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Maud Fagny, Marieke L. Kuijjer, Maïke Stam, Johann Joets, Olivier Turc,  
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# Identifying key tissue-specific, biological processes by integrating enhancer information in maize gene regulatory networks

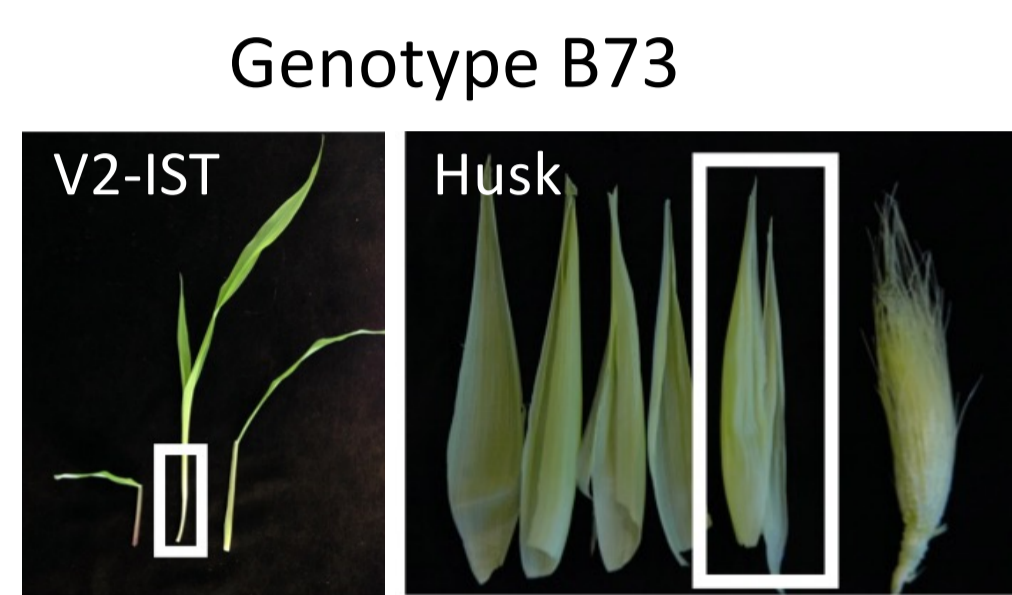
Maud Fagny<sup>1</sup>, Marieke L. Kuijjer<sup>2,3</sup>, Maike Stam<sup>4</sup>, Johann Joets<sup>1</sup>, Olivier Turc<sup>5</sup>, Julien Rozière<sup>1,6,7</sup>,  
Stéphanie Pateyron<sup>6,7</sup>, Anthony Venon<sup>1</sup> and Clémentine Vitte<sup>1</sup>. Contact: [clementine.vitte@inrae.fr](mailto:clementine.vitte@inrae.fr)

<sup>1</sup> Université Paris-Saclay, INRAE, CNRS, AgroParisTech, GQE – Le Moulon, Gif-sur-Yvette, France; <sup>2</sup> Centre for Molecular Medicine Norway (NCMM), Nordic EMBL Partnership, University of Oslo, Oslo, Norway; <sup>3</sup> Department of Pathology, Leiden University Medical Center, Leiden, Netherlands; <sup>4</sup> Plant Development and (Epi) Genetics, Swammerdam Institute for Life Sciences, University of Amsterdam, Amsterdam, Netherlands; <sup>5</sup> LEPSE, Université de Montpellier, INRAE, Institut Agro, Montpellier, France; <sup>6</sup> Université Paris-Saclay, CNRS, INRAE, Univ Evry, Institute of Plant Sciences Paris-Saclay (IPS2), Orsay, France; <sup>7</sup> Université de Paris, CNRS, INRAE, Institute of Plant Sciences Paris-Saclay (IPS2), Orsay, France

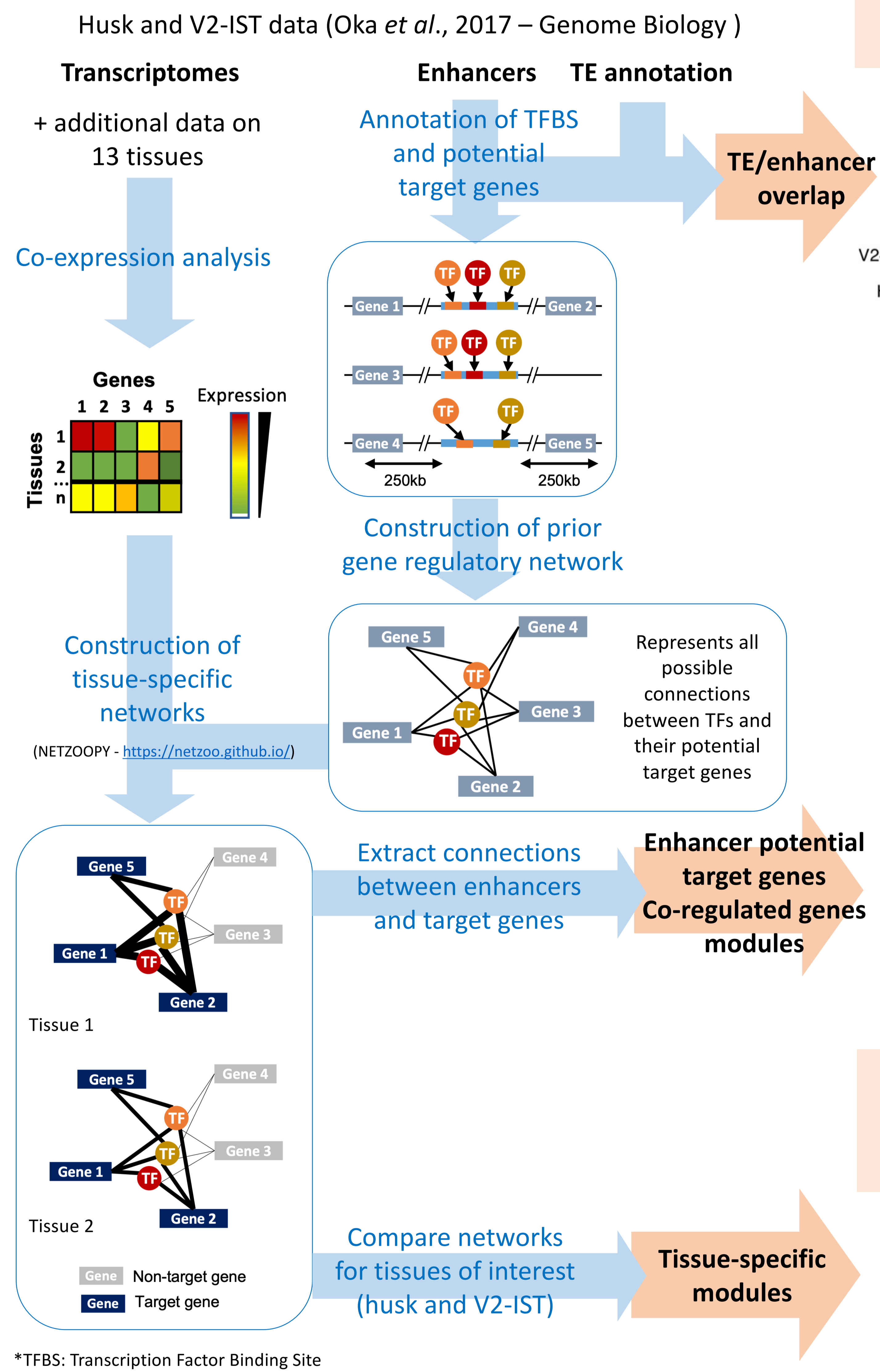
## Background and objectives

Enhancers are key regulators of the spatio-temporal coordination of gene expression, in particular during development. Their regulatory effect is mediated by the binding of transcription factors (TFs), which interact with target gene promoters through 3D-loops over long distances (2kb-1Mb). While enhancers have been identified as key players in the wiring of developmental gene regulatory networks in mammals, this question remains largely unexplored in plants. Transposable Elements (TEs) of various superfamilies have been proposed as a source of new *cis*-regulatory elements in plants and animals, but whether they contribute to the emergence of tissue-specific gene regulatory networks in plants remains to be fully elucidated.

Here, we investigate the enhancer-driven regulatory network of two maize tissues at different stages: leaves at seedling stage (V2-IST) and husks (bracts) at flowering. By integrating enhancer, transcription factors binding sites (TFBSs) annotation and mRNA-seq data using a systems biology approach, we model the regulatory relationships between TFs and their potential target genes, and identify regulatory modules specific to husk and V2-IST. This allows us to tackle two main questions: **What functions are regulated in a tissue-specific manner between husk and V2-IST, and what are the molecular players (genes, TFs, enhancers) involved? Do transposable elements contribute to enhancers and which biological function do they regulate?**



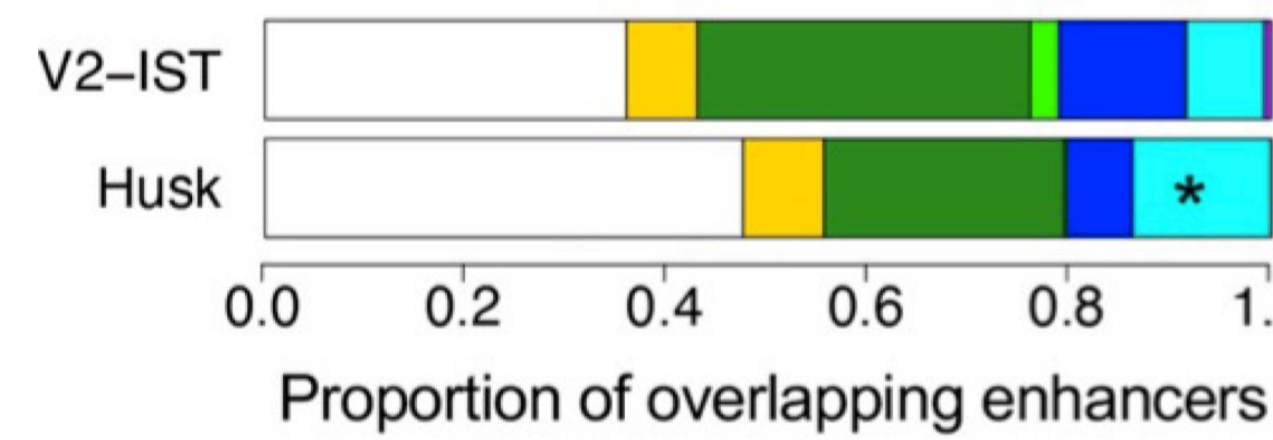
## Data and methods



## Transposable elements are a source of TFBS sequences in tissue-specific enhancers

Analysis at the order level :

Legend: None, Multiple, LTR, LINE, TIR, MITE, Helitron

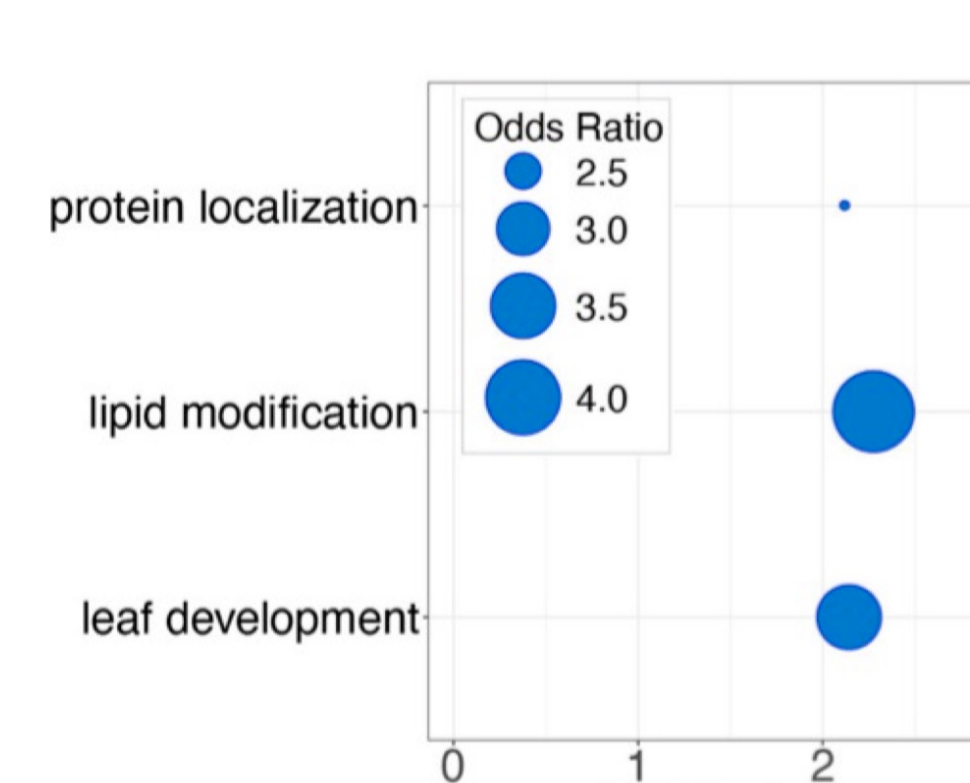


MITEs overlapping husk enhancers are enriched in putative TFBSs:

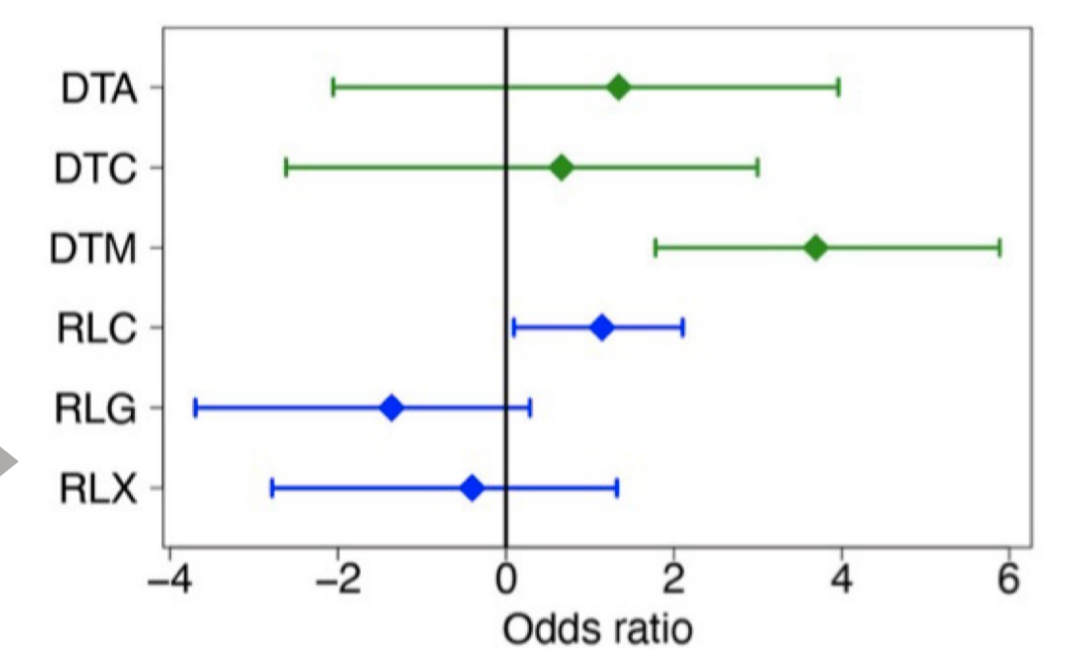
Closest TFBS motifs in *A. thaliana* :

- HB-like TFs
- MYB-like TFs
- MADS-like TFs

Target genes of husk enhancers overlapping MITEs with the MYB-like TFBS are enriched in mature leaf functions



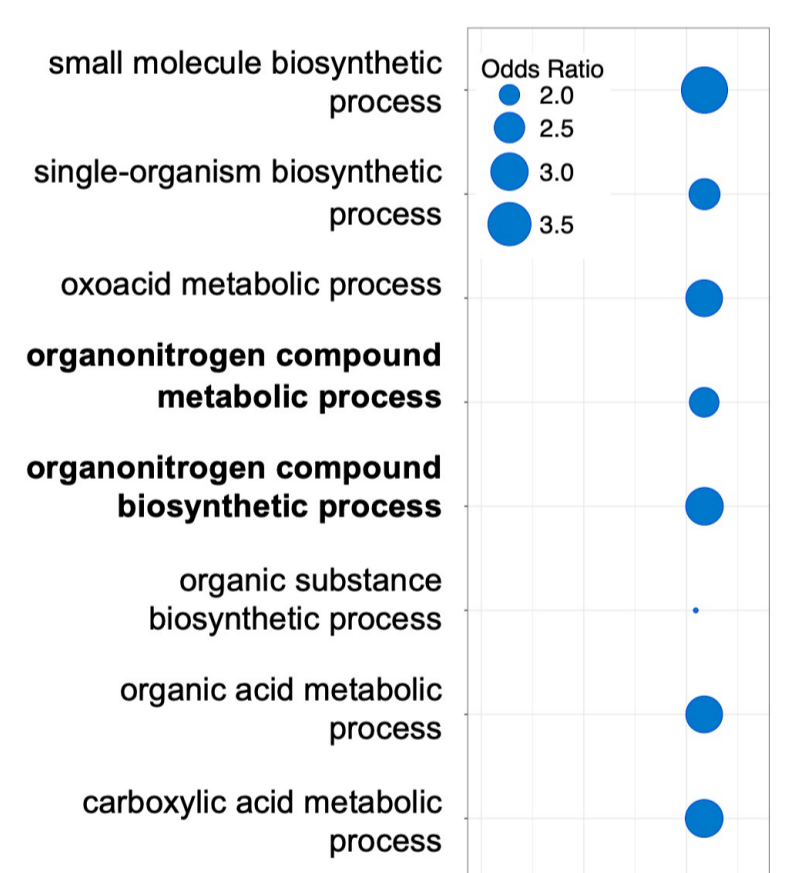
Analysis at the superfamily level :



V2-IST enhancers are enriched in *Mutator* DNA transposons

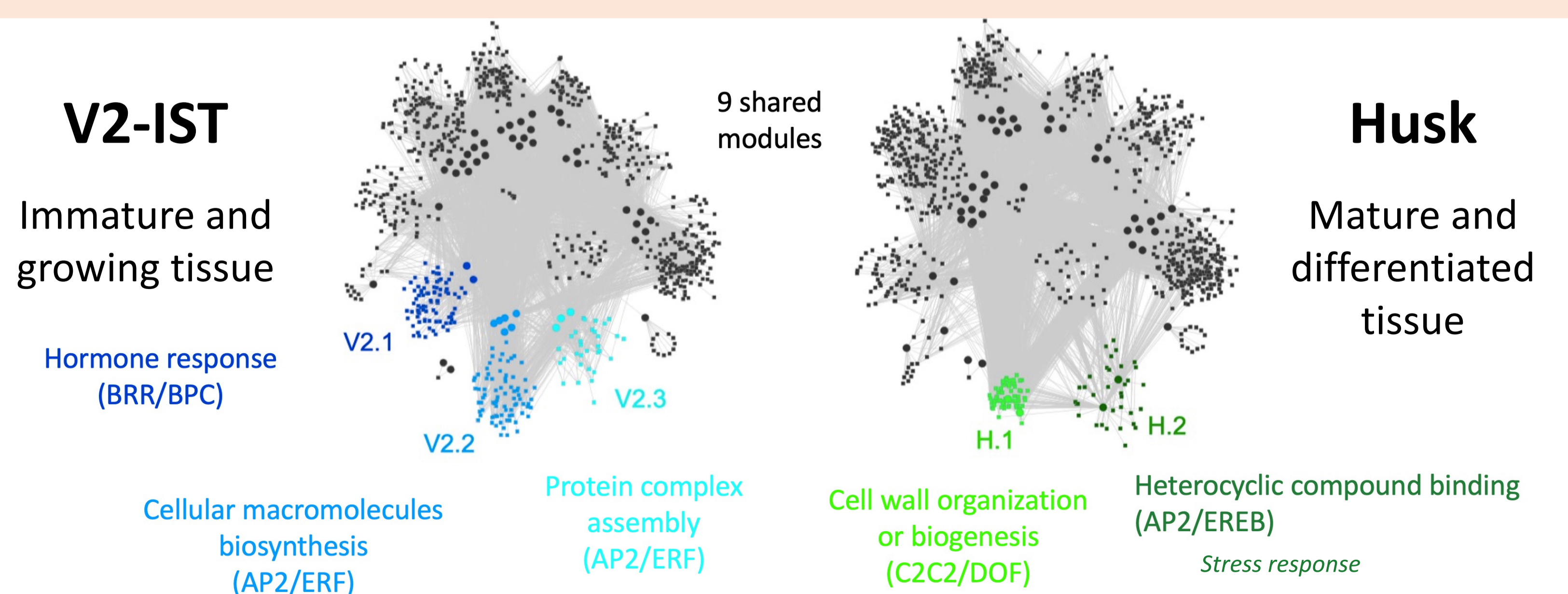
*Mutators* overlapping V2-IST enhancers are enriched in TFBS from the AP2/ERF family

Target genes of V2-IST enhancers overlapping *Mutator* are enriched in nitrogen-storage related functions



**Take home: Different TE superfamilies have shaped part of the regulatory network in the two tissues, TIR transposon *Mutator* in V2-IST, and MITE *Pif/Harbinger* in husk.**

## Tissue-specific regulatory modules highlight different biological functions in husk and V2-IST



**Take home: We identify regulatory modules corresponding to functions relevant to the tissue analyzed as well as the key players (groups of co-regulated genes and their key regulatory TFs) involved in these functions. In addition to the expected modules, we discover regulatory modules of unclear function, notably in husk, a tissue which functions besides ear protection remain poorly characterized.**

## Fundings and support