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Using non-additive effects in genome-wide association studies and genomic predictions to improve biotic stress tolerance in peach

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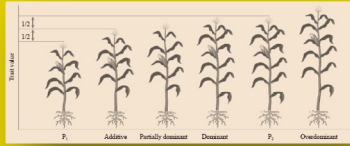
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Why working on non-additive effects in fruits trees ?



Heterosis and non-additive effects are exploited in maize breeding but not in fruit tree breeding yet (Priyadarshan, P.M., 2019)

To understand complex trait architectures

Non-additive genetics effects are involved in complex traits and heterosis

They include dominance, epistasis and contribute to inbreeding depression

Predicting non-additive effects is challenging

The Natural and Orthogonal Interactions Approach (NOIA, Vitezica et al. 2017) can alleviate the confounding between genetic effects



Strong pesticide reliance in peach

To improve peach tree resilience

- Harnessing together minor and major effects genes allows to design a **more durable plant immunity with large spectrum**
- Access to non-additive variance allows for a **better exploitation of the total genetic variance**
- The approach is particularly relevant for **clonally propagated crops** such as peach (*P. persica*).

How to work on non-additive effects in fruits trees ?

Plant material and disease phenotyping

1. **Multisite peach core-collection**, 192 accession genotyped with 16k SNP array
2. **Visual observations** of symptoms of 6 diseases and pests in different environments
3. **Pre-processing** : spatial corrections, extraction of maximum damage, transformation, G-BLUP (Y_g values)

Genetic diversity in peach core-collection



← Leaf curl disease on peach



Modeling non-additive effects

1 Variance decomposition – Model ADI_Inb :

$$Y_g = \mu + \beta \text{Inb}_g + A_g + D_g + AA_g + AD_g + DD_g + \varepsilon_g$$

$$A \sim N(0, \sigma_A^2 K_A), D \sim N(0, \sigma_D^2 K_D), \varepsilon \sim N(0, \sigma_\varepsilon^2 I)$$

$$AA \sim N(0, \sigma_{AA}^2 K_{AA}), AD \sim N(0, \sigma_{AD}^2 K_{AD}), DD \sim N(0, \sigma_{DD}^2 K_{DD})$$

$$A \perp D \perp AA \perp AD \perp DD \perp \varepsilon \quad \text{see detailed methods in Roth et al. 2022}$$

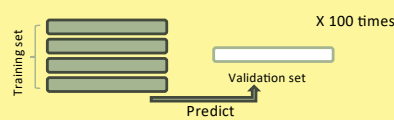
Comparison of 8 model declinations with NOIA approach :

A, A_Inb, AD, AD_Inb, ADAA, ADAA_Inb, ADI, ADI_Inb

Inb_g: percentage of homozygosity; β: associated regression coefficient; A_g and D_g: additive and dominant random effects associated to genotype g; AA_g, AD_g and DD_g: random effects modeling epistasis, accounting for additive by additive, additive by dominant and dominant by dominant effects, respectively; ε_g: random error; σ_A² ... σ_{DD}²: variance terms associated to genetic effects; K_A ... K_{DD}: kinship matrices corresponding to each genetic effect, after Vitezica et al. 2017.

2 Genomic predictions with 8 models

Via 5-fold cross validation on G-BLUPs



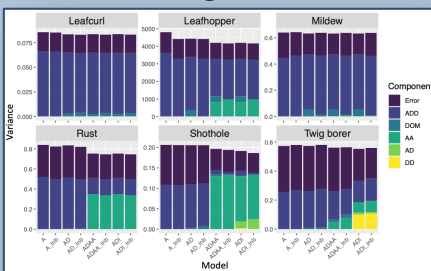
3 Genome-wide association (3 models)

using a recoding of SNP polymorphism

Allelic state	Additive model	Dominant model	Recessive model	Over-dominance model
a1a1	0	0	0	0
a1a2	1	2	0	1
a2a2	2	2	2	0

Are non-additive effects underlying trait architecture in peach biotic stress response ?

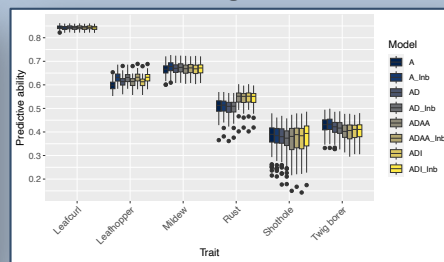
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Variance decomposition across 6 traits and 8 models

- **Total variance is stable** across the different models. **Heritability increases** when adding epistatic effects for rust, shothole and twig borer.
- The **fixed effect of inbreeding is significant for leafhopper and mildew**. Adding inbreeding affects dominance variance estimation for those traits.
- Among epistatic effects, **prevalence of additive by additive variance** but large confounding with additive variance.

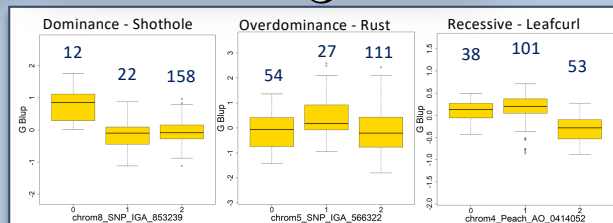
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← Results of 100 cross-validations across 6 traits and 8 models

- **High prediction accuracies for leaf curl** (mean PA = 0.84)
- Systematic improvement of accuracy using **inbreeding** for leafhopper damage (+0.03) and **additive by additive effects** for rust damage prediction (+0.04)
- **Overall low predictive ability for shothole and twig borer** damage with **degradation** of predictive ability using dominance and epistatic effects on twig borer damage (-0.03 to -0.01)

3



Serrie et al. in prep

← Examples of non-additive QTLs detected for 3 diseases using non-additive GWAS

- A total of 31 associations (QTL) found with the 3 non-additive models
- 56 % associations detected only with non-additive models, 16 % are also detected with the additive model
- No overlap between overdominance and additive QTLs

Conclusion and outlook

- ❖ Using non-additive effects in linear mixed models improves heritability and genomic predictions when using the NOIA approach, and allows to discover new associations
- ❖ Inbreeding is positively correlated to susceptibility to leafhopper which is a trait affected by vigor → This may imply **directional dominance mechanisms**
- ❖ A major recessive QTL on LG4 seems to underlie leaf curl tolerance (3), but additivity catches most genetic variance (1), providing highly accurate predictions in any model (2)



Next, we will use non-additive and inbreeding effects in **MARKER ASSISTED SELECTION** and **GENOMIC SELECTION** to better harness durable tolerance mechanisms in peach

Useful references:

Roth, M., Beugnot, A., Mary-Huard, T., Moreau, L., Charcosset, A., and Fiévet, J.B. (2022). Improving genomic predictions with inbreeding and nonadditive effects in two admixed maize hybrid populations in single and multi-environment contexts. *Genetics* 220: iyac018.

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Vitezica, Z.G., Legarra, A., Toro, M.A., and Varona, L. (2017). Orthogonal estimates of variances for additive, dominance, and epistatic effects in populations. *Genetics* 206, 1297–1307.