# ESTIMATION OF INBREEDING DEPRESSION ON FEMALE FERTILITY IN THE FINNISH AYRSHIRE POPULATION

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Running head: Inbreeding depression on fertility

## Summary

SNP data enable the estimation of inbreeding at the genome level. In this study, we estimated inbreeding levels for 19 075 Finnish Ayrshire cows genotyped with a low-density SNP panel (8K). The genotypes were imputed to 50K density, and after quality control, 39 144 SNPs remained for the analysis. Inbreeding coefficients were estimated for each animal based on the percentage of homozygous SNPs ($F_{PH}$), runs of homozygosity ($F_{ROH}$), and pedigree ($F_{PED}$). Phenotypic records were available for 13 712 animals including non-return rate (**NRR**), number of inseminations (**AIS**), and interval from first to last insemination (**IFL**) for heifers and up to three parities for cows, as well as interval from calving to first insemination (**ICF**) for cows. Average $F_{PED}$ was 0.02, $F_{ROH}$ 0.06, and $F_{PH}$ 0.63. A correlation of 0.71 was found between $F_{PED}$ and $F_{ROH}$, 0.66 between $F_{PED}$ and $F_{PH}$, and 0.94 between $F_{ROH}$ and $F_{PH}$. Pedigree-based inbreeding coefficients did not show inbreeding depression in any of the traits. However, when $F_{ROH}$ or $F_{PH}$ was used as a covariate, significant inbreeding depression was observed; a 10% increase in $F_{ROH}$ was associated with 5 days longer IFL0 and IFL1, 2 weeks longer IFL3, and 3 days longer ICF2 compared to non-inbred cows.


## Introduction

Mating of animals with common ancestors creates inbreeding. The inbreeding level, or inbreeding coefficient (F), of an animal refers to the probability that two alleles at a locus are identical by descent (IBD; Falconer &Mackay, 1996). Inbreeding depression, in turn, is defined as the impairment of fertility or any other phenotypic value caused by inbreeding within a population (Falconer &Mackay, 1996). Multiple studies have reported reduced fertility due to inbreeding. For example, McParland et al. (2007) found that the calving interval of cows increased by 0.7 days and their survival to second lactation decreased by 0.3% for each 1% increase in the inbreeding coefficient. Bjelland et al. (2013) reported an increase in days open from 1.06 to 1.76 days per 1% increase in the inbreeding coefficient. Pryce et al. (2014), observed that a 1% increase in the inbreeding coefficient lengthened the calving interval by 0.18 days. Moreover, single lethal recessive alleles can cause embryo or fetus abortions at any stage of gestation, thus increasing

the time between parturitions of the dam. Impaired fertility also reduces profitability, because the lifetime milk production of the cow decreases and the costs related to inseminations and veterinary treatments increase. In the worst case, the cow must be involuntarily culled due to poor fertility, which incurs further costs through replacements.

The traditional way to estimate inbreeding coefficients is to use pedigree information ($F_{PED}$). However, shallow or incomplete pedigree data may lead to an underestimation of inbreeding coefficients. An alternative method is to use single nucleotide polymorphism (SNP) marker data. The simplest estimate of genomic inbreeding is the percentage of homozygous alleles ($F_{PH}$), but $F_{PH}$ cannot distinguish between alleles that are identical by state (IBS) and those that are IBD. One way to overcome the problem is to look for continuous stretches of homozygous genotypes called runs of homozygosity (ROHs). Using ROHs increases the probability that the homozygosity is due to IBD, not IBS (Gibson, 2006). ROH length depends on the distance in generations to a common ancestor (Bjelland et al. 2013): a short ROH indicates that the common ancestor occurred several generations ago, whereas a long ROH reflects a more recent common ancestor (Purfield et al., 2012).

The objective of this study was to estimate inbreeding coefficients for Finnish Ayrshire cows from pedigree and genomic data, and to use this information to determine inbreeding depression of cow fertility traits in this cattle breed.

## Materials and methods

The genotypes, pedigree data, breed proportions, raw phenotypes, solutions for fixed effects, and estimates of (co)variance components were obtained from NAV, Nordic Cattle Genetic Evaluation (Aarhus, Denmark) and from Faba, The Finnish Animal Breeding Association (Vantaa, Finland).

### Animals

The present Red Dairy Cattle (RDC) population in Finland consists of the original Finnish Ayrshire (FAY) breed and Scandinavian and North American red breeds. Table 1 shows the number of

cows with genotypes and those with both genotypes and phenotypes, representing different proportions of the FAY breed. We used two sets of RDC cows in this study: one including all cows with both genotypes and phenotypes registered as Finnish RDC (RDCFIN; 13 712 cows), and the other including only those RDC cows with both genotypes and phenotypes and at least 50% of FAY based on the pedigree (FAY50; 7 547 cows). All cows were born between 2002 and 2014.

**Genomic data**

Genotyping was performed using the Illumina BovineLD v.2 BeadChip low-density panel (Illumina Inc., 2015), which contains 7 931 SNPs. To achieve 50K density, the genotypes were imputed by the Fimpute software (Sargolzaei et al., 2014) using the default values. The imputed genotypes were further pruned so that SNPs with minor allele frequency (MAF) of less than 0.05 or a P-value of the Chi-square test for Hardy-Weinberg equilibrium of less than 0.0001 were removed from the data. A total of 39 144 SNPs remained for the analysis.

**Phenotypic data**

We utilized Nordic fertility evaluation data for the RDC breed to select a sub-sample of Finnish RDC cows for this study. Phenotypes of female fertility were available for 1 805 454 animals. When combined with the available genomic data, the sub-sample comprised a total of 13 712 animals with both genotypes and phenotypes. Fertility traits included non-return rate at 56 days after first insemination (NRR), number of inseminations (AIS), and intervals (in days) from calving to first insemination (ICF) and from first to last insemination (IFL). Fertility traits were considered separately for heifers (lactation 0) and for cows with one to three lactations. Descriptive statistics of unadjusted observations for each trait at each parity for both sets (RDCFIN and FAY50) of data are given in Table 2. The negative and non-integer values for observations in Table 2 are due to pre-corrections of the records for heterogeneous variance due to country, year of first calving, and parity (Fogh et al., 2003).

Since the data set used in this study was a sub-sample of the full Nordic fertility evaluation model for RDC, the raw phenotypic values were adjusted for systematic effects prior to the estimation of inbreeding depression using the solutions of the full evaluation model. The adjusted systematic effects included herd-birth year (for heifers) or herd-year of first calving (for cows), insemination year-month (for all traits except ICF), calving year-month (ICF), and heifer's age at first insemination. Figure 1 shows the variation of the adjusted phenotypic values.

**Estimation of inbreeding coefficients**

Pedigree-based inbreeding coefficients were estimated from the pedigree, with an average depth of 10 generations for the genotyped animals. Only animals with the pedigree completeness value (MacCluer et al. 1983) of 0.80 or greater based on five generations were included in the analysis. Genomic inbreeding coefficients were estimated based on either homozygous SNPs ($F_{PH}$) or runs of homozygosity ($F_{ROH}$). The first measure, $F_{PH}$, was determined for each animal as the proportion of homozygous genotypes of all genotypes. The other measures of genomic inbreeding were ROH-based. ROHs were detected with three different parameter settings using PLINK v1.07 (Purcell et al., 2007). The first parameter setting (ROH_1) was based on those used by Purfield et al. (2012). A minimum density of 1 SNP per 120 kb was set to prevent low SNP density from affecting ROH length. Short ROHs were eliminated by setting the minimum ROH length to 500 kb, but without limiting the number of SNPs per ROH (the corresponding PLINK parameters are --homozyg-density 120 --homozyg-kb 500 --homozyg-snp 0). For the second and third settings we reduced the size of the sliding window to 20 SNPs and the minimum ROH length to 10kb, and increased the minimum density to 1 SNP per 1000 kb, as in the article by Zhang et al. (2015). The difference between the second and third settings was the minimum number of SNPs per ROH: 30 SNPs for ROH_2 and 100 SNPs for ROH_3 (the corresponding PLINK parameters are --homozyg-window-snp 20 --homozyg-density 1000 --homozyg-kb 10 --homozyg-snp 30 or 100). For all three settings we allowed one possible heterozygous genotype per window to account for potential errors in genotyping and imputation. Based on these three parameter settings ($F_{ROH\_1}$, $F_{ROH\_2}$ and

$F_{ROH\_3}$), the inbreeding coefficient estimates were determined as the sum of SNPs in the ROHs divided by the total number of SNPs.

### Estimation of inbreeding depression

Inbreeding depression was estimated by regressing the phenotypic values on the inbreeding coefficients. Inbreeding depression was estimated separately for each trait (NRR, AIS, ICF, and IFL) using the multi-lactation model, *i.e.* with heifer and cow traits jointly:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e},$$

where vector **y** contains the pre-adjusted phenotypes of a trait for each parity, **b** is a vector of fixed effects including the mean μ and the linear regression coefficient b for each parity, **a** is a vector of random additive genetic effects, and **e** is a vector of random residual effects. The matrix **X** includes the inbreeding coefficients, either $F_{PED}$, $F_{ROH\_1}$ or $F_{PH}$, for each animal, and **Z** is an incidence matrix that relates the appropriate effects to each observation. Furthermore, it was assumed that the random genetic effects were normally distributed with $N(\mathbf{0}, \mathbf{A} \otimes \mathbf{G})$, where **A** is the pedigree-based additive relationship matrix and **G** is the additive genetic variance-covariance matrix of the heifer and cow traits (*e.g.* between IFL0, IFL1, IFL2, and IFL3), and also that the random residual effects were normally distributed with $N(\mathbf{0}, \mathbf{R})$. Variances and covariances were the same as in the Nordic fertility evaluation (Muuttoranta et al., 2016). Genetic groups for animals with unknown parents were treated in the analysis as random effects. The statistical analyses were performed with the DMU program package (Madsen and Jensen, 2000).

## Results

### Runs of homozygosity

We used three settings in PLINK to detect ROHs in the population of 19 075 genotyped animals. The first setting (ROH_1) gave a total of 411 541 ROHs for all animals. The frequency distribution

of ROHs shorter than 50 Mb using the ROH_1 setting is shown in Figure 2. There were 783 ROHs longer than 50 Mb, with a maximum length of 125.1 Mb. The number of SNPs in the ROHs varied from 6 to 1 897. With the ROH_2 and ROH_3 settings, the total numbers of ROHs found for all animals were 838 383 and 165 843, respectively. ROH lengths varied from 0.9 Mb to 138 Mb for ROH_2, and from 3.3 Mb to 138 Mb for ROH_3. The number of SNPs in the ROHs varied from 30 to 2 123 for ROH_2 and from 100 to 2 123 for ROH_3.

**Inbreeding coefficients**

The average inbreeding coefficients of all RDCFIN animals were 0.02, 0.09, and 0.63 for $F_{PED}$, $F_{ROH}$, and $F_{PH}$, respectively (Table 3). The corresponding averages for FAY50 animals were 0.03, 0.10, and 0.63 (Table 3). Homozygosity-based estimates ($F_{PH}$) were on a different scale than the other estimates. $F_{PH}$ could have been adjusted for the expected amount of homozygosity (Purcell et al., 2007) or calculated from the genomic relationship matrix (VanRaden et al., 2011) to be on a similar scale as the other inbreeding coefficient estimates. However, using scaled values instead of raw values would not have affected the obtained results of inbreeding depression. ROH-based inbreeding coefficients showed more variation than the pedigree- and homozygosity-based estimates (Tables 3 and 4, and Figures 3 and 4). Among the tested ROH methods, the lowest average estimates of inbreeding coefficients were obtained for ROH_3 (0.04 for RDCFIN and 0.05 for FAY50) and the highest for ROH_2 (0.09 for RDCFIN and 0.1 for FAY50). The average of $F_{ROH\_1}$ was 0.06 for RDCFIN and 0.07 for FAY50 (Table 3).

Correlations between the pedigree-based and genomic measures of inbreeding coefficients for RDCFIN were moderate: 0.66 between $F_{PED}$ and $F_{PH}$ and 0.71 between $F_{PED}$ and $F_{ROH\_1}$ (Table 5). The corresponding correlations for FAY50 varied from 0.55 between $F_{PED}$ and $F_{PH}$ to 0.59 between $F_{PED}$ and $F_{ROH\_1}$ (Table 5). Very strong correlations were detected between all genomic measures using all RDCFIN animals: from 0.90 between $F_{ROH\_3}$ and $F_{PH}$ to 0.98 between $F_{ROH\_1}$ and $F_{ROH\_2}$. The use of only FAY50 animals resulted in almost equal correlations, from 0.89 ($F_{ROH\_3}$ and $F_{PH}$) to 0.98 ($F_{ROH\_1}$ and $F_{ROH\_2}$). Due to the very strong correlation between all ROH-

based estimates, only $F_{ROH\_1}$, which had the strongest correlation with $F_{PED}$, was selected for subsequent analysis.

### Inbreeding depression

There were large differences in the estimates of inbreeding depression between traits, parities, data sets, and measures of inbreeding (Tables 6–8). In general, no statistically significant results were obtained when $F_{PED}$ was used as a covariate in the model. The only exception was NRR1 in the FAY50 data set ($P<0.1$), with a deteriorating effect of approximately 0.9% per 1% increase of $F_{PED}$ (Table 6). $F_{PH}$ had a statistically significant effect on NRR1 in both data sets, deteriorating NRR1 by approximately 1.1% and 1.2% per 1% increase in $F_{PH}$ in the RDCFIN and FAY50 data sets, respectively (Table 6).

A high genetic correlation (0.91) has been reported between IFL, which measures the service period in days, and AIS, which measures the number of inseminations in the same period (Berry et al., 2014). The results for both traits were congruent in our study, and thus only the results of IFL are presented here (Table 7). In the RDCFIN animals, an increase of 1% in $F_{ROH\_1}$ lengthened IFL0 and IFL1 by approximately 0.4 and 0.5 days, respectively. Similarly, a 1% increase in $F_{PH}$ was associated with an increase of 0.9 days in IFL0 and of 1.1 days in IFL1. Using the FAY50 data set, the corresponding estimates were 0.4 days (IFL0 and $F_{ROH\_1}$), 0.6 days (IFL1 and $F_{ROH\_1}$), and 1.4 days (IFL1 and $F_{PH}$). Moreover, an increase of 1% in $F_{ROH\_1}$ and $F_{PH}$ increased IFL3 by 1.5 days and 3 days, respectively (Table 7).

Among the three ICF traits, only ICF2 showed statistically significant inbreeding depression with $F_{ROH\_1}$ as a covariate; a 1% increase in $F_{ROH\_1}$ increased ICF2 by 0.3 and 0.4 days in the RDCFIN or FAY50 data sets, respectively.

## Discussion

### Runs of homozygosity and inbreeding coefficient

ROH determination depends on the selected parameters. Consequently, we compared three different parameter settings which differed in the minimum requirements for the number of SNPs in ROH, ROH length, and SNP density in ROH. The obtained results indicate that the number of ROH segments increases with a decrease in the number of SNPs required to determine ROH. Eventually, the ROH-based estimates of inbreeding coefficients converge to $F_{PH}$ when ROH length diminishes to a single SNP. However, the possibility to detect ROH segments that are IBS but not IBD also increases along with a smaller number of required SNPs. The most stringent setting in our study was ROH_3, for which the minimum number of SNPs in ROH was set to 100. The largest number of ROH segments was found using ROH_2, which differed from ROH_3 only in terms of the minimum number of SNPs in ROH (30 instead of 100 SNPs). As expected, the estimates of inbreeding coefficients depended on these settings. ROH_3 gave the smallest average inbreeding coefficient, followed by ROH_1 and ROH_2.

The size of the sliding window may have had an effect on ROH lengths as well, since a SNP is included in a ROH only if 5% of the windows containing the SNP are completely homozygous (Howrigan et al., 2011). Additionally, Ferenčaković et al. (2013) showed that ROHs may depend on the density of the genotyping panel. In their study, a 50K panel gave a larger number of small (<4 Mb) ROH segments than a high-density panel. No differences between panels were obtained for ROHs longer than 4 Mb. The authors concluded that a 50K panel creates false positive findings of short ROHs, and therefore leads to an overestimation of $F_{ROH}$. In the present study, almost half (198 595 of 411 541) of ROHs (determined using the ROH_1 setting) were shorter than 5 Mb (Figure 2). This indicates that ROH_1, with average estimates of 0.06 for RDCFIN and 0.07 for FAY50, may overestimate the level of inbreeding. The ROH_2 analysis revealed twice as many ROHs as ROH_1, and presumably resulted in even higher overestimation of inbreeding (0.09 for RDCFIN and 0.10 for FAY50). In contrast, ROH_3 only detected ROHs longer than 3.3 Mb, which may have led to an underestimation of $F_{ROH,}$ with average values of 0.04 for RDCFIN and 0.05 for FAY50. With the ideal criteria for detecting ROHs, the average inbreeding coefficient estimate would probably have been somewhere between the $F_{ROH\_3}$ and

$F_{ROH\_1}$ values. We also tested if pruning of SNPs based on linkage disequilibrium (LD) has an effect on detection of ROHs and estimates of inbreeding depression. For this we repeated the ROH_1 analysis using the LD-pruned RDCFIN dataset (PLINK: --indep-pairwise 50 5 0.5, resulting in 29 390 SNPs). As a result, the correlation between $F_{ROH\_1}$ values from the LD-pruned and unpruned data was 0.98. Also the pruning had a very minor effect on the estimates of inbreeding depression *e.g.* for IFL0 the LD-pruned data gave 43.4 (SE=13.8) compared the estimate of 43.2 (SE=13.0) from the unpruned data. Despite the effect of panel density and the settings of ROH calling, many studies have concluded that $F_{ROH}$ provides the most effective and consistent measure of the inbreeding coefficient compared to other methods (e.g. Keller et al., 2011; Bjelland et al., 2013).

All inbreeding coefficients ($F_{PED}$, $F_{PH}$, $F_{ROH}$) calculated by the three methods were correlated, but the correlations were higher between genomic estimates (r = 0.89–0.98) than between pedigree and genomic estimates (r = 0.55–0.71). Similar high correlations have been reported in other studies as well. Bjelland et al. (2013) observed a correlation of 0.81 between genomic inbreeding measures ($F_{PH}$ and $F_{ROH}$), and Pryce et al. (2014) reported a corresponding correlation of 0.9. Keller et al. (2011) found that inbreeding coefficients calculated using ROH correlated strongly (0.6) with the homozygous mutation load, whereas the correlation between the homozygous mutation load and pedigree-based inbreeding coefficients was weak (0.25). Pryce et al. (2014) detected a correlation of 0.53 between $F_{PED}$ and $F_{ROH}$ and of 0.45 between $F_{PED}$ and $F_{PH}$, while Purfield et al. (2012) reported an even stronger positive correlation (0.73) between $F_{PED}$ and $F_{ROH}$. The correlations found in the present study between the genomic measures of inbreeding coefficients were consistent with previous studies, and correlations between estimates obtained by pedigree and genomic methods were almost as strong as those reported by Purfield et al. (2012).

**Inbreeding depression**

We observed virtually no inbreeding depression associated with $F_{PED}$ in the present study. However, the genomic measures of inbreeding coefficients revealed inbreeding depression on NRR1 ($F_{PH}$), ICF2 ($F_{ROH\_1}$), IFL0, IFL1, and IFL3 (both $F_{PH}$ and $F_{ROH\_1}$). The phenotypic data used in the present study were from field records. Therefore, the number of highly inbred cows was small and the analyses were based primarily on cows with low levels of inbreeding. As Cassell et al. (2003) noted, in such conditions, non-significant results are common. In general, power of regression coefficient depends on data size and dispersion of the dependent variable. In our case, the number of animals was bigger for heifers than for cows. This may explain the differences between the parities. Smaller dispersion of $F_{PED}$ than $F_{ROH\_1}$ may have resulted in reduced statistical power of pedigree based inbreeding depression estimation compared to genomic measures of inbreeding depression. Also, culling for poor fertility can create bias in estimates of inbreeding depression if the cause of poor fertility is inbreeding. This may be an additional explanation for differences between parities. Moreover, selection can create beneficial homozygosity at certain loci thus having an opposite effect on a trait compared to inbreeding based homozygosity. However, even though fertility traits are part of the current Nordic breeding goal, the effect of selection on our results is expected to be minimal.

Also Pryce et al. (2014) found differences between pedigree- and genome-based estimates of inbreeding depression, implying that the use of pedigree information probably underestimates inbreeding depression on female fertility. On the contrary, Ferenčaković et al. (2013) reported that the widely used Illumina BovineSNP50 BeadChip (Illumina Inc. 2016) overestimates the number of short ROHs and, consequently, the inbreeding coefficient. In addition, Pryce et al. (2014) reported that only ROHs longer than 60 SNPs or 3.5 Mb were associated with a decrease in milk yield independent of the overall level of homozygosity. They suggested that if inbreeding is due to an ancient common ancestor, selection has had an opportunity to purge deleterious mutations and therefore they did not find association between short ROHs and decrease in milk yield.

Among the studied fertility traits in the present study, NRR had a bimodal distribution even after adjustment for heterogeneous variance and systematic effects. The analysis with unadjusted data and logistic regression model might have resulted in more reliable estimates of inbreeding depression on NRR. However, the structure of the data (number of observations in the different classes of the systematic effects) did not allow this approach to be applied.

Thanks to its simplicity, the calving interval is among the most widely used fertility traits. Many studies have reported that inbreeding causes a lengthening of the calving interval (e.g. Smith et al., 1998; Wall et al., 2005; McParland et al., 2007; Pryce et al., 2014). The calving interval is defined as the interval from previous calving to conception (days open) and gestation length. Pereira et al. (2016) showed that increased inbreeding only affects days open, but not gestation length. Days open also comprises two periods: the interval from calving to first insemination and from first to last insemination, both of which were examined in the present study and revealed inbreeding depression. Bjelland et al. (2013) reported an increase of 1.76 and 1.72 days in days open per 1% increase in $F_{PH}$ and $F_{ROH}$, respectively. The corresponding results in the present study were approximately 0.3 days for ICF and approximately 0.5 days for IFL. Combining the estimates of inbreeding depression for the two intervals gave estimates from 0.59 (first parity and RDCFIN) to 0.94 (second parity and FAY50) with $F_{ROH\_1}$ and from 1.17 (first parity and RDCFIN) to 2.16 (second parity and FAY50) with $F_{PH}$. These results are in accordance with those of Bjelland et al. (2013).

In conclusion, we showed that genome-based estimates of inbreeding differ from pedigree-based estimates, and that genomic inbreeding estimates are associated with female fertility. Further examination of the effect of the density of the SNP panel and the length of ROHs on inbreeding depression would elucidate the role of inbreeding depression on fertility traits. It is possible that the sum of ROHs or homozygosity may not reveal all the harmful effects of inbreeding on fertility. We suggest that a more detailed intra-chromosomal approach (Kleinman-Ruiz et al., 2016) could reveal specific chromosomal regions that are strongly affected by inbreeding depression in Finnish Ayrshire cows.

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Figure legends

Figure 1. Box-plots of adjusted phenotypic values

Figure 2. Frequency distribution of ROH length using the first parameter setting. Only ROHs shorter than 50 Mb are presented.

Figure 3. Box-plots of inbreeding coefficients estimated with different methods for RDCFIN and FAY50 data sets

Figure 4. Scatter density plot of $F_{ROH\_1}$ and $F_{PED}$. Each point is colored by the frequency of observations.

**Table 1** Number of cows with different proportions of the Finnish Ayrshire (FAY) breed

| | Animals with genotypes | Animals with genotypes and phenotypes |
|---|---|---|
| RDCFIN[1] | 19 075 | 13 712 |
| At least 25% FAY | 18 393 | 13 199 |
| At least 50% FAY (FAY50) | 10 199 | 7 547 |
| At least 75% FAY | 420 | 372 |

[1]Red Dairy Cattle registered in Finland

**Table 2** Descriptive statistics of unadjusted fertility traits of genotyped RDCFIN / FAY50 cows (values for both data sets are presented if different)

| | | Number of animals | Mean | SD | Min | Max |
|---|---|---|---|---|---|---|
| NRR (%) | 0 | 13 368 / 7 358 | 62.1 / 61.5 | 47.4 / 47.6 | -1.3 | 100.5 |
| | 1 | 9 474 / 5 230 | 54.3 / 53.3 | 49.3 | 0.2 | 99.8 |
| | 2 | 5 043 / 2 949 | 53.0 / 52.2 | 49.2 / 49.3 | 0.3 | 99.8 |
| | 3 | 1 540 / 1 011 | 54.5 | 49.1 | 0.4 | 99.8 |
| AIS (n) | 0 | 13 261 / 7 301 | 1.8 | 1.1 | 1.0 | 5.2 |
| | 1 | 9 323 / 5 155 | 2.0 / 2.1 | 1.2 | 1.0 | 5.0 |
| | 2 | 4 918 / 2 891 | 2.1 | 1.2 / 1.3 | 1.0 | 5.0 |
| | 3 | 1 453 / 957 | 2.0 | 1.2 | 1.0 | 5.1 |
| ICF (days) | 1 | 9 453 / 5 220 | 85.9 / 86.5 | 28.4 / 28.6 | 19.1 | 189.4 |
| | 2 | 5 067 / 2 968 | 87.4 / 88.0 | 29.2 / 29.3 | 15.4 / 24.9 | 188.7 |
| | 3 | 1 509 / 991 | 86.3 / 87.8 | 28.0 / 28.3 | 23.1 / 24.2 | 188.5 |
| IFL (days) | 0 | 12 878 / 7 080 | 26.9 / 27.8 | 40.8 / 41.5 | -2.3 | 242.1 |
| | 1 | 9 546 / 5 267 | 40.1 / 41.7 | 56.2 / 56.9 | -5.1 | 251.6 |
| | 2 | 5 131 / 2 991 | 42.7 / 44.3 | 55.9 / 56.8 | -5.2 | 251.8 |
| | 3 | 1 567 / 1 028 | 41.0 / 41.8 | 54.1 / 55.0 | -6.5 | 258.0 |

**Table 3** Descriptive statistics of inbreeding coefficients estimated with different methods for RDCFIN / FAY50 data sets

| | Mean | SD | Min | Max |
|---|---|---|---|---|
| $F_{PED}$ | 0.02 / 0.03 | 0.01 / 0.01 | 0.0 / 0.0 | 0.29 / 0.29 |
| $F_{ROH\_1}$ | 0.06 / 0.07 | 0.03 / 0.02 | 0.001 / 0.01 | 0.28 / 0.28 |
| $F_{ROH\_2}$ | 0.09 / 0.10 | 0.03 / 0.02 | 0.008 / 0.03 | 0.30 / 0.30 |
| $F_{ROH\_3}$ | 0.04 / 0.05 | 0.02 / 0.02 | 0.003 /0.003 | 0.27 / 0.27 |
| $F_{PH}$ | 0.63 / 0.63 | 0.01 / 0.01 | 0.60 / 0.60 | 0.71 / 0.71 |

**Table 4** Frequency distribution of $F_{PED}$ (N_ $F_{PED}$) and $F_{ROH\_1}$ (N_$F_{ROH_1}$)

| Inbreeding coefficient class | N_$F_{PED}$ | N_$F_{ROH_1}$ |
|---|---|---|
| 0.00 | 21 | 2 |
| 0.00-0.01 | 2661 | 123 |
| 0.01-0.02 | 3503 | 379 |
| 0.02-0.03 | 3713 | 917 |
| 0.03-0.04 | 2204 | 1475 |
| 0.04-0.05 | 934 | 1893 |
| 0.05-0.06 | 676[1] | 2006 |
| 0.06-0.07 | | 2057 |
| 0.07-0.08 | | 1743 |
| 0.08-0.09 | | 1235 |
| 0.09-0.10 | | 784 |
| >0.10 | | 1098 |

[1] $F_{PED} > 0.05$

**Table 5** Correlations between different estimates of inbreeding based on RDCFIN / FAY50 data sets

| | $F_{PED}$ | $F_{ROH\_1}$ | $F_{ROH\_2}$ | $F_{ROH\_3}$ | FPH |
|---|---|---|---|---|---|
| $F_{PED}$ | 1 | | | | |
| $F_{ROH\_1}$ | 0.71 / 0.59 | 1 | | | |
| $F_{ROH\_2}$ | 0.70 / 0.58 | 0.98 / 0.98 | 1 | | |
| $F_{ROH\_3}$ | 0.69 / 0.57 | 0.96 / 0.95 | 0.92 / 0.92 | 1 | |
| $F_{PH}$ | 0.66 / 0.55 | 0.94 / 0.93 | 0.95 / 0.95 | 0.90 / 0.89 | 1 |

**Table 6** Estimates of inbreeding depression (SE in brackets) for non-return rate (NRR) in parities 0–3 for RDCFIN and FAY50 data sets

| | | $F_{PED}$ | $F_{ROH\_1}$ | $F_{PH}$ |
|---|---|---|---|---|
| NRR0 | RDCFIN | 18.0 (40.0) | -9.4 (17.1) | -17.1 (40.7) |
| | FAY50 | 27.4 (39.9) | 17.1 (22.4) | 64.3 (53.3) |
| NRR1 | RDCFIN | -60.9 (40.2) | -35.0 (22.4) | -106.5** (53.2) |
| | FAY50 | -93.6* (52.5) | -40.2 (29.7) | -118.9* (70.4) |
| NRR2 | RDCFIN | 7.8 (53.2) | -13.1 (29.8) | -43.7 (71.2) |
| | FAY50 | 83.5 (68.9) | -14.1 (39.2) | -45.4 (92.9) |
| NRR3 | RDCFIN | 38.4 (87.8) | 17.0 (51.1) | 21.6 (126.7) |
| | FAY50 | -7.6 (106.7) | -0.6 (64.3) | 10.9 (154.8) |

*P-values < 0.1, **P-value < 0.05, ***P-value < 0.01

**Table 7** Estimates of inbreeding depression (SE in brackets) for interval from first to last insemination (IFL) in parities 0–3 for RDCFIN and FAY50 data sets

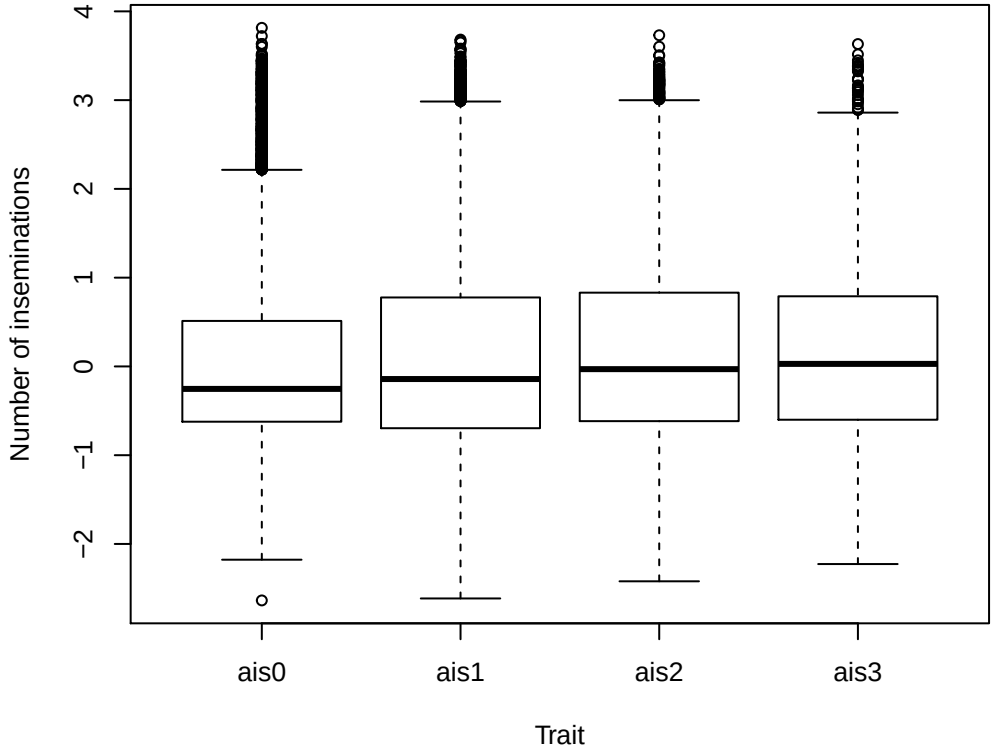
| | | $F_{PED}$ | $F_{ROH\_1}$ | $F_{PH}$ |
|---|---|---|---|---|
| IFL0 | RDCFIN | 28.6 (23.4) | 43.2***(13.0) | 89.1***(30.9) |
| | FAY50 | 8.7 (30.1) | 38.1**(17.0) | 62.2 (40.4) |
| IFL1 | RDCFIN | 41.2 (47.8) | 54.8**(26.6) | 110.0*(63.1) |
| | FAY50 | 53.3 (62.6) | 64.8*(35.1) | 139.6*(83.3) |
| IFL2 | RDCFIN | 2.7 (62.5) | 37.8 (34.8) | 111.3 (83.3) |
| | FAY50 | -32.6 (81.6) | 54.6 (46.0) | 148.5 (109.1) |
| IFL3 | RDCFIN | 27.7 (104.2) | 79.8 (60.6) | 217.6 (149.9) |
| | FAY50 | 148.5 (126.1) | 145.9* (75.8) | 326.1*(182.5) |

*P-values < 0.1, **P-value < 0.05, ***P-value < 0.01

**Table 8** Estimates of inbreeding depression (standard error in brackets) for interval from calving to first insemination (ICF) in parities 0–3 for RDCFIN and FAY50 data sets.

| | | $F_{PED}$ | $F_{ROH\_1}$ | $F_{PH}$ |
|---|---|---|---|---|
| ICF1 | RDCFIN | 15.1 (22.7) | 4.0 (12.6) | 7.1 (29.8) |
| | FAY50 | 4.8 (29.6) | 13.0 (16.6) | 15.9 (39.2) |
| ICF2 | RDCFIN | 20.4 (28.9) | 28.0*(16.1) | 44.4 (38.4) |
| | FAY50 | 8.6 (37.4) | 39.3*(21.1) | 65.7 (49.9) |
| ICF3 | RDCFIN | 15.6 (49.2) | -3.6 (28.3) | -8.3 (70.0) |
| | FAY50 | -18.3 (58.8) | -14.4 (35.0) | -30.0 (84.4) |

*P-values < 0.1, **P-value < 0.05, ***P-value < 0.01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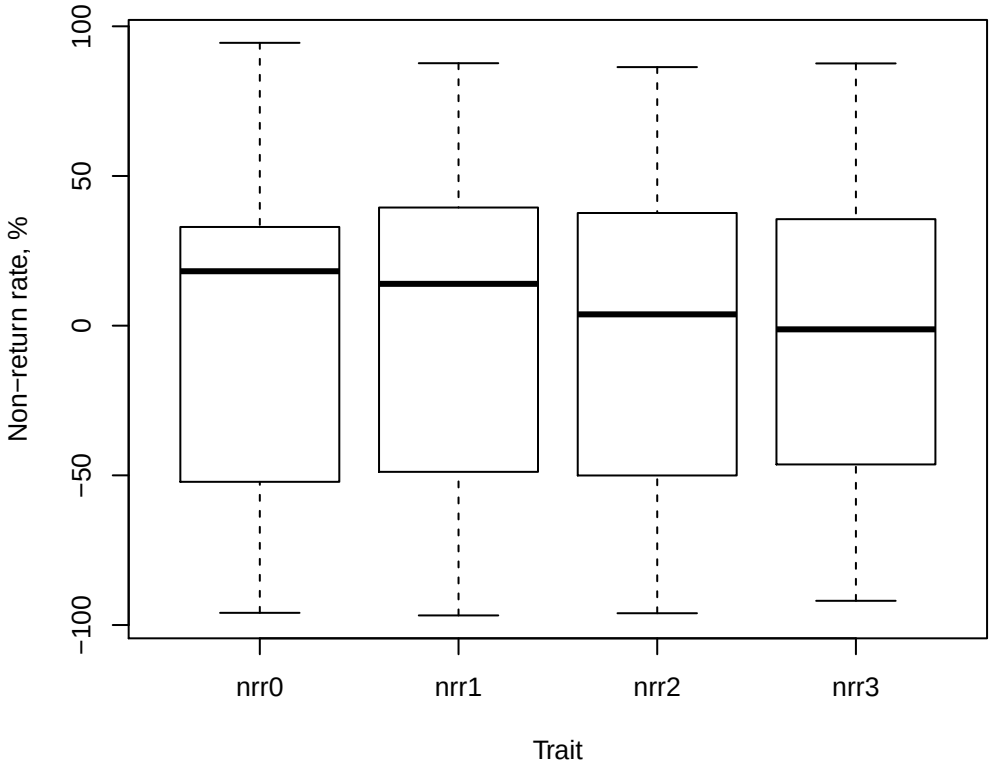
2
1
0
−1
−2
ais0
ais1
ais2
ais3
Trait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−100
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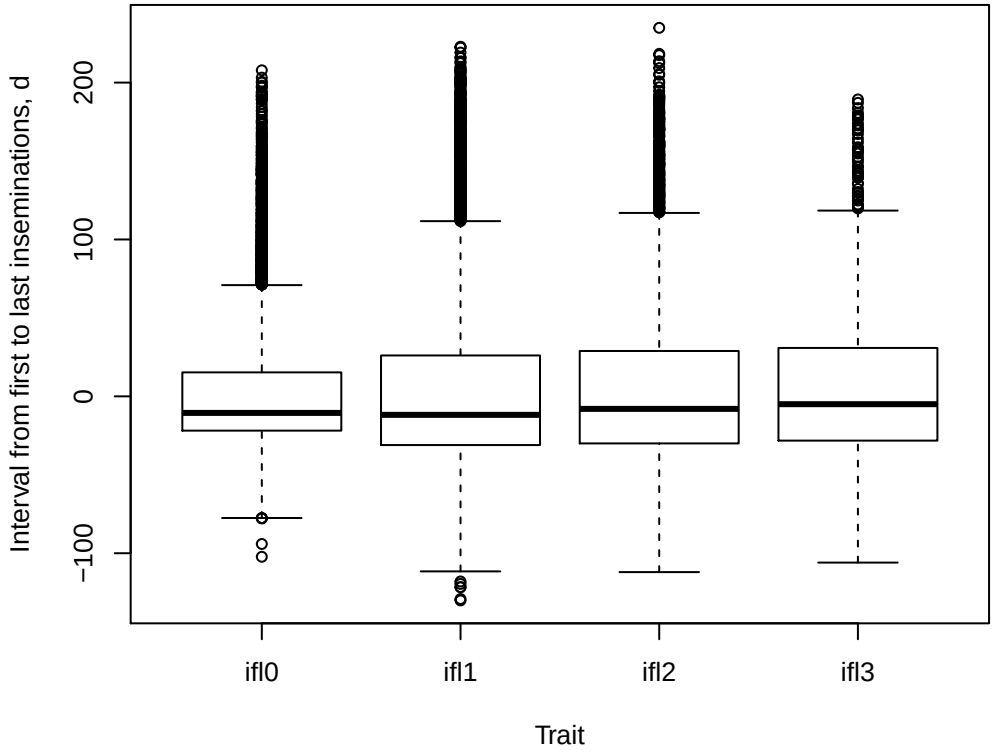
nrr1
nrr2
nrr3
Trait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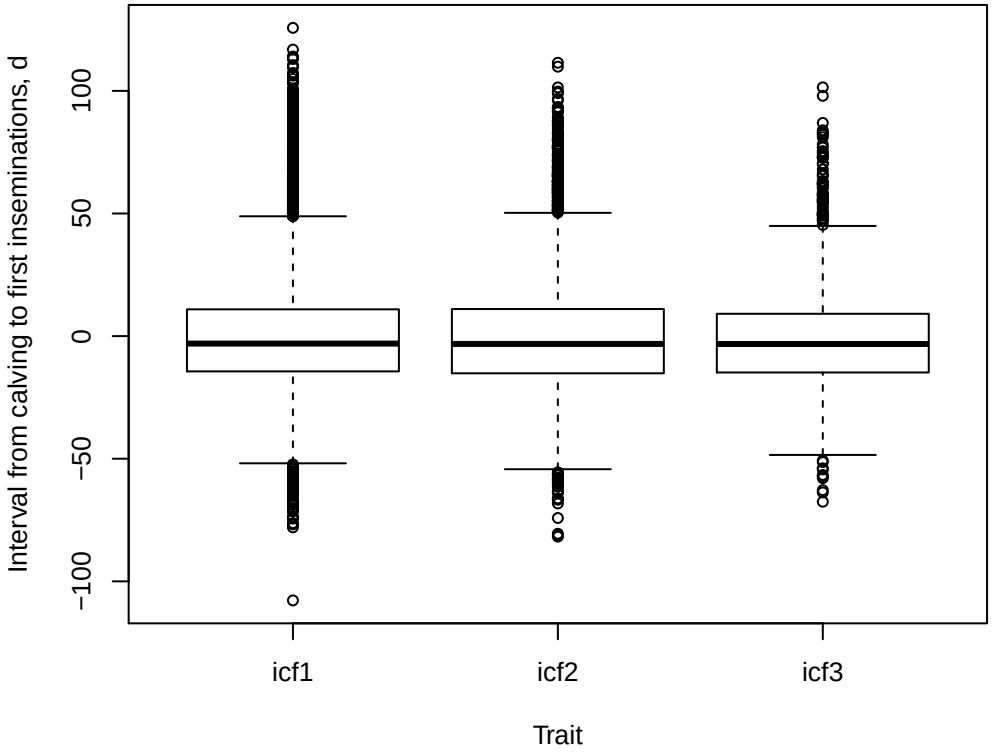
ifl0
ifl1
ifl2
ifl3
Trait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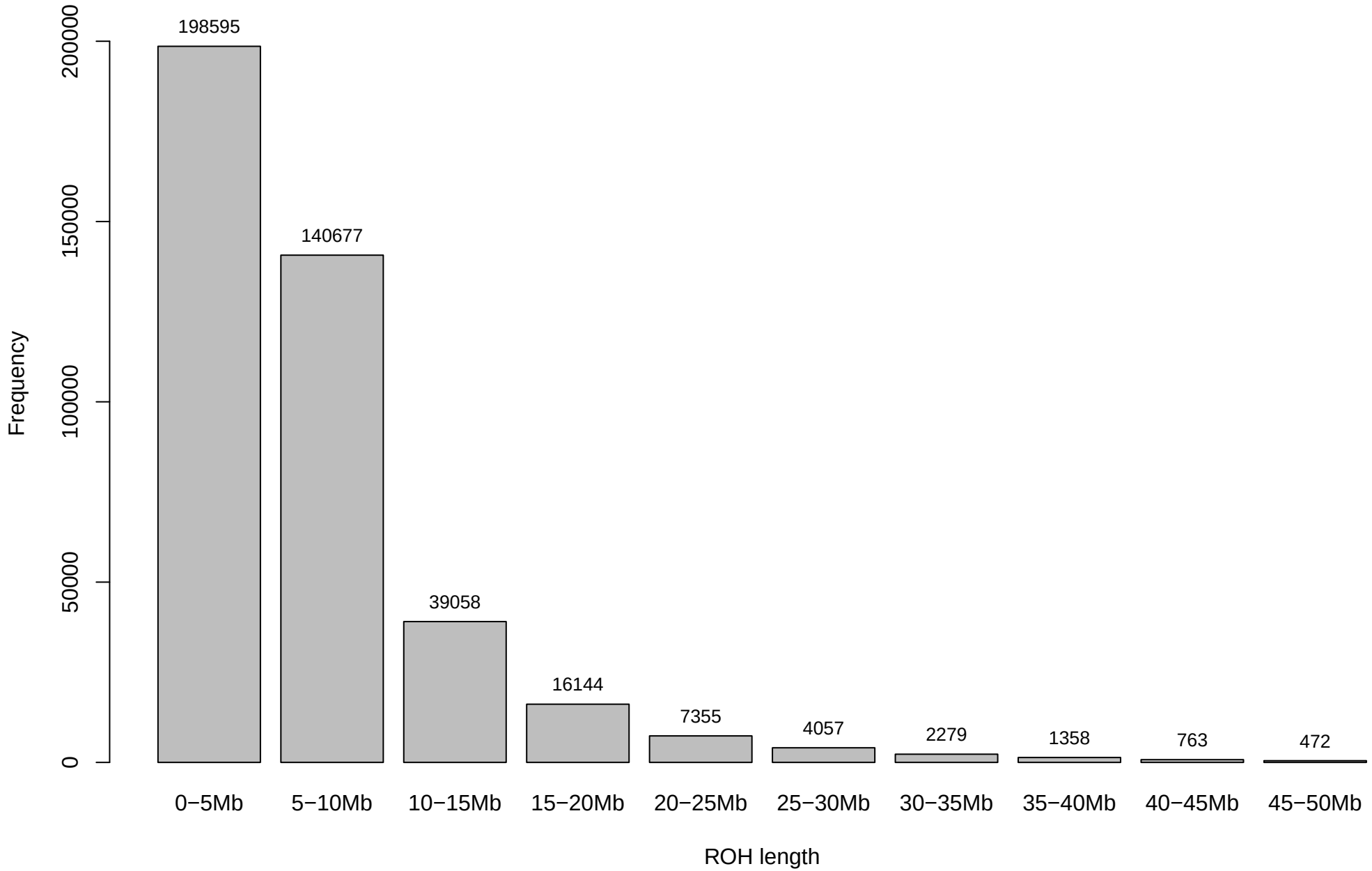
icf1
icf2
icf3
Trait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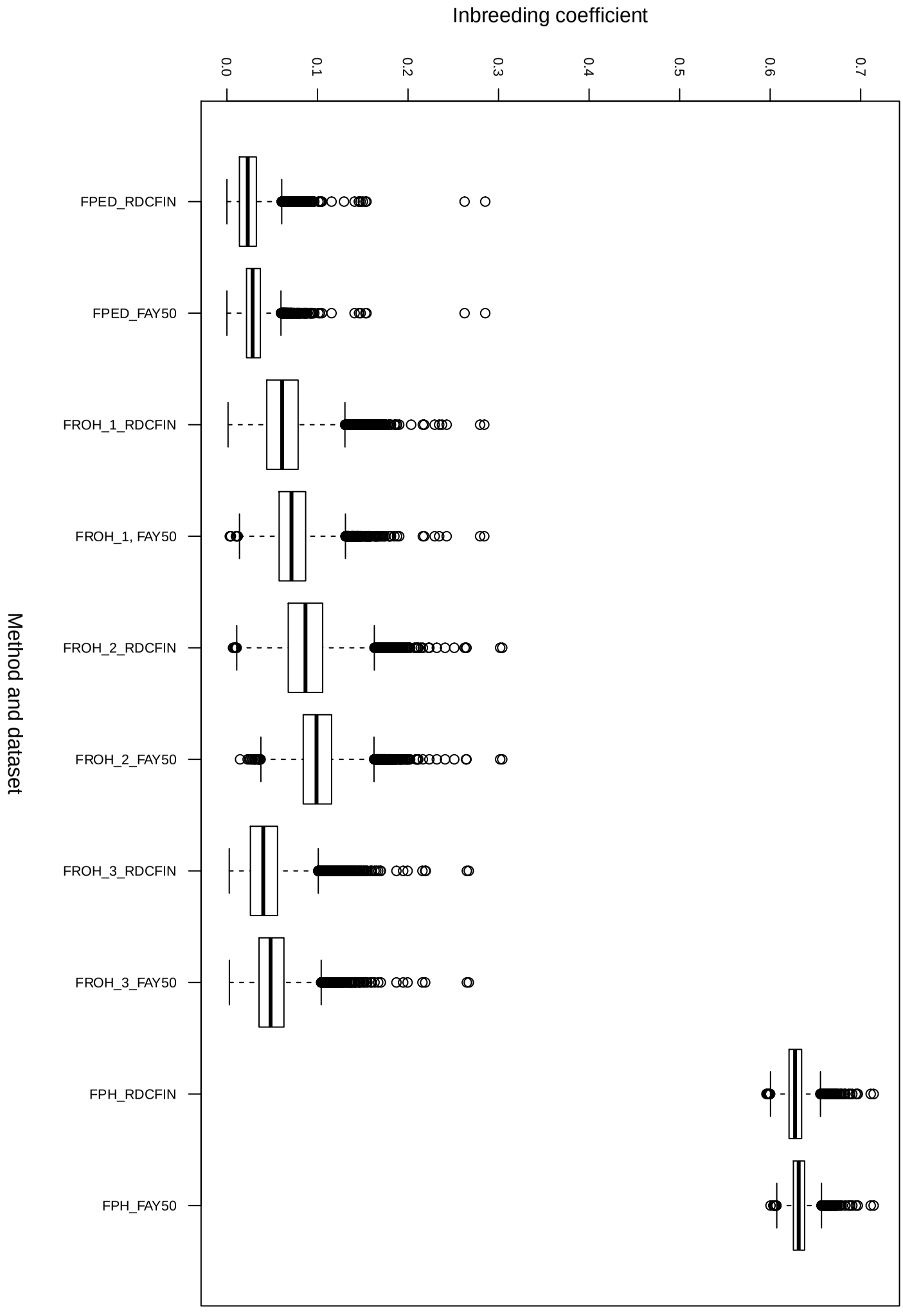
ROH length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0.4
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Method and dataset
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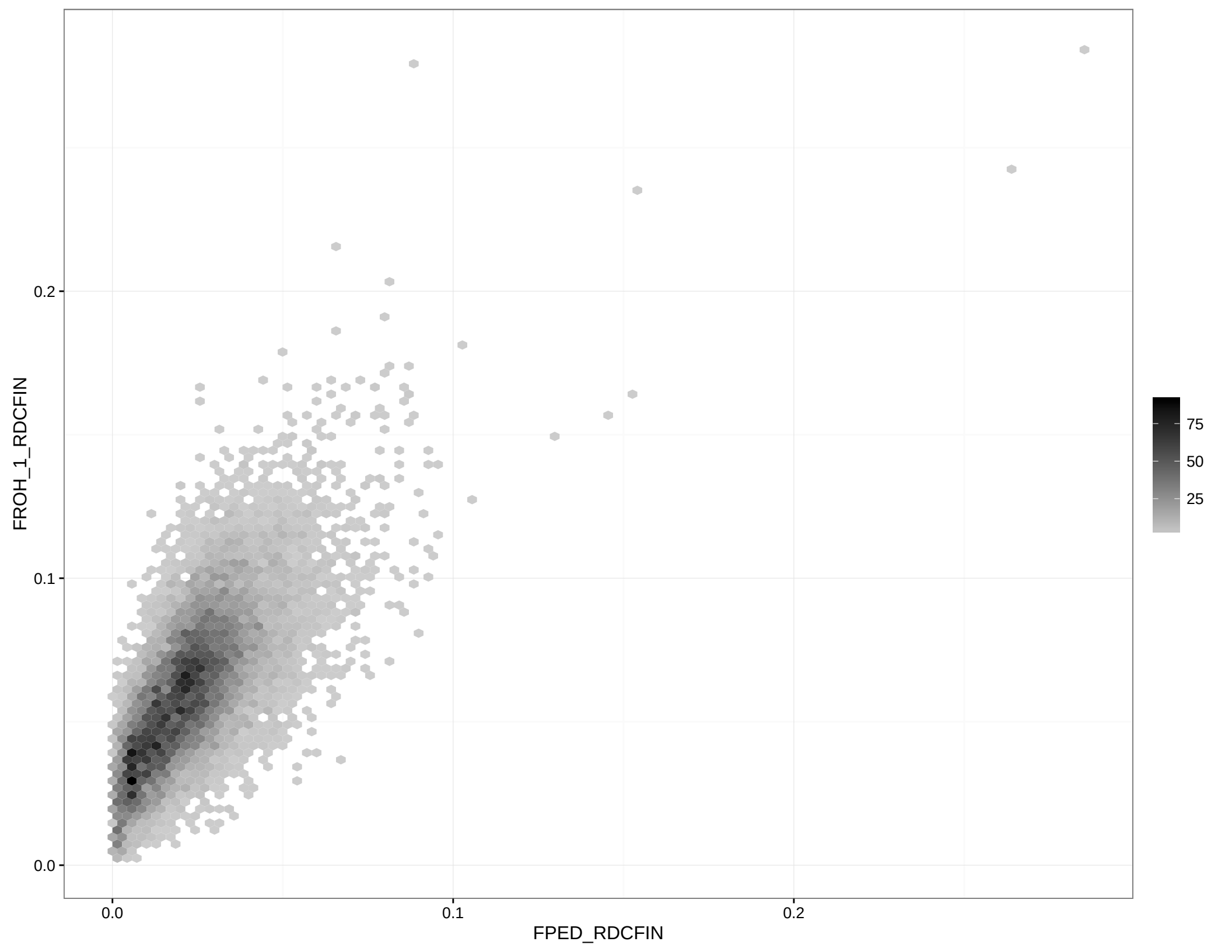
FPED_FAY50
FROH_1_RDCFIN
FROH_1, FAY50
FROH_2_RDCFIN
FROH_2_FAY50
FROH_3_RDCFIN
FROH_3_FAY50
FPH_RDCFIN
FPH_FAY50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25