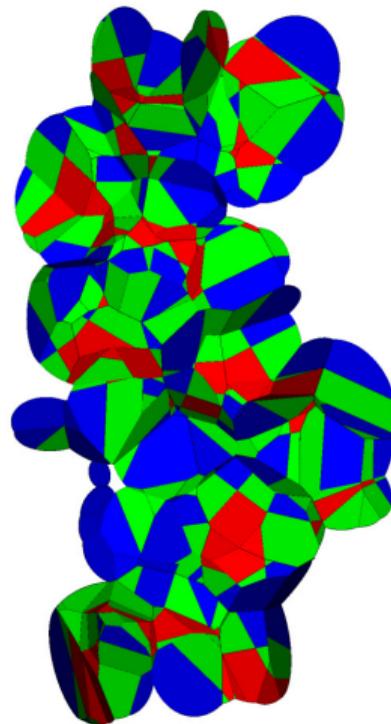


## Introducing contact sectors

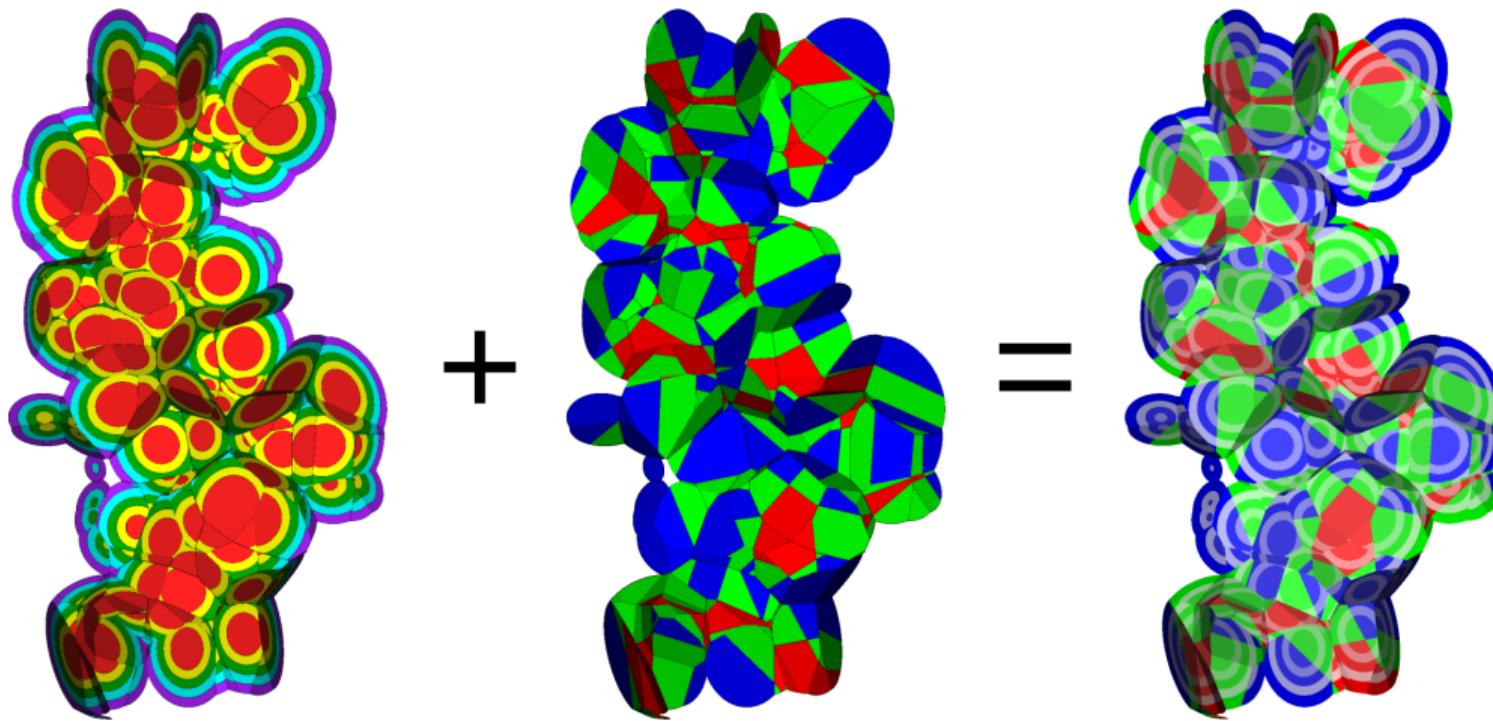
Simple contacts



Contact sectors



## Combining contact layers and sectors



## 5-fold cross-validation results of selection performance

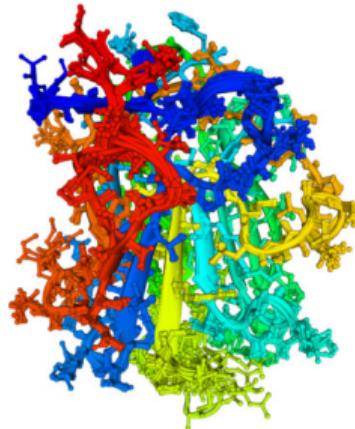
Method	Components	Correct selection rate	
		mean	std. deviation
Ideal selector		1	0
Random		0.04	0.017
Total area		0.05	0.016
Simple pseudo-energy	$P(\text{occur})$	0.53	0.039
	$P(\text{persist} \text{occur})$	0.56	0.035
	$P(\text{occur}) \cdot P(\text{persist} \text{occur})$	0.63	0.030
Extended geometry pseudo-energy	$P(\text{occur})$	0.80	0.006
	$P(\text{persist} \text{occur})$	0.77	0.025
	$P(\text{occur}) \cdot P(\text{persist} \text{occur})$	0.83	0.004

Progress: from **0.63** to **0.83**

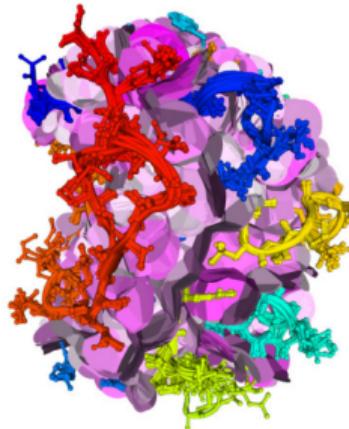
Predicting structural heterogeneity of protein contacts from  
singular static conformational models

# Contact area persistence values for PDB ensembles

Ensemble of conformations from PDB, based on a 90% sequence identity cluster

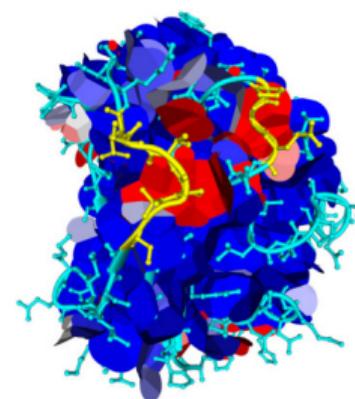


Residue-residue contact areas of every conformation, minimum seq. sep. = 6, colored by area

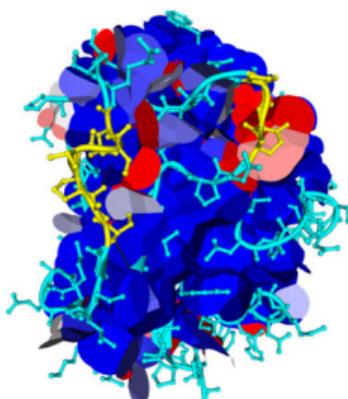


Residue-residue contact areas colored by ensemble-wide persistence

PDB ID = 1D2S



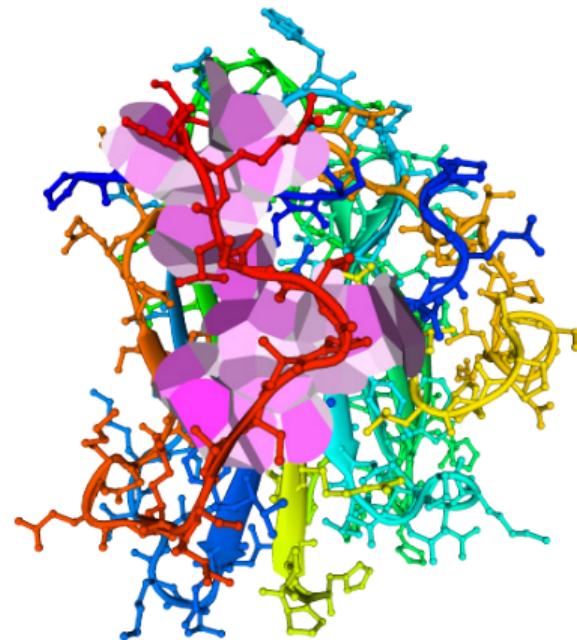
PDB ID = 6PYB



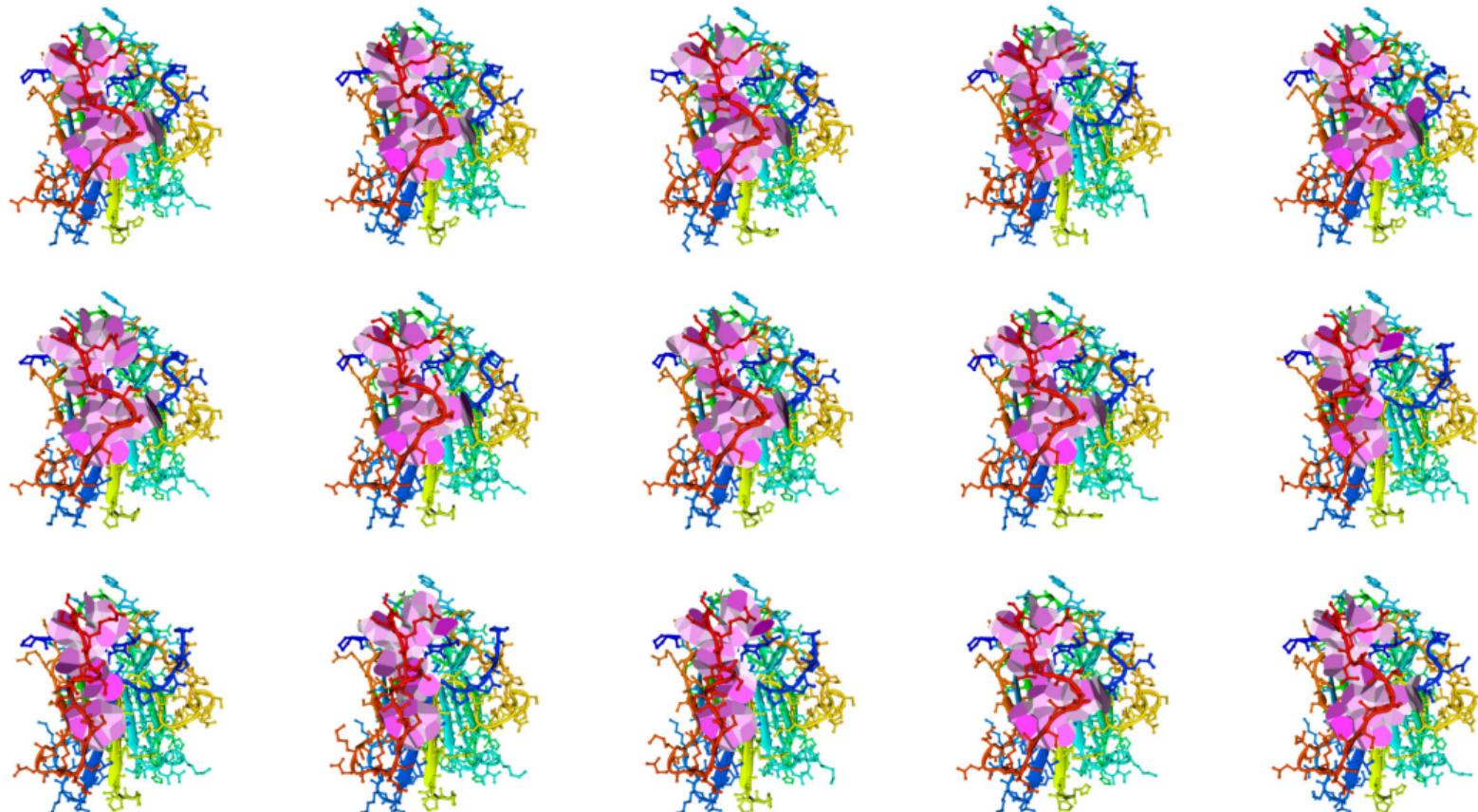
If a contact with ID  $\kappa = (\text{residue}_a, \text{residue}_b)$  is present in at least one conformation, and both  $\text{residue}_a$  and  $\text{residue}_b$  are present in at least two conformations, then  $\text{area}_{\min}(\kappa) \geq 0$  and  $\text{area}_{\max}(\kappa) > 0$  are available.

Then the ensemble-wide contact area persistence is defined as  $\text{persistence}(\kappa) = \frac{2 \cdot \text{area}_{\min}(\kappa)}{\text{area}_{\min}(\kappa) + \text{area}_{\max}(\kappa)}$

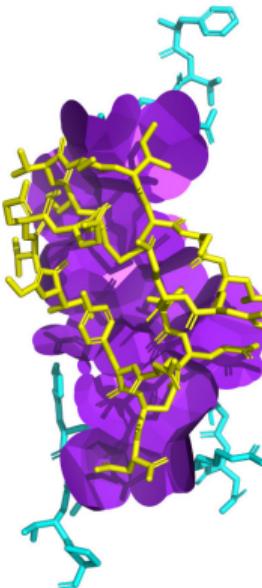
## Ensemble contacts for a sub-interface — risky animation



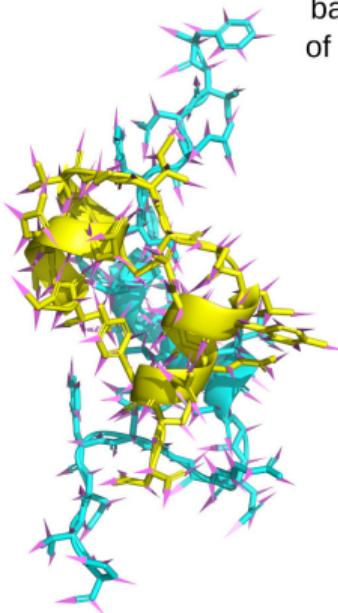
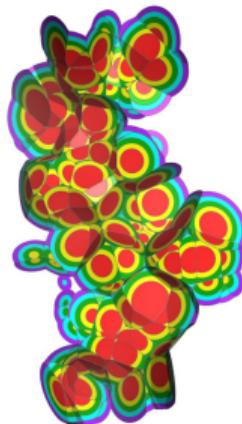
## Ensemble contacts for a sub-interface — reliable frames



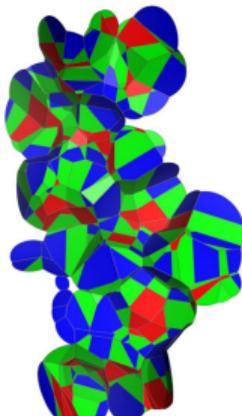
# Extended geometry of contacts



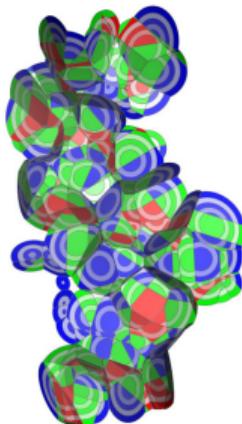
"Layers" of contacts  
based on distances  
from outer boundaries



"Sectors" of contacts  
based on halfspaces  
of directions of atoms

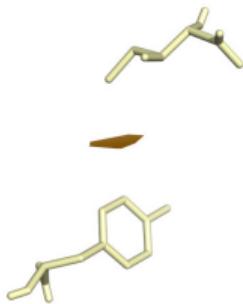


"Layers" and "Sectors"  
combined to define multiple  
geometric contact categories

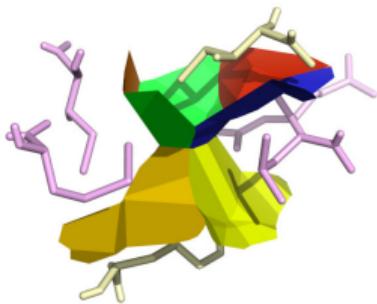


# Voronoi contacts block (VCBlock)

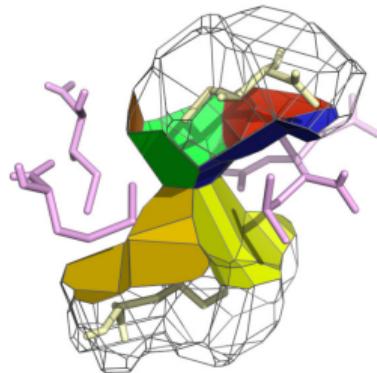
Tessellation-derived contact surface between two main residues



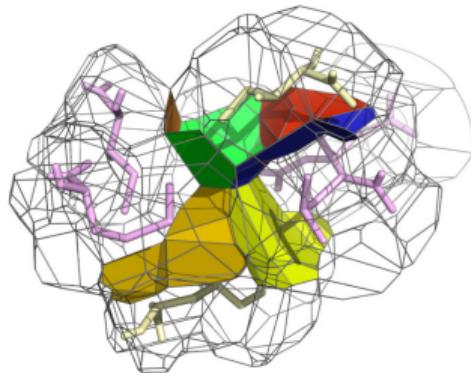
+ Adjacent contacts with shared residues (side residues)



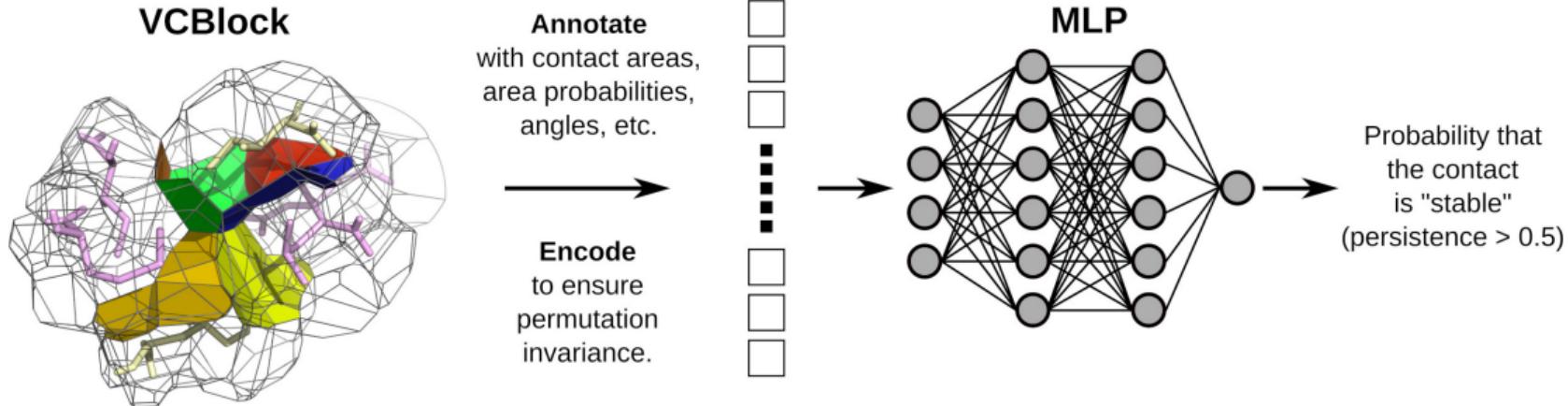
+ Interface of the main residues with the environment



+ Interface of the side residues with the environment

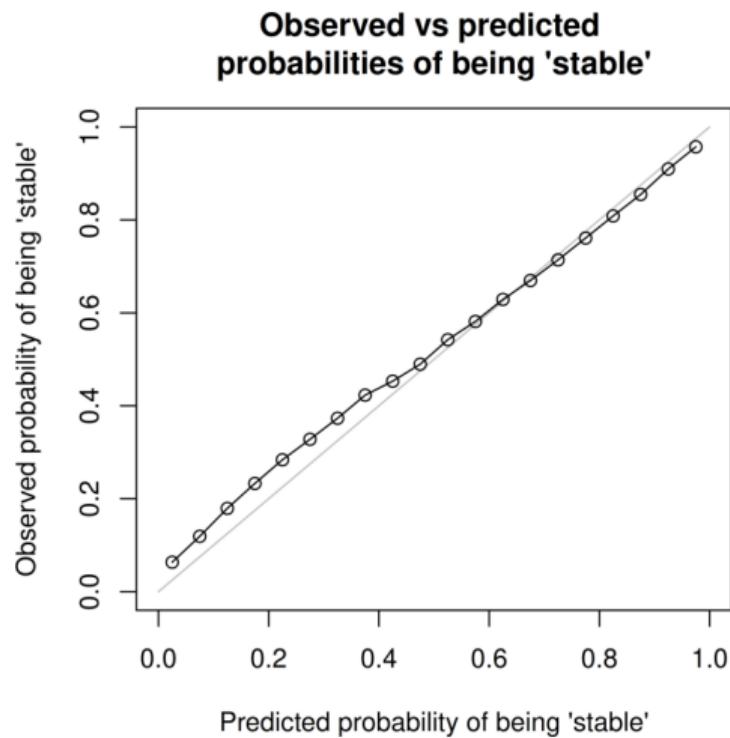
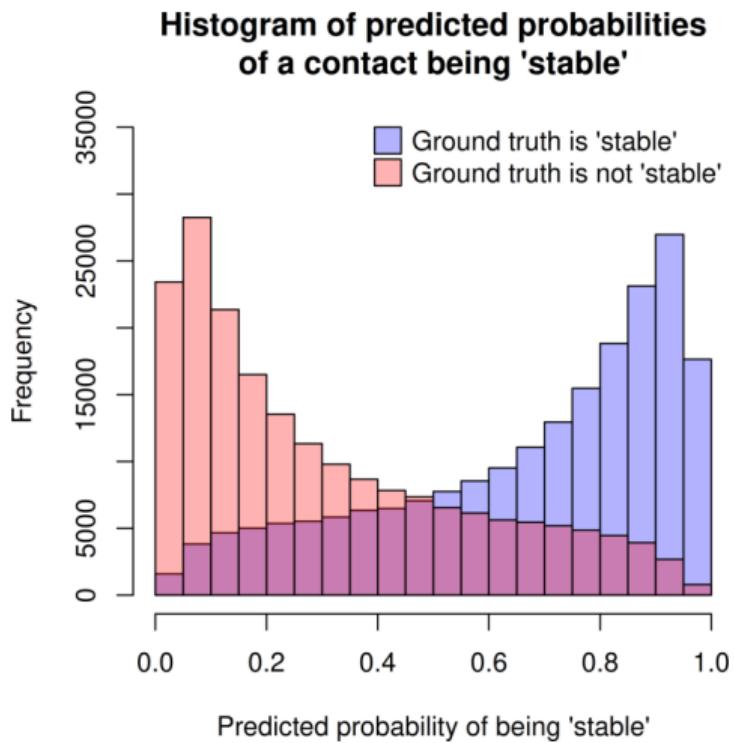


# VCBlock-based contacts stability predictor



Current MLP training/validation/testing was done using a set of  $\sim 2 \times 10^6$  VCBlocks sampled from  $\sim 2 \times 10^4$  protein ensembles collected from PDB. The data split was done respecting the 30% sequence identity-based clustering.

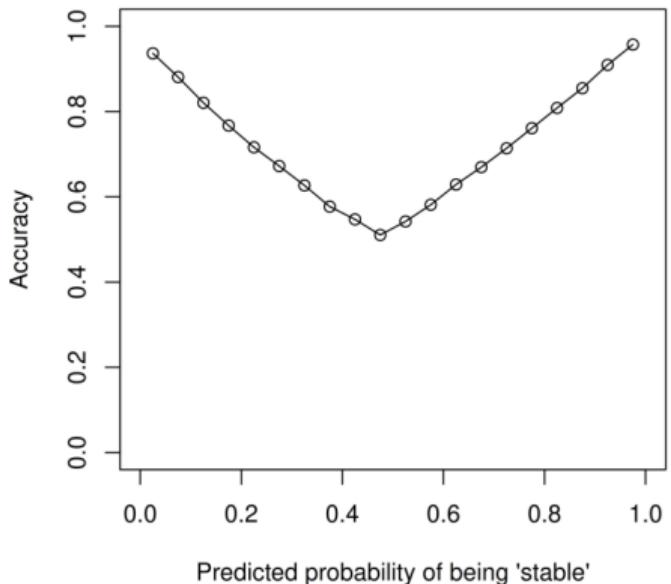
# Classifier performance on the testing set



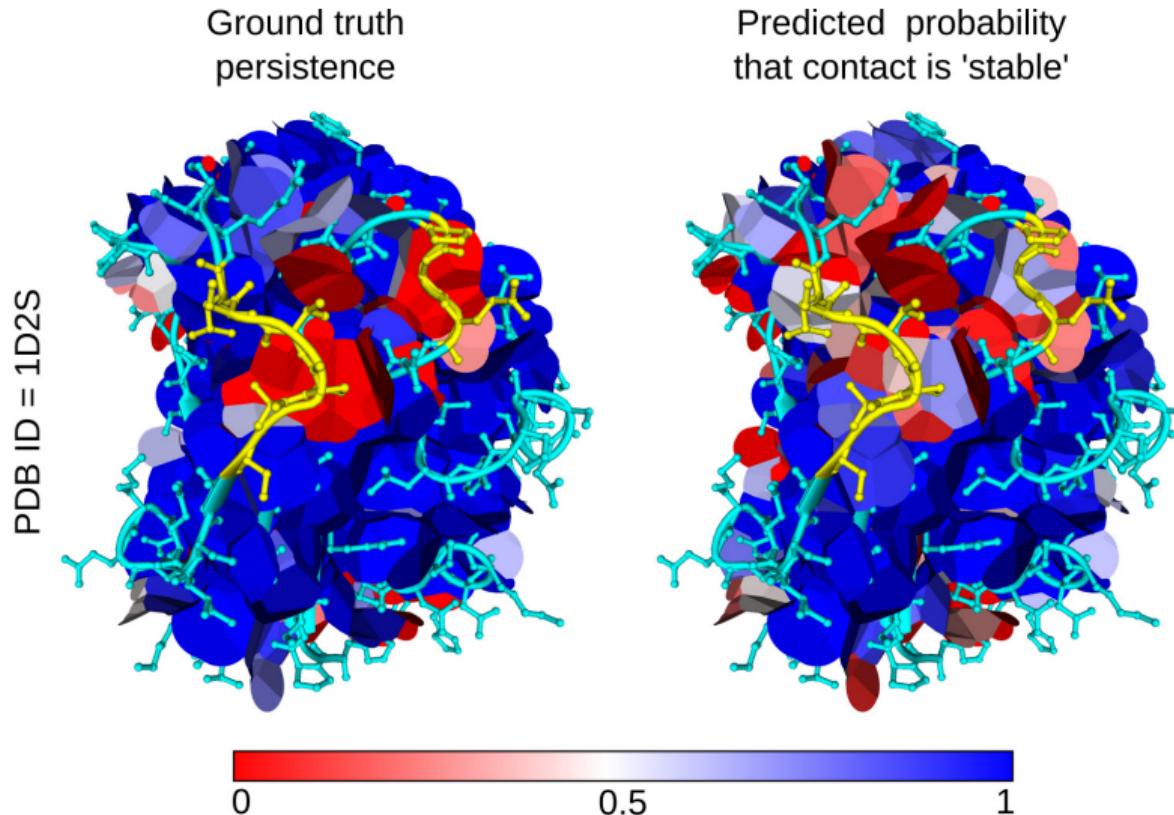
## Classifier performance on the testing set

Accuracy  $\sim 0.78$  overall, but extreme values are predicted more accurately

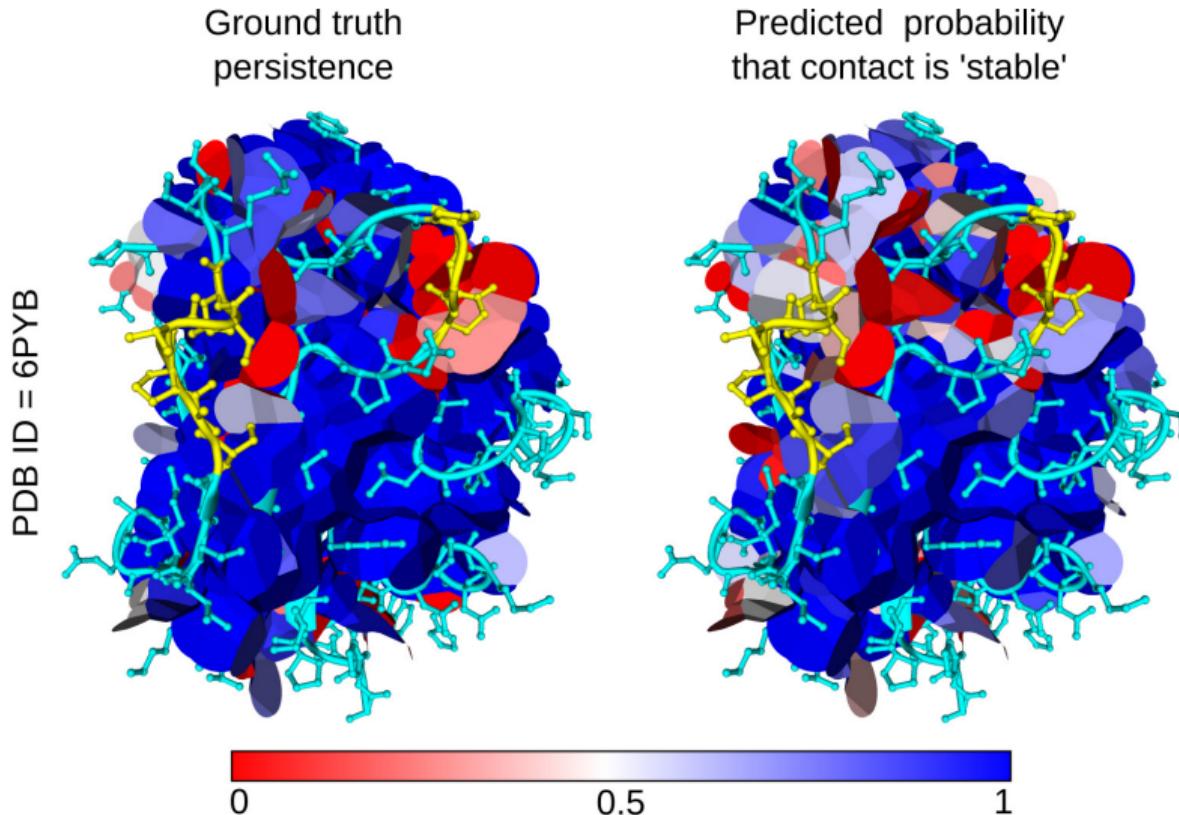
Accuracy vs predicted probability of being 'stable'



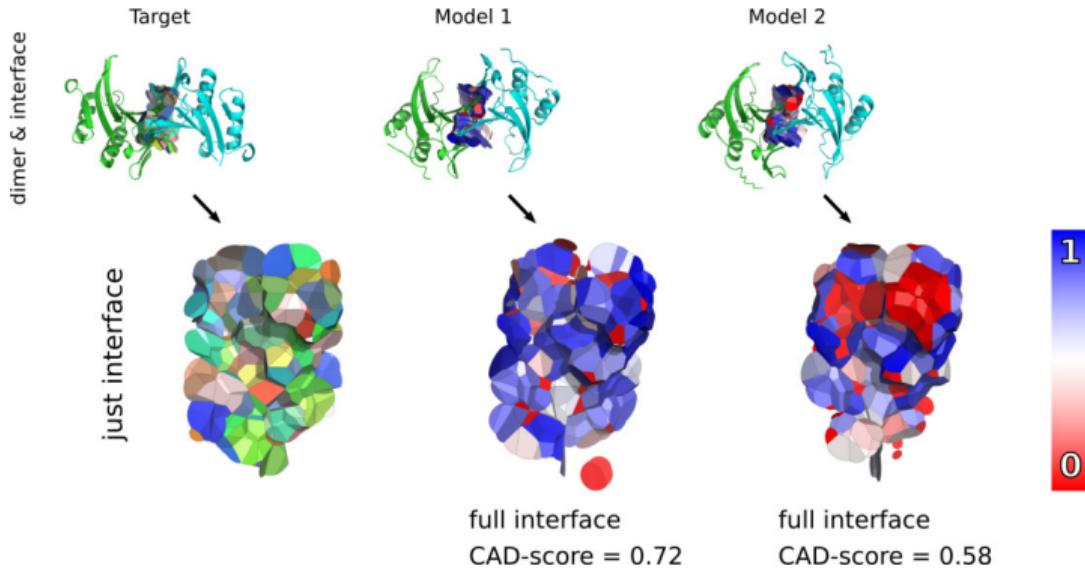
## Example of MLP predictions vs ground truth



## Example of MLP predictions vs ground truth



# Analyzing oligomeric predictions

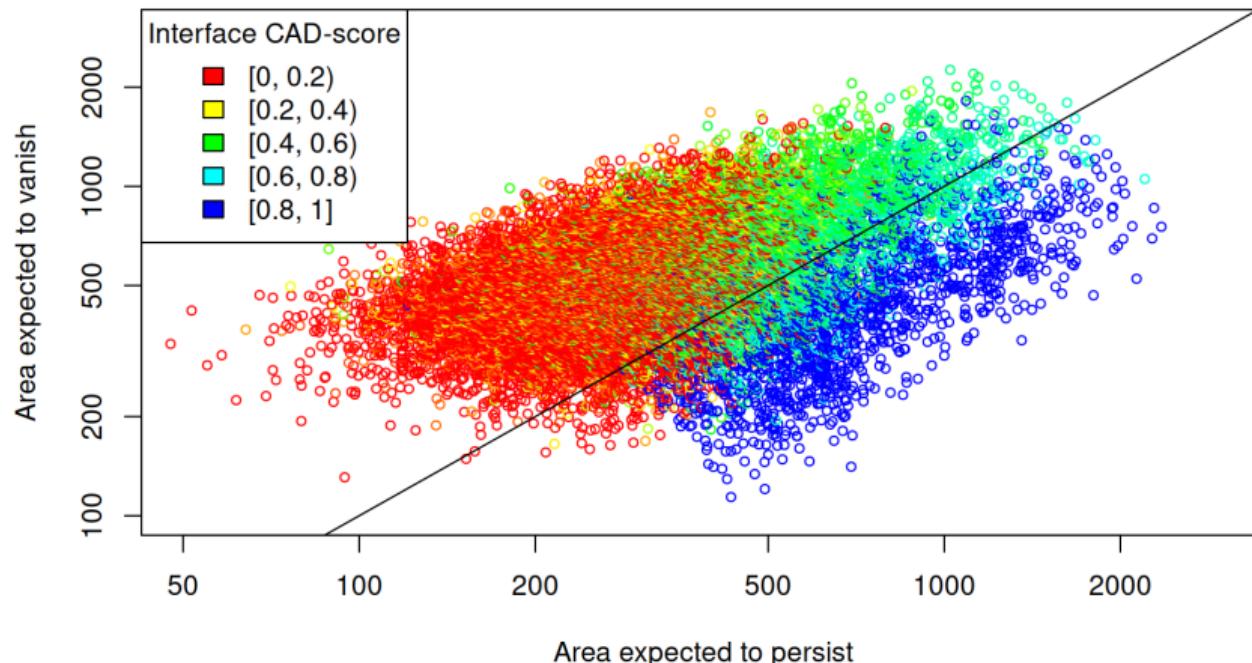


When we run VoroMarmotte software for inter-chain contacts, we get:

ID	area_expected_to_persist	area_expected_to_vanish	area_total	area_pseudoenergy_v1
target.pdb	736.036934416612	307.304285583388	1043.34122	-1330.24266560559
model1.pdb	514.899135986745	456.753564013255	971.6527	-192.57424709485
model2.pdb	399.674485370467	572.686044629533	972.36053	572.000273266142

# Interface area persistence predicted for native and redocked heterodimers

VoroMarmotte global scores for native and predicted inter-chain interfaces,  
colored by similarity to native interface (CAD-score)



## VoroMarmotte pseudoenergy

The VoroMarmotte pseudoenergy for a set of contacts  $K$  is calculated as follows:

$$E(K) = \sum_{k \in K} \text{area}(k) \cdot \log \frac{P_{\text{predicted}}(k \text{ persists}|k \text{ occurs})}{1 - P_{\text{predicted}}(k \text{ persists}|k \text{ occurs})} \quad (11)$$

We work with probabilities, but there are some relations to physics (constants omitted):

$$\Delta G \sim E(K) \quad (12)$$

$$K_D \sim \frac{1 - P_{\text{predicted}}(\text{interface persists}|\text{interface occurs})}{P_{\text{predicted}}(\text{interface persists}|\text{interface occurs})} \quad (13)$$

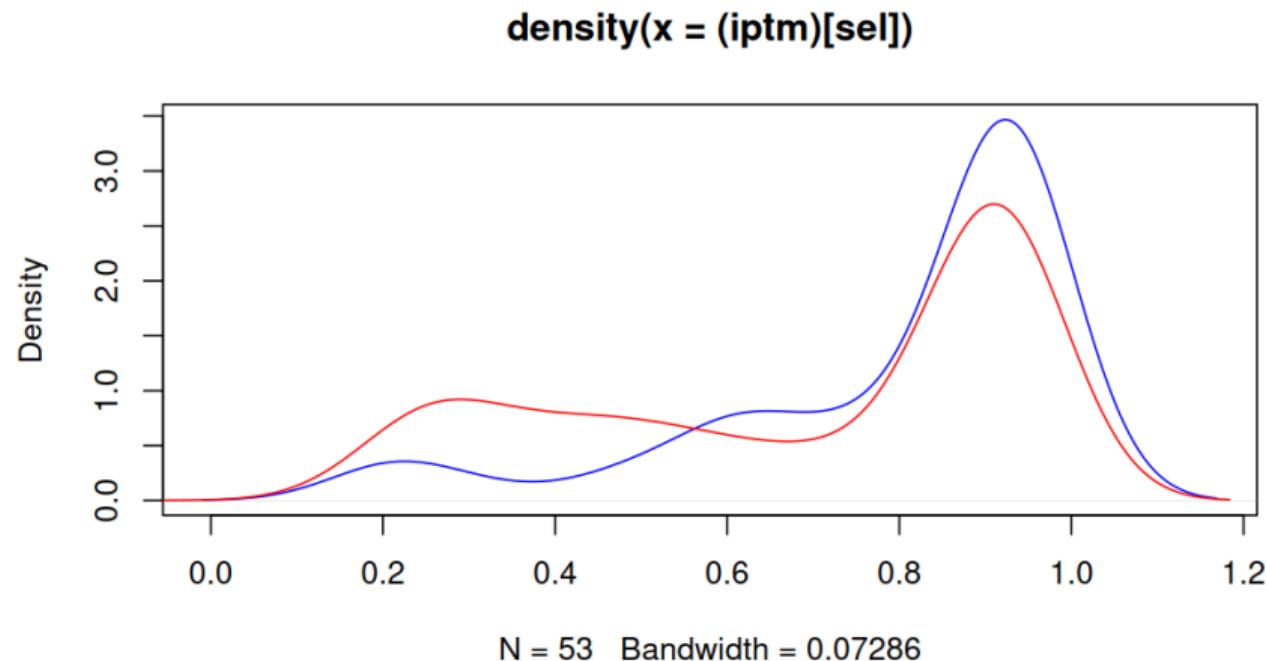
## Looking at the data from EGFR Protein Design Competition



- ▶ <https://foundry.adaptyvbio.com/competition>
- ▶ [https://github.com/adaptyvbio/egfr\\_competition\\_2](https://github.com/adaptyvbio/egfr_competition_2)
- ▶ There are 400 AF2 structural models of protein-binder complexes, each structure is annotated with experimental binding characterization results and with AF2 scores.
- ▶ There are about 50 binders and 350 non-binders.

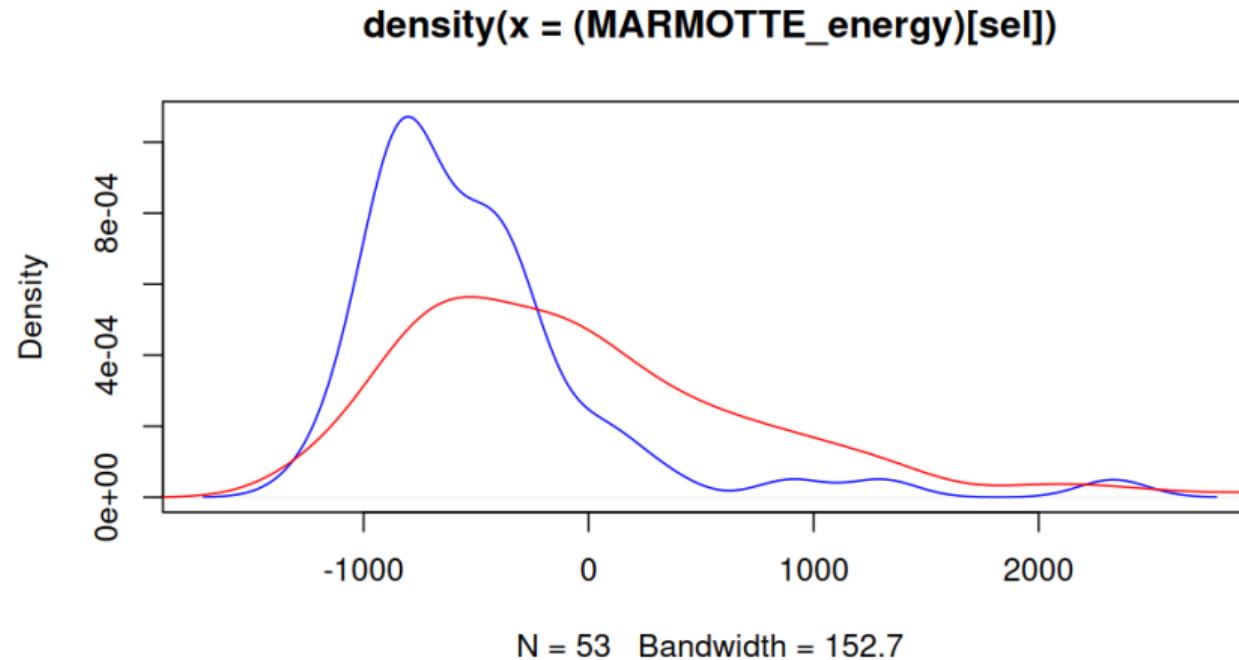
## Scores for binders and non-binders

Empirical densities of AF2 ipTM scores for binders and non-binders:



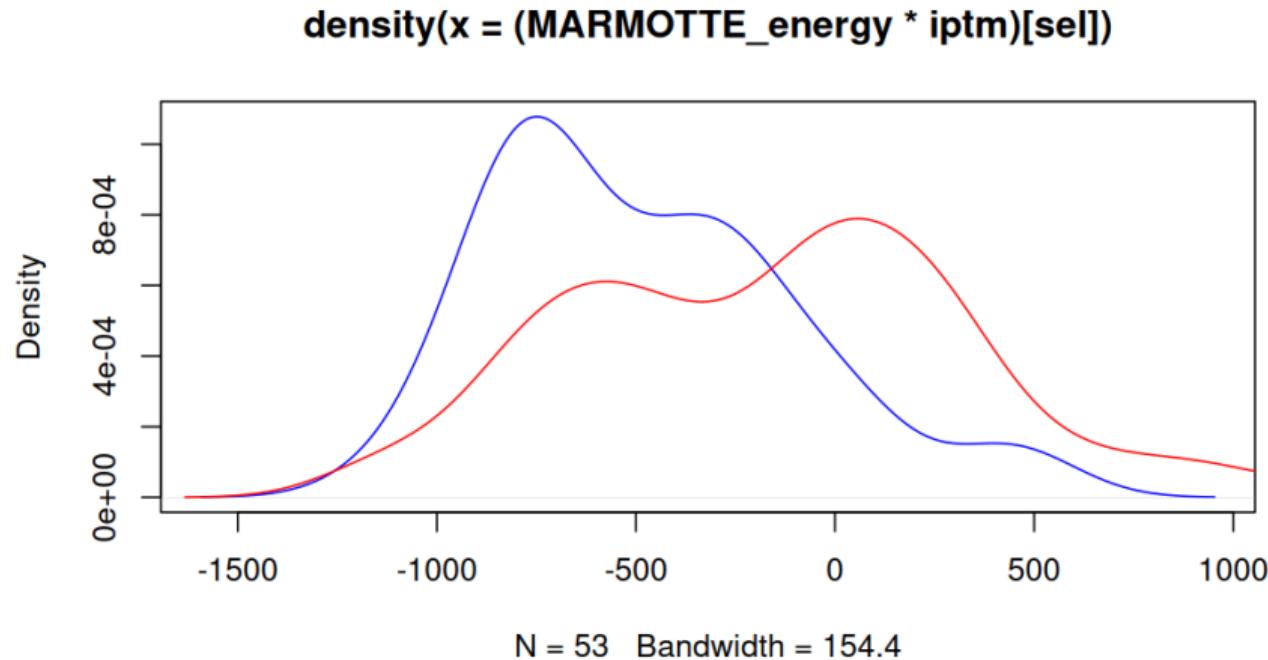
## Scores for binders and non-binders

Empirical densities of VoroMarmotte pseudoenergies for **binders** and **non-binders**:



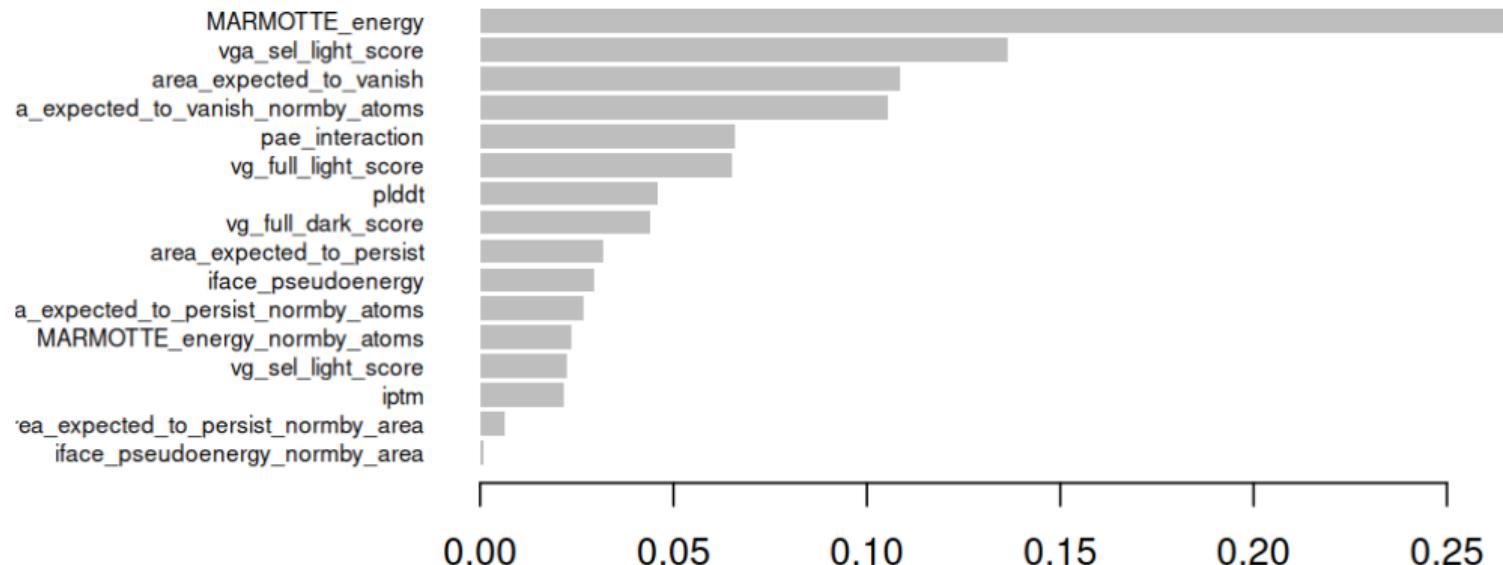
## Scores for binders and non-binders

Empirical densities of naive combo-scores for binders and non-binders:



## XGBoost analysis of importance of scores

An XGBoost-based binder/non-binder classifier was trained and cross-validated using various scores in input, the reported most important features were:



The classifier performance on test data is low, balanced accuracy is about 0.65.

## Final remarks (Oasis-like)

Definitely:

- ▶ Tessellation-derived contact area descriptors can be used to collect information about contact stability from ensembles of conformations in PDB, this information can improve scoring of protein-protein interfaces.
- ▶ The Voronoi Contacts Block can be used to predict stability of contacts in an ensemble.

Maybe:

- ▶ The predicted stability of contacts can be used to select better binders.
- ▶ The tessellation-based methodology for scoring interfaces can be used for protein design-related tasks.

# Thanks

Thank you!

CNRS Laboratoire Jean Kuntzmann:

- ▶ Sergei Grudinin
- ▶ The GruLab Team  
(<https://grulab.imag.fr>)

Useful links:

- ▶ <https://www.voronota.com>
- ▶ <https://www.kliment.lt>
- ▶ <https://www.bioinformatics.lt>



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the European Union