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PREDICTING THE DISTRIBUTION OF *PASPALUM GUENOARUM* (POACEAE) USING ENVIRONMENTAL VARIABLES AND ENSEMBLE SPECIES DISTRIBUTION MODELS

Predicción de la distribución de *Paspalum guenoarum* (Poaceae) utilizando variables ambientales y modelos de distribución ensamblados

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Summary: *Paspalum guenoarum* Arechav. is a perennial grass native to South America, highly valued for its year-round forage production and notable cold tolerance. In this study, we characterized its distribution, identified the main environmental drivers, and evaluated the predictive performance of different algorithms used to estimate its potential distribution. Using herbarium records and germplasm accessions together with environmental variables, we modeled its ecological niche using an ensemble modeling approach. Our results indicate that the species is mainly distributed in northeastern Argentina, southern Brazil, northern Uruguay, and Paraguay, and is associated with subtropical regions with no dry season. Bioclimatic variables, particularly precipitation of the wettest month and mean diurnal temperature range, were the most important predictors, whereas edaphic variables and elevation had a secondary influence. Ensemble models produced more robust predictions than individual algorithms; nevertheless, MaxEnt showed high predictive performance and ease of implementation. Overall, these findings provide a solid basis for understanding the species' distribution and environmental preferences, and offer a reference framework for future distribution modeling studies within the genus *Paspalum*.

Key words: BIOMOD2, ecological niche modeling, ensamble models, germplasm conservation, *Paspalum guenoarum*.

Resumen: *Paspalum guenoarum* Arechav. es una gramínea perenne nativa de América del Sur, altamente valorada por su producción continua de forraje durante todo el año y su notable tolerancia al frío. En este estudio, caracterizamos su distribución, identificamos las principales variables ambientales que la determinan y evaluamos el rendimiento predictivo de diferentes algoritmos utilizados para estimar su distribución potencial. A partir de registros de herbario y accesiones de germoplasma junto con variables ambientales, modelamos el nicho ecológico de la especie mediante un enfoque de modelado de consenso. Nuestros resultados indican que la especie se distribuye principalmente en el noreste de Argentina, el sur de Brasil, el norte de Uruguay y Paraguay, y se asocia a regiones subtropicales sin estación seca. Las variables bioclimáticas, particularmente la precipitación del mes más húmedo y el rango diurno de temperatura promedio, fueron los predictores más importantes, mientras que las variables edáficas y la elevación tuvieron una influencia secundaria. Los modelos de consenso produjeron predicciones más robustas que los algoritmos individuales; sin embargo, MaxEnt mostró un alto rendimiento predictivo y facilidad de implementación. En general, estos hallazgos proporcionan una base sólida para comprender la distribución y las preferencias ambientales de la especie, y ofrecen un marco de referencia para futuros estudios de modelado de distribución dentro del género *Paspalum*.

Palabras clave: BIOMOD2, conservación de germoplasma, modelado de nicho ecológico, modelos ensamblados, *Paspalum guenoarum*.

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Introduction

The South American Campos constitute an ecological region composed of temperate and subtropical grasslands of major importance for food production and the regional economy (Burkart, 1975; Paparamborda *et al.,* 2026). This region extends from southern Brazil to northeastern Argentina and Uruguay, and experiences climates characterized by warm summers and mild winters in so-called transitional zones (Overbeck *et al.,* 2007; Jaurena *et al.,* 2021; Quesenberry *et al.,* 2022). The botanical composition of the Campos is diverse; however, grasses of the genus *Paspalum* L. are particularly prominent and highly valued in livestock systems and breeding programs because of their high forage value and broad natural variability in these regions (Zuloaga & Morrone, 2005; Hojsgaard *et al.,* 2009). Most species are perennial and warm-season, with maximum biomass accumulation occurring during spring and summer, followed by a marked reduction in forage availability towards late autumn and winter (Burkart, 1975; Mislevy & Everett, 1981).

Paspalum guenoarum Arechav. inhabits these regions and is distinguished by its year-round forage production, palatability, and notable cold tolerance (Nabinger & Dall'Agnol, 2019; Scienza *et al.,* 2024). Records document its presence from southern Brazil to northern Argentina and Uruguay, and also in areas of Bolivia and Paraguay (Zuloaga & Morrone, 2005; Steiner *et al.,* 2017). Given its occurrence in humid subtropical regions, we hypothesize that the species inhabits or prefers humid environments with marked seasonal temperature variation, suggesting that precipitation and temperature are a key driver of its distribution. However, its distribution remains poorly characterized, as do the environmental variables that determine it. Improving knowledge of its geographic range and environmental preferences is essential for advancing germplasm collection and plant breeding programs, particularly in transitional zones, where populations experience high environmental variability, including droughts, flooding events, photoperiod, and extreme temperatures (Quesenberry *et al.,* 2022). Likewise, such knowledge is vital in these regions, which have suffered significant degradation due to land-use change (Overbeck *et al.,* 2007).

In this context, Ecological Niche Models (ENMs) have contributed substantially to understand the patterns that explain species' geographic ranges (Peterson *et al.,* 2011). These models relate species presence records to a set of environmental variables to identify areas of environmental suitability (Elith & Leathwick, 2009). Currently, several algorithms are used for this type of analysis; however, because each has inherent strengths and limitations, integrating multiple individual algorithms into an ensemble model is recommended to optimize performance and predictive capacity (Thuiller *et al.,* 2009; Huang *et al.,* 2024).

Although ecological niche models have been developed for certain species of the genus *Paspalum* (Lee *et al.,* 2016; Karunarathne *et al.,* 2020; Glison *et al.,* 2023), these studies have mainly relied on individual algorithms. Because the choice of method should not be arbitrary and predictions may vary among methods as a result of the inherent limitations of each algorithm (Elith *et al.,* 2006), integrative approaches are required to produce more robust projections of areas of environmental suitability (Konowalik & Nosol, 2021). The development of ensemble models has proven to be a valuable strategy for reducing uncertainty and increasing predictive robustness (Thuiller *et al.,* 2009). One widely used framework for implementing such ensemble approaches is BIOMOD2, an R-based platform that integrates multiple algorithms to model and project species distributions (Thuiller *et al.,* 2009). However, such approaches have not yet been applied to species of the genus *Paspalum*, such as *P. guenoarum*, which limits not only the identification of potential germplasm collection areas but also the understanding of its distribution and the environmental variables that shape it.

Considering these knowledge gaps, we aimed to (i) characterize the distribution of *P. guenoarum*, (ii) identify the environmental variables that determine its distribution as well as its ecological preferences, and (iii) evaluate the predictive performance of different modeling algorithms implemented in BIOMOD2 to estimate the species' distribution. This approach aims to provide a solid foundation for prioritizing areas for future germplasm collections of *P. guenoarum*, focused at preserving existing genetic diversity in the face of rapid habitat loss due to land-use changes, as well as providing a basis for future applications of ecological niche models in this group of plants.

Material and Methods

Occurrence records

A georeferenced database of *P. guenoarum* was compiled using records from the CTES herbarium of the Instituto de Botánica del Nordeste, the SI herbarium of the Instituto de Botánica Darwinion, and the MVJB herbarium of the Jardín Botánico de Montevideo. Primary occurrence data exclusively derived from herbarium specimens were then downloaded from the Global Biodiversity Information Facility (GBIF: https://doi.org/10.15468/dl.hdcbfn) and SpeciesLink (https://specieslink.net). In addition, georeferenced occurrences of germplasm accessions conserved in the BGCTES genebank of the Instituto de Botánica del Nordeste were included, as well as accessions maintained in other genebanks available through the Genesys portal (https://www.genesys-pgr.org). All records were subjected to a rigorous spatial quality control procedure using Google Earth Pro (version 7.3.6). Each occurrence was individually inspected to identify and remove duplicated coordinates. Only records from 1980 onwards were included (except for the type specimen), and those located in artificial environments (e.g., urban areas, botanical gardens, museums, or institutional coordinates) or outside the known natural distribution of the species were excluded. Based on this information, a database representing the natural distribution of *P. guenoarum* was generated (Table S1). For subsequent niche analyses, a geographic rarefaction filter was applied to the occurrence records using the Wallace platform (Kass *et al.,* 2018) to reduce spatial autocorrelation, with a single record retained within a 30 km radius. Spatial data editing, analysis, and visualization were performed in QGIS version 3.40 (QGIS Development Team). Finally, occurrence records were intersected with the global ecoregions map proposed by Olson *et al.* (2001) and with the Köppen-Geiger climate classification updated to a 1 arc-minute resolution (Beck *et al.,* 2023) to identify the ecoregions and climatic classes occupied by the species.

Environmental Variables

In this study, the 19 bioclimatic variables available from the WorldClim database version 2.1 (https://worldclim.org) were used at a spatial resolution of 2.5 arc-min. In addition, seven edaphic variables were obtained from the International Soil Reference and Information Centre portal (ISRIC; https://www.isric.org) at an original spatial resolution of 250 m (Hengl *et al.,* 2017), and these were subsequently resampled to a spatial resolution of 2.5 arc-min using bilinear interpolation implemented in the raster package (Hijmans, 2025) in R (R Core Team, 2025). A geophysical variable representing elevation, obtained from WorldClim (Fick & Hijmans, 2017), was also included. To reduce multicollinearity among environmental variables, a Pearson correlation analysis was performed on the 27 factors initially considered, and variables with correlation coefficients greater than 0.7 were excluded. Collinearity in the final set of selected variables was additionally assessed using the Variance Inflation Factor (VIF), ensuring that all predictors had VIF values below 10 (Dormann *et al.,* 2013). As a result, model construction relied on four bioclimatic predictors: Mean Diurnal Temperature Range (Bio2), Annual Precipitation (Bio12), Precipitation of the Wettest Month (Bio13), and Precipitation of the Warmest Quarter (Bio18); three edaphic predictors: soil pH (pH hox), cation exchange capacity (cecsol), and soil water content (awcts); and one geophysical variable corresponding to elevation (altitude).

BIOMOD2 Ensemble Models

To predict the potential distribution of *P. guenoarum*, the BIOMOD2 platform version 4.2.6 was used, which allows the integration of multiple statistical and machine-learning algorithms (Thuiller *et al.,* 2009; Zhang *et* *al.,* 2024). Five individual algorithms were evaluated: generalized boosting models (GBM), random forest (RF), maximum entropy implemented in R (MAXNET), generalized linear models (GLM), and flexible discriminant analysis (FDA), under two modeling approaches: one based exclusively on bioclimatic variables (bioclimatic model) and another that additionally included edaphic variables and elevation (combined model).

To delimit the calibration area (M area), the georeferenced database representing the natural distribution of the species was used (Table S1). The M area was defined by constructing a minimum convex polygon around the occurrence records and applying a 250 km buffer to represent the area potentially accessible to the species (Peterson *et al.,* 2011), considering its potential dispersal capacity and the historical connectivity among grassland-forest mosaics in southern South America. Pseudo-absence generation followed the surface range envelope (SRE) strategy using a quantile threshold of 0.025 (Yang *et al.,* 2025). Under this approach, 2,000 pseudo-absences were generated to ensure model stability and reduce sampling bias; the procedure was then repeated across ten independent replicates.

Because the default MaxEnt configuration may lead to model overfitting (Elith & Graham, 2009), the regularization multiplier and feature classes were calibrated using the ENMeval package (version 2.0.5) in R. Different combinations of feature classes and regularization values were evaluated, and the configuration including linear, quadratic, hinge, and product features (LQHP) with a regularization multiplier of 0.5 was selected, as the lowest corrected Akaike Information Criterion (AICc) was yielded and an optimal balance between model complexity and flexibility was achieved (Li *et al.,* 2025). The remaining models were calibrated using the bigboss optimization strategy, which allows automatic tuning of the internal parameters of each algorithm (Sari *et al.,* 2026). This procedure was implemented under a random cross-validation framework with ten repetitions, using 70% of the data for model training and 30% for performance evaluation (Yang *et al.,* 2025). The complete modeling workflow was documented following the ODMAP protocol (Fitzpatrick *et al.,* 2021), and is provided in Table S2 in the Supplementary Material.

Variables Importance

To identify the most relevant environmental variables shaping the distribution of *P. guenoarum*, predictor importance was estimated using a ten-permutation procedure implemented in BIOMOD2. In this method, the values of each environmental predictor are randomly permuted and the resulting decrease in model predictive performance is measured; a greater decrease indicates a higher relevance of the variable in shaping the species' ecological niche (Thuiller *et al.,* 2009). Response curves were then generated from the ensemble model to evaluate the relationship between each variable and environmental suitability for the species, while holding the remaining variables constant. In addition, values of each environmental predictor were extracted at occurrence sites of *P. guenoarum* within its natural distribution to characterize the environmental range occupied by the species (Silva *et al.,* 2023).

Model Performance Evaluation

To evaluate model performance, three metrics were employed: the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS), and the Kappa coefficient (Adhikari *et al.,* 2023; Yang *et al.,* 2025; Li *et al.,* 2026). AUC values range from 0 to 1, with values < 0.7 indicating poor model performance, values between 0.7 and 0.9 indicating moderate performance, and values > 0.9 indicating excellent performance (Zhao *et al.,* 2024). TSS was calculated as the sum of sensitivity (the probability of correctly predicting presence) and specificity (the probability of correctly predicting absence or background points), minus one (Chen *et al.,* 2026). Therefore, TSS values range from -1 to 1, with values greater than 0.75 indicating excellent model performance (Changjun *et al.,* 2021). As a threshold-dependent evaluation metric, the limitations of AUC are largely compensated for by TSS (Allouche *et al.,* 2006). Finally, the Kappa coefficient was used as a measure of agreement between model predictions and observed occurrences. Its values range from -1 to 1, with values above 0.75 indicating excellent performance (Yang *et al.,* 2025). To ensure high predictive and discriminatory ability, only models with TSS values greater than 0.75 and AUC values higher than 0.9 were selected for ensemble construction. Ensemble models were constructed using a weighted mean approach (EMwmean), in which individual models were weighted according to their predictive performance (TSS). Ensemble performance was evaluated using the same metrics applied to individual models (AUC, TSS, and Kappa). The threshold that maximized TSS was then used to convert continuous suitability maps into binary presence-absence maps (Zhang *et al.,* 2024). The resulting threshold values were 0.462 for the bioclimatic model and 0.477 for the combined model. All prediction maps were visualized and edited in QGIS version 3.40 (QGIS Development Team).

Results

Distribution of P. guenoarum

A total of 518 georeferenced occurrence records of *P. guenoarum* were compiled across its natural distribution. After rigorous quality control and spatial filtering, 124 reliable records distributed across five countries were retained: Argentina, Bolivia, Brazil, Paraguay, and Uruguay (Fig. 1). In Argentina, records occurred in the provinces of Corrientes (11), Misiones (11), Entre Ríos (1), and Santa Fe (1). In Bolivia, records were concentrated in the departments of Santa Cruz (12) and Chuquisaca (1). Brazil accounted for the highest number of occurrences, distributed across the states of São Paulo (19), Rio Grande do Sul (13), Goiás (9), Paraná (8), Mato Grosso do Sul (7), Santa Catarina (6), Bahia (5), Distrito Federal (4), Paraíba (2), Maranhão (1), Minas Gerais (1), Piauí (1), and Sergipe (1). In

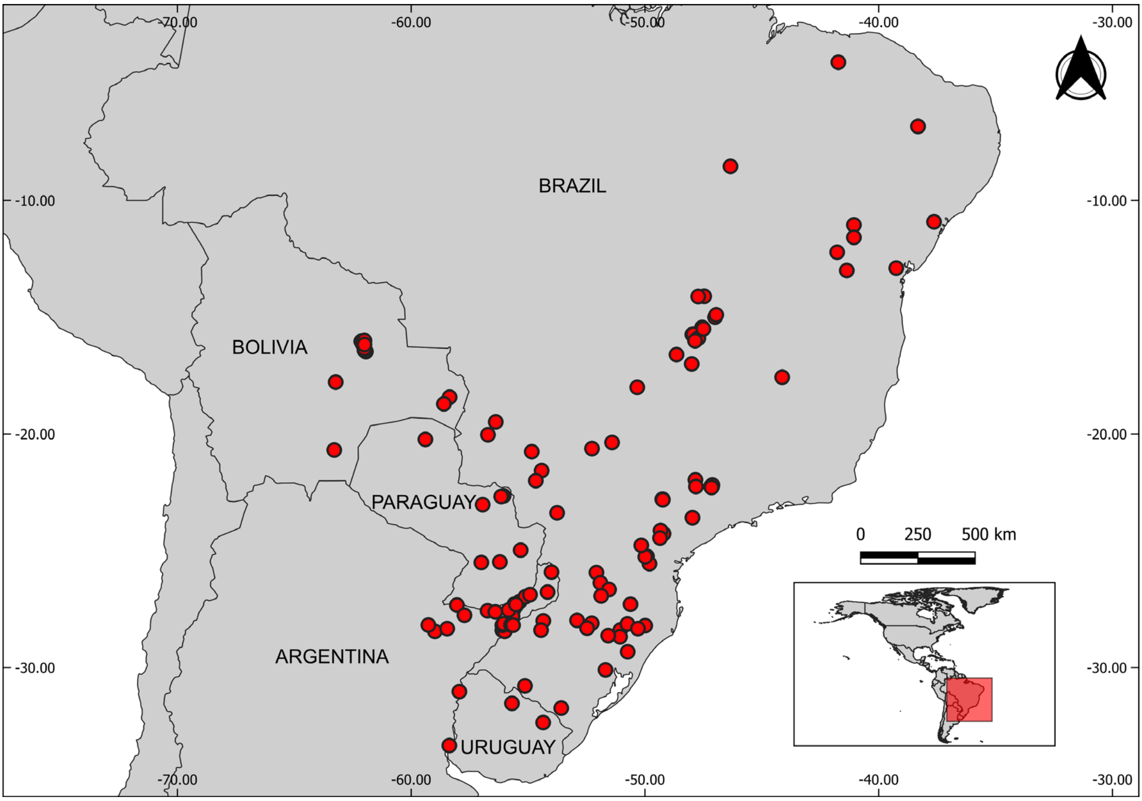

Fig. 1. Natural distribution of *Paspalum guenoarum* in South America. Red dots represent georeferenced occurrence records obtained from herbarium collections and germplasm accessions.

Paraguay, records occurred in six departments, including Amambay (2), Alto Paraguay (1), Alto Paraná (1), Caaguazú (1), Concepción (1), and Cordillera (1). In Uruguay, records were found in the departments of Tacuarembó (1), Cerro Largo (1), and Río Negro (1; type specimen, Arechavaleta 1894).

Paspalum guenoarum was primarily associated with the Araucaria Mixed Forests, which accounted for 23.61% of the occurrences, followed by the Upper Paraná Atlantic Forests (18.93%) and the Cerrado (17.30%). According to the Köppen-Geiger climate classification, the species showed affinity for temperate climates without a dry season (49.18%), including both hot-summer (Cfa) and warm-summer (Cfb) subtypes, followed by tropical savanna climates (40.98%), with a predominance of climates characterized by hot summers (Table 1).

Potentially Suitable Habitats for P. guenoarum

The bioclimatic model predicted a potential distribution of *P. guenoarum* covering 2,559,787 km², mainly concentrated in southern Brazil and encompassing the states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Minas Gerais, Goiás, Mato Grosso, and Mato Grosso do Sul. In Bolivia, suitable areas were restricted to the department of Santa Cruz. In Paraguay, suitability extended across almost the entire country, with the exception of the department of Boquerón. In Argentina, the potential distribution was limited to the northeastern provinces of Misiones and Corrientes and the eastern regions of Chaco and Formosa, whereas in Uruguay it was concentrated in the northern region, including the departments of Rivera, Tacuarembó, Cerro Largo, Treinta y Tres, and Lavalleja (Fig. 2A).

Table 1. Distribution of records across biogeographic and climatic units. Biogeographic units follow the ecoregion classification of Olson *et al.* (2001), while climatic units are based on the Köppen-Geiger classification updated by Beck *et al*. (2023).

	Classification	Percentage (%)
Ecoregions	Araucaria moist forests	23.61
	Alto Paraná Atlantic forests	18.93
	Cerrado	17.30
	Chiquitano dry forests	9.84
	Humid Chaco	6.56
	Southern Cone Mesopotamian savanna	6.56
	Uruguayan savanna	6.56
	Caatinga	4.10
	Dry Chaco	1.63
	Pantanal	1.63
	Bahia coastal forests	0.82
	Campos Rupestres montane savanna	0.82
	Espinal	0.82
	Maranhão Babaçu forests	0.82
	Classification	**Percentage (%)**
Climate	Tropical, savanna	40.98
	Temperate, no dry season, hot summer	34.43
	Temperate, no dry season, warm summer	14.75
	Temperate, dry winter, hot summer	3.28
	Tropical, monsoon	3.28
	Arid, steppe, hot	2.46
	Tropical, rainforest	0.82

When the model included edaphic variables and elevation, the potential distribution increased by 12.9% to 2,889,146 km², owing to a higher probability of occurrence in northern Argentina and central-southern Uruguay (Fig. 2B).

Environmental Variables

Bioclimatic factors were the main determinants of the ecological niche of *Paspalum guenoarum*. When we used only bioclimatic variables, model predictive performance was higher, with precipitation of the wettest month (Bio13) emerging as the variable with the greatest contribution (35.7%), followed by mean diurnal temperature range (Bio2; 30.3%), annual precipitation (Bio12; 29.6%), and precipitation of the warmest quarter (Bio18; 4.4%). In the model that incorporated edaphic variables and elevation, precipitation of the wettest month remained the most influential factor shaping the species' distribution (Bio13; 20.7%), followed by mean diurnal temperature range (Bio2; 19.4%), annual precipitation (Bio12; 18.7%), and precipitation of the warmest quarter (Bio18; 12.2%). Under this scenario, edaphic variables contributed secondarily, with soil pH (ph_hox; 10%), cation exchange capacity (cecsol; 8.5%), and soil water content (awcts; 7.4%) as the most relevant. Elevation showed the lowest contribution to the ensemble model (altitude; 3.1%).

The response curves described the climatic preferences of *P. guenoarum* (Fig. 3). The species prefers precipitation of approximately 100-200 mm during the wettest month of the year, corresponding to intermediate to relatively humid conditions within the study area, a mean diurnal temperature range of 7-10 °C, accumulated annual precipitation of 1,500-2,500 mm, and 400-800 mm of precipitation during the warmest quarter. With respect to the remaining factors, *P. guenoarum* shows a preference for slightly acidic to neutral soils (pH 4.5-6.5), moderate to high cation exchange capacity (10-20 cmolc kg^{-1}), high soil water retention capacity (40-45%), and elevations ranging from 500 to 3,000 m a.s.l.

The environmental range occupied by the species showed a high degree of concordance with the climatic preferences of the two main predictors of its distribution, precipitation of the wettest month and mean diurnal

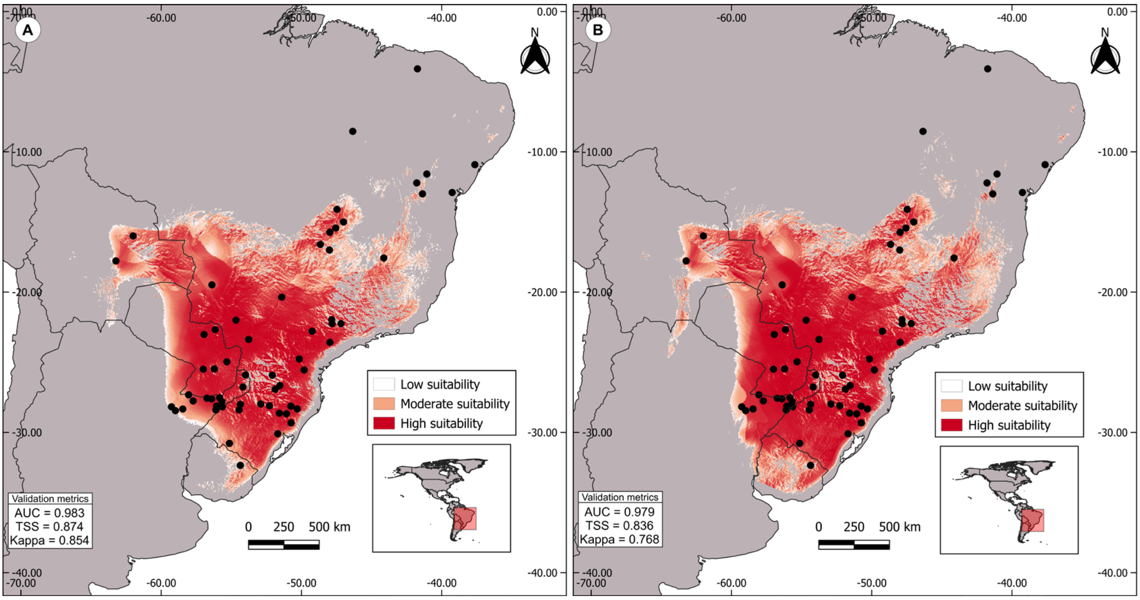

Fig. 2. Potential distribution of *Paspalum guenoarum*. A: Shows the predicted habitat suitability obtained using only bioclimatic variables. B: Presents the model including bioclimatic, edaphic, and geophysical variables. Black dots represent occurrence records used for model calibration.

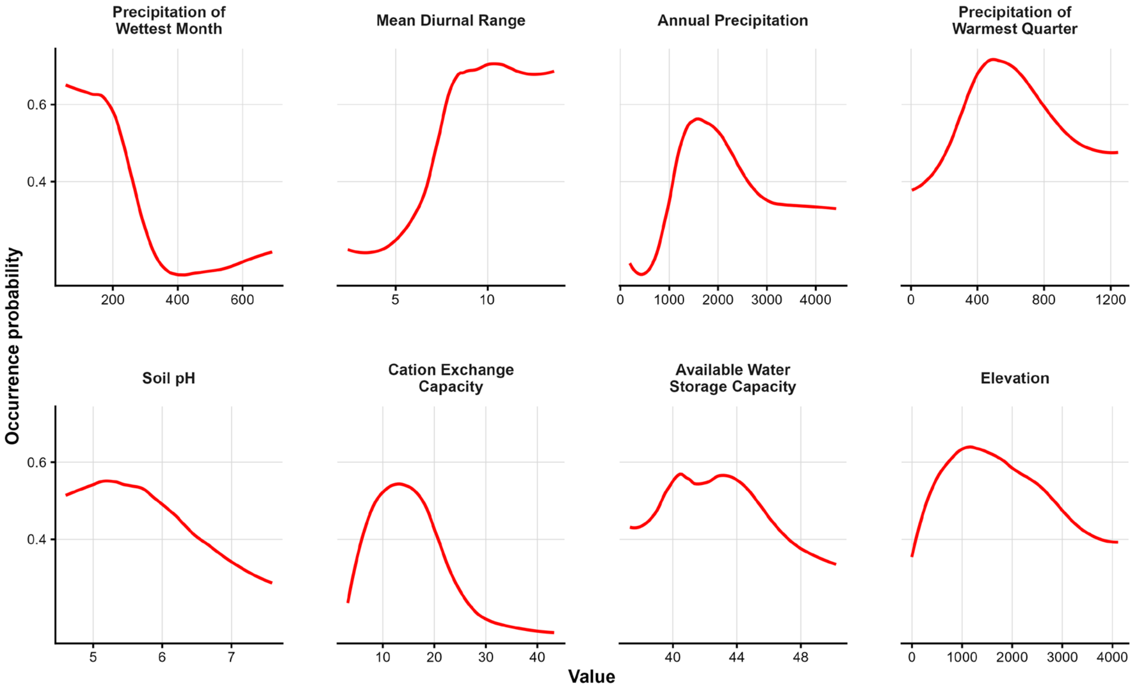

Fig. 3. Response curves of *Paspalum guenoarum* for the environmental predictors in the ecological niche model. The red lines illustrate the relationship between the predicted probability of occurrence (Y-axis) and the specific values of each environmental predictor (X-axis).

temperature range, as estimated by the response curves (Table 2). Nevertheless, occurrences of *P. guenoarum* were recorded in areas with annual precipitation below the optimal ranges indicated by the curves (464 mm) and with lower precipitation during the warmest quarter (50 mm), as well as in soils with low cation exchange capacity (4.7 cmolc kg^{-1}) and at elevations below the suitability ranges.

Model Performance Evaluation

Consensus modeling based exclusively on bioclimatic variables exhibited excellent statistical performance (AUC= 0.983;

Table 2. Descriptive statistics of environmental variables extracted at the occurrence locations of *Paspalum guenoarum*.

Variable	Mean	SD	Min	Max
Precipitation of Wettest Month (mm)	193.50	43.61	88.00	346.00
Mean Diurnal Range (°C)	11.30	0.80	6.79	12.73
Annual Precipitation (mm)	1403.15	271.48	464.00	1987.00
Precipitation of Warmest Quarter (mm)	431.98	102.65	50.00	614.00
Soil pH (H_2O)	5.48	0.35	5.00	6.68
Cation Exchange Capacity (cmolc/kg)	11.48	4.20	4.78	22.33
Available Water Capacity (%)	43.11	2.38	38.78	49.47
Elevation (m)	519.74	348.43	39.64	1257.08

*Mean, standard deviation (SD), minimum (Min), and maximum (Max) values were calculated for each environmental variable extracted at the 124 occurrence locations.

TSS= 0.874; Kappa= 0.854), indicating a high predictive capacity to identify areas of environmental suitability for *P. guenoarum* and strong reliability in spatial projections. At the individual level, the GBM, RF, and MAXNET algorithms achieved the highest accuracy, with AUC values exceeding 0.95 and TSS and Kappa metrics above 0.8 (Fig. 4A). Although the GLM and FDA models showed slightly lower performance, all algorithms exceeded the established accuracy thresholds. The combined model, which included edaphic variables and elevation, showed lower statistical performance than the bioclimatic model, but still demonstrated high predictive capacity for delineating the species' optimal habitat (AUC= 0.979; TSS = 0.836; Kappa = 0.768). Under this scenario, all algorithms maintained AUC values above 0.90; however, only GBM, RF, and MAXNET achieved TSS values greater than 0.75. In contrast, the GLM and FDA models exhibited the lowest performance, falling below the critical threshold values in some replicates (Fig. 4B).

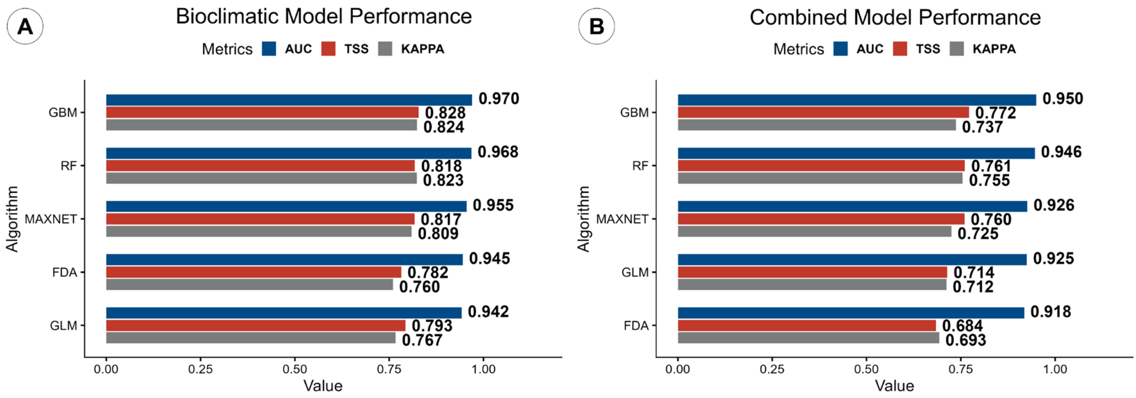

Fig. 4. Performance of the algorithms used to build the ensemble model. A: Models calibrated using bioclimatic variables only. B: Models calibrated using combined bioclimatic, edaphic, and geophysical variables. Bars represent mean values of AUC (blue), TSS (red), and Kappa (grey) for each algorithm.

Discussion

The distribution of *P. guenoarum* has been described in previous studies based on isolated occurrence records (Zuloaga & Morrone, 2005; Steiner *et al.,* 2017; Scienza *et al.,* 2024); however, the present study provides a delimitation derived from a comprehensive review of herbarium specimens and germplasm collections from major regional institutions. Our findings indicate that the natural distribution of the species includes northern Argentina, southern Brazil, Bolivia, Paraguay, and northern Uruguay. In addition, we recorded occurrence sites in central and northern regions of Brazil that do not coincide with the distribution traditionally proposed for the species (Zuloaga & Morrone, 2005; Steiner *et al.,* 2017). These discrepancies may be related to the taxonomic complexity of the Plicatula group within the genus *Paspalum*, which includes *P. guenoarum* together with other morphologically similar species, forming a variable complex of species and forms that remains poorly defined taxonomically (Sartor *et al.,* 2009). This complexity may have led to difficulties in accurate specimen identification (Aguilera *et al.,* 2011). Furthermore, the scarcity of records in Bolivia and Uruguay may reflect geographic biases associated with an uneven distribution of collection effort, which often concentrates in regions close to research centers with greater funding availability (Meyer *et al.,* 2015; Anderson *et al.,* 2020). This pattern agrees with findings from a recent review on the conservation of the genus *Paspalum*, which showed that major South American collections concentrate in Brazil and Argentina, and that *P. guenoarum* is not among the most represented species in the main germplasm banks (Acuña *et al.,* 2019).

Our results show that *P. guenoarum* occurs in humid forests of the Atlantic domain and in ecoregions such as the Cerrado and subtropical savannas. These findings highlights that the species is mainly associated with transitional zones between ecoregions, particularly in southern Brazil, where these regions occur as mosaics of subtropical grasslands, savannas, and forest patches (Overbeck *et al.,* 2007; Andrade *et al.,* 2019). Likewise, in Araucaria mixed forests, the presence of open clearings, together with disturbances such as grazing or fire, may favor the persistence of species such as *P. guenoarum* within forested landscapes (Müller *et al.,* 2024). The climatic analysis aligns with these results, indicating the species' plasticity in occupying environments ranging from temperate to humid tropical climates and, in particular, its preference for temperate climates without a dry season, which may explain its cold tolerance and continuous forage production throughout the year (Steiner *et al.,* 2017; Scienza *et al.,* 2024). This broad occurrence across both tropical savannas and temperate regions further confirms the considerable ecological plasticity of *P. guenoarum*, highlighting its ability to adapt to contrasting environmental regimes, as well as its potential value as a forage species across diverse ecological settings.

Ensemble models indicated that the potential distribution of *P. guenoarum* is mainly concentrated in southern Brazil, eastern Paraguay, northeastern Argentina, and northern Uruguay. This discrepancy between the distribution derived from herbarium collections and the ensemble predictions may be explained by the fact that records at tropical latitudes could correspond to cultivated areas or to misidentifications resulting from the taxonomic complexity of the Plicatula group (Sartor *et al.,* 2009; Aguilera *et al.,* 2011). This interpretation is further supported by the climatic conditions of northeastern Brazil, which are predominantly semi-arid and therefore inconsistent with the precipitation requirements identified for the species. In addition, these results underscore the importance of conducting future collection missions in tropical regions to clarify the taxonomic circumscription of these populations and confirm whether they indeed belong to the species. Likewise, there is a clear need to intensify collection missions in southern Brazilian states, particularly in Santa Catarina and Rio Grande do Sul, where the frequency of available records is low relative to the extensive areas that are environmentally suitable for the species. Such collections could benefit from the high natural variability of grasses of the genus *Paspalum* in these transitional zones (Hojsgaard *et al.,* 2009; Quesenberry *et al.,* 2022). Furthermore, the observed thermal and precipitation tolerance suggests adaptive genetic variability, which provides critical implications for breeding and conservation under future climate change scenarios.

Precipitation-related environmental variables showed the highest contribution to the ecological niche of *P. guenoarum*, which is expected given that mean annual precipitation is a major driver of grassland productivity (Knapp & Smith, 2001; Guido *et al.,* 2014). This pattern makes the species particularly sensitive to drought and flooding events and is reflected in the response curve for precipitation of the wettest month, which shows a marked decline in suitability above 200 mm. This trend also explains the absence of highly suitable areas at tropical latitudes, where excessive precipitation during the wettest months may limit the establishment of *P. guenoarum*. In addition, mean diurnal temperature range emerged as one of the main environmental predictors, which may explain the species' preference for temperate climates characterized by a wide daily thermal amplitude. By contrast, edaphic variables and elevation showed a secondary contribution to shaping the ecological niche of *P. guenoarum*. Nevertheless, the environmental range occupied by the species indicates a preference for acidic to neutral soils with high moisture retention capacity. With respect to elevation and cation exchange capacity, greater plasticity was observed, with the species occupying broader ranges, from mid-elevations to soils with highly variable fertility levels. Considering these environmental preferences, our results suggest that although *P. guenoarum* has been frequently recorded in regions such as the Cerrado and other seasonally dry environments, it preferentially occupies the wetter portion of its distribution range. This pattern is consistent with the strong contribution of precipitation-related variables to its ecological niche. The occurrence of the species in drier regions can be explained by a combination of factors, including taxonomic misclassification within the Plicatula group, the presence of cultivated populations beyond its natural range, and biases in sampling effort that affect the spatial distribution of records.

The ensemble model showed outstanding statistical performance under both the bioclimatic and combined approaches, highlighting the usefulness of ensemble modeling in improving predictive capacity and reducing the uncertainty associated with individual algorithms (Thuiller *et al.,* 2009; Zhang *et al.,* 2024). The superior performance of the bioclimatic model compared with the model that incorporated edaphic variables and elevation may be attributed both to the greater relevance of climatic factors in shaping the distribution of *P. guenoarum* and to limitations of globally available edaphic layers, which tend to show more heterogeneous spatial representation and a higher proportion of missing values than bioclimatic variables, thereby reducing model performance (Rota *et al.,* 2024).

At the individual level, the GBM, RF, and MAXNET algorithms showed the highest AUC and TSS values, in agreement with previous studies conducted on different species (Adhikari *et al.,* 2023; Huang *et al.,* 2024; Giraldo & Kucuker, 2025). This superior performance can be attributed to the fact that GBM and RF are regression tree–based methods capable of modeling nonlinear responses and complex interactions among environmental variables, as well as to the regularized maximum entropy approach of MAXNET, which allows complex relationships to be modeled while avoiding overfitting (Elith *et al.,* 2006). Accordingly, these results indicate that these algorithms are particularly useful for discriminating environmentally suitable areas for *P. guenoarum* from unsuitable ones. Nevertheless, although ensemble models implemented in BIOMOD2 increase predictive robustness and reduce uncertainty, their application involves greater methodological complexity and higher computational demand (Chen *et al.,* 2025). In this context, our results indicate that MaxEnt represents a methodologically efficient and operationally accessible alternative due to its intuitive interface and presence-background modeling framework; however, its correct application depends on rigorous calibration of feature classes and optimization of the regularization parameter to avoid overfitting and ensure robust predictions (Zhao *et al.,* 2021; Kang *et al.,* 2025). Finally, the differences observed among AUC, TSS, and the Kappa coefficient highlight the need to evaluate models using more than one performance metric (Konowalik & Nosol, 2021). While AUC provides a global measure of a model's discriminatory ability, threshold-dependent metrics such as TSS and Kappa are more sensitive to classification errors and to the choice of cut-off values, capturing additional aspects of predictive performance (Ábrego & Ovaskainen, 2023). This approach allowed the application of an objective criterion to define threshold values and to accurately discriminate environmentally suitable areas for *P. guenoarum* from unsuitable ones.

Together, these results delineate an ecological profile for *P. guenoarum*, characterized by its occurrence in subtropical forest-savanna mosaics and across a broad but structured precipitation gradient. Recognizing this environmental profile is essential not only for improving predictive modeling but also for guiding conservation strategies, particularly in transitional ecosystems that are increasingly threatened by land-use change (Overbeck *et al.,* 2007). Protecting and managing these environments may be crucial for maintaining natural populations and preserving the adaptive potential of the species.

Conclusions

The distribution of *P. guenoarum* is mainly concentrated in southern Brazil, eastern Paraguay, northeastern Argentina, and northern Uruguay, where it is associated with humid ecoregions of the Atlantic domain as well as with the Cerrado and subtropical savannas. The species shows a preference for subtropical climates, particularly temperate climates without a marked dry season. Bioclimatic factors, particularly precipitation of the wettest month, mean diurnal temperature range, and annual precipitation, are the main drivers of its distribution; although edaphic variables and elevation contribute to shaping its ecological niche, their influence is secondary.

Ensemble species distribution models constitute a robust tool for identifying environmentally suitable areas for *P. guenoarum*, while also indicating that individual algorithms such as MaxEnt and regression tree-based methods can provide reliable and methodologically efficient predictions.

Overall, this study contributes to the understanding of the distribution of *P. guenoarum* and the environmental factors that shape it, and evaluates the usefulness of ensemble species distribution models for identifying areas of environmental suitability. This information serves as a strategic basis for focusing and orienting targeted collection programs, and underscores the species' ecological plasticity for its conservation and use in breeding programs under climate change scenarios, especially given the significant habitat loss from land-use changes within its natural range. This information can support conservation and cultivation strategies for the species, as well as inform the application of distribution models to other species within the genus *Paspalum*.

Supplementary Material

Supplementary material are available at Bonplandia online and consist of the following:

Fig. S1. Individual model predictions for each algorithm used in the bioclimatic model (GBM, RF, MAXNET, FDA, and GLM), showing habitat suitability for *Paspalum guenoarum*.

Fig. S2. Individual model predictions for each algorithm used in the combined model (GBM, RF, MAXNET, FDA, and GLM), showing habitat suitability for *Paspalum guenoarum*.

Table S1. Geographic distribution of occurrence records of *Paspalum guenoarum* derived from herbarium specimens and germplasm collections.

Table S2. ODMAP (Overview, Data, Model, Assessment, and Prediction) metadata describing the methodology used in this study.

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Author Contribution

F. M. L. performed data curation and statistical analysis and wrote the original draft of the manuscript. F. M. L., F. M. and C. A. A., conceptualized the study. D. C. S. and M. D., contributed expert knowledge on the biology, ecology, and distribution of *P. guenoarum*. C. A. A. was responsible for project supervision and management. All authors contributed to the review and editing of the final manuscript.

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