

The influence of floral variation and geographic disjunction on the evolutionary dynamics of *Ronnbergia* and *Wittmackia* (Bromeliaceae: Bromelioideae)

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The *Ronnbergia* alliance is a lineage of two genera, *Ronnbergia* and *Wittmackia*, which diversified in three centres of distribution; the Pacific Forest, the Atlantic Forest and the Caribbean. In this study, we reconstructed the most plausible biogeographic scenario that explain the disjunct evolution of the *Ronnbergia* alliance in these centres of diversity. We also compared the evolutionary rate dynamics of lineage diversification and floral evolution in each of these areas. Our results suggested that the *Ronnbergia* alliance originated in the Atlantic Forest c. 5.2 Mya. *Ronnbergia* originated c. 3.5 Mya after a long-distance dispersal event to the Pacific Forest. The diversification of *Wittmackia* started in the Atlantic Forest, c. 3.2 Mya, and experienced more heterogeneous evolutionary rate dynamics than *Ronnbergia* during its radiation. In *Wittmackia* a long-distance dispersal from the Atlantic Forest to Jamaica gave rise to the Caribbean clade, which diversified rapidly and experienced significantly higher rates of floral evolution. This study helped in understanding how bromeliad diversification occurs differently among major centres of biodiversity. In our case, we found how the Caribbean is a much more dynamic area of diversification than the Atlantic Forest or the Pacific Forest.

KEYWORDS: bromeliad evolution – diversification rates – floral evolutionary rates – geographic disjunction – Neotropical biodiversity hotspots.

INTRODUCTION

The Neotropics are the most biodiverse region on earth and include more than one-third of all seed plant species (Govaerts, 2001). This astonishing diversity is heterogeneously distributed across the region and frequently concentrated in centres of diversity (Gentry, 1982; Antonelli & Sanmartín, 2011). Each of these centres of diversity offers unique biotic and abiotic conditions that promote the establishment and evolution of plant species and lineages (Antonelli & Sanmartín, 2011). However, many of these areas are highly endangered and classified as hotspots of biodiversity for conservation purposes because they host high levels of plant endemism and are subject

to a rapid loss of primary vegetation (Myers *et al.*, 2000). For this reason, it is a matter of urgency to understand the evolutionary mechanisms that give rise to and maintain biodiversity in these areas to propose informed actions to protect them. In this context, we present a study of the geographical range evolution, species diversification and phenotypic evolution of a lineage of bromeliads that mainly diversified in three of the most important hotspots of biodiversity of the Neotropics (the Caribbean, the Atlantic Forest and the Tumbes-Chocó-Magdalena region).

Bromeliaceae (c. 3500 species) are an excellent model to study evolutionary patterns in the Neotropics because they have diversified in almost every terrestrial biome in this region, producing a high number of endemic species and exhibiting a strong

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signal of adaptive diversification in the main lineages (Givnish *et al.*, 2014; Bouchenak-Khelladi *et al.*, 2015). Recent studies have focused on studying the evolution of the tank-epiphytic clade of berry-fruited bromeliads, also called core Bromelioideae (Schulte, Barfuss & Zizka, 2009; Sass & Specht, 2010; Silvestro, Zizka & Schulte, 2014; Givnish *et al.*, 2014; Heller *et al.*, 2015; Aguirre-Santoro, Michelangeli & Stevenson, 2016). These studies suggested that the diversification of this clade represents the most rapid event of adaptive radiation in Bromeliaceae, triggered by the acquisition of two key innovations (the epiphytic habit and the development of tank-forming rosettes) and potentiated by the previous acquisition of the CAM photosynthetic path, avian pollination and entangling seeds (Silvestro *et al.*, 2014; Givnish *et al.*, 2014). Moreover, this radiation extended across the low to medium elevation areas of the Neotropics, forming clades highly restricted to specific biogeographic regions (Sass & Specht, 2010; Heller *et al.*, 2015; Goetze *et al.*, 2016; Aguirre-Santoro *et al.*, 2016; Maciel *et al.*, 2018). Although these studies revealed important mechanisms for the overall evolution of this lineage, there is little information about the evolutionary processes at the species level because of the widespread taxonomic problems that characterize this group and the lack of well-established monophyletic infrafamilial groups. To overcome this limitation, we present a first approach to understand evolutionary mechanisms at the species level by studying a recently described lineage in core Bromelioideae, the *Ronnbergia* alliance (Aguirre-Santoro *et al.*, 2016).

The *Ronnbergia* alliance is one of the two main lineages of core Bromelioideae and comprises c. 70 species recently placed in *Ronnbergia* E.Morren & André and *Wittmackia* Mez (Aguirre-Santoro, 2017). One of the remarkable features of this lineage is that its main subclades show strong patterns of geographical isolation. The first clade, represented by *Ronnbergia*, comprises species mostly restricted to the Tumbes-Chocó-Magdalena biodiversity hotspot and adjacent forests. The second clade, *Wittmackia*, is composed of a grade of species endemic to the Atlantic Forest in eastern Brazil, the widespread species *Wittmackia lingulata* (L.) Mez and a nested monophyletic group endemic to the northern portion of Caribbean (the Caribbean clade; Fig. 1). This highly restricted geographical separation of the lineages in the *Ronnbergia* alliance provides an excellent case study for understanding biogeographic mechanisms that interconnect three centres of plant diversity (Atlantic Forest, Tumbes-Chocó-Magdalena and the Caribbean) and exploring how this geographical isolation affected the evolutionary dynamics in the lineages. Therefore, in this paper we revisit the phylogenetic study of the

Ronnbergia alliance to test hypotheses in biogeography and evolutionary dynamics in this group.

Given that each of the three centres of diversity offered different times and biotic and abiotic conditions for the diversification of lineages of the *Ronnbergia* alliance, it is expected that the evolutionary dynamics on each of these areas also occurred in a unique fashion. However, it is also possible that random evolution, extinction or niche conservatism make evolutionary dynamics among clades undistinguishable (Kozak & Wiens, 2006; Smith *et al.*, 2011; Mahler *et al.*, 2013). Detecting differences in evolutionary dynamics among clades is now possible with the development of new methods on macroevolution that provide a statistical framework for hypothesis testing (Harmon *et al.*, 2003; Alfaro *et al.*, 2009; Revell *et al.*, 2012; FitzJohn, 2012; Ingram & Mahler, 2013; Rabosky *et al.*, 2013, 2014a; Rabosky, 2014; Title & Rabosky, 2019). Here, we estimate and compare the overall rates of speciation of the lineages among centres of diversity to identify possible mechanisms that affected these rates after the geographical isolation of the lineages.

Besides the expected disparity in speciation rates, we also expect to find differences in the tempo and mode of evolution of adaptive traits among centres of diversity. Because the *Ronnbergia* alliance form part of the large adaptive radiation of core Bromelioideae, it has been suggested that its diversification is likely driven by the ability of the plants to colonize epiphytic habits, form tank rosettes and use the CAM photosynthetic pathway (Crayn, Winter & Smith, 2004; Quezada & Gianoli, 2011; Silvestro *et al.*, 2014; Givnish *et al.*, 2014; Crayn *et al.*, 2015). Moreover, characters that modulate the radiation in response to pollinators, herbivores or seed dispersers also played an important role in the diversification of lineages in Bromeliaceae (Benzing, 2000; Givnish *et al.*, 2014). For instance, the combination of colour and size of floral bracts and petals, organ armature, floral compression and the development of petal appendages may act synergistically to protect the flowers from predators and attract potential pollinators (Benzing, 2000). The function of these traits in the adaptive radiation of core Bromelioideae, however, has never been studied in a phylogenetic context. For this reason, we measured the heterogeneous floral variation observed in the *Ronnbergia* alliance, quantified the evolutionary rate dynamics of floral traits and compared these rates among lineages as an indirect way to explore the potential impact of pollinators and floral predators in the radiation of the group.

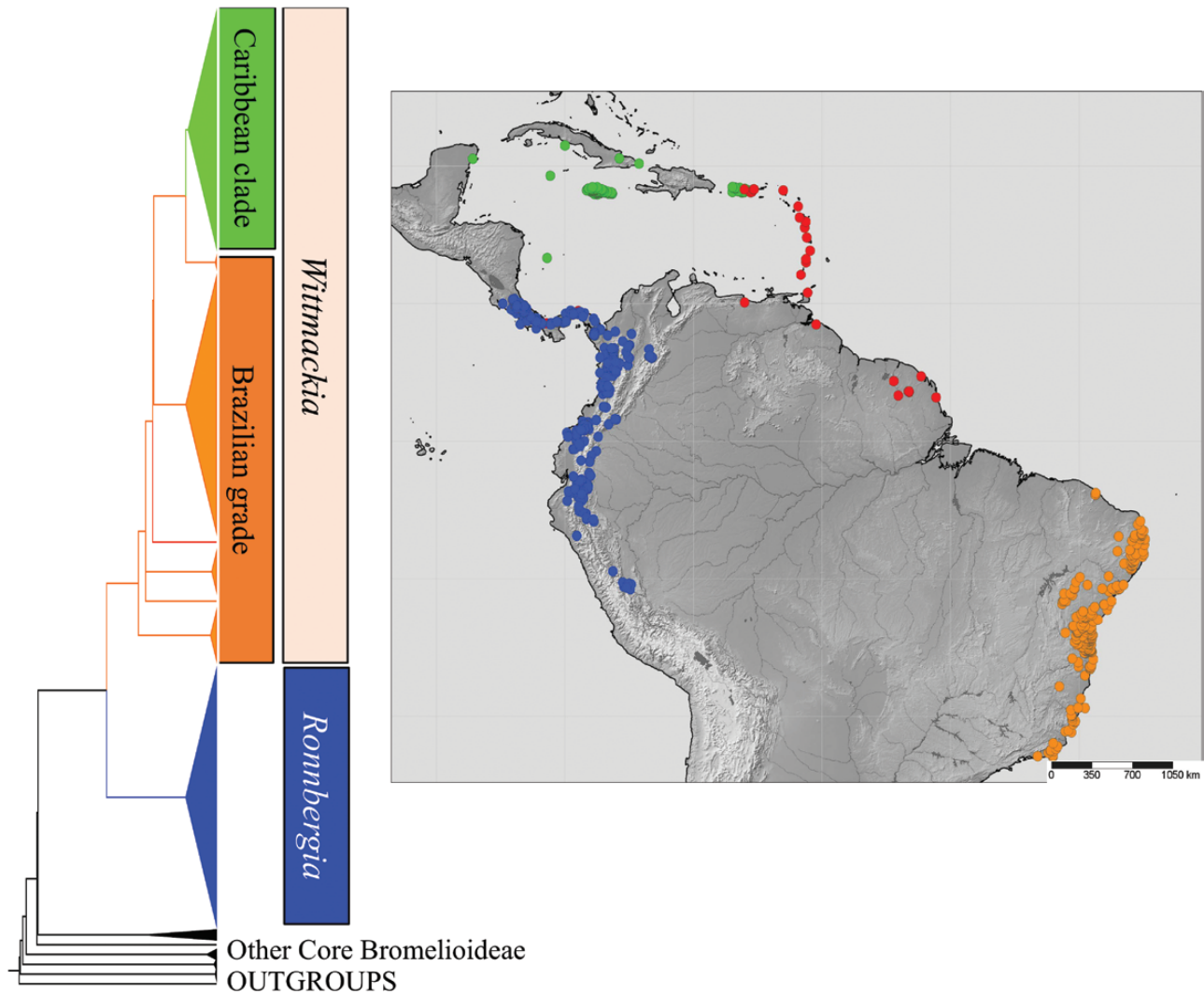


Figure 1. Phylogenetic tree, main clades and geographical distribution of the *Ronnbergia* alliance. The blue points in the map represent specimens of *Ronnbergia*; the orange points represent specimens of Brazilian *Wittmackia* species; the red points represent specimens of the widespread *Wittmackia lingulata*; the green points represent specimens of the Caribbean clade of *Wittmackia*. Modified from Aguirre-Santoro, Michelangeli & Stevenson, 2016.

In this paper, we seek to present the diversification of the *Ronnbergia* alliance as an empirical case that shows how evolutionary dynamics can be different but interconnected between the Caribbean, the Atlantic Forest and the Tumbes-Chocó-Magdalena biodiversity hotspots. We conducted a biogeographic analysis to provide a hypothesis of ancestral geographical range evolution, tested how diversification rates differ among these centres of diversity and compared the evolutionary dynamics of floral variation among these areas. We expect our results to be part of a holistic view helping in understanding the complex origin and preservation of Neotropical biodiversity hotspots and providing the basis to understand the outstanding

diversification of core Bromelioideae across tropical America.

MATERIAL AND METHODS

TIME-CALIBRATED PHYLOGENETIC TREE

Phylogenetic inference and divergence times estimation were conducted jointly through RevBayes (Höhna *et al.*, 2016). The DNA sequence data and initial taxon sampling used for this analysis was extracted from Aguirre-Santoro *et al.* (2016). Substitution matrix parameters were independently estimated for each gene, assuming a GTR+G+I model of nucleotide evolution. Speciation and extinction were modelled as

a birth-death process. Lognormal distributions were used as priors for diversification and turnover. We used a relaxed molecular clock for time-calibration, and thus each branch rate was modelled as a lognormal distribution in which parameters were drawn from a common set of hyperpriors. Because there are no known fossils of bromeliads that can be used to infer the absolute ages of clades, we specified two calibration points using the indirect calibrations from [Givnish *et al.* \(2014\)](#). First, we placed a normally distributed prior age of 9.4 Myr [standard deviation (SD): 0.5] for the crown of Bromelioideae at the root of the tree. Second, we used a uniform prior of 4–7 Myr for the crown age of the tank-epiphytic clade sister to *Acanthostachys* Link (also known as core Bromelioideae). Two independent MCMC runs were executed for 3 000 000 generations, tuning every 2000. The first 70 000 generations of each run were discarded as burn-in. Chain convergence was assessed with Tracer v.1.6 ([Rambaut & Drummond, 2003](#)). Subsequently, we combined the post-burn-in set of trees of the two runs in a single file using LogCombiner ([Bouckaert *et al.*, 2014](#)) and generated a time-calibrated maximum credibility tree (MCC) in TreeAnnotator ([Bouckaert *et al.*, 2014](#)) setting the branch lengths as the mean node ages across all trees. Finally, we pruned the duplicate accessions of the same species in the MCC tree to include only one representative specimen per species. For this selection, we conserved accessions represented by type specimens or wild-collected specimens identified by the first author. The final pruned MCC tree included 56 terminals, representing 17 *Ronnbergia* spp. and 39 *Wittmackia* spp. ([Supplementary Table 1](#)).

BIOGEOGRAPHY

To infer the most likely biogeographic scenario that explains the disjunct distribution in the *Ronnbergia* alliance, we defined nine areas of endemism based on the marked geographical structure observed in the clades of the phylogenetic tree. The first area, here named ‘Pacific Forest’, corresponds to the continuous range encompassed by the Tumbes-Chocó-Magdalena biodiversity hotspot, in addition to the adjacent forests of southern Costa Rica and Panama and the Inter-Andean and eastern slopes of the Andes of Ecuador to central Peru. The second area, here called ‘Atlantic Forest’, includes the Atlantic Forest and adjacent caatinga and semi-deciduous forests from Ceará to Rio Grande do Sul, Brazil. Except for the widespread *W. lingulata*, the remaining area occupied by the species of the *Ronnbergia* alliance is restricted to the Caribbean, which we separated into four areas: Puerto Rico, Jamaica, Cuba and western Caribbean. The last of these encompasses Grand Cayman, Providencia

Island (Colombia) and the Yucatán Peninsula of Mexico. Finally, we defined the following three areas to accommodate the distribution of some of the outgroup taxa and the widespread *W. lingulata*: northern Central America (except Yucatán), the Lesser Antilles and the Amazon.

Based on these areas of endemism, we inferred the evolution of geographical ranges in the time-calibrated MCC tree of the *Ronnbergia* alliance using the *R* package BioGeoBEARS ([Matzke, 2013](#); [R Development Core Team, 2015](#)). This package allows estimating ancestral areas across six different models of range evolution in a likelihood framework and chooses the best fitting model through standard model selection statistics [Akaike information criterion (AIC), likelihood ratio test etc.]. The three main models used in BioGeoBEARS were the dispersal-extinction-cladogenesis model (DEC; [Ree & Smith, 2008](#)); a probabilistic implementation of the dispersal-vicariance model (DIVALIKE; based on the model proposed by [Ronquist, 1997](#)) and a likelihood variation of the BayArea model (BAYAREA-like; based on the model described by [Landis *et al.*, 2013](#)). The remaining three models are nested in each of the first three models and include an additional parameter that represents a founder-event speciation (+ J; [Matzke, 2014](#)). We conducted biogeographic analyses under each model without specifying any constraints in direction or time for dispersal and assessed the fit of each model using the AIC corrected for sampling size (AICc). We selected the best biogeographic reconstruction as the one inferred using the model with the lowest AICc value. Finally, we plotted the marginal probabilities of the inferred ancestral areas on the time-calibrated MCC tree for further interpretation.

SPECIATION RATE DYNAMICS

To have a time-calibrated tree that only includes species of the *Ronnbergia* alliance, we pruned all the outgroups while conserving the original branch lengths using the *R* packages *ape* and *geiger* ([Paradis, Claude & Strimmer, 2004](#); [Harmon *et al.*, 2008](#)). This subsampled dataset included 56 species, representing nearly 80% of the species described in the *Ronnbergia* alliance ([Aguirre-Santoro, 2017](#)).

To compare to see whether the overall speciation rates were different among specific clades in the *Ronnbergia* alliance, we conducted a Bayesian analysis of macroevolutionary mixtures on the 56-species time-calibrated MCC tree ([Rabosky *et al.*, 2013](#); BMM; [Rabosky, 2014](#)). This method uses reversible-jump MCMC to explore simple to complex models that differ in the number of diversification regimes and select those models that improve the posterior probability over time. At the end of the analysis, BMM provides

a posterior distribution of rate regime scenarios that best fit the diversification dynamics of the *Ronnbergia* alliance, including an estimation of the speciation rates at any point of any branch across all samples of the posterior distribution. For this analysis, we chose appropriate priors on rate parameters for the phylogenetic tree using the function ‘setBAMMpriors’ from the R package BAMMtools (Rabosky *et al.*, 2014b). We also accounted for missing taxa by specifying that our taxonomic sampling represented 80% of the known diversity of the *Ronnbergia* alliance. Subsequently, we ran two MCMC analyses in BAMM v.2.2.0 (Rabosky, 2014) for 5 000 000 generations each, using a sampling frequency of 1000. We checked for convergence of the MCMC and appropriate effective sampling size of the log-likelihoods and number of shift events using the R package coda (Plummer *et al.*, 2006). The parameters and priors used to run BAMM are provided in Supplementary File 1.

All the analyses explained below were conducted on the output of the BAMM analysis using different functions of BAMMtools (Rabosky *et al.*, 2014b). We compared the overall speciation dynamics among clades in two ways. First, we generated rate through time plots (RTT plots) to compare the speciation rate estimates over time of *Ronnbergia* vs. *Wittmackia*, and the Caribbean clade vs. the remaining lineages of the *Ronnbergia* alliance (background lineages). Second, we quantified and localized significant rate shifts along the phylogenetic tree in a phylorate plot (a graphic that displays the mean of the marginal posterior density of speciation rates along the branches of the phylogenetic tree in a gradient of colours). The phylorate plot was generated in two steps: (1) summarizing the posterior distribution of the number of rate shifts to detect what rate shift count model has the higher posterior probability; and (2) exploring the 95% credible set of shift configurations and their frequencies sampled during the MCMC to detect the most likely locations of the rate shifts along the phylogenetic history of the *Ronnbergia* alliance.

FLORAL EVOLUTIONARY DYNAMICS

To study the evolutionary rates of floral traits along the phylogenetic tree of the *Ronnbergia* alliance, we measured 13 floral structures that possibly confer plasticity to the overall shape of the flower as a response to pollinators, herbivores and/or seed dispersers (Supplementary Table 1). We only measured one well-preserved individual flower per species because corollas are frequently absent or poorly conserved in herbarium specimens of bromeliads. In this way, for instance, we avoided using measurements of a single petal in combination with averages of other structures from many individuals. The latter can be potentially

problematic as most of the macroevolutionary methods used in this article do not take into account the variance when using averages. The raw measurements were log-transformed before all analyses. Because the petals and ovaries of *Ronnbergia* sp. nov. and *W. jamaicana* (L.B.Sm. & Proctor) Aguirre-Santoro are unknown, we inferred the measurements on these structures using the function ‘anc.ML’ of the R package phytools (Revell, 2012). This method uses maximum likelihood character reconstructions under a Brownian motion model to calculate tip states for a continuous character. Finally, we corrected for the allometric effect of flower size on the log-transformed measurements of all floral substructures using the phylogenetic size correction function ‘phyl.resid’ of phytools (Revell, 2012) and conserved the residual values for subsequent analyses.

To determine whether the variation of flower length and size-corrected floral structures can be attributed to the phylogenetic relationships of the species, we checked for phylogenetic signal on each trait using Blomberg’s K (Blomberg, Garland & Ives, 2003) and Pagel’s λ (Pagel, 1999) as implemented in the function ‘phylosig’ of phytools (Supplementary Table 2; Revell, 2012). Subsequently, we conducted a phylogenetic principal component analysis (pPCA) on the residuals of the floral structures with phylogenetic signal using the function ‘phyl.pca’ of phytools to reduce the number of floral variables into a smaller number of components. We obtained the PC scores for each species and conserved only the first two principal components (PC1 and PC2), as they explain 58% of the total variance of floral shape (Supplementary Table 2). In summary, our final morphological dataset for the evolutionary analyses consisted of three floral axes (the log-transformed measurements of flower length and the scores of the first two principal components representing floral shape).

To analyse the evolutionary rate dynamics of flower length and shape, we first visualized the variation of these phenotypic axes in a morphospace plot, which allows for the identification of general trends in floral evolution across the species of the *Ronnbergia* alliance. Then, we quantified the rates of phenotypic evolution for each floral axis and looked for distinct rate shifts across the phylogenetic tree using BAMM. For each analysis of floral evolutionary rate dynamics, we conducted two parallel BAMM runs for 5 000 000 generations with a sampling frequency of 1000, using appropriate priors from the ‘setBAMMpriors’ function of BAMMtools and checking MCMC convergence and effective sample size. As in the analysis of speciation rates, we performed comparisons of the overall rate of phenotypic evolution between *Ronnbergia* and *Wittmackia*, and between the Caribbean clade and its background lineages using RTT plots. We also summarized and displayed significant rate shifts in

floral evolution by generating phylorate plots and analysing the posterior probabilities of distinct rate shift counts and configurations.

RESULTS

DIVERGENCE TIME AND BIOGEOGRAPHY

The MCC tree of the RevBayes analysis (Supplementary Fig. 1) shows the origin of the *Ronnbergia* alliance in the early Pliocene, c. 5.2 Mya [95% highest posterior density interval (HPD): 4.4–5.9 Mya]; at this point *Ronnbergia* and *Wittmackia* diverged from each other. The diversification of *Ronnbergia* started c. 3.5 Mya (95% HPD: 2.9–4.1 Mya), whereas the cladogenesis of *Wittmackia* began later, c. 3.2 Mya (95% HPD: 2.6–3.8 Mya). The diversification of the Caribbean clade started in the early Pleistocene in *Wittmackia*, with a crown age of 1 Mya (95% HPD: 0.8–1.3 Mya).

The AICc comparisons of log-likelihood values obtained under different biogeographic models in BioGeoBEARS suggested that the DEC + J model is the best fit for our dataset (Table 1). Figure 2 shows the biogeographic history inferred under the DEC + J model. This estimation of ancestral geographical range evolution shows that the origin of the *Ronnbergia* alliance probably occurred in the Atlantic Forest. Subsequently, a dispersal event from the Atlantic Forest to the Pacific Forest gave rise to *Ronnbergia*, where its entire diversification took place. In the case of *Wittmackia*, the radiation of this lineage mainly occurred in the Atlantic Forests, except for two independent dispersals outside this region. One of these dispersal events corresponds to the recent migration of *W. lingulata* to northern South America, the Lesser Antilles and the Pacific Forest. The second and most significant dispersal event corresponds to the dispersal event, c. 0.8–1.8 Mya, from the Atlantic Forest to Jamaica, which gave rise to the Caribbean clade. Jamaica was reconstructed as the main centre for the diversification of the Caribbean clade, from where two independent

dispersals to Puerto Rico, one to Cuba and one to the western Caribbean (Grand Cayman + Providencia + the Yucatán Peninsula) occurred. The probabilities of the ancestral area reconstructions at all nodes of the MCC tree are provided in Supplementary File 2.

FLORAL MORPHOLOGY

The 14 measured traits showed phylogenetic signal and, therefore, could be used for further macroevolutionary analyses (Supplementary Table 2). The first principal component of the pPCA analysis (PC1) explains 34% of the variation of the floral substructures, and PC2 explains 24% of the variation. PC1 mainly summarizes the variation in width and length of the floral bracts, ovary and calyx width and sepal length (Supplementary Table 2). Species with long and wide floral bracts, wide flowers and long sepals, e.g. *R. veitchii* (Baker) Aguirre-Santoro and *W. urbaniana* (Mez) Aguirre-Santoro, have negative values on the PC1 axis, whereas species with narrow floral bracts, narrow flowers and short sepals, e.g. *R. drakeana* (André) Aguirre-Santoro and *W. lingulatoidea* (Leme & H.Luther) Aguirre-Santoro, have positive values on the same axis. PC2 mainly accounts for the variation in the length of the floral bracts and the length of sepal mucros (Supplementary Table 2). Species with small floral bracts and short sepal mucros, e.g. *R. drakeana* and *R. killipiana* L.B.Sm., show negative values of PC2, whereas species with long floral bracts and long sepal mucros, e.g. *R. deleonii* L.B.Sm. and *W. antillana* (Mez) Aguirre-Santoro, show positive values. The morphospace plots show that *Ronnbergia* spp. exhibit the largest phenotypic variation both in floral shape (PC1 and PC2) and flower length compared to *Wittmackia* (Fig. 3). Moreover, *Ronnbergia* tends to have longer flowers than *Wittmackia*, although there is an overlap. In *Wittmackia*, the species that emerged in the Atlantic Forest (Brazilian *Wittmackia*) and the Caribbean form separate clusters along the floral shape axes but overlap around low values of flower length. These clusters describe that the species in the Caribbean clade

Table 1. Likelihoods, parameter estimates, and model comparison statistics for the six biogeographic models fitted in BioGeoBEARS

Model	Ln likelihood	Degrees of freedom	P-value of likelihood ratio test	AICc	d	e	j
DEC	-219.47	2	Null model	443.03	0.013675157224547	0.00000	0
DEC+J	-206.46	3	3.40E-07	419.12	0.01052045255242	0.00000	0.00696166796603
DIVALIKE	-216.06	2	Null model	436.22	0.015158067399636	0.00000	0
DIVALIKE+J	-206.78	3	1.70E-05	419.76	0.011851909950309	0.00000	0.005639796825329
BAYAREALIKE	-257.18	2	Null model	518.46	0.01362455529215	0.00000	0
BAYAREALIKE+J	-213.92	3	1.40E-20	434.03	0.009381268859067	0.11632	0.010330727200993

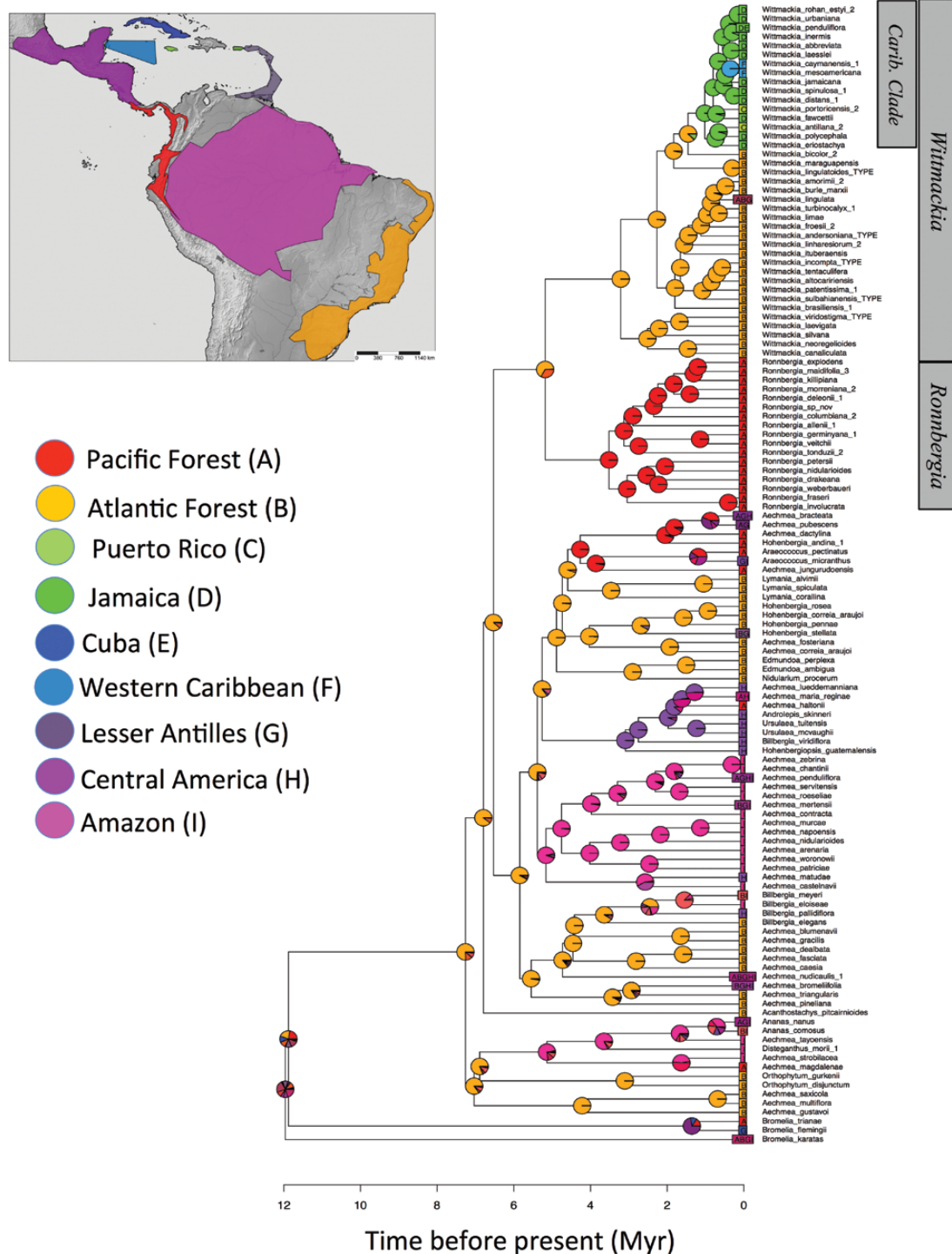


Figure 2. Areas of endemism and ancestral area reconstructions for the *Ronnbergia* alliance inferred with the DEC+J biogeographic model. The pies on the nodes of the phylogenetic tree represent the relative probability of the area of occurrence of a common ancestor.

tend to have wider and longer floral bracts, wider flowers and longer sepals than those species that originated in the Atlantic Forest.

EVOLUTIONARY RATE DYNAMICS

The BAMM analyses favoured a model with two speciation rate regimes across the phylogenetic tree

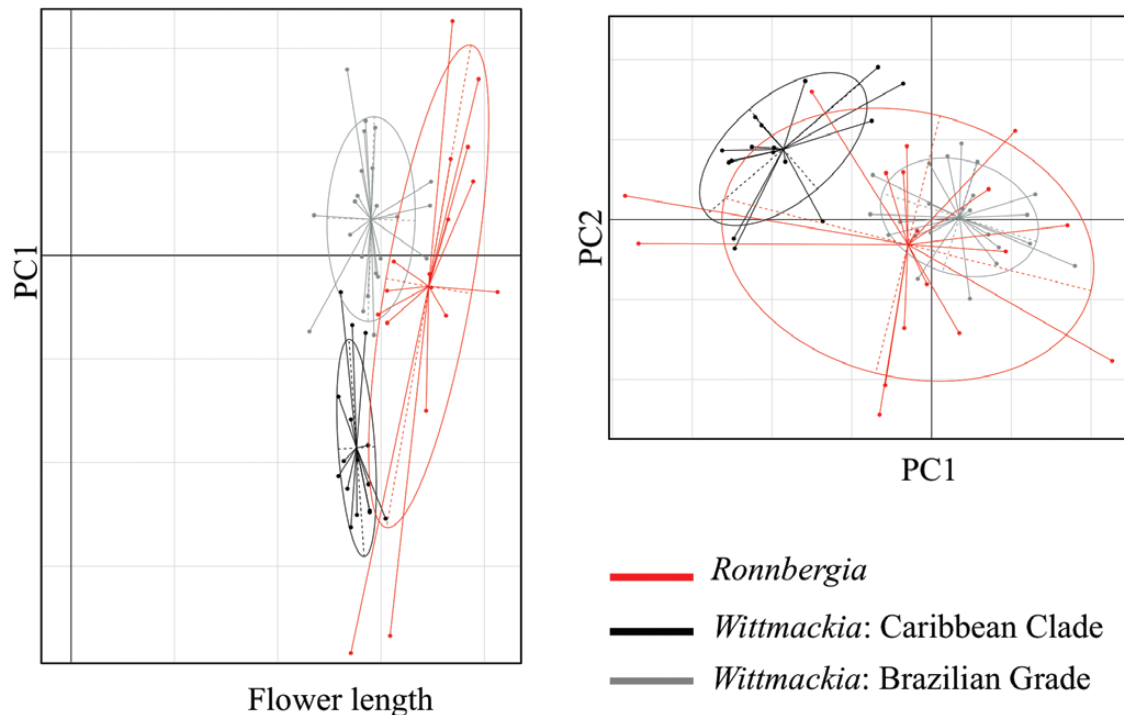


Figure 3. Morphospace of the three phenotypic axes studied for the *Ronnbergia* alliance: flower length, PC1 and PC2.

of the *Ronnbergia* alliance (posterior probability of models favouring two-rate regimes [PP]: 0.5) with a regime shift occurring at the core of the Brazilian radiation of *Wittmackia* (Figs 4A, 5A). The mean rate of speciation for the radiation of in *Wittmackia* is slightly faster than the rate in *Ronnbergia* (Supplementary Table 3). The RTT plots showed that the rates of speciation in *Ronnbergia* did not experience dramatic rate shifts and have a tendency to slow down over time, whereas the speciation rates in *Wittmackia* are more heterogeneous and have a tendency to remain constant over time (Fig. 4A). This difference is explained by the much faster speciation rate of the Caribbean clade compared to other background lineages of the *Ronnbergia* alliance (Table 2; Fig. 4E).

In the case of the phenotypic data, a single rate model (no rate shifts) was the most frequently sampled with posterior probabilities of 0.50 for flower length, 0.27 for PC1 and 0.51 for PC2 (Supplementary Table 3). However, a slight increase of phenotypic rates of PC1 was observed c. 1 Mya, during the radiation of the Caribbean clade (Figs 4G, 5C). This is not the case for the phenotypic rates of flower length and PC2, where the rate regimes are mostly similar across all lineages of the *Ronnbergia* alliance (Figs 4B, D, F, H, 5B, D).

DISCUSSION

ORIGIN OF THE *RONNBERGIA* ALLIANCE AND LONG-DISTANCE DISPERSAL TO THE PACIFIC FOREST

Our estimations of time divergence indicate that the major diversification events in the *Ronnbergia* alliance occurred during the Pliocene and Early Pleistocene (1.0–5.3 Mya). This is also the approximate time period in which most of the best-known recent radiations of angiosperms in the Neotropics occurred (Antonelli *et al.*, 2009; Hoorn *et al.*, 2010; Madriñán, Cortés & Richardson, 2013; Hazzi *et al.*, 2018). Specifically, the *Ronnbergia* alliance originated during the early radiation of core Bromelioideae in the Atlantic Forest, c. 5.0–5.5 Mya (Fig. 2). According to Givnish *et al.* (2014), the diversification of core Bromelioideae was influenced by the consolidation of the rainy, high-moisture, continuous forests in the Atlantic Forest of eastern Brazil. During this radiation, the main lineages of core Bromelioideae originated and, in many cases, were followed by rare cases of long-distance dispersal to other regions of the Neotropics (Sass & Specht, 2010).

In the case of the *Ronnbergia* alliance, the first long-dispersal event occurred to the Pacific Forest, resulting in the origin of *Ronnbergia*, c. 3.5 Mya (Fig. 2). The specific mechanisms that explain this exceptional geographical range shift are unknown, but

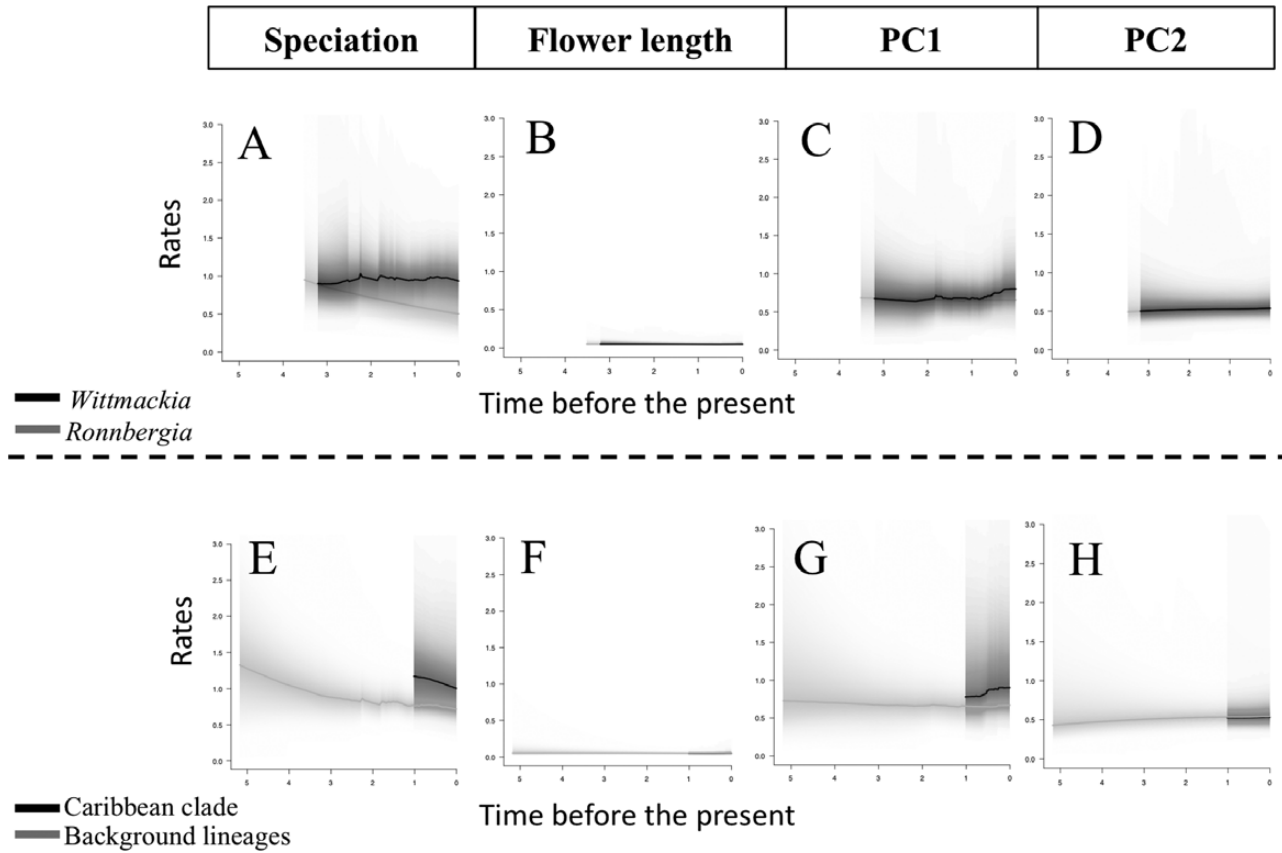


Figure 4. RTT plots comparing the rate variation over time of speciation and phenotypic traits of the main clades of the *Ronnbergia* alliance. A–D, Rate comparison over time of speciation and phenotypic traits of *Ronnbergia* vs. *Wittmackia*. E–H, Rate comparison over time of speciation and phenotypic traits of the Caribbean clade vs. background lineages (*Ronnbergia* + Brazilian grade of *Wittmackia*).

given the zoochorous seed dispersal syndrome of most Bromelioideae, an animal vector could have played an important role in this long-distance dispersal event. This dispersal scenario is plausible because there are not known species in the transitional zone between the Atlantic Forest and the Pacific Forest (e.g. the Amazon or the cerrado), and also because these two centres of diversity share similar environmental conditions (e.g. high precipitation, high soil fertility and mountainous topography), despite their separation (Gentry, 1982; Thomas & Britton, 2008; Hoorn *et al.*, 2010).

Several studies described floristic similarities between the Atlantic Forest and the Andes, but they mostly referred to high elevation and cold tolerant groups that migrated from the central Andes to the mountainous regions of the Atlantic Forest (Thorne, 1972; DeForest Safford, 1999; Fiaschi & Pirani, 2009). In the case of medium to low-elevation taxa, the reports of floristic similarities between the Pacific Forest and the Atlantic Forest are scarce, and they normally include a transitional zone in the Amazon (Gentry, 1982, 1992; Fiaschi & Pirani, 2009; Hoorn *et al.*, 2010;

Antonelli & Sanmartín, 2011). Therefore, the long-distance dispersal event that gave rise to *Ronnbergia* could be considered exceptional and provide a precedent to look for similar cases in other organisms. It must be noted, however, that four *Ronnbergia* spp. inhabit the mountainous western extreme of the Amazon-side slopes of the Andes: *R. campanulata* Gilmartin & H. Luther, *R. deleonii*, *R. drakeana* and *R. wuelfinghoffii* (E. Gross) Aguirre-Santoro, suggesting that an ancient occupancy of extinct taxa in the *Ronnbergia* alliance in the Amazon rainforest cannot be discarded.

DIVERSIFICATION OF *RONNBERGIA* IN THE PACIFIC FOREST

The start of the radiation of *Ronnbergia*, c. 3.5 Mya, coincides with the final uplift of the northern Andes, a factor that probably contributed to the isolation of this lineage in the humid forests of north-western South America. Although the specific sequence of biogeographic events that explain the distribution patterns of *Ronnbergia* still need to be formally assessed,

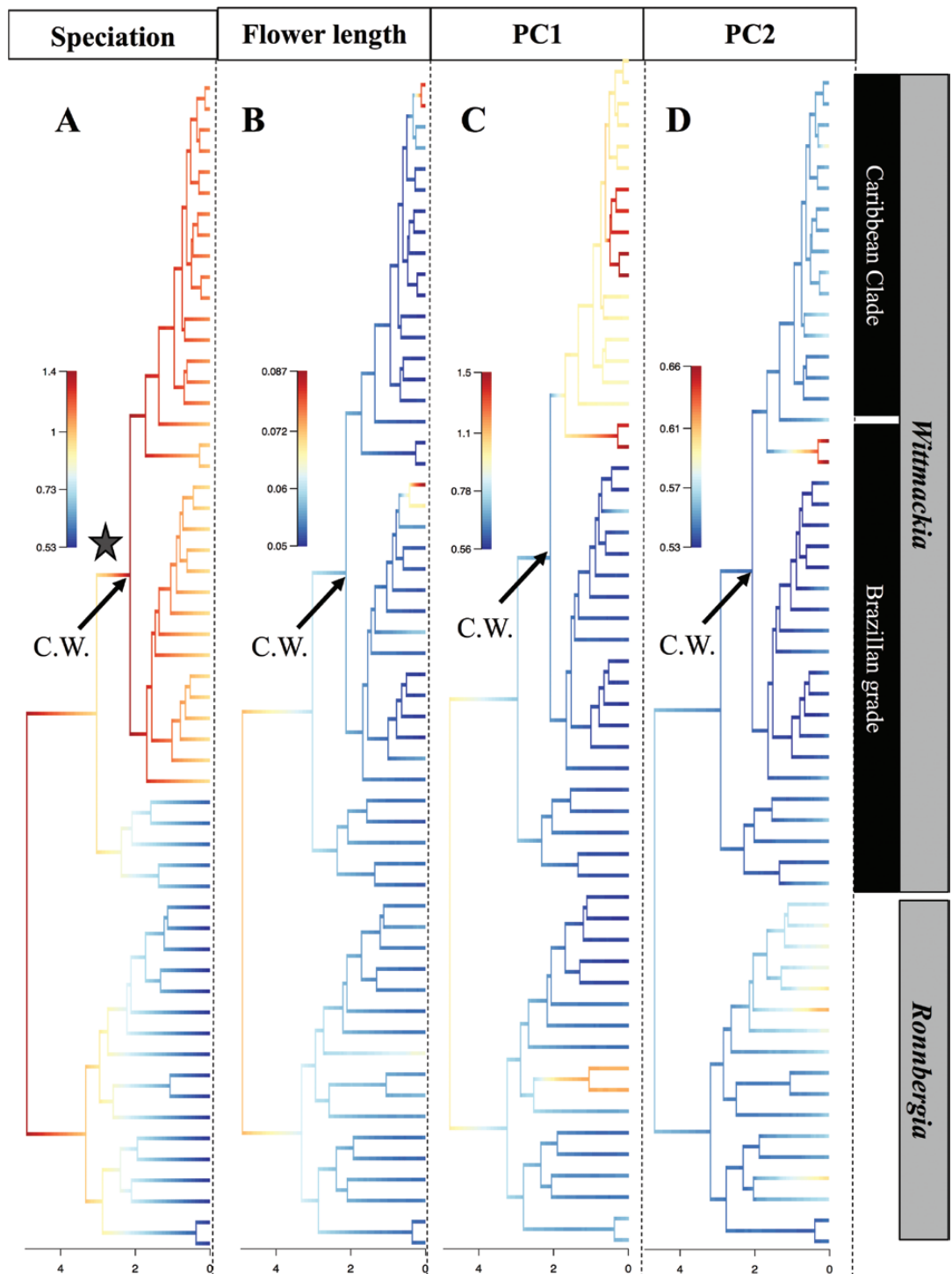


Figure 5. Phylorate plots of the rate dynamics of speciation and phenotypic traits along the branches of the phylogenetic tree. The bar next to each tree shows the range and intensity of the rate values (blue for low values and red for high values). The star indicates the node where a significant rate shift occurred. C.W. = core *Wittmackia*. A, Phylorate plot of speciation rates. B, Phylorate plot of phenotypic rates of flower length. C, Phylorate plot of phenotypic rates of PC1. D, Phylorate plot of phenotypic rates of PC2. Time scale bar at the bottom in millions of years.

Table 2. Estimated speciation and phenotypic rates for the *Ronnbergia* alliance and its main clades. The 95% confidence interval (C.I.) for each rate estimation is provided.

Clade	Speciation rates 95% C.I.		Phenotypic rates					
			Flower length	95% C.I.	PC1	95% C.I.	PC2	95% C.I.
<i>Ronnbergia</i> alliance	0.85	0.65–1.09	0.06	0.04–0.08	0.73	0.49–1.04	0.55	0.39–0.77
<i>Ronnbergia</i>	0.68	0.38–1.03	0.06	0.04–0.08	0.7	0.38–1.10	0.56	0.38–0.81
<i>Wittmackia</i>	1.01	0.68–1.41	0.05	0.04–0.07	0.76	0.52–1.10	0.55	0.39–0.77
Caribbean clade	1.16	0.61–2.07	0.05	0.04–0.07	1.06	0.55–2.14	0.55	0.39–0.79
Background (non-Caribbean)	0.81	0.61–1.06	0.05	0.04–0.08	0.69	0.42–1.03	0.55	0.39–0.78

the inferred phylogenetic relationships suggested a possible origin and major diversification of the genus in western Colombia. The colonization and subsequent speciation events to southern Ecuador and eastern Andes of Colombia probably occurred before the final rise of high slopes of the Andes c. 2–4 Mya (Garziona *et al.*, 2008), whereas the arrival in southern Central America probably happened after the final consolidation of the Panama Isthmus, c. 2–3 Mya (Montes *et al.*, 2012; Bacon *et al.*, 2015; O'Dea *et al.*, 2016).

Our results indicate that the rates of speciation in *Ronnbergia* are relatively constant and lower than those in *Wittmackia*, and they tend to slow down over time (Figs 4A, 5A). Slowdowns in diversification after the start of an adaptive radiation are expected according to the early-burst mode of evolution, in which ecological opportunity decreases as niches become filled and interspecific competition becomes stronger over time (Rabosky & Lovette, 2008; Glor, 2010; Burbrink & Pyron, 2010; Mahler *et al.*, 2013; Wellborn & Langerhans, 2015). This pattern is observed in the phylorate plot of speciation rate (Fig. 5A), which shows that during the split of *Ronnbergia* and *Wittmackia* the speciation rates were slightly faster, and that they subsequently decreased during the radiation of *Ronnbergia*.

Although slowdowns are also expected in the evolutionary rates of adaptive traits (Mahler *et al.*, 2013), this pattern is not evident in the evolution of floral structures of *Ronnbergia*, in which the phenotypic rates of the three floral axes remained invariable over time (Fig. 4B–D, F–H). This result indicates that rapid floral evolution in *Ronnbergia* was not a major force in the diversification of this genus. Despite this result, *Ronnbergia* showed wide floral variation, which indicates that although floral traits probably evolved in response to a high diversity of pollinators and herbivores, the phenotypic transitions were gradual and not always linked to speciation events (Fig. 3). In this case, the influence of non-adaptive mechanisms, such as geographical divergence may have played an important role in the diversification of *Ronnbergia* (Givnish, 2015). It is possible that high extinction rates also had an

influence on our estimations of phenotypic rate, but this effect was not directly assessed in this study.

DIVERSIFICATION OF *WITTMACKIA* IN THE ATLANTIC FOREST

The first two lineages of *Wittmackia* originated c. 3.2 Mya in the Atlantic Forest of north-eastern Brazil (Fig. 2). The first lineage, represented by five species endemic to humid mountainous forests in southern Bahia State, diversified similarly to *Ronnbergia*: with steady to slow speciation and phenotypic rates (Fig. 5A–D). This pattern is consistent with the early-burst mode of evolution discussed above for *Ronnbergia*, a lineage that diversified under similar environmental conditions to those of the Atlantic Forest in southern Bahia. The second lineage of *Wittmackia*, in contrast, diversified in a more heterogeneous fashion and across different environmental conditions, resulting in a lineage substantially richer in species number, called core *Wittmackia* from hereon (C.W. in Fig. 5).

Our diversification rate analysis identified the most recent common ancestor of core *Wittmackia* as the node that experienced the most significant rate shift across the *Ronnbergia* alliance, c. 2.5 Mya (Fig. 5A). At this point, the speciation rates of *Wittmackia* accelerated rapidly; later, they underwent a slight decrease in the lineages that continued diversifying in the Atlantic Forest but stayed high in the diversification of the Caribbean clade. It is possible that the initial acceleration on speciation rates reflects the effect of the Pleistocene glaciations in the Atlantic Forest, which produced multiple opportunities for speciation as a consequence of repeated events of major area fluctuation (Carnaval *et al.*, 2009; Batalha-Filho, Cabanne & Miyaki, 2012; Cabanne *et al.*, 2016).

Floral traits did not undergo significant rate shifts during the radiation of *Wittmackia* in the Atlantic Forest (Fig. 5B–D). The flowers in the Brazilian-centred *Wittmackia* spp. are not as phenotypically diverse as the flowers in *Ronnbergia* (Fig. 3). Moreover, the petals of the Brazilian species do not show

remarkable colour variation and rarely produce petal appendages (Aguirre-Santoro *et al.*, 2016). This reduced morphological spectrum, combined with constant phenotypic rates, indicates a tendency to conservatism for pollination and floral herbivory strategies during the diversification of *Wittmackia* in the Atlantic Forest, where speciation may have been driven by geographical shifts rather than rapid adaptation. This contrast between the large floral diversity in *Ronnbergia* and the reduced variation in *Wittmackia* coincides with the greater diversity of hummingbirds in north-western South America compared to the lower diversity in the Atlantic Forest, where they also act as the main pollinators of *Wittmackia* (McGuire *et al.*, 2014). This possible correlation between hummingbird diversity and floral variation in the *Ronnbergia* alliance, however, still needs to be assessed formally.

DIVERSIFICATION OF *WITTMACKIA* IN THE CARIBBEAN

The second major shift in geographical range in the *Ronnbergia* alliance was the long-distance dispersal from the Atlantic Forest to Jamaica, 0.8–1.8 Mya (Fig. 2). This type of dispersal is unusual and has rarely been reported in the literature for other groups of organisms (Acevedo-Rodríguez & Strong, 2008). Our biogeographic reconstruction and macroevolutionary analysis suggested that a founder event, followed by a remarkably rapid radiation with its centre in Jamaica, gave rise to the 17 species that comprise the Caribbean clade (Fig. 2). During the diversification of the Caribbean clade the speciation rates and phenotypic rates of PC1 were significantly faster than those of the background lineages (Figs 4A, G, 5A, C). This rapid and recent speciation, combined with rapid phenotypic change, is consistent with a pattern of adaptive diversification, a major evolutionary force for the origin of biodiversity in the Caribbean archipelago (Losos & Ricklefs, 2009; Mahler *et al.*, 2010, 2013; Filipowicz & Renner, 2012; Matos-Maravi *et al.*, 2014).

Most of the species that comprise the Caribbean clade are narrow endemics to three regions of Jamaica with contrasting environmental conditions: the hilly forest on limestone of the Cockpit Country (seven endemic species); the steep, igneous and metamorphic mountain chain of the Blue and John Crow mountains (two endemic species) and the coastal plains (three endemic species). This habitat specialization is common in adaptive radiations, in which species become rapidly adapted to specific niches as a function of ecological opportunity and interspecific competition. In the case of the Caribbean clade of *Wittmackia*, adaptation to these habitats may have been influenced by two factors: sufficient niche diversity, and rapid shifts in floral evolution in response to pollination and/or herbivory (Fig. 5C).

The species of the Caribbean clade occupy a restricted area in the morphospace of floral variation (Fig. 3). They have predominantly small flowers and form a cluster around the most negative values of the two PC floral axes. Moreover, they are morphologically different from the other lineages of *Ronnbergia* alliance because of their compact, strobilate spikes (Aguirre-Santoro, 2017). This constrained morphological variation in the Caribbean clade suggests a possible tendency of the flowers to evolve towards an optimum adaptive peak or, in contrast, the lack of sufficient time for the species to strongly diverge in morphology from each other. In our dataset, only the first floral shape axis (PC1) shows a slight rate increase that started after the radiation of the Caribbean clade (Figs 4G, 5C). The values on this axis describe the variation in structures that may be related to floral protection, such as long and wide floral bracts, wide and flattened flowers and robust sepals. This pattern indicates that floral protection probably played an important role in the evolution of the Caribbean clade, especially during the diversification in the heterogeneous habitats of Jamaica, where flower herbivores are also probably highly diverse.

It is possible that floral evolution in the Caribbean clade not only increased the chances of successful pollination, but may also be related to strategies for deterring undesired seed predators. Benzing (2000), for instance, mentioned that many berry-fruited bromeliads produce seeds that become inviable after consumption by animals; therefore, they developed strategies to attract dispersers interested in consuming the fruits externally, without detaching them from the infructescence. These strategies may include fruit compression, sepal persistence with pungent apical mucros and fruit explosiveness (as in *Ronnbergia*), among others. Although we did not measure fruits, the signature of some of these traits is also present in flowers, such as sepal mucros, floral compression, sepal size etc.

Only four Caribbean *Wittmackia* spp. are endemic to other Caribbean regions outside of Jamaica, namely Puerto Rico (two endemic species), Yucatán (one endemic species) and Grand Cayman and Providencia (one shared species). The lack of resolution in our phylogenetic data did not permit us to infer with confidence the sequence of events that led to the colonization of these areas. However, our data weakly favoured a scenario in which these events corresponded to independent dispersals, including two separate colonization events from Jamaica to Puerto Rico that gave rise to the two endemic species on the latter island. These two species exhibit contrasting morphologies, geographical distribution and habitat specialization, indicating that niche partitioning allowed the origin and co-occurrence

of these two species in the same island. In the case of the areas in the western Caribbean (Yucatán, Grand Cayman and Providencia), island size, the recency of the colonization events and inability to compete for resources against other species may be factors that explain the lack of more than one species co-existing in the same area. The latter two factors may also explain the absence of *Wittmackia* spp. on Hispaniola and the Bahamas and the presence of only one widespread species in Cuba [*W. penduliflora* (A. Rich.) Aguirre-Santoro]. Greater phylogenetic resolution is still necessary to understand the radiation of *Wittmackia* in the Caribbean, which might be determined not only by floral evolution, but also other traits related to adaptation to soil types and ecological interactions.

CONCLUSIONS

There are several issues that we did not address in our study, but deserve attention in future studies. First, we did not incorporate phylogenetic uncertainty. This is important because the phylogenetic relationships in the most recent lineages of the Brazilian radiation of *Wittmackia* and the Caribbean clade are still weakly supported. However, given that these are ‘shallow’ clades, we do not think that incorporating phylogenetic uncertainty would drastically change our results. Second, we did not measure the dynamics of extinction rates in the evolution of the *Ronnbergia* alliance; instead, we focused only in speciation and phenotypic rates. Obtaining accurate estimates of extinction is still a controversial issue and there are no robust methodologies to efficiently approach this problem (Rabosky, 2010). Third, we did not test the evolutionary dynamics of other potentially adaptive reproductive and vegetative structures. These characters include, for example, petal appendages, inflorescence branching, flower colour, pseudopetioles, the CAM photosynthetic pathway, formation of tank rosettes and epiphytism. These characters may have played a role as important as the floral traits assessed in this study and have the potential to reveal differential effects of adaptation across lineages in the *Ronnbergia* alliance.

The evolution of the *Ronnbergia* alliance is only one episode in the much larger adaptive radiation of core Bromelioideae. We demonstrated that species-level phylogenetic trees help identify the fine-scale processes that modulated this diversification. More importantly, our study helped revealing how diversification occurs *in situ* among centres of biodiversity with conservation priority. In our case, we found how the Caribbean, especially Jamaica, is a much more dynamic area of diversification compared to the Atlantic Forest and the Pacific Forest. In

the latter two areas, evolution seems to occur at a more constant pace, although it can be influenced by drastic climatic fluctuations, like in the lineages that diversified in the Atlantic Forest. The pattern of disjunct geographical range separation, followed by rapid *in situ* diversification, has occurred several times during the evolution of core Bromelioideae; for this reason, new species-level phylogenetic studies will still be necessary for revealing the tempo and mode of evolution of this adaptive radiation restricted to the Neotropics.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Supplementary File 1. Configuration file with priors and parameters used to run the diversification analyses in BAMM.

Supplementary File 2. Rdata file with the probabilities of the ancestral area reconstructions for each node. To open this file, run the script provided in the BioGeoBEARS webpage (<http://phylo.wikidot.com/biogeobears>).

Supplementary Figure 1. Chronogram generated from the Maximum Credibility Tree of the RevBayes, time-divergence analysis. Bars indicate the 95% confidence interval of the node ages estimated with a relaxed molecular clock model.

Supplementary Table 1. Species list, voucher information, morphological measurements, and PCA data used for the morphological and phylogenetic analyses. All raw measurements are in mm. Information in parenthesis next to the vouchers correspond to the herbarium where the collection is deposited or if the data were taken from a living collection (Liv.).

Supplementary Table 2. List of characters used in the morphological analyses with their respective scores of phylogenetic signal, p-values, and PCA loadings of the two first axes.

Supplementary Table 3. Posterior probabilities of the different rate regime models sampled for speciation rates, and flower length, PC1 and PC2 phenotypic rates.