

Resource availability and disturbance frequency shape evolution of plant life forms in Neotropical habitats

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Summary

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Received: 10 October 2023

Accepted: 30 January 2024

New Phytologist (2024)
doi: 10.1111/nph.19601

Key words: adaptation, *Chamaecrista*, climate, ecological opportunity, legumes, macroevolution, niche, South America.

- Organisms use diverse strategies to thrive in varying habitats. While life history theory partly explains these relationships, the combined impact of resource availability and disturbance frequency on life form strategy evolution has received limited attention.
- We use *Chamaecrista* species, a legume plant lineage with a high diversity of plant life forms in the Neotropics, and employ ecological niche modeling and comparative phylogenetic methods to examine the correlated evolution of plant life forms and environmental niches.
- Chamaephytes and phanerophytes have optima in environments characterized by moderate water and nutrient availability coupled with infrequent fire disturbances. By contrast, annual plants thrive in environments with scarce water and nutrients, alongside frequent fire disturbances. Similarly, geophyte species also show increased resistance to frequent fire disturbances, although they thrive in resource-rich environments.
- Our findings shed light on the evolution of plant strategies along environmental gradients, highlighting that annuals and geophytes respond differently to high incidences of fire disturbances, with one enduring it as seeds in a resource-limited habitat and the other relying on reserves and root resprouting systems in resource-abundant habitats. Furthermore, it deepens our understanding of how organisms evolve associated with their habitats, emphasizing a constraint posed by low-resource and high-disturbance environments.

Introduction

Plant form and function are exceptionally diverse in the tropics, but are unevenly spread across environmental gradients (Schulze, 1982; Ewel & Bigelow, 1996; Westoby *et al.*, 2002; Díaz *et al.*, 2016). The plant strategy theory predicts that plants have a set of functional features composing different strategies to survive in environments with varying resource availability and disturbance frequency (Grime, 1977). For instance, habitats that restrict biomass production due to low water and nutrient availability are often inhabited by plants with stress-tolerant strategies. Stress-tolerant plants are often perennial and grow slowly, keeping their organs for long periods. They often have some resource storage strategy, thus maximizing resource exploitation under temporarily favourable conditions (Grime, 1977). On the other hand, habitats that impose frequent losses of plant biomass via disturbance, such as fire or herbivory, are often inhabited by plants with a ruderal strategy. Ruderal plants, commonly annual plant species, are short-lived and grow fast, maximizing seed production over biomass accumulation (Grime, 1977; Friedman,

2020). Alternatively, disturbance-prone habitats are also often inhabited by plants with larger storage tissues, commonly underground organs, such as rhizomes, lignotubers, and xylospodia with a higher capacity to resprout (Bellingham & Sparrow, 2000; Pausas & Keeley, 2014). Finally, plants with competitor strategies inhabit habitats with greater resource availability and less disturbance frequency. These plants can obtain resources from the environment quickly and have a high investment in biomass, and most have a significant investment in height growing (Grime, 1977).

The traditional plant life form classification (Raunkjaer, 1934) has been commonly used as a proxy to plant strategies, allowing to test hypotheses regarding the relationship between habitats and plant traits (Schulze, 1982; Irl *et al.*, 2020; Shary *et al.*, 2020; Boyko *et al.*, 2023). This classification summarizes structural and functional traits that indicate habitat preferences and ecological and resistance plant strategies. For instance, therophytes life forms, here also called annual life forms, have rapid growth and greater investment in rapid reproduction that allow these species to escape disturbance events or unfavourable periods

over the year, such as dry seasons, through a high production of dormant seeds that germinate when favourable periods return (Friedman, 2020). Thus, annual life forms can also be classified as stressor escape because their life cycle is adjusted when environmental conditions favour their growth and reproduction (Bandurska, 2022). However, short growing seasons or frequent disturbances may prevent seed formation, so annual forms become less fit, and other life forms, like geophyte forms with underground buds and storage systems, can reach higher success under these conditions (Chapman & Crow, 1981; Tonnabel *et al.*, 2018). The water and photosynthates stored in the underground organs allow germinating buds to retake growth and biomass accumulation after disturbances (da Silva & Rossatto, 2019), favouring plant survival when resource availability is seasonally limited (Pausas *et al.*, 2018). Water and nutrient storage in the underground system of geophytes constitutes a stress avoidance strategy, preventing disruption in plant cells during unfavourable periods (Bandurska, 2022). On the other hand, nongeophytic perennial life forms that increase biomass allocation in height growth, such as chamaephytes and phanerophytes, are mainly found in habitats with high water availability and low disturbance intensity (Grime, 1977; Irl *et al.*, 2020). These habitats favour competitive strategies with plants with greater height investment, having more light acquisition and advantages over other plant life forms that do not invest in height growth (Schulze, 1982; Rees & Long, 1992).

Associations between plant life forms and habitats with varying resource availabilities and disturbance intensity have also been observed at the macroevolutionary scale. For instance, a recent multi-clade analysis revealed that annual life forms more often evolve in habitats prone to extreme heat (Boyko *et al.*, 2023). Similarly, the evolution of annual life forms among *Oenothera* species is associated with the occupation of arid regions (Evans *et al.*, 2005). Furthermore, the evolution of perennial forms during Montiaceae diversification is related to the occupation of montane habitats, where colder conditions limit biomass production (Ogburn & Edwards, 2015). Also, resprouting life forms in *Leucadendron*, *Mimosa*, and *Andira* evolved under increased fire frequency (Simon *et al.*, 2009; Tonnabel *et al.*, 2018). While there are insightful studies, the evolutionary dynamics of plant life forms and their environmental niches remain understudied, especially in the Neotropics. In addition to a few studies, it is necessary to detect potential limitations in the procedures adopted so far. For example, the dichotomy between annuals and perennials may be simplistic to capture specific correlation patterns between environmental features and life forms. For instance, certain environmental conditions, such as disturbance frequency, may select annuals and perennials with a resprouting strategy while excluding nonresprouting perennials (Keeley *et al.*, 2011). Moreover, different plant life forms can also evolve in response to multiple factors, including frequent disturbances in fire-prone habitats, leading to biomass loss and variable environmental resource availability, such as water and soil nitrogen, which could constrain plant biomass production. The impact of multiple environmental gradients on the evolution of life history strategies in plants, particularly whether they correlate with the

evolution of annuals, nonresprouting, and resprouting perennials, has been seldom explored, highlighting the existing knowledge gap.

The Neotropical region encompasses a wide range of environmental gradients and an enormous plant diversity (Hughes *et al.*, 2013; Morrone, 2014). The Neotropical flora is estimated to include c. 118 000 species of vascular plants (Raven *et al.*, 2020). This region encompasses a mosaic of physiognomies and habitats, spanning from tropical forests within the Amazonian domain to seasonally dry and warm forests in the Caatinga domain, and further to the climatically seasonal, rockier, and nutrient-poor soils found in the *Campos Rupestres* ('rocky fields') (Hughes *et al.*, 2013). Furthermore, the eastern Neotropics, that is the Chacoan subregion (Morrone *et al.*, 2022), have undergone significant climatic shifts in the last 30 million years (Myr), including glaciations and the Open Diagonal formation, a region with seasonal rainfall that stretches from northeastern Brazil to northern Argentina (Lavina & Fauth, 2011). In addition, some areas of the Neotropics have high endemism, such as the *Campos Rupestres*, a mountainous region in eastern Brazil recognized for its high floristic singularity (Colli-Silva *et al.*, 2019). This region harbours c. 5000 species (Silveira *et al.*, 2016; BFG *et al.*, 2018) with various life forms, including resprouting, shrub, and herbaceous species (Rapini *et al.*, 2008). Despite this vast floristic diversity in the Chacoan subregion, little is known about how evolutionary processes have shaped the evolution of the environmental niche and life form in diversified plant lineages.

This study explores a *Chamaecrista* lineage (Fabaceae) mainly occurring in the Chacoan subregion (Fig. 1a) to investigate whether plant life form evolution is associated with distinct changes in environmental niches. As each plant life form represents a distinct set of traits reflecting a plant strategy to inhabit different parts of environmental gradients, our general hypothesis is that the evolution of plant life forms occurs jointly with the evolution of the environmental niche. In this case, we would expect an absence of environmental niche conservatism (Crisp & Cook, 2012) since descendant lineages would occupy distinct environmental conditions from their ancestors due to transitions associated with the evolution of life forms. More specifically, we hypothesize that (1) Life forms with short-lived and lower biomass production, such as annual species, are evolutionarily correlated with seasonal environments with less resource availability over time, while perennial species with higher biomass production are evolutionarily associated with environments having greater resource availability; (2) Life forms with escape or avoidance strategies, such as rapid seed production in annuals or large underground storage systems in geophytes, are evolutionarily associated with environments having a higher disturbance frequency and less water availability during the dry season than species lacking these resistance strategies. Based on these hypotheses, we constructed three evolutionary predictions (see the *Materials and Methods* section) connecting the occupation of distinct environmental conditions with transitions across the four life forms found in *Chamaecrista*. Our primary motivation is to bridge a gap in understanding the evolution of multiple life forms across variable environmental and disturbance gradients.

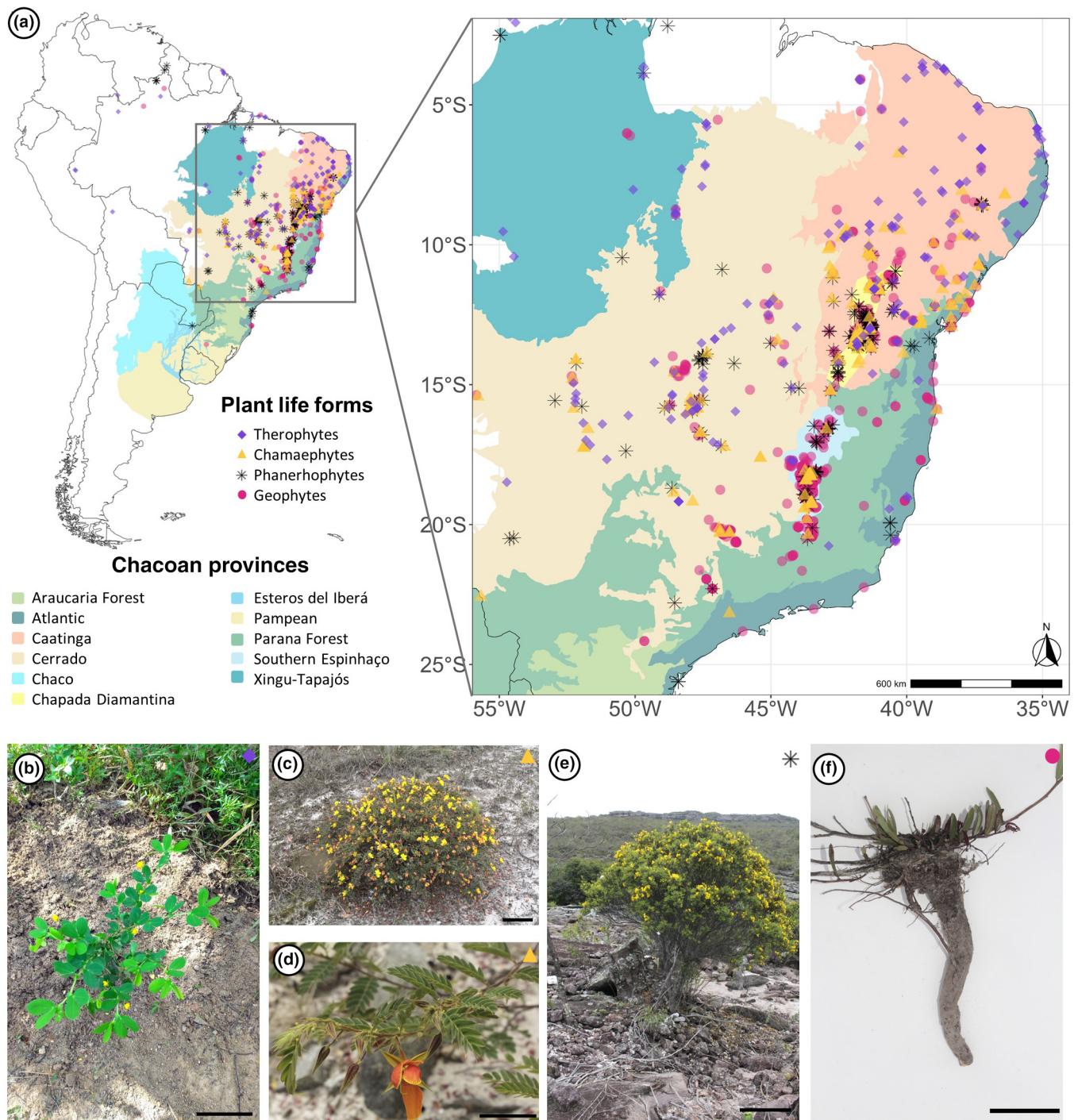


Fig. 1 The Chacoan subregion in the Neotropics and its provinces, as defined by Morrone (2014) and updated by Morrone *et al.* (2022), showing the distribution of occurrences of *Chamaecrista* species with different life forms. (a) Plant life form distribution along the provinces in the Chacoan subregion. Each colour in the map corresponds to a province, and each symbol corresponds to a different plant life form occurrence. The Campo rupestre vegetation includes the Chapada Diamantina and Southern Espinhaço provinces. (b) *Chamaecrista rotundifolia* (Pers.) Greene, a therophyte species. (c) *Chamaecrista ramosa* (Vogel) H.S.Irwin & Barneby, a chamaephyte species. (d) *Chamaecrista pascuorum* (Benth.) H.S.Irwin & Barneby, a chamaephyte species. (e) *Chamaecrista confertiformis* (H.S. Irwin & Barneby) Conc., L.P. Queiroz & G.P. Lewis, a phanerophyte species. (f) *Chamaecrista simpliflacta* H.S.Irwin & Barneby, a geophyte species. The xylopodium in the *C. simpliflacta* is a large woody underground structure. Bars: (b, c) 8.0 cm; (d) 3.0 cm; (e) 50.0 cm; (f) 10.0 cm.

Materials and Methods

Study group and phylogenetic background

Our study group is a lineage within *Chamaecrista* (L.) Moench (Fabaceae) encompassing 135 species (section *Baseophyllum* and section *Chamaecrista*) (Souza *et al.*, 2021), of which 68 occur in South America. This group includes sub-shrubs, shrubs, and tree species (Souza *et al.*, 2021), with many plant life forms (Fig. 1b–f). Some species have xylopodium, underground woody systems that harbour germinating buds, thus becoming able to regrow after disturbance events (Conceição *et al.*, 2009; Rando *et al.*, 2016; Souza *et al.*, 2021). This *Chamaecrista* lineage has diversified in the last 30 Myr (Rando *et al.*, 2016), likely originating in the Neotropics. In addition to the diversity of plant structure, species diversification occurred in the Chacoan subregion in the Neotropics (Fig. 1a). This region has a variety of ecosystems with wide environmental variation (Hughes *et al.*, 2013; Morrone, 2014).

We used a sample of 200 dated phylogenetic trees from the posterior distribution inferred in the Bayesian analysis (Vasconcelos *et al.*, 2020). This phylogenetic hypothesis is the most comprehensive dated tree available for the group, which used four molecular markers including 49 species (Rando *et al.*, 2016; Vasconcelos *et al.*, 2020). Divergence time was estimated using two calibration points (Rando *et al.*, 2016; Vasconcelos *et al.*, 2020). We pruned our sample of phylogenetic trees to our study group, sections *Baseophyllum*, and *Chamaecrista*, removing two species not occurring in South America. These two species (*C. caribae* (Northr.) Britton and *C. lineata* (Sw.) Greene) derived from a single dispersal event from South to Central America (Souza *et al.*, 2021), and have little relevance to understanding how the group evolved in South America. We retained a single terminal under *C. nictitans* (L.) Moench, eliminating a taxonomic synonym and two varieties due to the difficulty in recognizing and potential misidentification of infraspecific taxa (BFG *et al.*, 2022). Although infraspecific taxa commonly do not hold an evolutionary meaning (Hamilton & Reichard, 1992), this is often not the case in species-rich genera in the Neotropics, especially in the genus *Chamaecrista* (Baker-Méio & Marquis, 2012). Therefore, we kept some varieties in the phylogeny precisely because they indicate distinct evolutionary lineages, as in *C. tragacanthoides* var. *rasa* H.S.Irwin & Barneby and *C. tragacanthoides* (Mart. ex Benth.) H.S.Irwin & Barneby var. *tragacanthoides* or when varieties have different life forms (e.g. *C. desvauxii* varieties). In summary, the phylogenetic trees of *Chamaecrista* remained with 44 taxa. The name and authorship of all species used here are in Supporting Information Table S1.

Plant life form classification

We used the same classification utilized by Irl *et al.* (2020), which is an adaptation to the Raunkiaer system to classify *Chamaecrista* species into plant life forms. Hence, we considered four plant life forms:

(1) Therophyte: Annual woody plants whose shoot and root systems die after completing their life cycle, including seed production, in the favourable season of a single year.

- (2) Chamaephyte: Perennial woody plants smaller than 50 cm.
- (3) Phanerophyte: Perennial woody plants taller than 50 cm.
- (4) Geophyte: Perennial woody plants with reduced shoot system and developed root system that holds underground storage organs.

Our study considered *Chamaecrista* species as geophytes if plants have extensive woody root-holding buds, that is xylopodium (Conceição *et al.*, 2009; Rando *et al.*, 2016; Souza *et al.*, 2021). To classify species into those categories, we utilized the information provided by taxonomic revisions and other studies on *Chamaecrista*. The plant life form classification and the references used are in Table S1.

Characterizing environmental niches

To test our hypotheses linking plant life form evolution with environmental niche changes, we first characterize the species' β niche. The β niche is defined as macrohabitat and climate factors influencing larger-scale species distributions (Ackerly *et al.*, 2006). To do this, we use species occurrence data and environmental variables to build ecological niche models. The georeferenced occurrence data for species was extracted from three online databases: Global Biodiversity Information Facility (GBIF) (<http://gbif.org>), Reflora Virtual Herbarium (<http://reflora.jbrj.gov.br>), and Environmental Information Reference Center (<http://splink.cria.org.br>). The cleaning procedure in the occurrence data involved several filter steps that aimed to improve the final dataset, removing: (1) duplicate records, (2) records without expert identification, and (3) records missing accurate geographic information, that is missing or incorrect geographic coordinates or noninformed sampling locality (see Methods S1 for details on filters). After cleaning, we checked all occurrences on Google Earth to verify their plausibility. We also selected 10 environmental variables that characterize climatic, edaphic, and disturbance conditions that could potentially influence the niche occupation of each species. The spatial resolution used in environmental variables was 30 s (*c.* 1 km²). The 10 selected variables represented environmental gradients that can impact plant fitness via resource availability (water and nutrients), metabolic rates (temperature), and survival rates (fire frequency) (Guisan & Zimmermann, 2000; Mod *et al.*, 2016). Details of each environmental layer used in modelling are in Methods S1.

We built environmental niche models using the maximum entropy algorithm implemented in the MAXENT 3.4.4 (Phillips *et al.*, 2006; Phillips & Dudík, 2008). Maxent is an algorithm that uses species occurrence data and environmental variables to predict the environment suitability score of an area (Phillips *et al.*, 2006; Phillips & Dudík, 2008). We choose Maxent as a modelling algorithm because it is recognized for good results in inferring species niches (Searcy & Shaffer, 2016; Ray *et al.*, 2018; Ahmadi *et al.*, 2023), including in studies investigating niche evolution (Evans *et al.*, 2009; Mitchell *et al.*, 2018; Goren *et al.*, 2019; Grant & Kalisz, 2020). The Maxent algorithm uses the environmental layers to extract the environmental values in occurrence data and to create a background sample. Considering that the models would be built for multiple species and would

later be compared with each other and that the predicted suitability map generated by MAXENT with random background or by background weighting is consistent and comparable (Ahmadi *et al.*, 2023), we built our models with 10 thousand background points spread over our study area, that is South America. We excluded species with fewer than three occurrences, resulting in the removal of three species (*C. coriacea* (Benth.) H.S.Irwin & Barneby, *C. cytisoides* (DC. ex Collad.) H.S.Irwin & Barneby, and *C. unijuga* (Benth.) Conc., L.P. Queiroz & G.P. Lewis) from the phylogenetic trees. This left us with 41 taxa for modelling procedures and subsequent comparative phylogenetic analyses. As most species had few occurrences (mean occurrences per species = 30.19, SD = 19.60), we only utilized the ‘linear’ and ‘quadratic’ features in Maxent (Elith *et al.*, 2011). To avoid spatial pseudoreplication (Guisan *et al.*, 2017), we excluded occurrences in the same grid cell for each species. In summary, we used 1238 occurrences in the models. The species with the highest occurrences was *C. blanchetii* (Benth.) Conc., L.P. Queiroz & G.P. Lewis (82 occurrences), and the species with the lowest occurrences was *C. anceps* (Benth.) H.S.Irwin & Barneby (three occurrences). We evaluated models by cross-validation procedures, utilizing two metrics for model predictive performance. For species with > 10 occurrences, we applied 10-replicate cross-validation, splitting our occurrence data into training and testing and averaging AUC values over replicates. Average AUC values > 0.75 were considered a reliable predictive performance (Phillips & Dudík, 2008). For species with occurrences between 3 and 10, we applied a cross-validation with replicates equal to the number of occurrences. We then evaluated models by their average AUC values and the statistical tests proposed by (Pearson *et al.*, 2007), whose significant results indicated a reliable predictive performance. All details of environmental niche modelling and their results are provided in Methods S1.

The predicted suitability map generated by Maxent is a proxy for the environmental conditions necessary for a species to live and reproduce. Therefore, we can use it to quantify species’ tolerance or occupancy along species’ different environmental dimensions (Evans *et al.*, 2009; Warren, 2012). We used the quantitative metrics described by Evans *et al.* (2009) to extract the predicted niche occupancy profile of the species for the four environmental niche dimensions (Table 1). The predicted niche profile is a quantitative metric used to extract the environmental values from the suitability map, considering the probability of the species occurring in the study area (Evans *et al.*, 2009). We applied this procedure using the ‘pno’ function in the PHYLOCIM package (Heibl & Calenge, 2018).

Estimating the evolution of environmental niche

Our main hypothesis posits nonconservative evolution of species’ environmental niches. Initially, we assessed whether environmental niches were evolutionarily conserved in our study group using Warren *et al.* (2008) comparative methods. We employed the D and I metrics, measuring niche overlap on suitability map generated by environmental niche models. The D and I metrics vary from ‘0’ (no overlap) to ‘1’ (total overlap). D metric is based on

ecological literature and corresponds to Schoener’s (1968) statistic, while I metric is based on Hellinger distance (Warren *et al.*, 2008). Both metrics were chosen because, unlike D, the I metric do not carry any biological assumptions concerning the meaning of local species densities. We assessed niche evolution over the four environmental gradients by quantifying D and I metrics on niche occupancy profiles for each niche dimension (‘Characterizing environmental niches’ in the Materials and Methods section). To quantify niche conservatism, we calculated the age range correlation (ARC) between niche overlap metrics (D and I) and species divergence time (Fitzpatrick & Turelli, 2006; Warren *et al.*, 2008) using the ‘niche.overlap’ and ‘age.range.correlation’ functions in the PHYLOCIM package (Heibl & Calenge, 2018).

Estimating the evolution of plant life forms

To estimate the ancestral plant life forms in our study group, we used a Bayesian approach with stochastic character mapping (SIMMAP) (Bollback, 2006). First, we assessed which macroevolutionary model would better fit the evolution of plant life forms in each phylogenetic tree using the ‘corHMM’ function in the CORHMM package (Boyko & Beaulieu, 2021). This function was utilized to calculate maximum likelihood estimates of transition rates between life forms. In some models, we incorporated the ‘hidden’ rate changes (Boyko & Beaulieu, 2021). Altogether, we created nine models by adjusting the transition (Q) matrix. The initial three models assumed either equal (ER model), symmetric (SYM), or completely variable (ARD model) transition rates, presuming homogeneity in generating distinct states at the tips and ancestral nodes along the branches of the *Chamaecrista* clade. The subsequent six models incorporated heterogeneity – hidden rate changes – allowing multiple processes to influence plant life form evolution across the phylogeny. In these models, we included two rate categories (i.e. transition matrices), permitting variations between subclades in the phylogeny (R1 and R2, rate.cat = 2). Among them, the first models encompassed two equal-rate (ER/ER model), two symmetric-rate (SYM/SYM), and two all-different-rate (ARD/ARD model) matrices. We also constructed three mixed models: ER/SYM, ER/ARD, and SYM/ARD two-matrices. In all hidden rate change models, we allowed differences in the transitions between rate categories (R1 \rightarrow R2 and R2 \rightarrow R1). We selected the best-fit model by comparing the AICc values of each model in each phylogenetic tree (Burnham & Anderson, 2002).

In 99.5% of phylogenetic trees (199 of 200), the simplest ER model (equal rates without hidden rate changes) was selected as the best macroevolutionary model. Therefore, this model was used to reconstruct the ancestral state of plant life forms. To incorporate the uncertainty of phylogenetic reconstructions into ancestral state estimates, we generated 2000 stochastic character maps (SIMMAPs), 10 SIMMAPs for each phylogenetic tree under the ER model using the make.simmap function implemented in phytools (Revell, 2012). We used the ‘describe.simmap’ in the PHYTOOLS R package to summarize SIMMAP estimates (Revell, 2012).

Table 1 The four environmental niche axes used to quantify species' occupancy following Evans *et al.* (2009).

Code	Environmental variable	Biological interpretation	References
Bio18	Precipitation of the warmest quarter (mm)	Water availability during the plant growth period	Fick & Hijmans (2017)
Nitrogen	Nitrogen concentration in the first 30-cm soil profile (cg kg^{-1})	Soil nitrogen availability	Poggio <i>et al.</i> (2021)
Bio17	Precipitation of the driest quarter (mm)	Water deficit in dry season	Fick & Hijmans (2017)
Fire	Average annual fire frequency between the years 1999–2019 (number of fires yr^{-1})	Frequency of disturbances (plant aerial part loss)	BD Queimadas – INPE (https://queimadas.dgi.inpe.br/)

Evolutionary correlation between plant life form and environmental niche

We tested the evolutionary correlation between plant life forms and disturbance frequency and resource availability (see predictions in Table 2) using a model selection framework comparing different evolutionary models for continuous-scaled traits (Beaulieu *et al.*, 2012). As we are interested in investigating whether the evolution of different life forms is associated with the occupation of different environments, we modelled the evolution of niche occupancy (continuous traits) as a function of plant life forms (discrete traits). First, we transformed niche occupancy profiles (see 'Characterizing environmental niches' in the Materials and Methods section) to a natural logarithm scale. A natural logarithm scale is recommended because the phenotypic changes among species are represented proportionally (Harmon, 2018). Also, natural-log values better conform to the Brownian motion, an assumption underlying evolutionary models (O'Meara *et al.*, 2006; Harmon, 2018; Vasconcelos *et al.*, 2021). Second, we sampled 500 values of each environmental variable (Table 1) based on the probability of species' profile niche occupancy. We then calculated the mean and standard error for each environmental variable using our occupancy values samples, assigning a unique value to each species. Hence, we analysed continuous trait evolution in terms of the proportionality of changes over mean occupancy values. As for the discrete traits, we use each of the 2000 SIMMAP's to represent the estimated ancestral life form on nodes of phylogenetic trees.

We considered seven evolutionary models: two based on the Brownian motion (BM) and five based on the Ornstein–Uhlenbeck (OU) process. BM models essentially describe stochastic processes, that is when the phylogenetic distance among species explains the difference between species' traits. At the same time, OU models describe stochastic processes with additional directional processes, such as stabilizing selection or constraints. We also included the White noise (WN) model as the null model in our selection procedure to verify whether our data have no phylogenetic structure and whether trait values vary around a global mean (Cooper *et al.*, 2016; see also Grabowski *et al.*, 2023 for a fruitful discussion about the use of OU models). We fitted the evolutionary models to our data by utilizing the 'OUwie' function in the OUWIE package, and the null model was fitted with the 'fitContinuos' function in the GEIGER package. All models were fitted to all 2000 estimates of plant life forms evolution.

BM models assume that the traits evolve via stochastic changes over time, a process whose intensity is given by an evolutionary rate

(σ^2) (Harmon, 2018). OU models also assume that the traits evolve via stochastic changes over time, but they additionally consider directional changes towards some optimum value (θ) under some attraction force (α), thus restricting trait values around an optimum value (Beaulieu *et al.*, 2012). The seven evolutionary models applied to the data were: BM1, BM model with a single σ^2 value for all life forms; BMS, BM model with distinct σ^2 values for each life form; OU1, OU model with a single σ^2 , α and θ values for all life forms; OUM, OU model with a single σ^2 and α values for all life forms, but with distinct θ values for each life form; OUMA, OU model with a single σ^2 value for all life forms, but with distinct α and θ values for each life form; OUMV, OU model with a single α value for all life forms, but with distinct σ^2 and θ values for each life form; and OUMVA, OU model with distinct σ^2 , α and θ values for each life form (Beaulieu *et al.*, 2012). The best fit under BM or OU1 models would indicate that plant life forms and environmental niche optima have evolved independently in the study plant lineage. On the other hand, the best fit under the OUM, OUMA, OUMV, or OUMVA models would indicate plant life forms and environmental niche optima are evolutionarily correlated in the studied plant lineage. Finally, the best fit under the WN model would indicate that niche evolution is not associated with the lineage's evolutionary history.

To evaluate model reliability, we checked model estimates. We removed those that were biologically unrealistic, that is those that estimate the optimum value (θ) parameter outside the range of values occupied by species. We also checked the Hessian matrix associated with each model and discarded those with negative eigenvalues (Beaulieu *et al.*, 2012). Then, we evaluated the model fit to our data by the ΔAIC_c . We considered the lowest ΔAIC_c as the best fit. When ΔAIC_c difference between the best and second best models was smaller than two units, we consider it a tie and do not choose any model as the best (Burnham & Anderson, 2002; Alencar *et al.*, 2017). After evaluating model reliability and fit, we analysed parameter estimates under the best-fit model in each SIMMAP to verify our evolutionary predictions (Table 2). The predictions and interpretations related to our hypothesis are described in Table 2.

Results

Niche modelling and niche evolution

Overall, environmental niche models had a good predictive performance, with AUC values ranging from 0.81 to 1. Six species

Table 2 Predictions associating the evolution of plant life forms with environmental niche dimensions.

Predictions	Expected θ values	Biological interpretation
P1: Therophytes have their adaptive optimum in niches with lower water availability during the plant growing season (bio18) and lower soil nitrogen availability than perennial plant forms.	For bio18 and nitrogen axes: $\theta_{\text{therophytes}} < \theta_{\text{chamaephytes}}$, $\theta_{\text{phanerophytes}}$ and $\theta_{\text{geophytes}}$	Low availability of water and nitrogen resources limits plant growth. In general, perennial plant strategies are slow-growing and produce more biomass than annual plants, thus requiring high resource availability and becoming selectively disadvantageous in environments with low water and nutrient availability. By contrast, therophytes would be selectively favoured in these environments due to their short-lived and lower biomass production, reproducing soon during the growing season, allowing them to persist as seeds.
P2: Nonresprouting perennial strategies, that is chamaephytes and phanerophytes, have their adaptive optima in niches with a lower water deficit in the driest period (bio17) than therophytes and geophytes.	For the bio17 axis: $\theta_{\text{chamaephytes}}$ and $\theta_{\text{phanerophytes}}$ $> \theta_{\text{therophytes}}$ and $\theta_{\text{geophytes}}$	Chamaephytes and phanerophytes lack conspicuous resistance strategies to cope with water deficits in dry seasons more intense. By contrast, therophytes have an escape strategy through seed banks, while geophytes have an avoidance strategy with underground water-storing organs. Consequently, therophytes and geophytes would be favoured under more severe environments with dry seasons more intense.
P3: Resprouting perennial strategies, that is geophytes, or disturbance-scaping strategies, that is therophytes, have their adaptive optima in niches with higher fire frequency than chamaephytes and phanerophytes.	For the fire frequency axis: $\theta_{\text{therophytes}}$ and $\theta_{\text{geophytes}}$ $> \theta_{\text{chamaephytes}}$ and $\theta_{\text{phanerophytes}}$	Geophytes have a large underground storage organ with multiple buds that allow them to resprout after fire events and keep the plant alive during the dry season. Therophytes produce an extensive seed bank that can massively germinate and maintain populations under high fire frequency habitats. Thus, therophytes (scape strategy) and geophytes (avoidance strategy) would be selectively favoured in environments with high fire frequency.

Each prediction expects a set of θ parameter estimates from best-fit evolutionary models linked to its biological interpretation.

had models based on a few occurrences ($3 < n < 10$), with the AUC ranging from 0.83 (*C. anceps* (Benth.) H.S.Irwin & Barneby and *C. ulmea* H.S.Irwin & Barneby) to 1 (*C. lagotois* H.S.Irwin & Barneby). These species also attained significance under the evaluation proposed by (Pearson *et al.*, 2007), having good predictive performance. Seventeen species had between 10 and 30 occurrence points, and the AUC of these models ranged from 0.91 (*C. pilosa* (L.) Greene) to 0.99 (*C. confertiformis* (H.S. Irwin & Barneby) Conc., L.P. Queiroz & G.P. Lewis and *C. simpliciflora* H.S.Irwin & Barneby). Finally, 18 species had more than 30 occurrence points, and the AUC of these models ranged from 0.86 (*C. diphylla* (L.) Greene) to 0.99 (*C. potentilla* (Mart. ex Benth.) H.S.Irwin & Barneby). The table with the model performance for each species is available in Methods S1.

After excluding the three species with insufficient occurrences for niche modelling, our sample maintained 41 taxa representing 38 species and three varieties. The ARC analysis did not support a relationship between species' divergence time and the D and I niche overlap metrics, D ($f=0.50$; $P=0.99$) and I ($f=0.47$; $P=0.94$) (Fig. S1; Table S2), indicating that closely related species do not occupy more equal or similar environmental niches than those more distantly related. The ARC analyses based on unique dimensions of the environmental niche also did not support a relationship between species' divergence time and niche overlap metrics (Fig. S2; Table S2). Thus, we have evidence that the environmental niche is not conserved over time in this plant lineage.

The evolution of plant life forms

The model assuming equal transition rates among all plant life forms, ER, best fit our data (Table S3) and was used to reconstruct ancestral states in our sample of phylogenetic trees. ER-based SIMMAP analyses indicated conflicting different plant life forms for the last common ancestor of the *Chamaecrista* lineage, although the phanerophyte life form had been the most likely ancestral state inferred in 26.25% of the 2000 trees of the posterior distribution (Fig. 2). Transitions among plant life forms were overall common, with an average of 25 ($SD = 4.75$) transitions throughout phylogenetic trees. The most common transition was from the phanerophyte to the chamaephyte state (mean 2.43 $SD = 1.44$), while the least common transition was from the chamaephyte to the geophyte state (mean = 1.70, $SD = 1.40$). The geophyte life form evolved independently in clades A, B, and C, but the geophyte life form remained conserved in clade A. On the other hand, all other life forms evolved in clade B, which held the greatest number of transitions among life forms (Fig. 2).

The relationships between the evolution of life forms and environmental niches

OU-based models considering the four different life forms had the best fit for 3 of 4 environmental niche dimensions across the alternative SIMMAP reconstructions (Table S4). The OUM model had the best fit for water availability dimension in the

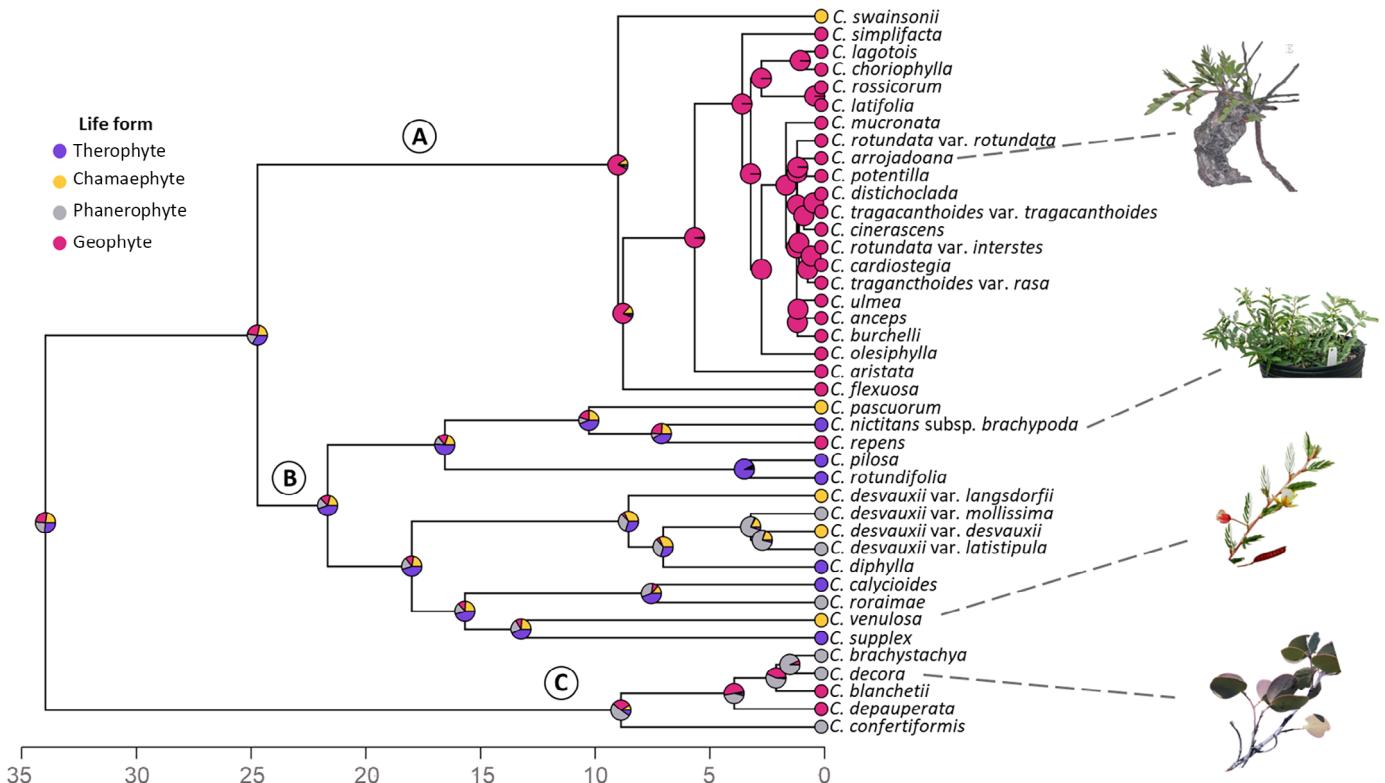


Fig. 2 Ancestral reconstruction of plant life forms in the *Chamaecrista* focal lineage. Ancestral state estimates are based on a summary of 2000 stochastic character mapping trees. Labels A, B and C indicate the three main clades in the phylogeny.

warmest period (bio18) and soil nitrogen dimension, and the OUMV model had the best fit for the fire frequency dimension. By contrast, the WN model (null model) had the best fit for the water niche dimension in the driest period (bio17) (Table 3). Except for the water niche dimension in the driest period (bio17), each plant life form was associated with a distinct evolutionary optimum (θ) of environmental niches. Evolutionary rates (σ^2) and optimum-attraction forces (α) did not differ among plant life forms for two niche dimensions (water availability in the warmest period and nitrogen). For the fire frequency dimension, the evolutionary rates (σ^2) differed among life forms.

The estimated evolutionary optima for therophytes displayed lower water availability and lower soil nitrogen availability than that estimated for all categories of perennial plants (Fig. 3a–d). The perennial life forms were associated with almost twice the water availability of the annual plants. Perennial plants also displayed optima with greater nitrogen availability than annual plants (*c.* 1.25×). Among the perennial plants, geophytes had the highest optima values for water availability (bio18) and soil nitrogen concentration (Fig. 3a,c).

Plant life forms also had distinct evolutionary optima for the fire frequency dimension. Therophytes and geophytes were associated with higher fire frequencies than chamaephytes and phanerophytes (Fig. 3d,e). Therophytes and geophytes occupy niches with 1.8 times and 2.5 times higher fire frequency values than chamaephytes and phanerophytes. Additionally, the rate of evolution of the fire frequency niche dimension was higher in

therophytes and geophytes than in the chamaephytes and phanerophytes (Table 3).

Discussion

We characterized the environmental niche of 41 taxa in the *Chamaecrista* phylogeny distributed over South America. We applied evolutionary models to investigate whether the evolution of plant life forms occurs with changes in four environmental dimensions of the species's niche representing resources and disturbance gradients for plants. The environmental niche is not conserved over time in the genus *Chamaecrista*. Instead, species' niches have evolved contrary to the expectations of niche conservatism, and the evolution of plant life forms was correlated with distinct optima in three environmental niche dimensions. More specifically, the evolution of geophytes was associated with higher water and nitrogen availability and higher fire frequency. On the other hand, the evolution of therophytes was associated with lower water and nitrogen availability and intermediate fire frequency. These patterns support our first and third predictions but not our second prediction.

Although niche conservatism is common in many plant lineages (Liu *et al.*, 2020), *Chamaecrista* species had a nonconserved niche evolution in the last 30 Myr with descendant lineages occupying distinct environmental conditions from those of ancestor lineages (Warren *et al.*, 2008). This evolutionary pattern depends on (1) the new habitat availability and (2) species'

Table 3 The four environmental niche axes and their respective best-fit evolutionary models and estimated parameters.

Environmental niche axes	Best-fit model	Percentage (%) of phylogenetic trees supporting the best- fit model	Evolutionary parameter estimates			
			Plant life forms	θ	σ^2	α
Bio18	OUM	37.6	Therophyte	188.8	0.14	0.72
			Chamaephyte	318.5	0.14	0.72
			Phanerophyte	353.7	0.14	0.72
			Geophyte	447.0	0.14	0.72
Nitrogen	OUM	51.2	Therophyte	136.8	0.55	11.84
			Chamaephyte	163.8	0.55	11.84
			Phanerophyte	168.4	0.55	11.84
			Geophyte	181.5	0.55	11.84
Bio17	WT	85.1	Therophyte	—	—	—
			Chamaephyte	—	—	—
			Phanerophyte	—	—	—
			Geophyte	—	—	—
Fire	OUMV	77.0	Therophyte	0.022	0.00014	1.004
			Chamaephyte	0.011	0.00009	1.004
			Phanerophyte	0.014	0.00006	1.004
			Geophyte	0.031	0.00116	1.004

Bio18 and Bio17 correspond to water availability in the warmest and driest quarters. Nitrogen corresponds to soil nitrogen availability, and fire corresponds to fire frequency in the environment. Together, these axes represent resources and disturbance gradients. Our results show that with the exception of the bio17 axis, all life forms evolved different adaptive optima along the environmental niche gradient. The reported percentage (%) represents the phylogenetic trees supporting the best-fit model, excluding ties. The evolutionary parameter estimates are the average value among the best-fit models. The best-fit model is determined based on the lowest ΔAIC_c value, with a lower value indicating a more favourable fit.

potential to diverge ecologically (Edwards & Donoghue, 2013). In the Neotropics, the relative availability of new habitats during *Chamaecrista* diversification correlates with geological and climatic processes in the last 30 Myr (Lavina & Fauth, 2011). These processes, including the Andean uplift and the Open Diagonal formation accentuated by Quaternary cycles, shaped the Neotropical region (Antonelli & Sanmartín, 2011; Lavina & Fauth, 2011). These newly available habitats likely imposed distinct selective pressures on plant lineages, influencing the evolution of life forms. Similar patterns in other Neotropical plant lineages, like *Mimosa* and *Andira*, show life form evolution in response to environmental changes, with resprouting life forms evolving under increased fire frequency during the open diagonal formation (Simon *et al.*, 2009). In *Lupinus* (Fabaceae), annual life forms are associated with the occupation of low-altitude xeric environments (Drummond, 2008), or in *Leucadendron* (Proteaceae), where resprouting life forms had their adaptive optima in high fire frequency habitats (Tonnabel *et al.*, 2018). Accordingly, our study demonstrates the concurrent evolution of *Chamaecrista*'s environmental niches and plant life forms, leading to a correlated pattern between life forms aligning with the newly available environmental conditions.

Plant life forms differ regarding biomass allocation and, therefore, become selectively advantageous in different environments. Supporting our first prediction, annual plants had their adaptive optimum towards low water and nitrogen availability, while perennials, mostly geophytes, had their adaptive optimum towards high water and nitrogen availability. This pattern might reflect distinct selective pressure favouring different plant life forms in each environment. The scarcity of water and nitrogen constrains

photosynthetic rates and carbon assimilation (Damatta *et al.*, 2002), impacting biomass allocation among plant organs (Dovrat *et al.*, 2019), especially in perennial plants with substantial height investment. On the other hand, annual plants produce less biomass than perennials and can grow and reproduce when water and nutrients are scarcer, allocating their biomass primarily to reproductive effort, completing their life cycle during short periods of resource availability (Friedman, 2020). This high reproductive input leads to annuals setting great seed banks for future favourable seasons, thus enduring and becoming selectively favoured in environments with low resource availability (Dovrat *et al.*, 2019). Yet, our results suggest that environments with high availability of resources must favour perennial plant species with an investment in height (aboveground organs) that outcompete annual ones. These perennial species have a competitive advantage over annual species due to the higher and steady investment in growth height throughout the whole year, negatively affecting the occurrence of annual species by limiting light and resources needed for seed germination and seedling development (Tilman, 1988; Rees & Long, 1992). Therefore, the non-occurrence of annual species in environments with high resource availability and few disturbance events would be related to a competitive disadvantage of annual species in relation to perennial species, as observed in some systems (Tilman, 1988; Rees & Long, 1992).

It is also interesting to note that among the perennial life forms, the geophyte is the life form that has an optimal niche with higher water and nutrient availability. For these plants, a high availability of resources might be necessary to develop and maintain underground storage organs. In the case of

Chamaecrista species, the geophyte plants mainly inhabit the Cerrado and Campos Rupestres (Fig. 1). Both regions are marked by seasonally dry periods and disturbance events. Thus, our results suggest that the maintenance and survival of the geophyte species

in these environments depend on a period of the year when water and nutrient availability is high.

Intense dry seasons in central regions of South America can impose water deficits for plants, limiting species distribution.

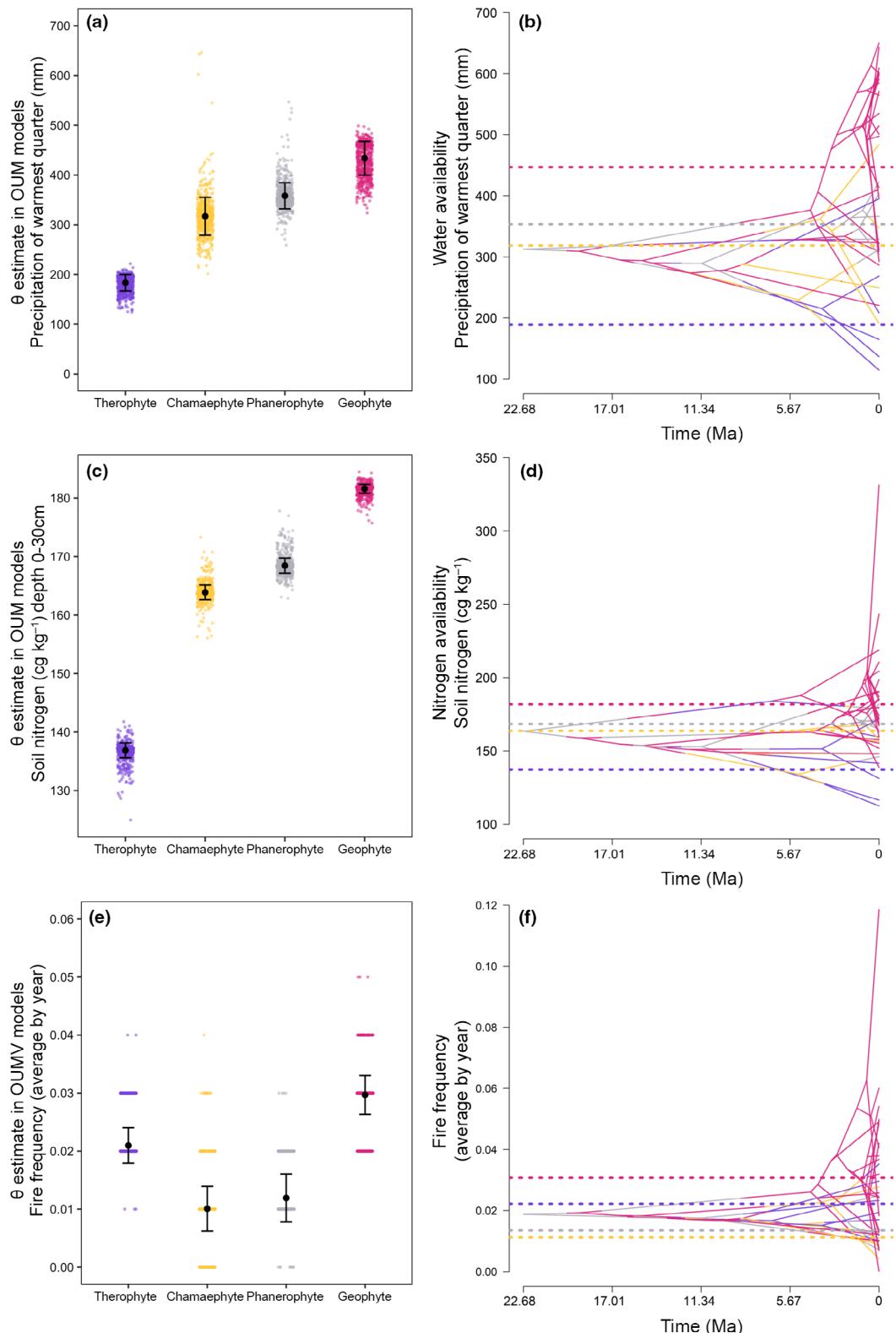


Fig. 3 Adaptive optima (θ) estimated in each niche dimension in which evolutionary models were selected as the best fit and the traitgram with a life form mapped joint the current niche. (a) The optima (θ) estimated by the OUM model for the bio18 dimension; (b) The traitgram with species position along the water availability gradient; (c) The optima (θ) estimated by the OUM model for the nitrogen availability dimension; (d) The traitgram with species position along the soil nitrogen availability gradient. (e) The optima (θ) estimated by the OUMV model for the fire frequency dimension; (f) The traitgram with species position along the fire frequency gradient. Colours represent each life form: purple: therophytes, yellow: chamaephytes, grey: phanerophytes and pink: geophytes. In graphs a, c and e, each dot corresponds to the theta value estimated by each model considered the best, excluding ties and the error bars correspond to SD. The dashed line in graphs b, d and f corresponds to theta mean value for each life form.

Unlike therophytes and geophytes, chamaephytes and phanerophytes lack conspicuous escape or avoidance strategies to cope with extreme dry seasons, such as a persistent seed bank or resource-storing organs. Our second prediction stated that chamaephytes and phanerophytes would have evolved niches characterized by dry seasons less intense. However, none of the tested evolutionary models was selected as the best for the water niche dimension in the driest period (bio17). Therefore, neither the phylogenetic pattern nor the plant life forms explain the evolution of species along the water gradient during dry seasons. Although the null model has a better fit to the data, the average range for the accumulated water in the driest period currently inhabited by *Chamaecrista* species corresponds to a small fraction (12.7–78.7 mm) of the total variation available in South America, which ranges from 0 to 1631 mm. A similar pattern was found for some Mimosoids lineages (Ringelberg *et al.*, 2023). This result highlights that the perennial *Chamaecrista* species studied here, independent of the life form, probably have some resistance strategy to deal with the intense water restriction during the dry seasons (Bandurska, 2022). Resistance strategies such as avoidance or tolerance often derive from the evolution of ecophysiological and cellular traits, such as thick tissue formation and osmotic adjustment or substances and proteins production, respectively, which protects against the negative effect of osmotic and ionic stresses (Micco & Aronne, 2012; Bandurska, 2022). In both cases, these mechanisms are undetectable under our life form classification. Furthermore, the focal *Chamaecrista* lineage diversified during the open diagonal formation in South America, probably descending from an ancestor inhabiting tropical rainforests (Conceição *et al.*, 2009). The open diagonal includes highly seasonal environments where dry seasons are more severe than those of adjacent tropical rainforests. Thus, the occurrence of species in an environment marked by very restricted precipitation in the driest period requires, regardless of the plant life form, that the species have some resistance strategies to survive during dry seasons.

Supporting our third prediction, geophytes and therophytes have higher optima values for fire frequency than nonresprouting perennials. Interestingly, our results also show that geophytes present higher optima values for fire frequency than therophytes. Under high fire frequency, therophytes would be disadvantaged because frequent fires can compromise the life cycle of these plants, preventing viable seed bank settings (Enright *et al.*, 2014). On the other hand, in the same scenario, geophytes may be selectively favoured because their underground woody system with root buds facilitates regeneration and regrowth after fire events (Pausas *et al.*, 2018). The resprouting of geophytes can reduce the risk of immaturity, for example the risk of dying before seed

production (Iwasa & Kubo, 1997; Ojeda *et al.*, 2005) since geophytes persist after the passage of fire, unlike therophytes plants. Furthermore, geophytes can grow faster and blossom earlier after fire events than plants emerging from the seed bank (Iwasa & Kubo, 1997; Lamont *et al.*, 2011; Pausas & Keeley, 2014). This feature increases its competitive advantage over not resprouting species. On the other hand, under lower fire frequency, that is, a larger interval between one fire to another, therophytes producing many seeds have advantages over species that do not produce seeds quickly (Pausas & Keeley, 2014). The short-lived of therophytes allows them to withstand fire disturbance via a persistent seed bank capable of germinating after fire passage (Pausas & Keeley, 2014). Thus, our results support the idea that geophytes and therophytes would better fit different fire regimes (Keeley *et al.*, 2011), albeit being fire-tolerant, in which therophytes would be selectively favoured under intermediate fire frequencies (Enright *et al.*, 2014).

Unexpectedly, given our prediction, we found that environments with low resource availability and high disturbance are less occupied, representing a restrictive ecological condition for the *Chamaecrista* lineage. Illustrating it, geophyte plants had adaptive optima towards the highest fire frequency and high resource availability, while therophyte plants had their adaptive optima towards intermediate fire frequency and the lowest resource availability. It corroborates plant strategy theory that predicts habitats with low resource availability and high disturbance rates would be unsuitable for all plant strategies because severe stress would prevent plant biomass recovery after disturbance events (Grime, 1977). A similar evolutionary pattern was recorded in a clade of Montiaceae, in which the evolution of succulent leaves, for example leaves with higher saturated water content (SWC), is associated with environments with greater resource availability (i.e. greater precipitation) and higher temperatures (i.e. potentially more stressful environments for plants) in relation to species that have lower SWC values (Ogburn & Edwards, 2015). Both succulent leaves of Montiaceae and the xylopodia of some *Chamaecrista* species (geophytes) are resource-storing organs that likely become selectively favourable in more intense seasonal environments marked by subsequent high and low resource availability periods. Thus, our study provides more empirical evidence that resource-storing organs are essential for species maintenance in disturbed and seasonal environments.

In sum, our results show that in a *Chamaecrista* lineage, annual species have evolved with environmental niches marked by lower resource availability and intermediate disturbance frequency, while geophyte species have evolved with environmental niches marked by high resource availability and high disturbance frequency. These results show a trade-off likely restricts

simultaneous plant adaptation to environmental niches with low resource availability and high disturbance. Although we could not distinguish between adaptation and exaptation scenarios, our findings indicate that different plant life forms and environmental niches evolve together. Our results also provide empirical evidence that niche evolution can occur at finer scales, along microhabitats, without necessarily involving a shift to different phytogeographic domains or biomes. Still, the niche change also depends on the evolution of plant functional traits. These findings may have important implications for understanding the environmental factors shaping plant evolution in the Neotropics. They could potentially inform why species occur in specific regions and not in others. From a future perspective, our results also help to understand how future environmental changes may affect plant form and function diversity.

Acknowledgements

We thank the colleagues from the *Laboratório de Interações Planta-Animal* (LIPA) at the Federal University of ABC (UFABC, Brazil) for feedback and discussions during the development of this study. Anonymous reviewers provided helpful comments on previous versions of this manuscript. This work is part of the doctoral thesis of LSP. This work was funded by a fellowship to LSP from the São Paulo Research Foundation (FAPESP/grant no. 2021/01573-0) and by research grants to AN of the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq/grant no. 434692/2018-2) and the São Paulo Research Foundation through a Young Investigators Grant (FAPESP/grant no. 2019/19544-7). SA was supported by Instituto Serrapilheira (grant no. 1709-21213). JGR was supported by FAPESB (process JCB0030/2016). RCP was supported by FAPESP (2019/18627-6 and 2018/02191-1).

Competing interests

None declared.

Author contributions

LSP, SA and AN conceived the idea and designed the study. AN provided funding for the study. LSP, RCP and JGR collected and organized the datasets. LSP conducted the analyses and led the writing of the manuscript. LSP, SA, TV and AN reviewed the drafts of the manuscript. LSP, SA, AN, TV, RCP and JGR contributed to the final version of the manuscript.

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Data availability

All our data and R scripts are available on the platform [github.com](https://github.com/luanaprochazka/plant-life-form-and-niche-evolution) at: <https://github.com/luanaprochazka/plant-life-form-and-niche-evolution>.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Correlation between niche overlap metrics and node age.

Fig. S2 Correlation between niche overlap metrics and node age in the four niche dimensions.

Methods S1 Details on niche modelling procedures.

Table S1 Classification of *Chamaecrista* species into plant life forms according to the literature.

Table S2 Parametric and Monte Carlo regression analyses between niche overlap metrics.

Table S3 Evolutionary transition models and their respective AICc and ΔAICc average values.

Table S4 The fitting metrics between eight evolutionary models and four niche axes across 2000 SIMMAP reconstruction.

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