1   **TITLE**
2   **Temperature predicts leaf shape in palms (Arecaceae)**
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33

34   **Abstract**

35   Leaves display a remarkable variety of shapes, each potentially relevant to the function of these

36   organs and with potential ecological advantages in certain climates. Studies correlating leaf

37   shape with either climate or allometric constraints (how size and shape relate) focus on

38   intraspecific variation or model organisms, and the drivers of leaf shape at a macroecological

39   scale remain poorly known. Here, we determine associations between climatic and allometric

40   factors with the evolution of leaf shape in a lineage with one of the highest diversities of leaf

41   shape known, the palms (family Arecaceae). We apply a Bayesian phylogenetic mixed model to

42   test for associations with leaf shapes (entire, pinnate, palmate, and costapalmate). We further

43   reconstruct the ancestral leaf shape in palms using multistate speciation and extinction models.

44   We find that high mean annual temperature correlates with dissected shapes. The ancestral leaf

45   shape is entire, and pinnate lineages originated multiple independent times after transitions into

46   polymorphism (species with entire or pinnate individuals). Finally, we compared the frequency

47   of shapes with global temperatures through time through the Cenozoic. Although mean annual

48   temperature has a positive effect on leaf dissection, the relative frequency of pinnate lineages

49   increased as global temperatures cooled through time, potentially through colonization of open

50   more seasonal habitats. Dissection could therefore be beneficial at high temperatures, where

51   other leaf shaped lineages would be highly vulnerable under increased global warming. This

52   study contributes to the understanding of leaf shape evolution and its drivers.

53

57   **1. Introduction**

58   Leaves are the engines of nearly all life on land. They capture carbon dioxide from the

59   atmosphere and convert it into readily accessible nutrients that sustain, directly or indirectly, the

60   functioning and health of ecosystems and their biota. The basic functions they carry out

61   – photosynthesis, transpiration and respiration – depend in turn on temperature and water

62   availability. Because they carry out such critical functions for the plants, leaves are most likely

63   under strong natural selection, resulting in morphological adaptations to the environmental

64   conditions.

65   Throughout the evolution of angiosperms, variation not only in length and width but also

66   in blade dissection (with simple and compound leaves as extremes), margin serration, and

67   contour (e.g. orbicular versus lanceolate leaves) have evolved numerous times independently

68   (Nicotra et al., 2011). Nonetheless, the drivers of leaf shape evolution are poorly known.

69   Research on the evolution and adaptation of leaf shape is often limited to a handful of species

70   (e.g. examples reviewed in Nicotra et al., 2011 and Chitwood & Sinha, 2016; Marcysiak, 2012;

71   Leigh et al., 2017), or to model organisms like *Arabidopsis* (Piazza et al., 2010), which prevents

72   generalization at a larger taxonomic scale.

73   General expectations regarding functionality can be drawn from examining the leaf

74   adaptations in different environments. Traits like leaf dissection, length and, effective width

75   (diameter of largest circle drawn within a leaf margin; Leigh et al., 2017) potentially change with

76   climate, which affects plant temperature regulation and interacts with water availability (Nicotra

77   et al., 2011; Peppe et al., 2011). For instance, plants in environments with extreme temperatures

78   tend to have small or dissected leaves to prevent leaves from reaching damaging temperatures

79   (Gates, 1986; Leigh et al., 2017; Wright et al., 2017). Deeply dissected leaves effectively

80   function as a collection of small leaf units, with faster heat loss through convection than entire

81   leaves of the same area (Givnish, 1979; Gurevitch & Schuepp, 1990), and are less likely to reach

82   damaging temperatures when exposed to extreme heat. Thus, shapes that reduce leaf damage at

83   high temperatures are expected to be beneficial in hot and dry environments (Nicotra et al., 2007;

84   2008; Leigh et al., 2017). Under drought conditions and in arid environments with limited water

85   availability for transpiration, stomata close and high temperatures threaten leaf function. In this

86   case, smaller or deeply dissected shapes reduce overheating and optimize the safety of the leaf

87   (Nardini & Luglio, 2014). Dissection could be beneficial also in species with large and wide

88   leaves that are optimized for high gas exchange, as dissection makes the transportation of water

89   to areas of the blade farthest from the rachis more effective (Givnish, 1979). In contrast, cool

90   climatic conditions may favor entire leaf shapes over dissected shapes, where leaf heating leads

91   to higher temperatures in the leaf compared to the air, which can be beneficial for photosynthesis

92   and growth.

93

94   Leaf shape, particularly size, can be tuned to maximize light capture in environments

95   with limited sunlight. This is particularly relevant for monopodial plants (non-branching plants

96   with a single stem or growth axis) that depend on leaf size or number to increase the total

97   photosynthetic area (Chazdon, 1985; Renninger & Phillips, 2016). However, leaf size is limited

98   by allometry where following Corner's rule, "the larger and sturdy an axis is, the larger and more

99   complicated are its appendages" (Corner, 1949; Tomlinson, 2006). Thus, to produce larger

100   leaves and capture more light, the plant needs to invest significant energy in leaf supporting

101   structures (e.g. petioles and rachis) that are strong enough to resist the stress from wind and rain

102   (Chazdon, 1986). In the forest understory, small leaves with entire shapes could be easier to

103   arrange to maximise light capture than dissected leaves. For very large leaves, dissection allows

104   the leaflets to move independently and reduce the drag produced by strong winds (Niklas, 1992;

105   Vogel, 2009; Blein et al., 2010). Corner's rule has been observed in the palm *Geonoma congesta,*

106   in which leaf size and dissection are positively correlated to stem diameter and crown height

107   (Chazdon, 1991a). Another relationship between dissection and allometry is described by the

108   "rapid growth hypothesis" (Givnish 1978, 1984; Niinemets, 1998), which states that dissection

109   allows plants to grow rapidly during periods of high light availability by maximizing light

110   capture while investing less in wood density. This association between dissection and growth has

111   been found in Amazonian trees (Malhado et al., 2010). Finally, it has been suggested that

112   dissection has varied ecological roles in herbivory: limiting how effectively herbivores feed

113   (Brown & Lawton, 1991), increasing the chance of herbivory via a correlation with leaf size and

114   growth (Rivero-Lynch et al., 1996), or reducing herbivory by acting like variegated leaves in that

115   patterns of discoloration "distort" the leaf's edges (Givnish, 1990; Campitelli et al., 2008).

116   Leaf shape results from trade-offs between physiological and allometric constraints,

117   phylogenetic history, and natural selection (Givnish, 1987; Tsukaya, 2006; Nicotra et al., 2011).

118   Whether leaf shapes have evolved in response to climatic or phylogenetic constraints, the

119   distribution of leaf shape and their evolution through time should reflect evolutionary processes.

120   In this study, we use palms (Arecaceae) to understand the macroevolutionary drivers of leaf

121   shape variation. Palms are tropical and subtropical, with 80% of the species distributed within a

122   15-30°C mean annual temperature range (Dransfield et al., 2008), and which exhibit high leaf

123   shape variation compared to other monocots (Horn et al., 2009; Gunawardena & Dengler, 2004).

124   Palms are primarily monopodial (i.e. do not branch) with non-deciduous leaves (Tomlinson,

125   2006; Dransfield et al., 2008), allowing us to control for the effect of branching strategies over

126   leaf-climate relationships.

127   Here, we hypothesise that dissection is beneficial in high temperatures. If this is the case,

128   we expect temperature to have a positive effect on the distribution of dissection throughout the

129   palm phylogeny. We also hypothesise that taller species are more likely to have dissected leaves

130   as dissection could allow for large leaves that scale with plant height. In this case, we expect

131   larger plants to be dissected because dissection allows for larger leaves that are more resistant to

132   mechanical damage and that have better weight distribution along the rachis, hence a positive

133   effect of plant height on dissection. We tested these predictions for extant taxa over geological

134   time scale. On the one hand, if our predictions are true, extant variations in climatic conditions

135   across ecoregions should predict the current distribution of palms and leaf shapes. On the other

136   hand, the evolution of leaf shapes through time since the origin of palms should reflect major

137   global climatic changes that occurred since the Late Cretaceous, when palms are thought to have

138   originated (Dransfield et al., 2008). Here, we contribute to the knowledge gap concerning

139   climatic factors and plant allometry. Understanding the evolution of leaf shape through past and

140   current environmental conditions provides a context for predicting plant responses to changing

141   climates (Chitwood & Sinha., 2016).

142   **2. Methods**

143   We conducted all GLMMs and ancestral trait reconstruction analyses at the species level

144   using a time-calibrated Maximum Clade Credibility tree generated from the tree distribution

145   generated originally by Faurby et al. (2016) and updated by Hill et al. (unpublished). The

146   phylogeny includes 2550 species that were used to annotate leaf shapes, recover coordinate

147   records from the Global Biodiversity Information Facility (GBIF), and estimate species medians

148   for the climatic and allometric variables. We standardized the taxonomic identifications across

149   all data sources using the Kew's World Checklist of Selected Plant Families (WCSP) for

150   Arecaceae (Govaerts et al., 2020). We removed all GBIF records which could not be

151   unambiguously assigned to any of the species accepted by the WCSP.

152

153   *Leaf shape in palms*

154   Leaf shape variation in palms can be described by three main features: size, plication and

155   dissection. For size, palm leaves can be as small as 15 cm in length (*Chamaedorea tuerckheimii,*

156   Dransfield et al., 2008), as wide as 8 m (in the cospalmate *Corypha umbraculifera*; Tomlinson,

157   2006), and as large as 25 m in length (*Raphia regalis*; Hallé, 1977). Plication refers to leaf

158 folding, leaf blades are folded like accordions as they develop, and the type of plication depends

159 on whether the folds are on the upper (induplicate) or lower (reduplicate) ridges. Plication is

160 highly phylogenetically conserved within subfamilies with very few exceptions; the only

161 induplicate subfamily is Coryphoideae (except for the tribe Trachycarpeae, Fig. 1), whereas

162 Calamoideae, Nypoideae, Ceroxyloideae, and Arecoideae are all reduplicate (Dransfield et al.,

163 2008). Finally, palm leaves are either entire or dissected. Dissected leaves usually form from

164 entire blades as they develop and can be pinnate, palmate or costapalmate depending on the

165 length of the leaf rachis and the presence of a costa (an extension of the leaf axis; Dransfield et

166 al., 2008). Interestingly, some palm species are polymorphic (within-species leaf shape variation

167 in which individuals have either entire or dissected leaves), but in such cases, polymorphism

168 only involves entire and pinnate shapes. For the latter, it is worth noting that genomic analyses

169 (e.g. Loiseau et al., 2019) have confirmed that at least some of them represent true

170 polymorphism within populations rather than issues of taxonomy with different taxa currently

171 grouped under one species name being polymorphic.

172

173 Based on the information available on Genera Palmarum II (Dransfield et al., 2008) and

174 PalmWeb (http://www.palmweb.org/, last consulted in October 2019), we classified all species

175 into "entire", "pinnate", "bipinnate", "palmate" (costapalmate and palmate), and "polymorphic"

176 categories, depending on their leaf shape. We merged the costapalmate and palmate shapes

177 because their leaf blades are highly similar and only differ in the costa. We removed the

178 bipinnate shape category from all analyses because the category includes only 14 out of the 2550

179 species. Of the species included, the large majority are pinnate (67.7%, Supporting Information

180 Table S1), followed by palmate and entire (22.19% and 5.5% respectively). Only 75 (3.87%)

181 species are polymorphic. They were included in the ancestral state estimation analyses but

182 excluded from the GLMMs because they cannot be assigned to a unique shape category in our

183 models (Supporting Information Table S2).

184

185 *Palm allometry data*

186 We annotated all species using the data in Palm_Traits v.1 (Kissling et al., 2019) and

187 scored maximum leaf number, maximum petiole length, plant height, and blade length variables.

188 We calculated plant height by adding the variables 'MaxStemHeight_m',

189 'Max_Petiole_length_m' and 'Max_Blade_Length_m', with 'MaxStemHeight_m' set to zero for

190 acaulescent species. We could annotate 47-77% of the species in the phylogeny depending on the

191 variable. Species without annotations were either not annotated in Palm_Traits v.1 or were

192 climbing species (465 species, Supporting Information Table S3); the latter removed because

193 their life strategies differ from the rest of palms and their stem height is not readily comparable.

194

195 *Climatic and ecoregion data*

196   We downloaded 885,130 occurrences of palm species from GBIF (last consulted, January

197 2019), from which we excluded fossil occurrences and data with missing coordinates. We used

198 the R package *CoordinateCleaner* (Zizka et al., 2019) to remove duplicate coordinates per

199 species, records nearby science institutions, coordinates on bodies of water, and coordinates in

200 city/country centroids, all using a buffer of 5000 m). We further used a custom Python script

201 (https://github.com/mftorres/palm_leaf) and the World Geographical Scheme for Recording

202 Plant Distributions maps (TDWG; Brummitt, 2001) to remove species coordinates falling outside

203 the botanical countries listed as their native areas in the WCSP database. We obtained 56,372

204 clean coordinate records representing 70% of the species (Supporting Information Table S4),

205 which we used to extract all WorldClim1.4 climatic variables with *dismo* v1.1.4 (Hijmans et al.,

206 2017) and *ade4* v1.7.15 (Dray & Dufour., 2007), both R packages (R Core Team, 2018). We

207 used the extracted WorldClim1.4 data to estimate the de Martonne's Aridity Index (de Martonne,

208 1925) for each record as the annual precipitation in mm divided by the mean annual temperature

209 in Celsius + 10. Finally, we estimated the species medians for every climatic variable from

210 which we could extract the information.

211

212   After annotating climatic and allometric variables for 1212 to 1439 species out of the

213 2550 species in the phylogeny (depending on record and data availability), we examined the

214 correlation between variables and chose for the models the variables with a Spearman's

215 coefficient < 0.7 (Supporting Information Fig. S1). We additionally estimated the variance

216 inflation factor for all variables using the function *vif* and removed those above a threshold of 0.7

217 (USDM v1.1.18; Naimi, 2015). We chose five climatic and two allometric variables: mean

218 annual temperature (°C), temperature seasonality ($\sigma*100$), annual precipitation (mm);

219 precipitation seasonality ($\sigma*100$), aridity (mm/°C), maximum leaf number, and plant height (m).

220 For our palm data, other climatic variables that we do not include in the models (like the

221 maximum and minimum temperature/precipitation of the warmest month) had a high Spearman's

222 correlation coefficient (> 0.7) to one or a few of the variables selected (Supporting Information

223 Fig. S1). Annual precipitation and aridity were highly correlated (Spearman's correlation

224 coefficient = 0.9; Supporting Information Fig. S1); however, because water stress increases the

225 damaging effect of high temperatures and can be a selective pressure for leaf shape, we removed

226 aridity from models that included precipitation and vice versa. Similarly, plant height was highly

227 correlated with the understory/canopy trait and we kept plant height as a proxy for

228 understory/canopy from here on. All variables included in the models were $\log^{10}$-transformed

229 (with the exception of mean annual temperature) and standardized to have zero mean and a

230 standard deviation of one (Supporting Information Table S4). Finally, we annotated the species

231 ecoregions based on Olson et al. (2001) and as described in Cássia-Silva et al. (2019).

232

233 *Generalized linear mixed models*

234 We fit a series of GLMMs using all selected variables (except for aridity and annual

235 precipitation, see Results), removing one variable in each iteration, to evaluate the effect. We

236 used logistic regressions to distinguish the variables associated with leaf shape using a series of

237 pairwise comparisons; pinnate (0) vs. palmate (1), entire (0) vs. palmate (1), and entire (0) vs.

238 pinnate (1). All regressions were done using Bayesian phylogenetic logistic regressions

239 implemented in the R package *MCMCglmmRAM* (Hadfield, 2015). For computational

240 constraints, we ran every model on 42 (Adams, 1979) phylogenies randomly selected from the

241 distribution of phylogenies generated by Faurby et al. (2016) and updated in Hill et al. (2021),

242 setting them as a random effect. For every model on the 42 phylogenies, we ran two independent

243 chains of 10,000,000 iterations each, with a thinning of 8,000, and a burn-in of 10% of the

244 sampling. Analyses were run at the Chalmers University of Technology cluster through the

245 Swedish National Infrastructure for Computing (SNIC; Gothenburg, Sweden). We ran the

246 models until the chains converged, here defined as effective sampling sizes for all variables

247 higher than 100, and autocorrelation between values lower than 0.2. We evaluated the

248 significance of the effects for every predictor variable based on whether the 2.5 and 97.5%

249 quartiles of the estimated density overlapped zero (Supporting Information Table S5).

250

251   *Ancestral state estimation*

252   In order to select an appropriate model for the ancestral trait estimation, we first used the

253   Multi-State Speciation and Extinction (MuSSE) model from the R package *diversitree* (FitzJohn,

254   2012) to compare speciation, extinction, and transition rates between leaf shapes. We adjusted

255   the leaf shape dataset to ensure we had enough power to estimate parameters: 1) We did not

256   include plication in the analyses due to its high phylogenetic clustering (Fig. 1; but see the

257   discussion about how all folded palmate leaves across plants are similar due to leaf folding inside

258   the bud in Couturier et al., 2011); 2) we created a "polymorphic" category for species exhibiting

259   more than one shape. 3) We excluded all species for which leaf shape information was

260   unavailable from the analyses. This resulted in a dataset containing 2543 species and four

261   character states: palmate (costapalmate + palmate), pinnate, entire and polymorphic.

262   Polymorphism only includes those species that have both pinnate and entire leaves, but never

263   palmate or costapalmate leaves. Hence, when designing the MuSSE models we assumed direct

264   transitions between palmate leaves and polymorphic states (pinnate + entire) to be impossible

265   and therefore constrained the corresponding transition parameters to zero. Because of the large

266   number of parameters for the MuSSE model remaining (18 parameters, Supporting Information

267   Fig. S2), we selected the best-fitting model using a backward model selection procedure on the

268   maximum clade credibility tree only. We started fitting a model in which all remaining

269   parameters were unconstrained, using maximum likelihood estimation (ML). We then proceeded

270   with reducing the model, one constraint at a time until the AIC score did not improve. At each

271   step, all models with one more constraint than the previous (more complex) model were fitted

272   and ranked according to their AIC scores. The model with the lowest AIC score was retained as

273   the base model for the next step, providing it was significantly lower ($\Delta AIC > 2$) than the best

274   model from the previous step. Using the best-fitting model as determined above, we performed

275   an MCMC analysis to compare posterior distributions of parameters. We ran the MCMC for

276   10,000,000 generations, sampling every 8,000 generations and a burnin of 1,100. We used the

277   ML parameter estimation as starting points for the MCMC. AIC scores for determining the best

278   MuSSE models stopped improving at the tenth step during the backward model selection

279   procedure, representing 315 models, of which six did not converge.

280

281   We used the best-fitting MuSSE model to estimate ancestral states across the tree. Based

282   on this ancestral state estimation we estimated the number and rate of transitions through time as

283   well as the relative frequency of lineages of each leaf type through time. To do so, we sampled

284   states at nodes 100 times, using the relative probabilities of leaf shape estimated for each node as

285   sampling probabilities. For each iteration, at each branch where a state transition occurred we

286   sampled a random timing from a uniform distribution for the event along that branch. Finally, for

287   each iteration, we counted the number of transitions happening within a 5 million year sliding

288   window to obtain the number of state transitions through time. We calculated the rate of

289   transition through time by dividing the number of transitions by the sum of branch lengths within

290   each time interval. We repeated the procedure for one iteration out of the 100, but instead of

291   calculating the number of transitions, we calculated the relative frequency of lineages exhibiting

292   each type of leaf shape through time. Finally, we compared the relative shape frequency through

293   time with the global temperature change scale computed for an ice-free ocean extrapolated by

294   Condamine et al. (2020) and based on data from Zachos et al. (2001).

295

296   **3. Results**

297   *Leaf shape and climate*

298   Palms are widely distributed across climatic gradients (except for habitats where extreme

299   frost occurs). However, leaf shapes are not distributed evenly throughout the geographic

300   distribution of the palm family (Figs. 1 and S7-10). The distribution of pinnate and palmate

301   species extends farther from the equator into areas of substantial water scarcity and regular

302   exposure to extreme temperatures. These areas include the tropical and subtropical moist and dry

303   broadleaf forests, temperate forests, grasslands and savannahs, and desert and xeric shrublands

304   (Supporting Information Fig. S10). Meanwhile, the distribution of entire-leaved species is

305   concentrated in tropical areas near the equator where annual temperature and precipitation are

306   more constant. We observe a similar pattern for all climatic variables considered here, in which

307   the species median distributions of pinnate and palmate species are wider than the species

308   median distributions of species with entire leaves (Supporting Information Fig. S3 and Table

309   S6). For mean annual temperatures for example, pinnate species range between 12.8°C and

310   27.7°C (14.9°C difference), palmates range between 13.8°C and 28.1°C (14.3°C difference), and

311   species with entire leaves range between 14.1°C and 27°C (12.9°C difference). However, the

312   median of the distribution for mean annual temperatures is higher for palmate (25.1°C), then

313   entire (24.6°C), and lowest for pinnate species (23.7°C).

314

315   The GLMMs identified a strong association between temperature and dissection when

316   considering entire and pinnate shapes and a less clear pattern when considering palmate in

317   combination with the other two shapes. When comparing entire versus pinnate shapes, the model

318   including all variables showed a significant positive association between mean annual

319   temperature and pinnate shape (P = 0.002). That means that high mean annual temperatures

320   make the pinnate shape more likely. The significance of the positive association persists even

321   when only climatic variables are considered (Figs. 2a and S4). When the model included one

322   climatic and one allometric variable, both had a significant association with pinnate shape.

323   However, when models included only a single variable, the only one that had a significant

324   positive association with pinnate shape was temperature seasonality (P = 0.001, Figs. 2c and S4).

325

326   When comparing pinnate versus palmate, none of the variables were significant when

327   they were all included in the same model. However, when considering only the climatic variables

328   and none of the allometric ones, mean annual temperature was significant and had a positive

329   association with palmate shapes (0.018 < P < 0.022). With this, palmate shape is more likely at

330   high mean annual temperatures, if only climate is considered. When the model included one

331   climatic and one allometric variable, the climatic variable had a significant positive association

332   with palmate shape (and negative with pinnate) if the allometric variable was plant height.

333   Considering one climatic variable together with maximum leaf number resulted in a lack of

334   significant associations (Fig. 2a). Finally, when comparing entire versus palmate shapes, none of

335   the variables had a significant effect regardless of the model (Fig. 2a-c, Supporting Information

336   Table S5).

337

338   No significant associations were found with precipitation and aridity unless each was

339   included in the model together with one more variable (Figs. 2a and S4), indicating that the

340   variation in leaf shape they explain is minimal. Precipitation and aridity had a significant and

341   positive effect in models when the other variables are plant height (pinnate versus palmate) and

342   leaf number (entire versus pinnate). However, the Spearman's correlation coefficient between

343   precipitation and plant height/leaf number, and those between aridity and the same two variables,

344   were small (-0.2 in all cases except between aridity and leaf number, which is -0.3). Finally, for

345   our data and all shape comparisons, the association between shape and temperature was not

346   restricted to annual mean estimates but potentially extends to other variables highly correlated

347   with mean annual temperature including the mean temperature of the coldest month, and the

348   mean temperatures of the driest, warmest, and coldest quarter (Spearman's correlation

349   coefficient = 0.9 for the variables mentioned; Supporting Information Fig. S1).

350

351   *Allometry and shape*

352   For our data, plant height was highly correlated with growth habit (Spearman's

353   correlation coefficient = 0.8), understory versus canopy (since most palms are found in forested

354   environments); therefore, we did not consider habit explicitly in the models. However, it is worth

355   noting that almost all species with entire leaves live in the understory, while pinnate and palmate

356   species live in both (Supporting Information Fig. S3). Pinnate and palmate species tend to be

357   much larger than species with entire leaves, with median heights of 8.7 m (74.4 m max) in

358   pinnate and 6.6 m (54.9 m max) in palmate species. In contrast, species with entire leaves have a

359   median height of 4.9 m and a maximum height of 39 m, leaf length included in all cases.

360   Regarding leaf number, pinnate and species with entire leaves have a similar median of 10.9

361   leaves (and a maximum of 55 and 41 respectively) while palmate species tend to have more, with

362   a median of 22 and a maximum of 75 leaves (*Livistona endauensis*; Kissling et al., 2019).

363

364   From the GLMMs, we only found a significant association between plant height and

365   shape when comparing entire and pinnate shapes and the direction of the effect changed

366   depending on which other variables were present in the model. Plant height had a significant

367   negative association with pinnate shape when all variables were considered in the model (P =

368   0.008); however, the effect of plant height was a lot smaller than the effect of mean annual

369   temperature (Figs. 2a-b and S4), suggesting that while high mean annual temperatures make

370   pinnate shapes more likely, large plant height make them less likely. Moreover, the directionality

371   of the association between plant height (or maximum leaf number) and pinnate shape varied. The

372   association was negative when models included mean annual temperature, annual precipitation,

373   aridity, and maximum leaf number; the effect was positive when the model included temperature

374   seasonality or precipitation seasonality (Fig. 2a). Only when the model included plant height and

375   nothing else, did it have a significant positive association with pinnate shape (P = 0.008, Fig. 2c).

376

377   *Ancestral state estimation*

378   The best-fitting model (Supporting Information Fig. S2) had nine parameters and resulted

379   from 1) merging the speciation rates for palmate, pinnate, and entire shapes; 2) merging the

380   extinction rates for entire and polymorphic shapes; and 3) constraining six transition parameters.

381   The resulting speciation rate of polymorphic species was more than twice higher than that of the

382   others (Supporting Information Fig. S5). Extinction rate for the polymorphic and entire shape

383   lineages was estimated as zero (lineage/unit of time, $l^{-1}my^{-1}$). Pinnate lineages had more than

384   twice the extinction rate of palmate lineages, which in turn was higher than the extinction rate for

385   entire lineages. The resulting net diversification for pinnate lineages was close to zero. Palmate

386   lineages followed with a mean net diversification estimated around 0.1 $l^{-1}my^{-1}$ and entire lineages

387   0.2. Polymorphic lineages clearly had the highest net diversification rate with a posterior

388   distribution averaging around 0.5 $l^{-1}my^{-1}$.

389

390   Ancestral state estimation based on the best fitting-model inferred entire leaves as the

391   most probable state at the root (Fig. 3). Interestingly, according to our model, pinnate leaf

392   lineages, the most common extant leaf type, originated multiple independent times from entire

393   leaves after polymorphic transition periods. We found that the overall rate of state transitions

394   through time remained relatively constant (Supporting Information Fig. S6). The relative

395   frequency plot (Fig. 4) shows that entire leaves dominated during the early period of

396   diversification, in the Late Cretaceous between 100-80 Million years ago (Mya). However, their

397   relative frequency decreased through time at a steady rate, slowly replaced mainly by pinnate

398   leaves since ca. 80 Mya. The first palmate lineages appeared after the pinnate lineages and their

399   relative frequency remained approximately the same through time, averaging around 0.1.

400

401   **4. Discussion**

402   In this study, we explore 1) the associations between leaf shape and climatic and

403   allometric drivers whilst controlling for phylogenetic relationships 2) reconstruct the ancestral

404   leaf shape of palms; and 3) compare shape frequencies and temperature trends through time. We

405 found that 1) temperature and not plant allometry drives leaf shape; 2) that the ancestor to all

406 palms likely had entire leaves; 3) and that trends in shape frequency do not mirror trends in

407 temperature through time (at least not among the lineages that survived until present day). These

408 findings support the hypothesis that temperature and not allometry explain extant leaf shape

409 distributions in palms and suggest shape as a potential adaptive response to heat.

410

411 *Leaf dissection and climate*

412 Species with dissected leaves, especially if pinnate, are more frequent where mean annual

413 temperatures are high (Fig. 2a). This is congruent with the wider geographic range of dissected

414 species compared to those with entire leaves; dissected leaf species are distributed throughout the

415 driest and most seasonal ranges where palms are found (Figs. S3 and S8-S10) and dissection is

416 likely an advantageous trait to avoid overheating (Nicotra et al., 2007; 2008; Leigh et al., 2017).

417 These papers note that deeply dissected palm leaves are analogous to compound or dissected

418 leaves in eudicots. The width of each pinnae is often narrower than the width of the whole leaf,

419 and under the same conditions, narrower leaves lose heat to the air faster and reach damaging

420 temperatures more rarely than wider leaves. During water scarcity or in dry environments,

421 avoiding damaging temperatures in the leaf surface is key for protecting the photosynthetic

422 machinery. Here, dissection allows species to withstand temperature extremes, seasonal

423 variation, and water stress (Figs. S3). In areas where water is available, like the moist forest

424 where all shapes occur, dissection is likely less crucial and has less advantage over other shapes.

425

426 The association between temperature and dissection is not significant when entire and

427 palmate shapes are compared (Figs. 2 and S4); there are three non-mutually exclusive

428 explanations for this. First, the discrete shape categories in our models might not capture the

429 continuous variation within shapes and could be insufficient for unveiling the climate-shape

430 association. For example, palmate-shape species within *Licuala* and *Saribus* are shallowly

431 dissected and resemble eudicot leaves with toothed margins that are closer to an entire shape.

432 Second, anatomical traits unrelated to shape could be the key adaptations to different

433 environments (Horn et al., 2009). The loss of non-lignified fiber bundles in the leaf mesophyll or

434 the presence of bridge-like veins connecting the adaxial and abaxial layers of the leaf, are traits

435 thought to be advantageous in dry environments (Kenzo et al., 2007; Horn et al., 2009). Different

436   species can evolve different strategies to respond to the same environmental challenges. Third,

437   the correlation between climate and shape are difficult to disentangle from a phylogenetic effect

438   due to a strong geographic structuring of related lineages, particularly in the case of the

439   Coryphoideae subfamily to which the majority of palmate and costapalmate species belong.

440   Models considering continuous variation and data on intra and interspecific variation in

441   dissection depth within palmate shapes are necessary to better understand the relationship

442   between climate and palmate shapes.

443

444   Leaf dissection and margin serration have been found to respond quickly to changes in

445   mean annual temperature in the eudicot *Acer rubrum* (Royer et al., 2009). Similar temperature-

446   shape associations have been explored in other eudicots (Nakayama et al., 2014; Chitwood &

447   Shina, 2016); however, research is lacking regarding monocots and the lineage-specific

448   mechanisms behind shape convergence across angiosperms hinders the comparisons between

449   monocots and eudicots (Conklin et al., 2019). A better understanding of the mechanisms by

450   which climate interacts with shape development will come from future studies addressing shape

451   variation quantitatively (Chitwood & Sinha., 2016; Kissling et al., 2018). Quantitative trait data

452   on leaf shape is still lacking for most palms, but data comprising intraspecific variation for some

453   morphological traits like that published in Lenters et al (2021), open the door to more

454   comprehensive analyses. Finally, global temperatures are likely to increase over the coming

455   decades. This could have implications over which palm lineages are able to survive in hotter

456   environments and which could perish. Most palm species that are currently naturalised in areas

457   outside their native distribution are those that originated in open and dry habitats, not in moist

458   forests (Fehr et al., 2020), and all have dissected leaf shapes. Understanding the association

459   between climate and shape and other leaf traits, is necessary to predict potential future

460   homogenization of palm communities in the face of climate change.

461

462   *Leaf shape and plant allometry*

463   We expected plant height to influence leaf shape via allometry (large plants have large

464   leaves that are likely dissected to avoid mechanical damage; Corner, 1949; Chazdon, 1991b).

465   Regarding allometry, plant height has a negative effect on dissection when pinnate and entire

466   shapes are compared, but the effect is comparatively smaller than that of mean annual

467 temperature and not observed in other models (Figs. 2 and S4). Tall heights are problematic at

468 extremely high temperatures and water scarcity because water transport and transpiration

469 becomes harder with increased plant height (hydraulic limitation hypothesis; Ryan & Yoder,

470 1997; Ryan, 2006; Olson et al., 2018). Because pinnate species are more likely at high mean

471 temperatures with potentially high water stress or seasonality in water availability, extremely tall

472 pinnate species are at a disadvantage. However, the positive association between tall heights and

473 dissection only appears when we account for seasonality in temperature or precipitation and

474 nothing else. There might be interactions between mean annual temperature, plant height, and

475 water availability for which we do not explicitly test there. Moreover, traits related with the

476 position, lignification, and structure of cells within the leaf tissue could provide the blade with a

477 resistance to mechanical damage that does not involve shape. This is the case for palmate and

478 cospalmate species, which have veins arranged in a network that provides better leaf support and

479 tolerance to hydraulic disruption (Sack et al., 2008), but data to test such effects systematically

480 across the family are sadly not available.

481 We also expected plant height to relate to dissection via the rapid growth hypothesis

482 (Givnish, 1978; 1984; Niinemets, 1998; Malhado et al., 2010). Malhado et al. (2010) tested this

483 hypothesis and found an association between dissection and both low wood density and rapid

484 diameter growth. Dissection is adaptive under favourable light conditions because producing

485 compound or dissected leaves is physiologically less expensive than branching and thus

486 promotes rapid vertical growth (Malhado et al., 2010). However, most palm species are

487 monopodial and are not under the same selection forces. Moreover, Malhado and coauthors

488 (2010) excluded all palms from their analyses and we cannot directly compare our results with

489 theirs.

490

Leaf shape evolution

492 We found that dissected leaf shapes evolved frequently during the history of palms, a

493 result consistent with previous research (Fig. 3). Using 178 taxa with pinnate or palmate species

494 only, Horn et al. (2009) reached the identical conclusion that shape is homoplasious and changes

495 between states fast.

496 According to our model and data available, early crown lineages of palms had entire

497 leaves, while palmate and pinnate shapes appeared later multiple times independently. The

498   earliest reliably dated and identified leaf fossil known to this day is that of *Sabalites carolinensis*

499   from the Santonian-Campanian (fossil dating from 86-82 Mya), which exhibits a costapalmate

500   shape (Berry, 1914). However, the oldest estimated appearance of palmate and costapalmate

501   lineages occured between 78-80 Mya and most likely corresponds to the stem of Coryphoideae,

502   slightly more recent than *S. carolinensis*. The earliest pinnate fossil appeared during the

503   Campanian (fossil date 76-70 Mya; Dransfield et al., 2008). According to our ancestral

504   estimation, the first pinnate leaves appeared with the emergence of polymorphic lineages

505   approximately 85 Mya, predating the oldest pinnate fossil. Fossils remain rare and provide at

506   best a minimum age for any taxon or morphological character; the absence of old fossils

507   exhibiting entire shapes is surprising and is explained either by the incomplete nature of the

508   fossil record or by our ancestral state estimation of leaf evolution. We note however that the

509   mismatch between the age of the palmate fossils and the emergence of its shape lineage can

510   result from the uncertainty around the time estimates in the phylogeny we used.

511   One interesting outcome of our model and ancestral state estimation is the role played by

512   polymorphic lineages. Polymorphism, which only concerns combinations of entire and pinnate

513   shapes, appears as a transitional state between these two shapes forming an evolutionary bridge

514   between ancestral lineages with non-polymorphic leaf shapes. Maximum Likelihood estimates of

515   transition parameters also indicate that there is a strong directionality; the highest transition rates

516   being from polymorphic toward pinnate shapes, the second highest was by transitions from entire

517   shapes towards polymorphism. As a result, polymorphic lineages are maintained in our ancestral

518   state estimation at a constant proportion of about 20% of all palm lineages throughout the history

519   of palm (although extant polymorphic species are around 3%). We also found that pinnate,

520   palmate, and entire lineages do not have significantly different speciation rates but polymorphic

521   lineages have an estimated speciation rate about five times higher than the others. In terms of

522   extinction however, pinnate lineages have the highest rate, followed by palmate and finally entire

523   and polymorphic lineages. These results suggest that the high number of extant pinnate lineages

524   do not result from high diversification rates, but from a high speciation rate of polymorphic

525   lineages combined with a high rate of independent transitions towards pinnate leaves.

526

527   *Leaf shape through time*

528   The first non-polymorphic pinnate lineages appeared only during the Cretaceous-
529   Paleogene transition period (Fig. 4). At that time, palms were dominated by entire leaves (70%
530   of lineages), and remained so until the Eocene-Oligocene transition period. The late Cretaceous
531   and the early Paleogene were periods of high global temperatures, with ever-wet tropical areas
532   distributed towards high latitudes. Palms thrived during this period forming the Palmae Province
533   that covered South America, Africa and India (Pan et al., 2006). The large extent of warm and
534   humid conditions may have promoted the initial diversification of entire leaves during the early
535   period of palms diversification.

536   During the Eocene and the Oligocene however, pinnate shapes rapidly became dominant
537   (Fig. 4). At the end of the Eocene, pinnate lineages represented about 40% of the lineages and
538   20% were entire. During the Eocene, global temperatures decreased at a relatively fast pace. The
539   increasing dominance of pinnate leaves during this period of global cooling refutes the
540   hypothesis that pinnate lineages would thrive during periods of warmer climate. We did not
541   identify a period of fast sudden evolutionary changes, also refuting the idea that a specific and
542   short event drove the evolutionary changes in leaf configuration.

543   We suggest that the turnover in leaf shapes was not a response to temperature variation
544   only but took place in the context of global climate and habitat changes happening throughout
545   the Cenozoic. Past the late Cretaceous and Paleocene during which palms reached their
546   maximum extent (Bogotá-Ángel et al., 2021), ever-wet forests started to contract toward lower
547   latitudes. Kissling et al. (2012) showed that the distribution of tropical rainforests only declined
548   during the last 50 My and in all tropical regions simultaneously. After the Early Eocene Climate
549   Optimum (47 Mya) and around the Eocene-Oligocene Transition (34 Mya), temperature and
550   wetness decreased at northern high latitudes (Pound & Salzmann, 2017; Hutchinson et al., 2021).
551   Seasonality at high latitudes also increased (Eldrett et al., 2009) and drier and temperate
552   environments expanded at the expense of tropical rainforests (Graham, 2011; Morley, 2011). As
553   such, pinnate lineages may have repeatedly evolved and diversified as a response to these new
554   conditions, which selected for palms adapted to drier environments, at least during parts of the
555   year (Cássia-Silva et al, 2019). The first occurrence of pinnate (ca. 80 Mya) and palmate shapes
556   (ca. 70 Mya) both predate the assemblage of dry forests (30-20 Mya; Becerra et al., 2005) and
557   savannahs (10 Mya; Pennington et al., 2006). Currently, palms with pinnate or palmate shapes

558   are found in dry and seasonal ecoregions such as the Tropical and Subtropical dry forests,

559   temperate regions, savannas, and deserts – all ecoregions in which species with entire leaves are

560   not present (Supporting Information Fig. S10).

561

562   **Conclusion**

563   We explored the drivers of leaf shape evolution in palms by testing for associations

564   between shape and current climatic and allometric variables, and by reconstructing the evolution

565   of shape throughout palm evolutionary history. We highlight the importance of considering

566   biotic and abiotic factors when studying the evolution of plant traits. In the case of palms, we

567   found that mean annual temperature is associated with leaf dissection. A small negative effect of

568   plant height on dissection may result from the inefficiency of large plant heights in high

569   temperatures due to water transport constraints. The ancestral state to all extant palms is inferred

570   as entire, from which pinnate shapes emerged via polymorphic states (species with both entire

571   and pinnate individuals) and became more frequent. Palmate species emerged from entire states

572   and their frequency remained constant. Palms are important representative taxa of the tropical

573   forests with more than 2,500 species distributed globally. Thus, exploring how its leaf shape

574   diversity emerged contributes to our understanding of shape and its adaptive potential, especially

575   in light of increasing climatic change and temperature extremes.

576

587

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805
806   **Tables**
807
808   Please see the tables in this shared file:
809   https://docs.google.com/spreadsheets/d/1QJLNBAhUBWG__Rcqfv2j0Ae_mR_7UaEmn6WvB
810   mBN5yU/edit?usp=sharing
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812

813 **FIGURES**

814 Figures are attached at the end in high resolution

815
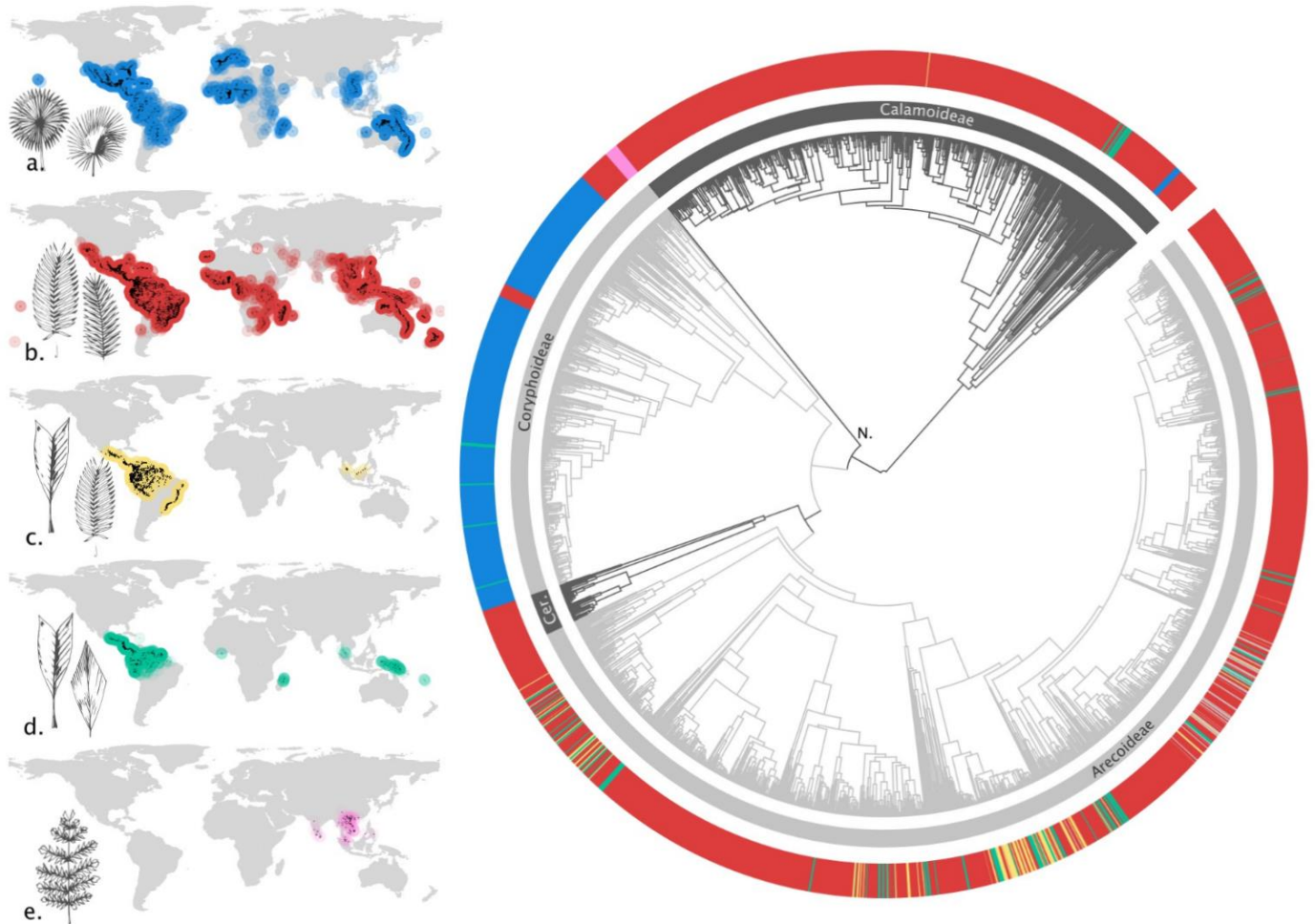
816

817 **Figure 1. Distribution of leaf shapes at a global scale and throughout the phylogeny of**
818 **Palms. Left:** The maps show the approximate distribution of shapes based on cleaned GBIF
819 records alone and the distribution of species with no coordinate records available is not reflected
820 here. Leaf silhouettes were taken from the illustrations in the Genera Palmarum (Dransfield et
821 al., 2008). **Right:** The calibrated maximum clade credibility tree of 2550 palm species generated
822 by Faurby et al. (2016). Dark and light greys are used to distinguish between subfamilies. The
823 outermost ring shows the distribution of leaf shapes across the phylogeny and follows the same
824 color scheme of the maps. **a)** Palmate + Costapalmate, **b)** Pinnate, **c)** Variable within species, **d)**
825 Entire, **e)** Bipinnate. **Cer.**= Ceroxyloideae. **N.**= Nypa.

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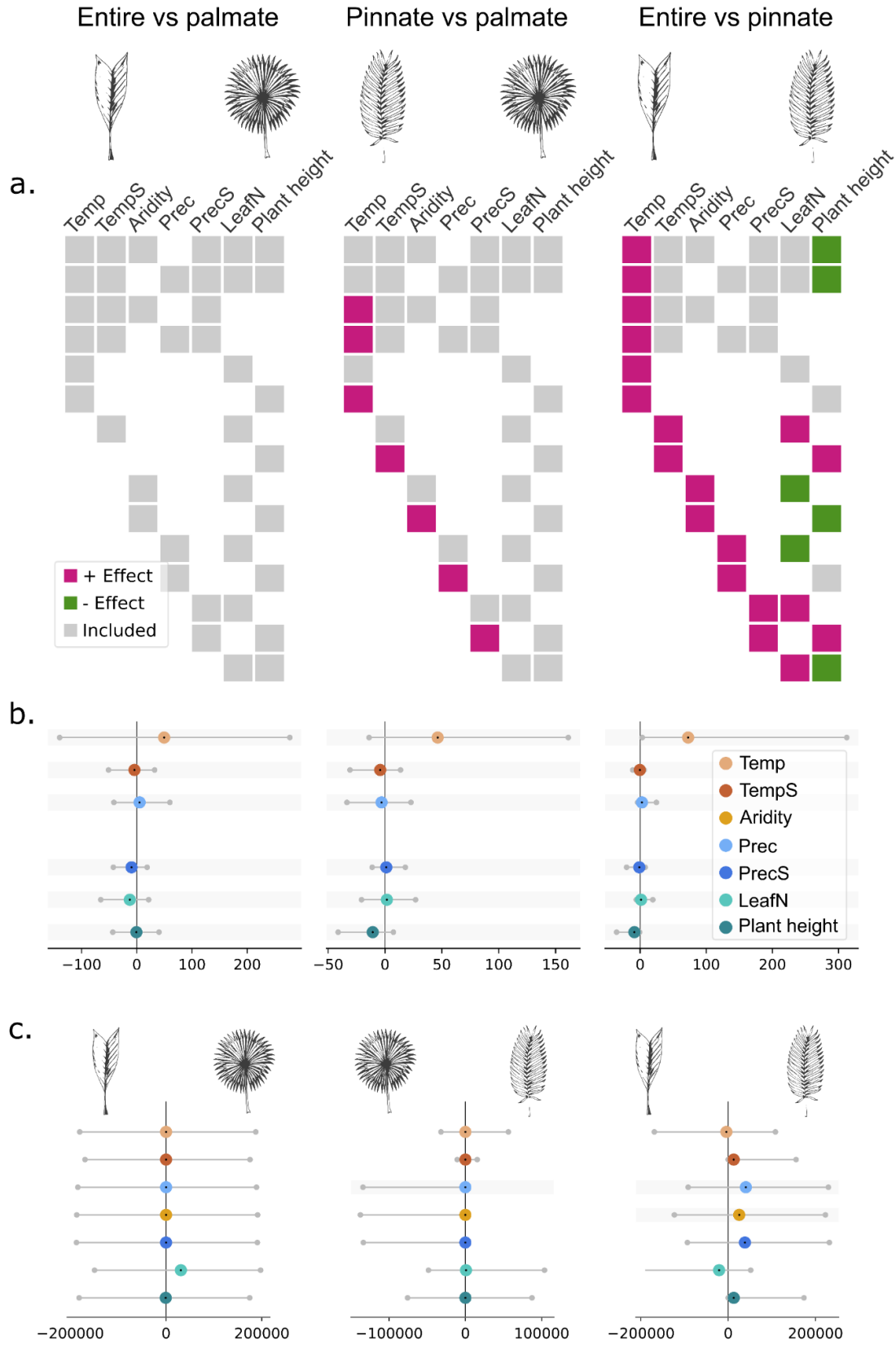
830 **Figure 2. Results of the Generalized Linear Mixed Models (GLMMs).** Leaf shapes show the

831 pair in the models (logistic regression; left = 0, right = 1). **a)** Summarised results from all

832 GLMMs ran; one model per row. Grey boxes represent variables included in each model with

833 non-significant effects, in magenta are the included variables with significant positive effects,

834 and in green the included variables with a significant negative effect. **b)** Distribution of estimates

835 for the most inclusive model (first row in **a**). The colour circle represents the median and the

836 horizontal bars span from the 2.5% to the 97.5% quantiles of the estimated distribution. Results

837 including Aridity instead of Precipitation are similar (Supporting Information Fig. S4). **c)**

838 Summarised results of the models including a single variable, with one model per row. Variables

839 are coded with the same colours as in **b)** and the leaf shapes coded as left = 0 and right = 1.

840 **Temp:** mean annual temperature; **TempS** = temperature seasonality; **Prec** = annual

841 precipitation; **PrecS** = Precipitation seasonality; **LeafN** = Maximum leaf number. Leaf

842 silhouettes were adapted from the illustrations in the Genera Palmarum (Dransfield et al., 2008).
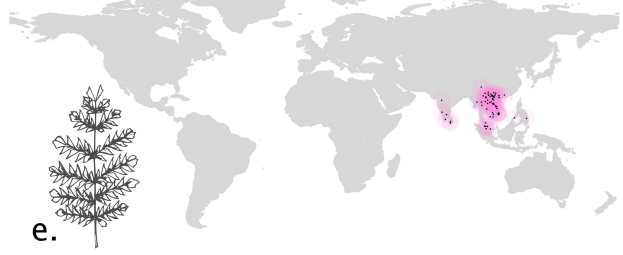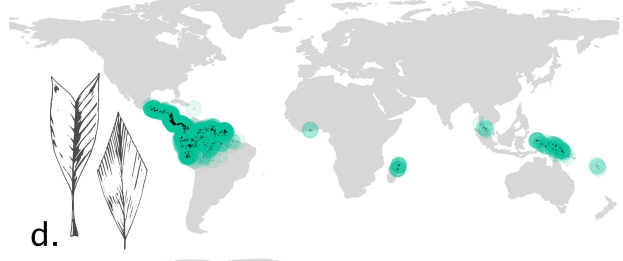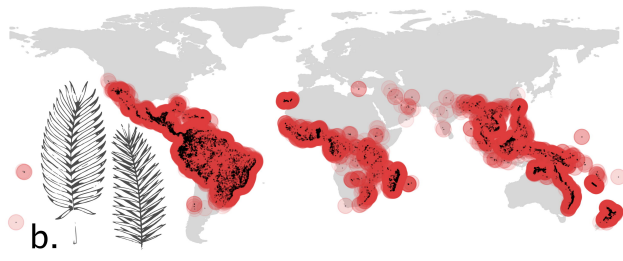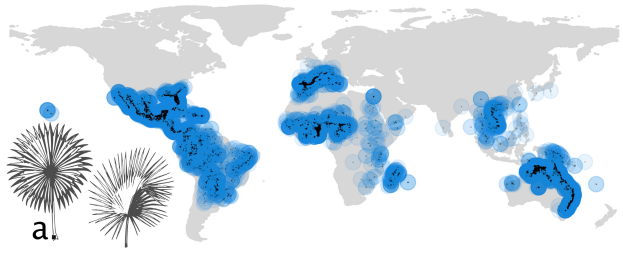
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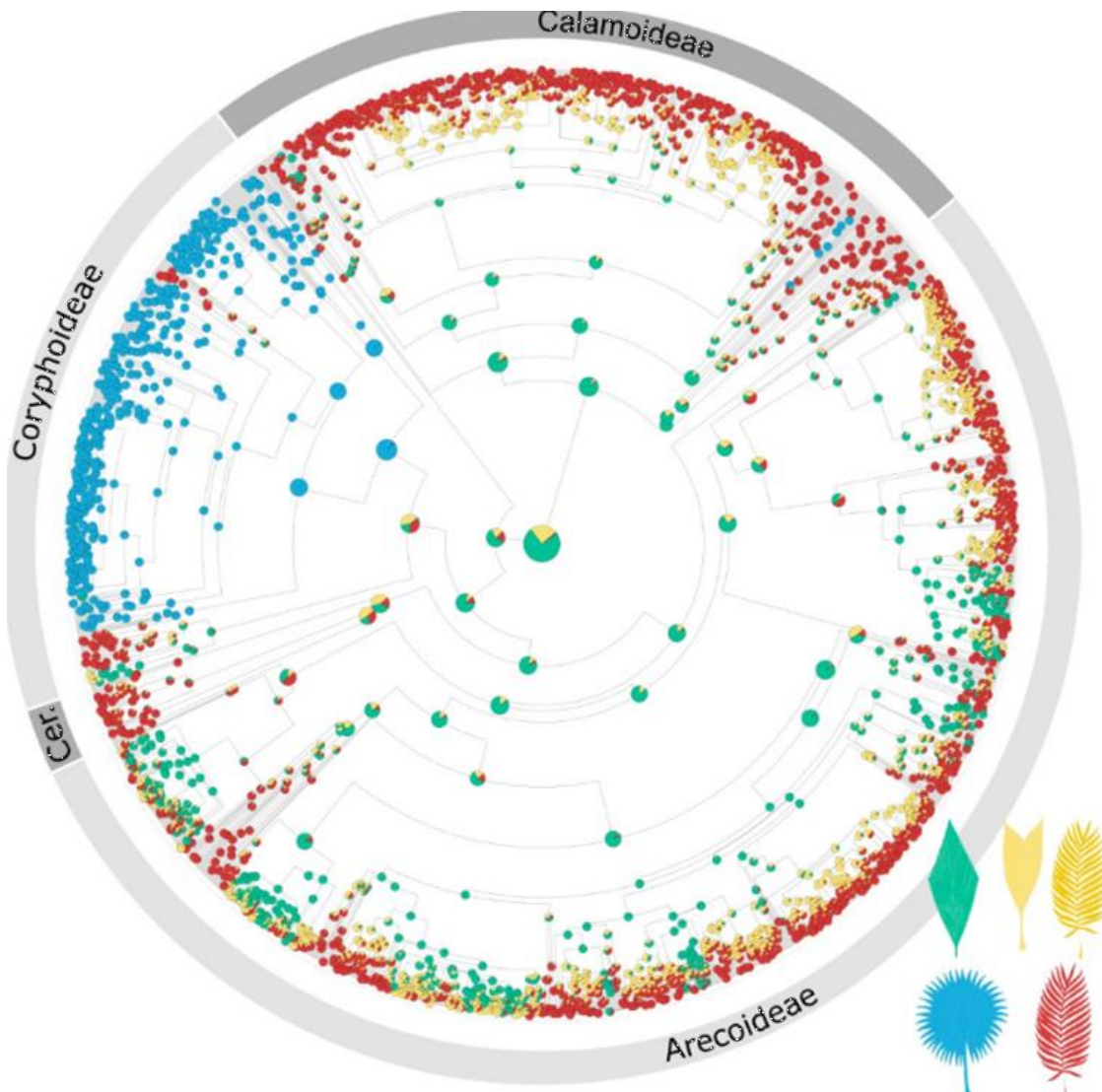
Figure 3. Ancestral state reconstruction of leaf shape across palms (Arecaceae) using the calibrated maximum clade credibility tree generated by Faurby et al., 2016. The pie charts show the probability of each state at the given node. States are color-coded as follows: **Blue** = Palmate (costapalmate+palmate); **red** = Pinnate; **green** =: Entire; **yellow** = Polymorphic (where individuals of the same species have either entire or pinnate leaves). **Cer.** = Ceroxyloideae.
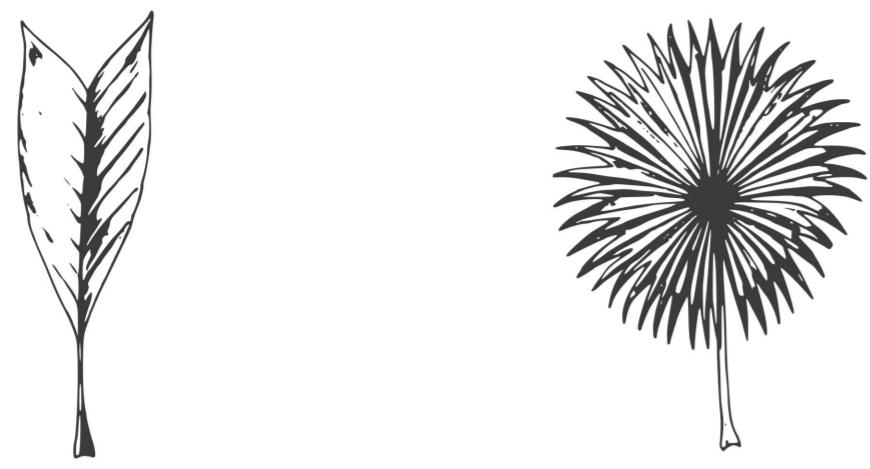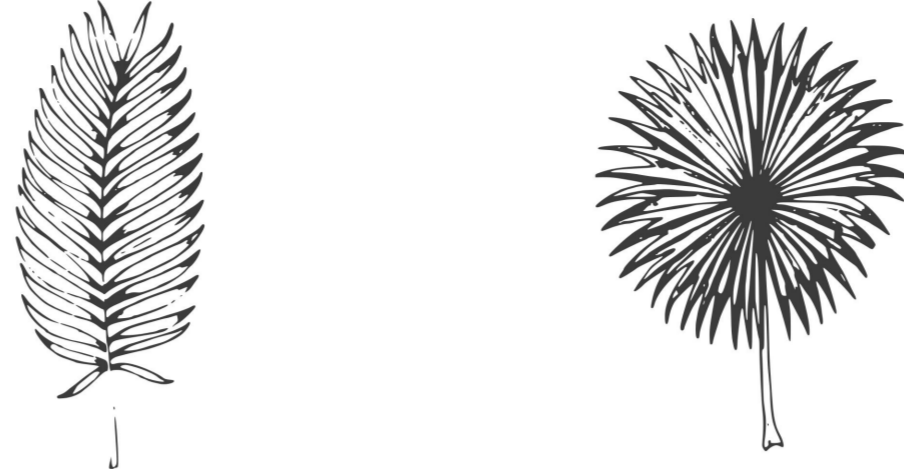
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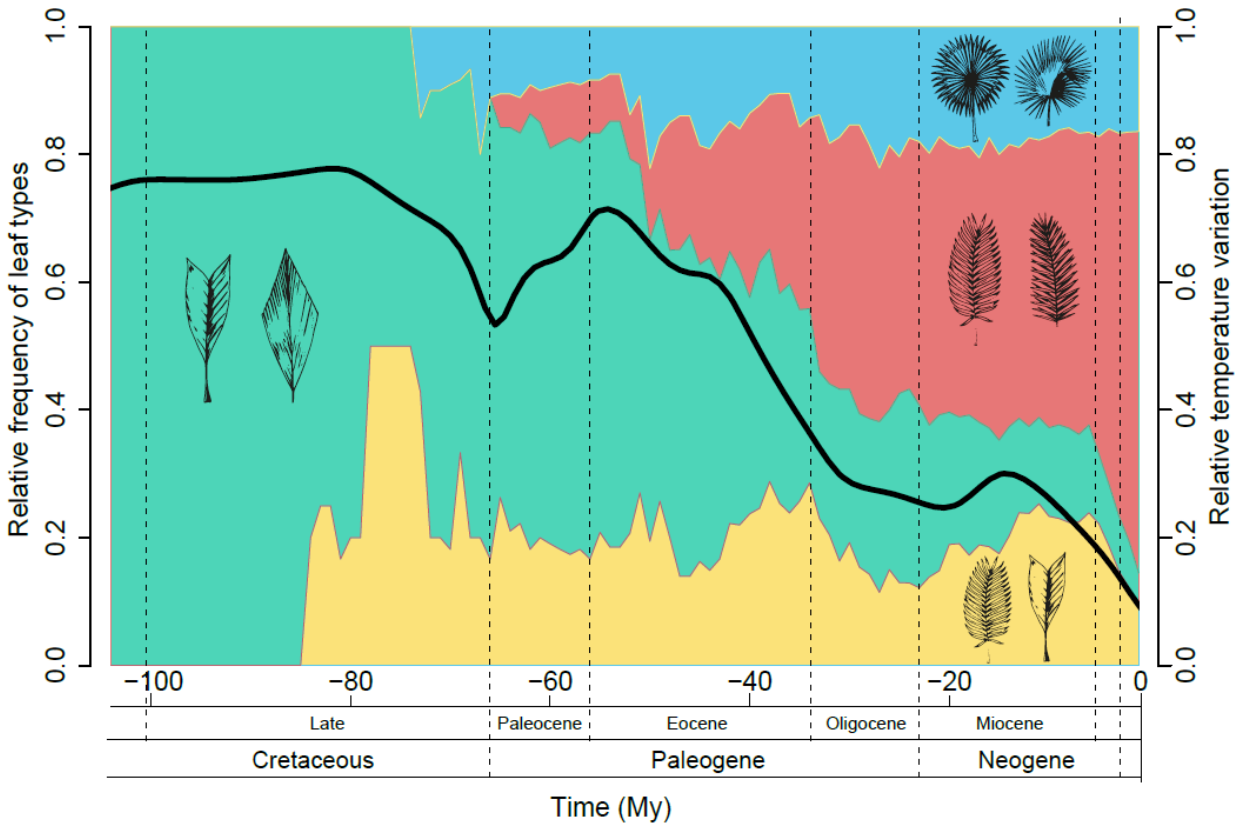
Figure 4. Relative frequency of lineages of each leaf shape through time. Frequencies were calculated from the ancestral state estimation performed using the best fitting model on the maximum clade credibility tree. **Blue** = Palmate (costapalmate+palmate); **red** = Pinnate; **green** =: Entire; **yellow** = Polymorphic (where individuals of the same species have either entire or pinnate leaves). **Note:** here the polymorphic state was split back into pinnate and entire leaves by assigning one or the other shape randomly.
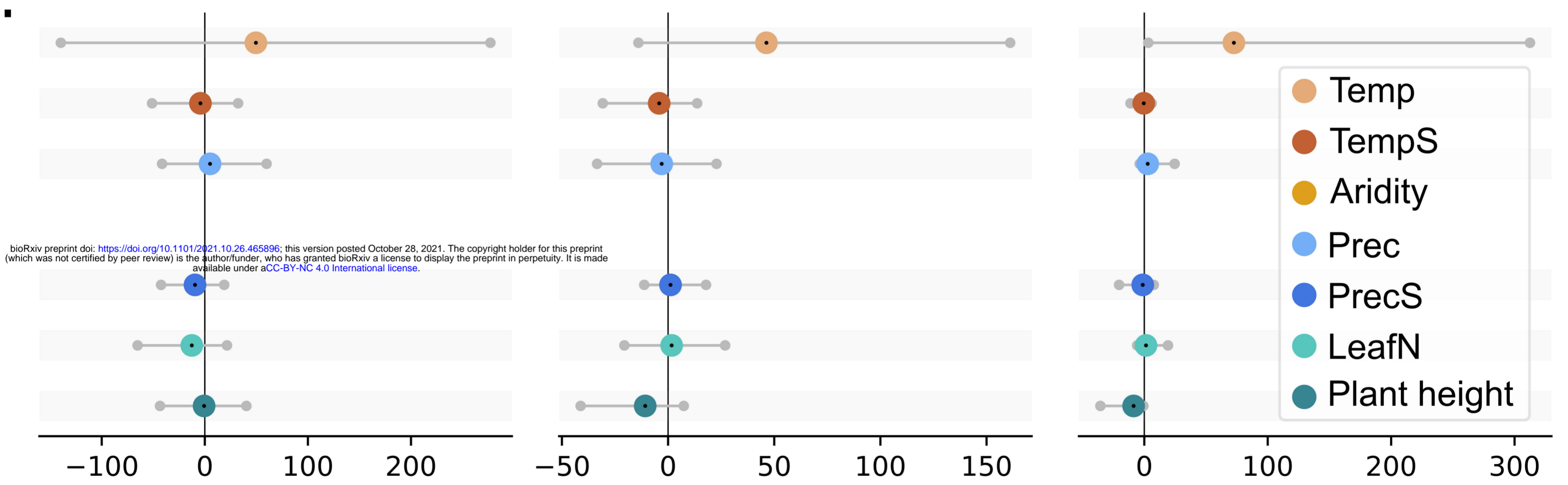
Entire vs palmate   Pinnate vs palmate   Entire vs pinnate

a.

Temp | TempS | Aridity | Prec | PrecS | LeafN | Plant height

+ Effect
- Effect
Included

b.

Temp
TempS
Aridity
Prec
PrecS
LeafN
Plant height

c.

Calamoideae

Coryphoideae

Cer.

Arecoideae