EDITORIAL

Will models of genetic evaluation and genomic selection 'converge'?

I would like to differentiate between two approaches of predicting breeding values. The focus is on the individual animal as it is the unit of selection. Breeders want to predict the value of future progeny, which will inherit half the breeding value (BV) of either parent. As BVs are not directly observable and treated as random variables, the strength of inheritance is usually measured as the covariance of BVs of animals belonging to successive generations. Before the genomic era, there was no way to discern the fraction of genome contributed differentially by an ancestor to the BV. Thus, it is assumed to be, for example, onequarter from grandparents to grand progeny, and so on. Such a black box model does not take into account the genetic architecture of the trait. A Gaussian density is obtained with a large number of additive gene effects. As the number is finite, the word infinitesimal used to name the model is unfortunate. The idea that an infinite number of gene effects are necessary to get a normal density evidences a confusion between a sampling and a limiting distribution. We will refer to the large sampling approach as topdown, which is parsimonious and reasonable when the focus of selection and prediction is the individual, not the gene. The use of markers in high density has produced a bottom-up approach (from the gene or QTL to the breeding value) starting with the so-called whole-genome regression methods. It is worthwhile to figure out when the two approaches 'converge'.

The bottom-up models can account for the genetic architecture of the trait, but with an expensive number of parameters and a problem of handling data for animals that do not have genomic information. Those predictions assume that markers are in Hardy–Weinberg (H–W) among themselves, but in linkage disequilibrium (LD) with the QTLs, which are mostly unknown! The need to account for the dependence structure (relatedness and LD is crucial. Gustavo de los Campos, Daniel Sorensen and Daniel Gianola (2015, *PLOS Genetics* **11**:1–21) ascertained the relationship between the classic heritability (h^2) and the genomic heritability (h_g^2) that results from using bottom-up models. Within a quantitative genetics framework, they obtained the relationship $h_g^2 = r^2 h^2 \le h^2$,

where r^2 is the squared correlation between genotypes at the marker locus and at the QTL, that is the fraction of heritability recovered by the markers. Therefore, the bottom-up model will not be entirely effective unless it can account for the full h^2 of the trait ($r^2 = 1$) and there is no 'missing heritability'.

In the top-down approach, the inheritance process is modelled by the average of parental BV plus a Mendelian residual. This 'error term' involves the variation in the contribution by grandparental genome, which after going through the corresponding parent, end up in grand progeny with an amount above or below 25%. Thus, without genomic data the information on the Mendelian residual comes from the phenotypic data on the individual itself, or on its progeny. We (Cantet and Vitezica, 2014, WCGALP10) showed that the Mendelian residuals of BVs predicted with genomic relationships have smaller or, at maximum, equal variance in comparison with the conventional animal model. The predictions of BV with phenotypes, pedigree and genomic information reduce the uncertainty due to recombination acting across generations. Would that increase the accuracy of prediction? Most likely. Notice, however, that there are methods that do not use all pedigree and genomic information. Consider the genomic relationship matrix (GRM) from single-step genomic BLUP. The predictor is close to 'convergence' between the approaches, and the model is apparently equivalent to whole-genome regression when markers are in H-W equilibrium. Elizabeth Thompson (2013, Genetics 194:301-326) observed that '- the GRM ... does not take the segmental nature of inheritance of DNA into account' and that 'permutation of the loci will not affect' the values of the elements of the matrix. Therefore, the information from IBD that account for LD seems to be the key to more precise genomic relationships. After all, IBD is evidence of common inheritance!

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