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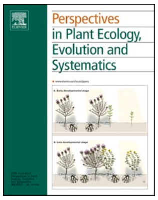

Similar diversification patterns in "sky islands": A comparative approach in lineages from *campo rupestre* and *campo de altitude*

Thuane Bochorny [a,f,*], Lucas F. Bacci [a,g], Marcelo Reginato [b], Thais Vasconcelos [c], Fabián A. Michelangeli [d], Renato Goldenberg [e]

[a] *Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, Universidade Estadual de Campinas, São Paulo 81530-900, Brazil*
[b] *Departamento de Botânica, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul 91501-970, Brazil*
[c] *Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI 48109, USA*
[d] *Institute of Systematic Botany, The New York Botanical Garden, Bronx, NY 10458-5126, USA*
[e] *Universidade Federal do Paraná, Departamento de Botânica, Centro Politécnico, Curitiba, Paraná 81531-970, Brazil*
[f] *Instituto de Pesquisa Jardim Botânico do Rio de Janeiro, DIPEQ, Rio de Janeiro 22460-030, Brazil*
[g] *Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA*

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ABSTRACT

Campo rupestre and *campo de altitude* are two highly diverse plant formations that are found in montane areas in eastern Brazil. These formations are associated with landscapes having different geological histories and are part of different phytogeographic domains under different climatic conditions. It is unclear however, whether lineages in each area have different diversification dynamics and climatic niche evolution. Here we analyze biogeographical history, climatic niche evolution and diversification dynamics of the Cambessedesieae (Melastomataceae), a clade with many endemics in each formation. We use a time-calibrated phylogenetic tree alongside carefully curated distribution points to estimate ancestral ranges and compare diversification dynamics and climatic niche evolution across the group, using models of geographical range evolution (BioGeoBEARS), diversification dynamics (BAMM, GeoSSE) and trait-evolution (l1ou). Our results show that Cambessedesieae is a relatively old (Early Eocene, 48 Mya) clade in comparison to other lineages of similar distribution. An initial split between lineages that are mainly endemic to either formation happened earlier, but, surprisingly, these two lineages have similar diversification dynamics and climatic niche evolution. Shifts in climatic regimes in extant lineages occurred more recently and are not associated with changes in diversification rates. Overall, we show that lineages endemic to montane areas and having different geological histories and in different climatic and phytogeographic contexts can have similar diversification patterns.

1. Introduction

Montane vegetation formations worldwide often have exceptional species richness and endemism, and so are the subjects of numerous studies on diversification dynamics (reviewed by Rahbek et al., 2019). Most studies focus on aspects of montane landscapes that can accelerate speciation and increase local endemism, such as the altitudinal gradient and that mountaintops create continental archipelago-like systems (also known as "sky-islands") that impose frequent barriers to gene flow (Madriñán et al., 2013; Merckx et al., 2015; Antonelli, 2015; Hoorn et al., 2018). Exceptional rates of speciation have also been linked to the process of orogeny itself (Hughes and Eastwood, 2006, but see Vasconcelos et al., 2020). Regardless of the age of the landscape, cyclical changes in climate are often thought to be responsible for creating opportunities for isolation and speciation over long periods of time in montane regions (e.g., Flantua et al., 2019; Muellner-Riehl et al., 2019; Dantas-Queiroz et al., 2021; Rull, 2005; Rull and Vegas-Villarrúbia, 2020).

The mountains of eastern Brazil are good study-systems for testing the role of geological age and climatic niche in the diversification of their endemic lineages. These tropical mountains of lower altitudes (between 900 and 3000 m a.s.l), or tropical snow-free mountains,

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* Corresponding author at: Programa de Pós-Graduação em Biologia Vegetal, Departamento de Botânica, Universidade Estadual de Campinas, São Paulo 81530-900, Brazil

E-mail addresses: tbochorny@gmail.com (T. Bochorny), lucasfbacci@gmail.com (L.F. Bacci), mreginato@ufrgs.br (M. Reginato), thais.nogales@gmail.com (T. Vasconcelos), fabian@nybg.org (F.A. Michelangeli), renato.goldenberg@gmail.com (R. Goldenberg).

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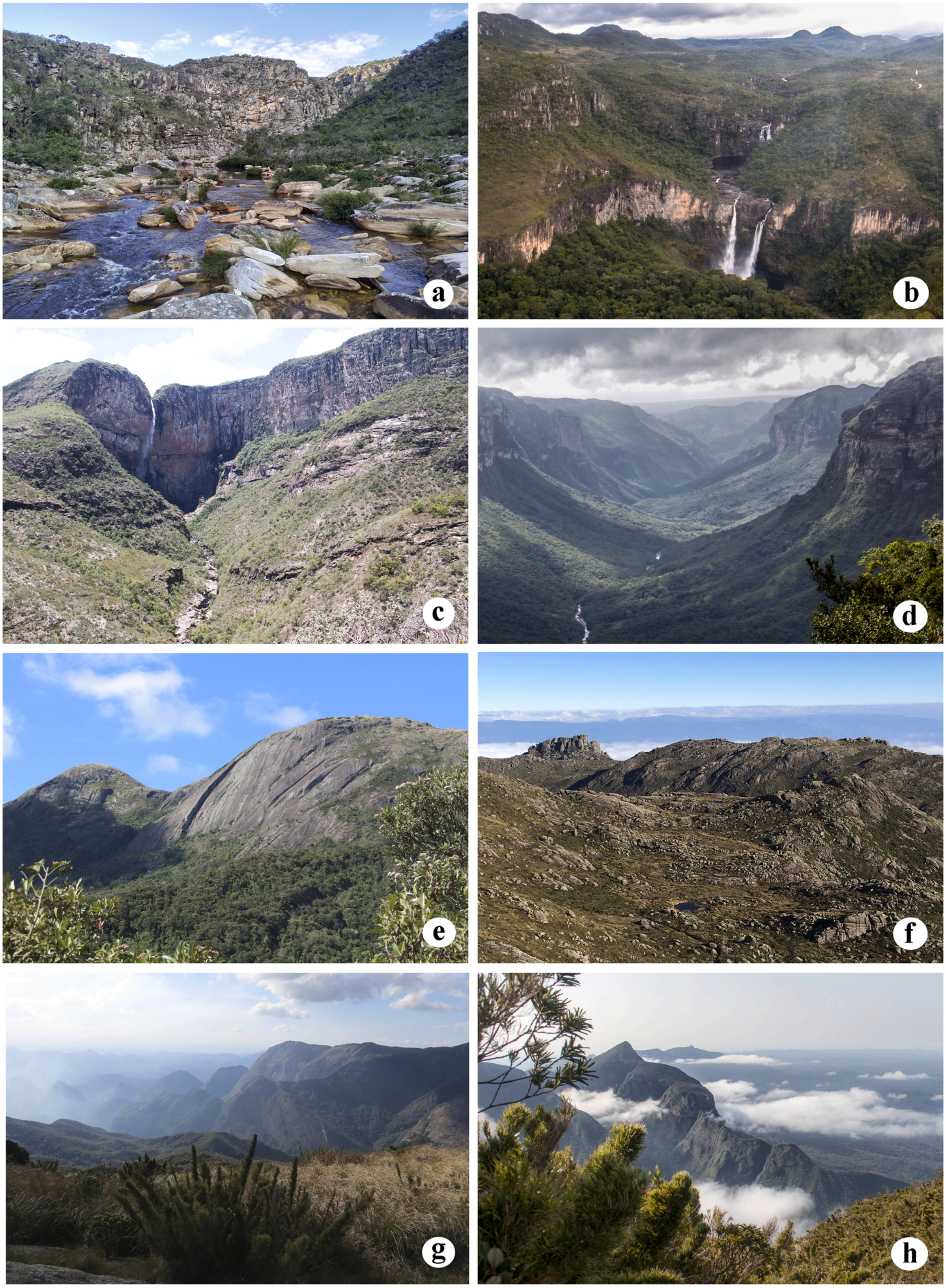

Fig. 1. Natural landscapes of *campos rupestres* and ***campos de altitude* in eastern Brazil.** A. Typical view of the brazilian rocky outcrops of *campo rupestre* in the Serra do Cipó National Park, Minas Gerais (November/2019). B. Quartzite-sandstone outcrops of *campo rupestre* in Chapada dos Veadeiros National Park, Goiás (January/ 2015). C, Serra do Tabuleiro State Park, Minas Gerais (November/2019) D. Chapada Diamantina National Park, Bahia (July/2019). E. Typical view of Brazilian granitic outcrops of *campo de altitude* in the Serra dos Órgãos National Park, Rio de Janeiro (February/2016). F. Itatiaia National Park, Rio de Janeiro (July/2017). G, H. Pico Paraná State Park, Paraná (September/2019).
(Photos by Thuane Bochorny).

exhibit naturally fragmented landscapes formed by open grassland (*campo*) islands in a forest or savanna matrix (McCormack et al., 2009). Two main montane open grassland formations are recognized here: *campo rupestre* and *campo de altitude* (Vasconcelos, 2011; BFG, 2021; Fig. 1). *Campo rupestre* is a low-growing, mostly herbaceous or shrubby vegetation on stony soils (Giulietti and Pirani, 1988; Silveira et al., 2016; Colli-Silva et al., 2019) found in the Espinhaço range and other patches in the Brazilian highlands. In its southern portion, the Espinhaço range is at the intersection of two biodiversity hotspots, the Cerrado and the Atlantic Forest (Silveira et al., 2016). In these areas, the more humid eastern slopes are covered by semi-deciduous Atlantic Forests, while the drier western and northern slopes comprise Cerrado and Caatinga domains. Areas of *campo rupestre* are among the most ancient landscapes on earth, and date from the Gondwana formation, nearly 640 Ma (Giulietti and Pirani, 1988; Pennington et al., 2000; Simon et al., 2009; Vasconcelos, 2011). Although this mountain system has long been tectonically stable, extreme weathering (Silveira et al., 2016) has resulted in constant landscape changing over time.

Campo de altitude comprises patches of high-altitude grasslands that are completely within the Atlantic Forest domain. Despite sharing some floristic elements with the *campo rupestre*, the *campo de altitude* is distinct in its geological formation (Benites et al., 2007; Alves and Kolbek, 2010) and the vegetation has closer affinities with the Páramos in the Andes (Safford, 2007). The *campo de altitude* occurs in areas that are generally associated with granitic or gneissic rocky outcrops usually found above 2000 m of elevation that occur mostly in the Mantiqueira and Serra do Mar ranges in south-eastern Brazil. These ranges originated during the Tertiary Period with large-scale uplifting in the Late Eocene or Oligocene (Giulietti et al., 1997; Safford, 1999; Caiafa and Silva, 2005; Vasconcelos, 2011), and so is considerably younger than the montane systems where *campo rupestre* occurs.

Although the floristics of the *campo rupestre* and the *campo de altitude* have been relatively well studied (Fiaschi and Pirani, 2009; Fiaschi et al., 2016), a lingering question is whether lineages in these two tropical montane systems have different diversification dynamics. The age and speed of diversification of montane lineages is often linked to the geological history of the mountain range itself, with faster diversification expected to be found in younger montane systems (e.g. Madriñán et al., 2013; Merckx et al., 2015). However, there is a gap in studies comparing the diversification dynamics of closely related lineages that are endemic to montane systems of different geological ages. Similarly, climate has been for long considered an important predictor for patterns of species distribution and diversification (Stebbins, 1974), but only now is it statistically possible to combine climatic variables and species diversification dynamics in a proper analytical framework (e.g. Vargas et al., 2020; Suissa et al., 2021).

Here, we compare diversification patterns in these open montane formations of eastern South America. Given their varying geological ages and climates, we predict that those lineages that are endemic to either *campo rupestre* or *campo de altitude* will have different diversification dynamics. Thus, we provide a time-calibrated overview of the evolutionary history of the diverse clade Cambessedesieae (Melastomataceae), with 69 species in three genera: *Cambessedesia* DC., *Huberia* DC. and *Merianthera* Kuhlm. (Bochorny et al., 2019). The evolutionary history of Cambessedesieae is strongly associated with the mountain ranges of eastern South America. The clade has two main lineages, one (with the greatest diversity) in the *campo rupestre* and the other in the *campo de altitude*, with most species having a micro-endemic distribution pattern (Bochorny et al., 2019). We use the evolutionary history of the Cambessedesieae to answer two main questions of the diversification dynamics of lineages endemic to either *campo rupestre* or *campo de altitude*: (1) Given their differences in climate and geology, do endemic lineages differ in their diversification patterns by formation? (2) And, are shifts in climatic niche evolution also associated with those diversification patterns? To answer these questions, we determine diversification rates, clade age, and climatic regimes associated with Cambessedesieae lineages.

Table 1
Details of secondary calibrations for the tribe Cambessedesieae and the genera *Cambessedesia*, *Huberia* and *Merianthera*.

Phylogenetic hypothesis	Clade	Minimum age (Mya)	Reference	Prior, mean (stdev)
Cambessedesieae tree	Root	46.3	Bacci et al. (2021)	Normal, 46.3 (1.0)
	Cambessedesieae	41.3	Bacci et al. (2021)	Normal, 41.3 (6.0)
	Huberia + *Merianthera*	36.3	Bacci et al. (2021)	Normal, 36.3 (4.0)
	Cambessedesia	23.2	This paper	Normal, 23.2 (6.0)
	Huberia	20.4	This paper	Normal, 20.4 (4.6)
	Merianthera	10.3	This paper	Normal, 10.3 (4.8)

2. Methods

2.1. Taxon sampling

The tribe Cambessedesieae comprises three genera: (1) *Cambessedesia* with 25 species that occur mostly in the *campo rupestre* of the Espinhaço range (Fidanza, 2009; Bochorny et al., 2019); (2) *Huberia* with 37 species, most of them from the *campo de altitude* of Serra do Mar and Serra da Mantiqueira (Baumgratz, 1999; Bochorny and Goldenberg, 2019) and four species occurring in the Andes of Ecuador and Peru at elevations between 1200 and 3350 m (Baumgratz, 2004); and (3) *Merianthera,* which comprises seven species largely endemic to granitic and gneissic inselbergs on rocky outcrops in the Atlantic Forest and two species in the *campo rupestre* of Minas Gerais state (Goldenberg et al., 2012).

2.2. Phylogenetic and dating analysis

To investigate the time of origin and diversification of the Cambessedesieae clade we relied on molecular dating. We used the molecular dataset in Bochorny et al. (2019) to infer a calibrated chronogram using 56 taxa of the 69 accepted species from the three genera of Cambessedesieae, including 81 % of the species in this clade. Phylogenetic analyses were based on six molecular markers: two nuclear ribosomal loci (the internal and external transcribed spacers, nrITS and nrETS), three plastid spacers (*atpF-atpH*, *psbK-psbI* and *trnS-trnG*) and a segment of a low-copy nuclear gene (*waxy*) – detailed in Supplementary material: Appendix 1, 2.

Phylogenetic analyses used Bayesian inference (BI) as implemented in the software BEAST v2.5.0 (Bouckaert et al., 2014) through CIPRES Science Gateway (Miller et al., 2010). The chronogram was calibrated using divergence times estimated for Cambessedesieae and close relatives from Bacci et al. (2021). Briefly, Bacci et al. (2021) estimated divergence times for a clade comprising the closely related tribes Cyphostyleae, Cambessedesiae and Bertolonieae. Two fossil records were used, both within Melastomataceae. The first one is a leaf fossil used to offset the most recent common ancestor (MRCA) of the family (except tribe Kibessieae). The second is a seed fossil used as a Melastomateae and Rhexieae crown prior (Berger et al., 2016). The inference of Bacci et al. (2021) included only 16 species of Cambessedesieae (vs. 56 included here), but we consider that to be a reliable estimate for the divergence times in this clade of Melastomataceae. Therefore, we followed a secondary calibration approach with three normally distributed priors set at the crown of Cambessedesieae and at the crown of each major clade (i.e. *Cambessedesia*, *Huberia* + *Merianthera* clade) with parameters based on the analysis of Bacci et al. (2021) (Table 1).

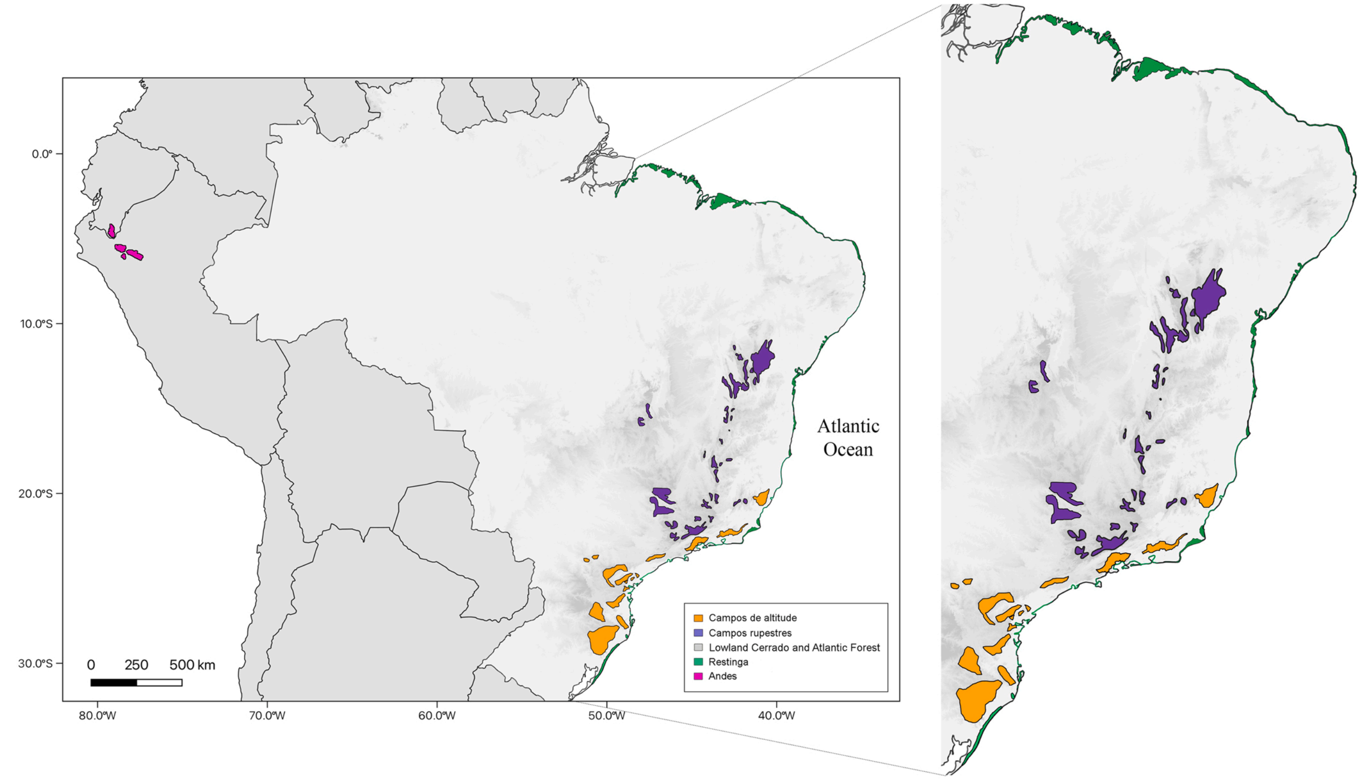

Fig. 2. Map of the biogeographical areas of this study. Biogeographical regions were coded by the distribution of Cambessedesieae (Melastomataceae).

The molecular clock prior was set to lognormal uncorrelated, the tree prior was set to Yule process, and the partitions were set accordingly. We ran three independent analyses of 100 million generations each, sampling every 5000 generations. Convergence was assessed in Tracer v.1.5 (Rambaut and Drummond, 2013), and runs were considered satisfactory with ESS values greater than 200. The stable posterior distributions of the independent runs were combined using LogCombiner v.1.7.5 and summarized using TreeAnnotator v.1.7.5 (Drummond et al., 2012). The consensus tree and associated posterior probabilities (PP) were generated using the standard burn-in of 10 % and visualized in FigTree v.1.4.0 (Rambaut, 2014).

2.3. Historical reconstructions

To analyze the historical biogeography of the group, a database of geographic distribution based on specimens of all sampled species was compiled using herbarium records and online data available through the biodiversity portals speciesLink (http://splink.cria.org.br/) and GBIF.org (2021). Distribution points were carefully curated and only specimens identified or reviewed by taxonomists of the group were considered. Distributional outlier records ("taxonomic suspicious") and specimens with coordinates matching the centroid of municipalities were considered inaccurate and deleted. Our final database contains 1125 occurrence points. We used the final database of reliable occurrence points to score a presence/absence matrix to be used as input in the historical biogeography analysis and to analyze shifts in climatic niche through time (see *Climatic Regimes* section below).

Biogeographical areas chosen for the analysis were derived from the literature (Fiaschi and Pirani, 2009; Fiaschi et al., 2016), as well as distribution patterns observed in other lineages (e.g. Asteraceae: Schilling et al., 2000, Melastomataceae: Fritsch et al., 2004, Apocynaceae: Rapini et al., 2007, Melastomataceae: Reginato et al., 2016). We coded the geographical range as: A - *Campos de altitude*, B - *Campos rupestres*, C - Lowland Cerrado and Atlantic Forest (considered here as the areas below 900 m elev., excluding restingas), D - Restingas, and E - Andes. (Fig. 1 indicates *campos rupestres* and *campos de altitude* in the mountains of eastern Brazil, Fig. 2 indicates coded biogeographical regions).

Ancestral range estimation was performed in R using the package BioGeoBEARS (Matzke, 2013). This package implements several models of geographic range evolution in a likelihood framework, while allowing to test which model best fits the geographical and phylogenetic data under analysis (Matzke, 2013). The species in our phylogenetic hypothesis were coded as present/absent in the biogeographical areas selected and this matrix was used for the ancestral range estimation. The Dispersal-Extinction Cladogenesis (DEC, Ree, 2005; Ree and Smith, 2008) and DEC+J (with the addition of a free parameter that accounts for founder-event speciation ("j") – Matzke, 2013) models were implemented. Both models have two free parameters ("d" and "e") specifying the rate of “dispersal” (range expansion) and “extinction” (range contraction) along the branches of the phylogeny, although with different assumptions at cladogenesis events (details in Matzke, 2013). All models were compared using the Akaike Information Criterion (AIC).

2.4. Diversification analyses

To test whether diversification dynamics in lineages distributed in the *campo rupestre* and *campo de altitude* are distinct, two approaches were taken. First, we used the Bayesian Analysis of Macroevolutionary Mixture (BAMM) to estimate speciation and extinction rates and to identify shifts in diversification rates (Rabosky et al., 2014). BAMM estimation of diversification rates through time without requiring a specific hypothesis about how rates differ among lineages. We accounted for incomplete taxon sampling by applying clade specific sampling fractions in each of the three clades: *Cambessedesia* (0.83), *Huberia* (0.73) and *Merianthera* (1.0). We ran BAMM with four reversible jump MCMC chains, each for five million generations. ESS values (> 200) were used to assess convergence. The posterior distribution was used to estimate the configuration of the diversification rate shifts, and alternative diversification models were compared using Bayes factors. Results were analyzed and plotted using the R package BAMMtools 2.0.2

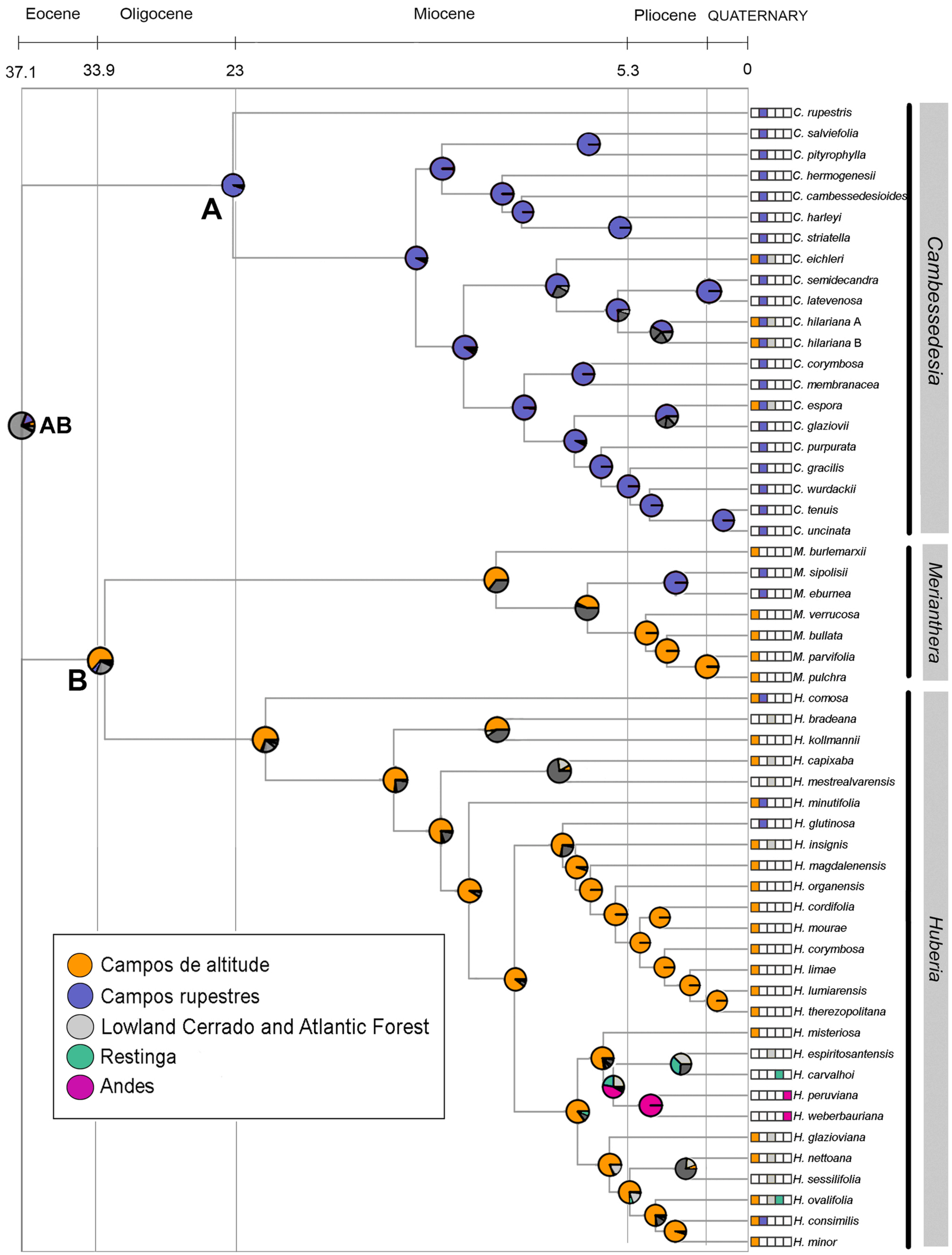

Fig. 3. Time-calibrated phylogeny of Cambessedesieae (inferred from *atpF-atpH*, ETS, ITS, *psbK-psbL*, *trnStrnG* and waxy molecular regions), ancestral range estimations and area coding. Pie charts on nodes represent ancestral areas derived from the BioGeoBEARS analysis and color code follows the legend on the map: A - Campo rupestre, B - Campo de altitude, C - Lowland Cerrado and Atlantic Forest, D - Restingas, E - Andes. Colored squares on tips represent the occurrence of that species in the delimited geographical area. Clades indicated as follows: A. *Cambessedesia* clade; B. *Merianthera* clade and C. *Huberia* clade.

Table 2
Model fit comparison of the ancestral range reconstruction of Cambessedesieae. LnL = log likelihood; n = Number of parameters. The best model in bold.

Model	LnL	n	d	e	J	x	n
DEC	-96.310	2	0.377	1e-12	0	0	0
DEC+j	**-93.341**	**3**	**0.310**	**1e-12**	**0.013**	**0**	**0**

(Rabosky et al., 2014).

Second, we used a method that explicitly test the hypothesis that dynamics of speciation and extinction are different between two selected areas. To that end, we used the Geographic State Speciation and Extinction: GeoSSE model (Goldberg et al., 2011) implemented in the "diversitree" package of the software R (R Core Team, 2018). The GeoSSE model combines features of the constant-rate birth-death model with a three-state Markov model and allows estimating speciation, extinction, and dispersal parameters across two geographical regions. For this analysis, we pruned the phylogeny so that only species occurring either on *campo rupestre*, *campo de altitude* or both were sampled, allowing us to examine whether related lineages at high-elevation bands experienced different diversification dynamics.

2.5. Climatic regimes

Climatic variables for each species were extracted from 19 bioclimatic layers of the WorldClim data set version 1.0 (Hijmans et al., 2005). Records were intersected to the layers using the R package raster (Hijmans, 2013) and the mean of each species was used in a principal component analysis (PCA) to convert a set of correlated climatic variables into a set of values of uncorrelated variables. We used the first three principal components of the climatic PCA and the phylogenetic hypothesis for the clade to identify shifts in climatic regime and test how conserved or labile is the climatic niche evolution in the group. We used a lasso-based method l1ou (Khabbazian et al., 2016; R package ℓ1ou) to detect possible climatic regime shifts within the clade. This method selects the number of shifts in phenotypic optima and their convergence under Ornstein–Uhlenbeck (OU) model on trees (Khabbazian et al., 2016). Both extraction of climatic values and the implementation of the ℓ1ou method were performed through the software R (R Core Team, 2018), using functions from several packages, such as ape (Paradis and Schliep, 2018), phytools (Revell, 2012), raster (Hijmans, 2018), maptools (Bivand and Lewin-Koh, 2017), rgeos (Bivand and Rundel, 2017) and phyloch (Heibl, 2008).

3. Results

3.1. Phylogenetic and dating analysis

Absolute age estimation yielded a stem age for Cambessedesieae in the Early Eocene, around 48.7 Mya (95 % HPD: 37–62; Supplementary material; Appendix 3). The age estimates for the most recent common ancestors (crown nodes) of each of the major lineages of Cambessedesieae were found to be slightly younger than the priors used in the calibration analyses. The crown node of Cambessedesieae is placed in the Late Eocene, around 37.1 Mya (95 % HPD = 36–44) (Fig. 3). The *Merianthera* + *Huberia* clade diverged from each other in the Early Oligocene, around 33.2 Mya (95 % HPD: 26–40). The crown group of *Cambessedesia* originated in the Oligocene-Miocene border, around 23.2 Mya (95 % HPD: 18–28). *Huberia* diversified around 20.4 Mya (95 % HPD: 15–25) and *Merianthera* is the most recent clade, diversifying around 10.9 Mya (95 % HPD: 7–15). Most of the cladogenic events that resulted in modern species are dated back from the Pliocene (between 5 and 2.5 Mya) and Miocene (between 23 and 5Mya).

3.2. Historical reconstruction

We compared the fitness of two biogeographical models (DEC and DEC+J), given the phylogenetic hypothesis and the distribution data of Cambessedesieae (log-likelihoods, number of free parameters, and AIC values in Table 2). The model with the best fit was the DEC with the addition of the founder effect (J) as a free parameter (DEC+J; Table 2). The ancestral area of Cambessedesieae was estimated to be a widespread range encompassing *campo rupestre* and *campo de altitude* with an initial vicariant event separating the *Huberia* + *Merianthera* clade and *Cambessedesia* (see Fig. 3). The *Cambessedesia* clade originated in the *campo rupestre*, with most of its cladogenetic events in this region and a few recent range expansions of widespread species to other areas. Only three *Cambessedesia* species present a wide distribution (e.g. *Cambessedesia eichleri*, *C. espora* and *C. hilariana*); all three occurring in *campo rupestre*, *campo de altitude* and in the low altitude areas surrounding those mountains.

The *Huberia* + *Merianthera* clade originated in the *campo de altitude*, with recent range expansions to the low areas of Cerrado and Atlantic Forest and *campo rupestre* (Fig. 3). Four species in this clade (*Huberia comosa*, *H. consimilis*, *H. glutinosa* and *H. minutifolia*) later dispersed back to the *campos rupestres*. Most range expansions or shifts to areas of lowland Cerrado and Atlantic Forest are dated from the Miocene-Pliocene. One single event of dispersal to the Andes was detected around 5 Mya. The Andean clade includes *Huberia peruviana* and *H. weberbaueriana*, which are restricted to the "cloud forests" of the Andes of Peru and Ecuador. Also, two species have dispersed to the lowland "restinga" of eastern Brazil in the Atlantic Forest (*Huberia carvalhoi* and *Huberia ovalifolia*). The *Merianthera* clade originated in the *campo de altitude* with a posterior expansion of a minor clade (*Merianthera sipolisii* + *Merianthera verrucosa*) back to the *campo rupestre*.

3.3. Diversification analyses

The diversification analysis of BAMM shows that net diversification rates are very similar across Cambessedesieae and indicates that no particular clade underwent a significant shift in diversification rates. The best shift configuration (Fig. 4, A) shows diversification rates increasing towards the present (0.33 species*mya^{-1} at the root vs. 0.42 species*mya^{-1} near the present). Conversely, the GeoSSE analysis comparing diversification and dispersal dynamics between the *campo de altitude* and the *campo rupestre* showed highly overlapping rates for all parameters (Fig. 4, B, C, D and, E). Model comparison based on AIC indicates that none of the rates are significantly different between areas. The fit of each model evaluated in the GeoSSE analysis is provided in Table 3.

3.4. Climatic regimes

The climatic PCA summarized 85.7 % of the variation in the three first components (PC1 = 39.9 %, PC2 = 25.5 % and PC3 =20.3 %). The variables contribution on each axis are given in Table 4 and Fig. 5 with the most important variables mainly related to precipitation seasonality, precipitation of warmest quarter and isothermality (a day-night and summer-winter oscillation temperatures). Climatic regime analysis in Fig. 5 A shown *Cambessedesia* clade with one climatic shift in a small subclade (*C. purpurata*, *C. gracilis*, *C. wurdackii*, *C. uncinata* and *C. tenuis*), which is endemic to the northern portion of the Espinhaço range. No climatic shifts were detected within *Merianthera*, whereas six different climatic shifts were higlighted within the *Huberia* clade, belonging to *H. insignis*, *H. carvalhoi*, *H. sessilifolia*, *H. ovalifolia* and the *H. cordifolia* + *H. mourae* and *H. peruviana* + *H. weberbaueriana* clades. Among those, only the shifts detected in *H. insignis* and *H. ovalifolia* were convergent. The three first components of the climatic PCA are plotted and color-coded according to the regimes in Fig. 5 A (Axis1, Axis2 and Axis3). Overall, climatic shifts do not coincide with changes in diversification

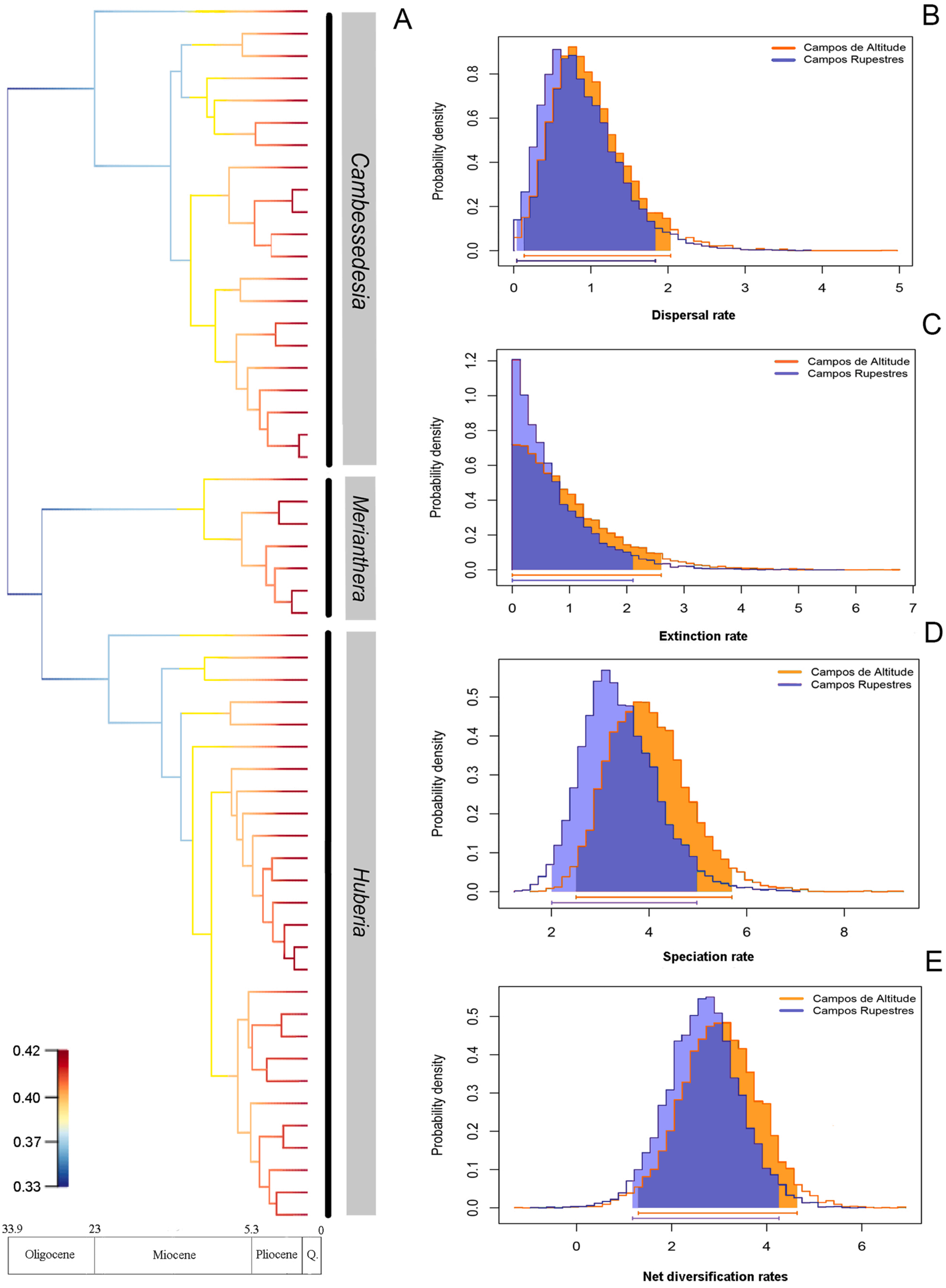

Fig. 4. A. Bayesian Analysis of Macroevolutionary Mixture (BAMM) showing diversification rates through time in Cambessedesieae. Posterior probability distributions for GeoSSe model in *campo de altitude* and *campo rupestre*. B. Dispersal rates; C. Extinction rates; D. Speciation rates and E. Net-diversification rates.

Table 3
Results of GeoSSE analysis of geographic diversification of Cambessedesieae in high altitude areas of "*campos de altitude*" and "*campos rupestres*". Eq.spec, eq.ext and eq. disp indicate models where equal rates (of speciation, extinction and dispersal, respectively) are expected between areas.

Model	Df	lnLik	AIC	ChiSq	Pr (>|Chi|)
full	7	21.653	57.307	NA	NA
eq.spec	5	22.090	54.181	0.874	0.645
eq.ext	6	21.774	55.549	0.241	0.622
eq.disp	6	21.661	55.322	0.015	0.901

Table 4
Climatic PCA loadings of the three first principal components (PC1, PC2 and PC3). Variables with less than 0.1 loadings value were omitted. Highest values for each PC in bold.

Climatic variable	PC1	PC2	PC3
Bio1: Annual Mean Temperature	–	0.190	–
Bio2: Mean Diurnal Range	–	0.291	0.161
Bio3: Isothermality	–	–	**0.366**
Bio4: Temperature Seasonality	0.194	–	–
Bio5: Max Temperature of Warmest Month	–	0.303	–
Bio6: Min Temperature of Coldest Month	–	–	–
Bio7: Temperature Annual Range	0.160	0.298	–
Bio8: Mean Temperature of Wettest Quarter	–	0.216	–
Bio9: Mean Temperature of Driest Quarter	–	0.103	–
Bio10: Mean Temperature of Warmest Quarter	–	0.206	–
Bio11: Mean Temperature of Coldest Quarter	–	0.144	–
Bio12: Annual Precipitation	0.214	–	–
Bio13: Precipitation of Wettest Month	0.246	0.238	–
Bio14: Precipitation of Driest Month	–	–	–
Bio15: Precipitation Seasonality	0.107	**0.365**	0.183
Bio16: Precipitation of Wettest Quarter	0.246	0.226	–
Bio17: Precipitation of Driest Quarter	–	–	–
Bio18: Precipitation of Warmest Quarter	**0.292**	0.127	–
Bio19: Precipitation of Coldest Quarter	–	–	–

dynamics in the group.

Climate niche regimes estimated for *Cambessedesia*, *Huberia* and *Merianthera* are shown in Fig. 5B. Overall, the three genera overlap in the climatic PCA, where *Merianthera* and *Huberia* have the greatest similarity, and *Cambessedesia* shows the greatest spread. Climatic regimes in Cambessedesieae were detected late in the history of the group with six shifts from the background (climatic regime in gray, here named background due to being the regime detected for the most recent ancestor of Cambessedesieae) to different regimes. The influence of each climatic variable on climatic space of Cambessedesieae is summarized in Fig. 5 C.

4. Discussion

4.1. Spatio-temporal evolution of Cambessedesieae

Cambessedesieae is a relatively old lineage relative to other tribes of Melastomataceae (Reginato et al., 2020), with origin estimated in the Early Eocene (48.7 Mya). An early split in the lineage (Late Eocene) divided the group into two clades with distinct biogeographical histories: one that diversified mainly in the *campo rupestre* and the other mainly in the *campo de altitude* (Fig. 3). After this initial split, radiation in both clades, giving origin to extant species, were predominantly restricted to each of those areas, with only recent dispersal to other regions. The timing of this first split roughly corresponds to the cooling phase during the Late Eocene-Early Oligocene (29–37 Ma) that climaxed with the Terminal Eocene Event (TEE), when major geological reorganization, such as the establishment of the Antarctic Circumpolar Current, caused changes in vegetation composition worldwide (Meseguer et al., 2013).

Our biogeographical analysis suggests that Cambessedesieae lineages tended to remain restricted to montane areas through their entire evolutionary history. Disjunct clade distribution between *campo rupestre* and *campo de altitude* is relatively common (Fiaschi and Pirani, 2009), with several genera and species shared among these "sky islands" in the Cerrado and Atlantic Forest domains (Giulietti and Pirani, 1988; Di Maio, 1996; Safford, 1999; Safford and Martinelli, 2000; Calió et al., 2008). Some other examples of plant taxa either restricted to *campo rupestre* and *campo de altitude* or with disjunct distribution between them include: *Wunderlichia* (Asteraceae), *Prepusa* (Gentianaceae), *Pseudotrimezia* (Iridaceae), *Luxemburgia* (Ochnaceae), *Bradea* and *Hindsia* (Rubiaceae), *Vellozia* (Velloziaceae) and *Xyris* (Xyridaceae) (Fiaschi and Pirani, 2009). Although dispersal events from the Andes to eastern Brazil have occurred in several groups (Thode et al., 2019, 2021), the opposite dispersal route is less common (e.g., *Leandra* s.str., Melastomataceae; Reginato and Michelangeli, 2018).

The biogeographic reconstruction of *Cambessedesia* suggests an ancient origin of the genus (around 23.2 Mya) and a more recent radiation and diversification in the *campo rupestre* of the Espinhaço range (around 16.7 Mya in the Mid-Miocene). It provides additional support for the possibility that some *campo rupestre* lineages may pre-date the diversification of the lower altitude Cerrado (Hughes et al., 2013). Other dated phylogenies of unrelated endemic lineages of *campo rupestre* similarly suggest old origins but recent radiation and diversification (Simon et al., 2009; Bitencourt and Rapini, 2013; Hughes et al., 2013; Souza et al., 2013; Bonatelli et al., 2014). Studies using time-calibrated phylogenies for *campo rupestre* lineages found species diversification concentrated in the Miocene (Rapini et al., 2007; Simon et al., 2009; Antonelli et al., 2010) or Pliocene and Pleistocene (Ribeiro et al., 2014; Rando et al., 2016; Vasconcelos et al., 2020).

In contrast, in the *campo de altitude* of the Atlantic Forest, the early diversification of the *Huberia* + *Merianthera* clade (around the early Oligocene 33.9 Mya) was concomitant with the initial uplift of the Serra do Mar and the Serra da Mantiqueira mountain ranges (Safford, 1999). The major uplift of the Serra do Mar and Serra da Mantiqueira in the Late Eocene may have favored radiation and colonization of environmentally heterogeneous niches. It may have opened an opportunity for Cambessedesieae to spread to the southeastern coastal highlands of Brazil, suggested by *Merianthera* and *Huberia* clades that diverged from each other around 33.2 Mya.

4.2. Conserved climatic niches between the campo rupestre and campo de altitude lineages

Although lineages linked to the *campo rupestre* and *campo de altitude* split at the beginning of Cambessedesieae diversification, it is interesting to note that both formations share similar climatic regimes for most of their evolutionary history (i.e. the background regime, Fig. 5). The *campo rupestre* and *campo de altitude* can be therefore considered

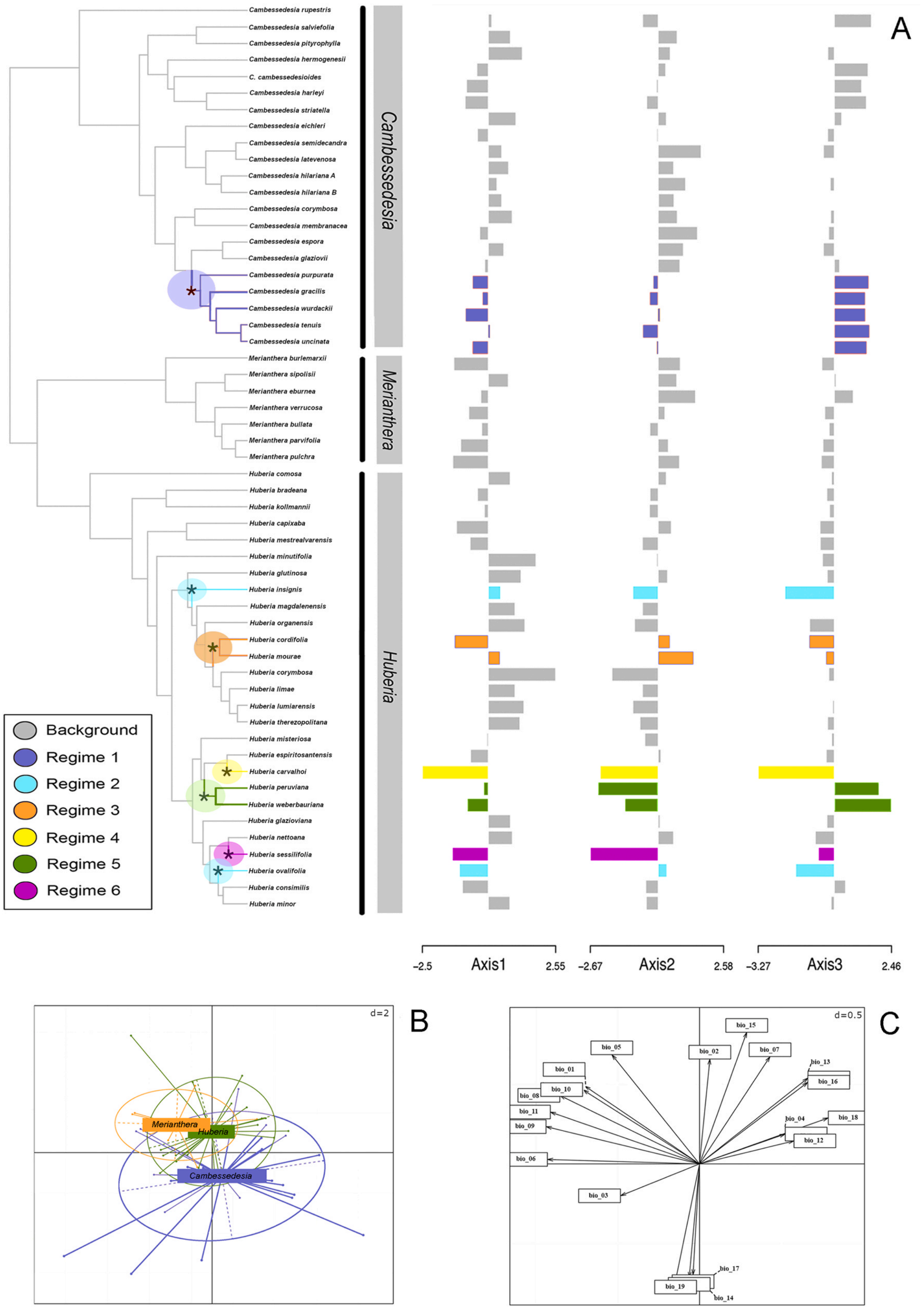

Fig. 5. A. Climatic regimes analysis, nodes colored following the legend. The bars for each terminal are the loadings of the first three axis from Principal Component Analysis (PCA). The background regime is colored in gray. The bars next to each terminal indicate their coordinates in the first three PCA axes. B. Climatic space of Cambessedesieae with the first three axes of the PCA plotted, colors following the regimes for each genera. C. PCA showing the importance of the 19 bioclimatic variables from the Worldclim database in the ordination. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

"climatic islands", and long-term niche conservatism (as indicated in other groups of Melastomataceae, such as *Leandra* Raddi *s.s.* and *Bertolonia* Raddi – Reginato, 2014; Bacci et al., 2021) was probably responsible for keeping most of the Cambessedesieae species restricted to these montane regions. Phylogenetic studies across angiosperms have shown that major ecological niches are more conserved through evolutionary history than previously expected, which has had important consequences for the assembly of local communities and regional species pools from which these are drawn (Donoghue, 2008). Niche conservatism, where closely related species have similar habitat requirements, implies that speciation does not necessarily result in evolutionary shifts across niche dimensions (Wiens and Graham, 2005). Thus, Donoghue (2008) suggests that, when faced with a changing environment, plant movement along habitat corridors may be favored over evolving adaptations while remaining in place.

To a certain extent, the diversification of Cambessedesieae seems to fit this scenario, with shifts to other climatic regimes occurring only close to the present and being mainly restricted to *Huberia*. We detected six shifts to five different climatic regimes in *Huberia* (Fig. 5 A). Only *H. insignis* and *H. ovalifolia* had convergent shifts (Regime 2). These two species are distributed in lower altitudes of the Atlantic Forest and represent the two most widespread species in the tribe in southeastern Brazil. Notably, the distributions of all of the remaining species of *Huberia* are highly restricted (Bochorny et al., 2019). The *Huberia cordifolia* + *H. mourae* clade (shift to Regime 3) is also notable for occurring in the *campo de altitude* of the Serra dos Órgãos range, where both species are found at the highest altitudes recorded for *Huberia* in the Atlantic Forest (around 2000 m elev., Bochorny et al., 2017) and also, *H. peruviana* + *H. weberbauriana* clade from the Andes of Ecuador and Peru (found between 1200 and 3350 m elev.). Other regime shifts indicate a trend of moving from generally open canopies to forests (e.g. Regimes 4 and 6), a trend also recently observed in other Myrtales clades (e.g. Gonçalves et al., 2020; Lima et al., 2021).

Excluding *Huberia*, the only other shift in climatic regime is found in *Cambessedesia*. One climatic shift occurred in a small clade (*C. purpurata*, *C. gracilis*, *C. wurdackii*, *C. uncinata* and *C. tenuis* – Fig. 5 A) endemic to the Chapada Diamantina province (northern Espinhaço Range; Colli-Silva et al., 2019). The climatic regime of the Espinhaço Range consists of markedly dry winters and wet summers (Giulietti and Pirani, 1988) and this shift could be associated with the decreasing rainfall towards the northern part of the range (Silveira et al., 2016). No climatic shifts were detected in the clade of the genus *Merianthera* (with most species occurring in inselbergs). Some studies (e.g. Parmentier and Hardy, 2009) indicated that phylogenetic niche conservatism has been an important factor for generating the observed phylogenetic structure in inselbergs. However, De Paula et al. (2021) found that climate not only change the conditions of the inselbergs, but also influences the structure of the matrix and therefore the pool of species that can colonize inselbergs from the surrounding vegetation (Burke, 2013; De Paula et al., 2016).

4.3. *Similar patterns of diversification between the campo rupestre and campo de altitude*

Our study is the first comparison of patterns of diversification between the *campo rupestre* and *campo de altitude*, the two most species-rich montane formations in eastern South America. An important, interesting result is the striking similarity in the tempo and mode of speciation in these two areas that are major centers of Cambessedesieae diversification. The GeoSSE analysis found no evidence for distinct diversification dynamics between lineages in the two areas, and so diversification scenarios were similar (Fig. 4, Table 3). The BAMM analysis also found similar diversification rates in the Cambessedesieae, indicating that the entire clade diversified at similar rates, albeit with increasing diversification rates towards the present. As previously discussed, the montane landscape of the *campo rupestre* is considerably older than that of the *campo de altitude* (Safford, 1999; Fiaschi and Pirani, 2009; Vasconcelos, 2011). These montane formations are also within distinct bioregions and climatic conditions, with the former mainly included in the Cerrado and Caatinga domains and the latter in the Atlantic Forest domain. Notwithstanding, we show that lineages in both mountain systems diversified similarly.

Shifts in diversification dynamics are historically associated with colonization of new areas where new ecological opportunities are found (Donoghue and Sanderson, 2015; Nürk et al., 2020). For instance, rapid radiation of plant lineages occurred in the hyper-diverse montane forests of the tropical Andes, such as in *Phlegmariurus* (Lycopodiaceae; Testo et al., 2018), Lobelioideae (Campanulaceae; Lagomarsino et al., 2016), and *Macrocarpaea* (Gentianaceae; Vieu et al., 2021). However, the several recent movements to different areas and climates observed in Cambessedesieae (especially in *Huberia*) did not change their diversification dynamics. Therefore, it remains unclear which factors are driving species diversification in this group. Nonetheless, we can offer at least three hypotheses for future studies. (1) Given the tendency of increased diversification towards the present, speciation in Cambessedesieae may be a result of a "species-pump", e.g. successive range expansions and contractions during periods of relative instability in the Quaternary that are responsible for diversification in other groups endemic to montane habitats (Stebbins, 1974; Toussaint et al., 2013). (2) Cambessedesieae have extreme flower diversity, which is likely to be associated with bee pollinators and their diversity (Bochorny et al., 2019). The wide diversity of colors, shapes and sizes of Melastomataceae connective appendages may have evolved by selection through male fitness (see Bochorny et al., 2021) and the dorsal stamen connective appendages in *Huberia* and *Merianthera*, and the bi-colored petals of *Cambessedesia*, may influence the diversification of the genera in high-altitude habitats. (3) Occasional events of dispersal and isolation between mountain tops act as "climatic islands," in addition to long-term niche conservatism, and were possibly responsible for keeping most Cambessedesieae species restricted to these montane regions, with speciation continuing at a somewhat even rate over time.

5. Conclusions

Here we showed that endemic lineages in montane areas with different geological histories and in different bioregions can diversify in similar ways. We therefore reject the hypothesis that diversification dynamics of lineages endemic to areas of different geological histories are necessarily distinct and found no evidence for shifts in diversification rates linked to shifts in climatic niche in Cambessedesieae. These results are remarkable because the tempo and mode of diversification of montane lineages is often linked to the age or stability of the landscape, where the timing of mountain uplift is stressed as the most important factor driving diversification. As a caveat, we note that Cambessedesieae is only one of several lineages with similar distributions in these areas, so this study should be considered a first step in comparing diversification patterns between mountain systems in eastern South America. Also, climatic shifts are difficult to detect in small phylogenetic trees and similar analyses should be applied to larger phylogenies. Studies that wish to build on these results should analyze a larger number of lineages to evaluate the role of diversification and transitions among habitats and to assess whether our results represent a generality or an exception to the rule. Accounting for the contribution of both climate and soil variables using species distribution modeling will also be crucial to understand the role of range contractions and expansions over time in the diversification of the group.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ppees.2022.125700.

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