Molecular Phylogenetics and Evolution 103 (2016) 55–63

Contents lists available at ScienceDirect

Molecular Phylogenetics and Evolution

journal homepage: www.elsevier.com/locate/ympev

Speciation dynamics and biogeography of Neotropical spiral gingers (Costaceae)

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ARTICLE INFO

Article history:
Received 25 April 2016
Revised 5 July 2016
Accepted 8 July 2016
Available online 9 July 2016

Keywords:
Diversification
Macroevolution
Phylogenetics
Zingiberales

ABSTRACT

Species can arise via the divisive effects of allopatry as well as due to ecological and/or reproductive character displacement within sympatric populations. Two separate lineages of Costaceae are native to the Neotropics; an early-diverging clade endemic to South America (consisting of ca. 16 species in the genera *Monocostus*, *Dimerocostus* and *Chamaecostus*); and the Neotropical *Costus* clade (ca. 50 species), a diverse assemblage of understory herbs comprising nearly half of total familial species richness. We use a robust dated molecular phylogeny containing most of currently known species to inform macroevolutionary reconstructions, enabling us to examine the context of speciation in Neotropical lineages. Analyses of speciation rate revealed a significant variation among clades, with a rate shift at the most recent common ancestor of the Neotropical *Costus* clade. There is an overall predominance of allopatric speciation in the South American clade, as most species display little range overlap. In contrast, sympatry is much higher within the Neotropical *Costus* clade, independent of node age. Our results show that speciation dynamics during the history of Costaceae is strongly heterogeneous, and we suggest that the *Costus* radiation in the Neotropics arose at varied geographic contexts.

1. Introduction

Global biodiversity flourishes in the Neotropical region as the result of an extensive and complex history of evolutionary trends, mediated by ecological processes (Ricklefs, 2004; Rull, 2011). Despite the extent and importance of the high species diversity found in the Neotropics, we are still in the early stages of our understanding of its origins (Antonelli and Sanmartín, 2011; Turchetto-Zolet et al., 2013). A critical component of this task is the examination of the environment-dependent evolutionary processes by which new biological species arise, i.e. speciation. Although the geography of speciation has long been debated (Barraclough and Nee, 2001; Coyne and Orr, 2004; Fitzpatrick et al., 2009), the phylogenetic approaches of the last few decades have greatly advanced the study of speciation (Nee et al., 1994; Ricklefs, 2007; Silvestro et al., 2011; Morlon et al., 2011; Paradis, 2011; Rabosky, 2014) and its relationship with geographic diversification (Barraclough and Vogler, 2000; Graham et al., 2004; Goldberg et al., 2011). Moreover, phylogenetic trees of extant taxa retain information about speciation dynamics through time (Rabosky, 2009, 2010; Cusimano and Renner, 2010).

Neotropical ecosystems have a conspicuous historical dynamic (Hoorn et al., 2010) with intense fluctuation both in overall magnitude and in plant diversity (Jaramillo et al., 2010; Antonelli and Sanmartín, 2011). Numerous mechanisms have been proposed to explain high species diversity in tropical systems (Mortiz et al., 2000, Antonelli and Sanmartin, 2011) and most studies focused on speciation assume allopatry as the predominant geographic mode of speciation (Coyne and Orr, 2004). Undeniably, Oligocene and Miocene were key periods for the development of modern Neotropical diversity (Antonelli et al., 2009; Hoorn et al., 2011) due to geographic alterations, especially Andean uplift and the consequent alterations of Amazonian River drainage patterns (Räsänen et al., 1990, 1992; Hoorn et al., 1995; Gregory-Wodzicki, 2000); ocean level rise and incursions into the South American continent (Flynn and Wyss, 1998; Wesselingh and Salo, 2006); and Central America geomorphological dynamics, such as volcanic activity that resulted in oceanic ground shallowing and the closing of the Isthmus of Panama (Montes et al., 2012; Bacon et al., 2013). In particular, ecological opportunities provided by the different environments and

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http://dx.doi.org/10.1016/j.ympev.2016.07.008
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microclimates available after the uplift of the Andes are believed to have resulted in the current high South American diversity (Gentry, 1982; Luteyn, 2002; Rauscher, 2002; Bell and Donoghue, 2005; Ortiz-Jaureguizar and Cladera, 2006; Hughes and Eastwood, 2006; Antonelli et al., 2009; Wagner et al., 2013). Estimates show that nearly half of the dated extant Neotropical species originated before the Pleistocene (Rull, 2008). Compared to this intense geographic and topographic dynamic during the Tertiary, significant environmental changes during the Quaternary have been more related to glacial cycles and their impact on species range continuity, which could potentially lead to allopatric speciation (Haffer, 2008). To some extent, a proportion of the Neotropical rainforests have also been shown to be ecologically stable over long periods of time (Carnaval et al., 2009; Couvreur et al., 2011).

Speciation often results from the evolution of reproductive isolation mechanisms, as once incipient species may not remain distinct entities in their absence (Coyne and Orr, 2004). An alternative to allopatric forces, ecological and reproductive character displacement in sympatry can also lead to speciation (Schluter, 2000; Wendt et al., 2002; Lovette et al., 2002; Pfennig and Servedio, 2013; Rabosky et al., 2014), and several phenotypic novelties have been associated with species radiations in plants (e.g. Toon et al., 2014; Werner et al., 2014; Bouchenak-Khelladi et al., 2014).

Adaptive divergence as a response to ecological factors, such as pollinators and habitat, commonly drives the evolution of prezygotic barriers in plants (Rieseberg and Willis, 2007; Surget-Groba and Kay, 2013). In particular, the interactions between plants and pollinators can drive adaptive divergence in floral traits and contribute to the maintenance of reproductive isolation among closely related sympatric species (Grant, 1981; Kay, 2006; Wendt et al., 2008). Pollinator preference can be a strong selection factor for reinforcement between sympatric closely related species (Hopkins and Rausher, 2012). Furthermore, speciation may also occur by lineage reticulation, instead of divergence (Stebbins, 1959; Arnold, 1992). Hybridization has been considered a key phenomenon in plant evolution because it results in large amounts of genetic recombination and may enable the establishment of new traits and evolutionary lineages (Grant, 1981; Ehrlich and Wilson, 1991; Soltis and Soltis, 1999). Hybridization and introgression in isolated populations could actually stimulate speciation by providing standing genetic variation that can contribute to ecological speciation (Seehausen, 2004; Palma-Silva et al., 2011). Moreover, flowering plants maintain genomes with considerable gene redundancy, much of which is likely the result of allopolyploidy or whole genome duplication (Soltis et al., 2003).

Spiral Gingers (Costaceae Nakai) comprises ca. 125 pantropically distributed species, with its center of species diversity located in South and Central America (ca. 65 Neotropical species, ca. 30 African, ca. 23 Southeast Asian). Few species have a broad geographic range, with most species locally restricted geographically and by habitat heterogeneity (Maas, 1972). Two Costaceae lineages inhabit the Neotropics: a small, early divergent clade primarily endemic to South America consisting of *Monocostus* K.Schum. (1 species), *Dimerocostus* Kuntze (3–5 species) and *Chamaecostus* C.D.Specht and D.W.Stev. (8 species); and the Neotropical *Costus* L. clade (ca. 50 species), which encompasses nearly half of the family's total species richness. Phylogenetic studies indicate that while Dimerocostus, *Monocostus* and *Chamaecostus* most likely have an Amazonian ancestral distribution (André et al., 2015), Neotropical *Costus* diverged from African *Costus* following a long distance dispersal event that occurred long after the final break up of the Gondwanan supercontinent (Kay et al., 2005; Specht, 2006a) and likely diversified from a Central American origin (Salzman et al., 2015).

Over 40 species of fossils have been identified as pertaining to the Zingiberales, comprising a record that extends from the Cretaceous to Pliocene (Berry, 1921a, 1921b, 1925; Reid and Chandler, 1926; Hickey and Peterson, 1978; Friis, 1988; Boyd, 1992; Manchester and Kress, 1993). However, lack of detailed data on extant and fossil morphology inhibits confidently determining familial affiliations of many taxa (Smith et al., 2013). Moreover, pollen - an important source of historical information - lacks an exine in Zingiberales, impeding efficient fossilization. Nevertheless, there is at least one potential Costaceae fossil available (Smith et al., 2013): a stem cast/mold from the Miocene of Trinidad (Berry, 1925).

Hummingbird pollination (ornithophily) has evolved several times in Neotropical *Costus* from bee pollinated (melittophily) ancestors (Kay et al., 2005; Salzman et al., 2015), and flower morphology accurately reflects pollination type (Kay and Schemske, 2003) mainly by diversity of coloration patterns marking the showy labellum (an organ comprised of five fused staminodes, Specht et al., 2012), and in overall flower aperture size (Kay et al., 2005; Specht, 2006a). This pollination shift has been suggested to be particularly important in diversification of Neotropical *Costus* (Kay and Schemske, 2003; Kay et al., 2005; Specht, 2006b; Salzman et al., 2015) but has not been investigated for the South American clade, i.e. *Dimerocostus*, *Monocostus* and *Chamaecostus*. Kay et al. (2005) proposed a scenario for the diversification of *Costus*, in which range shifts in response to environmental changes and rapid floral adaptation in geographic isolation could have promoted reproductive isolation among closely related species. Interestingly, Costaceae's South American clade is species-poor as compared to the Neotropical *Costus* clade (ca. 16 vs. 50 species), regardless of being older and having potentially experienced the same environmental changes.

While the Costaceae is an appropriate system for studying spatiotemporal diversification dynamics in the megadiverse Neotropical region, comprehensive and current chronological and biogeographic approaches for the analysis of Costaceae diversification have not yet been fully considered. Here, we examine the spatiotemporal context of speciation through a phylogenetic framework in two Neotropical Costaceae lineages (*Costus* and the South American clade) with significantly different extant species richness.

2. Methods

2.1. Taxonomic sampling, DNA extraction, amplification and sequencing

A total of 84 ingroup taxa were sampled, including nearly all known species from the South American clade, most of Neotropical and African *Costus* species, and a few representatives of Asian Costaceae. *Alpinia zerumbet* (Pers.) B.L. Burtt and R.M. Sm. and *Zingiber officinale* Roscoe (Zingiberaceae) were designated as outgroups. Available sequences were downloaded from GenBank (from Slazman et al., 2015; André et al., 2015). For the remaining taxa, total genomic DNA was isolated from silica-gel dried leaf tissue using CTAB extraction protocol (Doyle and Doyle, 1990). Regions of the chloroplast (trnL-trnLF, rps16-trnk) and nuclear (rpb2, ETS and ITS) genomes were amplified and sequenced using published primers (Taberlet et al., 1991; Shaw et al., 2007; Specht et al., 2001; Kay et al., 2005; White et al., 1990, respectively). Novel primers for the calmoduline (CAM) 23rd intron were designed following a long PCR protocol using Zingiberales primers cam33F and cam328R (Johansen, 2005; Salzman et al., 2015). PCR fragments were generated and sequenced on an Applied Biosystems® 3730 DNA Analyzer automated DNA sequencer at UC Berkeley's Museum of Vertebrate Zoology's Evolutionary Genetics Laboratory. Chromatogram files were examined for biases and possible errors using Geneious version 5.6.3 (Biomatters Ltd.). Alignments were made for each marker using MUSCLE algorithm (Edgar, 2004) implemented in Geneious and alignments were subsequently checked manually. Alignment regions that could not be unambiguously interpreted were excluded from analysis.

2.2. Phylogenetic inferences and speciation dynamics

Nucleotide sequences of the 2 plastid and 4 nuclear genetic markers were concatenated and analyzed under a Bayesian phylogenetic framework, using BEAST 1.7.4 (Drummond and Rambaut, 2007). Sequence data was partitioned to allow different models of sequence evolution for each region, based on likelihood analyses ran on jModelTest version 2.0 (Darriba et al., 2012) and selected with Bayesian information criterion. A relaxed clock with an uncorrelated lognormal model of rate variation was used and a Yule speciation process for branching rates was selected. Two fossil-based time to the most recent common ancestor (tmrca) calibrations were used; 45 ± 5 Ma for the Costaceae root (*Costus incertis*†; Berry, 1925) and 85 ± 5 Ma for *Alpinia* + *Zingiber* clade (*Zingiberopsis*†; Hickey and Peterson, 1978), and a CTMC rate prior was selected (Ferreira and Suchard, 2008). No monophyletic prior assignment was made. Markov chain Monte Carlo simulations were run twice independently for 5×10^7 generations and sampled every 5×10^3. These analyses were performed on the CIPRES Science Gateway (Miller et al., 2010). We assessed convergence of model parameters across the independent runs by analyzing plots of the marginal posterior distributions in Tracer version 1.5 (Rambaut and Drummond, 2007), and by ensuring high effective sample size values (ESS $\geqslant$ 200). Tracer was also used to assess burn-in levels. A maximum clade-credibility tree was obtained from the posterior sample of trees using TreeAnnotator version 1.7.4 (Drummond et al., 2012), and visualized on FigTree (http://tree.bio.ed.ac.uk/software/figtree/). Phylogenetic data is storaged at TreeBASE repository at http://purl.org/phylo/treebase/phylows/study/TB2:S19543.

The Bayesian Analysis of Macroevolutionary Mixtures (BAMM; Rabosky, 2014) was used for the analysis of speciation rates on the ultrametric phylogeny, accounting for non-random taxon sampling. This model assumes that changes in evolutionary regimes occur across the branches of phylogenetic trees under a compound Poisson process model of rate variation and explicitly allows rates to vary both through time and among lineages. Four MCMC chains were run for 5×10^7 generations and sampled every 5×10^3, using the BAMM default parameters.

2.3. Geography of speciation

Locality data for Neotropical Costaceae was downloaded from the Global Biodiversity Information Facility Data Portal (www.gbif.org, March 2014), and from examination of herbaria material (A; HAMAB; HEPH; IAN; IBGE; INPA; MG; MO; NY; R; RB; UB; UC; UFACPZ; UFG, acronyms follows Thiers, continuously updated).

Reconstruction of the geographical distribution of species at the time of speciation is obviously problematic, as the current distribution of a species is not necessarily a direct indicator of species' historical geographical range (Losos and Glor, 2003). We inferred the *potential* geographic distribution of species by ecological niche modeling (Austin, 1985; Graham et al., 2004; Phillips et al., 2006) instead of using geographic range maps based on locality data. We have inferred current distributions with ecological niche modeling to improve predictions of poorly known species distributions. Current distribution data is sampled some amount of time after the speciation event and during this time, species' ranges most likely have changed. Nonetheless, we can determine the role of geography in speciation by plotting and comparatively analyzing the amount of current range overlap for different sister species pairs across all nodes in a species-level phylogeny, which therefore span a range of time since speciation (Barraclough and Vogler, 2000; Fitzpatrick and Turelli, 2006; Anacker and Strauss, 2014).

Values from 43 environmental variables describing climate (Hijmans et al., 2005; Kriticos et al., 2012), soil (Global Soil Data Task Group, 2000) and net primary productivity (Imhoff and Bounoua, 2006) were extracted based on specimens' localities. After evaluating the correlation between each of the variables in R (R Core Team, 2014), we removed variables that had a coefficient $-0.75 \leqslant r \geqslant 0.75$, which resulted in 14 uncorrelated variables describing environmental variation. Extant species potential geographic distributions were modeled by maximum entropy in MAXENT version 3.3.3k (Phillips et al., 2006), with 25% of the data used for training. Thresholds for geographic ranges were estimated from median presence of 50 bootstrap replicates, in QGIS (Quantum GIS Development Team, www.qgis.org). We then calculated the degree of sympatry between sister clades (Chesser and Zink, 1994: area of overlap in geographic range/range size of clade with smaller range) for each node of the South American Clade and the Neotropical *Costus* clade.

Additionally, evolution of the geographic range of Costaceae was interpreted using historic biogeographic reconstruction. Ancestral ranges were inferred using the BioGeoBEARS package implemented in R (Matzke, 2013), which allows for both probabilistic inferences of models of range expansion and founder-event speciation (J). An unconstrained dispersal-extinction-clado genesis analysis (DEC and DEC+J; Ree et al., 2005; Ree and Smith, 2008; Ree and Sanmartín, 2009) and the Bayesian analysis for large number of areas (BAYAREA and BAYAREA+J; Landis et al., 2013) were run using the maximum clade credibility time-calibrated tree. The Likelihood Ratio Test (LRT) and the Akaike Information Criterion (AIC; Burnham and Anderson, 2002) were used to objectively compare models. Geographic distributions of the terminal taxa were coded based on environmental discontinuity of Neotropical regions and on extant Costaceae species distributions: (1) Central America and the Caribbean, (2) Amazonian, (3) Andean, (4) Central Brazilian Plateau and Atlantic Rainforests, (5) Africa, (6) Asia and Oceania. Costaceae from the Central Brazilian Plateau, which is dominated by savanna ecosystems, actually occur within gallery forests surrounding streams and rivers, and harbor mostly the same species as the Atlantic Rainforests. We set the maximum number of areas equal to four.

3. Results

We present a comprehensive multilocus phylogenetic estimate for Costaceae (Fig. 1), along with corresponding branch age estimates. The family Costaceae first diversified around 50 million years ago, in the Eocene, and the large *Costus* genus originated ca. 30 million years ago. The age of the most-recent common ancestor of Neotropical *Costus* is estimated to have occurred only ca. 10 million years ago. Furthermore, phylogenetic relationships inferred here reaffirm the monophyly of major lineages within Costaceae: i.e. the South American clade, *Costus*, and the Neotropical *Costus* clade.

The comprehensive phylogeny of Fig. 1 clearly shows the unbalanced distribution of extant species diversity, with most species belonging to the Neotropical *Costus* clade. The Bayesian Analysis of Macroevolutionary Mixtures (ESS LogLik = 816.295, ESS N Shifts = 901) favors a configuration with a single shift (posterior distribution = 0.6400).

Biogeographical models including founder-speciation (+J) are favored and BAYAREALIKE had greater likelihood compared to

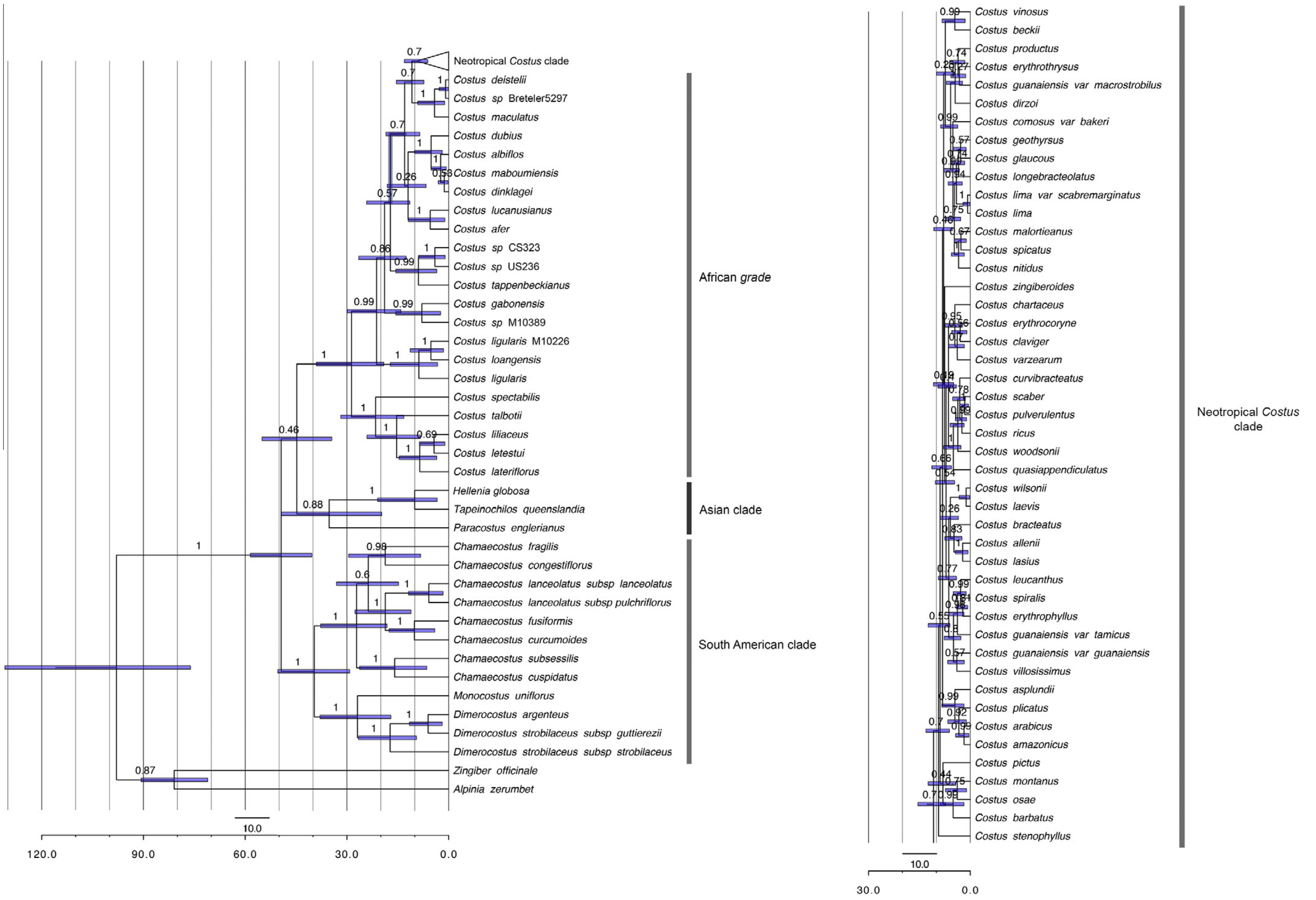

Fig. 1. Fossil calibrated maximum clade credibility tree estimated from 1000 trees. (A) Whole phylogeny with Neotropical *Costus* clade clumped; (B) Neotropical *Costus* clade. Numbers above branches refer to posterior probabilities. Blue bars denote node height probability density at 95%. Lower scale in million years before present. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

DEC models (BAYAREALIKE LnL = −158.034 with +J, and −180.826 without +J; DEC LnL = −165.89 with +J, and −174.02 without +J). Uncertainty in estimated ancestral range scenarios are indicated with pie charts, but we particularly discuss the biogeographical history of Costaceae based on the single scenario with highest likelihood (Fig. 2). Ancestral geographic state reconstructions indicate that the South American clade originated and diversified in the Amazon and the Andes (Fig. 2A). Neotropical *Costus* started to diversify (significant species accumulation indicated by the grey circle, Fig. 2B) in Central America from a long distance dispersal event from Africa. A comparison of speciation rates (Fig. 3) suggests four major rate patterns within Costaceae phylogeny; the South American clade rate, the Neotropical *Costus* clade rate, and two separate rate patterns within African *Costus*.

Degree of sympatry plots (Fig. 4A and B) point to the overall predominance of allopatric speciation in the South American clade (Fig. 4A), where most recently diverged species display little overlap in geographic ranges. In contrast, sympatry is much higher within the Neotropical *Costus* clade, independent of node age (Fig. 4B).

4. Discussion

As previously inferred (Specht et al., 2001; Specht, 2006b), an early lineage divergence event splits Costaceae into two major clades: a South American clade [(*Monocostus* + *Dimerocostus*) +*Chamaecostus*], and a large clade containing the remaining species of Costaceae. There are important differences between species of the early-diverging South American clade and the Neotropical *Costus* clade regarding their geographical distribution. Nearly half of the species richness of Neotropical *Costus* is endemic to Central America, with several predominantly South American species having large ranges that also include Central America. On the other hand, the distributions of *Chamaecostus*, *Dimerocostus* and *Monocostus* are almost entirely exclusive to South America with only a single species of *Dimerocostus* having a large range expanding into Central America.

The genus *Costus* maintains an amphi-Atlantic distribution, with ca. 29 known species in Africa (P.J.M. Maas and H. Maas, pers. com.) and ca. 51 in the Neotropics. This rare biogeographic condition (Renner, 2004) is shared, for example, with *Renealmia* L.f. (Zingiberaceae), which has ca. 15 species in Africa and 61 in the Neotropics (Maas, 1977). Särkinen et al. (2007) suggested that *Renealmia* acquired this distribution by an oceanic long-distance dispersal event from Africa to South America during the Miocene or Pliocene, and that speciation in the Neotropics might have been affected by the orogeny of the Andes. Notably, Specht (2006a) and Salzman et al. (2015) previously suggested an African origin for Neotropical *Costus*. Here, we also demonstrate a long distance dispersal from Africa to Central America ca. 10 million years ago. We also infer subsequent successive migration events from Central to South America, as well as some apparently recent range expansions by some species, such as *Costus scaber* Ruiz and Pav., that still maintain most of their distribution in South America.

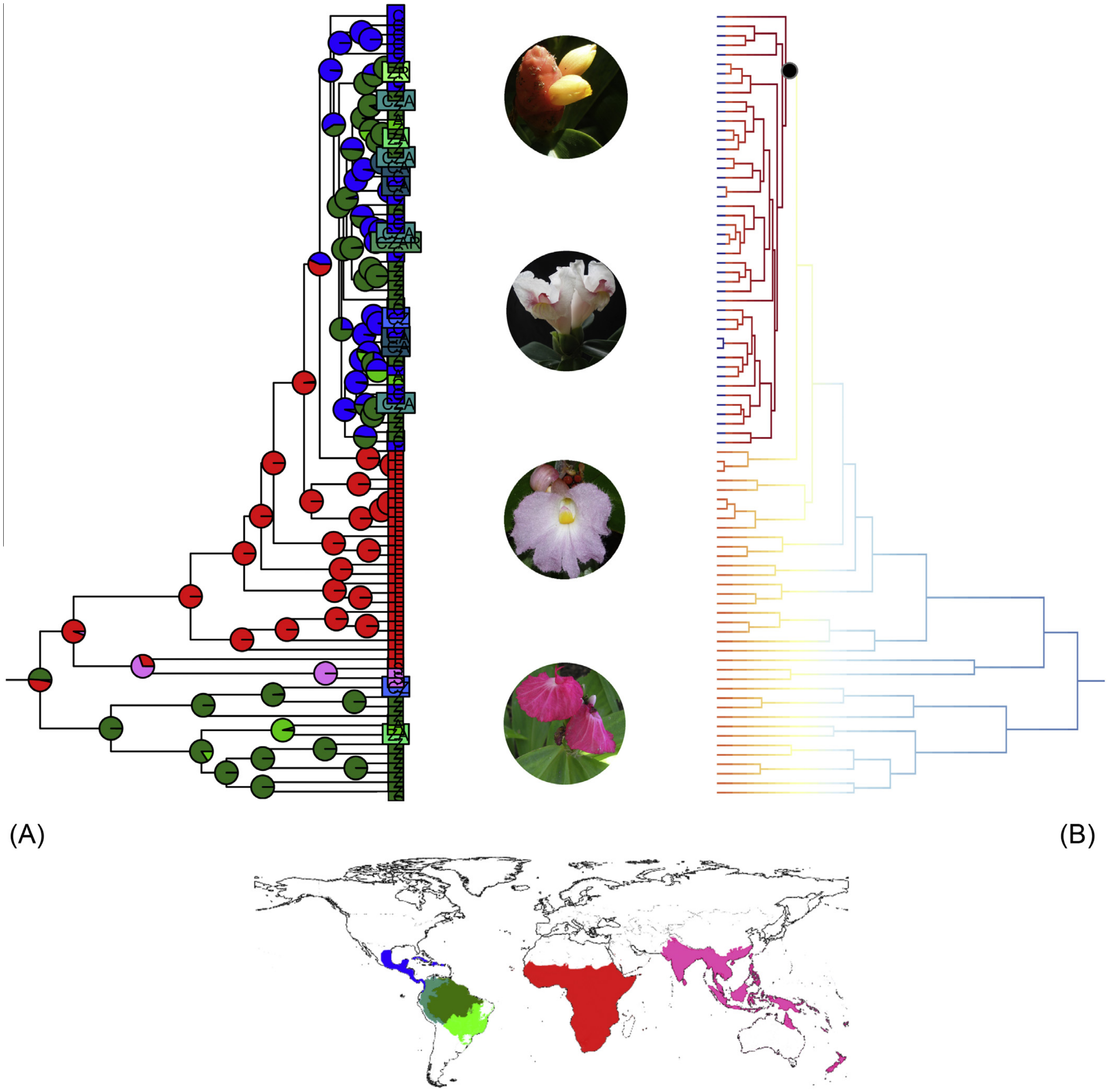

Fig. 2. Top: (A) Biogeographical analysis of Costaceae using BioGeoBEARS. (B) Phylorate plots for speciation rate using BAMM; colors at each point in time along branches denote instantaneous speciation rates, with warmer colors referring to faster rates; two distinct rate configurations account for most of the posterior probability of the data with the dark dot indicating the node of the single shift in configuration. Bottom: Geographic distribution of Costaceae included in biogeographic analysis: 🟦 Central America and the Caribbean, 🟩 Amazonian, 🟩 Andean, 🟩 Central Brazilian Plateau and Atlantic Rainforests, 🟥 Africa, 🟪 Asia and Oceania. Outgroups are not shown. Central images show representative Costaceae (top-down): *Costus scaber* Ruiz and Pav., *Costus arabicus* L., *Costus ligularis* Baker, *Chamaecostus lanceolatus* (Petersen) C.D. Specht and D.W. Stev. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Long-distance dispersal of plants, such as transatlantic ones, are challenging to research because they involve rare events determined by complex and highly stochastic processes. In fact, extreme climatic events and generalized long distance dispersal vectors are more likely to explain drastic deviations from a mean trend in dispersal, and therefore are likely to turn exceptionally rare dispersal events into reality (Nathan, 2006).

Disjunct transatlantic patterns have occasionally been ascribed to vicariance involving the break up of the Gondwanan supercontinent or continental rafting (Raven and Axelrod, 1974), but many tropical plant groups originated more recently (Givnish and Renner, 2004; Renner, 2004; Schrire et al., 2005; Christenhusz and Chase, 2013). Previous biogeographic and dating analysis of Costaceae used a strict molecular clock approach and the calibration points for converting relative to absolute ages were either based on the divergence time between Costaceae and Zingiberaceae as estimated in an ordinal analysis of Zingiberales (Specht, 2006a; Kress and Specht, 2006), or on an approximated date of the closing of the isthmus of Panama (assumed to be 3.5 Ma and coincident to *Costus* arrival in the Neotropics, by Kay

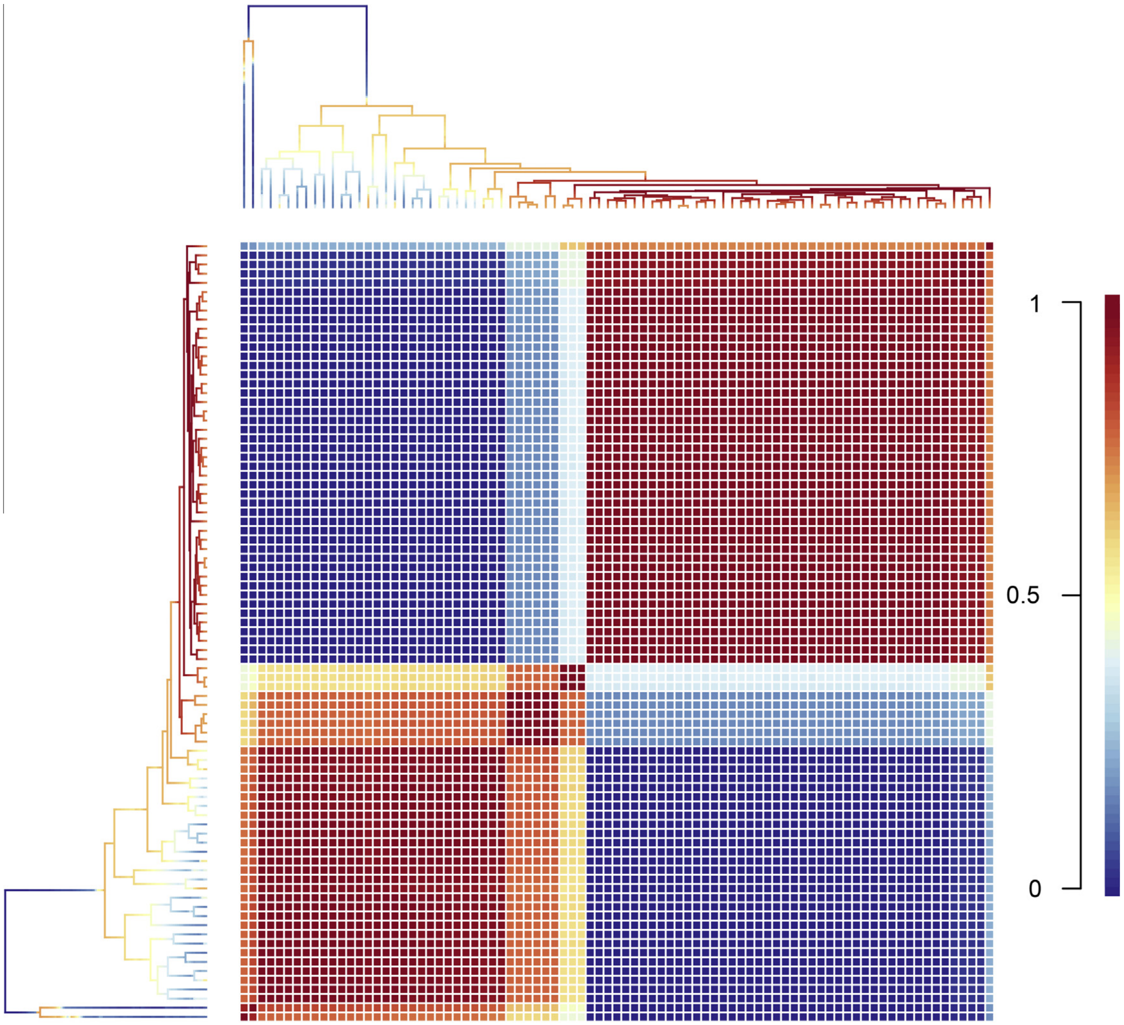

Fig. 3. Heterogeneous speciation rates within Costaceae phylogeny recovered using BAMM. Color bar and squares indicate proportion of similarity between rates. Colors at each point in time along branches of the phylogeny denote instantaneous speciation rates. Outgroup rate is underestimated due to limited sampling of outgroup clades. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

et al., 2005). The Specht (2006a) analysis suggested an initial diversification within Costaceae of approximately 65 million years ago, long after the final break up of the Gondwanan supercontinent (McLoughlin, 2001; Metcalfe, 1991) or the existence of a boreotropical dispersal route (ca. 50–40 My ago; Lavin and Luckow, 1993; Morley, 2003) with the Neotropical *Costus* dispersing from Africa approximately 33 Ma (33.66 ± 3.46) and undergoing its radiation approximately 22 ± 3 Ma. Using the closing of the Panama isthmus as a calibration point, Kay et al. (2005) found Neotropical *Costus* to be 4.6 Ma old. Additionally, using ITS substitution rates from across herbaceous taxa, Kay et al. (2005) estimated a date range for the divergence of subgenus *Costus* from the rest of the genus of ca. 1.5–7.1 Ma. Here, by using a relaxed molecular clock we inferred a younger age for the initial Costaceae diversification than proposed by Specht (2006a) and an older age of Neotropical *Costus* origin as compared to that proposed by Kay et al. (2005). Dates recovered in our analysis point to a recent oceanic long-distance dispersal (Lavin et al., 2004; Renner, 2004) as explicatory of Neotropical *Costus* origin.

Ancestral biogeographic state reconstruction strongly supports Central America as ancestral within the Neotropical *Costus* clade, suggesting that early diverging lineages evolved mostly in a dynamic and fragmented area. This clade has a remarkably young age given its large extant species diversity. Its origin is coincident with an abrupt decrease in global temperatures following the growth in Antarctic ice (Zachos et al., 2001; Katz et al., 2008; Jaramillo and Cardenas, 2013), and with tectonic activities in West Africa (Diester-Haass and Chamley, 1980; Pearson et al., 2008), as well as the intense geomorphological dynamics in Central and South America (Hoorn et al., 1995; Montes et al., 2012).

Despite this biogeographic background, our results indicate that a single morphological key innovation may not account for diversification within Costaceae and ecological and reproductive evolution in sympatry likely played more important roles in the speciation dynamics of this lineage. In fact, pollinator dissimilarity is generally sufficient to maintain pre-zygotic isolation between sympatric species (Sakai et al., 1999; Kay and Schemske, 2003), such that pollination shifts may be sufficient to successfully act as reproductive barriers between incipient species. Kay and Schemske (2008) report wide crossability within this clade and a propensity towards strong intrinsic postzygotic isolation seems unlikely. Salzman et al. (2015) showed a relative increase in diversification for lineages within Neotropical *Costus* that display specialized pollination morphologies as compared to the preseumed generalist pollination morphology. Well-developed pollination differentiation suggested by the floral morphology and overall reproductive biology has been confirmed in tested species but remains largely unverified for most species in the family

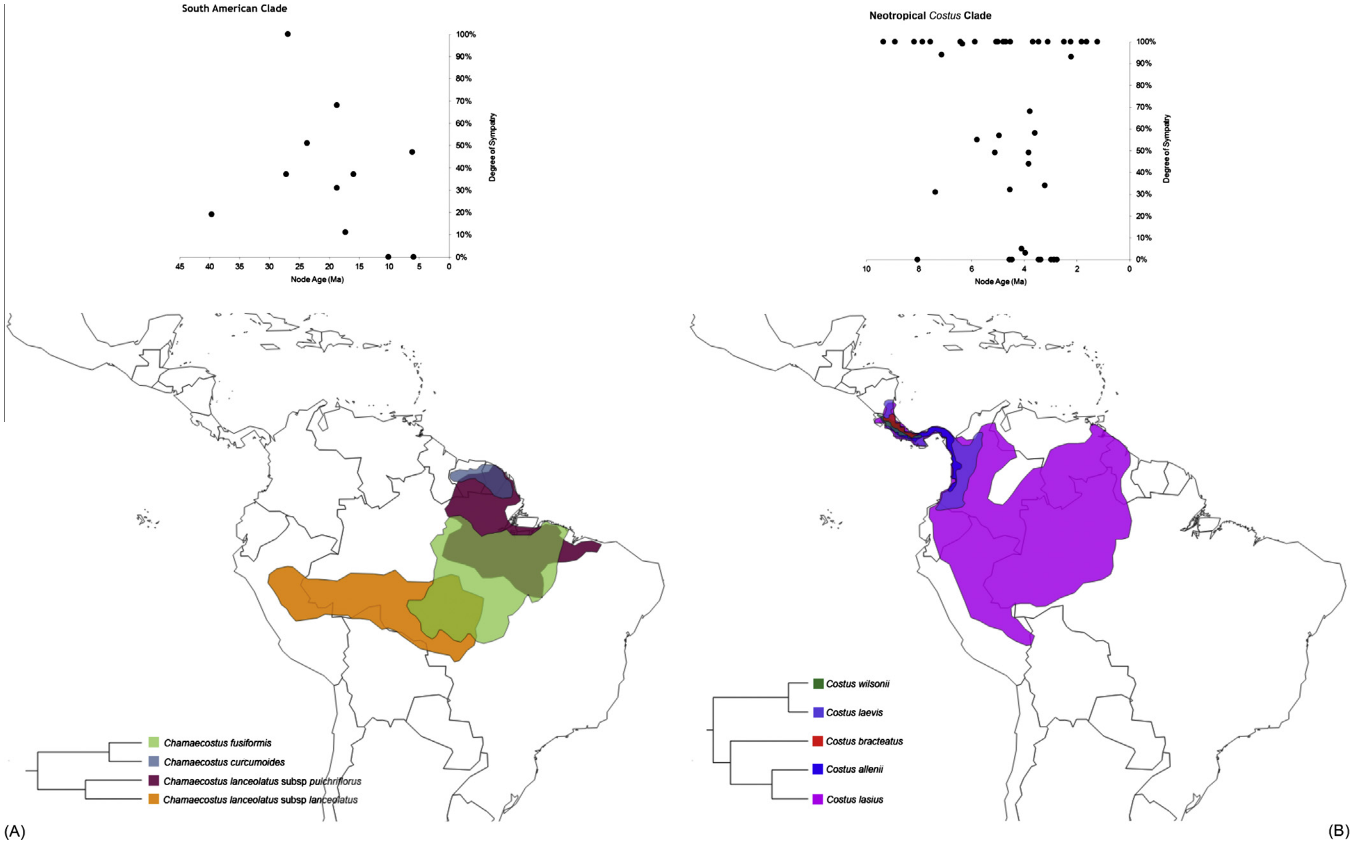

Fig. 4. Sympatry analysis of speciation in Neotropical *Costus* and the South American clades. Top: Degree of sympatry by node age for (A) the South American clade and (B) the Neotropical *Costus* clade. Bottom: Maps showing examples of recovered potential current distributions superimposed for one selected clade from *Chamaecostus* (A) and *Costus* (B).

(Kay and Schemske, 2003; Surget-Groba and Kay, 2013). Additionally, Chen and Schemske (2015) report local ecological isolation between two closely parapatric *Costus* species in Panama, indicating that divergent habitat adaptation can function in reproductive isolation even for species that share pollination traits.

Polyploidy may also result in the evolution of speciose lineages, since polyploids often exhibit ecological differentiation, high fecundity, perennial life history, and self-fertilization or asexual reproduction (Rieseberg and Willis, 2007). Polyploidy in Costaceae remains largely unverified, however, as we still do not know chromosome numbers for most species, and see variation within Neotropical species and between the New and the Old World *Costus* (Edeoga and Okoli, 2000).

Timing of the significant increase in diversification rate, coincident with the origin of the Neotropical *Costus* clade, further uncovers a scenario of *in situ* divergence, including multiple independent invasions to South America presumably occurring overland by the Panamanian land bridge, which indeed was likely already formed (Montes et al., 2012; Bacon et al., 2013). However, further ecological studies investigating tolerance limits to relevant environmental gradients across *Costus*, such as edaphic, climatic and topographic variables, will help better define evolution of particular ecological characters involved in spatial occurrence.

Sympatric speciation may have had a significant contribution to diversification in Costaceae, in addition to orogenic-driven allopatric processes. Based on the high importance of sympatric speciation for the diversification in the Neotropical *Costus* clade, its subclades could display characteristics that facilitate *in situ* diversification, such as susceptibility to the evolution of intrinsic barriers to reproduction, genes and genome duplications, or unusually high amounts of structured genetic diversity. Nonetheless, the founder effect of colonization of this key geographic region certainly presented new ecological niches for the *Costus* lineage.

Acknowledgements

T.A. received a scholarship grant from *Coordenação de Aperfeiçoamento de Pessoal de Nível Superior*. T.W. received a productivity grant from *Conselho Nacional de Desenvolvimento Científico e Tecnológico*. C.S. received funding from the National Geographic Society #8994-11, NSF DEB0866601, and UC Berkeley CNR-BSP, SPUR, and URAP. We are thankful to Heather Driscoll, Yizhuo Bastea-Forte, Tanya Renner, Irene Liao, Stacey Shen and Roxana Yockteng for help in selecting molecular markers and generating sequences.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ympev.2016.07.008.

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