



OPEN Factor analytic selection tools and environmental feature-integration enable holistic decision-making in *Eucalyptus* breeding

Saulo F. S. Chaves¹, Michelle B. Damacena², Kaio Olimpio G. Dias³,
Caio Varonill de Almada Oliveira⁴ & Leonardo L. Bhering³✉

Understanding the genotype-by-environment interaction (GEI) and considering it in the selection process is a *sine qua non* condition for the expansion of Brazilian eucalyptus silviculture. This study's objective is to select high-performance and stable eucalyptus clones based on a novel selection index that considers the Factor Analytic Selection Tools (FAST) and the clone's reliability. The investigation explores the nuances interplay of GEI and extends its insights by scrutinizing the relationship between latent factors and real environmental features. The analysis, conducted across seven trials in five Brazilian states involving 78 clones, employs FAST. The clonal selection was performed using an extended FAST index weighted by the clone's reliability. Further insights about GEI emerge from the integration of factor loadings with 25 environmental features through a principal component analysis. Ten clones, distinguished by high performance, stability, and reliability, have been selected across the target population of environments. The environmental features most closely associated with factor loadings, encompassing air temperature, radiation, and soil characteristics, emerge as pivotal drivers of GEI within this dataset. This study contributes insights to eucalyptus breeders, equipping them to enhance decision-making by harnessing a holistic understanding from the genotypes under evaluation to the diverse environments anticipated in commercial plantations.

Keywords Genotype-by-environment interaction, Factor analytic mixed models, tree breeding, reliability, environmental features

Brazilian silviculture is continuously growing. In 2022, the production value in silviculture increased by 14.9%, setting new national records, as reported by the Brazilian Institute of Geography and Statistics (IBGE). IBGE data also revealed that the planted forests' total area exceeds 9.5 million hectares, with a substantial 77% of this area dedicated to species from the *Eucalyptus* genus. Ensuring a sustainable and secure expansion of eucalyptus-planted forests necessitates the identification of clones adapted to environmental changes. These clones must be capable of withstanding various challenges posed by marginal environments, including factors such as drought, frost, poor soil quality (whether chemical or physical), and unfavourable weather conditions for optimal tree growth^{1,2}. This crucial task is typically achieved through rigorous testing of selection candidates in multi-environment trials (MET). These trials must be strategically installed in environments that accurately represent the conditions that clones may encounter in commercial plantations. In other words, MET should properly sample the genotype-by-environment interaction (GEI), the phenomenon that dictates the differential behavior of clones in response to different environmental stimuli³.

There are two main types of GEI: Scale-type, also known as simple or non-crossover, where changes in performance do not affect genotype ranking; and Rank-type, also called complex or crossover, where the opposite is true^{4,5}. Managing GEI is crucial, especially in situations where it is rank-type, as it requires statistical solutions that not only isolate these effects but also incorporate them into the selection process. Factor Analytic (FA)

¹Federal University of Viçosa, Department of Agronomy, Viçosa, MG, Brazil. ²Bracell MS Florestal, Campo Grande, MS, Brazil. ³Federal University of Viçosa, Department of General Biology, Viçosa, MG, Brazil. ⁴ArborGen Tecnologia Florestal, Bom Despacho, MG, Brazil. ✉email: leonardo.bhering@ufv.br

mixed models provide these solutions. This method was developed as an alternative to multivariate models and a mixed model counterpart to AMMI (Additive Main Effects and Multiplicative Interaction)^{6–9}. The core idea is to reduce dimensionality to a certain number of latent covariates (the factors) by leveraging the covariance between environments intrinsic to these factors¹⁰. FA considers genotypic heteroscedasticity and predicts a candidate's performance in an untested environment. For its mixed model framework, it successfully deals with unbalanced data and can leverage kinship or molecular information¹¹. Furthermore, Factor Analytic Selection Tools (FAST)¹² provide straightforward alternatives for precise decision-making in the search for high-performance and/or stable genotypes.

Factor analytic models primarily focus on understanding the “genotype” portion of GEI. However, an alternative approach to explore interaction dynamics is to examine the “environment” portion using data from environmental features. This paradigm has been evolving since the early '70s but gained significant traction in the last decade due to improved computational resources^{13–17}. The comprehensive approach involves integrating FA models with environmental information, bridging the “genotype” and “environment” aspects of GEI. This integration combines real environmental covariates with latent environmental covariates (the factors), offering a powerful tool for both prediction and inference^{2,18,19}. This integrated approach has proven beneficial in various contexts, such as defining breeding zones, studying genotypic responses to climatic changes, exploring the intricate relationship between genomics and environmental data and predicting the genotypic performance to new, untested environments^{18,19}. In the specific case of eucalyptus breeding, studies like that of Callister et al.² used FA models integrated with genomics and environmental data to delineate breeding zones for *Eucalyptus globulus* Labill. Another example of usage is reported by Costa e Silva et al.²⁰, who investigated how eucalyptus genotypes are influenced by changes in weather-related environmental features by regressing genotypic values onto climatic variables. Such integrated approaches hold promise for advancing our understanding of the complex interplay between genetics and environmental factors in tree breeding programs.

This study presents a unique application of the FAST methodology in the context of eucalyptus breeding. Notably, we extended FAST by integrating it with a candidate's reliability. This enhancement aimed to select eucalyptus clones with high performance, stability, and high-quality information, facilitating targeted recommendations across diverse environments and decreasing the risk of a flawed decision. Additionally, we delved into the dynamics of GEI by examining the relationship between known and latent environmental covariates. To achieve this, we adapted the methodology outlined by Bakare et al.²¹, integrating the outcomes of the FA model with environmental features in a single partial least squares regression.

Results

Single-environment trial analyses

The genotypic variance constituted the major portion of the total variance in all environments but E1 and E5 (Fig. 1A). Furthermore, the genotypic effects were significant in all analysed environments. Thirty-three distinct clones were among the top ten selections in individual environments, with clones C04 and C13 being the only ones consistently chosen across all environments (Fig. 1B).

FA outcomes

Model selection

The Akaike Information Criterion (AIC) exhibits minimal changes with the number of factors. Subtle increases in explanatory power are observed from FA3 onward. FA3, with an explanatory power of 87%, was selected as the model for further analysis (Fig. 2A). In this model, the first factor predominantly explained the variance in all environments except E6, where the second factor played a more prominent role. The contribution of the third factor was minor across all environments except E1 and E7 (Fig. 2B). The factor loadings of each environment in each of the chosen model's three factors are in the Supplementary Material (Table S1)

Heritability and pairwise genotypic correlations

The heritability varied from 0.65 to 0.72, and the coefficient of variation (CV) ranged from 0.04 to 0.12 (Fig. 3A), indicating good experimental precision. Genotypic correlations between environments ranged from 0.33 to 0.92, with E6 showing the most significant deviation from its peers. The closest relationship was observed between E5 and E3 (Fig. 3B).

Selection

Using the selection index, we selected the top ten clones for global performance and stability across environments (Fig. 4A), namely C13, C04, C03, C34, C16, C22, C27, C02, C33, and C17. These clones meet the three criteria considered for building the index: they have high global performance, can keep it acceptably high across environments, and have trustworthy information. Note that all selected clones beat the two commercial checks. The two clones that were consistently selected in all individual analyses were also selected by the index (C13 and C04). Notably, C13 is more stable than C04, as evidenced by the lower RMSD of C13, and the steeper slope of C04 in the latent regression plots of the second and third factors (Fig. 4B). The selection of these clones will provide an expected gain of 8.30%.

Environmental drivers of the GEI

Five components were selected for the partial least squares regression (PLSR) model, which explained over 90% of the total variance. The PLSR biplot (considering the first two components) revealed that features like TMAX, TMEAN, SPV, and HIRI are highly associated with the first factor, while PH, BDOD, ALT, TRANGE and CLAY are linked to the second factor (Fig. 5A). Notably, FA3 does not show substantial influence from any specific

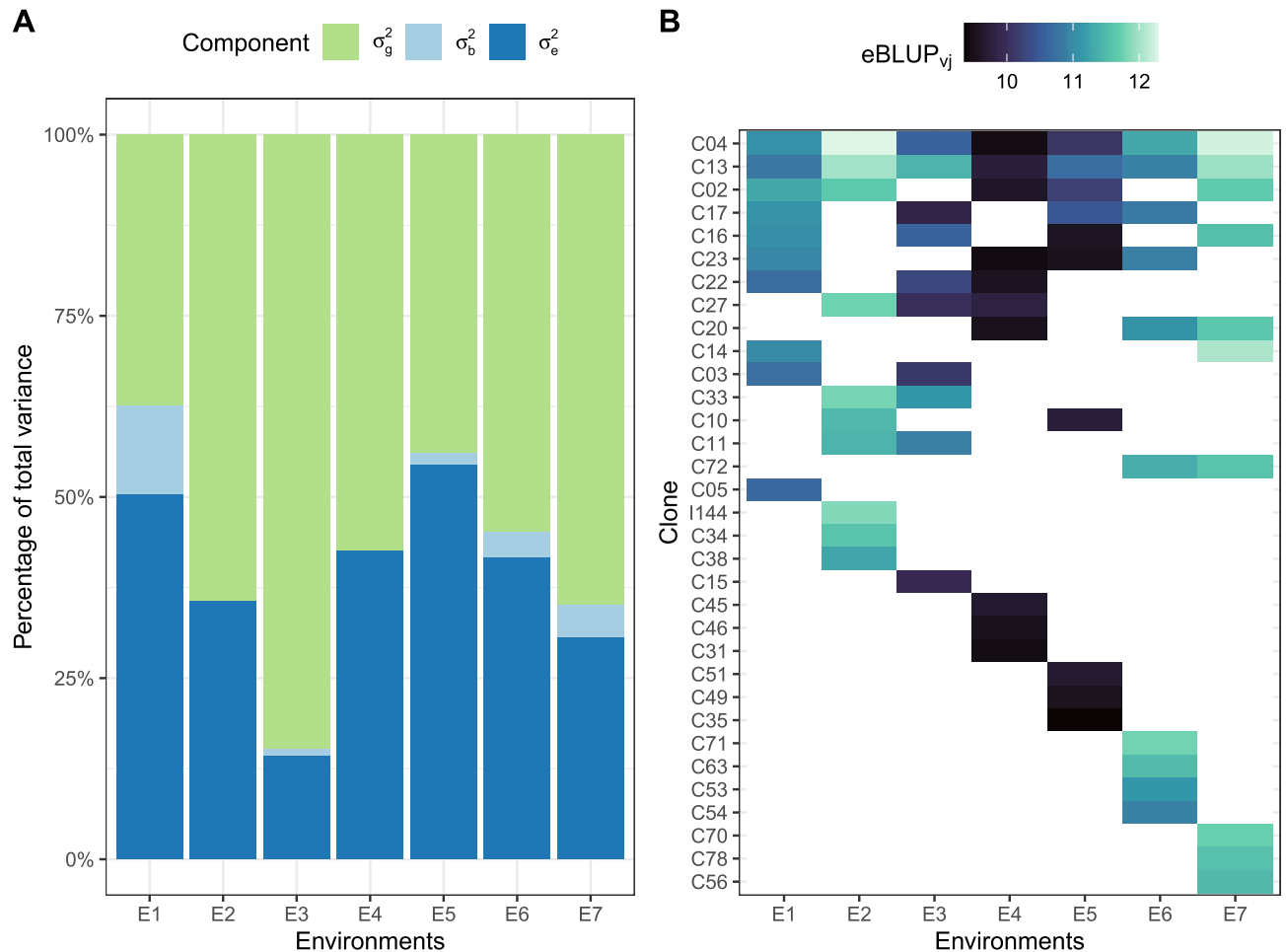


Figure 1. Results of the individual analyses per environment: **(A)** percentage of each variance component attributed to the total variance; and **(B)** performance of the top ten clones in each environment. In **(A)**, the genotypic variance was significant in all environments. In **(B)**, a blank cell indicates that the clone in the y -axis was not selected in the x -environment.

environmental feature, despite being closer to RH2M. Among the tested features, VPD, RH2M, CLAY, SAND, SPV and temperature-related features play crucial roles in driving GEI in the dataset. The spatial arrangement of environments in Fig. 5B shows how they are related based on the GEI and the environmental features. E6 and E5 seem to be the most different environments. In fact, E5 is the most geographically distant (see Fig. 7), and E6 has a marked drought period and was the most different regarding explanation dynamics in the FA models.

Discussion

This study establishes the efficacy of FAST for the selection and recommendation of eucalyptus clones across diverse environments. A novel aspect of this approach is the integration of FAST with the clone's reliability, introducing an additional criterion-information quality-in the decision-making process. Moreover, our investigation focuses on the environmental determinants of GEI by exploring the relationship between latent factors and actual environmental features, identifying the most influential factors driving differential phenotypic expression across environments.

When addressing GEI, two approaches come into play. The first entails an environment-specific strategy, focusing on recommendations to each environment based on individual analyses' outcomes, as depicted in Fig. 1. While optimal, this approach is often impractical due to financial constraints, making it challenging to run breeding programs for each environment separately. The second option involves leveraging biometrical solutions to consider data from all environments simultaneously and incorporate GEI into the decision-making process. Here, the objective is to identify candidates with consistently high and stable performance across all trials, as illustrated in Fig. 4. Factor analytic models are a gold standard method for implementing the latter alternative^{7,8,22}. This study outlines a recommended pipeline for eucalyptus breeders utilizing FA models: (1) initiate the process by selecting an appropriate model, determining the optimal number of factors based on explicative power (Fig. 2); (2) employ the selected model to explore experimental precision and the nature of GEI within the dataset (Fig. 3); and (3) utilize FAST for clonal selection, enabling a comprehensive assessment of high-performance and stability across diverse environments. Furthermore, breeders can compare selected clones' behaviour across environments with commercial checks using latent regression plots (Fig. 4).

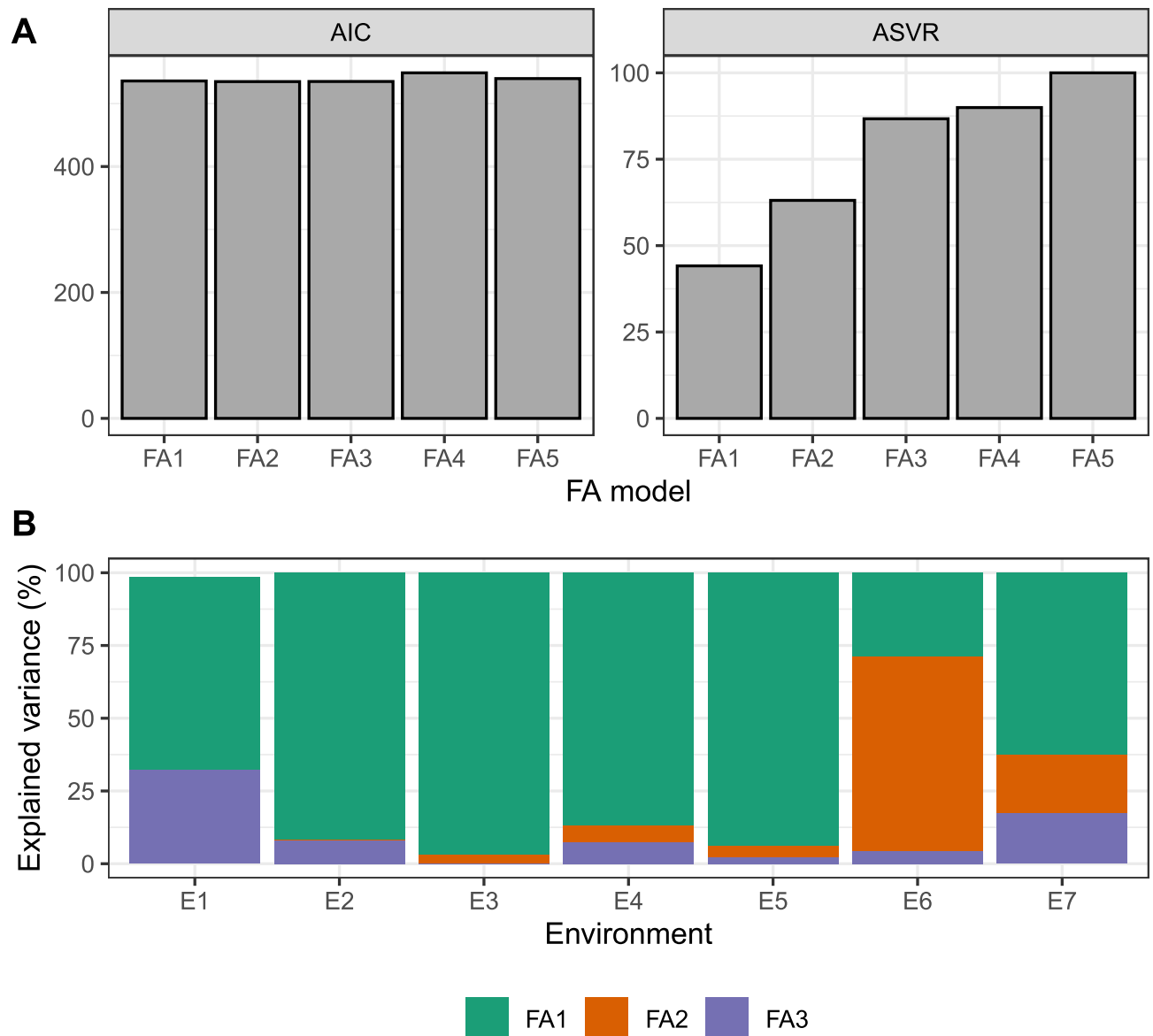


Figure 2. Selection of the proper number of factors for the FA model: (A) Akaike information criterion (AIC, left plot) and average semivariates ratio (ASVR, right plot), and (B) explained variance per factor and environment of the selected model (FA3).

The variability observed in genotypic correlations between environments underscores the nuanced nature of GEI in the dataset. While many correlations are positive and high (> 0.7), suggesting subtle changes in clonal performance in terms of genotypic value, breeders must not overlook the presence of GEI. The information provided in Fig. 1 emphasizes that the majority of selected clones differ across environments. This highlights that even subtle changes can impact clonal selection, and recommending suboptimal candidates may result in financial setbacks in eucalyptus silviculture. Selecting a low-performing clone over a promising one can have repercussions for at least seven years, the number of years to reach rotation age in commercial plantations. Environment E6 (Bocaiúva-MG) stood out as the location where clones exhibited the most divergent responses. Notably, it was the only environment in which the second factor held the highest explicative power (Fig. 2) and was somewhat poorly related to the other environments in the partial least squares regression (Fig. 5B). This specific site is characterized by a substantial temperature range and a distinct period with minimal precipitation, making it a preferred choice for testing clones for drought tolerance^{23,24}. The unique conditions of E6 likely contribute to the distinct behaviour observed in the second factor and the heightened variability in clonal responses.

The relationship illustrated in Fig. 3B represents the manifestation of genotypic responses to environmental influences. We integrated these responses with the actual environmental features of each environment to evaluate the environmental drivers of GEI in the dataset and establish a comprehensive relationship between environments (Fig. 5). Some crucial environmental features have been extensively discussed in the literature. Queiroz et al.²⁴ in Brazil found that temperatures between 6 °C and 31 °C are generally favourable for tree growth, but the optimum temperature range varies depending on the species or hybrid. For example, the most planted hybrid

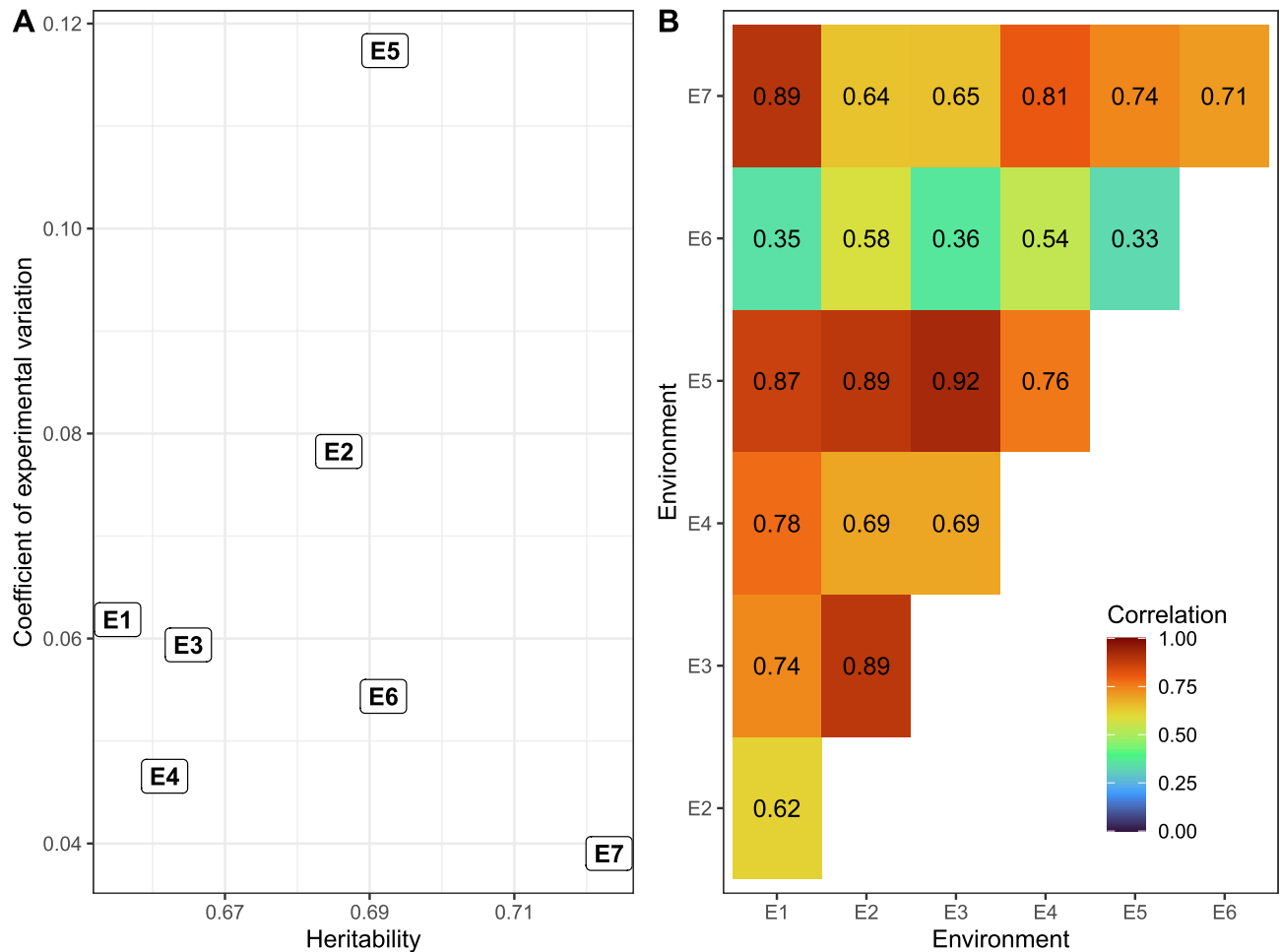


Figure 3. (A) The biplot illustrates the heritability (x-axis) and coefficient of experimental variation (in decimal scale, y-axis) for each environment. (B) The heatmap displays the pairwise correlation between environments. In the upper triangle, genotypic correlations are presented, while the lower triangle exhibits correlations derived from the relationship between environments based solely on environmental features.

in Brazil, *E. grandis* × *E. urophylla*, thrives in tropical conditions and requires higher temperatures for optimal growth. Mean temperature values outside this range can potentially damage eucalyptus through impacts on the photosynthetic apparatus and alterations in internal water relations, often associated with heatwaves, droughts, or frosts^{25–27}. Temperature changes are also correlated with shifts in latitude—approaching zero latitude tends to increase mean temperatures; and altitude—higher altitudes usually have lower temperatures. In the context of climate change, Elli et al.¹ identified temperature as a critical factor, projecting potential reductions in tree growth for plantations in the Brazilian Center-North region (latitudes closer to zero). Figure 5A also revealed an important role of features related to water relations (VPD and RH2M) and soil-related features. The relevance of these features evidences the susceptibility of eucalyptus forests to changes in water availability in both soil and atmosphere^{28–30}. It justifies the ongoing efforts in breeding eucalyptus for drought tolerance. It is noteworthy that the PLSR-FA integration, although recent, has been contributing significantly to understanding the relationship between GEI and real environmental variables, as outlined in Bakare et al.²¹ and Araújo et al.¹⁹.

The discussion addressed in the previous paragraph alert to a concerning scenario for plant breeding. According to the last report of the Intergovernmental Panel on Climate Change, the last fifty years had the most steep increase in temperatures in the last 2000 years³¹. Particularly in Brazil, droughts and heat waves are becoming more frequent^{32,33}. Given this fact, plant breeders should focus on developing genotypes that can keep performing acceptably whilst enduring extreme conditions. This is specially important for forest species, which stay in the field for several years (even decades). Breeding efforts are a must for reaching sustainable forestry. In this sense, enviromics initiatives are an important ally to appropriately address the genotype-by-environment interaction from both “genotype” and “environment” frameworks, instead of focusing only on the “genotype” as it is usually done^{2,19,34}.

The complexities arising from genotype-environment interactions underscore the importance of selecting stable candidates to mitigate financial risks. Poor decisions can lead to substantial investments in low-performing clones, making the selection of stable, high-performing candidates crucial for forestry companies operating in diverse environments. By opting for stable candidates, the number of clones needed for clonal seedling production is reduced, streamlining nursery processes and enhancing efficiency in large-scale projects. This not only

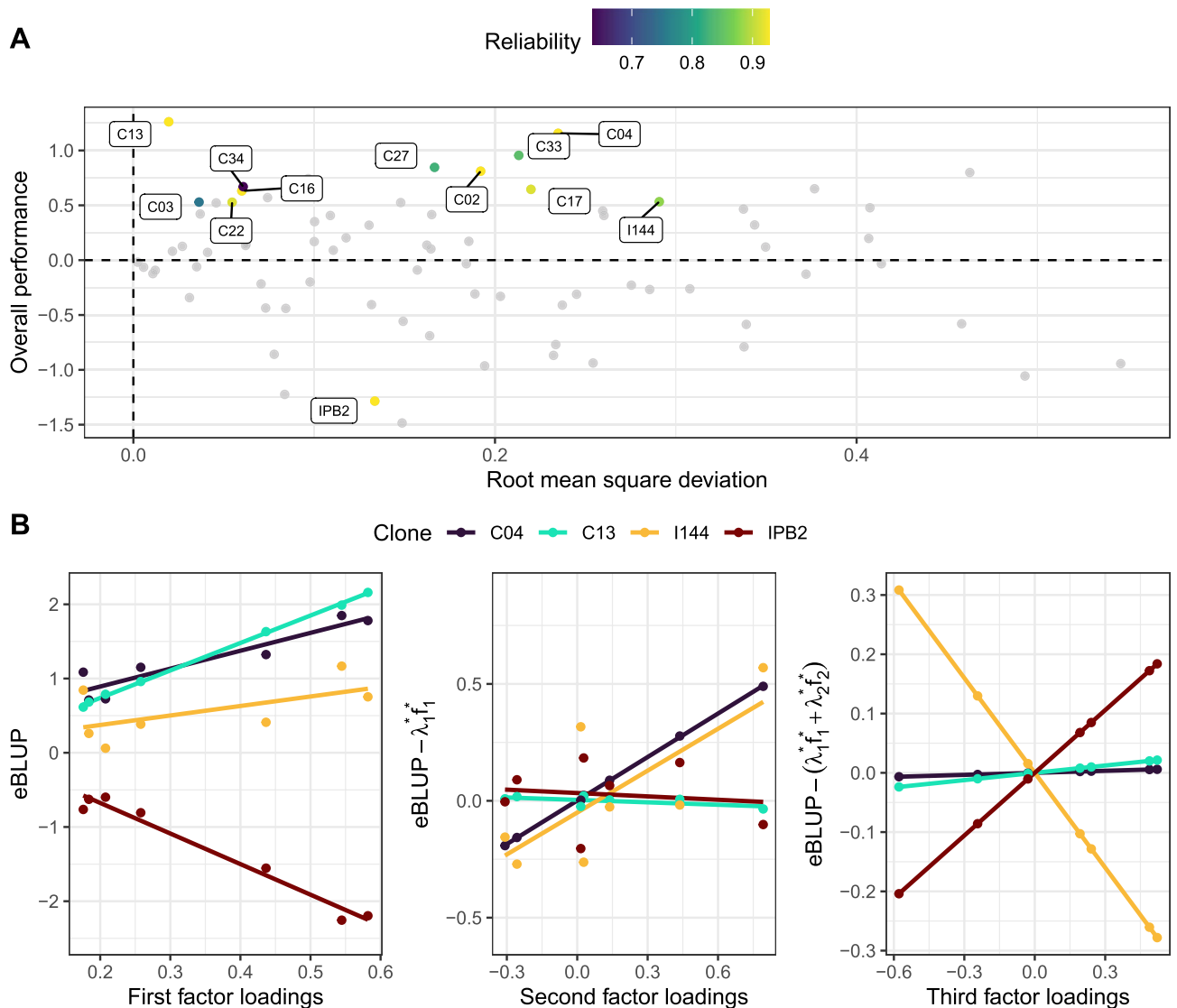


Figure 4. Overall performance vs root mean squared deviation (A), and latent regression plots comparing two top performers (C04 and C13) and two commercial checks (I144 and IPB2) (B). In (A), the higher the overall performance (or the more distant from zero in the y-axis), the better. Stable clones have low root mean squared deviation (global) (or closer to zero in the x-axis).

optimizes resource utilization but also facilitates a more adaptive response to climate change, a key element for sustainability and long-term success in the forestry sector. The selection process resulted in the identification of 10 high-performing clones with acceptable stability potential, outperforming both commercial checks. Notably, the clones outperformed I144, the most planted clone in Brazil, which validates their potential. With reliability exceeding 0.8 for all clones except C34, the selection was based on high-quality information.

Considering reliability becomes crucial due to the varied sampling of each clone across the trial network, as illustrated in Fig. 6. For instance, consider clone C50, which was only tested in environment E5. Since we did not have kinship information, the FA model will predict the performance of this clone in environments where it was not tested based on its performance in E5 and the covariance between this environments and the others^{35,36}. In a scenario where C50 performed exceptionally well, it would probably be selected in the FAST index. However, relying on C50 for recommendations to other environments entails risks. These environments might lack the specific factors present in E5 that contributed to C50's superior performance. In contrast, clone C13, tested and selected in all environments, exhibited consistent performance superior to commercial checks. With high reliability, the risk of C13 performing poorly in other environments is minimized. By incorporating the clones' reliability into the FAST index, the decision-making process is more robust, accounting for potential risks and ensuring informed selections³⁷. Enhancing the reliability of clone *per se* sampling is not solely dependent on direct evaluations. Utilizing kinship matrices, whether derived from pedigree or genomics, offers an avenue to capitalize on information from related clones, thereby refining allele sampling³⁸. Additionally, employing models that account for genetic interactions within the trial contributes to isolating a pure genotypic value, unburdened by indirect genetic effects³⁹. It is noteworthy that various methods are available to address risk in

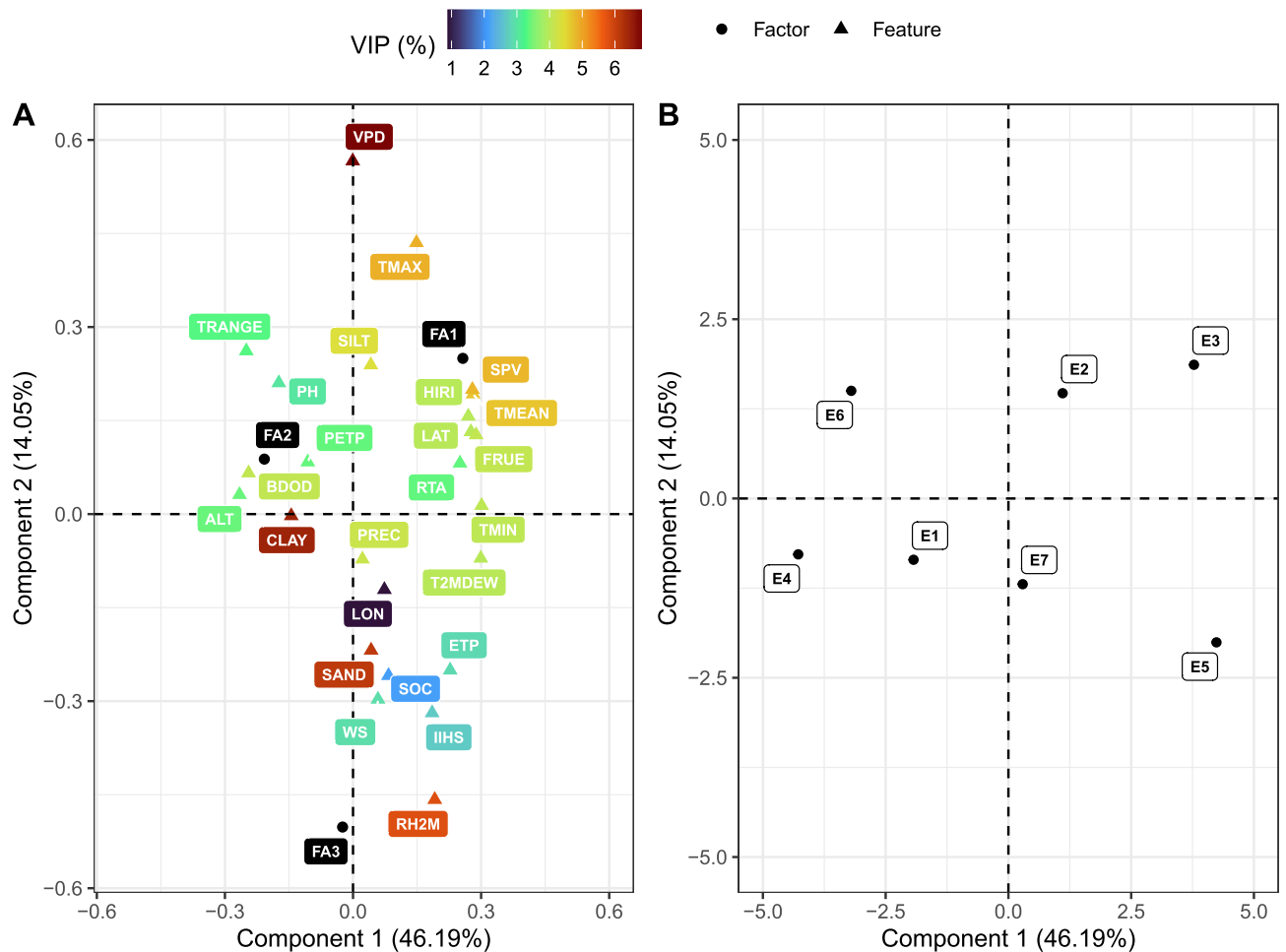


Figure 5. Results of partial least squares regression: (A) relationship between real (features) and latent (factors) environmental covariates (biplot of the predictors' and responses' loadings considering the first two components); and (B) relationship between environments based on both environmental features and factors (biplot of predictors' scores considering the first two components). FA1, FA2 and FA3 are the first, second and third factors, respectively. For the environmental features' acronyms, see Table 1. In (A), colour scale represents the variable importance in projection (VIP), in percentage, of each environmental feature.

plant breeding. For instance, the approach proposed by Dias et al.⁴⁰ harnesses the probabilistic foundation of the Bayesian framework, providing a comprehensive strategy to navigate uncertainties in the breeding process.

Methods

The dataset encompasses seven advanced clonal tests conducted in five Brazilian states (see Fig. 7). The clones used in these trials originate from breeding programs of various pulp companies located in different regions of Brazil, meaning they were tested and selected for a specific environmental range. ArborGen[®], the owner of the analyzed dataset, is a company that sells genetic material from both its own breeding program and partner companies. The objective of these trials was to evaluate the adaptation of tested clones to environmental conditions different from those in which they were initially tested. For confidentiality reasons, the clones' identifications have been coded. Only the two commercial checks, IPB2 and I144, retained their original identification as they are public domain. Most of the clones were *E. grandis* × *E. urophylla* hybrids, with some being pure *E. grandis* or *E. urophylla* (see Supplementary Material Table S2). The trials serve as representatives of diverse environmental conditions that clones may encounter in commercial plantations. Some environments are particularly critical: E1 and E6 are more prone to drought, while E2 is characterized by high heat and humidity. E5 uniquely represents the Northeastern region, and E3 the Northern region. Furthermore, four out of six biomes are represented in our dataset. Installed between February 2019 and February 2020, each trial was laid out in a randomized complete blocks design, featuring four repetitions and thirty-six plants per plot. Eight clones are consistent across all trials. The dataset exhibits a 46% connectivity (see Fig. 6). In this study, "trial" and "environment" are used interchangeably.

We measured the diameter at breast height (DBH) when the trees were 20 ~ 30 months old. It is important to note that all trees within a specific trial were measured at the same age, although the ages varied among different trials. The DBH was measured using a diametric tape.

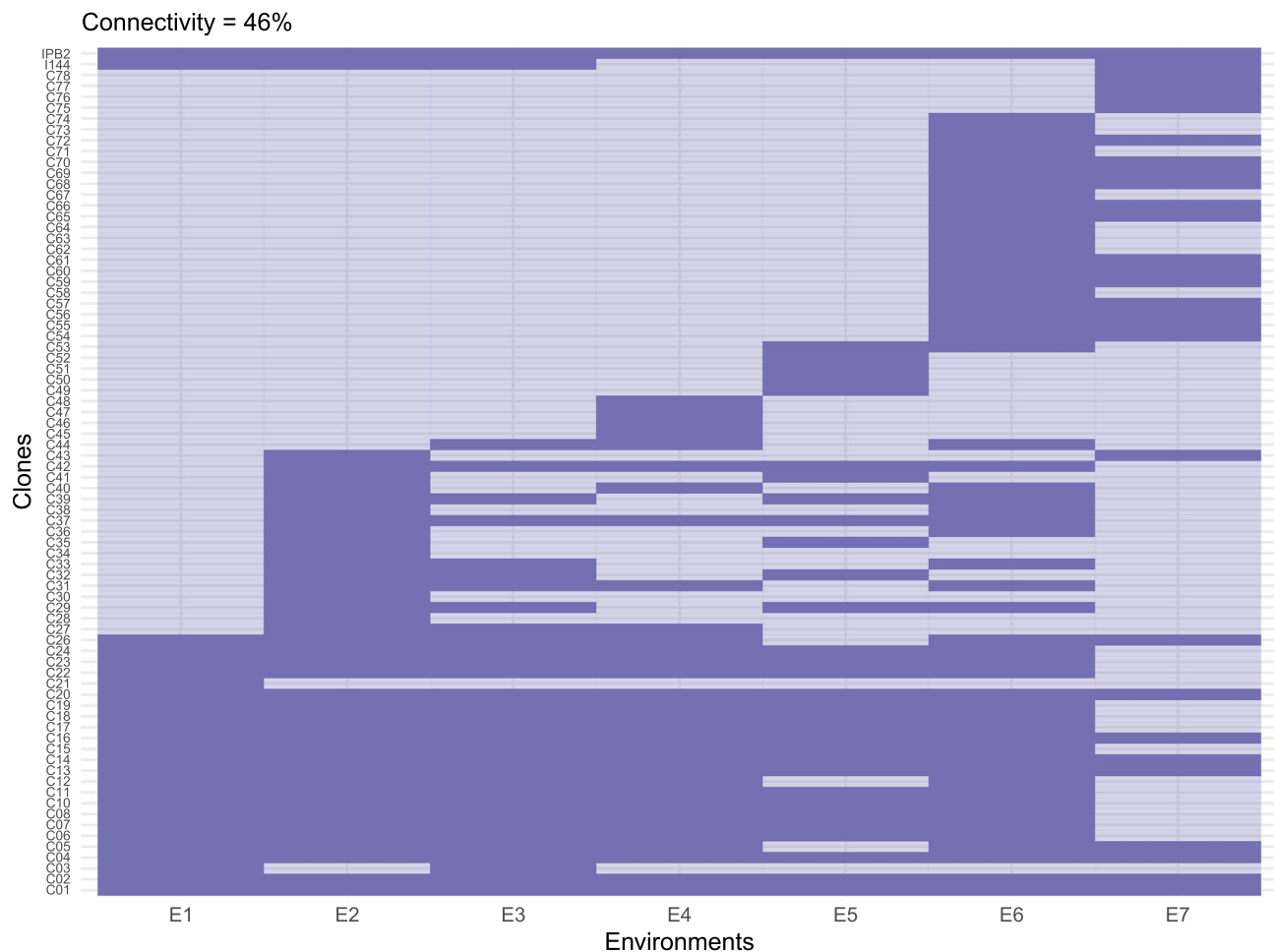


Figure 6. Heatmap depicting the connectivity in the dataset. Intense-coloured cells indicate the presence of the clone of the y-axis in the trial of the x-axis, and light-coloured cells, the absence. This heatmap was generated using the ggplot2 package, v. 3.5.1 (<https://ggplot2.tidyverse.org/articles/ggplot2.html>).

Environmental features

Utilizing coordinates (latitude and longitude) and information on sowing and data collection dates, we gathered data on 25 environmental features (refer to Table 1). Features pertaining to weather and climate throughout the established period (daily records) were obtained using the `EnvRtype` package⁴¹ in the R software environment version 4.3.2⁴². This package serves as a user-friendly tool for retrieving features from the NASAPOWER database⁴³. Additionally, soil-related features were acquired as rasters from `SoilGrids`⁴⁴ and processed using the `raster` package in R⁴⁵.

Statistical analyses

We used the mean DBH across plants within plots. In the mathematical notation below, V is the number of clones ($v = 1, 2, \dots, V$), J is the number of environments ($j = 1, 2, \dots, J$), R is the number of replicates ($r = 1, 2, \dots, R$), and N is the number of phenotypic observations, with $N = \sum_{j=1}^J N_j$, with N_j being the number of observations per environment. This distinction is necessary since the trials have different sizes. We performed all analyses under the linear mixed model framework, where the residual maximum likelihood⁴⁶ is used to estimate the variance components. These are necessary for predicting the best linear unbiased predictions (BLUPs) using Henderson's mixed model equation^{47,48}. These analyses were performed in the `ASReml-R` package⁴⁹.

Single-trial analyses

First, we fitted the following linear mixed model for single-trial analysis:

$$\mathbf{y} = \mu \mathbf{1} + \mathbf{Z}_1 \mathbf{b} + \mathbf{Z}_2 \mathbf{g} + \boldsymbol{\varepsilon} \quad (1)$$

where $\mathbf{y}$ is a $N_j \times 1$ vector of phenotypic records, μ is the model intercept, connected to $\mathbf{y}$ by a $N_j \times 1$ vector of ones; $\mathbf{b}$ is the vector of block random effects [$\mathbf{b} \sim N(\mathbf{0}, \sigma_b^2 \mathbf{I}_R)$], accompanied by its $N_j \times R$ incidence matrix $\mathbf{Z}_1$; $\mathbf{g}$ is the $V_j \times 1$ vector of random genotypic effects [$\mathbf{g} \sim N(\mathbf{0}, \sigma_g^2 \mathbf{I}_{V_j})$], connected to $\mathbf{y}$ by its $N_j \times V_j$ design matrix $\mathbf{Z}_2$; and $\boldsymbol{\varepsilon}$ is the $N_j \times 1$ vector of random residual effects [$\boldsymbol{\varepsilon} \sim N(\mathbf{0}, \sigma_\varepsilon^2 \mathbf{I}_{N_j})$].

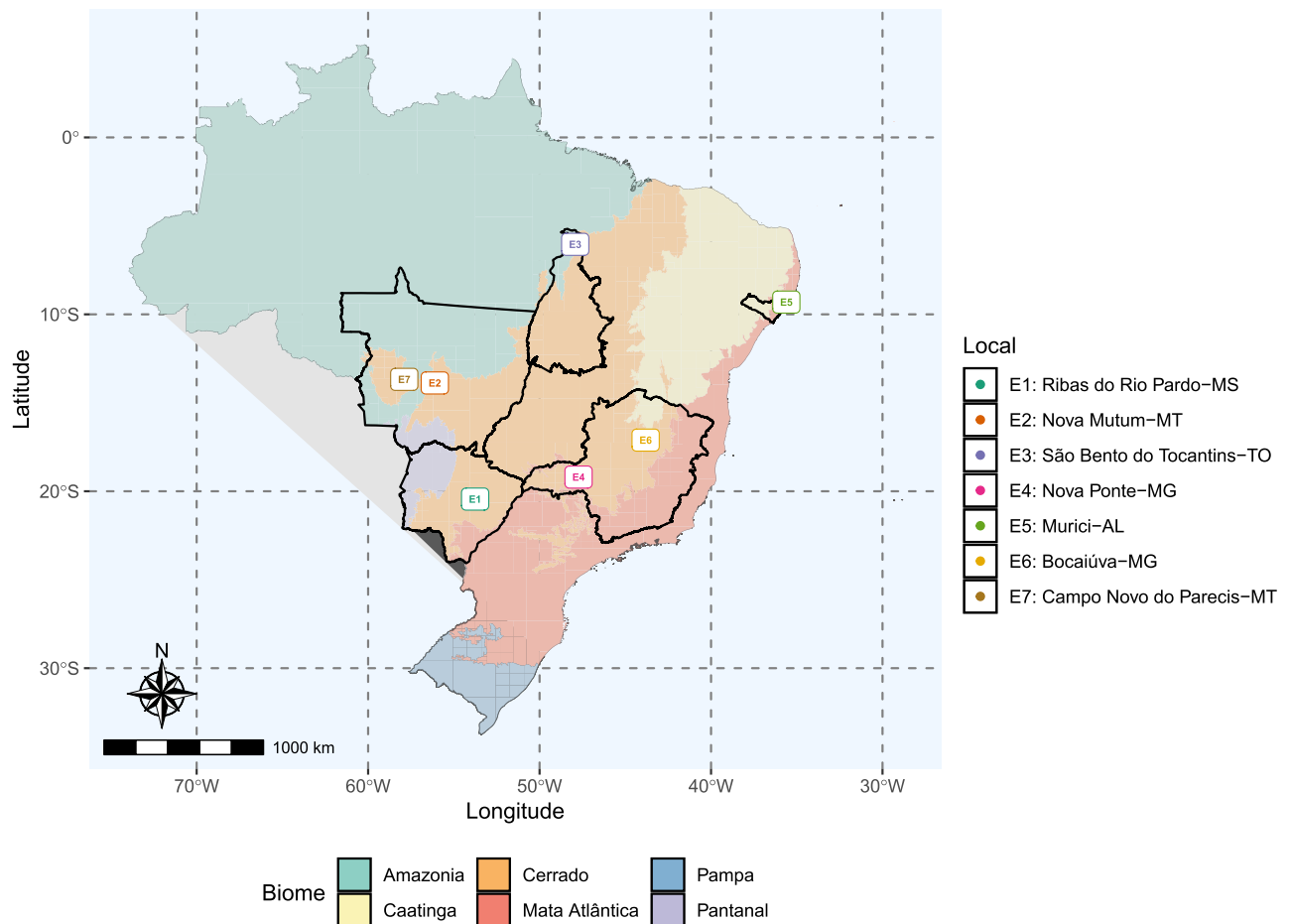


Figure 7. The map illustrates the locations of trials across Brazil. State borders are depicted by contours, with each colour signifying a distinct Brazilian biome. On the right, the legend provides details on the corresponding municipalities for each trial, while the map labels utilize codes specific to this study. This map was generated using the `ggplot2` package, v. 3.5.1 (<https://ggplot2.tidyverse.org/articles/ggplot2.html>), and the files publicly available at the [Brazilian Institute of Geography and Statistics website](https://biogeography.org/).

The individual analyses were conducted to assess the significance of genotypic effects in each trial using the likelihood ratio test. Additionally, we identified the top ten clones in each environment for subsequent comparison with the FAST outcomes (described in the following section).

Factor analytic linear mixed models

The FA model is described as follows:

$$\mathbf{y} = \mu \mathbf{1} + \mathbf{X}\mathbf{a} + \mathbf{Z}_1\mathbf{b} + \mathbf{Z}_2\mathbf{g} + \boldsymbol{\varepsilon} \quad (2)$$

where $\mathbf{a}$ is a $J \times 1$ vector of fixed environment effects, connected to $\mathbf{y}$ by its $N \times J$ incidence matrix $\mathbf{X}$. $\mathbf{a}$ contains the effects due to differences in geographical location, temporal variation and tree ages. The other terms, previously described in Eq. (1), have new dimensions: N_j is changed by N , and V_j is substituted by V . In addition, $\mathbf{b}$ and $\mathbf{g}$ are nested effects, so their dimensions are $RJ \times 1$ and $VJ \times 1$. Their incidence matrix changed accordingly. The conditional distribution of the random effects of Eq. (2) is:

$$\begin{bmatrix} \mathbf{b} \\ \mathbf{g} \\ \boldsymbol{\varepsilon} \end{bmatrix} \sim MVN \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \sigma_b^2 \mathbf{I}_J \otimes \mathbf{I}_R & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{\Lambda} \mathbf{D} \boldsymbol{\Lambda} + \boldsymbol{\Psi} \otimes \mathbf{I}_V & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \bigoplus_{j=1}^J \sigma_{\varepsilon_j}^2 \mathbf{I}_{N_j} \end{bmatrix} \right) \quad (3)$$

where $\mathbf{I}$ are identity matrices whose order is indicated by their subscripts, $\boldsymbol{\Lambda}$ is the $J \times K$ matrix of factor loadings ($\boldsymbol{\Lambda} = \{\lambda_{kj}\}$), $\mathbf{D}$ is the $K \times K$ diagonal matrix of factor scores variances ($\mathbf{D} = \{d_k\}$), $\boldsymbol{\Psi}$ is the $J \times J$ diagonal matrix of specific variances ($\boldsymbol{\Psi} = \{\psi_j\}$), $\otimes$ is the Kronecker product and $\bigoplus$ is the direct sum.

In Eq. (2), the eBLUPs are obtained using the following multiple regression:

$$\mathbf{g} = (\boldsymbol{\Lambda} \otimes \mathbf{I}_V) \mathbf{f} + \boldsymbol{\delta} \quad (4)$$

Feature	Acronym	Unit	Minimum	25% quartile	Mean	75% quartile	Maximum
Longitude	LON	°	− 57.8919	− 56.1094	− 49.5761	− 43.8150	− 35.6094
Latitude	LAT	°	− 20.4428	− 19.1983	− 14.6973	− 13.6750	− 6.0432
Altitude	ALT	m	102.00	389.00	511.72	670.00	993.00
Mean air temperature	TMEAN	°C	9.70	23.27	24.98	27.01	34.92
Maximum air temperature	TMAX	°C	14.33	28.26	30.73	32.95	42.49
Minimum air temperature	TMIN	°C	3.24	17.91	20.09	22.88	28.58
Dew point	T2MDEW	°C	− 7.08	14.03	17.62	21.47	24.87
Daily temperature range	TRANGE	°C/day	1.61	7.43	10.64	13.80	23.73
Wind speed	WS	m/s	0.18	0.89	1.84	2.50	5.91
Relative humidity	RH2M	%	17.56	57.44	68.02	80.81	94.44
Precipitation	PREC	mm/day	0.00	0.00	3.07	3.48	66.86
Horizontal infrared radiation intensity	HIRI	MJ/m²/day	255.18	371.52	388.17	410.41	453.37
Insolation incidence on a horizontal surface	IIHS	MJ/m²/day	1.97	16.88	19.51	22.55	32.21
Extraterrestrial radiation	RTA	MJ/m²/day	23.74	30.38	34.85	39.32	42.27
Vapour pressure deficit	VPD	kPa	0.10	0.76	1.37	1.75	4.68
Slope of saturation vapour pressure curve	SPV	kPa°C	0.08	0.18	0.20	0.21	0.31
Potential evapotranspiration	ETP	mm/day	0.87	7.66	8.94	10.38	14.79
Deficit by precipitation	PETP	mm/day	− 14.79	− 9.78	− 5.87	− 4.61	61.76
Effect of temperature on radiation use efficiency	FRUE	−	0.00	0.83	0.88	0.98	1.00
Soil organic content	SOC	g/kg	13.30	14.20	19.32	23.80	24.70
Silt content	SILT	%	14.00	15.00	21.37	28.00	36.00
Sand content	SAND	%	30.00	43.00	46.69	52.00	59.00
Clay content	CLAY	%	26.00	27.00	32.11	35.00	41.00
pH	PH	−	4.90	5.10	5.22	5.40	5.70
Bulk density of the fine earth fraction	BDOD	kg/dm³	1.20	1.30	1.31	1.40	1.40

Table 1. Environmental features considered in the analyses, and their respective minimum, 25% quartile, mean, 75% quartile and maximum values.

where $\mathbf{f}$ is the $VK \times 1$ vector of factor scores and $\boldsymbol{\delta}$ is the $VJ \times 1$ vector of lack-of-fit effects, associated to $\boldsymbol{\Psi}$. Factors need to be rotated when $k > 1$. We performed the rotation process based on the singular value decomposition, described by Smith et al.²². Henceforth, the matrix of rotated loadings will be represented by $\boldsymbol{\Lambda}^*$ ($\boldsymbol{\Lambda}^* = \{\lambda_{kj}^*\}$), and the vector of rotated scores will be represented by $\mathbf{f}^*$ ($\mathbf{f}^* = \{f_{kv}^*\}$). These replace $\boldsymbol{\Lambda}$ and $\mathbf{f}$ at Eqs. (4) and (3).

We selected the number of factors of the FA model based on its explicative power. Since parsimony tends to decrease as explicative power increases, we selected the model with more than 85% of explicative power that had the smaller K . For that, we used the average semivariances ratio⁵⁰. As an addendum for complementing information on the models' explicative power and parsimony, we computed the Akaike Information Criterion (AIC)⁵¹ and the percentage of explained variance per factor and per environment ($\%v_{jk}$), given by, respectively:

$$AIC = -2\text{Log}L + 2t \tag{5}$$

$$\%v_{jk} = \frac{\lambda_{kj}^{*2}}{\sum_{k=1}^K \lambda_{kj}^{*2} + \psi_j} \tag{6}$$

where $\text{Log}L$ is the logarithm of the maximum point of the residual likelihood function, and t is the number of parameters.

After defining the number of factors of the FA model, we computed the pairwise genotypic correlation between environments as follows⁵²:

$$\boldsymbol{\Upsilon} = \boldsymbol{\Phi}(\boldsymbol{\Lambda}^* \boldsymbol{\Delta} \boldsymbol{\Lambda}^* + \boldsymbol{\Psi}) \boldsymbol{\Phi} \tag{7}$$

where $\boldsymbol{\Upsilon}$ is a $J \times J$ matrix of pairwise genotypic correlations and $\boldsymbol{\Phi}$ is a $J \times J$ diagonal matrix whose elements are the inverse of the square roots of the diagonal elements of $\boldsymbol{\Lambda}^* \boldsymbol{\Delta} \boldsymbol{\Lambda}^* + \boldsymbol{\Psi}$.

Using the chosen model, we also computed the generalized heritability⁵³ and the experimental coefficient of experimental variation, given by, respectively:

$$H_j^2 = 1 - \frac{V(\Delta)}{2\sigma_{g_j}^2} \quad (8)$$

$$CV_j = \frac{\sqrt{\sigma_{e_j}^2}}{\mu_j} \quad (9)$$

where $V(\Delta)$ is the pairwise prediction error variance. The parameters described above are indexed by environment, for Eq. (2) provides environment-wise variances.

The extraction of outputs from the FA model was performed using a homemade function (`fa.outs`), available from https://github.com/saulo-chaves/May_b_useful/blob/main/fa.outs.R.

Factor analytic selection tools

To facilitate the selection process, we used the FAST¹². From the premise that the first factor resumes the genotypic main effect⁵⁴, we computed the overall performance of each clone as follows:

$$OP_v = \frac{1}{J} \sum_{j=1}^J \lambda_{1j}^* f_{1v}^* \quad (10)$$

Using the same premise previously mentioned, one may assume that the other factors represent stability. Assuming that a stable clone is the one that can have its performance easily predicted across environments, we measured the stability of a clone using the root mean squared deviation from a fictitious latent regression, given by:

$$RMSD_v = \sqrt{\frac{1}{J} \sum_{j=1}^J e_{vj}^2} \quad (11)$$

where e is the portion of $\mathbf{g}$ (Eq. 4) without $\lambda_{1j}^* f_{1v}^*$.

We associated these metrics with the reliability of the clone, given by:

$$r_v = 1 - \frac{PEV_v}{\bar{\sigma}_g^2} \quad (12)$$

where PEV_v is the prediction error variance of the v genotype, and $\bar{\sigma}_g^2$ is the mean genotypic variance across environments. Reliability is useful in the context of unbalanced data, a scenario that can be applied in this study.

We used OP_v , $RMSD_v$, and r_v in an index to perform the selection⁵⁰:

$$ID_v = \left(2 \frac{OP_v - \overline{OP}}{\sqrt{Var(OP)}} - \frac{RMSD_v - \overline{RMSD}}{\sqrt{Var(RMSD)}} \right) \times r_v \quad (13)$$

note that the FAST metrics are weighted by reliability. This additional consideration enhances confidence in the selection process, as it incorporates not only the performance itself but also the quality of the information.

After identifying the top-performing clones, we conducted a comparative analysis with the two commercial checks using latent regression plots⁵⁵. The number of plots corresponds to the number of factors, which is contingent on the selected model. The initial plot illustrates the latent regression between the eBLUPs ($\mathbf{g}$) and the first factor loadings. Subsequent plots feature $\mathbf{g} - \sum_{k=1}^{K-1} \lambda_{kj}^* f_{kv}^*$ on the y -axis and the k th factor loadings on the x -axis.

Linking FA to environmental features

We computed the mean of each feature for each environment and compiled them into $\mathbf{W}$, the $J \times P$ matrix representing environmental features, with P denoting the number of features. Then, we performed a partial least square regression (PLSR)—using the kernel algorithm^{56,57}—of the environmental features on the rotated factor loadings:

$$\mathbf{\Lambda}^* = \mathbf{W}\mathbf{B}^* + \mathbf{E} \quad (14)$$

where $\mathbf{B}^*$ is a matrix of coefficients and $\mathbf{E}$ is a matrix of residuals. The PLSR was fitted using the `pls` package⁵⁸. This analysis served the dual purpose of understanding the connection between factors and environmental features and inferring the relationship between environments using both real and latent environmental covariates. We also assessed the relative importance of each environmental feature to the underlying GEI variation in the dataset. For this purpose, we computed the variable importance in projection (VIP)⁵⁹, given by:

$$VIP_p = \sqrt{\frac{P \sum_{a=1}^A \left[SS_a \left(\frac{\omega_{ap}}{\|\boldsymbol{\omega}_a\|^2} \right) \right]}{\sum_{a=1}^A SS_a}} \quad (15)$$

where SS_a is the sum of squares explained by the a -th PLS component ($a = 1, 2, \dots, A$, and A is defined via leave-one-out cross-validation), ω_{ap} is the loading weight of the p -th feature in the a -th component, and $\boldsymbol{\omega}_a$ is a vector of loading weights in the a -th component. We transformed the VIPs to a percentage scale using $VIP_p(\%) = \frac{VIP_p^2}{\sum_p VIP_p^2} \times 100$. The VIP was computed using the `plsVarSel` package⁶⁰.

Ethical statement

The cultivated *Eucalyptus* spp. clones were provided by ArborGen[®]. We confirm that we have complied with all necessary regulations for this type of research.

Data availability

The data and the code are available from the corresponding author upon reasonable request.

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Author contributions

S.F.S.C. analysed the data; S.F.S.C. and M.B.D. wrote the first draft; K.O.G.D. and L.L.B. reviewed the drafts. All authors reviewed the final version of the manuscript.

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Competing interests

The authors declare no competing interests

Additional information

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Correspondence and requests for materials should be addressed to L.L.B.

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