



Pattern and timing of biogeographical history in the Neotropical tribe Bignonieae (Bignoniaceae)

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Despite an improving knowledge of species distribution patterns in the Neotropics, the processes that underlie these patterns remain uncertain. The tribe Bignonieae (Bignoniaceae), with 21 genera and *c.* 400 species, is the largest clade of lianas in the Neotropics. The group is an excellent model for biogeographical and evolutionary studies as it is widely distributed and exhibits high levels of morphological diversity. Here, we investigate the biogeographical history of Bignonieae using a tribe-wide time-calibrated phylogenetic tree as a basis for ancestral area reconstructions. We examine four hypotheses for the origin and subsequent biogeographical spread of the tribe. Our analyses suggest that the crown group of Bignonieae originated in South American rainforests approximately 50 Mya. Ancestral area reconstructions for the early divergences are equivocal, although the resulting *Adenocalymma*–*Neojobertia* and core Bignonieae clades appear to have occurred in eastern South America and lowland Amazonia, respectively. Our analyses suggest that, following this initial split, most lineages of Bignonieae have been repeatedly exchanged between biogeographical areas. These events occurred over a broad time span and are likely to have had multiple drivers; climate drying and the Andean Orogeny may have been particularly important for shaping overall diversity. In Bignonieae, contemporary distribution patterns appear to have been strongly influenced by Holocene environmental change. © 2012 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **171**, 154–170.

ADDITIONAL KEYWORDS: biogeography – divergence time estimates – lianas – Neotropical flora.

INTRODUCTION

The uneven distribution of species diversity has long intrigued biogeographers, evolutionary biologists and ecologists (Gaston, 2000). Patterns such as the latitudinal species gradient (e.g. Jablonski, Roy & Valentine, 2006; Wiens *et al.*, 2006), altitudinal species gradient (e.g. Rahbek, 1995; Vázquez & Givnish, 1998; Lomolino, 2001) and global biodiversity hotspots (Myers *et al.*, 2000) are well known and documented. However, despite an improving knowledge of these patterns, our understanding of their

causes and consequences is still fragmentary (Donoghue, 2008; Donoghue *et al.*, 2009).

The Neotropics host *c.* 37% of global plant species diversity (Richardson *et al.*, 2001) and high levels of diversity in many other groups of organisms (e.g. Grenyer *et al.*, 2006; Lamoreux *et al.*, 2006; Qian & Ricklefs, 2008). The concentration of diversity in the Neotropics has attracted the attention of scientists, with considerable effort directed towards both the documentation of patterns and, more recently, a better understanding of the underlying processes (e.g. Pennington *et al.*, 2004, 2010; Cody *et al.*, 2010; Hoorn *et al.*, 2010; Pennington & Dick, 2010; Rull, 2011). A wide variety of hypotheses have been sug-

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gested to explain patterns in the geographical distribution of plant diversity in the Neotropics (for reviews, see Haffer, 2008; Antonelli *et al.*, 2010; Antonelli & Sanmartín, 2011). However, only relatively recently has it become possible to test these hypotheses explicitly with phylogenetic methods (e.g. Richardson *et al.*, 2001; Davis *et al.*, 2002; Lavin, 2006; Dick *et al.*, 2007; Antonelli *et al.*, 2009; Simon *et al.*, 2009, 2011; Roncal *et al.*, 2010). These studies have helped to identify the processes underlying the assembly of Neotropical plant species diversity (Pennington & Dick, 2004; Wiens & Donoghue, 2004; Pennington, Richardson & Lavin, 2006; Antonelli & Sanmartín, 2011). They indicate that different biogeographical and environmental factors are important in different lineages (e.g. Pennington *et al.*, 2004; Särkinen *et al.*, 2007; Antonelli *et al.*, 2009; Roncal *et al.*, 2010), and that overall patterns reflect the complex history of Neotropical environments (Antonelli & Sanmartín, 2011).

Lianas are a critical element in Neotropical forest ecosystems. Plants with this growth form contribute approximately 25% of the species diversity and woody stem density in these forests (Schnitzer & Bongers, 2002). An improved understanding of the evolutionary history of groups that include lianas can therefore be expected to provide new insights into the origins and evolution of Neotropical ecosystems. Despite their importance, lianas have thus far not featured in studies of Neotropical biogeography. With 21 genera and *c.* 400 species (Lohmann & Taylor, 2013), the tribe Bignoniaceae (Bignoniaceae) is the largest single clade of lianas in the Neotropics (Lohmann, 2006). The tribe is exclusively New World in distribution, occurring from the southern USA to northern Chile and Argentina (Lohmann, 2006). Members of this clade occupy a wide array of humid and dry habitat types, ranging from rainforests (e.g. Atlantic coastal and Amazonian) to seasonally dry woodlands (e.g. caatinga and chaco) and savannas (e.g. cerrado). Individual species exhibit a variety of distribution patterns. Some species are locally endemic, while others have wide ranges. Similarly, some are restricted to a single habitat, whereas others occupy several broadly defined habitat types (Gentry, 1979). The size of the tribe in terms of species numbers and the range of distribution patterns make Bignoniaceae an excellent model for the investigation of Neotropical biogeography.

Two contrasting biogeographical hypotheses have been proposed to explain the current distribution of Bignoniaceae. The first suggests that the tribe originated in the coastal rainforests of eastern Brazil and subsequently spread westwards and northwards across South and Central America (Fig. 1A; Kubitzki, 1975; Gentry, 1982). This hypothesis is based on the

presence of putatively primitive species (e.g. *Perianthomega vellozoi* Bureau) in this region (Gentry, 1982). The second hypothesis is based on the observation that supposedly specialized forms [e.g. *Bignonia magnifica* (Sprague ex Steenis) L.G.Lohmann, *Bignonia longiflora* Cav.] occur in western South America. Atchley (1976) interpreted these as support for a western origin and later eastward expansion (Fig. 1B). Beyond these specific hypotheses, two observations suggest additional scenarios. First, as lowland Amazonia is the current centre of species diversity, it is possible that the clade originated there, and subsequently expanded its distribution (Fig. 1C). Indeed, such explanations based on the current centre of species diversity are among the most widely used to account for patterns of species diversity (as reviewed by Cain, 1944). Second, the presence of putative fossils of Bignoniaceae (e.g. Chaney & Sanborn, 1933) and a contemporary species, *Bignonia capreolata* L., in North America point to a North American origin and southward range expansion (Fig. 1D; Wolfe, 1975; Lavin & Luckow, 1993).

Each of these four scenarios makes specific testable predictions about the phylogeny of Bignoniaceae. For instance, if Bignoniaceae originated in the coastal rainforests of eastern Brazil, we would expect the earliest diverging lineages to occur there, and western lineages to have arisen more recently. In this study, we use a time-calibrated molecular phylogenetic tree and ancestral area reconstructions to evaluate the historical biogeography of Bignoniaceae. We discuss our results in the context of environmental change in the Neotropics and patterns in other plant groups.

MATERIAL AND METHODS

DATA MATRIX

We used the combined molecular dataset of Lohmann (2006) as the basis for our analysis. This dataset includes chloroplast *ndhF* and nuclear *PepC* sequences for 104 members of Bignoniaceae. To this data matrix we added *ndhF* sequences for *Perianthomega vellozoi* Bureau and three outgroups [*Jacaranda arborea* Urban, *Tabebuia sauuvallei* Britton and *Tecoma capensis* (Thunb.) Lindl.]. For these taxa, *PepC* sequences were coded as missing data. Details of the included taxa are provided in Supporting Information (Table S1), and the aligned sequence matrix is available from TreeBase (Study Accession 13300).

The taxon sampling of Lohmann (2006) aimed to represent genera and their morphological diversity. The matrix includes approximately one-quarter of the currently recognized species of Bignoniaceae and all but one of the 21 genera (the monotypic *Callichlamys* Miq. was not included; Lohmann & Taylor, 2013).

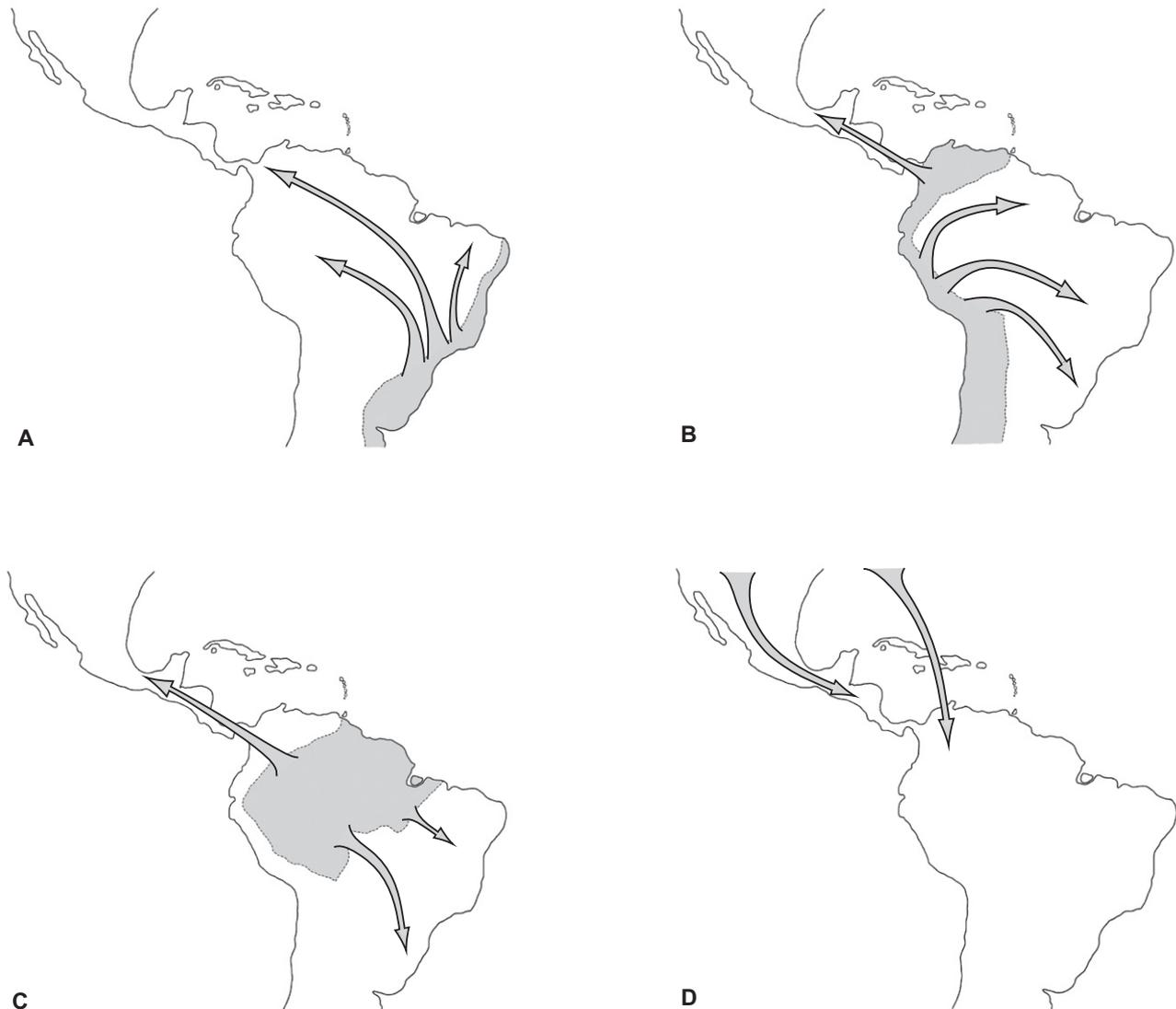


Figure 1. Hypothesized origins for the tribe Bignonieae. A, Origin in eastern South America and subsequent westward expansion (Gentry, 1982). B, Origin in western South America and subsequent eastward expansion (Atchley, 1976). C, Origin in lowland Amazonia and subsequent expansions. D, Origin in North America and subsequent southward dispersal to Central and South America.

This sampling also represents both the overall geographical distribution of the tribe and the range of distribution types characteristic of individual species (i.e. geographically widespread taxa and those with more restricted distributions, taxa restricted to a single habitat and those that occupy several). Therefore, our current sampling provides a framework for the study of broad biogeographical patterns in the Neotropics.

MOLECULAR ESTIMATES OF CLADE AGES

Preliminary investigations indicated that the two marker loci are not evolving in a clock-like fashion.

Likelihood ratio tests using these loci, either individually or combined, strongly rejected rate constancy across lineages ($P \ll 0.001$). In addition, preliminary BEAST analyses indicated that the posterior distribution of the covariance parameter for the uncorrelated log-normal relaxed clock bounded zero. This result suggests that rates are not autocorrelated, making methods that assume autocorrelation (e.g. penalized likelihood and MULTIDIVTIME) less appropriate. We therefore chose to use the uncorrelated log-normal model of rate evolution as implemented in BEAST (version 1.7.1; Drummond & Rambaut, 2007a) to simultaneously infer trees and associated divergence times.

For the BEAST analyses, we partitioned the data by locus. A GTR + I substitution model was applied to the *ndhF* partition and an HKY model to the *PepC* partition. Model parameters were unlinked across partitions. Three independent BEAST runs, each consisting of 2.0×10^7 generations, were sampled every 1000 generations (for a total of 2.0×10^4 sampled generations). The convergence of individual runs was assessed using Tracer v.1.5 (Drummond & Rambaut, 2007b) and by plotting the log posterior probability against the number of generations. Chains converged within the first 5.0×10^3 sampled generations in all cases; for subsequent analyses, we combined the post-burnin generations for the three runs, resulting in a final sample size of 4.5×10^4 generations. The effective sample sizes for both individual and combined post-burnin samples were > 300 for all parameters.

For the BEAST analyses, we constrained the ages of two nodes. The first calibration was based on a pollen grain from the Gatuncillo formation of Panama, described as ‘cf. *ParagonialArrabidaea*’ (Graham, 1985). The updated generic taxonomy (Lohmann & Taylor, 2013) places members of these two groups in several genera (*Cuspidaria* DC., *Fridericia* Mart., *Tanaecium* Sw. and *Xylophragma* Sprague). We therefore assigned this fossil to the crown node of the

corresponding *Xylophragma* and allies clade. The Gatuncillo formation is estimated to be 37.0–33.7 Myr old (Tripathi & Zachos, 2002); we applied this constraint using a log-normal prior with an offset value of 33.7 and a mean and standard deviation of 1.0. We also constrained the age of the root node using fossil evidence. In this case, we did not use a single fossil, but rather several fossils that are all approximately 50 Myr old (e.g. Wehr & Hopkins, 1994; Wehr, 1995; Wehr & Manchester, 1996; Wilf, 1997; Pigg & Wehr, 2002). These are the oldest fossils clearly recognizable as Bignoniaceae and, as such, provide appropriate minimum ages for the first diverging lineages in the family. We applied this constraint using a normal prior with a mean of 49 and standard deviation of 3.0.

SELECTION AND CODING OF BIOGEOGRAPHICAL AND HABITAT CHARACTER STATES

For our analyses, we defined five broad biogeographical areas. Four are based on those proposed by Gentry (1979) and reflect patterns of endemism in Bignoniaceae. The four areas are: (1) eastern South America; (2) the South American dry areas; (3) lowland Amazonia; and (4) western South America and Central America (Fig. 2). To these we added a fifth area,



Figure 2. Biogeographical areas proposed by Gentry (1979), reflecting patterns of endemism in Bignoniaceae.

North America, to account for the distribution of *Bignonia capreolata* L. We used distribution maps for the 105 taxa sampled in the molecular phylogeny of the tribe (Fig. S1) and used those maps as a basis to assign species to biogeographical regions. Our taxon sampling included a mixture of widespread species and those restricted to a single biogeographical area; widespread taxa were coded as polymorphic. To aid the interpretation of our biogeographical results, we determined whether species occurred in wet (e.g. lowland rainforest), dry (e.g. cerrado, seasonally dry forest) or both of these broad habitat categories. Assignments were based on the habitat data provided by Lohmann & Taylor (2013). Biogeographical and habitat information for the sampled Bignonieae is presented in Supporting Information (Table S2).

We acknowledge that our biogeographical areas differ from the more narrowly defined areas that have been used in other recent biogeographical studies (e.g. Antonelli *et al.*, 2009; Givnish *et al.*, 2011). However, we believe that the broad areas suggested by Gentry (1979) provide the most appropriate framework for biogeographical inference in this group. In Bignonieae, individual species tend not to be restricted to more narrowly defined areas; instead, they are often more widely distributed. For example, although the dry areas of South America can be subdivided into a number of smaller units (e.g. cerrado, caatinga and chaco), the same species of Bignonieae are often present in two or more of these subtypes. Preliminary analyses with more narrowly defined areas resulted in almost all terminal taxa being coded as polymorphic and even higher levels of uncertainty in area reconstructions.

BIOGEOGRAPHICAL RECONSTRUCTIONS

We used parsimony, statistical dispersal–vicariance analysis (S-DIVA; Yu, Harris & He, 2010) and Bayesian binary Markov chain Monte Carlo (MCMC) (BBM; Yu, Harris & He, 2011) to reconstruct the biogeographical history of Bignonieae. We used multiple approaches in order to limit the possibility of methodological biases influencing subsequent inferences. In each case, we performed analyses using the maximum clade credibility tree and a random subset of 1000 post-burnin trees from the combined BEAST runs. These analyses allowed us to account for uncertainty in both tree topology and age estimates (for S-DIVA and BBM only). For these analyses, we trimmed the three outgroups from our trees.

Preliminary parsimony reconstructions were performed in MacClade 4.08 (Maddison & Maddison, 2005) using both ACCTRAN and DELTRAN optimizations. The same general patterns were recovered in both cases; the few exceptions involved derived nodes,

and did not affect the overall reconstruction. We therefore performed additional parsimony analyses in Mesquite 2.74 (Maddison & Maddison, 2009). For these analyses, we optimized character states on 1000 trees randomly sampled from the combined BEAST runs. Ancestral states were then summarized on the maximum clade credibility tree.

S-DIVA and BBM analyses were performed in RASP (Yu *et al.*, 2011) using default parameters, the exceptions being that the maximum number of unit areas was set to five for both analyses and the number of BBM runs was set to 1.0×10^6 generations. Initial S-DIVA and BBM runs assumed a null distribution for the outgroup. To evaluate the influence of this assumption, we repeated analyses with alternative ancestral areas enforced. For both S-DIVA and BBM, we conducted six additional analyses, five in which the outgroup was assumed to have occurred in a single biogeographical area and one in which a widespread ancestor was assumed.

RESULTS

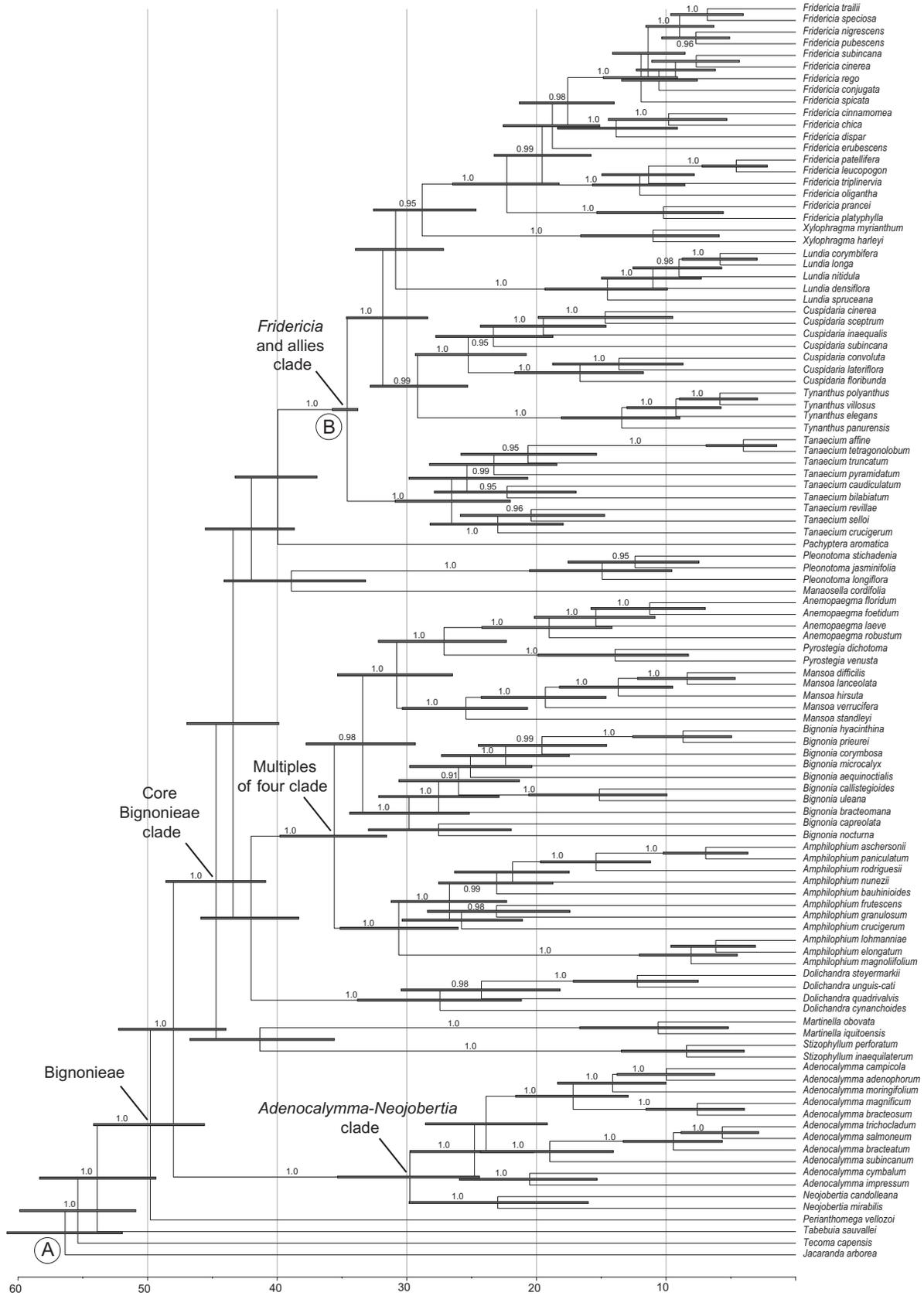
DIVERGENCE TIME ESTIMATION

Our divergence time analyses (Fig. 3; Table 1) suggest that the earliest diverging contemporary lineages in Bignonieae arose during the Eocene [95% highest posterior density (HPD), 54.2–45.6 Mya]. This age is consistent with older estimates for Lamiales as a whole (Magallón & Castillo, 2009). Most of the major clades in the tribe were established prior to 25 Mya. Contemporary species diversity is as much as 35 Myr old in some currently recognized genera (e.g. *Bignonia* L., *Adenocalymma* Mart. ex Meisn.), although it is much younger in others (e.g. *Xylophragma*).

BIOGEOGRAPHICAL RECONSTRUCTIONS

Ancestral area reconstructions based on S-DIVA are presented in Figures 4 and 5; those for parsimony and BBM are presented in Supporting Information (Figs S2–S4). A summary of reconstructions at key nodes is given in Table 1.

Parsimony reconstructions suggest that the earliest divergences in Bignonieae and the most recent common ancestor (MRCA) of the *Adenocalymma–Neojobertia* Baill. clade (corresponds to the SMANG clade of Lohmann, 2006) occurred in eastern South America (Fig. S2; Table 1). In the *Adenocalymma–Neojobertia* clade, colonizations of lowland Amazonia and the South American dry areas followed early diversification in eastern South America. The split between the *Adenocalymma–Neojobertia* and core Bignonieae lineages is accompanied by the colonization of lowland Amazonia by the core Bignonieae clade. Based on this analysis, much of the early diversifica-



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Figure 3. See caption on next page.

Figure 3. Maximum clade credibility tree for the tribe Bignoniaceae. Branch lengths are proportional to time, with grey bars indicating 95% highest posterior densities and posterior probabilities shown where these are above 0.90. Nodes A and B indicate fossil constraints used for divergence time estimation. Node A is based on the first earliest recognizably Bignoniaceae fossils; node B is based on fossil pollen from the Gatuncillo formation of Panama (see text for further details). Clade names either follow Lohmann (2006) or new names are introduced to accommodate recent nomenclatural changes.

tion in the core Bignoniaceae clade also occurred in lowland Amazonia. Colonizations of other biogeographical areas, such as the South American dry areas (i.e. the *Fridericia–Xylophragma* clade) and North America (i.e. *Bignonia capreolata*), occurred later. Reversals involving both eastern South America (e.g. the *Mansoa difficilis* Bureau & K.Schum.–*Mansoa hirsuta* DC. clade and *Tynanthus elegans* Miers) and lowland Amazonia [i.e. *Fridericia prancei* (A.H.Gentry) L.G.Lohmann, *F. spicata* (Bureau & K.Schum.) L.G.Lohmann and *F. trailii* (Sprague) L.G.Lohmann] are also observed.

In general, results from the BBM and parsimony analyses are similar. The BBM analysis using a null outgroup distribution recovers eastern Brazil as the most likely ancestral area for the basal nodes in Bignoniaceae and the *Adenocalymma–Neojobertia* clade (Fig. S2; Table 1). For the crown node of core Bignoniaceae, the BBM reconstruction implies a widespread distribution; a widespread ancestor (i.e. eastern South American and lowland Amazonian) is most likely, with both eastern South America and lowland Amazonia reconstructed with lower probabilities (Table 1). Outgroup distribution had little impact on nodal reconstructions, except when a widespread or lowland Amazonian outgroup was enforced (Fig. S3). In these analyses, levels of uncertainty differ across the phylogenetic tree. In many parts of the tree, there is strong support for area reconstructions. In others (e.g. in *Dolichandra* Cham. and the *Fridericia–Xylophragma* clade), there are higher levels of uncertainty associated with reconstructions. Again, BBM implies multiple colonizations of each biogeographical area.

Reconstructions based on S-DIVA (Fig. 4) are broadly similar to those of our other analyses. A notable difference, however, is the inference of widespread ancestors at the two basal-most nodes in Bignoniaceae (Table 1). Outgroup choice had a greater influence on area reconstructions in S-DIVA (Fig. 5). Patterns in the distribution of uncertainty in nodal reconstructions differ between S-DIVA and BBM. For example, in the *Fridericia–Xylophragma* clade, S-DIVA suggests a colonization of the dry areas, whereas BBM favours widespread ancestors at the same nodes. Conversely, in *Tanaecium* and *Cuspidaria*, S-DIVA reconstructions suggest greater uncertainty.

DISCUSSION

In this study, we estimated divergence times and reconstructed ancestral geographical distributions for the Neotropical tribe Bignoniaceae. Although these analyses have some limitations with respect to biogeographical inference (e.g. poor support for the more basal nodes, limited taxon sampling), they provide important general insights into the history of the tribe. Our analyses suggest a complex history involving repeated colonizations of several broadly defined biogeographical areas. These events have occurred over a broad time span, suggesting that a number of factors may have influenced the evolution of modern species diversity in Bignoniaceae. Below, we discuss the general patterns recovered and their potential explanations.

THE GEOGRAPHICAL ORIGIN OF BIGNONIAEAE

In this study, we considered four broad scenarios for the origin of Bignoniaceae. Three of these scenarios suggest that the tribe originated somewhere in South America, whereas the fourth implies a North American origin (Fig. 1). These alternative hypotheses can be summarized as two distinct questions. Did the Bignoniaceae originate in North or South America? If the tribe arose in South America, where did this event take place?

Our molecular age estimates suggest that the oldest divergences in Bignoniaceae are of Eocene age. We date the MRCA of the tribe to approximately 50 Mya (95% HPD, 54.2–45.6 Mya). This age is consistent with either a North or South American origin, as forests containing tropical elements covered most of South America and also occurred in North America during the Eocene (Romero, 1986; Morley, 2000; Jaramillo, Rueda & Mora, 2006). However, despite the existence of suitable habitats, none of our ancestral area reconstructions supports a North American origin (Figs 4, S2, S3). Even when a North American ancestor is enforced, the S-DIVA and BBM analyses favour a widespread (S-DIVA; Fig. 4) or eastern South American (BBM; Fig. S3) MRCA for Bignoniaceae. Instead, in almost all of our ancestral area reconstructions, a South American origin for Bignoniaceae is strongly favoured (Figs 4, 5, S2, S4).

Table 1. Age estimates and ancestral state reconstructions for key nodes

	Age estimate and 95% HPD	Probabilities for nodal reconstructions		
		Parsimony	BMM	S-DIVA
Major clades and numbered nodes				
Node 1, Bignonieae	49.8 54.2–45.7	A: 1.00	A: 0.96	ACD: 0.54 AC: 0.23 A: 0.23
Node 2	48.0 52.2–43.9	A: 1.00	A: 0.58 AC: 0.30 C: 0.10	ACD: 0.54 AC: 0.23 C: 0.23
Node 3, <i>Adenocalymma</i> – <i>Neojobertia</i> clade	29.8 35.3–24.4	A: 1.00	A: 0.67 AC: 0.26	A: 0.68 AC: 0.32
Node 4, Core Bignonieae clade	44.7 48.6–40.9	C: 0.63 Equivocal: 0.37	AC: 0.50 C: 0.28 A: 0.10	CD: 0.62 C: 0.36
Node 5	43.4 47.0–39.9	C: 0.75 Absent: 0.25	C: 0.47 AC: 0.44	C: 0.99
Node 6	41.3 46.7–35.6	C: 0.61 Absent: 0.39	ACD: 0.35 AC: 0.24 CD: 0.22	CD: 0.36 C: 0.36 D: 0.28
Multiples of four clade	35.6 39.8–31.6	C: 1.00	C: 0.65 AC: 0.19 BC: 0.09	C: 1.00
<i>Fridericia</i> and allies clade	30.9 34.0–27.2	C: 1.00	C: 0.93	C: 0.99
Crown nodes of genera				
<i>Adenocalymma</i>	24.7 29.7–20.2	A: 1.00	A: 0.46 AC: 0.41 C: 0.07	AC: 0.37 A: 0.36 C: 0.26
<i>Amphilophium</i>	30.6 35.1–26.0	C: 1.00	C: 0.65 AC: 0.19 BC: 0.08	C: 1.00
<i>Anemopaegma</i>	19.0 24.2–14.2	C: 1.00	C: 0.81 BC: 0.09	C: 1.00
<i>Bignonia</i>	29.8 34.4–25.2	C: 1.00	C: 0.79	C: 0.94 CE: 0.06
<i>Cuspidaria</i>	16.6 22.7–11.7	C: 1.00	BC: 0.44 C: 0.38 ABC: 0.09	C: 0.37 BC: 0.32 AC: 0.31
<i>Dolichandra</i>	27.4 33.8–21.6	C: 0.99	ABC: 0.57 AC: 0.12 AB: 0.12	BC: 0.33 AC: 0.33 ABC: 0.33
<i>Fridericia</i>	22.3 26.5–18.3	B: 0.95 Equivocal: 0.05	ABC: 0.52 AB: 0.25 BC: 0.12	B: 0.97
<i>Lundia</i>	14.5 19.3–9.9	C: 1.00	C: 0.92	C: 0.99
<i>Mansoa</i>	25.4 30.3–20.6	C: 1.00	CD: 0.63 C: 0.31	C: 1.00
<i>Pleonotoma</i>	14.9 20.5–9.6	C: 1.00	C: 0.91 AC: 0.08	C: 0.97
<i>Tanaecium</i>	26.5 30.9–22.0	C: 1.00	C: 0.89 CD: 0.07	C: 0.98
<i>Tynanthus</i>	13.4 18.1–8.9	C: 1.00	C: 0.95	C: 1.00

BMM, Bayesian binary Markov chain Monte Carlo; HPD, highest posterior density; S-DIVA, statistical dispersal–vicariance analysis.

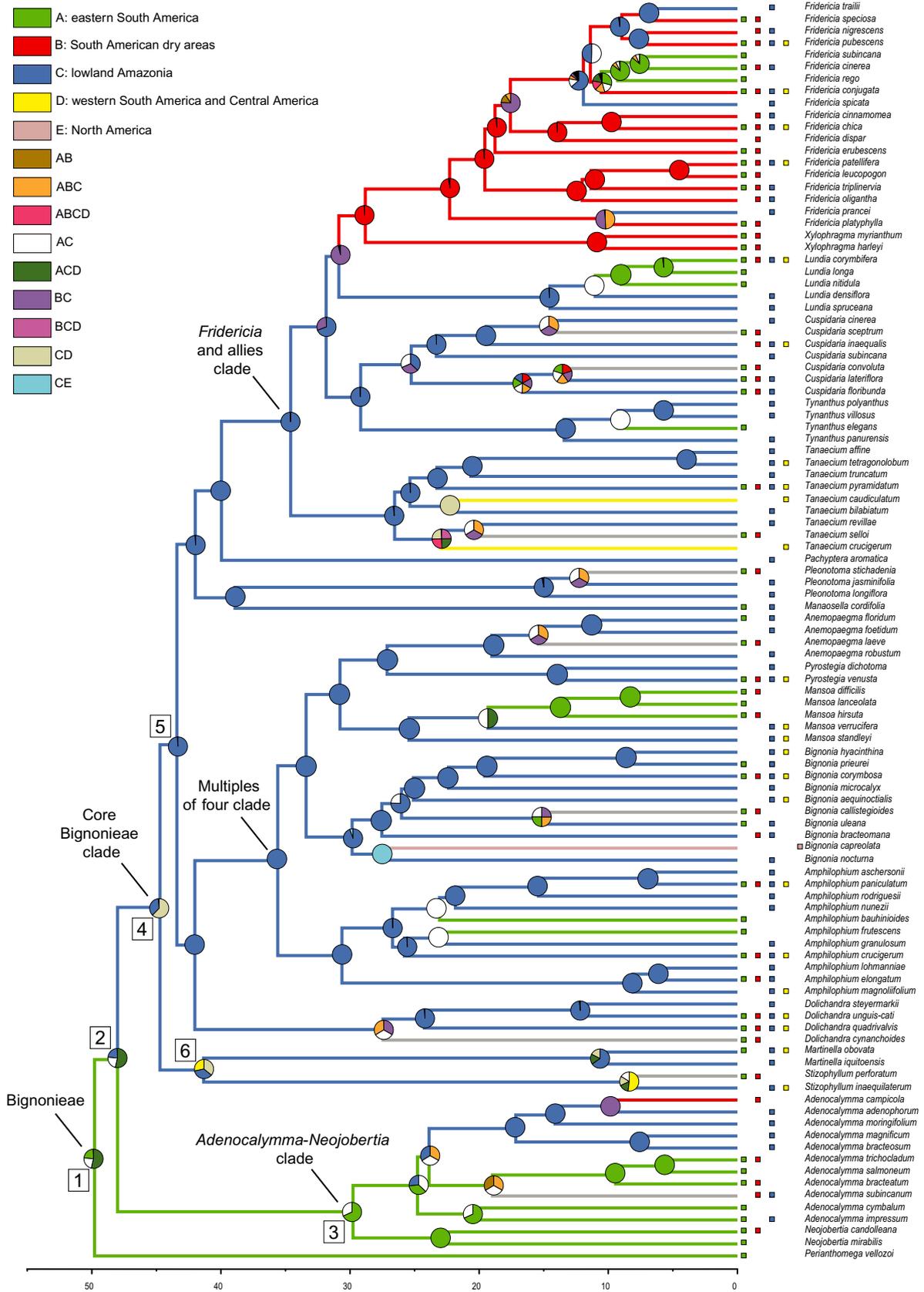


Figure 4. See caption on next page.

Figure 4. Ancestral state reconstructions based on maximum parsimony (using DELTRAN optimization) and statistical dispersal–vicariance analysis (S-DIVA) overlaid onto the maximum clade credibility chronogram from BEAST. Current distributions are indicated before the species names. The colour of the branches indicates inferred distributions of ancestral taxa using parsimony (grey lines indicate ambiguous parsimony reconstructions). Pie graphs report relative probabilities from the S-DIVA analysis; the three areas with highest probability are reported with the remaining areas (usually frequencies below 0.01) collectively marked in black. Nodes 1–6 are discussed in the text and reconstructions based on alternative outgroup distributions are shown in Figure 5.

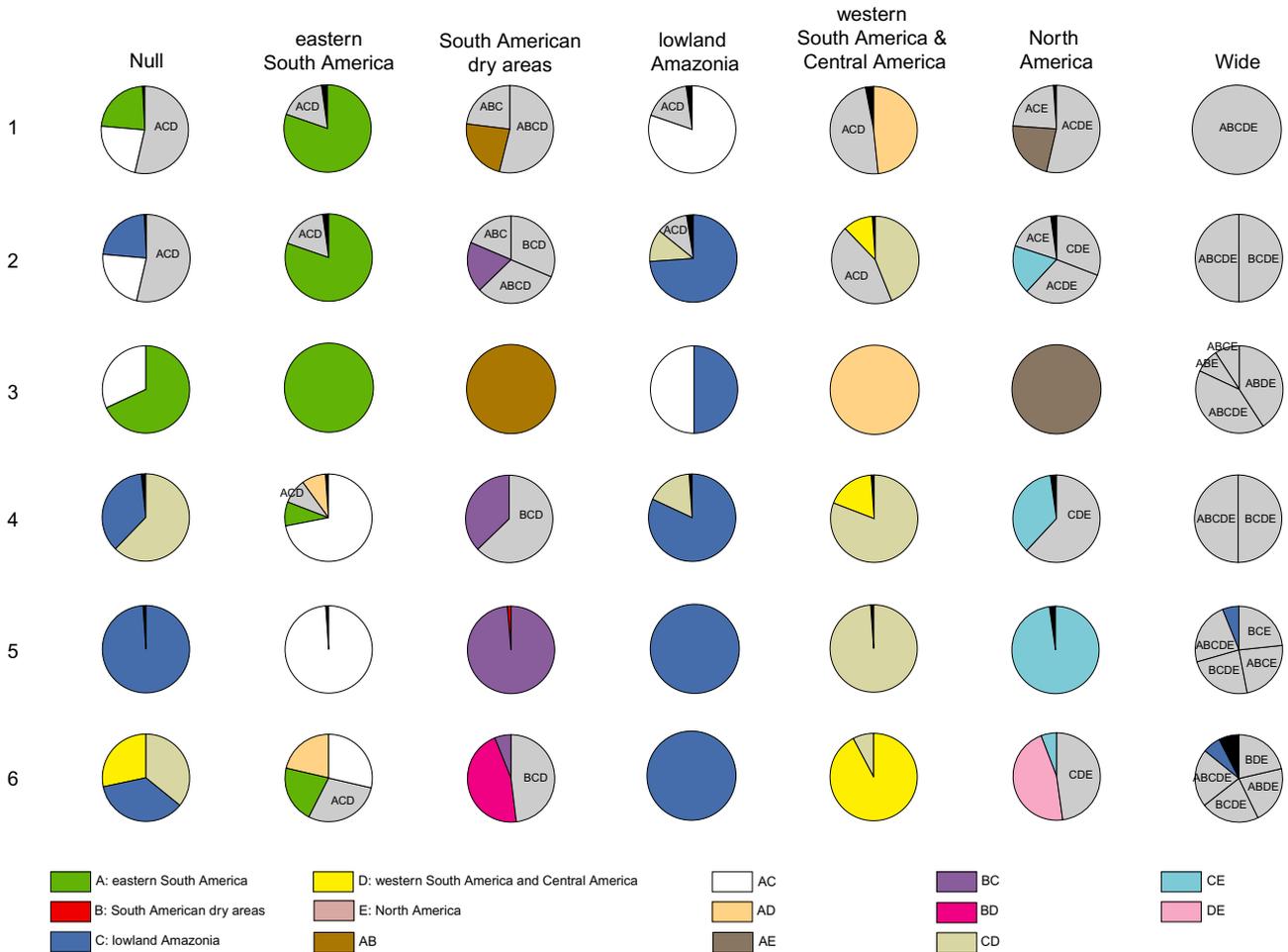


Figure 5. Ancestral state reconstructions for nodes 1–6 (marked in Fig. 4) based on statistical dispersal–vicariance analysis (S-DIVA) and assigning the outgroup to different biogeographical areas. Pie graphs report the proportional likelihood for reconstructions with $P > 0.01$; other reconstructions are collectively indicated in black. For clarity, reconstructions involving three or more of our biogeographical areas are shaded grey (widespread) and the inferred distributions are indicated with the corresponding letters.

Although our analyses provide no evidence for a North American origin, the fossil record is not inconsistent with this possibility. Specifically, there are two Eocene fossils [pollen from the Gatuncillo formation of Panama (Graham, 1985) and *Callichlamys* from the Goshen flora of Oregon (e.g. Chaney & Sanborn, 1933)] that appear to directly contradict our phylogeny-based ancestral area reconstructions. At face value, this conflict would seem to limit our ability

to confidently infer the biogeographical history of this clade. However, it is important to examine all the evidence carefully. In this case, both fossils are late Eocene in age (i.e. < 37 Myr old) and represent relatively derived lineages (i.e. the stem of the Multiples of four clade and nested within the *Fridericia* Mart. and allies clade). This makes it much more difficult to interpret these fossils as evidence for a common ancestor in North America c. 50 Mya. An alternative

explanation is that the lineages represented by these fossils and the single extant North American species, *Bignonia capreolata*, are the result of long-distance dispersal from South America. This latter scenario is consistent with our ancestral area reconstructions, with fossil evidence for the appearance and diversification of Bignoniaceae in South America during the Eocene (Romero, 1993) and with the derived position of North American taxa in a family-wide phylogenetic analysis (Olmstead *et al.*, 2009). The two scenarios also imply different patterns of dispersal and extinction. If we assume a North American origin, each of the lineages that diverged prior to *c.* 37 Mya must have independently dispersed southward and subsequently become extinct in North America. However, a South American origin requires a smaller number of northward dispersals and does not require widespread extinction. The latter would seem more parsimonious. Further analyses of the fossil record are clearly needed in order to distinguish between these two scenarios. However, at this point, a South American origin for the tribe provides a better explanation of the available data.

Unfortunately, our analyses do not unambiguously identify where in South America Bignoniaceae arose. Ancestral area reconstructions using both parsimony and BBM imply that the MRCA of Bignoniaceae occurred in eastern South America (Table 1; Figs S2, S3). In the BBM analyses, eastern South America remains the most likely ancestral area, unless a widespread or lowland Amazonian outgroup is enforced (Fig. S4). Our S-DIVA reconstructions also favour a widespread MRCA, although, in this case, the distribution of the ancestor is more strongly influenced by outgroup distribution (Table 1; Figs 4, 5). A combination of factors is likely to be responsible for difficulties in confidently resolving the distribution of the MRCA. Uncertainties in the underlying tree topology and associated age estimates are clearly important; relationships near the base of the tree are more poorly supported and the probability distributions for age estimates at many nodes are wide (Fig. 3). An additional complication is the large number of widespread contemporary species. Reconstruction of ancestral states in such situations is challenging and the outcomes are often strongly method dependent.

Although our reconstructions do not identify a unique ancestral area, they do strongly suggest that the MRCA occupied a South American rainforest habitat. None of our reconstructions offers support for an origin in the South American dry areas. Even when a dry area outgroup was enforced, our reconstructions still favoured a widespread ancestor (Figs 5, S4). A widespread forest ancestor makes sense, given that rainforest assemblages are thought to have been more or less continuous in South

America until the middle Miocene (Morley, 2000). However, the observation that lowland Amazonian and widespread taxa are generally derived in Bignoniaceae as a whole (Olmstead *et al.*, 2009) appears to favour a more restricted eastern South American ancestor. This latter suggestion is consistent with Gentry's (1982) biogeographical hypothesis and with recent phylogenetic studies that imply an eastern South American origin for various plant groups (for a review, see Fiaschi & Pirani, 2009). Even though the available data suggest an eastern South American origin for Bignoniaceae, confidently resolving where in South America the Bignoniaceae arose will require further phylogenetic studies and detailed analyses of South American palaeofloras.

THE SPREAD OF BIGNONIEAE IN THE NEOTROPICS

Our trees indicate that Bignoniaceae split into two major lineages (i.e. the core Bignoniaceae and *Adenocalymma-Neojobertia* clades; node 2) early in their history, and that relatively soon after this initial split there were further divergences in core Bignoniaceae (i.e. nodes 4–6). Age estimates suggest that these early divergences occurred during the mid and late Eocene (Table 1). Parsimony analyses indicate that the establishment of the core Bignoniaceae and *Adenocalymma-Neojobertia* clades was associated with geographical differentiation. That is, the MRCA of the *Adenocalymma-Neojobertia* clade is reconstructed as eastern South American and that of core Bignoniaceae as lowland Amazonian (Table 1; Fig. S2). However, neither the S-DIVA nor BBM analysis recovers this pattern clearly (Table 1; Figs 4, S3). Uncertainty in the ancestral area reconstructions at these early nodes is again likely to be caused by a combination of factors. Taken together with evidence for the wide distribution of rainforests during the Eocene, it is difficult to exclude widespread ancestors early in the evolution of Bignoniaceae.

Despite uncertainty at the basal nodes, our analyses consistently suggest that lineage diversity in core Bignoniaceae arose primarily in lowland Amazonia. Many of the nodes in this clade are reconstructed as lowland Amazonian with high likelihood (Figs 4, S2, S3). As our taxon sampling is incomplete, we must remain cautious about the exact nature and timing of the divergences in this group. However, it is clear from our analyses that diversification events in core Bignoniaceae are unlikely to have been associated with a single climatic or geological event. Diversification has occurred over such a broad time span that multiple drivers seem more likely. One possibility is that hydrological changes ~23–7 Mya (i.e. the Pebas and Acre systems; Hoorn *et al.*, 2010) were important for diversification in this clade. These changes have been associated with diversification in several groups of

birds, amphibians and plants (e.g. Antonelli *et al.*, 2010; Roncal *et al.*, 2010). Although this hypothesis is appealing, testing it may prove difficult, given the uncertainty in age estimates and the fact that these changes often overlap in time (Pennington & Dick, 2010).

Diversification of the core Bignoniaceae in lowland Amazonia was followed by multiple colonizations of the remaining biogeographical areas. Our analyses suggest that at least 13 such colonizations occurred from ~30.9 Mya (95% HPD, 34.0–27.2 Mya) onwards (Figs 4, S2, S3). In most cases, our reconstructions suggest that these events involved single species or small species groups within genera [e.g. *Amphilophium frutescens* (DC.) L.G.Lohmann, *Tanaecium caudiculatum* (Standl.) L.G.Lohmann, *Mansoa diffractilis–hirsuta* clade]. However, one event, the colonization of the South American dry areas by an ancestor of the *Fridericia–Xylophragma* clade, c. 30.9 Mya (95% HPD, 34.0–27.2 Mya), occurred prior to diversification of the two genera and has therefore affected a larger number of species. The timing of this event appears to coincide broadly with the cooling and drying of the climate in South America during the Oligocene (Morley, 2000; Jaramillo *et al.*, 2006). These changes are thought to have led to the establishment of open habitats well before modern savannas became important c. 24 Mya (van der Hammen, 1983; Jacobs, Kingston & Jacobs, 1999). The timing of divergences in the *Fridericia–Xylophragma* clade also often coincide with those for other savanna groups (Simon *et al.*, 2009). In addition to the *Fridericia–Xylophragma* clade, members of other genera of core Bignoniaceae have colonized the South American dry areas (e.g. *Bignonia*, *Cuspidaria*). Indeed, contemporary taxa with distributions that include the dry areas are widely distributed in this clade (Figs 4, S2, S3); these colonizations appear to have occurred much more recently than in the *Fridericia–Xylophragma* clade.

Members of core Bignoniaceae have also colonized western South America and Central America (Figs 4, S2, S3). Our analyses included two *Tanaecium* spp. restricted to this region. Divergence time estimates suggest that these may have originated as much as c. 25 Mya. If so, the establishment of these species seems likely to have resulted from dispersal prior to the formation of the Isthmus of Panama (Coates *et al.*, 1992) or isolation during the earliest stages of the Andean orogeny (Hoorn *et al.*, 2010). In addition to those sampled in this study, a further nine species of Bignoniaceae occur only in western South America and Central America (Lohmann & Taylor, 2013); it will be interesting to investigate whether these exhibit similar relationships. In contrast, 21 of the sampled species have distributions that include, but are not limited to, western South America and

Central America. Our analyses strongly suggest that these taxa represent more recent colonization events. The distributions of these taxa always include lowland Amazonia and this implies a close biogeographical link between these areas. We need improved sampling of both restricted and shared taxa if we are to examine the origins of these plants in more detail.

Our analyses show that the smaller *Adenocalymma–Neojobertia* clade has also expanded its range. In this clade, early divergences are generally reconstructed as eastern South American (Figs 4, S2, S3). In *Adenocalymma*, one subclade has colonized lowland Amazonia. This event is dated to c. 23.9 Mya (95% HPD, 28.6–19.2 Mya), well after the establishment of the dry areas, and therefore suggesting an origin by dispersal. One member of this clade [*Adenocalymma campicola* (Pilg.) L.G.Lohmann] has subsequently occupied the dry areas. In other lineages of the *Adenocalymma–Neojobertia* clade, there have been further colonizations of both lowland Amazonia and the dry areas.

CONTEMPORARY SPECIES DISTRIBUTIONS IN BIGNONIEAE

To date, most biogeographical studies involving Neotropical plants have focused on large, widely distributed groups (e.g. Perret, Chautems & Spichiger, 2006; Antonelli *et al.*, 2009; Givnish *et al.*, 2011). In these groups, individual species have more restricted distributions and often occur in just one of the regions that make up the distribution of the group as a whole. In contrast, Bignoniaceae contains a substantial proportion of broadly distributed species. In the current analyses, 47% (49/104) of the sampled Neotropical species are restricted to one biogeographical area, whereas 53% (55/104) occur in two or more areas (Fig. 4; Table S2).

Differences in niche conservatism may provide a partial explanation for contrasting distribution patterns in Bignoniaceae and previously studied groups (e.g. Perret *et al.*, 2006; Antonelli *et al.*, 2009; Givnish *et al.*, 2011). In these earlier studies, subclades are often biogeographically distinct, and this is consistent with strong niche conservatism having limited the ability of individual species to colonize other biogeographical areas. In contrast, the dynamic colonization history of Bignoniaceae and the widespread distributions of many of its species suggest reduced niche conservatism. Such an explanation is certainly consistent with the observation that a substantial number of species of Bignoniaceae occupy both wet (e.g. lowland rainforest) and dry (e.g. cerrado, seasonally dry forest) habitats. In our sample, 23% (24/105) of the species occur in both of

these habitat types with all but one also being widespread (Table S2). Differences between wet and dry habitats are thought to represent a significant adaptive barrier for Neotropical plant groups (Pennington, Lavin & Oliveira-Filho, 2009). Therefore, the observation that individual species are capable of occupying both wet and dry habitats suggests much broader tolerances in these taxa. Increased niche breadth in Bignoniaceae could be linked to growth form variation. Although the majority of Bignoniaceae are lianas, species with shrubby growth forms occur in a number of genera (e.g. *Adenocalymma*, *Anemopaegma* Mart. ex Meisn. and *Fridericia*). Such marked variation in growth form is relatively rare among Neotropical plant groups, but would seem likely to have important implications in terms of niche occupation.

Although the majority of Bignoniaceae species that occupy both wet and dry habitats are widespread, both widespread and restricted distributions are common in species that occur in either wet or dry habitats. In our sample, 31% (19/62) of wet habitat species are widespread and 69% (43/62) have restricted distributions. In contrast, 72% (13/18) of the dry habitat taxa are widespread and 28% (5/18) are restricted. We cannot rule out evolutionary explanations (e.g. retention or development of narrower tolerances) for the presence of both widespread and restricted species in Bignoniaceae as a whole. However, as widespread and restricted taxa occur widely on the phylogenetic tree, it is possible that other historical factors may have been more important. In particular, the past and present distributions of the habitats that these species occupy may represent important drivers of widespread and restricted distributions in Bignoniaceae.

For wet habitat taxa, the mixture of widespread and restricted distributions is consistent with increases in the extent of wet habitats during the Holocene (Mayle, Burbidge & Killeen, 2000; Mayle *et al.*, 2004). More specifically, if dispersal processes were not uniform across species, we would expect both widespread and restricted distributions to arise as individual species spread from their presumably more limited Pleistocene ranges at different rates. Most members of Bignoniaceae have seeds that are capable of being dispersed over considerable distances (Augspurger, 1986, 1989). However, differences in dispersal opportunities (e.g. single versus multiple initial populations) or mechanisms (e.g. wind versus water dispersal) could have resulted in differential rates of dispersal. In the case of dry habitat species, the observed pattern appears to better fit the contemporary distribution of these habitats. Specifically, as dry habitats (i.e. savannas or dry forests) occur in each of our biogeographical areas, we would expect a combination of widespread

and restricted distributions for dry habitat taxa. In the current sample, 13 of the 14 widespread dry habitat species occur in both the South American dry areas and eastern South America. These two areas share dry habitat types (e.g. cerrado and caatinga), and so it is understandable that they also share a substantial number of dry habitat taxa.

We are still some way from understanding contemporary species distributions in Bignoniaceae and in Neotropical plant groups more generally. However, the combination of niche breadth and Holocene environmental change provides an appealing explanation for the observed patterns in Bignoniaceae. Although more work is needed, differences in species distributions for this clade and other Neotropical plant groups suggest that studies of Bignoniaceae will provide insights of general interest. In particular, detailed analyses of the differences underlying restricted and widespread distributions in Bignoniaceae may be of importance.

CONCLUSIONS AND FUTURE DIRECTIONS

Our analyses represent a first step towards an understanding of the biogeographical history of Bignoniaceae. We have used a tribe-wide phylogenetic analysis to investigate general biogeographical patterns in this large Neotropical clade. We show that diversification occurred during a time period that was marked by several important changes in Neotropical environments (e.g. Hoorn *et al.*, 2010; Scotese, 2010). Drying of Neotropical climates and the Andean orogeny appear to have been important drivers of diversification, whereas contemporary distribution patterns may owe more to Holocene climates. Despite these general insights, a detailed understanding of the biogeographical processes that underlie diversity patterns in Bignoniaceae must await a more robust and thoroughly sampled phylogeny. In this respect, analyses of individual genera may provide important insights. To this end, detailed species-level phylogenies for several Bignoniaceae genera are being produced. These include *Anemopaegma* (Calió, Winkworth & Lohmann), *Bignonia* (Zuntini & Lohmann), *Dolichandra* (Fonseca & Lohmann), *Lundia* DC. (Kaehler, Michelangeli & Lohmann, 2012) and *Tynanthus* Miers (Medeiros & Lohmann).

Given that relatively few time-calibrated phylogenetic trees are available for Neotropical plant groups, and none for lianas, our results represent an important step towards a more comprehensive picture of Neotropical biogeography. The generation of time-calibrated phylogenetic trees for additional groups, especially those with similar distributions, is critical. Only with these will it be possible to examine the relative importance of specific factors involved in the biogeographical and diversification history of Neo-

tropical plant groups. It will be particularly interesting to see how the patterns exhibited by the largest clade of lianas in the Neotropics compare with those of other ecologically important elements in these communities.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. Distribution maps of the 105 species of Bignoniaceae sampled.

Figure S2. Ancestral state reconstructions based on maximum parsimony (using DELTRAN optimization) and a sample of 1000 post-burnin BEAST trees overlaid onto the maximum clade credibility chronogram from BEAST. Current distributions are indicated before the species names. The colour of the branches indicates inferred distributions of ancestral taxa using parsimony (grey lines indicate ambiguous parsimony reconstructions). Pie graphs report the proportion of trees in the post-burnin sample for which a given reconstruction was recovered; grey indicates that a node is absent and black that the reconstruction is equivocal in a proportion of the trees.

Figure S3. Ancestral state reconstructions based on maximum parsimony (using DELTRAN optimization) and the Bayesian binary Markov chain Monte Carlo (BBM) method overlaid onto the maximum clade credibility chronogram from BEAST. Current distributions are indicated before the species names. The colour of the branches indicates inferred distributions of ancestral taxa under parsimony (grey lines indicate ambiguous parsimony reconstructions). Pie graphs report relative probabilities from the BBM analysis; the three areas with highest probability are reported, with the remaining areas (usually frequencies below 0.01) collectively marked in black. Nodes 1–6 are discussed in the text and reconstructions based on alternative outgroup distributions are shown in Fig. S3.

Figure S4. Ancestral state reconstructions for nodes 1–6 (marked in Fig. S2) based on the Bayesian binary Markov chain Monte Carlo (BBM) method and assigning outgroups to different biogeographical areas. Pie graphs report the proportional likelihood for reconstructions with $P > 0.01$; other reconstructions are collectively indicated in black. For clarity, reconstructions involving three or more biogeographical areas are shaded grey (widespread) and the inferred distributions are indicated with the corresponding letters.

Table S1. Taxa, vouchers, localities and GenBank accession numbers for sampled Bignoniaceae and outgroups. Species names follow Lohmann & Taylor (2013).

Table S2. Habitat types and biogeographical distributions for sampled Bignoniaceae. We used the term ‘restricted’ to describe taxa that occur in a single biogeographical area and ‘widespread’ to describe those occupying two or more areas.