

Unlocking the Potential of Slovenian Maize Landraces: Exploring Diversity and Redundancy in the MRIZP Gene Bank

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ABSTRACT

The Gene Bank of the Maize Research Institute Zemun Polje (MRIZP) maintains 2,217 accessions of local maize landraces collected across the former Yugoslavia, including 103 accessions originating from Slovenia and collected between 1963 and 1989. The conservation of such an extensive collection presents significant logistical and economic challenges, particularly in terms of efficient characterization and evaluation. The development of cost-effective conservation strategies is therefore essential to ensure long-term preservation and to enhance the utilization of genetic resources in research and breeding programs. The objectives of this study were: (i) to analyse existing passport data of the Slovenian maize landrace gene pool; (ii) to examine its morphological diversity; and (iii) to identify redundant accessions and propose strategies for more efficient conservation. Analysis of passport and morphological data indicates that the Slovenian maize landrace collection is well structured, with low redundancy, likely reflecting effective coordination among collecting institutions. Multivariate, cluster and correspondence analysis, revealed distinct groups associated with specific geographic regions and historical introduction pathways, emphasizing the role of environmental factors in shaping diversity. The limited redundancy, together with pronounced morphological variability, highlights the uniqueness and breeding value of this material. These landraces exhibit adaptation to local agroecological conditions and possess traits of agronomic importance, such as early maturity, grain quality, and resilience, making them particularly relevant for breeding programs targeting temperate environments, organic production, and low-input systems. In conclusion, the Slovenian maize landrace collection conserved at MRIZP represents a valuable genetic resource with significant potential for sustainable maize breeding and crop improvement in temperate regions.

Keywords: diversity, efficient conservation, morphological markers, *Zea mays* L.

INTRODUCTION

The Gene Bank (BG) of the Maize Research Institute Zemun Polje (MRIZP) started as working collections for breeding activities and afterward expanded through collection activities and exchanges with other gene banks. Beside 3500 introduced genotypes, it maintains 2,217 accessions of local landraces collected in the former Yugoslavia, of which 103 accessions were collected in the period 1963-1989 in the Republic of Slovenia (Andjelković et al., 2017). A huge job was done in the past, but today, we are faced with the great challenge of preserving such a large collection (Singh et al., 2012). A large number of conserved accessions, being loaded with unfavourable traits, make numerous collections

almost useless for breeding and obtaining relevant results in a reasonable period of time, as well as from the aspect of economic justification of the characterisation and evaluation (van Hintum and Knüpffer, 1995; Greene and Pederson, 1996; Popović et al., 2020).

Establishing a cost-effective conservation system can reduce the risk that gene banks become “dead collections” that fail to fulfil their primary mission (Goodman, 1990). Efficient conservation strategies enable the long-term preservation, characterization, and wider use of genetic resources in research and breeding programmes. Molecular markers are effective tools towards this goal (Spooner et al., 2005; van Treuren et al., 2010; van Treuren and van Hintum, 2014). However, in a study of a large collection, the potential to

reduce necessary investments is to limit the molecular screening to the validation of potential duplicate groups determined by available data sources, such as passport and morphological data (McGregor et al., 2002). The passport data are good starting criteria when comparing accessions, followed by comparison based on traits related to kernel and plant morphology (van Hintum, 2000; Twumasi et al., 2017).

The agro-morphological or molecular data of genetic resources are usually being processed by different methods of multivariate statistics. Data reduction techniques (e.g. principal components analysis; correspondent analysis) are increasingly popular for visualising patterns of similarity or distance between individuals or subspecies within population-level studies of sequence data (van den Ende et al., 2023). Although the resulting two- or three-dimensional projections of “genospaces” typically capture only a reduced part of the total variance, they are usually preferred to dendrograms or trees, and to univariate indices of sequence divergence (Fay and Wu, 2003), due to the possibility of displaying continuous variability within and between defined groups (Babić et al., 2021).

The analysis of passport and morphological data of the gene pools collected in former Yugoslavia is in progress. The idea is to determine whether and to what extent the MRIZP collection of local maize landraces is burdened with redundant accessions. According to Babić et al. (2021), the Montenegrin maize landrace gene pool contains numerous morphologically similar and potentially redundant accessions. Three institutions were collecting accessions at different and simultaneous times, and the data suggested that there was no good coordination between them. Specifically, it occurred that two distinct institutions collected very similar maize accessions in the same location at the same or different dates, or that the same institution collected comparable accessions at various times. Aside from this unfavorable issue, significant variability was discovered within the MRIZP Montenegrin maize landrace collection, which no longer exists in farmers' fields or in the Montenegrin gene bank.

To build a cost-effective conservation system in the MRIZP Gene Bank, the aim of this study was to (i) analyse the existing passport data of the Slovenian maize landraces gene-pool (ii) evaluate their morphological diversity, and (iii) identify the most similar and redundant accessions and propose the next step in the process of establishing the cost-efficient conservation of this germplasm.

MATERIAL AND METHODS

This study focused on local maize landraces collected in Slovenia and maintained in the MRIZP gene bank. Since the passport data was absent for three accessions, the morphological characterization of 100 MRIZPGB accessions was performed in 2020 and 2021 using the CIMMYT/IBPGR Descriptors for Maize (IBPGR, 1991). Traits, developmental stages of plants, and methodology, as well as the minimal number of plants or plant parts necessary for evaluation are defined in the descriptors.

Landraces were sown in two rows, with 30 plants per row, in two replications, at the location of Zemun Polje, Serbia (44°52' N, 20°19' E, 81 m asl), located in the Pannonian 3 (PAN3) zone (Metzger et al., 2013) with a temperate continental climate and a slightly calcareous chernozem soil type. Standard cropping practices were applied.

The 28 phenotypic traits were evaluated: plant height, ear height, number of leaves above the ear, total number of leaves, number of ears per plant, leaf length, leaf width, tassel length, tassel peduncle length, length of the branching part of the tassel, number of primary tassel branches, kernel row number, number of kernels per row, ear length, ear width at the top of the ear, ear width in the middle of ear, ear width at the base of ear, cob width, rachis width, kernel length, kernel width, kernel thickness, kernel hardness, kernel dentiness, 1000-kernel weight, number of days to tasseling, and to silking.

Statistical Analyses

The hierarchical cluster analysis was applied on standardized values of observed morphological traits (all observed except

days for tasseling and silking) (Peeters and Martinelli, 1989). The squared Euclidean distances were calculated as a measure of the distances between landraces, whereas complete-linkage clustering was used as a grouping method. Correspondence analysis was performed according to coefficients of morphological similarity and results were displayed graphically (Greenacre, 1988). The main advantage of correspondence analysis is that it does not make assumptions about unit assignment and depicts continuous variability more precisely, which is especially important when there is extensive genetic exchange between geographically close populations (Blasius and Greenacre, 1998).

The statistical package IBM SPSS Statistics 25 was used for data analysis.

RESULTS

According to the MRIZP gene bank passport

Table 1. Passport data of the MRIZP maize landraces collected in Slovenia

Geographical area	Collecting/sponsoring institutions					Σ
	YAR and USDA	BFLj	AFING	MRIZP		
	Period of acquisition					
	‘60s	‘80s	‘70s	‘70s	‘80s	
Eastern Slovenia					11	11
Central Slovenia	12	9			1	22
Northern Slovenia	9	8				17
Southern Slovenia	3	1				4
West and coastal Slovenia	3		38	5		46
Σ	27	18	38	5	12	100

BFLj - Biotechnical Faculty Ljubljana; YAR - Yugoslav Association of Researchers; USDA - United States Department of Agriculture; AFING - Agricultural Forestry Institute Nova Gorica; MRIZP - Maize Research Institute Zemun Polje.

Cluster analysis applied to morphological data divided Slovenian maize landraces into four groups (Table 2). Average values of morphological traits per cluster are presented in Table 2. Cluster 1, as the most numerous group, encompassed 42 landraces collected by all collecting institutions in the whole territory of Slovenia, but predominantly in the central part and at low altitudes. The majority of landraces in Cluster 1 were dent and semi-dent types, characterized by long

data, 27, 43, and 30 maize accessions were collected in Slovenia during the 1960s, 1970s, and 1980s, respectively. The largest number of accessions (46) was collected in the western and coastal parts of Slovenia. The Yugoslav Association of Researchers (YAR) and the United States Department of Agriculture (USDA) collected 12 accessions in Central, nine in North, and three in the western and costal parts of the country during the 1960s. Biotechnical Faculty Ljubljana (BFLj) collected nine, eight, and one accessions in Central, North, and South Slovenia.

The Agricultural Forestry Institute Nova Gorica (AFING) collected accessions in the western and coastal parts of Slovenia (38). The MRIZP, collected 5 accessions in West and Coastal Slovenia during the 1970s, 11 in Eastern Slovenia and one in Central Slovenia in the 1980s (Table 1).

ears and kernels, and days to tasseling between 60 and 68. Cluster 2 encompassed 11 early and ultra-early flint landraces, collected mainly in the Northern and Southern parts of Slovenia during the first collecting missions in the 1960s. The third cluster consisted of 14 flint and flint-like landraces acquired primarily by the Biotechnical Faculty of Ljubljana in 1980 in the Celje, Radovljica, and Postojina regions at altitudes ranging from 550 to 600 meters. Three accessions

from third cluster were collected by YAR and USDA in the municipalities of Postojna and Tolmin in the 1960s. The fourth Cluster encompassed distinct long season dents, unique in their morphological profiles: the robust plant, long kernel length, and so on. At

the same time, this is also a numerous group (33 accessions), collected in West and Coastal Slovenia, usually by the Agricultural Forestry Institute Nova Gorica in the 1970s. Just three of them were collected in the 1960s by YAR and USDA.

Table 2. Average values of evaluated morphological traits per cluster

Evaluated traits	Average values per cluster			
	1	2	3	4
Plant height	202.94	170.63	201.25	249.67
Ear height	76.39	57.79	69.13	102.05
Number of leaves above the ear	5.62	4.95	6.00	6.40
Total number of leaves	16.38	14.09	16.36	18.56
Number of ears per plant	1.22	1.40	1.17	1.26
Leaf length	76.69	68.79	79.15	86.08
Leaf width	8.94	7.86	8.95	9.59
Tassel length	57.11	53.30	59.37	61.37
Tassel peduncle length	22.87	21.79	22.20	22.84
Length of the branching part of tassel	34.24	31.52	37.17	38.53
Number of primary tassel branches	15.44	15.00	14.97	20.70
Kernel row number	12.15	12.91	12.49	12.10
Number of kernels per row 1	35.99	27.66	30.26	36.34
Number of kernels per row 2	36.67	28.21	30.86	36.90
Ear length	17.58	13.52	17.16	17.42
Ear width at the top of ear	3.47	3.15	3.77	4.01
Ear width in the middle of ear	3.98	3.55	4.37	4.62
Ear width at the base of ear	4.29	3.81	4.74	4.99
Cob width	2.30	2.14	2.75	2.46
Rachis width	1.93	1.81	2.37	2.02
Kernel length	1.02	0.87	0.99	1.27
Kernel width	0.93	0.82	1.03	1.02
Kernel thickness	0.45	0.47	0.53	0.44
Kernel hardness	3.42	4.03	3.75	2.34
Kernel dentiness	2.56	1.96	2.25	3.55
1000-kernel weight	329.52	243.00	383.86	430.55
Days to tasseling	64.40	55.45	62.21	73.45
Days to silking	67.07	58.27	66.21	76.27
Number of landraces per cluster	42	11	14	33

Cluster analysis assigned evaluated landraces to certain groups although continuous variability in morphological data existed. In such cases or in situations where significant genetic exchange between geographically close populations is expected

(Blasius and Greenacre, 1998) correspondent analysis is more suitable for presenting data. The first three dimensions of correspondence analysis captured 84%, 6%, and 5% of data inertia (variability).

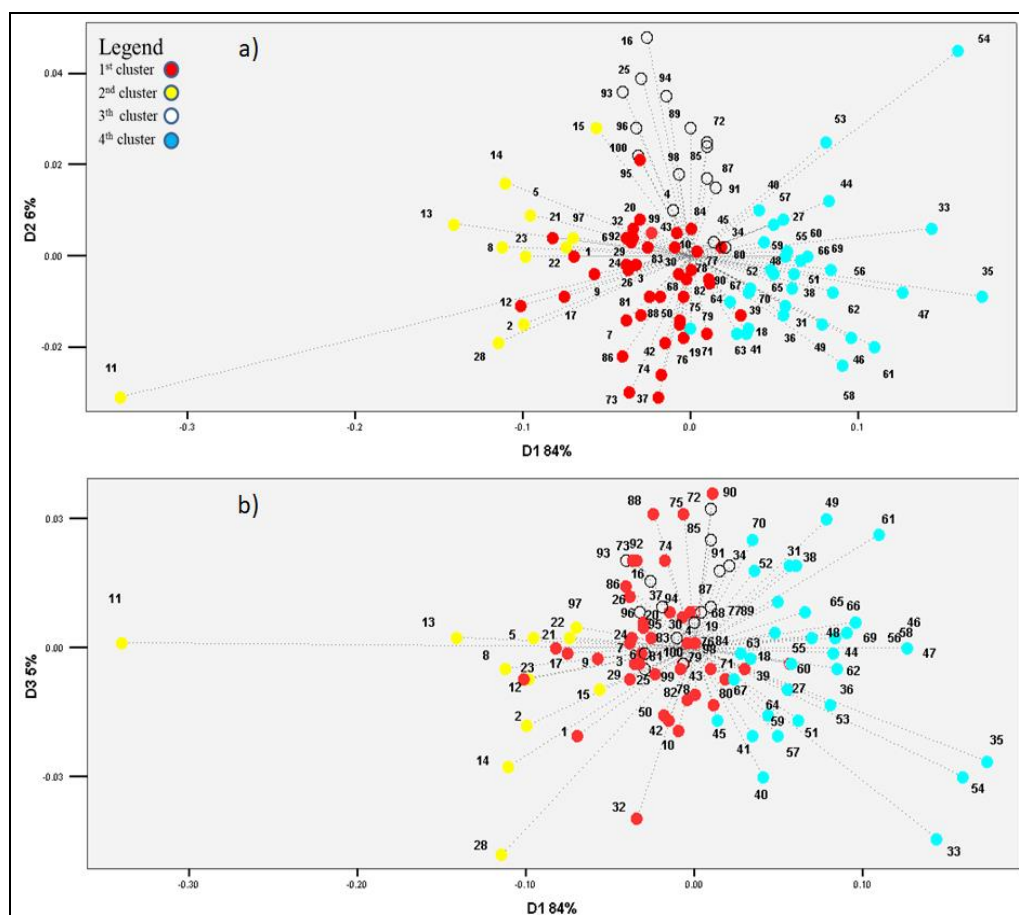


Figure 1 (a, b). Distribution of maize landraces according to the correspondence analysis

Alignment to specific clusters is indicated by distinct marker colours in the correspondence analysis plots (Figure 1a, b). In both graphs, the first cluster (red) occupies a central position, with its territory overlapping predominantly with cluster three (Figure 1b), and to a much lesser extent with clusters two and four. In certain cases, population points assigned to different clusters (e.g. 100 and 95) are located very close to each other in the plot (Figure 1a), indicating a high degree of similarity across most morphological traits. Passport data and the reference grain collection further reveal that these two populations were collected by the same institution, at the same time and from the same municipality, differing only in grain colour.

Within the two largest clusters (clusters 1 and 4), the highest frequency of overlapping

or closely positioned accession points is observed, suggesting the presence of potentially redundant samples. It is also evident that certain landraces assigned to the first cluster (e.g. landrace 39) show greater similarity to landraces from the fourth cluster (e.g. 18, 41, 63) than to some members of their own cluster (e.g. landrace 12) (Figure 1a, b). Furthermore, the positioning of landraces 12, 17, 1, 21, and 9, although assigned to the first cluster, indicates a higher morphological similarity to landraces of the second cluster than to those within their assigned group. Examination of the raw morphological data and the reference grain collection confirms that these landraces are small-grained flints, which explains their closer resemblance to genotypes from the second cluster rather than those from the first.

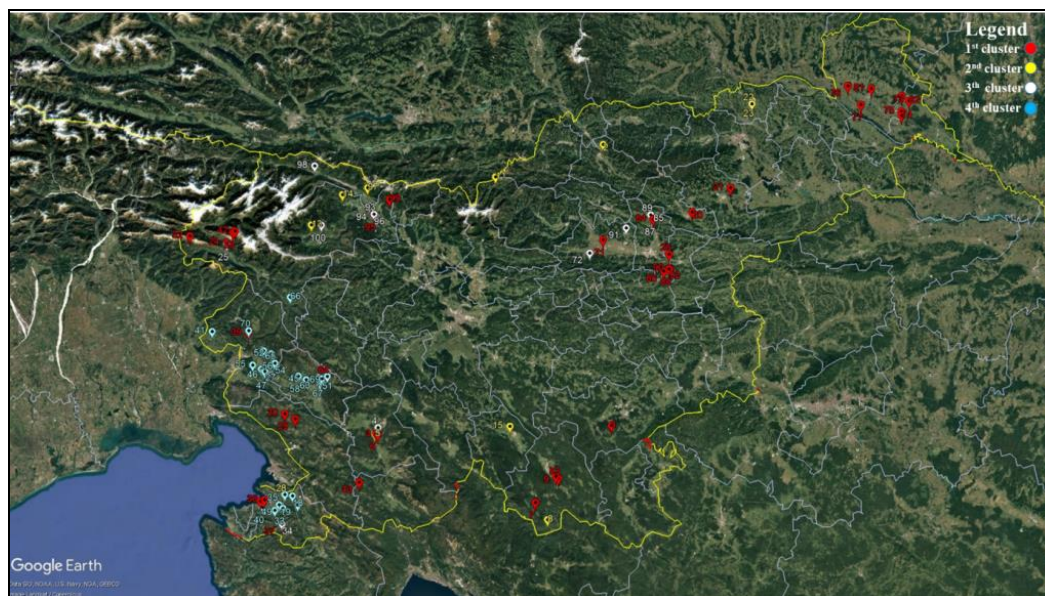


Figure 2. Map of maize landraces collecting sites

The geographical map illustrates the collection sites of the landraces, with cluster membership indicated by different colours (Figure 2). Clear patterns can be observed in the spatial distribution of the clusters. Landraces belonging to the first and most numerous cluster are distributed across the entire territory of Slovenia, with a predominance in the central and western regions. In contrast, landraces of the least numerous cluster (cluster 2, yellow) were mainly collected from hilly and mountainous areas, particularly along the borders with Croatia and Austria. The collection sites of landraces from the third cluster (white) are generally located at higher altitudes. Meanwhile, landraces of the fourth cluster (blue) were primarily collected in western Slovenia, especially in the coastal region and near the border with Italy.

A more comprehensive further analysis of squared Euclidean distance matrices, passport data, and referent seed collection, pointed out that were 19% (eight) and 10% (four) of possible redundant accessions in the first and fourth clusters. There was no determined redundancy in the second cluster, while in the third cluster, only one possible case was found. According to passport data, these redundant accessions typically occur when samples are collected by different organizations or when the same collecting institution collects in different locations.

DISCUSSION

Considering the passport data, it can be concluded that the collection of Slovenian maize landraces was well organized, with effective coordination among the collecting and sponsoring institutions. Such a coordinated approach resulted in a low level of redundancy, i.e., a limited number of duplicate or potentially duplicate accessions. These redundancies were predominantly observed within the first cluster, which occupies a central position in the plot of correspondence analysis of morphological similarities (red points) (Figure 1a, b).

Combining passport data and cluster analysis, it can be seen that the earliest collecting missions (1960s) collected predominantly landraces classified in the 1st and 2nd clusters (12 and 9 accessions), while the landraces of the 3rd and 4th clusters were less represented (3 accessions each). In the collecting missions organized in the 1970s and 1980s, the landraces of 1st and 4th clusters prevailed (32 and 30 accessions, respectively). Also, in this period 79% (11 accessions) of the 3rd cluster were collected by the Biotechnical Faculty of Ljubljana (BFLj) (Table 2).

Numerous authors consider morphological markers to be unreliable indicators of genetic relationships (Nagy et al., 2003; Babić et al., 2016; El-Esawi et al., 2023). The most

commonly mentioned causes are low polymorphism, expression influenced by environmental factors, high selection pressure, observers' subjectivity, and limitations of the established evaluation systems (Božović et al., 2022; Perić et al., 2025). However, based on the obtained results, it is possible to gain insight into which maize types were grown in Slovenia prior to the introduction of hybrids varieties, as well as how the process of natural hybridization of different maize types, grown at that time, occurred. Based on the collecting sites, the number of collected landraces and their grouping, it can be assumed that in the early 1960s, small-grain flint varieties were predominantly grown at higher altitudes. At that time, only a small number of South American dent types were cultivated in the western and coastal parts of Slovenia, while the dent types of the American corn belt were slightly cultivated in central and eastern Slovenia, along the Hungarian border. Since the results revealed that early flint landraces did not mix much with other material, they could be proposed as unique germplasm for enriching breeding collections that deal with early material (Babić et al., 2022).

The distribution of specific landrace types collected across different time periods suggests that the earliest maize introductions to Slovenia were most likely small-grained, short-season flint types. Subsequently, a more intensive spread of higher-yielding dent types occurred, including American Corn Belt dents introduced from the direction of Hungary, as well as South American dent types introduced via Italy. Flint varieties with slightly longer vegetation and more robust plants (3rd cluster) were mostly collected later (1970s and 1980s), suggesting that these maize types were introduced later in Slovenia.

The sites of collection can also indicate the routes of introduction, i.e., the dents of South America were brought to Slovenia by sea from Italy, while the dents of the American Corn Belt most likely arrived overland from Hungary. Previous research indicates the existence of two introductory

routes to Europe: one from the Caribbean via Southern Europe and one to Central Europe with material from North America (Tenailon and Charcosset, 2011; Brandenburg et al., 2017). Although our analysis suggested possible routes of maize introduction into Slovenia, the results also indicated that distinct maize types became established under locally favorable edaphic and climatic conditions. In line with this, Takou et al. (2025) reported that genetic diversity is primarily shaped by local environmental factors rather than by introduction routes.

According to our results, a strong concordance was observed between collection sites and cluster affiliation. The presence of regions on the correspondence analysis plot where points of the first and third clusters overlap (Figure 1a, b), indicates similarities in their morphological profiles, as well as evident gene flow between these groups. Passport data indicated that these landraces were predominantly collected in geographically proximate regions. Similar lengths of growing-season and synchronized anthesis and silking times (Table 2) likely facilitated spontaneous crossing between these two geographically close landraces groups. Genotypes derived from the previously described crosses may possess specific traits of importance for maize breeding in temperate climate regions. Hadi (2006), in a comprehensive review of maize germplasm, concluded that, primarily due to differences in growing season length and climatic conditions, the varieties cultivated in Eastern Central Europe differ from those in the American Corn Belt and other European regions.

In contrast, the short growing season of the 2nd cluster landraces and the prolonged growing season of the 4th cluster landraces (Table 2) constituted a natural barrier to hybridization, as reflected in their clear separation on the correspondence analysis plot. Also, the geographical map shows the spatial distance of the cultivation/collection area of the landraces of clusters 2 and 4, which represents an additional barrier for their crossings.

The widest genetic and morphological diversity within a species occurs in natural conditions as a result of a continuous process of crossing, mutations, and natural selection (Mayer et al., 2020). The small number of identified redundant accessions and the great morphological diversity indicated that the collection of the Slovenian maize landraces, preserved in the MRIZP gene bank, is a unique collection with great potential for modern maize breeding. Existing variability can be used to create a broad-based initial material for well-targeted breeding objectives: early maturity, grain quality improvement, and creation of ideotypes suitable for organic and *low-input* production.

The application of modern methodologies developed within conventional breeding, such as molecular markers, NIR spectroscopy, remote-sensing based phenotyping, laboratory methods for assessing technological and nutritional quality, as well as approaches grounded in quantitative genetics and associative mapping, can substantially enhance the accuracy of conserved germplasm evaluation and facilitate the development of improved maize varieties (Costa et al., 2015; Allier et al., 2020; Balconi et al., 2024; Popović et al., 2025).

CONCLUSIONS

The analysis of passport and morphological data indicates that the Slovenian maize landrace collection maintained in the MRIZP gene bank is well-organized, with minimal redundancy attributable to effective coordination among collecting institutions. Morphological clustering and correspondence analysis revealed distinct genetic groups corresponding to specific geographic regions and historical introduction routes, highlighting the diversity shaped by edaphic and climatic factors across Slovenia.

The relatively low level of redundancy, combined with the observed morphological diversity, underscores the uniqueness and breeding potential of this collection. The landraces reflect a natural adaptation to local conditions and possess valuable traits such as early maturity, grain quality, and resilience,

making them a vital resource for modern maize breeding programs targeted at temperate climates, organic farming, and *low-input* systems.

Overall, the Slovenian maize landrace collection represents a valuable genetic reservoir with significant potential to support sustainable maize breeding efforts and crop improvement in temperate regions.

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