

# Improving germplasm representativeness in the *Desmanthus virgatus* (L.) Willd. complex using a validated model

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## Short Report

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# Abstract

The study of native plant genetic resources with forage value has become increasingly important in the last few years, especially in legume species that contribute to the sustainability of agricultural systems. Species of the *Desmanthus virgatus* (L.) Willd. complex are known for their forage potential. In Argentina, the complex includes several native species that are important for grazing systems. Germplasm collections of species of the complex are available; however, the genetic representativeness of the conserved material is unknown. In this work, we evaluated the ecogeographic representativeness of germplasm collections of species of the *D. virgatus* complex native to Argentina by developing an Ecogeographic Land Characterization map (ELC), which was validated with genetic and morphological data. There was consensus between the ecogeographic categories of the ELC map and the molecular and morphological data. The germplasm collections of species of the *D. virgatus* complex native to Argentina show a good ecogeographic representativeness; however, some ecogeographic categories still need to be represented, which should be targeted in further collection missions.

## Introduction

The study of native plant genetic resources with forage value has gained importance in the research agenda of groups from different countries (Butler and Muir 2012; Marinoni et al. 2019; Muir et al. 2014; Nichols et al. 2007; Shelton, Franzel, and Peters 2005). In particular, legume species have shown to be essential for production systems, since they not only improve the quality of the animal diet, but also contribute to biological nitrogen fixation (Pensiero and Zabala 2017), being a key tool for the sustainability and restoration of degraded grasslands (Bhullar et al. 2009; Rao and Hodgkin 2002). In Argentina, approximately 732 legume species have been recorded, with 156 being endemic (Zuloaga and Morrone 1999). Several of these species have been recognized for their forage potential; hence, they have been subjected to domestication processes with the aim to introduce them into crop systems and improve forage quality (Zabala et al. 2010). Species of the genus *Desmanthus* have been found to have great forage potential, especially in tropical and subtropical regions. For instance, in the north of Australia, the possible introduction of this genus into grazing systems was studied; as a result, three cultivars were made available in 1991: *D. virgatus* cv. *Marc*, *D. leptophyllus* cv. *Bayamo*, and *D. pubescens* cv. *Uman* (Burt 1993; Jones and Clem 1997). Furthermore, in the USA, four *D. bicornutus* cultivars were developed (Ocumpaugh et al. 2004), whereas in Argentina, two cultivars were developed: *D. leptophyllus* (DLBT) and *D. virgatus* (DV7059).

At the taxonomic level, *D. virgatus* (L.) Willd. is a complex that includes four species native to Argentina: *Desmanthus acuminatus* Benth., *Desmanthus papalaceus* (Lindm.) Burkart, *Desmanthus tatuhyensis* Hoehne var. *tatuhyensis* and *D. virgatus* (sensu stricto) (Luckow 1993; Zuloaga and Morrone 1999). Of these species, all but *D. tatuhyensis* have shown forage potential. Despite this limitation, *D. tatuhyensis* is a valuable plant genetic resource due to its tolerance to salinity and flooding (Zabala et al. 2010).

The germplasm of these species has been included in collections for decades. The Australian Pastures Genebank (APG), the Embrapa Tabuleiros Costeiros (CPATC) and the Centro Internacional de Agricultura Tropical (CIAT) hold almost the total of germplasm collections of the *D. virgatus* complex (Genesys 2025). In Argentina, the germplasm bank “Ing. Agr. José M. Alonso” has a unique collection of the *D. virgatus* complex, with 80 accessions (FAO 2010; Zabala et al. 2010) obtained in numerous collection missions. However, despite the information obtained for the complex and the conserved germplasm, the representativeness of the conserved genetic variability is unknown.

Determining the genetic representativeness of a species in a germplasm collection is essential for evaluating the genetic variability of the collected populations with respect to those occurring in nature. However, since the variability existing in nature is unknown, complementary or alternative approaches have been proposed to evaluate the genetic representativeness in ecogeographic terms (Parra-Quijano et al. 2012). This characterization is based on the analysis of environmental information of the sites where populations grow, which is obtained from georeferenced ecogeographic data (Steiner and Greene 1996). Ecogeographic representativeness is related to the abiotic adaptation process and, indirectly, to genotypic aspects (Parra-Quijano et al. 2012a). The relationship between environmental conditions, genes and phenotypic expressions due to natural selection and local adaptation (Greene and Hart 1999) offers a biological basis for this approach. Thus, in the absence of genetic data, combining spatial data with ecogeographic information allows us to estimate the genetic representativeness in ecogeographical terms. This combination is a valid approach to the understanding and study of phenotypic and genotypic diversity in germplasm collections.

Ecogeographic land characterization (ELC) maps have been widely used for that purpose (García et al. 2017; Marinoni et al. 2015, 2021; Naranjo Quinaluisa et al. 2018; Orquera et al. 2025; Parra-Quijano et al. 2012; Rubio Teso et al. 2022). This method helps identify possible bias in *ex situ* collections; thus, it allows us to focus collection efforts on the areas where they are most necessary and to establish representative collections. While the method is a good approximation to the situation in nature, validating the tool with genetic data is desirable.

Model validation has been demonstrated to be an efficient and useful tool to identify and characterize patterns of genetic and phenotypic variation. Naranjo et al. (1990) and Assefa et al. (2003) highlight how techniques contribute to the identification of variability within germplasm collections. Recently, Orquera et al. (2024) developed an easy-to-apply method to validate ELC maps.

In this work, an ELC was developed for the *D. virgatus* complex in Argentina; it was validated with genetic data and used to evaluate the representativeness of the conserved germplasm.

## Materials and methods

### Study area and occurrence data

The study was conducted in the area of occurrence of the *Desmanthus virgatus* complex in Argentina. Species occurrence data were collected from the “Ing. Agr. José M. Alonso” Germplasm Bank of the Facultad de Ciencias Agrarias de la Universidad Nacional del Litoral, from the GENESYS global genebank (<https://www.genesys-pgr.org/>), the Documenta Florae Australis database (<http://www.darwin.edu.ar/iris>), and the Global Biodiversity Information Facility (GBIF) database (<http://data.gbif.org/>).

Records were evaluated with GEOQUAL in the CAPFITOGEN3 tool package (Parra-Quijano et al. 2020) with the aim to remove geographic inconsistencies, using the method described by Marinoni et al. (2021). Data that were duplicated, inconsistent or that lacked coordinates were removed from the analysis.

## Variable selection and development of the ELC map

The construction of the ELC map requires the availability of ecogeographic variables closely associated with the distribution of the species complex as well as the occurrence dataset. We used the tool SelecVar in the package CAPFITOGEN3. The set of CAPFITOGEN3 tools (<https://www.capfitogen.net/es/>) comprises 80 bioclimatic layers from the database WorldClim v 2.1 (<https://www.worldclim.org/data/worldclim21.html>), 66 soil layers from the Harmonized World Soil Database version 1.21 (<https://iiasa.ac.at/web/home/research/researchPrograms/water/HWSD.html>) and SoilGrids (<https://soilgrids.org>), and 33 geophysical variables from Worldclim v2.1 and SRTM v3 (<http://srtm.csi.cgiar.org/>). The map was constructed using georeferenced layers with a cell resolution of 30 arc seconds ( $\sim 1 \times 1$  km at the equator).

Ecogeographic variables for the elaboration of the ELC map were selected following Marinoni et al. (2021) and Orquera et al. (2025). The importance of each variable was determined via a Random Forest classification, using the mean decrease accuracy (MDA) of each variable (Cutler et al. 2007). Half of the variables with the lowest MDA ranking values were discarded (except for the geophysical component, which only includes five variables). Finally, the variables that were significantly correlated ( $P \leq 0.01$ ; correlation coefficient ( $r$ )  $\geq |\pm 0.5|$ ) were discarded, and those with the highest MDA value and highest weight in the components 1 and 2 of the Principal Component Analysis (PCA) were retained, thereby ensuring a minimum of three variables per component.

The layers of the selected variables were cropped using the distribution area of the species in Argentina with the tool rLayer of the kit CAPFITOGEN3.

Finally, the ELC map of the *D. virgatus* complex was built with the variables retained at the end of the process, using the ELC maps tools. The number of optimum groups was determined with the successive non-hierarchical K-means clustering method, and the optimum number of clusters was defined using the Bayesian Information Criterion (BIC), with a maximum of four clusters per component. The groups

obtained for each component were combined to generate the final ecogeographic categories of the ELC map. Vector and raster layers were processed using QGIS 3.28.15 (QGIS Development Team 2022).

## **Morphological and genetic validation of the ELC map (dup: abstract ?)**

The map was validated following the method described by Orquera et al. (2025), with the morphological data obtained by Zabala et al. (2008), who included the analysis of 26 populations of *D. virgatus*, *D. acuminatus* and *D. paspalaceus* collected in Argentina. Fourteen quantitative, vegetative and reproductive morphological traits were used. In addition, information of 14 ISSR molecular markers provided by Tomas et al. (2011) from the same populations was used. The morphological data and the ecogeographic variables selected were subjected to a PCA, and molecular data were analyzed using a Principal Coordinate Analysis (PCoA). To evaluate the consensus between datasets, the first six principal components and coordinates were used to perform a consensus analysis between ecogeographic, morphological and genetic variation via a Generalized Procrustes Analysis (Gower 1975).

## **Analysis of ecogeographic representativeness**

Once the ELC map was elaborated and validated, the ecogeographic category (EC) for each occurrence record was extracted using the raster analysis tool in the QGIS Processing Toolbox. To evaluate the representativeness of the conserved germplasm, the frequency of occurrence of accessions of germplasm conserved in genebanks (observed frequency) was compared with the total frequency of occurrence points (expected frequency) of each category, using the chi-square test (Hernández-Salinas et al. 2022; Marinoni et al. 2015). The ideal scenario is one in which the accessions conserved in germplasm banks are distributed in a proportions that exactly reflects the total frequency of occurrence of each ecogeographic category. However, this is not always the case, and some categories can be under- or overrepresented, or even not be conserved at all. Identifying gaps in germplasm collections would allow us to optimize sampling design to establish priorities in collection missions.

## **Results**

### **Development of the ELC map**

Of the 425 presence records, those belonging to the same species and that were at a distance of less than 5 km were removed, since they are considered to belong to the same population. Of the remaining 314 records (Fig. 1), 48 belong to germplasm bank accessions.

Table 1 presents the bioclimatic, edaphic and geophysical variables selected to generate the ELC map. Details of the process are described in Supplementary Material. The resulting ELC map consisted of 36 (Fig. 2) ecogeographical categories in the distribution area of the complex.

Table 1  
Ecogeographic variables used to design the  
Ecogeographic Land Characterization (ELC) map

| Component   | Variables                             |
|-------------|---------------------------------------|
| Bioclimatic | Min Temperature of Coldest Month      |
|             | Annual Precipitation                  |
|             | Mean Temperature of Driest Quarter    |
| Edaphic     | Topsoil Sand Fraction                 |
|             | Topsoil total exchangeable bases      |
|             | Topsoil CEC (soil)                    |
| Geophysical | Latitude for the cell centroid        |
|             | Annual solar radiation                |
|             | Elevation. Meters above the sea level |

## Morphological and genetic validation of the ELC map

The Multivariate Analysis of Variance and the Bonferroni-corrected Hotelling's a posteriori test revealed significant differences ( $P < 0.01$ ) between categories, and the Wilks' Lambda value was of 0.01 ( $\eta^2 = 0.01$ ;  $P < 0.0001$ ). These differences were supported by the Generalized Procrustes Analysis, where consensus was 84% between morphological and ecogeographic data, 80% between genetic and ecogeographic data, and 73% among the three datasets.

## Evaluation of ecogeographic representativeness

Occurrence was observed in 27 of the 36 ECs resulting from the ELC map. Of them, 7 are not represented in germplasm banks (Fig. 3).

The Chi square test showed no significant differences in distribution between conserved accessions and the expected frequency ( $P < 0.0001$ ), indicating a satisfactory alignment between expected and observed frequencies ( $P < 0.05$ ).

## Discussion

Ecogeographic characterization maps have been found to be key tools for the conservation and management of natural genetic resources. In this work, we present the first report of the distribution of the *Desmanthus virgatus* complex in ecogeographic zones, providing a fundamental guide for its conservation and sustainable use. The method used, based on tools of the CAPFITOGEN3 package and

on multivariate techniques, has been previously validated for the spatial analysis of ecogeographic diversity (García et al. 2017; Marinoni et al. 2015; Orquera et al. 2025; Mauricio Parra-Quijano et al. 2012). This methodology is useful for designing optimized germplasm collections, characterizing ecogeographic diversity of germplasm (Naranjo Quinaluisa et al. 2018; Rubio Teso et al. 2022) and giving priority to regions for in situ and ex situ conservation (Nduche et al. 2023).

The ELC map of the *D. virgatus* complex has revealed a notable variability across its distribution range, suggesting a great genetic diversity of the complex in Argentina (Korona 1996; Mauricio Parra-Quijano et al. 2012). However, a high number of records in a given area does not necessarily indicate optimum environmental conditions; by contrast, it might reveal sampling bias, since sampling is conducted mostly in areas of easy access (Hijmans 2012).

The analysis of ecogeographic representativeness has allowed us to detect over-, under- and unrepresented zones in the genebank collections. This finding is fundamental to plan long-term collection and conservation strategies, ensuring a suitable representation of the genetic variability of *D. virgatus* and promoting cooperation between genebanks and other key actors (Gallo 2024; Rahman et al. 2021).

The high consensus found between the environmental and genetic data sets reinforces the value of these models as a provisional tool when genetic data are not available, since they are a good approximation to the adaptive scenario of species. The application of validated models is essential in programs aiming at the conservation and use of plant genetic resources.

## Declarations

## Competing Interests

The authors have not financial interests to disclose.

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## Author Contribution

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Maria Ayelen Velazquez, Ricardo Orquera and Lorena Marinoni. The first draft of the manuscript was written by Maria Ayelen Velazquez and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

# Data Availability

The datasets generated during and/or analysed during the current study are available in the CONICET repository.

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## Figures

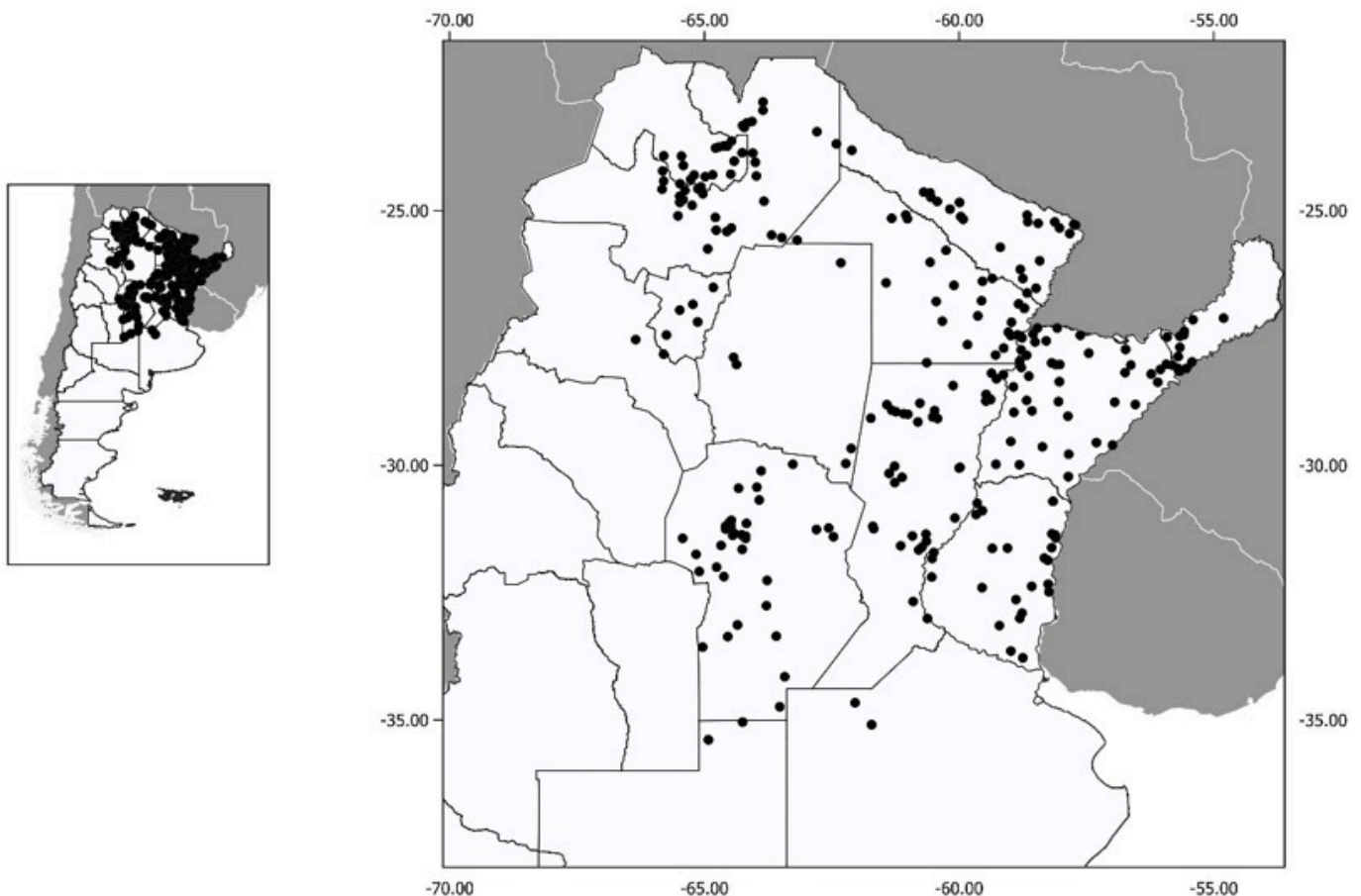


Figure 1

Map of occurrence (black points) of the *Desmanthus virgatus* complex in Argentina

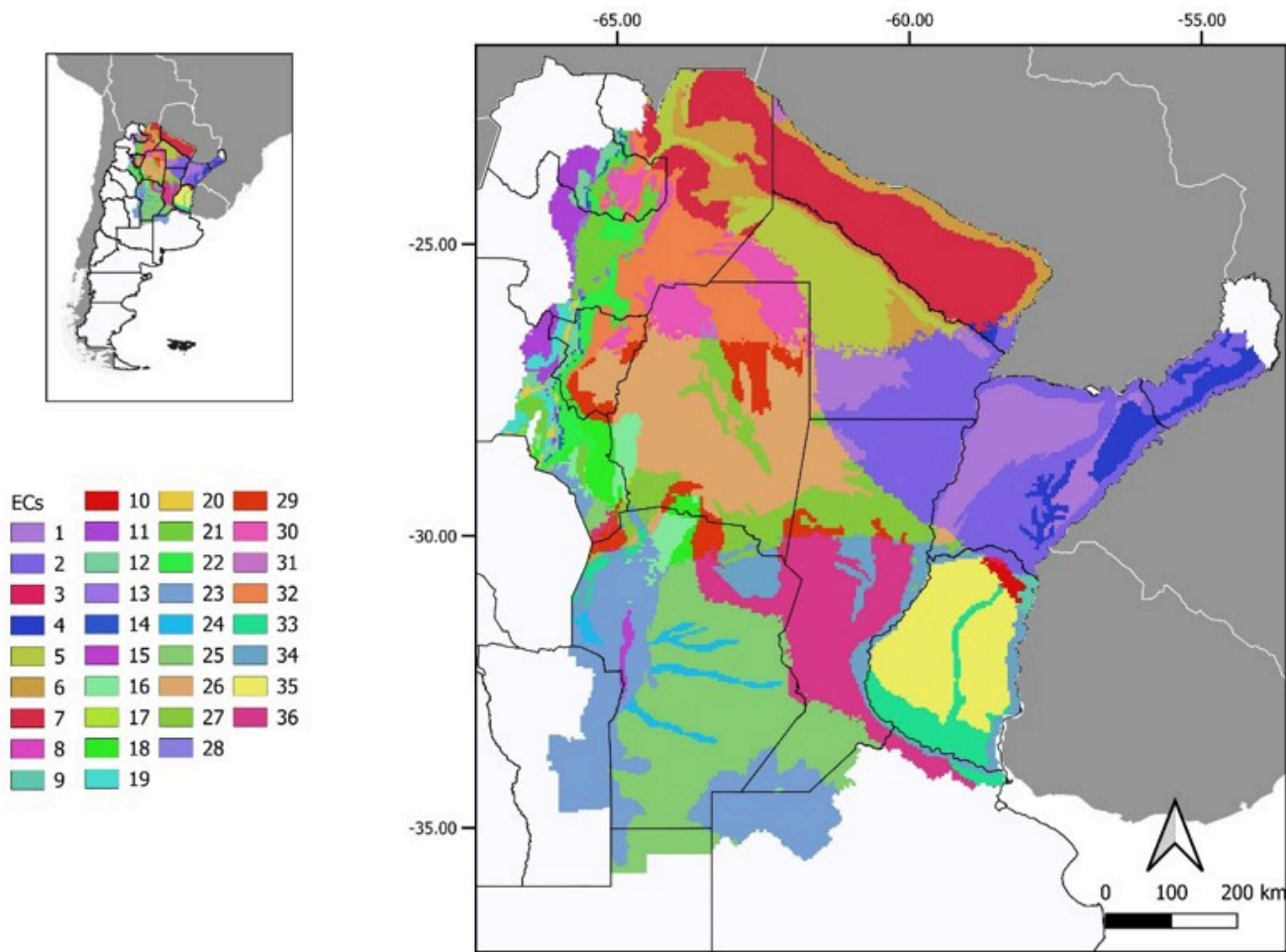


Figure 2

Ecogeographic Land Characterization (ELC) map of the distribution area of the *Desmanthus virgatus* complex in Argentina.

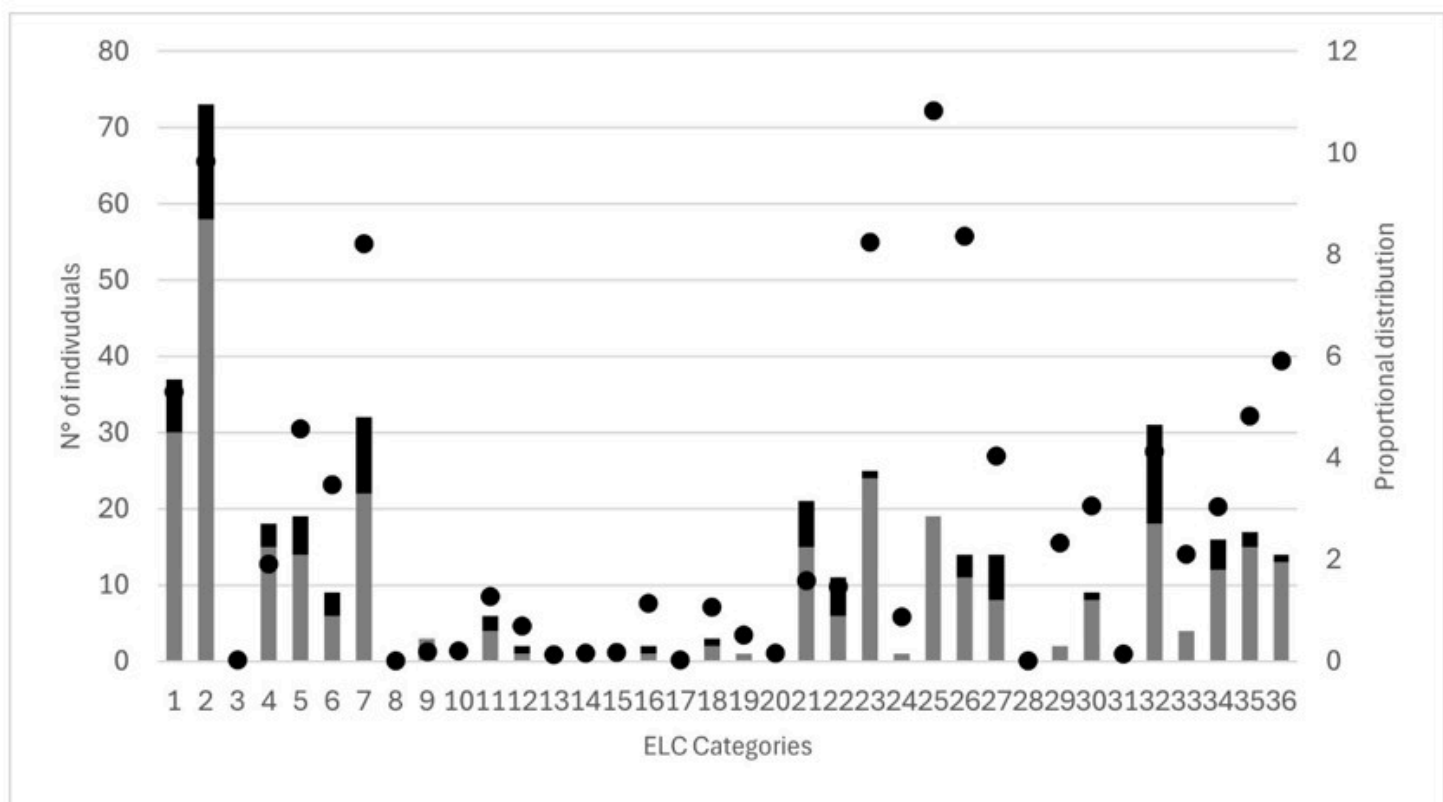


**Figure 3**

Frequency distribution among ELC map categories (x-axis). Grey bars represent the total percentage of occurrences, and black bars represent the percentages of accessions conserved in the germplasm banks. Circles stand for proportional distribution of each category in the ELC map.