

A New Methodological Approach to Detect Microcenters and Regions of Maize Genetic Diversity in Different Areas of Lowland South America

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Abstract Microcenters of diversity of crop plants are small geographic areas, while regions of diversity are large and relatively diffuse areas that conserve high or moderate genetic diversity, respectively. This study aimed to identify microcenters and regions of maize diversity in different areas of lowland South America, in Brazil and Uruguay, proposing a new methodological approach based on ethnobotanical, morphological, and molecular indicators and genetic diversity indices. The collection areas considered microcenters were surrounded by a buffer of 50 km (area: 7,850 km²) and the regions by buffers of 150 km (area: 70,650 km²) to 300 km (area: 282,600 km²). The study was carried out in parts of the biomes of Amazonia, Caatinga, Cerrado, Atlantic Forest, and Pampa. A total of 261 farmers participated, of whom 129 were interviewed. Four microcenters and four regions of maize diversity were identified, showing: (i) richness and genetic diversity of landraces (mostly unique to each region) and richness of maize races; (ii) the presence of landraces under diversification by current human action as diagnosed by sociocultural aspects and diversity of uses attributed to landraces; and, (iii) maize germplasm conservation areas, on microregional and regional geographic scales. Indicators of *strengths*, *weaknesses*, *opportunities*, and *threats* were identified in the areas involved in the study.

Key Words: Conservation, Diversity indices, Genetic resources, Landraces, Methodology, *Zea mays* spp. *mays*

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Introduction

Maize (*Zea mays* spp. *mays* L.; family Poaceae) domestication originated in Southwest Mexico 9,000 years before present (BP) (Matsuoka et al. 2002; Piperno et al. 2009), and the species was dispersed to South America at least ~7,150 years BP in Ecuador (Pearsall and Piperno 1990), ~6,850 years BP in lowland Bolivia (Lombardo et al. 2020), ~5,300 years BP in Rondônia, Brazil (Hilbert et al. 2017) and ~4,190 years BP in Uruguay (Iriarte et al. 2004). Genetic diversity of maize is distributed in different crop systems across the Americas (Bedoya et al. 2017; Bracco et al. 2016; Costa et al. 2022; Kato et al. 2009; Kistler et al. 2018; van Heerwaarden et al. 2011; Vigouroux et al. 2008) and around the world (Mir et al. 2013). The lowlands of South America, which include areas with altitudes below 1,500 m above sea level, are considered a secondary center of genetic diversity in maize (Brieger et al. 1958; Paterniani and Goodman 1977). A recent study involving archeological and molecular data considered Southwestern Amazonia a center of maize diversification (Kistler et al. 2018). Several recent studies on the genetic diversity of maize in lowland South America (Bedoya et al. 2017; Bracco et al. 2016; Kistler et al. 2018; van Heerwaarden et al. 2011) focused predominantly on ex situ collections and did not extensively explore the genetic diversity of maize conserved in situ/on farm in this region. We hypothesized that there are microcenters and regions of maize diversity in lowland South America, given the species' ample distribution (Costa et al. 2022) and history of landrace cultivation.

Different concepts and hypotheses about centers of diversity of crop species were presented throughout the twentieth century, and these concepts, as well as methodological proposals, continue to evolve in the twenty-first century. Vavilov always considered that there was a close relationship between the genetic diversity of cultivated plants and human societies (Vavilov 1951, 1992). Diversity centers refer to centers of germplasm accumulation and in situ domestication (Harlan 1971; Hawkes 1983) by human populations that obtain, cultivate, and improve their crops to guarantee food security (Clement 1999). To characterize an area as a center of diversity, genetic, biological, sociocultural,

ecological, and evolutionary factors are essential (Serratos 2009).

Diversity centers can involve different levels of spatial coverage—macrogeographic, mesogeographic, and microgeographic—where concentrations of diversity can be categorized (Harlan 1992). The regions considered centers of diversity are associated with relatively restricted areas with high diversity, and the microcenters of diversity are related to very restricted geographic areas, within which significant diversity is accumulated (Harlan 1971, 1992). Following the ideas of Hawkes (1983), Clement (1999) proposed a hierarchy of concentrations of diversity: (1) “minor centers of diversity” (like Harlan's (1971) microcenters), defined as small areas with moderate to high concentrations of diversity; (2) “regions of diversity,” considered extensive and relatively diffuse areas with moderate concentrations of diversity; and (3) “centers of diversity,” considered extensive areas with high concentrations of diversity.

A microcenter can cover an area of 1,000 to 10,000 km², according to Zimmerer and Douches (1991). In this case, the concentration of diversity is related to a specific human culture with associated management practices and uses, and therefore can be considered a center of accumulation over time (Clement 1999). In the Peruvian Altiplano, for example, microcenters often correspond to municipalities' political departments that reflect past and present patterns of economic and socio-cultural organization (Zimmerer and Douches 1991). The genetic diversity identified in the microcenters of diversity is shaped by human-eco-geographic aspects (interaction between society and the eco-geographic space), which involve ethnic groups whose inhabitants share a local identity and cultural traits, social relationships, land use and organization, and various economic factors (Zimmerer and Douches 1991; Zimmerer and de Hann 2017).

However, these genetic resources are vulnerable to losses within the farming system in which they are inserted, mainly because of the industrialization of agriculture, where family farmers have replaced their local varieties with commercial cultivars (John and Babu 2021). To identify priority areas for conservation, methodological approaches used in different surveys (Jarvis et al. 2008; Maxted and Vincent 2021;

Pacicco et al. 2018; Pironon et al. 2020) have considered parameters of richness and indices to measure diversity and mapped areas with the highest concentrations of diversity.

A survey involving data from 26 traditional communities from different continents (Africa, North America, South America, Asia, and Europe) used indicators and indices as measures of richness and genetic diversity and showed that an important diversity of landraces of 27 species is conserved by family farmers in small areas, indicating priority areas for agrobiodiversity conservation (Jarvis et al. 2008). This study was based on information generated from databases, unlike our study, which was carried out with data collected in situ, providing a more detailed and current characterization of the diversity present in these areas. Similar studies, conducted by Costa et al. (2017) and Silva et al. (2017, 2020a) in southern Brazil, found an abundance of maize landraces conserved in situ/on farm by family farmers in the microcenter of diversity identified in the region. One of these studies included a wide sample of family farmers in two municipalities using a methodological approach called the *Census of Diversity*, which is based on ethnobotanical data (Costa et al. 2017). This differs from the approach of our study, which combined data from ethnobotany with morphological and molecular data, including indices of genetic diversity and a much wider geographic coverage. Indicators and genetic diversity indices are useful tools to jointly analyze different variables and measure diversity in time and space (Brown 2008; Jarvis et al. 2008). The development of efficient conservation strategies requires a detailed understanding of the spatial patterns of genetic diversity (Altieri and Koohafkan 2008). In the case of maize, the distribution of landraces in agricultural landscapes can be an indicator of patterns of richness and uniformity of genetic diversity maintained in situ/on farm.

The dispersal of cultivated species is associated with diversification in different environmental and sociocultural contexts. A recent study showed the existence of inter-regional connections among different genetic groups of maize influenced by the expansion of the speakers of Tupi, Macro-Gê, and Arawak indigenous languages, where—from an apparent origin in Southwestern Amazonia—different migratory routes emerged and dispersed maize through

the Cerrado, Atlantic Forest, Caatinga, and Pampa biomes (Costa et al. 2022). Considering the expansion of the species in this part of the continent, the present research was developed with the objective of identifying microcenters and regions of maize diversity, proposing a new methodology involving ethnobotanical, morphological, molecular indicators, and diversity indices, to expand knowledge about the genetic diversity of the species conserved in situ/on farm in different areas, and in different biomes of lowland South America.

Materials and Methods

SAMPLING

Collections of maize landraces conserved by local communities were conducted in parts of five South American biomes (Amazonia, Cerrado, Caatinga, Atlantic Forest, and Pampa), including *ribeirinhos* (traditional communities along riversides in Amazonia), *quilombolas* (a quilombo is a Brazilian hinterland settlement founded by people of African origin), and agrarian reform settlers (Table 1). The collections were carried out in eight areas, including different municipalities and/or sections, which we call “localities,” and which were grouped as follows: (i) being involved in the same networks, which promote exchanges of local varieties among farmers; and (ii) related biocultural contexts. For this reason, diversity indicators and indices were calculated by collection area. It is important to clarify that we did not conduct an extensive survey in the whole region of lowland South America, but instead chose these areas considering the criteria described above, and previous knowledge that these areas would be important for maize conservation.

The term landraces is used in this study to refer to local varieties traditionally managed and reproduced by family farmers (Costa et al. 2017, 2021). The term maize race refers to a set of local varieties with common genetic characteristics, adapted to certain environmental conditions associated with particular social and cultural contexts (Lima 2016). The study was conducted with 261 family farmers who participated in seven *Workshops for Maize Race Conservation*, 129 interviewees who

TABLE 1. COLLECTION AREA CODE, COLLECTION AREAS, BIOMES, NUMBER OF FAMILY FARMERS PARTICIPATING IN THE RESEARCH (NFFP), NUMBER OF FAMILY FARMERS INTERVIEWED (NFFI), AND NUMBER OF FAMILY FARMERS WHO PARTICIPATED IN THE ANALYSIS OF *STRENGTHS*, *OPPORTUNITIES*, *WEAKNESSES*, AND *THREATS* (SWOT) IN BRAZIL AND URUGUAY

| Area code | Collection areas ¹ | Biome | NFFP | NFFI | SWOT ² |
|-----------|-------------------------------|-----------------|------|------|-------------------|
| Brazil | | | | | |
| I | 1 locality, RO | Amazonia | 12 | 12 | – |
| II | 7 locations in PB | Caatinga | 50 | 20 | – |
| III | 10 locations in MS | Cerrado | 66 | 15 | 66 |
| IVa | 6 locations in MG | Atlantic Forest | 55 | 15 | 30 |
| IVb | 1 locality in RS | Atlantic Forest | 40 | 28 | 40 |
| Uruguay | | | | | |
| Va | 7 locations, TA/RV | Pampa | 14 | 13 | 14 |
| Vb | 4 locations, RO/TT | Pampa | 14 | 14 | – |
| Vc | 1 locality, CA | Pampa | 10 | 12 | – |
| Total | 37 locations | | 261 | 129 | 150 |

¹Collection areas, including municipalities and/or sections (localities) involved in the research: (I) Amazonia—Gua-jará-Mirim, in Rondônia; (II) Caatinga—Esperança*, Solânea, Arara, Queimadas, Alagoa Nova, Remígio and Montadas, in Paraíba; (III) Cerrado—Juti*, Campo Grande, Maracaju, Sidrolândia, Mundo Novo, Porto Murinho, Rio Brillhante, Itaquiraí, Dourados and Caarapó, in Mato Grosso do Sul; (IVa) Atlantic Forest—Divino*, Carangola, Simonesia, Lajinha, Conceição de Ipanema and Sem Peixe, in Minas Gerais; (IVb) Atlantic Forest—Ibarama*, in Rio Grande do Sul; and in Uruguay, (Va) Pampa—sections Cuarta, Sexta, Doce, Trece, in Tacuarembó; Tercera, Segunda and Novena, in Rivera; (Vb) Pampa—Quinta, in Treinta y Tres; and municipalities of Castillos, Rocha, Velazquez, in Rocha; and (Vc) Pampa—Tala*, in Canelones. *Municipalities/sections where the workshops were held. In the region of Tacuarembó/Rivera (Va), the Workshop was strategically held in the Primeira section*, in Tacuarembó, and in Rocha/Treinta y Tres (Vb), in La Paloma*, Rocha. ²Not applicable (-) was assigned to SWOT (*Strengths*, *Opportunities*, *Weaknesses*, and *Threats*), referring to areas where SWOT analysis was not carried out during the *Workshops for Maize Races Conservation*, due to lack of space or time

collaborated in the ethnobotanical characterization, and 150 farmers who participated in the analysis of *Strengths*, *Weaknesses*, *Opportunities*, and *Threats* (SWOT) (Table 1). The *Workshops* were set up as training spaces about maize races and were designed for farmers, technicians, extensionists, researchers, teachers, and students. This training was carried out in the form of didactic workshops, in which the project proposal, the history of maize (origin, domestication, dispersal, and diversification), the background of studies of maize races in Brazil and Uruguay, and the main challenges for the conservation of agrobiodiversity were presented.

Sampling is an important process in genetic diversity studies and can have a significant impact on the indices calculated to assess this genetic diversity (Bashalkhanov et al. 2009; Franco et al. 2006). Small sample sizes can

lead to errors in estimating genetic diversity because they do not adequately capture the genetic variability present in an area, leading to an underestimation of diversity. On the other hand, a large sample may not add significant information. The number of family farmers who participated in each area was determined by the indication of local partners, logistics, and the family farmers' own interest in participating and collaborating with the research, which is reflected in the heterogeneous sampling and diversity results presented in this study. This heterogeneous sampling also led to differences in the number of ears examined in the phenotypic and genotypic analyses per area, which can be considered a vulnerability. Data on farmers' profiles, such as age, ethnicity/origin, and farming experience, are presented in Table 2 and in Supplementary Data Table S1. Farming experiences included

agriculture, horticulture, fishing, extractivism, livestock, fruit cultivation, handcraft, rubber extraction, and hunting, among others. The farmers' origins varied among Brazilian, Uruguayan, Bolivian, Indigenous, Peruvian, Paraguayan, Portuguese, Afro-descendant, German, Italian, Polish, Spanish, Mixed Race, European, and Criollo. The two most spoken languages were Portuguese (Brazil) and Spanish (Uruguay), but we also interviewed indigenous farmers speaking Guarani in the Cerrado region in Brazil. The average age of farmers varied between 48 (Cerrado biome) and 64 (Amazonia biome) years.

To carry out germplasm collections and ethnobotanical characterization, two strategies were developed: the first, during the *Workshop*, and the second, during in situ visits to the interviewees' properties. At the *Workshops*, family farmers were invited to bring the ears of each landrace they conserved. Farmers were instructed to carry out the selection of ears, when possible, at the time of harvest, always choosing those that they considered representative of the landrace. During the collections, an attempt was made to obtain the maximum diversity of maize landraces present in each area, since the collections were carried out with the objective of classifying the maize races. For the landraces that were not stored on the ear, a quantity of threshed seeds was collected for molecular characterization and ex situ conservation, and for those landraces in which the farmers did not have a stock of ears and/or seeds, only the interview was carried out, recording the presence of that landrace in the collection area. The team carried out in situ visits and a total of seven workshops in the areas selected, except in Amazonia, where the only strategy for collecting and interviewing was carried out in situ, in riverside communities of the Rio Ouro Preto Agroextractive Reserve (Rio Ouro Preto RESEX), in Guajará-Mirim, Rondônia, Brazil. The collection was supported by a collaborative research network of the project, involving universities, organizations that work with family farming, research, and extension institutions, which was called the Collaborative Research Network of the Interdisciplinary Group of Studies in Agrobiodiversity.

ETHNOBOTANICAL CHARACTERIZATION

Ethnobotanical characterization was carried out through semi-structured interviews, using a questionnaire (Supplementary Data Appendix S1), composed of questions that involved the identification of farmers and the collection of information about the maize landraces, including: local name, origin, time of cultivation, uses and records associated with cultivation, and the history of maize in the region (Supplementary Data Table S2). Ethnobotanical data were analyzed with descriptive statistics.

PHENOTYPIC CHARACTERIZATION

For each landrace, five ears were collected, according to the availability of cobs at the time of collection. A total of 284 maize landraces (212 in Brazil and 72 in Uruguay) were phenotypically characterized (Supplementary Data Table S3). The phenotypic characterization was performed using 19 morphological descriptors of the ear and grain, considered keys for the classification of maize races (Bird and Goodman 1977; Silva et al. 2017, 2020b), with ten qualitative and nine quantitative characteristics (Table 3).

The classification of maize races used in the present study was developed by Silva et al. (2020b), where data analysis was performed separately for each grain type and for each country, except for popcorn, in which data from Brazil and Uruguay were considered together. The analyses included qualitative variables obtained from the absolute frequencies of each variation/category within the characteristic, with the highest frequency value (mode) being adopted to characterize the variety for that variable. For quantitative variables, the arithmetic means were estimated.

MOLECULAR CHARACTERIZATION

Molecular characterization was performed on 209 maize accessions, 120 from Brazil and 89 from Uruguay. DNA extraction of local varieties was conducted by gathering a leaf *bulk* of 30 individuals from each accession (Bedoya et al. 2017). After collection, the leaves were freeze-dried and

TABLE 2. PROFILES OF FAMILY FARMERS INTERVIEWED IN BRAZIL AND URUGUAY

| Area code | Biome | Farming experience | Ethnicity/origin | Language | Farmer's average age | Gender ¹ | NFFI ² |
|-----------|-------------------------------|--|---|---------------------|----------------------|---------------------|-------------------|
| Brazil | | | | | | | |
| I | Amazonia | Agriculture, fishing, extractivism, handicraft, rubber tappers, babassu oil, hunting | Brazilian, Bolivian, Indigenous, Peruvian, Portuguese | Portuguese | 64 | Female | 3 |
| | | | | | | Male | 6 |
| | | | | | | Male and female | 3 |
| II | Caatinga | Agriculture, animal production, dairy production, agroecological fair, livestock, seed sales | Brazilian | Portuguese | 55 | Female | 3 |
| | | | | | | Male | 14 |
| | | | | | | Male and female | 3 |
| III | Cerrado | Agriculture, dairy production, grains, fruit cultivation, olericultures, horticulture, handicraft, livestock, manioc | Indigenous, Italian, Paraguayan | Guarani, Portuguese | 48 | Female | 4 |
| | | | | | | Male | 8 |
| | | | | | | Male and Female | 3 |
| IVa | Atlantic Forest | Agriculture, coffee, maize, manioc, beans, dairy, horticulture, fruit cultivation, flour house | Afro-descendant, Brazilian, German, Italian, Indigenous | Portuguese | 50 | Female | 3 |
| | | | | | | Male | 10 |
| | | | | | | Male and female | 2 |
| IVb | Pampa-Atlantic Forest Ecotone | Agriculture, beans, maize, manioc, horticulture, livestock, forage crops, fruit cultivation, handicraft, olericulture, tobacco | Brazilian, German, Italian, Polish, Spanish, Mixed Race | Portuguese | 55 | Female | 6 |
| | | | | | | Male | 21 |
| | | | | | | Male and female | 1 |

Table 2. (continued)

| Area code | Biome | Farming experience | Ethnicity/origin | Language | Farmer's average age | Gender ¹ | NFFI ² |
|-----------|-------|---|--|---------------------|----------------------|---------------------|-------------------|
| Uruguay | | | | | | | |
| Va | Pampa | Livestock and dairy, horticulture, tobacco | Brazilian, Criollo, European, Italian, Spanish, Mixed Race | Portuguese, Spanish | 59 | Female | 5 |
| | | | | | | Male | 8 |
| Vb | Pampa | Livestock and dairy, canned foods, horticulture | Italian, Polish, Spanish, Mixed Race | Spanish | 54 | Female | 5 |
| | | | | | | Male | 9 |
| Vc | Pampa | Aviculture, forage crops, horticulture, livestock | European, Spanish | Spanish | 57 | Female | 3 |
| | | | | | | Male | 8 |
| | | | | | | Male and female | 1 |
| Total | | | | | | | 129 |

¹Gender: (1) "Male," when only the man participated in the interview; (2) "Female," when only the woman participated in the interview; and (3) "Male and female," when the couple participated in the interview together. ²Number of family farmers interviewed

TABLE 3. MORPHOLOGICAL DESCRIPTORS USED TO CHARACTERIZE EARS AND GRAINS TO CLASSIFY MAIZE RACES FROM BRAZIL AND URUGUAY (SILVA ET AL. 2020B)

| | Qualitative descriptors | Quantitative descriptors |
|----------------|-----------------------------------|--------------------------|
| Ear | Kernel color texture (crown) | Number of grains per row |
| | Kernel crown color | Ear length (cm) |
| | Grain type (endosperm) | Ear diameter (cm) |
| | Ear shape | Cob diameter (cm) |
| | Kernel row arrangement | Rachis diameter (cm) |
| | Cob color | Number of rows |
| Kernel (grain) | Pericarp color | Kernel length (mm) |
| | Grain color | Kernel width (mm) |
| | Kernel shape | Kernel thickness (mm) |
| | Kernel shape of the upper surface | |

sent to the *Genetic Analysis Service for Agriculture* (SAGA) of CIMMYT, located in Mexico, where DNA extraction and molecular characterization were performed. The samples were extracted using the modified CTAB method (Doyle and Doyle 1990). Molecular characterization was performed by DArTseq technology (Al-Beyroutiová et al. 2016; Sansaloni et al. 2011), using the *HiSeq 2500* sequencer from *Illumina*

(<http://www.illumina.com>). SNP markers were identified de novo by comparing the sequences of fragments present in genomic libraries obtained in this assay, and processed later in the analytical pipeline (DArTsoft14). Thus, SNP calling was done completely independent of any reference genome, which makes this strategy an excellent resource to evaluate the genetic diversity of any species (Sansaloni et al. 2020).

Markers were filtered based on the following criteria: *Call Rate* (proportion of samples for which the corresponding marker information does not correspond to missing data) ≥ 0.95 ; *RepAvg* (proportion of replicated technical assay pairs for which the marker score is consistent) ≥ 0.85 ; *AvgPIC* (average of polymorphism information content of reference alleles and SNPs) > 0 . Molecular characterization resulted in 50,696 SNP markers, and from the filters, 5313 SNPs were selected for statistical analysis (Supplementary Data Table S4). The genetic diversity parameters observed heterozygosity (H_O) and Nei's (1978) genetic diversity index (D) (or expected heterozygosity— H_E) were estimated using hierfstat (Goudet 2005) and poppr (Kamvar et al. 2014) for R (R Development Core Team 2015). In this study, the diversity parameters were considered indicators of genetic diversity, since the samples were extracted through *bulks* of individuals, which formed a composite sample representative of each accession and did not allow identifying changes in populations such as erosion or genetic drift.

GENETIC DIVERSITY INDICES AS METHODOLOGICAL TOOLS FOR IDENTIFYING MICROCENTERS AND REGIONS OF MAIZE DIVERSITY

Indicators are obtained by measuring individual or collective variables from data collections to generate information with the potential to guide decisions and actions in each context (Brown 2008). Decisions related to the genetic diversity of cultivated plants are taken at the local, national, and international levels (Brown 2008). Genetic diversity indicators can be used to guide these decisions, monitor the conservation of genetic resources available to farmers, and signal problems for conservation. In the case of plant genetic resources for food and agriculture, FAO suggests three types of indicators: (i) Indicators that measure the current state of permanent genetic diversity, *in situ* (in fields or natural areas) and *ex situ* (in germplasm banks or gene banks); (ii) indicators that monitor changes over time, in particular indicators of the rate of loss of diversity or genetic erosion; and (iii) indicators that assess diversity in space (Brown 2008). From the ethnobotanical, phenotypic, and molecular characterizations, the following indicators of genetic diversity were

generated in each collection area: (i) ethnobotanical indicators: average number of landraces per farmer (*NLF*), richness of local names (*RLN*), richness of unique names (*RUN*), richness of culinary uses (*RCU*), richness of origin (*RO*), and average time of cultivation (*ATC*); (ii) phenotypic indicators: richness of grain color (*RGC*), richness of grain type (*RGT*), race richness (*RR*), richness of unique races (*RUR*), and Shannon index of qualitative descriptors (*H'QD*); and (iii) molecular indicators: Nei's (1978) genetic diversity index (D) and observed heterozygosity (H_O). The *RUN* and *RUR* indicators involve the "exclusive" character corresponding to local names and races with a presence identified exclusively in a collection area. The *H'QD* indicator considered the following qualitative descriptors: kernel color texture, kernel color, grain type, ear shape, kernel row arrangement, cob color, pericarp color, grain color, kernel shape, and kernel shape of the upper surface. We considered the *H'QD* because these descriptors are considered key to classifying maize races. Richness represents a direct measure of diversity that should be understood as the number of observed diversity units and has been widely used to estimate the diversity of plant populations (Frankel et al. 1995).

Genetic diversity indices were generated for each collection area (Brown 2008; Jarvis et al. 2008; Pacicco et al. 2018), based on the data obtained for each indicator (Fig. 1). This was the methodological tool proposed by this study for the characterization of microcenters and regions of diversity, which can be used and adapted to the study of other species. For each ethnobotanical and phenotypic indicator, the Shannon diversity index (H') was calculated (Shannon 1948). For the molecular indicators, the genetic diversity index of Nei (1978) (D) and the observed heterozygosity (H_O) were considered. From the arithmetic means of the ethnobotanical, phenotypic, and molecular indices, a single index was generated for each category, called "Ethno Index," "Pheno Index," and "Mol Index," respectively. The arithmetic means of these indices were obtained with the aim of estimating a local mean value of reference per collection area. The H' was calculated using the PAST software version 4.0 (Hammer et al. 2001), which considers the following formula:

$$H' = \sum_{i=1}^s p_i \ln p_i$$

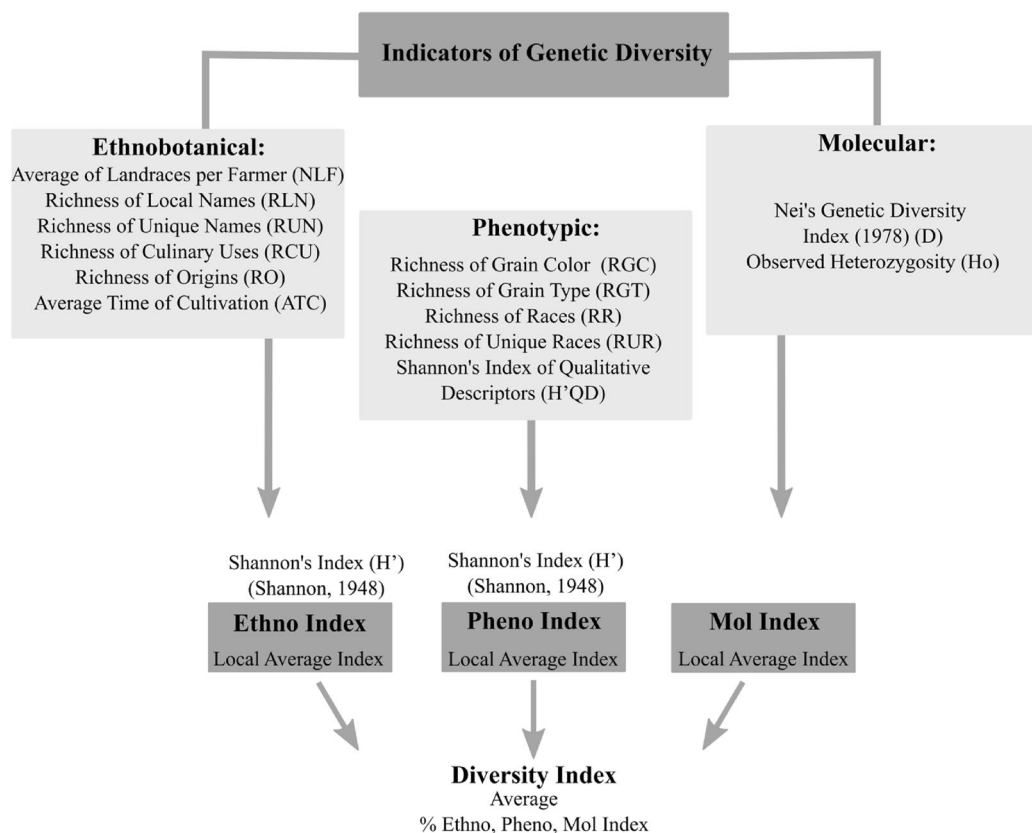


Fig. 1. Diversity index presented as a methodological tool for characterizing the microcenters and regions of maize diversity in lowland South America. The arithmetic means of the genetic diversity indices generated based on the data obtained for each ethnobotanical, phenotypic, and molecular indicator were considered to obtain the local average indices: (i) Ethno Index = $[(NLF + RLN + RUN + RCU + RO + ATC) / 6]$; (ii) Pheno Index = $[(RGC + RGT + RR + RUR + H'QD) / 5]$; and (iii) Mol Index = $[(D + H_o) / 2]$. The different local average indices were weighted by estimating the percentage of these indices, and then the arithmetic averages were estimated, generating the “Diversity Index,” as a reference value of genetic diversity per collection area

where p_i is the relative abundance (proportion) of landrace i in the sample; $p_i = n_i / N$; n_i is the number of individuals of landrace i ; N is the total number of individuals in the sample.

The Shannon index (H') is used to measure variability based on the richness and frequency with which a variable or character occurs (Brown 2008; Jarvis et al. 2008). This index allows for comparisons between different areas, which can be correlated with other factors, such as ecogeographic and cultural contexts (Li et al. 2002; Vilaró et al. 2020). In this study, H' corresponds to a diversity index used to quantify diversity in categorical data and considers the respective proportions

of landraces in each class of analyzed variable within the study area (richness and abundance). The Shannon index has been used in other studies to estimate the diversity of maize populations based on morphological characteristics (Costa et al. 2017; Li et al. 2002; Vilaró et al. 2020).

A weighted measure of diversity was used by estimating the percentage of each index (Ethno, Pheno, and Mol), and we considered the average percentage of the three indices as a reference measure of diversity for each area (Supplementary Data Table S5). The percentage referring to each Index (Ethno, Pheno, and Mol) was estimated using the following calculation:

$$\% = \frac{\text{Index (Ethno, Pheno or Mol)}}{\text{Maximum Observed Index (Ethno, Pheno or Mol)}} \times 100$$

Then, “the arithmetic means of these three indices were estimated, generating a reference value of the genetic diversity “Diversity Index” per collection area (Fig. 1). Based on the diversity indices, areas of high diversity were considered > 70%; moderate diversity areas > 35% and < 70%; and areas of low diversity < 35%.

In this study, we considered the terms microcenters (Harlan 1992) and minor centers of diversity (Clement 1999; Hawkes 1983) as synonymous, and we will use the term microcenters of diversity. Areas < 10,000 km² were considered microcenters and areas > 10,000 km² are regions, according to Zimmerer and Douches (1991). The collection areas grouped by biocultural context and related farmer seed networks were surrounded by buffers of 50 km (area: 7850 km²), 150 km (area: 70,650 km²), and 300 km (area: 282,600 km²), with the areas constituted by the 50 km buffers considered microcentres and the others as regions. Biocultural contexts involve interrelated biological and cultural manifestations that co-evolve within complex social-ecological systems (Maffi 2015). Farmer seed networks transfer seed from domesticated or undomesticated plants via farmer-to-farmer gifting, swapping, bartering, or purchase, as well as via trading or sale, which occurs outside of the commercial seed sector and formal regulation (Coomes et al. 2015). A map of the geographic distribution of the identified microcenters and regions of diversity was prepared using QGIS software (<http://qgisbrasil.org>). The areas related to the microcenters and regions of diversity and the research locations encircled by the 50 km, 150 km, and 300 km buffers were projected on the map, considering the levels of diversity identified by the genetic diversity indices for these areas.

ANALYSIS OF STRENGTHS, WEAKNESSES, OPPORTUNITIES, AND THREATS FOR THE CONSERVATION OF AGROBIODIVERSITY

SWOT analysis, an acronym for “*Strengths, Weaknesses, Opportunities, and Threats*,” is a tool used to identify and analyze internal and external factors that can impact the viability of objectives, projects, institutions, or organizations and has

been used as a technique for strategic planning (Fig. 2) (FAO 2006, 2018). This analysis provides a picture of current “reality” and, therefore, serves as a tool for analyzing a situation (or environment) and a diagnosis (Jacobsen et al. 2015; Schroeder et al. 2013; Valverde et al. 2015). During the *Workshops for Maize Races Conservation* and with the participation of 150 farmers in three of the collection areas in Brazil (III: Mato Grosso do Sul, 66 participants; IVa: Minas Gerais, 30; and IVb: Rio Grande do Sul, 40) and one collection area in Uruguay (Va: Tacuarembó, 14) (Table 1), the SWOT analysis was performed with the objective of identifying the main challenges that farmers face in the conservation of agrobiodiversity, especially in relation to landraces. This activity was not carried out in the other areas due to a lack of time during the *Workshops*. Participants were divided into subgroups that varied according to the number of participants, municipality, community, and/or other criteria, such as women’s groups and youth groups. Each subgroup had the collaboration of a facilitator, and the teams, after discussing the proposal, presented the topics identified and the summary of the discussion to the plenary. Interviewing 150 farmers across these areas is somewhat limited, but it did provide important data in terms of *Strengths, Weaknesses, Opportunities, and Threats*.

Results

ETHNOBOTANICAL, PHENOTYPIC, AND MOLECULAR CHARACTERIZATION OF MAIZE DIVERSITY

The ethnobotanical characterization allowed the identification of 386 maize landraces conserved in situ/on farm by family farmers (Supplementary Data Table S2). The geographic distribution of landraces (Fig. 3) was concentrated in smaller areas, which were classified as microcenters (buffer: 50 km), including areas I, II, IVb, and Vc, and less concentrated in more extensive areas (buffers: 150 km and 300 km), III, IVa, Va, and Vb. The ears shown on the map indicate

| SWOT | Enhancing factors | Inhibiting factors |
|-------------------------|--|--|
| Internal factors | STRENGTHS <i>Internal attributes and resources that support a successful outcome</i> | WEAKNESSES <i>Internal attributes and resources that work against a successful outcome</i> |
| External factors | OPPORTUNITIES <i>External factors that can be used as an advantage</i> | THREATS <i>External factors that could jeopardize success</i> |

Fig. 2. Methodological approach of the SWOT analysis (FAO 2006, 2018) used with the objective of identifying the main challenges that farmers face for the conservation of agrobiodiversity in lowland South America

the richness of maize races based on phenotypic characterization. A maize race is composed of a set of landraces, and for representation in this figure, only one ear of each race was selected to represent it. This illustration has no direct relation to the number of landraces in each area.

The genetic diversity of maize landraces was evaluated using ethnobotanical, phenotypic, and molecular indicators per collection area (Supplementary Data Table S6). Among the study areas, the average number of landraces conserved per farmer ranged from one (Pampa, Vc) to four (Mata Atlântica, IVa). A richness of 120 local names attributed to the landraces from Brazil and 39 from Uruguay was identified. In Brazil, the richness of local names ranged from 17 in the Caatinga and Amazonia to 47 in the Atlantic Forest (IVa), and in the Pampa (Uruguay), from 8 to 25. Among the names identified, 134 were exclusive to the areas of Brazil and Uruguay, and only 23 were common to two or more collection areas. The unique names ranged from 4 in the Pampa (Vc) to 33 in the Atlantic Forest (IVa) (Supplementary Data Table S7).

The uses and preferences attributed to the landraces are associated with the characteristics that farmers consider important, especially for food, which influence the selection of their landraces. Thirty-four culinary use values associated with the landraces were identified, represented by direct food uses, culinary potential, and food attributes that are appreciated by farmers (Supplementary Data Table S6). The top four

were “Corn on the cob” (24%), *Pamonha/Curau* (11%), “Cake/Bread” (10%), and “Flour” (8%). The area with the greatest richness of uses was Amazonia (20), followed by the Atlantic Forest-IVa (18) and Caatinga (15) (Table 4 and Supplementary Data Table S6).

The networks of origin of maize landraces correspond to the sources from which farmers obtain their seeds and can be considered an indicator of diversity, as gene flow can promote diversity (Louette et al. 1997). Thus, the richness of origin configures the circulation networks of landraces among farmers in an area. In this study, farmers obtained their seeds mainly through “Family Heritage” (21%), “Neighbors” (16%), “Seed Exchange Meetings” (11%), and “Exchanges between Friends/Relatives” (11%). These results demonstrate that the main source for obtaining the landraces is the region itself (endogenous origin). However, some farmers also introduced landraces from other areas, where 26 (7%) landraces had an exogenous origin; that is, they migrated from other areas and even from other countries, such as Bolivia, Peru, and Argentina.

The growing time for the landraces is associated with their adaptation to the ecological conditions and sociocultural aspects specific to each area. Landraces with minimum, average, and maximum conservation times of 1, 15, and 100 years, respectively, were identified. The average times of the collection areas ranged from 8 years in the Cerrado to 36 years in Amazonia. The maximum time of 100 years was observed

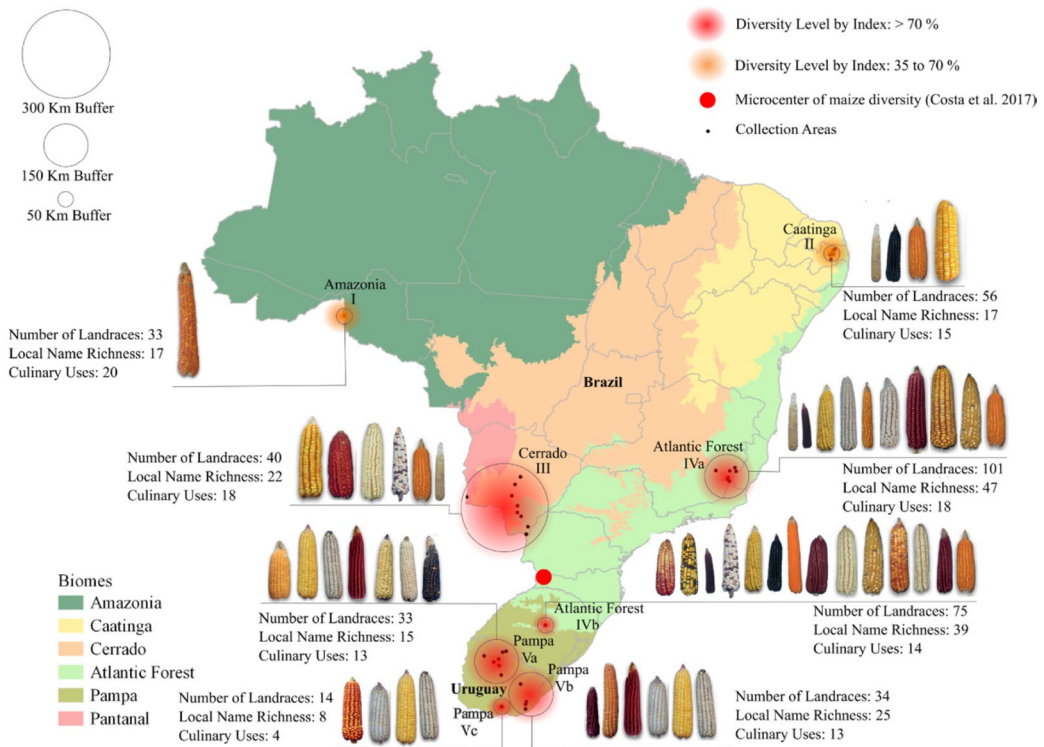


Fig. 3. Microcenters and regions of maize genetic diversity identified in different biomes of lowland South America. The collection areas considered microcenters were surrounded by a buffer of 50 km (area: 7850 km²) and the regions by buffers of 150 km (area: 70,650 km²) and 300 km (area: 282,600 km²), and the levels of diversity identified by the indices were projected on the map. The ears show the richness of maize races present in each microcenter or region, based on phenotypic characterization. The colors at the base of the map represent the distribution of biomes in Brazil and Uruguay (IBGE 2021)

in the Cerrado and the Atlantic Forest (IVa). The results also revealed that (i) 50% of the landraces are cultivated from 0 to 5 years by the same family, (ii) 15% from 6 to 10 years, (iii) 20% from 11 to 30 years, and (iv) 15% have been cultivating them for over 30 years.

Regarding the destination and use of the production, the landraces are used mainly for “Family Food” (44%), that is the direct use as human food in the most diverse ways; “Animal Food” (33%), in the form of silage, grain, and feed; and “Sale” (16%), of seeds, grains, straw for handicrafts, corn on the cob, flour, and hominy, among others. The less frequent categories occurred locally: “Seed Donation” in the Caatinga, Atlantic Forest (IVa), and Pampa (Vb); “Multiplication of Seeds” only in the Cerrado and Pampa (Va); and “Handicrafts” in the

Atlantic Forest (IVb) and Amazonia. Associated with culinary and agronomic attributes, farmers indicated at least 16 reasons why the conservation of landraces is carried out, the four main ones being “Animals like it” (31%), related to palatability; “Conservation of diversity” (15%), related to aspects relevant to the maintenance and richness of species diversity, such as conserving more than two landraces; “Family Tradition” (14%), related to cultural values derived from customs, traditions, and family heritage; and “Seed autonomy” (11%), whether political, economic, and/or related to food security.

Regarding the farming systems, 78% of the landraces are managed in “swiddens/farm plots,” 18% in “homegardens,” and 3% in the “forest” (recently opened smaller swiddens), with the latter category being observed only in Amazonia

(100%), and in the Cerrado (3%), where landraces are cultivated in the “forest,” in combination with other species within a system of shifting cultivation. This category coincides with the presence of indigenous and ribeirinho communities in these states, since in the other collection areas, these actors were not interviewed. In the Atlantic Forest (IVb) and the Caatinga, 100% of the landraces are managed in “swidens/farm plots.” Maize is grown singly or intercropped with one or more species, such as beans (*Phaseolus vulgaris*), fava beans (*Vicia faba*), pumpkins (*Cucurbita* spp.), manioc (*Manihot esculenta*), sweet potatoes (*Ipomoea batatas*), and coffee (*Coffea arabica*). Proportionally, the management of landraces in homegardens was higher in Uruguay (43%) than in Brazil (8%).

Twenty-nine criteria that farmers use to select their seeds for cultivation were identified, and the three with the highest percentage of citations were as follows: “Ear size” (19%), “Grain uniformity” (17%), and “Healthy ear” (12%). Twenty-two selection criteria (76%) mentioned by farmers were related to the characteristics of the ear and grain, agreeing with the key scientific descriptors used to identify maize races (Bird and Goodman 1977).

The phenotypic characterization showed high variation for the descriptors evaluated in the maize landraces. We characterized 4 landraces in collection area I (Rondonia), 48 in area II (Paraíba), 16 in area III (Mato Grosso do Sul), 85 in area IVa (Minas Gerais), 59 in area IVb (Rio Grande do Sul), 30 in area Va (Tacuarembó/Rivera), 25 in area Vb (Rocha/Treinta y Tres), and 14 in area Vc (Canelones). Considering all the collection areas, 11 grain colors were identified: yellow (32%), orange (27%), white (17%), red (6%), light yellow (5.6%), purple (5.3%), brown (3%), black (1.4%), pink (1%), wine (1%) and cream (0.7%); and for grain type, a total of 8 types were observed: dent (51%), semi-dent (16%), flint (11%), semi-flint (11%), flinty (7%), popcorn (7%), tunicate (0.7%), and sweet (0.3%). The areas that presented the highest values for grain color were the Atlantic Forest, IVa (9) and IVb (8), Caatinga (6), Cerrado (6), and Pampa, Vb (6); and for grain type, the highest values were found in the Atlantic Forest, IVa (6) and IVb (5), Caatinga (5), Cerrado (5), and Pampa, Va (5). The Shannon index based on the ten qualitative phenotypic descriptors showed the highest values in the Atlantic Forest, IVa (1.20) and IVb (1.15), Pampa, Vb (1.08), and Caatinga (1.03).

The maize races were characterized with 19 descriptors, which combined gave identity to different groups of landraces. In total, 25 maize races were identified in Brazil and 10 in Uruguay. The richness of races per area ranged from 1 to 14, with the highest richness identified in the Atlantic Forest, IVb (14) and IVa (10), and in the Pampa, Va (7). The areas that showed the greatest richness of unique races were the Atlantic Forest, IVb (7) and IVa (4), and Cerrado (3) (Supplementary Data Table S8). The number of rows 22 and 26, characterized for race classification, were identified only in the Atlantic Forest (IVb). Likewise, the interlocked arrangement of grains was observed only in Amazonia, as noted in previous studies (Brieger et al. 1958; Costa et al. 2021; Paterniani and Goodman 1977). The sweet grain type was identified only in the Atlantic Forest (IVb).

For the molecular indicators, we genotyped 8 accessions in collection area I (Rondonia), 25 in area II (Paraíba), 15 in area III (Mato Grosso do Sul), 46 in area IVa (Minas Gerais), 26 in area IVb (Rio Grande do Sul), in Brazil, and 50 in area Va (Tacuarembó/Rivera), 22 in area Vb (Rocha/Treinta y Tres), and 17 in area Vc (Canelones), in Uruguay. The highest genetic diversity values were observed in the Pampa, Vc ($H_O=0.333$ and $D=0.219$) and Va ($H_O=0.302$ and $D=0.214$), Atlantic Forest, IVa ($H_O=0.281$ and $D=0.205$), Caatinga ($H_O=0.243$ and $D=0.188$), and Pampa, Vb ($H_O=0.230$ and $D=0.196$). The molecular data was further explored in another study, which aimed to identify dispersal patterns of maize genetic diversity in this part of the continent (Costa et al., 2022). The genetic groups were structured according to the predominance of endosperm types (popcorn, flinty, flint/semi-flint). The genomic analyses suggested different dispersal patterns for each endosperm type and can be associated with hypotheses of expansions of different indigenous groups (Costa et al., 2022).

MICROCENTERS OF MAIZE GENETIC DIVERSITY IN LOWLAND SOUTH AMERICA

Based on ethnobotanical, phenotypic, and molecular indicators (Supplementary Data Table S6), different indices of genetic diversity were calculated (Table 5) with the purpose of characterizing the diversity of maize present in these areas, as well as obtaining parameters

TABLE 4. CULINARY USES AND ATTRIBUTES OF LOCAL MAIZE LANDRACES IDENTIFIED IN LOWLANDS OF SOUTH AMERICA

| Area code | Collection areas ¹ | Biome | Culinary uses and attributes |
|-----------|-------------------------------|-----------------|--|
| Brazil | | | |
| I | 1 locality, RO | Amazonia | Uses: corn on the cob, pamonha/curau*, cake/bread, hominy, cuscuz*, chicha*, porridge, munguzá (chá de burro)*, toasted, polenta/angu*, flour, soup, cream, popcorn, xerém*, maize meal; attributes: sweet, flavor, consistency, pops well |
| II | 7 locations, PB | Caatinga | Uses: corn on the cob, pamonha/curau*, hominy, polenta/angu*, cake/bread/broa, fuba, cuscuz*, munguzá*, maize meal, cornstarch, popcorn; attributes: sweet, soft, taste, consistency |
| III | 10 locations, MS | Cerrado | Uses: cake/bread, boiled maize, polenta/angu*, maize meal, pamonha/curau*, flour, hominy, canjicão, canjiquinha*, chicha*, chipa*, cream, popcorn; attributes: soft, flavor, sweet, consistency, pops well |
| IVa | 6 locations, MG | Atlantic forest | Uses: corn on the cob, cake/bread, porridge, flour, canjiquinha*, pamonha/curau*, polenta/angu*, maize meal, canjicão*, popcorn, beiju flour*, hominy, cuscuz*, pudding, cornstarch; attributes: softness, taste, pops well |
| IVb | 1 location, RS | Atlantic forest | Uses: flour, corn on the cob, softness, cake/bread, polenta/angu*, hominy, popcorn, porridge, pamonha/curau*, soup, juice; attributes: sweet, taste, healthy/nutritious |
| Uruguay | | | |
| Va | 7 locations, TA/RV | Pampa | Uses: corn on the cob, flour, polenta/angu*, cake/bread, hominy, gofio*, popcorn, torta frita*; attributes: taste, sweet, consistency, soft, healthy/nutritious |
| Vb | 4 locations, RO/TT | Pampa | Uses: corn on the cob, flour, locro*, popcorn, hominy, polenta/angu*, soup, puchero*; attributes: taste, sweet, healthy/nutritious, consistency, soft |
| Vc | 1 locality, CA | Pampa | Uses: puchero*; attributes: flavor, healthy/nutritious, soft |

¹Collection areas, including municipalities and/or sections (localities) involved in the research: (I) Amazonia—Guajará-Mirim, in Rondônia; (II) Caatinga—Esperança, Solânea, Arara, Queimadas, Alagoa Nova, Remígio and Montadas, in Paraíba; (III) Cerrado—Juti, Campo Grande, Maracaju, Sidrolândia, Mundo Novo, Porto Murinho, Rio Brilhante, Itaquiraí, Dourados and Caarapó, in Mato Grosso do Sul; (IVa) Atlantic Forest—Divino, Carangola, Simonesia, Lajinha, Conceição de Ipanema and Sem Peixe, in Minas Gerais; (IVb) Atlantic Forest—Ibarama, in Rio Grande do Sul; and in Uruguay, (Va) Pampa—sections Cuarta, Sexta, Doce, Trece, in Tacuarembó; Tercera, Segunda and Novena, in Rivera; (Vb) Pampa—Quinta, in Treinta y Tres; and municipalities of Castillos, Rocha, Velazquez, in Rocha; and (Vc) Pampa—Tala, in Canelones. *Typical culinary uses of maize (in alphabetical order): canjicão (a delicacy whose method of preparation is similar to hominy), canjiquinha (a Brazilian delicacy, typical of some regions, which consists of coarsely ground maize until it crumbles, cooked with pork—usually ribs—and other homemade seasonings), chicha (fermented drink of indigenous origin), chipa (pie prepared with crushed boiled maize, onion, cheese and milk, cooked in the oven), Cuscuz (prepared with semolina—incomplete grinding – maize grain), beiju flour (flaked maize flour), gofio (a type of roasted maize flour, consumed with hot milk and sugar or only with sugar), locro (a stew made from pumpkin, beans and maize kernels), accompanied with meat, garlic and oregano and sometimes tomato sauce); Guarani indigenous people prepare it with poultry and vegetables), munguzá (porridge), munguzá (chá de burro) (porridge made with Brazil nut milk (*Bertholletia excelsa*) and maize), pamonha/curau (a delicacy prepared with crushed boiled maize, seasoned with sugar or salt, then boiled and rolled in maize husks or banana leaves), puchero (stew with meat, bacon, cabbage, corn on the cob, onions, celery, carrots, sweet potatoes, squash, and potatoes; all these ingredients cut into large pieces are cooked), fried pie (dough usually prepared with wheat flour; sometimes, it can be mixed with maize flour and fried) and xerém (dish made with grains of dry maize broken in the pestle, cooked in water and salt; it can be served with milk or accompanied by chicken or roast beef)

TABLE 5. MAIZE GENETIC DIVERSITY IN MICROCENTERS AND REGIONS IN LOWLAND SOUTH AMERICA BASED ON ETHNOBOTANICAL, PHENOTYPIC, AND MOLECULAR INDICATORS AND INDICES

| Area code | Collection areas ¹ | Biome | Ethnobotanical indices (H') ² | | | | | Phenotypic indices (H') ³ | | | | | Molecular indices ⁴ | | | Diversity index | | | |
|--------------|-------------------------------|-----------------|--|------|------|------|------|--------------------------------------|-------------|------|------|------|--------------------------------|------|-------------|-----------------|-------|-------|-----------|
| | | | NLF | RLN | RUN | RCU | RO | ATC | Ethno Index | RGC | RGT | RR | RUR | H'DQ | Pheno Index | | D | Ho | Mol Index |
| Brazil | | | | | | | | | | | | | | | | | | | |
| Microcenters | | | | | | | | | | | | | | | | | | | |
| I | 1 locality, RO | Amazonia | 3 | 2.65 | 2.26 | 1.79 | 1.79 | 1.3 | 2.13 | 1.39 | 0.69 | 0 | 0 | 0.84 | 0.58 | 0.123 | 0.13 | 0.127 | 56.45 |
| II | 7 locations, PB | Caatinga | 2 | 2.19 | 1.91 | 1.66 | 1.66 | 1.31 | 1.79 | 1.36 | 1.16 | 0.31 | 0 | 1.03 | 0.77 | 0.188 | 0.243 | 0.216 | 67.41 |
| IVb | 1 location, RS | Atlantic Forest | 3 | 3.37 | 3.19 | 2.17 | 2.17 | 1.23 | 2.52 | 1.58 | 1.10 | 1.93 | 1.22 | 1.15 | 1.39 | 0.202 | 0.254 | 0.228 | 93.05 |
| Regions | | | | | | | | | | | | | | | | | | | |
| III | 10 locations, MS | Cerrado | 3 | 2.79 | 2.49 | 1.84 | 2.1 | 0.9 | 2.19 | 1.54 | 1.47 | 1.38 | 0.64 | 0.89 | 1.18 | 0.176 | 0.181 | 0.178 | 77.76 |
| IVa | 6 locations, MG | Atlantic Forest | 4 | 3.5 | 3.25 | 1.86 | 1.86 | 1.17 | 2.61 | 1.61 | 1.57 | 1.53 | 0.86 | 1.2 | 1.35 | 0.205 | 0.281 | 0.243 | 95.06 |
| Uruguay | | | | | | | | | | | | | | | | | | | |
| Microcenter | | | | | | | | | | | | | | | | | | | |
| Vc | 1 locality, CA | Pampa | 1 | 1.84 | 1.39 | 1.43 | 1.43 | 1.31 | 1.40 | 1.03 | 1.36 | 1.18 | 0 | 0.78 | 1.00 | 0.219 | 0.333 | 0.276 | 75.19 |
| Regions | | | | | | | | | | | | | | | | | | | |
| Va | 7 locations, TARV | Pampa | 2 | 2.52 | 1.98 | 1.58 | 1.58 | 1.24 | 1.82 | 1.48 | 1.46 | 1.63 | 0.69 | 0.93 | 1.26 | 0.214 | 0.302 | 0.258 | 84.62 |
| Vb | 4 locations, RO/TT | Pampa | 2 | 3.09 | 2.81 | 1.69 | 1.69 | 1.21 | 2.08 | 1.51 | 1.27 | 1.54 | 0 | 1.08 | 1.16 | 0.196 | 0.23 | 0.213 | 80.11 |

¹ Collection areas, including municipalities and/or sections (localities) involved in the research; Please refer to Table 1; ² ethnobotanical indicators: average number of landraces per farmer (NLF), richness of local names (RLN), richness of unique names (RUN), richness of culinary uses (RCU), richness of origin (RO), average time of cultivation (ATC); ³ phenotypic indicators: richness of grain color (RGC); richness of grain type (RGT); race richness (RR); richness of unique races (RUR); Shannon index of qualitative descriptors (H'DQ); ⁴ molecular indicators: Nei's (1978) genetic diversity index (D) and observed heterozygosity (H_o); diversity index generated from the average value of ethnobotanical indices (Ethno Index), genetic diversity index generated from the average value of phenotypic indices (Pheno Index) and genetic diversity index generated from the average value of molecular indices (Mol Index)

to identify microcenters and regions of maize diversity in lowland South America. The highest values of the Ethno Index were observed in the following areas: the Atlantic Forest, IVa (2.61) and IVb (2.52), Cerrado (2.19), Amazonia (2.13), and Pampa, Vb (2.08); the highest values of the Pheno Index were found in the Atlantic Forest, IVb (1.39) and IVa (1.35), Pampa, Va (1.26), Cerrado (1.18), and Pampa, Vb (1.16); and those of the Mol Index were in the Pampa, Vc (0.276) and Va (0.258), and the Atlantic Forest, IVa (0.243) and IVb (0.228). The two areas of the Atlantic Forest, IVa and IVb, that had the highest diversity of culinary uses (H') and the highest Ethno Indices correspond to the areas that had the highest Pheno Indices but did not have the highest Mol Indices, as observed in the Pampa, Va and Vc (Fig. 4 and Table 5). These results show how diversity is dynamic in all indices and areas. All geographic areas in this study were considered important for conservation. A given area may not have the highest diversity for a specific indicator, but it may excel for others. This is why it is important to use different indices when looking at microcenters or regions of diversity for any crop.

The results show that sampling for the different indices can influence diversity, although we observed contrasts, such as those in the ethnobotanical and molecular indices. The highest Ethno Indices, observed in the Atlantic Forest, IVa and IVb, and Cerrado, corresponded to the regions with the highest sampling in the ethnobotanical characterization. However, Amazonia presented one of the highest Ethno Indexes despite having the second lowest sampling. Canelones, which also had one of the smallest sample sizes, had the highest Mol Index of all the regions. On the other hand, the two highest Pheno indices were obtained in the regions with the highest sampling, and the lowest Pheno Index was observed in the least sampled region. These results suggest a tendency for sampling to influence phenotypic indices more than ethnobotanical and molecular indices.

The parameters evaluated together highlight the diversity of maize landraces (Fig. 4; Supplementary Data Table S5). The average percentage of the diversity of the three indices (Ethno, Pheno, and Mol Index) ranged from 56.45% (Amazonia) to 95.06% (Atlantic Forest, IVa) and presented a general average of 79%, considering all areas.

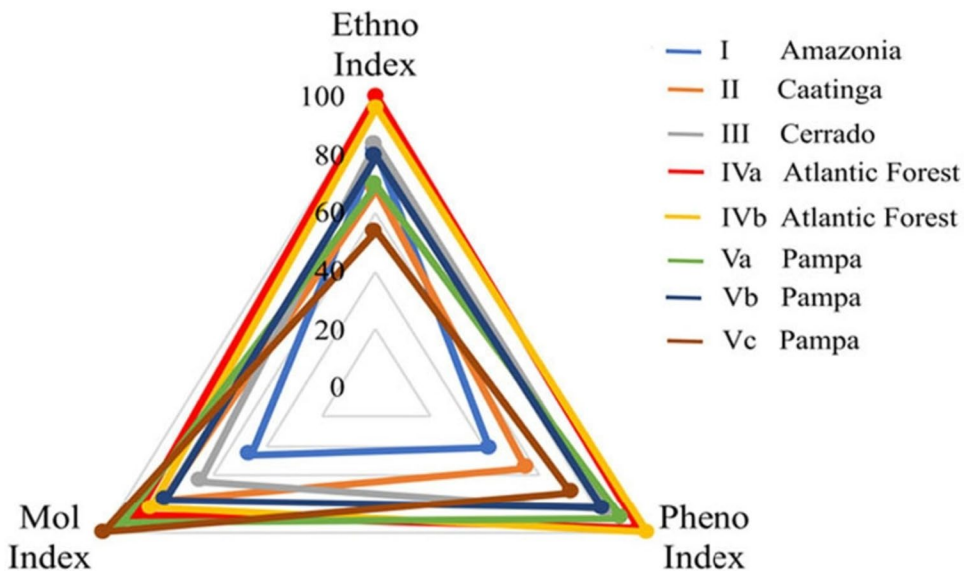


Fig. 4. Percentage of maize genetic diversity, considering the ethnobotanical “Ethno Index,” phenotypic “Pheno Index,” and molecular “Mol Index” indices, in the microcenters (I, II, IVb, and Vc) and regions (III, IVa, Va, and Vb) of species diversity in lowland South America. The weighted average percentages of diversity calculations used to calculate the diversity index are presented in Supplementary Data Table S5

Regarding the previously defined criteria, the areas involving the Cerrado, Atlantic Forest, and Pampa (III, IVa, IVb, Va, Vb, and Vc) showed high diversity (> 70%); the Amazonia and Caatinga areas (I and II) showed moderate diversity (35 to 70%); and no area showed low diversity (< 35%). Based on the criteria considered and on the concepts presented by Clement (1999), the collection areas of Amazonia (I), Caatinga (II), Atlantic Forest (IVb), and Pampa (Vc) were considered microcenters of maize genetic diversity, as they present high and moderate genetic diversity, on a microregional scale, and the Cerrado (III), Atlantic Forest (IVa), and Pampa (Va and Vb) areas were considered regions of diversity, as they present high genetic diversity on a regional scale, involving larger and more diffuse areas. These sites conserve a considerable diversity of landraces and races, many of which are exclusive to the studied areas. These areas present dynamic sociocultural contexts, as demonstrated by the ethnobotanical characterization, which certainly contributes strongly to the identification of four microcenters and four regions of maize genetic diversity (Fig. 2 and Table 5).

The microcenter located in Amazonia presented the greatest richness of culinary uses (20), the longest average cultivation time (36 years), and a wealth of 17 local names assigned to the landraces, in addition to an exclusive race observed in this area (*Entrelaçado*; Costa et al., 2021). The Cerrado region of diversity stood out for presenting the second highest richness of culinary uses, together with the Atlantic Forest region (IVa), in Southeastern Brazil. The region also stood out for presenting the second-highest average number of landraces per farmer, together with Amazonia and the Atlantic Forest (IVb), the second-highest richness of origin of the landraces, and the second-highest richness of grain type, together with the Caatinga, Atlantic Forest (IVb), and Pampa (Va) areas.

The Atlantic Forest region (IVa), in Southeastern Brazil, stood out in the ethnobotanical indicators for presenting the highest average number of landraces per farmer, the greatest richness of local names, and, together with the Atlantic Forest microcenter (IVb), located in Southern Brazil, the greatest richness of unique names and origin of landraces. In the phenotypic indices,

it stood out for presenting the highest richness of grain type, races, and the highest Shannon index of qualitative descriptors, in addition to the second-highest richness of grain color. It also stood out for having the highest molecular indices among the microcenters in Brazil. And it was the microcenter that presented the highest average percentage of the diversity of the Ethno, Pheno, and Mol indices (95.1%), followed by the other microcenter of the Atlantic Forest (IVb) (93.1%).

The Atlantic Forest microcenter (IVb), in the South, obtained the second-highest average percentage of diversity and was distinguished in several ethnobotanical, phenotypic (showing the greatest richness of grain color, races, and unique races), and molecular indicators. The Caatinga microcenter obtained the second highest richness of grain type, together with the other microcenters already mentioned, and, as in Amazonia, it presented a richness of 17 local names and an exclusive race, with an important diversity of landraces within the race. These landraces are adapted to the semi-arid environment and thus constitute important germplasm adapted to drought and high temperatures to adapt to climate change.

In Uruguay, considering only the three sampled areas, the region located in the east of the country (Vb) presented the greatest richness of local names, unique names, and the longest average cultivation time, in addition to the greatest richness of grain color and the Shannon index of qualitative descriptors. And the second-highest average cultivation time among all eight areas sampled in both countries. The microcenter (Vc) located in the Canelones area stood out for presenting the highest molecular indices among the eight areas. This area also had the lowest number of farmers interviewed in the survey, which may have influenced the lower diversity values of the Ethno and Pheno indices observed. The northern Uruguayan region (Va) included the only places where the flour maize races in the country were identified, presenting the second-highest value for molecular indices and the third-highest race richness among the eight sampled collection areas, in addition to the highest race richness among the areas of Uruguay.

ANALYSIS OF STRENGTHS, WEAKNESSES, OPPORTUNITIES, AND THREATS FOR AGROBIODIVERSITY CONSERVATION

The SWOT analysis was carried out to identify the main challenges that farmers face for agrobiodiversity conservation, especially in relation to maize landraces (Supplementary Data Table S9). The SWOT analysis allowed the identification of 63 topics for *strengths*, 59 for *weaknesses*, 51 for *opportunities*, and 44 for *threats* to agrobiodiversity conservation (Supplementary Data Table S9). *Strengths* and *opportunities* support the conservation of landraces in family farmer communities. The places involved in the research stood out for the local production of landrace seeds, diversification of farming production, and hosting organizations of family farmers that work in the conservation of traditional knowledge, in the search for knowledge on agroecological practices, in the development of actions that promote the exchange of experiences among farmers, and in the cherishing of healthy food. The main difficulties (*weaknesses* and *threats*) for conservation are associated with the lack of projects and public incentives for local associations, the strong presence of monocultures and the expansion of transgenic seeds, rural exodus, especially of young people, access to drinking water, and territorial insecurity (in the case of indigenous communities).

Discussion

MICROCENTERS OF MAIZE GENETIC DIVERSITY IN LOWLAND SOUTH AMERICA

The ethnobotanical, phenotypic, and molecular indicators showed the existence of high and moderate maize genetic diversity in the sampled collection areas in different biomes of lowland South America. To determine the microcenters and regions of diversity, the size of the collection areas was considered, within which the indicators and indices identified: (i) the richness and genetic diversity of landraces (mostly exclusive to the respective areas), (ii) landrace diversification due to current human action diagnosed by sociocultural aspects (origin, cultivation time, uses, and management), and (iii) conservation

areas and accumulation of maize germplasm on a microregional and regional scale. The ethnobotanical characterization showed that all areas studied are involved in dynamic farming systems, as demonstrated by the richness of the origins of landraces (network of circulation of landraces), the richness of uses attributed to the landraces, and management carried out by farmers, as observed in other studies (Costa et al. 2017, 2021; Louette et al. 1997; Louette and Smale 2000). The phenotypic indicators showed genetic diversity evaluated through different maize descriptors. These parameters demonstrated that the areas involved in this study conserve significant genetic diversity, as observed in regions considered important areas of diversity for the species in Mexico (Bellon et al. 2003; Dzub-Aguilar et al. 2016; Gomez et al. 2000; Louette et al. 1997; Perales et al. 2003) and in southern Brazil (Costa et al. 2017) and in large germplasm collections (Li et al. 2002; Vilaró et al. 2020) (Table 6). The molecular indicators were high, although the values of $D (H_E)$ were higher in Mexico (0.338) (Arca et al. 2020), compared to the present study (which ranged from 0.123 to 0.219) (Table 6), which is expected because Mexico is the region where the process of domestication and diversification of maize originated (Kistler et al. 2018; Piperno et al. 2009).

Harlan (1992) considered South America to be a non-center of diversity, where farming was so widely distributed that no clear center could be identified. However, he recognized that a complex mosaic of cultural diversity was present on this continent, although he did not present a map with a proposal of this mosaic. Giacometti (1992) proposed 10 centers of diversity for fruit species in Brazil, illustrated by Clement (1999), within which are areas encompassing three microcenters (I, II, and IVb) and two regions (III and IVa) of maize diversity identified by the present study for Brazil. Considering the geographic distribution of indigenous language families proposed by Eriksen (2011), Southwestern Amazonia was inhabited in the past by Indigenous People of the Arawak, Tupi, and Pano languages, and the other areas involved in this study were inhabited by Indigenous People of the Tupi and Macro-Jê languages (Eriksen 2011). The Santa Catarina microcenter (Costa et al. 2017) and the diversity region located in the Cerrado, identified by this study, are located close to the “Brasil-Paraguay” center, proposed by Vavilov (1992). This region

TABLE 6. COMPARATIVE ANALYSIS OF DIFFERENT LEVELS OF GENETIC DIVERSITY, CONSIDERING INDICATORS AND INDICES AMONG DIFFERENT AREAS, LARGE MAIZE GERmplasm COLLECTIONS, AND THE MICROCENTERS AND REGIONS OF MAIZE GENETIC DIVERSITY IN LOWLAND SOUTH AMERICA

| Grain color | | |
|---|--------------------------|-----------------------------|
| Areas | Richness | References |
| Brazil—Microcenters and regions of genetic diversity | 4 to 9 | * |
| Uruguay—Microcenters and regions of genetic diversity | 2 to 6 | * |
| Brazil – Microcenter of genetic diversity of Santa Catarina | 7 | Costa et al. (2017) |
| Mexico—Guanajuato | 5 | Gomez et al. (2000) |
| Mexico—Oaxaca | 4 | Bellon et al. (2003) |
| Mexico—Yucatán | 4 | Dzib-Aguilar et al. (2016) |
| Mexico—Cuzapala | 3 | Louette et al. (1997) |
| Grain type | | |
| Areas/collections | H' | References |
| Brazil—microcenters and regions of genetic diversity | 0.69 to 1.57 | * |
| Uruguay—microcenters and regions of genetic diversity | 1.27 to 1.46 | * |
| Brazil—microcenter of genetic diversity of Santa Catarina | 0.73 | Costa et al. (2017) |
| Chile—germplasm collection | 1.69 | Vilaró et al. (2020) |
| Bolivia—germplasm collection | 1.54 | Vilaró et al. (2020) |
| Paraguay—germplasm collection | 1.49 | Vilaró et al. (2020) |
| North of Argentina—germplasm collection | 1.39 | Vilaró et al. (2020) |
| Brazil—germplasm collection | 1.36 | Vilaró et al. (2020) |
| Uruguay—germplasm collection | 1.26 | Vilaró et al. (2020) |
| China—germplasm collection | 1.41 | Li et al. (2002) |
| American countries – China germplasm collection | 1.08 | Li et al. (2002) |
| Europe countries—China germplasm collection | 1.08 | Li et al. (2002) |
| Asian countries—China germplasm collection | 1.31 | Li et al. (2002) |
| African countries—China germplasm collection | 1.31 | Li et al. (2002) |
| Oceania countries—China germplasm collection | 1.31 | Li et al. (2002) |
| Races | | |
| Areas | Richness | References |
| Brazil—microcenters and regions of genetic diversity | 1 to 14 | * |
| Uruguay—microcenters and regions of genetic diversity | 4 to 7 | * |
| Mexico—11 biogeographical regions | 1 to 13 | Perales and Golicher (2014) |
| Time of cultivation | | |
| Areas | Average and maximum time | References |
| Brazil—microcenters and regions of genetic diversity | 16 and 100 | * |
| Uruguay—microcenters and regions of genetic diversity | 14 and 80 | * |
| Brazil—microcenter of genetic diversity of Santa Catarina | 10 and 100 | Costa et al. (2017) |
| Mexico – Oaxaca | 25 and 67 | Bellon et al. (2003) |
| Genetic diversity index of Nei (1978) | | |
| Areas | D (He) | References |
| Brazil—microcenters and regions of genetic diversity | 0.123 to 0.205 | * |
| Uruguay—microcenters and regions of genetic diversity | 0.196 to 0.219 | * |
| Mexico | 0.338 | Arca et al. (2020) |

*Data obtained in the present study aimed at identifying microcenters and regions of diversity in lowland South America

is associated with high population densities of indigenous Guarani (a Tupi language) and various other cultures, within which high genetic diversity has been conserved, according to Giacometti (1992). Northwestern Argentina is considered another area of diversity, supported by maize cultivation (Brieger et al. 1958). The Brazilian coast, in turn, was occupied by populations from the Tupi language trunk (Castro and Silva et al. 2020). According to Giacometti (1992), a region of diversity may have extended across southeastern Brazil.

The ancient presence of maize in Southwestern Amazonia is confirmed by different archeological records (Hilbert et al. 2017; Lombardo et al. 2020), reaching up to ~6850 years BP (Lombardo et al. 2020). However, archeological records of maize are scarce in the other areas of this study. Archeological evidence for maize from 4190 years BP was identified in Rocha, eastern Uruguay (Iriarte et al. 2004). In the Peruaçu Valley, a region on the left bank of the São Francisco River in Minas Gerais, Brazil, there are traces of the presence of maize for at least 990 years BP (Bush et al. 2000; Freitas et al. 2003). And, on the coast of Santa Catarina, southern Brazil, maize was identified from 1390 years BP (Wesolowski et al. 2010). Future studies aiming to understand the relationship between modern maize landraces and archeological maize may reveal the functions of genes associated with maize diversification processes in lowland South America. These genes are selected during and after domestication and are involved with the mechanisms of species adaptation to different environmental conditions and human cultural practices, promoting species diversification (Meyer and Purugganan 2013) and the origin of native local races. Such studies are in progress by the team involved in the present study.

MAIN CHALLENGES FOR CONSERVATION IN LOWLAND SOUTH AMERICA

The present study involved different eco-geographic contexts and biomes (Amazonia, Cerrado, Caatinga, Atlantic Forest, and Pampa), as well as sociocultural contexts, within which different profiles of family farmers were included: traditional farmers, *quilombolas*, agrarian reform settlers, and *ribeirinhos*. All these

elements, environmental and human, acted in the diversification process and shaped the diversity of landraces present in each microcenter and region of diversity. The ethnobotanical characterization showed that all areas contain maize landraces with unique local names (Supplementary Data Table S7) and races (Supplementary Data Table S8), which indicates that each location has its own diversity since the variety name and race are considered indicators of diversity and important markers of diversity characterization (Costa et al. 2021). On the other hand, different areas also share common names and races, such as the Avati Moroti race (floury grain) present in the Cerrado and Atlantic Forest, the Avati Pichingá race (popcorn grain) in the Caatinga, Cerrado, and Atlantic Forest, and the Cateto complex (flint grain) in the Caatinga, Cerrado, and Atlantic Forest (IVa and IVb), which demonstrates the dynamics and interregional sharing of maize diversity.

The main *weaknesses* (internal factors) and *threats* (external factors) for the conservation of agrobiodiversity identified (Supplementary Data Table S9) can be considered agents of genetic erosion (Brown 2008). The surroundings of these areas are characterized by the expansion of large areas of monoculture. The genetic diversity of cultivated species has suffered losses related to the industrialization of agriculture (John and Babu 2021) and climate change (Altieri and Koohafkan 2008). A study involving family farmers in the Atlantic Forest, in southeastern Brazil, observed that the number of landraces cultivated by farmers in different areas was influenced by socioeconomic, ecogeographic, cultural, and climate change factors (Cavalcanti et al. 2021). The microcenters and regions of diversity identified in the present study involve areas from the Cerrado, Atlantic Forest, and Amazonia that are already included in areas identified as biodiversity *hotspots* (Myers et al. 2000), which correspond to areas with great biodiversity that are threatened with extinction and are considered a priority for conservation programs (Myers 1990; Myers et al. 2000).

The *strengths* (internal factors) and *opportunities* (external factors) (Supplementary Data Table S9) identified by the SWOT analysis are agents that promote agrobiodiversity conservation in the collection areas. The microcenter located in Southwestern Amazonia, for example,

is surrounded by an extractive reserve (RESEX), characterized by the presence of *ribeirinho* farmers. This area has been recognized as a center of diversification of cultivated species by other studies (Clement et al. 2016; Kistler et al. 2018; Lombardo et al. 2020). A previous study reported an important richness of landraces belonging to the *Entrelaçado* race, which is being conserved by traditional and indigenous farmers who inhabit the area (Costa et al. 2021). In the Cerrado, the region of diversity identified involves the presence of family farmers, agrarian reform settlers, and Indigenous People, the latter from the municipality of Caarapó, where the *Te'yikue* (in Guarani this means “old village” or “place that was home”) indigenous village is located. Currently, rural communities in the region have three community seed banks, located in the municipalities of Juti, Caarapó, and Sidrolândia.

The Atlantic Forest region (IVa), in southeastern Brazil, is in the Zona da Mata, in Minas Gerais. A history of local initiatives has contributed to the development of agroecology and the conservation of landraces in the region, which was legally recognized in 2018 as an Agroecological and Organic Production Pole (Minas Gerais 2018). The microcenter identified in the Atlantic Forest (IVb), in southern Brazil, involved the municipality of Ibarama, in Rio Grande do Sul. The municipality is strongly marked by the presence of family farmers engaged in a historic movement that aims to promote the conservation of agrobiodiversity with the support of local organizations. In the Caatinga, the research was carried out in Serra da Borborema, in Paraíba. This area contains a network of 63 family community seed banks, mobilized by the articulation of farmers and local organizations as a strategy for coexistence with the semi-arid region. Local farmers have discussed the creation of transgenic-free communities in the territory. This collection area, as well as the Amazonian area, presented a unique race with an important diversity of landraces within the race that are adapted to the semi-arid environment and thus constitute important germplasm adapted to drought and high temperatures to adapt to climate change.

In Uruguay, where the entire country is in the Pampa biome, the indication of microcenters and regions of maize diversity is unprecedented. The departments of Rocha and Treinta y Tres (Vb) contain 35% of the country's protected areas (SISNAP

2021) and an important native forest of Palmares de Butiá (*Butia capitata*), a characteristic ecosystem dominated by the butiá palm with associated species of plants and animals that are distributed across plains, mountains, and wetlands (Rivas et al. 2017; Sosinski et al. 2019). In this region, there is also the Banhados do Leste Biosphere Reserve, declared as such in 1976 by the United Nations Educational, Scientific, and Cultural Organization (UNESCO). In the department of Rocha, the archeological records of maize indicate the ancient presence of the species in the region (Iriarte et al. 2004). In Canelones, the National Institution of Human Rights and Warden (Ombudsman) declared the municipality of Tala (Vc) to be an area free of transgenic soy (Uruguay 2019). This process may favor the declaration of transgenic-free areas, also involving maize. Rivera and Tacuarembó (Va) were the only places where Uruguayan floury maize was identified. The northern (Tacuarembó and Rivera) and eastern (Rocha and Treinta y Tres) regions of the country have ample intra-regional ecogeographic and cultural diversity. Therefore, we suggest future studies to understand how maize diversity is structured and distributed within these local contexts and to verify whether other microcenters of diversity, both for maize and for other species, exist in these areas.

Microcenters and regions of diversity are the result of traditional family farming systems that involve landscapes and managed agroecosystems, farming products, social networks, food systems, and knowledge (Altieri and Koohafkan 2008; Koohafkan and Cruz 2011). In addition, they preserve cultural traditions and a wide diversity of uses associated with agrobiodiversity (Altieri and Koohafkan 2008; Koohafkan and Cruz 2011). In 2018, the traditional agricultural system of the Espinhaço Mountain Range in the state of Minas Gerais, also known as “Gatherers of Sempre-Vivas Flowers,” was the first Brazilian agricultural system internationally recognized as a Globally Important Agricultural Heritage System (GIAHS) by FAO (2021). The conservation of landraces carried out by farmers brings benefits to rural communities, the environment, and ecosystem services (Raymond et al. 2009; Wallace 2007). Considering that agrobiodiversity is not generally considered in the formulation and creation of protected areas, Santilli (2011) discussed the importance of establishing “agrobiodiversity reserves or zones,” which would correspond to

the creation of a category within the National System of Conservation Units destined for the conservation and management of agrobiodiversity (Santilli 2011). Areas identified as microcenters and regions of cultivated species diversity may be recognized as “agrobiodiversity reserves or zones,” with the aim of establishing a basis for the recognition of these areas and subsidizing public policies aimed at dynamic conservation and sustainable management of these agroecosystems.

Conclusions

This study identified ample maize genetic diversity and identified four microcenters and four regions of maize diversity in different biomes (Amazonia, Cerrado, Caatinga, Atlantic Forest, and Pampa) of lowland South America. For the identification of microcenters and regions of genetic diversity, the size of the collection areas and the diversity diagnosed by means of ethnobotanical, phenotypic, and molecular indicators and indices were considered, within which the following were identified: (i) genetic richness and diversity of maize landraces (mostly exclusive to the respective areas) and races, (ii) presence of active landrace diversification due to current human action as diagnosed by ethnobotanical indicators, and (iii) areas of conservation of maize germplasm on a microregional and regional geographic scale. The methodology presented here can be used for the characterization of microcenters of maize diversity in other areas, as well as for other crops. The indicators of *weaknesses* and *threats* to the conservation of agrobiodiversity identified in the areas involved in this study demonstrate that these areas are vulnerable to genetic erosion and therefore should receive greater attention when planning the conservation of agrobiodiversity.

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Author Contribution

FMC, NCAS, RV, and EAV planned and designed the research. FMC, NCAS, and RV collected and prepared the South American lowland material and conducted

the statistical data analysis. FMC, NCAS, RV, EAV, and CRC contributed to the drafting of the manuscript, including the review, support for the interpretation, and discussion of the results. All authors reviewed and contributed to the final manuscript.

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Data Availability

The authors confirm that the data supporting the findings of this study are available within the article and its [supplementary materials](#).

Declarations

Ethics Approval This research was approved by the Ethics Committee for Research with Human Beings of ESALQ/USP in December 2016; by the National Research Ethics Commission (CONEP), CAAE process 60382016.2.0000.5395; by the National System of Authorization and Information on Biodiversity (SisBio) (registration no. 61447-1); and was registered in the National System for the Management of Genetic Heritage and Associated Traditional Knowledge (SisGen) (registration no. AD2EF0B). Before each interview, family farmers signed the free and informed consent form.

Conflict of Interest

The authors declare no competing interests.

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