



Ecological and Spatial Patterns Associated with Diversification of the Shrub Genus *Tetraglochin* along Southern-Central Andes (Rosaceae)

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Abstract

In addition to the degree of geographical isolation (sympatry, parapatry, allopatry and peripatry), ecology can be an important factor promoting diversification of lineages, both by niche divergence as well as niche conservatism. *Tetraglochin* is a genus of shrubs with six species distributed along the Southern and Central Andes, from Peru to southern Argentina and central Chile. Although monophyly of the genus as the identity of its species are well established, spatiotemporal framework for its diversification and the potential role of the ecology and geography in the speciation process remain unknown. In the present study we analyzed diversification times and historical biogeography of the genus, and conducted different climatic niche and geographical range comparisons among its species to determine possible patterns associated with speciation. Results support the Pleistocene diversification, early along the Southern Andes and the Patagonian Steppe and subsequently in the Central Andes. Climatic niche divergence did not prove to be a major factor promoting speciation, but rather the phylogenetic niche conservatism. Our analyses also favored the sympatric model of speciation, although patterns from geographical range evolution are difficult to interpret due to the lability on the ancestral distributions, and therefore micro-allopatric or parapatric divergence associated with the glacial-interglacial cycles and climatic oscillations throughout the Quaternary should not be discarded. Other potential factors associated with diversification of *Tetraglochin* are also discussed.

Keywords Niche divergence · Phylogenetic niche conservatism · Pleistocene · Patagonian steppe · The Andes · South America

Introduction

A central objective of evolutionary biology is to understand the relative roles of ecology and geography in speciation (Coyne and Orr 2004; Nosil 2012). Traditionally, studies have focused on distinguishing modes of speciation associated to the degree of geographical range overlap and the potential gene flow during speciation (i.e. allopatric—including vicariant and peripatric, parapatric, and sympatric

speciation patterns; e.g. Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006; Kisel and Barraclough 2010; Phillimore 2014). The allopatric model, in where populations become separated and reproductive isolation accumulates in the absence of gene flow, has long been considered the most plausible (Jordan 1905; Mayr 1959; Gentry 1982). Over time, however, this view has been changed by different studies suggesting that speciation in non allopatric scenarios might be more common than usually recognized (Turelli et al. 2001; Coyne and Orr 2004; Bolnick and Fitzpatrick 2007; Fitzpatrick et al. 2008, 2009; Luebert et al. 2014; Rosser et al. 2015; André et al. 2016). Nevertheless, the increasing phylogenetic evidence suggests that ecology, more than geography, is responsible for driving diversification (Wiens 2004a; Donoghue 2008; Crisp et al. 2009; Crisp and Cook 2012; Pyron et al. 2015). Ecological adaptation to local environments is an important process promoting divergence in nature (Rundle and Nosil 2005; Schluter 2001; Nosil 2012; Pyron et al. 2015), and numerous studies

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demonstrate its importance in plant diversification (Levin 2003; Givnish 2010; Schemske 2010; Ramsey 2011). Specifically, plants may be more affected by small-scale environmental heterogeneity than mobile organisms, increasing the relative significance of ecological differentiation (Anacker and Strauss 2014). In this context, ecological speciation models establish that divergent natural selection drives the emergence of reproductive isolation between populations as a consequence of adaptation to different ecological niches (Schluter 2009; Rundle and Nosil 2005). Under niche divergence, populations depart from their ancestral climatic niche to occupy different climatic regimes along at least one axis of multidimensional niche space, leading to a rapid ecological divergence that may eventually result in complete reproductive isolation (Nosil and Harmon 2009; Pyron et al. 2015; Cox et al. 2014; Wang et al. 2017). Alternatively, adaptation to the ecological niche can also promotes speciation by phylogenetic niche conservatism (PCN) (Wiens 2004a; Wiens and Graham 2005; Pyron et al. 2015; Kozak and Wiens 2006), defined as the tendency of closely related species to retain characteristics of their fundamental niche over time (Peterson et al. 1999; Peterson 2011; Wiens 2004a; Wiens and Graham 2005; Wiens et al. 2010). Under niche conservatism, ecological constraints play a role in speciation, particularly during periods of environmental change, limiting adaptation to new climatic conditions (Wiens 2004a; Pyron et al. 2015). In this case, allopatric and/or parapatric speciation occurs when ancestral distributional ranges become fragmented isolating the populations (e.g. along elevational gradients during periods of warming or orogeny), and incipient species fail to adapt to novel environmental conditions that would facilitate the maintenance of gene flow (Wiens 2004b; Pyron et al. 2015). Therefore, the relative contributions of niche divergence and niche conservatism during the speciation processes should consequently affect the diversification of lineages and shape the degree of niche similarity between the members of a clade (Culumber and Tobler 2016). Furthermore, either under niche divergence or conservatism, if geography has served as a means of reproductive isolation, closely related species should exhibit lower range overlap (Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006). Thus, analyzing the patterns of similarity exhibited by ecological niches and geographical ranges in closely related species can provide insights into the relative roles of geography and ecology during the speciation process (Grossenbacher et al. 2014; Anacker and Strauss 2014).

Tetraglochin Poepp. (Rosaceae: Rosoideae: Sanguisorbeae) is a South American genus of shrubs comprising six species distributed along the Central and Southern Andes from Peru to southern Argentina and central Chile (Cialdella and Pometti 2017) (Fig. 1). The genus is morphologically defined by including shrubby plants, frequently thorny, with deciduous leaves on long branches (macroblasts), and

persistent leaves on short branches (brachyblasts) (Fig. 2). The flowers are apetalous and the fruit is an achene enclosed by the dried receptacle or hypanthium (Cialdella and Pometti 2017) (Fig. 2f). Recently, Acosta et al. (2016) recovered, using molecular data, the monophyly of *Tetraglochin* and showed its phylogenetic relationship with the genera *Margyricarpus* Ruiz & Pav., *Acaena* Mutis ex L., and *Polylepis* Ruiz & Pav. within subtribe Sanguisorbinae. Species of this genus are common elements of the Andean-Patagonian biogeographical domain (Cabrera and Willink 1973), and are primarily distributed in two areas: the southern Andes of Argentina and Chile including the Patagonian steppe (~30° to 50° lat) from sea level to ca. 3200 m [*T. acanthocarpa* (Speg.) Spegazzini, *T. alata* (Gillies ex Hook. and Arn.) Kuntze, and *T. caespitosa* Philippi], and the central Andes of Peru, Bolivia, and northern Argentina (~28° to 8° lat) from ca. 2200 to 4700 m [*T. andina* Cialdella, *T. cristata* (Britton) Rothmaler, and *T. inermis* (I. M. Johnst.) Rothmaler]. However, within these primary areas, species also show variation in their habitat and distribution, inhabiting at least in seven different ecoregions (sensu Olson et al. 2001): Central Andean wet puna, Central Andean dry puna, Central Andean puna, High Monte, Low Monte, Southern Andean steppe, and Patagonian steppe. These areas provide highly diverse habitats for the evolution and diversification of *Tetraglochin*, as well as numerous plant lineages of different families (Luebert and Weigend 2014). Additionally, species of the genus also exhibit considerable range asymmetry, as evident in the wide distribution range of *T. cristata* from northern Peru to Argentina, and the micro-endemic distributions of *T. inermis* or *T. acanthocarpa*, which are restricted to the Puna of northwestern Argentina and the southern portion of the Patagonian steppe, respectively. However, possible processes associated with its evolution cannot be inferred because the spatiotemporal framework for its diversification along the South-Central Andes and the potential ecological and geographical factors related are still unknown.

In this study, we explore the roles of geography and ecology on the diversification of *Tetraglochin*, analyzing the time-course and geography of its diversification, and the patterns associated to the climatic niche and geographical range evolution. For this purpose we conducted phylogenetic analyses with divergence time and ancestral range estimations, together with climatic niche and geographical range comparisons. Because it has been reported that tests of niche overlap using geographical projections derived from species distribution modelling (SDM) techniques are likely to vary depending on the extent and distribution of environmental gradients in the study area (Broennimann et al. 2012), we used climate data processed both by ordination and SDM techniques that represent the environmental (E) and geographical (G) spaces, respectively. Results of these analyses allowed us to elucidate the ecological and geographical

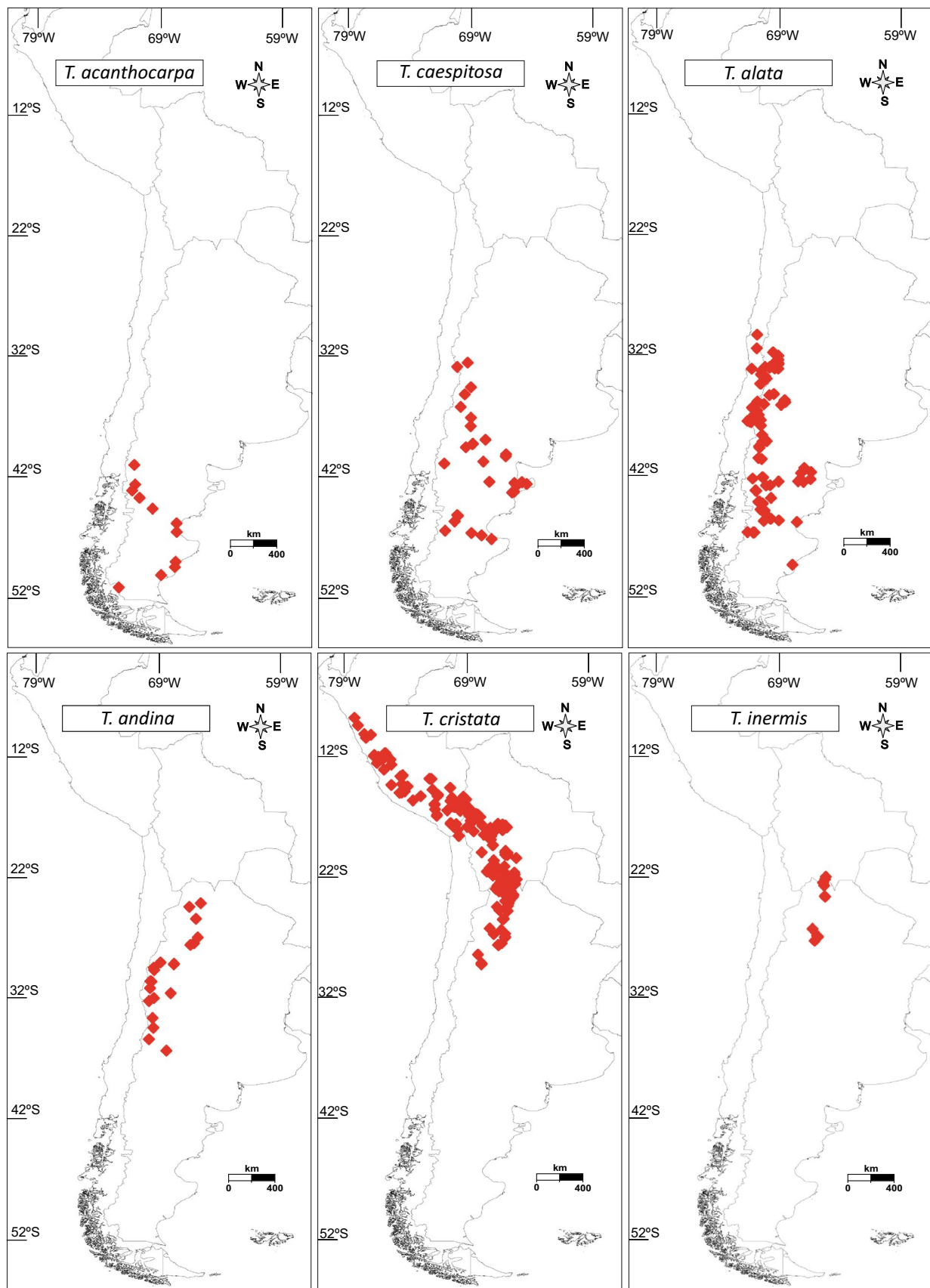


Fig. 1 Distribution maps of *Tetraglochin* species. Dots represent specimen records for the different species

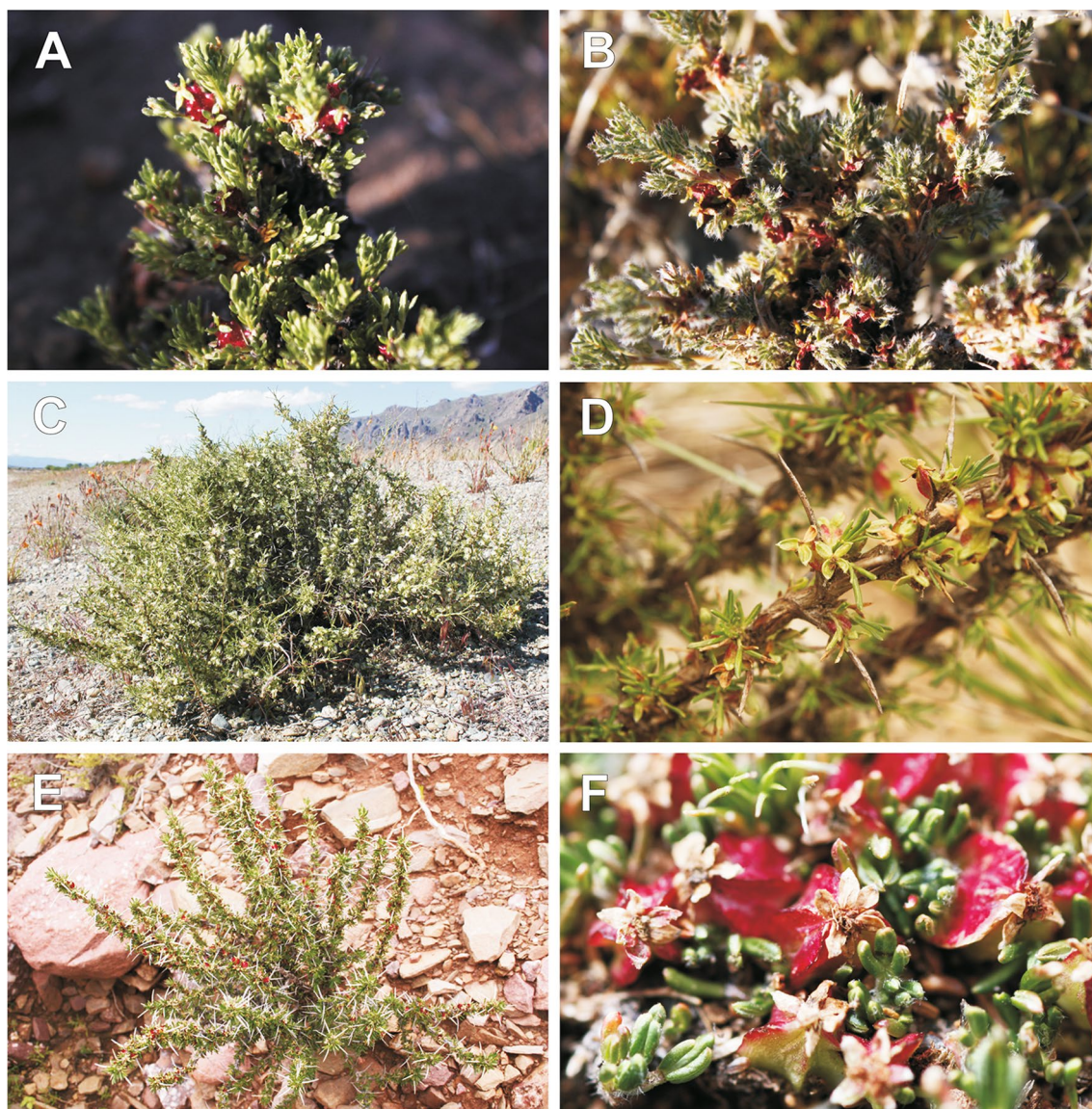


Fig. 2 Photographs of *Tetraglochin* species taken in the field. **a** *T. acanthocarpa* (F.O. Zuloaga 15553, SI). **b** *T. caespitosa* (F.O. Zuloaga 14653, SI). **c** *T. alata* (F.O. Zuloaga 15661, SI). **d** *T. andina*

(F.O. Zuloaga 12961, SI). **e** *T. cristata* (F.O. Zuloaga 9142, SI). **f** *T. inermis* (F.O. Zuloaga 10797, SI)

patterns associated with the diversification of *Tetraglochin*, contributing to understanding evolutionary and ecological aspects of the Southern-Central Andean Flora.

Materials and Methods

Phylogenetic Analyses and Divergence Time Estimation

For phylogenetic analyses of *Tetraglochin*, we used the ITS and *trnL-F* sequences generated in Acosta et al. (2016). These alignments include sequences from 18 specimens

representing the six species included in the genus according to the recent taxonomic treatment of Cialdella and Pometti (2017): *T. acanthocarpa* (one specimen), *T. alata* (eight), *T. andina* (four), *T. caespitosa* (one), *T. cristata* (three), and *T. inermis* (one). Specimens of *T. ameghinoi* were treated under *T. alata* because the former was considered as a subspecies of the latter by Cialdella and Pometti (2017) and both taxa share similar geographical distribution. Additionally, alignments include representatives of the closely related genera *Polylepis*, *Acaena*, and *Margyricarpus* and other members of subfamily Rosoideae. Datasets used in the phylogenetic analyses have a total of 58 sequences, GenBank accession numbers are provided in Appendix 1 (Electronic Supplementary

Material), and all aligned matrices are available online from Dryad Digital Repository (<https://doi.org/10.5061/dryad.sd69mc7>).

The species tree of *Tetraglochin* was estimated using the coalescent-based method implemented in *BEAST extension (Heled and Drummond 2009) of BEAST v1.8.2 (Drummond et al. 2012). Nucleotide substitution models selected in jModeltest2 2.1.3 (Darriba et al. 2012) based on (AIC) scores were GTR + G (ITS) and GTR + I + G (*trnL-F*). Coalescent species tree analyses were conducted using all nucleotide substitution, clock, and tree models unlinked across partitions (ITS and *trnL-F*). We used an uncorrelated log-normal clock model (UCLN), a yule process for the species tree prior, and the piecewise linear and constant root for the population size model. To estimate divergence times for *Tetraglochin*, we used three calibrations on the species tree: (1) Zhang et al. (2017) studied phylogenetic relationships and divergence times in Rosaceae using plastid phylogenomics. The authors reported an age of 75.78 Mya (95% HPD: 74.45–78.14 Mya) for the crown node of subfamily Rosoideae. This age was used as secondary calibration to calibrate the root node (crown node of Rosoideae) using a normal prior distribution of mean = 75.78 Mya and SD = 1.25. (2) The mesofossil of *Rosa germerensis* belongs to the Challis Volcanics Formation in Custer County, Idaho, has been assigned to the Early Eocene (56–47.8 Mya) (Edelman 1975). This fossil was used to calibrate the stem node of *Rosa* (following Xiang et al. 2016 and; Zhang et al. 2017) under a lognormal prior distribution with offset = 47.8 Mya, SD = 1 and a 95% upper bound = 75.78 Mya associated with the age reported for the crown node of Rosoideae by Zhang et al. (2017). (3) Microfossils of *Acaena* sp. were found in Cullen Formation in Tierra del Fuego, Argentina, and originally assigned to Middle Eocene (Zetter et al. 1999). However, sediments of Cullen Formation are now considered to be from the Late Oligocene to Middle Miocene (28.1–16 Mya), according to radiometric and palynological data (Zamaloa 2000). This fossil was used to calibrate the stem node of *Acaena* under a lognormal prior with offset = 16 Mya, SD = 1 and a 95% upper bound = 49.17 Mya, this upper bound associated with the age reported by Zhang et al. (2017) for the MRCA of tribes Roseae, Potentilleae, and Agrimonieae.

Six runs were conducted in BEAST using 100 million generations and sampling every 50,000. The first 25% of each run was discarded as burn-in, and effective sample size (ESS) > 200 was checked in Tracer v1.6 (Rambaut et al. 2013). Replicates were combined using LogCombiner 1.8.2 and the species trees were visualized in DensiTree v2.2.5 (Bouckaert and Heled 2014). The maximum clade credibility (MCC) species tree was calculated using TreeAnnotator 1.8.2. BEAST analyses were conducted in the CIPRES Science Gateway v3.3 (<http://www.phylo.org/>) (Miller et al.

2010). All the XML file for BEAST analyses and the trees obtained are available from the Dryad Digital Repository (<https://doi.org/10.5061/dryad.sd69mc7>).

Biogeographical Analyses

For biogeographical analyses of *Tetraglochin*, we identified two major areas along the Andes relevant for the genus: the central Andes (Andean mountains extending south of the Amotape–Huancabamba zone into Andes of Argentina and Chile, ~29° lat) and the southern Andes and Patagonia (Andes of Argentina and Chile from ~29° to ~55° lat together the Patagonian Steppe) (Luebert and Weigend 2014). Species occurrences used in this study have been compiled mainly from the examination of herbarium specimens deposited at BA, BAA, BAB, CONC, CORD, CTES, LIL, LP, LPB, MERL, SI, USM (herbarium abbreviations from Thiers 2018) and the systematic revisions of the genus (Rothmaler 1939; Acosta et al. 2016; Cialdella and Pometti 2017). Additionally, local floras were also consulted (Zardini 1973; Novara 1993; Grondona 1984; Kiesling 1994), checklists (Gereau 1993; Marticorena 2008; Romoleroux et al. 2014), and the Global Biodiversity Information Facility (GBIF) (accessed on July 2017).

Analyses were conducted using the package BioGeoBEARS v0.2.1 (Matzke 2013) implemented in R 3.3.1 (R Core Team 2016) which allows comparison of different models of ancestral-range estimation. Each model allows for a subset of different biogeographical possibilities, such as within-area speciation, dispersal, vicariance and extinction. These biogeographical processes are implemented in an ML framework as free parameters that are estimated from the data (Matzke 2012, 2014). We used six different models: DEC, DEC + J, DIVA, DIVA + J, BayArea, BayArea + J (J models include a j parameter controlling founder-event speciation, Matzke 2014), the maximum number of areas restricted to the maximum number of regions observed among extant taxa (two), and non-temporal stratification. Reconstructions were calculated on the MCC tree and 100 species trees randomly subsampled from the posterior distributions, and pruned to include only members of *Tetraglochin*. Fit of the models was compared using the Akaike information criterion corrected for sample size (AICc). In addition, since our primary goal from the biogeographical analyses is to estimate the number and type of biogeographical events through diversification of *Tetraglochin* (e.g. within-area speciation, vicariance, and dispersal), we used biogeographical stochastic mapping (BSM) (Dupin et al. 2017) under the best fit model (DEC, see results). Event frequencies were estimated on the MCC tree and the 100 randomly subsampled trees

conducting 1000 BSMs on each tree, and taking the mean and the standard deviation of event counts.

Species Occurrence and Environmental Data

For niche comparisons in *Tetraglochin* along the geographical and environmental spaces, we used species occurrences obtained from the examination of specimens deposited in different herbaria, taxonomic revisions, local floras, and the Global Biodiversity Information Facility (GBIF) (see previous section). All records were mapped using QGIS v2.18.12 “Las Palmas” (Quantum GIS Development Team 2016) for visual inspection. In cases of specimens with no GPS coordinates but exact locality names, records were georeferenced using Google Earth Pro v7.3.0.3832 (<https://www.google.com.ar/intl/en/earth/>). After removing duplicates and occurrences closer to 30 arc-seconds (~1 km), we obtained a total of 388 data points, with an average of 65 data point per species (*T. acanthocarpa*: 12, *T. alata*: 92, *T. andina*: 22, *T. caespitosa*: 32, *T. cristata*: 217, *T. inermis*: 13) (dataset available in Table S1 of Electronic Supplementary Material available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.sd69mc7>). Information on the current climatic conditions within the study area was extracted from the recently developed CHELSA v1.2 climatic dataset (Karger et al. 2017a, b). These data is suitable for studies in mountain areas because incorporates orographic predictors as wind field and valley exposition, increasing accuracy of species range prediction, principally for the precipitation pattern (Karger et al. 2017a). Values of all 19 bioclimatic variables were extracted from the area defined by a minimum convex polygon enclosing all species records with 50-km buffer zone (ca. 07°36′–51°06′ lat, 70°36′–63°48′ long, Fig. S1, Electronic Supplementary Material). Additionally, we also included data from the annual aridity index (IA) and potential evapotranspiration (PET) database (Trabucco and Zomer 2009) (<http://www.cgiar-csi.org>) at the same resolution. Data extraction and manipulation were done using the packages adehabitatHR v0.4.14 (Calenge 2006), raster v2.5.8 (Hijmans 2016), sp v1.2.4 (Bivand et al. 2013), and maptools v0.8.41 (Bivand and Lewin-Koh 2017), implemented in R.

Niche Comparisons in the Environmental (E) Space

Niche comparisons among species of *Tetraglochin* in the (E)-space were estimated using the PCA-env approach of Broennimann et al. (2012), in which a principal component analysis is calibrated on the entire environmental space (in our case, 19 bioclim variables from CHELSA + IA + PET)

included in the study area (the 50 km-buffered minimum convex polygon enclosing all *Tetraglochin* species occurrences for this work, Fig. S1). We considered the first three principal components (PC), and we divided this environmental space in a grid of 100×100 cells, in which each cell corresponds to a unique vector of the available environmental conditions in the study area. Because the number of species occurrences can be biased, resulting in an under- or over-estimation of the species density, a kernel-density function is applied for smoothing the density of occurrences for each of the cells in the environmental space (see Broennimann et al. 2012 for details on the methodology and the kernel-density estimator). The density grids for each species were used subsequently to compute the niche overlap by means of the Schoener’s *D* statistic (Schoener 1970; reviewed in; Warren et al. 2008). Schoener’s *D* ranges from 0 (no overlap) to 1 (complete overlap). Similarity of climatic niches along the (E)-space was analyzed using the background similarity test (Warren et al. 2008) to assess whether the climatic niches among species are less similar (divergent) or more similar (conserved) than expected by chance, accounting for the differences in the surrounding environmental conditions. For this test, we used 1000 repetitions, and null hypothesis was rejected if niche overlap of the observed value was lower or greater than the 95% of simulated values. All these analyses were conducted using the ecospat v2.1.1 package (Broennimann et al. 2016; Di Cola et al. 2017). Furthermore, comparisons of environmental niche overlaps among species were also visualized using density profiles computed for each bioclimatic niche axis in the sm v2.2.5.4 package (Bowman and Azzalini 2014) and the niche breadth for each species was quantified as the sum of its variances on the first three PC (niche breadth $sp_a = \sigma^2_{a(PC1)} + \sigma^2_{a(PC2)} + \sigma^2_{a(PC3)}$). Finally, we conducted agglomerative hierarchical clustering with the unweighted pair-group average (UPGMA) algorithm and a distance matrix composed by the niche overlap estimation (Schoener’s *D* metric) between each pair of species, to compare the species composition of the climatic-niche clusters versus the clades recovered in the phylogenetic analyses. Cluster analyses were conducted using the R package cluster v.2.0.5 (Maechler et al. 2016).

Niche Comparisons in the Geographical (G) Space

For niche comparisons in the (G)-space, we applied species distribution modelling (SDM) to model distribution of *Tetraglochin* species using the maximum entropy algorithm implemented in Maxent v3.4.1 (Phillips et al. 2017). Because inclusion of the 21 bioclimatic variables (19 bioclim + IA + PET) in the SDM can be problematic due to high degrees of collinearity among predictors (Heikkinen et al.

2006), we performed initial analyses on all 21 variables and then chose climatic variables that contribute most in the Maxent models using jackknife test, and with a Spearman's rank correlation coefficient (ρ) < 0.7. Eight variables were selected for the SDM analyses: annual mean temperature (BIO1), mean diurnal range (BIO2), isothermality (BIO3), temperature seasonality (BIO4), mean temperature of driest quarter (BIO9), annual precipitation (BIO12), precipitation of coldest quarter (BIO19), and potential evapotranspiration (PET). Each Maxent analysis was performed using 10 cross validation runs with a maximum iterations of 1000, and all other options were left as default (logistic output, convergence threshold of 1.10^{-5} , 1.10^4 background points, regularization multiplier of 1, default prevalence of 0.5, and autofeatures). The area under the receiver operating characteristic curve (AUC) was used as a measure of model performance, and variable contribution to SDM was evaluated both through permutation importance and jackknife tests.

We used two complementary approaches to conduct niche comparison based in the SDM predictions. Firstly, we conducted the background similarity test in the phyloclim v0.9.4 package (Heibl and Calenge 2013) using the ecological niche models obtained for each species, the Schoener's D index, and 1000 replicates. The null hypothesis of niche similarity by chance was rejected when observed values for D index were significantly different (lower or greater) than the 95% of the pseudoreplicated data sets. Secondly, we generated the predicted niche occupancy (PNO) profiles in phyloclim following the methodology proposed by Evans et al. (2005). In order to obtain a PNO profile per variable, median suitability projections obtained for each species in the SDM were integrated with each of the eight variables and binned into 100 evenly space categories. From each PNO profile, we extracted 1000 random values associated with its probability distribution. The PNO profiles for each species were used to estimate ancestral climatic tolerances as proposed Evans et al. (2009) on the MCC species tree and using 1000 randomly subsampled trees to incorporate uncertainty from phylogenetic relationships and divergence times. The ancestral tolerances were estimated in phyloclim using a maximum likelihood approach under a model of Brownian motion evolution and 100 random samples from the PNO profiles. Finally, to summarize niche occupancy in the multivariate (G)-space, we estimated the weighted means of the PNOs for each species and environmental variables, and analyzed them in a phylogenetic principal component analysis (pPCA) using the phytools v0.6.20 package (Revell 2012) and the ML estimation of lambda (Pagel 1999) to obtain the correlation structure.

Geographical Range Overlap

Because patterns of geographical range overlap and niche similarity between closely related species are complementary to delineate speciation processes (Lynch 1989; Chesser and Zink 1994; Barraclough and Vogler 2000; Fitzpatrick and Turelli 2006; Kozak and Wiens 2006; Anacker and Strauss 2014; Grossenbacher et al. 2014; Spalink et al. 2016), we calculated the species range overlap among *Tetraglochin* species using binary presence/absence maps of each species derived from the SDM predictions. Since the choice of a threshold is a topic of ongoing debate, we used the threshold indicating maximum training sensitivity plus specificity, which is considered as a more robust approach (Liu et al. 2005, 2013). The degree of range overlap between two species was estimated as the ratio of the area shared by both species to the area of the smaller ranged species (Barraclough and Vogler 2000). In this way, if one distribution range is contained within another, overlap is one (100%). Finally, we evaluated correlation between range overlap and divergence times using two alternative approaches. First, we used the modified age-range correlation (ARC) method proposed by Fitzpatrick and Turelli (2006) and implemented in the package phyloclim. In this method slopes and intercept derived from a linear model can be used to characterize the predominant geographical speciation pattern (allopatric versus sympatric). Analyses were conducting using the range overlap estimations, the MCC tree, and 1000 dated phylogenies randomly subsampled from the posterior distributions, while the significance of the intercept and the slope was assessed via Monte Carlo simulation using 1000 random permutation of the **overlap matrix under the null hypothesis of no phylogenetic signal**. Alternatively, we used the Mantel test under the null hypothesis that divergence time between two species is unrelated to the range overlap of the same two species. Time of the most recent common ancestor (MRCA) for each species pair was calculated from the MCC tree and the 1000 dated phylogenies and the Mantel test between range overlap and divergence time matrices were conducted in the R package vegan v2.4.3 (Oksanen et al. 2017) using 10,000 permutations and the Spearman rank correlation coefficient.

Results

Phylogeny and Divergence Times

Results from species tree analyses were congruent with the concatenated analyses of Acosta et al. (2016), recovering the monophyly of *Tetraglochin* (PP: 0.87) and its inclusion in a clade together genera *Margyricarpus*, *Acaena* and *Polylepis*

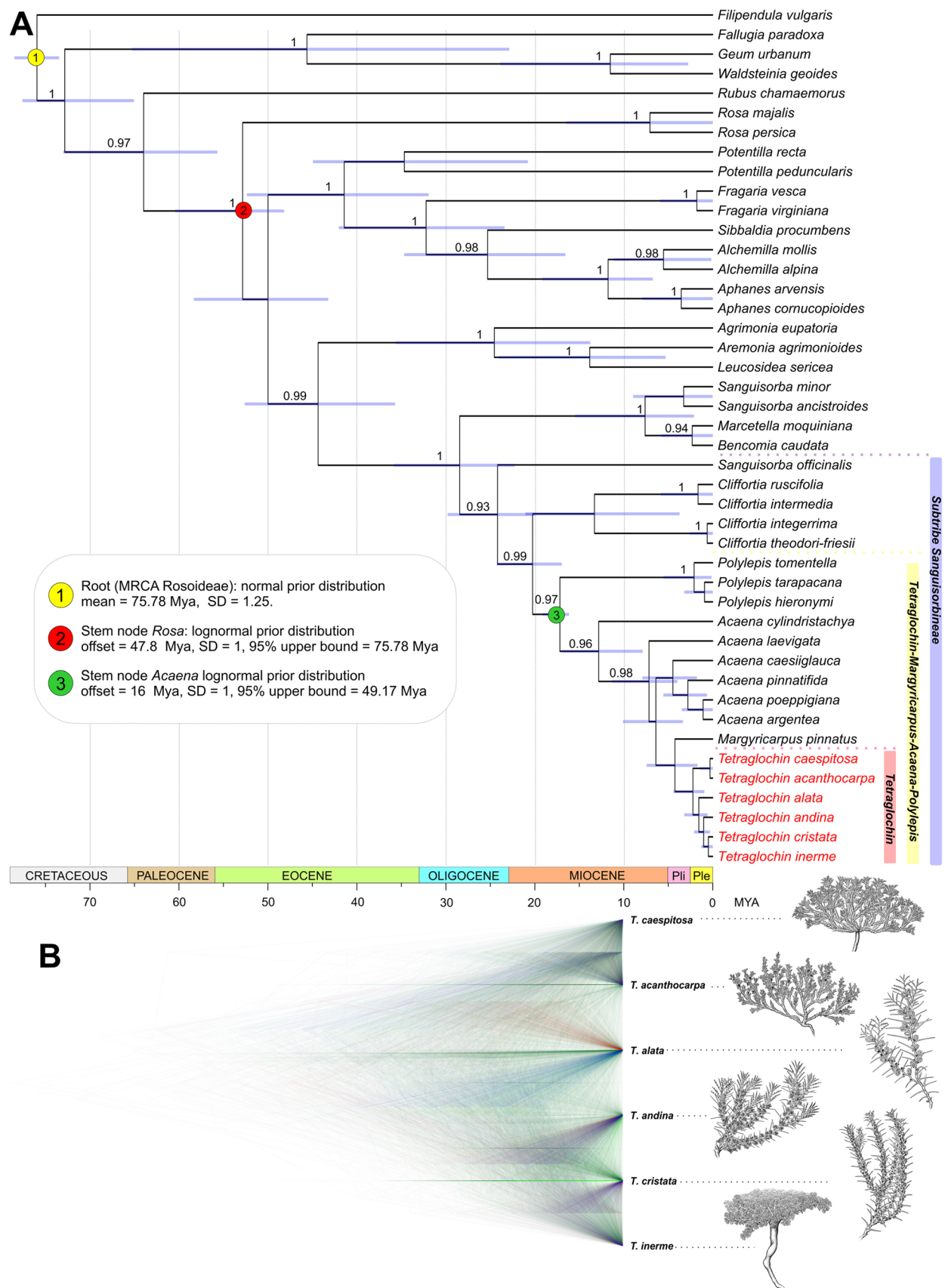


Fig. 3 Species trees estimated from nuclear ribosomal ITS and plastid *trnL-F* regions using the multispecies coalescent method implemented in *BEAST v1.8.2, uncorrelated log-normal relaxed clock model, and three node-age calibrations. **a** Maximum clade credibility (MCC) species tree. Shaded horizontal bars show the 95% highest posterior densities of divergence times and Bayesian posterior probability (PP) values > 0.90 are given at each node. Numbers in circles show nodes used for calibration. **b** Set of 9000 species trees obtained in *BEAST and plotted using DensiTree v2.2.5. *Pli* Pliocene, *Ple* Pleistocene

(PP: 0.97) (Fig. 3a). Within *Tetraglochin*, two main clades were obtained, one composed by the Southern Andean-Patagonian species *T. acanthocarpa* and *T. caespitosa* (PP: 0.82) and the other by the species *T. alata* (Southern Andes), *T. andina* (Southern-Central Andes), *T. cristata*, and *T. inermis* (both restricted to Central Andes) (PP < 0.5) (Fig. 3a). Additionally, species inhabiting the Central Andes (*T. andina*, *T. cristata*, and *T. inermis*) were also included in a clade (PP = 0.7). Competing topologies obtained in the analyses primarily included *T. alata* as sister of the “*T. acanthocarpa*–*T. caespitosa*” clade, or presented alternative positions within the “*T. andina*–*T. cristata*–*T. inermis*” clade (Fig. 3b). Divergence time estimations placed the stem node of *Tetraglochin* (MRCA of *Tetraglochin*–*Margyricarpus*) mainly in the Pliocene [median = 4.25 Mya, 95% highest posterior density (HPD) = 7.44–1.72 Mya], while diversification within the genus was recovered in the early Pleistocene (crown node of *Tetraglochin* 2.23 Mya, 95%HPD: 4.43–0.95 Mya) (Fig. 3a). Ages obtained for other Rosoideae taxa included in the analyses were congruent to the divergence times reported by Zhang et al. (2017).

Ancestral Range Estimation

Of the six biogeographical models evaluated using BioGeoBears, the DEC model resulted the best supported, followed by the DIVA model (AIC_{c_{wt}} = 0.53 and 0.39 respectively, Table 1) showing the importance of the cladogenetic changes in the historical biogeography of the genus. The inclusion of the “jump dispersal” parameter did not improve the models (DEC + j, DIVA + j, and BayArea + j) (Table 1), suggesting for diversification of *Tetraglochin* that models with founder-event speciation (cladogenetic “jump” dispersal) are not adequate to account for movements to new areas. Ancestral range estimation under the DEC model (Fig. 4) recovered the Southern Andes (including the Patagonian steppe) as the most probable ancestral area of the MRCA of *Tetraglochin* (p = 0.77) and its early diversification during the Pleistocene. Subsequent diversification involved an anagenetic range expansion to central Andes of the MRCA of “*T. andina*–*T. cristata*–*T. inermis*” (p = 0.91) clade around 1.5–1 Mya aprox, and a later event of sympatric subset

speciation to the Central Andes for the MRCA of the “*T. cristata*–*T. inermis*” clade. BSM analyses revealed that more common biogeographical events within *Tetraglochin* comprise within area-speciation (71% of total events), of which 49% correspond to “narrow” speciation (daughter lineages inherit the same ancestral range), and 22% to subset speciation (one of the two daughter lineage inherit only a subset of the ancestral range) primarily due to the isolation of the “*T. cristata*–*T. inermis*” clade in the Central Andes (Table S2, Electronic Supplementary Material). Dispersals events (anagenetic range expansions) represented 19% of total events, whereas vicariance was represented only by the 10% (Table S2). Within dispersals, the route from Southern Andes to Central Andes was more frequent (68%) than the reverse way (32%), while for the within-area subset speciation events, the Southern-Central Andes → Central Andes diversification was greater (75%) than the Southern-Central Andes → Southern Andes route (25%).

Niche Comparisons in the Environmental (E) Space

Eigenvalues and variable loadings obtained in the PCA-env approach are shown in Table S3 (Electronic Supplementary Material). The first three PCs accounted for 80.16% of the niche variation (33.81% and 29.44%, and 16.91%, respectively). Variable loadings (Table S3 and Fig. S2 of Electronic Supplementary Material) showed that the first component was primarily influenced by variables associated with the precipitation and humidity, such as the annual precipitation (BIO12), the precipitation availability over atmospheric water demand defined by the aridity index (IA), and the precipitation of wettest quarter/month (BIO16, BIO13). The second PC showed the higher correlation with the variables related to temperature, as the annual mean temperature (BIO1), the min/mean temperature of coldest month/quarter (BIO6/BIO11), and the temperature of the warmest quarter (BIO10). The third component was associated mainly to variables describing the temperature oscillations, as the isothermality (day-to-night temperature variation relative to the annual variation, BIO3) and the temperature seasonality (temperature change over the course of the year, BIO4). Thus, in the (E)-space, environments with higher precipitations and lower aridity load negatively in the first PC, while in the second PC load negatively the lower temperatures, and in the third PC load positively environments with higher isothermality and lower temperature seasonality (Fig. S2, Electronic Supplementary Material).

Climatic niches occupied by *Tetraglochin* species in the (E)-space are shown in the Figs. 4 and S2, S3 (Electronic Supplementary Material). The greatest species separation was obtained along the PC3 (temperature variation) showing two main groups, one composed by *T. cristata* and *T. inermis* (the Central Andean species), and associated to the higher

Table 1 Comparison of the fit of the models tested in BioGeoBE-ARS, all including or not founder-event speciation (“+j”)

Model	LnL	AICc	Δ AICc	ω_i
DEC	−4.38	16.77	0	0.53
DEC+j	−4.32	26.63	9.86	0.00
DIVA	−4.7	17.39	0.62	0.39
DIVA+j	−4.54	27.09	10.32	0.00
BayArea	−6.33	20.67	3.9	0.08
BayArea+j	−5.26	28.52	11.75	0.00

Log-likelihood $\ln(L)$, Akaike information criterion corrected for sample size (AICc), difference in AICc value compared with the best model (Δ AICc), and the Akaike weights (ω_i) showing the relative likelihood of each model

isothermality and the lower temperature seasonality of the Central Andes; and the other including the southern Andean species *T. acanthocarpa*, *T. alata*, and *T. caespitosa* in where isothermality is lower and temperature seasonality is greater. (Fig. 4, S2, S3). Specimens of *T. andina* were mixed between these two groups. The two remaining components (PC1 “precipitation” and PC2 “temperature”) showed a lower species differentiation (Fig. 4, S2, S3). Niche-similarity test based in PCs1–2 did not recover more dissimilarity between niches of different species than expected by chance (accounting for the differences in the surrounding environmental conditions) (Table 2), nevertheless niches of Central Andean (*T. cristata* and *T. inermis*) and Southern Andean species (*T. acanthocarpa*, *T. alata*, and *T. caespitosa*) were significantly dissimilar when PC3 was included (Table 2). Only the niche of *T. andina* was not differentiated from those of the remaining species. Cluster analyses using the niche overlap measures (Schoener’s D) showed two main clusters (Fig. S4, Electronic Supplementary Material), separating the Southern and Central Andean species, while *T. andina* was included both with the Southern Andean (with PCs 1–3 and 2–3) or the Central Andean species (with PC1–2). Finally, niche breadth measures for each species along the (E)-space recovered the largest niche breadth for *T. andina* and the smallest one for *T. acanthocarpa* (Fig. S5, Electronic Supplementary Material).

Niche Comparisons in the Geographical (G) Space

Values of the AUC obtained in the SDM for *Tetraglochin* species ranged from 0.997 (*T. inermis*) to 0.914 (*T. caespitosa*) indicating a good model performance (Table S4 and Fig. S6 of Electronic Supplementary Material). The annual mean temperature (BIO1) presented high contribution to the SDM of most *Tetraglochin* species, showing its importance on the distribution of the entire genus (Table S4). The isothermality (BIO3) was the variable that contributed most to the SDM of the Southern Andean species, while the mean

temperature of driest quarter (BIO9) was for the Central Andean species (Table S4). Other variables with high contribution in the SDMs were associated to single species as the annual precipitation (BIO12) for *T. caespitosa*, or the potential evapotranspiration (PET—ability of the atmosphere to remove water through evapotranspiration processes) for *T. acanthocarpa*. Background similarity test using the distribution models for each *Tetraglochin* species recovered significant similarity within the Southern or Central Andean species groups, but also showed significant differentiation between the species of these two regions (Table 3). Results from PNO profiles and ancestral climatic tolerance reconstructions (Fig. 5 and S7 of Electronic Supplementary material) showed that Central and Southern Andean species are differentiated in the E-space, mainly by the values of BIO3, BIO4, BIO9, and BIO19 (precipitation of coldest quarter), while niche values of *T. andina* shared affinity with both groups. This pattern was also recovered by the phylogenetic principal component analysis, mainly along the PC1 associated to BIO3, BIO9, and BIO19 (Fig. S8, Electronic Supplementary Material).

Geographical Range Overlap

Species range estimations using the SDMs and the maximum training sensitivity plus specificity as threshold showed that the largest ranges were obtained for *T. caespitosa*, *T. alata* and *T. cristata*, while *T. inermis* and *T. andina* presented the smallest ones (Figs. S5 and S9, S10, Electronic Supplementary Material). Age-range correlation analyses recovered a pattern of sympatric speciation (intercept higher than 0.5 and negative slope) for the MCC species tree and 869 of the 1000 trees analyzed (Fig. 6), however the null hypothesis (no phylogenetic signal of geographical range) was not rejected under the Monte Carlo resampling ($p_{\text{intercept}} = 0.102$, $p_{\text{slope}} = 0.226$). Finally, the Mantel test recovered significant correlation between species range overlap and divergence time for the MCC tree ($\rho = -0.595$, $p = 0.038$) and 647 of the 1000 trees analyzed ($p < 0.05$, ρ 95% CI -0.480 , -0.744).

Discussion

South American terrestrial ecosystems experienced drastic transformations in the Cenozoic, during which events occurred in the Neogene and later by the Pleistocene had enormous effects on the diversification of the local biodiversity (Hoorn et al. 2010; Antonelli and Sanmartín 2011; Rull 2011; Hazzi et al. 2018). The Neogene presented strong climatic, tectonic, and geographical changes, mainly related to events such as the middle Miocene climatic optimum (Zachos et al. 2001), the uplift of the Andes (Jordan

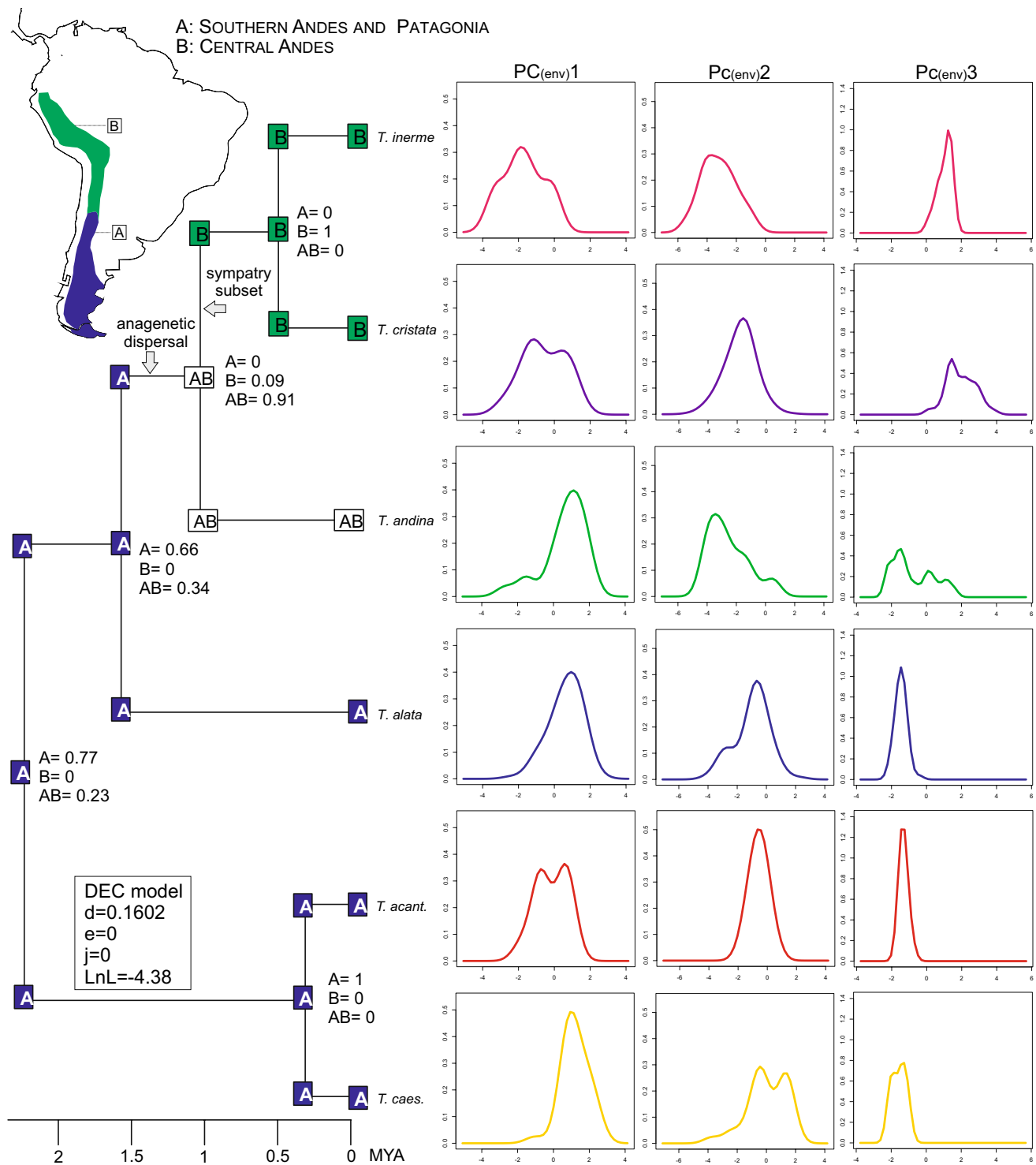


Fig. 4 Biogeography of *Tetraglochin* species and their climatic niches along the environmental (E) space. Left: ancestral range estimation (ARE) on the *Tetraglochin* chronogram using the DEC model in BioGeoBEARS. States at nodes (squares) represent the area with highest ML probability before the instantaneous speciation event, whereas those on branches represent the state of the descendant lineage immediately after speciation. Squares with more than one letter refer to ancestral areas composed of more than one biogeographical area. Boxes to the left of taxon names indicate areas of tip species. Probabilities of ancestral areas are shown to the right of nodes. Right: density plots computed for each *Tetraglochin* species using the PC_{env}1, PC_{env}2, and PC_{env}3

Table 2 Pairwise niche overlap values using the Schoener's D metric and *p*-values of niche similarity test for species of *Tetraglochin* in the environmental (E) space

Comparison A–B	PCenv1–2			PCenv1–3			PCenv2–3		
	Overlap (D)	Niche similarity		Overlap (D)	Niche similarity		Overlap (D)	Niche similarity	
		A → B	B → A		A → B	B → A		A → B	B → A
<i>T. acanthocarpa</i> – <i>T. caespitosa</i>	0.368	0.120	0.594	0.402	0.098	0.150	0.271	0.032^a	0.020^a
<i>T. acanthocarpa</i> – <i>T. alata</i>	0.497	0.026^a	0.100	0.617	0.038^a	0.092	0.434	0.016^a	0.066
<i>T. acanthocarpa</i> – <i>T. andina</i>	0.125	0.843	0.927	0.174	0.735	0.519	0.068	0.262	0.312
<i>T. acanthocarpa</i> – <i>T. cristata</i>	0.341	0.052	0.056	0.000	< 0.001^b	< 0.001^b	0.000	< 0.001^b	< 0.001^b
<i>T. acanthocarpa</i> – <i>T. inerme</i>	0.105	0.354	0.123	0.000	< 0.001^b	< 0.001^b	0.000	< 0.001^b	< 0.001^b
<i>T. caespitosa</i> – <i>T. alata</i>	0.615	0.216	0.076	0.670	0.094	0.076	0.604	0.066	0.076
<i>T. caespitosa</i> – <i>T. andina</i>	0.258	0.789	0.793	0.337	0.900	0.689	0.237	0.731	0.392
<i>T. caespitosa</i> – <i>T. cristata</i>	0.235	0.222	0.060	0.000	< 0.001^b	< 0.001^b	0.000	< 0.001^b	< 0.001^b
<i>T. caespitosa</i> – <i>T. inerme</i>	0.048	0.599	0.711	0.000	< 0.001^b	< 0.001^b	0.000	< 0.001^b	< 0.001^b
<i>T. alata</i> – <i>T. andina</i>	0.443	0.839	0.980	0.393	0.609	0.458	0.371	0.344	0.304
<i>T. alata</i> – <i>T. cristata</i>	0.509	0.134	0.018^a	0.000	0.804	0.671	0.000	< 0.001^b	< 0.001^b
<i>T. alata</i> – <i>T. inerme</i>	0.169	0.446	0.573	0.000	< 0.001^b	< 0.001^b	0.000	< 0.001^b	< 0.001^b
<i>T. andina</i> – <i>T. cristata</i>	0.443	0.579	0.897	0.167	0.655	0.910	0.165	0.436	0.424
<i>T. andina</i> – <i>T. inerme</i>	0.267	0.623	0.494	0.101	0.274	0.454	0.141	0.256	0.671
<i>T. cristata</i> – <i>T. inerme</i>	0.408	0.274	0.266	0.251	0.052	< 0.001^b	0.350	0.070	0.152

Comparisons under similarity test with $p < 0.05$ (in bold) indicate that niches of species A and B are more dissimilar or similar than expected by chance

^aMore similar than expected by chance

^bMore dissimilar than expected by chance

Table 3 Pairwise niche overlap values using the Schoener's D metric and *p*-values of niche similarity test for species of *Tetraglochin* in the geographic (G) space

Comparison A–B	Overlap (D)	Niche similarity	
		A → B	B → A
<i>T. acanthocarpa</i> – <i>T. caespitosa</i>	0.580	< 0.001^a	< 0.001^a
<i>T. acanthocarpa</i> – <i>T. alata</i>	0.501	< 0.001^a	< 0.001^a
<i>T. acanthocarpa</i> – <i>T. andina</i>	0.152	< 0.001^b	0.044^b
<i>T. acanthocarpa</i> – <i>T. cristata</i>	0.015	< 0.001^b	< 0.001^b
<i>T. acanthocarpa</i> – <i>T. inerme</i>	0.050	< 0.001^b	< 0.001^b
<i>T. caespitosa</i> – <i>T. alata</i>	0.605	< 0.001^a	< 0.001^a
<i>T. caespitosa</i> – <i>T. andina</i>	0.322	0.713	< 0.001^a
<i>T. caespitosa</i> – <i>T. cristata</i>	0.025	< 0.001^b	< 0.001^b
<i>T. caespitosa</i> – <i>T. inerme</i>	0.079	< 0.001^b	< 0.001^b
<i>T. alata</i> – <i>T. andina</i>	0.436	< 0.001^a	< 0.001^a
<i>T. alata</i> – <i>T. cristata</i>	0.040	< 0.001^b	< 0.001^b
<i>T. alata</i> – <i>T. inerme</i>	0.098	< 0.001^b	< 0.001^b
<i>T. andina</i> – <i>T. cristata</i>	0.195	0.851	< 0.001^b
<i>T. andina</i> – <i>T. inerme</i>	0.341	< 0.001^a	< 0.001^a
<i>T. cristata</i> – <i>T. inerme</i>	0.415	< 0.001^a	< 0.001^a

Comparisons under similarity test with $p < 0.05$ (in bold) indicate that niches of species A and B are more dissimilar or similar than expected by chance

^aMore similar than expected by chance

^bMore dissimilar than expected by chance

et al. 2001; Blisniuk et al. 2005; Graham 2009; Encinas et al. 2013; Gregory-Wodzicki 2000; Graham et al. 2001; Garzone et al. 2008; Leier et al. 2013), marine ingressions into the continent (Del Río et al. 2013; Uba et al. 2009), and changes in the Amazonian drainage system (Hoorn et al. 2010). On the other hand, the Pleistocene also presented significant environmental alterations due to climatic oscillations (Zachos et al. 2001), glacial-interglacial cycles (Rabassa 2008; Rutter et al. 2012) and changes in the sea level and the seashores (Ponce et al. 2011; Rabassa and Ponce 2013). The most supported scenario for the diversification of *Tetraglochin* recovered from our dated phylogenies and ancestral range estimations placed it during the Pleistocene, early along the Southern Andes and the Patagonian steppe, and subsequently along the Central Andes as a result of a Southern to Central Andean dispersal. These results suggest that diversification in this genus could be associated to quaternary glaciations and the successive glacial expansions and retreats. Regarding the Southern Andes and Patagonia, glaciations began in the late Miocene-early Pliocene, followed by successive expansion/retraction events (Rutter et al. 2012), and with the major expansion of the ice from the Andes, the Great Patagonian Glaciation (GPG), during the Pleistocene (~1.5 to 1 Mya) (Rabassa 2008; Rabassa et al. 2011; Rutter et al. 2012). Additionally, early Pleistocene glaciations were also recovered for the Central

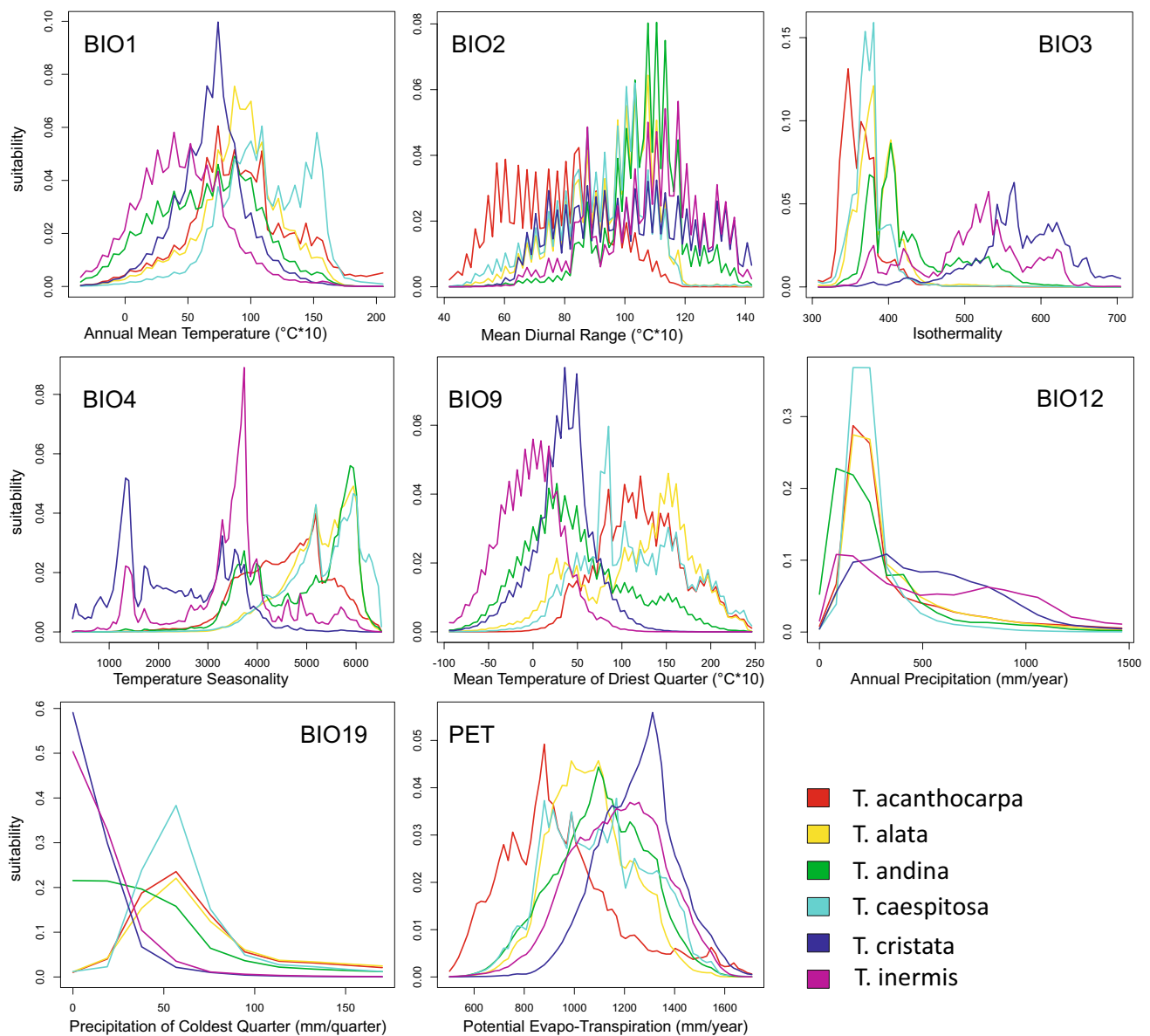


Fig. 5 Predicted niche occupancy (PNO) profiles of eight climatic variables included in the SDM analyses (geographical space) for *Tetraglochin* species. Horizontal axis of PNO profiles shows values of each variable and vertical axis represented the predicted suitability that each species has for this climatic variable. *BIO1* annual mean

temperature, *BIO2* mean diurnal range, *BIO3* isothermality, *BIO4* temperature seasonality, *BIO9* mean temperature of driest quarter, *BIO12* annual precipitation, *BIO19* precipitation of coldest quarter, and PET: potential evapotranspiration

Andes of Bolivia approx. 2.6 Mya (Rutter et al. 2012). These quaternary events have been identified as important driving forces in the evolution of the Southern/Central Andean and Patagonian lineages (Sérsic et al. 2011; Luebert and Weigend 2014).

Within subtribe Sanguisorbinae, a similar pattern of diversification can be found in the closely related *Polylepis*, a genus of small trees and shrubs with ca. 15–30 species growing throughout Northern and Central Andes from Venezuela to Argentina (Simpson 1979; Kessler 1995; Kessler

and Schmidt-Lebuhn 2006), which presumably diverged during the Pliocene–Pleistocene (Simpson 1986; Kerr 2004; Zhang et al. 2017). Diversification in the genus *Acaena* appears to have begun during the Miocene and involved several long-distance dispersal events (Kerr 2004; Jauregui-Lazo 2015). This genus of herbaceous plants includes ca. 45 species distributed primarily in Southern South America and New Zealand, but with species also found in northern South America, Central America, North America, Africa, Australia, the Subantarctic Islands, and Hawaii (Grondona 1964;

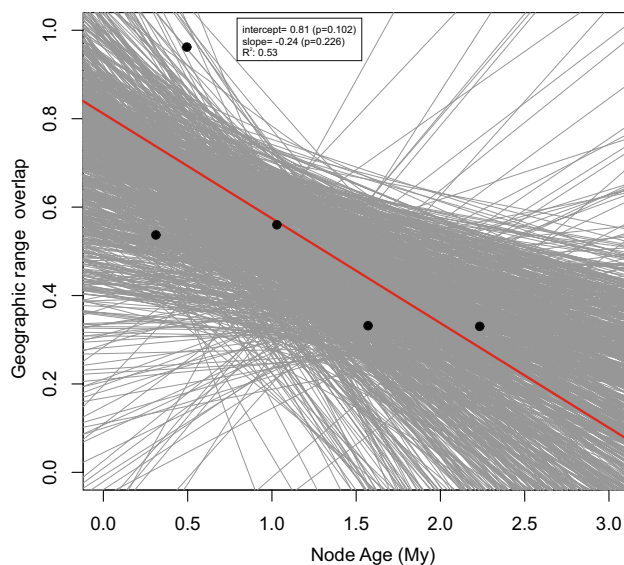


Fig. 6 Result of age range correlation (ARC) analyses which present phylogenetic signal of geographical range overlap in function of time (Mya). Each dot represents a node of the phylogenetic tree. Red line and values shown within the box correspond to the fitted regression obtained using the MCC species tree. Gray lines correspond to the fitted regressions using the 1000 subsampled posterior trees

Jauregui-Lazo 2015). *Margyricarpus*, recovered as sister group of *Tetraglochin* in Acosta et al. (2016) and in this work, includes only two species native to South America, *M. pinnatus* inhabiting in Argentina, Bolivia, Brazil, Chile, Ecuador, Peru, and Uruguay; and *M. digymus* endemic of the Juan Fernández islands (Marticorena 2008). Both genera are easily distinguished by the drupaceous fleshy fruits of *Margyricarpus* and the achene enclosed by the dried receptacle of *Tetraglochin* (Cialdella and Pometti 2017). Our analyses placed the divergence between these two genera (stem node of *Tetraglochin*) mainly along the Pliocene, with the subsequent restriction of *Tetraglochin* species to the Southern Andes/Patagonia and the Central Andes, while *Margyricarpus* (specifically *M. pinnatus*) also extended its geographical range to the eastern regions of the Southern Cone.

Our climatic niche comparisons for both the environmental (E) and geographical (G) spaces suggest that the niche is conserved throughout the diversification of the genus, recovering only substantial changes between the southern Andean species and the Central Andean lineage. Species from lineages that have diversified within the same Andean region (Southern Andes-Patagonia or Central Andes) do not show significant niche differences, on the contrary, closely related species (sister species, i.e. “*T. acanthocarpa*–*T. caespitosa*” and “*T. cristata*–*T. inermis*”) usually exhibit significant similarity along the different niche dimensions. This suggests that ecological divergence is not a major factor associated to the speciation of *Tetraglochin*. Under ecological

speciation, reproductive isolation between two populations evolves by divergent ecologically based selection (Rundle and Nosil 2005; Schluter 2009; Nosil 2012). Alternatively, results seem to support the presence of phylogenetic niche conservatism (PNC) in the evolution of the genus, evidenced by the tendency of the species to retain similar ecological niches over evolutionary time (Peterson et al. 1999; Wiens 2004a). The presence of PCN has been reported for different plant groups (e.g. Alexandre et al. 2017; Kolanowska et al. 2017; Salariato and Zuloaga 2017); and referred as a potential promoter of speciation when species fail to adapt to novel ecological conditions. Under this speciation mechanism, geographical ranges becomes fragmented and initially isolated into allopatric populations that can become future new lineages (Wiens 2004a; Wiens and Graham 2005; Pyron et al. 2015). Glacial cycles and climatic oscillations during the quaternary, in combination with PCN, could have promoted habitat fragmentation in *Tetraglochin* species, leading to the isolation of populations with suppression or reduction of gene flow, as already indicated for different plant lineages from the Southern Andes and Patagonia (Sérsic et al. 2011). However, PNC in *Tetraglochin* must be interpreted with caution because niche divergence may have occurred along an ecological dimension not included in our analyses (as some factor at a finer environmental/geographical scale); and allopatry need not be caused by unsuitable climatic conditions (Jezkova and Wiens 2018), allopatric populations may be separated by other geographic/physical barriers not related to climate (e.g., populations separated by river barriers) (Hazzi et al. 2018).

Alternatively, results from geographical range overlap among the species of *Tetraglochin* favored a sympatric pattern of speciation. The association between divergence times and geographical range overlap detected using the Mantel test, as well as the presence of sympatric ranges between young sister species seems to support the predominance of diversification without substantial geographical isolation. However, since species ranges can expand, contract, and change considerably through time (Losos and Glor 2003), the current geographical range of a species is not necessarily an indicator of its historical distribution. Therefore, current sympatry is not sufficient evidence to support that speciation occurred sympatrically. As a result, Pleistocene refuge hypothesis (PRH—Haffer 1969) with initial allopatric or parapatric divergence presumably associated with PCN, and subsequent range expansion and sympatry should not be discarded for *Tetraglochin*.

An additional factor that could play an important role in the diversification of *Tetraglochin* is the occurrence of hybridization and polyploid speciation. This mechanism of speciation has been reported as particularly frequent in plants since polyploids frequently exhibit ecological differentiation, local dispersal, high fecundity, perennial life

history, and self-fertilization (Mallet 2007; Rieseberg and Willis 2007). Unfortunately polyploidy in *Tetraglochin* is largely unverified and there are still no chromosome numbers reported for its species. However, this phenomenon is widespread in many genera of Rosaceae (Vamosi and Dickinson 2006; Dickinson et al. 2007) such as *Alchemilla* (Gehrke et al. 2008), *Crataegus* (Talent and Dickinson 2005), *Rosa* (Ritz et al. 2004), and the closely related *Acaena*, *Polylepis*, and *Margyricarpus* (Crawford et al. 1993; Kerr 2004; Schmidt-Lebuhn et al. 2010). Interestingly, *T. andina*, which exhibits morphological affinities with both *T. alata* and *T. cristata* (Cialdella and Pometti 2017), is extended from the northern portion of the southern Andes to the Southern portion on the Central Andes, in agreement with the geographical boundaries of *T. alata* and *T. cristata* and their contact zone. *Tetraglochin andina* was the only species in the genus that presented a climatic niche with elements from both the Southern and Central Andes, showing the largest niche breadth and the second smallest geographical range after *T. inermis*. Since hybrids can colonize unfilled ecological niches or adaptive peaks, reducing the gene flow with their parent species (Mallet 2007), this evidence could suggest a hybrid origin for *T. andina*. Nevertheless, molecular data analyzed in this work does not enable us to infer potential allopolyploidization events in *Tetraglochin*, and future studies, using for example sequences from low-copy nuclear genes, are needed to study these processes.

Analyses conducted in this work suggest a complex pattern of diversification in *Tetraglochin*, with different spatial, ecological and genetic factors affecting divergence. However, our analyses support the Pleistocene diversification of *Tetraglochin*, first along the Southern Andes and the Patagonian Steppe and subsequently in the Central Andes. Ecological divergence does not appear to have been a major factor promoting speciation, but rather, the phylogenetic niche conservatism. The Pleistocene refuge hypothesis cannot be discarded to explain diversification of *Tetraglochin*, and while sympatry was favored as geographical model for speciation, allopatric or parapatric divergence associated with the glacial cycles and climatic oscillations are also possible, mainly under the refuge hypothesis. In addition, the niche analyses suggest that polyploidy speciation events could have occurred throughout the diversification of the genus; however, additional phylogenetic and cytogenetic studies are necessary to corroborate this hypothesis. Our study contribute to understanding the evolutionary history of *Tetraglochin* in particular, and the Southern and Central Andean flora in general. New analyses also including members of the genera *Polylepis*, *Acaena*, and *Margyricarpus* can help to elucidate general and particular trends in the diversification history of this clade, detect potential shifts in their diversification

rates, and identify the nature of the factors associated with these changes.

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Data Accessibility All data generated for this study are available online from Dryad Digital Repository (<https://doi.org/10.5061/dryad.sd69mc7>), and the electronic supplementary material.

Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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