

# Climatic niche evolution in the Andean genus *Menonvillea* (Cremolobeae: Brassicaceae)

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**Abstract** The study of how climatic niches change over evolutionary time has recently attracted the interest of many researchers. Different methodologies have been employed principally to analyze the temporal dynamics of the niche and specially to test for the presence of phylogenetic niche conservatism. *Menonvillea*, a genus of Brassicaceae including 24 species, is distributed primarily along the Andes of Argentina and Chile, with some taxa growing in southern Patagonia and others in the Atacama Desert and the Chilean Matorral. The genus is highly diversified morphologically but also presents a remarkably wide ecological range, growing from the high Andean elevations, to the dry coastal deserts in Chile, or the Patagonia Steppe in Argentina. In this study, we used molecular phylogenies together with climatic data to study climatic niche evolution in the genus. The results show that the main climatic niche shifts in *Menonvillea* occurred between the sections *Cuneata-Scapigera* and sect. *Menonvillea* throughout the Mid-Late Miocene, and associated with the two main geographical distribution centers of the genus: the highlands of the central-southern Andes and the Atacama Desert-Chilean Matorral, respectively. Climatic niches in these lineages were mainly differentiated by the aridity and potential evapotranspiration, the minimum temperatures of the coldest month, and the temperature annual range and seasonality. Niche evolution in

*Menonvillea* deviated from a Brownian motion process, with most of the climatic dimension best-fitting to an Ornstein-Uhlenbeck model of multiple adaptive peaks. Our results also indicated that higher aridity levels and lower annual temperature ranges were associated with the evolution of the annual habit, as exemplified by the distribution of sect. *Menonvillea*. Finally, the results suggested that climatic niche evolution in *Menonvillea* exhibited some degree of phylogenetic niche conservatism, fundamentally within the two main lineages (sect. *Menonvillea* and sects. *Cuneata-Scapigera*).

**Keywords** Andes · Atacama Desert · Cruciferae · Patagonian steppe · Phylogenetic niche conservatism · Species distribution modeling

## Introduction

Over the past decade, studies of climatic niche evolution have increased substantially, integrating both phylogenetic and ecological data (e.g., Evans et al. 2009; Boucher et al. 2012; Schnitzler et al. 2012; Ahmadzadeh et al. 2013; Nyári and Reddy 2013; Rato et al. 2015; Algar and Mahler 2015). The climatic niche, defined as the set of environmental conditions associated with the occurrence of a given species (Grinnellian niche, Hutchinson 1978; Soberón 2007), and resulting from the cumulative effects of the physiological tolerance in response to climate (Ackerly 2003), has long been a central concept in ecology. Notably, the study of how climatic niches change over evolutionary time has recently attracted the interest of many researchers (e.g., Hoffmann 2005; Knouft et al. 2006; Pearman et al. 2008; Vieites et al. 2009; Smith and Donoghue 2010). Quantification of climatic niches can be done using several methodologies, such as dimension-reducing techniques (e.g., principal component analyses, Duran et al. 2013). Of

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these, the use of species distribution modeling (SDM) approaches has become popular, allowing to incorporate the potential climatic niche of a species derived from its realized niche (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Elith and Leathwick 2009) and consequently to explore the factors that influence the evolution and geographical distribution of a given species (Evans et al. 2009; Joly et al. 2013; Title and Burns 2015). Several approaches can be used to study the niche evolution, the most common ones involve (1) conducting ancestral state reconstructions; (2) assessing phylogenetic signal of the different niche dimensions (e.g., using Pagel's  $\lambda$  or Blomberg's  $K$ ) (see Kamilar and Cooper 2013; Münkemüller et al. 2012); (3) measuring the relative fit of different models of niche evolution, such as Brownian motion (BM) and Ornstein-Uhlenbeck (OU) (Cooper et al. 2010); and (4) studying the rates of niche evolution among lineages and over the evolutionary timescale (O'Meara et al. 2006; Rabosky et al. 2013). These methods have been employed principally to analyze the temporal dynamics of the niche (e.g., Evans et al. 2009; Vieites et al. 2009; Schnitzler et al. 2012; Duran et al. 2013, Algar and Mahler 2015) and specially to test for the presence of phylogenetic niche conservatism (PNC) (Losos 2008; Ackerly 2009; Cooper et al. 2010; Wiens et al. 2010; Münkemüller et al. 2015). PCN can be defined as the tendency of species to retain characteristics of their fundamental niche over time (i.e., low rates of climatic niche evolution) (Harvey and Pagel 1991; Wiens and Graham 2005), contrasting with patterns of niche divergence where the evolutionary lineages depart from their ancestral climatic niche to occupy different climatic regimes (Peterson et al. 1999; Peterson 2011). Frequent niche divergence within a clade may lead to speciation and increase the rate of climatic niche evolution (Hutter et al. 2013). Therefore, niche evolution and PNC studies enable us to understand how the climatic niche of lineages changes over evolutionary time, but also to determine the implications of the present and future climatic change over biodiversity and conservation (Guisan et al. 2013).

*Menonvillea* DC., a genus of Brassicaceae with 24 species, is distributed primarily along the Andes of Argentina and Chile, with some taxa growing in southern Patagonia and others in the Atacama Desert and Chilean Matorral (Rollins 1955; Salariato et al. 2014). This genus, together with *Aimara* Salariato & Al-Shehbaz and *Cremolobus* DC., is included in tribe Cremolobeae, which forms with tribes Eudemeae and Schizopetaleae a South American endemic lineage shown by Salariato et al. (2016) to represent the first Brassicaceae lineage to colonize South America in the Early Miocene (around 18–20 Mya), diversifying around Early-Mid Miocene in the central and southern Andes and the Atacama-Sechura desert.

*Menonvillea* is highly diversified morphologically, particularly in its habit, leaves, flowers, and fruit. Furthermore, the ecological range of the genus is remarkably wide, with species growing at high Andean elevations (up to 5300 m), in the dry

coastal deserts of Atacama in Chile, or in the Patagonia Steppe in Argentina (Salariato et al. 2014). As shown by Salariato et al. (2013), *Menonvillea* includes three main lineages, corresponding to sects. *Cuneata*, *Menonvillea*, and *Scapigera*, which are strongly supported by molecular data and several morphological characters. While early diversification of *Menonvillea* was reported during Early-Mid Miocene, diversification of its sections dates back to Late Miocene-Pleistocene and correlates with the final Andean uplift (Salariato et al. 2016). Also, different geographical patterns are present in the sections of *Menonvillea* (Fig. 1). Species of sect. *Menonvillea* are Chilean endemics that mainly grow at moderate to low altitudes principally in the Atacama Desert and the Chilean Matorral, with a few species reaching the Andean highlands. By contrast, species of sects. *Scapigera* and *Cuneata* are distributed along the Andes of Argentina and Chile. Species of sect. *Scapigera* are found particularly at high altitudes reaching ca. 4500 m in the central portion of the Andes in Argentina and Chile, in the Altoandina, Prepuna, and Puna biogeographical provinces (sensu Cabrera and Willink 1973) and northern Patagonia. Species of sect. *Cuneata* are widely distributed and occupy the most variable ecological ranges in the genus; they grow from the northern Altoandina and Puna regions of Jujuy (Argentina) and Antofagasta (Chile) to southern Patagonia in Santa Cruz Province and the Magallanes Region, from ca. 500 to 5300 m.

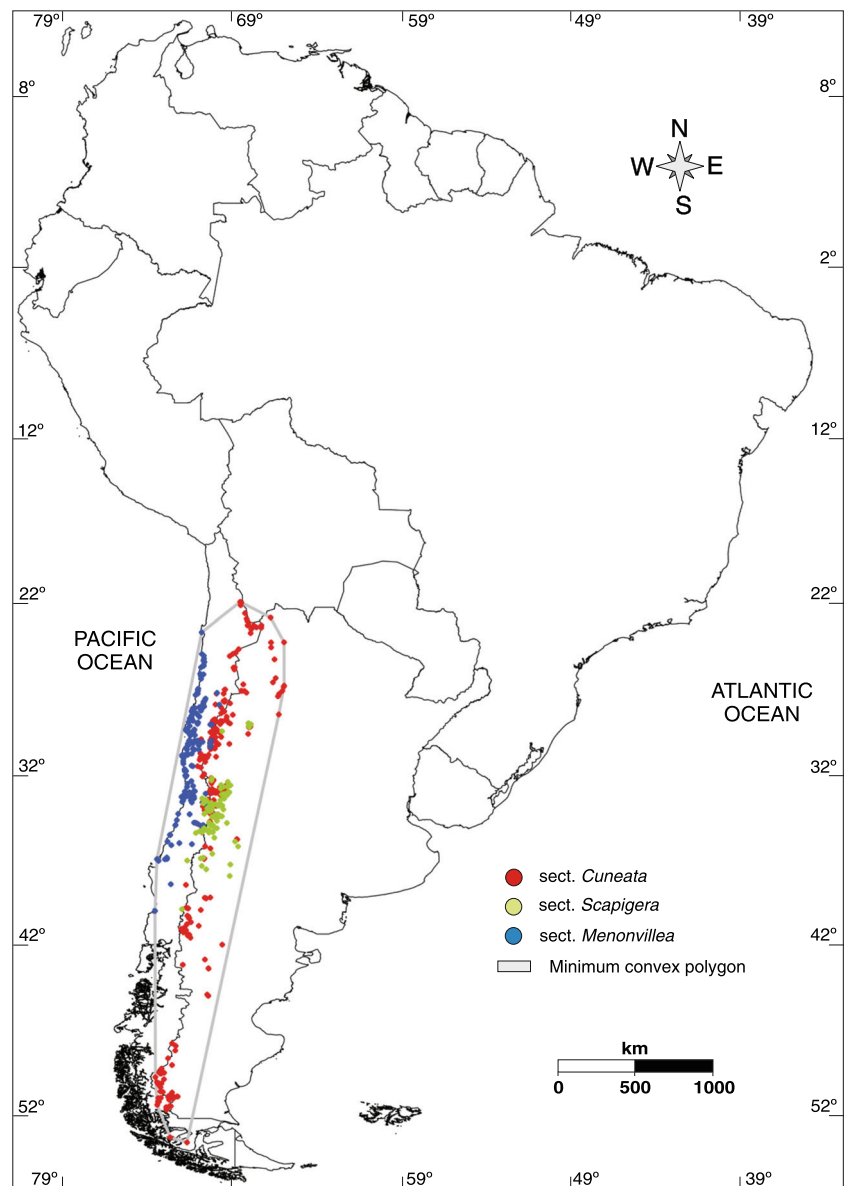
Given that *Menonvillea* species occupy different ecological habitats through the central-southern Andes and associated areas, such as the Atacama Desert and the Patagonian steppe, an analysis of the niche evolution in this genus would increase the knowledge about the tempo and mode of evolutionary patterns and processes in that part of the Andes. In this paper, we utilized information on the phylogenetic relationships, climatic data processed both by ordination and SDM techniques, and phylogenetic comparative methods to study climatic niche evolution in *Menonvillea*. Specifically, we employ a series of methodologies that involve (1) niche overlap comparisons, (2) evaluation of phylogenetic signal, (3) fit of different macroevolutionary models, and (4) estimation of the rates of climatic niche evolution. As a result, our main goals were to determine the main climatic factors associated with the niches of different lineages, to examine the evolutionary dynamics of climatic niches in time and space, and to detect potential PNC or niche divergence events.

## Materials and methods

### Species occurrence and environmental data

Species occurrences used in this study have been mostly extracted from the taxonomic revision of the genus (Salariato et al. 2014) and included data from specimens deposited in

**Fig. 1** Geographical area analyzed in the climatic niche analyses. *Red, green, and blue dots* correspond to species of sects. *Cuneata*, *Scapigera*, and *Menonvillea*, respectively. Delimited area corresponds to the minimum convex polygon enclosing the entire distribution of *Menonvillea* species



different herbaria (B, BAA, BAB, BH, BM, BCRU, CONC, CORD, E, F, G, GH, K, KW, LE, LIL, LP, MEL, MERL, MO, NY, P, PR, S, SGO, SI, SRFA, U, UC, UPS, US) (herbarium acronyms follow Thiers 2015). Subspecies of *Menonvillea scapigera* (subsp. *scapigera* and subsp. *longipes*) were included as separate taxa in the analyses because they occupy different habitats (Salariato et al. 2014). All records were mapped using Diva-GIS v7.5 (Hijmans et al. 2012) for visual inspection. In cases of specimens with no GPS coordinates but exact locality names, records have been georeferenced using Google Earth 7.1. After removing duplicates and occurrences closer to 0.5' (~1 km), we obtained a total of 808 records, with an average of 35 data point per species, ranging from 5 (*Menonvillea famatinensis* and *Menonvillea frigida*) to 185 (*Menonvillea cuneata*) (dataset available in Appendix 1 of Supplementary material, and from the Dryad Digital Repository: doi:10.5061

/dryad.c5271). *Menonvillea macrocarpa* and *Menonvillea zuloagaensis* are only known from their type collections (only one record each), and therefore, they were excluded from the niche overlap analyses and the SDM estimations.

Information on the current climatic conditions within the study area was extracted from the WorldClim database v1.4 (Hijmans et al. 2005) with a resolution of 30". Values of all 19 bioclimatic variables and altitude were extracted from the area defined by a minimum convex polygon enclosing all species records (Fig. 1). Additionally, we also include 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 (Calenge 2006), raster (Hijmans 2015), sp (Bivand et al. 2013), and maptools (Bivand and Lewin-Koh 2015), implemented in R 3.2.1 (R Core Team 2015).

## Niche overlap comparisons

Climate niche overlaps between species and sections of *Menonvillea* were estimated using the PCA-env approach proposed by Broennimann et al. (2012) in which a principal component analysis is calibrated on the entire environmental space present in the study area (the minimum convex polygon enclosing all *Menonvillea* species occurrences in this work). We consider the first two main principal components (PC), and we divided this environmental space in a grid of  $100 \times 100$  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 overestimation 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 (or section) 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). All niche overlap estimations were conducted using the ecospat package (Broennimann et al. 2015).

First, in order to study niche affinities among species of *Menonvillea*, we used the R package cluster (Maechler et al. 2015) to conduct agglomerative hierarchical clustering using the unweighted pair-group average (UPGMA) algorithm and a matrix composed by the niche overlap estimation among all species. Additionally, a Mantel test was used to evaluate the correlation between niche overlap and divergence times. For this, time of the most recent common ancestor (MRCA) for each species pair was calculated using 1000 dated phylogenies randomly subsampled from the posterior distributions of trees obtained in the BEAST analyses (see below). Mantel test between niche overlap and divergence time matrices were conducted in the R package Vegan (Oksanen et al. 2015) using 10,000 permutations and the Spearman rank correlation coefficient. Second, to analyze niche affinities between sections of *Menonvillea*, we used the niche similarity test (Warren et al. 2008) implemented in ecospat to assess whether the climatic niches of *Menonvillea* sections are dissimilar or more similar than expected by change. For this test, we used 1000 repetitions, and null hypothesis was rejected if niche overlap of the observed value was greater or smaller than the 95 % of simulated values. Additionally, comparisons of environmental niche overlaps among sections were visualized using density profiles computed for each bioclimatic niche axis in the sm package (Bowman and Azzalini 2014).

## Species distribution modeling

Because inclusion of the 22 bioclimatic variables (19 BIOCLIM + altitude + IA + PET) in the SDM can be

problematic due to high degrees of collinearity among predictors (Heikkinen et al. 2006), we used the niche dimensions obtained in the PCA analyses based on all 22 standardized bioclimatic variables extracted from the study area. The first five PCs, accounting for more than 95 % of the variation (for PCA results, see Table 1), were included as predictors in the SDM analyses. To perform SDM for each species, we selected the maximum entropy algorithm implemented in Maxent 3.3.3k (Phillips et al. 2006). 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.

## Phylogeny

For phylogenetic analyses of *Menonvillea*, we used ITS, *trnL-F*, *trnH-psbA* intergenic spacer, and *rps16* intron sequences for 24 taxa (23 spp. and 1 subsp.) representing more than 95 % of taxa included in the genus (only *Menonvillea zuloagaensis* could not be sequenced). Although the sequences were taken mainly from Salariato et al. (2013, 2016), additional 29 new sequences were generated for this study (GenBank accession numbers are provided in Table S1, Supplementary material). Protocols for extraction, amplification, and DNA sequencing are described in Salariato et al. (2015). Each species was represented by one to three specimens (see S1). Species of the genera *Xerodraba*, *Aimara*, and *Cremolobus* were included as outgroups following the phylogenetic relationships of the Cremolobeae-Eudemeae-Schizopetaleae clade presented in Salariato et al. (2016). Sequence alignments were generated using the phylogeny-aware alignment algorithm implemented in the program PRANK (Löytynoja 2014) and subsequently checked and improved manually using BioEdit. All aligned matrices are available online from Dryad Digital Repository (doi:10.5061/dryad.c5271) and TreeBase (<http://purl.org/phylo/treebase/phyloWS/study/TB2:S18952>). Nucleotide substitution models selected in jModeltest2 2.1.6 based on (AIC) scores were SYM + G (ITS), TPM1uf + G (*trnL-F*), TPM1uf + G (*trnH-psbA*), and TIM1 + G (*rps16* intron). Because coalescent-based methods have demonstrated to be more accurate for species tree topology estimation (Heled and Drummond 2010), and divergence times can be overestimated with gene-tree-based approaches that do not correct for genetic divergence that predates speciation (especially for recent divergence events) (McCormack et al. 2011; Angelis and Dos Reis 2015), we estimated the species tree of *Menonvillea* using the coalescent-based method implemented in \*BEAST extension (Heled and Drummond 2010) of BEAST v2.3.0 (Bouckaert et al. 2014). All nucleotide substitution models were unlinked across loci, and an uncorrelated log-normal clock model

**Table 1** Loadings on the first five components obtained from the principal component analysis using bioclimatic variables extracted from the study area (minimum convex polygon enclosing the *Menonvillea* species distribution)

Variables	PC1	PC2	PC3	PC4	PC5
Annual mean temperature (BIO1)	-0.25	0.26	0.04	0.11	-0.11
Mean diurnal range (BIO2)	-0.22	-0.05	0.32	-0.31	0.19
Isothermality (BIO3)	0.00	-0.20	0.46	0.17	-0.04
Temperature seasonality (BIO4)	-0.19	0.14	-0.23	-0.40	0.23
Max temperature of warmest month (BIO5)	-0.26	0.24	0.02	-0.08	0.09
Min temperature of coldest month (BIO6)	-0.12	0.29	-0.04	0.38	-0.12
Temperature annual range (BIO7)	-0.25	0.08	0.05	-0.42	0.22
Mean temperature of wettest quarter (BIO8)	-0.24	0.16	0.14	-0.09	-0.40
Mean temperature of driest quarter (BIO9)	-0.07	0.21	-0.10	0.38	0.42
Mean temperature of warmest quarter (BIO10)	-0.26	0.26	-0.03	0.00	-0.02
Mean temperature of coldest quarter (BIO11)	-0.21	0.25	0.11	0.26	-0.18
Annual precipitation (BIO12)	0.24	0.26	0.13	-0.07	0.08
Precipitation of wettest month (BIO13)	0.21	0.25	0.22	-0.03	0.23
Precipitation of driest month (BIO14)	0.27	0.20	-0.03	-0.12	-0.20
Precipitation seasonality (BIO15)	-0.08	-0.05	0.49	0.17	0.02
Precipitation of wettest quarter (BIO16)	0.21	0.25	0.21	-0.03	0.22
Precipitation of driest quarter (BIO17)	0.27	0.20	-0.02	-0.12	-0.17
Precipitation of warmest quarter (BIO18)	0.14	0.24	0.11	-0.27	-0.42
Precipitation of coldest quarter (BIO19)	0.24	0.22	0.16	0.04	0.30
Altitude (ALT)	0.04	-0.29	0.37	-0.10	-0.03
Annual aridity index (IA)	0.28	0.21	0.07	-0.07	-0.07
Potential evapotranspiration (PET)	-0.28	0.15	0.24	-0.07	0.00
Variance (%)	38.83	29.05	12.65	9.79	5.46
Cumulative proportion (%)	38.83	67.88	80.52	90.31	95.77

(UCLN) was assigned to each sampled locus. We linked the tree model for the three chloroplast regions (*trnL-F*, *trnH-psbA*, *rps16* intron) because they are genetically linked, and we set separate tree models for the chloroplast dataset and the nuclear ribosomal ITS region. A birth-death process was used for the species tree prior, and the piecewise linear and constant root was used for the population size model. To estimate divergence times, we used two secondary calibrations from Salariato et al. (2016) on the species tree: we calibrate (1) the root node (MRCA of tribes Eudemeae and Cremolobeae) using a normal prior distribution of mean = 17.74 Mya and SD = 2, and (2) the crown node of *Menonvillea* with a normal prior distribution of mean = 15.94 Mya and SD = 1.9. These ages were obtained in the divergence time analyses for the Cremolobeae-Eudemeae-Schizopetaleae clade (CES clade) of Salariato et al. (2016) using a broad sampling of Brassicaceae and several fossil-based calibrations. Detailed dating rationale and strategy used to obtain these ages is given in Salariato et al. (2016) and Franzke et al. (2016). Four runs were conducted in BEAST using 200 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 2.3.0, and the species maximum clade credibility

tree (MCCT) was calculated using TreeAnnotator 2.3.0. Alternatively, the dataset was also analyzed using concatenated analyses in BEAST, applying the same priors and settings for nucleotide and clock models. All phylogenetic trees are available online from Dryad Digital Repository (doi:10.5061/dryad.c5271) and TreeBase (<http://purl.org/phylo/treebase/phylovs/study/TB2:S18952>).

### Niche evolution

For the studies of climatic niche evolution in *Menonvillea*, we first generated the predicted niche occupancy (PNO) profiles using the phyloclim package (Heibl and Calenge 2013), following the methodology proposed by Evans et al. (2009). In order to obtain a PNO profile per principal component (PC), median probability projections obtained for each species in the SDM were integrated with each of the five PCs and binned into 100 evenly space categories. From each PNO profile and species, we extracted the weighted mean and 1000 random values associated with its probability distribution. In the case of *M. macrocarpa*, which was not included in the SDM analyses because it is known only for the type collection, we included in the evolutionary analyses the values of the environmental components corresponding to its type locality.

Additionally, to assess differences between PNOs of different sections, we conducted a permutational MANOVA test (PERMANOVA) using the mean PNO values of each species in *vegan* package.

First, we performed ancestral state reconstructions of climatic niche evolution under maximum likelihood (ML) estimation, using the MCCT and the mean PNO values for each climatic component in the R package *phytools* (*fastAnc* function) (Revell 2012). Second, we evaluated the phylogenetic signal of the five climatic components using Pagel's  $\lambda$  index (Pagel 1999). This index ranges from 0 to 1, indicating no phylogenetic signal when  $\lambda = 0$ , and phylogenetic pattern as expected under Brownian motion when  $\lambda = 1$ . Pagel's  $\lambda$  was calculated for the 1000 randomly subsampled posterior trees from the Bayesian analyses, and using the 1000 sampled values from each PNO profiles in *phytools*. Lambda ( $\lambda$ ) values observed were compared to those obtained from 1000 data simulations under Brownian motion.

Second, to investigate the mode of evolution along each climatic niche component, we fit five alternative models of evolution to the PNO values of each climatic PC: (1) a Brownian motion model (BM), in which traits evolve as a random walk process and niche disparity accumulates approximately linearly through time (Felsenstein 1985); (2) a "single-peak" OU, that assumes niche evolution has been constrained toward a single adaptive peak (Hansen 1997; Butler and King 2004); (3) a "multi-peak" Ornstein-Uhlenbeck model (OUM), which supports the presence of multiple adaptive peaks (Beaulieu et al. 2012); (4) an early-burst model (EB), which predicts that rates of niche diversification have decreased exponentially through time (Harmon et al. 2010); and (5) a white noise model (WN), in which the niche evolution is independent from phylogenetic relationships (no covariance structure among species). Fit of these models was estimated both on the MCCT using the mean PNO values for each PC, and over the 1000 trees using the 1000 randomly sampled PNO values. Calculations were conducted using the R packages *geiger* (Harmon et al. 2008) (BM, OU, EB, and WN models) and *surface* (Ingram and Mahler 2013) (OUM model), and the best-fitting model was chosen using the Akaike information criterion corrected for small sample size (AICc). In case of models with multiple adaptive peaks, *surface* algorithm indentified lineages in which regime shifts may have occurred without a priori assignment. Results observed were compared to those obtained from 1000 data simulations under Brownian motion.

In order to evaluate the relations of climatic niche with life history of *Menonvillea* species, we used phylogenetic logistic regression, which allows predictions for a binary-dependent variable (i.e., life history) to be made from continuous independent variable (i.e., climatic PCs). For this, we used the method of Ives and Garland (2010) implemented in the *phylolm* package (Ho and Ané 2014) with 1000 bootstrap

replicates. We assigned values for habit (dependent variable) following Evans et al. (2005) (potentially perennial "iteroparous" = 0, obligately annual "semelparous" = 1), while the mean PNO values for the five climatic PCs were included as independent variables. Models were compared using the AIC and significance within each model was determined with a threshold of 0.05.

Finally, in order to estimate and detect changes in the rates of climatic niche evolution, we analyzed the mean PNO values of the five PCs on the MCCT using BMM 2.3.0 (Rabosky 2014). BMM uses reversible-jump Markov chain Monte Carlo (rjMCMC) to select between models that vary in the number of evolutionary regimes, assuming that changes in evolutionary regimes occur across branches of the phylogenetic trees under a compound Poisson process, and accounting for variation in the rate of trait evolution ( $\beta$ ) through time and among lineages (Rabosky et al. 2013, 2014). Priors for the BMM analysis were set using the R package *BAMMtools* (Rabosky et al. 2015) (*poissonRatePrior* = 1.0, *betaInitPrior* = 0.17, *betaShiftPrior* = 0.07). We ran the MCMC for ten million generations with four MCMC and a sampling frequency of 10,000. Convergence was visualized in R by plotting the log-likelihood trace of the MCMC output file, discarding the first 10 % of samples as burn-in. ESS >200 from the remaining samples was checked using the R package *CODA* (Plummer et al. 2006). For each climatic component, we calculated the phylorate and rate-through-time plots, identified the 95 % credible set of distinct rate-shift configurations, and computed the Bayes factors contrasting models with different numbers of shifts.

## Results

### Niche overlap comparisons

Eigenvalues and variable loadings for the PCA are shown in the Table 1. The first two PCs accounted for 67.88 % of the niche variation (38.83 and 29.04 %, respectively), while the first five PCs explained 95.77 %. Variable loadings (Table 1) showed that the first component was primarily influenced by variables associated with the humidity and precipitation as the PET (ability of the atmosphere to remove water through evapotranspiration processes) (Fig. S1A), the aridity index (IA) (precipitation availability over atmospheric water demand), and the precipitation of the driest quarter (BIO17), and secondarily by variables related to the highest temperatures such as max temperature of the warmest quarter (BIO5). The second PC shows high correlation with altitude and temperature, especially with min temperature of coldest month (BIO6), mean temperature of warmest quarter (BIO10), and annual mean temperature (BIO1) (Table 1, Fig. S1B). Thus, in

the first PC, environments with higher aridity load negatively, while in the second PC, the high altitude environments with lower temperatures load negatively, especially in winter. Regarding the remaining components, PC3 was mostly influenced by precipitation seasonality (BIO15) and isothermality (BIO3), while PC4 by temperature annual range (BIO7) and temperature seasonality (BIO4), and PC5 by the mean temperature of the driest quarter (BIO9), the precipitation of the warmest quarter (BIO18), and the mean temperature of the wettest quarter (BIO8) (Table 1, Fig. S1C–E).

Niches for each species in the climatic space calculated by the PCA-env technique are shown in the Supplementary material (Figs. S2–S3). Cluster analyses for species using the niche overlap measures (Schoener's *D*) show three main clusters (Fig. 2a): one integer exclusively by the southern Andean species of sect. *Cuneata*, another including species of both sects. *Cuneata* and *Scapigera* from the central Andes, and a third cluster including all Chilean endemic species of sect. *Menonvillea* plus lowland-inhabiting *M. longipes* (sect. *Scapigera*) and *Menonvillea patagonica* (sect. *Cuneata*). Niche overlap was high between sects. *Cuneata* and *Scapigera* and low between them and sect. *Menonvillea* (Fig. 2b–e); the niche similarity test recovered significant similarities only for sects. *Scapigera* and *Cuneata* ( $p = 0.002$ ). Finally, the Mantel test recovered significant correlation between niche overlap and divergence time (median  $\rho = -0.506$ ,  $p < 0.01$ , 95 % CI =  $-0.279, -0.517$ ).

### Species distribution modeling

Values of the AUC obtained for each species ranged from 0.89 to 1 (mean = 0.97), indicating good model performance (Table S2 and Figs. S4–S5, Supplementary material). The contribution of the five PCs used to the distribution models ranged from 0 to 96.9 %, and while there was no a unique response in variable preference between species, the prevailing tendency was that PC4 contributes mostly to species of sect. *Menonvillea*; PC2, PC3, and PC5 contribute to species of sect. *Scapigera*; and PC1, PC2, PC3, and PC5 contribute to species of sect. *Cuneata* (Table S2). Results of the PERMANOVA test using the mean PNO values for the five climatic dimensions showed that both sects. *Scapigera* and *Cuneata* differ significantly from sect. *Menonvillea* ( $p < 0.001$ ), while significant differences between the first two sections were rejected ( $p = 0.885$ ).

### Phylogeny

Species trees obtained for *Menonvillea* were congruent with topologies reported in Salaria et al. (2013, 2016) (Fig. 3). The genus included three main lineages corresponding to sections *Menonvillea*, *Cuneata*, and *Scapigera* (posterior probability “pp” = 1 for all sections), the last two sister (pp = 0.98).

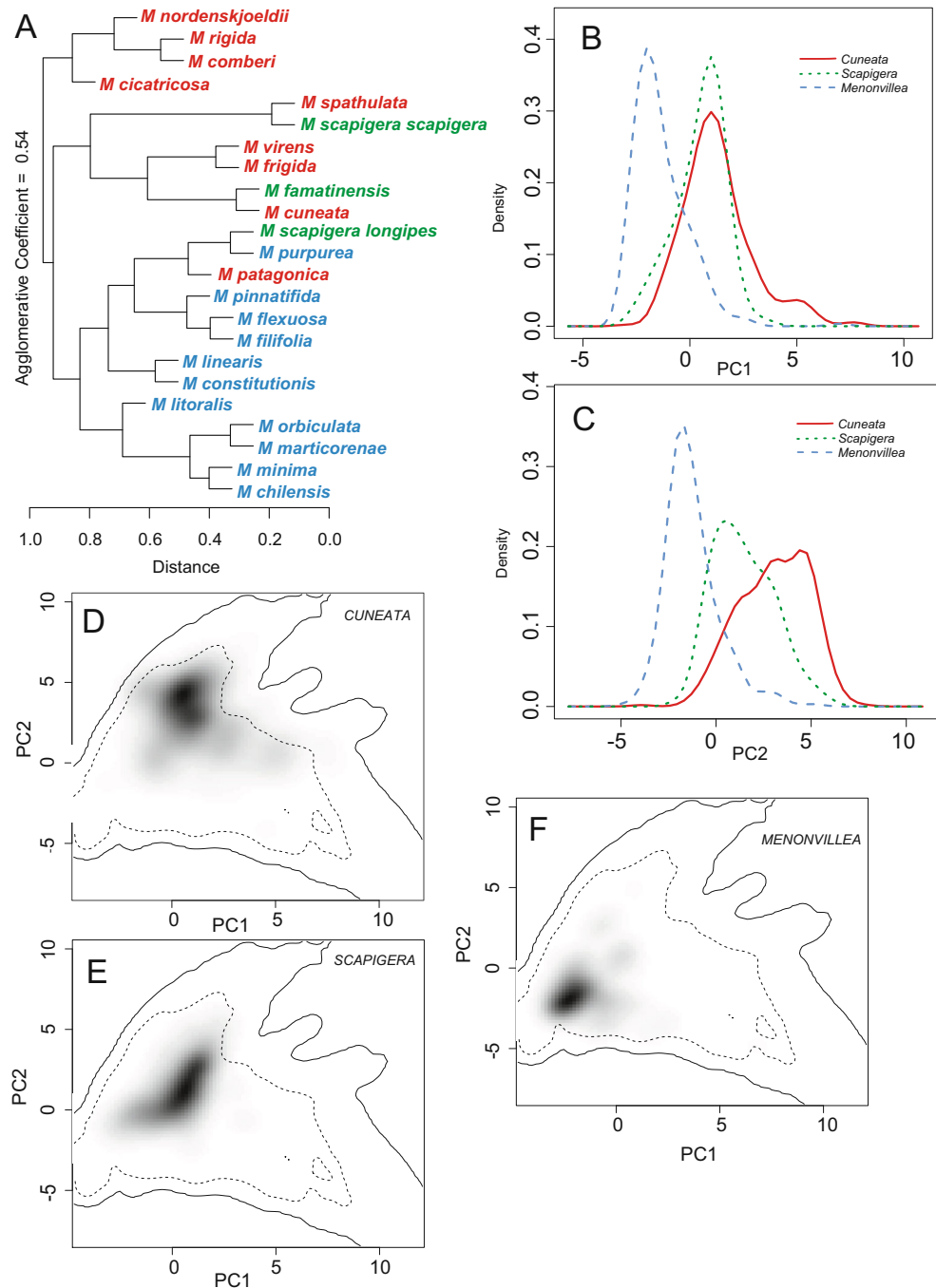
Divergence times for the crown node of the genus were 14.62 Mya (median) (HPD95% 12.77–16.45), while ages for crown nodes of sects. *Menonvillea*, *Cuneata*, and *Scapigera* were 5.32 Mya (2.14–8.97), 6.27 Mya (4.26–8.49), and 1.15 Mya (0.28–2.32), respectively. Topologies from the concatenated analyses (Fig. S6, Supplementary material) were similar to the species tree, and divergence times for *Menonvillea* sections in the concatenated analyses were slightly older (1–2 My approx.). The main difference between the two methods was the divergence time of the clade composed by sect. *Menonvillea* excluding *Menonvillea minima*, in which species tree analyses recovered a crown node age of 1.02 Mya (0.41–1.74) vs. 4.56 Mya (2.17–6.92) in the concatenated analyses.

### Niche evolution

Ancestral state reconstructions (Figs. 4 and S7 of Supplementary material) for PC1, PC2, and PC4 differentiated sects. *Cuneata* and *Scapigera* from sect. *Menonvillea*, while PC3 changes within sect. *Cuneata* and PC5 was highly variable within the entire genus. Phylogenetic signal (Pagel's  $\lambda$ ) recovered over the 1000 trees and using the 1000 PNO values was moderate in PC1, PC2, and PC4 and closer to zero in PC3 and PC5 (Table 2). The comparisons of model fit based on the AICc (Table 2) indicated that the BM model was rejected in all PCs ( $p < 0.01$ ). The OU model with multiple selective optima (OUM) was preferred in PC1, PC2, and PC4, while PC3 and PC5 fitted a WN, where climatic components change regardless of shared ancestry between species. For climatic components best described by an OUM model, the number of different optima more frequently selected was two followed by three. In these analyses, sects. *Cuneata* and *Scapigera* always presented a distinct regime from sect. *Menonvillea* (Fig. 5). When a third optimum was recovered, PC1 shows additional shift regimen for the *M. rigida*-*Menonvillea nordenskoeldii* clade, PC2 for the *M. frigida*-*M. virens*-*Menonvillea cuneata*-*M. macrocarpa* clade, and PC4 for sect. *Menonvillea* excluding *M. minima*. Additionally, surface analyses using multivariate data (PC1 + PC2 + PC4) also selected models with two and three different peaks in which sects. *Cuneata*-*Scapigera* and sect. *Menonvillea* also resulted under distinct regimens, and the third optimum was assigned, similar to the PC2, to the *M. frigida*-*M. virens*-*M. cuneata*-*M. macrocarpa* clade (Fig. 5). Results from simulated data were differentiated from empirical data, showing a phylogenetic signal closer to 1 and the BM model as the most frequently best-fitted model (Table 2).

Using phylogenetic logistic regression, life history in *Menonvillea* was best predicted by the aridity component (PC1) (Table 3; estimate slope coefficient  $B_1 = -0.83$ ,  $p = 0.022$ ) and the temperature annual variation component

**Fig. 2** Results from the niche overlap analyses obtained using the PCA-env method. **a** Agglomerative hierarchical clustering using UPGMA algorithm and the niche overlap estimations (Schoener's *D* index) among all species. Species names in red, green, and blue belong to sects. *Cuneata*, *Scapigera*, and *Menonvillea*, respectively. **b, c** Density plots computed for sects. *Cuneata*, *Scapigera*, and *Menonvillea* using the PC1 (**b**) and PC2 (**c**). **d–f** Climatic niche of the three *Menonvillea* sections produced by the two main axes of the PCA-env. For each section, the gray to black shading represents the grid cell density of the species occurrence (black being the highest density). The first dashed line represents the 50 % of the available environment and the solid line represents the 100 %.



(PC4) ( $B_1 = 0.57$ ,  $p = 0.024$ ). These results indicate that lower values for PC1 (higher aridity) and PC4 (lower annual temperature range) are associated with the annual habit. On the other hand, models including the PC3 and PC5 as independent variables showed the lowest fit to predict the life history.

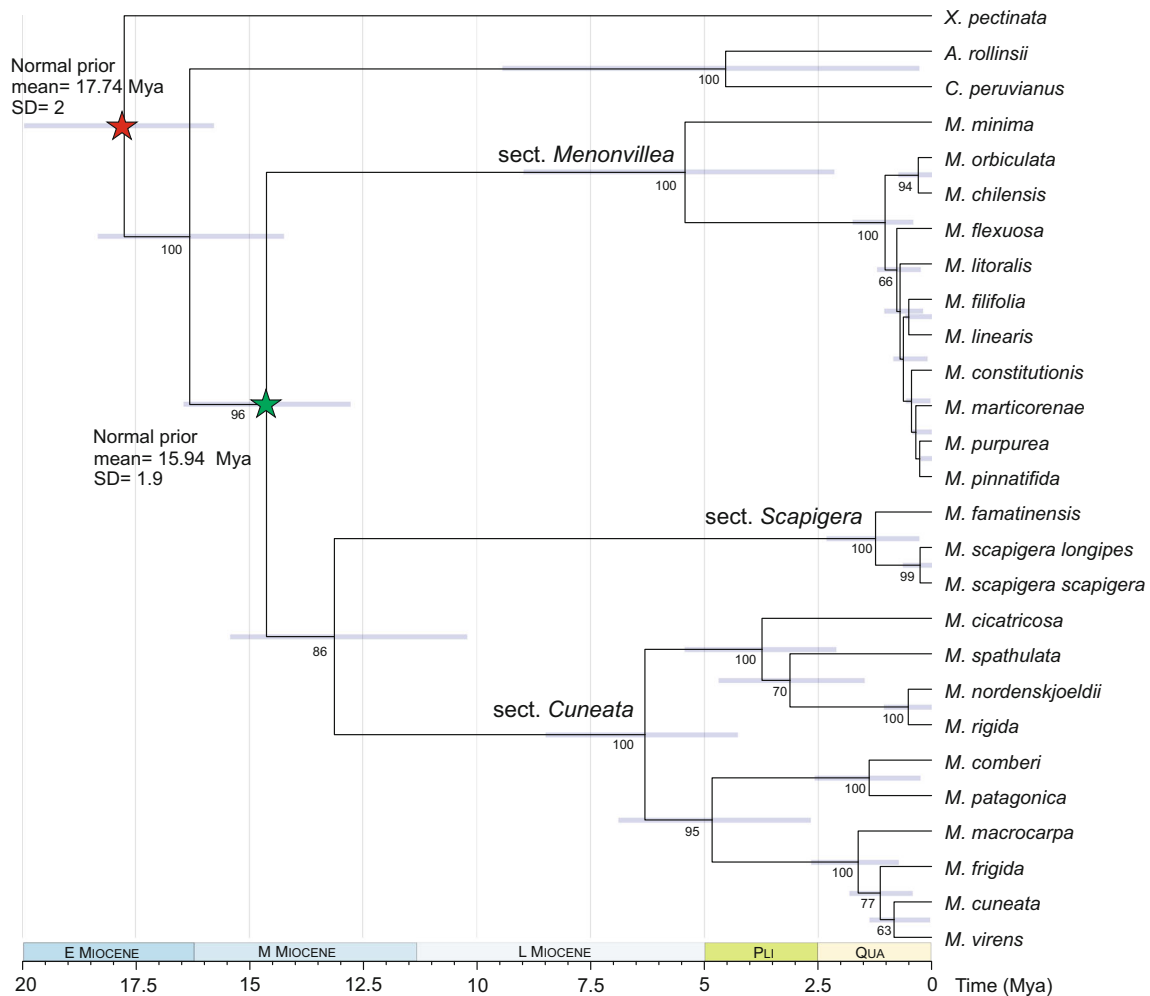
Finally, the BAMM analyses favored models without rate shifts in the niche evolution of all PCs, excepting PC4 (Fig. 6). For this component, analyses favored models with two regimes and a rate shift placed on the crown node of sect. *Menonvillea* (posterior probability of shift configuration = 0.65, frequency

in the 95 % credible set = 0.70). Bayes factor values also favored models with no rate shift for PCs 1–3 and 5 ( $2 \ln \text{BF} < 0$ ), and with one rate shift for PC4 ( $2 \ln \text{BF} = 13.52$ ).

## Discussion

The analyses conducted in this study provide a comprehensive view of how climatic niches evolved over the evolutionary history of *Menonvillea*. The results show that the main





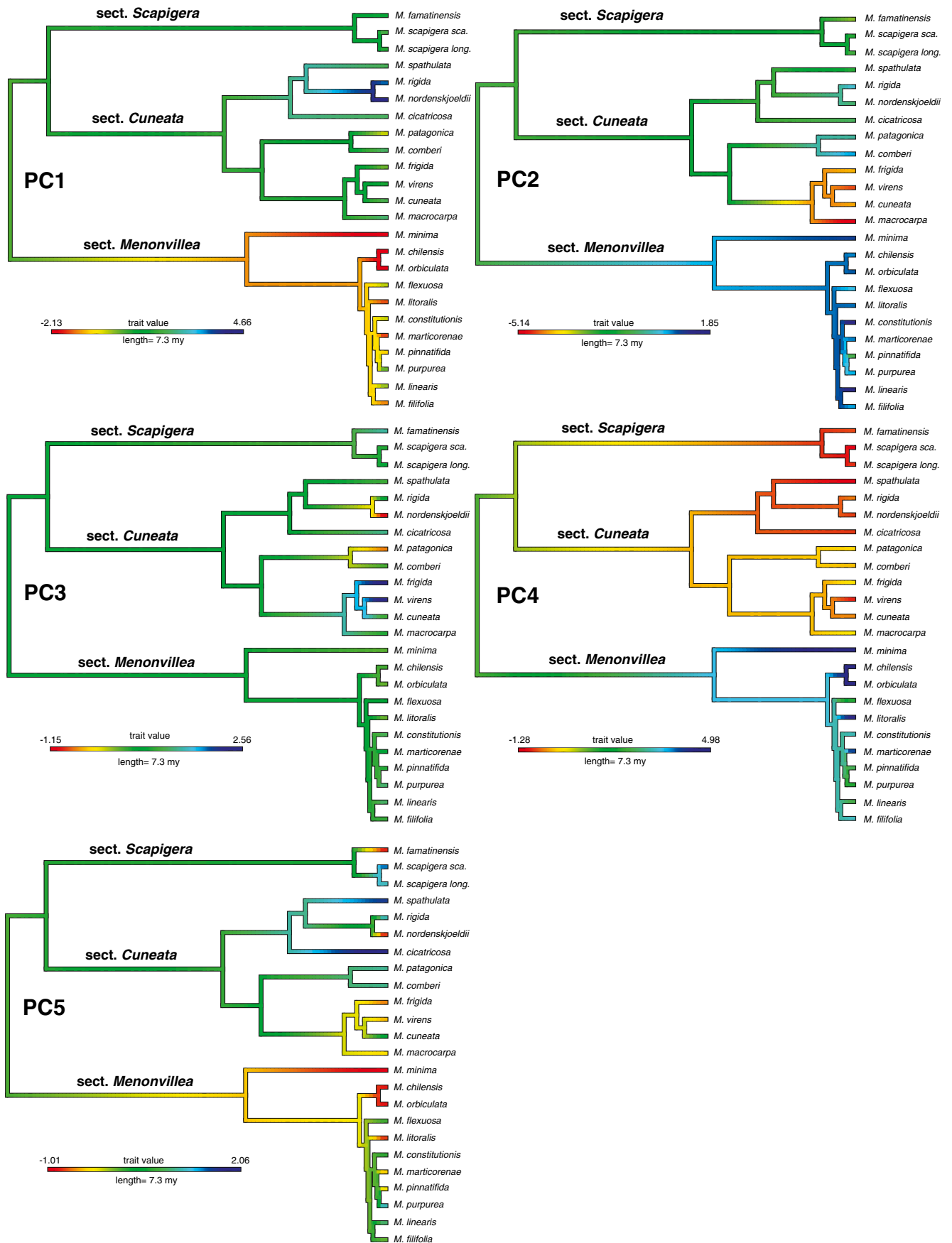
**Fig. 3** Maximum clade credibility species tree (MCCT) estimated from nuclear ribosomal ITS and three chloroplast DNA regions (*trnL-F*, *trnH-psbA*, *rps16 intron*) using the multispecies coalescent method implemented in \*BEAST, uncorrelated log-normal relaxed clock model, and two

secondary calibrations under normal prior distributions. *Shaded horizontal bars* show the 95 % highest posterior densities of divergence times and *stars* indicate nodes used for secondary calibration. Bayesian posterior support values >50 % are given at each node

climatic niche shift in *Menonvillea* occurred between the *Cuneata-Scapigera* clade and sect. *Menonvillea* throughout the Mid-Late Miocene, and it was associated with the two principal geographical distributions in the genus: the highlands of central-southern Andes and the Atacama Desert together with the Chilean Matorral. The climatic niche of sect. *Menonvillea* was primarily differentiated from niche of the *Cuneata-Scapigera* lineage by the higher aridity and PET, the higher temperatures (mainly in winter), and the smaller temperature annual range—seasonality (Fig. S1, Supplementary material). Species of this section are Chilean endemics mostly distributed between 27° S and 36° S at 0–2500 m elevations.

The Atacama Desert is characterized by its hyperaridity, with annual precipitation less than 100 mm, sporadic rain, and the regular formation of stratus clouds from September to December providing moisture for plant growth in the mountains and steppe coastal slopes (Rundel et al. 1991). Hyperaridity in this region is due to the lack of rainfall, but it is also related to the high PET (Houston and Hartley

2003). Arid to semiarid conditions of the Atacama Desert can be traced back to the late Jurassic (150 Mya) (Hartley et al. 2005). However, the hyperarid climate regime did not appear until Mid to the Late Miocene (15–10 Mya) as a consequence of the rain shadow originated by the Andean orogeny and the effects of the Humboldt current and the Pacific Anticyclone (Houston and Hartley 2003; Reich et al. 2009, Schlunegger et al. 2010). Based on the ages determined here and in Salaria et al. (2016), diversification of sect. *Menonvillea* occurred around the Late Miocene-Pliocene, when hyperaridification of this region was well established. The aridity decreased for species inhabiting the Chilean Matorral (central Chile from ~30° S to ~39° S), where precipitations increased from north to south. However, the climatic niche of sect. *Menonvillea* remained differentiated from the other sections essentially by the temperate Mediterranean climate (Armesto et al. 2007), with dry summers, lower temperature seasonality, and relatively higher temperatures in winter.



**Fig. 4** Ancestral state reconstructions of main climatic PCs for *Menonvillea*. Colors of branches reflect values of PC scores estimated by maximum likelihood on the MCCT. Variable loadings are indicated in Table 1

Climatic niches in sects. *Cuneata* and *Scapigera* were similar, with most of the species distributed between 1000 and 5300 m in the highlands of the central-southern Andes and occupying the Altoandina, Puneña, and Patagonica biogeographical provinces of Cabrera and Willink (1973). Regimens of these regions are characterized by the low temperatures, especially in winter, and a great temperature variation throughout the year. Aridity decreased from north to south and from east to west in the southern Andes, and the PET values are lower than in the Atacama Desert and the central Chilean Matorral. While most of the uplift of the southern Andes occurred in Early-Mid Miocene (~17–14 Mya) (Jordan et al. 2001; Blisniuk et al. 2005; Graham 2009; Encinas et al. 2013), the central Andes obtained more than half of their current elevation in the Late Miocene (~10–6 Mya) (Gregory-Wodzicki 2000; Graham et al. 2001; Garzzone et al. 2008; Leier et al. 2013). Basal diversification of the genus, as well as MRCA of the *Cuneata-Scapigera* clade, occurred in the Mid Miocene during the southern Andes orogeny and before the main uplift of the central Andes, as the latter was approximately half of the present altitude (Graham 2009). Nevertheless, diversification of sect. *Cuneata* took place in the Late Miocene, in agreement with the central Andean orogeny, and after the Mid Miocene climatic optimum (15–17 Mya) when the global climate became cooler (Zachos et al. 2001). On the other hand,

**Table 2** Mean Pagel's  $\lambda$  values and frequency of macroevolutionary models selected for each principal component, using 1000 posterior Bayesian trees and 1000 PC values randomly sampled from the predicted niche occupancy (PNO) profiles

PC	Pagel's $\lambda$	% model selection				
		BM	EB	WN	OU	OUM
PC1	0.45	0.1	0	20.1	11.2	<i>68.6</i>
PC2	0.59	0	0	16.2	14.5	<i>69.3</i>
PC3	<0.01	0	0	<i>64.9</i>	13.4	21.7
PC4	0.57	0	0	0.7	0.1	<i>99.2</i>
PC5	<0.01	0	0	<i>84.6</i>	8.6	6.8
PC1 (sim)	0.96	<i>58.8</i>	1.4	0.5	14.1	25.2
PC2 (sim)	0.97	<i>60.5</i>	0.9	0.5	13.1	25
PC3 (sim)	0.97	<i>60.9</i>	1.1	0.3	11.9	25.8
PC4 (sim)	0.97	<i>63.4</i>	1.1	0	12	23.5
PC5 (sim)	0.98	<i>62.4</i>	0.9	0.1	12	24.6

Most frequently selected models for each PC are shown in italics

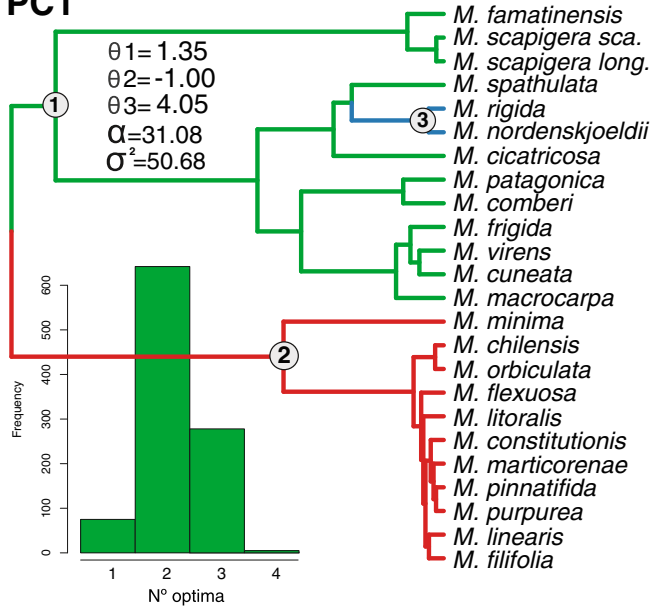
*BM* Brownian motion, *EB* early burst, *WN* white noise, *OU* Ornstein-Uhlenbeck with one adaptative peak, *OUM* Ornstein-Uhlenbeck with multiple adaptative peaks

diversification of sect. *Scapigera* in the Pleistocene was likely associated with the climatic fluctuations and the glacial cycles with alternate expansion and retreat of the ice shields (Haselton et al. 2002; Rabassa et al. 2011).

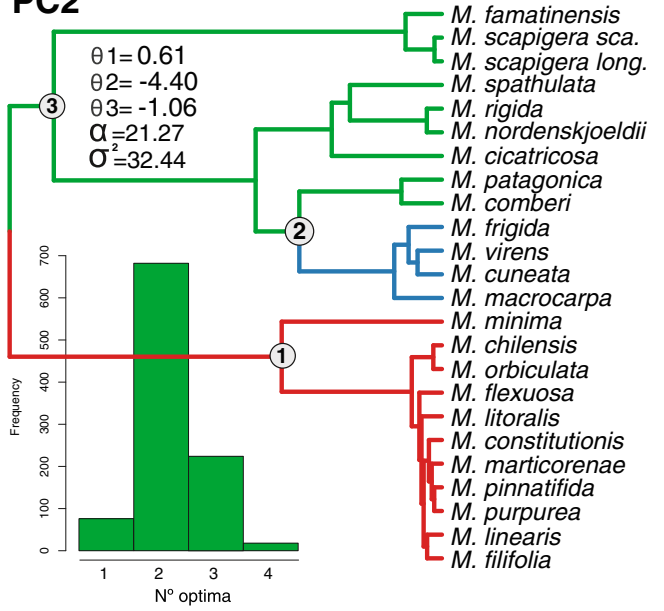
Niche evolution in *Menonvillea* was inconsistent with a Brownian motion process. Climatic components showing higher phylogenetic signal and separating the main niches (PC1, PC2, PC4) best-fitted an Ornstein-Uhlenbeck model, in which niche evolution within each main lineage (sect. *Menonvillea* and sects. *Cuneata-Scapigera*) was governed by a different adaptive optimum. Climatic differences between the two regions placed different constraints on niche evolution, suggesting the presence of niche conservatism in the history of these two lineages. Salariato et al. (2016) estimated the ancestral areas for the CES clade and reported that MRCA of sect. *Menonvillea* was likely distributed in the Atacama Desert with subsequent dispersals to the central Andes and the Chilean Matorral, while MRCA of sects. *Cuneata-Scapigera* resulted in the southern Andes. Afterwards, MRCA of sect. *Cuneata* originated in the southern Andes, with subsequent range expansion to the central Andes, while the MRCA of sect. *Scapigera* diversified in the central Andes. These biogeographic reconstructions, together with the divergence times obtained, suggest that the ancestral environmental conditions inhabited by the MRCAs of sect. *Menonvillea* and sects. *Cuneata-Scapigera* (lowland-arid areas and highland-cool areas, respectively) are consistent with the two different adaptive peaks recovered for these lineages.

Perhaps one of the major functional traits related to these selective regimens is the life form (annual vs. perennial). According to phylogenetic logistic regression, life history is strongly related with variables of PC1 (primarily dominated by the PET and aridity) and PC4 (mostly associated with the temperature annual range and seasonality). Specifically, our results indicated that the evolution of the annual habit is associated with higher aridity levels and lower annual temperature ranges, both of which conditions are principally presented in the distribution of sect. *Menonvillea*. Species in sect. *Scapigera* are all perennials, and only two out of ten species in sect. *Cuneata* (*Menonvillea comberi* and *M. patagonica*) are annual, while five of 11 species of sect. *Menonvillea* are annuals, with two perennial species (*Menonvillea orbiculata* and *Menonvillea pinnatifida*) that less frequently grow as annual (Salarinato et al. 2014). Annuals are common in desert floras and apparently are better adapted than perennials to lowland areas associated with arid conditions and fluctuation in water availability, while perennials are better adapted to cooler and wetter environments of alpine habitats (Cole 1954; Schaffer and Gadgil 1975). Ancestral life form reconstructions for the CES clade (Cremolobaeae-Eudemeae-Schizopetaleae) (Salarinato et al. 2016) showed that the perennial habit was favored in MRCA of the genus *Menonvillea* and sects. *Cuneata* and *Scapigera*, while in sect. *Menonvillea*,

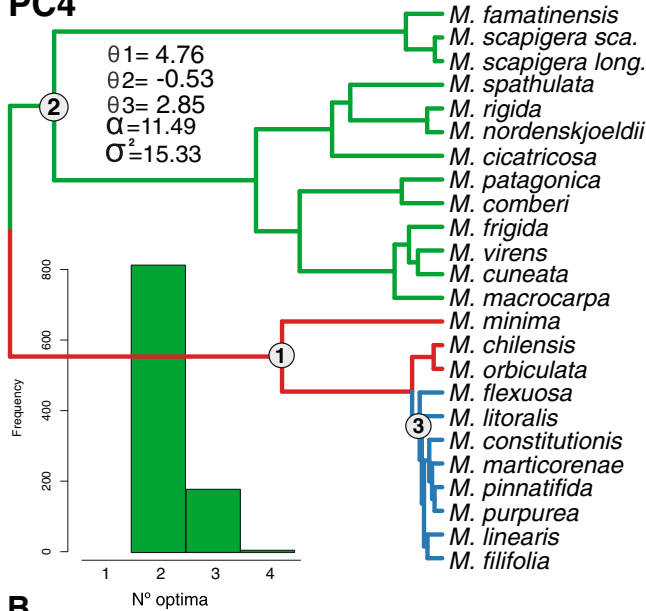
**A**  
**PC1**



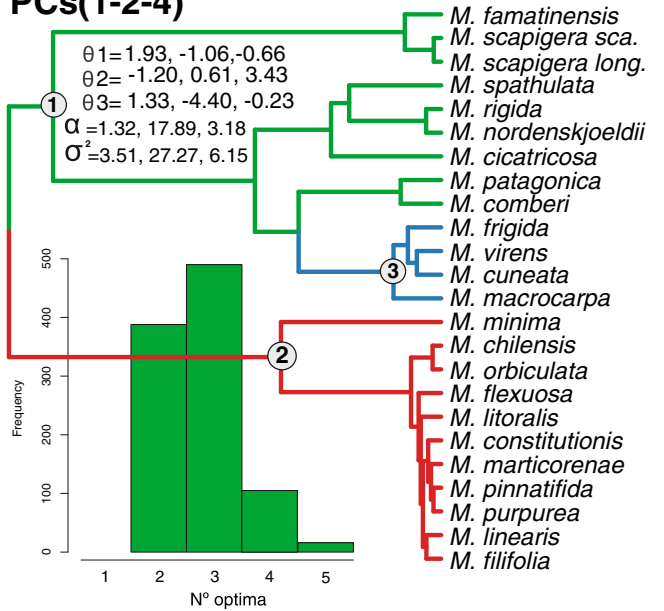
**PC2**



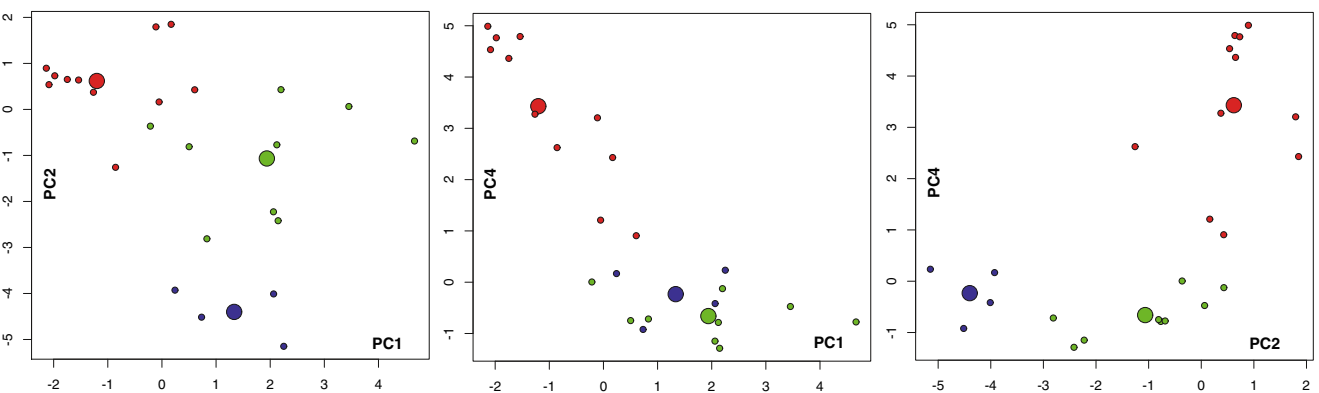
**PC4**



**PCs(1-2-4)**



**B**



**Fig. 5** SURFACE analyses of climatic PCs that best-fitted to a multiple OU model. **a** MCC trees showing different regimes painted onto the branches for analyses with PC1, PC2, PC4, and PC1 + PC2 + PC4 data. Numbers on branches indicate the order in which regime shifts were added. Histograms show frequency of the number of regimes selected over 1000 Bayesian posterior trees and PC values. Symbols:  $\theta$  = optimum trait value,  $\alpha$  = rate of adaptation to optima,  $\sigma^2$  = rate of stochastic evolution. **b** Trait values for each species (*small circles*) and estimated optima (*large circles*) using PC1 + PC2 + PC4 data, with regime colors matching those in the tree

reconstructions were ambiguous. However, their results suggest that the annual habit seems to have originated independently from the perennial one several times within the CES clade, specifically for *Menonvillea* in sect. *Menonvillea* and the *M. patagonica*-*M. comberi* clade of sect. *Cuneata*. While switches from annual to perennial habit have been linked to expansion into mountainous habitats (Drummond et al. 2012), perennial to annual life cycle transitions have been connected with range expansion from mountainous to arid lowland areas (Evans et al. 2005; Lo Presti and Oberprieler 2009; Özüdoğru et al. 2015). Additional adaptive traits linked to these main climatic niches can be the reduction of leaf surface area and the tomentose “arachnoid” trichomes in sect. *Menonvillea* (adaptations to arid environments), or the rhizome-like stems and the thick-woody caudices of sects. *Cuneata* and *Scapigera* (adaptations to alpine climate with rigorous winters) (Salariato et al. 2014). The results suggest that the main morphological specialization in *Menonvillea* is related with the climatic niche occupied by the species. The closely related tribe Eudemeae, which includes exclusively perennial species, diversified along the Andes without colonizing the desert regions or the adjacent Chilean Matorral, and its absence could be due to insufficient adaptation to hyperarid conditions (Salariato et al. 2015). On the other hand, the tribe Schizopetaleae, which includes both perennial and annual species, is distributed primarily in the Atacama Desert and Chilean Matorral, and its species are well adapted to grow under hyperarid conditions (Toro-Núñez et al. 2013).

In addition to the main niche differentiation between sect. *Menonvillea* and sects. *Cuneata*-*Scapigera*, secondary niche changes have occurred within the different sections. Niche

overlap analyses revealed that the species with more differentiated climatic niche dimensions were *Menonvillea purpurea* (sect. *Menonvillea*), *M. patagonica* (sect. *Cuneata*), and *M. scapigera* subsp. *longipes* (sect. *Scapigera*). *M. purpurea* has the southernmost distribution in its section, and it grows in the Chilean regions IV (Coquimbo), V (Valparaíso), Metropolitana de Santiago, VI (Libertador O’Higgins), VII (Maule), and IX (Araucanía), on rocky areas and cliffs at elevations between 50 and 2800 m (Salariato et al. 2014). Aridity in the southern distribution of this species is significantly lower than in the central and northern regions. Alternatively, *M. patagonica* is the only species of sect. *Cuneata* that grows at low to moderate elevations (500–2500 m) of west-central Patagonia in the Argentinean provinces Neuquén, Río Negro, and Chubut. In this area, aridity is higher than in the southern Andean slopes due to the rain shadow effect (Blisniuk et al. 2005). *M. scapigera* subsp. *longipes* (central Chile and Argentina) is characterized by inhabiting lower altitudes (1100–2500 m) in contrast to 2500–4500 m for other species of the section.

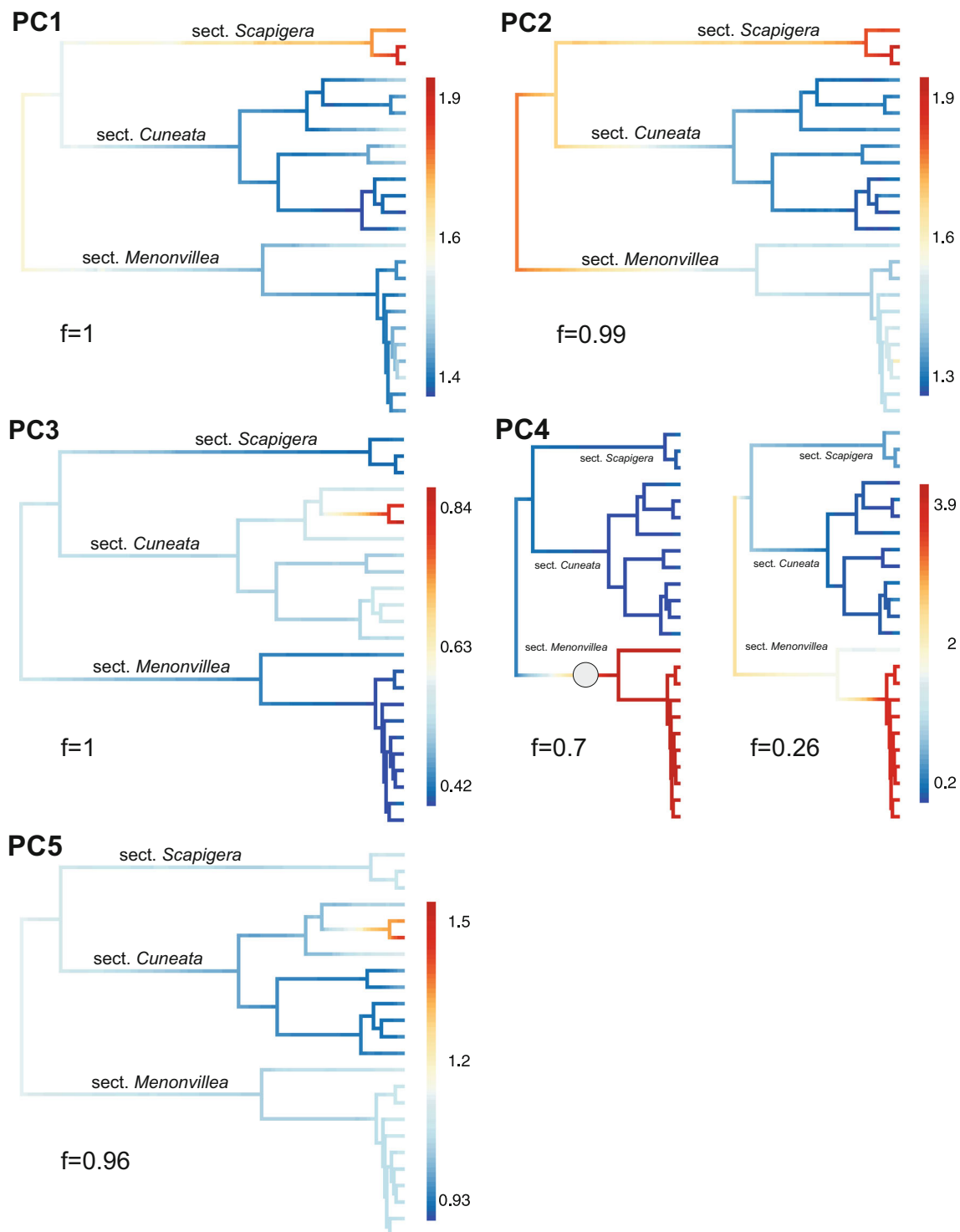
Evolution of the most influent climatic dimensions (PC1, PC2, PC4) also presents shifts within the sections. The aridity component (PC1) changes to the highest values (lowest aridity) in the *M. rigida*-*M. nordenskjoeldii* clade of sect. *Cuneata*, which is characterized by having a different adaptive regime from the remaining *Cuneata*-*Scapigera* clade. These two species grow in the southern part of the southern Andes, where precipitations are higher. They inhabit the Altoandina biogeographical province (Cabrera and Willink 1973), and *M. nordenskjoeldii* reaches Santa Cruz Province in Argentina and the XII Region (Magallanes y Antártica Chilena) in Chile to 53° S latitude. Although PC2, which is mainly related to the minimum temperatures and altitude, is primarily differentiated between sect. *Menonvillea* and sects. *Cuneata* and *Scapigera*, the clade *M. frigida*-*M. virens*-*M. cuneata*-*M. macrocarpa* was characterized by lower temperatures associated with higher altitudes, which is reflected by the different adaptive optimum recovered for this clade. These four species inhabit the central Andes of Argentina and Chile (~21° S–34° S) between 2000 and 5300 m and reach the highest altitude for the entire genus. Regarding the PC4, this component also presented variation within sect. *Menonvillea*, and it is mainly linked to the eastern species that live near the coast and the species that also grow in the west between the slopes of the Chilean coast range and the Andes.

The climatic PCs mainly dominated by precipitation seasonality/isothermality (PC3) and temperature of driest quarter/precipitation of warmest quarter (PC5) obtained the lowest phylogenetic signal (PS) and best-fitted to a white noise model. This would suggest that these climatic dimensions change independent of phylogenetic relationships (data with no covariance structure among species). However, Münkemüller et al. (2015) showed that when niches evolve according to an OU process with a single optimum and

**Table 3** Phylogenetic logistic regression using the life history of *Menonvillea* species (perennial vs. annual) as dependent variable, and the climatic PC as predictors

Predictor	AIC	$B_1$	$p$ value
PC1	24.15	<i>-0.84</i>	<i>0.02</i>
PC2	29.77	0.69	0.06
PC3	30.18	-1.25	0.10
PC4	25.06	<i>0.57</i>	<i>0.02</i>
PC5	34.95	-0.67	0.11

$B_1$  values correspond to the estimated slope, and results indicated in italics are significantly different from 0 ( $p < 0.05$ )



**Fig. 6** Phylorates plots for climatic niche evolution from the 95 % credible shift sets recovered by BAMM, with associated posterior probabilities ( $f$ ). Color at each point in time along the branches

denotes instantaneous rates of phenotypic evolution. Only credible shift set of PC4 presented a shift in the rate of climatic niche evolution (the gray circle indicates location of estimated rate shift)

moderate-high strength of selection ( $\alpha$ ), PS results in low values and the OU model can be misidentified as WN. Values of  $\alpha$  recovered for PC3 and PC5 (0.52 and 3.15, respectively), coupled with the low variance of these components within the *Menonvillea* distribution and that OU was the

second most frequently fitted model, seem to indicate that evolution in these variables follows a single optimum OU model characterized by an optimum associate for the entire genus. In PC3, precipitation seasonality (BIO15) and isothermality (BIO3) mean diurnal range relative to mean

annual range) presented little variation, mainly included within sect. *Cuneata* (Figs. 4 and S1C). The higher values were for the northernmost central Andean species *M. frigida* and *M. virens* (which are also distributed at the highest altitude ~3000–5300 m), and the lowest values were for the southernmost Andean species *M. nordenskjöldii* and *M. patagonica*. In the case of PC5, the values slightly varied within the three sections. The temperature of driest quarter (BIO9) presented temporal differentiation because the driest season in central Andes corresponds to winter, while in southern Andes and Atacama Desert/Chilean Matorral, it corresponds to summer. The other main variable, precipitation of warmest quarter (BIO18), usually presented lower values for the entire distribution of *Menonvillea* (Fig. S1E), corresponding with the South American Arid Diagonal (Chacón et al. 2012).

Except for the annual temperature range component (PC4), other climatic PCs did not register significant changes in the evolutionary rates. For these PCs, evolutionary rates were similar among different sections and over time. These results could be interpreted as support for PNC; however, evolutionary rates are useful for comparing the relative speed of niche evolution between clades and through time, but similar to phylogenetic signal, it cannot provide an absolute measure of PNC because it depends on the model of niche evolution assumed (Hunt 2012; Münkemüller et al. 2015). Alternatively, rate change detected in the temperature seasonality (PC4) for sect. *Menonvillea* would be associated with the east-west distribution discussed above and the high altitudinal variation within the section, where species such as *M. minima*, *Menonvillea chilensis*, *Menonvillea litoralis*, and *Menonvillea marticorenae* grow closely to the coast between 0 and 800 m, and others, such as *Menonvillea flexuosa*, *M. pinnatifida*, *M. purpurea*, and *Menonvillea linearis* also inhabit the slopes of the Chilean coast range and the Andes reaching between 2300 and 3700 m.

There is great debate on how to identify absolute presence or absence of PNC and the best methods to test it (Cooper et al. 2010; Münkemüller et al. 2015). Wiens (2008) and Wiens et al. (2010) indicated that a pattern expected under the BM model is sufficient to state the presence of PNC, while Losos (2008) suggested that there should be additional constraints, as strong stabilizing selection under OU models, to argue for PNC. Jara-Arancio et al. (2013) studied the climatic niche evolution in the genus *Leucocoryne* (Alliaceae), which presents a similar distribution to the species of sect. *Menonvillea* throughout the eastern Atacama Desert and central Chile. They reported for *Leucocoryne* two independent incursions into the Atacama Desert from central Chile in the Late Miocene and Pliocene, where the shifts were from wetter to the drier biome. While climatic variables in their analyses best-fitted one-optimum OU model, Jara-Arancio et al. (2013) concluded that climatic niche evolution in *Leucocoryne* is characterized by a low level of phylogenetic conservatism. From a quantitative perspective, our results suggest that climatic niche evolution in the genus

*Menonvillea* presents some degree of PNC, mainly within the lineages “sect. *Menonvillea*” and “sects. *Cuneata-Scapigera*” for variables of PC1, PC2, and PC4, and along the entire genus for those of PC3 and PC5. Nonetheless, climatic niche shifts are still present within the *Menonvillea* sections, underlining the dynamic nature of climatic niche evolution in this genus. Future comparisons across other Andean Brassicaceae and different plant groups could indicate whether or not this is a general pattern of the southern-central Andean lineages.

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**Data archiving** Data used in this paper are archived in TreeBase (<http://purl.org/phylo/treebase/phyloids/study/TB2:S18952>) and Dryad (doi:10.5061/dryad.c5271).

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