

**TALITA ESTÉFANI ZUNINO SANTANA**

**FARM-LEVEL ANALYSIS OF ENVIRONMENTAL DESCRIPTORS TO  
INVESTIGATE GENOTYPE BY ENVIRONMENT INTERACTION IN PASTURE-  
RAISED BEEF CATTLE**

Thesis submitted to the Animal Science Graduate Program of the Universidade Federal de Viçosa in partial fulfillment of the requirements for the degree of *Doctor Scientiae*.

Adviser: Renata Veroneze

Co-adviser: Gilberto R. de Oliveira Menezes

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Renata Veroneze  
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In memory of  
**Luiz Otávio Campos da Silva** and  
**Fabyano Fonseca e Silva.**

I dedicate.

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“Climb the mountain not to plant your flag, but to embrace the challenge, enjoy the air and behold the view. Climb it so you can see the world, not so the world can see you.”

**David McCullough Jr.**

## ABSTRACT

SANTANA, Talita Estefani Zunino, D.Sc., Universidade Federal de Viçosa, July, 2024. **Farm-level analysis of environmental descriptors to investigate genotype by environment interaction in pasture-raised beef cattle.** Adviser: Renata Veroneze. Co-adviser: Gilberto R. de Oliveira Menezes.

In beef cattle breeding programs, the environmental effects are commonly adjusted by considering the combined effects of herd, year, and season, referred to as the contemporary group (CG). Nonetheless, several other macro-environmental factors are known, such as climate, soil moisture, temperature, precipitation, farm management practices and facilities, etc. Such known environmental effects can be directly accounted for in the genetic evaluation models. The first objective of this study was to assess environmental and farm management factors for the evaluation of yearling weight (YW) in pasture-raised Nellore cattle across tropical savanna in South America. The dataset analyzed encompassed animal phenotypes, pedigree, climate and soil classifications, elevation, and detailed information related to farm management practices at the animal-rearing locations. Explanatory variables were selected based on three steps: (1) evaluation of each variable's contribution to explaining the variance among farms, (2) assessment of collinearity among farm management descriptors, and finally (3) comparison of models using a stepwise selection procedure. The results indicate that soil classification (SOIL), elevation (ELE), animal breeding technician (TEC), years enrolled in the breeding program (YEN), no-till farming (NTI), period of the breeding season (PBS), and reproduction technique (RTC) are deemed important to better describe the macro-environmental effects contributing to variation across farms. Indeed, when environmental and farm management descriptors were simultaneously included in the model, they explained 41.5% of the farm variance. This finding reveals the real source of environmental variation commonly accounted for by CG in the genetic evaluations. This suitable characterization of environmental factors might be especially important in the context of genotype by environment interaction (GxE). In this sense, we also aimed to identify relevant environmental conditions (EC) for Nellore cattle using farm-level environmental descriptors via divisive hierarchical clustering analyses, estimate genetic parameters related to growth, reproductive, and carcass traits, and investigate the presence of GxE by comparing rankings of estimated breeding value (EBV) of bulls among identified ECs using either BLUP or ssGBLUP methods. The evaluated traits included YW, scrotal circumference (SC), age at first calving

(AFC), ribeye area (REA), backfat thickness (FAT), and marbling score (MARB). The optimal clustering of farm-level descriptors grouped farms into two EC. Subsequently, a bi-trait linear model was used to investigate the GxE. The lowest genetic correlation was observed for AFC ( $0.31 \pm 0.09$ ), followed by YW ( $0.37 \pm 0.05$ ), and REA ( $0.62 \pm 0.08$ ), indicating traits largely affected by GxE. The Spearman's correlations for EBVs of bulls were generally low across evaluated traits using either BLUP or ssGBLUP. The percentage of common bulls for EBVs ranked within the TOP5%, TOP10%, and TOP25% categories was most pronounced within the TOP5% ranking using either BLUP or ssGBLUP. AFC exhibited the highest degree of re-ranking, followed by YW and REA, across both methods and all ranking categories, indicating a higher influence of GxE on these traits. These findings highlight the importance of including environmental factors in genetic evaluations of AFC, YW, and REA traits to select animals more adapted to different environmental conditions.

**Keywords:** climate, farm management practices, Nellore, GxE interaction, survey research

## RESUMO

SANTANA, Talita Estéfani Zunino, D.Sc., Universidade Federal de Viçosa, julho de 2024. **Análise de descritores ambientais em nível de fazenda para investigar a interação genótipo por ambiente em bovinos de corte criados a pasto.** Orientadora: Renata Veroneze. Coorientador: Gilberto R. de Oliveira Menezes.

Nos programas de melhoramento genético de bovinos de corte, os efeitos ambientais são comumente ajustados considerando os efeitos combinados de rebanho, ano e estação, referidos como o grupo contemporâneo (GC). No entanto, vários outros fatores macro ambientais são conhecidos, como clima, umidade do solo, temperatura, precipitação, práticas e instalações de manejo da fazenda entre outros. Esses efeitos ambientais conhecidos podem ser diretamente considerados nos modelos de avaliação genética. O primeiro objetivo deste estudo foi avaliar fatores ambientais e de manejo da fazenda para a avaliação do peso ao sobreano (PS) em gado Nelore criado a pasto na savana tropical da América do Sul. O conjunto de dados analisado abrangeu fenótipos animais, pedigree, classificações de clima e solo, elevação e informações detalhadas relacionadas às práticas de manejo da fazenda nos locais de criação dos animais. As variáveis explicativas foram selecionadas com base em três etapas: (1) avaliação da contribuição de cada variável para a explicação da variância entre fazendas, (2) avaliação da colinearidade entre descritores de manejo da fazenda e, finalmente, (3) comparação de modelos usando um procedimento de seleção passo a passo. Os resultados indicam que a classificação do solo (SOLO), elevação (ELE), técnico de melhoramento animal (TEC), anos inscritos no programa de melhoramento (AIN), plantio direto (PD), período da estação de reprodução (PEM) e técnica de reprodução (TCR) são considerados importantes para melhor descrever os efeitos macro ambientais que contribuem para a variação entre as fazendas. De fato, quando os descritores ambientais e de manejo da fazenda foram incluídos simultaneamente no modelo, eles explicaram 41,5% da variância da fazenda. Este achado revela a verdadeira fonte de variação ambiental comumente considerada pelo GC nas avaliações genéticas. Essa caracterização adequada dos fatores ambientais pode ser especialmente importante no contexto da interação genótipo por ambiente (GxA). Nesse sentido, também objetivamos identificar condições ambientais relevantes (CA) para o gado Nelore usando descritores ambientais a nível de fazenda por meio de análises de clustering hierárquico divisivo, estimar parâmetros genéticos relacionados a características de crescimento, reprodutivas e de carcaça, e investigar a presença de GxA comparando rankings de valores genéticos estimados (VGE) de touros entre CAs identificadas usando métodos BLUP ou ssGBLUP. As características avaliadas incluíram

PS, circunferência escrotal (CE), idade ao primeiro parto (IPP), área de olho de lombo (AOL), espessura de gordura dorsal (EGS) e marmoreio (MAR). O agrupamento ideal dos descritores a nível de fazenda agrupou as fazendas em duas CAs. Subsequentemente, um modelo linear de duas características foi usado para investigar a GxA. A menor correlação genética foi observada para IPP ( $0,31 \pm 0,09$ ), seguida por PS ( $0,37 \pm 0,05$ ) e AOL ( $0,62 \pm 0,08$ ), indicando características amplamente afetadas por GxA. As correlações de Spearman para VGEs de touros foram geralmente baixas entre as características avaliadas usando BLUP ou ssGBLUP. A porcentagem de touros comuns para VGEs classificados nas categorias TOP5%, TOP10% e TOP25% foi mais pronunciada na classificação TOP5% usando BLUP ou ssGBLUP. IPP exibiu o maior grau de reclassificação, seguida por PS e AOL, em ambos os métodos e todas as categorias de classificação, indicando uma maior influência de GxA nessas características. Esses achados destacam a importância de incluir fatores ambientais nas avaliações genéticas das características IPP, PS e AOL para selecionar animais mais adaptados a diferentes condições ambientais.

**Palavras-chave:** clima; práticas de manejo da fazenda; Nelore; interação GxE; pesquisa de levantamento.

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## CHAPTER 1

### GENERAL INTRODUCTION

#### 1.1.Introduction

The phenotypic expression of a quantitative trait of an animal is determined by the joint effect of genetics and environmental factors. A central component of livestock breeding programs is the estimation of breeding values, defined as the sum of the additive effects of all contributing alleles across the loci affecting the trait (Falconer, 1996). Estimated breeding values (EBV) can be computed based on the pedigree-based additive relationship between animals, or using genomic information (Meuwissen et al., 2001; Legarra et al., 2009). In beef cattle breeding programs, the environmental effects are commonly adjusted for by considering the combined effects of herd, year, and season, referred to as the contemporary group (CG). Nonetheless, several other macro-environmental factors are known and could be used in the genetic evaluation, such as climate, soil moisture, temperature, precipitation, farm management practices and facilities, etc. (Mulder et al., 2013). Such known environmental effects can be directly accounted for in the genetic evaluation models.

A suitable characterization of environmental factors is especially important in the context of genotype by environmental interaction (GxE). In the presence of GxE, the phenotypic value of a genotype will change according to environmental conditions. Two different models have been widely used in the literature to study GxE: multitrait mixed models and reaction norm models; both models require phenotypes to be recorded on the same or correlated animals in, at least, two different environments (Hayes et al., 2016). The multitrait approach accounts for GxE based on genetic correlations, where the performance of a genotype for a trait under different EC is treated as distinct yet correlated traits (Falconer, 1952). If the environment can be categorized, such as pasture versus feedlot, intensive versus extensive production systems, different countries, or other EC groups, the multitrait models can be straightforwardly applied. This method has advantages in terms of computational demand and interpretation of results, being user-friendly for commercial breeding programs. Conversely, a reaction norm model is recommended when the environment is more accurately represented by a continuous variate, such as temperature humidity indices (Falconer, 1990). This model can accommodate an infinite number of environments through covariance functions (Kirkpatrick et

al., 1990), allowing the phenotypic expression of a genotype to be modeled as a function of the environment (Falconer, 1990). That is, predictions are feasible even when phenotypes have not been evaluated across all environments, as long as pedigree (or genomic) information is available.

Global reports indicate that three of the current top five beef-producing countries (i.e., Brazil, China, and India) primarily raise their cattle in (sub)tropical regions and diverse production systems, ranging from intensive feedlots to extensive grass-based farming (Gilbert et al., 2018; Robinson et al., 2018). High temperatures, high humidity, and distinct variations in rainfall (dry and wet seasons) characterize (sub)tropical climates (Alvares et al., 2013). These conditions expose cattle to several challenges, including heat stress, negative energy balance due to seasonal pasture variations, and infestations of ectoparasites (e.g., ticks and flies) and endoparasites, which require tailored breeding and management strategies. Raising cattle in these challenging environments may contribute to genetic variation in phenotypic plasticity resulting in GxE.

Overall, studies suggest the need to further consider GxE in genetic evaluations of beef cattle affecting growth (Cardoso and Tempelman, 2012; Williams et al., 2012; Chiaia et al, 2015; Raidan et al., 2015; Oliveira et al., 2018; Braz et al 2021) and female reproductive traits (Chiaia et al, 2015; Fennewald et al 2018; Mota et al., 2020; Carvalho Filho et al., 2024). In contrast, GxE models are less important for traits related to male reproduction (Chiaia et al, 2015; Raidan et al., 2015; Santana et al., 2015; Nascimento et al. 2022) and carcass (Ibi et al. 2005). However, these studies often do not include information about farm-specific management practices, which could provide a better understanding of the GxE within different production systems. In addition, they usually adopt reaction norms and use CG solutions as environmental gradient, which makes the practical implementation difficult.

## **1.2.Thesis objectives**

The overarching objective of this thesis was to better understand the environmental, farm management, and genetic aspects of growth, reproductive, and carcass traits in Nellore cattle. The main specific objectives of this thesis were to:

- I. Assess environmental and farm management factors for the evaluation of yearling weight (YW) in pasture-raised Nellore cattle across tropical savanna in South America;

- II. Identify relevant environmental conditions (EC) for Nellore cattle using farm-level environmental descriptors via divisive hierarchical clustering analyses;
- III. Estimate genetic parameters related to growth, reproductive, and carcass traits;
- IV. Investigate the presence of genotype by environment interaction (GxE) by comparing rankings of estimated breeding value (EBV) of bulls among identified ECs using either BLUP or ssGBLUP methods.

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## CHAPTER 2

### COMPREHENSIVE FARM-LEVEL ANALYSIS OF ENVIRONMENTAL DESCRIPTORS FOR DEVELOPING AN EFFICIENT GENETIC EVALUATION OF PASTURE-RAISED BEEF CATTLE

#### 2.1. Abstract

The main objective of this study was to assess environmental and farm management factors for the evaluation of yearling weight (YW) in pasture-raised Nellore cattle across tropical savanna in South America. The dataset analyzed encompassed animal phenotypes, pedigree, climate and soil classifications, elevation, and detailed information related to farm management practices at the animal-rearing locations. Explanatory variables were selected based on three steps: (1) evaluation of each variable's contribution to explaining the variance among farms, (2) assessment of collinearity among farm management descriptors, and finally (3) comparison of models using a stepwise selection procedure. The results indicate that soil classification (SOIL), elevation (ELE), animal breeding technician (TEC), years enrolled in the breeding program (YEN), no-till farming (NTI), period of the breeding season (PBS), and reproduction technique (RTC) are deemed important to better describe the macro-environmental effects contributing to variation across farms. Among them, TEC and NTI were directly or indirectly associated ( $P < 0.05$ ) with several descriptors of soil, supplemental feeding, and reproduction management. Indeed, when environmental and farm management descriptors were simultaneously included in the model, they explained 41.5% of the farm variance. This finding reveals the real source of environmental variation commonly accounted for by CG in the genetic evaluations. This suitable characterization of environmental factors might be especially important in the context of genotype by environmental interaction (GxE), but also for forecasting animal performance under different environmental conditions.

**Keywords:** climate; farm management practices; yearling weight; Nellore; GxE interaction; survey research

#### 2.2. Introduction

Pasture-raised beef cattle experience substantial environmental variability, influencing their growth, health, and productivity (Greenwood 2021). Factors such as climate, soil quality,

forage availability, and water resources can vary widely across regions and seasons. Adaptive management practices are required to ensure optimal cattle performance and sustainable beef production across environments. Hence, beef production in such variable environments demands a comprehensive understanding of how these factors interact with cattle genetics and management strategies.

The phenotypic expression of a quantitative trait of an animal is determined by the joint effect of genetics and environmental factors. A central component of livestock breeding programs is the estimation of breeding values, defined as the sum of the additive effects of all contributing alleles across the loci affecting the trait (Falconer, 1996). Estimated breeding values (EBV) can be computed based on the pedigree-based additive relationship between animals, or using genomic information (Meuwissen et al., 2001; Legarra et al., 2009). In beef cattle breeding programs, the environmental effects are commonly adjusted for by considering the combined effects of herd, year, and season, referred to as the contemporary group (CG). Nonetheless, several other macro-environmental factors are known, such as climate, soil moisture, temperature, precipitation, farm management practices and facilities, etc. (Mulder et al., 2013). Such known environmental effects can be directly accounted for in the genetic evaluation models.

A suitable characterization of environmental factors is especially important in the context of genotype by environmental interaction (GxE). In the presence of GxE, the phenotypic value of a genotype will change according to environmental conditions. The estimated average performance of contemporary groups (CG) has been widely used to build environmental gradient to address GxE in beef cattle (Cardoso and Tempelman, 2012; Chiaia et al., 2015; Oliveira et al., 2018; Mota et al., 2020; Nascimento et al., 2022). In contrast, alternative environmental descriptors have been proposed for dairy cattle (Fikse et al., 2003; Erbe et al., 2021), swine (Fragomeni et al., 2016; Tiezzi et al., 2020; Freitas et al., 2021, 2023), and have been extensively utilized in plant breeding (Jarquín et al., 2014; Crossa et al., 2017; Costa-Neto et al., 2021; Resende et al., 2021, 2024). However, these studies often do not include information about farm-specific management practices, such as grazing strategies, feed supplementation protocols, herd health management, and breeding techniques, that might significantly influence production outcomes. In this regard, the main objective of this study was to assess environmental and farm management factors for the evaluation of yearling weight (YW) in pasture-raised Nellore cattle across tropical savanna in South America.

## 2.3. Material and methods

Animal Care and Use Committee approval was not necessary for this study because the data provided for statistical analysis came from an existing database belonging to Embrapa-Geneplus beef cattle breeding program.

### 2.3.1. Data collection

The dataset included information from different sources encompassing animal phenotypes, pedigree and geographic location, climate, soil classification, elevation at the animal-rearing locations, as well as descriptors related to farm management practices. More details regarding these sources of information can be found in the subsequent sections. For a more in-depth data description exploration, please refer to Table 1.

#### 2.3.1.1. Animal data

Phenotypes of yearling weight (YW) and pedigree information from Nellore cattle reared in pastures across Brazil, Bolivia, and Paraguay were provided by the Embrapa-Geneplus beef cattle breeding program (Campo Grande, MS, Brazil). The YW mean  $\pm$  standard deviation (SD) was  $305.10 \pm 67.26$  kg, with animals being measured at approximately  $485.6 \pm 43.9$  days of age from 1999 to 2021.

Contemporary groups were established by combining the month and year at measurement (farm and sex were included as additional factors). Records of animals in CGs with fewer than 40 observations were excluded from the analysis to ensure statistical robustness. After data editing, 143,332 animals with records from 60 farms were available for analysis, which included 180 animals from Bolivia, 1,403 from Paraguay, and 141,749 from Brazil, including the following states (with counts within parentheses): Acre (550), Bahia (4,202), Goiás (2,740), Maranhão (1,175), Minas Gerais (2,316), Mato Grosso do Sul (56,301), Mato Grosso (28,202), Pará (7,788), Paraná (10,039), Rio de Janeiro (2,478), Rondônia (3,782), São Paulo (15,299), and Tocantins (6,877). Pedigree information comprised three generations, resulting in a total of 253,027 animals in the additive relationship matrix.

#### 2.3.1.2. Survey data

The survey targeted 118 Nellore cattle producers enrolled in the Embrapa-Geneplus beef cattle breeding program. The objective was to collect geographic locations representing the central points of their farms (based on the World Geodetic System 1984 – WGS84) and

obtain detailed information regarding soil, feeding, and reproduction management protocols implemented on their respective farms. Additionally, the survey included questions concerning reproductive efficiency measures.

Those who consented to engage in the survey received preliminary instructions via phone communication. Subsequently, a web-based survey, designed through Google Forms, was emailed to them. The form comprised sixty questions, including short-answer, multiple-choice, and checkbox responses, were categorized into five sections:

- General information: Farm ID, breeding program technician, number of years enrolled to the Embrapa-Genepplus beef cattle breeding program, geographic coordinates, total land area, the land area allocated to livestock, and type of production system.
- Soil management: Questions covering the utilization of native grasslands, tillage, no-till farming, contour farming, crop rotation, or other practices.
- Supplementation feeding by animal category: Including mineral mix, a combination of mineral mix and urea, protein, or protein and energy sources in the supplements for calves, heifers, cows, and sires.
- Reproduction management: Adoption of breeding seasons and their period and length, number of females exposed to breeding, bull-to-cow ratio, use of synchronization protocols or other reproduction techniques, age and weight of heifers (at the first mating) and cows.
- Reproductive outcomes: Encompassing conception rate for heifers, primiparous, and multiparous cows in the breeding season.

During the period spanning from October to December 2021, a total of 80 beef cattle breeders completed the survey.

#### 2.3.1.3. Environmental data

We collected environmental data, including the Köppen-Geiger climate classification (CLI), soil classification (SOIL), and elevation (ELE) based on the geographical locations of farms.

The Köppen-Geiger climate classification is one of the most common climate classification systems in the world (Köppen, 1936), which has recently been updated (Peel et al., 2007). This classification categorizes global climate zones based on temperature, precipitation, and vegetation patterns. It employs a combination of letters to denote different

climate types, with the main categories being A (tropical or equatorial), B (arid or dry), C (warm/mild temperate), D (continental), and E (polar). Each major zone is further subdivided based on temperature or dryness characteristics. Out of the twelve climate classifications documented in Brazil, as identified by Álvares et al. (2013), four were observed at the locations included in this dataset, as illustrated on the map in Figure 1a.

The soil class for the rearing locations was extracted from the World Reference Base for Soil Resources – WRB, an international soil classification system established by the International Union of Soil Sciences (IUSS, 2015). Shaped by the legend of the FAO/UNESCO-ISRIC Soil Map of the World (FAO, 1988), this system operates on two levels. The first level comprises 32 Reference Soil Groups (RSGs), while the second level combines the RSG with specific qualifiers. This approach provides a comprehensive framework for classifying and characterizing soils, encompassing key features such as soil horizons, properties, and environmental contexts; for a detailed description, please visit: <https://soilgrids.org/>. Among the 57 soil classifications recognized across South America, 12 were found at the farms studied, as illustrated on the map in Figure 1b.

Lastly, the elevation ( $289.80 \pm 127.37$  m), defined as vertical distance above sea level, was collected using the R package “elevatr” (Hollister et al., 2023).

The Köppen-Geiger climate classification, soil classification, and elevation were defined as environmental descriptors.

#### 2.3.1.4. Farm management data

The farm management descriptors were extracted from the survey data. Continuous variables were converted into categorical variables, ensuring that each question had at least three affirmative responses for at least one class. After data editing, 25 questions remained for the characterization of farm management. Table 2 provides a complete description of variables concerning farm management protocols.

#### 2.3.2. Selection of environment and farm management descriptors

The process of identifying optimal farm-level environmental and management descriptors for the genetic evaluation of YW was conducted through three sequential steps:

(1) Each descriptor was individually included as a fixed effect in a general statistical model. The decision to retain a descriptor was based on its capacity to explain at least 5% of the

variance among farms. The general statistical model employed for this assessment can be written as:  $\mathbf{y}^* = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_f\mathbf{f} + \mathbf{e}$ , where  $\mathbf{y}^*$  is the vector of the phenotypes adjusted for random additive genetic effects calculated using the BLUPF90+ software (Misztal et al., 2018);  $\boldsymbol{\beta}$  is a vector with fixed effects of sex, CG, age (linear covariate) at measurement and the evaluated descriptor;  $\mathbf{f}$  is a vector of random farm effects, assumed to follow  $N(\mathbf{0}, \mathbf{I}\sigma_f^2)$ , where  $\sigma_f^2$  is the farm variance; and  $\mathbf{e}$  is the residual vector assumed  $N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ . The  $\mathbf{X}$  and  $\mathbf{Z}_f$  are known incidence matrices related to fixed and farm effects, respectively. Estimation of fixed effects and variance components was performed utilizing the Maximum Likelihood (ML) method through the application of the *lmer* function, available in the R package “lme4” (Bates et al., 2015).

(2) Considering that farm management descriptors can be associated with each other, we used the Chi-Square test (at a 5% significance level) to identify and prune highly associated variables, thereby reducing collinearity and redundant information (McHugh, 2013).

(3) Model comparison and variable selection were performed using a stepwise selection procedure for each group of variables independently, either environmental or farm management descriptors. The relevance of fixed effects was assessed based on the Akaike Information Criterion – AIC (Akaike, 1973). The least-squares means for the fixed effects in the final model were obtained using the R package “emmeans” (Lenth, 2024).

### 2.3.3. Statistical analysis

After the definition of the relevant environment and farm management descriptors to be included in the genetic evaluation of YW, final model comparisons were made including these effects in a benchmark model (BM) described as:

$$\mathbf{y} = \mathbf{X}\boldsymbol{\beta} + \mathbf{Z}_a\mathbf{a} + \mathbf{Z}_f\mathbf{f} + \mathbf{e}$$

where  $\mathbf{y}$  is the vector of the YW observations;  $\boldsymbol{\beta}$  is a vector with fixed effects of sex, CG, age (linear covariate) at measurement, and the relevant descriptors identified in the last step;  $\mathbf{a}$  is a vector of random additive genetic effects, assumed to follow  $N(\mathbf{0}, \mathbf{A}\sigma_a^2)$ , where  $\sigma_a^2$  is the additive genetic variance and  $\mathbf{A}$  is the numerator relationship matrix;  $\mathbf{f}$  is a vector of random farm effects, assumed to follow  $N(\mathbf{0}, \mathbf{I}\sigma_f^2)$ , where  $\sigma_f^2$  is the farm variance and  $\mathbf{I}$  stands for an identity matrix; and  $\mathbf{e}$  is the residual vector assumed  $N(\mathbf{0}, \mathbf{I}\sigma_e^2)$ . The  $\mathbf{X}$ ,  $\mathbf{Z}_a$  and  $\mathbf{Z}_f$  are known incidence matrices related to fixed, additive genetic, and farm effects, respectively.

In this study, the variance components and breeding values were estimated using the Restricted Maximum Likelihood/Best Linear Unbiased Prediction (REML/BLUP) method, implemented on the BLUPF90+ software (Misztal et al., 2014). Estimates of the within-farm heritability ( $h_w^2$ ) were calculated according to Visscher and Goddard (1993) as follows:  $h_w^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2}$ , where  $\hat{\sigma}_a^2$  and  $\hat{\sigma}_e^2$  are the estimates of the additive genetic and residual variances, respectively. The model comparisons were performed using the AIC and the proportion of farm variance explained by the fixed effects. Further details will be provided in subsequent sections.

## 2.4. Results

### 2.4.1. Description of survey data outcomes

Sixty-eight percent of the targeted beef cattle breeders completed the survey. After the data editing, information from 60 farms was used for assessing farm management descriptors of Nellore cattle producers. These farms have been enrolled in the Embrapa-Genepplus beef cattle breeding program since the following periods: 1996 – 2000 (15%), 2001 – 2005 (10%), 2006 – 2010 (21.7%), 2011 – 2015 (21.7%), and 2016 – 2020 (31.7%). Eleven technicians with animal breeding expertise assist these farms. Among them, one technician supported 23% of all farms.

The majority of the sampled farms were located in Mato Grosso do Sul state, accounting for 23 farms (38%), followed by the states of Mato Grosso and São Paulo with 7 farms (11.7%) each, Bahia and Rondônia with 4 farms (6.7%) each, Paraná with 3 farms (5%), and Goiás, Pará, and Rio de Janeiro with 2 farms (3.3%) each. Furthermore, single-farm representation was observed from Acre, Maranhão, Minas Gerais, and Tocantins states, as well as from Bolivia and Paraguay (1.7% each). Concerning the use of the total land area, the breeders indicated allocating small (6.7%; with a total land range from 130 to 2,024 ha), medium (36.7%; with a total land range from 191 to 3,300 ha), or large (56.7%; with a total land range from 1,062 to 77,000 ha) areas to livestock production. Within these areas, 85% of the animals are raised within pasture-based systems, while the remaining animals are integrated into crop-livestock production systems.

Notably, the pasture is the main feed source used in the diets of the farms that answered the survey. In this context, the producers have adopted several soil management practices intending to enhance forage quality and production and soil conservation, such as pasture

recovery and renewal (73%), fertilization (65%), tillage (63%), natural resources conservation (50%), contour farming (48%), crop rotation (47%), no-till farming (32%), native grasslands (20%), and irrigation (5%).

Supplemental feeding was observed across all animal categories described in the survey. Breeders supplemented their animals with at least a mineral source for calves (46.7%), heifers (48.3%), cows (36.7%), and sires (40%). Furthermore, additional supplements included urea for heifers (15%), cows (25%), and sires (11.7%); protein for calves (13.3%), heifers (18.3%), cows (15%), and sires (15%); and protein-energy for calves (6.7%), heifers (8.3%), cows (8.3%), and sires (16.7%). Some supplemental strategies combined more than two sources: mineral, protein, and protein-energy for calves (13.3%) and sires (5%); mineral, mineral and urea, and protein for cows (5%), and sires (5%); and mineral, mineral and urea, protein, and protein-energy for heifers (10%), cows (10%), and sires (6.7%). In the calf category, 20% of the animals received exclusively protein sources.

All our respondents indicated the adoption of breeding season on their farms, either in the short (51.7%) or long term (48.3%), as a strategy of reproduction management. Among these, the most frequent breeding season periods were from October to January (21.7%); October to February (20%); and November to February (13.3%). Furthermore, September to December and November to March were reported by 6.7% each, while December to March, October to March, September to January, and September to March were each reported by 5%.

October to December and September to February were reported by 3.3% each, and January to March, August to January, and October to April were reported by 1.7% each. The most commonly adopted reproduction technique was the combined use of fixed-time artificial insemination, resynchronization protocols, and herd bulls (86.7%), followed by fixed-time artificial insemination and herd bulls (11.7%). Only one farm indicated the exclusive use of natural service. In vitro fertilization was also observed as a reproduction technique (51.7%). An average of 887 heifers and cows were exposed to the breeding season, with the number of females varying from a minimum of 50 to a maximum of 3500. The cows entered the breeding season with an average weight of  $497.2 \pm 49.9$  kg, while the average age and weight of the heifers at the first mating were  $18.8 \pm 4.79$  mo (Minimum = 11 mo; Maximum = 28 mo) and  $325.4 \pm 41.86$  kg (Minimum = 250 kg; Maximum = 430 kg), respectively. When herd bulls were used during the breeding season, an average bull-to-cow ratio of  $1:31 \pm 1:12$  cows were employed (Minimum = 1:15 cows; Maximum = 1:80 cows).

Concerning reproduction outcomes, the average conception rate to fixed-time artificial insemination was  $55\% \pm 15.4\%$ ,  $52.6\% \pm 14.1\%$ , and  $61.3\% \pm 12.9\%$  for heifers, primiparous, and multiparous cows, respectively. The average conception rate by the completion of the breeding season was  $81.3\% \pm 10.6\%$ ,  $75.4\% \pm 9.6\%$ , and  $84.5\% \pm 6.1\%$  for heifers, primiparous, and multiparous cows, respectively.

#### 2.4.2. Selection of environment and farm management descriptors

The main findings obtained from the descriptor selection procedure are presented in Tables 3, 4, and 5. Table 3 presents the estimates of variance components and AIC concerning each environmental and farm management descriptor evaluated from the general statistical model. This model used phenotype corrected by random animal additive effect and included the random effect of farm beside the fixed effects. The inclusion of different fixed effects explained from 0.77% to 36.89% of the farm variance, while the residual variance was unchanged. The breeding program technician (TEC), period of the breeding season (PBS), SOIL, ELE, and age of the heifer at the first mating (AHF) were the predominant contributors, accounting for 36.9%, 27.9%, 23.9%, 19.5%, and 18.7% of farm variance, respectively. Although some effects did not improve the model goodness-of-fit, they did contribute significantly to explaining farm variance. Among them, PBS and SOIL displayed the inferior fit despite being ranked, respectively, as the second and third most influential variables. Consequently, these effects were retained in the selection procedure in pursuit of a more comprehensive understanding.

The Chi-square test was utilized to investigate the associations among pre-selected farm management descriptors (Table 4). Whenever a marginal association was significant, we called it a direct association. On the other hand, when two variables did not present a significant marginal association, but both were significantly associated with a third variable, we referred to this as an indirect association. TEC exhibited direct associations with the period of use of established pasture (PEP), contour farming (CON), irrigation (IRR), and calf supplemental feeding (CFSF), while no-till farming (NTI) was directly linked to crop rotation (CRO) and fertilization (FER). Moreover, TEC presented indirect associations with FER, in vitro fertilization (INF), and weight of heifer at first mating (WHF) via PEP, AHF via CON, and cow supplemental feeding (CWSF) and bull supplemental feeding (BSF) via CFSF. Indirect associations were also observed between NTI, FER, and WHF via CRO, as well as between NTI, INF, and WHF via FER. No significant associations were found for years enrolled (YEN),

PBS, and reproduction technique (RTC) effects. Therefore, TEC can be seen as a descriptor of TEC, PEP, CON, IRR, FER, INF, WHF, AHF, CFSF, CWSF, and BSF, while NTI as a descriptor of NTI, CRO, FER, WHF, and INF. In summary, the key farm management descriptors identified included TEC, YEN, NTI, PBS, and RTC.

Key farm management and environment descriptors were exhaustively subjected to the stepwise procedure to model comparisons (Table 5). The inclusion of composite descriptors was powerful in explaining the farm variance, ranging from 20.6% to 37.9%, 12.6% to 69.1%, and 70.2% to 82.9% when considering environmental, key farm management descriptors, and their combination, respectively. In all models, the residual variance estimates were not affected by the inclusion of either environment or management descriptors (Table 5). The optimal model related to environmental descriptors was identified as “SOIL + ELE”, which explains nearly double the farm variance compared to the best model in terms of goodness-of-fit (“CLI + ELE”). However, SOIL + ELE showed only a marginal increase in the AIC. In terms of farm management descriptors, the superior fit was consistently achieved through the inclusion of “TEC + NTI”, “TEC + NTI + RTC”, “TEC + YEN + NTI + PBS” or “TEC + YEN + NTI + PBS + RTC”. Among them, the proportion of farm variance explained by the included fixed effects ranged from 42.1% in the simplest model (TEC + NTI) to 69.0% in the complete model.

The optimal model for characterizing the farm-level environment was selected based on the interaction between environmental descriptors and the complete model encompassing farm management descriptors. The chosen model comprises "SOIL + ELE + TEC + YEN + NTI + PBS + RTC". It exhibited the highest level of goodness-of-fit and elucidated the third-largest proportion of farm variance among all models examined. Therefore, based on the BM and the relevant farm-level descriptors above-mentioned, we defined the environmental (EM), farm management (FM), and environmental-farm management (EFM) models, as detailed in Table 6. Additionally, as the TEC effect is confounded with many other factors (Table 4), we also run supplementary analyses by omitting TEC to investigate the potential effect of other factors. The results are presented in the Supplementary Material Table S1. In summary, when TEC was excluded from the model, the factors PEP, YEN, NTI, CFSF, and PBS were the ones that better explain the variance across farms.

For completeness, Supplementary Material Table S1 provides the variance components estimates, their standard errors, the models' goodness-of-fit, AIC, and the

proportion of farm variance explained by different combinations of environmental and farm management descriptors.

#### 2.4.3. Model comparison

The variance components and within-farm heritability estimates are detailed in Table 7. Consistent with observations in the variable selection procedure, farm management and environmental descriptors significantly influenced farm variance across all models under study. EFM explained the largest proportion of variance attributed to farms (41.5%), followed by FM (37.3%), and EM (24.7%). The inclusion of farm management and environmental descriptors improved the goodness-of-fit in the same order. Furthermore, the included descriptors did not affect the estimates of additive genetic and residual variance components. The overall estimates (kg<sup>2</sup>) of additive genetic and residual variances were  $678.38 \pm 15.29$  and  $1,254.05 \pm 10.98$ , respectively, implying similar within-farm heritability estimates across models of  $0.35 \pm 0.01$ .

## 2.5. Discussion

### 2.5.1. Description of survey data outcomes

This study includes farm management and environmental descriptors and cattle performance data from 60 farms that completed the survey and have recorded animals in the Embrapa-Genepplus dataset. The survey enhances the characterization of farm environments, aiming to integrate this information into the breeding program with a focus on GxE. Additionally, it provides valuable insights into the practices of farms enrolled in the Embrapa-Genepplus breeding program. This understanding allows for a comparative analysis of these practices against those of commercial beef producers and may offer opportunities for improving data records.

These farms enrolled in the Embrapa-Genepplus beef cattle breeding program in different years, but a considerable proportion of them (31.7%) joined the Embrapa-Genepplus program more recently, between 2016 and 2020. This substantial increase in enrollment might be attributed to initiatives by Brazilian beef cattle producers to enhance productivity and sustainability in response to the robust growth observed in the meat market. Indeed, in 2022, the Brazilian beef cattle agribusiness turnover was US\$ 198.12 billion, where US\$ 920.8 million is attributed to revenue generated by genetically improved animals (ABIEC, 2024). By comparison, the total revenue from genetically improved animals accumulated in Brazil from 2019 to 2021 was US\$ 938.6 million (ABIEC, 2024).

In assessing the geographical distribution, production system, and herd size of the studied farms, we observed that the majority of farms and recorded animals are located in the states MG and MS, under grazing systems, which reflects the distribution of livestock heads and pasture areas in Brazil. According to the Brazilian Institute of Geography and Statistics (IBGE, 2022), the states MG and MS in the Central-West region of Brazil accounted for 52.68 million heads (22.5% of the Brazilian total) across ~35 million hectares of pasture (LAPIG/UFG, 2024). Furthermore, the Embrapa-Genepplus beef cattle breeding program and the National Center of Research on Beef Cattle (CNPGC), both overseen by the Brazilian Agricultural Research Corporation (EMBRAPA), are located in the city of Campo Grande, the capital of MS. This strategic hub, with research and robust networks, may have contributed for the higher concentration of farms enrolled in the breeding program in Mato Grosso do Sul state.

Regarding the size of the studied farms, according to Brazilian Law 8.629 (1993) for rural property areas, the majority of farms in this study are classified as large (80%), followed by medium (18.3%), and a minor group categorized as small farms (1.7%). Nevertheless, some large farms have allocated small to moderate areas for beef cattle, suggesting that livestock production may not be their main business focus, or the presence of native vegetation, permanent preservation, or legal reservation areas.

The Brazilian beef cattle production system includes breeding, rearing, and finishing stages. The feedlot, when used, is typically employed during the finishing stage only. In 2022, Brazil, the world's second-largest beef producer, achieved a production milestone of 10.8 million tonnes of carcass-weight equivalent, with the national herd size increasing by 3.3%, and the pasture area decreasing by 5.7% (ABIEC, 2024). A significant proportion (82.8%) of the slaughtered animals were pasture-raised (ABIEC, 2024), demonstrating the importance of grasslands for Brazilian livestock production. In this context, the studied farms indicate the use of several soil management practices, such as soil conservation (e.g., crop rotation and contour farming), low-carbon agriculture techniques (e.g., pasture recovery and renewal, no-till farming, and integrated crop-livestock systems), and management improvements (e.g., fertilization and irrigation). These practices are implemented with the intention of increasing forage biomass, as well as enhancing soil organic carbon storage, which helps sustain soil fertility, conserve water quality, and mitigate greenhouse gas emissions (Conant et al., 2001; Ogle et al., 2004; Komatsuzaki and Ohta, 2007). Moreover, supplemental feeding patterns observed across the farms, primarily relying on mineral sources, highlight the critical need for the availability of high-quality forage for all animal categories. Complementary, in recent years,

the agribusiness for beef cattle has spent more money on fertilizer, plant protection products, and seeds in comparison with the expenses on nutrition supplements (ABIEC, 2024). These trends indicate efforts of the beef cattle industry to enhance efficiency by adopting technologies focused on tropical environments, sustaining biodiversity, and minimizing the use of natural resources.

In addition, reproduction management practices might help to improve the efficiency of cow-calf and full-cycle beef cattle production systems, while also contributing to the genetic progress of the herd. In this sense, adopting a defined breeding season, employing reproductive techniques, and focusing on reproductive and nutritional management practices for heifers and primiparous cows can be useful in decreasing female reproductive failure (Diskin and Kenny, 2014; Moorey and Biase, 2020).

Concerning breeding season timing, our data indicate that the breeders choose to schedule it during the rainy summer (between October and March in the tropical climate zone). This timing corresponds to the period of abundant and high-quality pasture, which is desired for heifers and cows with increased energy requirements to support gestation (Schmidt et al., 2018). Consequently, the birth season occurs during the dry winter, providing an advantage for the calves by decreasing the incidence of diseases (e.g., pneumonia), ticks, and endoparasites (Lorenz et al. 2011; Siqueira et al., 2021).

Many target farms reported the use of fixed-time artificial insemination (FTAI) and embryo transfer alongside the breeding season. In FTAI, ovulation and insemination are synchronized in females through the use of hormonal treatments, allowing for controlled and simultaneous artificial mating (Pursley et al., 1995). This technology enhances reproductive efficiency while enabling breeders to select superior sires within and across different herds (Bó and Baruselli, 2014). On the other hand, embryo transfer aims to accelerate genetic progress and optimize breeding outcomes throughout the collection and transfer of embryos from genetically superior donors to recipient females (Nicholas and Smith, 1983).

The lifetime reproductive efficiency of females is closely associated with the reproductive success of heifers (Núñez-Dominguez et al., 1991; Wathes et al., 2014). In this study, the farms have exposed their heifers to the first mating earlier, on average, than Brazilian farms raising Nelore females supported by animal breeding programs (Schmidt et al., 2018; Costa et al., 2020; Mota et al., 2020), including Embrapa-Genepplus (Ramos et al., 2021). Considering a gestation length of about 292 days (Paschal et al., 1991), it is expected that the

studied heifers will have an age at first calving (AFC) of approximately 28 mo. This AFC suggests that the surveyed farms adjust their reproductive management to identify sexually precocious females.

Regarding reproductive efficiency, the farms in this study achieved higher conception rates under artificial insemination and by the completion of the breeding season compared to commercial farms across South America, as reported by Zoetis (2023) and Inttegra (2023). According to the beef cattle FTAI report published by Zoetis (2023), the average pregnancy rates for heifers, primiparous and multiparous cows in FTAI are 45.7%, 46.1%, and 53.8%, respectively. The benchmark published by Inttegra (2023), which includes data from over 2 million *B. indicus*, *B. taurus* purebreds, and *B. indicus* × *B. taurus* crossbred animals, shows average conception rates until the completion of the breeding season of 77.6%, 73.3%, and 79.8% of exposed heifers, primiparous and multiparous cows, respectively. The superior reproductive performance observed in the farms studied might be attributed to effective nutritional, reproduction, and health management within the farm, as well as favorable genetic factors.

#### 2.5.2. Selection of environment and farm management descriptors

The variable selection procedure included descriptors of environment (climate and soil classifications, as well as elevation) and farm management, assessed based on the survey research (Table 2). The Maximum Likelihood (ML) methods was used to fit and compare the different models. Although REML is commonly preferred for variance component estimation, it is less suitable for comparing models with different fixed effects (Patterson and Thompson, 1971; Harville, 1977). By using ML, we can directly compare the likelihoods of models when the fixed effects structure is modified, facilitating the evaluation of different model specifications. In evaluating goodness-of-fit, the variance explained by the fixed effect was defined as a complementary selection criterion to AIC. Information criteria, such as AIC, do not provide information on the variance explained by the model (Orelien and Edwards, 2008), and they are not comparable across different datasets (Nakagawa and Cuthill, 2007). Therefore, the variance explained by fixed effects might enhance our assessment by providing a direct measure of the model's explanatory capability, thereby complementing the information derived from AIC.

The results obtained in the first step of variable selection (Table 3) indicate that all studied descriptors are associated with YW at a farm level, even though some farm management

descriptors presented a low impact on of explained farm variance. Among them, heifer supplemental feeding and the length of the breeding season are factors related to female fertility (Deutscher et al., 1991; Butler, 2014; Moorey and Biase, 2020), thus, although it did not have a big impact on YW it might be important in the study of reproduction traits. Likewise, while the production system (grazing or crop-livestock) showed slight importance, several studies have reported that the crop-livestock system significantly contributes to the maintenance of productivity, as well as the recovery and renewal of degraded pastures, resulting in improved performance of grazing animals (Sulc and Tracy, 2007; de Faccio Carvalho et al., 2010; Sekaran et al., 2021). The integrated crop-livestock system is a complex agricultural approach with diverse components, including soil, plants, animals, management practices, and climate. To better understand the contribution of this system to economically important traits, future survey research should incorporate detailed information on aspects such as the timing of grazing and planting, stocking density (AU/ha), type of crops and forage, and other factors.

Regarding the environmental descriptors analyzed, the climate classification exhibited a low impact in the model comparisons. This might be attributed to the limitation of farm distribution across climates in your dataset (Figure 1). Our data cover only four classes of climate from the twelve described in Brazil (Álvares et al., 2013), where the “Tropical zone, savannah – Aw” is predominantly represented in terms of number of farms ( $N = 28$ ), as well as recorded animals (Table 1). Therefore, additional research should be performed across more diverse geographical locations to support our findings.

After in-depth model comparisons, we identify that including simultaneously SOIL and ELE in the model as significant environmental descriptors, and TEC, YEN, NTI, PBS, and RTC as farm management descriptors.

### 2.5.3. Model comparison

The studied descriptors partially characterize the farm environment affecting YW, highlighting the farm management practices (TEC, YEN, NTI, PBS, and RTC) as a significant source of environmental variation. In agreement with the findings by Aiken et al. (2020) on forecasting beef production and quality, technical advising plays an important role in enhancing production outcomes through strategic decision-making. Specifically, the expert guidance provided by the TEC is closely associated with soil management practices, supplemental feeding, as well as herd reproduction management (Table 4). Decisions based on these management practices can collectively boost overall productivity and optimize resource

utilization. These findings suggest that the role of the technician within the Embrapa-Geneplus breeding program extends beyond genetic selection. Technicians might be pivotal agents in the dissemination of technologies and knowledge related to production management.

The number of years that each farm has been enrolled in the animal breeding program also was relevant to understanding the environmental variation accounting by the farm on YW. Although no statistically significant differences were found for years enrolled (Supplementary Material Table S2), the data indicated that farms longer in the Embrapa-Geneplus breeding program have higher YW averages compared to the more recent farms. This suggests that farms with longer enrollment might be effectively using genetic evaluation tools to select superior animals, as well as leveraging expert guidance provided by the Embrapa-Geneplus team to make better decisions. In contrast, more recent farms may still need to consolidate the use of these tools and require time to identify selection gains due to the generational interval in beef cattle.

In terms of soil management practices, NTI, CRO, and CON demonstrated varying levels of importance (Table 3). These practices are frequently implemented together with the aim of soil conservation. NTI and CON enhance soil structure and water-holding capacity, while the cover crops facilitated by CRO increase soil carbon and nitrogen content, positively affecting soil microbial activity (Giller et al., 2015). The PEP also showed significant importance to the farm environment. This variable might be linked to the degradation of pastures, which is often a result of prolonged and intensive use without adequate management practices over time (Teague et al., 2011). Indeed, PEP demonstrated a direct association with FER and IRR, which are practices that can avoid nutrient leaching and soil degradation, thereby contributing to the long-term productivity of pastures.

Concerning reproduction management, our findings suggest that breeders who adopt intensive artificial insemination (AI) practices can benefit from using superior genetics bulls (Supplementary Material Table S2). Although we do not observe differences in mean across the reproduction classes evaluated, we can observe high standard error for the natural service class, indicating that we have fewer homogenous animals regarding YW, which might be due to the use of animals with high variation regarding breeding values. Artificial insemination techniques can accelerate genetic gain by facilitating the transmission of alleles to offspring and enabling breeders to access a diverse pool of superior genetics from other herds.

Lastly, we identified SOIL and ELE as significant descriptors of environmental variation affecting YW. In line with our findings, Aiken et al. (2020) highlighted soil quality as a crucial predictor of the age at finishing in beef cattle. The quality and quantity of forage available, which are critical for cattle growth and development, are directly influenced by soil characteristics. Different soil classes exhibit varying levels of nutrients, water retention capacities, and pH levels, all of which are essential factors determining forage quality. Elevation also plays a significant role in environmental variation. Higher elevations typically result in cooler temperatures and varying precipitation patterns, both of which influence the types of grasses that can grow and their phenology response (Munson and Lexine Long, 2017). Cooler temperatures at higher elevations can slow down forage growth but can also reduce the stress on cattle, potentially enhancing growth rates (Godde et al., 2021). Understanding the impact of elevation might be important for optimizing grazing strategies and selecting animals best suited for specific altitudinal ranges.

Regarding variance components, the inclusion of the relevant farm-level descriptors did not affect the additive genetic and residual variances in the studied models (EM, FM or EFM). In this sense, the within-farm heritability estimates obtained for YW are slightly lower than the heritabilities reported by Boligon et al. (2010) and Marestone et al. (2022) using the conventional CG to account for the environmental effects in a Nellore cattle population. Nonetheless, our heritability estimates are within the range of values found by Chiaia et al. (2015) and Oliveira et al. (2018) under the reaction-norm GxE. Indeed, when environmental and farm management descriptors were simultaneously included in the model, they explained a significant proportion of the farm variance. This finding reveals the real source of environmental variation commonly accounted by CG in the genetic evaluations. A suitable characterization of environmental factors is especially important in the context of GxE, but also for forecasting animal performance under different environmental conditions. Currently, the estimated average performance of CG has been widely used to build environmental gradient to address GxE in beef cattle (Cardoso and Tempelman, 2012; Chiaia et al., 2015; Oliveira et al., 2018; Mota et al., 2020; Nascimento et al., 2022). However, these studies often do not include information about either environment factors or farm-specific management practices, which this study has revealed to be a significant source of environmental variation. The environmental effects can be easily assessed using open-source tools based on remote sensing and geographical information systems, enabling breeders to include macro-environmental effects (e.g., soil, climate, and weather information) into genetic evaluations within the GxE

framework (Costa-Neto et al., 2021; Resende et al., 2021; Resende et al., 2024). However, understanding farm-specific management practices requires a targeted approach such as a survey. In this regard, conducting surveys directly from beef producers enhances the characterization of farm environments, aiming to integrate this information into the breeding program with a focus on GxE, and also provides valuable insights into the practices of farms enrolled in the Embrapa-Geneplus breeding program. Certainly, the survey research needs periodic updates because the management practices adopted by breeders can change. Furthermore, analyzing data from detailed surveys presents challenges, especially when the surveys include numerous nominal variables. Nevertheless, the survey might engage beef producers to increase their involvement and investment in animal breeding programs. Consequently, this collaboration might lead to better implementation of recommended practices and more widespread adoption of superior genotypes. Furthermore, leveraging farm-level surveys might help geneticists and breeders gain a comprehensive understanding of how environmental factors interact with economically important traits under diverse farming conditions over time.

## **2.6. Conclusion**

Extensive farm-level analysis revealed seven environmental (SOIL and ELE) and farm management descriptors (TEC, YEN, NTI, PBS and RTC) as deemed important to better describe the macro-environmental effects contributing to variation across farms. Among them, TEC and NTI were directly or indirectly associated ( $P < 0.05$ ) with several descriptors of soil, supplemental feeding, and reproduction management. This findings reveals the real source of environmental variation commonly accounted by CG in the genetic evaluations. This suitable characterization of environmental factors might be especially important in the context of genotype by environmental interaction (GxE), but also for forecasting animal performance under different environmental conditions.

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## Tables

**Table 1.** Summary of data from the Nellore cattle population used in the present study.

Item	N
<i>Animals</i>	
Animals in the pedigree file	253,027
Sires with progeny	22,584
Dams with progeny	111,053
Contemporary group (CG)	163
Farms in the survey with recorded animals	60
<i>Koppen-Geiger Climate Classification</i>	
Tropical zone, monsoon (Am)	9,237
Tropical zone, savannah (Aw)	68,875
Temperate zone, without dry season, hot summer (Cfa)	44,509
Temperate zone, dry winter, hot summer (Cwa)	20,711
<i>Soil Classification based on World Reference Base for Soil Resources</i>	
Orthic Acrisols (Ao)	8,799
Ferric Acrisols (Ap)	1,099
Acric Ferralsols (Fa)	16,299
Orthic Ferralsols (Fo)	39,262
Rhodic Ferralsols (Fr)	22,233
Xanthic Ferralsols (Fx)	1,312
Luvic Phaeozems (Hl)	851
Lithosols (I)	4,611
Ferric Luvisols (Lf)	17,820
Ferralic Arenosols (Qf)	22,463
Dystric Planosols (Wd)	1,403
Eutric Planosols (We)	7,180

**Table 2.** Description of explanatory variables assessed by the survey conducted with 80 farmers enrolled in the Embrapa-Genepplus Nellore cattle breeding program from October to December 2021.

<b>Explanatory variables</b>	<b>Description</b>	<b>Number of levels</b>
<i>General information</i>		
Animal breeding technician	The technician affiliated with Embrapa-Genepplus who provides animal breeding guidance to the farm	11
Years enrolled in the Embrapa-Genepplus	The time categorized in 5-year increments, ranging from less than 5 to 25 years	5
Livestock land area	The land area allocated for livestock categorized into classes: small (100 ha) medium (101 – 999 ha) large ( $\geq$ 1000 ha)	3
Production system	Adopting grazing or crop-livestock as a production system	2
<i>Soil management</i>		
Period of use of established pasture	The time categorized in 5-year increments, ranging from less than 5 to 20 years	4
Native grasslands	Choosing exclusively native grasslands for pasture use (yes/no)	2
Tillage	Adopting tillage as a soil management method (yes/no)	2
No-till farming	Adopting no-till farming as a soil management method (yes/no)	2
Contour farming	Adopting contour farming as a soil management method (yes/no)	2
Crop rotation	Adopting crop rotation as a soil management method (yes/no)	2

<b>Explanatory variables</b>	<b>Description</b>	<b>Number of levels</b>
Pasture recovery and renewal	Adopting methods for recovery and renewal of degraded pastures (yes/no)	2
Fertilization	Adopting fertilization (yes/no)	2
Irrigation	Adopting irrigation (yes/no)	2
Natural resource conservation	Adopting buffer strips, riparian forest buffers, or stabilization of gullies and slopes for natural resources conservation (yes/no)	2
<i>Supplemental feeding<sup>1</sup></i>		
Mineral	Inclusion of mineral mix in the supplement (yes/no)	2
Mineral and urea	Inclusion of mineral mix and urea in the supplement (yes/no)	2
Protein	Inclusion of any protein source in the supplement (yes/no)	2
Protein-energy	Inclusion of both protein and energy source in the supplement (yes/no)	2
<i>Reproduction management</i>		
Breeding season	Adopting breeding season for a reproduction management strategy (yes/no)	2
Period of the breeding season	The time is categorized in various monthly increments (e.g.: October to February)	14
Length of the breeding season	The number of months is categorized as short-term (up to 4), and long-term (from 5 to 7)	2
Reproduction technique	The use of reproduction techniques is categorized into classes: Natural service (exclusively) Fixed-time artificial insemination and herd bulls Fixed-time artificial insemination, resynchronization protocols, and herd bulls	3

<b>Explanatory variables</b>	<b>Description</b>	<b>Number of levels</b>
In vitro fertilization	Use of in vitro fertilization as a reproduction technique (yes/no)	2
Age of heifer	The age of the heifer at the first mating is categorized into classes: 12 – 14 mo 16 – 18 mo 20 – 22 mo 24 – 26 mo	4
Weight of heifer	The weight of the heifer at the first mating is categorized into classes: $\leq 300$ kg 301 – 329 kg 330 – 359 kg 360 – 389 kg $\geq 390$ kg	5

1. Supplemental feeding was assessed for each animal category. As a previous step of farm management descriptor selection, the questions were merged and reclassified based on the animal category, resulting in new four descriptors: Supplemental feeding for calves (5 levels), heifers (5 levels), cows (6 levels), and sires (7 levels).

**Table 3.** Maximum likelihood estimates of farm variance ( $\sigma_f^2$ ), residual variance ( $\sigma_e^2$ ) and their standard deviations, and Akaike Information Criterion (AIC), analyzed from the general statistical model concerning each climate and farm management descriptor. The entries are ordered based on the proportion of farm variance explained (PVE) by the included fixed effect on yearling weight (kg) evaluated in Nellore cattle.

<b>Model</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
General Statistical Model	1467.88	38.31	1577.12	39.71	1462980	-
<i>Environmental descriptors</i>						
Soil classification	1117.71	33.43	1577.13	39.71	1462986	23.86
Elevation	1182.25	34.38	1577.12	39.71	1462969	19.46
Climate classification	1333.94	36.52	1577.12	39.71	1462981	9.12
<i>Farm management descriptors</i>						
Animal breeding technicians	926.38	30.44	1577.13	39.71	1462973	36.89
Period of the breeding season	1058.78	32.54	1577.12	39.71	1462987	27.87
Age of heifer	1193.35	34.54	1577.12	39.71	1462974	18.70
Period of use established pasture	1264.45	35.56	1577.12	39.71	1462977	13.86
Weight of heifer	1281.54	35.80	1577.13	39.71	1462980	12.69
Irrigation	1292.68	35.95	1577.12	39.71	1462975	11.94
Bull supplemental feeding	1306.74	36.15	1577.12	39.71	1462985	10.98
Contour farming	1312.55	36.23	1577.12	39.71	1462976	10.58
Calf supplemental feeding	1320.13	36.33	1577.12	39.71	1462982	10.07

<b>Model</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
Fertilization	1323.88	36.39	1577.12	39.71	1462976	9.81
No-till farming	1336.92	36.56	1577.12	39.71	1462977	8.92
In vitro fertilization	1368.76	37.00	1577.12	39.71	1462978	6.75
Years enrolled in the Embrapa-Genepplus	1365.00	36.95	1577.12	39.71	1462984	7.01
Cow supplemental feeding	1370.63	37.02	1577.12	39.71	1462986	6.63
Crop rotation	1385.41	37.22	1577.12	39.71	1462979	5.62
Reproduction technique	1388.82	37.27	1577.12	39.71	1462981	5.39
Production system	1400.42	37.42	1577.12	39.71	1462980	4.60
Tillage	1423.26	37.73	1577.12	39.71	1462980	3.04
Livestock land area	1403.50	37.46	1577.12	39.71	1462982	4.39
Heifer supplemental feeding	1424.87	37.75	1577.12	39.71	1462987	2.93
Native grasslands	1451.72	38.10	1577.12	39.71	1462982	1.10
Natural resources conservation	1453.87	38.13	1577.12	39.71	1462982	0.95
Pasture recovery and renewal	1455.16	38.15	1577.12	39.71	1462982	0.87
Length of the breeding season	1456.51	38.16	1577.12	39.71	1462982	0.77

**Table 4.** The Chi-squared test of independence, corresponding *p-values* within parentheses (upper diagonal), and chi-squared value (lower diagonal) for the pre-selected farm management descriptors.

	<b>TEC</b>	<b>YEN</b>	<b>PEP</b>	<b>NTI</b>	<b>CON</b>	<b>CRO</b>	<b>FER</b>	<b>IRR</b>	<b>CFSF</b>	<b>CWSF</b>	<b>BSF</b>	<b>PBS</b>	<b>RTC</b>	<b>INF</b>	<b>AHF</b>	<b>WHF</b>
<b>TEC</b>		0.56	0.02*	0.55	0.03*	0.17	0.20	0*	0.01*	0.21	0.43	0.23	0.82	0.45	0.10	0.61
<b>YEN</b>	38.05		0.47	0.67	0.70	0.09	0.49	0.75	0.60	0.21	0.48	0.33	0.18	0.31	0.87	0.39
<b>PEP</b>	47.69	11.65		0.54	0.09	0.16	0.04*	0*	0.64	0.78	0.33	0.40	0.21	0.07	0.67	0.65
<b>NTI</b>	8.85	2.34	2.16		0.20	0.04*	0.02*	0.48	0.51	0.54	0.73	0.24	0.77	0.86	0.12	0.18
<b>CON</b>	19.50	2.18	6.60	1.66		0*	0*	0.21	0.64	0.17	0	0.29	0.33	0*	0.03*	0.12
<b>CRO</b>	14.01	8.15	5.18	4.09	13.01		0.02*	0.91	0.33	0.76	0.22	0.72	0.55	0.62	0.64	0.04*
<b>FER</b>	13.53	3.44	8.22	5.83	17.17	5.44		0.49	0.56	0.97	0.09	0.10	0.34	0.01*	0.08	0.02*
<b>IRR</b>	26.42	1.91	20.53	0.49	1.55	0.01	0.47		0.46	0.36	0.41	0.76	0.78	0.95	0.59	0.78
<b>CFSF</b>	64.43	14.03	9.67	3.28	2.51	4.59	2.99	3.61		0*	0*	0.14	0.98	0.19	0.34	0.62
<b>CWSF</b>	57.74	24.78	10.54	4.05	7.76	2.61	0.89	5.52	58.49		0*	0.36	0.87	0.07	0.07	0.16
<b>BSF</b>	61.40	23.72	19.99	3.60	18.71	8.27	11.07	6.14	53.07	133.36		0.96	0.92	0.34	0.14	0.52
<b>PBS</b>	141.61	55.83	40.53	16.2	15.36	9.69	20	9.12	63.22	68.51	57.11		0.99	0.29	0.33	0.62
<b>RTC</b>	14.27	11.31	8.41	0.52	2.22	1.19	2.17	0.49	2.08	5.26	5.90	11.90		0.33	0.60	0.97
<b>INF</b>	9.85	4.80	7.04	0.03	8.04	0.25	6.34	0	6.06	10.10	6.76	15.36	2.22		0.21	0.09
<b>AHF</b>	40.30	6.84	6.67	5.81	8.71	1.70	6.62	1.90	13.39	23.47	24.62	42.21	4.58	4.58		0.18
<b>WHF</b>	36.84	17.01	9.62	6.30	7.40	10.21	11.32	1.75	13.72	26.32	22.98	48.29	2.37	8.15	16.20	

TEC= animal breeding technician; YEN= years enrolled in the Embrapa-Genepplus; PEP= period of use established pasture; NTI= no-till farming; CON= contour farming; CRO= crop rotation; FER= fertilization; IRR= irrigation; CFSF= calf supplemental feeding; CWSF= cow supplemental feeding; BSF= bull supplemental feeding; PBS= period of the breeding season; RTC= reproduction technique; INF= in vitro fertilization; AHF= age of heifer at first mating; WHF= weight of heifer at first mating. \*P-value < 0.05.

**Table 5.** Maximum likelihood estimates of farm variance ( $\sigma_f^2$ ), residual variance ( $\sigma_e^2$ ) and their standard deviations (SD), and the Akaike Information Criterion – AIC analyzed from the general statistical model concerning the combinations among the environmental and key farm management descriptors. The entries are ordered based on the proportion of farm variance explained (PVE) by the included fixed effects on yearling weight (kg) evaluated in Nellore cattle.

<b>Model</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
General Statistical Model	1467.88	38.31	1577.12	39.71	1462980	-
<i>Environmental descriptors</i>						
SOIL, ELE	912.04	30.20	1577.13	39.71	1462976	37.87
CLI, SOIL	1101.84	33.19	1577.15	39.71	1462991	24.94
CLI, ELE	1165.25	34.14	1577.13	39.71	1462975	20.62
<i>Farm management descriptors</i>						
TEC, YEN, NTI, PBS, RTC	454.00	21.31	1577.13	39.71	1462970	69.07
TEC, YEN, NTI, PBS	483.24	21.98	1577.13	39.71	1462970	67.08
TEC, YEN, PBS, RTC	524.69	22.91	1577.13	39.71	1462977	64.26
TEC, YEN, PBS	547.80	23.41	1577.13	39.71	1462975	62.68
TEC, NTI, PBS, RTC	576.00	24.00	1577.13	39.71	1462976	60.76
TEC, PBS, RTC	603.19	24.56	1577.13	39.71	1462977	58.91
TEC, NTI, PBS	618.40	24.87	1577.13	39.71	1462977	57.87
TEC, PBS	646.02	25.42	1577.13	39.71	1462977	55.99

<b>Model</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
TEC, YEN, NTI, RTC	732.16	27.06	1577.13	39.71	1462973	50.12
YEN, NTI, PBS, RTC	772.60	27.80	1577.13	39.71	1462982	47.37
TEC, YEN, NTI	779.01	27.91	1577.13	39.71	1462972	46.93
TEC, NTI, RTC	799.62	28.28	1577.13	39.71	1462970	45.53
TEC, YEN, RTC	810.30	28.47	1577.13	39.71	1462977	44.80
YEN, NTI, PBS	842.54	29.03	1577.13	39.71	1462983	42.60
TEC, NTI	849.34	29.14	1577.13	39.71	1462970	42.14
TEC, YEN	861.96	29.36	1577.13	39.71	1462977	41.28
TEC, RTC	864.32	29.40	1577.13	39.71	1462973	41.12
YEN, PBS, RTC	871.81	29.53	1577.13	39.71	1462987	40.61
YEN, PBS	925.73	30.43	1577.13	39.71	1462987	36.93
NTI, PBS, RTC	945.28	30.75	1577.13	39.71	1462986	35.60
PBS, RTC	1002.56	31.66	1577.12	39.71	1462987	31.70
NTI, PBS	1008.87	31.76	1577.13	39.71	1462986	31.27
YEN, NTI, RTC	1148.89	33.90	1577.12	39.71	1462980	21.73
YEN, NTI	1228.80	35.05	1577.12	39.71	1462980	16.29
NTI, RTC	1263.97	35.55	1577.12	39.71	1462977	13.89
YEN, RTC	1283.22	35.82	1577.12	39.71	1462984	12.58
<i>Environmental and farm management descriptors</i>						
CLI, SOIL, ELE, TEC YEN, NTI, PBS, RTC	250.64	15.83	1577.13	39.71	1462965	82.92

<b>Model</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
CLI, SOIL, TEC YEN, NTI, PBS, RTC	260.14	16.13	1577.13	39.71	1462965	82.28
SOIL, ELE, TEC YEN, NTI, PBS, RTC	265.28	16.29	1577.13	39.71	1462962	81.93
SOIL, TEC YEN, NTI, PBS, RTC	284.43	16.86	1577.13	39.71	1462964	80.62
CLI, ELE, TEC YEN, NTI, PBS, RTC	422.27	20.55	1577.13	39.71	1462974	71.23
CLI, TEC YEN, NTI, PBS, RTC	432.49	20.80	1577.13	39.71	1462973	70.54
ELE, TEC YEN, NTI, PBS, RTC	437.70	20.92	1577.13	39.71	1462970	70.18

CLI= Köppen-Geiger climate classification; SOIL= Soil classification, ELE= elevation; TEC = animal breeding technicians; YEN = years enrolled; NTI = no-till farming; PBS = period of the breeding season; RTC = reproduction technique.

**Table 6.** Random and fixed effects used in modeling yearling weight (kg) evaluated in Nellore cattle.

<b>Model</b>	<b>Fixed effects</b>	<b>Random effects</b>
Benchmark	AGE, S, CG	<i>a, f</i>
Environmental	AGE, S, CG, SOIL, ELE	<i>a, f</i>
Farm Management	AGE, S, CG, TEC, YEN, NTI, PBS, RTC	<i>a, f</i>
Environmental and Farm Management	AGE, S, CG, SOIL, ELE, TEC, YEN, NTI, PBS, RTC	<i>a, f</i>

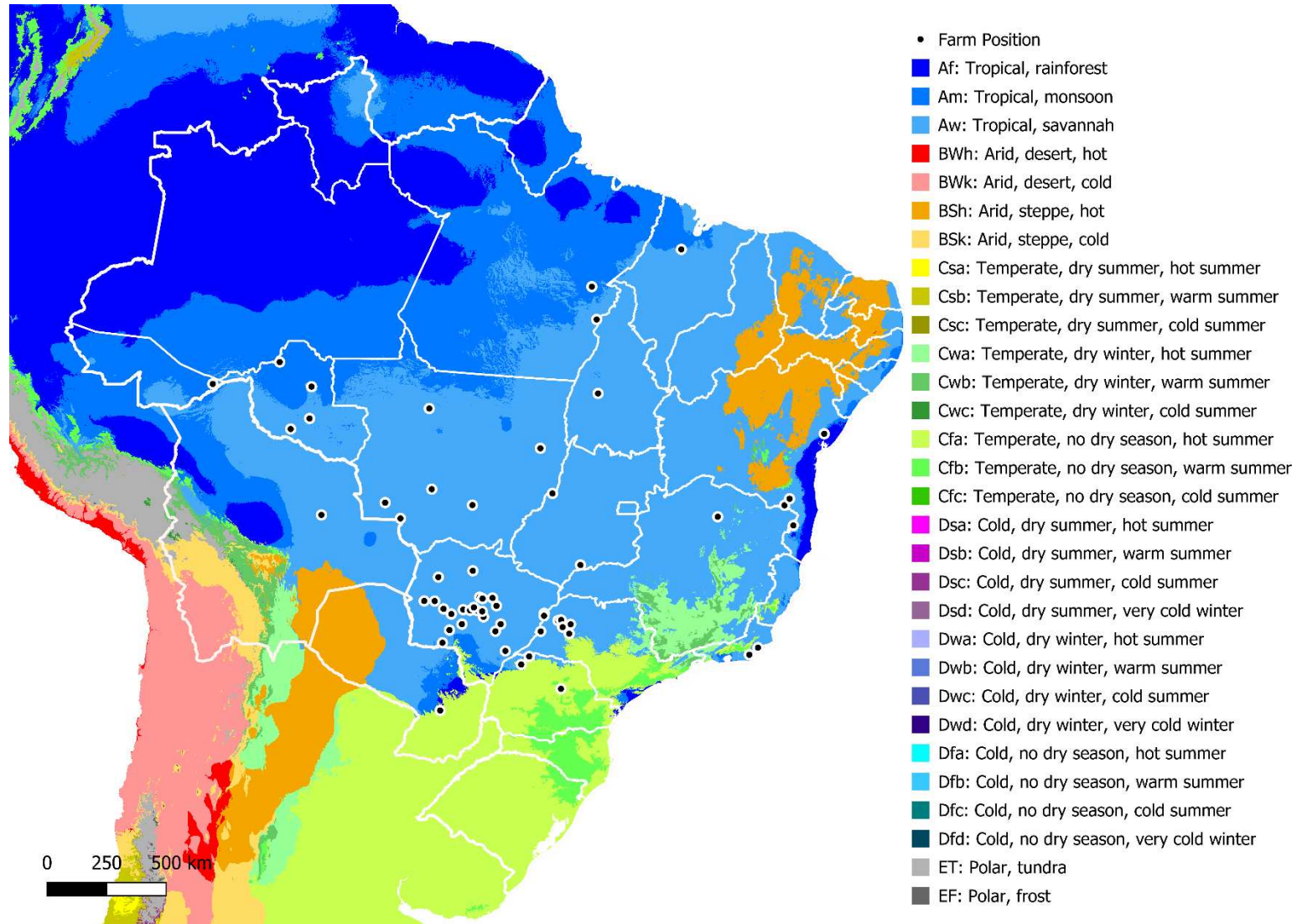
AGE= age at measurement (linear covariate); S= sex; CG= contemporary group; SOIL= soil classification based on World Reference Base for Soil Resources; ELE= Elevation (linear covariate); TEC= animal breeding technician; YEN= years enrolled in the Embrapa-Genepplus; NTI= no-till farming; PBS= period of breeding season; RTC= reproduction technique.

*a*= additive genetic effect and *f*= farm effect.

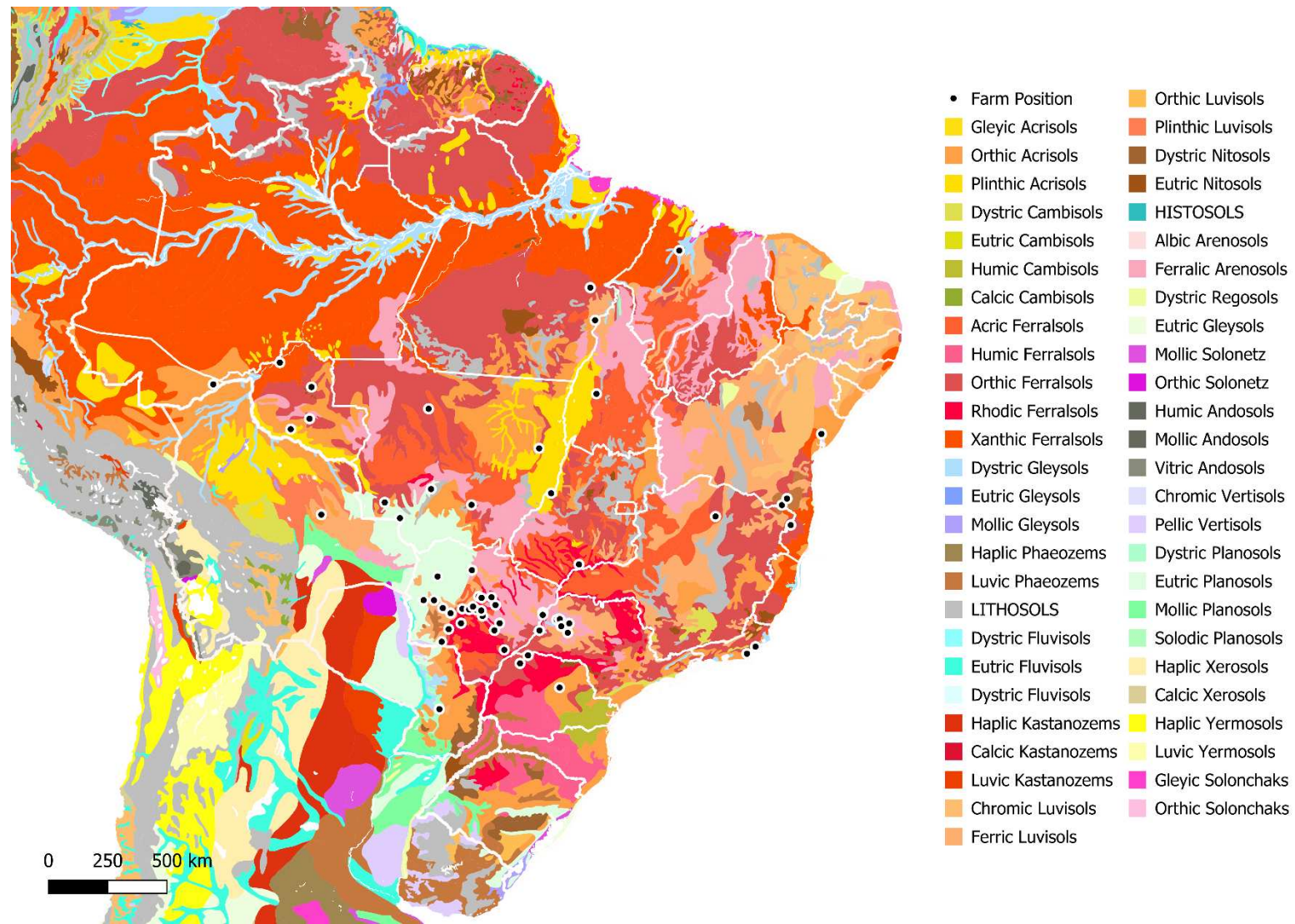
**Table 7.** Restricted Maximum likelihood estimates of additive genetic variance ( $\sigma_a^2$ ), farm variance ( $\sigma_f^2$ ), residual variance ( $\sigma_e^2$ ), within-farm heritability ( $h_w^2$ ), and their standard deviations, and Akaike Information Criterion (AIC) analyzed from different models. The entries are ordered based on the proportion of farm variance explained (PVE) by the included fixed effects on yearling weight (kg) evaluated in Nellore cattle.

<b>Model</b>	$\sigma_a^2$	<b>SD</b>	$\sigma_f^2$	<b>SD</b>	$\sigma_e^2$	<b>SD</b>	$h_w^2$	<b>SD</b>	<b>AIC</b>	<b>PVE</b>
Benchmark	678.48	15.29	1263.80	233.89	1254.00	10.98	0.35	0.01	1475996	0
Environmental	678.41	15.28	951.63	197.51	1254.00	10.98	0.35	0.01	1475886	24.70
Farm Management	678.34	15.29	792.92	209.67	1254.10	10.98	0.35	0.01	1475704	37.26
Environmental and Farm Management	678.27	15.29	740.00	255.64	1254.10	10.98	0.35	0.01	1475600	41.45

## Figures



**Figure 1A** – Koppen-Geiger climate classification and farm locations included in the study.



**Figure 1B** – Soil classification and farm locations included in the study.

## Supplementary material

**Supplementary Material Table S1.** Maximum likelihood estimates obtained in the variable selection procedure.

Available online:

<https://docs.google.com/spreadsheets/d/1n8nhw4zVhIhTGGXQqpYZqtT1I9AX-vzf/edit?usp=sharing&oid=114748748347088121814&rtpof=true&sd=true>

**Supplementary Material Table S2.** Least-square means (SE) of the fixed effects on yearling body weight (kg) evaluated in Nellore cattle (Obtained by the Maximum likelihood method using the general statistical model combined with selected environmental and farm management descriptors).

Model factors	<i>p-value</i>	Level	Estimate (SE)
Age at measurement	<0.001	-	0.1140 (0.003)
Elevation	<0.05	-	0.0853 (0.038)
Sex	<0.001	Male	312.79 (19.16)
		Female	269.38 (19.16)
Soil classification	NS	Orthic Acrisols (Ao)	254.23 (23.64)
		Ferric Acrisols (Ap)	317.99 (47.98)
		Acric Ferralsols (Fa)	276.87 (24.68)
		Orthic Ferralsols (Fo)	261.86 (25.90)
		Rhodic Ferralsols (Fr)	304.99 (28.16)
		Xanthic Ferralsols (Fx)	287.07 (59.31)
		Luvic Phaeozems (Hl)	305.64 (47.51)
		Lithosols (I)	268.91 (42.93)
		Ferric Luvisols (Lf)	276.77 (27.44)
		Ferralic Arenosols (Qf)	281.25 (23.27)
		Dystric Planosols (Wd)	354.24 (54.54)
		Eutric Planosols (We)	303.17 (33.82)
Animal breeding technician	NS	A	299.15 (25.53)
		B	293.07 (23.54)
		C	282.55 (32.93)
		D	308.46 (19.77)

		E	332.61 (32.84)
		F	252.78 (32.37)
		G	276.74 (37.02)
		H	262.21 (50.59)
		I	303.81 (38.39)
		J	304.60 (38.79)
		K	285.92 (24.74)
Enrolled years at Embrapa- Geneplus	NS	1996 – 2000	287.83 (27.07)
		2001 – 2005	309.00 (24.29)
		2006 – 2010	290.83 (24.43)
		2011 – 2015	297.49 (23.65)
		2016 – 2020	270.26 (19.45)
No-till farming	NS	Yes	299.14 (22.58)
		No	283.03 (19.05)
Period of breeding season	NS	January to March	309.15 (93.74)
		August to January	334.69 (58.58)
		September to December	272.47 (31.99)
		September to January	257.81 (31.72)
		September to February	353.54 (48.10)
		September to March	285.55 (32.98)
		October to December	276.21 (33.89)
		October to January	290.46 (23.15)
		October to February	285.51 (20.85)
		October to March	236.59 (29.83)
		October to April	313.39 (59.91)
		November to February	302.97 (23.05)
		November to March	274.04 (27.16)
		December to March	282.77 (30.65)
Reproduction technique	NS	1	264.90 (40.64)
		2	292.54 (21.36)
		3	315.80 (12.93)

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1= Natural service (exclusively); 2= Fixed-time artificial insemination and herd bulls; 3= Fixed-time artificial insemination, resynchronization protocols, and herd bulls. NS = no significant.

## CHAPTER 3

### EXPLORING FARM-LEVEL ENVIRONMENTAL DATA TO INVESTIGATE GENOTYPE BY ENVIRONMENT INTERACTION FOR GROWTH, REPRODUCTIVE, AND CARCASS TRAITS IN NELLORE CATTLE

#### 3.1. Abstract

In this study, we aimed to (1) identify relevant environmental conditions (EC) for Nellore cattle using farm-level environmental descriptors via divisive hierarchical clustering analyses, (2) estimate genetic parameters related to growth, reproductive, and carcass traits, and (3) investigate the presence of genotype by environment interaction (GxE) by comparing rankings of estimated breeding value (EBV) of bulls among identified ECs using either BLUP or ssGBLUP methods. The evaluated traits included yearling weight (YW), scrotal circumference (SC), age at first calving (AFC), ribeye area (REA), backfat thickness (FAT), and marbling score (MARB). Divisive hierarchical clustering analyses were used to determine the EC experienced by the animals using farm-level descriptors accounting for environmental factors (climate and soil classifications, and elevation) and 26 farm management practices (encompassing general, soil management, supplemental feeding, and reproduction management information). The optimal clustering of farm-level descriptors grouped farms into two EC, labeled ENV1 and ENV2. Subsequently, a bi-trait linear model was used to investigate the GxE. The estimates of heritability for all traits, except for AFC and FAT, were higher for animals raised on ENV1 compared to those in ENV2. Statistically significant differences were found for YW, AFC, and MARB using an approximation test. The lowest genetic correlation was observed for AFC ( $0.31 \pm 0.09$ ), followed by YW ( $0.37 \pm 0.05$ ), and REA ( $0.62 \pm 0.08$ ), indicating traits largely affected by GxE. Moderate to high genetic correlations were observed for SC ( $0.80 \pm 0.04$ ), FAT ( $0.88 \pm 0.07$ ), and MARB ( $0.95 \pm 0.04$ ). The Spearman's correlations for EBVs of bulls were generally low, ranging from -0.03 to 0.38 across evaluated traits, using either BLUP or ssGBLUP. The percentage of common bulls for EBVs ranked within the TOP5%, TOP10%, and TOP25% categories was most pronounced within the TOP5% ranking using either BLUP or ssGBLUP. AFC exhibited the highest degree of re-ranking, followed by YW and REA, across both methods and all ranking categories, indicating a higher influence of GxE on these traits. These findings highlight the importance of including environmental factors

into genetic evaluations of AFC, YW, and REA traits to select animals more adapted to different environmental conditions.

**Keywords:** GxE interaction; farm management; multitrait model; animal breeding; pasture-raised beef cattle

### 3.2. Introduction

The most common model in beef cattle genetic evaluations assumes that the performance of different genotypes uniformly changes across different environments (Falconer and Mackay, 1996). However, genotype by environment interaction (GxE) may occur when genotypes are exposed to diverse environmental conditions (EC), perhaps leading to re-ranking among selection candidates (Hayes et al., 2016).

Two different models have been widely used in the literature to study GxE: multitrait mixed models and reaction norm models; both models require phenotypes to be recorded on the same or correlated animals in, at least, two different environments (Hayes et al., 2016). The multitrait approach accounts for GxE based on genetic correlations, where the performance of a genotype for a trait under different EC is treated as distinct yet correlated traits (Falconer, 1952). If the environment can be categorized, such as pasture versus feedlot, intensive versus extensive production systems, different countries, or other EC groups, the multitrait models can be straightforwardly applied. This method has advantages in terms of computational demand and interpretation of results, being user-friendly for commercial breeding programs. Conversely, a reaction norm model is recommended when the environment is more accurately represented by a continuous variate, such as temperature humidity indices (Falconer, 1990). This model can accommodate an infinite number of environments through covariance functions (Kirkpatrick et al., 1990), allowing the phenotypic expression of a genotype to be modeled as a function of the environment (Falconer, 1990). That is, predictions are feasible even when phenotypes have not been evaluated across all environments, as long as pedigree (or genomic) information is available.

In both methods, genetic correlations can be used to assess differences the occurrence of GxE. According to Robertson (1959), a genetic correlation below 0.8 for a trait across different environments indicates significant re-ranking due to GxE, justifying the need of selection based on a breeding value for a specific environment. Extreme variations in climate (e.g., temperate versus tropical), soils and pasture quality, and management (e.g., farm input

level), may be conditions that lead to low genetic correlations for the same trait across environments (Burrow 2012; Raidan et al., 2015; Hayes et al., 2016).

Global reports indicate that three of the current top five beef-producing countries (i.e., Brazil, China, and India) primarily raise their cattle in (sub)tropical regions and diverse production systems, ranging from intensive feedlots to extensive grass-based farming (Gilbert et al., 2018; Robinson et al., 2018). High temperatures, high humidity, and distinct variations in rainfall (dry and wet seasons) characterize (sub)tropical climates (Alvares et al., 2013). These conditions expose cattle to several challenges, including heat stress, negative energy balance due to seasonal pasture variations, and infestations of ectoparasites (e.g., ticks and flies) and endoparasites, which require tailored breeding and management strategies. Raising cattle in these challenging environments may contribute to genetic variation in phenotypic plasticity resulting in GxE.

Overall, studies suggest the need to further consider GxE in genetic evaluations of beef cattle affecting growth (Cardoso and Tempelman, 2012; Williams et al., 2012; Chiaia et al., 2015; Raidan et al., 2015; Oliveira et al., 2018; Braz et al 2021) and female reproductive traits (Chiaia et al., 2015; Fennewald et al 2018; Mota et al., 2020; Carvalho Filho et al., 2024). In contrast, GxE models are less important for traits related to male reproduction (Chiaia et al., 2015; Raidan et al., 2015; Santana et al., 2015; Nascimento et al. 2022) and carcass (Ibi et al. 2005). However, these studies often do not include information about farm-specific management practices, which could provide a better understanding of the GxE within different production systems. In addition, they usually adopt reaction norms and use contemporary groups solutions as environmental gradient, which make the practical implementation difficult.

In this study, we aimed to (1) identify relevant environmental conditions (EC) for Nellore cattle using farm-level environmental descriptors via divisive hierarchical clustering analyses, (2) estimate genetic parameters related to growth, reproductive, and carcass traits, and (3) investigate the presence of genotype by environment interaction (GxE) by comparing rankings of estimated breeding value (EBV) of bulls among identified ECs using either BLUP or ssGBLUP methods.

### **3.3. Material and methods**

Animal Care and Use Committee approval was not obtained for this study because all data provided came from an existing database.

### 3.3.1. Animal and phenotypes

Phenotypic data from Nelore cattle raised in pastures across Brazil (covering all regions: North, Northeast, Midwest, Southeast, and South), as well as Bolivia, and Paraguay, were provided by the Embrapa-Genepplus beef cattle breeding program (Campo Grande, MS, Brazil). The recorded animals were born between 1991 and 2021 across 60 farms with a high diversity of management and different environmental conditions.

The evaluated traits included yearling weight (YB), scrotal circumference (SC), age at first calving (AFC), ribeye area (REA), backfat thickness (FAT), and marbling score (MARB). Carcass traits were measured via ultrasound by a certified technician on the longissimus thoracis muscle between the 12th and 13th ribs on the left side of the animal, according to the method proposed by Perkins et al. (1992). Images were taken with an Aloka® 500V real-time ultrasound machine, equipped with a 17.2-cm, 3.5-MHz linear transducer, and interpreted using Beef Image Analysis® software.

The contemporary groups (CG) were formed by the concatenation of year and season (spring: October to December, summer: January to March, autumn: April to June, and winter: July to September) at measurement. CGs with fewer than three individuals, those consisting of unique information from sex and farm, and records deviating  $\pm 3.5$  SD from the mean of the evaluated traits were removed from the analyses.

### 3.3.2. Pedigree and genotypes

The pedigree included 2,104,030 animals, which representing 25 generations. A total of 79,104 animals were genotyped using low- to high-density genome-wide bovine genotyping arrays (Table 1). The quality control (QC) of genotype data consisted of removing single nucleotide polymorphism (SNP) with a genotype call below 0.9, a call rate below 0.95, minor allele frequency (MAF) lower than 0.05, difference between observed and expected heterozygous frequencies  $\pm$  three standard deviations, and a Hardy–Weinberg equilibrium *p*-value less than  $10^{-6}$ . The snpStats R package (Clayton, 2014) and the BLUPF90 family software (Misztal et al., 2014) were utilized for performing the genomic QC and pedigree consistency analysis.

Missing genotypes from either SNP panel were imputed using the BovineHD BeadChip (Illumina, San Diego, CA, USA) as a reference panel, which contains 777,962 SNPs mapped to the ARSUCD1.2 bovine genome reference assembly (Rosen et al., 2020). In the

genotype imputation procedure, we included an SNP panel found in both the high-density and, at least, one low- or medium-density panel. The FImpute software was used to perform the genotype imputations and detect parent-progeny conflicts (Sargolzaei et al., 2014). Average imputation accuracy, assessed by Pearson's correlation between imputed and observed genotypes in a random cross-validation analysis, exceeded 97%. After QC, 93,386 SNPs for 72,958 animals (male= 28,101; female= 44857) remained for statistical analysis.

### 3.3.3. Environmental clustering

Divisive hierarchical clustering analyses were used to determine the environmental conditions (EC) experienced by the animals using farm-level descriptors accounting for several environmental (climate and soil classifications, and elevation) and farm management variables (animal breeding technician, enrolled years at the Embrapa-Genepus, livestock land area, production system, period of use established pasture, native grasslands, tillage, no-till farming, contour farming, crop rotation, pasture recovery and renewal, fertilization, irrigation, natural resource conservation, mineral supplement, mineral and urea supplement, protein supplement, protein-energy supplement, breeding season, period of the breeding season, length of the breeding season, reproduction technique, in vitro fertilization, and age and weight of heifer at the first mating), as described by Santana (2024). Gower's distance was employed to measure dissimilarities between farms, due to its capacity to accommodate diverse data types (i.e., binary, ordinal, or continuous variables) within the same dataset (Gower, 1971). The DIANA clustering algorithm was employed to assess the sample clusters (Kaufman and Rousseeuw 1990). The algorithm starts by grouping all data points into a single cluster. It then iteratively splits this cluster into smaller clusters based on Gower's distance, continuing until the number of clusters matches the number of samples. The result is a hierarchy of clusters that can be represented in a tree structure called a dendrogram. The root of the dendrogram represents the initial single cluster, and the leaves represent the final clusters. The optimal number of clusters was defined using the Calinski–Harabasz index (Caliński & Harabasz, 1974), and the robustness of the resulting partition was assessed using the Silhouette coefficient (Rousseeuw, 1987). Afterward, the optimal clustering of farm-level descriptors grouped farms into two EC, labeled ENV1 and ENV2. This cluster analysis was implemented in the R package “cluster” (Maechler et al., 2023).

### 3.3.4. Statistical analysis

Assuming that the performance of a genotype for a trait in ENV1 and ENV2 represents distinct but correlated traits, bi-variate linear models were utilized to estimate (co)variance components and predict breeding values. The general two-trait model in this context is defined as follows:

$$\begin{bmatrix} y_1 \\ y_2 \end{bmatrix} = \begin{bmatrix} \mathbf{X}_1 & 0 \\ 0 & \mathbf{X}_2 \end{bmatrix} \begin{bmatrix} b_1 \\ b_2 \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_1 & 0 \\ 0 & \mathbf{Z}_2 \end{bmatrix} \begin{bmatrix} a_1 \\ a_2 \end{bmatrix} + \begin{bmatrix} \mathbf{W}_1 & 0 \\ 0 & \mathbf{W}_2 \end{bmatrix} \begin{bmatrix} f_1 \\ f_2 \end{bmatrix} + \begin{bmatrix} e_1 \\ e_2 \end{bmatrix}$$

where,  $y_i$  is a vector of phenotypes for the  $i$ th EC (i.e., ENV1 and ENV2),  $b_i$  is a vector with fixed effects of sex, contemporary group, and age (linear covariate) at measurement for the  $i$ th EC, except SC and AFC which were assumed only CG;  $a_i$  is a vector of random additive genetic effects for the  $i$ th EC,  $f_i$  is a vector of random farm effects for the  $i$ th EC, and  $e_i$  is a vector of residuals for the  $i$ th EC. The  $\mathbf{X}_i$ ,  $\mathbf{Z}_i$  and  $\mathbf{W}_i$  are known incidence matrices relating records of the  $i$ th EC to fixed, additive genetic, and farm effects, respectively. The assumptions regarding the random effects are as follows:  $\begin{bmatrix} a_1 \\ a_2 \end{bmatrix} \sim N(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A})$ , where

$\mathbf{G}_0 = \begin{bmatrix} \sigma_{a_1}^2 & \sigma_{a_{1,2}} \\ \sigma_{a_{2,1}} & \sigma_{a_2}^2 \end{bmatrix}$  represents the matrix of additive genetic variance and covariance between

EC;  $\begin{bmatrix} f_1 \\ f_2 \end{bmatrix} \sim N(\mathbf{0}, \mathbf{F}_0 \otimes \mathbf{I})$ , where  $\mathbf{F}_0 = \begin{bmatrix} \sigma_{f_1}^2 & 0 \\ 0 & \sigma_{f_2}^2 \end{bmatrix}$  represents the matrix of farm variance between

EC; and  $\begin{bmatrix} e_1 \\ e_2 \end{bmatrix} \sim N(\mathbf{0}, \mathbf{R}_0 \otimes \mathbf{I})$ , where  $\mathbf{R}_0 = \begin{bmatrix} \sigma_{e_1}^2 & 0 \\ 0 & \sigma_{e_2}^2 \end{bmatrix}$  represents the matrix of residual variance

between EC. Where  $\sigma^2$  refers to variance and  $\sigma$  refers to covariance,  $\mathbf{A}$  is the pedigree-based relationship matrix,  $\mathbf{I}$  is an identity matrix, and  $\otimes$  is the notation of Kronecker product. The farm and residual covariances are equal to zero since evaluated animals have no performance records in either EC (they remain on the unique farm and EC throughout their life).

The presented multitrait model was extended to include data from genotyped animals, replacing  $\mathbf{A}$  with  $\mathbf{H}$ , which is a hybrid relationship matrix that combines both pedigree and genomic information. The inverse of the  $\mathbf{H}$  matrix can be written as follows (Aguilar et al., 2010):

$$\mathbf{H}^{-1} = \mathbf{A}^{-1} + \begin{bmatrix} 0 & 0 \\ 0 & \tau(\alpha \mathbf{G} - \beta \mathbf{A}_{22})^{-1} - \omega \mathbf{A}_{22}^{-1} \end{bmatrix},$$

where  $\mathbf{A}_{22}^{-1}$  is the inverse matrix of the pedigree-based relationship matrix  $\mathbf{A}$  for the genotyped animals, and  $\mathbf{G}^{-1}$  is the inverse of the genomic relationship matrix  $\mathbf{G}$  calculated

based on the first method proposed by VanRaden (2008).  $\mathbf{H}^{-1}$  was computed using the following parameters:  $\tau = 1$ ,  $\alpha = 0.95$ ,  $\beta = 0.05$  and  $\omega = 1$  (Misztal et al., 2014).

(Co)variance components for all traits were estimated using the restricted maximum likelihood (REML) method. The estimated breeding values (EBV) were assessed using the best linear unbiased prediction (BLUP) method, and the genomic estimated breeding values (GEBV) were obtained using the single-step genomic best linear unbiased prediction (ssGBLUP) method. These analyses were performed in the BLUPF90 suite programs (Misztal et al., 2014). For each trait, estimates of genetic correlation ( $r_{g_{1,2}}$ ), and within-farm heritability ( $h_w^2$ ) for the  $i$ th EC is given, respectively, by:  $r_{g_{1,2}} = \frac{\sigma_{a_{1,2}}}{\sqrt{\sigma_{a_1}^2 \sigma_{a_2}^2}}$  and  $h_w^2 = \frac{\hat{\sigma}_a^2}{\hat{\sigma}_a^2 + \hat{\sigma}_e^2}$ , where  $\hat{\sigma}_a^2$  is the estimate of the additive genetic variance, and  $\hat{\sigma}_e^2$  is the estimate of the residual variance (Visscher and Goddard, 1993). To assess differences in within-heritability estimates, a Gaussian approximation test was employed with a significance level of 5%. The p-value was computed using  $p = 2 \times \Phi(-|z|)$ , where  $z$  represents the z-score and  $\Phi$  denotes the cumulative distribution function of the standard normal distribution. Spearman's correlations and the percentage of common bulls ranked within the top 5% (TOP5%), top 10% (TOP10%), and top 25% (TOP25%) of EBVs were computed to compare bull rankings between two environmental conditions for each evaluated trait using either BLUP or ssGBLUP. The rank comparison analysis included only bulls with at least five recorded offspring in each environment (ENV1 and ENV2) per trait.

### 3.4. Results

#### 3.4.1. Descriptive statistics

Descriptive statistics for evaluated traits measured in Nellore cattle raised on two ECs are presented in Table 2. The geographical location of farms included in the dataset is shown in Figure 1.

#### 3.4.2. Environmental clustering

We used divisive hierarchical clustering with 29 farm-level environmental and management descriptors to partition the farms into two ECs (Figure 1). Table 3 shows the number of farms included by farm-level environmental descriptor for each EC. ENV1 is mainly composed of farms located in the temperate climate zones without a dry season and with a hot summer (Cfa) and with a dry winter with a hot summer (Cwa), followed by the tropical zone of

savannah (Aw), according to the climate classification proposed by Köppen-Geiger (1936). These farms are also situated in regions with ferralic arenosols (Qf) and rhodic ferralsols (Fr) soils (IUSS, 2015), at an average elevation of  $349 \pm 151$  meters. In contrast, ENV2 is defined by farms located in the Aw climate class, and regions characterized by orthic acrisols (Ao) and orthic ferralsols (Fo) soils, at an average elevation of  $251 \pm 143$  meters. Regarding farm management practices, ENV1 predominantly encompasses farms that allocate large grassland or crop-livestock areas to beef cattle breeding. The farms in ENV1 implement several soil management practices (including no-till farming, contour farming, crop rotation, fertilization, irrigation, and natural resource conservation), and have a diverse supplemental feeding strategy that includes calves, heifers, cows, and sires. Furthermore, farms in ENV1 usually expose their heifers to the first mating between 12 and 14 months of age, with a target weight of up to 329 kg. Conversely, ENV2 consists of farms that exclusively raise animals for breeding purposes on medium to large grassland areas. These farms employ minimal, or no soil management practices, and the primary supplement feeding for all animal categories is mineral mix. In terms of reproduction management, farms in ENV2 use breeding season and introduce their heifers to the first mating between 24 and 26 months of age, with varying weights of up to 329 kg.

### 3.4.3. Genetic parameters

Table 4 presents the estimates of (co)variance components, within-farm heritability, and additive genetic correlations between two ECs for each evaluated trait. The additive genetic and residual variances for all traits were higher in the animals raised on ENV1 when compared to the animals raised on ENV2, except for the additive genetic variance for AFC. On the other hand, the farm variances were higher in animals raised on ENV2 when compared to the animals raised on ENV1, except for SC and FAT. The within-farm heritability estimates ranged from 0.12 (FAT) to 0.38 (MARB). The within-farm heritability estimates for all traits, except for AFC and FAT, were higher in the animals raised on ENV1 compared to those in ENV2. Significant differences were statistically confirmed for YW, AFC, and MARB using the Gaussian approximation test. MARB, SC, REA, and YW had moderate within-farm heritability estimates of 0.38, 0.34, 0.27, and 0.25, respectively, in animals raised in ENV1. In ENV2, MARB and SC also had moderate within-farm heritability estimates of 0.31 and 0.30, respectively. Low within-farm heritability estimates of 0.13 and 0.12 were observed for FAT and AFC in animals raised in ENV1. The heritability estimates for animals raised in ENV2 were 0.19 for REA, 0.18 for YW, 0.16 for AFC, and 0.13 for FAT. Concerning genetic correlations, the lowest was observed for AFC ( $0.31 \pm 0.09$ ), followed by YW ( $0.37 \pm 0.05$ ),

and REA ( $0.62 \pm 0.08$ ), which seem to be largely affected by GxE. Moderate to high genetic correlations were observed for SC ( $0.80 \pm 0.04$ ), FAT ( $0.88 \pm 0.07$ ), and MARB ( $0.95 \pm 0.04$ ), which suggested the absence of GxE.

#### 3.4.4. Re-rank comparisons

The re-rank comparisons were performed using bulls with at least five recorded offspring in each environment per trait. The Spearman's correlations for EBVs of bulls were generally low, ranging from -0.03 to 0.38 across evaluated traits, using either BLUP or ssGBLUP. (Table 5). The largest difference between methods was observed in MARB (0.16), followed by FAT (0.15), AFC (0.14), REA (0.13), YW (0.12), and SC (0.05). By comparison, ssGBLUP exhibited higher Spearman's correlations for YW (0.08), SC (0.10), and MARB (0.39), and lower correlations for AFC (-0.01), REA (0.04), and FAT (0.05). Table 6 presents the percentage of common bulls for EBVs ranked within the TOP5%, TOP10%, and TOP25% categories. The variation in the percentage of common bulls between BLUP and ssGBLUP was most pronounced within the TOP5% ranking. AFC exhibited the highest degree of re-ranking, followed by YW and REA, across both methods and all ranking categories (TOP5%, TOP10%, and TOP25%). In contrast, MARB, FAT, and SC demonstrated the least re-ranking, indicating a lower influence of GxE on these traits which is in line with the genetic correlations results.

### 3.5. Discussion

#### 3.5.1. Genetic parameters

Estimates of variance components for growth (YW), reproduction (SC and AFC), and carcass traits (REA, FAT, and MARB) were obtained using the REML/BLUP method with a two-trait model that assumes distinct but correlated traits in each environment (ENV1 and ENV2) to understand GxE in Nelore cattle. The varying estimates of additive genetic and phenotypic variances in ENV1 and ENV2 suggest the presence of GxE effects for all evaluated traits (Bowman, 1972). The genetic variance was higher in ENV1 than in ENV2, except for AFC. This observation aligns with findings in the literature by Lemos et al. (2015), Raidan et al. (2015), Chiaia et al. (2018), Oliveira et al. (2018), and Nascimento et al. (2022) which indicate that estimates of variance components in Nelore cattle for growth and reproductive traits increase as EC become more favorable. According to Raidan et al. (2015) the unfavorable environment could limit the expression of genetic differences, resulting in lower genetic additive variance in comparison to the favorable environment.

For AFC we observed a distinct behavior, with significantly higher estimates of additive genetic variance and heritability for AFC in the constrained EC (i.e., ENV2). AFC is highly influenced by the farmer decisions regarding the moment (age and weight) to start breeding the heifers. In our farm level environmental description, we can observe that in ENV2 the heifers are typically first mated at 24 – 26 mo, compared to 12 – 14 mo in ENV1. It is possible that a significant proportion of heifers in ENV1 had not enough opportunities to breed, limiting the expression of genetic differences. Genetic selection for female sexual precocity is a recent development for Nellore cattle in Brazil (Nogueira et al., 2023), while the historical average age of puberty for Zebu cattle is 25 months (Sartori et al., 2010). Concerning heritability estimates, AFC and MARB exhibited low and moderate heritability, respectively, in agreement with those reported in the literature for Nellore cattle (Tonussi et al., 2015; Buzanskas et al., 2017; Mota et al., 2018; Londoño-Gil et al., 2022; Marestone et al., 2022). In contrast, heritability estimates for YW, SC, REA and FAT were lower than those reported in previous studies that did not account for GxE effects in Nellore cattle raised on pasture. For instance, Rojas de Oliveira et al. (2018), Schmidt et al. (2018) and Ramos et al. (2021) reported heritability estimates ranging from 0.34 to 0.48 for YW, and from 0.39 to 0.56 for SC. Caetano et al. (2013), Buzanskas et al. (2017), Rojas de Oliveira et al. (2018), Ramos et al. (2021), and Marestone et al. (2022) reported heritability estimates ranging from 0.30 to 0.35 for REA, and from 0.14 to 0.29 for FAT.

Our findings indicate the existence of GxE in AFC, YW, and REA, whereas it appears to be less important for SC, FAT, and MARB following the correlation thresholds established by Robertson (1959). In simulated scenarios for dairy cattle, Mulder and Bijma (2006) showed that long-term cooperation between equal-sized breeding programs in different environments was feasible with genetic correlations higher than 0.80 to 0.90, leading to result in up to 15% extra genetic gain. Conversely, when genetic correlations were as low as 0.40 to 0.60, the benefits of collaboration with breeding programs in different environments decreased over time (Mulder and Bijma 2006). The findings by Mulder and Bijma (2006) highlight the importance of tailoring genetic selection strategies for AFC, YW, and REA distinctly in ENV1 and ENV2.

Diaz et al. (2011), Williams et al. (2012), and Raidan et al. (2015) found weak evidence of GxE using a multitrait approach for growth traits in beef cattle, including Nellore raised in five states across Brazil, Angus at low versus high altitudes in USA, and Nellore raised in pasture versus feedlot, respectively. These authors estimated genetic correlations of 0.67 to 0.75 for YW (Diaz et al., 2011), 0.76 for the post-weaning gain, (Williams et al., 2012), and 0.75 for

final weight (Raidan et al., 2015). It shows the importance of a good definition of the EC to be able to detect GxE. In our work, multiple factors were used for defining the EC, including environmental descriptors such as climate and soil classifications, and elevation, as well as management descriptors related to general information, soil management, supplemental feeding by animal category, and reproduction management.

On the other hand, studies employing CG as an environmental descriptor in reaction norm models corroborate our results. Pegolo et al. (2011) estimated genetic correlations between extreme environments of 0.24 for weight at 450 days, while estimates of 0.26 to 0.42 for YW in Nellore cattle were obtained by Chiaia et al. (2015), Lemos et al. (2015) and Oliveira et al. (2018). Studies show that GxE effect is more important for traits related to fitness, such as female fertility (Heile-Mariam et al., 2008). AFC exhibited the lowest correlation between environments (0.31), which is similar to AFC estimates of genetic correlations between extreme environments ranging from 0.10 to 0.25 (Chiaia et al., 2015; Lemos et al., 2015; Mota et al., 2020). On the other hand, SC exhibits consistently high genetic correlations across extreme environments (Chiaia et al., 2015; Raidan et al., 2015; Santana Jr et al., 2015; Nascimento et al., 2022). Studies of GxE in carcass traits are limited, but Ibi et al. (2015) reported high genetic correlations for REA, FAT, and MARB measured in Japanese Black cattle between the Tohoku and Kyushu regions in Japan. However, no estimates of genetic parameters for carcass traits in Nellore cattle considering GxE were found in the literature.

### 3.5.2. Re-rank comparisons

The inclusion of genomic information into genetic evaluations improves the connectedness among herds, allowing more accurate estimation of an individual's breeding value across environments, even with small coefficients of genomic relationship (Yu et al. 2017). Hence, it is expected that EBVs obtained by BLUP and ssGBLUP will be different (Mota et al., 2016; Macedo Mota et al., 2020, and Nascimento et al., 2022). Nevertheless, there is an agreement between these models in selecting the best animals (Oliveira et al., 2018).

The low Spearman's correlations for EBV obtained using either BLUP or ssGBLUP reinforce the presence of GxE at some level for all evaluated traits, mainly those previously indicated by low genetic correlation (AFC, YW, and REA). These results demonstrate a large change in the ranking of bulls between the two EC, that it is bulls selected based on EBVs for the ENV1 may not be the best animal for ENV2 (Table 5). In contrast, rank correlations above 0.9 for AFC, YW, and SC were obtained by Lemos et al. (2015) and for SC by Nascimento et

al. (2022) between environments with low, medium, and high restrictions. According to these authors, a univariate-trait model could be used for the genetic evaluation of YW, AFC, and SC in Nellore cattle.

Nevertheless, in this study, the percentage of common bulls ranked by EBVs across different categories indicates that AFC, YW, and REA require caution in the genetic selection under two EC. For instance, in AFC less than 50% of the TOP25% will be selected in common using EBVs for both environments. Thus, the selection of bulls for AFC without considering the environment that the progeny will be raised may restrict the genetic gain for this trait.

The stability of rankings for MARB, FAT, and SC between environments suggests that these traits are less affected by GxE, making them more reliable for selection across diverse conditions. Furthermore, the highest-ranking bulls (TOP5%) were more susceptible to re-ranking in either BLUP or ssGBLUP. These observed trends align with the genetic and re-ranking correlations estimated earlier, reinforcing the need for tailored genetic selection strategies for AFC, YW, and REA under different ECs. The higher susceptibility of these traits to GxE highlights the importance of incorporating environmental factors into genetic evaluations to enhance the robustness of selection decisions.

Overall, these findings emphasize the critical role of GxE in influencing the genetic evaluation and selection of bulls, particularly for traits AFC, YW, and REA. Breeding programs should consider these interactions to optimize genetic gain and ensure consistent performance across varying environmental conditions. In this paper, we propose an easy and efficient way to provide genetic evaluations considering GxE. The environmental data for each farm can be extracted from public databases at the moment that the producer enrolls in the breeding program based on its location. The management data should be collected through a survey and the producers can be helped by the technicians in this task and it can be updated if the producers change management practices. The grouping analysis can be incorporated in the breeding program kit tools and it can be programmed to inform the producers which is the EC of his farm and provide EBVs for his specific EC. In comparison to reaction norms this method has lower computational demand and it is easier to interpret and use, since in reaction norms it can be hard to establish which EC the farm belongs to.

### **3.6. Conclusion**

This study identified two distinct EC based on farm-level environmental and management descriptors at Nelore cattle-rearing locations. The estimates of genetic parameters within these EC provided evidence for GxE affecting AFC, YW, and REA traits in Nelore cattle. The low Spearman's correlations observed for EBV obtained using either BLUP or ssGBLUP method reinforce the presence of GxE at some level for all evaluated traits, mainly those indicated by low genetic correlation. The top-ranking bulls (TOP5%) demonstrated more susceptibility to re-ranking for AFC, YW, and REA in either BLUP or ssGBLUP. These findings highlight the importance of incorporating environmental factors into genetic evaluations to enhance the robustness of selection decisions and increase genetic gains.

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## Tables

**Table 1.** Number of single nucleotide genotyping polymorphism (SNP) and genotyped animals for each genome-wide bovine genotyping array in the present study.

<b>SNP Panel</b>	<b>Panel SNP count</b>	<b>N</b>
Zoetis SNP low-density chip v4	18819	186
GeneSeek® Genomic Profiler™ Bovine LD v3 (26 K)	26151	1376
Z-chip v2	27533	1705
Zoetis Custom SNP chip ZL5	29842	17088
GeneSeek® Genomic Profiler™ Bovine LD v3 (30 K)	30108	3879
Zoetis SNP low-density chip v5	30754	149
GeneSeek® Genomic Profiler™ indicus (35 K)	35339	33650
Illumina BovineSNP50 BeadChip v2	54001	697
GeneSeek® Genomic Profiler™ indicus (50 K)	54791	11573
GeneSeek® Genomic Profiler™ HDi (75 K)	70092	24
Zoetis Custom SNP chip ZM2	74653	1171
Illumina BovineHD BeadChip	777962	1449

**Table 2.** Descriptive statistics for yearling weight (YW), scrotal circumference (SC), age at first calving (AFC), ribeye area (REA), backfat thickness (FAT), and marbling score (MARB) measured in Nellore cattle raised on two environmental conditions (ENV1 or ENV2).

<b>Trait</b>	<b>N</b>	<b>N of farms</b>	<b>Mean <math>\pm</math> SD</b>	<b>Minimum</b>	<b>Maximum</b>
YW, kg					
<i>ENV1</i>	95,084	30	319.49 $\pm$ 70.48	69.49	540.09
<i>ENV2</i>	68,939	30	282.22 $\pm$ 53.62	74.35	539.40
SC, cm					
<i>ENV1</i>	38,843	30	26.54 $\pm$ 4.49	12.00	42.50
<i>ENV2</i>	24,640	30	25.09 $\pm$ 3.96	10.00	41.00
AFC, days					
<i>ENV1</i>	40,657	30	1,124 $\pm$ 166.24	777.87	1,619
<i>ENV2</i>	35,614	29	1,164 $\pm$ 167.51	777.87	1,620
REA, cm <sup>2</sup>					
<i>ENV1</i>	23,166	17	58.38 $\pm$ 11.86	12.50	99.06
<i>ENV2</i>	9,361	13	49.44 $\pm$ 11.35	15.12	94.55
FAT, mm					
<i>ENV1</i>	22,798	17	3.21 $\pm$ 1.53	0.5836	9.02
<i>ENV2</i>	9,360	13	2.18 $\pm$ 0.66	0.5080	8.89
MARB, %					
<i>ENV1</i>	14,779	14	2.26 $\pm$ 0.82	0.2200	4.92
<i>ENV2</i>	8,630	13	2.02 $\pm$ 0.76	0.1300	4.38

**Table 3.** Number of farms by farm-level environmental descriptor for each environmental condition (ENV1 and ENV2) obtained by divisive hierarchical clustering analyses.

Item	ENV1	ENV2
<b>Environmental descriptors</b>		
Climate		
Tropical zone, monsoon (Am)	0	5
Tropical zone, savannah (Aw)	10	18
Temperate zone, without dry season, hot summer (Cfa)	12	6
Temperate zone, dry winter, hot summer (Cwa)	8	1
Soil classification		
Orthic Acrisols (Ao)	3	6
Ferric Acrisols (Ap)	1	0
Acric Ferralsols (Fa)	4	3
Orthic Ferralsols (Fo)	4	6
Rhodic Ferralsols (Fr)	5	3
Xanthic Ferralsols (Fx)	0	2
Luvic Phaeozems (Hl)	0	2
Lithosols (I)	0	1
Ferric Luvisols (Lf)	3	2
Ferralic Arenosols (Qf)	7	3
Dystric Planosols (Wd)	1	0
Eutric Planosols (We)	2	2
Elevation, mean $\pm$ SD	349 $\pm$ 151	251 $\pm$ 143
<b>Farm management descriptors<sup>1</sup></b>		
<i>General information</i>		
Enrolled years at Embrapa-Genepplus		
1996-2000	6	3
2001-2005	3	3
2006-2010	7	6
2011-2015	6	7
2016-2020	8	11
Livestock land area		
Large	20	14

Item	ENV1	ENV2
Medium	8	14
Small	2	2
Production system		
Crop-Livestock	9	0
Grazing	21	30
<i>Soil management</i>		
Period of use established pasture		
5	7	1
10	12	15
15	5	6
20	6	8
Native grasslands		
No	24	24
Yes	6	6
Tillage		
No	11	11
Yes	19	19
No-till farming		
No	15	26
Yes	15	4
Contour farming		
No	3	28
Yes	27	2
Crop rotation		
No	7	25
Yes	23	5
Pasture recovery and renewal		
No	6	10
Yes	24	20
Fertilization		
No	1	20
Yes	29	10

Item	ENV1	ENV2
Irrigation		
No	27	30
Yes	3	0
Natural resource conservation		
No	13	17
Yes	17	13
<i>Supplemental feeding</i>		
Mineral	9	15
Mineral and urea	4	3
Protein	8	9
Protein-energy	9	3
<i>Reproduction management</i>		
Breeding season		
No	0	0
Yes	30	30
Period of the breeding season		
Length of the breeding season		
Long	18	11
Short	12	19
Reproduction technique		
Natural service (exclusively)	1	0
Fixed-time artificial insemination (FTAI) and herd bulls	2	5
FTAI, resynchronization protocols, and herd bulls	27	25
In vitro fertilization		
No	8	23
Yes	22	7
Age of heifer		
12 – 14 mo	15	6
16 – 18 mo	4	6
20 – 22 mo	4	5
24 – 26 mo	7	13
Weight of heifer		

Item	ENV1	ENV2
$\leq 300$ kg	12	10
301 – 329 kg	10	6
330 – 359 kg	2	9
360 – 389 kg	6	2
$\geq 390$ kg	0	3

1. For privacy reasons, information concerning animal breeding technicians has been omitted.

**Table 4.** Estimates and standard errors of (co)variance components, within-farm heritability, and genetic correlation ( $r_{g_1g_2}$ ) for evaluated traits measured in Nellore cattle raised under two environmental conditions.<sup>1</sup>

Trait	Additive genetic (co)variances			Farm variances		Residual variances		Within-farm Heritability		$r_{g_1g_2}$
	ENV1	ENV2	$\sigma_{a_1a_2}$	ENV1	ENV2	ENV1	ENV2	ENV1	ENV2	
YW, kg	811.36 ± 20.7	490.26 ± 16.9	235.20 ± 31.7	1,085.8 ± 286.7	1,173.6 ± 310.0	1,322.6 ± 14.1	1,084.3 ± 12.6	0.38 ± 0.02	0.31 ± 0.02	0.37 ± 0.05
SC, cm	4.83 ± 0.20	3.94 ± 0.21	3.50 ± 0.21	3.96 ± 1.06	3.92 ± 1.07	5.47 ± 0.14	5.16 ± 0.15	0.47 ± 0.03	0.43 ± 0.03	0.80 ± 0.04
AFC, days	3,349 ± 244	4,414 ± 285	1,176 ± 350	1,107 ± 313	3,406 ± 955	20,885 ± 232	19,451 ± 256	0.14 ± 0.01	0.18 ± 0.01	0.31 ± 0.09
REA, cm <sup>2</sup>	28.36 ± 1.56	18.07 ± 1.76	14.25 ± 2.07	31.10 ± 11.26	48.04 ± 21.71	48.47 ± 1.11	35.25 ± 1.37	0.37 ± 0.03	0.34 ± 0.05	0.62 ± 0.08
FAT, cm	0.239 ± 0.020	0.053 ± 0.074	0.099 ± 0.012	0.695 ± 0.250	0.095 ± 0.043	1.068 ± 0.017	0.264 ± 0.007	0.18 ± 0.02	0.17 ± 0.02	0.88 ± 0.07
MARB, %	0.206 ± 0.012	0.160 ± 0.014	0.172 ± 0.012	0.015 ± 0.007	0.076 ± 0.037	0.320 ± 0.009	0.281 ± 0.011	0.39 ± 0.02	0.36 ± 0.03	0.95 ± 0.04

1. YW = yearling weight, SC = scrotal circumference, AFC = age at first calving, REA = ribeye area, FAT = backfat thickness and MARB = marbling score. Farm and residual covariances for all traits are equal to zero since evaluated animals have no performance records in both EC (they remain on the unique farm and EC throughout their life).

**Table 5.** Spearman correlations for estimated breeding values (EBV) of bulls between two environmental conditions, obtained using either BLUP or ssGBLUP for each evaluated trait measured in Nellore cattle.<sup>1</sup>

<b>Trait</b>	<b>N</b>	<b>BLUP</b>	<b>ssGBLUP</b>
YW, kg	482	-0.0354	0.0859
SC, cm	298	0.0470	0.0993
AFC, days	366	0.1295	-0.0061
REA, cm <sup>2</sup>	111	0.1739	0.0401
FAT, cm	111	0.2108	0.0537
MARB, %	102	0.2261	0.3881

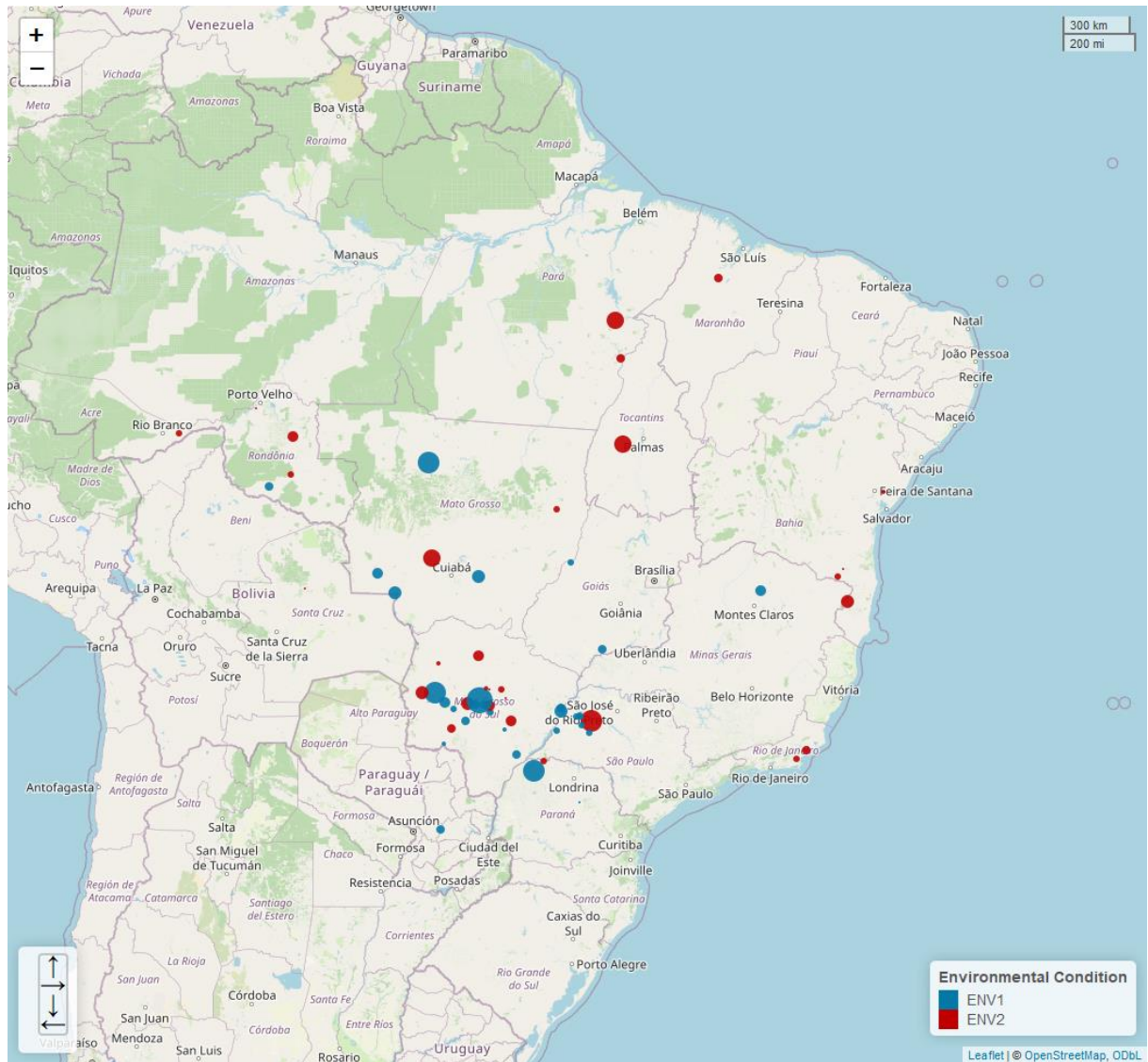
1. YW = yearling weight, SC = scrotal circumference, AFC = age at first calving, REA = ribeye area, FAT = backfat thickness and MARB = marbling score. N = Number of bulls. Only bulls with, at least, 5 recorded offspring in each environment per trait.

**Table 6.** The percentage of common bulls for estimated breeding values (EBV) between two environmental conditions ranked as 5% (TOP5%), 10% (TOP10%), and 25% (TOP25%), obtained using either BLUP or ssGBLUP for each evaluated trait measured in Nellore cattle.<sup>1</sup>

	TOP5%			TOP10%			TOP25%		
	N	BLUP	ssGBLUP	N	BLUP	ssGBLUP	N	BLUP	ssGBLUP
YW, kg	24	33.3	50.0	48	54.2	50.0	120	53.3	62.5
SC, cm	15	60.0	53.3	30	73.3	70.0	74	75.7	79.7
AFC, d	18	11.1	22.2	37	18.9	18.9	92	44.6	43.5
REA, cm <sup>2</sup>	6	50.0	66.7	11	63.6	63.6	28	67.9	71.4
FAT, cm	6	83.3	83.3	11	90.9	100	28	78.6	85.7
MARB, %	5	80.0	100.0	10	80.0	80.0	26	96.1	96.2

1. YW = yearling weight, SC = scrotal circumference, AFC = age at first calving, REA = ribeye area, FAT = backfat thickness and MARB = marbling score. N = Number of bulls. Only bulls with, at least, five recorded offspring in each environment per trait.

## Figures



**Figure 1** – Geographical location of farms colored by environmental conditions assessed by divisive hierarchical clustering and sized by the number of recorded animals.

## CHAPTER 4

### GENERAL CONCLUSIONS

#### 4.1. Conclusions

Na extensive farm-level analysis revealed seven environmental (SOIL and ELE) and farm management descriptors (TEC, YEN, NTI, PBS, and RTC) as deemed important to better describe the macro-environmental effects contributing to variation across farms. Among them, TEC and NTI were directly or indirectly associated with several descriptors of soil, supplemental feeding, and reproduction management. These findings reveal the real source of environmental variation commonly accounted for by CG in the genetic evaluations.

This suitable characterization of environmental factors was important in the context of GxEI conditions. In this study, we also identified two distinct EC based on farm-level environmental and management descriptors at Nellore cattle-rearing locations. The estimates of genetic parameters within these EC provided evidence for GxE affecting AFC, YW, and REA traits in Nellore cattle. The low Spearman's correlations observed for EBV obtained using either BLUP or ssGBLUP method reinforce the presence of GxE at some level for all evaluated traits, mainly those indicated by low genetic correlation. The top-ranking bulls (TOP5%) demonstrated more susceptibility to re-ranking for AFC, YW, and REA in either BLUP or ssGBLUP. These findings highlight the importance of incorporating environmental factors into genetic evaluations to enhance the robustness of selection decisions and increase genetic gains.