


Research Article

Linking South American dry regions by the Gran Chaco: Insights from the evolutionary history and ecological diversification of *Gomphrena* s.str. (Gomphrenoideae, Amaranthaceae)

María J. Bena^{1,2*} , Matias C. Baranzelli¹, Santiago M. Costas¹, Andrea Cosacov¹, María C. Acosta¹, Andrés Moreira-Muñoz³, and Alicia N. Sérsic¹

¹Laboratorio de Ecología Evolutiva—Biología Floral, Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Universidad Nacional de Córdoba, Av. Vélez Sarsfield 1611, Córdoba, Argentina

²Instituto de Botánica Darwinion (CONICET—ANCEFN), Labarden 200, San Isidro B1642HYD, Buenos Aires, Argentina

³Instituto de Geografía, Pontificia Universidad Católica de Valparaíso, Av. Brasil, Valparaíso 2241, Chile

*Author for correspondence. E-mail: mjuliabena@gmail.com

Received 20 March 2023; Accepted 15 August 2023

Abstract Geoclimatic events driving South American aridization have generated biota differentiation due to barriers and new environment formation. New environments allow species climatic niche evolution, or the geographical expansion of an existing one. Understanding the role these processes play may clarify the evolution of South American biota. *Gomphrena* L. ranges across almost all the continent's arid environments. We tested whether South American drylands are biogeographically connected through the Gran Chaco but, due to different aridity levels, lineage diversification could have also been associated with the evolution of climatic niches and morphological or physiological traits. With available data, we generated a dated phylogeny, estimated ancestral ranges, performed diversification analyses, reconstructed ancestral states of two characters, and examined if niches have changed between lineages. Results showed that *Gomphrena* diversified throughout the easternmost South American drylands ~15.4 Ma, and subsequently three independent clades colonized the western arid regions during the last Andean pulse, and after the marine transgressions (~4.8–0.4 Ma) via the Gran Chaco. The colonization implied an increase in the diversification rate of annuals over perennials and the progressive east–west differentiation of the occupied climatic niche. This diversification was influenced by C₄ photosynthesis, which could have acted as a niche opener to conquer new environments after the Paranaean Sea withdrew. Spatiotemporal patterns found in *Gomphrena* suggest that geographical expansion and evolution of climatic niches played a common but decoupled role in promoting diversification. These results show that the Gran Chaco may have acted as a historical connection linking South American drylands.

Key words: arid-adapted clade, Chaco, climatic niche evolution, dry diagonals, *Gomphrena*, habit evolution.

1 Introduction

The species diversity within and among biomes and environments that we observe today has been modulated by the interaction of biotic, climatic, and geological factors over time (Benton, 2009). These events have modified the historical landscape, driving biota differentiation due to the formation of barriers or the creation and expansion of new environments. The emergence of new environments and new abiotic conditions available may imply niche evolution during biota differentiation (Lörch et al., 2021) or it may just involve the spatial expansion of an existing climatic niche (Glade-Vargas et al., 2021; Salariato et al., 2022). In particular, the environmental aridization that took place since the late

Miocene (Ortiz-Jaureguizar & Cladera, 2006; Hoorn et al., 2010; Achimón et al., 2018) has been put forth as the cause of diversification in several plant groups worldwide (e.g., *Euphorbia* L., Euphorbiaceae, Garrick et al., 2009; *Pugionium* Gaertn., Brassicaceae, Wang et al., 2013; Barnadesioideae, Asteraceae, Lörch et al., 2021; *Anarthrophyllum* Benth., Fabaceae, Achimón et al., 2018; Atacama endemic taxa, Luebert & Weigend, 2014; *Mutisia* L. f., Moreira-Muñoz et al., 2020; Atripliceae, Amaranthaceae, Brignone et al., 2022). However, it is difficult to decouple the role of climatic factors (i.e., diversification with niche differentiation) from the role of the spatial expansion of an existing niche (i.e., diversification with niche conservatism) and establish which may have been the main driver of biota diversification.

South American arid systems have a long evolutionary history, acting as centers of diversification for many plant lineages and including several globally important hotspots of plant diversity (Abraham et al., 2020). Throughout the continent, dry and arid lands configure two clearly defined diagonals (Fig. 1A). One of these refers to the concatenation of the Caatinga, Cerrado, and Gran Chaco regions, from northeastern Brazil to northwestern Argentina (eastern South American Dry Diagonal; eSADD). The second dry diagonal refers to the Coastal deserts, Puna, Prepuna, Monte Desert, and Patagonian Steppe territories from southwestern Ecuador to southeastern Argentina (western South American Dry Diagonal; wSADD; Sarmiento, 1975; Werneck, 2011; Abraham et al., 2020; Luebert, 2021). The eSADD is generally more humid than the wSADD and has more pronounced rainfall seasonality, with precipitation concentrated in summer, while the wSADD tends to be less seasonal due to year-round aridity, with little precipitation largely occurring in winter (Luebert, 2021)—the concepts “dry” and “arid” to define both diagonals are here employed in a

wide sense, referring to geographical areas that comprise whether arid lands, drylands, or humid regions that become arid or semiarid during a dry season.

The connection between South American arid regions was affected by marine transgressions and several alluvial systems during the final period of their establishment (Mid Miocene–Early Pliocene; 5–11 Ma, Iriondo, 1992; Hernández et al., 2005). Three successive Atlantic marine transgressions were recorded in the area that corresponds to central and northern Argentina, Uruguay, the eastern slopes of the rising Andes of northern Bolivia, southern Peru, and Venezuela (Ortiz-Jaureguizar & Cladera, 2006). These geological events, concomitant with the stabilization of arid climatic conditions throughout the continent, promoted the appearance and disappearance of barriers that connected the two arid systems (i.e., eSADD and wSADD). Specifically, the extensive flooded area of the last marine transgression called the “Paranaean Sea” (see Kessous et al., 2020), was followed by spread plains, creating new terrestrial environments in the area of the Gran Chaco. Faced with this scenario, we ask

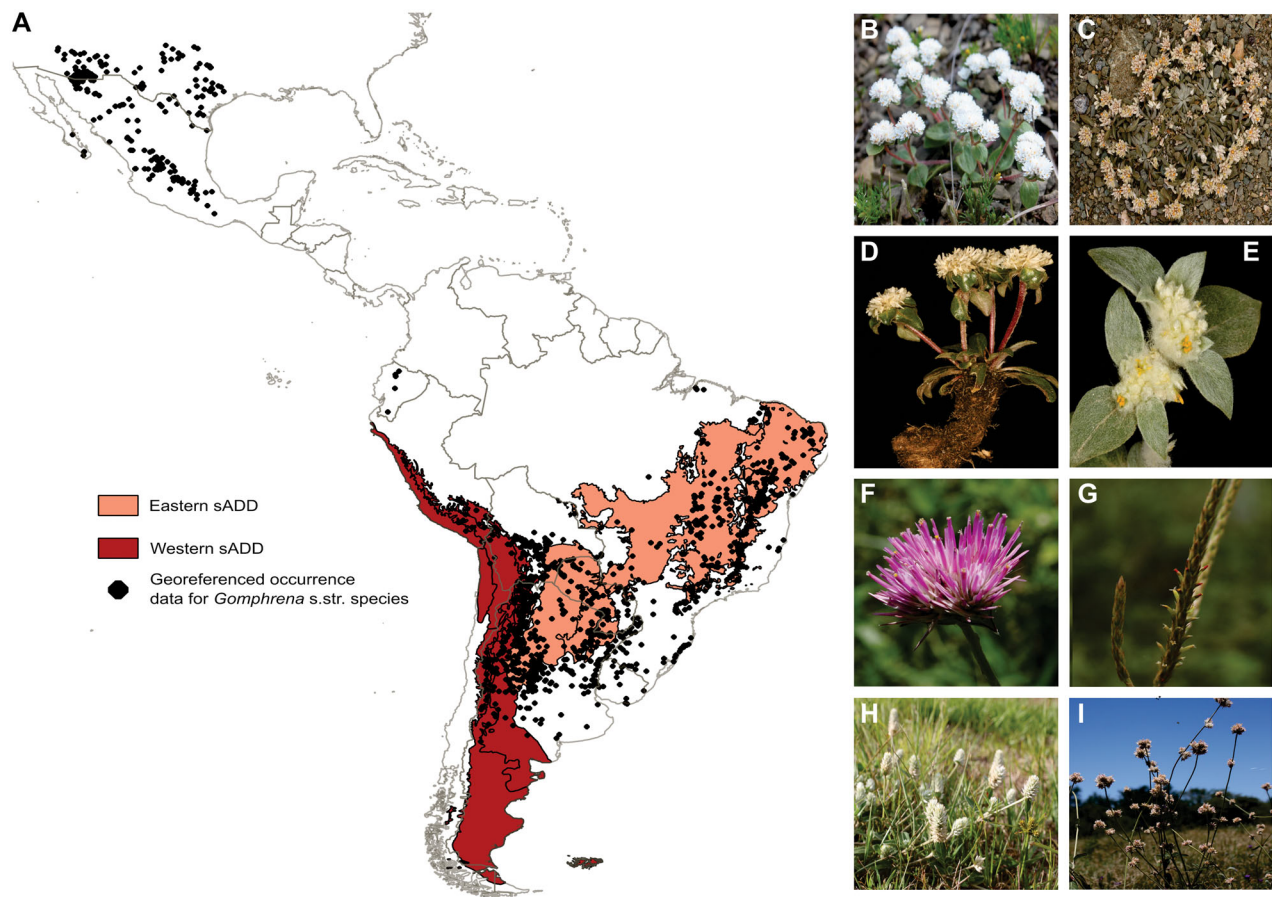


Fig. 1. A, Geographic distribution of the genus *Gomphrena* s.str. in America. Black dots indicate species occurrences, and colored areas indicate Eastern and Western South American Dry Diagonals (SADDs). Ecoregions encompassed by the SADDs follow Luebert's (2021) description, with the addition of the Central Andean Puna and Central Andean wet Puna (Olson et al., 2001) to the wSADD. Plants' images correspond to B, *Gomphrena phaeotricha*. C, *Gomphrena pumila*. D, *Gomphrena meyeniana*. E, *Gomphrena mendocina*. F, *Gomphrena haenkeana*. G, *Gomphrena graminea*. H, *Gomphrena celosioides*. I, *Gomphrena perennis*. Credits: (B) Juan Manuel Acosta; (C, D) Christian Zanotti; (E) Diego Salariato; (F, G) Fernando Omar Zuloaga; (H, I) Lone Aagesen.

whether the emerging land that corresponds to the Gran Chaco acted as a biogeographical connection, making the exchange of lineages between the two arid diagonals possible. Moreover, did the establishment of the Gran Chaco imply the appearance of a new climatic niche, or simply the spatial expansion of an existing one? By answering these questions, we aim to contribute to understanding the role of the Gran Chaco in the diversification of South American biota, an issue relatively unexplored or only recently explored (see Luebert, 2021; Griotti et al., 2023).

Even though the floristic composition shared between the eastern and western dry diagonals seems weak (Sarmiento, 1975; Ab'Saber, 1977; Prado & Gibbs, 1993; Prado, 2000; Linares-Palomino et al., 2003; Pennington et al., 2009; Linares-Palomino et al., 2011, 2015; Dryflor et al., 2016), several taxonomic groups have been recorded with taxa distributed in both arid regions (plants: *Skytanthus* Meyen, Apocynaceae, Prado, 2003; Paniceae, Poaceae, Zuloaga et al., 2007; *Leandra* Raddi, Melastomataceae, Reginato & Michelangeli, 2019; *Bulnesia* Gay, Zygophyllaceae, Böhnert et al., 2020; animals: Rhophitinae, Halictidae, Zanella & Martins, 2003). Among arid-adapted taxa, the plant genus *Gomphrena* L. (Gomphrenoideae, Amaranthaceae Juss.) is distributed in most environments of both dry diagonals (except the Coastal Deserts and Patagonian Steppe in the wSADD; Fig. 1A) and is one of the most widespread and species-rich genera within the Amaranthaceae family, composed of approximately 120 species (globally), including subshrubs and herbs (both perennial and annual; Figs. 1A–1H). There is a high richness of *Gomphrena* s.str. species in the Central Andes, the Argentine and Bolivian Puna, and the Caatinga and Cerrado habitats in Brazil (Acosta & Bena, 2020). The most recent ancestor of the genus was estimated to have emerged around 15.1 Ma (Ortuño & Borsch, 2020). Given the geographical distribution of *Gomphrena* s.str. in South America and its estimated origin, the genus constitutes an ideal system to understand the role of the Gran Chaco in connecting arid environments in both dry diagonals over time. Moreover, the independent evolution of traits such as annual habit, taproots, and tuberose roots among *Gomphrena* s.str. species (Pedersen, 2016; Acosta & Bena, 2020) suggests a direct link between the genus's diversification and the evolution of arid South American environments. Furthermore, Bena et al. (2017) found evidence for a climatic niche change of C_4 Gomphrenoideae into more arid environments than those occupied by their C_3 sister lineages, as well as a niche expansion into regions with colder winter climates. In this context, it has been proposed that C_4 photosynthesis appears to act as a niche opener, initially facilitating a geographic expansion of the inherited niche, whereas specialization to adapt to the new environment, through morphological or physiological changes, may be a delayed process that could generate speciation in the new habitat (Lundgren et al., 2015).

According to previous studies, the genus *Gomphrena* s.str. probably diversified in the New World tropics (Bena et al., 2020; Ortuño & Borsch, 2020). We, therefore, argue that the genus first diversified along the eastern South American drylands and subsequently colonized the western arid regions through the Gran Chaco as a biogeographical connection after Atlantic marine transgressions withdrew.

Thus, our main expectations are that (i) the ancestral distribution range of the genus was composed of regions throughout eSADD; (ii) the species and clades that currently inhabit wSADD regions are young lineages within *Gomphrena* s.str., and diversified during the most recent Andean pulses (7–2.5 Ma; Hoorn et al., 2022; Pérez-Escobar et al., 2022) and after marine transgressions (15.5–7 Ma; Ortiz-Jaureguizar & Cladera, 2006); (iii) the ancestors of wSADD lineages were in the Gran Chaco; (iv) there were morphological, physiological, and climatic niche changes between lineages inhabiting the different SADDs; and (v) there was a change in the diversification rates during colonization of the new wSADD environments. To test these predictions, we reproduced the existent dated phylogeny of *Gomphrena* s.str. (Ortuño & Borsch, 2020), we estimated divergence times and ancestral distribution ranges, performed ancestral state reconstructions of the habit and the photosynthetic pathway, and carried out a diversification analysis to elucidate the biogeographic history of the genus in South America. We also used distributional and bioclimatic data and niche modeling algorithms to compare climatic niches among *Gomphrena* s.str. clades and determine the role climatic niche evolution has played in the genus's diversification within the arid regions of South America.

2 Material and Methods

2.1 Phylogenetic and divergence time estimation

Using open-source data, we reconstructed the phylogenetic relationships and estimated the divergence times among *Gomphrena* s.str. species employing an extended data set of the subfamily Gomphrenoideae, and closely related subfamilies among Amaranthaceae s.l. ($n_{\text{taxa}} = 148$; Table S1). We searched GenBank for all available sequences of *trnL-F*, *rpl16*, and *matK* regions ($n_{\text{sequences}} = 311$; Table S1). In total, we analyzed 41 species as the ingroup (33 American species of *Gomphrena* s.str.; two species of *Guilleminea*; and six *Gomphrena* from Australia, Table S1). Additionally, we included 107 species of the Amaranthaceae s.l. as outgroups, from which 44 are gathered within the subfamily gomphrenoideae and the remaining 63 from further subfamilies (Table S1). Sequences were initially aligned with ClustalX v.2.0 (Larkin et al., 2007) under default settings and then adjusted manually using Bioedit v.7.0.9.0 (Hall, 1999). The phylogenetic analyses were performed through Bayesian approaches implemented in the software BEAST v.1.7.5 (Bayesian Evolutionary Analysis by Sampling Trees; Drummond & Rambaut, 2007). We used a concatenated data set, allowing each partition an independent substitution model. The parameters for these were set based on the program jModelTest2 v.2.1.6 (Posada & Crandall, 1998) implemented in the CIPRES portal (cyberinfrastructure for phylogenetic research; Miller et al., 2010). The best substitution models were HKY + I + G for *matK*, and HKY + G for *trnL-F* and *rpl16*. The relaxed Bayesian clock was implemented, with rates for each branch drawn independently from a lognormal distribution (Drummond et al., 2006). A “birth and death” prior was set for branch lengths. Since there are no known Gomphrenoideae fossils, we defined three secondary calibration points by using the age estimates of Di Vincenzo

Table 1 Clades and their age ranges employed for secondary calibration of the molecular clock (taken from Di Vincenzo et al., 2018)

Clade	Age range (lower–upper Ma)	Mean	SD
Achyranthoids + Gomphrenoids	21.42–33.86	27.7	2.0
Achyranthoids	15.79–27.89	22.2	2.0
Amaranthoids	17.12–34.30	25.7	2.0

et al. (2018): the age for the crown group of the Achyranthoids + Gomphrenoids clade; the age for the crown group of Achyranthoids; and the age of the Amaranthoids (Table 1). Age distribution priors for the secondary calibration points were included with “normal” age distributions equal to the 95% highest posterior densities interval (HPD). We ran the analysis with 50×10^6 generations, with a Yule tree prior, starting with a random tree and sampling parameters every 5000 steps. The convergence of the Markov chain Monte Carlo (MCMC) runs and the adequacy of the burn-in length were confirmed using the program Tracer v.1.7 (Rambaut et al., 2018). The maximum clade credibility tree (MCCT) was calculated using TreeAnnotator v1.7.5 (Drummond et al., 2012), excluding the first 25% of the sampled trees (burn-in fraction of 0.25).

2.2 Ancestral range estimations

For these analyses, we focused on the American species of *Gomphrena* s.str. We defined seven areas encompassing the current distribution of the genus in America, taking into account ecoregions (Olson et al., 2001), aridity values (United Nations Environment Programme aridity index [UNEP], 1993), and an altitude gradient along the Andean region across the western SADD: (i) North America; (ii) Andean region above 2600 masl; (iii) Andean region up to 2600 masl; (iv) Dry Chaco; (v) Humid Chaco; (vi) Brazilian Cerrado, and adjacent ecoregions; and (vii) Caatinga and adjacent (buffer) areas (see Fig. 2A; Table S2). We used the R package BioGeoBEARS (Matzke, 2013) to compare biogeographical models and estimate ancestral ranges of the American species of *Gomphrena* s.str. This package implements maximum likelihood methods that replicate the key assumptions of the three most widely used methods in historical biogeography, namely dispersal–extinction–cladogenesis (DEC; Ree & Smith, 2008), dispersal–vicariance analysis (DIVA; Ronquist, 1997), and BayArea (Bayesian Inference of Historical Biogeography for Discrete Areas; Landis et al., 2013), allowing comparison among them. DIVA and BayArea are not identical to their original formulation and are referred to as DIVALIKE and BAYAREALIKE in BioGeoBEARS (Matzke, 2013). Collectively, these models allow for a wide range of processes, including within-area speciation, vicariance, range expansion (dispersal to a new area), and range contraction (extinction in an area). We also tested models with and without founder-event speciation, which is incorporated with the j parameter. In such an event, range switching (e.g., from South America to North America) occurs with a lineage-splitting event (a node in the phylogeny), leaving one daughter lineage in a

new range and the other daughter lineage retaining the ancestral range. Such range-switching events are restricted to nodes, as it is considered unlikely that an entire lineage would simultaneously disperse to a new area and go extinct in its ancestral area (Matzke, 2014).

We set the maximum range size to four because this is the current maximum number of areas occupied by the analyzed taxa. We incorporated time-stratified dispersal multiplier matrices in the model fitting to account for the changing distances between the regions over geological time. We constrained our analysis based on the most critical geoclimatic events during the Andean uplift pulses by dividing the multiplier matrix into four time periods: (i) 17.5–15.5 Ma, defined by the genus diversification (Ortuño & Borsch, 2020); (ii) 15.5–7 Ma, defined by the Middle and Late Miocene Atlantic marine transgressions recorded in southern South America (the “Paranaean Sea”) (Ortiz-Jaureguizar & Cladera, 2006; Kessous et al., 2020); (iii) 7–2.5 Ma, defined by the culmination of the Andean uplift (Hoorn et al., 2022; Pérez-Escobar et al., 2022); and (iv) 2.5–0.1 Ma, defined by the cyclical Pleistocene glaciations (Rabassa, 2008). The dispersal multiplier matrices for each of these strata give the relative probability of dispersal between areas and are roughly scaled to represent the relative distance between the areas during each time slice. We tested a total of 12 models (Table 2), which varied in the number and types of free parameters included. The free parameters were d (the base rate of range expansion), j (the per-event weight of founder-event speciation at cladogenesis; Matzke, 2014), e (the rate of range contraction), and w (exponent on manual dispersal multipliers (Matzke, 2014). We used the corrected Akaike information criterion (AICc; Burnham & Anderson, 2002) to select among the models; the best-fit model with the lowest AICc score was used to infer the relative probabilities of ancestral ranges within the phylogeny.

2.3 Traits evolution

Based on the existing bibliography, we characterized the habit (annual/perennial) and photosynthetic pathway (C_3/C_4) of each species (including taxa not sampled in the phylogeny) and assessed their distribution across each of the defined areas (1–7, Fig. 2A). We subsequently performed ancestral state reconstructions of the binary traits: habit (annual = 0; perennial = 1), and photosynthetic pathway ($C_3 = 0$; $C_4 = 1$) of the taxa sampled in the phylogeny. We used the stochastic character mapping approach (SCM, Huelsenbeck et al., 2003) across the MCCT and 1000 trees randomly selected from the posterior distribution of the Bayesian MCMC searches, pruned to the core *Gomphrena* s.str. topology. The analyses were conducted using maximum likelihood with “corHMM” and “makeSimmap” implemented with the R package corHMM (Beaulieu et al., 2017). We tested three alternative transition models for each binary trait: equal rates, all permitted transitions to occur at the same rate; SYM (symmetric), backward and forward transitions occur at the same rate; and ARD (all-rates-different), allowing transitions to occur at different rates. In all cases, we used the Yang rooting method to fix the root state probabilities. This approach uses the estimated transition rates to set weights at the root (Yang et al., 2006; Beaulieu et al., 2017).

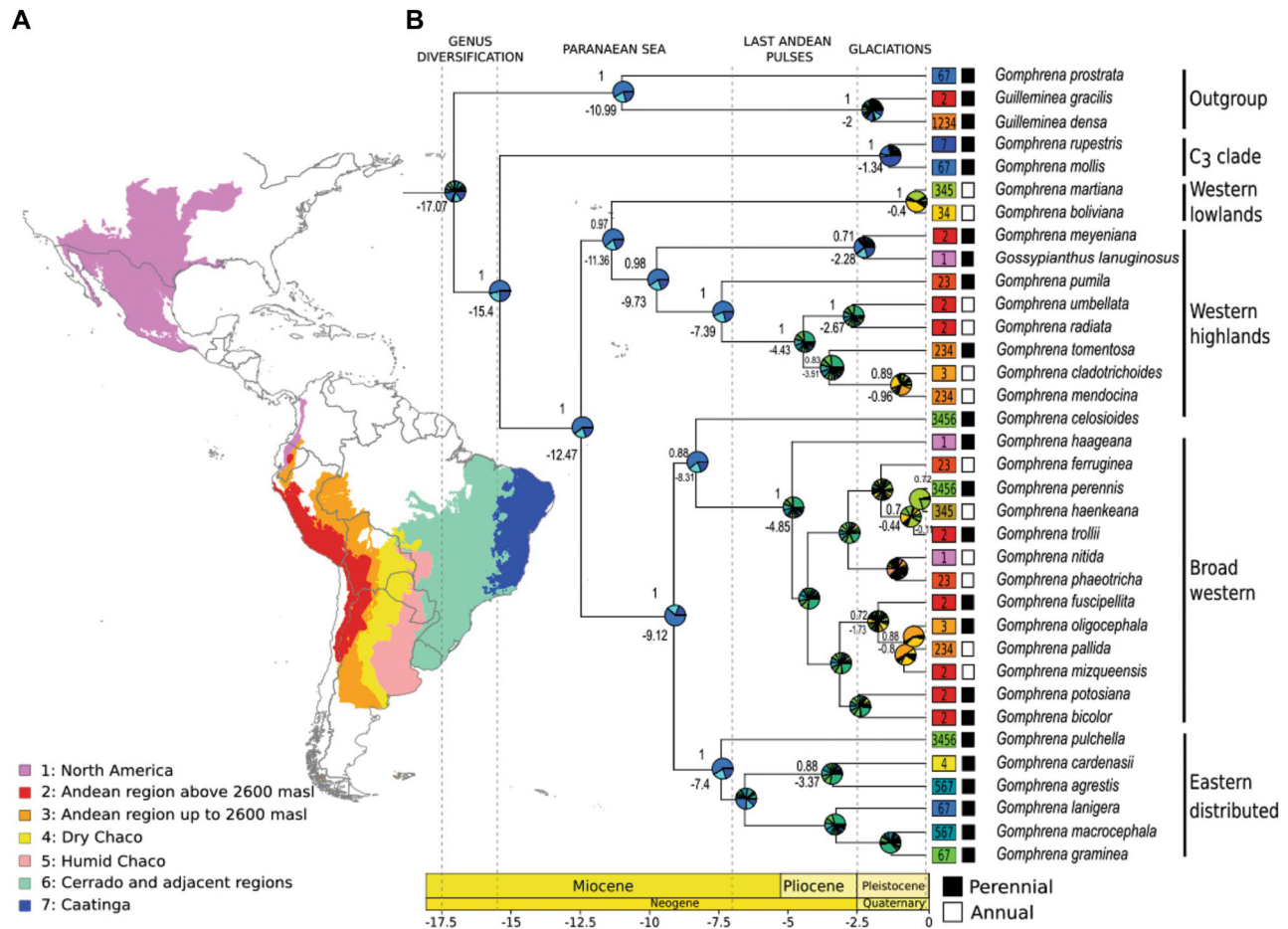


Fig. 2. **A**, Areas that encompass the distribution of the genus *Gomphrena* s.str. in America, which were considered to perform the ancestral range estimation. **B**, Maximum clade credibility tree pruned to the American core of *Gomphrena* s.str. Numbers above branches indicate posterior probabilities, and below branches indicate node ages. Only nodes with posterior probability ≥ 0.7 are shown. Periods considered for the time stratification of the ancestral range estimates are indicated above the figure and with vertical dotted lines. Pie charts show posterior probabilities obtained for each possible ancestral range in each node. The geographic areas defined (A) are indicated in colored boxes (1–7). Color scale and numbers indicate the areas defined for the ancestral range estimation including the combination of areas (additional colors). Colored boxes near the tips show the current distribution ranges of the species.

Table 2 Biogeographical models were tested, along with estimated parameters, log-likelihoods, and AICc values

Model	LnL	# parameters	D ^a	E ^b	J ^c	W ^d	AICc
DEC_TS	-286.306	2	0.082	0.125	0	1	576.987
DEC + J_TS	-246.187	3	0.910	0.5875	0	1	499.149
DEC_TS_W	-248.627	3	0.148	0.148	0	0.334	504.028
DEC + J_TS_W	-237.075	4	0.606	0.486	0.445	0.395	483.483
DIVALIKE_TS	-265.709	2	0.266	0.367	0	1	535.792
DIVALIKE + J_TS	-248.483	3	0.985	0.624	1.393	1	503.740
DIVALIKE_TS_W	-249.889	3	0.211	0.179	0	0.075	506.553
DIVALIKE + J_TS_W	-242.347	4	0.306	0.294	0.7294	0.249	494.027
BAYAREALIKE_TS	-252.958	2	0.301	0.482	0	1	510.292
BAYAREALIKE + J_TS	-248.670	3	0.312	0.303	0.537	1	504.114
BAYAREALIKE_TS_W	-231.909	3	0.489	0.501	0	0.353	470.592
BAYAREALIKE + J_TS_W	-234.038	4	0.314	0.371	0.3951	0.2743	477.409

Models were classified according to the number of free parameters. In bold italics are the best model and the estimated parameters under that model. AICc, corrected Akaike information criterion; ^aRate of range expansion; ^bRate of range contraction; ^cRelative per-event weight of jump dispersal; ^dExponent on manual dispersal multipliers (modifies *d* and *j*).

After obtaining a set of three models (for each trait), we used the AICc weight of each model to calculate the model-averaged marginal probabilities at the nodes (i.e., integrating the three models according to their AICc weights, see Table S3). We performed 1000 SCM simulations for the MCCT and 10 SCM simulations for each of the 1000 sampled trees to account for phylogenetic uncertainty. We used the *describe.simmmap* function of the R package *phytools* (Revell, 2012), which averages the state frequencies across all simulations, to calculate the posterior probability (PP) of each trait state on the selected nodes.

2.4 Diversification analyses

2.4.1 Nontrait dependent

We used MEDUSA (Modeling evolutionary diversification using stepwise akaike information criterion; Alfaro et al., 2009; Pennell et al., 2014) to identify shifts in diversification rates along branches of the genus *Gomphrena* s.str. This analysis was conducted using 1000 trees randomly selected from the posterior distribution of the Bayesian MCMC tree searches in BEAST, pruned to the core *Gomphrena* s.str. topology. The mixed models of either birth–death or Yule and the AICc criteria were used in the analyses. After initially fitting a constant rate birth–death model of diversification to the phylogenetic tree, MEDUSA uses a step-wise addition algorithm to infer phylogenetic local shifts in the rates of two diversification parameters: net diversification ($r = \lambda - \mu$) and relative extinction ($\epsilon = \mu/\lambda$), where λ is the speciation rate (birth) and μ is the rate of extinction (death). Rate shifts are retained if including the shift substantially improves the AICc score (Burnham & Anderson, 2002). MEDUSA requires that all missing species are assigned to a tip clade in the full tree. For this reason, we used comprehensive systematic resources (Foster, 1958; de Siqueira, 1992; Palmer, 1998; Acosta & Bena, 2020) to map the missing species richness. We were able to account for a large proportion of known species of *Gomphrena* s.str. Among Brazilian species, we included species of the *Gomphrena* section according to de Siqueira (1992). Other sections are probably grouped among the paraphyletic *Gomphrena*, which is not part of this study. Inferences of rate heterogeneity in the diversification process are drawn from the compilation of MEDUSA analyses across our full bootstrapped distribution of time-calibrated trees ($n = 1000$). We performed a “lineages through time” plot across 1000 randomly sampled trees used in the MEDUSA analyses. We plotted both lineages' raw and log scales with 95% confidence interval (CI). For this, we used the *phytools* package as implemented in R.

2.4.2 Trait dependent

Rate heterogeneity across clades can reflect the existence of trait-dependent diversification. We tested whether the habit and photosynthetic pathway are associated with changes in diversification rates in *Gomphrena* s.str. For this purpose, we used the binary speciation and extinction (BiSSE) models (Maddison et al., 2007) implemented with the R package *diversitree* (FitzJohn, 2012). We evaluated eight BiSSE models using maximum likelihood searches for each trait: (i) null model: speciation (λ), extinction (μ), and transition (q) rates were constrained to be equal; (ii) full model: all parameters are free to vary; (iii) lambda.free model: λ was allowed to

vary between character states while μ and q remained equal between states; (iv) mu.free model: μ was allowed to vary, while λ and q remained equal; (v) q.free model: q was allowed to vary, while λ and μ remained equal; (vi) lambda.mu.free model: λ and μ were allowed to vary, while q rates were constrained to be equal; (vii) lambda.q.free model: λ and q were allowed to vary, while μ rates were constrained to be equal; and (viii) mu.q.free model: μ and q were allowed to vary, while λ rates were constrained to be equal. The best-fit model was selected considering the lowest AICc value. We conducted a Bayesian BiSSE analysis with the best-fit model for each trait, and we obtained the posterior distributions of the parameters with the purpose of examining the CI of the estimations. This was run for 10 000 generations using an exponential prior (FitzJohn et al., 2009), and the first 10% were discarded as burn-in. PP distribution plots for λ , μ , q , and net diversification (r) rates were computed. Because our sampling was incomplete, all the BiSSE calculations were corrected using an implemented sampling fraction argument (*sampling.f*), for which a sampling fraction for each state was incorporated (i.e., the number of C_3 and C_4 species included over the total number of extant C_3 and C_4 species in *Gomphrena* s.str.).

2.5 Climatic niche comparison

Climatic variables to characterize and compare the fundamental niches of the main clades of *Gomphrena* s.str. were the 19 climatic variables with a 30 arcsec (~1 km) derived from high-resolution climatologies for the earth's land surface areas (CHELSA) for 1979–2013 (<https://chelsa-climate.org/bioclim/>; Karger et al., 2017). We downloaded a total of 971 georeferenced occurrence data for *Gomphrena* s.str. species corresponding to 28 species of the main clades detected in phylogenetic analyses (see Table S1b, Section 3) from the Global Biodiversity Information Facility (<https://www.gbif.org/>; GBIF, 2021a, 2021b). We eliminated duplicates and records with incomplete geographical information using QGIS v.2.18.12 (QGIS, 2009). We retained 736 presence records after this purging procedure (see details in Table S1b; Fig. 1A).

We examined whether there have been niche changes between the *Gomphrena* s.str. clades that inhabit the two different SADDs. We used two complemented tests to do this: Niche Overlap Test (NOT) and niche divergence test (NDT; Brown & Carnaval, 2019). Both allowed identifying climatic niche variations caused by both niche divergence or less evident factors such as climatic or geographic space limitations. NOT compares the realized niche of two different species or clades within their geographic distribution by considering the entire accessible environmental space (E-space). The NDT evaluates the same thing, but in the only portion of the environmental space that is shared by two species or clades when they are given a common environmental backdrop (i.e., analogous environmental spaces), enabling us to assess whether their occupied niches are equal or not under the same climatic background (Vaissi, 2022). If the NOT shows significant differences, this supports the argument that the two species occupy different niches (i.e., if the niches are equivalent or not equivalent), whereas if NDT shows significant results, it implies that the

fundamental niches of two species that share a common environmental space are divergent.

To do this, both tests calculated: (i) Niche Similarity Index (Schoener's D-metric), which quantifies the similarity between climatic niches of two species or clades in either G-space or E-space. Schoener's D-metric varies from 0 to 1, with 0 indicating niche divergence and 1 indicating niche equivalence (Brown & Carnaval, 2019). Niche Equivalency Tests were performed to determine whether this index is statistically significant—a one-tailed statistical test that evaluates the null hypothesis that the niches are equal. It compares the similarity of the niche observed between the species (Schoener's D-metric) with the frequency distribution constructed by resampling the points of occurrence of the groups to be compared randomly. (ii) Also, NOT and NDT calculate Background Tests that compare the observed Schoener's D-metric between clades with random changes in the spatial distribution of the second clade in geographic space. This evaluates how the change in the geographic space, and changes in the environmental space occupied impact the niche differences. In other words, it creates a null distribution of the E-space available in the species' habitat and compares it with the niche similarity between clades. With this, the test evaluates whether the compared niches are more different than would be expected given the underlying environmental differences between them. This test measures the ability of the Niche Equivalency Test to detect differences based on the available environmental space.

We performed all ecological niche comparisons among the main recovered *Gomphrena* s.str. clades (see Section 3) using the R package *Humboldt* (Brown & Carnaval, 2019). We used the *reduc.vars* function for each comparison, which selects the most important climatic variables for comparing each group. After this, a principal component analysis was performed to assess equivalency and similarity between the realized niches of *Gomphrena* s.str. clades in total (NOT) and shared (NDT) E-space using the *humboldt.doitall* function.

3 Results

3.1 Phylogenetic relationships and divergence times

The age of the subfamily Gomphrenoideae was inferred to be 30.56 Ma (28.93–33.86, 95% HPD, Fig. S1). The group that comprises the genus *Guilleminia* and the species *Gomphrena prostrata* shows as a sister clade of *Gomphrena* s.str. (Fig. 2B) that split 17.07 Ma (14.59–19.46, 95% HPD, Fig. 2B). Within *Gomphrena* s.str. the basal clade was composed of two taxa from the eSADD (*Gomphrena rupestris* and *Gomphrena mollis*, named “C₃ clade”), which diverged 15.4 Ma (13.02–17.9, 95% HPD, Fig. 2B). Among the remaining species of *Gomphrena* s.str., the phylogenetic analyses revealed two main lineages that diverged 12.47 Ma (10.45–14.5 Ma 95% HPD, Fig. 2B). The first of these lineages split into two main clades around 11.36 Ma (9.17–13.61 Ma 95% HPD, Fig. 2B), which mostly inhabit the Andean region. One of these is composed of high-altitude species (“western highlands” clade, WH), and the other of lowland species (“western lowlands” clade, WL). The WH diversified 9.73 Ma (7.43–12.15 Ma 95% HPD, Fig. 2B)

and contains the Andean species of *Gomphrena* s.str. that reach the highest altitudes within the genus (above 2600 masl), among which several are annual (Fig. 2B). An exception within the WH clade is the Caribbean species *Gossypianthus lanuginosus*, which was placed at the base of the clade. The WL is composed of two species (*G. martiana* and *G. boliviana*) whose distribution throughout the Andean region does not exceed altitudes of 2600 masl.

The second main lineage of *Gomphrena* s.str. diverged around 9.12 Ma (7.25–11.01 Ma 95% HPD, Fig. 2B) and split into a clade composed of many species that inhabit the eSADD, an “eastern distributed” clade (ED clade), and a “broad western” clade (BW) that reaches both the western and the eastern dry diagonals (Fig. 2B). The ED clade is composed of species across the ecoregions of Caatinga, Cerrado, and Atlantic Forest, as well as Chaco and Mesopotamian savanna (*Gomphrena agrestis*, *Gomphrena arborescens*, *Gomphrena cardenasii*, *Gomphrena macrocephala*, *Gomphrena lanigera*, *Gomphrena graminea*, *Gomphrena pulchella*). The BW clade consists of species from the Andean Puna, Prepuna, Yungas, high Monte, and Bolivian montane dry forests (*Gomphrena bicolor*, *Gomphrena fuscipellita*, *Gomphrena mizqueensis*, *Gomphrena oligocephala*, *Gomphrena pallida*, *Gomphrena phaeotricha*, *Gomphrena potosiana*, *Gomphrena trollii*), as well as others that occupy the Chaco region (*Gomphrena haenkeana*, *Gomphrena perennis*) and species with a very wide distribution from the Chaco to the Paraná flooded Savanna (*Gomphrena celosioides*). This clade also includes two taxa from the southern portion of North America (*Gomphrena haageana*, *Gomphrena nitida*).

3.2 Ancestral range estimations

Regarding the Biogeobears analyses, the AICc model selection supported the BAYAREALIKE+W model as the best fit (Table 2). Ancestral range estimations under this best-fitting model showed that the most probable ancestral range for *Gomphrena* s.str. is along the eSADD (15.4 Ma, areas “67,” PP = 0.534, Fig. 2B). Moreover, the four principal clades described above (WL, WH, BW, and ED) would also have their shared ancestors distributed along the eSADD (area “67,” PP = 0.604, Fig. 2B). Among these clades, the Chaco region was retrieved as part of the ancestral range by the BW clade since 4.85 Ma (i.e., dry and humid Chaco, Cerrado, and Caatinga; areas “4567”; PP = 0.265; Fig. 2B), with the exception of *G. celosioides*, whose most probable range still was the combination of Cerrado and Caatinga (area “67,” PP = 0.606; Fig. 2B). Around 4.43 Ma, the common ancestor of the subclade (within the WH clade) composed of *Gomphrena tomentosa*, *Gomphrena cladotrichoides*, *Gomphrena mendocina*, *Gomphrena umbellata*, *Gomphrena radiata* also retrieved the Chaco as part of the most probable ancestral range (areas: “4567”, PP = 0.273; Fig. 2B). Among the ED clade the Chaco region was colonized more recently, around 3.37 Ma, by *G. cardenasii* within a subclade comprised together with *G. agrestis* (areas: “4567”, PP = 0.281; Fig. 2B).

After the colonization of the Chaco, the final colonization of the Andean region took place only very recently, from around 1 Ma to the present. Inside the WH clade, the subclade *G. umbellata*+*G. radiata* still showed their ancestor's most probable range along the combination

of Chaco and eastern regions (areas: “4567”, PP = 0.237; Fig. 2B), while its sister subclade composed by *G. cladotrichoides* + *G. mendocina* would have colonized the Andean region by 0.96 Ma (Andean region up to 2600 masl; area: “3”, PP = 0.239; Fig. 2). Regarding the BW clade, one subclade nested within it (*G. perennis* + *G. haenkeana* + *G. trolli*) would have colonized the lower Andean region around 0.44 Ma but with a high uncertainty in the results (areas: “345”, PP = 0.22; Fig. 2B). The other subclade nested among the BW (*G. fuscipellita*, *G. oligocephala*, *G. pallida*, *G. mizqueensis*) also showed high uncertainty in its ancestral range around 1.73 Ma which would have been along the Dry Chaco (area “4,” PP = 0.109; Fig. 2B). But the colonization of the Andean region by the subclade conformed by *G. oligocephala*, *G. pallida*, *G. mizqueensis* would have happened around 0.8 Ma (most probable range: Andean region up to 2600 masl; area “3” PP = 0.47; Fig. 2B). The WL clade would have colonized the Andean region even more recently, around 0.4 Ma (most probable range Dry Chaco and Andean region up to 2600 masl, areas “34” PP = 0.424; Fig. 2B).

3.3 Evolution of traits

Considering the areas defined, we found a higher percentage of annual species in the westernmost areas (i.e., areas 2, 3, and 4, Figs. 2, 3), while the eastern area was almost exclusively occupied by perennials (areas 6 and 7) (Figs. 2, 3). Ancestral state reconstruction for the habit showed an equal probability of being annual or perennial for the core *Gomphrena* s.str. over the 1000 trees, while the node of the basal C₃ clade (*G. mollis* + *G. rupestris*) showed higher probabilities of being perennial (Fig. 4A; Table S3a). The ancestral state of the clades BW, ED, and WH also showed slightly higher probabilities of being perennial (Fig. 4A; Table S3a), but the ancestor of the WL clade had a higher probability of being annual (Fig. 4A; Table S3a). Some very recent nodes within BW and WH were inferred to have more probabilities of being annual. Withal, the probabilities of being annual increased from around 5 Ma to the present among most of the westernmost clades (Fig. 4). The ancestral state reconstruction of the photosynthetic pathway displayed very low or null uncertainty, with the ancestral state of the core *Gomphrena* s.str. showing the C₄ pathway, with a reversion to C₃ in the basal clade. All

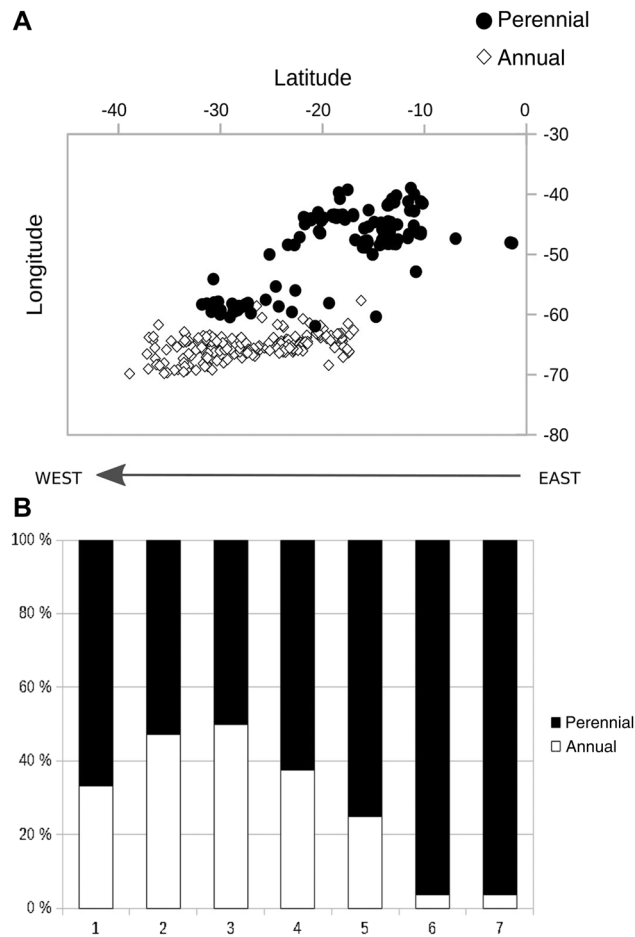


Fig. 3. Quantification of annual and perennial species along the area of interest. **A**, South American coordinates occupied by annual and perennial species (DNA under-sampled species are also included). **B**, Percentage of annual and perennial species along each area defined. 1, North America; 2, Andean region above 2600 masl; 3, Andean region up to 2600 masl; 4, Dry Chaco; 5, Humid Chaco; 6, Brazilian Cerrado and adjacent regions; 7, Caatinga and adjacent (buffer) areas.

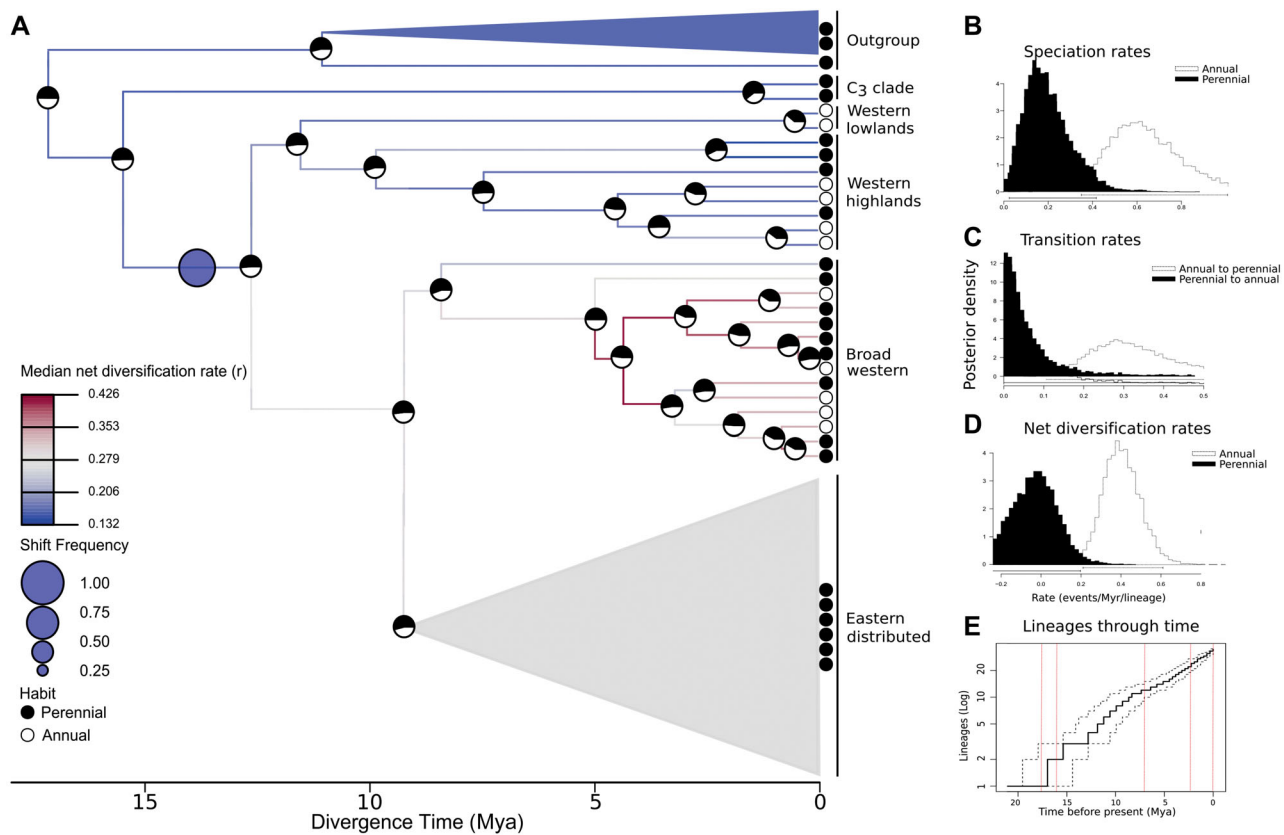


Fig. 4. **A**, Character mapping retrieved from Simmap over the maximum clade credibility tree, and diversification rate shifts retrieved from MEDUSA analyses along 1000 randomly sampled trees. Pie charts at nodes indicate the Posterior Probability (PP) of each “habit” state. The blue circle indicates the inferred position of rate shift increases found in more than 30% of the trees. Circles are scaled according to the proportion of trees in which the shift was detected. Branches are color-coded according to the median value of the net diversification rate (r) obtained from MEDUSA optimizations (see legend). Condensed branches represent the subsampled clades for whose species richness was mapped (see Section 2). Circles near tips indicate the habit of the sampled taxa. **B**, PP distributions for speciation rates. **C**, Transition rates. **D**, Net diversification rates of annual and perennial species. The bars at the bottom of the distributions correspond to the 95% credibility intervals. **E**, Lineages through time plot for *Gomphrena s.str.* (log scale). Vertical red lines indicate the time periods considered for the ancestral range estimation. Black dotted lines account for the 95% credibility intervals.

remnants of *Gomphrena s.str.* clades appeared to have C_4 ancestral states (Table S3a-c; Fig. S2).

3.4 Diversification analyses

3.4.1 Nontrait dependent

The MEDUSA diversification analyses provided evidence of heterogeneity in evolutionary rates across the phylogeny. We found one period among the South American *Gomphrena s.str.* where the diversification tempo changes ~ 12.47 Ma (blue circle near node, Fig. 4; Table S4). We also found rate increases in a second clade, but they correspond to the radiation of *Gomphrena* beyond America (*Gomphrena brachystylis*; *Gomphrena canescens*; *Gomphrena flaccida*; *Gomphrena muscoides*; *Gomphrena vermicularis*, Fig. S1; Table S4).

3.4.2 Trait dependent

Results from the Bisse analyses provided evidence of a trait-dependent diversification associated with the plant habit,

where the annuals showed a higher speciation rate than perennials (annuals $\lambda_0 = 0.608$, perennials $\lambda_1 = 0.183$) and the transition rate was higher from perennials to annuals than vice versa ($q_{01} = 0.249$, $q_{10} = 0$) (best-fit model: “lambda.q-free”) (Figs. 4B–4D; Table S5). We did not find evidence of changes in diversification associated with the photosynthetic pathway (Fig. S4). The log-lineages through time plot shows an acceleration in the number of lineages from approximately 5 Ma to the present (Fig. 4E).

3.5 Climatic niche comparison

The comparisons showed that the occupied climatic niches of C_3 (basal clade) and C_4 *Gomphrena s.str.* clades (BW, ED, WH, and WL) are quite different even in the portion of the E-space that is shared by both clades (i.e., niche divergence; Table 3; Fig. 5A). There were two clear trends in the climatic niche evolution within the C_4 species and clades after this initial divergence of the climatic niche within *Gomphrena s.str.* On the one hand, the colonization of new areas by the species of

Table 3 Schoener's D and p values of the Niche Overlap Test (NOT; equivalency and background statistic) and Niche Divergence Test (equivalency and background statistic) for all *Gomphrena* s.str. clades comparisons

Clades comparison	Niche Overlap Test				Niche Divergence Test				Interpretation following Brown & Carnaval (2019)
	Schoener's D		Background statistic p values		Schoener's D		Background statistic p values		
	1 → 2	2 → 1	1 → 2	2 → 1	1 → 2	2 → 1	1 → 2	2 → 1	
C ₃ vs. C ₄	0.054	0.623	0.247	0.505	0.119	0.009	0.644	0.644	Evidence that the species' niches have diverged
BW vs. ED	0.462	0.999	0.039	0.039	0.408	0.980	0.009	0.049	Strong evidence that the niches are equivalent
BW vs. WH	0.311	0.762	0.287	0.999	0.358	0.980	0.089	0.109	Suggests the niches are equivalent
BW vs. WL	0.377	0.999	0.129	0.089	0.339	0.802	0.148	0.169	Suggests the niches are equivalent
ED vs. WH	0.199	0.002	0.683	0.861	0.197	0.951	0.921	0.999	Supports the hypothesis that the current niches are not equivalent
ED vs. WL	0.295	0.001	0.129	0.287	0.337	0.901	0.406	0.089	Supports the hypothesis that the current niches are not equivalent
WH vs. WL	0.275	0.941	0.960	0.386	0.274	0.040	0.426	0.465	Evidence that the species' niches have diverged

Brown & Carnaval (2019) interpretation is included based on the result of all the calculated indices. Significant values are shown in bold. See complement results in Figure 4. BW, broad western; ED, eastern distribution clades; WH, western highlands; WL, western lowlands.

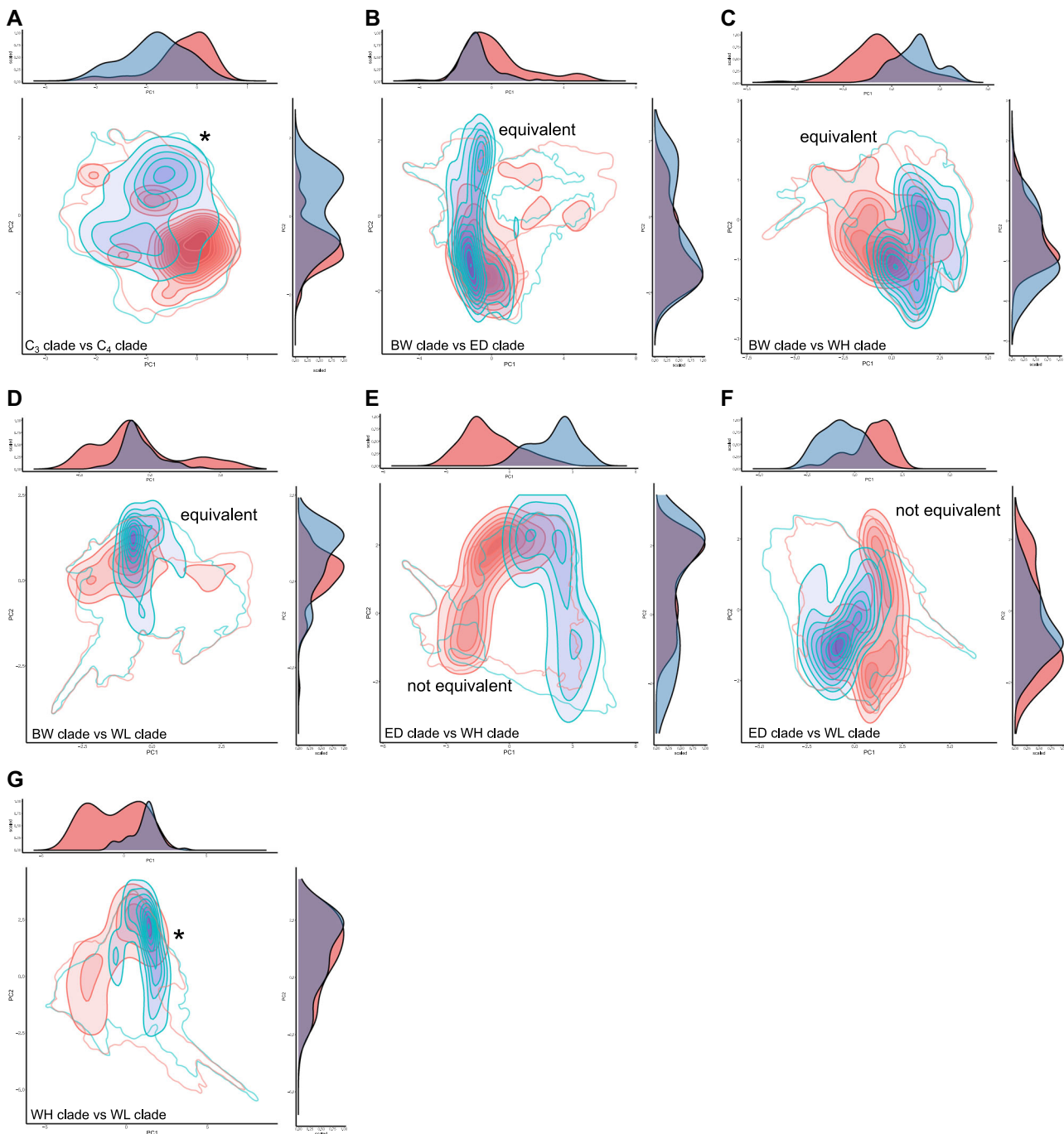


Fig. 5. Overlap density plots showing climatic niche comparison among *Gomphrena* s.str. clades: C₃ clade (C₃), C₄ clade (C₄), western highlands clade (WH), western lowlands clade (WL), broad western clade (BW), and eastern distributed clade (ED). Each plot shows one comparison: **A**, C₃ versus C₄. **B**, BW versus ED. **C**, BW versus WH. **D**, BW versus WL. **E**, ED versus WH. **F**, ED versus WL. **G**, WH versus WL. Each plot shows the E-space density occupied for each clade (in red clade 1 and blue clade 2 for each comparison) summarized in two principal components (PC). Lines representing the kernel density isopleths from 1% to 100% kernel densities, where full isopleths is the E-space occupied for the clades and the empty is the background E-space. Next to each PC, histogram density plots display the E-space occupied by each clade. See additional results in Table 3 of the main manuscript. Equivalent: clades occupy similar climatic niches; Not equivalent: clades occupy different niches without evidence of divergence among them; *Clades occupy different niches as a result of divergent evolution.

the BW clade apparently implied no climatic niche changes, neither for its sister lineage ED clade nor the WH and WL clades (i.e., equivalent niches, Table 3; Figs. 5B–5D). On the other, considerable differentiation in the complete E-space was observed between the ED clade versus WH and WL clades, indicating niche changes (i.e., not equivalent niches; Table 3; Figs. 5E, 5F). However, in the shared environments, there is no evidence that the species' niches may have diverged (Table 3; Figs. 5E, 5F). Finally, divergences in the climatic niche occupied were observed between WH and WL clades (i.e., niche divergence, Table 3; Fig. 5G).

4 Discussion

We provided a phylogenetic comparative analysis of the diversification and colonization history of *Gomphrena* s.str. across South American dry and arid environments. The results showed that the genus *Gomphrena* s.str. first diversified along the easternmost region of the eSADD (Brazilian Caatinga and Cerrado regions) and subsequently colonized the wSADD (Monte Desert, Puna, and Prepuna regions) around 5 Ma probably via the Gran Chaco, during the last Andean pulses and after the last marine transgressions (~7 Ma; Ortiz-Jaureguizar & Cladera, 2006; Hoorn et al., 2022). Following ancestral state reconstructions, diversification rate estimations, and climatic niche comparisons, we found that the colonization of this new arid environment implied an increase in the rate of diversification of annual over perennial species and progressive east–west differentiation of the occupied climatic niche. This progressive differentiation was probably facilitated by the group's C_4 condition, which acted as a niche opener for the conquest of new western arid environments (Bena et al., 2017). The draining of the Paranaean Sea meant the removal of a barrier that allowed the settlement of the western arid region but also brought climatic niche changes among the clades. The spatiotemporal diversification pattern found in *Gomphrena* s.str., therefore, suggests a common, but temporarily decoupled role of landscape change and niche differentiation in fostering biota diversification. Taken together, these results indicate that the Gran Chaco region may have acted as an arid biogeographical connection to conquer new arid environments and as a link between South American dry and arid regions (Luebert, 2021).

In general, the relationships among the main clades of the subfamily Gomphrenoideae and the diversification dates obtained in this work were concordant with previous studies (Bena et al., 2017, 2020; Ortuño & Borsch, 2020). In *Gomphrena* s.str., species with a mainly western distribution were grouped in different clades (referred to here as WL, WH, and BW) than easternmost species (clade ED), reinforcing the results of Bena et al. (2020), which had previously identified them as “high” and “low-Andean” clades, respectively. *Gomphrena* s.str. originated around 15.4 Ma across the eastern South American drylands (Brazilian Caatinga and Cerrado). During the Middle Miocene (ca. 17 Ma), South American landscapes were modified by climatic and geological events that drastically influenced the evolution of the flora (Ortiz-Jaureguizar & Cladera, 2006).

The global climate cooling, the reestablishment of a major ice sheet in Antarctica, the re-widening of the Drake Passage, the establishment of the Humboldt current, and obviously the Andean uplift, resulted in the hyperaridization of vast areas across the continent (Gregory-Wodzicki, 2000; Zachos et al., 2001; Lagabriele et al., 2009). The Andean Mountain range successively uplifted between 14 and 10 Ma (Quechua phase I) forming a major barrier to moisture-laden South Pacific winds (Ortiz Jaureguizar & Cladera, 2006). In eastern South America, all these events would have caused major climate changes, intensifying the dry conditions and increasing temperature differences between winter and summer (Hernández et al., 2005; Le Roux, 2012). Under this scenario of increasing aridity and seasonality, the genus *Gomphrena* diversified and gained a new photosynthetic strategy, the C_4 pathway. As was suggested by Bena et al. (2017), the model for the evolution of C_4 photosynthesis in the subfamily Gomphrenoideae seems to have evolved in humid habitats but facilitated an expansion into arid ones. Thus, species with a pre-existing C_4 condition found a favorable environment for their expansion and evolution in the new habitats.

Around 7.5 Ma, during the Late Miocene-Early Pliocene, the broad flooded surface of the “Paranaean Sea” was followed by vast plains, starting the “Age of the Southern Plains” (Ortiz-Jaureguizar & Cladera, 2006). This event eliminated a barrier to the dispersion, which allowed the colonization of western areas of the continent. Our biogeographical reconstruction suggests that the wSADD was apparently colonized through the Gran Chaco by two independent colonizations of *Gomphrena* s.str. (~4.85 and 4.43 Ma, BW, and WH clades, respectively). Ortuño & Borsch (2020) also showed two independent colonizations of the western SADD by the genus *Gomphrena* s.str. Here, we reinforced this phylogenetic pattern within a biogeographical context and provided the first estimation of *Gomphrena* s.str. ancestral range. Once the Paranaean Sea retired, the ancestral distributions of the genus would have extended from the Cerrado and Caatinga biomes to the Chaco and subsequently diversified into the Andean region after the mountain range achieved its current height. The connection between the Chaco, Caatinga, and Cerrado biomes has been treated in previous studies as a “savanna corridor” (Schmidt & Inger, 1951), “diagonal of open formations” (Vanzolini, 1963), or “dry diagonal” (Prado & Gibbs, 1993). However, the connection between these regions and the western SADD biomes has been scarcely documented. Also, a link between the Andean and Atlantic forests through the current Cerrado–Chaco transition has been reported, supporting that the connection was recurrent (Trujillo-Arias et al., 2018). Still, the connectivity between dry open biomes from eastern and western South America has been hardly documented. An alternative scenario would be that *Gomphrena* reached the WL (Area 3) through the seasonally dry tropical forests in the inter-Andean dry valleys—not through the Chaco plain—however, we did not find support for this hypothesis. The lack of studies centered on these connections emphasizes the importance of the present (and further) analyses that focus on biological groups with a distribution between open habitats of both western and eastern SADDs.

The ability of plants to conquer new arid environments is usually acquired through morphological and physiological differentiation. In this sense, most of the *Gomphrena* s.str. species show the C_4 photosynthetic pathway (Sage, 2016) and only ~5% (5 C_3 /92 C_4) are C_3 . According to our diversification analyses, there was a shift in *Gomphrena* s.str. diversification rate around 12 Ma, which coincides with the C_3 – C_4 transition in the genus. However, C_4 photosynthesis evolved earlier within the Gomphrenoideae subfamily (~20 Ma, genus *Froelichia*) and the pattern seen in *Gomphrena* s.str. seems to be a reversal to the ancestral C_3 condition (Ortuño & Borsch, 2020). Additionally, the trait-dependent diversification analyses did not show changes associated with the photosynthetic pathway either. At the global scale, the expansion of C_4 plants occurred 8–4 Ma at the Miocene–Pliocene boundary (Osborne & Beerling, 2006; Behrensmeyer et al., 2007), probably associated with the declining CO_2 levels, during the late Neogene and the increase in summer-dominated rainfall regimes (Latorre, 1997). In South America, these conditions coincided with the withdrawal of the Paranaean Sea (~7.5 Ma) and the last pulses of the Andean uplift (~5 Ma), implying that the expansion of C_4 lineages in *Gomphrena* s.str. was promoted not only by the local conditions but by a combination of climatic and geological events that occurred at both global and regional scales. We observed an increase in the number of *Gomphrena* s.str. lineages in synchrony with the most recent Andean pulses (~5 Ma) and the aridization of the continent. While the central Andes probably did not become extremely dry until very late in the Quaternary, pockets of arid habitats developed relatively early in inter-Andean valleys (Simpson, 1983). These valleys formed a scattered network from the northernmost regions of Colombia to central Chile and Argentina and were undoubtedly important in providing migration routes for taxa preadapted to arid conditions that eventually colonized the dry altiplano (e.g., Griotti et al., 2023). Consequently, the C_4 condition in *Gomphrena* s.str. may have improved chances of survival in the new environments by acting as a “niche opener,” and the results observed here reflect a delayed speciation process throughout the new habitat (Bena et al., 2017). Nontrait-dependent analyses did not detect rate shifts between western and eastern-distributed clades. This could be because, while there was an expansion toward western arid environments, species restricted to the eastern drylands continued their diversification *in situ*. However, this hypothesis remains to be tested by including the missing Brazilian taxa in the phylogeny.

Even though the ED lineage is not fully sampled, most *Gomphrena* species from Brazil are known to be perennial herbs or subshrubs (de Siqueira, 1992; Senna et al., 2015). The thickened subterranean systems have bud shoot-forming potential, providing the sprout of new shoots after an adverse period, like a severe drought or fire. Also, it is known that nearly 50% of the herbaceous and subshrub species from the Cerrado have these systems (Vilhalva & Appezzato-da-Glória, 2006), which may have been a strategy for the frequent periods of fire in that region. Interestingly, when evaluating trait-dependent rate shifts, we found an increase in the diversification rate associated with the annual habit. Also, the ancestral state reconstruction indicated that the

ancestral probability of being annual only equaled the probability of being perennial around 5 Ma and subsequently surpassed it among the most recent subclades within the BW and WH clades. The annual habit evolved independently several times within the genus, but only among clades that colonized the wSADD, suggesting a morphological divergence between SADDs. The annual life form seems to be mostly associated with plants occurring in dry or seasonally dry environments along the Andean influence zone, indicating the adaptive nature of the plants, which only appear in the wet season. Multiple origins of annuals have also been observed in other lineages of angiosperms radiating into areas with geographical patterns of dry environments such as *Nemesia* Vent. (Scrophulariaceae; Datson et al., 2008). Additionally, half of the C_4 species that reach arid regions are annuals that may complete their life cycles under brief periods of rain, and several of the climatic wide-ranging perennials have been collected in microsites such as creeks and riverbanks in the drier part of their ranges (Aagesen et al., 2016).

The distributions of most species are either shrinking or expanding in response to environmental conditions. However, most studies that compare the climatic niches assume that the species have reached a balance, but niche similarity measurement may be biased toward more common (more represented) habitat types. The niche comparison method used here allowed us to evaluate how much species differ in their climatic niches, without assuming that they are in balance (Brown & Carnaval, 2019). In this way, we were able to more accurately evaluate whether the clades of interest have evolved different niches or whether they occupy separate climatic niches because of differences in life history, biological interactions, or the environments available. The climatic niche comparisons performed demonstrated that the occupied niches of C_3 and C_4 *Gomphrena* s.str. clades are different even in the portion of their shared E-space (i.e., niche divergence *sensu* Brown & Carnaval, 2019). Whereas the C_3 clade is composed of just two species restricted to the Cerrado biome, the C_4 clade is constituted by the vast majority of species that are distributed along a variety of environments (including the Cerrado). In this sense, an infraspecific investigation among *Alloteropsis semialata* found that, while non- C_4 individuals remained confined to a limited geographic area and restricted ecological conditions, C_4 individuals dispersed across an expanded range of environments encompassing the ancestral one (Lundgren et al., 2015). Additionally, among C_4 *Gomphrena* s.str. species and clades, there were two clear trends of niche differentiation: the colonization of wSADD via niche conservatism in the BW clade, and via niche differentiation including adaptive divergence in the ED, WH, and WL clades, revealing an interplay between niche conservatism and divergence in the climatic niche evolution of the genus when shaping their distribution across the different arid environments of the continent (e.g., Aagesen et al., 2016; Salaria et al., 2022). Interestingly, WH and WL consist of species grouped along the Andean influence zone, so these results indicate a somewhat recent niche change throughout the newly colonized area, a product of the Andean uplift that generated new environments for colonization (Lörch et al., 2021). The high-altitude areas occupied by the species

of the WH clade constitute a new niche generated as a consequence of the Andean uplift (Pérez-Escobar et al., 2022). This expansion out of the Chacoan domain, highlights the importance of neotropical lineages in the high Andean flora, as most contributions on this topic concern Laurasian lineages that have reached the high Andes after the latest uplift.

Withal, our study shows that the historical diversification pattern of *Gomphrena* s.str. in South America consisted of an expansion toward western arid environments once geographical barriers disappeared, and a posterior niche change among the new habitats. However, these expansions and niche changes were decoupled in space and time. The C_4 condition was a key trait to start the east–west colonization, and the multiple shifts to the annual habit were essential to autochthonous speciation within the new western environments. This work provides the first evidence that the Gran Chaco operates as a biogeographical connection, linking the east and west open arid environments of South America.

Acknowledgements

This work was supported by the National Ministry of Science and Technology (FONCYT-PICT- 2018-0890 to A.N.S, and PICT-2017-1051 to M.J.B). A.M.-M. is supported by ANID-FONDECYT No 1221879. M.C.B., A.C, C.A, S.C., and A.N.S. would like to thank the National Council for Scientific and Technological Research (CONICET), Argentina. We acknowledge the valuable suggestions of Dr. L. Aagesen and an anonymous reviewer to improve the manuscript and thank Dr. N. Brignone for his help on the diversification analyses.

References

- Aagesen L, Biganzoli F, Bena MJ, Godoy-Bürki AC, Reinheimer R, Zuloaga FO. 2016. Macro-climatic distribution limits show both niche expansion and niche specialization among C_4 panicoids. *PLoS One* 11: e0151075.
- Abraham EM, Rodríguez MD, Rubio MC, Guida-Johnson B, Gomez L, Rubio C. 2020. Disentangling the concept of “South American Arid Diagonal”. *Journal of Arid Environments* 175: 104089.
- Ab'Saber AN. 1977. Os domínios morfoclimáticos na América do Sul. Primeira aproximação. *Geomorfologia* 53: 1–23.
- Achimón F, Johnson LA, Cocucci AA, Sérsic AN, Baranzelli MC. 2018. Species tree phylogeny, character evolution, and biogeography of the Patagonian genus *Anarthrophyllum* Benth. (Fabaceae). *Organisms Diversity and Evolution* 18: 71–86.
- Acosta JM, Bena MJ. 2020. *Gomphrena*. Amaranthaceae. In: Zuloaga FO, Belgrano MJ eds. *Flora Vascular de la República Argentina*. Buenos Aires: Estudio Sigma S.R.L. 72–104.
- Alfaro ME, Santini F, Brock C, Alamillo H, Dornburg A, Rabosky DL, Carnevale G, Harmon LJ. 2009. Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proceedings of the National Academy of Sciences of the United States of America* 106: 13410–13414.
- Beaulieu JM, Oliver JC, O'Meara B, Beaulieu MJ. 2017. Package ‘corHMM’. Analysis of binary character evolution. <https://cran.r-project.org/web/packages/corHMM/corHMM.pdf>
- Behrensmeyer AK, Quade J, Cerling TE, Kappelman J, Khan IA, Copeland P, Roe L, Hicks J, Stubblefield P, Willis BJ, Latorre C. 2007. The structure and rate of late Miocene expansion of C_4 plants: Evidence from lateral variation in stable isotopes in paleosols of the Siwalik Group, northern Pakistan. *Bulletin of the Geological Society of America* 119: 1486–1505.
- Bena MJ, Acosta JM, Aagesen L. 2017. Macro-climatic niche limits and the evolution of C_4 photosynthesis in Gomphrenoideae (Amaranthaceae). *Botanical Journal of the Linnean Society* 184: 283–297.
- Bena MJ, Ortuño T, Acosta JM. 2020. Disentangling the taxonomic variations within the high-andean complex *Gomphrena meyeniana*. *Systematic Botany* 45: 294–305.
- Benton MJ. 2009. The Red Queen and the Court Jester: Species diversity and the role of biotic and abiotic factors through time. *Science* 323: 728–732.
- Böhnert T, Weigend M, Merklinger F, Quandt D, Luebert F. 2020. Historical assembly of Zygophyllaceae in the Atacama Desert. *Frontiers of Biogeography* 12(3): e45197.
- Brignone NF, Pozner R, Denham SS. 2022. Macroevolutionary trends and diversification dynamics in *Atripliceae* (Amaranthaceae s.l., Chenopodioideae): A first approach. *Annals of Botany* 130: 199–214.
- Brown JL, Carnaval AC. 2019. A tale of two niches: Methods, concepts, and evolution. *Frontiers of Biogeography* 11(4): e44158.
- Burnham KP, Anderson DR. 2002. *Model selection and multimodel inference: A practical information-theoretic approach*. New York: Springer.
- Datson PM, Murray BG, Steiner KE. 2008. Climate and the evolution of annual/perennial life-histories in *Nemesia* (Scrophulariaceae). *Plant Systematics and Evolution* 270: 39–57.
- de Siqueira JC. 1992. O gênero *Gomphrena* L. (Amaranthaceae) no Brasil. *Pesquisas Botânica* 43: 5–197.
- Di Vincenzo V, Gruenstaedl M, Nauheimer L, Wondrafrash M, Kamau P, Demissew S, Borsch T. 2018. Evolutionary diversification of the African achyranthoid clade (Amaranthaceae) in the context of sterile flower evolution and epizoochory. *Annals of Botany* 122(1): 69–85.
- Drummond AJ, Ho SYW, Phillips MJ, Rambaut A. 2006. Relaxed phylogenetics and dating with confidence. *PLoS Biology* 4: e88.
- Drummond AJ, Rambaut A. 2007. BEAST: Bayesian evolutionary analysis by sampling trees. *BMC Evolutionary Biology* 7: 1–8.
- Drummond AJ, Suchard MA, Xie D, Rambaut A. 2012. Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution* 29: 1969–1973.
- Dryflor KBR, Delgado-Salinas A, Dexter KG, Linares-Palomino R, Oliveira-Filho A, Prado D, Pullan M, Quintana C, Riina R, Rodríguez MGM, Weintritt J, Acevedo-Rodríguez P, Adarve J, Álvarez E, Aranguren B A, Arteaga JC, Aymard G, Castaño A, Ceballos-Mago N, Cogollo A, Cuadros H, Delgado F, Devia W, Dueñas H, Fajardo L, Fernández A, Fernández MA, Franklin J, Freid EH, Galetti LA, Gonto R, González-M R, Graveson R, Helmer EH, Idárraga A, López R, Marcano-Vega H, Martínez OG, Maturo HM, McDonald M, McLaren K, Melo O, Mijares F, Moggi V, Molina D, Moreno NDP, Nassar JM, Neves DM, Oakley LJ, Oatham M, Olvera-Luna AR, Pezzini FF, Dominguez OJR, Ríos ME, Rivera O, Rodríguez N, Rojas A, Särkinen T, Sánchez R, Smith M, Vargas C, Villanueva B, Pennington RT. 2016. Plant diversity patterns in neotropical dry forests and their conservation implications. *Science* 353: 1383–1387.
- FitzJohn RG. 2012. Diversitree: Comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* 3: 1084–1092.
- FitzJohn RG, Maddison WP, Otto SP. 2009. Estimating trait-dependent speciation and extinction rates from incompletely resolved phylogenies. *Systematic Biology* 58: 595–611.

- Foster RC. 1958. *A catalogue of the ferns and flowering plants of Bolivia*. Cambridge, USA: Contributions from the Gray Herbarium of Harvard University. 184: 1–223.
- Garrick RC, Nason JD, Meadows CA, Dyer RJ. 2009. Not just vicariance: Phylogeography of a Sonoran Desert euphorb indicates a major role of range expansion along the Baja peninsula. *Molecular Ecology* 18: 1916–1931.
- GBIF. 2021a. GBIF occurrence download [online]. Available from <https://doi.org/10.15468/dl.p43qkx> [accessed 13 October 2021].
- GBIF. 2021b. GBIF occurrence download [online]. Available from <https://doi.org/10.15468/dl.s57c7ms> [accessed 13 October 2021].
- Glade-Vargas NS, Rojas C, Jara-Arancio P, Vidal P, Arroyo MTK, Hinojosa LF. 2021. Biogeography of *Argylia* D. Don (Bignoniaceae): Diversification, Andean uplift and niche conservatism. *Frontiers in Plant Science* 12: 1–15.
- Gregory-Wodzicki K. M. 2000. Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin* 112(7): 1091–1105.
- Griotti M, Ceccarelli SF, Roig-Juñent S. 2023. Following the aridity: Historical biogeography and diversification of the Philodromidae spider genus *Petrichus* in South America. *Molecular Phylogenetics and Evolution* 180: 107684.
- Hall TA. 1999. BioEdit: A user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.
- Hernández RM, Jordan TE, Dalenz Farjat A, Echavarría L, Idleman BD, Reynolds JH. 2005. Age, distribution, tectonics, and eustatic controls of the Paranense and Caribbean marine transgressions in southern Bolivia and Argentina. *Journal of South American Earth Sciences* 19: 495–512.
- Hoom C, Palazzesi L, Silvestro D. 2022. Editorial preface to special issue: Exploring the impact of Andean uplift and climate on life evolution and landscape modification: From Amazonia to Patagonia. *Global and Planetary Change* 211: 103759.
- Hoom C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson CL, Figueiredo JP, Jaramillo C, Riff D, Negri FR, Hooghiemstra H, Lundberg J, Stadler T, Särkinen T, Antonelli A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* 330(6006): 927–931.
- Huelsenbeck JP, Nielsen R, Bollback JP. 2003. Stochastic mapping of morphological characters. *Systematic Biology* 52: 131–158.
- Iriondo MH. 1992. El Chaco. *Holoceno* 1: 50–63.
- Karger DN, Conrad O, Böhrer J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M. 2017. Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4(1): 1–20.
- Kessous IM, Neves B, Couto DR, Paixão-Souza B, Pederneiras LC, Moura RL, Barfuss MHJ, Salgueiro F, Costa AF. 2020. Historical biogeography of a Brazilian lineage of Tillandsioideae (subtribe Vrieseinae, Bromeliaceae): The Paranaean Sea hypothesized as the main vicariant event. *Botanical Journal of the Linnean Society* 192: 625–641.
- Lagabrielle Y, Goddés Y, Donnadié Y, Malavieille J, Suarez M. 2009. The tectonic history of Drake Passage and its possible impacts on global climate. *Earth and Planetary Science Letters* 279(3–4): 197–211.
- Landis MJL, Matzke NJ, Moore BR, Huelsenbeck JP. 2013. Bayesian analysis of biogeography when the number of areas is large. *Systematic Biology* 62: 789–804.
- Larkin MA, Blackshields G, Brown NP, Chenna R, McGettigan PA, McWilliam H, Valentin F, Wallace IM, Wilm A, Lopez R, Thompson JD, Gibson TJ, Higgins DG. 2007. Clustal W and Clustal X version 2.0. *Bioinformatics* 23: 2947–2948.
- Latorre C. 1997. The expansion of C_4 grasses and global change in the late Miocene: Stable isotope evidence from the Americas. *Earth and Planetary Science Letters* 146: 83–96.
- Le Roux JP. 2012. A review of tertiary climate changes in southern South America and the Antarctic Peninsula. Part 2: Continental conditions. *Sedimentary Geology* 247–248: 21–38.
- Linares-Palomino R, Aybar D, Morales Ruiz EJ. 2015. Floristics of neotropical seasonally dry forests: A perspective from complete vascular plant inventories. *Phytocoenologia* 45: 251–267.
- Linares-Palomino R, Oliveira-Filho AT, Pennington RT. 2011. Neotropical seasonally dry forests: Diversity, endemism, and biogeography of woody plants. In: Dirzo R, Young HS, Mooney HA, Ceballos M eds. *Seasonally dry tropical forests*. Washington DC: Island Press. 3–21.
- Linares-Palomino R, Pennington RT, Bridgewater S. 2003. The phylogeography of the seasonally dry tropical forests in Equatorial Pacific South America. *Candollea* 58: 473–499.
- Lörch M, Mutke J, Weigend M, Luebert F. 2021. Historical biogeography and climatic differentiation of the *Fulcaldea-Archidasphyllum-Arnaldoa* clade of *Barnadesioideae* (Asteraceae) suggest a Miocene, aridity-mediated Andean disjunction associated with climatic niche shifts. *Global and Planetary Change* 201: 103495.
- Luebert F. 2021. The two South American dry diagonals. *Frontiers of Biogeography* 13(4): e51267.
- Luebert F, Weigend M. 2014. Phylogenetic insights into Andean plant diversification. *Frontiers in Ecology and Evolution* 2: 1–17.
- Lundgren MR, Besnard G, Ripley BS, Lehmann CER, Chatelet DS, Kynast RG, Namaganda M, Vorontsova MS, Hall RC, Elia J, Osborne CP, Christin P-A. 2015. Photosynthetic innovation broadens the niche within a single species. *Ecology Letters* 18: 1021–1029.
- Maddison WP, Midford PE, Otto SP. 2007. Estimating a binary character's effect on speciation and extinction. *Systematic Biology* 56(5): 701–710.
- Matzke NJ. 2013. *BioGeoBEARS: BioGeography with Bayesian (and likelihood) evolutionary analysis in R scripts*. Berkeley, CA: University of California.
- Matzke NJ. 2014. Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Systematic Biology* 63: 951–970.
- Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. *Gateway computing environments workshop (GCE)*. 1–8.
- Moreira-Muñoz A, Scherson RA, Luebert F, Román MJ, Monge M, Diazgranados M, Silva H. 2020. Biogeography, phylogenetic relationships, and morphological analyses of the South American genus *Mutisia* L.f. (Asteraceae) shows early connections of two disjunct biodiversity hotspots. *Organisms Diversity and Evolution* 20: 639–656.
- Olson DM, Dinerstein E, Wikramanayake ED, Burgess ND, Powell GV, Underwood EC, D'Amico JA, Itoua I, Strand HE, Morrison JC, Loucks CJ, Allnutt TF, Ricketts TH, Kura Y, Lamoreux JF, Wettengel WW, Hedao P, Kassem KR. 2001. Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51: 933–938.

- Ortiz-Jaureguizar E, Cladera GA. 2006. Paleoenvironmental evolution of southern South America during the Cenozoic. *Journal of Arid Environments* 66: 498–532.
- Ortuño T, Borsch T. 2020. *Gomphrena* (Amaranthaceae, Gomphrenoideae) diversified as a C_4 lineage in the New World tropics with specializations in floral and inflorescence morphology, and an escape to Australia. *Willdenowia* 50: 345–381.
- Osborne CP, Beerling DJ. 2006. Nature's green revolution: The remarkable evolutionary rise of C_4 plants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 361: 173–194.
- Palmer J. 1998. A taxonomic revision of *Gomphrena* (Amaranthaceae) in Australia. *Australian Systematic Botany* 11(1): 73–151.
- Pennell MW, Eastman JM, Slater GJ, Brown JW, Uyeda JC, FitzJohn RG, Alfaro ME, Harmon LJ. 2014. geiger v2. 0: An expanded suite of methods for fitting macroevolutionary models to phylogenetic trees. *Bioinformatics* 30: 2216–2218.
- Pedersen TM. 2016. Amaranthaceae. In: Ramella L ed. *Flora del Paraguay*. Genève. Ville de Genève: Conservatoire et Jardin botaniques. 9–256.
- Pennington RT, Lavin M, Oliveira-Filho A. 2009. Woody plant diversity, evolution, and ecology in the tropics: Perspectives from seasonally dry tropical forests. *Annual Review of Ecology, Evolution and Systematics* 40: 437–457.
- Pérez-Escobar OA, Zizka A, Bermúdez MA, Meseguer AS, Condamine FL, Hoorn C, Hooghiemstra H, Pu Y, Bogarín D, Boschman LM, Pennington RT, Antonelli A, Chomicki G. 2022. The Andes through time: Evolution and distribution of Andean floras. *Trends in Plant Science* 27: 364–378.
- Posada D, Crandall KA. 1998. MODELTEST: Testing the model of DNA substitution. *Bioinformatics* 14: 817–818.
- Prado DE. 2000. Seasonally dry forests of tropical South America: From forgotten ecosystems to a new phytogeographic unit. *Edinburgh Journal of Botany* 57: 437–461.
- Prado DE. 2003. As caatingas da América do Sul. *Ecologia e conservação da Caatinga* 2: 3–74.
- Prado DE, Gibbs PE. 1993. Patterns of species distributions in the dry seasonal forests of South America. *Annals of the Missouri Botanical Garden* 80(4): 902–927.
- QGIS. 2009. Geographic Information System. QGIS Association [online]. Available from <http://www.qgis.org>
- Rabassa J. 2008. Late cenozoic glaciations in Patagonia and Tierra del Fuego. *Developments in Quaternary Sciences* 11: 151–204.
- Rambaut A, Drummond AJ, Xie D, Baele G, Suchard MA. 2018. Posterior summarization in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67: 901–904.
- Ree RH, Smith SA. 2008. Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Systematic Biology* 57: 4–14.
- Reginato M, Michelangeli FA. 2019. Pleistocene range expansions might explain striking disjunctions between eastern Brazil, Andes and Mesoamerica in *Leandra* s.str. (Melastomataceae). *Journal of Systematics and Evolution* 57: 646–654.
- Revell LJ. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution* 2: 217–223.
- Ronquist F. 1997. Dispersal-vicariance analysis: A new approach to the quantification of historical biogeography. *Systematic Biology* 46: 195–203.
- Sage RF. 2016. A portrait of the C_4 photosynthetic family on the 50th anniversary of its discovery: Species number, evolutionary lineages, and Hall of Fame. *Journal of Experimental Botany* 67: 4039–4056.
- Salariato DL, Trinidad H, Cano A, Zuloaga FO, Al-Shehbaz IA. 2022. Interplay between conservatism and divergence in climatic niche evolution of Brassicaceae tribe Eudemeae shaped their distribution across the different environments of the Andes. *Botanical Journal of the Linnean Society* 200: 314–343.
- Sarmiento G. 1975. The dry plant formations of South America and their floristic connections. *Journal of Biogeography* 2(4): 233–251.
- Schmidt KP, Inger RF. 1951. Amphibians and reptiles of the Hopkins-Branner expedition to Brazil. *Fieldiana Zoologica* 31: 439–465.
- Senna L, de Siqueira JC, Marchioreto MS. 2015. *Gomphrena*. In: Lista de Espécies da Flora do Brasil. Jardim Botânico do Rio de Janeiro [online]. Available from <https://floradobrasil.jbrj.gov.br/> [accessed 15 November 2021].
- Simpson BB. 1983. An historical phytogeography of the high Andean flora. *Revista Chilena de Historia Natural* 56(10): 109–122.
- Townsend CC. 1993. Amaranthaceae. In: Kubitzki K ed. *Families and genera of vascular plants*. Berlin: Springer. 2: 70–91.
- Trujillo-Arias N, Calderón L, Santos FR, Miyaki CY, Aleixo A, Witt CC, Tubaro PL, Cabanne GS. 2018. Forest corridors between the central Andes and the southern Atlantic Forest enabled dispersal and peripatric diversification without niche divergence in a passerine. *Molecular Phylogenetics and Evolution* 128: 221–232.
- The United Nations Environment Programme (UNEP). 1993. *World Atlas of desertification*. London: The United Nations Environment Programme.
- Vaissi S. 2022. The role of climatic niche divergence in the speciation of the genus *Neurergus*: An inter- and intraspecific survey. *Evolutionary Ecology* 36: 389–407.
- Vanzolini PE. 1963. Problemas faunísticos do Cerrado. *Simpósio sobre o Cerrado* 307: 1.
- Vilhalva DAA, Appezzato-da-Glória B. 2006. Morfo-anatomia do sistema subterrâneo de *Calea verticillata* (Klatt) Pruski e *Isostigma megapotamicum* (Spreng.) Sherff—Asteraceae. *Revista Brasileira de Botânica* 29: 39–47.
- Wang Q, Abbott RJ, Yu QS, Lin K, Liu JQ. 2013. Pleistocene climate change and the origin of two desert plant species, *Pugionium cornutum* and *Pugionium dolabratum* (Brassicaceae), in north-west China. *New Phytologist* 199: 277–287.
- Werneck FP. 2011. The diversification of eastern South American open vegetation biomes: Historical biogeography and perspectives. *Quaternary Science Reviews* 30: 1630–1648.
- Yang J, Twohey P, Engler D, Musuvathi M. 2006. Using model checking to find serious file system errors. *ACM Transactions on Computer Systems* 24: 393–423.
- Zachos J, Pagani M, Sloan L, Thomas E, Billups K. 2001. Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* 292: 686–693.
- Zanella FCV, Martins FC. 2003. Abelhas da Caatinga: biogeografia, ecologia e conservação. In: Leal IR, Tabarelli M, Silva JMC eds. *Ecologia e conservação da Caatinga*. Recife: Editora Universitária da UFPE. 75–134.
- Zuloaga F, Morrone O, Davidse G, Pennington S. 2007. Classification and Biogeography of Panicoideae (Poaceae) in the New World. *Aliso* 23(1): 503–529.

Supplementary Material

The following supplementary material is available online for this article at <http://onlinelibrary.wiley.com/doi/10.1111/jse.13023/supinfo>:

Fig. S1. Extended phylogeny of the Gomphrenoideae subfamily and allies showing divergence times and 95% highest posterior densities intervals (blue bars). Numbers above branches indicate posterior probabilities, and below branches indicate node ages. Only nodes with posterior probability ≥ 0.7 are shown. The shaded area indicates the *Gomphrena* s.str. Clade. Secondary calibration points are marked with an arrow.

Fig. S2. Character mapping of the photosynthetic pathway over the maximum clade credibility tree, obtained from Simmap.

Fig. S3. Probabilities at nodes of being annual or perennial retrieved from the Simmap analyses over 1000 randomly selected trees. C₃ clade; BW, broad western clade; ED, eastern distributed clade; WH, western highlands clade; WL, western lowlands clade.

Fig. S4. Posterior probability distribution of speciation, extinction, and transition rates for the photosynthetic pathway. Posterior distributions were computed using Markov chain Monte Carlo analysis for the best-fitting Bisse model. Bars below each distribution correspond to the shaded area and represent the 95% confidence interval of each estimated parameter.

Table S1. (a) GenBank accession numbers for Amaranthaceae s.l. from the extended data set and the Australian species of *Gomphrena* (indicated with an asterisk). Subfamily and tribe classification follows Townsend (1993); (b) GenBank accession numbers, morphological, physiological traits, and distribution information of the American *Gomphrena* s.str. and its sister lineage (*Guilleminea* clade).

Table S2. Ecorregions (Olson et al., 2001), aridity (according to United Nations Environment Programme aridity index,

UNEP), and elevation values, considered to perform the bioregionalization of the species occurrences and the consequent estimation of the ancestral ranges.

Table S3. Probabilities at nodes from ancestral-states reconstructions over the 1,000 trees sampled, (a) model-averaged probabilities at the main nodes, obtained by integrating the three models according to their corrected Akaike information criterion weights. Posterior probability > 0.5 for each node are highlighted in bold; (b) distribution of probabilities for the trait “habit”; and (c) distribution of probabilities for the trait “photosynthesis”, among the sampled trees, segregated by each model. Node names are BW, broad western; ED, eastern-distributed; WH, western highlands; WL, western lowlands. See Fig. S2 for further numerical node codes.

Table S4. Clades in which a shift in the net diversification rate (r) was modeled in at least 30% of the trees (of 1000 total) in MEDUSA analyses. Values of r are interpreted as net speciation events per million years.

Table S5. Model fit comparisons of the Bisse analyses for the trait “habit.” For each model, we denote the degrees of freedom (DF), the log-likelihood (logLik), the Akaike information criterion corrected for sample size (corrected Akaike information criterion [AICc]), the Δ AIC, the Akaike weights (AICw), and the model parameters values: speciation (λ), extinction (μ), and transitions (q) rates (in Ma^{-1}) for states 0 (annual) and 1 (perennial). The best-fit model is highlighted in bold, identified by the lowest AICc and Δ AIC = 0.