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Pre-adaptation and adaptation shape trait-environment matching in the Neotropics

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Abstract

Aim: Functional traits shape the distribution of taxa across environments. However, it remains unclear whether trait and environmental niche evolution are correlated, and what happened first: trait change facilitating environment shifts (pre-adaptation) or environmental change leading to trait change (adaptation). We focus on a species-rich Neotropical legume radiation to shed light on this enigma.

Location: Neotropics.

Time Period: Cenozoic.

Major Taxa Studied: Fabaceae: Papilionoideae: *Swartzia*.

Methods: We assembled leaflet, fruit and petal size data from monographs and herbarium collections for 86 to 96% of the c. 180 *Swartzia* species, inferred a dated *Swartzia* phylogenetic tree from existing DNA sequences covering 38% of the species and integrated these with distribution, soil and climate data. We used phylogenetic linear regression to quantify trait–environment relationships and applied comparative methods to evaluate modes of correlated evolution between traits and environments.

Results: Leaflet and petal size were strongly linked to climate, while fruit size was not associated with climate or soil characteristics. Evolutionary transitions to relatively low rainfall and low temperature environments were conditional on the evolution of small leaflets, whereas transitions to wet and warm environments were preceded by the evolution of larger leaflets. In contrast, transitions to the warmest or coldest environments were followed, rather than preceded, by petal loss.

Main Conclusion: Our results show that the macroevolution of functional traits has influenced the broad-scale distribution of *Swartzia* across Neotropical rainforest, seasonally dry, montane and inundated habitats. We suggest that trait evolution is conditional on environmental change but both pre-adaptive and adaptive processes may occur. These processes are important to understand the distribution of diversity at both regional (e.g. Amazonia) and global biogeographical scales.

KEYWORDS
biome, community assembly, evolutionary transition rates, exaptation, Fabaceae, functional trait, macroevolution, trait evolution

1 | INTRODUCTION

Functional diversity is high in tropical ecosystems due to a spectacular richness of species and forms. This includes diversity in floral traits, fruits, wood anatomy and leaves (Chartier et al., 2021; Lim et al., 2020; Onstein et al., 2019; Swenson et al. 2012). This functional diversity may have resulted, at least in part, from major climatic and geological events during earth history that influenced trait evolution and diversification (Ackerly, 2004; Benton et al., 2022; Blonder et al., 2014; Carvalho et al., 2021; Onstein et al., 2022). Conversely, the evolution of novel traits may also have predisposed lineages to colonize and establish in new environments, if those traits provided a fitness advantage in the new environment ('pre-adaptation' or 'exaptation', Gould & Vrba, 1982). For example, traits related to frost tolerance such as smaller xylem vessels presumably evolved in response to drought in arid conditions, paving the way for the radiation of angiosperms into colder habitats (Zanne et al., 2014). It is thus expected that the evolution of plant traits has been shaped by environmental changes and potential shifts to new environmental conditions (e.g. Blonder et al., 2014; Onstein et al., 2022).

The distribution of plant taxa with particular functional traits is often associated with the environmental conditions in those places (i.e. 'trait–environment matching'), to achieve optimal physiological and ecological performance (Díaz et al., 2016). For instance, leaf size, a key trait involved in photosynthesis and transpiration, declines towards hot and dry environments but increases in warm and wet places (Givnish, 1984). Small leaves are favoured in dry environments because they prevent overheating due to a small boundary layer and thereby reduce the risk of physiological damage when temperatures are high (Wright et al., 2017). In addition, factors other than climate, such as herbivory (Moles & Westoby, 2000) and soil nutrient content (Fonseca et al., 2000) can influence leaf size.

In contrast to vegetative traits, reproductive traits may show a stronger association with the biotic environment. For example, fruit size and seed mass increase towards the tropics (Moles et al., 2007), which is likely linked to the predominance of vertebrate-mediated seed dispersal. Nevertheless, large, heavy seeds also provide an advantage in shady, dry and nutrient-poor environments, as they allow seedlings to establish and grow under stressful or competitive conditions, such as in species-rich rainforest understories (Westoby et al., 2002). Similarly, floral display (e.g. flower size and number) is linked to pollination, and as such can affect outcrossing and inbreeding (Goodwillie et al., 2010). Nevertheless, high temperatures and drought may reduce flower size to avoid water loss from transpiration (Descamps et al., 2020). Thus, despite the overwhelming evidence for biotic factors shaping the distribution and evolution of reproductive plant traits (Goodwillie et al., 2010; Lim et al., 2020), abiotic conditions may play a role as well.

Trait–environment matching in assemblages may result from correlated evolution due to in situ trait evolution, with species adapting while tracking the changing environment in their assemblage ('adaptive' scenario). Alternatively, trait–environment matching has resulted from immigration of taxa that already evolved suitable traits that matched the assemblage environment ('pre-adaptive' scenario) (Ackerly, 2004; Donoghue, 2008). Whether trait matching has resulted primarily from pre-adaptive or adaptive processes remains unclear, as the outcome depends on the rate of immigration of pre-adapted lineages in relation to the rate of in situ trait evolution (Donoghue, 2008). For example, in the _Caesalpinia_ legume group, trans-oceanic dispersal of pre-adapted lineages was common across the continentally isolated succulent biome, demonstrating that moving with pre-existing traits (i.e. deciduousness) is easier than evolving this trait (Gagnon et al., 2019). Similarly, sclerophyllous leaves with low specific leaf areas evolved prior to the onset of the Mediterranean climate in California's chaparral vegetation, with only few trait shifts occurring adaptively (i.e. after the onset of the Mediterranean climate) (Ackerly, 2004). Thus, given sufficient macroevolutionary time to allow dispersal across biogeographic barriers, pre-adaptation may be a common mechanism shaping the functional and phylogenetic composition of communities across biogeographical realms and regional assemblages (Donoghue, 2008).

Here, we assess whether adaptive or pre-adaptive processes in relation to the abiotic environment have shaped present-day trait–environment matching in a Neotropical legume radiation. We focus on the genus _Swartzia_ Schreb. (Papilionoidae), a speciose legume clade predominant in Neotropical rainforests, comprising c. 180 species distributed from southern Mexico and the Caribbean islands to southern Brazil and Bolivia (Torke & Schaal, 2008). Despite its predominance in rainforest, _Swartzia_ species also occur in savannas, dry forests, coastal scrub and pre-montane forests (Cowan, 1967; Torke & Mansano, 2009), so it has spread among biomes through its evolution. Morphologically, _Swartzia_ is characterized by flowers displaying dimorphic stamens—a trait associated with pollination by insects (Luo et al., 2008), absence of petals in some species (Tucker, 2003), arillate seeds and pinnately compound leaves with a single terminal leaflet or unifoliolate leaves by suppression of the lateral leaflets (Torke & Mansano, 2009). _Swartzia_ seeds (or occasionally whole fruits) are primarily dispersed by frugivorous vertebrates and occasionally by water (Chapman, 1989; Williamson et al., 1999). Because of their species richness, distribution across environments and striking morphological variation, _Swartzia_ represents an excellent model system to understand the relationships between functional traits and environments, and whether pre-adaptive or adaptive macroevolutionary processes have shaped them.

First, we hypothesize (**H1**) that the distribution of both vegetative and reproductive traits is associated with abiotic environmental conditions, indicative of trait–environment matching. Specifically, we expect that species with smaller leaflets, fruits and petals occur at lower temperatures, drier conditions and on soils low in nutrients, due to constraints on growth and survival in harsh conditions. Second, we hypothesize (**H2**) that the traits and matching environments identified in **H1** have evolved under a model of correlated evolution, suggesting that trait and environmental niche evolution are linked. Finally, we hypothesize (**H3**) that pre-adaptation is the predominant mode to explain trait–environment matching during the evolutionary radiation of _Swartzia_. Specifically, we expect trait

change (i.e. leaflet size change, fruit size change, and the loss/gain of petals) to precede the macroevolutionary transition to the matching abiotic environment, because such traits may be prerequisites for the colonization and establishment of plants into harsh environments, given sufficient macroevolutionary time to disperse (Donoghue, 2008).

2 | MATERIALS AND METHODS

2.1 | Phylogenetic reconstruction and dating

To reconstruct a *Swartzia* phylogeny, we followed the taxonomic classification by Torke & Schaal (2008) and Torke & Mansano (2009), and used previously published data on the internal transcribed spacer region of nuclear ribosomal DNA (ITS1, 5.8 s, and ITS2) and plastid genes (*atpB–rbcL* spacer, *trnL* intron, and the *trnL–F* spacer) (www.treebase.org, study ID S2154). This included genetic data for 81 *Swartzia* taxa (69 described species, 8 undescribed species, and 7 subspecies/variants), taxa from related genera in the swartzioid clade (*Ateleia*, *Bobgunia*, *Bocoa*, *Candolleodendron*, *Cyathostegia*, *Fairchildia* and *Trischidium*) and taxa used as outgroups (*Amburana ceaerensis*, *Baphia kirkii*, *Castanospermum australe*, *Cordyla haraka*, *Dipteryx odorata*, *Holocalyx balansae*, *Styphnolobium japonicum* and *Vatairea fusca*). We used BEAST 2 (Bouckaert et al., 2014) to obtain a dated phylogeny. To calibrate the phylogeny, we set the crown node of the Swartzioid clade to an age of 48.9 million years ago (Ma), following age inferences across the legume phylogeny (Lavin et al., 2005). BEAST was run until all parameters reached convergence, and a maximum clade credibility (MCC) tree with mean heights was obtained and used in subsequent analysis after removing the outgroups. More details on phylogenetic reconstruction and dating and the set of trees used can be found in the Supporting Information, supplementary methods, and supplementary files 1 to 5.

2.2 | Environmental niche data

We used curated herbarium specimens to assemble a total of 3688 occurrences for 156 *Swartzia* taxa (including subspecies and varieties. See Supporting Information, supplementary file 6). Samples lacking coordinates but containing precise location descriptions (e.g. on rivers, villages, nature reserves, indigenous territories and key geographical features) were georeferenced using the scientific literature, recompilations of historical maps on botanical expeditions, and online maps. Climatic (WorldClim 2 database, Fick & Hijmans, 2017) and soil (SoilGrids 2.0 portal, Poggio et al., 2021, at a range depth of 0–5 cm) variables were extracted for taxa that had at least five occurrences. We selected environmental variables related to water deficit (annual precipitation), soil texture (clay and sand content), soil fertility (nitrogen content) and temperature (annual mean temperature), as those strongly affect plant growth and survival. We excluded precipitation seasonality and temperature seasonality from

the final models, because including them resulted in increased collinearity among variables, and preliminary analyses indicated that they were not associated with the studied traits. For each taxon, we averaged each environmental variable across all occurrences, to reflect a taxon's climatic and soil environmental niche. More details on the extraction of environmental data can be found in Supporting Information, supplementary methods.

2.3 | Functional trait data

We extracted functional traits on leaflet, fruit and petal dimensions (length and width) from monographs, other literature and herbarium specimens for *Swartzia* taxa, resulting in trait data for 176, 116 and 153 taxa, respectively, for each trait. Although measurements from non-fresh herbarium material may introduce errors (Heberling, 2022), our results are unlikely to be affected by the inclusion of fruit and leaflet measurements from herbarium specimens because the number of species with herbarium data was small (4 taxa for leaflet, 17 taxa for fruit measurements, Supporting information Table S1). For extracting trait data from monographs, we developed a text-mining approach in R (for details, see Supporting Information, supplementary methods). Leaflet size, rather than the whole leaf, was used because it represents the 'functional' unit in compound-leaved species that determines the boundary layer relevant for transpiration and to avoid over-heating. We calculated leaflet area by multiplying blade length and width, as this generally predicts blade size in plants (Shi et al., 2019). We applied this to both minimum (minimum length * minimum width) and maximum (maximum length * maximum width) values, and then averaged these to obtain a single leaflet value per taxon. For this calculation, we only included non-basal leaflets because of data availability and because basal leaflet sizes are often significantly smaller than non-basal leaflets. For fruits and petals, we used the maximum width as a proxy for size, because of data availability. For fruits, we used 'width' rather than 'length', because fruit length in *Swartzia* is strongly influenced by the number of seeds that develop within a fruit and therefore highly variable within species. Subsequently, trait, environmental and phylogenetic data were merged for each trait separately for subsequent analyses, covering 61 (33.8%) to 64 (35.5%) species (Supporting information Table S1). All trait data, script for text mining and references are provided in the Supporting Information, supplementary files 7 to 15.

2.4 | Relationship between functional traits and environments

We used phylogenetic generalized least squares (PGLS) regression models to evaluate the relationship between environment and traits (**H1**), using the function 'pgls' in the R package 'caper' (Orme et al., 2018). The PGLS model incorporates a co-variance matrix of shared branch lengths among species into the estimate terms of the model to correct for the non-independence of data due to shared

ancestry. Trait variation is assumed to follow a Brownian motion model of evolution (i.e. variation between tips accumulates at a rate proportional to the length of the branches), however, as this assumption is not necessarily true, caper allows scaling of the internal branches of the tree to find the best fit to the data (Orme et al., 2018). For this, we used a non-fixed lambda parameter estimated by maximum likelihood to multiply the internal branch lengths of the phylogenetic tree and account for the estimated degree of phylogenetic structure in the data. Specifically, to explain interspecific variation in leaflet, fruit and petal sizes, we included our selected environmental variables (i.e. annual mean temperature, annual precipitation, nitrogen content, clay content and sand content) as predictor variables. In order to improve the normality of the model residuals, we applied transformations to variables that deviated from a normal distribution (i.e. square-root for temperature, cube-root for precipitation, inverse of nitrogen content, cube-root for leaflet area, logarithm of fruit width and logarithm of petal width + 1). As the maximum width of apetalous species (i.e. species lacking petals) was recorded as 0 cm, we applied the logarithm transformation of the response variable plus one unit. For petals, we performed the analysis twice, once when including and once when excluding the species lacking petals. When only including species with petals, the addition of one unit to petal width was not applied. To evaluate the relationship between predictors and response variables, we fitted all possible models (combinations of predictor variables) using the 'dredge' function in the R package 'MumIn' (Barton, 2009). The subset of models with the lowest Akaike information criterion (AICc) values (i.e. models with AICc difference <2 from the best model) were used in model averaging, using the 'model.avg' function. As the best models do not necessarily include the same predictor variables, we used conditional averaging (Burnham & Anderson, 1998) to estimate the overall effect of a predictor variable on the response trait (i.e. effect is averaged across models that included this predictor).

2.5 | Correlated evolution between trait and environment transitions

To test whether traits and associated environments have evolved under a model of correlated evolution (**H2**), we used BayesTraits (version 3.0.2, Pagel & Meade, 2006, 2019) implemented in the R package 'bayes traits wrapper' (Griffin, 2018). We focused on trait and environmental variables that showed significant relationships in the PGLS. These included leaflet size in relation to annual mean temperature and annual precipitation, and petal size in relation to annual mean temperature. We transformed the continuous variables into discrete character states to compare the "discrete independent" (i.e. uncorrelated evolution) with the "discrete dependent" (i.e. correlated evolution) models in BayesTraits. We explored a moving window of thresholds to classify species into binary environmental states, ranging from low to high quantile values (25%, 35.66%, 50%, 64.34% and 75% quantiles) and performed the analyses across these thresholds. For leaflets, we used the fifty percent quantile as

threshold (i.e. 65.25 cm^2) to classify species as having small leaflets (trait values equal to or below the threshold) and large leaflets (trait values above the threshold). For petals, no threshold was needed because we classified species according to petal presence (i.e. petalous species) and petal absence (i.e. apetalous species).

We calculated Bayes Factors (BF) of models for each trait–environment relationship, and for each environmental threshold, to assess whether a model of independent or dependent evolution was supported. Support for the dependent model would indicate that transitions between environmental states are dependent on transitions in trait states, whereas support for the independent model would suggest that environment and trait evolved independently. We ran a Bayesian Markov Chain Monte Carlo (MCMC) for five parallel runs for each model, on 1000 post-burn-in phylogenetic trees from the BEAST analysis sampled equally across 11,000,000 iterations, and discarded a burn-in of 10% iterations. Trees were scaled to have mean branch lengths of 0.1 to facilitate the inference of rates (Pagel & Meade, 2019). We used a reversible jump uniform hyper prior (ranging from 0 to 10) to seed the values of the mean and variance of a gamma prior for all rate parameters. The mean marginal likelihood of the five runs for the dependent and independent models were used to assess the significance of the trait–environment correlated evolution by calculating the log (BF). A log BF >2 indicates positive, >5 strong and > 10 very strong evidence (Kass & Raftery, 1995) in support of a model of correlated evolution. To test the sensitivity of our results to the classification of variables into discrete states, we also evaluated the continuous correlated evolution model in BayesTraits. We used the same configuration as in the discrete data analysis but excluded the reversible jump uniform hyper prior because it is only applicable to the inference of discrete trait state rates. Marginal likelihoods were obtained for a model where a correlation between the trait and the environment was set to zero (i.e. no correlated evolution) and one where the correlation was estimated. Each model was run five times and a mean marginal likelihood for both models was obtained to calculate the BF and assess the significance of correlated evolution. Additional information on the BayesTraits configuration can be found in the Supporting Information, supplementary methods.

2.6 | Pre-adaptation and adaptation during correlated evolution

To test whether a model of pre-adaptation (i.e. trait shift precedes environmental shift) or adaptation (i.e. environment shift precedes trait shift) was supported (**H3**), we extracted the inferred transition rates (i.e. evolutionary rates from one environmental state to the other, and from one trait state to the other) for the model of dependent evolution, and repeated this for each trait–environment analysis across the moving window of environmental thresholds. If trait evolution is dependent on the environment (i.e. adaptation model), then trait transition rates should be conditional on a lineage being present in a specific environmental state. Formally, this means that

the transition rate difference between rate Q_{12} (e.g. evolution from small to large leaves in dry places) and Q_{34} (e.g. evolution from small to large leaves in wet places) should significantly differ from 0 (i.e. across 65%–95% iterations and phylogenies). Similarly, if the difference between transition rates Q_{21} (e.g. evolution from large to small leaves in dry places) and Q_{43} (e.g. evolution from large to small leaves in wet places) is significantly different from 0, this would support an adaptation model (Figure 1). In contrast, if environmental niche evolution is dependent on the trait (i.e. pre-adaptation model), then the environmental transition should be conditional on a lineage possessing a specific trait state. Formally, this means that the transition rate difference between rate Q_{13} (e.g. evolution from dry to wet places when large leaves are present) and Q_{24} (e.g. evolution from dry to wet places when small leaves are present), or between rate Q_{31} (e.g. evolution from wet to dry places when large leaves are present) and Q_{42} (e.g. evolution from wet to dry places when large leaves are present) should differ from 0 to support a pre-adaptation model (Figure 1). We calculated these rate differences across iterations and phylogenies to determine the most likely direction of change for a given trait–environment relationship.

2.7 | Ancestral state reconstructions

To illustrate trait evolution in *Swartzia* and matching environments, we carried out ancestral state reconstructions on the 1000 post-burn-in phylogenetic trees for the threshold configuration with the best BF obtained in the correlated evolution analysis (i.e. 25% for leaflet size in relation to annual precipitation, 64.34% for leaflet size in relation to annual mean temperature, and 35.66% for petals in relation to annual mean temperature). The ancestral states were inferred with an unequal transition rate model, a MCMC run and the same configuration on iterations and priors from the previous section, using the "Multistate" option in BayesTraits, and scaling trees to have mean branch lengths of 0.001. Inferred probabilities were averaged across trees for each state and node and summarized on the MCC tree for illustration purposes.

3 | RESULTS

### 3.1 | Phylogenetic inference

Phylogenetic relationships resulting from the Bayesian reconstruction in BEAST were generally concordant with results obtained by Torke & Schaal (2008), with well resolved branches and high support from posterior probabilities on the majority of phylogenetic splits (Supporting information, supplementary file 3).

3.2 | Trait–environment matching

We found support for the hypothesis (**H1**) that interspecific variation in both vegetative (i.e. leaflet) and reproductive (i.e. petal) traits was explained by variation in abiotic environmental conditions after accounting for phylogenetic non-independence, thus supporting trait–environment matching in *Swartzia*. Specifically, for leaflets, there was a significant positive effect of annual mean temperature and annual precipitation on leaflet size (Figure 2a,b, Supporting Information Table S2). The best PGLS model (AICc = 183, lambda = 0, $df = 63$, adj. R-square = 0.24, $F = 11.51$, $p = 5.48e-05$) included only these two predictors (Supporting Information Table S3). For fruits, no predictor variable was significant, but there was a marginal positive effect of sand content on fruit width ($p = 0.08$,
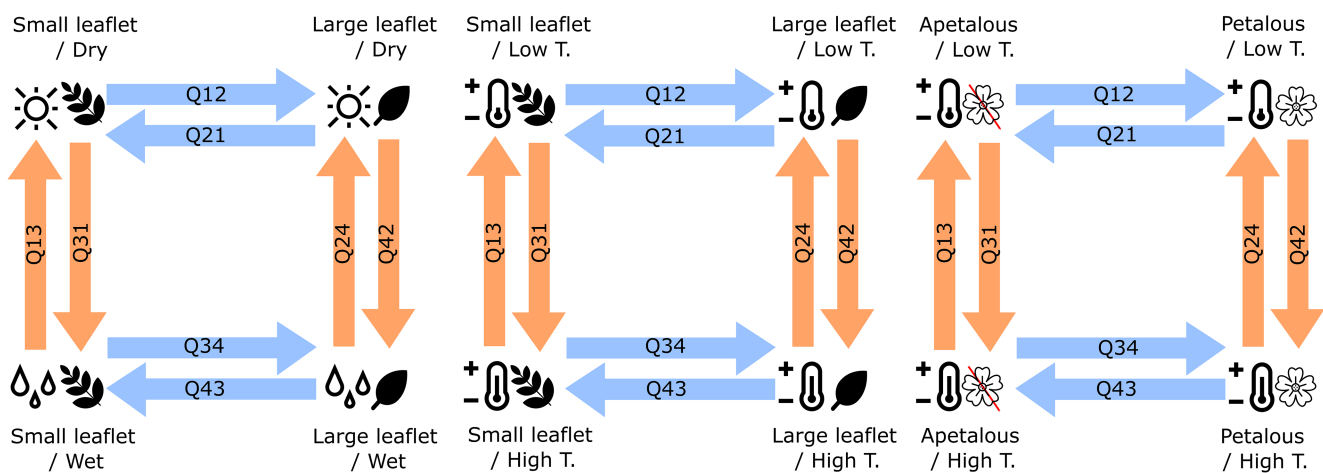
FIGURE 1 Transition rates in the dependent (correlated) evolution model, inferred using BayesTraits. Orange arrows refer to events where environmental transitions occur conditional on the presence of a particular trait state, whereas blue arrows refer to events where trait evolution occurs conditional on the presence of a particular environmental state. If rates Q13 and Q24 or rates Q31 and Q42 differ, this would support a 'pre-adaptation' scenario because shifts to new environments are conditional on trait states. Similarly, if rates Q12 and Q34 or rates Q21 and Q43 differ, this would support an 'adaptation' scenario because shifts to new trait states are conditional on environmental states.
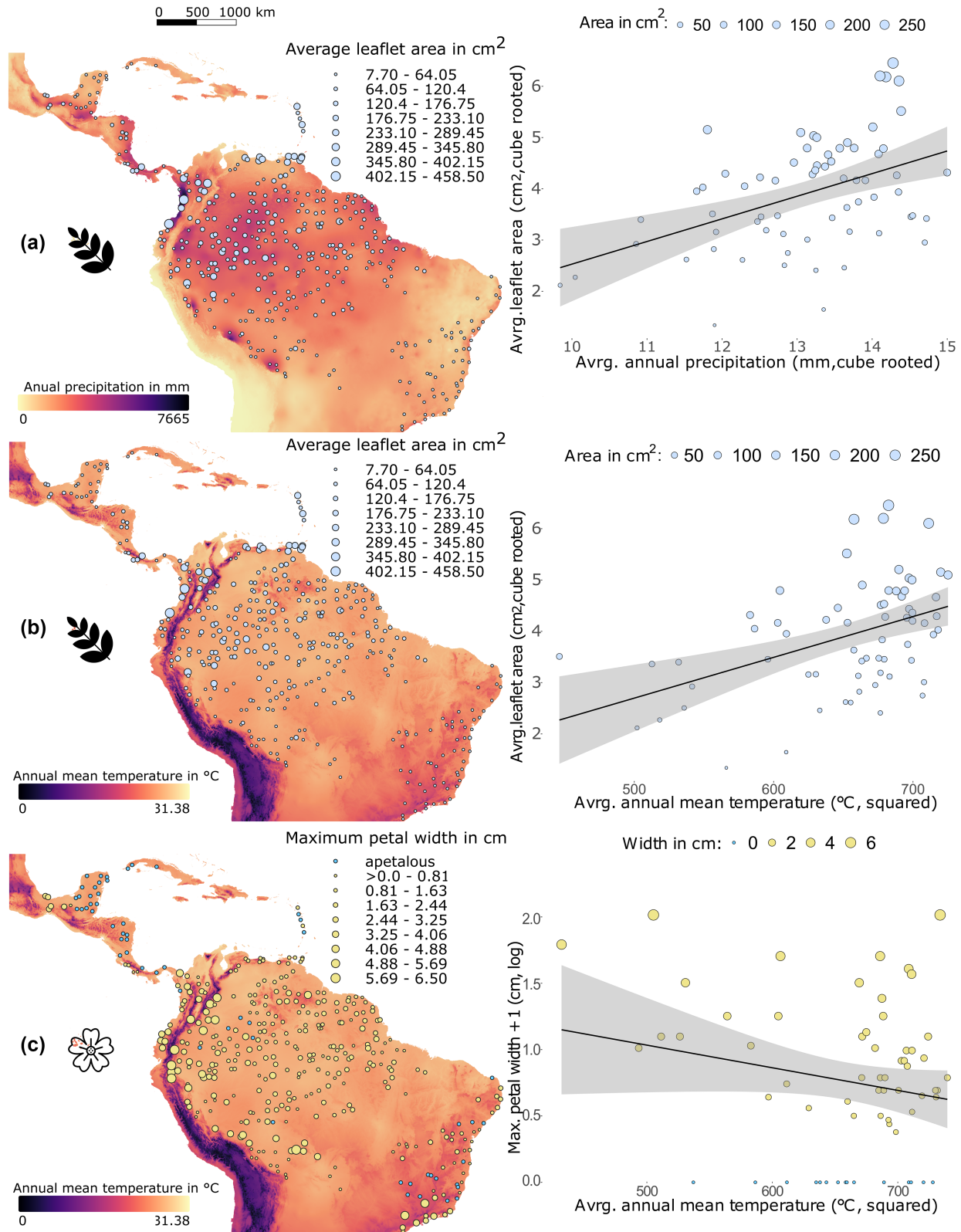
FIGURE 2 Trait–environment matching in *Swartzia*. Only traits and environments that indicated a significant relationship after accounting for phylogenetic non-independence using phylogenetic generalized least squares (PGLS) regression are shown. Panels on the left depict leaflet area (light blue, a & b) and maximum petal width (yellow, c) distributed across the Neotropical region and across its matching abiotic environmental predictor. Dots in the map represent a thinned version with averaged trait values across neighbouring occurrences for each trait to reduce overlap (i.e. close occurrences were averaged for the trait using the points thinning algorithm from SAGA in QGIS). Panels on the right show a fitted regression line for the trait–environment relationships after correcting for phylogenetic relatedness. Species included in the panels on the right comprise a subset of species with phylogenetic data, while the set used for the panels on the left include all species for which trait and occurrence data were available. Avrg. = average; max. = maximum.

Supporting Information Table S2). The best PGLS model (AICc = 57.4, lambda = 0.791, df = 61, adj. R-square = 0.04, F = 2.43, p = 0.09) included sand content and annual precipitation as predictors of fruit width (Supporting Information Table S3). For petals, there was a negative effect of annual mean temperature on petal size (Figure 1C and Supporting Information Table S2). The best PGLS models (AICc = 54.4, lambda = 1, df = 61, adj. R-square = 0.09, F = 7.48, p = 0.008 including all petalous/apetalous species; AICc = 83.5, lambda = 1, df = 46, adj. R-square = 0.15, F = 9.42, p = 0.003 including only petalous species) included only annual mean temperature as a predictor (see Supporting Information Table S3).

3.3 | Correlated evolution between traits and environments

Supporting **H2**, we found that trait–environment relationships followed a model of dependent, correlated evolution with a BF support >2 for most of the analyses across the moving window of environmental thresholds (Figure 3). Specifically, correlated evolution was supported when using environmental thresholds of 25%, 35.66%, 64.34% and 75% for precipitation to leaflet size, all thresholds for annual mean temperature to leaflet size, and thresholds of 35.66%, 50% or 64.34% for annual mean temperature to the presence or absence of petals. This suggests that model results are partially dependent on threshold values to define 'high' or 'low' environmental values, that is, when defining 'wet' or 'dry' or 'warm' or 'cold' conditions. BF support for the continuous trait correlated evolution models was also >2 for all trait-environment combinations (i.e. BF = 6.32 for annual precipitation in relation to leaflet size, BF = 2.17 for annual mean temperature in relation to leaflet size, and BF = 8.25 for annual mean temperature in relation to petal size), suggesting that our results are not biased by data categorization into discrete states.

Transition rates for the dependent (correlated) evolution models indicated strong and consistent support for a pre-adaptation scenario for leaflet size in relation to annual precipitation and annual mean temperature, thus consistent with **H3** (Figure 3a,b,d,e). Specifically, posterior rate differences indicated $Q_{13}-Q_{24}<0$ (64.34% and 75% threshold models, BF = 2.72 and 3.54 for precipitation in Figure 3a; 50%, 64.34% and 75% threshold models, BF = 4.77, 8.67 and 6.35 for temperature in Figure 3b) and $Q_{31}-Q_{42}>0$ (25% and 35.66% threshold models, BF = 7.65 and 3.04 for precipitation in Figure 3d; and 25%, 35.66% and 50% threshold models, BF = 4.12, 6.05 and 4.77 for temperature in Figure 3e). These results suggest that small leaflets enabled the evolutionary transition to the driest and coldest environments, and large leaflets the transition to the wettest and warmest environments (Figure 4). In contrast, transition rate inferences did not support adaptation scenarios for this trait because posterior rate differences $Q_{12}-Q_{34}$ and $Q_{21}-Q_{43}$ overlapped with zero for all threshold models (Figure 3g,h,j,k).

Interestingly, for the presence or absence of petals, transition rates for the dependent (correlated) evolution model indicated strong and consistent support for an adaptation scenario in relation to annual mean temperature, thus contrasting expectations from **H3** (Figure 3i,l).

Specifically, posterior rate differences indicated $Q_{12}-Q_{34}>0$ (35.66% threshold, BF = 5.89 in Figure 3i) and $Q_{21}-Q_{43}>0$ (35.66% and 50% thresholds, BF = 5.89 and 3.4 in Figure 3l) but also $Q_{21}-Q_{43}<0$ (64.34% threshold, BF = 4.11 in Figure 3l). These results suggest that gaining or losing petals can occur after colonizing cold environments but colonizing the warmest environments promotes petal loss only. Furthermore, transition rate inferences did not support a pre-adaptation scenario, because posterior rate differences $Q_{13}-Q_{24}$ and $Q_{31}-Q_{42}$ overlapped with zero for all threshold models (Figure 3c,f).

## 3.4 | Ancestral state reconstructions

The ancestral state reconstructions illustrate multiple transitions of trait and environment states across the *Swartzia* phylogeny (Figure 4). Specifically, we found at least three shifts from small to large leaflets (taking place between 24–21, 19–7.5 and 11–0 Ma), three shifts from large to small leaflets (19.6–11, 17–11 and 9–0 Ma), and two transitions to the apetalous state (22–18 and 14–11 Ma). Similarly, we found two transitions to wet environments (19–7.5 and 15.8–0 Ma), four transitions to dry environments (18–15.8, 17–11, 13–0 and 11.8–0 Ma), two transitions to low temperature environments (14–10 and 11–0 Ma), and three transitions to high temperature environments (18–16, 17–14 and 7.5–0 Ma). In addition, several transitions with uncertain direction occurred (grey highlighted nodes in Figure 4).

4 | DISCUSSION

We integrated a novel trait database with phylogenetic and species distribution data to evaluate whether trait–environment matching has resulted from correlated evolution, using an iconic Neotropical legume radiation—*Swartzia*—as a study system. Our results suggest that leaf and petal sizes across *Swartzia* taxa closely match climatic conditions (Figure 2), but fruit size did not show a significant match with climate or soil. Furthermore, we found strong support for correlated evolution between leaflet size, presence or absence of petals, and climate niche evolution, with leaflet size evolution supporting a pre-adaptation scenario (trait shift precedes environmental shift), and petals following an adaptive scenario (trait shift follows the environmental shift) (Figures 1, 3 and 4). These results suggest that trait–environment matching of *Swartzia* species across the Neotropics has resulted from long-term macroevolutionary processes in which lineages either tracked environments to which they were pre-adapted or adapted morphologically after the transition to a new environment.

4.1 | Eco-evolutionary associations between traits and the environment

We found that small leaflets have allowed *Swartzia* to colonize the driest and coolest conditions of its current distribution (e.g. seasonally dry forests, savannas and coastal scrubs), whereas the evolution
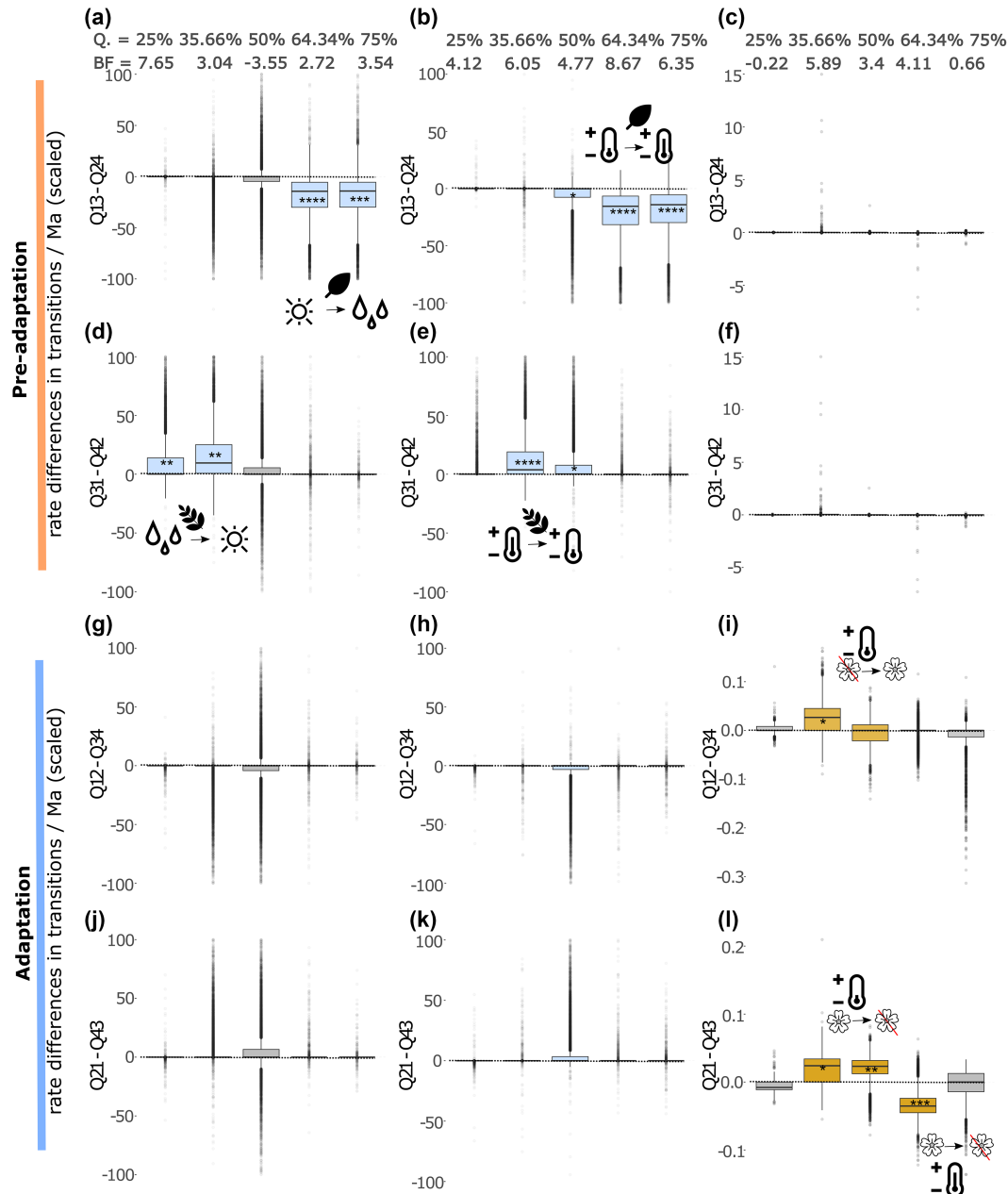
FIGURE 3 Transition rate differences for models of correlated evolution supporting pre-adaptation or adaptation in *Swartzia*. Correlated evolution between leaf size and precipitation (a, d, g, and j), leaf size and temperature (b, e, h, and k) and presence/absence of petals and temperature (c, f, i, and l). Boxplots show differences in transition rates based on 125,000 iterations across five independent runs and after removing a 10% burn-in. Rates were sampled each 2000 iteration across 1000 *Swartzia* phylogenetic trees. The pre-adaptation scenario (environmental niche transitions are allowed and trait states are fixed), are highlighted by the orange bars (Q_{13}–Q_{24} and Q_{31}–Q_{42}, see Figure 1), and the adaptation scenario (trait state transitions are allowed and the environmental niche is fixed) highlighted by the blue bars (Q_{12}–Q_{34} and Q_{21}–Q_{43}, see Figure 1). Silhouettes above or below boxplots illustrate the pre-adaptation/adaptation scenario, with the top silhouettes referring to the fixed condition (e.g. small leaves), and the arrow underneath referring to the transition (e.g. from wet to dry environments). Rates are sorted on the x-axes by the threshold model that was used to classify species into binary environmental states (25%, 35.66%, 50%, 64.34% and 75%). For example, 25% indicates that 25% of the species with the lowest environment values (e.g. mean annual precipitation) obtained the 'low' (e.g. dry) state, whereas the remaining species were assigned to the 'high' (e.g. wet) state. Rates are proportional to the factor used to scale the tree (i.e. scaled to have mean branch lengths of 0.1), and therefore represent a much higher number of transitions per million years (Ma) than the observed number of transitions (Figure 4). The Bayes factor (BF) support for each of the threshold models is indicated above the boxplots. Only threshold models with BF >2 supported dependent (correlated) evolution between trait and environment, in which case boxplots were coloured (blue for leaflets, yellow for petals). When there was no support for correlated evolution (i.e. independent model), boxplots are depicted in grey. All boxplots with a black asterix indicate that transition rate differences deviated from 0 (i.e. *65%–75%, **75%–85%, ***85%95%, or ****>95% of posterior rate differences higher or lower than 0), thus supporting either a pre-adaptation or adaptation scenario.

of large leaflets facilitated the transition to the wettest and warmest environments (e.g. tropical rainforests from northwestern Amazonia and the Pacific Chocó rainforests). These results imply that environmental conditions related to water and temperature stress have imposed constraints to the establishment of *Swartzia* species with certain leaf sizes across climatic gradients. Our findings are consistent with global angiosperm-wide patterns of leaf size, with larger leaves found in species occupying warmer and wetter places, and smaller ones in drier and colder habitats (Wright et al., 2017). Similarly, water stress explains substantial variation in drought-related functional traits in Neotropical rainforest tree communities, with drier plots composed of mostly small-leaved species with high wood densities (i.e. in southeastern Atlantic forests and Caribbean islands) and large-leaved species with low wood densities present in remarkably wet communities (i.e. Chocó and northwestern Amazonia) (Pinho et al., 2021). Thus, leaflet size, possibly in combination with drought-related traits such as water potential and leaf and stem hydraulic conductivity (Vargas et al.,2022), is key to the assembly of *Swartzia* across Neotropical biomes, and important for the assembly of plant communities more generally (Fontes et al., 2020; Wright et al., 2017).

In contrast, petals were first lost after *Swartzia* colonized the warmest extremes of its distribution, even though several reversals by apetalous lineages into cold habitats occurred subsequently (e.g. to colder regions in the southern or northernmost latitudes of its distribution, Figures 2 and 4). Our results suggest that heat stress rather than drought stress is more constraining for petal size (Figure 2), as large petals may suffer from inefficient heat regulation via transpiration (Descamps et al., 2020). Although we did not test for the effect of pollinators or insect florivores and their eco-morphological traits on petal size (Boaventura et al., 2022), the negative relationship between temperature and petal size may be indirect, via temperature constraining both pollinator and floral morphology. For instance, both petal and pollinator body size correlate positively with altitude as temperature decreased in the papilionid legume *Cytisus scoparius*, suggesting an advantage for larger petals and insect body sizes in colder environments (Malo & Baonza, 2002).

We did not find a role of climate or soil on the distribution of *Swartzia* fruit sizes. We suggest that the potential co-diversification of *Swartzia* with vertebrate seed dispersers and their eco-morphological traits, similar to palms (Lim et al., 2020) and Annonaceae (Onstein et al., 2019), may provide a better explanation for *Swartzia* fruit size distribution because fruit traits may be strongly shaped by vertebrate dispersal guilds (van der Pijl, 1969).

4.2 | Correlated evolution between traits and the environment

We found support for correlated evolution between leaflet size, petals and environmental shifts during the diversification of *Swartzia* (Figures 3 and 4), which was initiated ca. 26.39 Ma (34.78–18.63 Ma,

95% highest posterior density interval—see Supporting Information, supplementary file 4). Furthermore, trait and environment shifts were not clustered at specific time periods, suggesting that regional or local changes in Neotropical (micro-) climates and environments, rather than global paleoclimatic events, probably accompanied these transitions. Ecological processes that operate over evolutionary timescales may have played a key role throughout *Swartzia's* diversification, as has been suggested for other legume groups (Pennington et al., 2009, Pennington & Lavin, 2016) and more widely in Amazonian trees (Baker et al., 2014). Other selective forces, beyond the reach of our study, such as herbivory, may also have influenced trait evolution, because of trade-offs in plant resource allocation (e.g. defence vs. growth investment) and the evolution of trait optima in plant communities (Fine et al., 2006). Unfortunately, it remains challenging to infer historical environmental and trait shifts based on extant data only; implementing paleoclimatic and fossil trait data in trait–environment correlated evolution models may improve inferences of past dynamics (Landis et al., 2021).

4.3 | Pre-adaptive and adaptive mechanisms in shaping trait evolution in Neotropical radiations

Support for a pre-adaptive role of leaflet size in *Swartzia* may indicate that this trait is 'exapted' to its current function, which may be different from the function it was originally selected for (Gould & Vrba, 1982). *Swartzia* most likely originated in wet Amazonian rainforests (Figure 4), representing its centre of diversity today (Torke & Schaal, 2008). Smaller leaflet sizes in rainforest *Swartzia* therefore facilitated the later transition to drier habitats, but the initial selective pressure for small leaflets in rainforests remains unclear. Possibly, intense herbivory pressures select for small leaves, because they are less attractive or suitable to host diverse insect herbivores (Brown & Hartley Lawton, 1991) (Moran & Southwood, 1982), and spend less time in the leaf expanding stage when herbivory is most detrimental for leaves (Moles & Westoby, 2000). Indeed, interactions between plants and insect herbivores are old, and probably originated before the emergence of the modern closed-canopy rainforest in the late Cretaceous (Carvalho et al., 2021). Many additional selective pressures have probably acted on leaf size evolution and distribution across assemblages, such as light availability or microclimatic conditions (Díaz et al., 2016). Moreover, phylogenetic, genetic and developmental constraints, as well as allometric effects of plant size and architecture, may also have influenced leaf size variation within and across ecological communities (Díaz et al., 2016; Westoby et al., 2002).

In contrast to leaves, we found evidence for adaptive processes related to temperature during the evolutionary loss of petals (Figure 3). Petal loss is common in flowers with reduced complexity, such as those in *Swartzia*, and has occurred several times during angiosperm evolution, in contrast to petal gains (Endress, 2011; Zhang et al., 2013). Indeed, petal loss can be advantageous in energy-limited environments that experience high heat stress or high risk
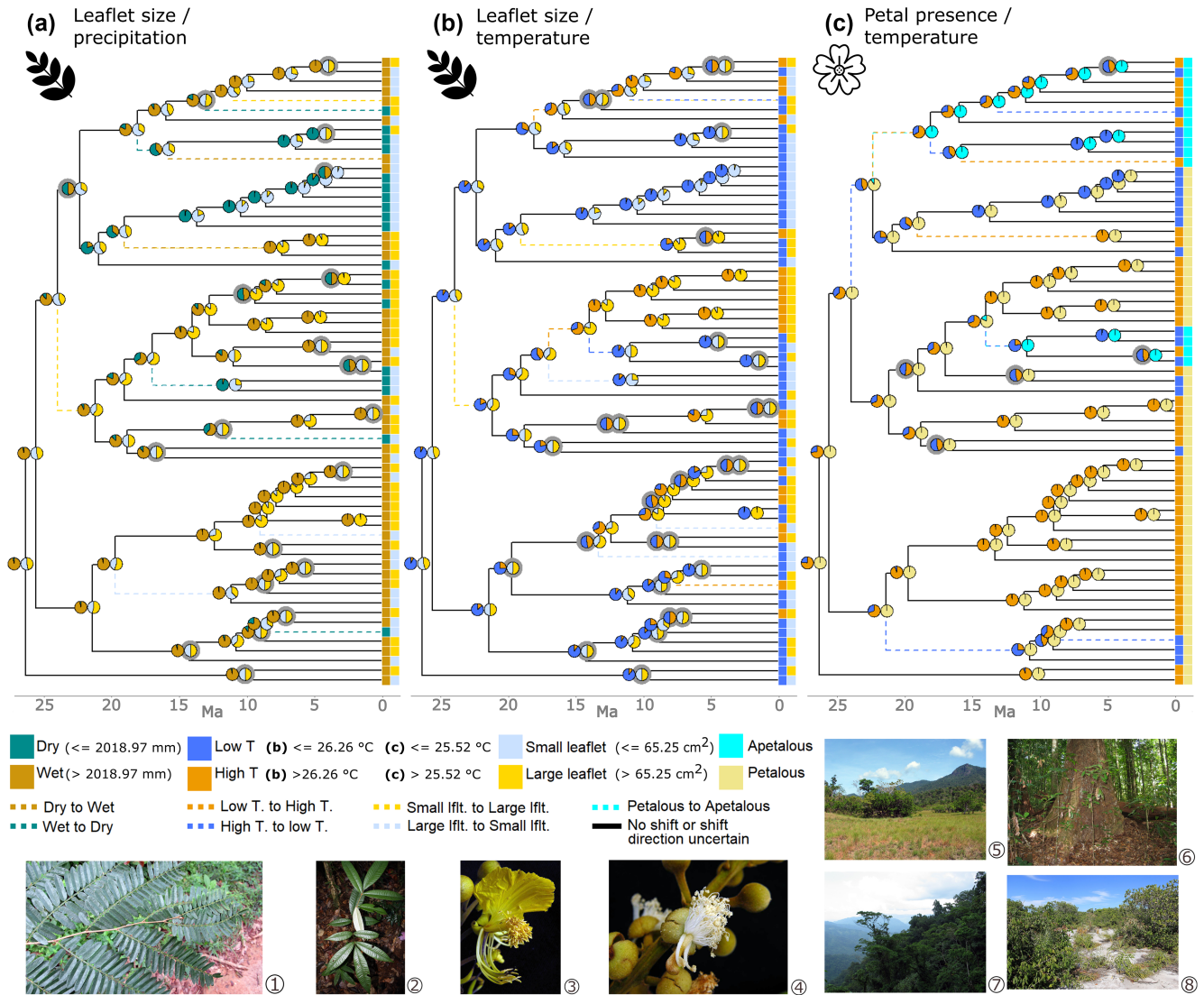
FIGURE 4 Ancestral state reconstructions of traits and matching environments in *Swartzia*. States were inferred with the "Multistate" function in BayesTraits across 1000 *Swartzia* phylogenetic trees. A time scale in units of million years ago (Ma) illustrates *Swartzia* evolution on the MCC tree. Reconstructions were made for the threshold configuration with the best support from Bayes factors in the correlated evolution analysis (i.e. 25% for leaflet size in relation to annual precipitation, 64.34% for leaflet size in relation to annual mean temperature and 35.66% for petals in relation to annual mean temperature). Branches highlighted in colour indicate trait or environmental transitions from parental to descending node. Nodes highlighted in grey represent ambiguous parental nodes (i.e. uncertain ancestral state with probability between 0.45 and 0.55) for which descending nodes differ in their trait states (i.e. implying trait change from parental to descending node, but the direction of change is uncertain). Photographs correspond to: (1) small leaflets from *Swartzia prolata*, (2) large leaflets from *Swartzia flavescens*, (3) petalous flowers from *Swartzia macrocarpa*, (4) apetalous flowers from *Swartzia sericea*, (5) savanna landscape from Guyana (6) rainforest landscape with a tree trunk of *Swartzia leiocalycina*, (7) montane environment from México, (8) restinga landscape from the Atlantic coast in Brazil. Pictures are under a creative common licence, and full attributions can be found in the Supporting Information, supplementary file 16. T = temperature; lflt = leaflet.

of florivory, because petal production demands energy (Hamann et al., 2021). In addition, petal loss could occur in the absence of pollinator-mediated selection pressures, e.g. if species evolved other means to spread pollen or attract pollinators (Zhang et al., 2013). In fact, visual cues by dimorphic stamens (rather than petals) and chemical signals (i.e. volatiles) are involved in pollinator attraction in *Swartzia* (Basso-Alves et al., 2022). Finally, petal loss may be under positive selection due to reduced herbivory and increased resource allocation (Cabin et al., 2022).

5 | CONCLUSIONS

We provided macroevolutionary evidence that both adaptive and pre-adaptive processes in functional trait evolution have influenced the assembly of the species-rich genus *Swartzia* across its Neotropical habitats. This is similar to leaf shapes and freeze-tolerance facilitating transitions to temperate biomes (Schmerler et al., 2012, Zanne et al., 2014) and sclerophyllous leaves to Mediterranean-type environments (Ackerly et al., 2004). *Swartzia* originated in the Amazon

rain forest and our analyses suggest that shifts from Amazonia to neighbouring biomes (Antonelli et al., 2018), such as savannas, dry forests and cloud forests, are underlain by both adaptive and pre-adaptive trait changes. However, we argue that such evolutionary transitions do not only operate at broad-scale biogeographical scales and among major biomes but also at more local scales across ecological gradients within biomes, such as rainforests. Subsequently, these trait–environment transitions may favour speciation, by isolating populations across divergent environments or traits (Nosil et al., 2016). We suggest that understanding trait variation across spatial scales, and the underlying evolutionary processes that may explain this variation, requires the integration of phylogenetic comparative methods (Ackerly & Monson, 2003) with detailed ecological data on traits, species composition and species interactions (e.g. Díaz et al., 2016).

AUTHOR CONTRIBUTIONS

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest for this article.

DATA AVAILABILITY STATEMENT

Phylogenetic data (BEAST configuration file, MCC tree and posterior set of trees), trait, environment, and occurrence data, and R script to extract trait data from monographs can be found in the supplementary files in Dryad repository: https://doi.org/10.5061/dryad.vhhmgqnzq.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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