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Performance of genomic selection under a single-step approach in autochthonous Spanish beef cattle populations

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Summary

This study evaluated different strategies for implementing a single-step genomic selection programme in two autochthonous Spanish beef cattle populations (Pirenaica—Pi and Rubia Gallega—RG). The strategies were compared in terms of accuracy attained under different scenarios by simulating genomic data over the known genealogy. Several genotyping approaches were tested, as well as, other factors like marker density, effective population size, mutation rate and heritability of the trait. The results obtained showed gains in accuracy with respect to pedigree BLUP evaluation in all cases. The greatest benefit was obtained when the candidates to selection had their genotypes included in the evaluation. Moreover, genotyping the individuals with the most accurate predictions maximized the gains but other suboptimal strategies also yielded satisfactory results. Furthermore, the gains in accuracy increased with the marker density reaching a plateau at around 50,000 markers. Likewise, the effective population size and the mutation rate have also shown an effect, both increasing the accuracy with decreasing values of these population parameters. Finally, the results obtained for the RG population showed greater gains compared to the Pi population, probably attributed to the wider implantation of artificial insemination.

KEYWORDS
accuracy, BLUP, cattle, genomic selection

1 | INTRODUCTION

The Genomic Selection (GS) methodology (Meuwissen, Hayes, & Goddard, 2001) has already shown to be a promising development for animal breeding. In fact, the dairy cattle industry has quickly incorporated it into their selection schemes to produce highly accurate genomic breeding values (GEBVs) for young bulls (Hayes, Bowman, Chamberlain, & Goddard, 2009; Spelman, Hayes, & Berry, 2013; VanRaden et al., 2009) and pig companies have started using it regularly in elite populations (Hidalgo et al., 2015; Ostersen et al., 2011; Tusell et al., 2016).

However, the beef cattle industry has been more reluctant in the implementation of this technology due to several reasons (Berry, Garcia, & Garrick, 2016). Compared to dairy cattle, most of the beef cattle breeds have a limited population size and the use of artificial insemination (AI) is not as widely spread. These phenomena contribute to the poor connectedness among and within populations. In fact, the usual dairy cattle strategy to evaluate very young bulls, as an alternative of progeny testing (Hayes et al., 2009), cannot be automatically mimicked. Thus, the appeal for implementing a GS programme should be specifically tested in each population.

The first attempts to implement GS (Meuwissen et al., 2001) involved a two-step approach: first, markers' effects had to be estimated from a training population and, next, the results were used to derive the genomic EBVs on

testing populations. Later on, Habier, Fernando, and Dekkers (2007) probe that the standard mixed-model equations (Henderson, 1984) can be easily adapted to incorporate genomic information through a genomic relationship matrix (**G**) and lead to predictions of GEBVs equivalent to the Gaussian regularization proposed by Meuwissen et al. (2001). Further, Legarra, Aguilar, and Misztal (2009) and Aguilar et al. (2010) developed an extension of this model denoted as single-step GBLUP, which allows predicting at the same time the breeding values for genotyped and non-genotyped individuals.

This latter approach could be useful for populations that cannot support a broad genotyping effort due to their small size and/or poor connectedness. To test so, we developed a large simulation experiment under different strategies. Our ultimate goal was to investigate the potential application of a single-step genomic selection programme in two Spanish autochthonous populations (*Pirenaica*—Pi and *Rubia Gallega*—RG).

2 | MATERIALS AND METHODS

2.1 | Pedigree and phenotypic information

We used the genealogical and phenotypic data on birthweight available for two populations, *Pirenaica* and *Rubia Gallega*. The data for *Rubia Gallega* comprised of 92,046 individuals in the genealogy and 64,030 birthweight data. The systematic effects considered for this trait in the current genetic evaluation model were (i) sex with two levels, (ii) age of dam with 16 levels and (iii) a random herd-year-season (HYS) effect with 10,160 levels. Likewise, the data for *Pirenaica* included 55,203 individuals in the genealogy and 32,702 birthweight records. The systematic effects considered were the same with 2, 16 and 5,343 levels, respectively. These data were used to frame the following simulation study.

2.2 | Simulation

First, an historical population of 100 individuals that evolved under random mating for 500 generations was simulated for each breed with the objective of generating linkage disequilibrium, as suggested by Meuwissen et al. (2001). The simulated genome comprised of 30 chromosomes with 2,000 markers each, from which 100 were randomly selected as causative mutations (QTLs). The QTL effects were drawn from a Gaussian distribution with mean zero and variance one. The mutation rate for both markers and causative mutations was fixed at 2.5×10^{-3}. These parameters were chosen to obtain genotypes of around 50,000 (50k) neutral markers mimicking the information provided by the *BovineSNP50 BeadChip* (Illumina INC, San Diego, CA, USA).

In the last generation, the individuals were randomly mated to generate a simulated genome for each of the founders of the actual Pi and RG recorded populations. After that, the genomic information of the remaining individuals of the populations was obtained by gene-dropping (MacCluer, Vandeburg, Read, & Ryder, 1986) over the available recorded pedigree. Thus, the last historical generation of the evolving population was used as the base for the individuals that comprise the recent genealogy of the population. This procedure allowed obtaining simulated genotypes for markers and QTL for pseudo-populations with the same genealogical structure as the actual ones.

In addition, phenotypic records were simulated for each individual that had a recorded phenotype on the real data set. Thus, they replicate the actual distribution of records across systematic, herd-year-season (HYS) and additive genetic effects. They were generated by summing a general mean (1,000), the effects of the QTLs, according to their specific genotype, and a residual drawn from a Gaussian distribution with zero mean, and a variance adequate to create two traits with heritability 0.1 and 0.4. Finally, the breeding values and the genotypes for all individuals in the pedigree were recorded. Note that all systematic effects were set to zero, although the distribution of the amount of phenotypic information available for its estimation replicated the real populations.

2.3 | Single step

The data provided by the simulation study was analysed by standard BLUP (Henderson, 1984) and by single-step GBLUP—ssGBLUP (Aguilar et al., 2010). Both analyses were performed using the BLUPf90 suite of programmes (Misztal et al., 2015).

The model used for all analyses was

$$\boldsymbol{y} = \boldsymbol{Xb} + \boldsymbol{Z_1 m} + \boldsymbol{Z_2 u} + \boldsymbol{e},$$

Where $\boldsymbol{y}$ is the vector of phenotypes, $\boldsymbol{b}$ is the vector of the systematic effects, sex with two levels and age of dam with 16 levels, $\boldsymbol{m}$ is the vector of the herd-year-season random effect with 5,343 and 10,160 levels for Pi and RG, respectively, $\boldsymbol{u}$ is the vector of additive genetic effects and $\boldsymbol{e}$ is the vector of errors. $\boldsymbol{X}$, $\boldsymbol{Z_1}$ and $\boldsymbol{Z_2}$ are the incidence matrices for $\boldsymbol{b}$, $\boldsymbol{m}$ and $\boldsymbol{u}$, respectively.

The only difference between ssGBLUP and BLUP is that in ssGBLUP, the inverse of the numerator relationship matrix $\mathbf{A}^{-1}$ is replaced in the mixed-model equations by matrix $\mathbf{H}^{-1}$ defined as:

$$\mathbf{H^{-1}} = \mathbf{A^{-1}} + \begin{bmatrix} \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{G^{-1}} - \mathbf{A_{22}^{-1}} \end{bmatrix}$$

where $\mathbf{G}$ is the genomic relationship matrix and $\mathbf{A}_{22}$ is the numerator relationship matrix for the genotyped individuals.

The default parameter options of the BLUPf90 software such as minor allele frequency of 0.05, individual and SNP call rate of 0.90 and **H** matrix scaling parameters ($\alpha = 0.05$ and $\beta = 0.95$) were used in all cases. In addition, variance components were assumed to be known.

2.4 | Simulation scenarios

We first developed several base scenarios of simulation by changing the following parameters:

1. Heritability of the trait ($h^2 = .1$ and .4)
2. Reference population: number of historical individuals genotyped (4,000, 2,000, 1,000, 500 and 250)
3. Genotypes for sires and dams of the candidates to selection (Yes or No) not included in the reference population.
4. Genotypes for the actual candidates to selection (Yes or No).
5. Phenotypic records for the candidates to selection (Yes or No).

The simulation strategy assumed that the populations had a reference genotyped population of varying size (from 250 to 4,000 individuals), and, after that, decisions to genotype the parents of the candidates or the candidates themselves had to be taken.

Combining all of them, the total number of cases of simulation was 80, plus four cases of standard BLUP evaluation (two heritabilities, either including or not the phenotypic records of the candidates to selection). In this study, the genotyped individuals were selected according to the estimated prediction error variance (PEV) achieved from a standard BLUP evaluation. Thus, the individuals were first ranked according to their PEV, and the bottom—or with lower PEV—4,000, 2,000, 1,000, 500 and 250, regarding the case of simulation, were next selected to be genotyped (this strategy is referred to as Top Historical—TH).

In addition, we performed a sensitivity analysis by comparing the results of each of these base scenarios with some other alternatives. These alternatives included.

1. Replacing the Top Historical (TH) individuals with the individuals with lower PEV, but born exclusively from 2010 to 2013 (Top Recent—TR).
2. Replacing the Top Historical individuals with a random sample of individuals born between 2010 and 2013 (Random Recent—RR)
3. Three combinations of the RR and TH strategies that included one-quarter, one-half or three-quarters of TH individuals combined with RR individuals.
4. Five alternative marker densities including: 4,000 (4k), 10,000 (10k), 23,000 (23k), 100,000 (100k) and 200,000 (200k) neutral markers.
5. Two alternative effective population sizes (Ne) in the simulation of the historical population (50 and 200)
6. Two alternative mutation rates for markers and QTL (1×10^{-3} and 4×10^{-3}).

A total of 20 replicates were simulated for each one of the scenarios described.

2.5 | Validation

The alternative procedures studied were compared in terms of the accuracy of the predictions, calculated as the Pearson correlation between the estimated breeding values and the simulated breeding values for the individuals born in last available year—2014. These individuals were considered the actual candidates to selection (579 and 1,738 animals for Pi and RG, respectively).

3 | RESULTS AND DISCUSSION

The data sets of the two populations used in this study differ significantly in their structure as it can be seen in Table 1. RG uses notably more artificial insemination (AI) than Pi, as it is reflected on the pedigree structure. The number of sires used for reproduction represents the 1.81% (1,669 animals) of the total number of males for RG, whereas they represent up to the 5.45% (3,010) for the Pi. Moreover, the average number of offspring per sire is 47.82 (*SD* = 225) for RG and just 17.21 (*SD* = 39.64) for Pi. To reinforce this statement, Figure 1 shows the number of offspring born in the year 2014 per sire for both populations. In RG, 283 sires have 1738 offspring (average 6.14 offspring per sire) while in Pi, 145 sires have 579 (average 3.99 offspring per sire).

3.1 | Standard BLUP evaluation

First, we performed a standard BLUP evaluation in each population and for each trait in order to define a reference

TABLE 1 Comparison of the pedigree structures between the Rubia Gallega (RG) and the Pirenaica (Pi) populations

	RG	Pi
No. of animals	92,046	55,203
No. of generations	16	25
Total no. of males	25,678	18,837
Sires (with offspring)	1,669	3,010
Mean no of offspring (*SD*)	47.82 (225)	17.21 (39.64)
Total no of females	66,368	36,366
Dams (with offspring)	35,156	23,373
Mean no of offspring (*SD*)	2.27 (1.68)	2.24 (1.8)

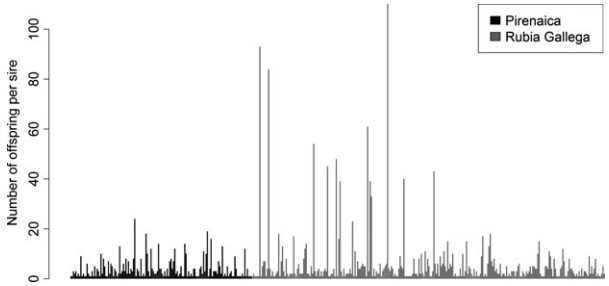

FIGURE 1 Number of offspring born in the year 2014 per sire

point to compare the results of the alternative genotyping strategies. The results are presented in Table 2 and ranged between 0.446 and 0.727. It should be noted the high accuracy achieved when candidates to selection were not phenotyped (0.446 to 0.550). The cause of these high accuracies is the amount of phenotyped half-sibs of the candidates to selection (49.2 ± 65.3 and 314.5 ± 648.5 for Pi and RG, respectively). Moreover, it can be observed that the accuracy of prediction for the individuals born in 2014 was very similar between populations when the heritability was larger (h^2 = .4), but there were remarkable differences between them for the low heritability cases (h^2 = .10). The reason for this latter difference can be attributed to the genealogical structure of the RG population. The more extended prevalence of AI implies a larger accuracy in the prediction of the breeding values of sires simply due to the larger half-sib family size, as pointed out above. This larger accuracy is reflected on the accuracies of their offspring. The effect is more evident with lower heritability, because more progeny is needed to achieve a larger accuracy (Falconer & Mackay, 1996). In addition, and as it was expected, the accuracy of the cases of simulation that included the phenotypes of the candidates to selection was larger. Finally, as it was also expected, the accuracy was larger for the scenarios with h^2 = .4 than with h^2 = .1.

3.2 | Base scenarios

The detailed results of the average accuracy of prediction among candidates to selection for all cases of simulation are presented in Tables S1 to S4. First of all, it is worth to mention that the bias of the prediction of breeding vales was almost null. In fact, the slope of the regression between true and predicted was always very close to 1. All these results are summarized in Figure 2, where the average accuracy and its confidence interval for each base scenario are depicted relative to the standard BLUP procedure. Overall, it can be observed that the accuracy of candidates to selection was always larger than the one provided by the standard BLUP procedure. In contrast, the two-step approach of genomic selection requires a minimum number

TABLE 2 Average accuracies (*SD*) obtained from the standard BLUP evaluation

	Trait A h^2 = .4		Trait B h^2 = .1	
	Without 2014 data	With 2014 data	Without 2014 data	With 2014 data
Pi	0.554 (0.011)	0.724 (0.004)	0.446 (0.013)	0.515 (0.011)
RG	0.550 (0.010)	0.727 (0.004)	0.479 (0.012)	0.549 (0.007)

of genotyped and phenotyped individuals to compete with the pedigree-based approaches, as probed by Daetwyler, Villanueva, and Woolliams (2008). So, the appropriateness of the single-step approach (Aguilar et al., 2010) for populations that cannot afford huge genotyping efforts, like the Spanish autochthonous beef cattle breeds, is very clear.

As expected, the increase of accuracy is greater as the number of genotyped individuals increases. However, it should be noted that this gain is only worthy when the candidates to selection are genotyped. In fact, the maximum gain obtained without genotyping the candidates to selection and their parents was just 2.5 ± 0.4% (Pi, 4000 genotyped individuals, h^2 = .1) and this figure only increased up to 9.6 ± 1.0% when the genotypes of the sires and dams of the candidates to selection were added. On the contrary, and for the same scenario, the increase of accuracy goes up to 23.9 ± 2.2% (4000 TH + candidates to selection genotyped) and 24.8 ± 2.2% (4000 TH + sires and dams + candidates to selection). When records from candidates to selection were included in the analyses, these differences were always smaller. It should be noted that the sires and dams of the candidates to selection were frequently included in the group of genotyped individuals and, therefore, only slight differences were found between this genotyping strategy and the one that did not include them. Genotyping all candidate individuals could be an important effort for the breeders associations. Nonetheless, it is important to mention that the imputation techniques work very efficiently (Khatkar, Moser, Hayes, & Raadsma, 2012; Mulder, Calus, Druet, & Schrooten, 2012) even with low-density panels. Thus, a genotyping strategy that uses low-density chips for candidate individuals combined with imputation techniques can be appropriate for these breeders associations.

Comparing the performance of the method with respect to the heritability of the trait, it can be observed that the rate of increase of accuracy is greater for h^2 = .4 than for h^2 = .1 when the records of the candidates to selection are not included in the analysis. This means that the number of genotyped individuals required for traits with lower heritability is greater because of the poorer information provided by the phenotypes when heritability is low. The well-established strategies of genomic selection in dairy cattle (Hayes et al.,

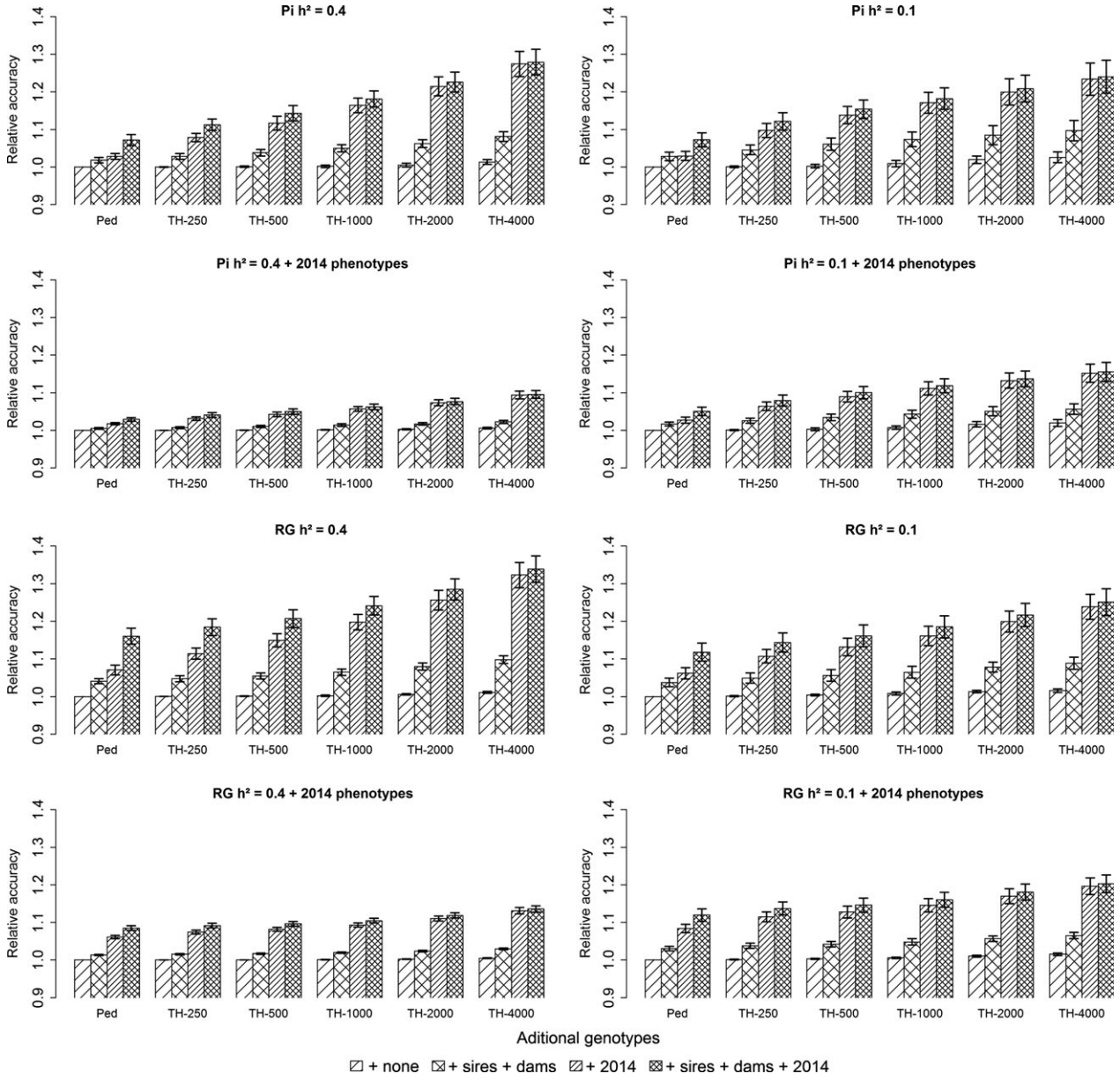

FIGURE 2 Relative accuracy with respect to the standard BLUP procedure for the different alternatives of the base scenario. RG: Rubia Gallega; Pi: Pirenaica; ped: standard BLUP evaluation; TH-250: 250 "Top Historical" genotypes; TH-500: 500 "Top Historical" genotypes; TH-1000: 1000 "Top Historical" genotypes; TH-2000: 2000 "Top Historical" genotypes; TH-4000: 4000 "Top Historical" genotypes; +none: no additional genotypes included; +sires+dams: genotypes of the parents of the candidates to selection included; +2014: genotypes of the candidates to selection included

2009) involve training the prediction equation on sires with extremely high accuracies, overcoming the informativeness of each individual phenotype by averaging over a huge number of daughters. This strategy cannot be replicated with the population structure of smaller populations. On the other hand, when the records of the candidates to selection are included in the analysis, the rate of increase in accuracy is greater for the cases of simulation that involved a lower heritability. The cause of this difference can be attributed to the higher base accuracy for phenotyped individuals with a moderate or high heritability (h^2 = .4).

Moreover, and as it was expected, the gain in accuracy is considerably greater when the records of the candidates to selection are not included in the analysis. This specific scenario tries to represent traits that are measured late in life (i.e., maternal traits) or difficult and expensive to measure (i.e., carcass traits, disease resistance). As an example, the maximum gain in accuracy for non-phenotyped candidates to selection was 36.5 ± 1.7% (RG, 4000 TH, + sires and dams + candidates to selection, h^2 = .4) whereas in the same scenario but with candidates recorded, the percentage of increase was just 14.1 ± 0.4%. This result confirms the

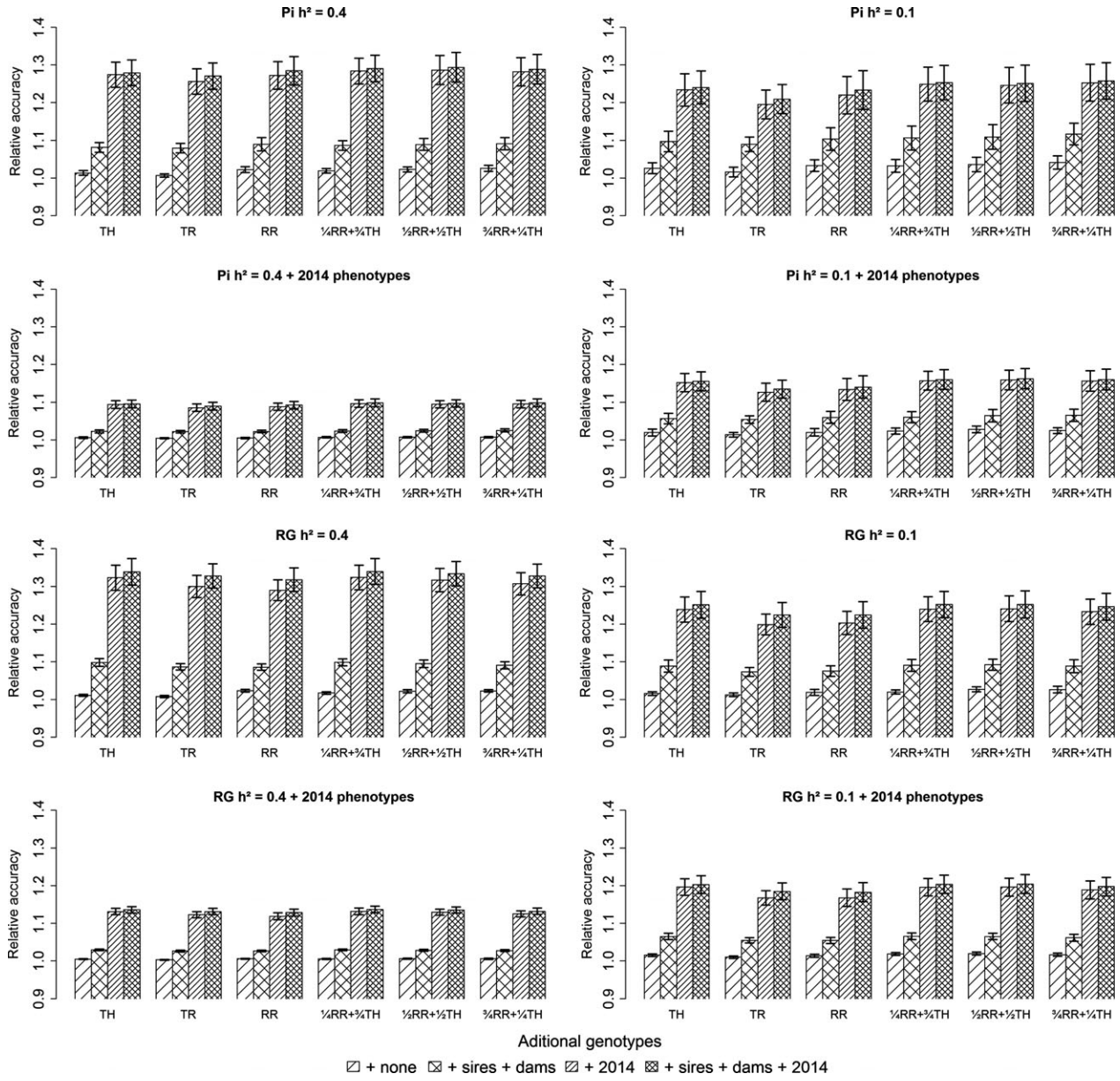

FIGURE 3 Sensitivity analysis with respect to the genotyping strategies. RG: Rubia Gallega; Pi: Pirenaica; TH: "Top Historical"; TR: "Top Recent"; RR: "Random Recent"; Size of reference sets: 4,000; +none: no additional genotypes included; +sires+dams: genotypes of the parents of the candidates to selection included; +2014: genotypes of the candidates to selection included

appropriateness of the GS for traits that cannot be easily measured on the candidates to selection.

Finally, it is relevant to note that the gain in accuracy was generally greater for RG than for Pi, even when both populations started with the same base level of accuracy, such as when they are analysed with a standard BLUP without genotypic information and with $h^2 = .4$. As before, the cause of this difference must be attributed to the genealogical structure of the RG population. Due to the wider application of AI, in this breed, a smaller number of individuals contributed greater to the extant population genetic diversity. These individuals contribute to the increase of the average accuracy of the candidates to selection through the genomic relationship matrix, which can be considered as an improved estimate of the true genetic relationship between individuals, based on SNP markers instead of only the pedigree information (Legarra, Christensen, Aguilar, & Misztal, 2014), and by the detection of older relationships hidden in the pedigree information.

3.3 | Sensitivity analysis

The results of the base scenario analysis covered a wide range of variables. However, it should be noted that they were conditioned to a set of predefined simulation

parameters. Thus, and in order to extract more general conclusions, we performed a sensitivity analysis with respect to the following variables: (i) the method of choice of genotyped individuals, (ii) the marker density, (iii) the effective population size along the evolutionary history of the population and (iv) the mutation rates for QTL and SNP markers.

The results of the sensitivity analysis with respect to the genotyping strategy are presented in Figure 3. As it can be observed, there were no relevant differences in accuracy regarding the method of choice of genotyped individuals when compared to the base strategy of sampling from the full historical population (TH individuals). It can be noted only a slight reduction of accuracy for lower heritabilities (h^2 = .1) when the TH individuals are replaced by RT and RR, that disappear when just one-quarter of TH individuals were included in the genotyped subset. The consequences of this result imply that, although the most informative individuals (with lower PEV) provide a better accuracy, the results are robust enough to suboptimal genotyping strategies forced by the availability of biological samples of older individuals.

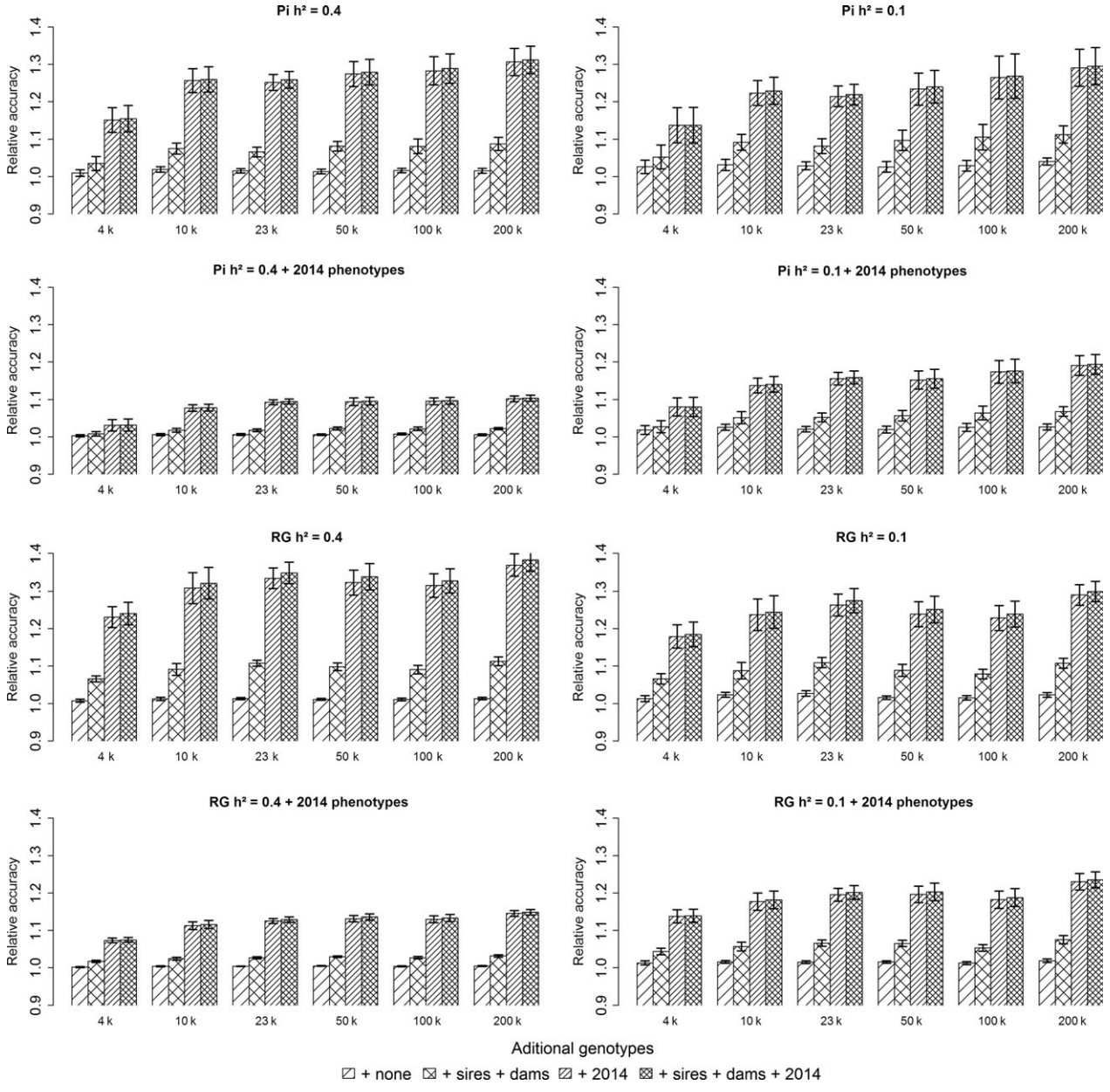

FIGURE 4 Sensitivity analysis with respect to the marker density. Genotype set used: TH 4,000 genotypes; RG: Rubia Gallega; Pi: Pirenaica; 4k: 4,000 SNPs; 10k: 10,000 SNPs; 23k: 23,000 SNPs; 50k: 50,000 SNPs; 100k: 100,000 SNPs; 200k: 200,000 SNPs; +none: no additional genotypes included; +sires+dams: genotypes of the parents of the candidates to selection included; +2014: genotypes of the candidates to selection included

The second sensitivity analysis was focused on the marker density, as the base simulation scenario tried to represent the density that can be obtained by the *BovineSNP50K BeadChip*. The results are presented in Figure 4. The main conclusion of this analysis is that the accuracy of GS increases with marker density, but it reaches a plateau at around 50k. Further increases of accuracy were small for denser chips. This result confirms the postulates of Cañas-Álvarez et al. (2016) who suggested that the Spanish autochthonous beef cattle populations need at least 38,000 segregating SNP markers. Thus, the potential increase that can be obtained from higher densities can be considered negligible, as it was also suggested by Solberg, Sonesson, Woolliams, and Meuwissen (2008), even for unrelated individuals (Meuwissen, 2009).

Further, the results of the sensitivity analysis with respect to effective size of the evolutionary historical population are presented in Figure 5. As it can be observed, there was a reduction in accuracy as the Ne increases as predicted by Solberg et al. (2008). These authors proposed that equivalent accuracies can be obtained as a function of Ne × L (number of markers). Thus, doubling or halving the effective size implies that double or half of the markers are needed to achieve the same accuracy. The Ne of the

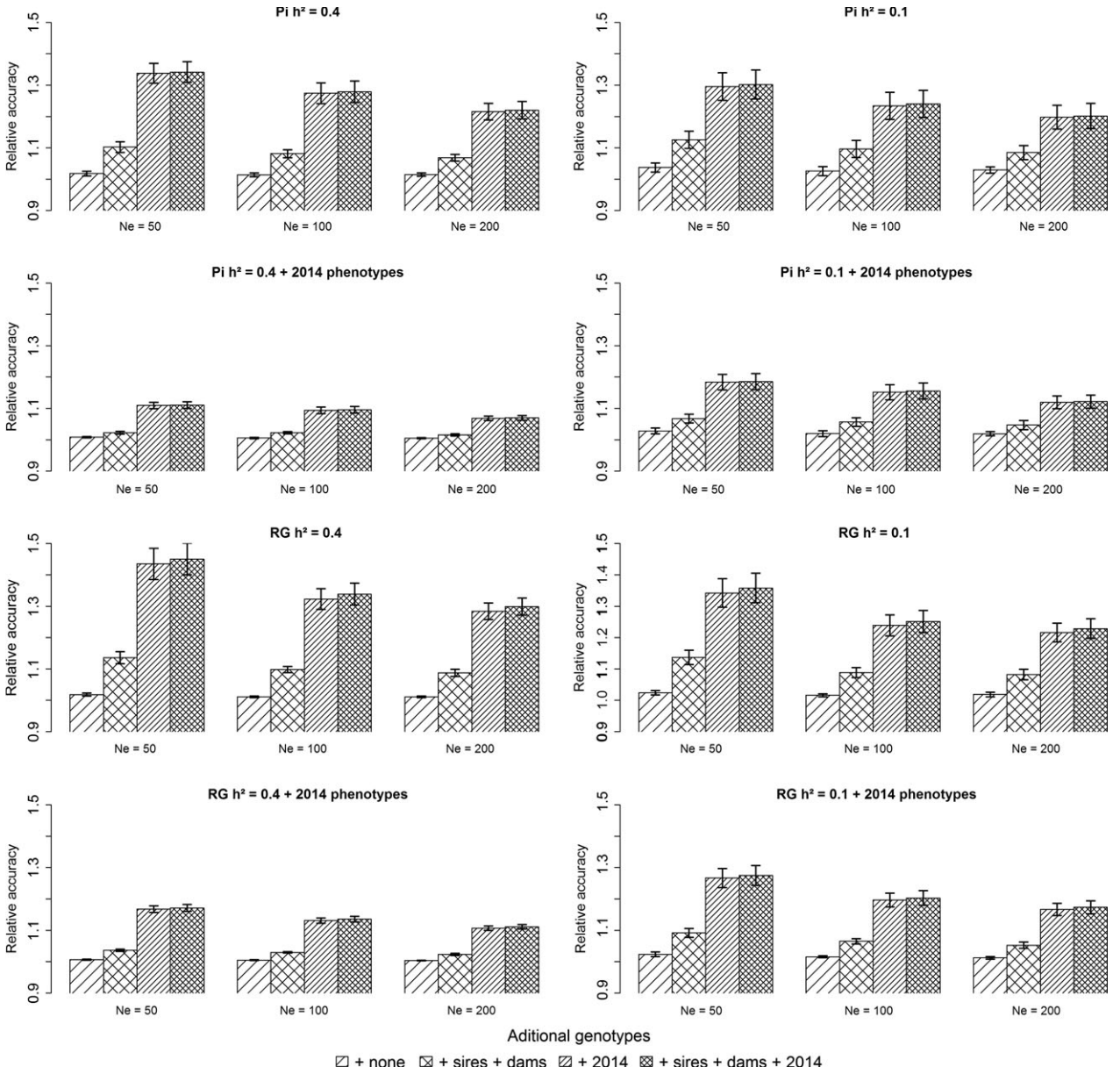

FIGURE 5 Sensitivity analysis with respect to effective population size. Genotype set used: TH 4,000 genotypes; RG: Rubia Gallega; Pi: Pirenaica; Ne: effective population size; +none: no additional genotypes included; +sires+dams: genotypes of the parents of the candidates to selection included; +2014: genotypes of the candidates to selection included

Spanish autochthonous populations was estimated between 26 and 47 (Cañas-Álvarez et al., 2016) and, as a consequence, the results of the base simulation study presented earlier can be considered as a conservative estimation of the potential gain in accuracy.

Finally, the last sensitivity analysis was devoted to mutation rate. The results are presented in Figure 6. The results showed only small differences in the accuracy when the mutation rate varied. However, there was a clear tendency to produce higher accuracies for lower mutation rates. The reason for those differences can be attributed to the fact that higher mutation rates provide lower LD between SNP markers and QTL. However, the assumed mutation rates were extremely high with respect to estimations in the literature (Hodgkinson & Eyre-Walker, 2011; Kumar & Subramanian, 2002), and, as before, this result ensures that the output of our base simulation study consists of a conservative estimation of the potential increase of accuracy that can be achieved with GS in the Spanish autochthonous beef cattle populations.

4 | CONCLUSIONS

The results of this study showed a potential benefit in terms of gain in accuracy by implementing a GS

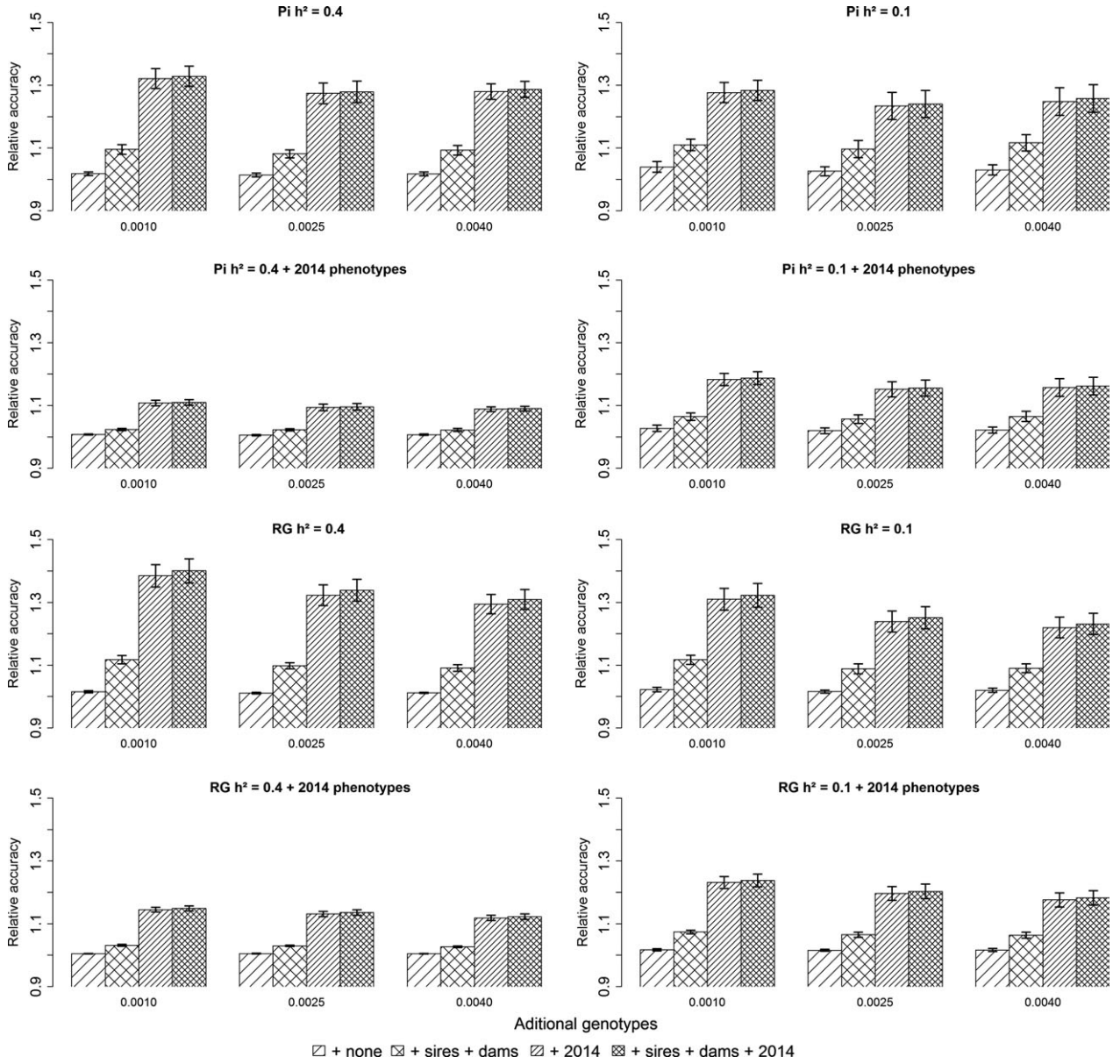

FIGURE 6 Sensitivity analysis with respect to mutation rate. Genotype set used: TH 4,000 genotypes; RG: Rubia Gallega; Pi: Pirenaica; Mutation rates tested = 1×10^{-3}, 2.5×10^{-3}, 4×10^{-3}; +none: no additional genotypes included; +sires+dams: genotypes of the parents of the candidates to selection included; +2014: genotypes of the candidates to selection included

programme for the Spanish autochthonous populations, even though the genotyping efforts that can be achieved by the breeders association are intermediate to low. This improvement can be achieved through the implementation of the single-step genomic selection approach (Aguilar et al., 2010; Legarra et al., 2009) that combines genomic- and pedigree-based relationships into the same relationship matrix. Under this approach, the pedigree-based relationship matrix sets a lower bound of accuracy, and it is improved as more individuals with genotypes are incorporated into the genomic evaluation. As expected, the GS approach has been found to be more relevant for traits with low heritability or when records for the candidates to selection are not available, and only when the candidates to selection are genotyped. Finally, it is important to mention that the potential benefits of GS is greater for RG than for Pi populations, because of the genealogical structure that is provided by the wider implantation of AI. So, a parallel increase of the rate of AI along with the genotyping efforts will lead to a greater success of GS in populations with a low percentage of AI.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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