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1 **Andean orogeny and the diversification of lowland neotropical rain forest trees:**
2 **a case study in Sapotaceae.**

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31 **ABSTRACT**

32 Understanding how species diversify and evolve in biodiversity hotspots like the
33 lowland rain forest in the Neotropics is critical for conservation in times of
34 unprecedented threats. To determine how the Andean uplift, the formation of the
35 Panama land bridge, and Pleistocene climatic fluctuations affected dispersal and
36 diversification, in the subfamily Chrysophylloideae, we generated a dated phylogeny
37 of 123 Sapotaceae species and inferred diversification rates. Sapotaceae is a good
38 model to test biogeographic hypotheses in the lowland rain forests as it predominantly
39 occurs <1000m altitude, and it is an abundant and diverse group in this biome. A total
40 of 146 Chrysophylloideae accessions were collected in previously under-explored
41 areas, generating one of the most complete data sets in terms of geographic sampling
42 for neotropical Sapotaceae. Our results suggest that migration between lineages to the
43 east and the west of the Andes' Eastern Cordillera, occurred before and after periods
44 of major uplift, indicating that the Andes did not represent a significant barrier to
45 dispersal for Sapotaceae, although it may have promoted vicariance in some cases.
46 Dispersal between South and Central America occurred mainly prior to the formation
47 of the Panama land bridge, suggesting that this event did not affect migration patterns
48 in Chrysophylloideae. We detected three shifts in diversification rates in the
49 phylogeny, however they do not occur at times indicating that Andean uplift during
50 the middle Miocene and climatic changes during the Pleistocene affected
51 diversification in Chrysophylloideae. Finally, some species with restricted
52 distributions appear to be phylogenetically nested within species with broader ranges,
53 thus our data provide insights into patterns of speciation in rain forest trees. Our study
54 improves our understanding of the effects of mountain barriers and climatic changes

55 on the origins of plant diversity, and provides crucial data from areas excluded from
56 previous biogeographic studies in the Neotropics.

57 **Keywords:** Andes, diversification, Neotropics, Panama land bridge, Pleistocene,
58 Sapotaceae, rain forest.

59

60 INTRODUCTION

61 The lowland rain forest biome in northern South America hosts some of the most
62 species-rich floras in the world, and it is represented by the forests in the
63 biogeographic units of Chocó, Amazon, Catatumbo, and Guiana. These forests are
64 separated from one another by three branches of the Andean mountain range (Fig. 1),
65 and are suggested to have been formed by distinct ecological and evolutionary
66 processes (Hernández-Camacho et al., 1992; Morrone, 2001; Bernal et al., 2016; Lasso
67 et al., 2018, Pérez-Escobar et al., 2019). These areas are considered of great
68 conservation and economic value (Bernal et al., 2016), and to aid conservation in times
69 of unprecedented threats, it is critical to understand how their species diversity is
70 distributed and has evolved. However, due to decades of civil conflict in countries like
71 Colombia and lack of safe access to these areas, samples from these forests have not
72 been included in previous studies, and consequently the patterns and processes driving
73 the distribution of this vegetation are still unclear.

74 Previous work suggests that dispersal and diversification patterns of plant species in
75 the Neotropics have been affected by the uplift of the Andes e.g. *Crematoperma* (Pirie
76 et al., 2006), *Dussia* (Winterton et al., 2014), Orchids (Pérez-Escobar et al., 2017),
77 palms (Bacon et al., 2018), Malvaceae (Richardson et al. 2015; Hoorn et al., 2019),

78 *Begonia* (Moonlight et al., 2018) and multiple paramo lineages (Madriñán et al 2013).
79 The Andean orogeny occurred in well differentiated phases (Gregory-Wodzicki, 2000;
80 Mora et al., 2010), but it was generally initiated by major tectonic movements during
81 the late Oligocene after the break-up of the Farallones plate, and the subsequent
82 increment in convergence rates at the margins of the newly created Cocos and Nazca
83 plates (Hoorn et al., 1995; Wortel, 1984). The northern part of the Andes now divides
84 into the Eastern, Central and Western Cordilleras (Fig. 1). The Eastern Cordillera was
85 formed as a continuous range in the middle Miocene (Winship, 1990; Hoorn et al.,
86 1995; Albert et al., 2006), although the easternmost part (the Merida Andes) might not
87 have reached 3000 m elevation until *ca.* 5–2 Ma, achieving their current *ca.* 5000 m
88 elevation even later (Kroonenberg, 1990). The Central Cordillera reached its current
89 altitude during the late Miocene at *ca.* 10–4 Ma (Kroonenberg, 1990), creating
90 altitudinal belts that at their lower points formed the Magdalena and Cauca valleys.
91 This orogeny was partially contemporary to the accretion of the Western Cordillera, a
92 process that initiated during the Oligocene and early Miocene, and caused the creation
93 of high-altitude habitats, above *ca.* 4000 m, during the late Miocene (Kroonenberg,
94 1990; Graham, 2011). These uplifts are presumed to have had a significant impact on
95 biogeographic patterns, especially as a physical barrier to dispersal of lowland
96 restricted organisms (Pirie et al., 2006; Pennington et al., 2010). The Eastern Cordillera
97 might have had the most profound effect as a barrier, because it reaches northern
98 coastal areas, whereas the other cordilleras do not and hence could be circumvented at
99 their northern ends (Fig 1).

100 Miocene tectonic activity also generated the Panama Land Bridge (Hoorn et al., 1995;
101 Farris et al., 2012), and together with the Andean orogeny redirected the Amazon and

102 Orinoco rivers, which had previously emptied together into the Maracaibo basin near
103 the northern tip of South America (Hoorn et al., 1995; Díaz de Gamero, 1996; Hoorn
104 et al., 2010). The formation of the Panama Isthmus was followed by climatic changes
105 during the Pleistocene with cold dry climates during glacial periods alternating with
106 warm wet periods during interglacials.

107 All of these events may have altered the paleogeography or climate in northern South
108 America, creating novel habitats, while opening or closing migration routes (Hoorn et
109 al., 1995; 2010). Habitat fragmentation would hence have occurred at varying scales,
110 from the large scale separation of the previously continuous lowland rain forests now
111 separated in the Amazon, the inter-Andean valleys, and Chocó, to more local effects
112 such as range changes during Pleistocene climatic fluctuations, and the development
113 of drier climatic zones in inter-Andean valleys (Haffer, 1969; Prance, 1973;
114 Richardson et al., 2001 but see Colinvaux et al., 2001; Pennington & Dick, 2004;
115 Whinnett et al., 2005). These events may have influenced species diversification, but
116 knowledge of how these factors affected the evolutionary history of the lowland rain
117 forest of northern South America is far from complete.

118 Sapotaceae is a pantropical family of trees mainly restricted to lowland tropical rain
119 forest, thought to have first diversified in Asia at *ca.* 67.1–105 Ma (Richardson et al.,
120 2014). It comprises three subfamilies (Pennington, 1991; Faria et al., 2017), among
121 which Chrysophylloideae is the most abundant in the Neotropics. This subfamily
122 originated in Africa, with crown divergence occurring around 78 Ma, then reaching
123 the Americas, perhaps via long distance trans-oceanic dispersal in the late Cretaceous
124 (Bartish et al., 2011). The subfamily has since become widespread and diverse in

125 northern South America, where it is distributed almost exclusively in lowland rain
126 forest. This restricted distribution makes it a perfect model for studying the effects of
127 various geological and climatic processes on evolution and speciation within South
128 American lowland rain forests.

129 This study aims to explore the dispersal and diversification history of
130 Chrysophylloideae, and relate it to the geographical and climatic changes discussed
131 above (Fig. 2). To achieve this, species of Chrysophylloideae were sampled from
132 previously unexplored areas of lowland rain forests. Here we present the first data set
133 for neotropical Sapotaceae that includes collections from major areas of lowland rain
134 forest on both sides of the Andes and the inter-Andean valleys. A dated phylogeny
135 based on ITS sequences was constructed and used along with diversification rates
136 analyses to test these hypotheses. We hypothesize signatures of diversification,
137 vicariance or migration caused by different geological or climatic events:

138 (i) if phylogenetic splits were caused by the uplift of the Eastern Cordillera of the
139 Andes, creating habitats too high for the family and causing vicariance (Fig 2), then
140 splits would have increased after *ca.* 12 Ma when this mountain range reached an
141 elevation higher than about 2000 m (upper altitudinal limit of Sapotaceae's range).

142 (ii) if the formation of the Isthmus of Panama created a terrestrial migration route for
143 taxa previously unable to disperse across water, then evidence for migration between
144 South and Central America would be found mainly after the uplift of the Panamanian
145 land bridge at *ca.* 13–15 Ma, although the land bridge formation is thought by some to
146 have occurred much later (Coates & Obando, 1996).

147 (iii) if the uplift of the Andes affected diversification rates in Chrysophylloideae, then
148 shifts in diversification rates would be found after the middle Miocene and during
149 periods of major tectonic activity in northern South America.

150 (iv) if periodic range contractions during the Pleistocene led to diversification, then
151 increased diversification rates would be found in this epoch.

152 **MATERIALS AND METHODS**

153 A total of 146 Chrysophylloideae accessions were collected in the previously under-
154 explored Chocó, Magdalena Valley, Catatumbo, Amazon and Macarena lowland rain
155 forests of Colombia, generating one of the most complete data sets in terms of
156 geographic sampling for neotropical Sapotaceae. Internal transcribed spacers of rDNA
157 (ITS) sequence data was produced for the new collections. The remaining sequences
158 were obtained from previous phylogenetic studies on Chrysophylloideae (Swenson et
159 al., 2008; Gonzalez et al., 2009) and GenBank. We chose to focus our study on ITS
160 data because it was the more variable marker (e.g. Armstrong et al 2014), and the large
161 amount of plastid data required to get a similar number of informative characters was
162 beyond the scope of the present study. The full data set contains 400 accessions, with
163 378 individuals of neotropical Chrysophylloideae, and 22 from paleotropical
164 Sapotaceae. Our data set represents 101 Chrysophylloideae species, 100% of the
165 currently recognised neotropical genera, and 30% of the currently recognised species,
166 including 71% of the known species in Colombia. A list of taxa and voucher specimen
167 information is shown in Appendix 1.

168 **DNA isolation, amplification and sequencing**

169 Leaf tissue from fresh silica-gel-dried collections was ground into a powder. Total
170 DNA was isolated with the DNeasy® Plant Mini Kit (QIAGEN) following the
171 manufacturer's procedures. The nuclear ITS region was amplified using primer pairs
172 ITS5 and ITS8. PCR reactions were carried out in 20µL volume reactions, by adding
173 2µl of dNTPs, 2 µl of 10x NH4 reaction buffer, 0.6 µl of MgCl₂, 1.5 µl of each primer
174 (10µM), 4µl of CES, 0.3µl of Biotaq DNA polymerase buffer, 7.1 µl double distilled
175 H₂O (ddH₂O) and 1µl of DNA. The thermal cycling profile was: 3 minutes at 94°C
176 (denaturing) followed by 29 cycles of 1 minute at 94°C (denaturation), 1 minute at
177 55°C (annealing) and 1.5 minutes at 72°C (extension), and an additional termination
178 step of 5 minutes at 72°C. The amplified fragments were electrophoresed on a 1%
179 agarose gel to check for quantity. PCR products were then purified with ExoSAP-IT®
180 (USB Corporation) which was added directly and incubated at 37°C for 15 minutes
181 followed by 80°C for 15 minutes. PCR templates were used for the cycle-sequencing
182 reactions using BigDye® Terminator v3.1 Cycle Sequencing Kit (Applied Biosystems,
183 Inc.) and then were run on an ABI PRISM 310 sequencer (Applied Biosystems, Inc.).
184 One of the samples in this study (*Chrysophyllum colombianum*) had two bands on the
185 PCR gel. These were excised and sequenced separately (*C. colombianum* a and b). We
186 detected no other examples of multiple copies of ITS in the samples used in this study.

187 **Sequence alignment and phylogenetic analysis**

188 DNA sequences were assembled and edited using Geneious 10.1.2 (Kearse et al.,
189 2012), automatically aligned using MUSCLE and edited manually with BioEdit (Hall,
190 1999). *Sarcosperma laurinum* was used as the outgroup in all analyses as it has been
191 shown to be the sister to all other Sapotaceae (Anderberg & Swenson, 2003).

192 Outgroups in other families could not be used because their ITS sequences could not
193 be aligned unambiguously with our Sapotaceae data.

194 Bayesian analyses were carried out with MrBayes v3.2.6 (Huelsenbeck & Ronquist,
195 2001; Ronquist & Huelsenbeck, 2003) through the CIPRES gateway (Miller et al.,
196 2010). A general time reversible (GTR) model with a gamma distribution and invariant
197 sites was identified as the best-fit substitution model in jModelTest (Darriba et al.,
198 2012). Four independent runs of four MCMC chains were set to run for 30,000,000
199 cycles, sampling the Markov chain every 3000 cycles (10,000 samples) and saving
200 branch lengths. After determining using Tracer v1.6 (Rambaut et al., 2014) that a burn-
201 in of 25% sufficed to reach stationarity, the remaining samples were saved and used
202 to construct a Maximum Clade Credibility tree. The average standard deviation was
203 calculated every 30,000 generations, 1000 calculations in total. Tree probabilities were
204 calculated and credibility intervals were set as a fraction of the highest posterior
205 density. Clade support was represented by posterior probability (pp.) values, with weak
206 and strong support indicated by pp. values of 50 to 95%, and over 95%, respectively
207 (Swenson et al., 2008). ESS values were checked in Tracer v.1.6 and all parameters
208 reached values >200.

209 **Divergence time estimation**

210 Divergence times were estimated using Bayesian dating analyses in BEAST v1.10.5
211 (Drummond & Rambaut, 2007). The XML (eXtensible Mark-up Language) input file
212 was generated in BEAUti v1.10.5. The length of the chain was set to 40,000,000
213 cycles, logging parameters and printing to screen every 4000 cycles. An extra run of
214 additional 40,000,000 cycles was set and combined with the first run to achieve ESS

215 values higher than 200 for all parameters. A general time reversible (GTR) substitution
216 model with a gamma distribution and invariant sites was used. Gamma categories
217 were set to four and base frequencies were estimated. To test clock models and tree
218 priors, Bayes Factors were calculated using path sampling and stepping-stone
219 sampling. The clock model and tree priors that best fit our data were an uncorrelated
220 relaxed clock with a lognormal distribution, using a speciation birth-death process.
221 This model allows for changes in rates along the branches, and a speciation birth-death
222 process accounts for background extinction. Priors for model parameters and statistics
223 used a lognormal distribution for all fossil-based calibration points and a normal
224 distribution for the secondary calibration point (Ho, 2007; Ho & Phillips, 2009).

225 Two fossil calibration points were used along with a secondary calibration point based
226 on a dated phylogeny of a broader sample of asterids that utilized six well characterized
227 fossils (Bremer et al., 2004). *Psilatricolporites maculosus* (Chrysophylloideae) has a
228 more or less continuous sequence at the late Paleocene-early Eocene transition in the
229 Maracaibo Basin in western Venezuela (Rull, 1997; Rull, 2000). The record of
230 *Psilatricolporites* from Venezuela is probably the oldest reliably dated representative
231 of Chrysophylloideae from the New World. Therefore, an offset with an age estimate
232 of 55 Ma was used at the crown node that included all members in the New World
233 (node B, Fig. 3). A mean of 0.001 was set so that 95% of the intervals in the log-normal
234 distribution would include values between the estimated age and the latest boundary
235 of the Late Paleocene. Pollen of *Psilastephanocolporites malacanthoides*, reported
236 from the upper Eocene of Nigeria (Jan du Chêne, 1978), was assigned to *Malacantha*
237 *alnifolia* (synonym of the accepted name *Pouteria alnifolia*). The stem node of *P.*
238 *alnifolia* was therefore constrained to an offset of 35 Ma and a mean of 0.001 (node

239 C, Fig. 3), so that 95% of the intervals in the log-normal distribution would include
240 values between the estimated age and the latest boundary of the Late Eocene. Finally,
241 the crown root node of the phylogeny was dated using a secondary calibration point of
242 102 Ma for the stem node of Sapotaceae, obtained from a dated phylogeny of asterids
243 by Bremer et al. and Bremer (2004, 2009). Because we did not have any
244 representatives of taxa that are sister to Sapotaceae in our analysis we could not recover
245 the stem node, and therefore applied the age of the stem node of Sapotaceae to the
246 crown root node of the phylogeny. We acknowledge that this may bias our estimates
247 towards the oldest possible age. The normal distribution was set with a mean of 102
248 and a standard deviation of three, so 95% of the intervals in a normal distribution
249 would include the age estimated by Bremer et al. and Bremer (2004, 2009) \pm five
250 years (node A, Fig. 3).

251 **Ancestral Range Reconstruction**

252 Ancestral range reconstructions were carried out using the R package BioGeoBEARS
253 v1.1.1 (Matzke, 2018). Areas were defined based on previous evidence suggesting
254 evolutionary distinction (see introduction), and on isolation due to ocean, mountain or
255 dry climate barriers: Amazon, Atlantic Forest, Catatumbo, Guyanas, Macarena, West
256 Indies, Central America, Chocó, Cauca Valley, Magdalena Valley, Asia, and Africa
257 (Fig. 3). The MCC tree obtained in the BEAST analyses was used as an input tree. The
258 maximum number of areas was set to three as this was the maximum number of areas
259 where any given taxon was found in our phylogeny. The DEC, DIVALIKE and
260 BAYAREALIKE models were evaluated, and the model with the lowest AIC value
261 was selected. Models including the “j” parameter were not used considering the
262 conceptual and methodological issues introduced by them (Ree and Sanmartín, 2018).

263 **Diversification Rates**

264 We used BAMM 2.5.0 (Rabosky, 2014) to identify and quantify changes in
265 evolutionary rates. BAMM uses a Markov chain Monte Carlo (MCMC) to compare
266 evolutionary models of diversification. We ran a speciation-extinction model with a
267 global sampling fraction of 0.3 to account for incomplete taxon sampling. Priors were
268 set using the setBAMMpriors function in R (R Core Team, 2018). The analyses were
269 run for 50,000,000 generations and 4 Markov chains. The mcmc output and the event
270 file were written with a frequency of 5,000. To analyse the output, we used the R
271 package BAMMtools v2.1.6 (Rabosky et al., 2014). Using BAMMtools v2.1.6 we
272 checked for convergence, computed the 95% credible set of shift configurations, and
273 extracted the best configuration. To identify the number of rate shifts we calculated
274 the Bayes Factor and compared among models. Changes in rates through time were
275 plotted using the plotRateThroughTime function.

276

277 Issues related to the reliability of BAMM analyses were raised on previous studies
278 (e.g. Rabosky 2014; Moore et al. 2016; Meyer et al. 2018 and Rabosky 2019) however
279 under the parameters specified for our analyses with an expected number of shifts = 1,
280 these issues should not hinder determination of patterns of diversification (Rabosky et
281 al. 2017), except in cases where small rate shifts occurred. To account for that and
282 other concerns related to BAMM, we also inferred branch specific diversification rates
283 using RevBayes v10 (Höhna et al., 2016). RevBayes uses a MCMC under a birth-death
284 process with diversification rates changing among branches. We used the time-
285 calibrated phylogeny generated in BEAST as a starting tree, and the root age parameter
286 was derived from it. The rate categories were set to six, and the effect of varying the

287 number of rates categories from 3-10, was tested. To account for incomplete taxon
288 sampling, the total number of species was set as the total number of species currently
289 accepted for Sapotaceae. Diversification rates were calculated using the
290 `fnDiscretizeDistribution`, and results were visualised using the R package `RevGadgets`
291 `v1`.

292

293 **RESULTS**

294 **Divergence Time Estimation**

295 Analyses were performed on a matrix of 400 accessions and 1151 characters. The
296 basal nodes of the phylogeny are weakly supported, but posterior probability values
297 increase in younger clades. Thirty-two splits between west-Andean and east-Andean
298 taxa were found from *ca.* 24 Ma onwards, of which 18 had posterior probability (pp.)
299 values higher than 0.9 (Table 1; Fig. 4a–c). Fifteen splits among lineages in Central
300 America and South America were found from *ca.* 33 Ma, nine of them with pp. > 0.9
301 (Fig. 4a). Lastly, ten splits in neotropical Sapotaceae occurred during the Pleistocene
302 epoch, seven of them with pp. > 0.9. Splits were considered at all levels in the
303 phylogeny as divergence at deeper time scales, before the occurrence of major tectonic
304 events in the Miocene and climatic changes in the Pleistocene, and closer to the
305 present, after these events, both provided evidence to explore the role of putative
306 drivers in the evolution of Chrysophylloideae. Splits were identified based on the
307 divergence time estimation and on the ancestral range reconstruction.

308 We found two major neotropical clades derived from African lineages at *ca.* 44 Ma
309 (Fig. 4a Node e, pp. 0.17) and *ca.* 47 Ma (Node p. Fig. 4a, pp. 0.13), respectively.

310 Additionally, a well-supported neotropical clade nested within the Asian Sapotaceae
311 was found and includes taxa from the Amazon, Magdalena Valley and Chocó (*ca.* 8.1
312 [2.89–12.96 HPD] Ma, Fig. 4a Node b, pp. 1).

313 The earliest well-supported split between Chocó and any other area in the Neotropics
314 occurred at *ca.* 33 (24.18–40.64 HPD) Ma (Fig. 4b Node w, pp. 0.99), between Chocó
315 and Central America (pp. 0.99). Further splits between Chocó and the Guyanas
316 occurred between *ca.* 13 and 6.5 Ma (Table 1). Well supported splits between Chocó
317 and Central America occurred at 28 Ma (20.68–36.33 HPD; Fig. 4a Node x, pp. 0.96),
318 and more recently at *ca.* 5.6 Ma (1.11–9.76 HPD; Fig. 4a Node f, pp. 0.99), 2.7 (0.69–
319 3.70 HPD) Ma (0.69–3.70 HPD; Fig. 4c Node am, pp. 1), and 2 (0.23, 2.75 HPD) Ma
320 (Fig. 4b Node u, pp. 1).

321 Three well supported splits between Central America and other areas in South America
322 occurred at *ca.* 15.9 (9.64–21.13 HPD), 13 (7.24–18.06 HPD) and 9.4 (3.66–14.79
323 HPD) Ma (Fig. 4c Nodes an, ao, ak). Six additional splits among lineages in Central
324 America and South America were found from 27.1 Ma to 1.6 Ma, but without strong
325 statistical support (Fig. 4a,b, Nodes aa, o, ai, k, aj).

326 The oldest split between lineages from Chocó and the Amazon occurred at *ca.* 24
327 (15.9–31.37 HPD) Ma (Fig. 4b Node ae, pp. 0.87). However, this and a later split at
328 *ca.* 23.7 (15.95–30.56 HPD) Ma (Fig. 4b Node ap) are weakly supported (pp. 0.87 and
329 0.89, respectively). Node y (Fig. 4b) is the earliest well supported (pp. 0.99) split
330 between lineages from Chocó and the Amazon at *ca.* 21.6 (12.62–29.78 HPD) Ma. Six
331 additional well-supported splits between taxa in Chocó and the Amazon were found
332 between *ca.* 16 and 1.4 Ma (Table 1). Eight splits with $pp. < 0.9$ occurred between taxa

333 in the Amazon and Chocó from *ca.* 19.7 (35.08–46.19 HPD) Ma to *ca.* 5.1 Ma (Fig.
334 4a,b,c Nodes av, az, g, ab, ag).

335 The oldest split between Chocó and other areas in northern South America such as the
336 Cauca valley was found at *ca.* 6.8 (2.84–9.64 HPD) Ma (Fig. 4b Node t, pp. 1), and
337 between Chocó and Magdalena Valley at *ca.* 14.3 (7.47–20.29 HPD) Ma (Fig. 4b Node
338 ac, pp. 1). Another split between Chocó and Magdalena Valley occurred at *ca.* 2.4
339 (0.55–3.17 HPD) Ma (Fig. 4a Node r, pp. 0.95).

340 Node z (Fig. 4b) at *ca.* 23 (12.68–34.53 HPD) Ma (pp. 0.73) indicates the time when
341 lineages in the Magdalena valley and the Atlantic forest in Brazil last shared a common
342 ancestor. The earliest split between taxa in the Magdalena valley and the Amazon
343 occurred at 8.1 (2.89–12.96 HPD) Ma (Fig. 4a Node b, pp. 1), taxa shared between
344 these areas also diverged later at *ca.* 6.1 Ma (2.45–8.92 HPD; Fig. 4b Node ad, pp. 1).
345 The age of node s (Fig. 4a) at *ca.* 1.5 (0.05–1.11 HPD) Ma (pp. 0.99) represents a
346 younger split between lineages from the Magdalena valley and Macarena.

347 Two main clades of lineages from Macarena are represented by nodes ba and bd (Fig.
348 4c). Node ba represents the most recent common ancestor shared between lineages
349 from Macarena and Chocó/Amazon at *ca.* 8.2 Ma. This relationship is weakly
350 supported (pp. 0.05). Node bd indicates the most recent common ancestor shared
351 between taxa in Catatumbo and in Macarena at *ca.* 3.9 (1.33–5.48 HPD) Ma (pp. 1).
352 Taxa in Macarena were found to also share a common ancestor with taxa in the
353 Amazon at *ca.* 4 Ma (pp.1) and in Chocó at *ca.* 4.8 (1.79–7 HPD) Ma (Fig. 4d Node
354 V, pp. 1) and 2.4 (0.55, 3.17) Ma (Fig. 4a Node r, pp. 0.95).

355 Catatumbo lineages (Fig. 4c Node be) diverged from lineages from Chocó at *ca.* 6.5
356 (2.83, 9.43 HPD) Ma (Fig. 4c Node bf, pp. 0.98). The stem node of that clade was
357 found at *ca.* 12 Ma (pp. 0.96) and represents the split between taxa in the Guyanas and
358 clade 4.13. Taxa from Catatumbo split from taxa in the Magdalena valley at *ca.* 4.9
359 (1.90, 6.78 HPD) and 7.8 (1.90 – 6.78 HPD) Ma (Fig. 4c Nodes ar and aq, pp. 1 and
360 0.3). Lineages from Los Llanos split from taxa from the Amazon at *ca.* 1 Ma (Fig. 4a
361 Node n, pp. 0.1 and Node l, pp. 0.11), 1.2 (0.01, 1.49 HPD) Ma (Fig. 4a Node m. pp.
362 0.95), 5.9 Ma (Node j. pp. 0.12) and 7 (3.95, 9.68 HPD) Ma (Node i. pp. 0.96).

363 **Ancestral Range Reconstruction**

364 A dispersal–extinction–cladogenesis (DEC) model was found as the best-fit model in
365 our analyses (DEC AIC: 1406, DIVALIKE AIC: 1585, BAYAREALIKE AIC: 1734).
366 The ancestral area for Sapotaceae was reconstructed as Asia (Fig. 4a Node a) with an
367 independent colonization to the Amazon in the Neotropics (Fig. 4a Node b), and two
368 colonisations to Africa (Fig. 4a Node c and d). Our results are consistent with two
369 migrations from Africa to the Neotropics, first to the Amazon (Fig. 4a Node e and p)
370 and from the Amazon to other areas in South and Central America, and the West
371 Indies. After arrival to Central America, Chrysophylloideae colonised Choco and after
372 arrival to the Atlantic Forest it colonised the Magdalena Valley. Direct dispersal from
373 the Amazon was reconstructed for the Guianas and Macarena, and this was followed
374 by multiple dispersals between South and Central America, and the West Indies (Table
375 1, Fig. 4. and Divergence Time Estimation section)

376

377 **Diversification Rates**

378 In our phylogeny the probability of a null model was too low and it could not be
379 calculated by BAMM. However, BAMM sampled models with 1:5 and 7 shift regimes,
380 favouring a model with a single shift at the basal node of the Neotropical groups (Fig.
381 3). Branch specific speciation rates calculated by RevBayes recovered two additional
382 shifts in diversification during the late Miocene at ca. 6-8 Ma (Fig. 3), for lineages in
383 the Catatumbo and Macarena forests. Changes in diversification rates coinciding with
384 periods of major uplift of the Andes, the closure of the Isthmus of Panama, or
385 Pleistocene climatic changes were not supported (Fig. 3).

386

387 **DISCUSSION**

388 The uplift of the Andes, the formation of the panama land bridge and climatic changes
389 in the Pleistocene reconfigured the Neotropics generating barriers that could prevent
390 or facilitate dispersal and promote diversification. In our analyses however, we did not
391 find evidence supporting the hypotheses of increases in diversification rates caused by
392 the Andean uplift or Pleistocene climatic changes. Our data suggest that dispersal has
393 played an important role in the evolutionary history of neotropical Chrysophylloideae
394 at various scales, with deep signatures in our phylogeny from the arrival of the
395 subfamily to South America possibly via trans-oceanic dispersal, and migration events
396 across the Andes and the Panama land bridge, to fine patterns of evolution within and
397 between species across Sapotaceae's geographical range.

398

399 The earliest record for a possible Sapotaceae migration from Asia to the Neotropics
400 was found in a well-supported neotropical clade nested within a clade of Asian species

401 with a stem node age of *ca.* 60 (56–67 HDP) Ma. We found evidence for further and
402 later migration to the Neotropics from Africa at *ca.* 47 and 44 Ma. Arrival in the
403 Neotropics was accompanied by a significant shift in diversification rates (Fig. 3),
404 although this may be an artefact of low sampling of palaeotropical lineages. These
405 dispersal events postdate the physical isolation of South America from Africa, and
406 coincided with the existence of the megathermal boreotropical rain forest in the
407 northern hemisphere during the Palaeocene/Eocene (Wolfe, 1975). However, one
408 would expect South American lineages to be nested within Central American ones if
409 South America had been colonized from northern boreotropical regions. According to
410 the ancestral reconstruction in BioGeoBEARS, the earliest occurrence of Sapotaceae
411 in the Neotropics was in the region currently occupied by the Amazon basin (Fig. 4
412 and Table 1). Hence, Sapotaceae could have dispersed instead via oceanic currents
413 from Africa to the eastern coast of South America as previously suggested for the
414 Sapotaceae genus *Manilkara* (Armstrong et al., 2014) (Table 1). Chrysophylloideae
415 then migrated on multiple occasions to Central America, to the West Indies, and other
416 areas in South America.

417 Evidence suggesting a strong role of dispersal in Chrysophylloideae's history, was also
418 found at fine scales in our phylogeny where we identified non-monophyletic species
419 with wider distributions, which may be the ancestors of species with narrower ranges
420 that are phylogenetically nested within them. This pattern deserves further study and
421 in our work was found in species such as *Chrysophyllum cainito* that is nested within
422 *C. argenteum*, *Micropholis casiquariensis* that is nested within *M. guyanensis*, and
423 *Pouteria reticulata* and *P. cainito* that are nested within the more broadly distributed
424 *P. guianensis*. Wide distributional ranges in lowland rain forest could be the result of

425 dispersal events followed by successful colonisation in areas where empty spaces were
426 created after periods of frequent disturbance (Pennington & Lavin, 2016). Isolation
427 and drift or strong selection may be sufficient to lead to species formation in peripheral
428 populations.

429

430 **Trans-Andean Vicariance (Hypothesis i)**

431 Thirty-two splits were found between taxa at either side of the Eastern Cordillera from
432 *ca.* 24 (15.9–31.37 HPD) Ma onwards (Fig. 4 and 5, and Table 1). Twenty-six of those
433 (14 with $pp.>0.9$ and 14 with $pp.<0.9$) occurred from *ca.* 12 Ma onwards (Table 1).
434 We acknowledge that the total number of splits would vary if additional collections
435 were added, yet our phylogeny includes 30% of the currently recognised species in
436 neotropical Chrysophylloideae, including 71% of the known species in Colombia, one
437 of the most species-rich areas and where the Andes branched in three ranges separating
438 important fragments of lowland rain forest. This suggests that our analyses have
439 recovered important evidence for migration across mountain barriers and reject a
440 hypothesis of vicariance caused by the uplift of the Eastern Cordillera (Fig. 2). Under
441 this hypothesis we would expect splits on either side to have occurred mainly from *ca.*
442 12 Ma. Timing of isolation across the Cordillera in our analyses is spread through time
443 rather than concentrated at one point as a vicariance model would predict (Fig. 5). This
444 indicates that the Andes were not a significant barrier to dispersal, and that isolation
445 of Sapotaceae lineages on either side of the Andes's Eastern Cordillera after the middle
446 Miocene, the time frame of major uplift in northern South America, occurred only in
447 some cases. Frequent dispersal among areas separated by the Andes has been reported
448 in other studies by Fine et al. (2014), Dexter et al. (2017), Hazzi et al. (2018), Pérez-

449 Escobar et al. (2019), and like Serrano et al. (2018) they indicate that migration may
450 have prevented provincialism in Sapotaceae's species distribution (but see e.g. Trénel
451 et al., 2007; Albert et al., 2006; Pirie et al., 2006; Arrivillaga et al., 2002; Winterton
452 et al., 2014; De-Silva et al., 2016).

453 Migration in Chrysophylloideae between areas to the west of the Eastern Cordillera,
454 i.e. Chocó, and the inter-Andean valleys, would not have been limited by altitude as
455 these areas are all connected by fragments of lowland rain forest. These fragments are
456 in the departments of Antioquia, Cordoba and Bolivar (Gentry, 1982) (Fig. 1).
457 Dispersal between Chocó and other areas in northern South America has also been
458 reported in other taxa such as Arecaceae and Burseraceae (Fine et al., 2014; Dexter et
459 al., 2017; Bacon et al., 2018). Trans-Andean migration of Sapotaceae between areas
460 that are not connected by corridors of lowland rain forest such as Catatumbo and the
461 inter-Andean valleys, could have occurred through mountain passes where altitudes in
462 the Eastern Cordillera are lower (Hazzi et al., 2018; Serrano et al., 2018) (red bars Fig.
463 1, Fig. 4).

464 **Migration across the Panama Isthmus (Hypothesis ii)**

465 Fifteen migration events, nine of them well supported, were found between Central
466 and South America (Fig. 4 and 5). The formation of the Isthmus of Panama is regarded
467 as a key event for Neotropical biotic evolution because it allowed the interchange of
468 terrestrial species between North and South America (Simpson, 1980). According to
469 Coates & Obando (1996) the formation of the Isthmus of Panama did not occur in one
470 single event, but was reportedly completed in the Middle Pliocene at around 3.4–3.1
471 Ma. However, more recent studies based on river deposit evidence from Northern

472 South America, indicate that the land bridge may actually have been formed at around
473 13–15 ma. The migration events found in our phylogeny occurred from *ca.* 33 (24.18–
474 40.64 HPD) Ma (Node w, Fig 4b.) onwards, prior to and after the closure of the
475 Panama land bridge, assuming a date of closure of *ca.* 13–15 Ma (Hoorn C & Flantua,
476 2015; Bacon et al., 2015). Our results corroborate Cody *et al.* (2010) who compared
477 plant and animal migration patterns across the isthmus, and found that dispersal of
478 plant taxa was spread through the Cenozoic and often preceded the formation of the
479 land bridge (whether regarded as occurring at 3 Ma or 13–15 Ma). They are also
480 similar to those of Bartish (2011) who suggested that the closure of the Central
481 American Seaway initiated a possible route for migration but was not essential for the
482 expansion of Sapotaceae’s distributional range. Considering that there is evidence for
483 transatlantic dispersal in Sapotaceae (e.g. Bartish et al., 2011), migration could have
484 taken place from South America to Central and North America, directly across the
485 relatively narrow seaway present before the formation of the Isthmus of Panama.

486 **Diversification after the Andean uplift (Hypothesis iii)**

487 Sapotaceae diversified at a constant rate until about 49.5 Ma when arrival in the
488 Neotropics coincided with shifts in diversification rates (Figs. 3 and 5). Two additional
489 diversification shifts occurred in the late Miocene in clades representing taxa at the
490 Macarena and Catatumbo forests. The hypothesis of increased diversification rates
491 being associated with periods of major uplift in the Andes was not supported. Because
492 Sapotaceae does not generally occur above 2000 m in South America, it would not
493 have been affected by the creation of novel montane habitats by the Andean uplift.
494 This uplift could however have affected the evolution of Chrysophylloideae and other

495 lowland rain forest restricted taxa by altering the edaphic and hydrological systems in
496 lowland areas (Burnham & Graham, 1999; Hoorn et al., 2010), but the effects of these
497 alterations did not significantly increase diversification rates in our analyses.

498

499 **Pleistocene Diversification (Hypothesis iv)**

500 Despite early work suggesting that speciation in animals from the lowland rain forest
501 of South America mostly predates the Pleistocene (Moritz et al., 2000), more recently
502 examples have accumulated suggesting origin of neotropical rain forest species during
503 the Pleistocene including in *Inga* (Fabaceae), *Guatteria* (Annonaceae) and Meliaceae
504 (Richardson et al., 2001; Erkens et al., 2007; Koenen et al., 2015). Thirteen splits
505 (seven with $pp.>0.9$) among South American Sapotaceae occurred during the
506 Pleistocene (Fig. 5). Our results add to a building picture that species diversification
507 in neotropical trees has occurred recently, and Pleistocene dates for speciation in
508 Sapotaceae (Fig. 5 and Table 1) are consistent in timing with a speciation model driven
509 by climatic changes. However, Pleistocene speciation is not responsible for the
510 majority of Sapotaceae speciation as early, “refuge theory” models of neotropical
511 speciation hypothesised (Haffer, 1969; Prance, 1973; Richardson et al., 2001; Pérez-
512 Escobar et al., 2019).

513 **Conclusions**

514 The study of patterns of evolution in northern South America, is fundamental to our
515 understanding of the origins of the great plant diversity of the Neotropics. Yet, due to
516 decades of civil conflict in countries like Colombia, the addition of plant collections
517 from forests on both sides of the Andes, was highly restricted in this area. Here we

518 addressed this gap and tested hypotheses focussed on the role of geographic barriers
519 and climatic changes, in the biogeographic history of the Chrysophylloideae subfamily
520 in Sapotaceae. Our results uncover patterns suggesting a strong role for dispersal in
521 the history of neotropical Sapotaceae and the lowland rain forest biome, where they
522 are most abundant.

523

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880 **Author Contributions**

881 Conceived and designed the experiments: JER, JS. Generated the data and ran analyses

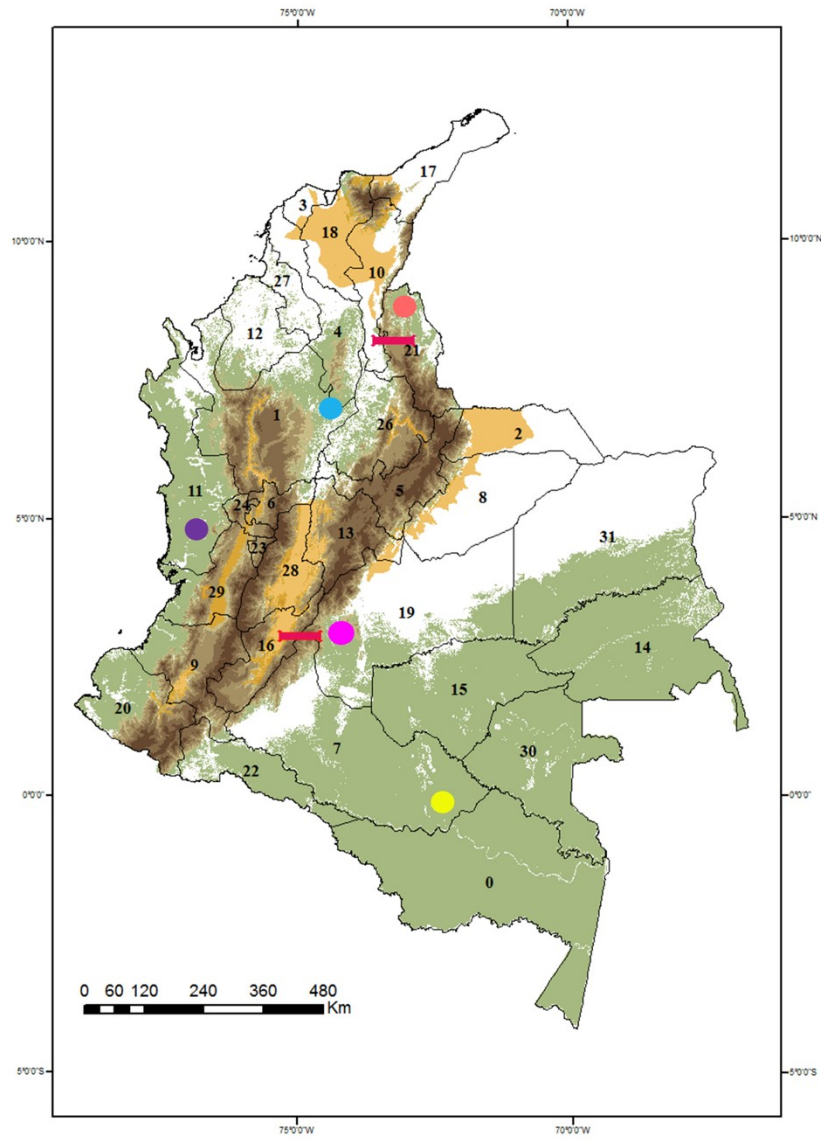
882 JS. Wrote the paper: JS, JER, RTP, RIM, RCB, GAM, JAH, IVB, MG, JC, SM, DC,

883 SDC.










884

885 **Figure 1.** Lowland rain forests of Colombia. Coloured dots indicate the fragments of
886 lowland rain forest that can be found in Colombia. These areas are characterised by
887 evergreen vegetation occurring under *ca.* 800 meters above sea level, which is
888 dominated by angiosperm tree species adapted to low fluctuations in temperature, high
889 precipitation (more than 2000 mm per year), with high beta and alpha diversity and an
890 abundance of lianas and epiphytes (Burnham & Johnson, 2004; IDEAM et al., 2007;
891 Reynel et al., 2013). Brown shades represent major mountain ranges, from north to
892 south: Sierra Nevada de Santa Marta, Eastern, Western, and Central Cordilleras. Areas
893 in yellow represent areas of dry forest. Red bars represent areas of low elevation in the
894 Andes below 1000 m. Black solid lines represent the administrative division of
895 Colombia into municipalities 0: Amazonas, 1: Antioquia, 2: Arauca, 3: Atlantico, 4:
896 Bolivar, 5: Boyaca, 6: Caldas, 7: Caquetá, 8: Casanare, 9: Cauca, 10: Cesar, 11: Chocó,
897 12: Cordoba, 13: Cundinamarca, 14: Guainía, 15: Guaviare, 16: Huila, 17: La Guajira,
898 18: Magdalena, 19: Meta, 20: Nariño, 21: Norte de Santander, 22: Putumayo, 23:
899 Quindio, 24: Risaralda, 26: Santander, 27: Sucre, 28: Tolima, 29: Valle del Cauca, 30:
900 Vaupes, 31: Vichada. Fragments of lowland rain forest are depicted as proposed by
901 IDEAM *et al.* (2017), and dry forest areas were adapted from the WWF Ecorregions
902 (Olson et al., 2001).

903



KEY

- | | |
|---|--|
|  Other Biomes |  Choco |
|  Mountain forest |  Amazon |
|  Lowland Rain Forest |  Macarena |
|  Tropical Dry Forest |  Catatumbo |
| |  Inter-Andean valleys |
| |  Points of low altitude |

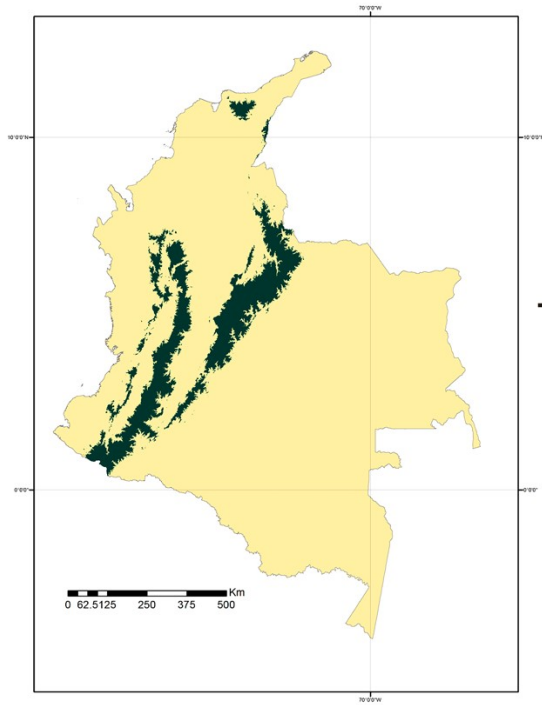
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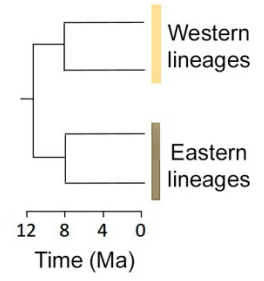
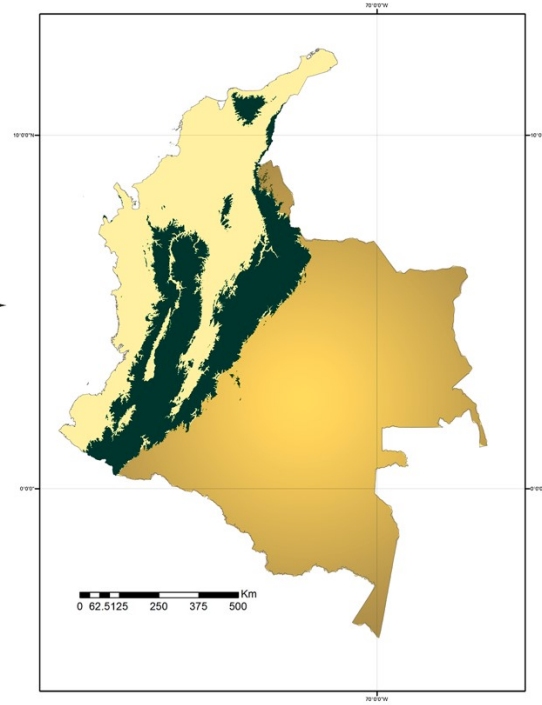
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907 **Figure 2.** Hypothetical phylogenetic splits assuming speciation events due to the
908 Andean uplift without subsequent dispersal. Panel A. representing Andean
909 configuration and hypothetical species distribution (yellow) before the early-middle
910 Miocene, and Panel B. representing Andean configuration and hypothetical species
911 distribution (shades of yellow) after early-middle Miocene when the Andes reached
912 current elevations. If the evolution of Sapotaceae was affected by early and middle
913 Miocene orogeny without subsequent dispersal, dichotomies in the phylogeny would
914 occur at *ca.* 12 Ma when the Eastern Cordillera was high enough to have prevented
915 migration.

A.



B.

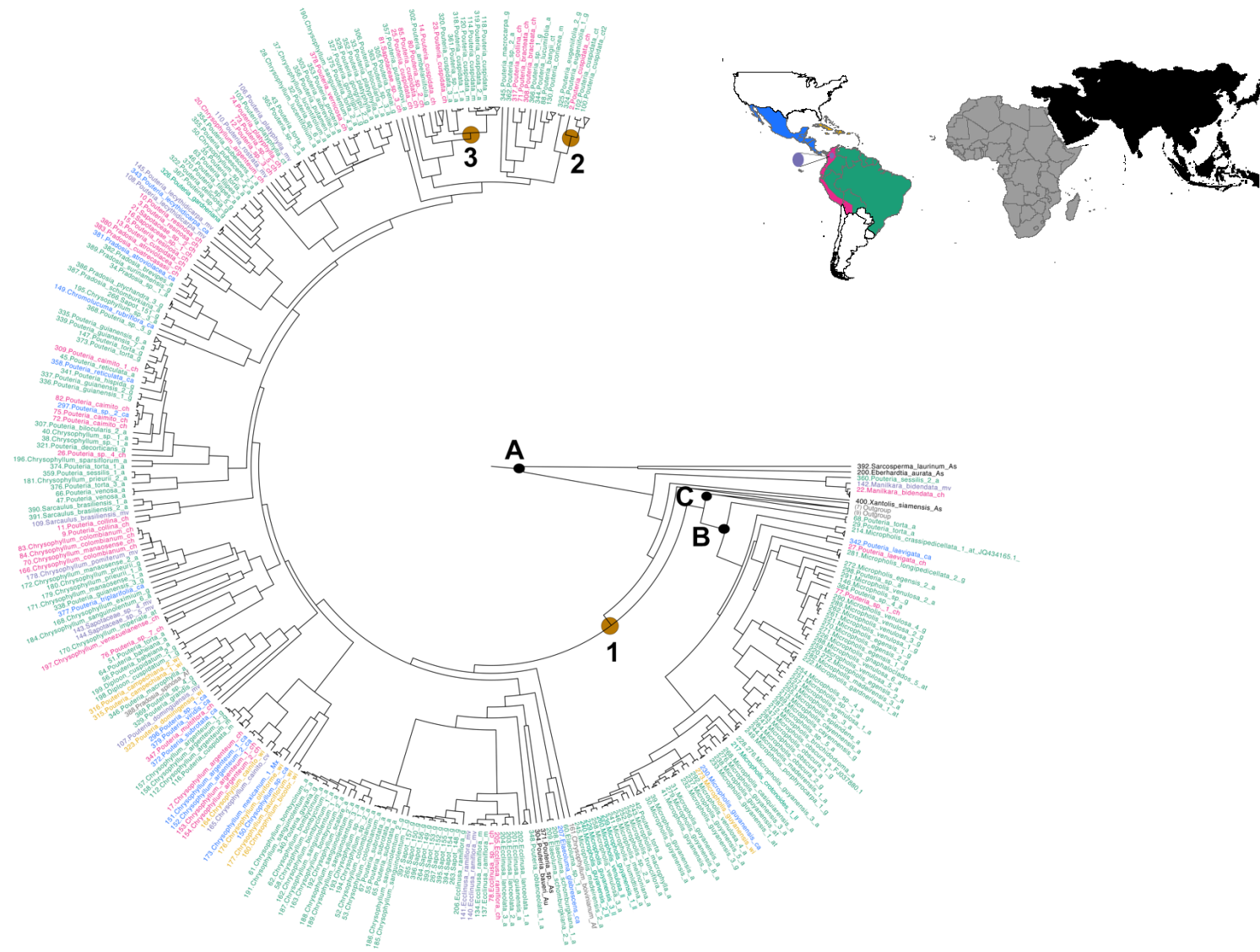


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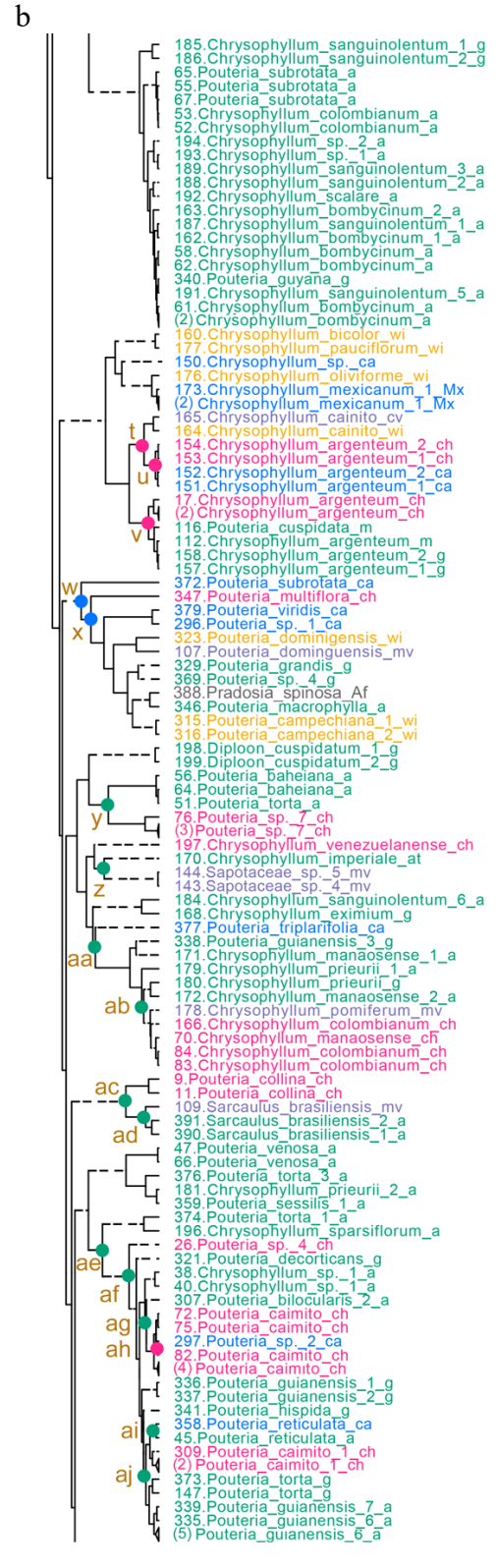
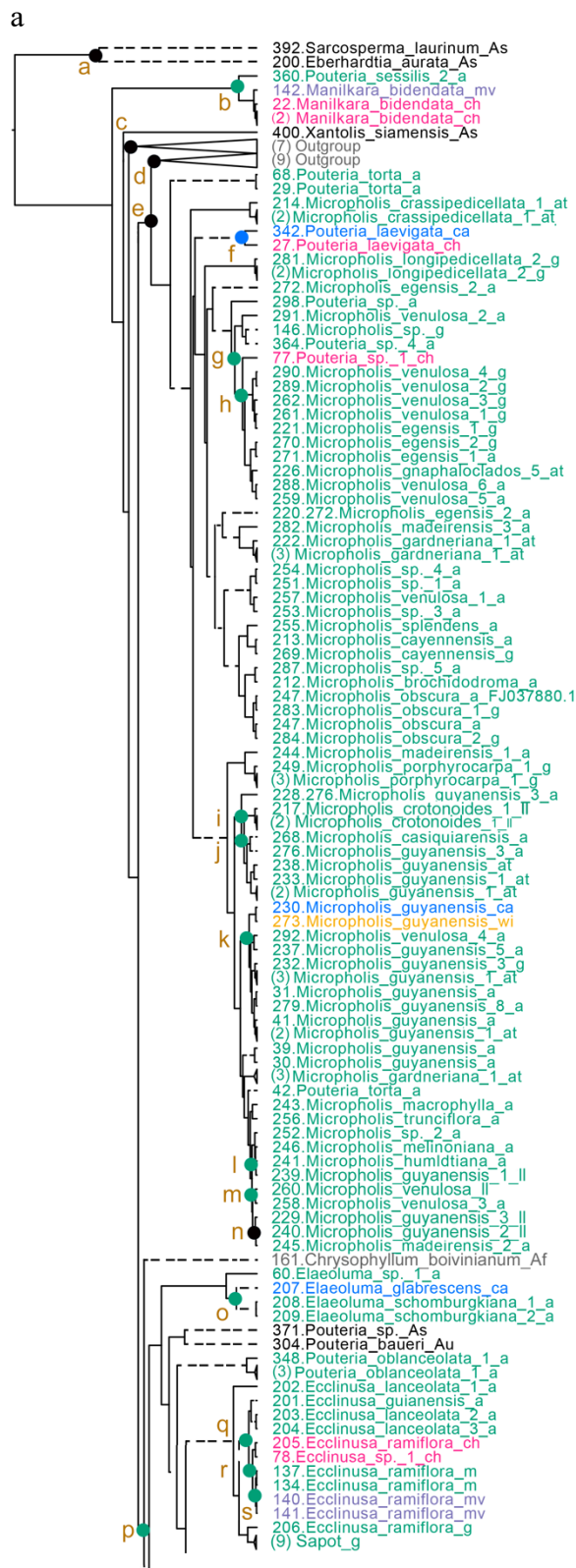
918 **Figure 3.** Maximum clade credibility tree from the BEAST analysis indicating
919 relationships among neotropical Sapotaceae lineages. Three calibration points are
920 indicated: node A – age estimate of Sapotaceae following Bremer et al. (2004); node
921 B – Neotropical pollen; node C – *Malacantha alnifolia* pollen. Colours in tips and the
922 map represent in pink: areas to the west of the Eastern Cordillera, in green: areas to
923 the east of the Eastern Cordillera, in purple: inter-Andean valleys, in blue: Central
924 America, in yellow: West Indies, in grey: Africa, and in black: Asia. Brown circles
925 represent shifts in diversification rates recovered by (1) BAMM 2.5, and (2 and 3) by
926 RevBayes 10. The colour palette was chosen using the colorblindFriendly function in
927 the R package RColorBrewer 2.0.

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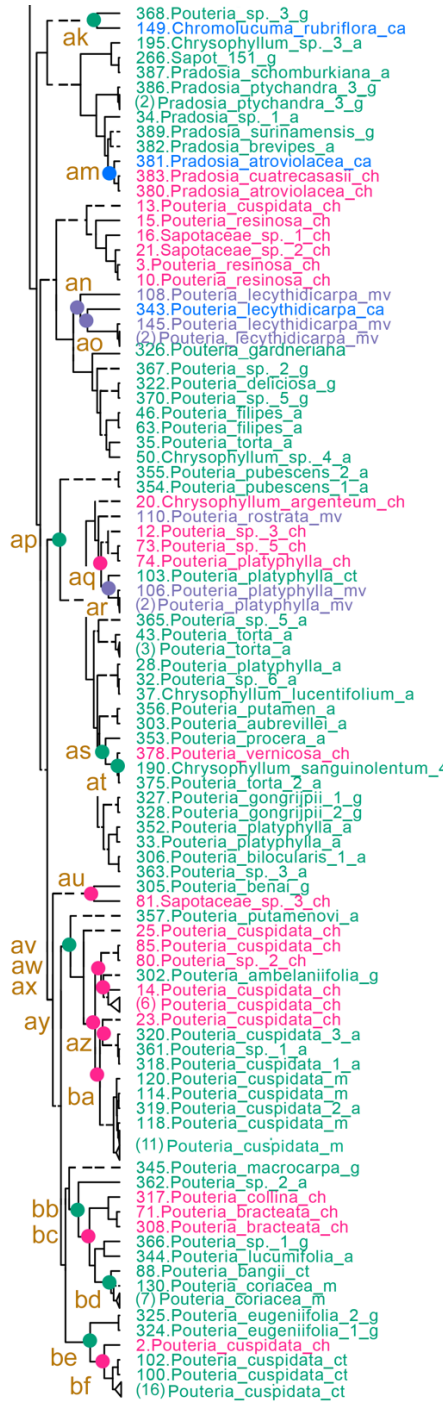


930 **Figure 4.** Maximum clade credibility tree from the BEAST analyses. Support across
931 the phylogeny is indicated by dotted (pp<0.9) and solid lines (pp>0.9). Letters
932 represent splits across the Panama Isthmus (assuming a date of *ca.* 13 – 15 Ma for its
933 formation), splits among areas at the east and west of the Eastern Cordillera, and splits
934 between the Paleotropics and the Neotropics. Colours in tips, nodes and the map
935 represent in pink: areas at the west of the Eastern Cordillera, in green: areas at the east
936 of the Eastern Cordillera, in purple: inter-Andean valleys, in blue: Central America, in
937 yellow: West Indies, in grey: Africa, and in black: Asia. Colours of circles on the
938 nodes represent the ancestral area of highest likelihood as estimated in BioGeoBears
939 v.1.1.1. The colour palette was chosen using the colorblindFriendly function in the R
940 package RColorBrewer v2.0. Letters after names indicate the following regions: a.
941 Amazonia, Af. Africa, As. Asia, at. Atlantic forest, Au. Australia, ca. Central America,
942 ch. Choco, ct. Catatumbo, cv. Cauca Valley, g. Guianas, ll. Llanos, m. Macarena, mv.
943 Magdalena Valley, wi. West Indies.

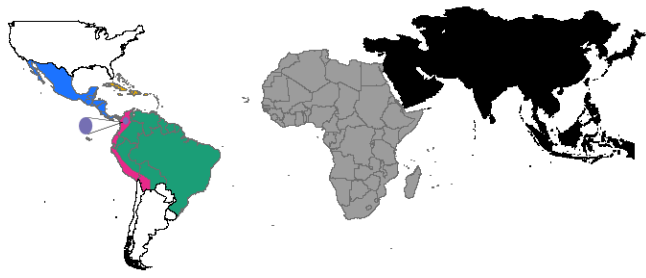
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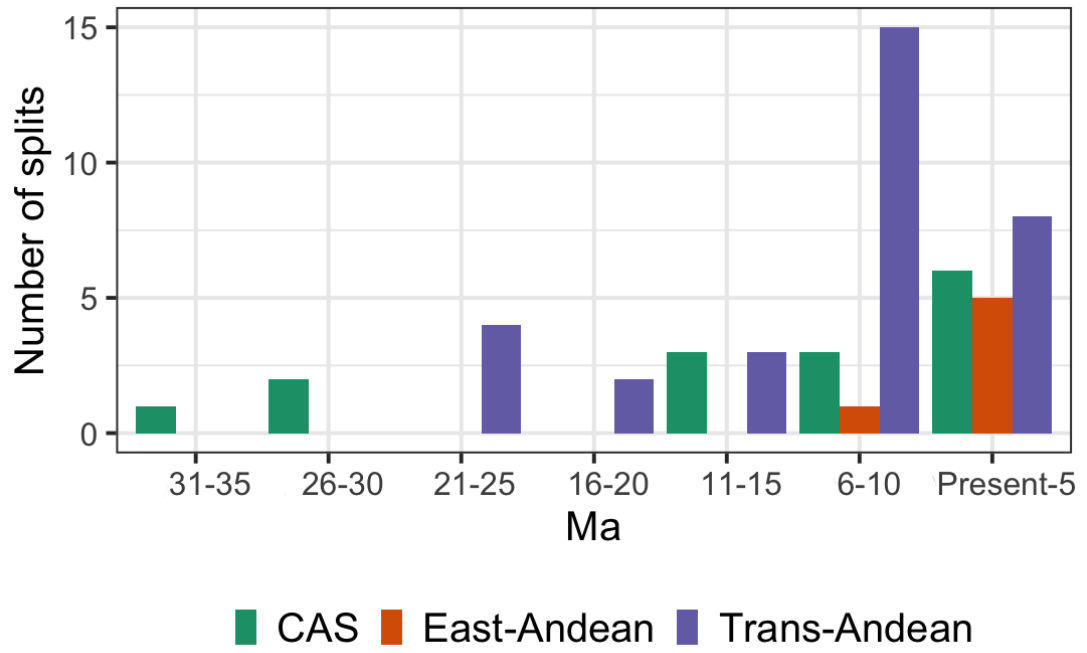


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949 **Figure 5.** Number of phylogenetic splits found in Sapotaceae through geological time
950 in northern South America. Types of splits were divided into Trans Andean: between
951 Cauca valley/Chocó/Magdalena Valley and Amazon/Atlantic forest/Catatumbo/
952 Llanos/Macarena; east-Andean: between Amazon, Atlantic forest, Catatumbo, Llanos
953 and Macarena; and Across CAS (Central American Seaway): between Central
954 America/Mexico and South American areas.

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958

960 **Table 1.** Summary of the divergence time estimation. Divergence time estimation
 961 analyses were carried out using BEAST v1.8.4. HPD are given for those nodes with
 962 Posterior Probability values higher than 0.7. Splits were divided into: Trans-Andean
 963 (between Chocó/Cauca valley/Magdalena Valley and Amazon/Atlantic forest/
 964 Macarena/Catatumbo); east-Andean (between Amazon, Catatumbo, and Macarena);
 965 Across the Panama Isthmus (between Central America and South American areas);
 966 trans-Atlantic (between Paleotropics and Neotropics); and Paleotropical for areas in
 967 Africa and Asia.

Node	Posterior probability	Mean age and HPD (Mya)	Type of split	Ancestral Area (highest likelihood)
a	0.83	65.66 [35.22, 94.92]	Trans-Atlantic	Asia
aa	0.19	27.1	Panama Isthmus	Amazon
ab	0.32	6.93	Trans-Andean	Amazon
ac	1	14.3 [7.47, 20.29]	Trans-Andean	Amazon
ad	1	6.11 [2.45, 8.92]	Trans-Andean	Amazon
ae	0.87	24 [15.9, 31.37]	Trans-Andean	Amazon
af	0.86	13.01 [6.99, 19.49]	Panama Isthmus	Amazon
ag	0.25	5.8	Trans-Andean	Amazon
ah	0.2	1.1	Panama Isthmus	Chocó
ai	0.23	1.6	Panama Isthmus	Amazon
aj	0.39	6	Trans-Andean	Guianas
ak	1	9.4 [3.66, 14.79]	Panama Isthmus	Guianas

Node	Posterior probability	Mean age and HPD (Mya)	Type of split	Ancestral Area (highest likelihood)
am	1	2.7 [0.69, 3.70]	Panama Isthmus	Central America
an	0.95	15.9 [9.64, 21.13]	Panama Isthmus	Magdalena valley
ao	0.92	13.1 [7.24, 18.06]	Panama Isthmus	Magdalena valley
ap	0.89	23.7 [15.95, 30.56]	Trans-Andean	Amazon
aq	0.3	7.8	Trans-Andean	Chocó
ar	1	4.96 [1.90, 6.78]	Trans-Andean	Magdalena valley
as	0.99	6 [2.74, 8.41]	Trans-Andean	Amazon
at	1	1.4 [0.06, 1.76]	Trans-Andean	Amazon
au	1	10.65 [4.5, 16.12]	Panama Isthmus	Chocó
av	0.15	19.79	Trans-Andean	Amazon
aw	0.71	7.84 [4.18, 10.31]	Trans-Andean	Chocó
ax	0.39	6.94	Trans-Andean	Chocó
ay	0.04	7.2	Trans-Andean	Chocó
az	0.35	10.16	Trans-Andean	Chocó
b	1	8.1 [2.89, 12.96]	Trans-Andean	Amazon
ba	0.05	8.2	Trans-Andean	Chocó
bb	1	16 [11.09, 20.74]	Trans-Andean	Amazon
bc	0.99	12.3 [7.74, 15.61]	Trans-Andean	Chocó
bd	1	3.9 [1.33, 5.48]	Trans-Andean	Catatumbo
be	0.96	12.1 [6.4, 17.07]	Trans-Andean	Guyanas
bf	0.98	6.5 [2.83, 9.43]	Trans-Andean	Chocó
c	0.34	50	Paleotropical	Africa
d	0.88	40 [35.08, 46.19]	Paleotropical	Africa

Node	Posterior probability	Mean age and HPD (Mya)	Type of split	Ancestral Area (highest likelihood)
e	0.17	44	Trans-Atlantic	Africa
f	0.99	5.6 [1.11, 9.76]	Panama Isthmus	Central America
g	0.41	9.74	Trans-Andean	Amazon
h	0.98	6.57 [3.24, 8.07]	Trans-Andean	Amazon
i	0.96	7 [3.95, 9.68]	East-Andean	Amazon
j	0.12	5.9	East-Andean	Amazon
k	0.03	3.8	Panama Isthmus	Amazon
l	0.11	1	East-Andean	Amazon
m	0.95	1.2 [0.01, 1.49]	East-Andean	Amazon
n	0.1	1	East-Andean	Llanos
o	0.48	9.09	Panama Isthmus	Amazon
p	0.13	47	Trans-Atlantic	Africa
q	1	4 [1.49, 5.47]	Trans-Andean	Amazon
r	0.95	2.4 [0.55, 3.17]	Trans-Andean	Amazon
s	0.99	1.5 [0.05, 1.11]	Trans-Andean	Macarena
t	1	6.8 [2.84, 9.64]	Trans-Andean	Chocó
u	1	2 [0.23, 2.75]	Panama Isthmus	Chocó
v	1	4.8 [1.79, 7]	Trans-Andean	Chocó
w	0.99	33 [24.18, 40.64]	Panama Isthmus	Central America
x	0.96	28 [20.68, 36.33]	Panama Isthmus	Central America
y	0.99	21.6 [12.62, 29.78]	Trans-Andean	Amazon
z	0.73	23 [12.68, 34.53]	Trans-Andean	Atlantic forest