Global Succulent Biome phylogenetic conservatism across the pantropical Caesalpinia Group (Leguminosae)

Edeline Gagnon[1,2,5] (ID), Jens J. Ringelberg[3], Anne Bruneau[1] (ID), Gwilym P. Lewis[4] and Colin E. Hughes[3] (ID)

[1]Institut de Recherche en Biologie Végétale & Département de Sciences Biologiques, Université de Montréal, H1X 2B2 Montréal, QC, Canada; [2]Département de Biologie, Université de Moncton, E1A 3E9 Moncton, NB, Canada; [3]Department of Systematic & Evolutionary Botany, University of Zurich, Zollikerstrasse 107, 8008 Zurich, Switzerland; [4]Comparative Plant and Fungal Biology Department, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, UK; [5]Present address: Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh EH3 5LR, UK

Summary

• The extent to which phylogenetic biome conservatism vs biome shifting determines global patterns of biodiversity remains poorly understood. To address this question, we investigated the biogeography and trajectories of biome and growth form evolution across the Caesalpinia Group (Leguminosae), a clade of 225 species of trees, shrubs and lianas distributed across the Rainforest, Succulent, Temperate and Savanna Biomes. We focused especially on the little-known Succulent Biome, an assemblage of succulent-rich, grass-poor, seasonally dry tropical vegetation distributed disjunctly across the Neotropics, Africa, Arabia and Madagascar.

• We reconstructed a time-calibrated phylogeny, assembled species occurrence data and assigned species to areas, biomes and growth forms. These data are used to estimate the frequency of transcontinental disjunctions, biome shifts and evolutionary transitions between growth forms and test for phylogenetic biome conservatism and correlated evolution of growth forms and biome shifts.

• We uncovered a pattern of strong phylogenetic Succulent Biome conservatism. We showed that transcontinental disjunctions confined within the Succulent Biome are frequent and that biome shifts to the Savanna, Rainforest and Temperate Biomes are infrequent and closely associated with shifts in plant growth forms.

• Our results suggest that the Succulent Biome comprises an ecologically constrained evolutionary arena spanning large geographical disjunctions across the tropics.

Introduction

Explanations for global-scale patterns of biodiversity have shifted from primarily geo-historical vicariance-dispersal explanations in favour of ecological and metacommunity processes as prominent factors shaping the distribution of clades and geographical phylogenetic structure (Lavin *et al.*, 2004; Wiens & Donoghue, 2004; Pennington *et al.*, 2006; Donoghue, 2008; Donoghue & Edwards, 2014), as revealed by patterns of taxon-biome relationships (Lavin *et al.*, 2004; Schrire *et al.*, 2005). An important corollary of these patterns is that phylogenetic biome or niche conservatism, that is, 'the extent to which species retain ancestral ecological traits and environmental distributions' (Crisp *et al.*, 2009) (see also Wiens *et al.*, 2010; Donoghue & Edwards, 2014), has been important in determining the global distribution of lineages (Wiens & Donoghue, 2004; Donoghue, 2008; Crisp *et al.*, 2009; Donoghue & Edwards, 2014). There is widespread empirical evidence for global-scale biome conservatism in plants, e.g. clades occupying southern hemisphere biomes (Crisp *et al.*, 2009), clades restricted to the tropics (Wiens & Donoghue, 2004), temperate clades (Donoghue & Smith, 2004), mangroves

(Ricklefs *et al.*, 2006) and seasonally dry tropical forest lineages (Lavin *et al.*, 2004; Pennington *et al.*, 2006, 2009), suggesting that phylogenetic biome conservatism played a prominent role in shaping the distributions of lineages. However, in other clades, biome shifts appear to be frequent and niche evolution pervasive (e.g. Simon *et al.*, 2009; Holstein & Renner, 2011; Weeks *et al.*, 2014; Ogburn & Edwards, 2015; Cardillo *et al.*, 2017). The reasons why conservatism appears more prevalent in some lineages than others remain poorly understood, but involve methodological issues of scale and biome definition, as well as biological reasons. These include the interplay between geographical distance, surface area, connectivity and ages of biomes, the ecological suitability of source and target areas, lineage specific variation in adaptability and dispersal ability (Weeks *et al.*, 2014) and variation in the relative openness of biomes (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014). Furthermore, increasing taxon sampling often reveals higher frequencies of biome shifts than those tallied from sparsely sampled phylogenies, especially as biome shifts can be phylogenetically clustered (Donoghue & Edwards, 2014). To address these questions, phylogenies with dense sampling of species and detailed distribution maps are

needed (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014).

One of the most striking examples of possible global phylogenetic biome conservatism is the multiple plant clades largely restricted to the Succulent Biome *sensu* Schrire *et al.* (2005). This biome encompasses a range of seasonally dry tropical vegetation, from medium stature closed-canopy deciduous forests – exemplified by Neotropical seasonally dry tropical forests (SDTFs) (Pennington *et al.*, 2000, 2006, 2009; Särkinen *et al.*, 2011; DRYFLOR, 2016; Dexter *et al.*, 2018; Silva de Miranda *et al.*, 2018) – to lower stature open thorn and cactus scrub and thicket vegetation, together grouped as seasonally dry tropical forest and woodland (SDTFW rather than SDTF) (de Queiroz *et al.*, 2017). As defined by Schrire *et al.* (2005), this biome includes vegetation types historically referred to by different names, including in Africa, thicket, bushland and scrubland *sensu* White (1983) – notably Somali-Masai *Acacia-Commiphora* deciduous bushland and thicket, broadly corresponding to the Arid Flora of Linder (2014). In the Neotropics, the Succulent Biome includes the seasonally dry tropical forest (bosque seco caducifolio), Caatinga in Brazil, mata acatingada, cuabal in Cuba, matorral in Tamaulipas, Mexico and bosque espinoso. These were equated as belonging within a single biome by Schrire *et al.* (2005; see Lock, 2006; Pennington *et al.*, 2006, 2009, 2018). The Succulent Biome occupies a highly fragmented distribution (Fig. 1f) in the Somali-Masai region of the Horn of Africa including Socotra, the southern fringes of Arabia, the southwest African Karoo-Namib and western Madagascar in the Old World (White, 1983; Schrire *et al.*, 2005), plus seasonally dry tropical parts of the Neotropics (maps in Pennington *et al.*, 2000; Schrire *et al.*, 2005; Linares-Palomino *et al.*, 2011; Särkinen *et al.*, 2011; DRYFLOR, 2016; de Queiroz *et al.*, 2017; Silva de Miranda *et al.*, 2018).

These areas share frost-free, strongly seasonal climates with a dry season of 5 to 9 months (rainfall < 100 mm per month) and mean annual rainfall generally < 1200 mm (Oliveira-Filho *et al.*, 2013; Dexter *et al.*, 2018) and largely fire intolerant vegetation that is deciduous, dominated by small-leaved, often spinescent trees, notably rich in stem succulents and poor in grasses (few, inconspicuous and usually ephemeral) (Lavin *et al.*, 2004; Schrire *et al.*, 2005; Pennington *et al.*, 2006, 2009, 2018; Oliveira-Filho *et al.*, 2013; de Queiroz *et al.*, 2017; Dexter *et al.*, 2018). These characteristics distinguish this biome from the Rainforest, Savanna (equivalent to the Grass Biome) and Temperate Biomes of Schrire *et al.* (2005). The Savanna Biome corresponding to tropical savanna (including Miombo woodland *sensu* White, 1983) also occurs in seasonally dry climates but lacks stem succulents and has a continuous C_4-grass ground layer that is fire prone and supports grazing, disturbance factors that select for distinctive plant functional traits including geoxyles and thick bark (Simon *et al.*, 2009; Lehmann *et al.*, 2011; Simon & Pennington, 2012) and spinescence (Charles-Dominique *et al.*, 2016). The Succulent Biome is absent from Australia and Asia (except in Arabia and parts of Pakistan and NW India), where areas sometimes classified as dry forests (Bastin *et al.*, 2017) are fire prone with a conspicuous grass layer and lack stem succulents; these have clear functional affinities to savanna (Pennington *et al.*, 2009, 2018; Dexter *et al.*, 2015; Griffith *et al.*, 2017).

The repeated pattern of clades tracking the Succulent Biome across transcontinental disjunctions was first documented by Lavin *et al.* (2004), based on a handful of legume lineages, including the combined *Leucaena* and *Dichrostachys* clade, the genus *Chapmannia* and the *Diphysa-Ormocarpum* clade and was further discussed by Pennington *et al.* (2006, 2009). These patterns suggested that the plant lineages occupying the Succulent Biome are biome conserved across continents, but this has not been explicitly tested and the generality of these patterns remains to be explored. Other authors have doubted the existence of a global seasonally dry tropical biome based on the lack of obvious floristic identity (Dexter *et al.*, 2015). Indeed, the Succulent Biome remains a neglected concept rarely discussed in the wider literature on biome definition and largely confined to studies of legumes (but see Thiv *et al.*, 2011; Hernández-Hernández *et al.*, 2014).

Alongside documenting the extent of phylogenetic biome conservatism vs biome switching, investigating evolutionary shifts in traits associated with biome shifts can provide insights into what determines geographic and phylogenetic turnover of clades. Evolutionary shifts in key plant functional traits (e.g. growth form, deciduousness, frost, drought and fire tolerance) are often required to overcome the adaptive barriers delimiting biomes (e.g. Edwards & Smith, 2010; Onstein *et al.*, 2014; Zanne *et al.*, 2014; Ogburn & Edwards, 2015) and confluences between biome and trait shifts are to be expected (Donoghue & Sanderson, 2015). However, there are limited data documenting evolutionary trajectories of functional traits in relation to biome switching (Edwards & Donoghue, 2013; Donoghue & Edwards, 2014; Ogburn & Edwards, 2015). It has also been suggested that biome switching can trigger shifts in diversification rates (e.g. Koenen *et al.*, 2013), that trajectories of diversification may differ between biomes (e.g. Hughes *et al.*, 2013; Dexter *et al.*, 2017) and that clades occupying the Succulent Biome show constantly slow rates of diversification (Koenen *et al.*, 2013), but none of these hypotheses has been tested in more than a handful of clades.

Here we focus on the Caesalpinia Group (Leguminosae: subfamily Caesalpinioideae; *sensu* LPWG, 2017) to investigate the idea that the Succulent Biome forms a global evolutionary arena inhabited by seasonally dry tropical phylogenetically conserved plant clades. The pantropical Caesalpinia Group comprises *c.* 225 species of multi-stemmed shrubs and small trees, lianas and functionally herbaceous suffrutices (Fig. 1). The group was recently re-classified into 26 genera (Gagnon *et al.*, 2016), nine of which are monospecific. Species are characterized by diverse plant defense mechanisms including deflexed prickles, spines, spinescent shoots and glandular trichomes; zygomorphic, generally bisexual and predominantly bee-pollinated flowers; a range of fruit morphologies and seed dispersal mechanisms (explosively or passively dehiscent or indehiscent pods, wind dispersed samaras (*Pterolobium*), seeds that are buoyant and capable of long-distance dispersal by sea (*Guilandina bonduc* and allies)). The clade includes several economically important tree species and most notably *Paubrasilia echinata* – the national tree of Brazil –
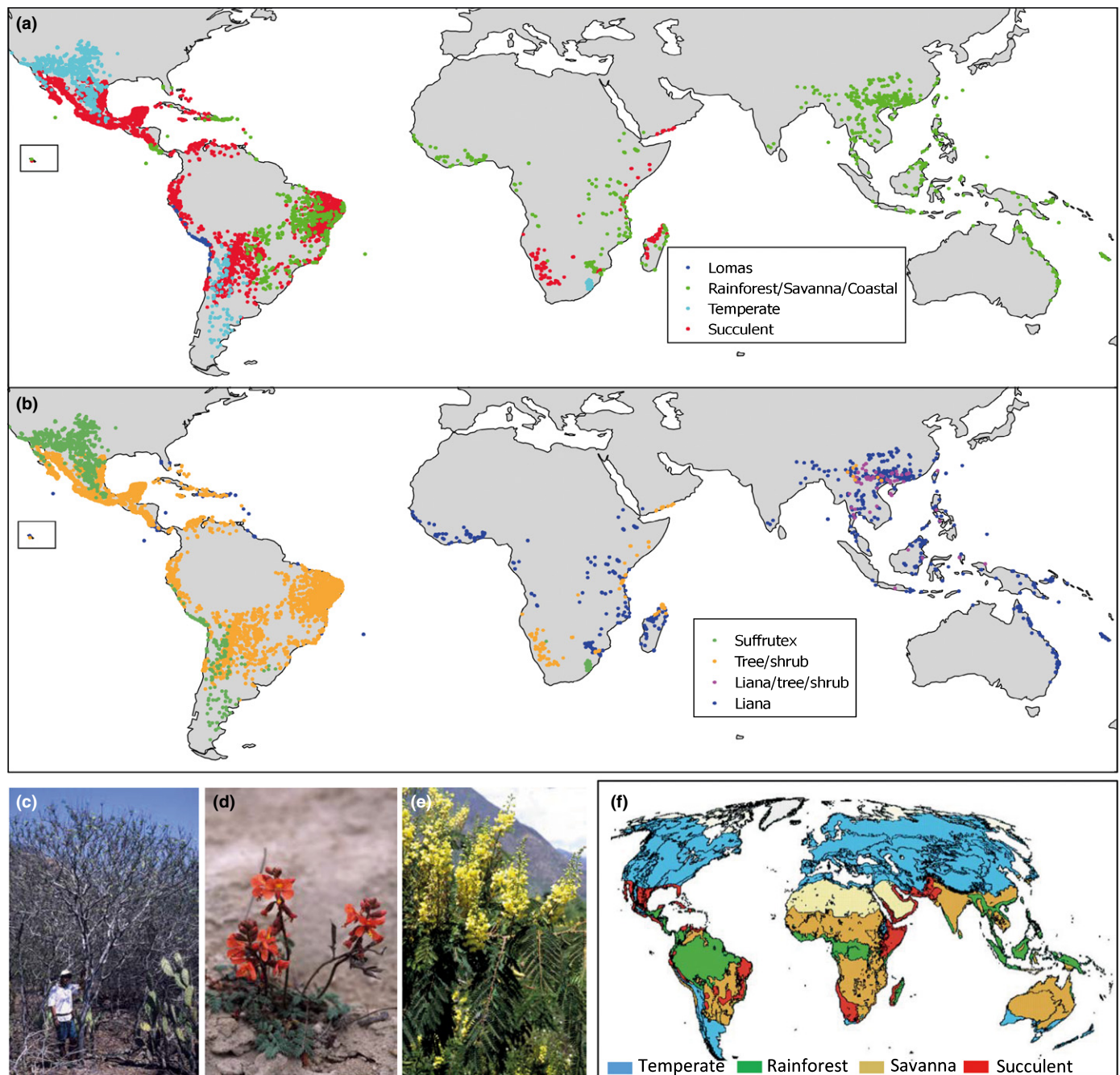
Fig. 1 Distribution of the pantropical Caesalpina Group across biomes and plant growth forms, based on 17 260 species occurrence records (see the Materials and Methods section); widely cultivated/naturalized species whose native ranges are poorly understood (*Caesalpinia pulcherrima* and *Biancaea decapetala*) were removed before mapping (a) Distribution map with species assigned to one or more of the four major biomes of Schrire *et al.* (2005) (see the Materials and Methods section). (b) Map with species assigned to growth form categories. (c–e) Growth forms of the Caesalpinia Group: (c) *Erythrostemon coccineus*, a small deciduous tree typical of seasonally dry tropical forest (Succulent Biome), coastal Oaxaca, Mexico; (d) *Hoffmannseggia miranda*, a functionally herbaceous suffrutex arising from a woody caudex, Lomas formations, coastal Peru. (e) *Biancaea decapetala*, a woody liana, probably native to India, here photographed in central Peru where cultivated as an ornamental. (f) Biome map of Schrire *et al.* (2005), with Savanna equivalent to Schrire's Grass Biome. Photographs (c–e) Colin Hughes; map in (f) courtesy of Brian Schrire.

whose wood is used to make violin bows. Many subclades within the Caesalpinia Group are restricted to the Succulent Biome (Fig. 1, Supporting Information Fig. S1). Subsets of species also occur in tropical savannas, rain forests, coastal mangroves or other shoreline habitats and frost-prone warm temperate drylands (Simpson *et al.*, 2005, 2006) (Fig. 1). While there appears to be a

predilection for the Succulent Biome, the historical biogeography and trajectories of diversification of this large pantropical clade across biomes remain poorly understood.

Recent studies by Gagnon *et al.* (2013, 2016) that generated a robust phylogeny sampling all 26 genera and 75% of species, provide the opportunity to examine geo-temporal patterns of

diversification across the Caesalpinia Group, the extent to which niches are conserved across continents, the evolutionary dynamics of biome shifts and whether evolutionary transitions in plant growth forms coincide with biome shifts. More specifically, we tested whether Succulent Biome phylogenetic conservatism is prevalent within and between continents across the Caesalpinia Group and assessed how other features of this clade – phylogenetic geographical structure and species diversification rates – match predictions from other Succulent Biome lineages. To do this we generated a densely sampled time-calibrated phylogeny, reconstructed the historical biogeography, biome shifts and the evolution of plant growth forms and tested for phylogenetic biome conservatism. We also estimated lineage diversification rates in relation to the evolution of biome and plant growth form and tested the correlation between the evolution of these characters across the phylogeny.

Materials and Methods

Species occurrence data and distribution maps

A taxonomic checklist including synonyms was assembled from Gagnon *et al.* (2016), plus additional synonymy (Brummitt & Ross, 1973; Ulibarri, 1996; Lewis, 1998; Simpson, 1998; Simpson & Lewis, 2003; Clark, 2016; Contreras-Jiménez *et al.*, 2017; Sotuyo *et al.*, 2017a,b). Most genera of the Caesalpinia Group benefit from recent taxonomic revisions (see Gagnon *et al.*, 2016), except for *Cenostigma*, *Guilandina* and the Ticanto clade. This list was used to obtain species occurrence records and assign records linked to synonyms to accepted names.

Vouchered (Basis of Record: Preserved Specimen) occurrence records were downloaded from the Global Biodiversity Information Facility (GBIF, 2017), SEINet (http://swbiodiversity.org/seinet) and DryFlor (http://www.dryflor.info/). To improve accuracy, the distribution of each species was mapped and checked against monographs or expert knowledge and obvious outliers removed. Occurrence points located in the sea, in botanical gardens, on the centroid of a country, or with coordinates only at the level of degrees, were removed. Data handling was performed in R (R Core Team, 2018; data available on Canadensys, doi: 10.5886/dpjv5u).

Biome definitions

Species were assigned primarily to the four global biomes of Schrire *et al.* (2005), the Succulent, Savanna (equivalent to

Schrire's Grass Biome), Rainforest and Temperate Biomes, but three other biomes were considered. First, we assigned species occurring in mangrove and other coastal habitats to a distinct Coastal Biome. Second, although the Succulent Biome includes open cactus and thorn scrub and thicket vegetation (e.g. parts of the Sonoran Desert, Baja California and the Namib-Karoo where rainfall is sufficient to maintain an open cover of woody shrubs and stem succulents), desert areas with lower rainfall, lacking such elements, were excluded. On this basis the Atacama−Sechura desert in South America, with its unusual fog-dependent Lomas formations (Rundel *et al.*, 1991), is here viewed as a unique biome following Guerrero *et al.* (2013). The three suffrutex *Hoffmannseggia* species sampled from the Lomas were assigned to this unique biome.

Finally, there is debate about the South American Chaco (Kuemmerle *et al.*, 2017; Pennington *et al.*, 2017) and its recognition as a separate biome based on floristic distinctions, frost occurrence and unusual fine-textured, sometimes alkaline or saline soils with impeded drainage and seasonal waterlogging (Prado, 1993a, b; Prado & Gibbs, 1993; Pennington *et al.*, 2000, 2017; Linares-Palomino *et al.*, 2011; Särkinen *et al.*, 2011; DRYFLOR, 2016; Silva de Miranda *et al.*, 2018). Although superficially uniform, the vast Chaco plains are heterogeneous: frost occurrence and soils prone to waterlogging and salinity are patchily distributed suggesting a mosaic of habitats that, in parts, resemble the Succulent Biome. It is also not uncommon for prominent woody species to span the Chaco and adjacent SDTF (e.g. *Libidibia paraguariensis*, *Parkinsonia praecox*, *Mimozyganthus carinatus*). Therefore, despite the distinctiveness of the Chaco, we included it in the Succulent Biome because it shares its key attributes of deciduousness, strong rainfall seasonality and vegetation that is grass poor, fire free with the presence of stem succulents. In our analyses of phylogenetic conservatism, we also tested whether coding the four species of the Caesalpinia Group occurring in the Chaco (*Denisophytum stuckertii*, *Erythrostemon coluteifolius*, *Libidibia paraguariensis* and *Lophocarpinia aculeatifolia*) would impact these analyses. It did not affect the results (Table 1; Fig. S2).

Biome and growth form assignments

Species distribution maps were used alongside the biome map of Schrire *et al.* (2005) to assign species to biomes (Table S1), with consultation of floras, taxonomic revisions, other maps (White, 1983; Linares-Palomino *et al.*, 2011; Särkinen *et al.*, 2011), elevation and vegetation data from herbarium labels,

Table 1 Numbers of biome shifts across the Caesalpinia Group obtained with observed and randomized biome data for a sample of 200 trees, using different models and biome definitions (see the Materials and Methods section).

	Equal rates model		Symmetrical model		Equal rates model + Chaco	
	Original	Randomized	Original	Randomized	Original	Randomized
1st Quartile	28.25	66.52	52.83	118.5	33.06	71.40
Median	28.78	68.27	65.23	199.9	33.68	73.19
3rd Quartile	29.44	69.87	94.62	482.9	34.41	74.87

co-occurrence with stem succulents and field observations. For most species, assignment to a single biome was straightforward and unambiguous. For a few species of *Hoffmannseggia* and *Pomaria* from the physiographically heterogeneous dry canyons of the Mexican Sierra Madre Oriental, where the boundaries between the Succulent and Temperate Biomes are less clear-cut, assignments to the Succulent Biome were more tentative. A few species span more than one biome and one taxon had insufficient data to assign to biome (*Cenostigma pluviosum* var. *peltophoroide*s) (Table S1).

Species were assigned to one of three growth form categories: tree/shrub, suffrutex (usually functionally herbaceous from a basal woody caudex, or perennial herbs) and liana, or if polymorphic scored as tree/shrub/liana, based on field observations, herbarium data, floras, taxonomic revisions and Simpson *et al.* (2004) for *Hoffmannseggia*.

Biome and growth form distribution maps were generated in QGIS (Quantum GIS Development Team, 2017) using the TomBio plugin (Burkmar, 2014) (Fig. 1).

Time-calibrated phylogeny

The concatenated DNA sequence alignment of Gagnon *et al.* (2016), which included five plastid loci (*rps16,* the *trnD-trnT* intergenic spacer, *ycf6-psbM,* the *matK* gene and *3′-trnK* intron, the *trnL-trnF* intron-spacer region) and the 5.8S subunit and flanking internal transcribed spacers ITS1 and ITS2 of nrDNA, were pruned to 202 accessions to remove population sampling while retaining all 168 species plus 10 subspecies and varieties, representing all 26 genera plus the Ticanto clade (a provisional name for a 27$^{\text{th}}$ genus awaiting further study) and nine outgroup taxa from Caesalpinioideae *sensu* LPWG (2017) (Table S1). All except seven accessions have sequences for at least two loci. Ambiguous alignment regions were removed (Gagnon *et al.*, 2016).

Time-calibrated phylogenies were constructed using BEAST v.1.8.4 (Drummond *et al.*, 2012) with two data partitions – the five plastid loci and ITS – applying the GTR+I+G model to both partitions based on the Aikake Criterion in JMODELTEST2 (Darriba *et al.*, 2012). Analyses used an uncorrelated log normal relaxed clock and a birth−death speciation tree prior. A diffuse prior was used to estimate the UCLD.mean (exponential prior distribution, mean 10, initial value 1.0). To avoid problems of low likelihood at the start, a fixed tree topology including age calibrations was specified (Methods S1).

The phylogeny was calibrated using two previously used fossil priors (Bruneau *et al.*, 2008; Simon *et al.*, 2009) on the stem nodes of the genera *Mezoneuron* and *Senna* (see Methods S1). In addition, the root height of the tree, corresponding to the crown node of subfamily Caesalpinioideae *sensu* LPWG (2017), was constrained using a uniform prior with maximum age 60.8 Ma and minimum 45 Ma, based on higher level legume time trees (Lavin *et al.*, 2005; Bruneau *et al.*, 2008; Simon *et al.*, 2009), which estimated the divergence of Caesalpinioideae at 58.6 Ma (58.8–58.5, 95% higher posterior density) in line with the earliest definitive caesalpinioid legume fossils at 58 Ma (Herendeen, 1992; Wing *et al.*, 2009).

Ancestral state and area reconstructions

Biome and growth form ancestral states were inferred using BEAST 1.8.4, with four replicate searches of 30 million generations, sampling every 1000 generations. Characters with polymorphic states were included by manually editing the xml file to the corresponding ambiguity codes for character states.

To locate and estimate the number and timing of transcontinental disjunctions, we reconstructed ancestral areas using both the continuous time Markov Chain (CTMC) phylogeographic model (Lemey *et al.*, 2009) in BEAST 1.8.4 and compared various biogeographical models in BIOGEOBEARS (see Methods S1; areas defined as in Fig. S2).

Phylogenetic biome conservatism

How to measure and test for phylogenetic biome (or niche) conservatism remains contentious with several methods proposed (e.g. Wiens & Graham, 2005; Losos, 2008; Crisp *et al.*, 2009; Wiens *et al.*, 2010; Crisp & Cook, 2012). Here we used two approaches: analysis of the total number of biome shifts against a null distribution and assessment of phylogenetic signal. While neither method alone provides an entirely robust or satisfactory way to measure biome conservatism (e.g. Losos, 2008; Revell *et al.*, 2008; Münkemüller *et al.*, 2015),when considered together they provide a useful approach to quantify and statistically evaluate the levels of biome conservatism across a phylogeny.

To assess the number of biome shifts we used stochastic character mapping implemented in the function make.simmap in the PHYTOOLS R package (Revell, 2012), which allows for polymorphic/missing character states. All analyses were performed over 200 trees randomly selected from the posterior distribution of the BEAST output to account for phylogenetic uncertainty, pruned to 193 tips (outgroup removed). The number of biome shifts per tree was compared with a null distribution obtained by randomizing tip states and re-running the analysis 99 times. A significantly lower number of biome shifts obtained with the original data compared with the randomized data provides evidence for biome conservatism (Maddison & Slatkin, 1991). make.simmap was run with 200 simulations per analysis under an equal rates model ('ER') and a symmetrical model ('SYM').

Phylogenetic signal was measured using the fitDiscrete function in GEIGER (Harmon *et al.*, 2008) which estimates Pagel's lambda (Pagel, 1999). High phylogenetic signal is indicative of conservatism (but see Revell *et al.*, 2008; Losos, 2008). As fitDiscrete does not allow missing/polymorphic character states and because 28 taxa were assigned to more than one biome, each of these taxa was randomly assigned one of its possible states per tree and the analyses were repeated 100 times. Tree branch lengths were transformed to fit the observed lambda as well as a lambda of 0 and 1 using the rescale function and the best-fitting lambda was picked using the Akaike Information Criterion (Akaike, 1974). fitDiscrete was also run with the ER and SYM models.

Correlated evolution

Several methods exist to test for correlated evolution between two characters, but none allows testing of two categorical multistate characters as we have here for growth forms and biomes. To circumvent this problem, we grouped the biomes and growth forms each into two categories and examined possible associations between growth form and biome by testing the transition from tropical to temperate biomes against woody to suffrutex growth forms. Species were reassigned to one of these two categories for each character. Correlated evolution was assessed using Pagel's test (Pagel, 1994) implemented in the fitPagel function in PHYTOOLS (Revell, 2012). Five taxa could not be unambiguously assigned to a character state for either biome or growth form, so fitPagel was run for all 32 possible combinations of character states for these taxa, using the 'FITMK' method, 200 trees, with both the ER model and the all rates different ('ARD') model.

Diversification rates analyses

The maximum clade credibility BEAST tree was used to explore the evolutionary dynamics of the Caesalpinia Group and test for shifts in species diversification rates through time and among lineages. A lineage-through-time plot (LTT) was generated with PHYTOOLS (Revell, 2012) to visualize the trajectory of lineage accumulation over time. To detect variation in diversification rates through time across the tree as a whole, RPANDA (v.1.3, Morlon et al., 2016) was used to compare the fit of constant-rate and variable-rates of speciation and extinction models (starting parameters values listed in Table S2). A complementary diversification rates analysis was conducted with BAMM v.2.5.0 (Rabosky, 2014; Rabosky et al., 2017) to estimate the posterior distribution of diversification rate shift configurations, with each representing the likelihood of different scenarios of rate shifts occurring at different points along the phylogeny (with zero, one, two, or more possible shifts) under different birth−death models (see Methods S1 and Table S3 for details).

Results

Geographical distributions of plant growth forms across biomes

In total, 17 260 species occurrence records, spanning > 200 species and infraspecific taxa and all 26 genera, were assembled to generate distribution maps (Fig. 1). These show that the Caesalpinia Group is pantropically distributed with only minor incursions, involving just four genera, into the temperate biome, presenting a clear signal of tropical niche conservatism (Figs 1–3). The group is virtually absent from Amazonia and poorly represented in rain forests in the Neotropics and Africa, but more common in rainforest in SE Asia, where a clade of lianas occurs. These distributions suggest an association between biomes and growth forms: species in the Succulent biome are almost all trees or woody shrubs; the Temperate and Lomas biomes group all the suffrutex species; species in the

Rainforest Biome are primarily woody lianas; and in the Savanna Biome both trees and lianas occur (Figs 1, 3).

Time-calibrated phylogeny and ancestral areas

The time-calibrated phylogeny (Fig. 2) estimates the crown age of the Caesalpinia Group to be early Eocene, at 54.78 Ma (95% highest posterior density: 53.27–56.27 Ma). Many subclades within the Caesalpinia Group show striking transcontinental disjunctions (Fig. S1) and there is strong geographical structure across the phylogeny (Fig. 2). For example, all the Asian species are placed in one clade containing all the liana species and, aside from one species in the Caribbean, the two major subclades within *Erythrostemon* group species from North America and South America. Other clades show similar geographical structure with subclades confined to individual areas of the Succulent Biome (Fig. 2).

The BIOGEOBEARS analysis found the dispersal−extinction−cladogenesis (DEC) model to have the best fit (Table S4) and the ancestral area reconstruction using this model (Fig. 2) was very similar to the Continuous-Time Markov Chain (CTMC) reconstruction in BEAST (results not shown). In total, 49 transcontinental disjunctions were identified based on a dispersal or range expansion event between nodes on the phylogeny (Figs 2, 4). Of the 49 transcontinental disjunctions, only two were accompanied by a switch in biome. Fifty-seven percent of within-biome transcontinental disjunctions occurred in the Succulent Biome (Figs 2, 4). Ages of the transcontinental disjunctions span the Eocene to the present with higher frequency in the last 10 Ma (Fig. 4).

Phylogenetic biome conservatism

More than half of the 225 species of the Caesalpinia Group occur in the Succulent Biome (142 species) with fewer species in the other biomes (Savanna, 39; Rainforest, 40; Coastal, 12; Lomas, 3). The number of biome shifts observed on our phylogeny is always significantly lower than the number of shifts obtained with randomized tip states, independent of the model used and regardless of whether the Chaco is scored as a separate biome or not (Table 1; Fig. S3), suggesting phylogenetic biome conservatism.

The median Pagel's lambda obtained using the ER model is 0.77. This lambda was picked as the best-fitting lambda for all 100 randomizations for 99% of the tree sample. For the remaining 1% of trees this value of lambda was also the best fit for 99 randomizations, whereas a lambda of 1 was a better fit for two individual randomizations. Treating the Chaco as a separate biome did not significantly change these results (median lambda = 0.77, best fit for all randomizations for 99.5% of trees, lambda of 1 better fit for one randomization of remaining trees). Using the SYM model resulted in a median lambda of 0.76, best fit for all randomizations for 91% of all trees, one or two randomizations per tree of the remaining trees fit better with a lambda of 1, also suggesting phylogenetic biome conservatism.
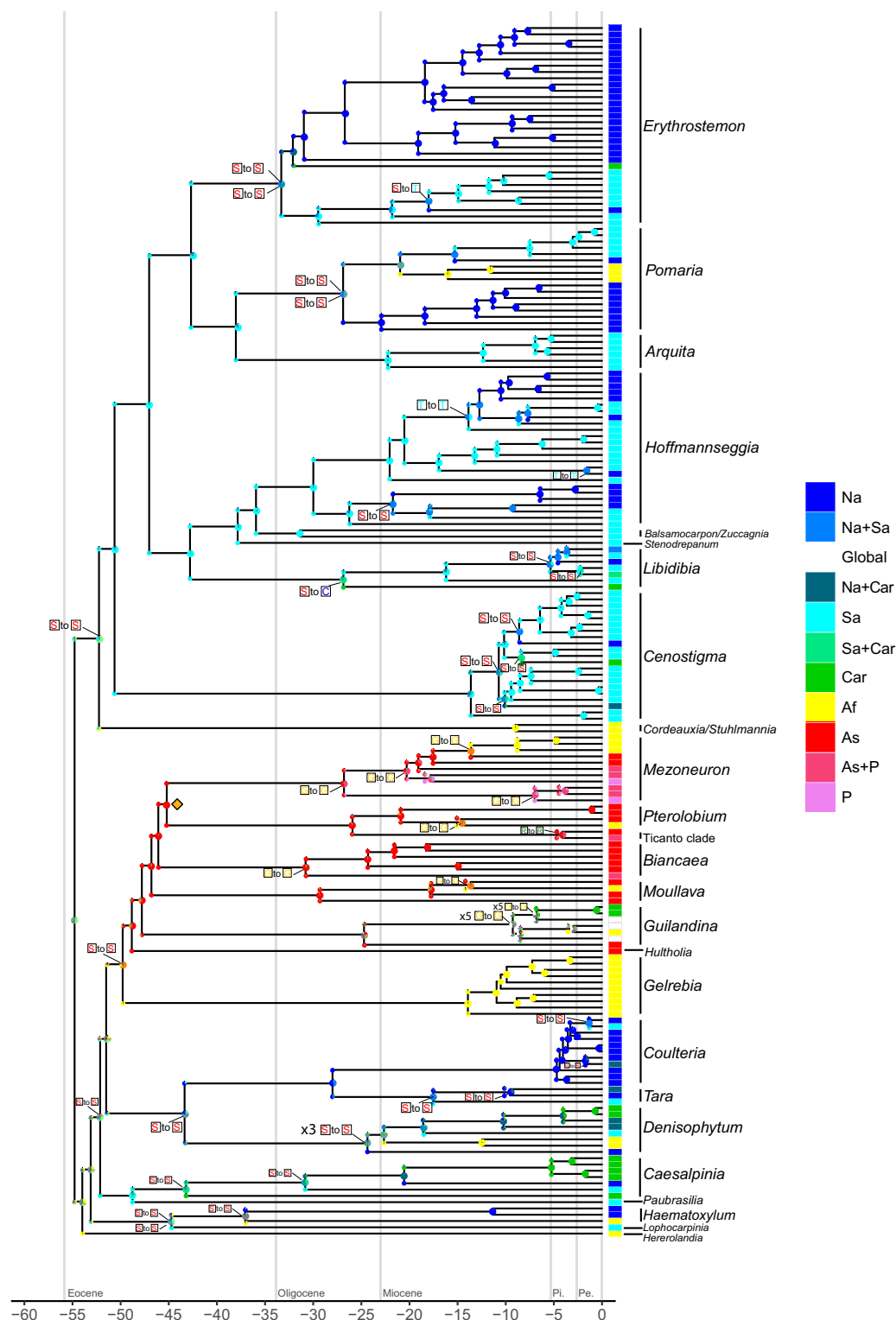
Fig. 2 Time-calibrated phylogeny of the Caesalpinia Group, showing the maximum clade credibility tree generated in BEAST 1.8.4, with the outgroup removed; grey lines along the time scale represent the boundaries between Pleistocene (Pe.), Pliocene (Pi.) and other geological epochs. The orange diamond represents the stem node of the Mezoneuron clade that was used to calibrate the analysis based on Eocene fossil *Mezoneuron* fruits from Herendeen & Dilcher (1991). The second fossil constraint is not shown here as it was placed within the outgroup, but is indicated in Fig. S8. Pie charts represent ancestral area reconstructions from the DEC model from the BIOGEOBEARS analysis. Boxes at tips are coloured according to the geographic areas occupied by the terminal taxon, as indicated by the color legend (Sa, South America; Na, North America; Car, Caribbean; Af, Africa; As,Asia; P, Pacific-Australian region). In addition, the edges/nodes on the phylogeny where transcontinental disjunctions are postulated, as inferred by the DEC model, are marked with a pair of boxes indicating whether or not these transcontinental disjunctions were accompanied with biome switches and which biomes were involved (S, Succulent (red); T, Temperate (light blue); G, Savanna (yellow); R, Rainforest (green), C, Coastal (purple)).
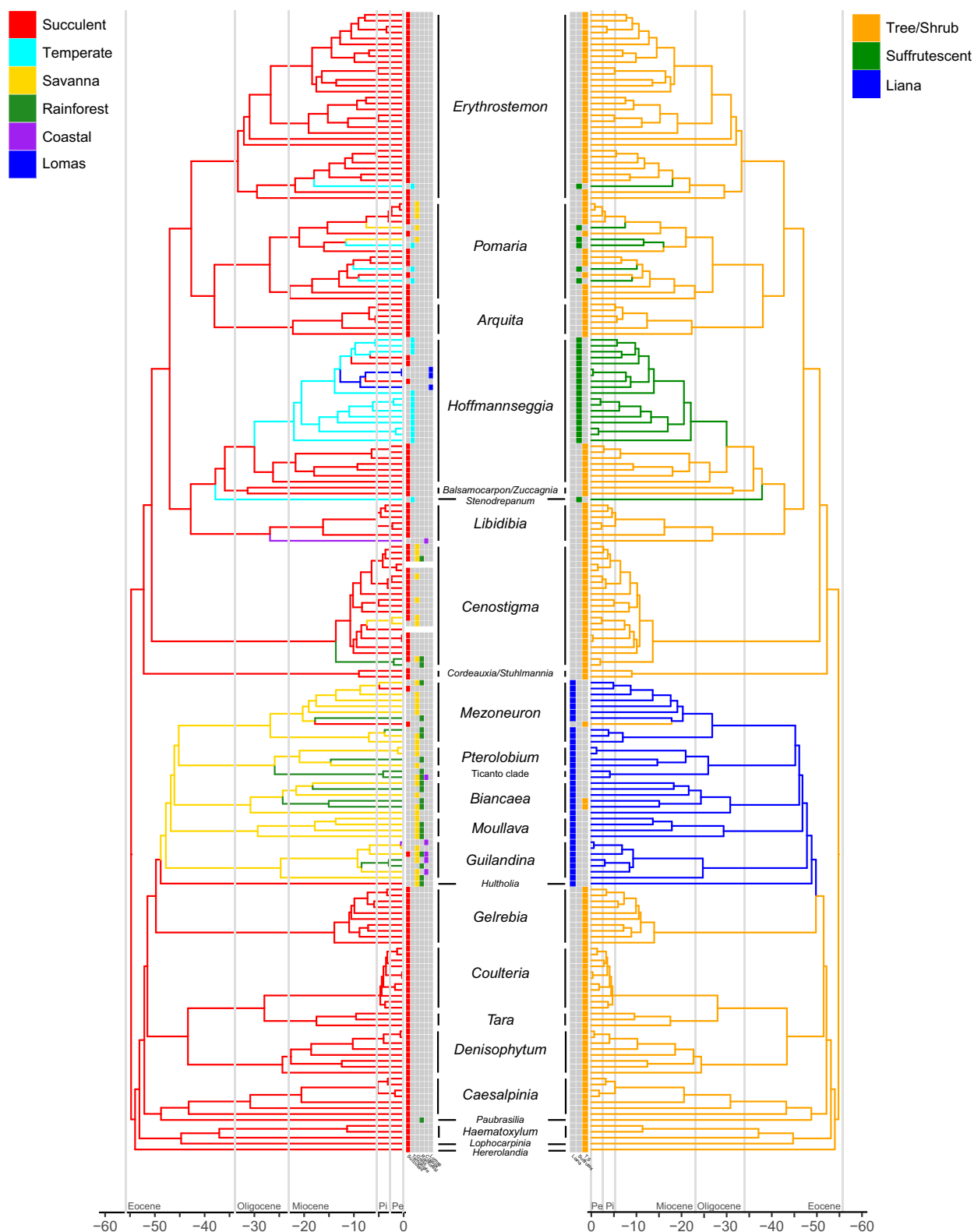
Fig. 3 Time-calibrated Bayesian ancestral state reconstructions of biomes (left) and plant growth forms (right), displayed on the maximum clade credibility generated in BEAST 1.8.4, with outgroup. Grey lines along the time scale represent the boundaries between the Pleistocene (Pe.), Pliocene (Pi.) and other geological epochs. Columns of boxes at tip terminals represent how each taxon was scored, with grey boxes indicating an absence of the character state in question; white boxes indicate that we were unable to assign biomes for the taxon in question.
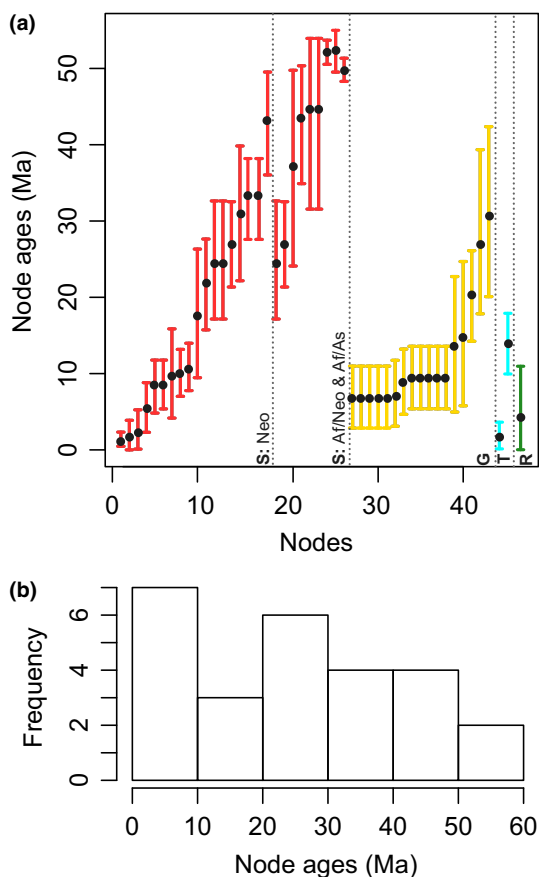
Fig. 4 Ages of transcontinental disjunctions within the same biome. (a) Scatterplot of the ages of transcontinental dispersal events within biomes, with bars representing the 95% highest probability density of the node ages, as estimated by Beast analysis; red, Succulent Biome (S); light blue, Temperate Biome (T); yellow, Savanna Biome (G); green, Rainforest Biome (R). For the Succulent Biome, the type of transcontinental disjunction is specified: Neo refers to transcontinental disjunctions between South America, North America and the Caribbean; Af/Neo refers to disjunctions between the Neotropics and Africa; As/Neo refers to disjunctions between Asia and the Neotropics; Af/As refers to disjunctions between Africa and Asia. (b) Histogram of the ages of transcontinental disjunctions within the Succulent biome. Ma, million years.

Correlated evolution

For every tree and all possible combinations of polymorphic character states, the null hypothesis of uncorrelated evolution could be rejected (with an α of 0.05) for both the SYM and the ARD models, suggesting a correlation between growth form (woody vs suffrutex) and biome (tropical vs temperate) transitions. The number and locations of these correlated shifts is uncertain due to phylogenetic uncertainty within *Pomaria* and *Hoffmannseggia* (Fig. S4), but this does not affect the overall conclusion of a significant biome/growth form shift correlation.
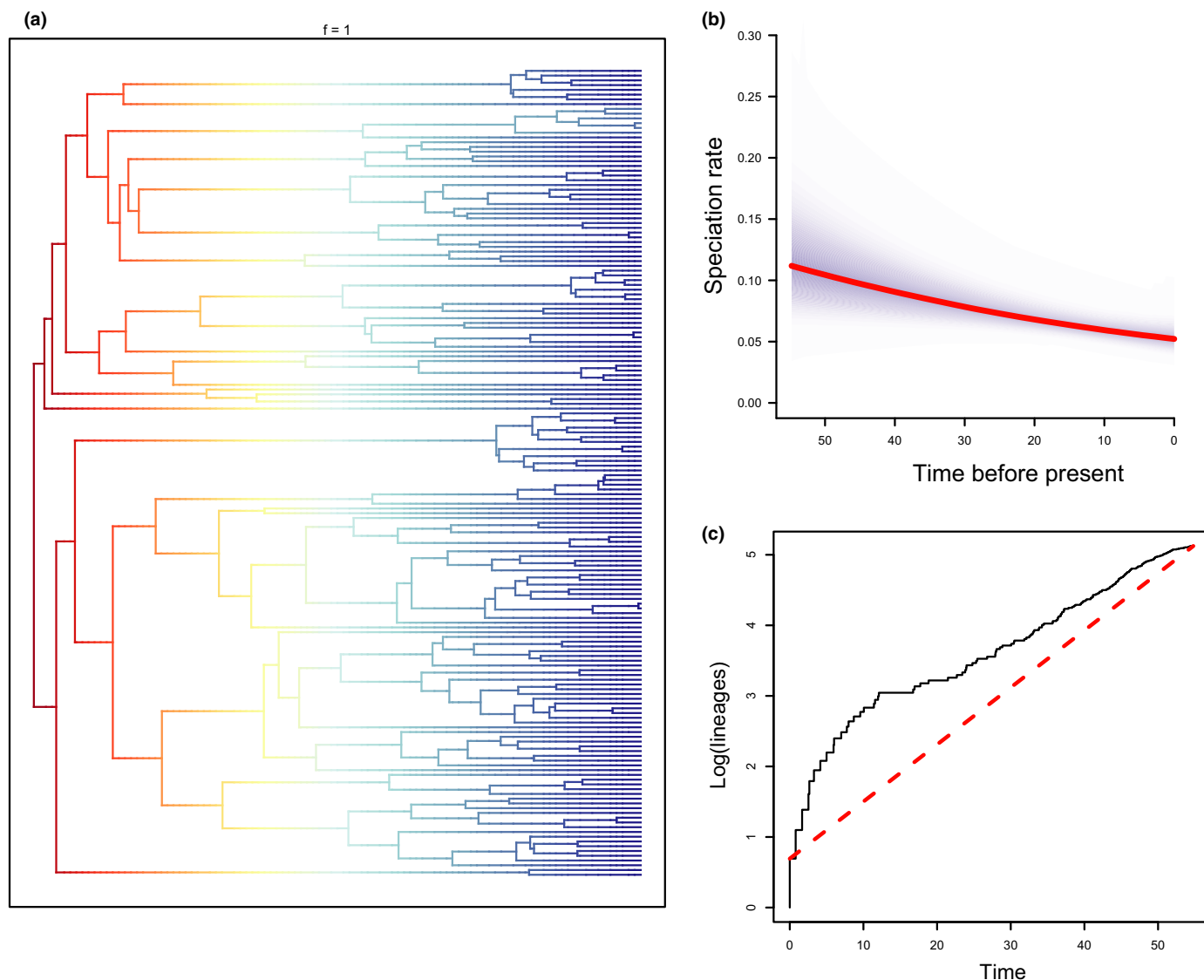
Diversification rates

Over the phylogeny as a whole, after an initial rapid diversification of lineages in the Eocene, rates of diversification remained

relatively constant, slowly declining through time (Fig. 5). While the best model according to the RPANDA analysis was the Pure Birth model with an exponential variation in speciation, it was not found to be significantly better than the Pure Birth model with constant or linearly variable speciation rates (ΔAICc < 1; see Table S5). BAMM analysis showed no evidence for diversification rate shifts across the Caesalpinia Group (Fig. S5), with Bayes Factors values for model comparisons well below 1.0 for all sets with one or more shifts and only the model with no shifts found in the 95% clade credibility sets (Fig. 5). The macroevolutionary cohort analysis and the cumulative probability shift tree did show that the clades corresponding to *Guilandina* and *Coulteria* seem to have slightly different macroevolutionary rate regimes than the rest of the group (Figs S6, S7).

Discussion

Transcontinental geographic disjunctions among closely related taxa, as seen in the Caesalpinia Group (Figs 1, 2, S1), have intrigued biogeographers and fueled the central debate between dispersal and vicariance for more than two centuries. Here, using a densely sampled phylogeny and detailed species occurrence data for this pantropical legume clade of 225 species, we show that most of the 49 postulated transcontinental disjunctions have more to do with shared biomes than tectonic history. More than 60% of species of the Caesalpinia Group are restricted to the Succulent Biome; 47 of 49 transcontinental disjunctions are within the same biome and 27 are within the Succulent Biome; the total number of within-biome transcontinental geographical disjunctions is higher than the total number of biome shifts whether within or between continents (Fig. 3); overall, there are more transcontinental geographical disjunctions than shifts between biomes; and estimates of the number and phylogenetic distribution of biome shifts and phylogenetic signal show significant support for phylogenetic biome conservatism (Figs 2, 4, S3). These results suggest that it has been easier for Caesalpinia Group taxa to occupy similar habitats on other continents than for lineages in different but geographically adjacent biomes to shift and adapt, in line with the *easier to move than evolve* mantra of biome conservatism proposed by Donoghue (2008). In the case of the Succulent Biome, strong phylogenetic conservatism is especially striking given the highly fragmented distribution of this biome which spans large transcontinental disjunctions across an archipelago of geographically isolated patches (Fig. 1).

Although the concept and initial delimitation of the Succulent Biome were founded on distributions of just a few legume lineages (Lavin, *et al.*, 2004), our results add significantly to this tally of Succulent Biome clades. Several other plant clades also have Succulent Biome distributions, including the *Bursera-Commiphora* clade (Burseraceae) (De Nova *et al.*, 2012; Weeks *et al.*, 2014) and *Thamnosa* (Rutaceae) (Thiv *et al.*, 2011), alongside geographically restricted clades within the Neotropics, e.g. Robinioid legumes (Lavin, 2006; Pennington *et al.*, 2009), the genera *Loxopterygium* (Anacardiaceae), *Pereskia* (Cactaceae) (Pennington *et al.*, 2004) and Cactaceae in general (Hernández-Hernández *et al.*, 2014) and within Africa and adjacent regions, e.g. *Moringa* (Moringaceae)

Fig. 5 (a) The 95% credible set of distinct shift configurations as found by the BAMM 2.5.0 diversification analysis, from the analysis of the maximum clade credibility tree of the Caesalpinia Group phylogeny; the frequency (f) of each distinct shift configuration is indicated and the colors represent the evolutionary rates along the branches (with blue/cool colors representing slower diversification rates and red/warm colors representing higher diversification rates). (b) The rate-through-time plot generated by BAMM 2.5.0, with shaded areas representing the confidence on evolutionary rate reconstructions across time. (c) The lineage-through-time (LTT) plot of the Caesalpinia Group generated on a log scale, using PHYTOOLS (Revell, 2012), based on the maximum clade credibility tree generated in BEAST, with the red dashed line representing linear growth.

(Olsen, 2002) and clades within *Euphorbia* (Euphorbiaceae) (Bruyns *et al.*, 2011). Further work is needed to test for phylogenetic biome conservatism across these and other clades.

Many questions remain about how biomes are defined, with differing emphases on floristic composition, physiognomy, functional traits, climate, soils, fire and phylogenetic distinctiveness (e.g. Olson *et al.*, 2001; Lehmann *et al.*, 2011, 2014; Särkinen *et al.*, 2011; Hughes *et al.*, 2013; Daru *et al.*, 2016; Higgins *et al.*, 2016; Moncrieff *et al.*, 2016; Silva de Miranda *et al.*, 2018). Choice of biome classification influences assessment of phylogenetic biome conservatism and selecting what biome classification to use depends on the questions being addressed. The three main lowland tropical biomes used here – Succulent, Savanna and Rainforest – are broad compared with other systems (e.g. WWF

Ecoregions; Olson *et al.*, 2001; Dinerstein *et al.*, 2017). These biomes reflect the major precipitation and rainfall seasonality gradients dictating vegetation stature and deciduousness and fire occurrence and herbivory, which together result in major functional differences between the grass-rich, fire-prone, succulent-poor Savanna Biome and the grass-poor, fire-free, succulent-rich Succulent Biome (Dexter *et al.*, 2018; Pennington *et al.*, 2018). More finely grained biomes (e.g. Dinerstein *et al.*, 2017) inevitably show much greater biome lability (e.g. Cardillo *et al.*, 2017), but in our view these ecoregions are better viewed as geographical subdivisions of more meaningful global biomes for understanding global plant distribution patterns, in line with recent merging of these ecoregions into biomes (Pennington *et al.*, 2018).

Nonetheless, many questions remain about how the Succulent Biome is defined and while the Schrire *et al.* (2005) map is a useful starting point, there is a clear need for a more accurate and objective map of this biome (Särkinen *et al.*, 2011; Silva de Miranda *et al.*, 2018). In addition, although assignment of the Chaco species to the Succulent Biome or to a distinct Chaco Biome makes no difference to the pattern of phylogenetic biome conservatism observed here, the affinities of the Chaco remain enigmatic and in need of further work (Kuemmerle *et al.*, 2017; Pennington *et al.*, 2017; Silva de Miranda *et al.*, 2018).

In a family-wide analysis of biome shifts in legumes, Schrire *et al.* (2005) suggested that the Succulent Biome was of central importance in the evolution of the family because many Succulent Biome clades were postulated to be older and often subtending Rainforest, Savanna and Temperate Biome lineages. They proposed that legumes originated in an arid belt surrounding the Tethys Seaway that spanned the Equator during the Eocene (56–43 Ma). Ancestral biome reconstructions, which depict the entire backbone of the Caesalpinia Group phylogeny as occupying the Succulent Biome (Fig. 3), might be taken to imply that the Succulent Biome has been present since the Eocene period, potentially in line with Schrire's hypothesis of a Tethys Seaway dry tropical ancestral legume biome. However, caution is required when inferring biome origins from phylogenies (Donoghue & Edwards, 2014) and divergence time analyses are notoriously sensitive to model choice and biases in taxon and gene sampling. The age estimated here for the Caesalpinia Group (54.78 Ma) is somewhat older than previous estimates from higher-level legume time trees (Bruneau *et al.*, 2008; Simon *et al.*, 2009), perhaps due to node density artifacts introduced by uneven outgroup versus ingroup taxon sampling in the Caesalpinia Group phylogeny that will tend to overestimate the age of the ingroup. It is notable that time-calibrated phylogenies of stem succulent plant lineages (Cactaceae, Agaves, Didiereaceae, *Euphorbia*), one of the key defining elements of the modern Succulent Biome, suggest younger Oligocene origins with more recent Miocene radiations (Arakaki *et al.*, 2011; Bruyns *et al.*, 2011; Hernández-Hernández *et al.*, 2014). These synchronous trajectories across geographically and phylogenetically independent stem succulent lineages were linked to Oligocene and Miocene global cooling and expansion of drought-prone vegetation (Arakaki *et al.*, 2011). This suggests that the modern Succulent Biome probably emerged during the Oligocene, becoming fully established in the late Miocene. Mid- to late-Miocene ages have been estimated for other Succulent Biome transcontinental legume clades (Lavin *et al.*, 2004) and correspond with late Oligocene and mid-Miocene ages of Succulent Biome lineages in Mexico (Willis *et al.*, 2014) and the Caatinga (de Queiroz *et al.*, 2017) and Miocene fossil assemblages from Ecuador containing fossil fruits that closely resemble the extant Andean Succulent Biome species (Burnham, 1995; Burnham & Carranco, 2004). With the bulk of evidence suggesting an Oligocene origin of the modern Succulent Biome, it seems possible that the Caesalpinia Group occupied some sort of proto-seasonally dry tropical biome in the Eocene, potentially lacking stem succulents and not readily equated with the modern Succulent Biome, but likely linked to the start of global aridification in

the mid-Eocene. It is notable that fossil fruits assigned to Caesalpinia Group lineages (*Mezoneuron* and *Caesalpinia*) have been recovered from mid-Eocene (45 Ma) strata at a number of localities in North America (Herendeen & Dilcher, 1991), including from the Green River putative dry tropical fossil flora of Utah (45–48 Ma) (Graham, 1999), suggesting that the Caesalpinia Group was present in North America soon after the group first appeared and that a proto-seasonally dry tropical forest could have been present in North America in the mid-Eocene. Such a scenario is compatible with the Boreotropics hypothesis (Lavin & Luckow, 1993) and with mid-Eocene age estimates for the split between Neotropical *Bursera* and Old World *Commiphora*, another group with Boreotropical Eocene fossils that shows striking amphi-Atlantic Succulent Biome phylogenetic conservatism (Weeks *et al.*, 2005, 2014; De Nova *et al.*, 2012). Similar dilemmas surround inferences of the age of tropical rain forests (Davis *et al.*, 2005; Couvreur *et al.*, 2011) and other biomes, suggesting a need for careful integration of multiple lines of evidence (Donoghue & Edwards, 2014). For the Succulent Biome, such multiple lines of evidence suggest persistence at least since the Miocene with nonanalog precursor dry tropical vegetation present in the Eocene when the Caesalpinia Group started to diversify.

The limited number of biome shifts into the Savanna Biome in the Neotropics, all of them within *Cenostigma*, occurred within the last 8 Ma (Fig. 3) coinciding with the recent assembly of the Cerrado from the late Miocene (Simon *et al.*, 2009). The shift into savanna and then rainforest in the large liana clade in Asia (Fig. 3) is older, dating back to the Eocene and is characterised by frequent shifts between savanna and rainforest in line with the lability of Savanna and Rainforest Biome shifts more generally (Simon *et al.*, 2009; de la Estrella *et al.*, 2017).

Clades occupying the Succulent Biome comprise deciduous woody trees and shrubs often displaying a conspicuous burst of post-drought leaf flushing triggered by relatively small amounts of precipitation (Oliveira-Filho *et al.*, 2013), a life history strategy well adapted to the seasonal drought distinguishing this biome. Across the Caesalpinia Group there is strong concordance between biomes and plant growth forms (Figs 1, 3) and shifts from tropical to temperate are closely correlated with shifts from woody to suffrutex growth forms. Although not tested quantitatively, the single transition to liana growth form is also closely associated with the shift into the Savanna Biome in Asia (Figs 1, 3) and subsequently persists in Asian rainforest lineages. These results reflect evidence that biome shifts often coincide with evolutionary shifts in plant life history strategies to overcome adaptive barriers associated with biome boundaries. For example, numerous shifts into the Savanna Biome are associated with transitions from trees to fire-adapted functionally herbaceous geoxyles (Simon *et al.*, 2009; Simon & Pennington, 2012; Maurin *et al.*, 2014; Pennington & Hughes, 2014). Similarly, repeated evolution of woody perennials from herbaceous annuals is closely associated with shifts from lowland to montane habitats (e.g. Hughes & Atchison, 2015). In the Caesalpinia Group shifts from tropical to frost-prone temperate habitats were apparently facilitated by shifts from trees to functionally herbaceous subshrubs (Fig. 3).

Similarly, the shift to liana growth form coincides with a shift into Savanna biomes in Asia (Fig. 3). Although the adaptive significance of this shift is less clear, it is notable that liana clades in other groups, such as Calamoid palms, are also distributed mainly in Asia (Couvreur *et al.*, 2015), potentially linked to open canopy disturbance regimes (Oliveira-Filho *et al.*, 2013) and Dipterocarp dominated rainforests.

Our results are very much in line with the emerging view of the Succulent Biome as relatively stable and ecologically resilient over long evolutionary timescales, as originally conceived by Lavin *et al.* (2004). A notable hallmark of Succulent Biome plant lineages is that they show geographically structured phylogenies, with small subclades of species restricted to disjunct pockets of Succulent Biome habitats (Lavin *et al.*, 2004; Lavin, 2006; Pennington *et al.*, 2006, 2009; Särkinen *et al.*, 2011; De Nova *et al.*, 2012; Dexter *et al.*, 2017), as found for the Caesalpinia Group (Fig. 2). These patterns have been interpreted in terms of dispersal limitation and low rates of immigration across the highly fragmented Succulent Biome, with occasional successful long-distance dispersal facilitated by evolutionary persistence of Succulent Biome vegetation across these areas (Lavin, 2006; Pennington *et al.*, 2009). This is borne out by the high levels of range-restricted species endemism (β diversity) across the Succulent Biome (DRYFLOR, 2016; Marshall *et al.*, 2016). The Caesalpinia Group has apparently diversified at a relatively constant and slow rate in line with other Succulent Biome lineages. In tribe Robinieae, a clade with strong Succulent Biome affinities (Lavin, 2006), a decrease in net species diversification rate has been documented (Koenen *et al.*, 2013) and slow and constant diversification rates are observed for Succulent Biome tree partitions in tribe Indigofereae and the genera *Mimosa* and *Calliandra*. In these groups nested Succulent Biome to the Savanna and Temperate Biome transitions are associated with shifts to higher rates of diversification (Koenen *et al.*, 2013).

The Succulent Biome is separated from other biomes by significant drought related adaptive barriers and notably the evolution of deciduousness involving the energetically costly production of short-lived leaves to facilitate rapid photosynthesis during the brief favourable wet season and to survive long periods of drought (McKey, 1994). This depends on the potentially key adaptation of rapid burst post-dry season leaf flushing characteristic of many Succulent Biome plant lineages, including the Caesalpinia Group, which involves sensitive responses to small rainfall events at the beginning of the rainy season (McKey, 1994; Oliveira-Filho *et al.*, 2014). This combination of attributes may result in strong phylogenetic Succulent Biome conservatism of lineages transcontinentally (Pennington *et al.*, 2006, 2009), as exemplified by detailed phylogenetic and biogeographic analysis of the pantropical Caesalpinia Group.

Author contributions

EG, JJR, AB, GPL and CEH planned and designed the research. EG, JJR, CEH collected and analysed the data. EG and CEH wrote the manuscript, with constructive feedback and revisions from AB, JJR and GPL.

ORCID

Anne Bruneau https://orcid.org/0000-0001-5547-0796
Edeline Gagnon https://orcid.org/0000-0003-3212-9688
Colin E. Hughes https://orcid.org/0000-0002-9701-0699

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Supporting Information

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

Fig. S1 Maps showing the distributions of transcontinental clades and geographical disjunctions across the Caesalpinia Group.

Fig. S2 Geographic areas defined for the BioGeoBEARS DEC and Beast CTMC analyses.

Fig. S3 Plots comparing the number of biome shifts per tree to a null distribution obtained by randomizing tip states.

Fig. S4 Bayesian consensus tree from MrBayes analysis (Gagnon *et al.*, 2016), with 408 taxa and posterior probabilities indicated below nodes in italics, with the exception of nodes that are with a green diamond, indicating posterior probability support of 0.95 and higher; nodes with less than 0.5 posterior probability support shown as polytomies.

Fig. S5 Bar plot of prior and posterior probabilities for the number of shifts inferred by Bamm.

Fig. S6 Macroevolutionary cohort analysis of the Caesalpinia Group in Bamm.

Fig. S7 Cumulative probability shifts tree from the Bamm analysis.

Fig. S8 Time-calibrated maximum clade credibility tree generated in Beast, with all 202 taxa initially included in the phylogeny; node ages indicated in bold above branches; red diamonds on node indicate placement of fossil calibrations along the stem nodes of *Mezoneuron* and *Senna*.

Methods S1 Justification of fossil calibrations and priors; detailed phylogenetic methods. Biogeography analysis.

Table S1 Growth and biome forms assigned to all taxa of the Caesalpinia Group.

Table S2 Starting parameter values for the Rpanda analysis.

Table S3 Sampling fractions estimated for each genus of the Caesalpinia Group, as specified in the Bamm analysis.

Table S4 Models tested in BioGeoBEARS package in R.

Table S5 Models of diversification tested using Rpanda.

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