

Foundations of Sequence Bioinformatics

“The Human Pangenome Project - For an inclusive genomics”

University of Milano - Bicocca



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July 9, 2026



Funded by
the European Union

Outline

1. Introduction
2. Structural variants calling
3. Pitfalls of structural variants evaluation
4. Pangenome graph augmentation
5. Conclusions

Introduction

Who am I?



INSTITUT
Pasteur



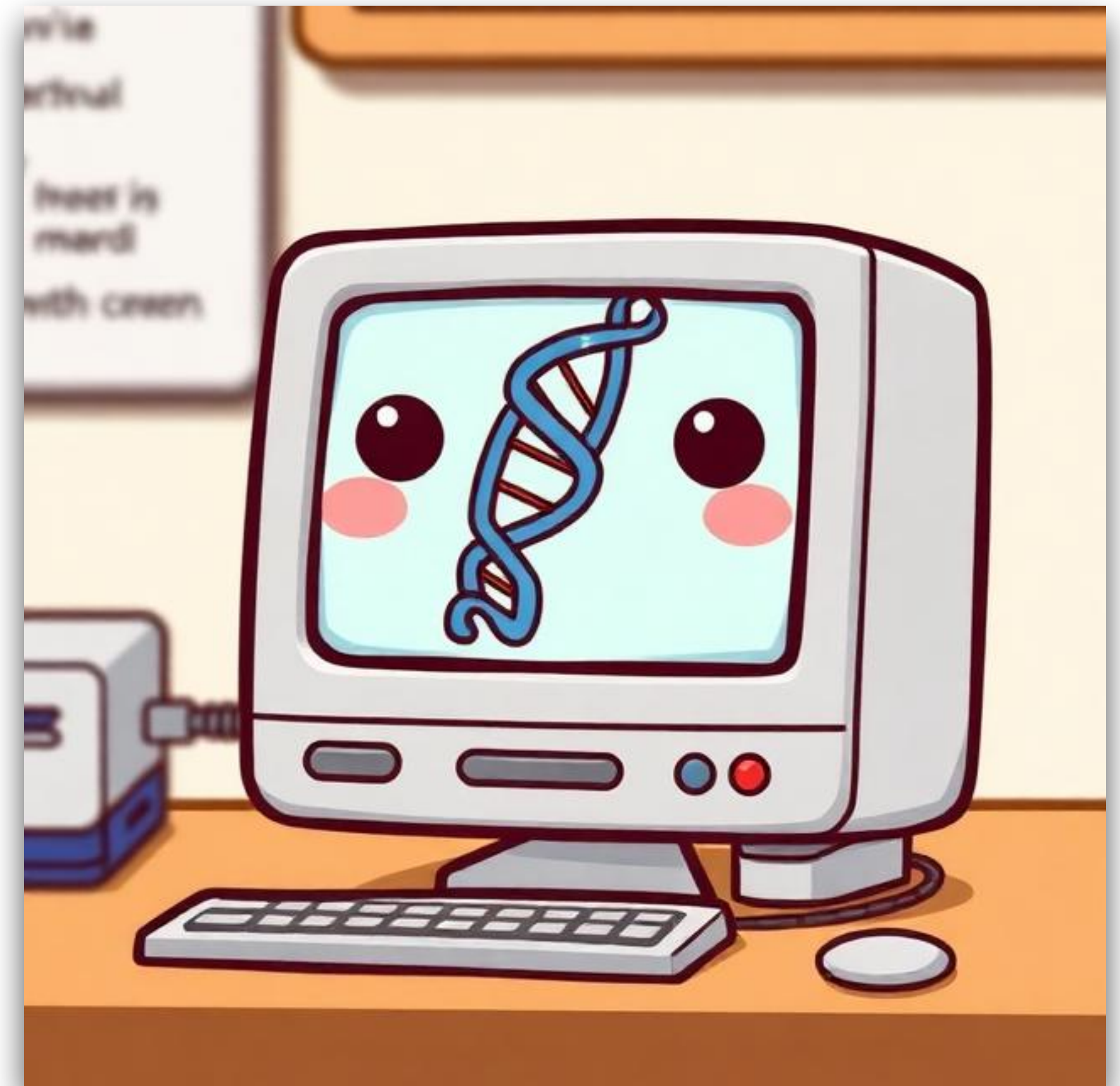
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MSc and PhD in
Computer Science

Sequence Bioinformatics

Sequence Bioinformatics

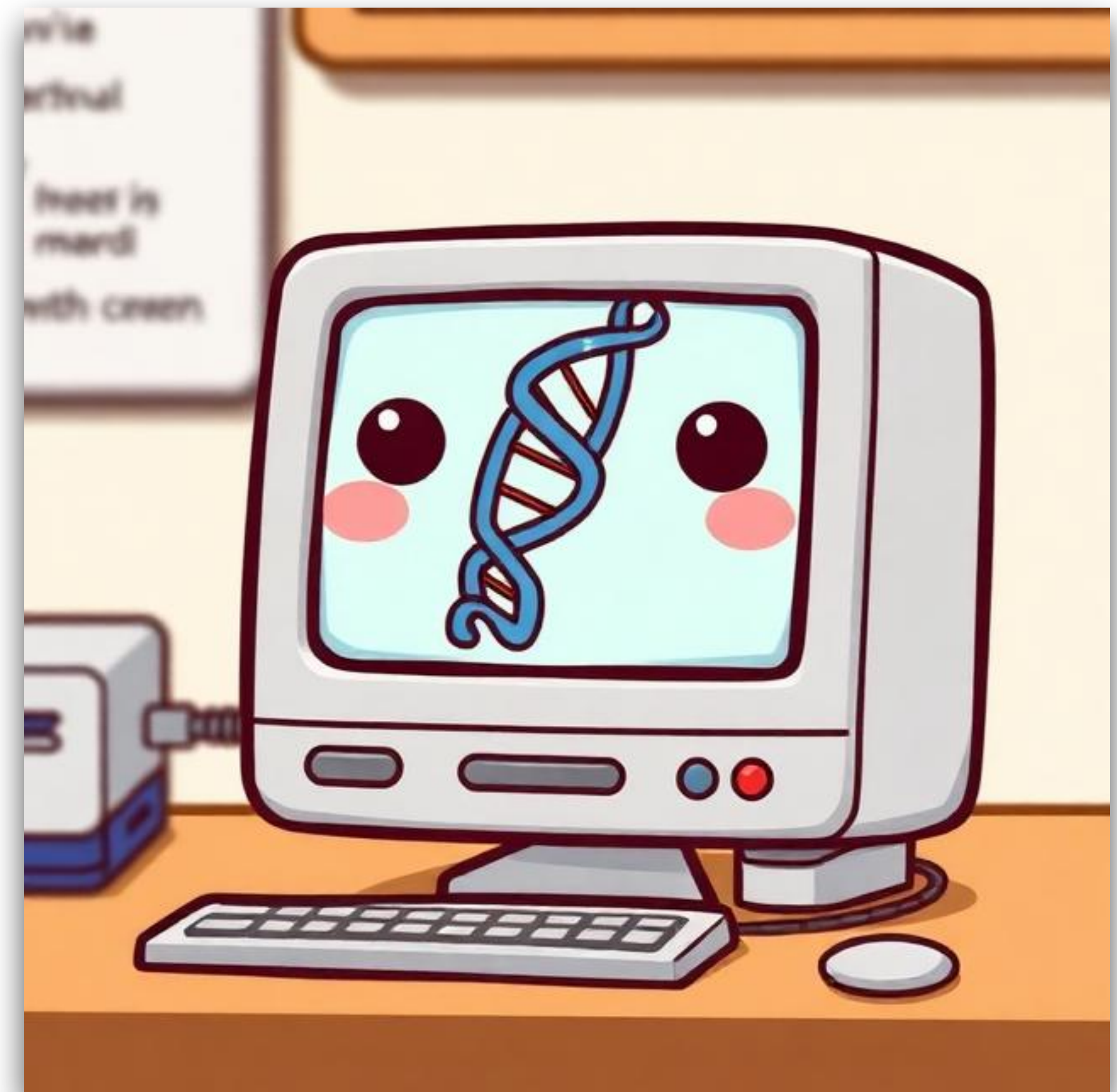
Use computers to analyze DNA



Sequence Bioinformatics

Use computers to analyze DNA

Extract knowledge from sequencing data
faster and better

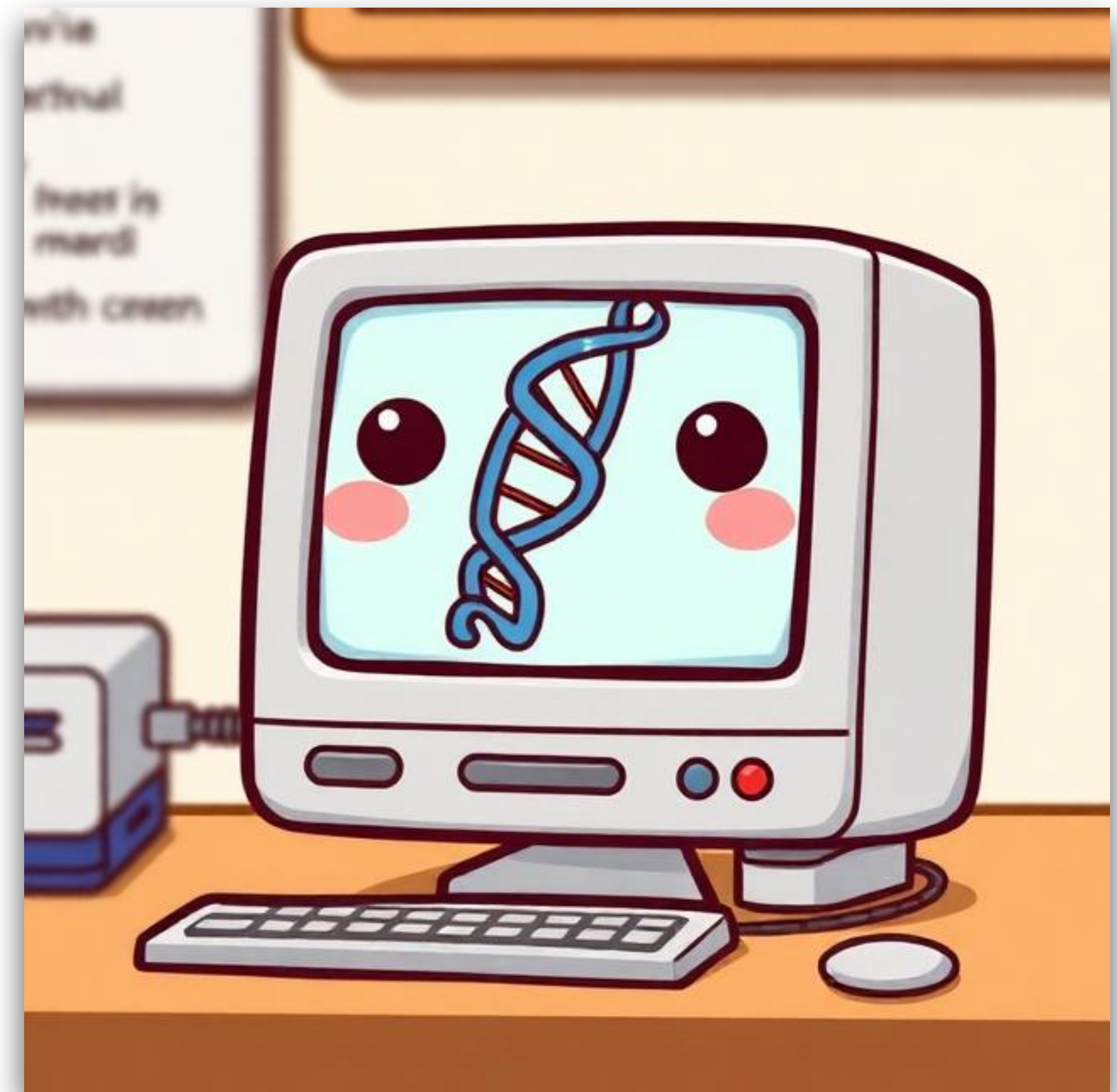


Sequence Bioinformatics

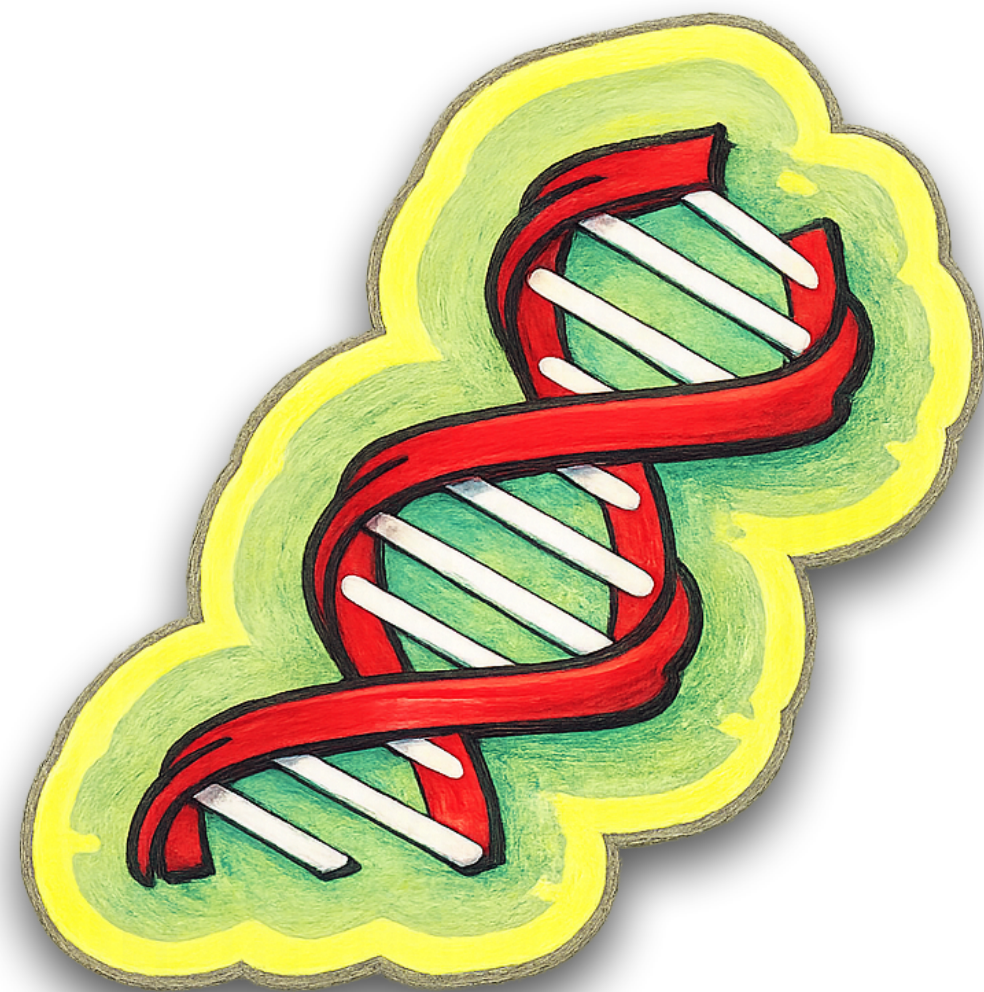
Use computers to analyze DNA

Extract knowledge from sequencing data
faster and better

Develop algorithms and data structures for the
analysis of sequencing data



Sequence Bioinformatics



*(DNA, genome, haplotype,
individual, ...)*

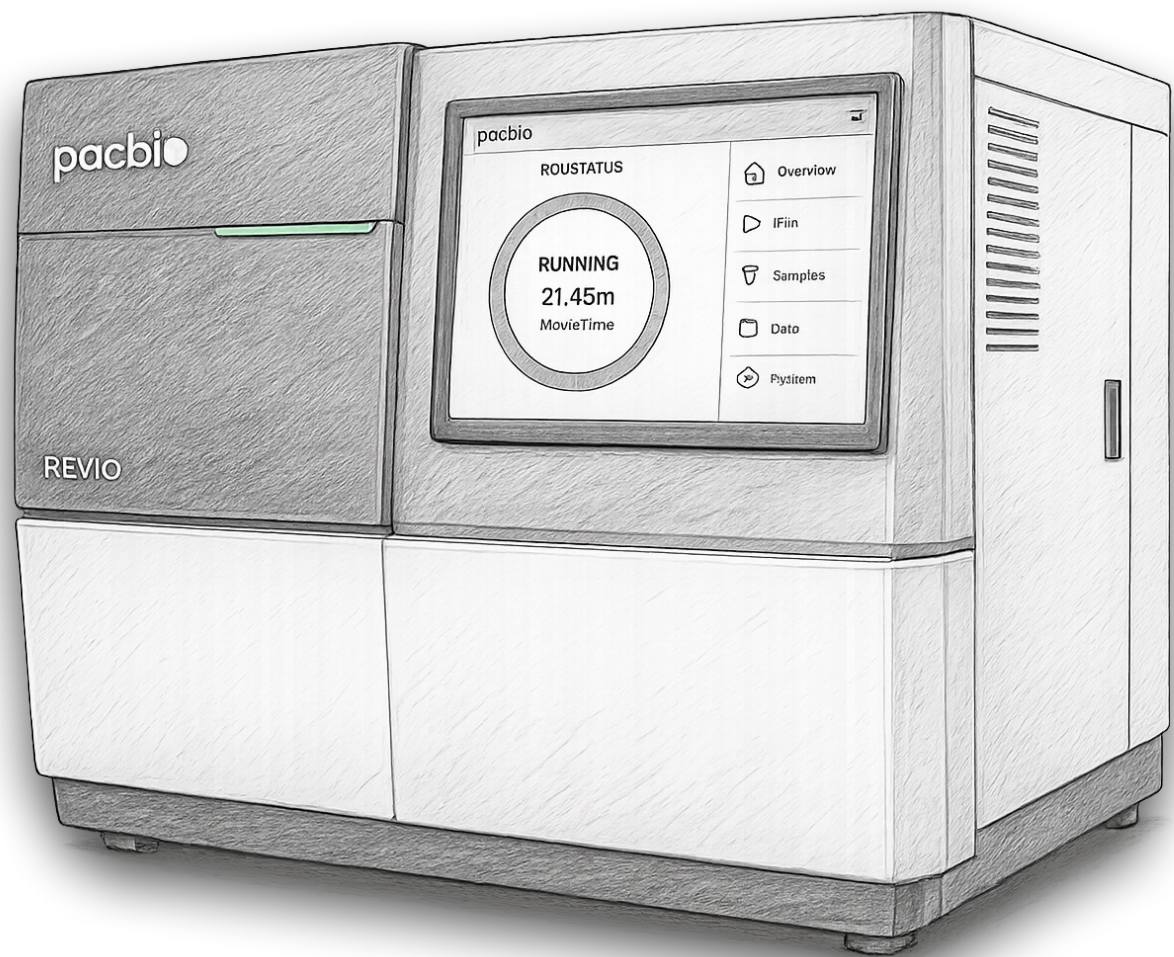
```
>chr1
```

```
TAGGGAGGTATCACAAGCTAGCTTGCACCAAAAACAAGttcaaattaacttttttttagGAGTAACTAtcaattttctcctt  
tctttccatgAAAGTTGGACAATCTTTCCCGACATCTATGAAGCCTAATCTTAATAAAAATCAAGTCTTTCTGTACAATTA  
AGGGGCTGAAGGGCCCCATCCTCCTGCCTGGCGCTGCCACGGACAGCCATTCTGCATGACTGAAGCTTCTGCTTTCCCTG  
AGCAGCAGGGAGGTCACACACTGAGACGCCGGTGGCCCGATGCCCCAGAGCACAAGGCAAATGCTGGTTCCTGCTCACCA  
CTTCGTCCTCGGTCCAGCACTTCTCGATGAGCTTGGGCACAGGCTTCTTCACCAGGCGCTGCAGGGCTTTGCCAGCATCG  
TAACCGCTTTTCATGcagctaaaacaacaattatAGTTAGCTAACTGCACCAAATAACAGACAGGACACAATCAATCC  
AAGGCAAGCTCCTCATTGACTATCTCCACAGAAGAGTCAGGAAAGGGGCACTGAGACTCCATCATTTCAGTAGGGCGCAG  
GAATTTGTTCTCATCCAAGACCACCCTATCCCAACCCCTATTCTACTCACtctgggagagggaggcaggcaaGGCAGAAA  
ATATTTTGGCAAAGATAGGAATAGGATTCCCCTATATTCCcataaagcaaacatttagggaatgtttggccccgcccagt  
gctcaggacattccatgcaatcattatcttacttaatcctatggggaaagtattctctcatttaattctacgggttaggag  
ctatcatcgccctacttcacagatgaggaaactgaggcacagaaagatcaagtaaagatgttcaccacactgagccagca  
ggtggtgaagccaagactccaacccagCCAGGAGGACCCCTACTCTTGCCTCATTCTCCGCAAAGCAGCGTAAAGTCACA  
CTATAAAATTTAAgagcttttttaaagaaagtaagtCTGTAATAGTATGCTAGTTTTTCAGTACATATGAATAAAGATGCA  
GGTTTATCTACATATTCCCTTTAGGACCAGACTTGTTTCTTGTCAAAGCTAATCAACTTTTCTCACCCCTGCGTCTTTTCA  
ACCCTGTGTAGTGTCTGGCACCATGGACACCTTCCACCTCGCAAAGATGCTCCAGACACTCCAAGTTTCTGAGTTCCAA  
CTTGCAGATAATGTAGAGAAACAGCAGGTACAAAGATCCTCCTGCTCTATCTACCTCCCCATACTGTGGCTGTCACTCAG  
AATTCTCATTGGAAATCCACCTTTCCTGTACACATCTAGTCTTCTTACACAAAGATTGGCTTTGTCTAAGACTTGCATCT  
GCGAGTCGATCGACTGAGCGAGCATCGTCGATTCTGTACGTATCTAGCGCGCCGAGTATATAGAGAGATCCTGCGCATCA  
ATATATACGCAGACTACAGCATCGCTAGCTATGACCGTAAGCTTCAGTCGATGCTAGCTAGCTGATCGTATACGTCAGCT
```

```
...
```

String = Sequence of Characters

Sequence Bioinformatics



(Sequencing data, read samples, read, ...)

```
@m84046_230427_194942_s2/157944423/ccs
TAAACCAAGAATAAAATTCTAAGCCCCACAGCCGATCGCGTGGACCCCGCCTCTGGGCCAAAGGGATTCCAGAGAAA...
+
IDIIDIIIIIIII2IIIIIIIIII7IIIIIDIIIIIIIIIIIIIIII<IID$IIDIDIIIIIIII<IIIIIDIIIIIIII...
@m54329U_230327_190242/29624753/ccs
TGAGCATGAGTGAACATGTGTGCATGAATGTGAGTATGATTTGGGTGTGTATGAGTGTGAATGTGTGCACGAGTGTA...
+
~v~|x~~}~a~~d~on~~~~~}~~~~}~~p~~h~~~~~h~~~~u~{x~~~~~y~...
@m84046_230427_194942_s2/102303621/ccs
GTATAGTCGGGGCATGCCCTCTTCTAGCCGCTGGGAGCACTACAGGATCCTCTTTGCTCACAGTGTAGTGGCAGCAC...
+
D7DIIDII2IIID2DD7IIIDDIDII7<IDD7+IIIDD++D7DI+IID+IID$D<DDDDIDIDIIIIID<$2IDIID...
@m54329U_230330_133121/154273907/ccs
GATCCTCTTGCTCACAGTGTAGTGGCAGCACGACAGGGCACTGCAGGGTCCTCTTGCTCATGGTGTGGTGCCCGTAC...
+
~~~~~{~~~f~~~~~...
@m84046_230424_215157_s4/143851749/ccs
TCTGACATTTTATTGCAGAGGGAATGATTGGGGCATCTTCAGAGGAGTTCTAGGGTGAGGGAACGATTAATTGGAA...
+
IIIDIII<IIIIIIIIIIIDI7IIIIIII7I7IIIIIIIIIIIIIDII2DIIII7IIIIIDIIIIIIIIIIIDI<I<I...
...
```

Goal of this talk

Prove that **Computer Science** is essential
to turn biological data into reliable biological insight

(CS: algorithms and data structures, problem formulation and modelling, scalable computation...)

“Don’t ask the barber whether you need a haircut” - Daniel S. Greenberg

Structural variants calling

Denti et al. Nature Methods (2023)

Disclaimer

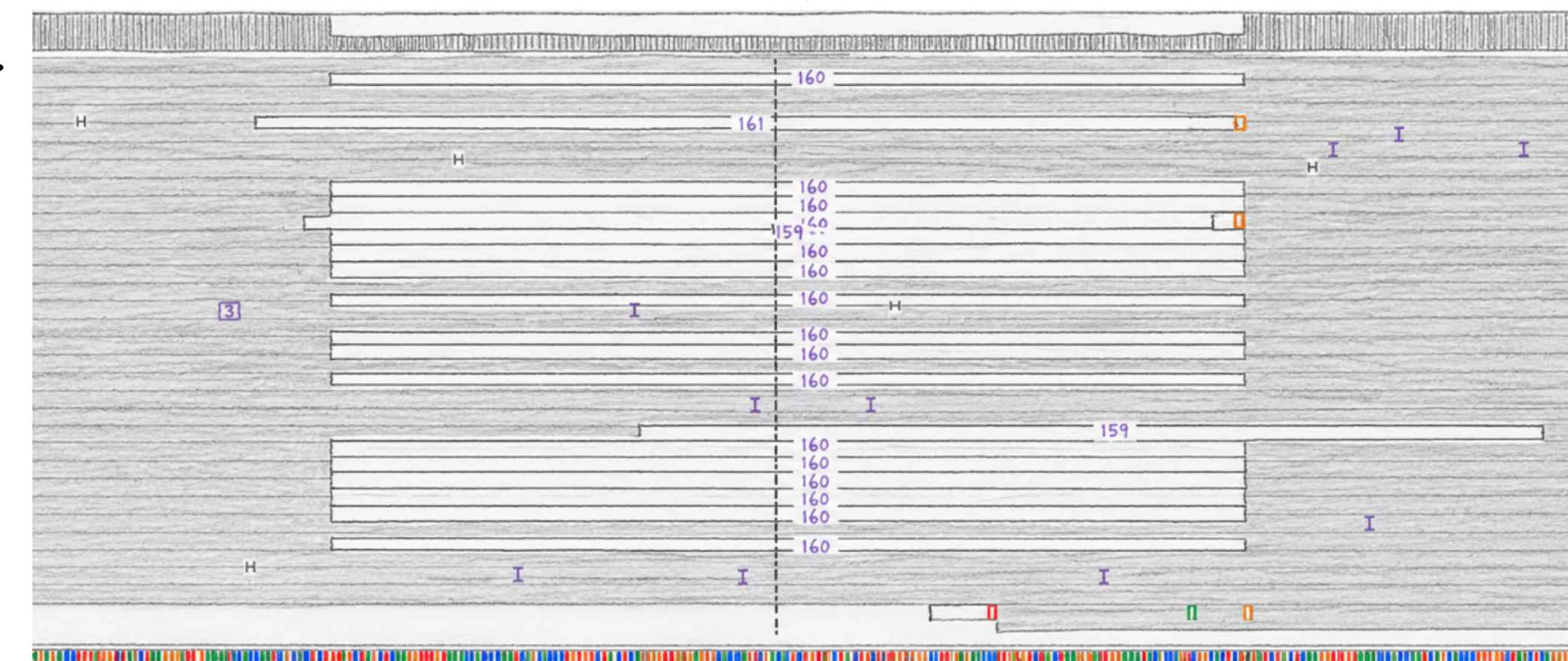
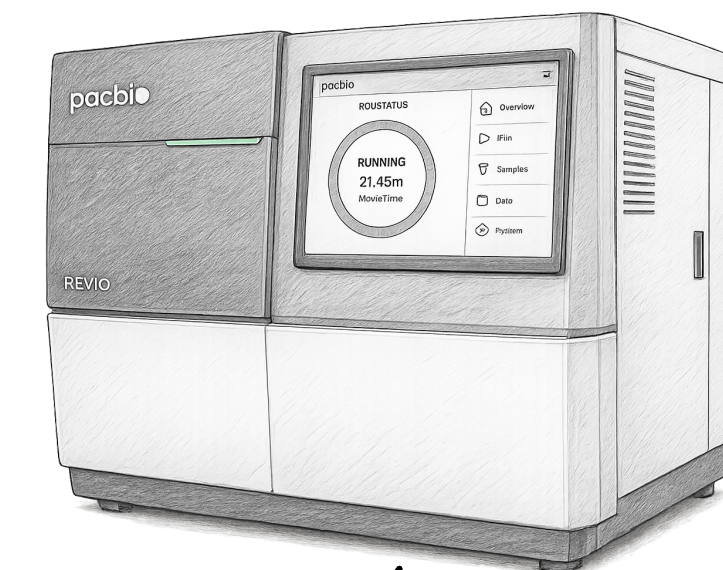
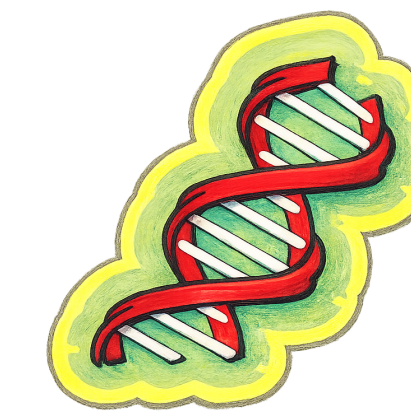
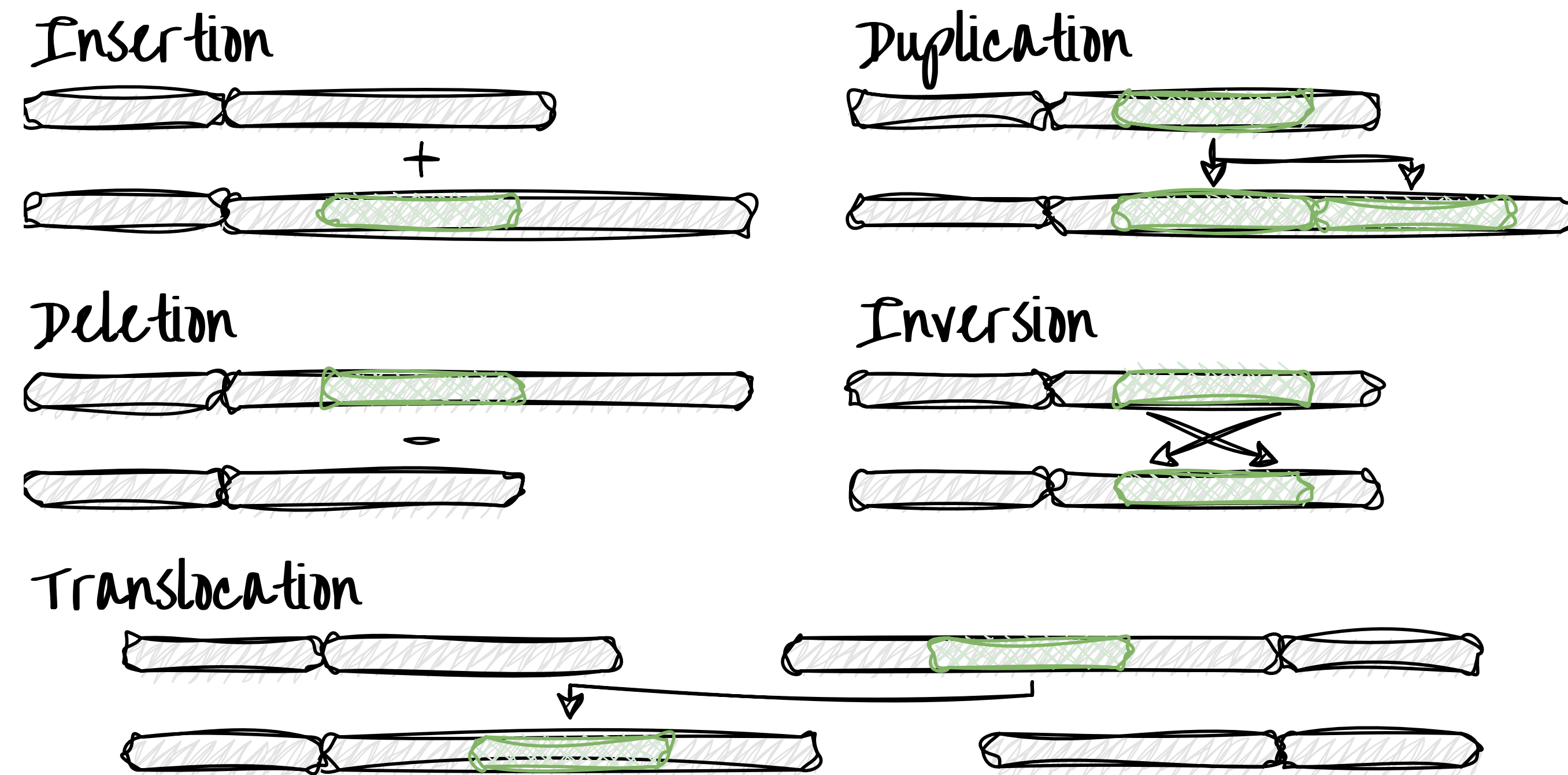
!! This first section does not cover pangenomics !!

Single linear reference - but still a nice introduction to why CS is essential
(pangenomics just make things worse 😅)

Structural Variants calling

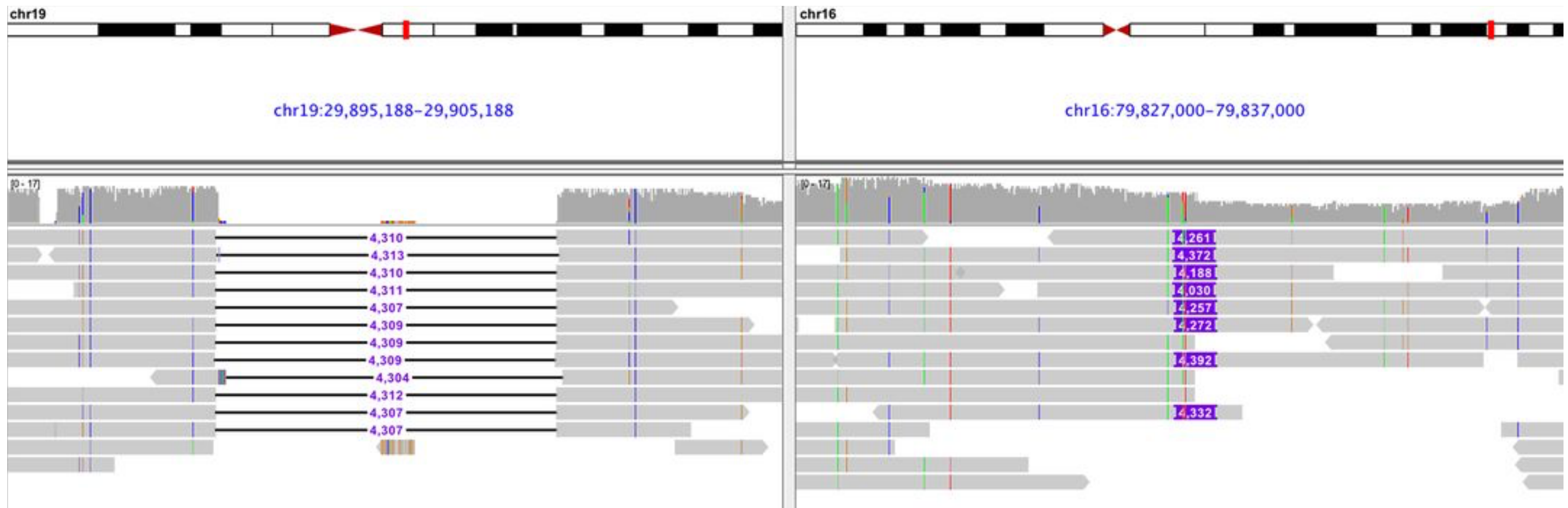
Large ($\geq 50bp$) genomic rearrangements

→ To find in sequencing reads



Why?

Structural Variations play a crucial role in **genetic disorders** and **cancer**

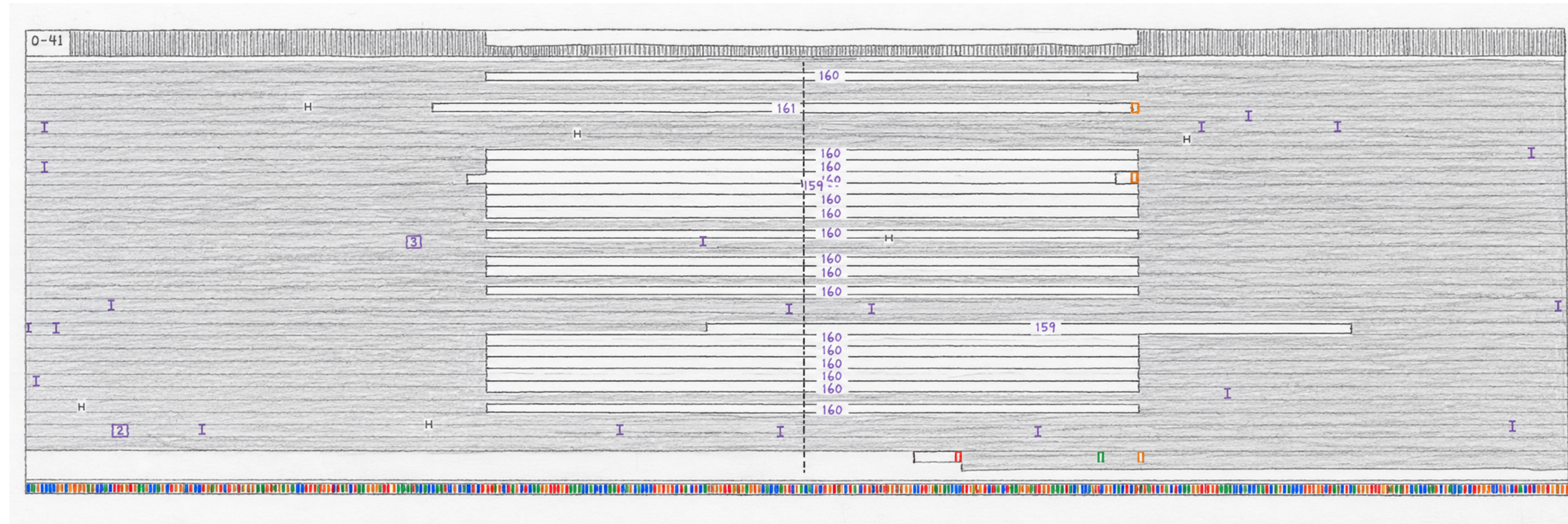


4.3kb translocation in the SK-BR-3 breast cancer cell line

State-of-the-art

Many alignment-based approaches *for short and long reads*

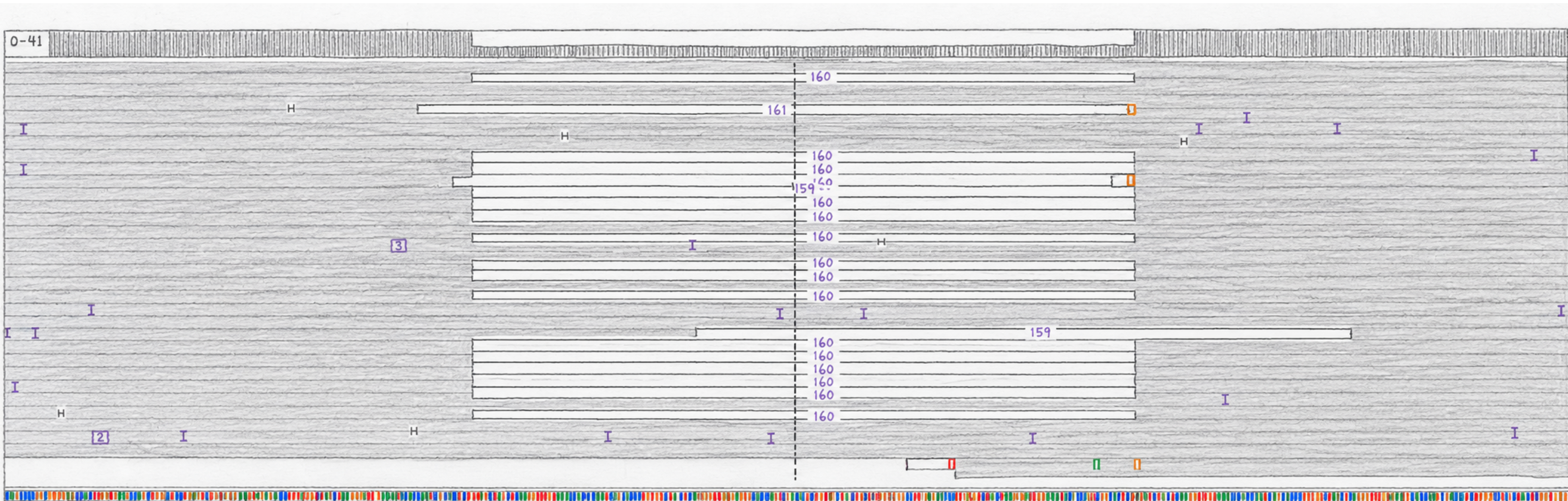
[Manta, DELLY, Lumpy, cuteSV, pbsv, sniffles, debreak, SVDSS, sawfish, ...]



Limitations:

- SVs detection in challenging/repetitive regions of the genome
- SVs with different alleles on two haplotypes (heterozygous events)

Key Idea



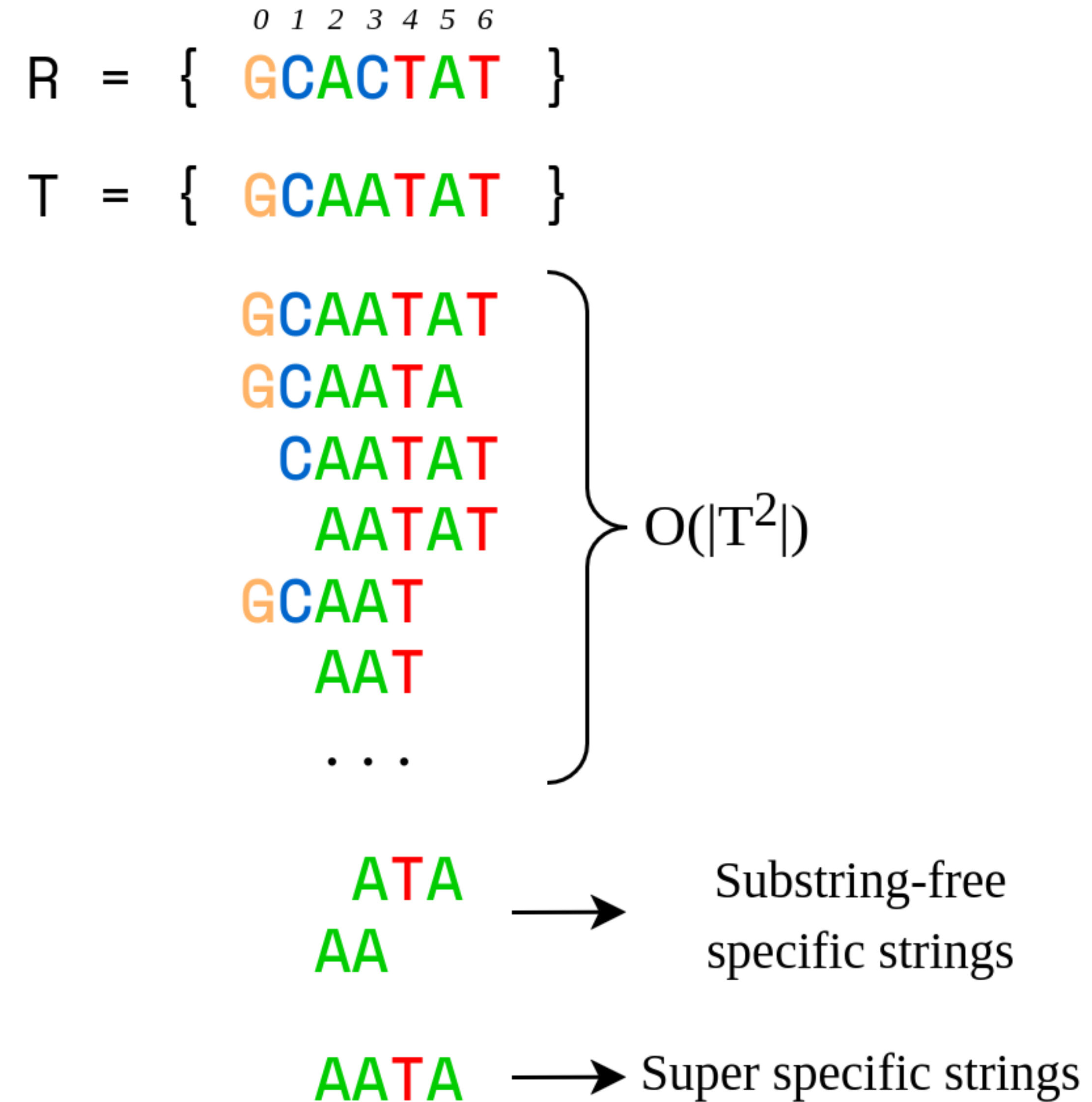
SVs can be seen as **differences** between the reference and the reads
(let's try to characterize them)

Specific strings

Given two sets of strings (R, T) ,
a **specific string** is any substring:

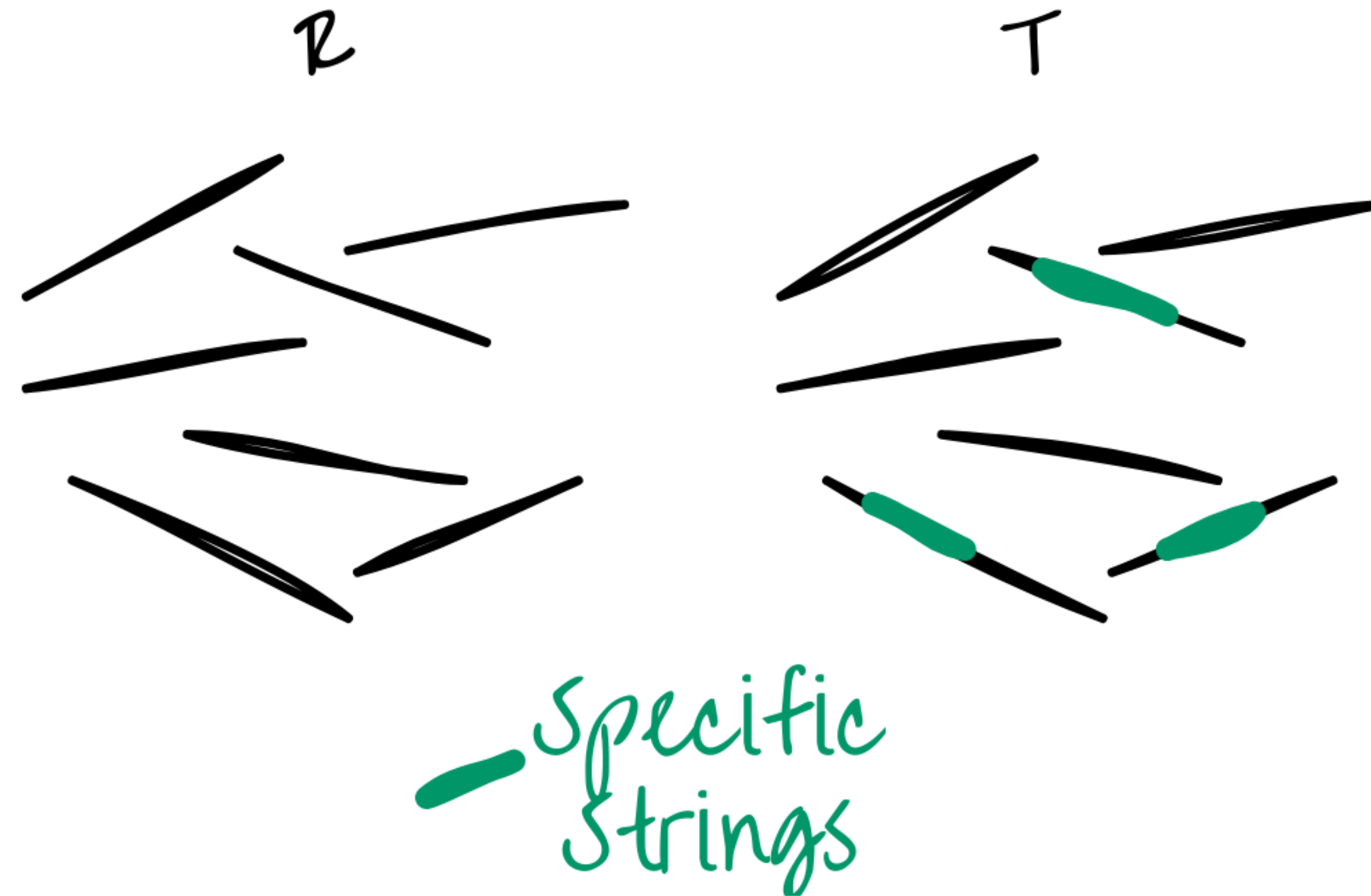
- (i) occurring in T and not occurring in R (*substring*)
- (ii) s.t. no other specific string is contained in it
(i.e., it is the *shortest*)

+ merge all specific strings overlapping on $t \in T$



Specific strings

Any portion of a string in the **Target** that cannot be found in the **Reference**



If R is the **reference genome** and T the **reads**,
then specific strings pinpoint (mostly) all variations

How to compute specific strings?

- **Human genome:** ~3 billion base pairs
- **PacBio HiFi, 30x:** ~6 million, ~15000bp-long

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How to compute specific strings efficiently? *Use specialized data structure (FMD-Index*)*

***Disclaimer:** *there are alternatives, not covered here :)*

FM-Index

Full-text index for a string:

- *efficient storing of full input*
- *efficient querying for substrings*

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Occurrence matrix + Counts vector
(single genome: ~60GB*)

	Rotations	BWT	\$	a	b	n
0	\$banana	a	0	1	0	0
1	a\$banan	n	0	1	0	1
2	ana\$ban	n	0	1	0	2
3	anana\$b	b	0	1	1	2
4	banana\$	\$	1	1	1	2
5	na\$bana	a	1	2	1	2
6	nana\$ba	a	1	3	1	2
Counts:			0	1	4	5

*What about indexing multiple genomes (i.e., a pangenome)?

FM-Index

Full-text index for a string:

- *efficient storing of full input*
- *efficient querying for substrings*

Occurrence matrix + Counts vector
(single genome: ~60GB*)

Advanced CS techniques

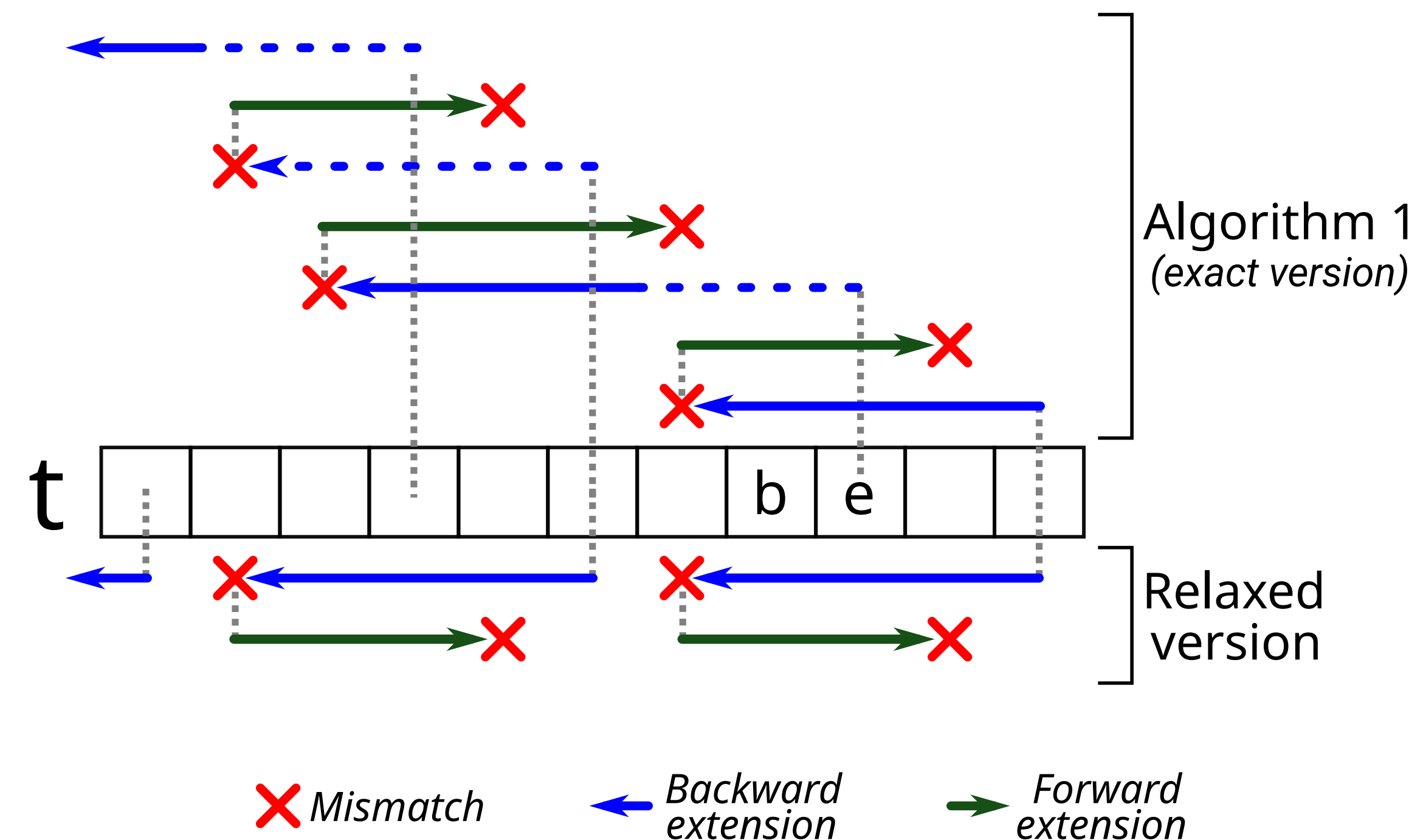
wavelet tree/matrix, B+-trees, run-length compression...
(single genome: <3GB)

	Rotations	BWT	\$	a	b	n
0	\$banana	a	0	1	0	0
1	a\$banan	n	0	1	0	1
2	ana\$ban	n	0	1	0	2
3	anana\$b	b	0	1	1	2
4	banana\$	\$	1	1	1	2
5	na\$bana	a	1	2	1	2
6	nana\$ba	a	1	3	1	2
Counts:			0	1	4	5

*What about indexing multiple genomes (i.e., a pangenome)?

Ping-Pong algorithm

- Based on **minimality property**
- Complexity: $O(n^2)$
we like to be pessimistic :)
- In practice: $O(n)$



SVDSS

Combination of old and new ideas:

- *Alignment-based error correction*
- *FM-index*
- *Specific strings*
- *Sweep-line clustering*
- *Partial order alignment*
- *Dual affine-gap sequence alignment*

Higher recall, comparable precision

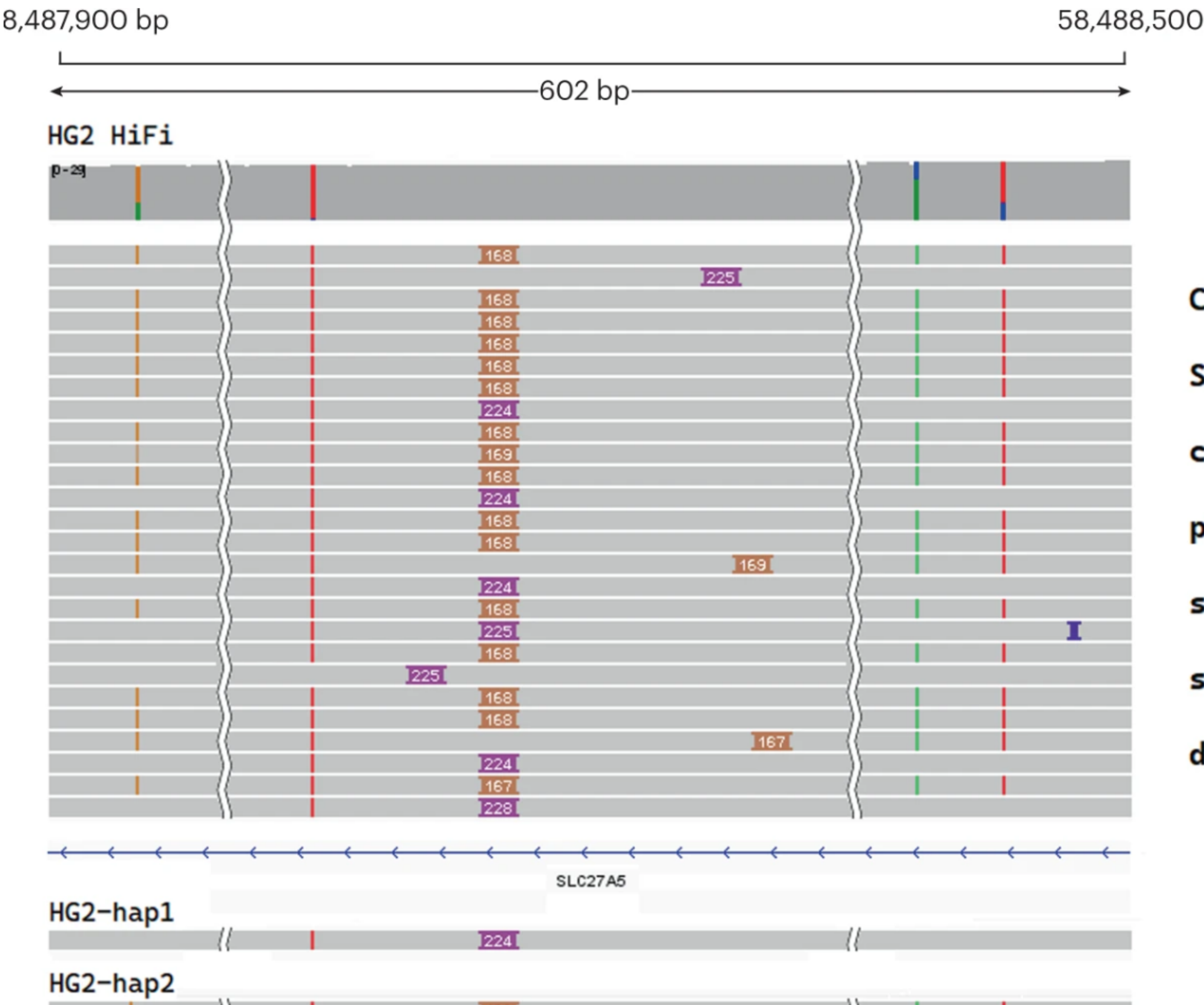
Region	Tool	HG002			HG007			CHM13		
		P	R	F1	P	R	F1	P	R	F1
Full Genome	SVDSS	88.4	78.2	83.0	90.1	76.5	82.7	87.3	84.6	86.0
	cuteSV	86.0	68.6	76.3	88.3	68.1	76.9	87.1	79.7	83.2
	pbsv	86.9	68.8	76.8	84.9	68.6	75.9	84.6	82.7	83.6
	sniffles	82.0	67.3	73.9	86.7	64.1	73.7	86.4	81.4	83.8
	SVIM	83.5	65.1	73.2	84.9	64.7	73.4	90.1	79.9	84.7
	debreak	88.6	67.5	76.6	90.1	64.2	75.0	83.7	79.6	81.6
Tier 1	SVDSS	95.2	85.5	90.1	95.2	82.7	88.5	95.3	93.4	94.5
	cuteSV	90.9	82.9	86.7	93.0	79.9	86.0	94.8	93.1	93.9
	pbsv	95.7	83.1	89.0	89.7	80.5	84.9	94.0	93.7	93.9
	sniffles	87.7	81.1	84.3	92.3	75.9	83.3	87.2	93.6	90.3
	SVIM	90.1	81.1	85.4	91.5	77.9	84.2	96.6	92.5	94.5
	debreak	96.8	82.5	89.1	96.2	76.4	85.2	93.7	93.0	93.3
Extended Tier 2	SVDSS	82.7	72.3	77.2	84.6	70.2	76.7	80.3	77.4	78.8
	cuteSV	80.9	57.0	66.9	82.3	56.0	66.6	79.9	68.1	73.6
	pbsv	78.4	57.2	66.1	78.8	56.4	65.7	76.0	73.3	74.6
	sniffles	77.8	56.1	65.2	80.3	52.1	63.2	72.7	73.2	72.9
	SVIM	76.4	52.0	61.9	76.2	51.2	61.2	83.4	69.3	75.7
	debreak	80.4	55.3	65.5	82.3	51.9	63.7	74.4	68.1	71.1

R: +9%, +12%, +2%

R: +2%, +2%, +0%

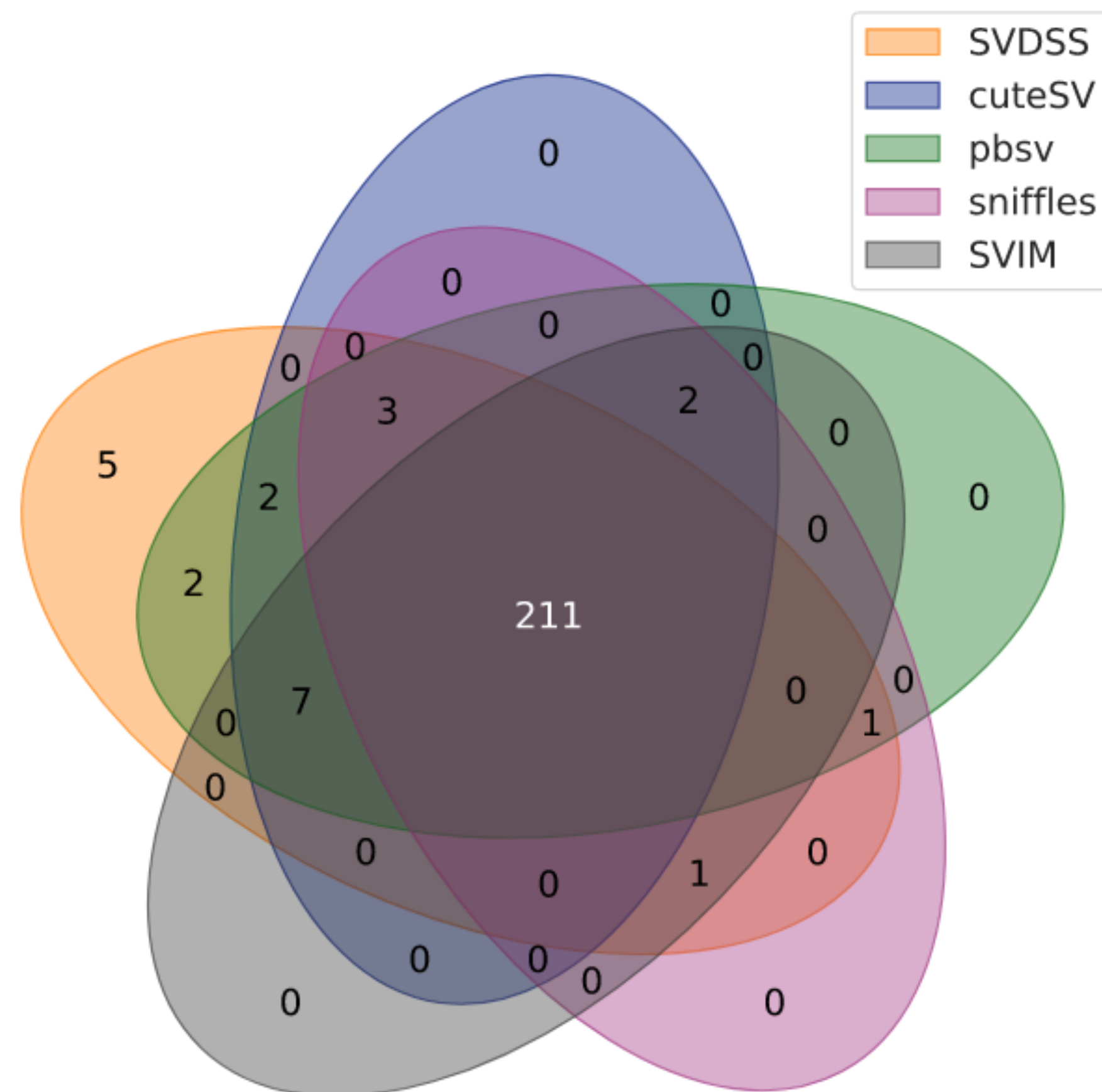
R: +15%, +14%, +4%
(challenging regions)

Heterozygous (1/2) calls

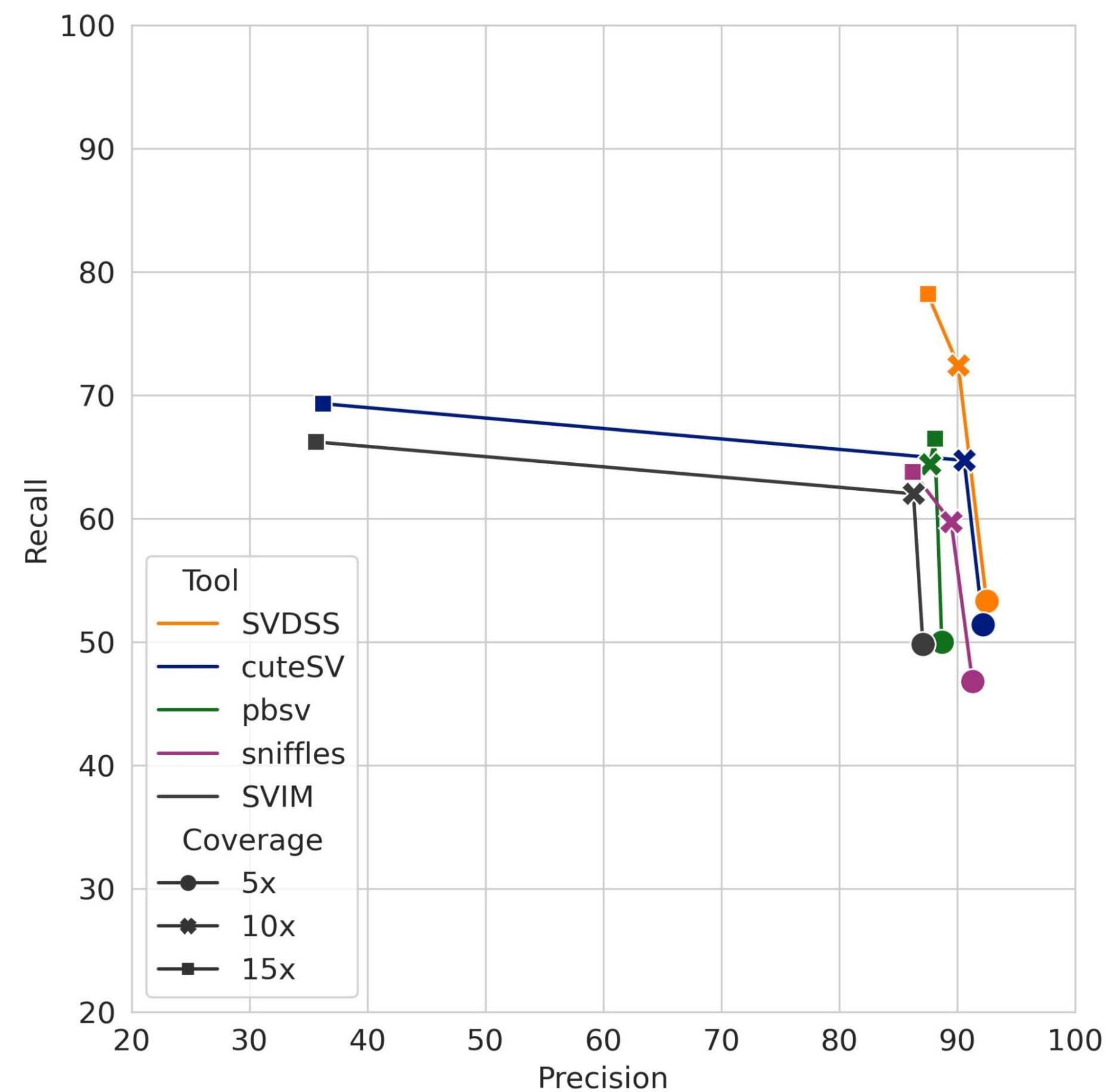


CMRG:	chr19:58488284	SVLEN=168,224	GT	1/2
SVDSS:	chr19:58488284	SVLEN=168,224	GT	1/2
cuteSV:	chr19:58488291	SVLEN=185	GT	0/1
pbsv:	chr19:58488284	SVLEN=168	GT	0/1
svim:	chr19:58488290	SVLEN=185	GT	0/1
sniffles:	chr19:58488285	SVLEN=168	GT	0/1
debreak:	chr19:58488290	SVLEN=185	GT	1/1

Other results



(i) *Best recall for challenging medically relevant SVs*

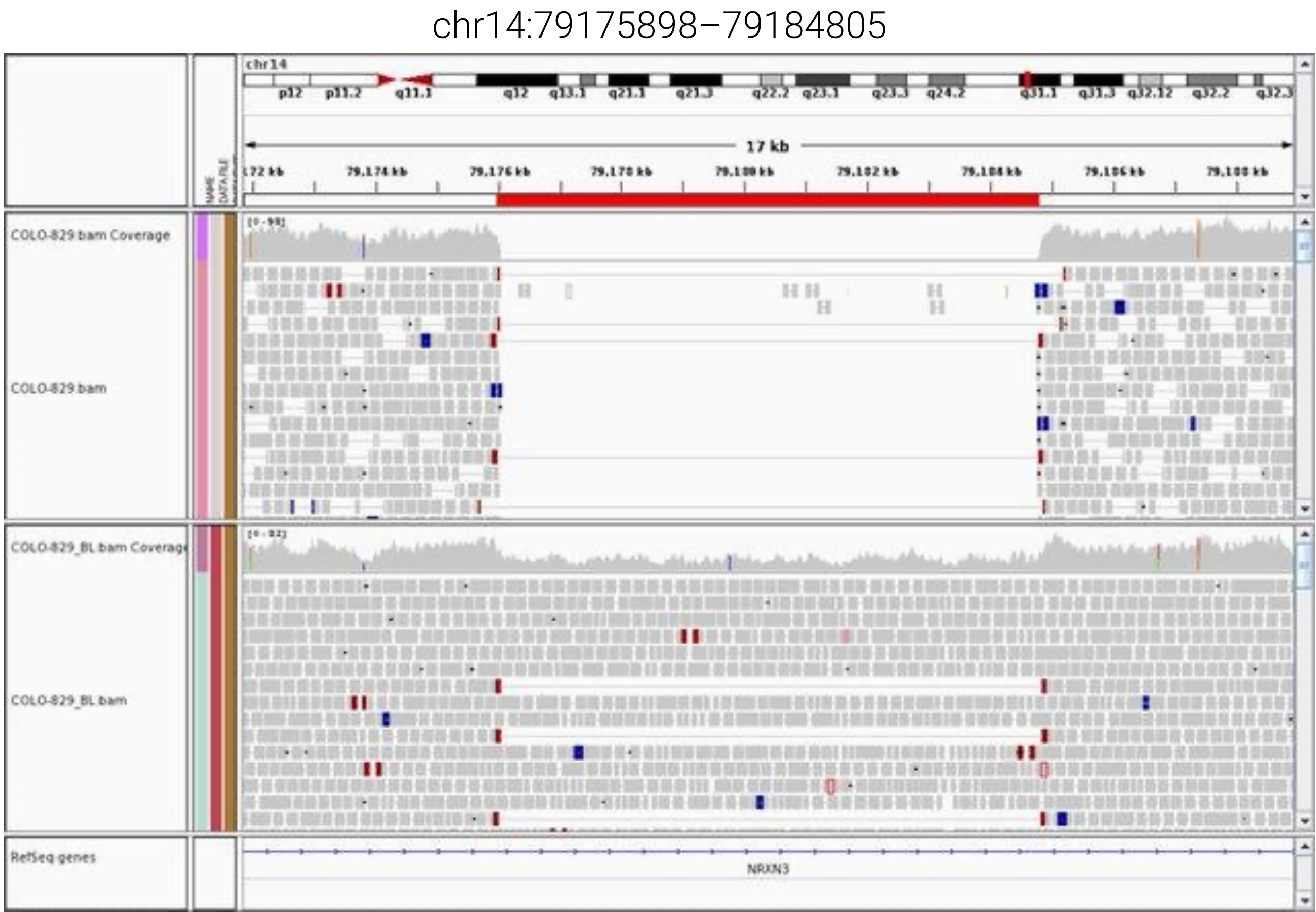


(ii) *Best calling performance even at 5x coverage*

Future: Somatic SV calling



Davide Monti

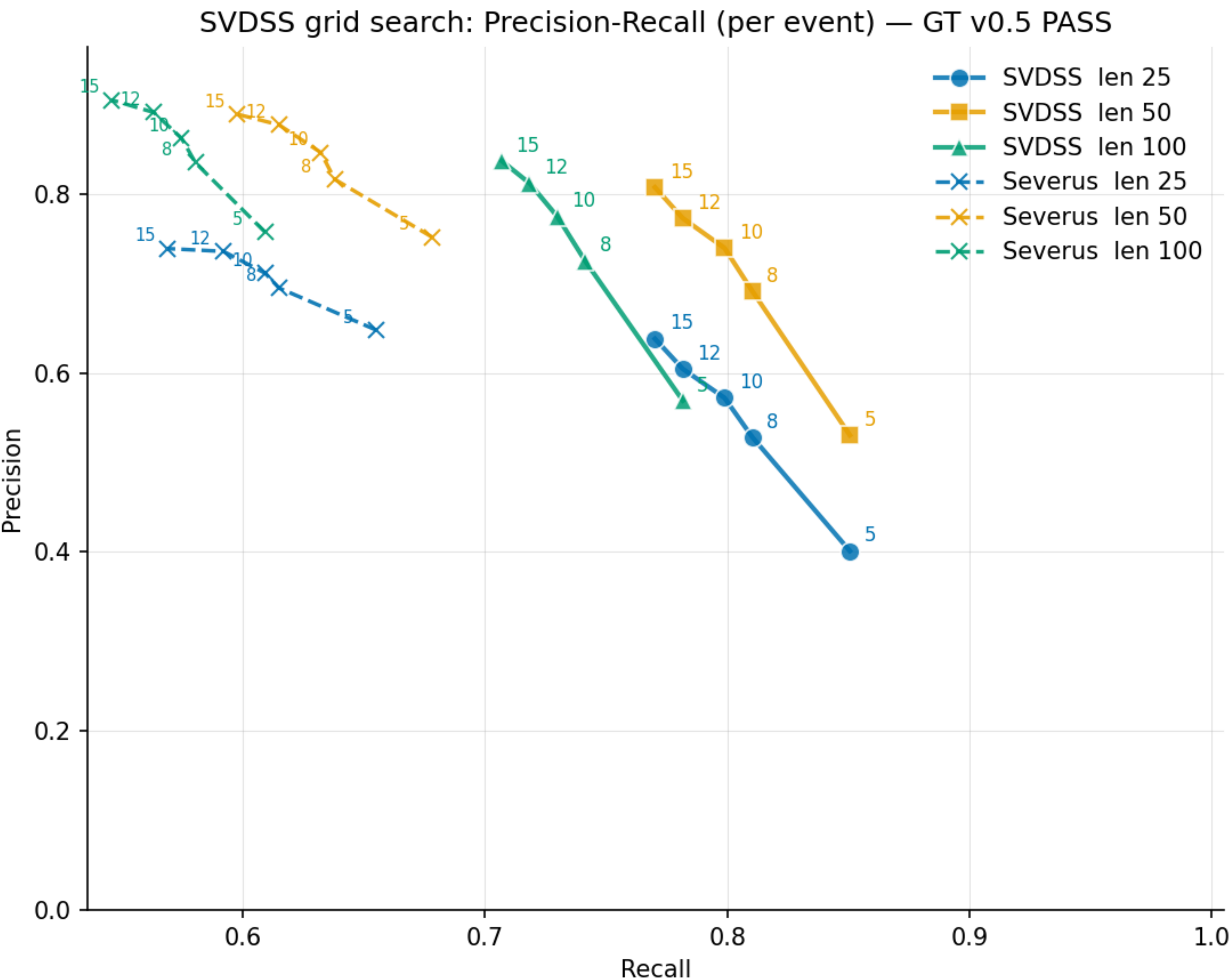


~9kb deletions (LOH event) in gene NRXN3 (metastatic melanoma cancer)

Future: Somatic SV calling



Davide Monti



Pitfalls of SVs evaluation

Denti et al. bioRxiv (2025)
(currently under review @Nature Communications)

Entering a gray(ish) zone

Until now, everything I presented seems **perfect!**

Problem ➡ Solution ➡ Good results

Entering a gray(ish) zone

Until now, everything I presented seems **perfect!**

Problem ➡ Solution ➡ Good results

Are we sure we are correct?

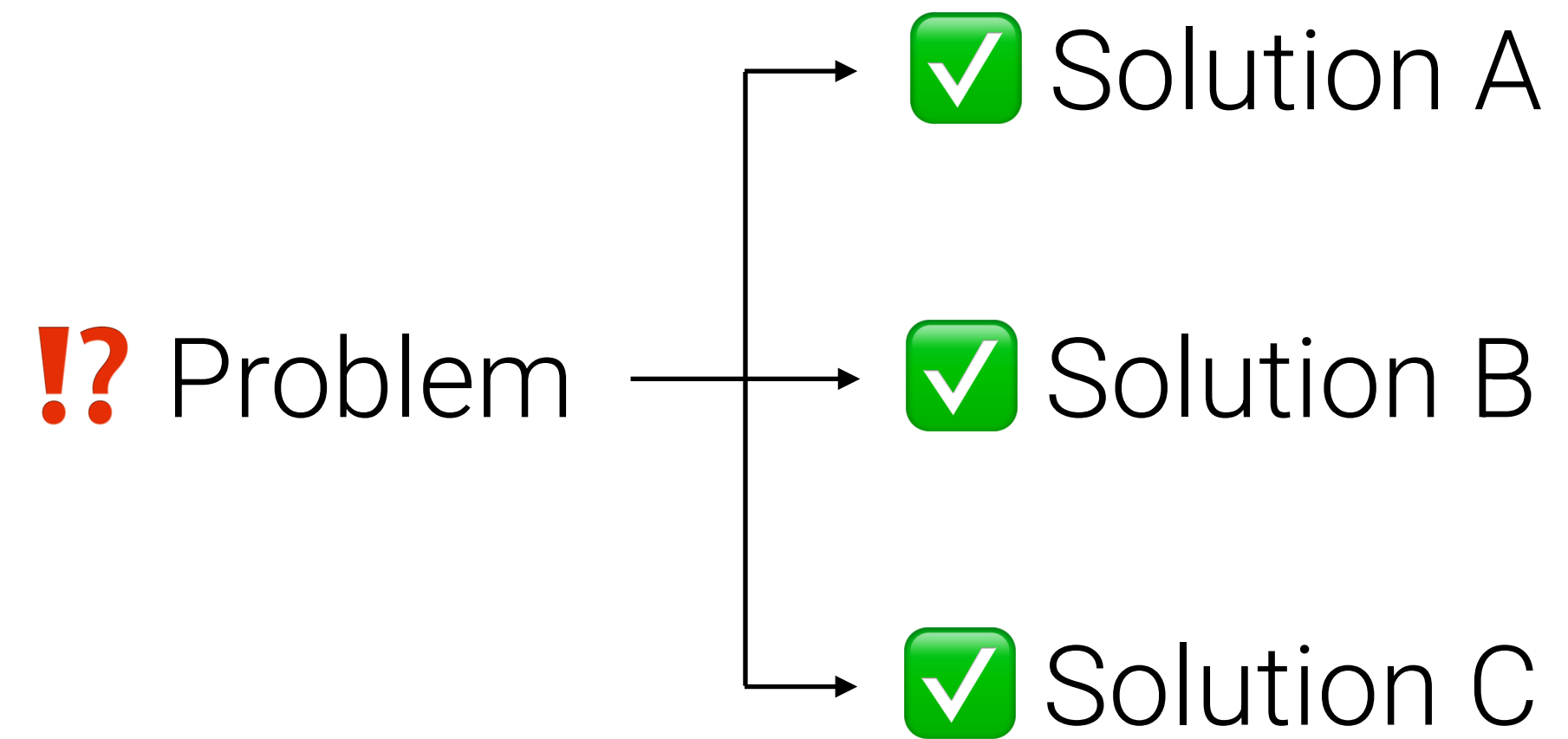
No solution, just a(n expected?) problem*

**This will be a recurrent theme in this second section 😊*

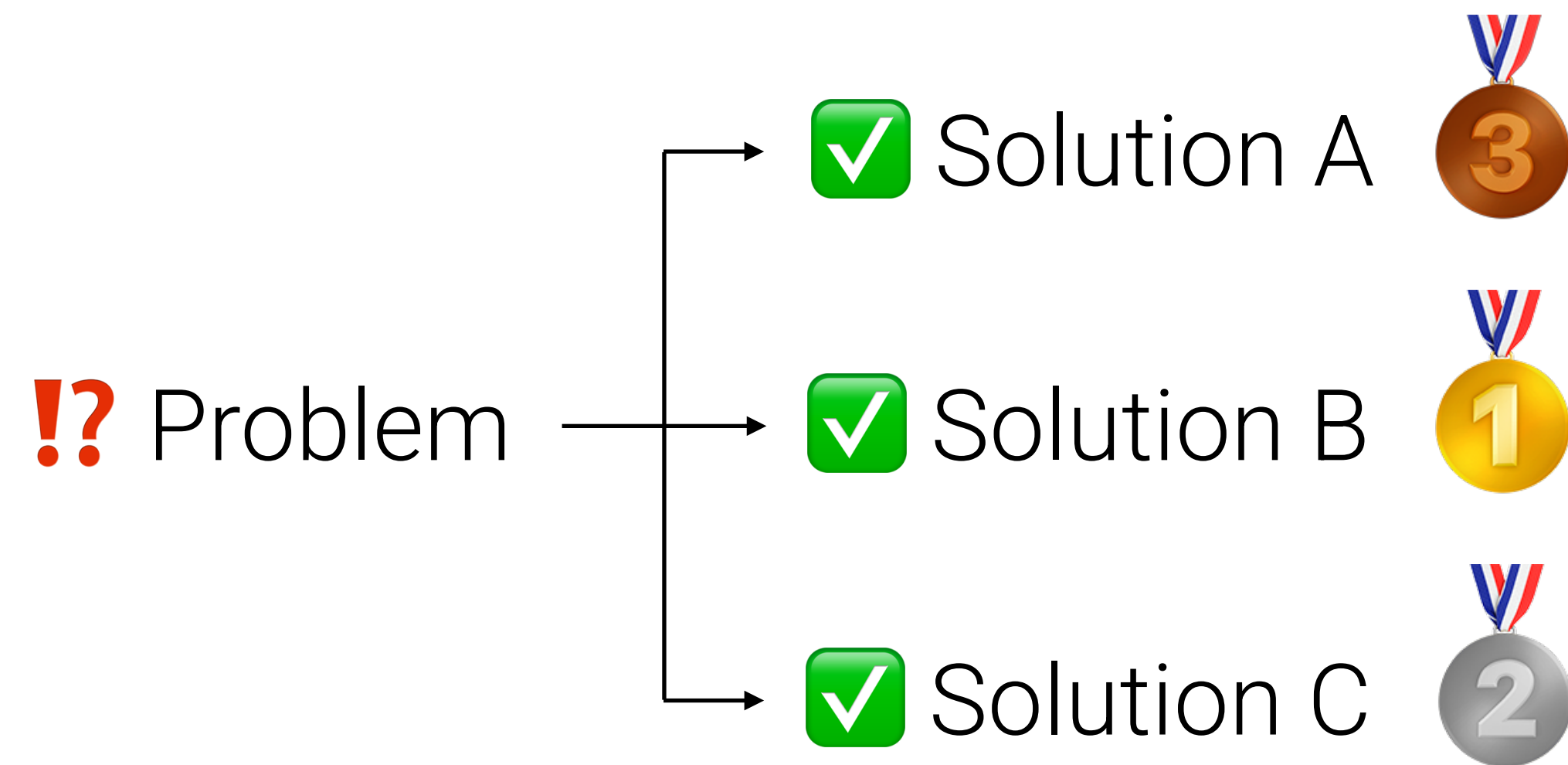
Context

! Problem

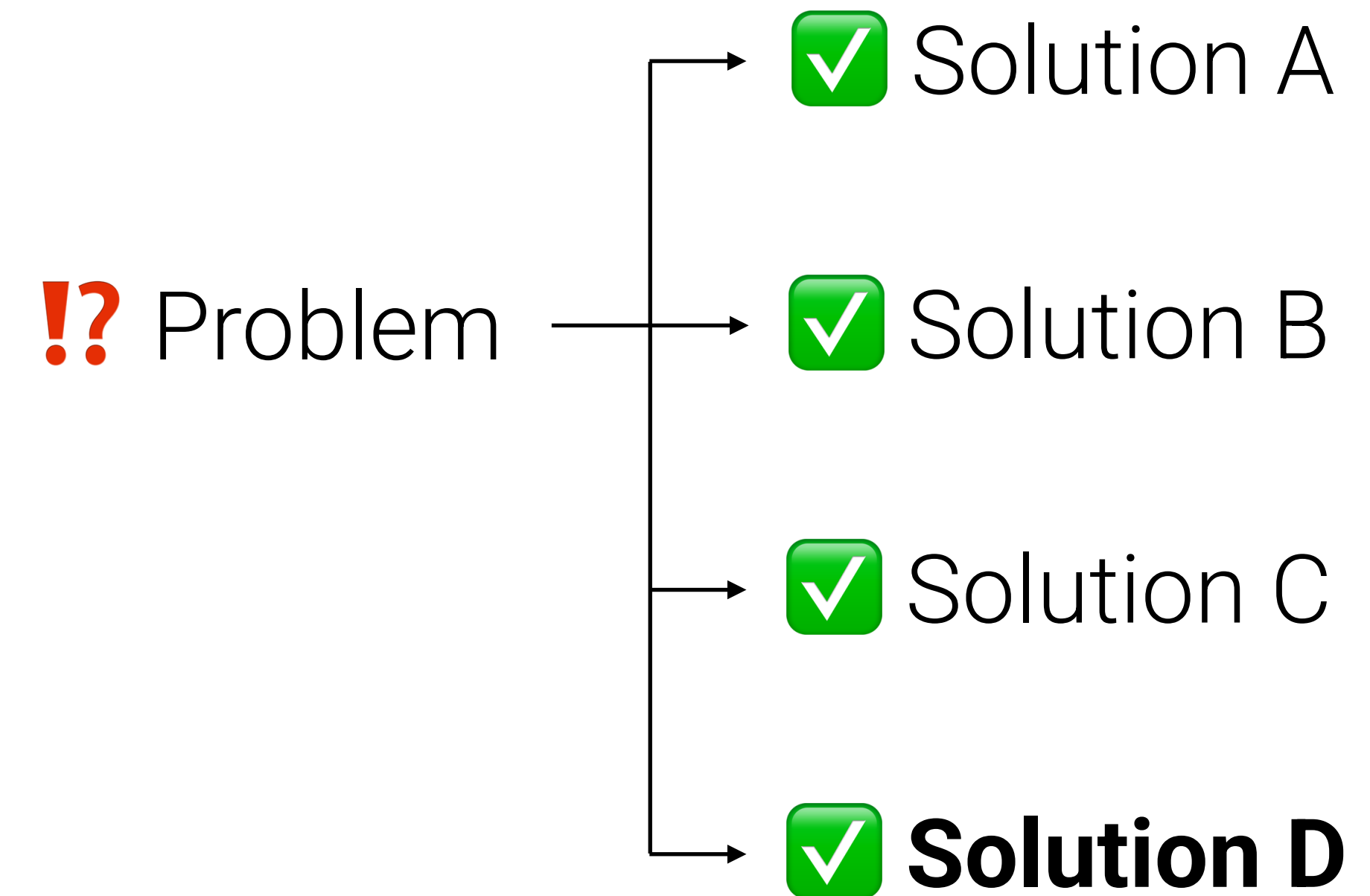
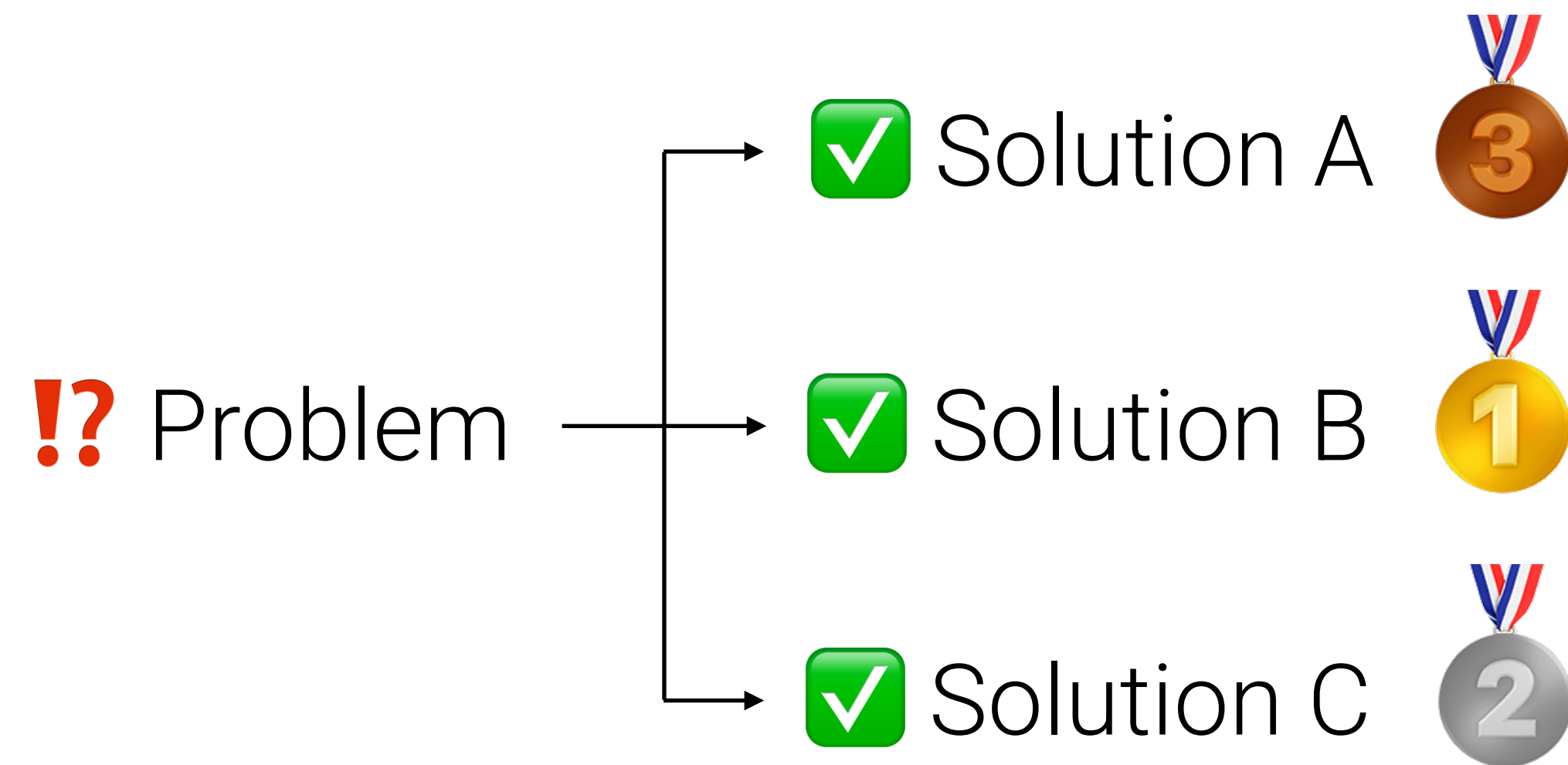
Context



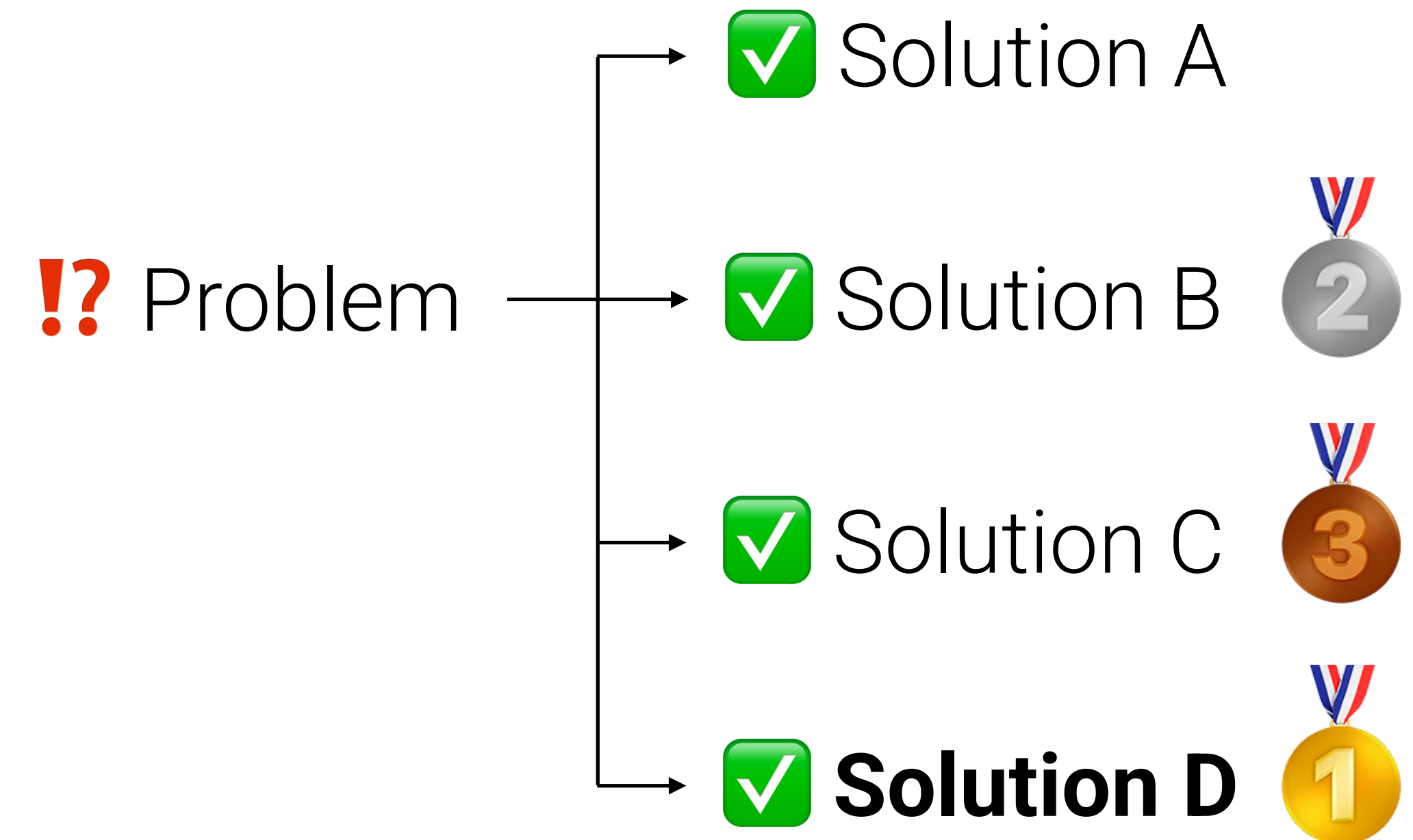
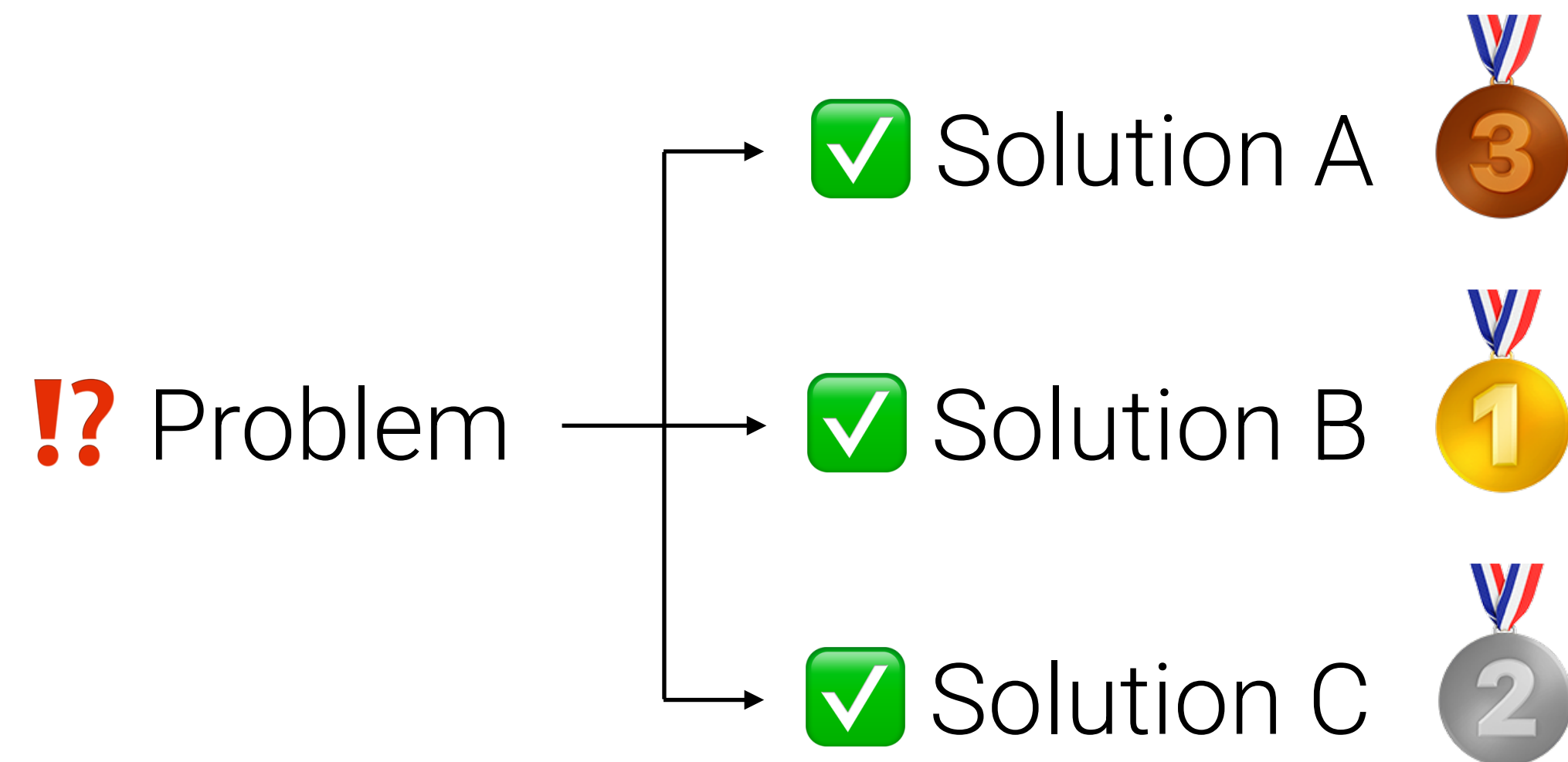
Context



Context

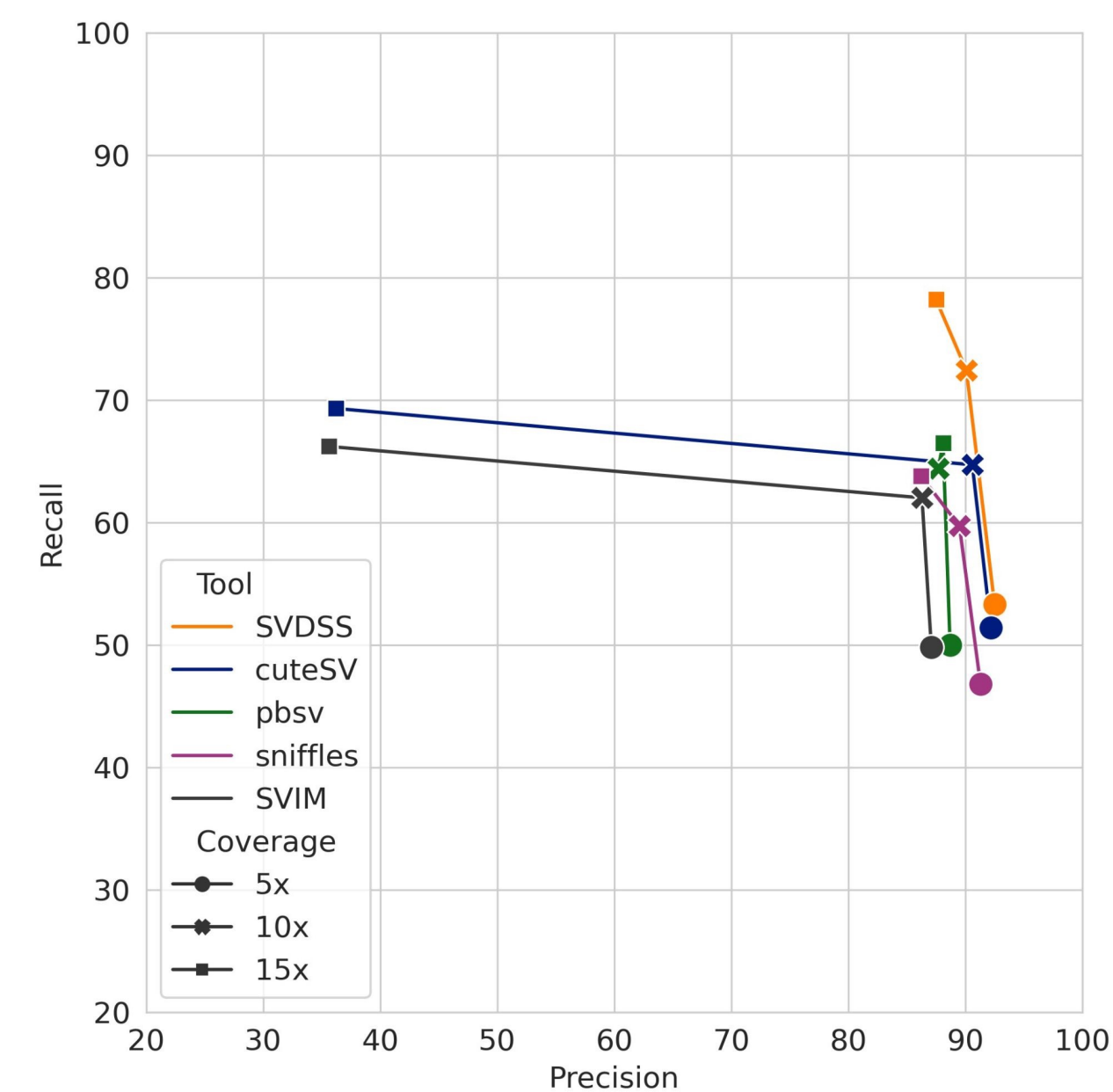


Context

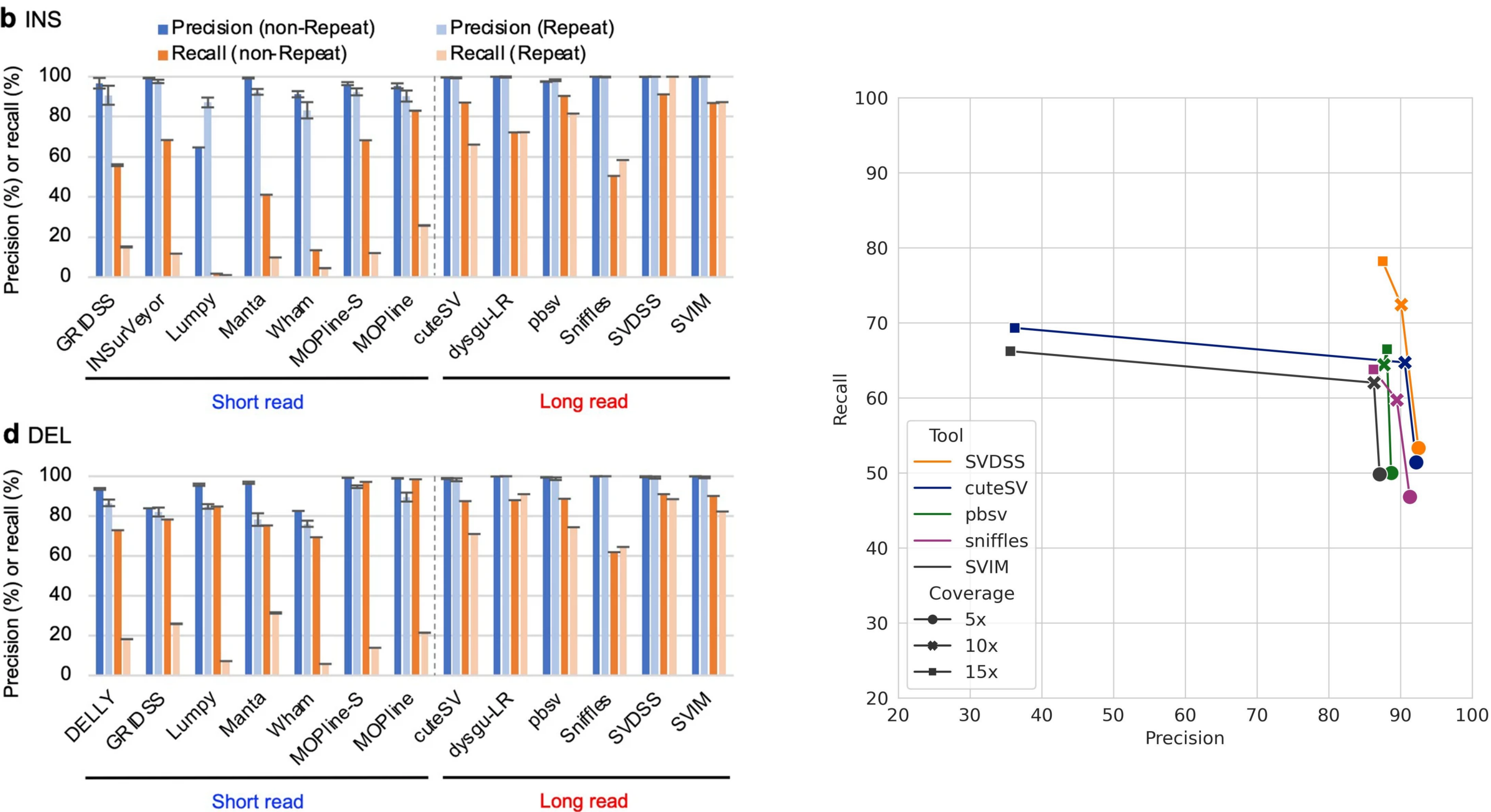


Ranking among solutions should be preserved

Inconsistent Ranking

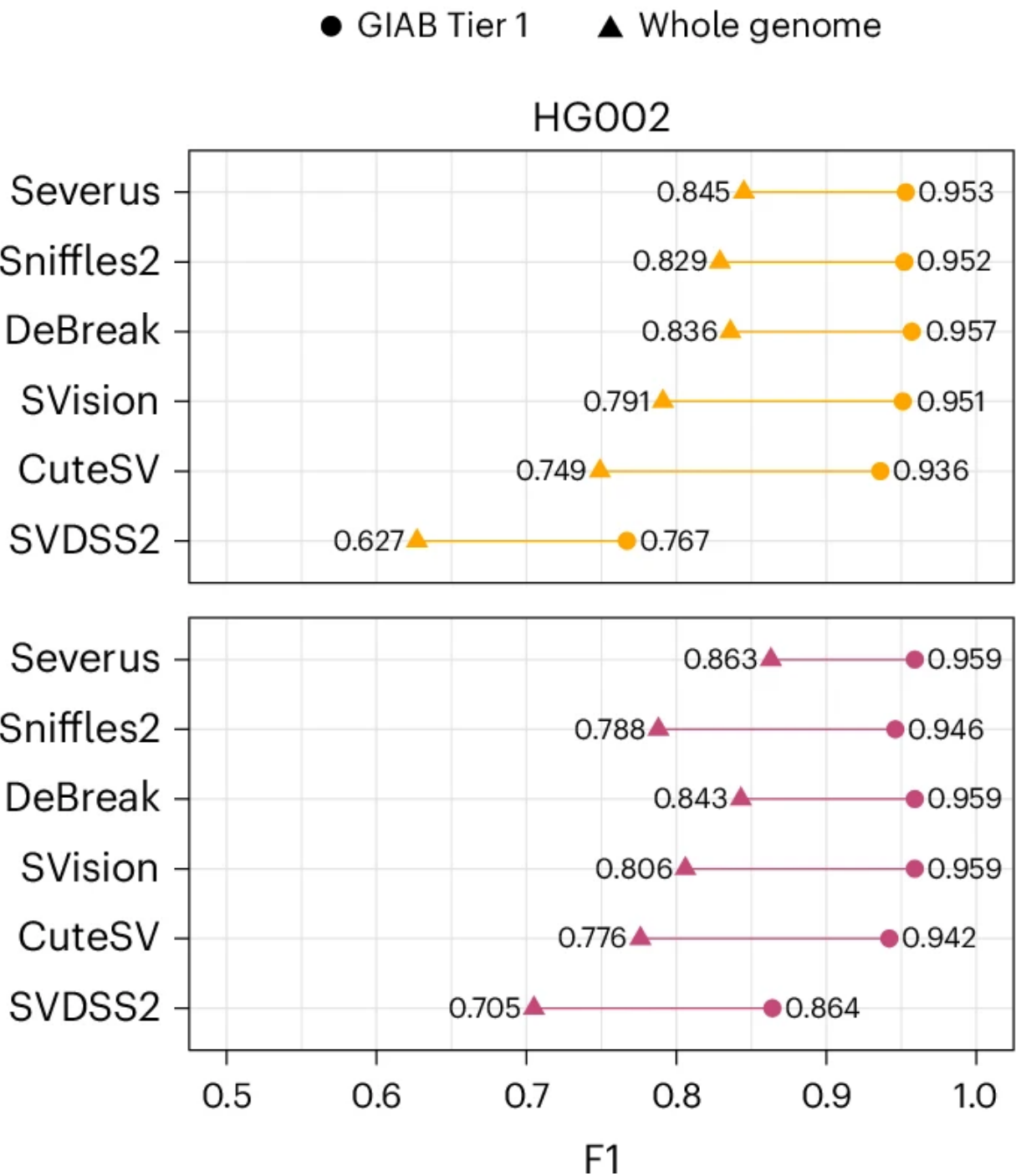
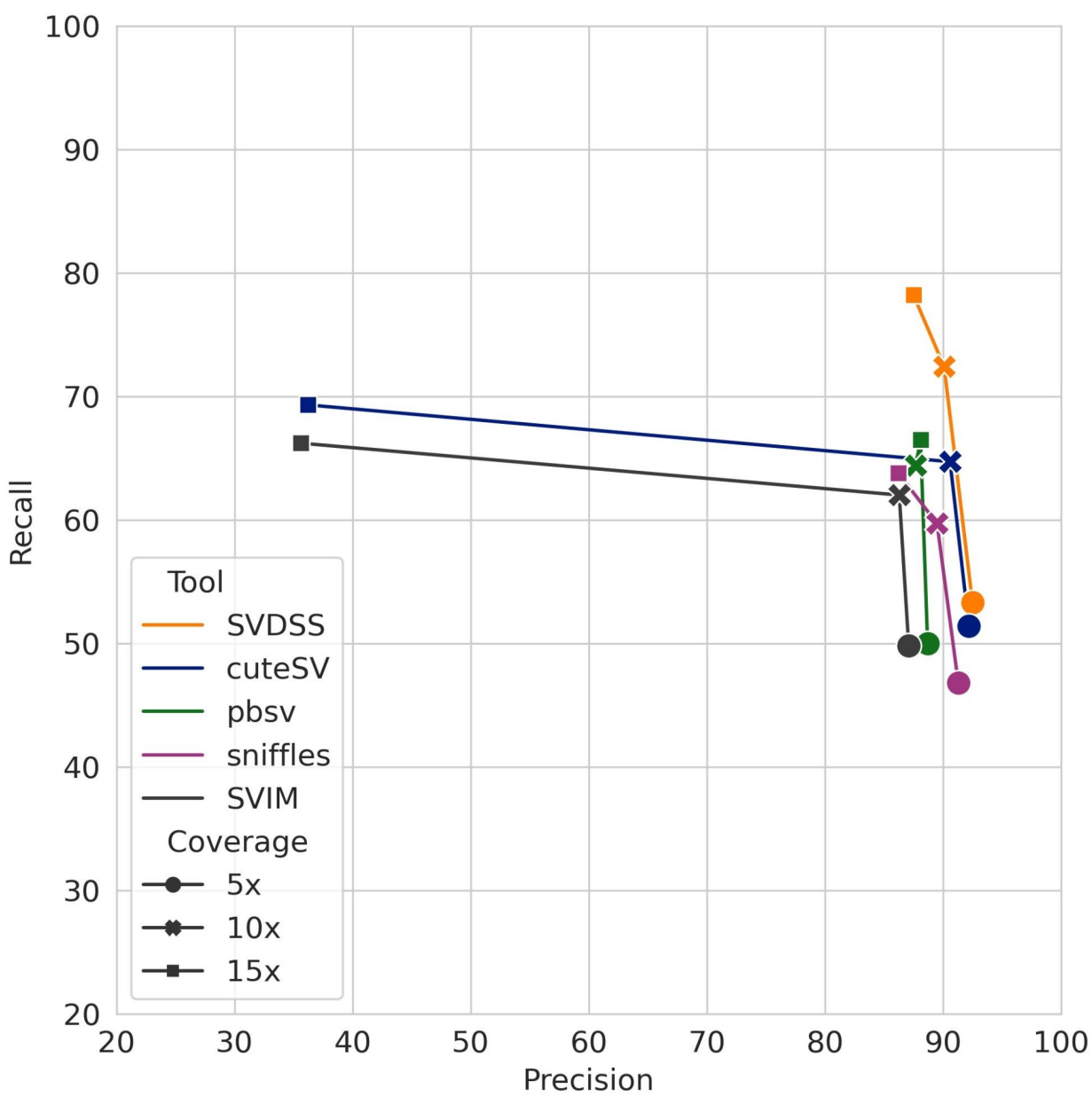
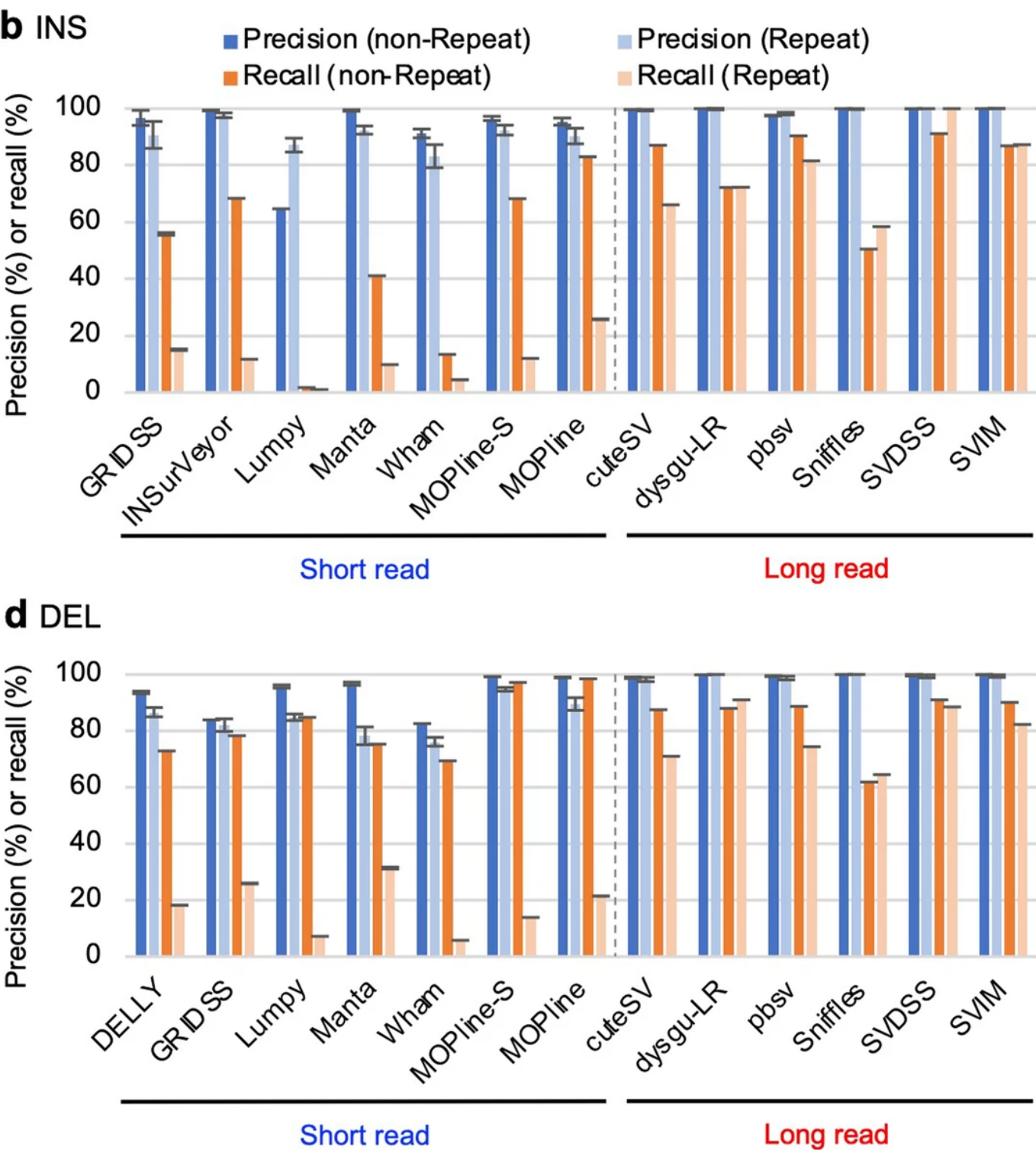


Inconsistent Ranking



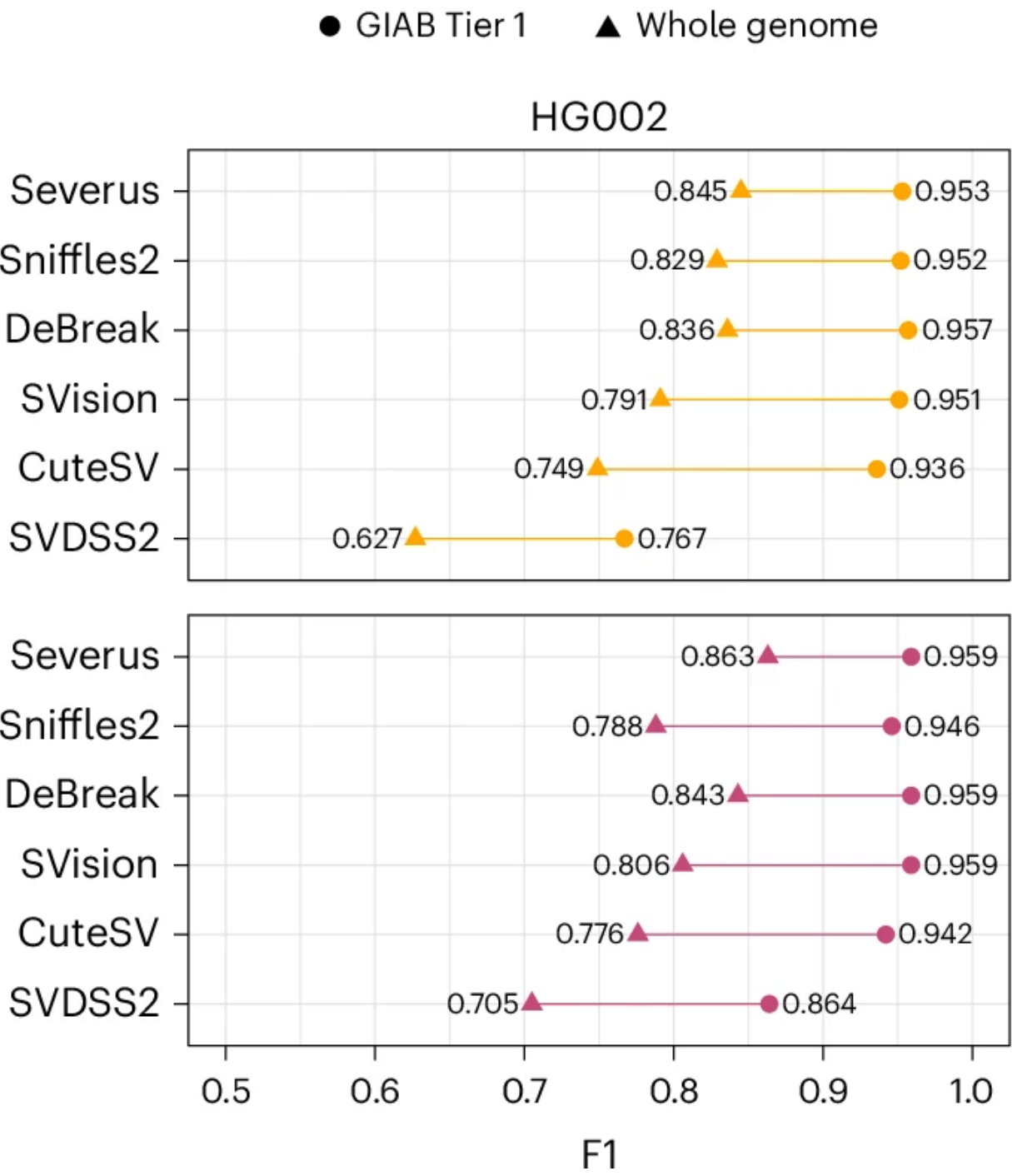
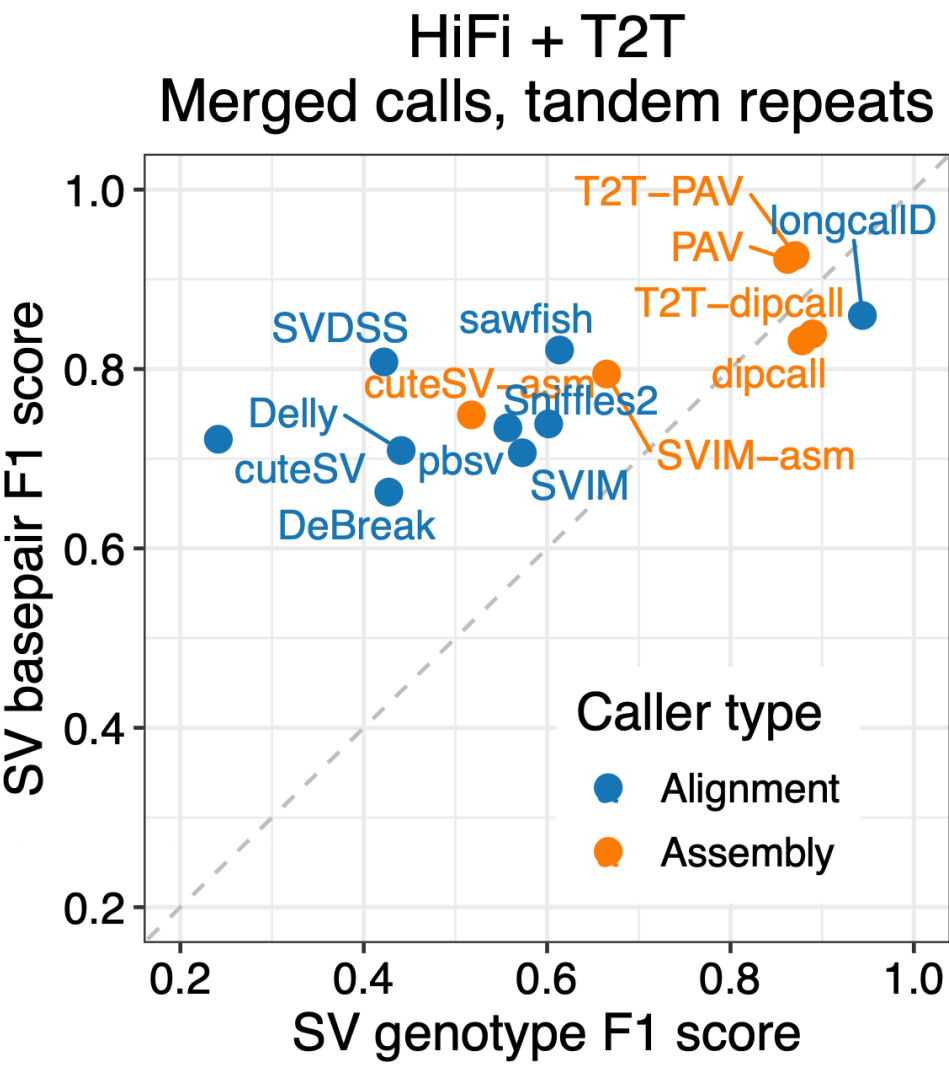
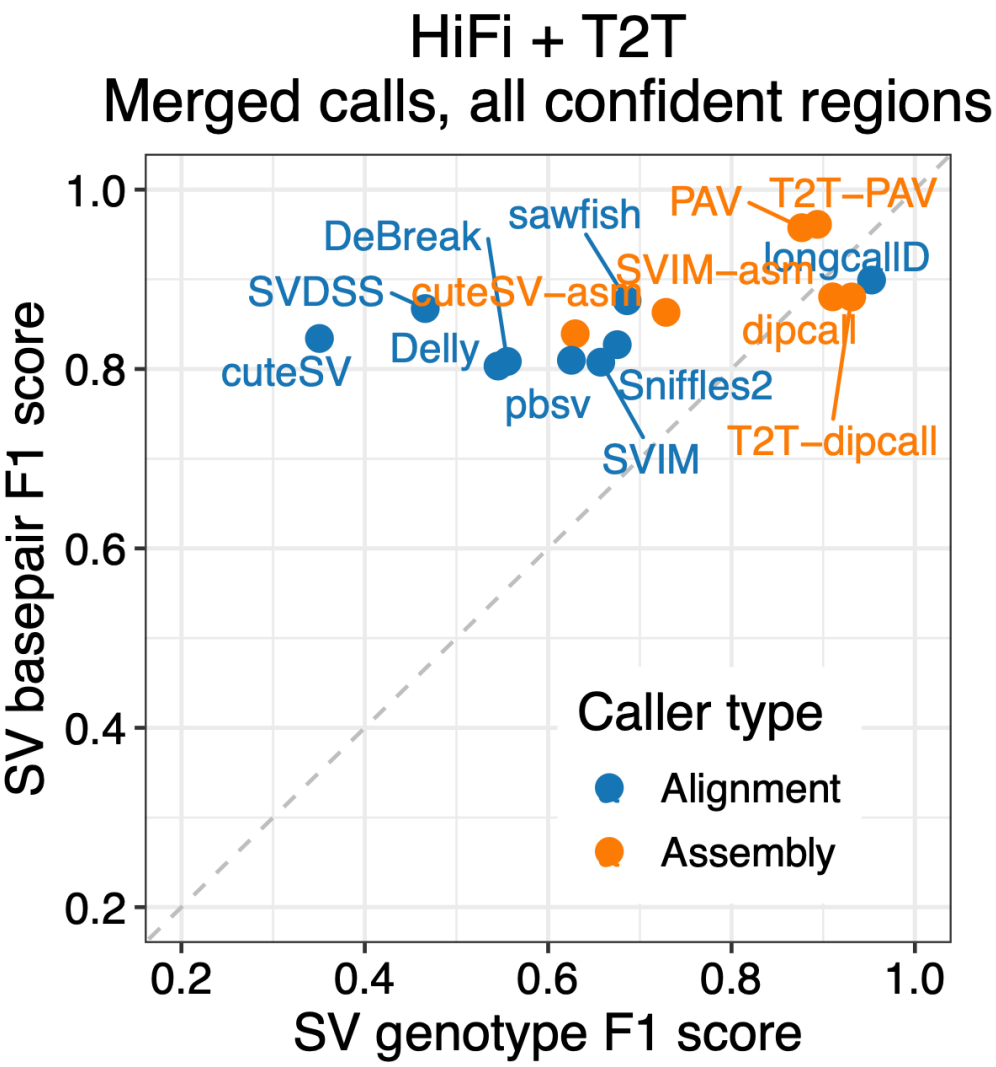
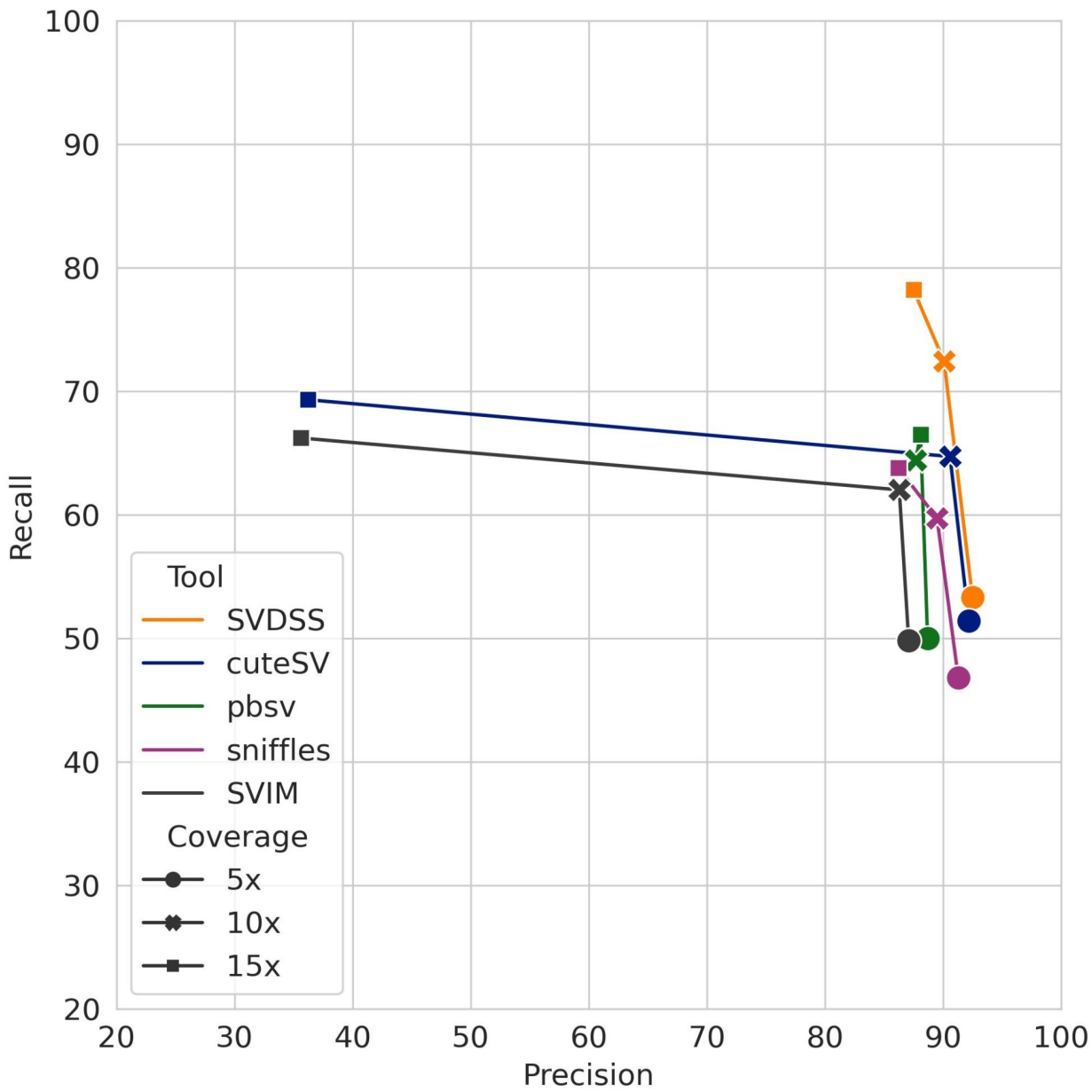
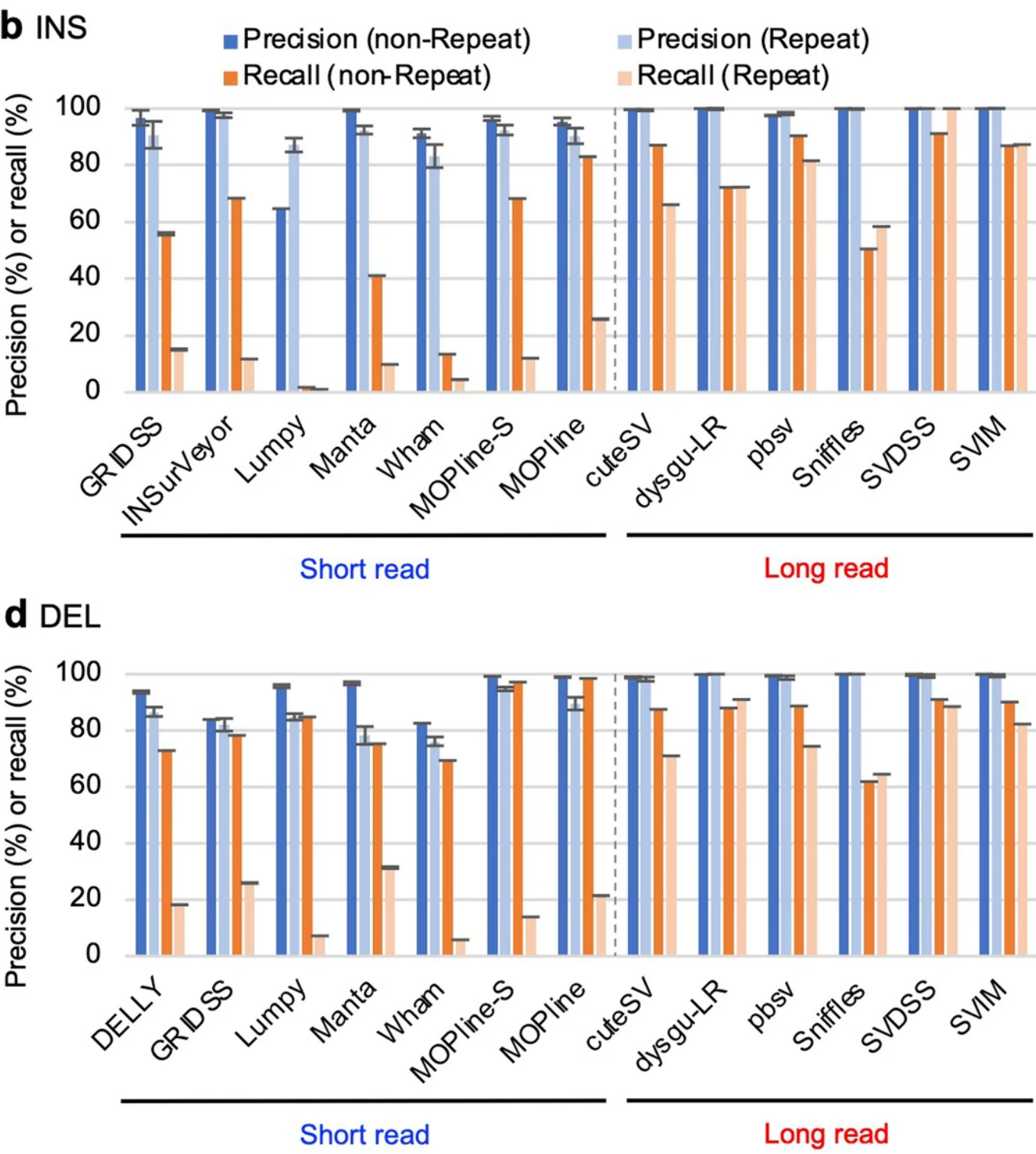
Denti et al. Nature Methods (2023)
Kosugi and Chikashi. Human Genome Variation (2024)

Inconsistent Ranking



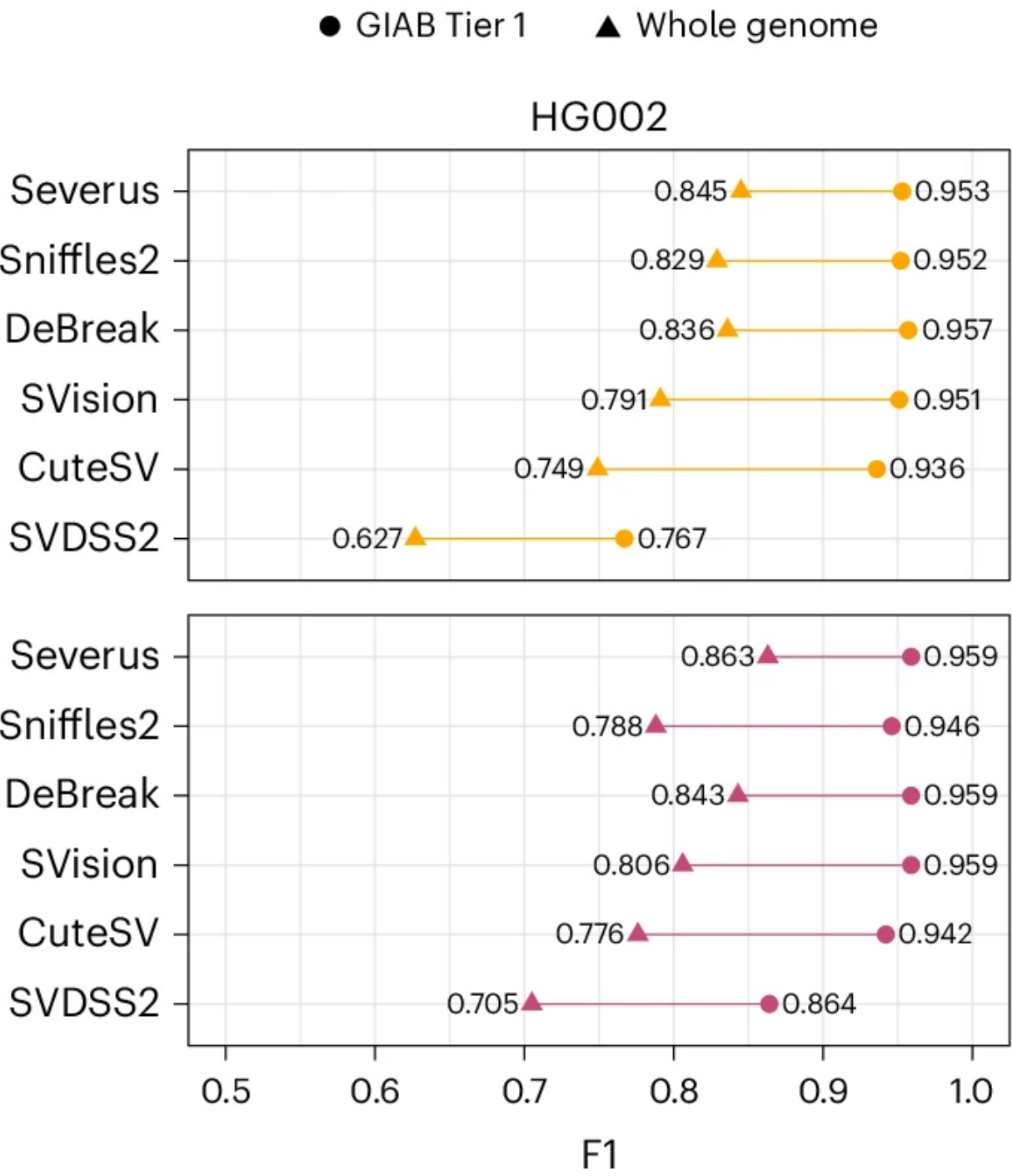
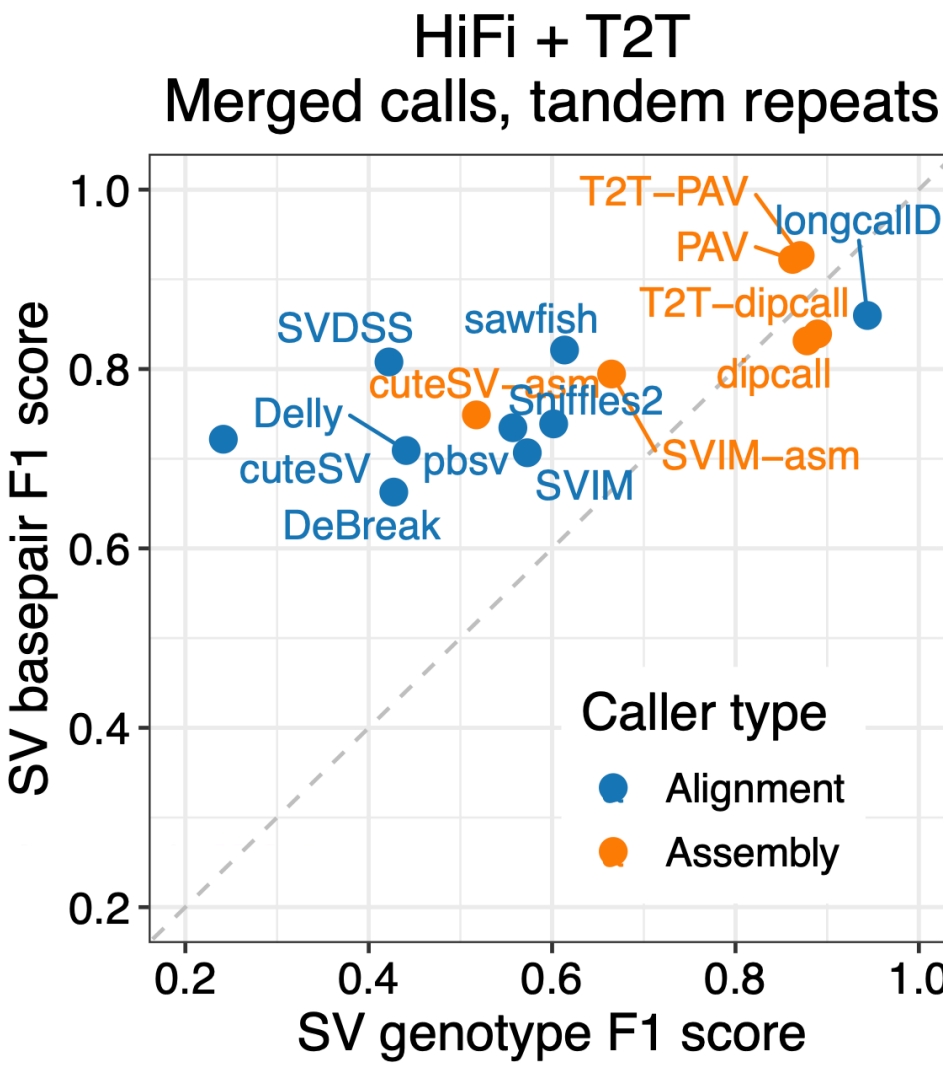
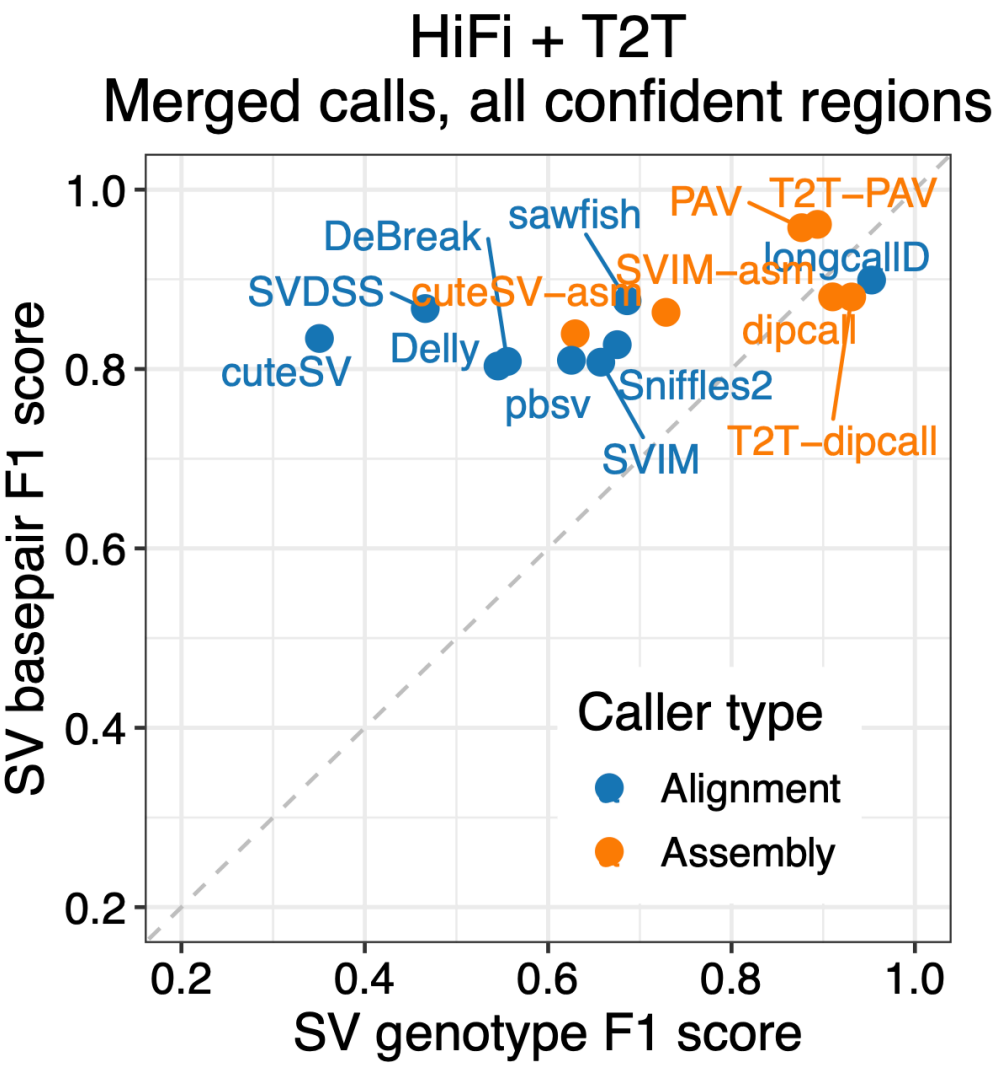
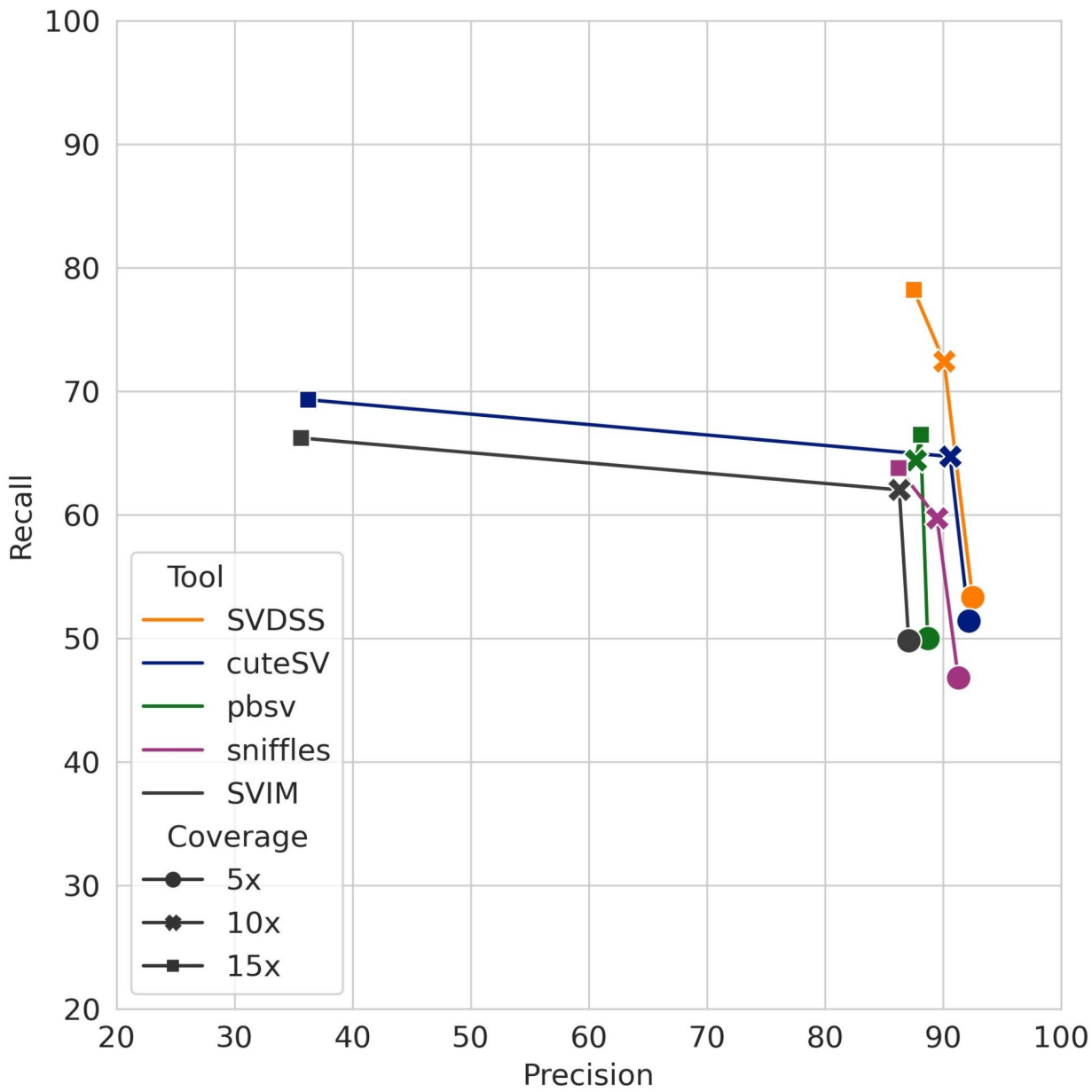
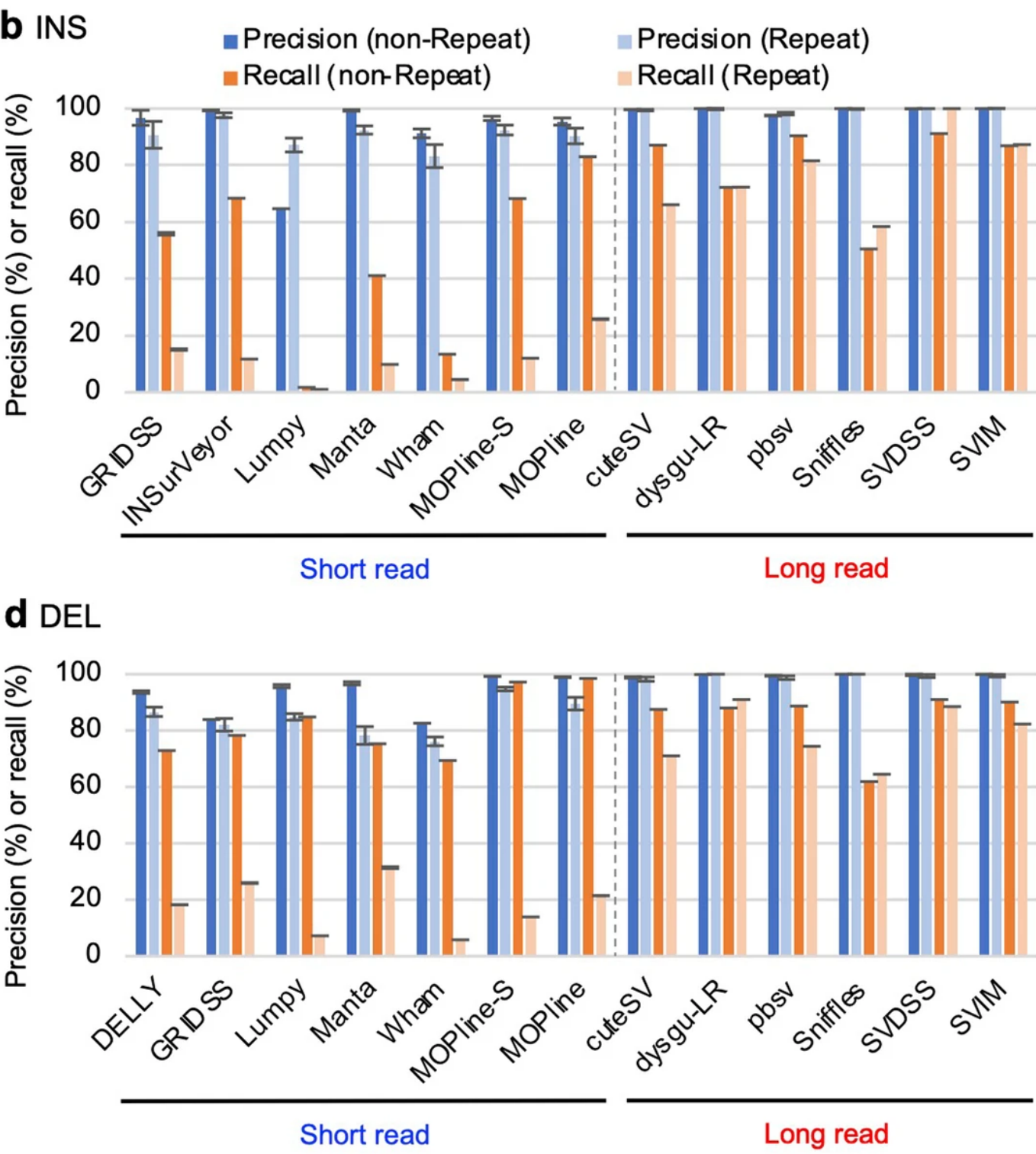
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Denti et al. Nature Methods (2023)
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Can we trust these results?

Where is the problem?

- Issue with our problem definition? (*No clear formulation for this biological problem?*)

Where is the problem?

- Issue with our problem definition? *(No clear formulation for this biological problem?)*
- Modelling problem? *(Are we oversimplifying?)*

Where is the problem?

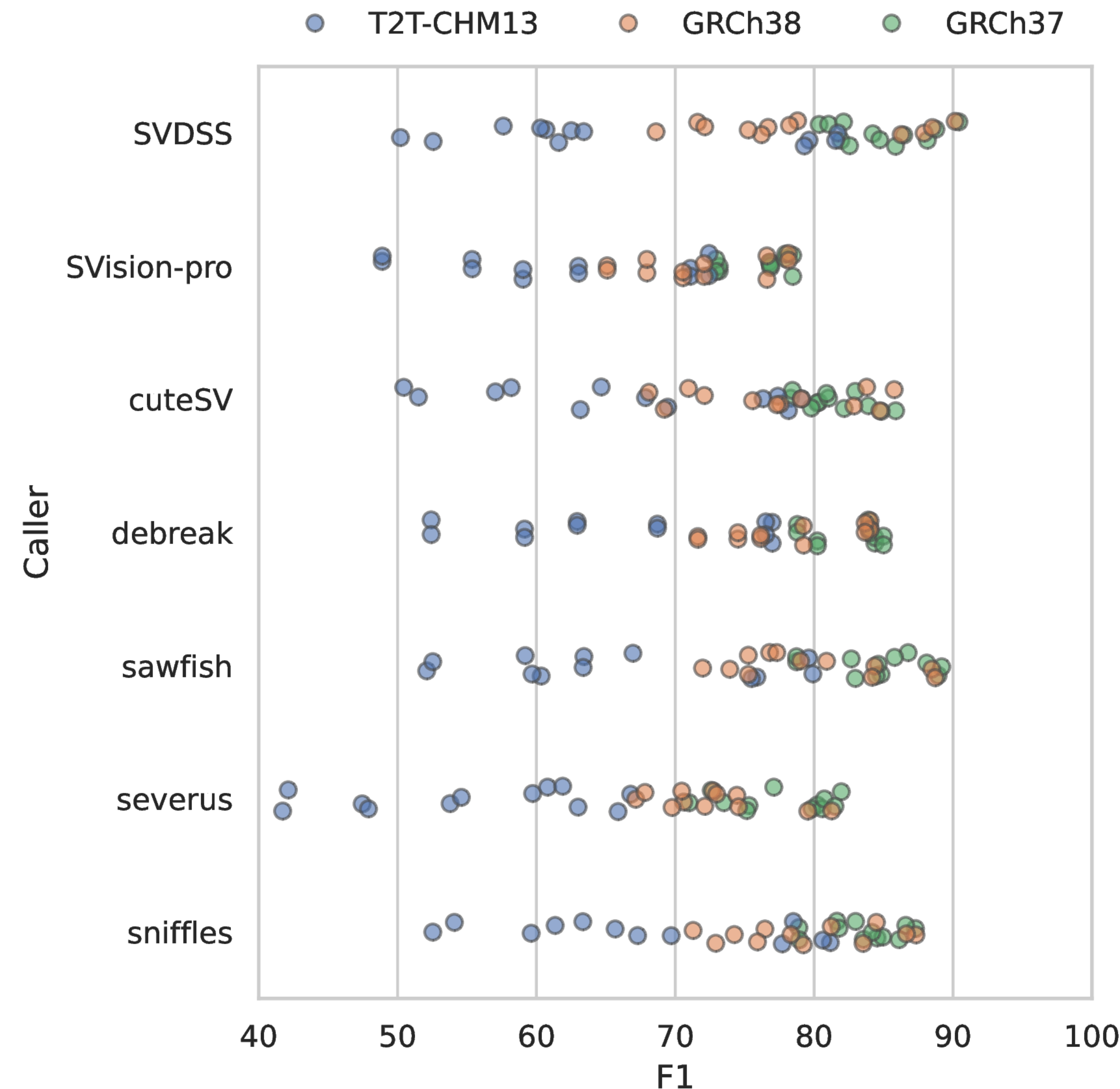
- Issue with our problem definition? *(No clear formulation for this biological problem?)*
- Modelling problem? *(Are we oversimplifying?)*
- Issue with evaluations?

Causes of these discrepancies

Performance depends on:

- ground truth
- reference version
- regions of the reference
- benchmark parameters

This even when applied to same sample



Causes of these discrepancies

Performance depends on:

- ground truth
- reference version
- regions of the reference
- benchmark parameters

This even when applied to same sample

		T2T-CHM13					
		Full genome			Confident regions		
w/o harmonization	SVDSS	6	4	5	1	1	4
	SVision-pro	5	6	6	6	6	6
	cuteSV	2	2	4	4	3	5
	debreak	1	3	2	3	4	3
	sawfish	4	5	3	5	5	2
	severus	7	7	7	7	7	7
	sniffles	3	1	1	2	2	1
w/ harmonization	SVDSS	5	5	2	1	1	2
	SVision-pro	6	6	6	6	6	6
	cuteSV	2	2	5	4	4	5
	debreak	3	4	4	5	5	4
	sawfish	4	3	3	3	3	3
	severus	7	7	7	7	7	7
	sniffles	1	1	1	2	2	1
		dipcall	SVIM-asm	hapdiff	dipcall	SVIM-asm	hapdiff

Causes of these discrepancies

Performance depends on:

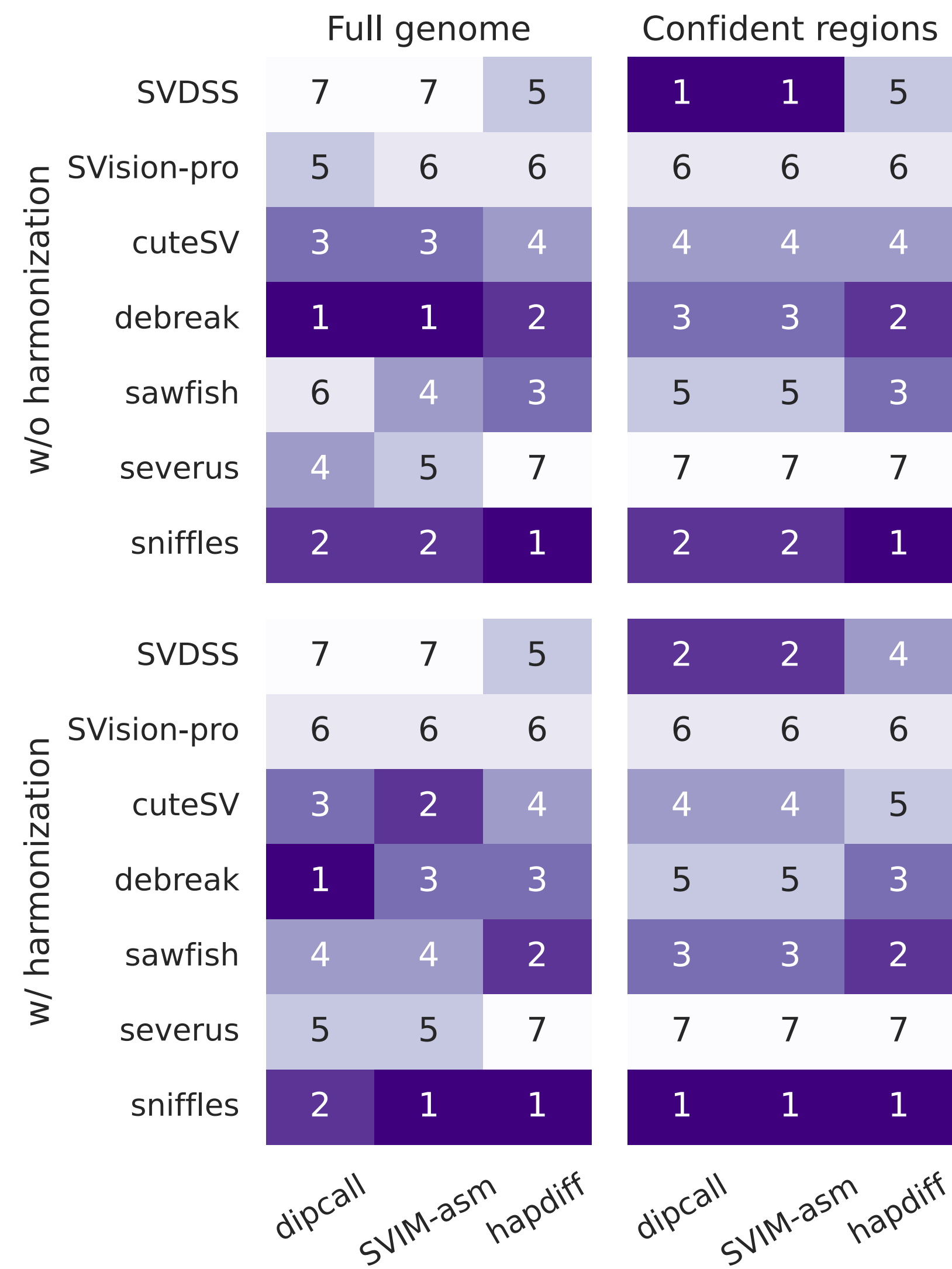
- ground truth
- reference version
- regions of the reference
- benchmark parameters

This even when applied to same sample

		T2T-CHM13					
		Full genome			Confident regions		
w/o harmonization	SVDSS	6	4	5	1	1	4
	SVision-pro	5	6	6	6	6	6
	cuteSV	2	2	4	4	3	5
	debreak	1	3	2	3	4	3
	sawfish	4	5	3	5	5	2
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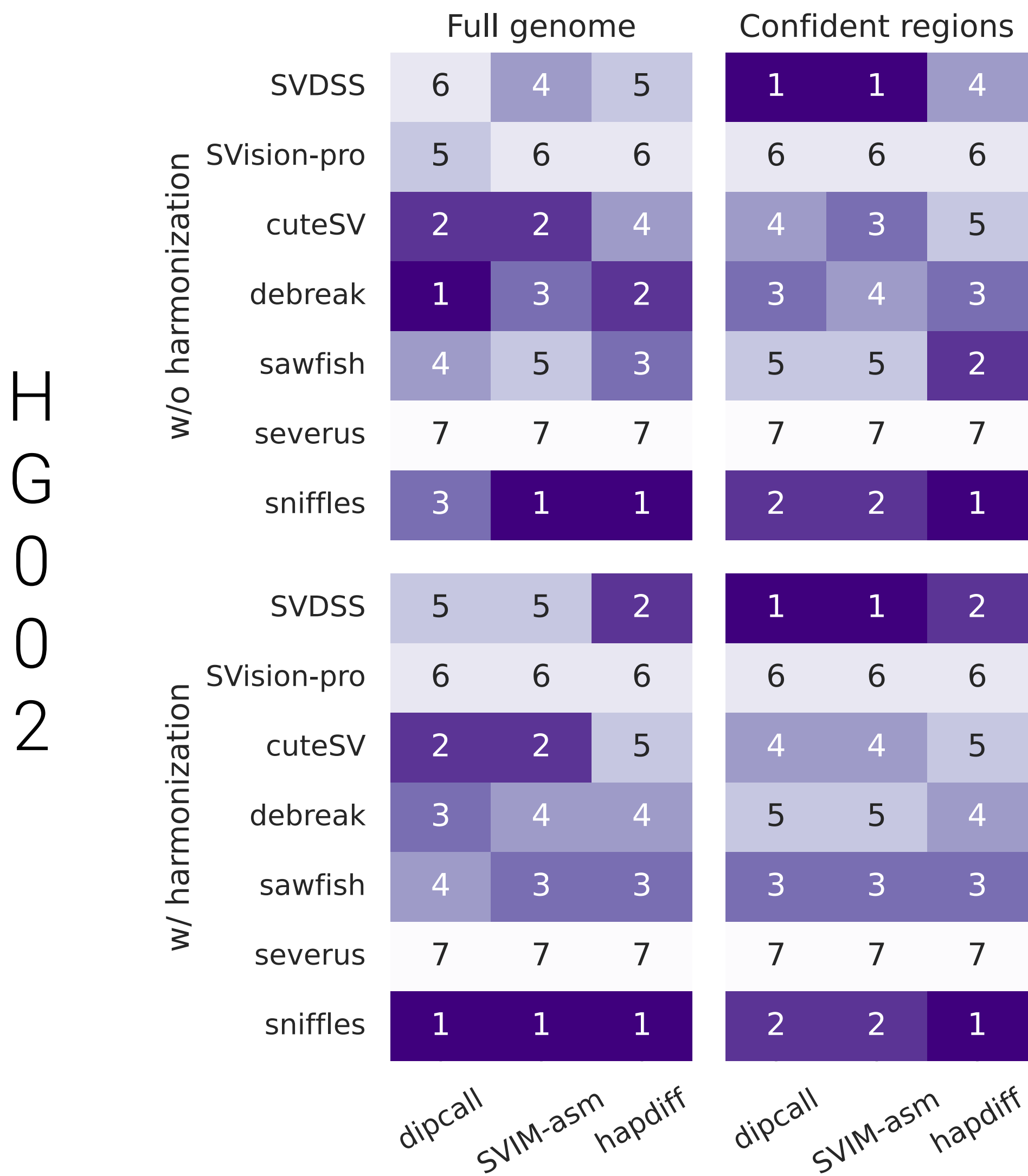
Different results for different individuals

T2T-CHM13



N
A
1
2
8
7
8

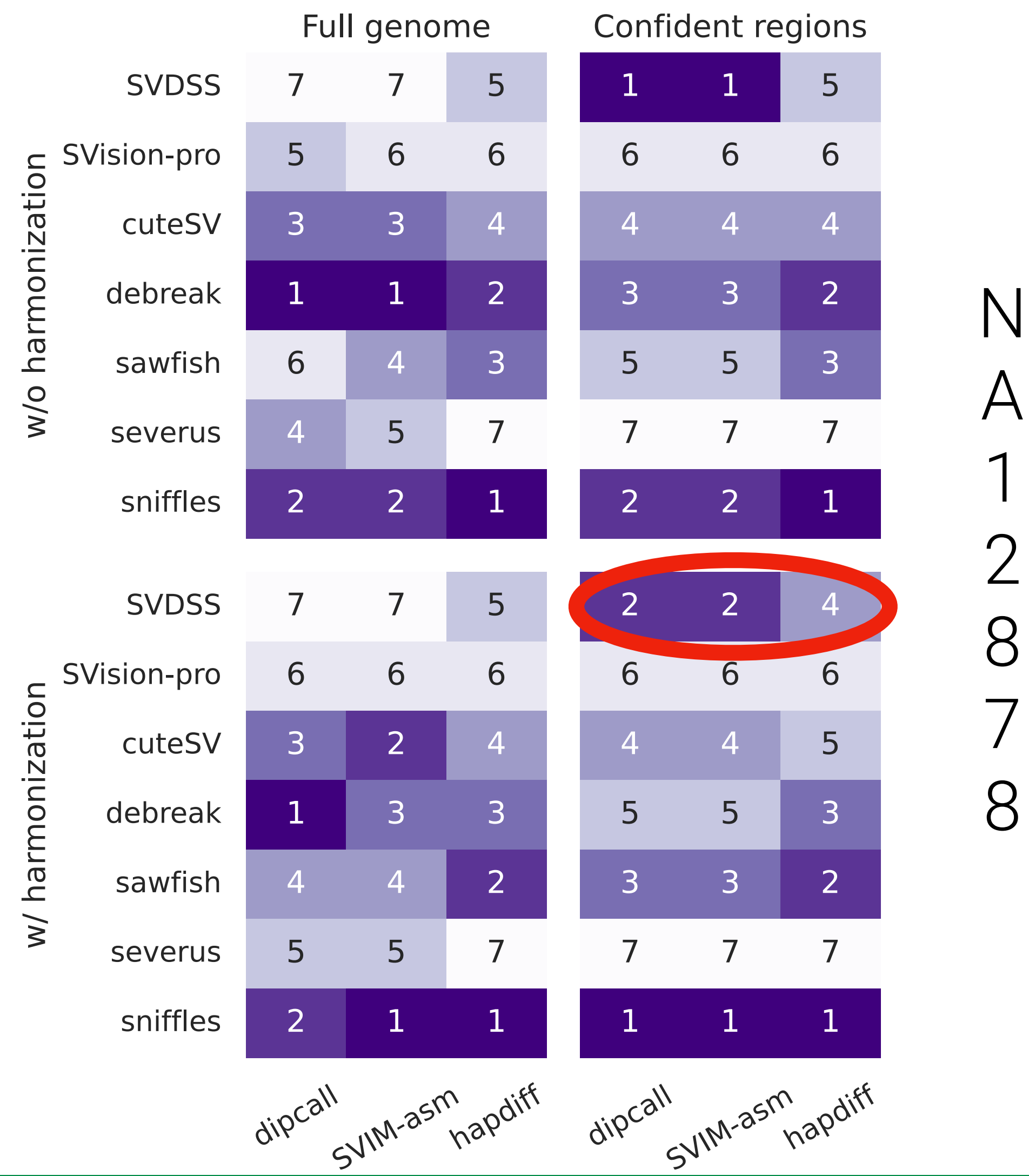
T2T-CHM13



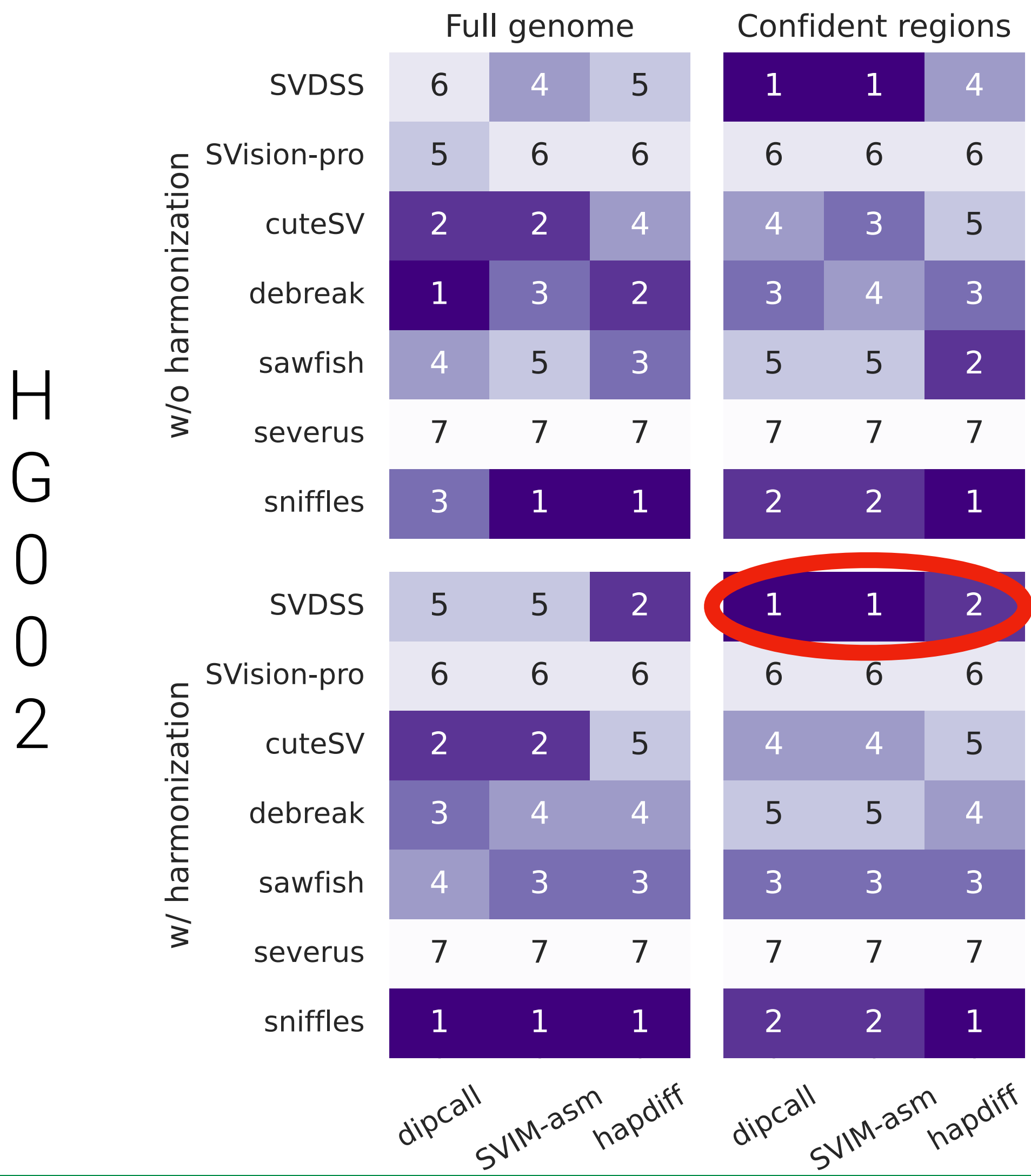
H
G
0
0
2

Different results for different individuals

T2T-CHM13



T2T-CHM13



My (expected) takes

- Results are not readily transferable across ground truths
- Evaluation against a single ground truth is insufficient
- No caller was best in every tested scenario

My (expected) takes and questions

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Can pangenomic help us?

- We need to scale to more individuals (*2 individuals already took some time*)
- What should we expect? Will rankings converge or diverge further?

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Unfortunately, I have more questions than answers here, but I hope my point was clear

Pangenome graph augmentation

Denti et al. bioRxiv (2025)

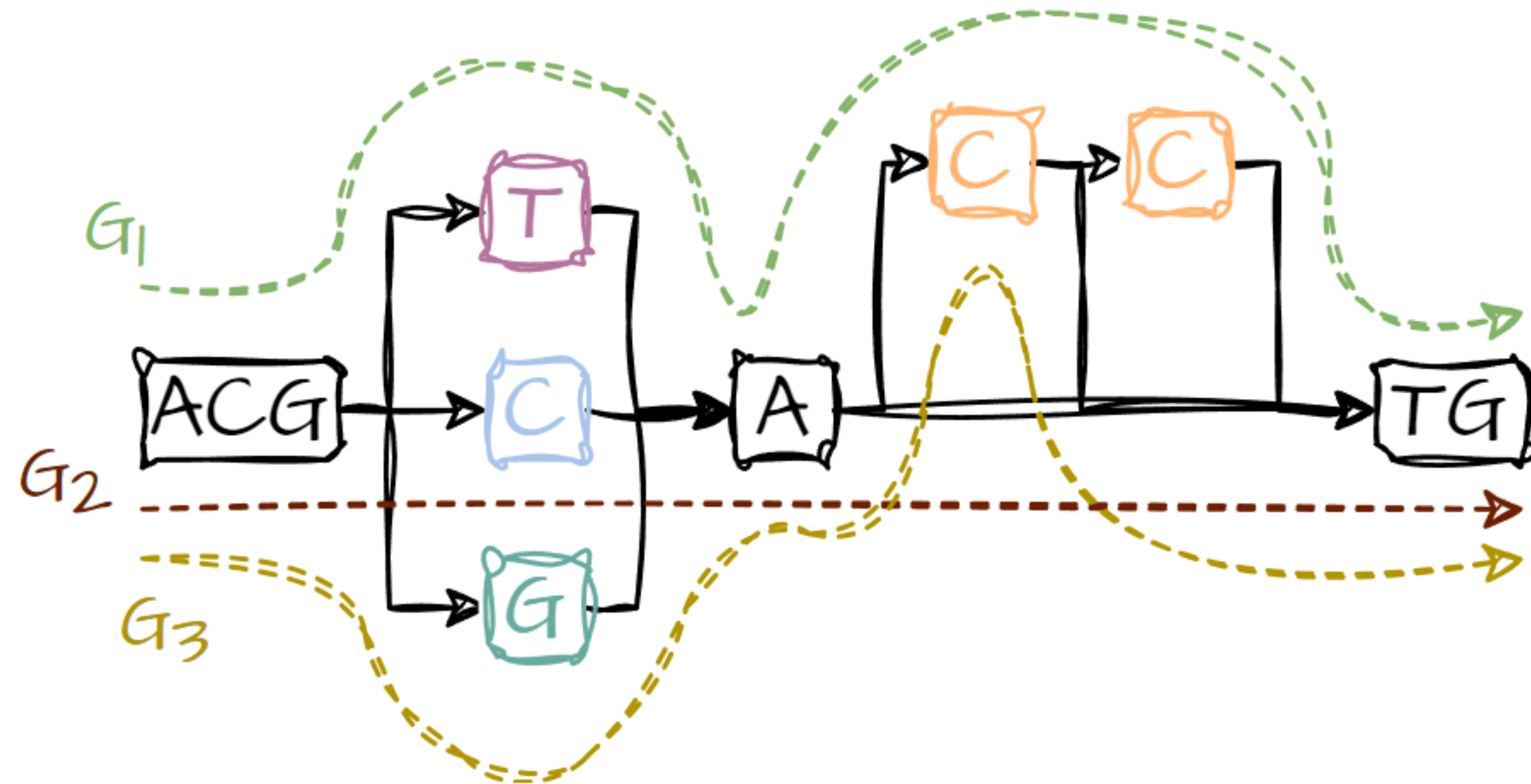
What is a pangenome?

A pangenome is a collection of genome

$G_1 = \text{ACG}\textcolor{violet}{T}\textcolor{orange}{A}\textcolor{orange}{C}\textcolor{orange}{C}\textcolor{violet}{T}\textcolor{violet}{G}$

$G_2 = \text{ACG}\textcolor{blue}{C}\textcolor{blue}{A}\textcolor{blue}{T}\textcolor{blue}{G}$

$G_3 = \text{ACG}\textcolor{teal}{G}\textcolor{teal}{A}\textcolor{orange}{C}\textcolor{orange}{T}\textcolor{orange}{G}$



“most **[graph] paths** are unlikely recombinations of true haplotypes”*

genome == haplotype == assembly == path

Why do we need pangenomes?

*“No single genome can **represent the diversity** in the human population. Using a single reference genome creates **reference biases**, adversely affecting [...] the **accuracy of genetic analyses**”*

How to build a pangenome graph?

Multiple genomes $\rightsquigarrow$ pangenome graph

MSA-based:

- Pandora *(Colquhoun et al. 2021)*
- panpa *(Dabbaghie et al. 2023)*
- pangeblocks *(Avila et al. 2024)*

All-vs-all:

- pggb *(Garrison et al. 2024)*

Progressive:

- minigraph *(Li et al. 2020)*
- minigraph-cactus *(Hickey et al. 2024)*

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!! High-quality assemblies required !!

All-vs-all:

- pggb *(Garrison et al. 2024)*

- *costly (high coverage + multiple seq.tech.)*
- *computationally expensive*

Progressive:

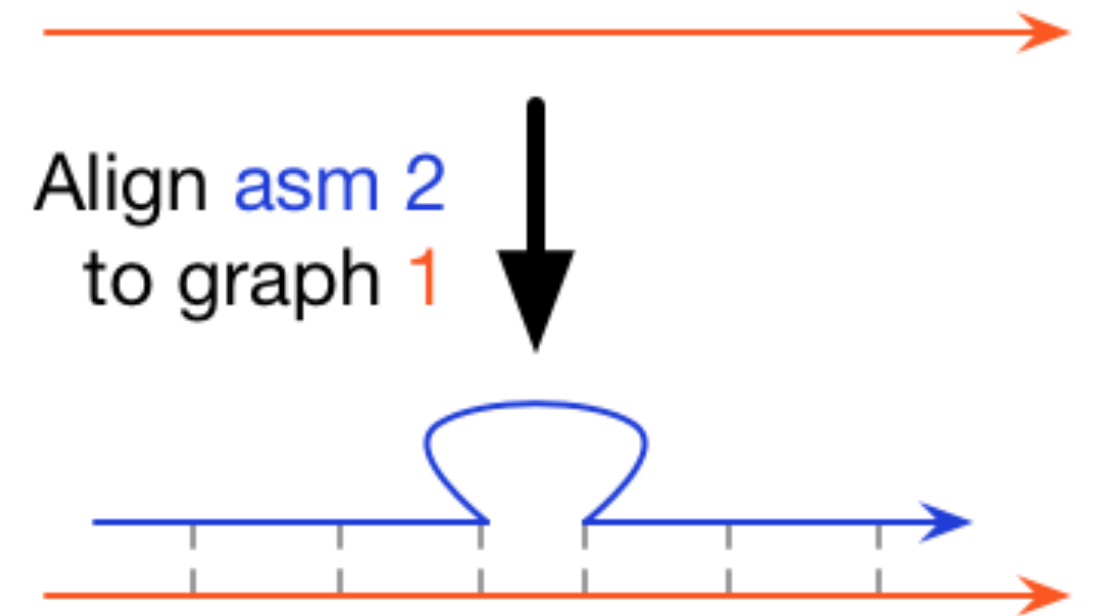
- minigraph *(Li et al. 2020)*
- minigraph-cactus *(Hickey et al. 2024)*

Progressive construction

A graph can be progressively constructed by iteratively aligning and inserting one genome at the time

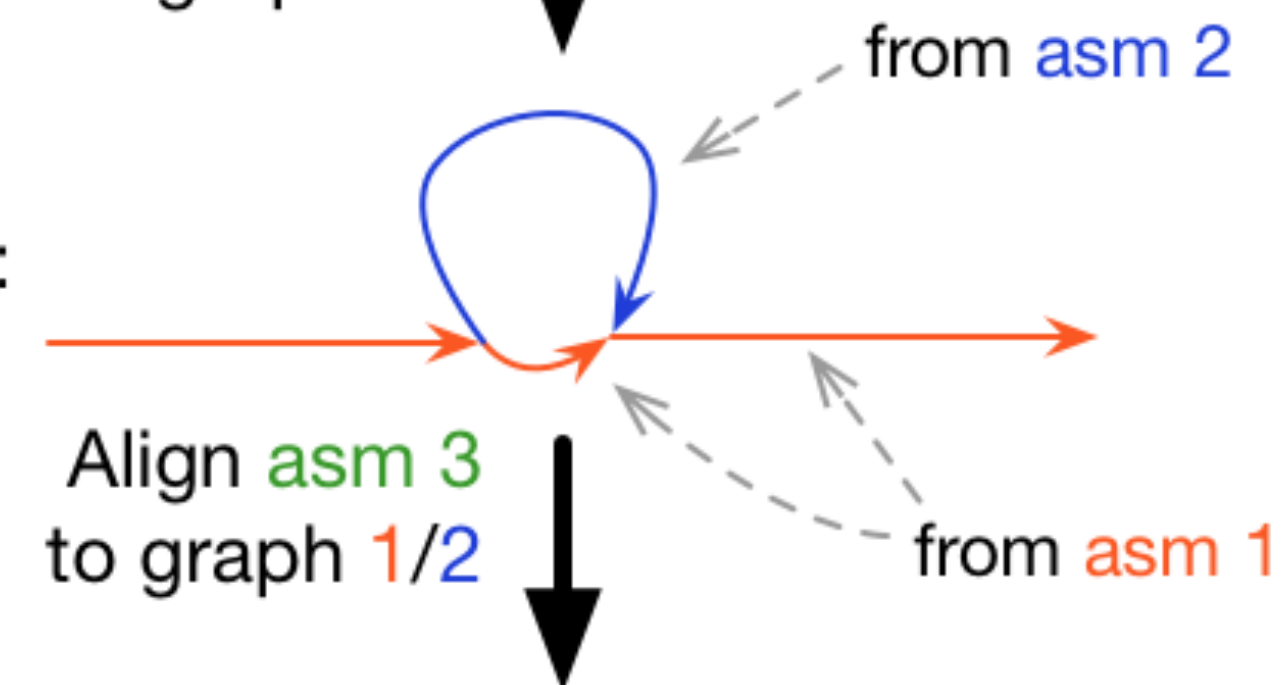


Graph 1
(asm 1):



Construct
graph 1/2

Coarse
graph 1/2:



Construct
graph 1/2/3

Coarse
graph 1/2/3:

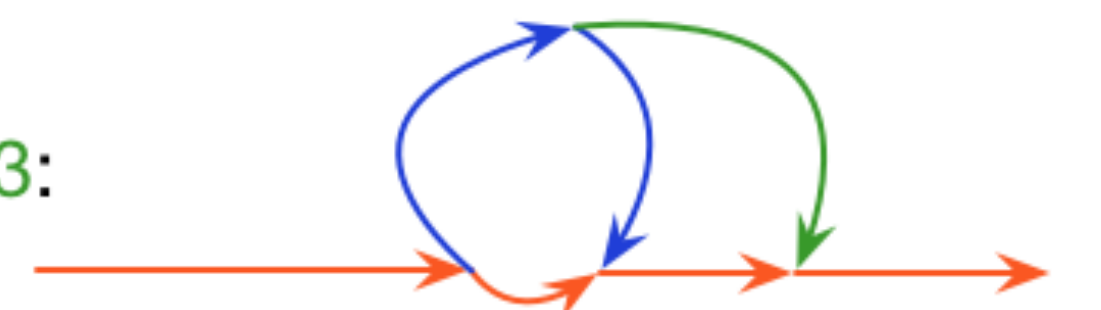


Image from github.com/lh3/minigraph

Progressive construction from long reads

My long-term vision:

no need to assemble new samples if we exploit already assembled genomes

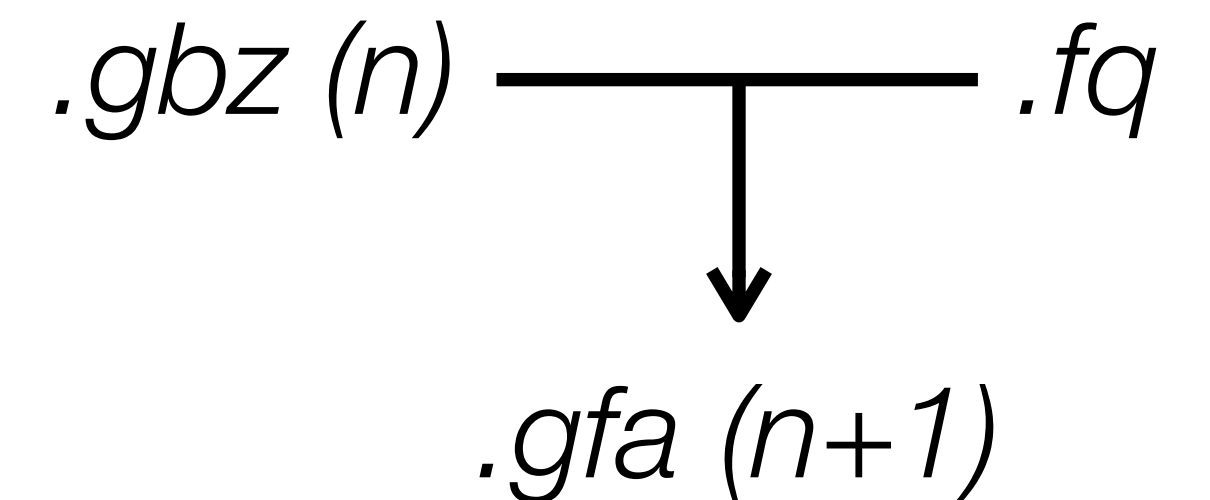
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My current goal:

assembly-free and alignment-free approach for augmenting a pangenome graph



Progressive construction from long reads

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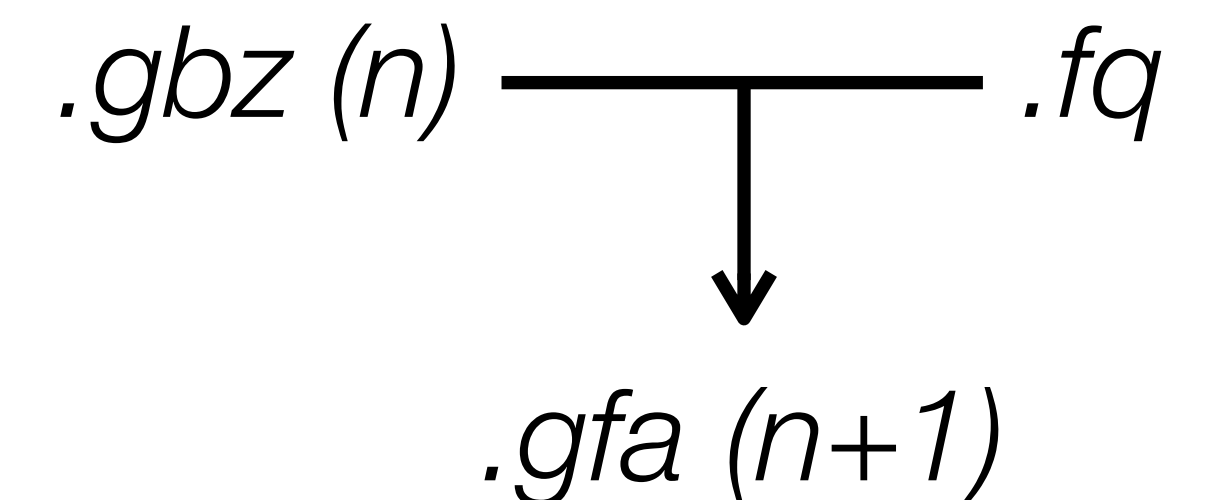
Several questions:

how can we...

pinpoint differences with known genomes?

locate such differences in the graph?

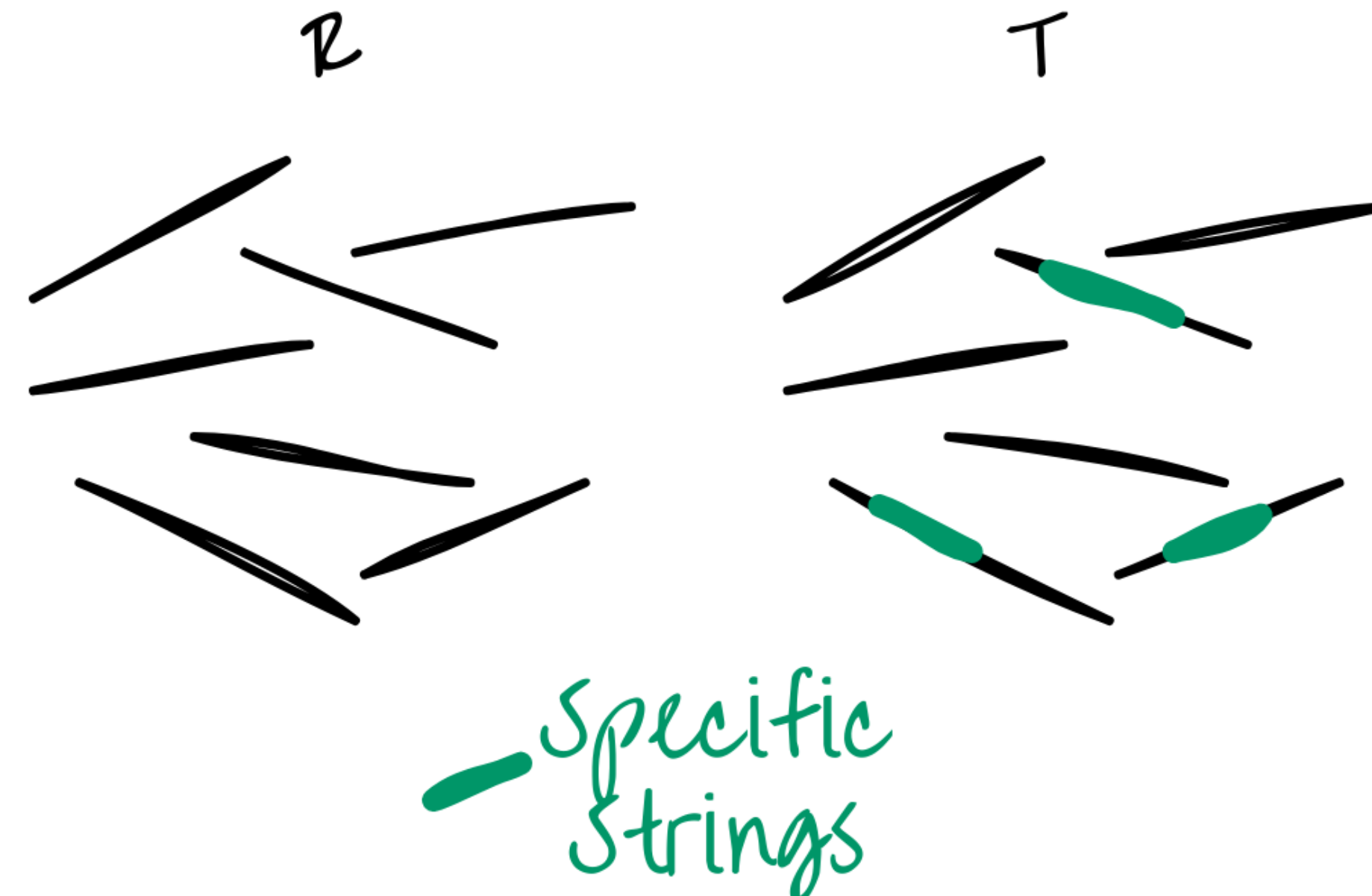
summarize information coming from different reads?



Specific strings

Specific strings pinpoint **any difference** between two sets of strings

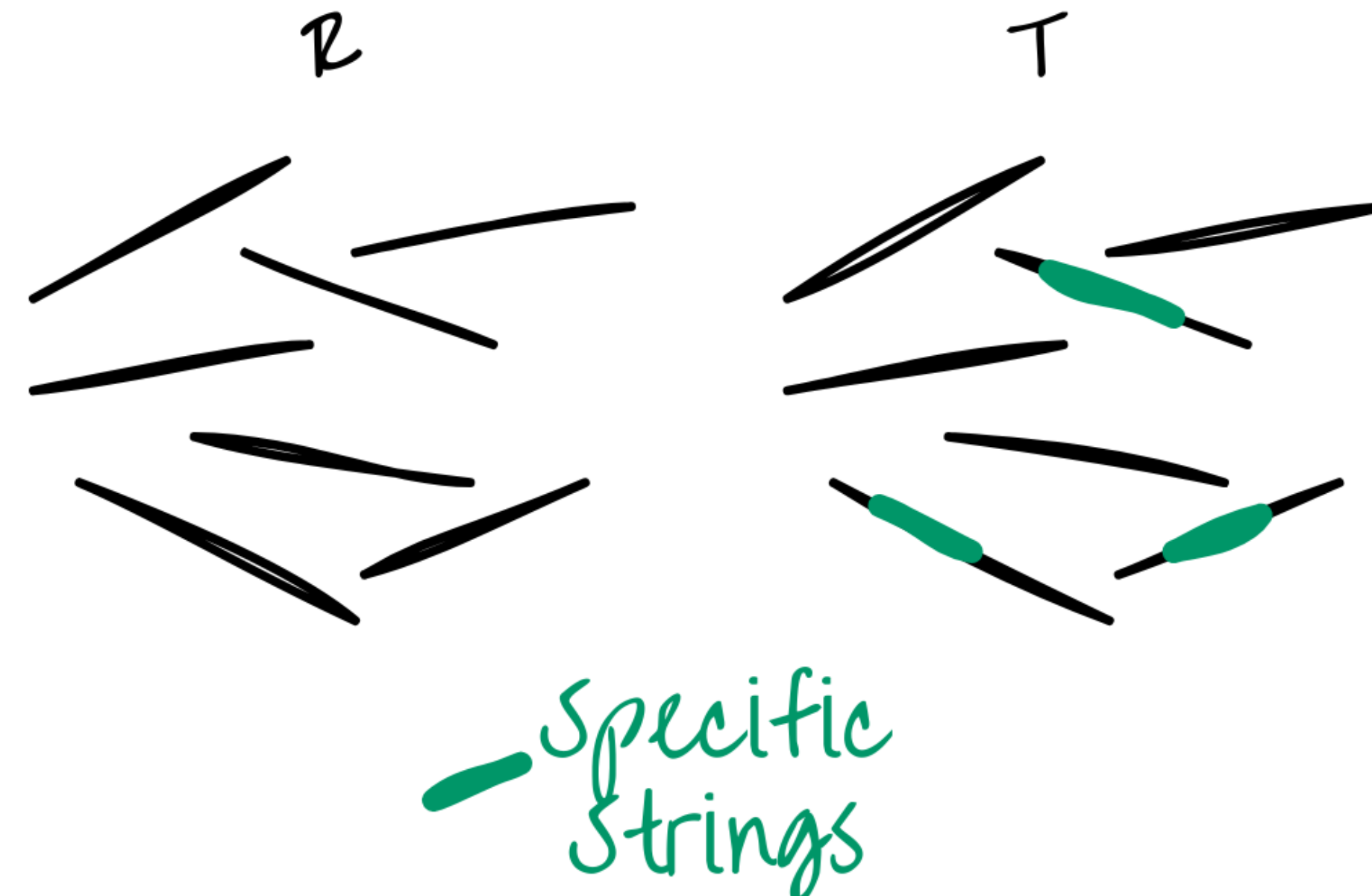
if we index a reference genome, they pinpoint (mostly) all variations of a sample



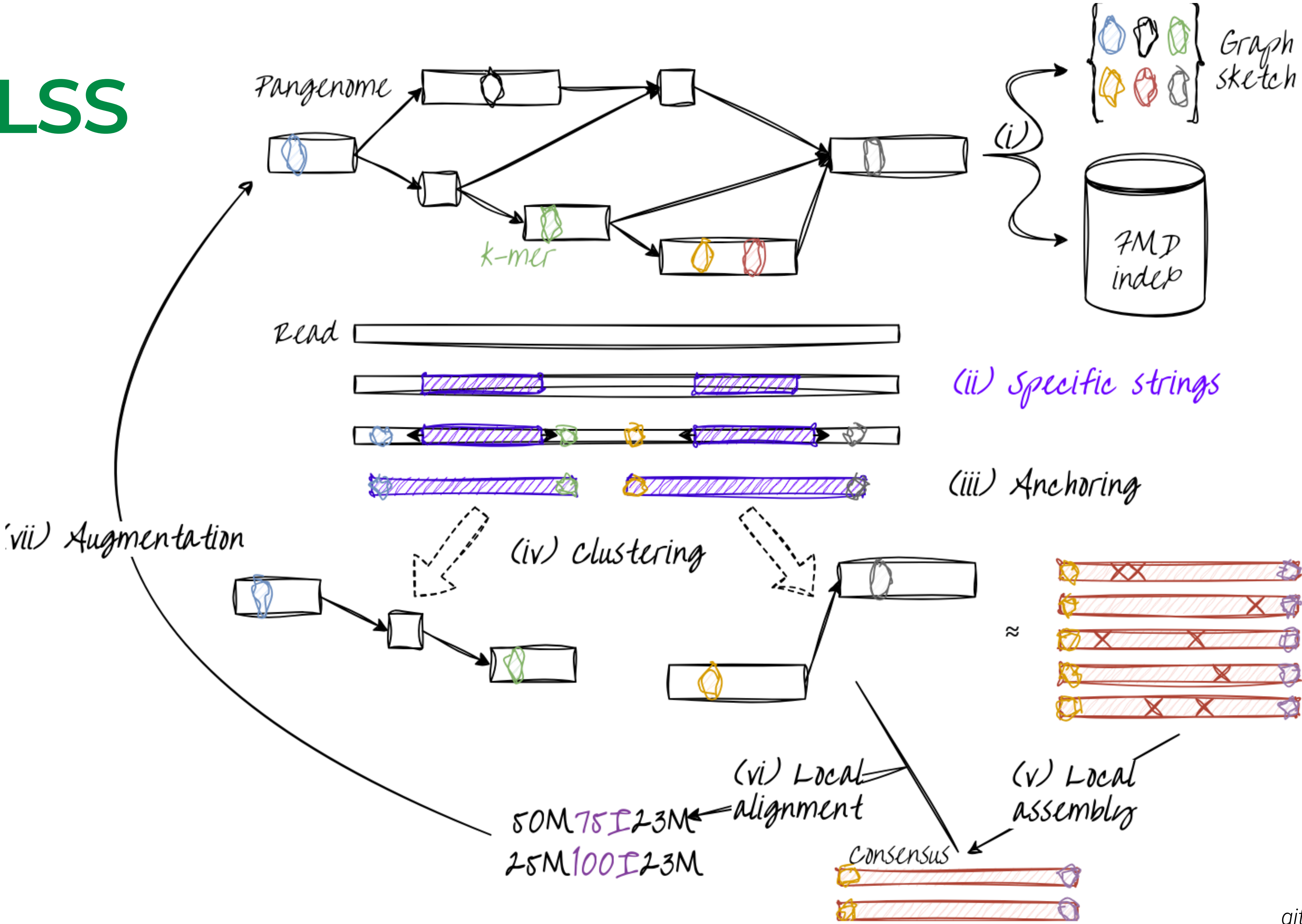
Specific strings

Specific strings pinpoint **any difference** between two sets of strings

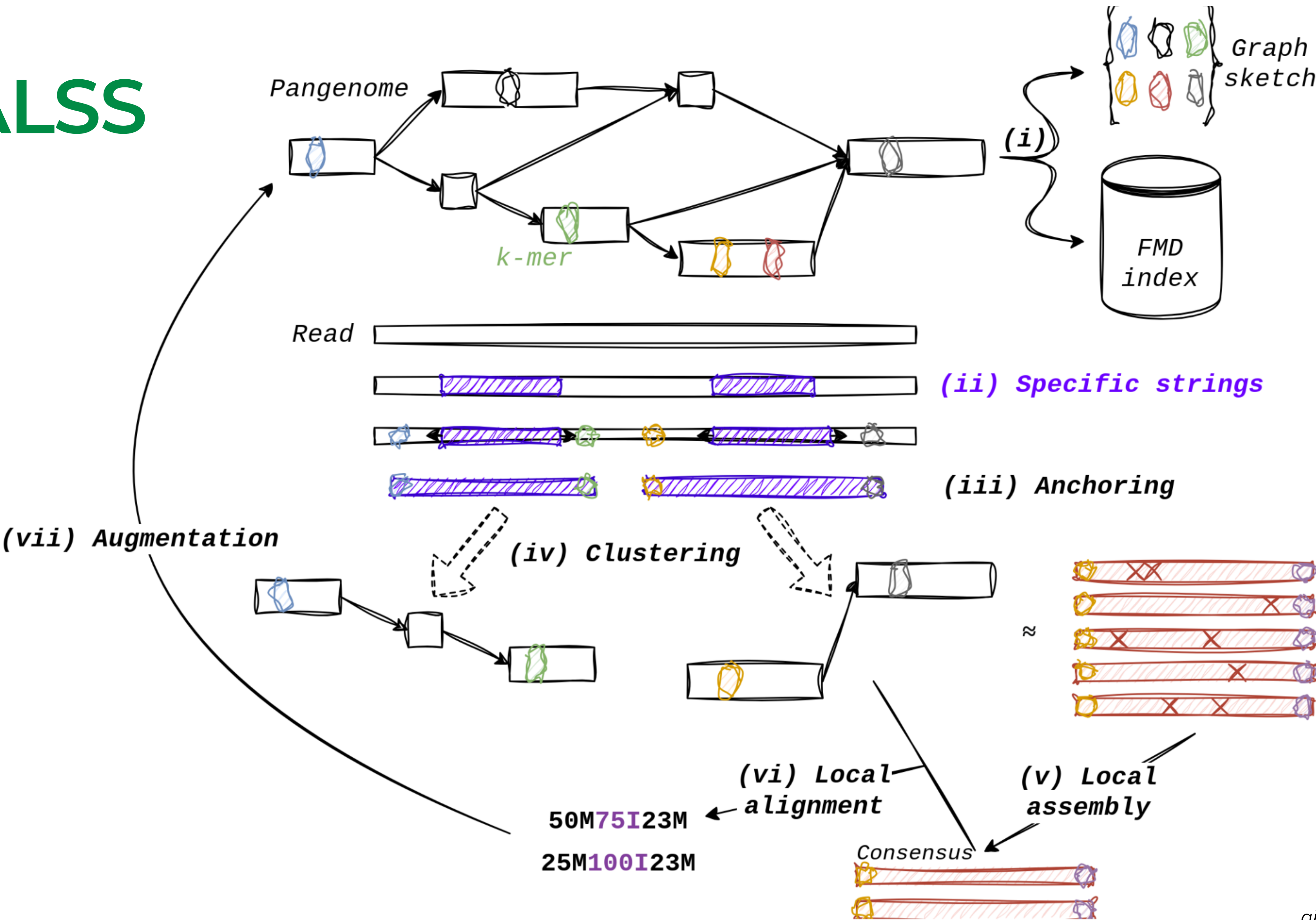
*if we index a reference **pan**genome, they pinpoint (mostly) all **novel** variations of a sample*



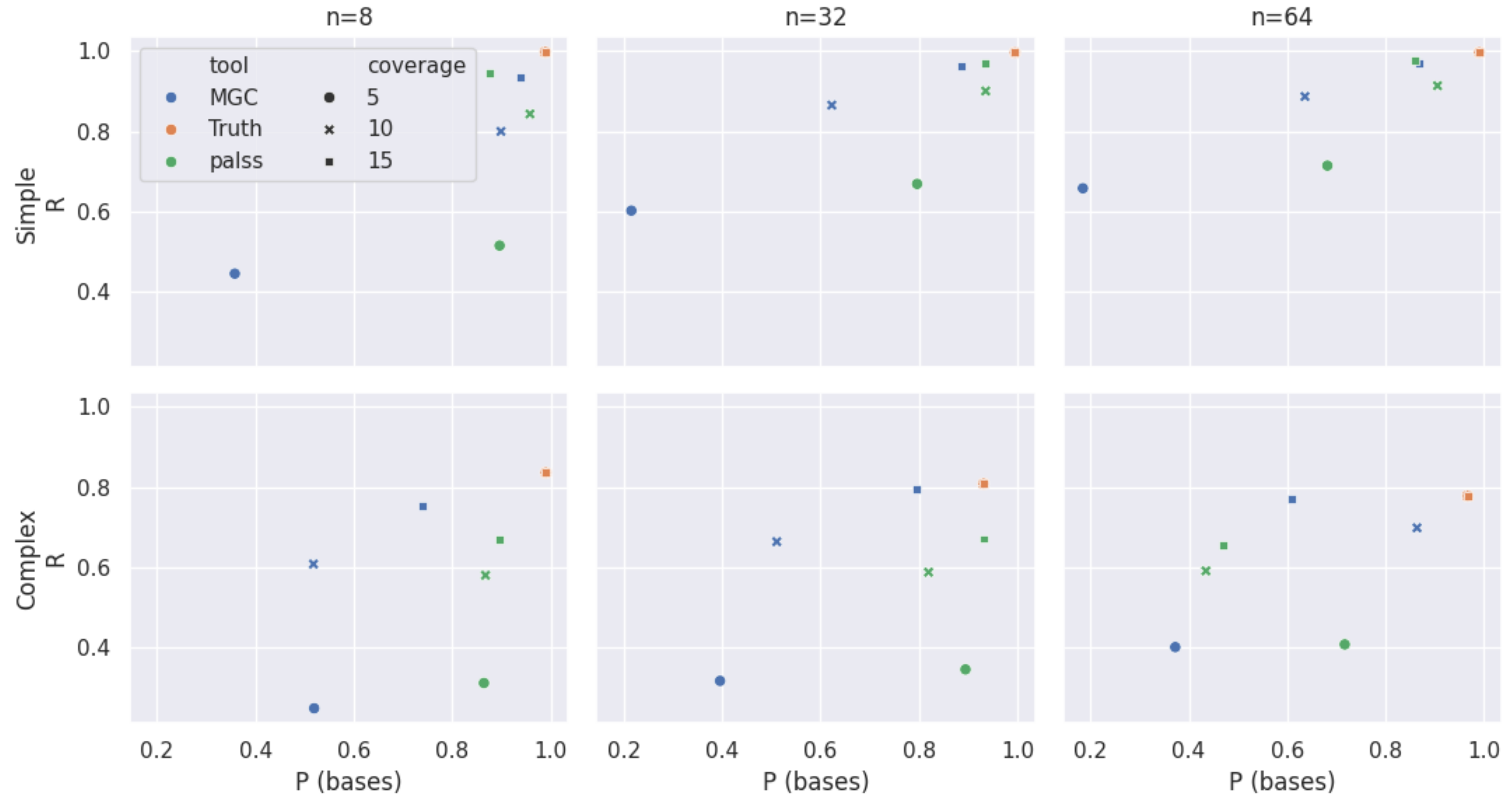
PALSS



PALSS



Augmentation accuracy *(chr20, simulated)*



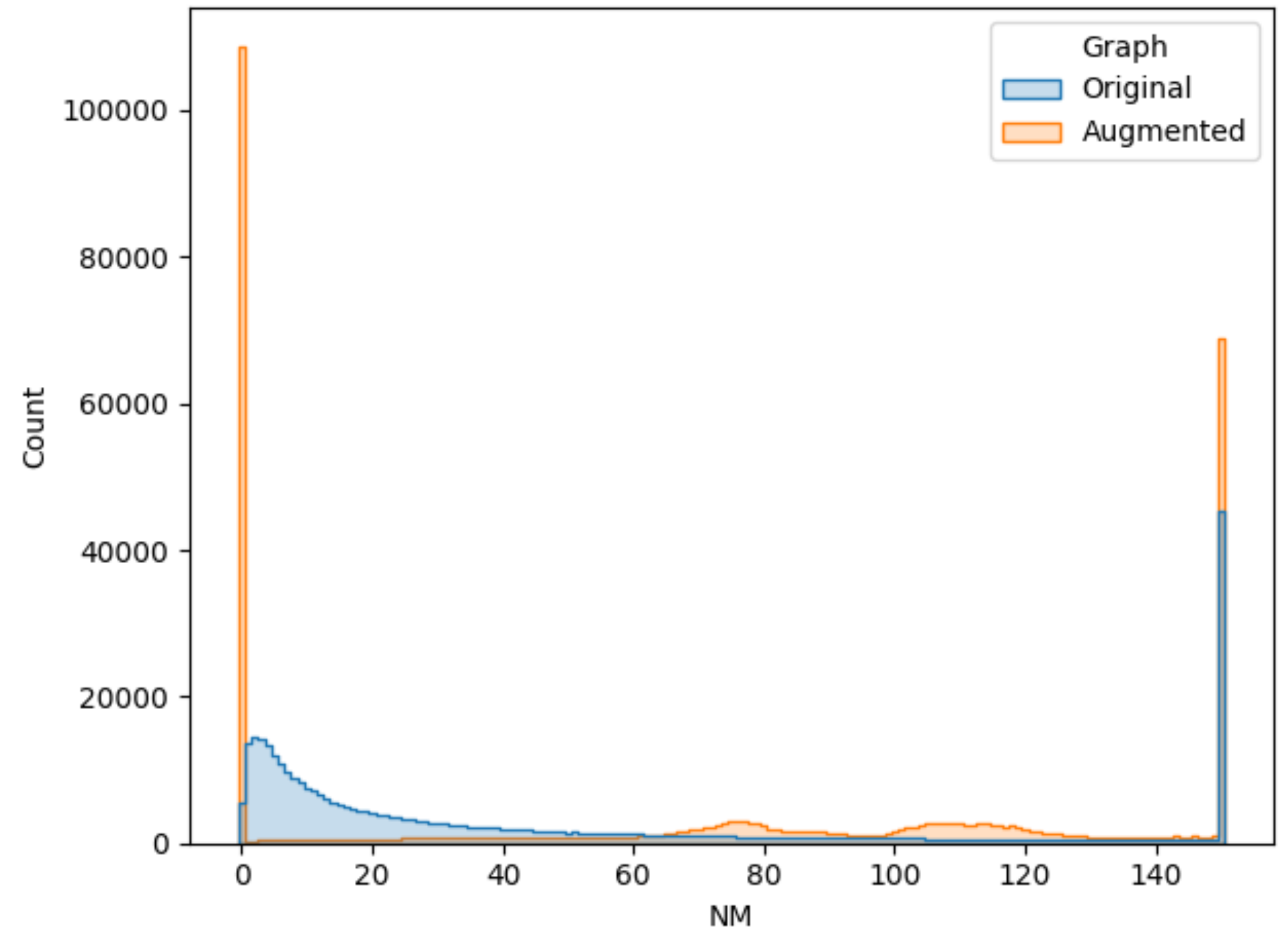
HPRCv2 + NA12878 (10x)

Pangenome augmentation:

2 days and 133GB (+6 days for FMD-index)

Pangenome construction:

10h and 140GB per assembly + 3 days



Read alignment accuracy

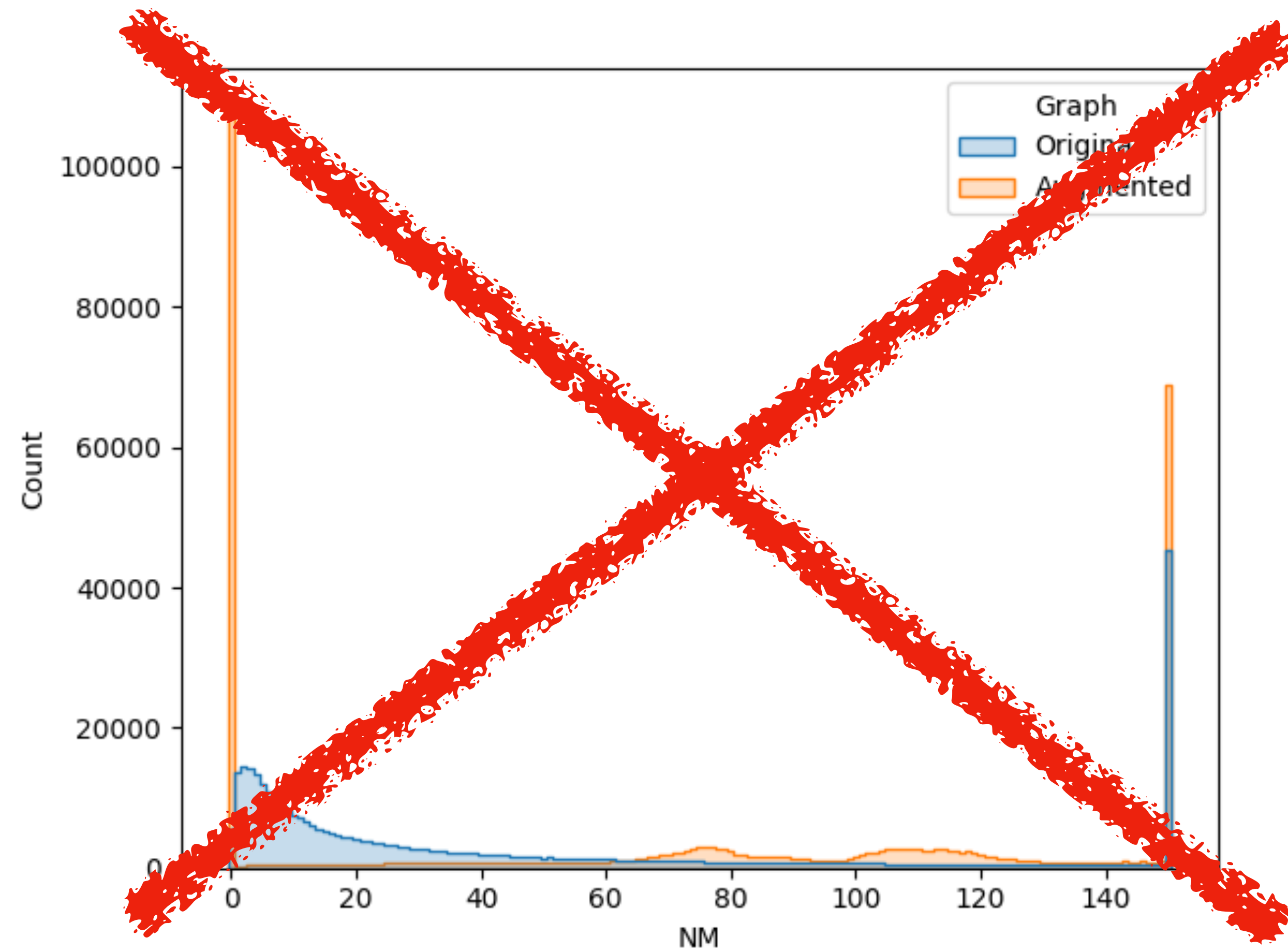
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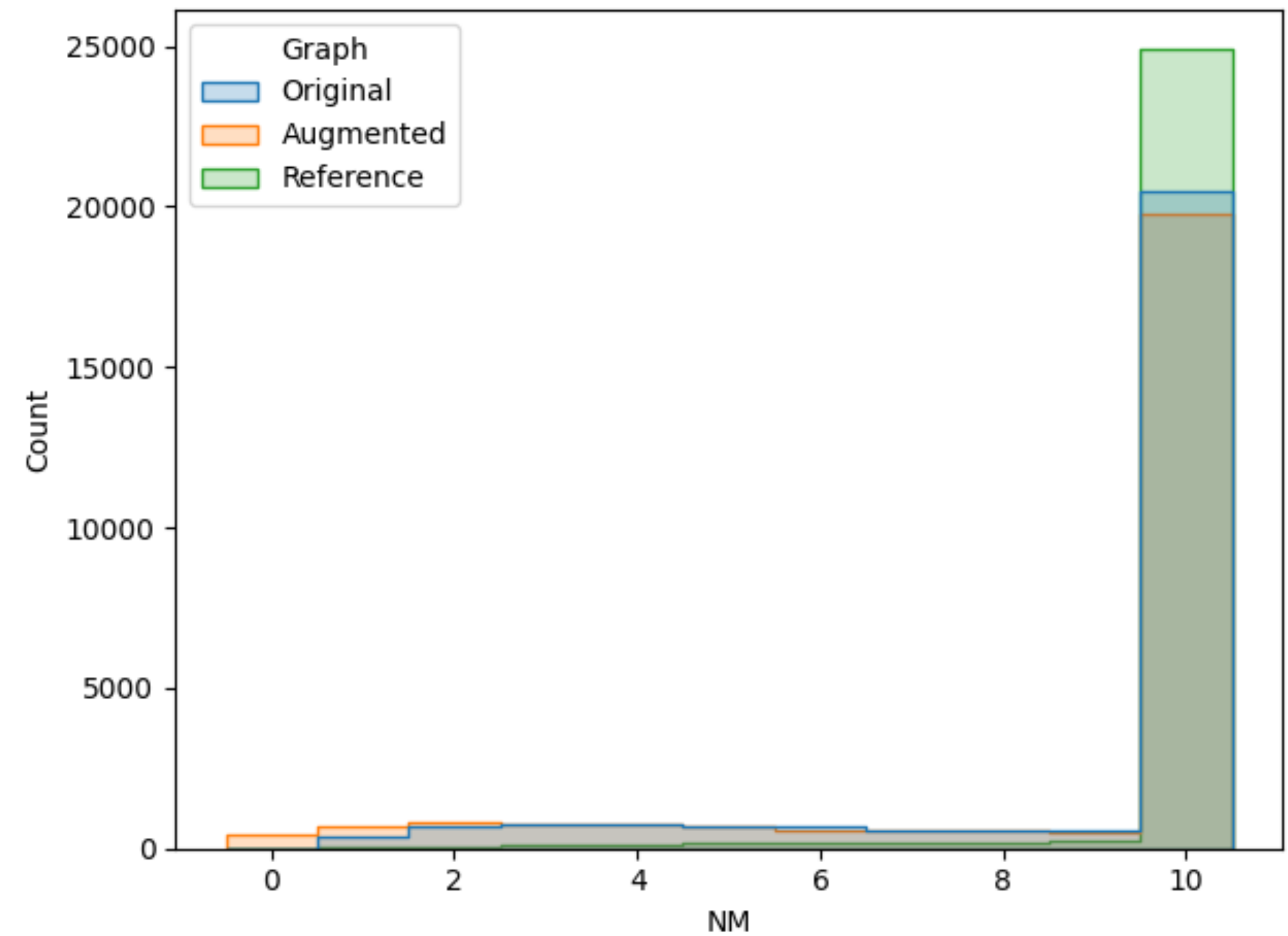
HPRCv2 + NA12878 (10x) - Chr5

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Read alignment accuracy

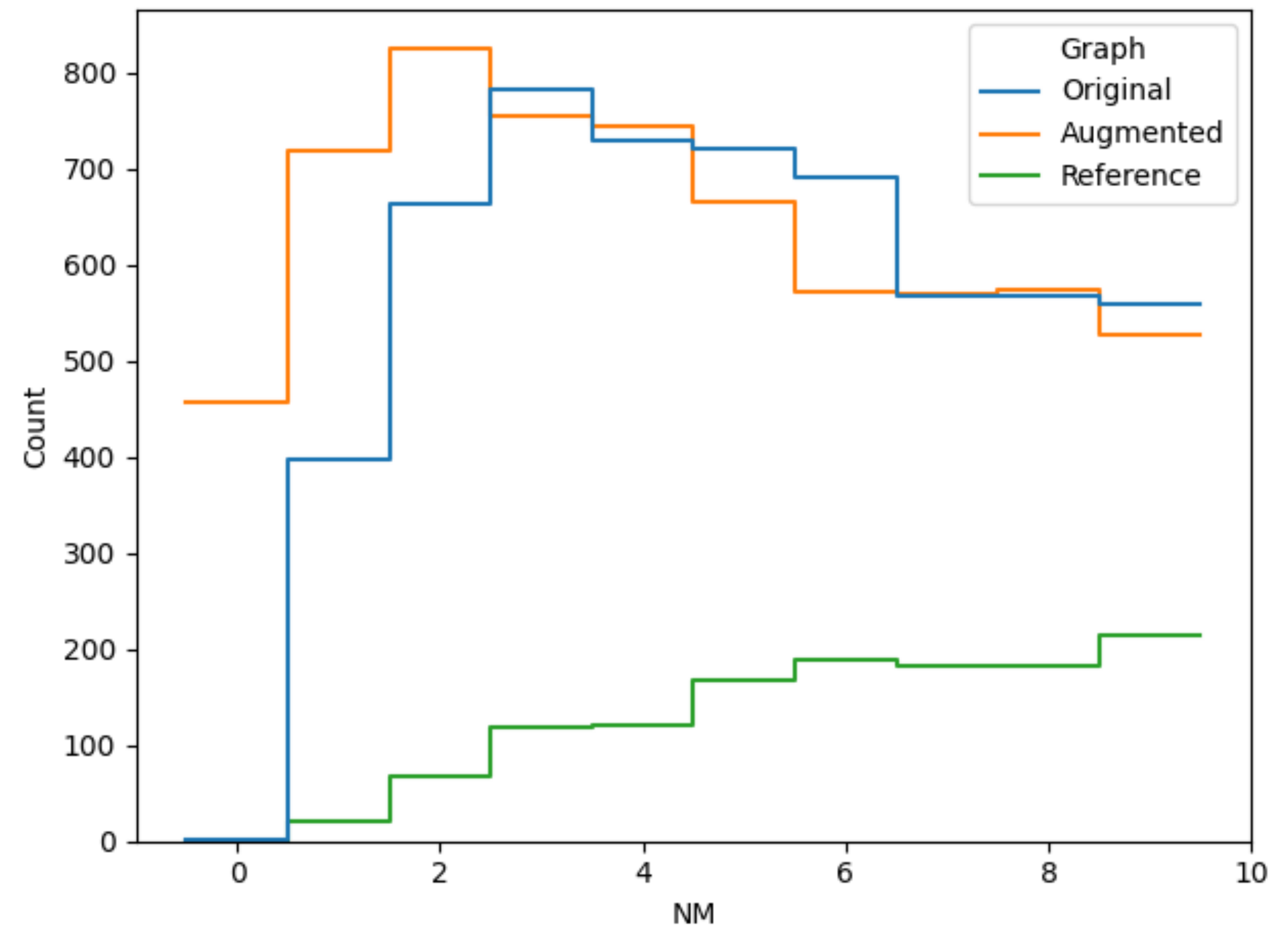
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Read alignment accuracy

Work-in-progress

- Evaluation on multiple chromosomes (*running...*)
- Improve scalability
- Include full haplotype paths in augmented graph

Pangenome graphs can be augmented using long reads
(good results with low coverage)

Conclusions

Key takeaways

1. Computer science is...

- the foundation of sequence bioinformatics
- essential for making new discoveries

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1. Computer science is...

- the foundation of sequence bioinformatics
- essential for making new discoveries

2. Pangenomics (*availability of multiple genomes*)

- can help us improve our understanding
- is also posing additional challenges

3. Computer science is not always perfect



Thank you!

I hope I have convinced you :)

Questions?



**Funded by
the European Union**