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Spatiotemporal seed transfer zones as an efficient restoration strategy in response to climate change

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Abstract. Restoration of wild plant populations in a changing environment is not a simple task, and it becomes increasingly complex and challenging in the context of climate change. In the present study, a spatiotemporal approach was used to delimit provisional seed transfer zones (STZs), for restoration activities involving two wild perennial grasses in Argentina. Ecogeographical land characterization maps were built specifically for the two species of *Trichloris* genus for the present bioclimatic conditions to define the different STZs; then, they were projected for two future climate scenarios (2050 and 2070). This allowed us to identify populations occurring in cells that underwent changes in ecogeographical categories, potential future beneficiaries of germplasm, and populations that could be used as corresponding source populations under the present conditions. Finally, the conservation status of populations was surveyed and a germplasm collection for future restoration activities was proposed. For the 2050 scenario, for *Trichloris crinita*, 32 potential beneficiary populations belonging to nine changing categories were identified, whereas for *Trichloris pluriflora*, four changing categories determined seven beneficiary populations. The number of changing categories and, consequently, the beneficiary populations increased in the 2070 scenario in both species. Several potential seed source populations are already stored in Argentine germplasm banks, but there is little representation of potential beneficiary populations. Spatial locations of still non-conserved populations, both seed sources and beneficiaries, were prioritized for future germplasm collecting missions. This novel approach used for *Trichloris* spp. can also be adopted for other species for collection and/or restoration purposes in the light of climate change.

Key words: conservation; germplasm sourcing; optimized collecting; threatened populations; *Trichloris crinita*; *Trichloris pluriflora*.

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Introduction

In the last decades, global warming has caused impacts on natural and anthropogenic systems across all continents and oceans (IPCC 2014). Particularly in Argentina, mean temperature increased by about 0.5°C in the last century and precipitations increased on average 5 mm/yr (Barros et al. 2008, Doyle et al. 2012), showing a displacement of isotherms and isohyets to the west and southwest of the country. Projected changes suggest trends of increasing temperature

and extreme intensity and frequency of rainfall events (IPCC 2014, Barros et al. 2015).

The rate of climate change is likely to exceed the species' capacity to adapt to such change (Davis and Shaw 2001). Accordingly, predicting the response of wild plant genetic resources to those changes has become an active field of research (Bellard et al. 2012, Guittar et al. 2016). A wild plant genetic resource is defined as any genetic material of plant origin that has undergone a long process of natural selection and adaptation to variations in the local environment and that has potential for ecosystem restoration and plant breeding (Brown and Marshall 1986, Handel et al. 1994). Since survival of wild plant genetic resources depends only on their adaptation abilities, they may be highly vulnerable to climate change if natural populations do not have sufficient genetic diversity to cope with change.

Threatened plant species persistence in their natural habitats depends on genetic diversity of the adaptive traits (Jump and Peñuelas 2005). If a given population has low genetic diversity and shows signs of maladaptation, resulting in lower fitness, a reinforcement action may be necessary. This reinforcement will be successful only if the germplasm used for rehabilitation is compatible with that of the target population and has the adaptive capacity to survive in the environment where it occurs (Bower et al. 2014).

Seed transfer zone (STZ) is a methodological approach that has been developed for accurately detecting well-adapted wild plant genetic resources to be used in restoration of ecosystems subjected to environmental changes (Havens et al. 2015). A STZ is a geographical area within which germplasm of a native population can be translocated to similar environmental scenarios with minimal risk of maladaptation (Kramer and Havens 2009, St. Clair et al. 2013, Havens et al. 2015). Species exhibit wide spatial and temporal variation in local patterns of adaptation, which are related to a number of biotic and abiotic factors (Hanson et al. 2017). Since genetic information on target wild plant species previous to collection or restoration activities is often lacking, population differentiation in terms of abiotic adaptation (the basis of the STZ approach) can indirectly reflect genetic variation (Peeters et al. 1990).

The first approaches to provide seed zones in order to avert or prevent failures in planting date from early 20th century (Bates 1930, Fowells 1946). Over the years, assorted approaches were used to delimit STZs with different specificity levels. Provisional STZs are based on assumptions about ecogeographical features that are important across species distribution range, and they are widely used by restoration managers because empirical species-specific zones based on genecological studies often are not available for most species and because of the time and effort to develop them (Vogel et al. 2005, Bower et al. 2014, Omernik and Griffith 2014, Doherty et al. 2017, Gibson and Nelson 2017, Germino et al. 2019, Cevallos et al. 2020). Some studies about genetic and phenotypic differentiation can be used to support provisional STZs and seed transfer guidelines (Johnson et al. 2004, Doherty et al. 2017, Durka et al. 2017), but the cost and time involved in the empirical species-specific approaches lead managers to use provisional STZs to support decisions in restoration activities. On the other hand, studies only based on genetic studies cannot provide clearer patterns to develop species-specific STZs (Jørgensen et al. 2016). This is particularly important when facing the challenge to enhance the use of wild plant materials in revegetation in some countries where STZ-based tools are inexistent. For instance, this is the case of Argentina, where restorations and revegetation activities are yet established by ecogeographical regions or the use of local genotypes as the best source for revegetation. Although the latter can be seen as a valid method, it becomes insufficient in the face of changing climate.

Several guidelines for germplasm collection and transfer based on the use of ecoregions as a parameter to delimit STZs have been proposed (Erickson et al. 2004, Johnson et al. 2010, Miller et al. 2011). However, the environmental categorization that provides an ecoregion may be too broad to detect certain limiting environmental factors and adaptive patterns (Parra-Quijano et al. 2012*a*). On the other hand, sensitivity to limiting environmental factors varies among species; therefore, a species-specific approach is necessary, such as the one developed by García et al. (2017) for the conservation of plant genetic resources based on the use of ecogeographical

land characterization (ELC) maps. Ecogeographical land characterization maps can be created for one species or a group of phylogenetically related species using ecogeographical variables closely related to species distribution, providing a helpful characterization of different environmental scenarios where the target species occurs in a given territory (García et al. 2017, Parra-Quijano et al. 2018).

As aforementioned, the first studies based on STZs were limited to present-time situations and covered only the spatial dimensions (Withrow-Robinson and Johnson 2006, Bower et al. 2014). However, under the current conditions of rapid climate change, the temporal dimension adds to the spatial one. This approach consists of producing STZs, whose present environmental characteristics are maintained in the future conditions. Thus, the spatial limits for seed transfer within a zone are defined for different time periods (Potter and Hargrove 2012, Havens et al. 2015, Richardson and Chaney 2018, Shryock et al. 2018).

Seed zones have been widely applied in forestry over time, but their use for herbaceous species is recent (Erickson et al. 2004, St. Clair et al. 2013, Bower et al. 2014, Durka et al. 2017, Erickson and Halford 2020). In Argentina, STZ approaches have also been mainly developed for tree species (Pastorino 2012, Azpilicueta et al. 2013, Atkinson et al. 2018). The use of wild forage species for rangeland rehabilitation is essential for the restoration of ecosystems modified by climate change. In Argentina, rangelands are mostly covered with gramineous species. Particularly, species of the genus *Trichloris* (Poaceae), *T. crinita* (lag.) Parodi, and *T. pluriflora* E. Fourn are C4 perennial grasses with a disjunct distribution in Argentine and USA rangelands (Lloyd-Reilley 2011, Quiroga et al. 2018). Both species are highly autogamous (Gutiérrez et al. 2016, Kozub et al. 2017), and they are distributed in semiarid rangelands, but only *T. crinita* grows in arid (150 mm of annual rainfall) and saline environments (Rúgolo and Molina 2012, Marinoni et al. 2015, 2020). Although both species have good forage quality for livestock production in arid and semiarid rangelands (Kunst et al. 1995, Quiroga et al. 2013, Kozub et al. 2018*b*), *T. crinita* has been more studied because of its tolerance to extreme environmental conditions. Genetic studies in the latter species are scarce and do not include representative populations along the distribution range (Cavagnaro et al. 2006, Kozub et al. 2018*a*), and they are lacking in *T. pluriflora* (Tomas et al. 2012). In a previous study, we found adaptive differentiation in seed mass in populations of *T. crinita* and *T. pluriflora* along their distribution range. Thus, seed mass of populations was found to be related to certain climatic and geophysical variables, such as latitude, altitude, rainfall, and temperature (Marinoni et al. 2018). Given the wide distribution of *Trichloris* species in Argentina and their forage value for livestock production, the study of the effects of climate change across their distribution range provides a valuable contribution to the design of management strategies for rangelands and wild plant genetic resources.

With the goal of optimal conservation and use of the genetic resources of two important native forage species, the present study aimed at (1) defining provisional spatiotemporal STZs for *T. crinita* and *T. pluriflora*; (2) based on the resulting STZs, determining the origin of germplasm to be used for rangelands restoration under a climate change scenario; and (3) identifying the current priorities for germplasm collection based on the vulnerabilities associated with climate change.

Materials and Methods

Spatial data of species occurrences

The study was conducted using the georeferenced occurrence dataset of the genus *Trichloris* in Argentina generated by Marinoni et al. (2015). Occurrence data were updated using the Global Biodiversity Information Facility (GBIF) database (http://data.gbif.org/), the Documenta Florae Australis database (http://www.darwin.edu.ar/iris/), which gathers data from Argentine herbaria, and local germplasm banks, from the Instituto Nacional de Tecnología Agropecuaria (INTA), the Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA), and the Facultad de Ciencias Agrarias of the Universidad Nacional del Litoral (FCA-UNL; see occurrence databases in Appendix S1: Tables S1, S2). A total of 305 and 99 occurrence records were obtained for *T. crinita* and *T. pluriflora*, respectively (Fig. 1), which were processed using GEOQUAL

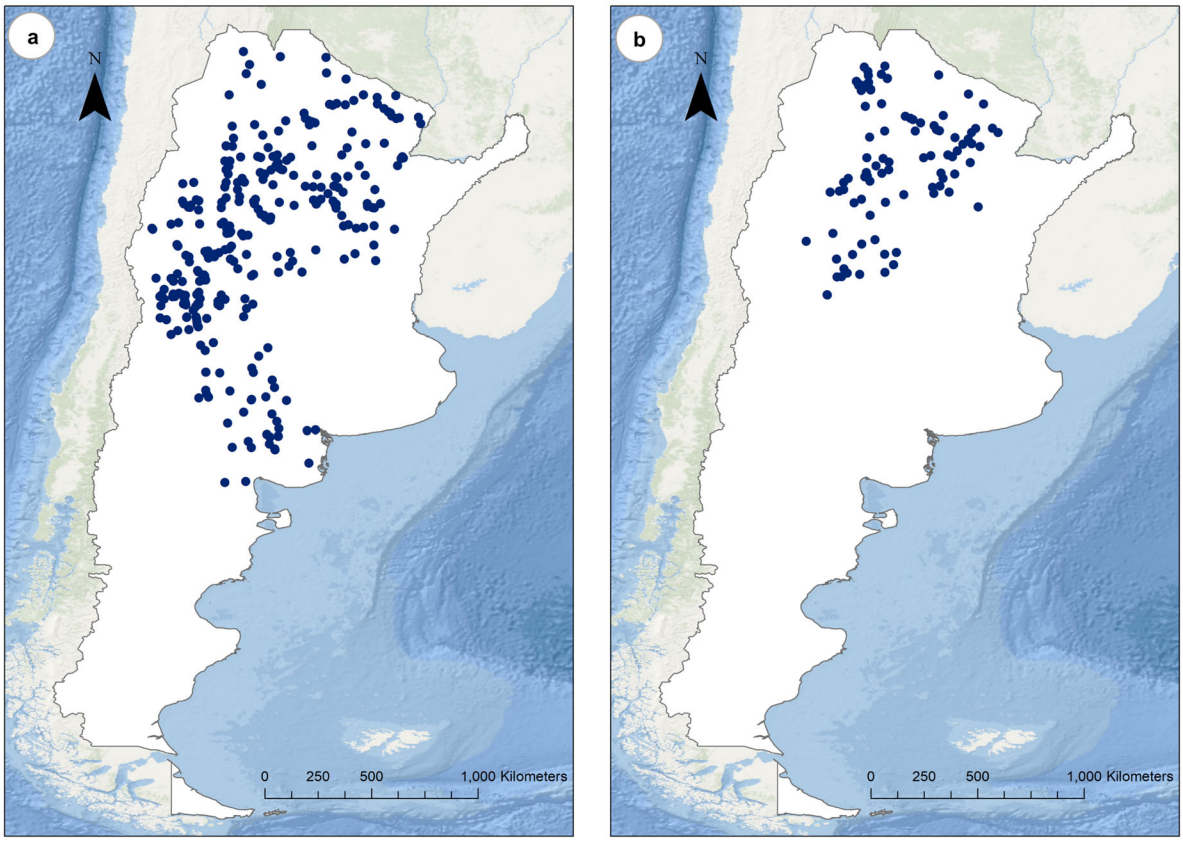


Fig. 1. Species distribution maps: (a) occurrence dataset of *Trichloris crinita* and (b) occurrence dataset of *Trichloris pluriflora*.

from CAPFITOGEN toolkit (http://www.capfitogen.net/es) to assess georeferencing quality (Parra-Quijano et al. 2018). This tool generates a parameter called TOTALQUAL100 for each occurrence record, which ranges from 0 (low accuracy georeferenced data, mistaken coordinates, or inconsistencies between coordinates and the associated locality names) to 100 (theoretically optimum quality data). Occurrence data with TOTALQUAL100 < 70 were discarded from analysis.

Present and future ecogeographical data

For each georeferenced occurrence record, ecogeographical data were extracted from layers with a grid cell size of 2.5 arc-minutes (~5 × 5 km at the equator). A total of 20 bioclimatic, 15 edaphic, and 5 geophysical variables were gathered from various sources compiled in the CAPFITOGEN toolkit (Appendix S2: Table S1). Edaphic and geophysical layers were obtained from Harmonized World Soil Database (http://webarchive.iiasa.ac.at/Research/LUC/External-World-soil-database/HTML, FAO et al. 2012) and Digital Elevation Model of Shuttle Radar Topography Mission (http://www.srtm.csi.cgiar.org), respectively. Bioclimatic layers for the present conditions were obtained from version 2.0 of WorldClim database (http://www.worldclim.org, Fick and Hijmans 2017), whereas projected bioclimatic layers for future conditions were obtained from version 1.4 (Hijmans et al. 2005), since they were not available for version 2.0. To analyze future climate conditions, the values of the BCC-CSM1-1, CCSM4, HadGEM2-AO, HadGEM2-ES, IPSL-CM5A-LR, MIROC5, MRI-CGCM3, and NorESM1-M GCMs of the Coupled Model Intercomparison Project Phase 5 (CMIP5) were averaged. Assembly of these GCMs was successfully used by Aguirre et al. (2017), and

some of these GCMs were used in studies for South America and Argentina (Maenza et al. 2017, Rivera et al. 2017). The RCPs 4.5 (optimistic) and 8.5 (pessimistic) scenarios projected for 2050 and 2070, respectively, were the selected future scenarios. RCP 4.5 was the scenario selected for 2050 because it predicts that emissions will peak by that year and then will stabilize, whereas RCP 8.5 predicts that emissions will continue to rise (Thomson et al. 2011, IPCC 2014, Thomas et al. 2017).

Variable selection process

To determine the most important variables influencing plant distribution and detect redundancies, random forest classification and bivariate correlations were, respectively, performed for each species and within each ecogeographical component (i.e., bioclimatic, edaphic, and geophysical; García et al. 2017), with the data extracted for the present conditions. First, the importance of each variable in the random forest classification was determined via the mean decrease in the accuracy (MDA) of each variable (Cutler et al. 2007). Half of the variables presenting the lowest values in the MDA ranking were discarded (except for the geophysical component, which only contains five variables). Then, the variables that were significantly correlated (P value ≤ 0.01; correlation coefficient $(r) \geq |\pm 0.5|$) were discarded in a stepwise procedure, and the variable with the highest value in the MDA ranking was retained. These analyses were performed using R software (R Core Team 2014), and the randomForest (randomForest package) and cor.test (stats package) functions (R code in Data S1).

Spatiotemporal seed transfer zone delineation

The Tzones tool from CAPFITOGEN toolkit was used to construct both present and future ELC maps of Argentina. An ELC map characterizes a given territory through the delineation of areas with similar environmental characteristics, referred to as ecogeographical categories (Parra-Quijano et al. 2018). First, the ELC map for the present conditions was generated with the previously selected ecogeographical variables. Each bioclimatic, edaphic, and geophysical component was subjected to a cluster analysis to determine the optimal number of groups (derived from combinations of selected variables). Clustering was performed using successive non-hierarchical *K*-means, and the Bayesian information criterion was used to determine the optimal number of groups. Tzones uses the find.clusters function from adegenet package (Jombart et al. 2015) to perform this process. Then, the groups obtained for each component were combined to generate the ecogeographical categories of ELC map for the present conditions.

The bioclimatic component is the only one that changes over time, and for which a modification in the spatial distribution of bioclimatic groups is expected for future projections. A random forest algorithm was used to determine a grouping pattern between ELC map categories and the present bioclimatic variables used for ELC map construction. Then, this pattern was used to project the bioclimatic categories onto the future ELC maps for both climate change scenarios (ensemble of GCM for RCP 4.5/2050 and RCP 8.5/2070). This procedure was followed separately for each *Trichloris* species and allowed us to have homologous ecogeographical categories for both present and future ELC maps. The parameters used to generate the present and corresponding future ELC maps using the Tzones tool are included in Appendix S3: Tables S1, S2 for reproducibility purposes.

The ecogeographical categories of ELC maps defined the different STZs for *Trichloris* species. Thus, seeds from populations belonging to one ecogeographical category, and, consequently, to one STZ, can be transferred to other populations of the same category/STZ with minimum risk of maladaptation (Withrow-Robinson and Johnson 2006, Bower et al. 2014). The temporal dimension is provided by the homology between ecogeographical categories of the present and future ELC maps, which allows seed transfer from present to future adaptive scenarios (Fig. 2).

Use of spatiotemporal STZs

We assumed that populations occurring in locations where the ecogeographical categories changed between present and future ELC maps would be maladapted and threatened as a result of a rapid change in climate conditions. Thus, these populations were identified as potential beneficiary populations. In parallel, we identified as suitable seed source populations those currently located in the same ecogeographical

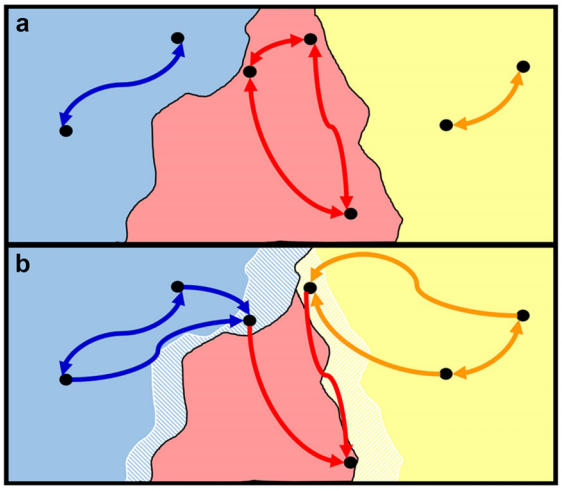


Fig. 2. Germplasm flow between populations (black points) according to seed transfer zone (STZ) structure. The arrows indicate the potential germplasm flow within STZs: (a) potential germplasm flow under present conditions (1950–2000) among populations occurring in three different STZs (solid blue, red, and yellow areas), and (b) potential germplasm flow across spatiotemporal STZs under a climate change scenario. Dashed blue and yellow areas illustrate areas changing from red to blue and yellow STZs, respectively, due to climate change. The tail of the arrows indicates present seed sources that can be used to reinforce future beneficiary populations (head of arrows).

categories as those where potential beneficiary populations will occur in the future. The latter will be used for assisted germplasm transfer if local populations become maladapted to the new conditions resulting from climate change. In this context, the identification and collection of suitable seed sources at present will allow us to use this germplasm for restoration plans in the future.

Ex situ conservation assessment

The ex situ conservation status of germplasm from seed source populations and potential beneficiary populations was checked in local germplasm banks from INTA, ADIZA, and FCA-UNL in Argentina. For each studied species, populations that are currently not conserved ex situ were identified for their prioritization in future optimized collecting designs (OCDs; Marinoni et al. 2015, García et al. 2017).

Table 1. Ecogeographical variables used to construct ELC maps for *Trichloris crinita* and *Trichloris pluriflora*.

Component	Variables	
	Trichloris crinita	*Trichloris pluriflora*
Bioclimatic	Isothermality	Minimum temperature of coldest month
	Maximum temperature of warmest month	Annual temperature range
	Rainfall during the wettest month	Rainfall during the driest month
	Seasonality of rainfall	
Edaphic	Clay content in surface soil	Silt content in surface soil
	Saturation of bases in surface soil	Clay cation exchange capacity in surface soil
	Salinity of surface soil	Saturation of bases in surface soil
		Salinity of surface soil
Geophysical	Longitude	Longitude
	Latitude	Latitude
	Gradient of the land surface	Average solar radiation
	Average solar radiation	

Note: ELC, ecogeographical land characterization.

Results

The ecogeographical variables selected as the most important by random forest and bivariate correlations analysis for *T. crinita* and *T. pluriflora* included four and three bioclimatic variables, three and four edaphic variables, and four and three geophysical variables, respectively (Table 1). The values of mean decrease in accuracy and correlation used in the selection process are included in Appendix S4. For this procedure, one occurrence record of the *T. crinita* dataset was discarded due to low georeferencing quality, whereas no records were discarded for *T. pluriflora*. Thus, a total of 304 and 99 occurrence records were finally used for *T. crinita* and *T. pluriflora*, respectively.

Spatiotemporal seed transfer zone delineation

The ELC map for the present conditions consisted of 52 ecogeographical categories for *T. crinita* and 45 for *T. pluriflora* (Fig. 3), which were defined by a set of descriptive statistics

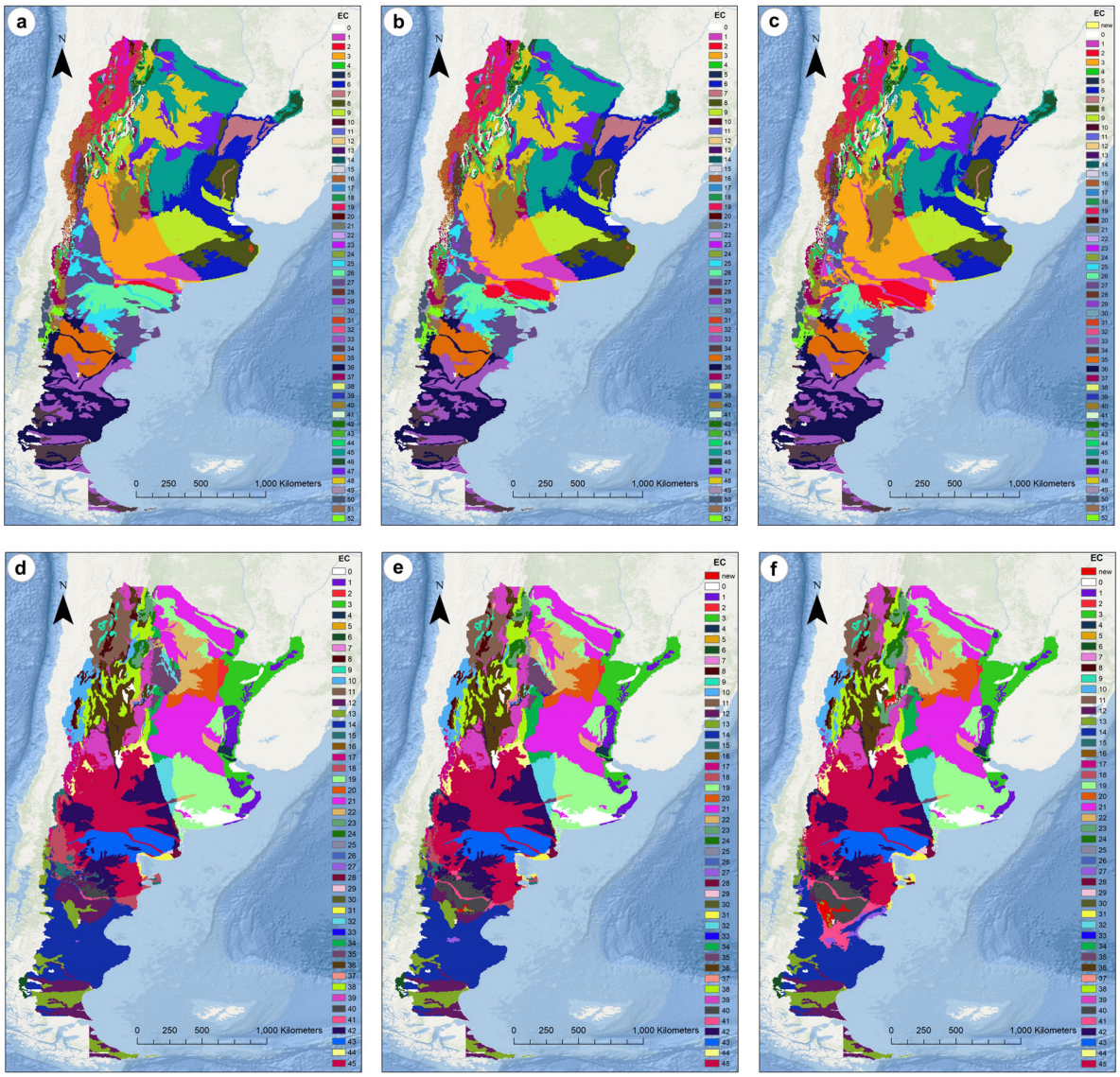


Fig. 3. Ecogeographical land characterization maps generated for *Trichloris crinita* with ecogeographical data from (a) present, (b) RCP 4.5 scenario for 2050, and (c) RCP 8.5 scenario for 2070, and for *Trichloris pluriflora* with ecogeographical data from (d) present, (e) RCP 4.5 scenario for 2050, and (f) RCP scenario 8.5 for 2070.

and specific ranges for each of the environmental variables included in the classification (Appendix S5). In both species, the combination of bioclimatic variables generated four bioclimatic groups, whose geographic extent differed depending on the temporal setting (Fig. 4).

The categories of ELC maps projected for different future scenarios varied in extent and number of cells with respect to those found in the ELC map for the present conditions for *T. crinita* and *T. pluriflora* (Fig. 3). One new EC was detected for RCP 8.5/2070 scenario for *T. crinita* and for both scenarios (RCP 4.5/2050 and RCP 8.5/2070) for *T. pluriflora*. New ECs in future ELC maps are generated by new combinations of bioclimatic, edaphic, and geophysical groups not reported for the current conditions. In all cases, the changes were more evident as changes in the frequency and distribution of the present-time

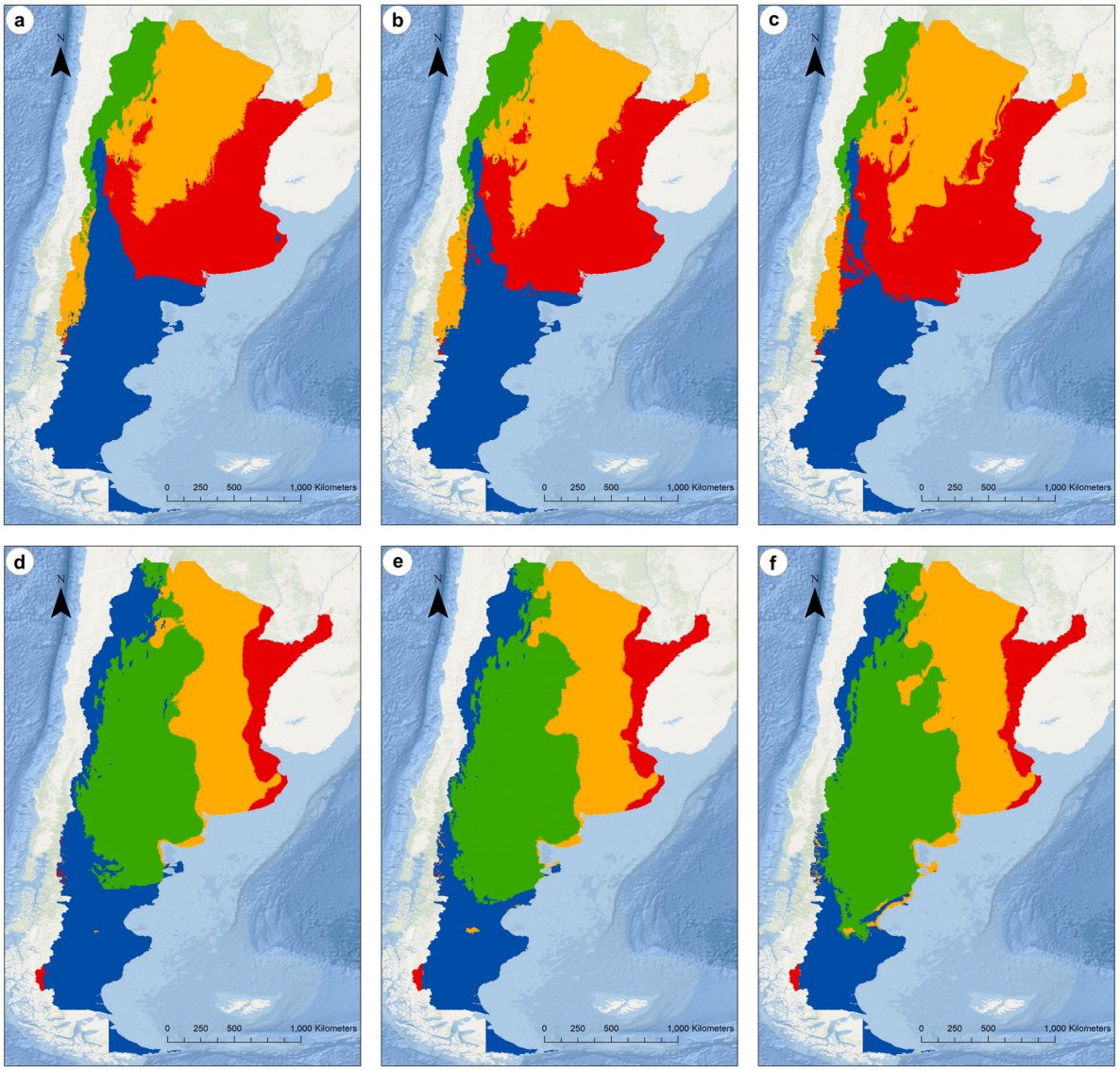


Fig. 4. Bioclimatic groups derived from combination of bioclimatic variables, used to generate ecogeographical land characterization maps for *Trichloris crinita*: (a) present, (b) RCP 4.5 scenario for 2050, and (c) RCP 8.5 scenario for 2070, and for *Trichloris pluriflora*: (d) present, (e) RCP scenario 4.5 for 2050, and (f) RCP 8.5 scenario for 2070.

categories rather than as emergence of new categories. The frequency histograms for both species and for all scenarios are provided in Appendix S5: Fig. S1.

For *T. crinita*, occurrence data were recorded in 24 categories of the present ELC map. In both future projections, occurrences were found in the same ecogeographical categories, but with different frequencies in several of them. In the RCP 8.5/2070 scenarios, no occurrences were found for the category no. 8 (Table 2). Occurrences of *T. pluriflora* were found in 15 categories of the present ELC map, and changes in the frequencies in both future scenarios were also observed, as well as missing categories (Table 3). Thus, the 24 and 15 ecogeographical categories where species occur (*T. crinita* and *T. pluriflora*, respectively) under present conditions define the species-

Table 2. Number of populations of *Trichloris crinita* within each ecogeographical category of ELC maps for the present time and both future projections (RCP 4.5/2050 and RCP 8.5/2070 scenarios).

Ecogeographical categories	Present time	Future projection RCP 4.5/2050	Future projection RCP 8.5/2070
0	1	1	1
1	9	9	9
2	2	9	9
3	72	75	75
5	1	1	1
6	11	10	6
8	3	5	0†
9	10	5	7
16	1	1	1
19	3	3	2
20	1	1	1
23	1	1	1
25	3	2	2
26	8	1	1
27	5	2	1
28	2	2	1
29	2	2	2
37	6	7	7
40	25	25	26
41	8	8	9
44	10	10	11
45	46	47	51
47	20	18	23
48	53	58	56

Note: ELC, ecogeographical land characterization.
† Non-represented category in the RCP 8.5/2070 scenario.

Table 3. Number of populations of *Trichloris pluriflora* within each ecogeographical category of ELC maps for the present time and both future projections (RCP 4.5/2050 and RCP 8.5/2070 scenarios).

Ecogeographical categories	Present time	Future projection RCP 4.5/2050	Future projection RCP 8.5/2070
8	1	0†	0†
19	4	4	5
20	3	3	3
21	15	15	14
22	17	17	20
23	12	15	18
24	3	3	4
25	1	1	2
32	1	1	0†
34	4	4	5
35	4	4	1
36	9	7	4
38	11	11	10
39	12	12	11
45	1	1	1

Note: ELC, ecogeographical land characterization.
† Non-represented category in the RCP 4.5/2050 scenario.
‡ Non-represented category in the RCP 8.5/2070 scenario.

specific STZs. The identification number of the ecogeographical categories was used to identify the different STZs.

Use of spatiotemporal STZs

In *T. crinita*, 32 potential beneficiary populations were identified in 10 STZs that undergo changes in their distribution for the RCP 4.5/2050 scenario (Fig. 5a, Table 4). For RCP 8.5/2070, 37 potentially beneficiary populations were found, located in 12 sites that changed STZs (Fig. 5b, Table 4). Consequently, 226 and 261 potential seed source populations belonging to 9 and 11 different STZs were identified for the optimistic (Fig. 5c) and pessimistic scenarios (Fig. 5d), respectively (Table 4). Similarly, for *T. pluriflora*, 7 and 15 potential beneficiary populations were identified for RCP 4.5/2050 (Fig. 6a) and RCP 8.5/2070 (Fig. 6b) scenarios located in 5 and 8 sites that changed STZs, respectively (Table 5). Accordingly, 40 and 56 potential seed source populations belonging to 4 and 7 different STZs were identified to be used for future restorations, for the optimistic (Fig. 6c) and pessimistic (Fig. 6d) scenarios, respectively (Table 5).

Optimized collecting design

According to the occurrence database compiled for the present study (Appendix S1), the germplasm banks of INTA and IADIZA currently contain 11 (R. E. Quiroga, *personal communication*) and 96 (P. C. Kozub, *personal communication*) accessions of *T. crinita*, respectively, whereas the germplasm bank of FCA-UNL has a *Trichloris* collection with 53 accessions of *T. crinita* and 29 accessions of *T. pluriflora* (J. M. Zabala, *personal communication*).

In *T. crinita*, 23 of the 32 threatened populations identified as potential beneficiary for the RCP 4.5/2050 scenario are already conserved in germplasm banks, as well as 56% of the seed source populations, except for populations from the STZ no. 8. Seed source populations from all spatiotemporal STZs for the RCP 8.5/2070

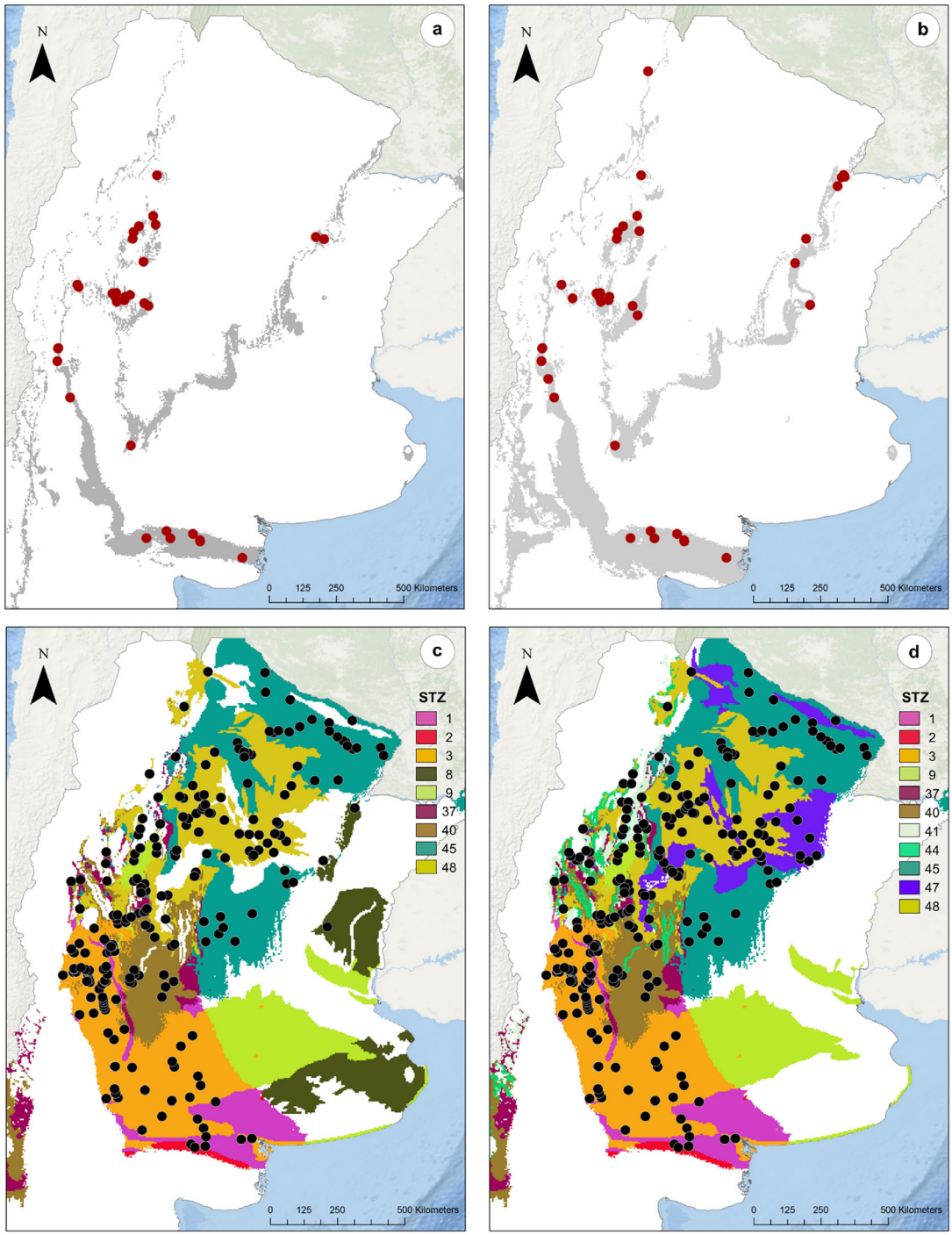


Fig. 5. Climate change impact on distribution of *Trichloris crinita*. Changes in seed transfer zones (STZs; gray zones) and threatened populations—potential beneficiary populations—(red points) for (a) RCP 4.5 scenario for 2050 and (b) RCP 8.5 scenario for 2070. Spatiotemporal STZs and potential seed source populations (black points) for (c) RCP 4.5 scenario for 2050 and (d) RCP 8.5 scenario for 2070.

Table 4. Description of spatiotemporal seed transfer zones (STZs) in *Trichloris crinite*.

Future scenario	Changing STZ	No. of threatened populations	Conservation status†	Future STZ	No. of seed source populations	Conservation status†
RCP 4.5 2050	25	1	1	1	9	7
	26	7	3	2	2	1
	27	3	3	3	72	59
	40	3	3	3	72	59
	47	2	1	8	3	0
	48	3	3	9	10	10
	1	1	0	37	6	5
	3	3	0	40	25	17
	6	1	1	45	46	12
	9	8	8	48	53	15
	Total	32	23		226	126
RCP 8.5 2070	25	1	1	1	9	7
	26	7	3	2	2	1
	27	4	4	3	72	59
	40	2	2	3	72	59
	48	3	3	9	10	10
	1	1	0	37	6	5
	3	3	0	40	25	17
	28	1	1	41	8	3
	19	1	0	44	10	6
	6	5	2	45	46	12
	8	3	0	47	20	9
	9	6	6	48	53	15
	Total	37	18		261	144

Notes: The number of threatened populations (potential beneficiaries) occurring in changing STZs is indicated and the number of potential seed source populations for future restorations is detailed, out of a total of 304 populations recorded. Conservation status is also provided.

† Number of accessions stored at germplasm banks of the Instituto Nacional de Tecnología Agropecuaria (INTA), the Instituto Argentino de Investigaciones de Zonas Áridas (IADIZA), and the Facultad de Ciencias Agrarias of the Universidad Nacional del Litoral (FCA-UNL).

scenario are conserved, and so are 22 of the 37 threatened populations (Table 4).

However, in *T. pluriflora*, there is no availability of germplasm of seed source populations from the STZ no. 34 (RCP 4.5/2050) or no. 25 (RCP 8.5/2070). Moreover, because only the germplasm bank of FCA-UNL stores accessions of *T. pluriflora*, there is a significant lack of potential beneficiary populations. Only one of the seven populations identified for the optimistic scenario and two of the 15 populations detected for the pessimistic scenario are already conserved (Table 5). Populations from almost all spatiotemporal STZs for seed sourcing for future scenarios are already conserved in germplasm banks, accounting for 25% (RCP 4.5/2050) and 18% (RCP 8.5/2070) of total occurrences.

The 34 target populations (still not conserved ex situ) for both species and future projections, either threatened (potential beneficiary) or seed source populations, are detailed in Fig. 7. As it can be observed, most prioritized populations coincided for both future projections, and some additional ones appeared for the pessimistic future scenario.

Discussion

In the present study, we used ELC maps for delimiting provisional STZs, specifically for two native forage species of the genus *Trichloris* as a case study. This approach allowed us to define, qualitatively and objectively, ecogeographically homologous areas for present and future climatic conditions, projected for two of the most widely used scenarios for the study of the impact of climate change (Akhter et al. 2017, Thomas et al. 2017). The proposed approach produces STZ maps useful for present (spatial) and present-future (spatiotemporal) transfers. In this study, we

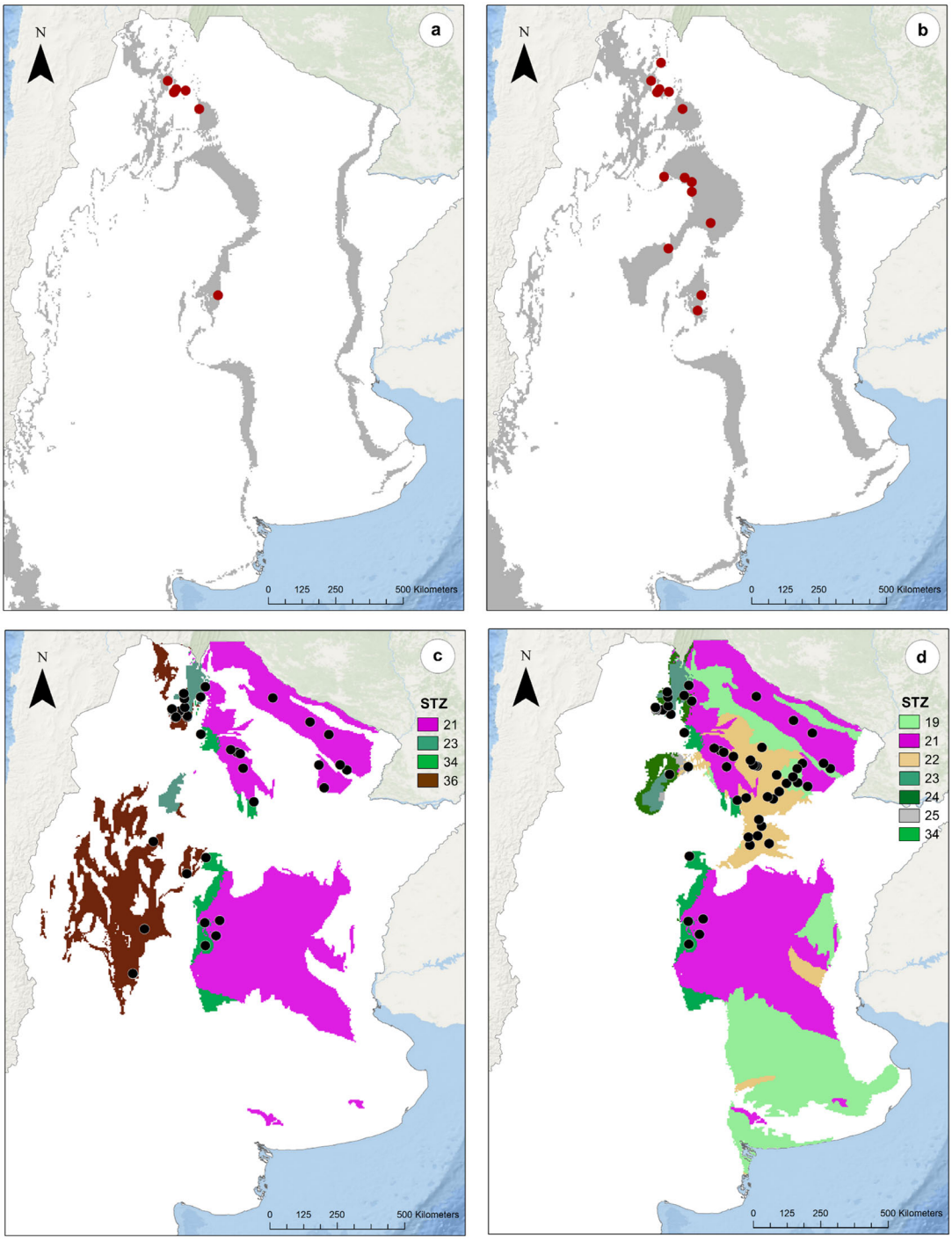


Fig. 6. Climate change impact on *Trichloris pluriflora* distribution. Changing seed transfer zones (STZs; gray zones) and threatened populations—potential beneficiary populations—(red points) for (a) RCP 4.5 scenario for 2050 and (b) RCP 8.5 scenario for 2070. Spatiotemporal STZs and potential seed source populations (black points) for (c) RCP 4.5 scenario for 2050 and (d) RCP 8.5 scenario for 2070.

Table 5. Description of spatiotemporal seed transfer zones (STZs) in *Trichloris pluriflora*.

Future scenario	Changing STZ	No. of threatened populations	Conservation status†	Future STZ	No. of seed source populations	Conservation status†
RCP 4.5 2050	34	1	0	21	15	3
	36	3	1	23	12	1
	8	1	0	23	12	1
	21	1	0	34	4	0
	23	1	0	36	9	6
	Total	7	1		40	10
RCP 8.5 2070	32	1	0	19	4	1
	34	1	0	21	15	3
	35	3	0	22	17	4
	36	5	2	23	12	1
	8	1	0	23	12	1
	38	1	0	24	3	1
	39	1	0	25	1	0
	21	2	0	34	4	0
	Total	15	2		56	10

Notes: The number of threatened populations (potential beneficiaries) occurring in changing STZs is indicated and the number of potential seed source populations for future restorations is detailed, out of a total of 99 populations recorded. Conservation status is also provided.

† Number of accessions stored at germplasm banks of the Facultad de Ciencias Agrarias of the Universidad Nacional del Litoral (FCA-UNL).

focused on the use of the spatiotemporal approach; we assumed some populations as threatened in the future because they occur in locations that will undergo a change in STZs, and detected appropriate seed sources in the present that would be required for the reinforcement of such threatened populations in the future. Seed transfer would be necessary when potential beneficiary populations show signs of maladaptation (i.e., negative demographic trends, loss of genetic diversity). The continuous monitoring of threatened populations, besides the ex situ conservation measures, should ensure timely decision making.

Patterns of genetic variation differ among species and are closely related to reproductive and dispersal systems. It is known that in autogamous species, genetic diversity is higher among than within populations. An autogamous population is composed of highly homozygous lines (Loveless and Hamrick 1984, Falconer and Mackay 2006); therefore, a local habitat is occupied by the best adapted lines (Allard et al. 1968). Although some studies revealed substantial genetic variation between populations of both *Trichloris* species (Cavagnaro et al. 2006, Tomas et al. 2012, Kozub et al. 2018*a*), variation within threatened populations may not be enough to face rapid climatic changes; therefore, germplasm collection and management plans are imperative (Erickson and Halford 2020).

Several studies have focused on the development of species-specific STZs, using multivariate statistics, algorithms, and clustering analysis to define patterns of climatic similarity and providing a guide for transfer of germplasm, giving priority to sources for restoration of natural ecosystems (Doherty et al. 2017, Crow et al. 2018, Shryock et al. 2018). However, in our study, as in that of Coulston and Riitters (2005) and Potter and Hargrove (2012), we included geophysical and edaphic variables, which have important implications in the geographic distribution and adaptation patterns in plants. These variables should also be taken into account, since germplasm will be transferred to environments with specific geophysical and soil conditions; ignoring them can lead to maladaptation. Here we performed a cluster analysis separately for each component (i.e., bioclimatic, edaphic, and geophysical), which allowed us to find the optimal set of variables that defines the real structure of the underlying groups (Raftery and Dean 2006, Dean et al. 2018) and a balanced contribution for each component. This is particularly important in both *Trichloris* species, since

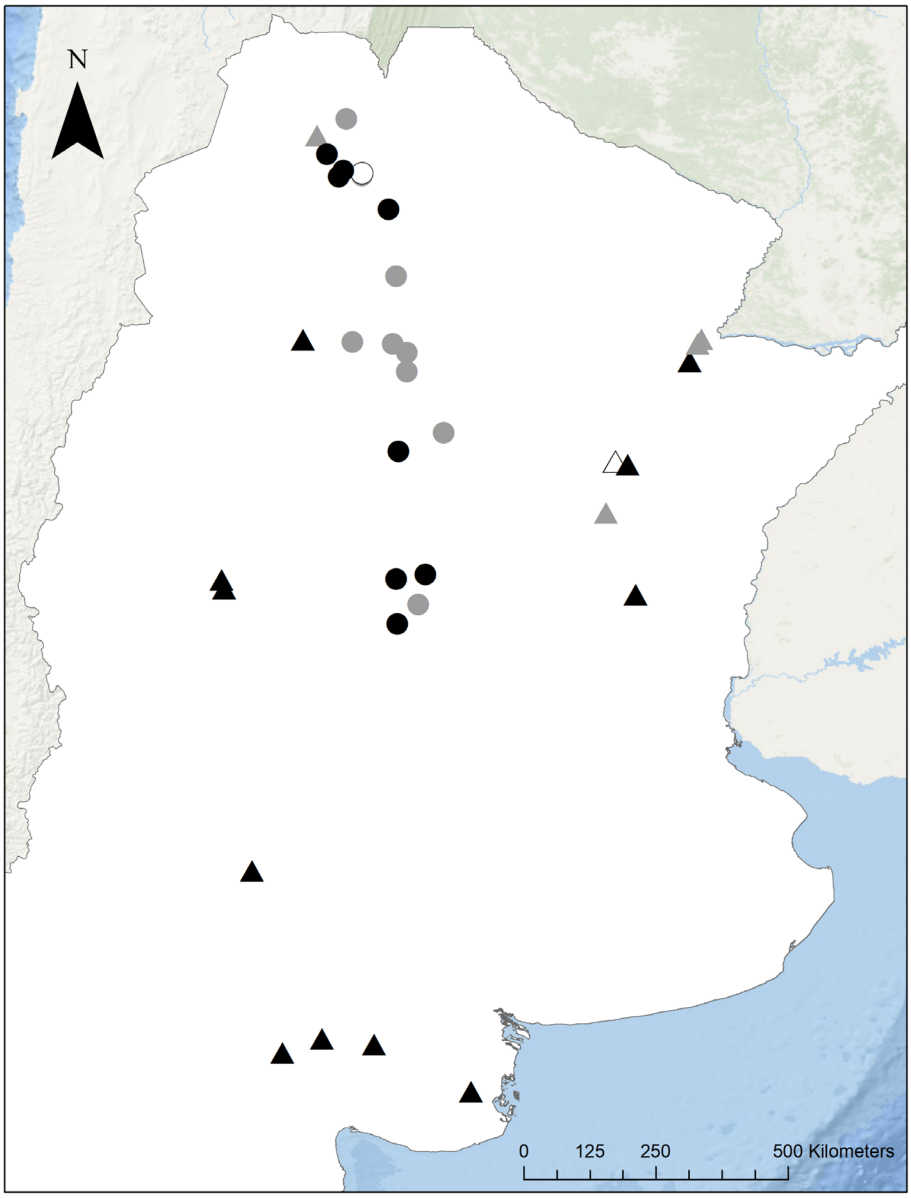


Fig. 7. Final target populations for an optimized collecting design for *Trichloris crinita* (triangles) and *Trichloris pluriflora* (circles). Solid black symbols represent prioritized populations in both future scenarios (RCP 4.5/2050 and RCP 8.5/2070), empty symbols show populations only prioritized for RCP 4.5 scenario, and solid gray symbols represent populations prioritized only for RCP 8.5 scenario.

geophysical and bioclimatic factors have been associated with adaptive genetic variation in seed weight, a critical trait of plant's life history related to fitness across plant species (Marinoni et al. 2018) as well as with adaptive traits associated with tolerance to water and salt stress (Marinoni et al. 2020).

Regardless of the method used for STZ development, for most of the species used in restoration projects, the results are often a best guess, given the lack of a true understanding of adaptive variation (Broadhurst et al. 2008). Although some studies relating adaptive genetic variation to geographical and climatic variables have been

performed (Hamann et al. 2011, St. Clair et al. 2013, Massatti et al. 2020), the genetic characterization of each population of every species used for restoration, though a valuable conservation task, is often logistically and economically unfeasible (McKay et al. 2005). This approach is not often practical, since in the frame of germplasm collecting, extensive genetic characterization may lead to redundancy (Jaramillo and Baena 2000, Parra-Quijano 2011), and resources for this task are a limiting factor (Vogel et al. 2005). However, validation of the delineated STZs in terms of genetic differentiation is essential (Massatti et al. 2020, Yoko et al. 2020) especially in the context of climate change. Here we present provisional spatiotemporal STZs as a first step in seed transfer guidance for restoration purposes of Argentinian rangelands in response to climate change. In the near future, reciprocal transplant experiments within and between designated STZs and genetic diversity and functional traits analyses will be carried out to validate the ecogeographical approach used in the present study. Although the results of the present study will allow us to collect and conserve germplasm from populations for seed sourcing and endangered populations, the final application of the spatiotemporal STZs will be subject to the results of the aforementioned adaptive traits evaluation studies.

The usefulness of ELC maps for OCD has been previously reported (Parra-Quijano et al. 2012*b*, Marinoni et al. 2015, Phillips et al. 2016, García et al. 2017, Quinaluisa et al. 2018); here we present a new application within the frame of OCD in the scenario of climate change. In the present study, we used this OCD approach as a strategy to mitigate the negative impacts of climate change in native forage grasses of the genus *Trichloris*. Because of the uncertainty about the direction and potential impact of climate change on species distribution (Harris et al. 2006), we assessed two possible scenarios, an optimistic (RCP 4.5) and a pessimistic (RCP 8.5) one, and prioritized the threatened populations (potential beneficiaries of germplasm) and seed source populations (for possible future restorations) for germplasm collection. Regarding seed source populations, germplasm collection from currently non-represented STZs is imperative to assist the beneficiary populations. Collecting all potential threatened populations is also recommended to respond to the risk of maladaptation and loss of genetic diversity. Finally, the target populations to consider for the OCD will depend on the future scenario that is assumed. We propose a first step involving the germplasm collection of populations in common for both future scenarios; then, the remaining prioritized populations for optimistic and pessimistic scenario, in accordance with the economic resources' availability, the most limiting factor in collection activities.

Climate change poses a new challenge in terms of collection, conservation, and management of the most suitable populations for ensuring restoration success. For years, the idea that local or the nearest sourced seed would be better adapted to the restoration site prevailed (Mortlock 2000). However, in the era of global warming, when ecosystems are subject to rapid changes in environmental conditions, local genotypes are potentially less optimal than other genotypes already exposed at their sites of origin to the conditions that will prevail in the future (Sgro et al. 2011). Here, we suggest a reasonable seed transfer strategy for two native forage grasses to guarantee rangeland resilience to climate change. The proposed approach is feasible for use in other species and helps to promote the use of native plant genetic resources.

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Literature Cited

Aguirre, N., P. Eguiguren, J. Maita, T. Ojeda, N. Sanamiego, M. Furniss, and Z. Aguirre. 2017. Potential impacts to dry forest species distribution under two climate change scenarios in southern Ecuador. Neotropical Biodiversity 3:18–29.

Akhter, S., M. A. McDonald, P. van Breugel, S. Sohel, E. D. Kjær, and R. Mariott. 2017. Habitat distribution modelling to identify areas of high conservation value under climate change for *Mangifera sylvatica* Roxb. of Bangladesh. Land Use Policy 60:223–232.

Allard, R. W., S. K. Jain, and P. L. Workman. 1968. The genetics of inbreeding populations. Advances in Genetics 14:55–131.

Atkinson, R., E. Thomas, J. Cornelius, R. Zamora, and M. Franco Chuaire. 2018. Fit for purpose seed supply systems for the implementation of landscape restoration under Initiative 20x20: an analysis of national seed systems in Mexico, Guatemala, Costa Rica, Colombia, Peru, Chile and Argentina. World Resources Institute, Bioversity International, ICRAF, Lima, Peru. https://cgspace.cgiar.org/bitstream/handle/10568/93037/Fit-for-purpose_Atkinson__may2018.pdf?sequence=3

Azpilicueta, M. M., L. A. Gallo, M. Van Zonneveld, E. Thomas, C. Moreno, and P. Marchelli. 2013. Management of *Nothofagus* genetic resources: definition of genetic zones based on a combination of nuclear and chloroplast marker data. Forest Ecology and Management 302:414–424.

Barros, V. R., J. A. Boninsegna, I. A. Camilloni, M. Chidiak, G. O. Magrín, and M. Rusticucci. 2015. Climate change in Argentina: trends, projections, impacts and adaptation. Wires Climate Change 6:151–169.

Barros, V. R., M. E. Doyle, and I. Camilloni. 2008. Precipitation trends in southeastern South America: relationship with ENSO phases and the low-level circulation. Theoretical and Applied Climatology 93:19–33.

Bates, C. G. 1930. The frost hardiness of geographic strains of Norway pine. Journal of Forestry 28:327–333.

Bellard, C., C. Bertelsmeier, P. Leadley, W. Thuiller, and F. Courchamp. 2012. Impacts of climate change on the future of biodiversity. Ecology Letters 15:365–377.

Bower, A. D., J. B. S. Clair, and V. Erickson. 2014. Generalized provisional seed zones for native plants. Ecological Applications 24:913–919.

Broadhurst, L. M., A. Lowe, D. J. Coates, S. A. Cunningham, M. McDonald, P. A. Vesk, and C. Yates. 2008. Seed supply for broadscale restoration: maximizing evolutionary potential. Evolutionary Applications 1:587–597.

Brown, A. H. D., and D. R. Marshall. 1986. Wild species as genetic resources for plant breeding. Pages 9–15 *in* N. Z. Agronomy Society Special Publication No. 5. Proceedings of the Plant Breeding Symposium DSIR. Agronomy Society of New Zealand, Lincoln, New Zealand.

Cavagnaro, P. F., J. B. Cavagnaro, J. L. Lemes, R. W. Masuelli, and C. B. Passera. 2006. Genetic diversity among varieties of the native forage grass *Trichloris crinita* based on AFLP markers, morphological characters, and quantitative agronomic traits. Genome 498:906–918.

Cevallos, D., Á. Bede-Fazekas, E. Tanács, K. Szitár, M. Halassy, A. Kövendi-Jakó, and K. Török. 2020. Seed transfer zones based on environmental variables better reflect variability in vegetation than administrative units: evidence from Hungary. Restoration Ecology 28:911–918.

Coulston, J. W., and K. H. Riitters. 2005. Preserving biodiversity under current and future climates: a case study. Global Ecology and Biogeography 14:31–38.

Crow, T. M., S. E. Albeke, C. A. Buerkle, and K. M. Hufford. 2018. Provisional methods to guide species-specific seed transfer in ecological restoration. Ecosphere 9:e02059.

Cutler, D. R., T. C. Edwards Jr., K. H. Beard, A. Cutler, K. T. Hess, J. Gibson, and J. J. Lawler. 2007. Random forests for classification in ecology. Ecology 88:2783–2792.

Davis, M. B., and R. G. Shaw. 2001. Range shifts and adaptive responses to Quaternary climate change. Science 292:673–679.

Dean, N., A. E. Raftery, and L. Scrucca. 2018. Package 'clustvarsel', variable selection for Model-Based clustering. Version 2.3.3. http://cran.r-project.org/web/packages/clustvarsel/clustvarsel.pdf

Doherty, K. D., B. J. Butterfield, and T. E. Wood. 2017. Matching seed to site by climate similarity: techniques to prioritize plant materials development and use in restoration. Ecological Applications 27:1010–1023.

Doyle, M. E., R. I. Saurral, and V. R. Barros. 2012. Trends in the distributions of aggregated monthly precipitation over the La Plata Basin. International Journal of Climatology 32:2149–2162.

Durka, W., S. G. Michalski, K. W. Berendzen, O. Bossdorf, A. Bucharova, J.-M. Hermann, N. Hölzel, and J. Kollmann. 2017. Genetic differentiation within multiple common grassland plants supports seed transfer zones for ecological restoration. Journal of Applied Ecology 54:116–126.

Erickson, V. J., and A. Halford. 2020. Seed planning, sourcing, and procurement. Restoration Ecology 28:219–227.

Erickson, V. J., N. L. Mandel, and F. C. Sorensen. 2004. Landscape patterns of phenotypic variation and population structuring in a selfing grass, *Elymus glaucus* (blue wildrye). Canadian Journal of Botany 82:1776–1789.

Falconer, D. S., and T. F. C. Mackay. 2006. Introduction to quantitative genetics. Fourth edition. Addison Wesley Longman Limited, Harlow, UK.

FAO, IIASA, ISRIC, ISSCAS, and JRC. 2012. Harmonized World Soil Database. Version 1.2. FAO, Rome, Italy and IIASA, Laxenburg, Austria.

Fick, S. E., and R. J. Hijmans. 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. International Journal of Climatology 37:4302–4315.

Fowells, H. A. 1946. Forest tree seed collection zones in California. Research note. No. 51. California Forest and Range Experiment Station, Berkeley, California, USA.

García, R. M., M. Parra-Quijano, and J. M. Iriondo. 2017. A multispecies collecting strategy for crop wild relatives based on complementary areas with a high density of ecogeographical gaps. Crop Science 57:1059–1069.

Germino, M. J., A. M. Moser, and A. R. Sands. 2019. Adaptive variation, including local adaptation, requires decades to become evident in common gardens. Ecological Applications 29:e01842.

Gibson, A., and C. R. Nelson. 2017. Comparing provisional seed transfer zone strategies for a commonly seeded grass, *Pseudoroegneria spicata*. Natural Areas Journal 37:188–199.

Guittar, J., D. Goldberg, K. Klanderud, R. J. Telford, and V. Vandvik. 2016. Can trait patterns along gradients predict plant community responses to climate change? Ecology 97:2791–2801.

Gutiérrez, H. F., G. A. Richard, and M. C. Cerino. 2016. Sistema reproductivo de *Trichloris* (Poaceae, Chloridoideae, Chlorideae). Boletín de la Sociedad Argentina de Botánica 51:111–122.

Hamann, A., T. Gylander, and P. Y. Chen. 2011. Developing seed zones and transfer guidelines with multivariate regression trees. Tree Genetics and Genomes 7:399–408.

Handel, S. N., G. R. Robinson, and A. J. Beattie. 1994. Biodiversity resources for restoration ecology. Restoration Ecology 2:230–241.

Hanson, J. O., J. R. Rhodes, C. Riginos, and R. A. Fuller. 2017. Environmental and geographic variables are effective surrogates for genetic variation in conservation planning. Proceedings of the National Academy of Sciences USA 114:12755–12760.

Harris, J. A., R. J. Hobbs, E. Higgs, and J. Aronson. 2006. Ecological restoration and global climate change. Restoration Ecology 14:170–176.

Havens, K., P. Vitt, S. Still, A. T. Kramer, J. B. Fant, and K. Schatz. 2015. Seed sourcing for restoration in an era of climate change. Natural Areas Journal 35:122–134.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones, and A. Jarvis. 2005. Very high-resolution interpolated climate surfaces for global land areas. International Journal of Climatology 25:1965–1978.

IPCC. 2014. Climate change 2014: Synthesis report. *In* Core Writing Team, R. K. Pachauri, and L. A. Meyer, editors. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland.

Jaramillo, S., and M. Baena. 2000. Material de apoyo a la capacitación en conservación *ex situ* de recursos fitogenéticos. https://www.bioversityinternational.org/e-library/publications/detail/material-de-apoyo-a-la-capacitacion-en-conservacion-ex-situ-de-recursos-fitogeneticos/

Johnson, G. R., F. C. Sorensen, J. B. St Clair, and R. C. Cronn. 2004. Pacific Northwest forest tree seed zones. A template for native plants? Native Plants Journal 5:131–140.

Johnson, R., L. Stritch, P. Olwell, S. Lambert, M. E. Horning, and R. Cronn. 2010. What are the best seed sources for ecosystem restoration on BLM and USFS lands? Native Plants Journal 11:117–131.

Jombart, T., Z. N. Kamvar, R. Lustrik, C. Collins, M. P. Beugin, B. Knaus, and F. Caboli. 2015. Adegenet: exploratory analysis of genetic and genomic data. R package version 2.0. https://cran.r-project.org/web/packages/adegenet/

Jørgensen, M. H., A. Elameen, N. Hofman, S. Klemsdal, S. Malaval, and S. Fjellheim. 2016. What's the meaning of local? Using molecular markers to define seed transfer zones for ecological restoration in Norway. Evolutionary Applications 9:673–684.

Jump, A. S., and J. Peñuelas. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. Ecology Letters 8:1010–1020.

Kozub, P. C., K. Barboza, J. B. Cavagnaro, and P. F. Cavagnaro. 2017. Reproductive biology of the native forage grass *Trichloris crinita* (Poaceae, Chloridoideae). Plant Biology 19:444–453.

Kozub, P. C., K. Barboza, J. B. Cavagnaro, and P. F. Cavagnaro. 2018*a*. Development and characterization of SSR markers for *Trichloris crinita* using sequence data from related grass species. Revista de la Facultad de Ciencias Agrarias de la UNC 50:1–16.

Kozub, P. C., J. B. Cavagnaro, and P. F. Cavagnaro. 2018*b*. Exploiting genetic and physiological variation of the native forage grass *Trichloris crinita* for revegetation in arid and semi-arid regions: an integrative review. Grass and Forage Science 73:257–271.

Kramer, A. T., and K. Havens. 2009. Plant conservation genetics in a changing world. Trends in Plant Science 14:599–607.

Kunst, C., R. Renolfi, H. Pérez, and F. Dalla Tea. 1995. Preferencia de bovinos por gramíneas nativas de bosques y arbustales de la región chaqueña occidental. Revista Argentina de Producción Animal 15:110–113.

Lloyd-Reilley, J. 2011. Plant guide for multiflower false Rhodes grass. *Trichloris pluriflora* E. Fourn. . .. USDA-Natural Resources Conservation Service, E. "Kika" de la Garza Plant Materials Center, Kingsville, Texas, USA. https://plants.usda.gov/plantguide/pdf/pg_trpl3.pdf

Loveless, M. D., and J. L. Hamrick. 1984. Ecological determinants of genetic structure in plant populations. Annual Review of Ecology and Systematics 15:65–95.

Maenza, R. A., E. A. Agosta, and M. L. Bettolli. 2017. Climate change and precipitation variability over the western 'Pampas' in Argentina. International Journal of Climatology 37:445–463.

Marinoni, L., A. Bortoluzzi, M. Parra-Quijano, J. M. Zabala, and J. F. Pensiero. 2015. Evaluation and improvement of the ecogeographical representativeness of a collection of the genus *Trichloris* in Argentina. Genetic Resources and Crop Evolution 62:593–604.

Marinoni, L. D. R., G. A. Richard, D. Bustos, E. L. Taleisnik, J. F. Pensiero, and J. M. Zabala. 2020. Differential response of *Trichloris* ecotypes from different habitats to drought and salt stress. Theoretical and Experimental Plant Physiology 32:213–229.

Marinoni, L., J. M. Zabala, M. Parra-Quijano, R. J. Fernández, and J. F. Pensiero. 2018. Genetic and environmental variation of seed weight in *Trichloris* species (Chloridoideae, Poaceae) and its association with seedling stress tolerance. Plant Ecology and Diversity 11:173–184.

Massatti, R., R. K. Shriver, D. E. Winkler, B. A. Richardson, and J. B. Bradford. 2020. Assessment of population genetics and climatic variability can refine climate-informed seed transfer guidelines. Restoration Ecology 28:485–493.

McKay, J. K., C. E. Christian, S. Harrison, and K. J. Rice. 2005. "How local is local?"—a review of practical and conceptual issues in the genetics of restoration. Restoration Ecology 13:432–440.

Miller, S. A., A. Bartow, M. Gisler, K. Ward, A. S. Young, and T. N. Kaye. 2011. Can an ecoregion serve as a seed transfer zone? Evidence from a common garden study with five native species. Restoration Ecology 19:268–276.

Mortlock, B. W. 2000. Local seed for revegetation: Where will all that seed come from? Ecological Management and Restoration 1:93–101.

Omernik, J. M., and G. E. Griffith. 2014. Ecoregions of the conterminous United States: evolution of a hierarchical spatial framework. Environmental Management 54:1249–1266.

Parra-Quijano, M. 2011. Colecta Optimizada de los Recursos Fitogenéticos. http://www.agrobiodiversidad.org/Documentos/ParraQuijano2011_ColectaOptimizadaRecursosFitogeneticos.pdf

Parra-Quijano, M., J. M. Iriondo, and E. Torres. 2012*a*. Improving representativeness of genebank collections through species distribution models, gap analysis and ecogeographical maps. Biodiversity and Conservation 21:79–96.

Parra-Quijano, M., J. M. Iriondo, and E. Torres. 2012*b*. Ecogeographical land characterization maps as a tool for assessing plant adaptation and their implications in agrobiodiversity studies. Genetic Resources and Crop Evolution 59:205–217.

Parra-Quijano, M., E. Torres Lamas, J. M. Iriondo Alegría, and F. López. 2018. CAPFITOGEN, Programme to strengthen national Plant Genetic Resource Capacities in Latin America, Version 2.0. http://www.capfitogen.net/es

Pastorino, M. J. 2012. How many seed transfer zones are necessary for the preservation of the genetic identity of *Austrocedrus chilensis* natural populations in Argentina? Restoration Ecology 20:551–554.

Peeters, J. P., H. G. Wilkes, and N. W. Galwey. 1990. The use of ecogeographical data in the exploitation of variation from gene banks. Theoretical and Applied Genetics 80:110–112.

Phillips, J., Å. Asdal, J. Magos Brehm, M. Rasmussen, and N. Maxted. 2016. *In situ* and *ex situ* diversity analysis of priority crop wild relatives in Norway. Diversity and Distributions 22:1112–1126.

Potter, K. M., and W. W. Hargrove. 2012. Determining suitable locations for seed transfer under climate change: a global quantitative method. New Forests 43:581–599.

Quinaluisa, E. J. N., C. G. T. Bastidas, R. J. V. Feria, Y. C. Pérez, A. H. D. Pilla, E. J. B. Borja, and N. J. P. Andrade. 2018. Caracterización eco-geográfica de Melloco (*Ullucus tuberosus* C.) en la región alto Andina del Ecuador. La Técnica: Revista de Agrociencia 19:31–46.

Quiroga, R. E., R. J. Fernández, R. A. Golluscio, and L. J. Blanco. 2013. Differential water-use strategies and drought resistance in *Trichloris crinita* plants from contrasting aridity origins. Plant Ecology 214:1027–1035.

Quiroga, R. E., A. C. Premoli, and R. J. Fernández. 2018. Climatic niche shift in the amphitropical disjunct grass *Trichloris crinita*. PLOS ONE 13: e0199811.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raftery, A. E., and N. Dean. 2006. Variable selection for model-based clustering. Journal of the American Statistical Association 101:168–178.

Richardson, B. A., and L. Chaney. 2018. Climate-based seed transfer of a widespread shrub: population shifts, restoration strategies, and the trailing edge. Ecological Applications 28:2165–2174.

Rivera, J. A., D. Araneo, O. Penalba, and R. Villalba. 2017. Linking climate variations with the hydrological cycle over the semi-arid Central Andes of Argentina. Past, present and future, with emphasis on streamflow droughts. *In* 19th EGU General Assembly, Proceedings from the conference held 23-28 April, Vienna, Austria. European Geosciences Union, Vienna, Austria.

Rúgolo, Z. E., and A. Molina. 2012. Trichloris. Pages 167–169 *in* F. O. Zuloaga, Z. E. Rúgolo, and A. M. R. Anton, editors. Flora vascular de la República Argentina. Volume 3, Tomo 1. Monocotyledoneae. Aristidoidea a Pharoidea. First edition. Gráficamente Ediciones, Córdoba, Argentina.

Sgro, C. M., A. J. Lowe, and A. A. Hoffmann. 2011. Building evolutionary resilience for conserving biodiversity under climate change. Evolutionary Applications 4:326–337.

Shryock, D. F., L. A. DeFalco, and T. C. Esque. 2018. Spatial decision-support tools to guide restoration and seed-sourcing in the Desert Southwest. Ecosphere 9:e02453.

St. Clair, J. B., F. F. Kilkenny, R. C. Johnson, N. L. Shaw, and G. Weaver. 2013. Genetic variation in adaptive traits and seed transfer zones for *Pseudoroegneria spicata* (bluebunch wheatgrass) in the northwestern United States. Evolutionary Applications 6:933–948.

Thomas, E., E. Tovar, C. Villafañe, J. L. Bocanegra, and R. Moreno. 2017. Distribution, genetic diversity and potential spatiotemporal scale of alien gene flow in crop wild relatives of rice (*Oryza* spp.) in Colombia. Rice 10:13.

Thomson, A. M., et al. 2011. RCP4. 5: a pathway for stabilization of radiative forcing by 2100. Climatic Change 109:77–94.

Tomas, P. A., F. Vaccari, J. M. Zabala, J. A. Giavedoni, and J. F. Pensiero. 2012. Análisis de la variación genética en accesiones nativas de *Trichloris crinita* y *T. pluriflora* mediante marcadores moleculares ISSR. Jornadas Latinoamericanas de Recursos Genéticos, Mejoramiento y Biotecnología de Especies Forrajeras, Pergamino, Buenos Aires, Argentina.

Vogel, K. P., M. R. Schmer, and R. B. Mitchell. 2005. Plant adaptation regions: ecological and climatic classification of plant materials. Rangeland Ecology and Management 58:315–319.

Withrow-Robinson, B., and R. Johnson. 2006. Selecting native plant materials for restoration projects: ensuring local adaptation and maintaining genetic diversity. Publication EM 8885-E. Oregon State University Extension Service, Corvallis, Oregon, USA.

Yoko, Z. G., K. L. Volk, N. A. Dochtermann, and J. A. Hamilton. 2020. The importance of quantitative trait differentiation in restoration: Landscape heterogeneity and functional traits inform seed transfer guidelines. AoB Plants 12:plaa009.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3462/full

Appendix S1