

RESEARCH PAPER



Transitions between biomes are common and directional in Bombacoideae (Malvaceae)

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Funding information

German Research Foundation, Grant/Award Number: DFG FZT 118 and 2017-04980; Knut and Alice Wallenberg Foundation; Swedish Foundation for Strategic Research; Royal Botanic Gardens; Kew. CDB; Swedish Research Council

Handling Editor: Luis Valente

Abstract

Aim: To quantify evolutionary transitions between tropical evergreen rain forest and seasonally dry biomes, to test whether biome transitions affect lineage diversification and to examine the robustness of these results to methodological choices.

Location: The tropics.

Time period: The Cenozoic.

Major taxa studied: The plant subfamily Bombacoideae (Malvaceae).

Methods: We inferred ancestral biomes based on a fossil-dated molecular phylogeny of 103 species (59% of the clade) and recorded the number of transitions among biomes using biogeographical stochastic mapping based on the dispersal-extinction-cladogenesis model. We then estimated diversification rates using state-specific speciation and extinction rate (SSE) methods. Furthermore, we tested the sensitivity of the results to model choice, phylogenetic uncertainty, measurement error and biome definition.

Results: We found numerous transitions from evergreen rain forest to seasonally dry biomes, and fewer in the opposite direction. These results were robust to methodological choices. Biome type did not influence diversification rates, although this result was subject to uncertainty, especially related to model choice and biome definition.

Main conclusions: Our results contradict the idea of evolutionary biome conservatism in Bombacoideae, and support previous findings that evergreen rain forests serve as a source for the flora of seasonally dry biomes. The impact of biome classification and biome definition on the results suggest caution when using a biome concept for biogeographical reconstruction and diversification rate analysis.

KEYWORDS

biome connectivity, biome shift, diversification, rain forest, seasonality, seasonally dry biomes, tropical biodiversity

Christine D. Bacon and Alexandre Antonelli are senior authors on this paper

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1 | INTRODUCTION

Evolutionary transitions among biomes have been suggested as critical for the generation of plant diversity (Donoghue & Edwards, 2014). In particular, a high connectivity of biota among biomes in tropical America (the Neotropics) might have been essential for the assembly of its globally outstanding diversity (Antonelli et al., 2018; Zizka, 2019). Biomes are vegetation units defined by functionally similar plant groups and similar environmental conditions (Moncrieff, Hickler, & Higgins, 2015). Although the definition, meaning and delimitation of biomes remain controversial (Moncrieff et al., 2015; Mucina, 2019), they are often used to understand how broad-scale ecological niches change in evolutionary time (e.g. Bacon, 2013).

Generally, species tend to retain their ancestral ecological niche over time (Wiens & Donoghue, 2004). Therefore biome transitions – the shift of evolutionary lineages into new biomes – have been considered rare, especially in some biomes such as seasonally dry tropical forests (Crisp & Cook, 2012; Gagnon, Ringelberg, Bruneau, Lewis, & Hughes, 2019). Environmental dissimilarity might be a major factor limiting interchange of plant lineages among biomes (Crisp et al., 2009) and within the frost-free tropics, seasonal water availability may be particularly important constraining factor (Hughes, Pennington, & Antonelli, 2013; Olmstead, 2013).

Three major lowland tropical biomes are evergreen tropical rain forests, seasonally dry tropical forest and savanna (including tropical grass- and shrublands). Despite key differences in some ecological drivers (e.g. fire frequency), savanna and seasonally dry forest share a marked seasonality in water availability, which sets them apart from evergreen rain forest (Pennington, Lehmann, & Rowland, 2018). This raises a broader question of transitions into and out of regions with a seasonally dry climate (Pennington et al., 2018).

Previous studies give a mixed picture of the prevalence of biome transitions among seasonally dry biomes and evergreen tropical rain forests in plants. On the one hand, the phylogenetic composition of seasonally dry and rain forest sites across the tropics suggests a separation of these environments through evolutionary time (Slik et al., 2018). This could reflect that rainfall seasonality is a major determinant of the floristic composition of tropical forests (e.g. Morley, 2000), and dry climate is an important phylogenetic constraint to plant evolution for many lineages (Cássia-Silva, Freitas, Alves, Bacon, & Collevatti, 2019; Olmstead, 2013; Qian, Jin, & Ricklefs, 2017). However, transitions from evergreen rain forest to seasonally dry biomes, especially savanna, are known from plant lineages in the Neotropics (Bacon, Moraes R., Jaramillo, & Antonelli, 2017; Lohmann, Bell, Calió, & Winkworth, 2013), Africa (Estrella, Forest, Wieringa, Fougère-Danezan, & Bruneau, 2017; Monthe et al., 2019; Veranso-Libalah, Kadereit, Stone, & Couvreur, 2018), and Australia (Crisp et al., 2019) and the floristic study of Dexter et al. (2015) suggests permeability of lowland tropical biomes globally.

Evolutionary adaptations to any new biome may be difficult to evolve, but once a lineage is established, one might expect it to diversify (Moore & Donoghue, 2007), for instance, due to the release from competitors and herbivores, or adaptive radiation in the new environment. Indeed, a link between biome transitions and increased diversification has been found in some taxa such as Fabaceae (Koenen et al., 2013), Proteaceae (Onstein et al., 2016) and Malvaceae (Areces-Berazain & Ackerman, 2017), but not in others, for example, *Protea* (Valente et al., 2010). In the Neotropics, the repeated adaptation to seasonally dry habitats has been hypothesized as an important mechanism of plant diversification, in particular, in savannas (Areces-Berazain & Ackerman, 2017), and in the Paleotropics aridification and transitions to seasonally dry biomes seem to have increased diversification in some groups (Abrams et al., 2019; García-Aloy et al., 2017). Little is known for seasonally dry forests, (Dexter et al., 2015), which seem to be relatively isolated through time and space (Pennington & Hughes, 2014).

In summary, while biome transitions are an integral process in the assembly of tropical biodiversity, there is much we do not know about transitions to seasonally dry biomes and their impact on lineage diversification. Here, we quantify the number of biome transitions in the Bombacoideae, a subfamily of the Malvaceae with a centre of diversity in the Neotropics. We test two hypotheses related to the effect of biome transitions among evergreen rain forest and seasonally dry biomes on diversification.

1. Transitions from evergreen rain forests into seasonally dry biomes occur multiple times and are more common than vice-versa. We expect this because of the older age of evergreen rain forests and results from prior studies identifying savannas as lineage sinks, especially in the Neotropics (Donoghue & Edwards, 2014; Freitas, Bacon, Souza-Neto, & Collevatti, 2019; Pennington & Hughes, 2014).
2. Transitions from evergreen rain forest to seasonally dry biomes increased net diversification due to competitive release and adaptive radiation. An increased diversification after biome transitions has been documented in other lineages (Cardillo et al., 2017; Souza-Neto, Cianciaruso, & Collevatti, 2016).

2 | MATERIALS AND METHODS

2.1 | Study group

The Bombacoideae is distributed across all tropical regions, with approximately 90% of its species richness in the Neotropics, thus reflecting the general pattern of globally outstanding plant diversity in this region. Furthermore, the Bombacoideae occur in a variety of different habitats suggesting multiple biome transitions ensuring a sufficiently large sample to estimate directionality in transitions.

We followed the taxonomy of Bombacoideae by Robyns (1963) updated with recent revisions when necessary (www.tropicos.org).



org). In total, our list comprised 174 accepted species in 17 genera (Appendix S1).

2.2 | Phylogenetic reconstruction and dating

We obtained DNA sequences from two nuclear (ETS and ITS) and three chloroplast markers (*matK*, *trnS-trnG* and *trnL-trnF*) for 103 species (59% of Bombacoideae, including all genera) from Carvalho-Sobrinho et al. (2016). We aligned the sequences using MUSCLE v3.6 (Edgar, 2004) with manual adjustment (Simmons, 2004). We partitioned the nuclear data by locus to allow for variation in substitution models and analysed the chloroplast markers as a single unit separate from the nuclear genes.

We used BEAST v. 1.8.1 (Drummond, Suchard, Xie, & Rambaut, 2012) for phylogenetic inference and divergence time estimation, with an MCMC of 200 million generations, sampling every 10,000 with a burn-in of 10% chosen after checking chain convergence. We used an uncorrelated lognormal molecular clock model, a Yule pure-birth speciation model with no starting tree, the GTR + γ model of nucleotide substitution with four rate categories, and default operators. We chose an uncorrelated clock, due to the combination of chloroplast and nuclear markers. We included *Chiranthodendron pentadactylon*, *Fremontodendron californicum*, *Hampea appendiculata*, *Patinoa sphaerocarpa*, *Pentaplaris doroteae* and *Phragmotheca ecuadorensis*; as well as *Sterculia lanceolata* and *Sterculia nobilis* as more distant outgroups to root the tree. To enable dating of the clades as presented in the most recent phylogenetic revision of the Bombacoideae (Carvalho-Sobrinho et al., 2016), we constrained the monophyly of three clades: (a) *Ceiba*, (b) the clade comprising *Pseudobombax* and *Pochota*, and (c) the clade comprising *Ceiba*, *Neobuchia*, *Pochota* and *Pseudobombax* (Figure S2.1, Appendix S2).

The use of fossils allows for a minimum constraint on a clade's age, where non-uniform (e.g. exponential) prior probability densities are most often used (e.g. Warnock, Parham, Joyce, Lyson, & Donoghue, 2015). We dated the phylogeny using two fossil calibration points: (a) a macro-fossil of *Malvaciphyllum macondicus* (Wing, Herrera, Jaramillo, Gómez-Navarro, & Labandeira, 2009) at the crown node of the clade comprising Malvoideae and Bombacoideae (exponential prior, mean 0.7 and an offset of 58 mya; Carvalho, Herrera, Jaramillo, Wing, & Callejas, 2011); and (b) a flower fossil (Lima & Salard-Cheboldaeff, 1981) at the crown node of the clade comprising *Ceiba*, *Eriotheca*, *Pachira*, *Pochota*, *Pseudobombax* and *Spirotheca* (exponential prior, mean of 2.3, offset 41.3 mya, Figure S2.1 in Appendix S2).

2.3 | Geographical distribution

We compiled geographical localities of Bombacoideae from our own fieldwork and public databases (www.gbif.org, biendata.org, Gilles et al., 2016; Conservatoire et Jardin Botaniques de la Ville de Genève & South African National Biodiversity Institute Pretoria, 2017; Schmidt

et al., 2017). We used the *rgbif* package v1.1.0 (Chamberlain, 2017) in R (R Core Team, 2019) to obtain records from www.gbif.org (GBIF.org, 2018). We only included records filed as the accepted species names and used the *taxize* R-package v0.9.5 (Chamberlain & Szöcs, 2013) to resolve spelling errors in the species names. We merged sub-specific ranks under the accepted species name, and restricted species' occurrences to the native species range on a regional level based on our field experience and the literature. We retained only one record per species per site and cleaned occurrence records geographically using the *CoordinateCleaner* R-package v2.0-7 (Zizka et al., 2019). To visualize the global species richness of Bombacoideae, we generated species ranges from the occurrence records using geospheric convex hulls clipped to coastlines using the *CalcRange* function of the *speciesgeocodeR* R-package v2.0-10 (Töpel et al., 2017), using a 50km buffer for species with less than 3 occurrences.

2.4 | Biome classification

Based on the occurrence records and a widely used global biome definition (Olson et al., 2001), we classified species as: evergreen rain forest present in 'Tropical and subtropical moist broadleaf forests'; seasonally dry forest present in 'Tropical and subtropical dry broadleaf forests' or 'Deserts and xeric shrublands'; or savanna present in 'Tropical and subtropical grasslands, savanna and shrubland'. To account for outlier individuals and imprecision in geographical coordinates, we counted a species as present in a biome, if at least 5% of its records occurred there. We treated seasonally dry forest and savanna differently for the ancestral state reconstruction, because they differ in their ecology (Pennington et al., 2018, i.e. the presence of fire) and because they might differ in their affinities with evergreen rain forest. However, since we were interested in transitions among evergreen rain forest and seasonally dry biomes we combined these two biomes as seasonally dry biomes (SDB) for the estimation of diversification rates. We justify this with the potential importance of rainfall seasonality in the diversification of flowering plants (Areces-Berazain & Ackerman, 2017) and because Bombacoideae are often used as indicator species of evergreen rain forest in the fossil record (Morley, 2000). Furthermore, a more fine-scale biome classification would lead to reduced statistical power and classification accuracy of species to biomes (Silva de Miranda et al., 2018).

2.5 | Ancestral biome estimation

We used biogeographical stochastic mapping based on the dispersal-cladogenesis-extinction model (DEC) as implemented in BioGeoBEARS v1.1.2 (Dupin et al., 2017; Matzke, 2016) to reconstruct ancestral biomes on the phylogeny. Because there is good evidence for an older age of evergreen forests as compared to savanna and seasonally dry tropical forest, as well as fossil evidence that the Bombacoideae are ancestrally a rain forest group (Wing et al., 2009), we used a time-stratified model together with an

areas-allowed-matrix, and limited the group to evergreen rain forest before the Miocene (23.03 mya). We used 1,000 stochastic replicates on the maximum clade credibility tree from the BEAST analysis. To quantify the number of biome transitions (Hypothesis 1), we counted the number of transitions from evergreen rain forest into either seasonally dry biomes and vice versa, inferred by the biogeographical stochastic mapping.

2.6 | Diversification rate estimation

We used the GeoHiSSE model (Caetano, O'Meara, & Beaulieu, 2018) as implemented in the `GeoHiSSE` function of the `hisse` v.1.9.6 R-package (Beaulieu & O'Meara, 2016), to estimate state-specific diversification and extinction rates from the phylogeny, and hence the impact of biomes on diversification (Hypothesis 2). GeoHiSSE estimates speciation and extinction rates dependent on geographical trait states, as well as transition rates among states while allowing for widespread ancestors and taking sampling frequencies into account. We chose GeoHiSSE above other SSE methods, since it (a) can account for widespread species, (b) can include 'concealed traits' and therefore is less prone to false positives (Caetano et al., 2018), and (c) has a limited number of parameters suited for our moderate-sized phylogeny. To account for incomplete phylogenetic sampling, we calculated the fraction of evergreen rain forest and seasonally dry biome species sampled in the phylogeny from the total number of Bombacoideae species and included this information using the `sampling.f` argument of the `GeoHiSSE` function ($f_{EFB} = 0.438$, $f_{SDB} = 0.938$, $f_{widespread} = 0.767$).

To test the effect of biome state on diversification rate, we fitted five different models to the maximum clade credibility phylogeny, and compared their fit using the Akaike Information Criterion corrected for small sampling size (AICc): (a) a null model with no concealed trait and all rates equal, (b) a model with no concealed trait and all speciation and extirpation rates equal, but different transition rates, (c) a canonical GeoSSE model with no concealed traits, but different speciation, extirpation and transition rates, (d) a GeoHiSSE model with one concealed trait, equal speciation and extirpation rates but different transition rates, and (e) a full GeoHiSSE model with one concealed trait and different speciation, extirpation and transition rates.

2.7 | Reliability of the results

We tested the sensitivity of our conclusions to four potential caveats and sources of uncertainty.

1. Model choice. Model choice can affect the ancestral biome reconstruction and diversification rate estimates (Davis, Midford, & Maddison, 2013; Herrera-Alsina, Els, & Etienne, 2019). To test its effect on ancestral biome reconstruction, we reconstructed ancestral biomes using stochastic character mapping and the

model-averaged marginal reconstructions from the GeoHiSSE models which we used to estimate diversification rates. To test the effect of model choice on diversification rate estimates, we ran analyses using the BiSSE (Maddison, Midford, & Otto, 2007), HiSSE (Beaulieu & O'Meara, 2016) and FiSSE (Rabosky & Goldberg, 2017) models.

2. Phylogenetic uncertainty. Phylogenetic relationships are never known with certainty, especially in groups undergoing rapid radiations. To test the effect of phylogenetic uncertainty we ran analyses, reconstructing ancestral biomes and estimating state-dependent diversification rates on 100 randomly sampled phylogenies from the posterior distribution of the phylogenetic reconstruction, using the same biome classification and model as for the main analyses.
3. Measurement error/biome classification. Assigning species to biomes is challenging, because it is unclear when a species should be considered as present in a biome (is one record sufficient?) and because of the low precision of biome delimitations, the uncertainty of geographical coordinates and interdigitation of biomes (e.g. gallery forests (rain forest) within savanna). To test the impact of these issues, we repeated the ancestral biome reconstruction and the diversification rate estimation across 100 stochastic replicates. For each replicate, we classified the recent species (the tips of the phylogeny) into biomes based on the fraction of collection records assigned to each biome, and otherwise used the same specifications as for the main analysis ('record-based' biome classification hereafter).
4. Biome definition. To evaluate the sensitivity of our conclusions to alternative biome definitions, we repeated the ancestral biome estimation and the diversification rate estimation using: (a) a biome definition based on remote sensing of phenology and leaf area index (Buitenwerf & Higgins, 2016, 'phenology-based' hereafter), where we considered species as occupying the evergreen rain forest biome if they occurred in pixels classified as the 'Evergreen high leaf area index biome' or 'Mixed' and as occupying seasonally dry biomes if they occurred in 'Deciduous' pixels, and (b) a classification based on our own experience in the field ('expert-based' hereafter). See Appendix S1 for the expert-based classification and Figures S2.2 and S2.3 in Appendix S2 for a map of the ecoregion-based and phenology-based definitions.

See Appendix S4 for more detail on the tests related to the ancestral biome reconstruction and Appendix S5 for more detail on the tests related to diversification rate estimation.

3 | RESULTS

3.1 | Temporal evolution and recent biogeography

We inferred the root age of the Bombacoideae between 53.5 and 59.3 mya (Ma), close to the fossil constraint for the crown node of Bombacoideae + Malvoideae (58 Ma). Most branches in the

reconstructed phylogeny were well supported, with some exceptions in *Ceiba*, *Eriotheca* and *Pachira* (Figure S2.3 in Appendix S2). The results suggested recent radiations (in the last 2.6 Ma) within *Ceiba* (including *C. crispiflora*, *C. erianthos*, *C. glaziovii*, *C. pubiflora*, *C. rubriflora*, *C. speciosa* and *C. ventricosa* and *Pseudobombax* (including *P. longiflorum*, *P. campestre*, *P. majus* and *P. petropolitanum*).

We found 14,865 high-quality occurrence records for 172 species (98% of the Bombacoideae; max. 3,062 records for *C. pentandra*; median of 19 per species; Figure S2.4, Appendix S2 for geographical sampling intensity; Appendix S3 for species range maps). The range maps confirmed Amazonia and the Atlantic forest as centres of Bombacoideae diversity (Figure 1).

We found the majority of species to be evergreen rain forest biome (EFB) specialists (73, 42% all species with occurrence information) or generalists occurring in the EFB and seasonally dry biomes (SDB, 73 species). Some genera were enriched in rain forest specialists: *Catostemma* (12/71% of the genus), *Scleronema* (4/67%) and *Pachira* (25/56%). *Ceiba* (14/73%) was especially enriched in generalists. Fewer species were specialists in SDB (16/9%), especially *Adansonia* (4/50%) and *Pseudobombax* (5/20%). The results were dependent on the biome classification and definition. The proportion of specialists increased when using the *record-based* biome classification (generalist: 6%; EFB: 58%; SDB: 22%), and the *expert-based* biome definition (generalist: 2%; EFB: 49%; SDB: 50%, Table 1).

3.2 | Ancestral biome reconstruction and biome transitions

Biome transitions occurred multiple times in different groups of Bombacoideae (Figure 2), for instance, *Eriotheca*, *Ceiba* and *Pseudobombax*. The 95% quantile of recorded transitions from

EFB to SDB ranged from 38–52 (mean 46) and 11–25 transitions from SDB to EFB (mean = 18; Table 1). The findings of multiple transitions between EFB and SDB, and more transitions from SDB to EFB were consistent across all uncertainty tests (Table 1, Appendix S4).

We found transitions towards SDB shortly after they were allowed in the model, in the early Miocene, with shifts to seasonally dry forest beginning slightly earlier (17.3–23.0 Ma) than to savanna (15.3–23.0 Ma). The first shifts back to EFB occurred later (2.5–17.4 Ma). The timing of the first transitions to SDB in the early Miocene were consistent across phylogenetic and biome classification uncertainty as well as biome definitions (Table 1). Alternative ancestral biome reconstructions using different methodology do not exclude transitions to SDB specialists already in the early Miocene, but suggests most transitions during the Late Miocene.

3.3 | Diversification rate analyses

We found no significant effect of biome state on the diversification rates. The best-fitting GeoHiSSE model had no trait-dependent speciation, unequal transition rates and one concealed trait. The lack of significant difference in diversification rates between EFB and SDB in the Bombacoideae was robust to phylogenetic uncertainty and biome classification (Table 2). However, this conclusion was sensitive to (a) model choice (HiSSE suggested higher diversification rates in SDB, whereas FiSSE rejected state-dependent diversification), (b) phylogenetic uncertainty (only 65% of the replicates agreed on the same model), and (c) biome definition (the *phenology-based* definition suggested higher rates in EFB whereas the *expert-based* definition suggested higher rates in SDB).

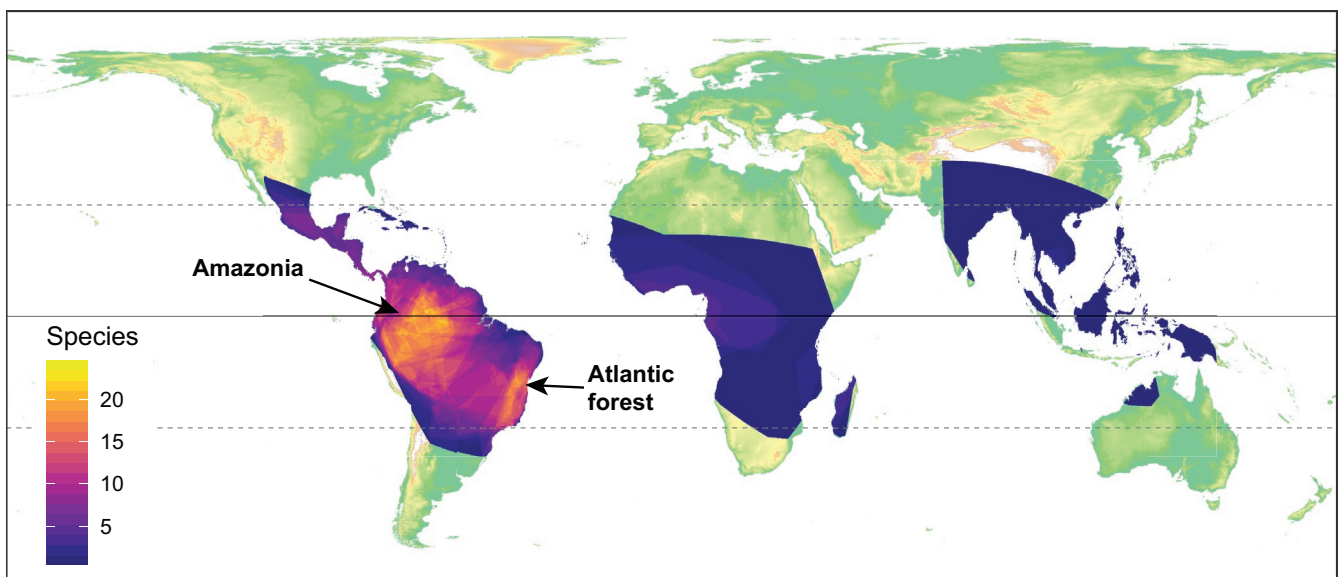


FIGURE 1 Global distribution and species richness of the Bombacoideae. The map is in Behrmann projection and produced by the overlay of species range maps estimated from point occurrence data using convex hull polygons. The centre of diversity is in tropical America, especially in Amazonia and the Atlantic forest in Coastal Brazil

TABLE 1 Biome transitions in Bombacoideae among evergreen rain forest (EFB) and seasonally dry biomes (SDB), the latter including seasonally dry forest (SDF) and savanna (SAV)

Index	Main analysis	Phylogenetic uncertainty	Measurement error	Biome definition	
				Phenology	Expert
EFB specialists	73	73	99.9	43	50
SAV specialists	2	2	14.4	NA	15
SDF specialists	9	9	20.4	NA	35
SDB specialists (SAV or SDF)	16	16	36.8	21	52
Generalist species (SDB \ EFB)	73	73	11.6	98	2
Total number of transitions	80–89 (84.1)	79–88 (83.3)	34–48 (40.6)	61–69 (64.7)	20–25 (22.5)
Transitions to EFB	11–25 (18.0)	8–23 (15.4)	3–11 (6.82)	NA	1–5 (2.9)
Transitions to SDF	30–42 (35.9)	31–44 (37.5)	13–23 (17.8)	NA	7–12 (9.2)
Transitions to SAV	26–34 (30.2)	26–34 (30.4)	12–20 (16.3)	NA	9–13 (10.4)
EFB → SDB	38–52 (45.6)	40–55 (47.5)	16–28 (21.9)	38–53 (46.5)	9–15 (11.6)
SDB → EFB	11–25 (18.0)	8–23 (15.2)	2–11 (6.57)	10–27 (18.2)	1–5 (2.8)

Note: The columns represent different analyses to test the effect of different types of uncertainty. Main analysis: A reconstruction of ancestral biomes using biogeographic stochastic mapping based on a DEC model. Phylogenetic uncertainty: 100 replicates of the main analyses using randomly sampled phylogenetic trees from the posterior distribution of the phylogenetic reconstruction. Biome classification: 100 replicates with stochastic assignment of tips to biomes based on the number of occurrence records available. Biome definition: replications of the main analysis using two alternative biome definitions based on remote sensing (Phenology) or expert knowledge of the study species (Expert).

All analyses suggested unequal transition rates between EFB and SDB. However, the direction and strength of the difference varied strongly with all methodological choices (Table 2). While our main analyses, and the additional HiSSE analyses suggested higher transition rates from SDB to EFB, the direction was reversed when using a *phenology-based* biome definition. For phylogenetic uncertainty and biome classification, the direction was variable and the absolute diversification and transition rates varied by orders of magnitude among the individual replicates (Figure S5.10 in Appendix S5).

4 | DISCUSSION

Here, we tested hypotheses on the role of biome transitions in the evolutionary of the tropical plant group Bombacoideae. We found support for multiple independent transitions among the evergreen rain forest (EFB) and seasonally dry biomes (SDB) and more transitions from EFB to SDB than vice-versa (Hypothesis 1). We rejected the hypothesis that biomes differ in net diversification (Hypothesis 2).

4.1 | Temporal evolution

The root-age of Bombacoideae is consistent with the dating of its sister Malvoideae to the late Cretaceous (Areces-Berzain & Ackerman, 2017). Furthermore, a Paleocene or earlier origin of the Malvaceae (Bombacoideae + Malvoideae) and the Bombacoideae clade, as we inferred, is supported by fossils of those groups in North America

and South America at least since the Paleocene (Carvalho et al., 2011) and possibly much earlier (Vega, García-Barrera, Perrilliat, & C., Coutiño, M. A., & Mariño-Pérez, R., 2006). However, there is uncertainty on the placement of some fossils (either within Bombacoideae or within the former Bombacaceae, a broader group including some lineages now considered Malvoideae). Furthermore, our use of exponential priors on the two macrofossil calibrations constrained by the age of the strata they were derived from implies high confidence in their age, which seems justified in this case because the fossil specimens are well-preserved and present clear morphological synapomorphies allowing for their assignment to a specific nodes on the phylogeny. Additionally, the stratum the Malvaciphyllum fossil is derived from is temporally well-defined (Wing et al., 2009). Using less informative priors, at least with respect to maximum age, would likely shift divergences in the group to somewhat older ages.

The Bombacoideae have a relatively rich fossil record compared to other plant groups, especially for pollen (Jaramillo, Rueda, & Torres, 2011). Unfortunately, it is generally difficult to place pollen fossils in relation to recent taxa, due to high homoplasy in Malvaceae pollen morphology (Saba, 2007), making the full integration of fossil and molecular data challenging. However, our results on the number and direction of biome shifts should be robust to uncertainties in phylogenetic dating.

4.2 | Biome transitions

Our findings suggest caution using Bombacoideae fossils as indicators of past evergreen rain forests (e.g. Morley, 2000; Pross et al., 2012), unless these fossils have biome-specific traits. The number

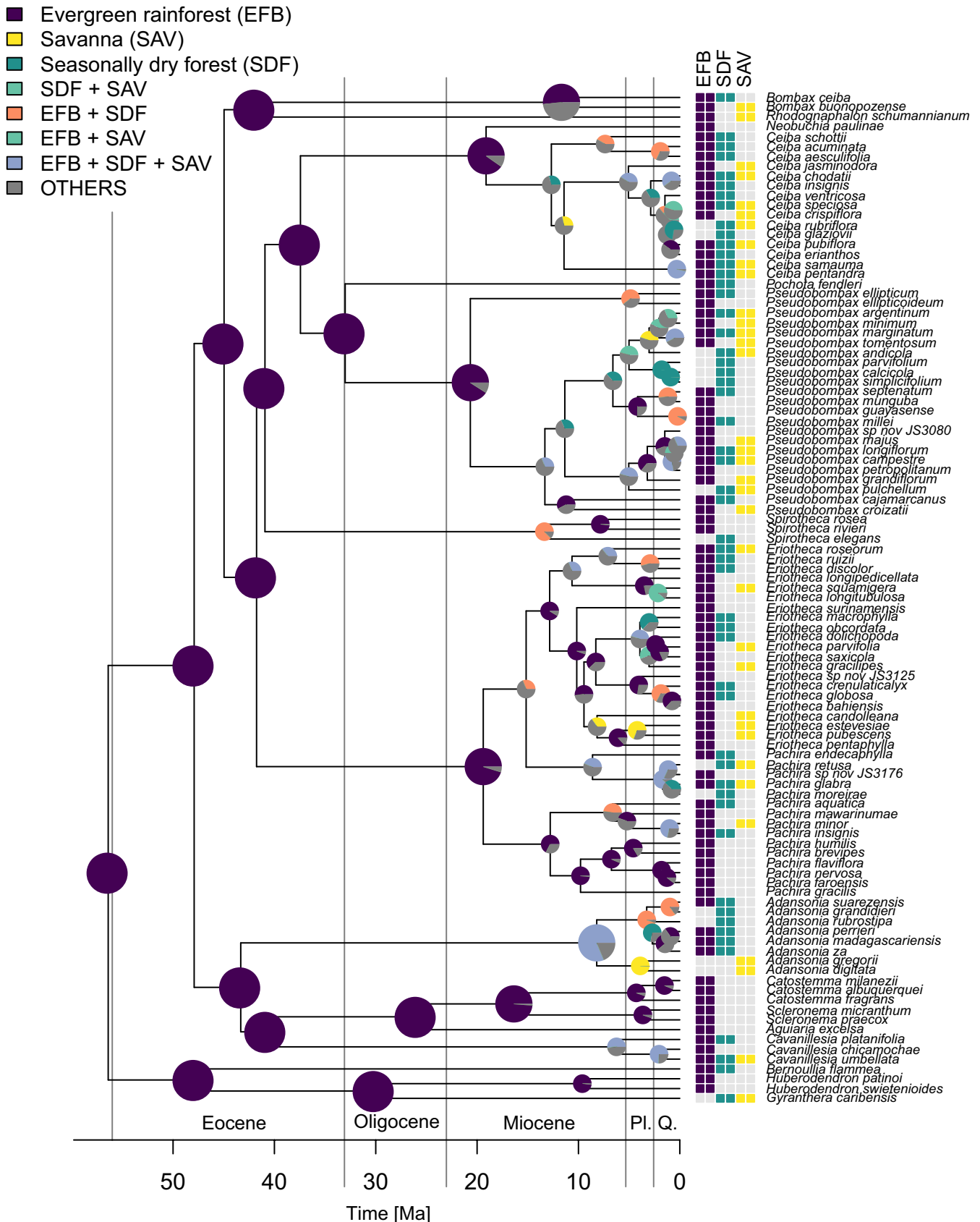


FIGURE 2 Biome evolution in Bombacoideae. The evergreen rain forest is represented in purple, seasonally dry forest ('Seasonally dry tropical and subtropical forest' and 'Deserts and Xeric Shrublands', Olson et al., 2001) in blue and savanna in yellow. Dispersals into seasonally dry forest and savanna were allowed from the beginning of the Miocene onward based on fossil information. There are multiple independent transitions into seasonally dry biomes, especially in the last 10 million years

TABLE 2 Evolutionary transition and diversification rates among evergreen rain forest (EFB) and seasonally dry biomes (SDB), the latter including seasonally dry tropical forest (SDF) and savanna (SAV) in Bombacoideae

Index	Main analysis (GeoHiSSE)		Model choice		Phylogenetic uncertainty		Biome definition	
	FISSE	HiSSE	FISSE	HiSSE	Measurement error	Phenology	Expert	
EFB specialists	73	115	115	73	99.5	43	48	
SDB specialists (SAV or SDF)	28	59	59	28	38.5	21	55	
Generalist species (SDB \ EFB)	73	NA	NA	73	36.0	98	71	
Preferred model	equal diversification, unequal transitions, concealed trait	trait-dependent diversification, unequal transitions, no concealed trait	equal diversification	equal diversification, unequal transition, concealed trait (65%)	equal diversification, unequal transition, concealed trait (94%)	trait-dependent diversification, unequal transition, no concealed trait	trait-dependent diversification, unequal transitions, no concealed trait	
Diversification	equal	SDB > EFB	equal	equal	equal	EFB > SDB	SDB > EFB	
Transitions	EFB → generalist < SDB → generalist	EFB → SDB < SDB → EFB	NA	variable	variable	EFB → generalist > SDB → generalist	dependent on concealed trait	
Concealed trait	yes	no	NA	yes	yes	no	yes	

Note: The Table shows the results of various state-specific speciation and extinction models, and the impact of different uncertainties on the analysis. See text for details.

of biome transitions among EFB and SDB are high, at least at the large scale (Figure 2, Table 1), especially compared to other similar-sized groups (Cardillo et al., 2017; Estrella et al., 2017), which is likely partly due to how we chose to account for widespread species and to our use of biogeographical stochastic mapping, which reconstructs anagenetic events along branches, rather than just counting shifts observed at nodes (which represent the minimum number of shifts).

Our results from the biogeographical stochastic mapping suggest more transitions towards seasonally dry biomes than the reverse. This fits with expectations based on the age of the biomes and observations from other lineages (Pennington & Hughes, 2014; Simon & Pennington, 2012). The evergreen rain forests of Amazonia – one of the diversity centres of Bombacoideae – have been suggested as a regional and global species source, ‘pumping lineages’ into other biomes (Antonelli et al., 2018, 2015). Cases in which specific lineages have shown asymmetry in the direction of biome transitions have been suggested to indicate the presence of enabler traits that facilitate biome transitions and the establishment in a new biome (Donoghue & Edwards, 2014). Thus, an interesting question is what enabler traits preadapt Bombacoideae to seasonally dry environments. A candidate is parenchymatous wood that can readily yield the succulent stem habit typical of seasonally dry tropical forests. Further possible candidates are large fruit and seeds, and high dispersal capacity.

Model choice partly affected the ancestral biome reconstruction, with GeoHiSSE suggesting the majority of lineages as generalist rather than rain forest specialist (Figure S4.6 in Appendix S4). This seems unlikely and might be due to the unconstrained treatment of time and biome age. The inferred importance of generalist species likely also relates to the finding of a higher transition rate from SDB to EFB suggested by the main GeoHiSSE analysis. In general, the qualitative conclusions based on the ancestral biome reconstruction using biogeographical stochastic mapping were robust to uncertainty in phylogenetic reconstruction, biome classification and biome definition. However, the number of reconstructed transitions was sensitive to biome classification and definition, and the total number of transitions was considerably lower when using a record-based biome-classification or expert-based biome definition. This change in absolute number likely reflects the lower number of recent generalist species scored by these schemes: both methods tend to favour species' classifications as specialists. In the case of the record-based biome classification, most species predominantly occur in one biome, and in the case of the expert-based biome definition, this might be caused by a focus on micro-habitat in the site classification (for instance slope and local moisture availability).

Each biome definition has advantages and challenges, but biome classifications based on spatially explicit biome definitions (the *ecoregion* and *phenology*-based definitions in our case) and specimen data are more reproducible, less influenced by researcher biases, and better suited to computational investigations of uncertainty in downstream analyses, than *expert-based*



approaches. Importantly, the different results for the absolute number of biome transitions and the diversification rates we observed with the *expert-based* classification call for further exploration of how biome delimitation and identification might influence our understanding of actual transitions in habitats and highlight the need for caution when interpreting quantitative results of biome transition analyses.

4.3 | Biomes and diversification

We did not find a significant relation between diversification rate and biome type, rejecting the hypothesis that biome transitions into seasonally dry biomes are a driver of increased diversification, although this finding is subject to uncertainty. This could reflect a lack of statistical power or indicate that other factors besides the adaptation leading to evolutionary radiations in seasonally dry conditions are the main drivers of diversification in Bombacoideae, contrasting with results from other Malvaceae (Areces-Berzain & Ackerman, 2017). Other potential drivers of diversification in Bombacoideae include plant-pollinator interactions, fruit/seed evolution and changes in ploidy level (Carvalho-Sobrinho et al., 2016; Costa, Oliveira, Carvalho-Sobrinho, & Souza, 2017).

The transition and diversification rate analyses were sensitive to all types of tested uncertainty. This was partly expected due to the different specifications of the models (especially if they account for generalist species) and the resulting changes in the classification of tip trait states, as well as the relatively small size of our phylogeny (Davis et al., 2013). However, these results were also surprising, especially concerning sensitivity to model choice on the qualitative conclusions (Table S5.2, Appendix S5) as well as the effect of phylogenetic uncertainty and biome classification on the estimated rates (Figure S5.10, Appendix S5). Reasons for the sensitivity of the diversification rate analyses to model choice and uncertainty deserve more study, but the results indicate that we currently lack evidence that biome alters diversification rate in Bombacoideae.

5 | CONCLUSIONS

We show that evergreen rain forest – seasonally dry biome transitions are common in Bombacoideae, especially within the Neotropics. These findings are robust to methodological choices and support the view that the evergreen rain forest-seasonally dry biome boundary is permeable for this plant lineage on evolutionary time scales. Furthermore, this permeability is directional with transitions from evergreen rain forest to seasonally dry biomes being more common than the reverse.

Our results also demonstrate that model choice as well as different biome classifications and biome definitions can lead to qualitatively different conclusions, stressing the importance of carefully selecting a biome-scoring scheme that is suitable for the question

at hand and testing its sensitive to methodological choices and assumptions.

DATA ACCESSIBILITY STATEMENT

A species list is available in the Supporting material (Appendix S1). The DNA alignments, the shapefiles of species ranges and all analyses scripts with input data are available from zenodo (<https://zenodo.org/record/2634308#.Xku300p7mHt>)

ACKNOWLEDGEMENTS


We thank two anonymous reviewers and the subject editor for helpful comments on the manuscript. We thank Francisco Velasquez for preliminary analyses and discussion of the results, Søren Faurby for help with analyses in an earlier version of the manuscript and Ivana Kirchmair for helpful comments on the manuscript. We thank C. Chatelain for sharing occurrence data from the Africa plant database, Jan Wieringa for sharing records from WAG and all data contributors to GBIF and species link for their effort in collecting, digitizing, and providing specimens used in this study. AZ is thankful for funding by iDiv via the German Research Foundation (DFG FZT 118), specifically through sDiv, the Synthesis Centre of iDiv. AA is supported by grants from the Swedish Research Council, the Knut and Alice Wallenberg Foundation, the Swedish Foundation for Strategic Research and the Royal Botanic Gardens, Kew. CDB acknowledges funding from the Swedish Research Council (2017-04980).

AUTHOR CONTRIBUTIONS

AZ and CDB designed the study with contribution from all authors. JCS and AZ gathered the data. JCS provided the field-based biome classification. CDB reconstructed and dated the phylogeny, AZ analysed the data, and all authors interpreted the results. AZ wrote the manuscript with contributions from all authors.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Zizka A, Carvalho-Sobrinho JG, Toby Pennington R, et al. Transitions between biomes are common and directional in Bombacoideae (Malvaceae). *J Biogeogr.* 2020;00:1–12. <https://doi.org/10.1111/jbi.13815>