TITLE

Plant height predicts leaf shape in palms (Arecaceae)

Running title:

Height predicts leaf shape in palms

Authors

Maria Fernanda Torres Jiménez[1,2,3], Nicolas Chazot[1,2], Thaise Emilio[4], Johan Uddling Fredin[1,2], Alexandre Antonelli[1,2,5,6], Søren Faurby[1,2*], Christine D. Bacon[1,2*]

*Shared last authorship

Author institutions

[1]Department of Biological and Environmental Sciences, University of Gothenburg, Box 461, SE-405 30 Gothenburg, Sweden

[2]Gothenburg Global Biodiversity Centre, Box 461, SE-405 30 Gothenburg, Sweden

[3]Institute of Biosciences, Life Sciences Centre, Vilnius University, 10257 Vilnius, Lithuania

[4]Programa Nacional de Pós-Doutorado (PNPD), Programa de Pós-Graduação em Ecologia, Instituto de Biologia, Universidade Estadual de Campinas (UNICAMP)

[5]Department of Plant Sciences, University of Oxford, South Parks Road, OX1 3RB Oxford, United Kingdom

[6]Royal Botanical Gardens Kew, TW9 3AE Richmond, United Kingdom

Running title:

Height predicts leaf shape in palms

Abstract

Aim: Leaves display a remarkable variety of shapes, each with potential ecological advantages in certain climates. Studies correlating leaf shape with either climate or height constraints have focused on intraspecific variation, while the macroecological drivers of shape remain poorly known. Here, we determine associations between climate and plant height with the evolution of leaf shape in a lineage with high species and morphological diversity.

Location: Global.

Time period: Cretaceous to contemporary.

Major taxa studied: Palms (Arecaceae).

Methods: We apply a Bayesian phylogenetic mixed model to test for associations between climate and leaf shape (entire, pinnate, palmate, and costapalmate). We further reconstruct the ancestral leaf shape using multistate speciation and extinction models and compare the frequency of shapes with global temperatures through time.

Results: We find that plant height associates with dissected shapes, and that annual precipitation correlates with pinnate shapes. The ancestral leaf shape is likely entire or polymorphic. Pinnate lineages originated multiple times after transitions from entire-leaved to either polymorphic (species with entire-leaved or pinnate individuals) or pinnate shapes.

Main conclusions: Palms that are tall and live in humid regions are more likely to have pinnate leaves. Through geological time scales, temperature did not play a role in determining leaf shapes. This study contributes to our understanding of how the diversity of leaf shapes is linked to biological and climatic factors.

Keywords

Arecaceae, annual precipitation, dissection, leaf shape, macroevolution, MuSSE, palms, plant height.

1. Introduction

Leaves are the engines of most life on land. They capture atmospheric carbon dioxide and convert it into accessible nutrients that sustain ecosystem functioning and health. The basic functions they carry out –photosynthesis, transpiration, and respiration –depend on temperature and water availability. Because they carry out such critical functions, leaves are likely under strong natural selection, resulting in morphological adaptations to environmental conditions (Nicotra et al., 2011). Throughout angiosperm evolution, variation not only in length and width but also in blade dissection, have evolved numerous times independently (Nicotra et al., 2011). Nonetheless, the drivers of leaf shape evolution and its adaptive potential are poorly known, with research being limited to a handful of species or to model eudicots (Nicotra et al., 2011; Chitwood & Sinha, 2016; Leigh et al., 2017), hindering generalisations at a larger taxonomic scale.

General expectations regarding leaf function can be drawn from examining their adaptations in different environments. Traits like leaf dissection, length and effective width (diameter of the largest circle drawn within a leaf margin; Leigh et al., 2017) vary across climates, which affects plant temperature regulation and interacts with water availability (Nicotra et al., 2011; Peppe et al., 2011). In environments with extremely high temperatures plants tend to have small or dissected leaves to avoid reaching damaging temperatures (Leigh et al., 2017; Wright et al., 2017). Deeply dissected leaves effectively function as a collection of small leaf units, with faster heat loss through convection than entire-shaped leaves of the same area (Givnish, 1979; Gurevitch & Schuepp, 1990), and are less likely to reach damaging temperatures when exposed to extreme heat. Thus, shapes that reduce damage at high temperatures are expected to be beneficial in hot and dry environments (Nicotra et al., 2007; 2008; Leigh et al., 2017). Under drought conditions where water for transpiration is limited, stomata close and compounding high temperatures threaten leaf function. In such cases, smaller or deeply dissected shapes reduce overheating and optimise leaf safety (Nardini & Luglio, 2014). Species with large and wide leaves, optimised for high gas exchange, could benefit from dissection as this makes water transportation to blade areas farthest from the rachis more effective (Givnish, 1979). In

contrast, cool climatic conditions may favour entire-leaved shapes over dissected, where leaf heating is not extreme and wide photosynthetic surfaces are beneficial.

Leaf shape and size may also be optimised to maximise light capture. This is particularly relevant for monopodial plants (non-branching plants with a single growth axis) or understory species that depend on leaf size, leaf angle, or number to increase the total photosynthetic area (Givnish, 1988; Valladares et al., 2002; Renninger & Phillips, 2016). However, leaf size is limited by allometry (the proportional change in size or shape of different parts of an organism). Corner's rule states that "the larger and sturdy an axis is, the larger and more complicated are its appendages" (Corner, 1949; Tomlinson, 2006). For large leaves, dissection allows the leaflets to move independently and reduce the drag from strong winds (Niklas, 1992; Vogel, 2009). Corner's rule has been observed in the palm *Geonoma congesta,* in which leaf size and dissection are positively correlated to stem diameter and crown height (Chazdon, 1991a). Another relationship between dissection and allometry is described by the "rapid growth hypothesis" (Givnish 1984; Niinemets, 1998), which states that dissection (or compound leaves) allows plants to grow rapidly during periods of high light availability because investing in longer rachises is energetically cheaper than investing in wood density and branching (Malhado et al., 2010). Moreover, longer petioles or rachises (Givnish, 1988) and optimal trade-offs between leaves' (or leaflets') angle and self-shade (Valladares et al., 2002), could be alternative strategies of understorey species for maximising light capture.

Leaf shape results from trade-offs between physiological and allometric constraints, phylogenetic history, and natural selection (Givnish, 1987; Tsukaya, 2006; Nicotra et al., 2011). Whether leaf shapes have evolved in response to climate or allometry via natural selection or are phylogenetically constrained, leaf shape geographic distribution and its evolution through time should reflect which evolutionary process prevails.

Here, we use palms (Arecaceae) to understand the macroevolutionary drivers of leaf shape variation. Palms are an ideal group to address this question given their wide distribution and morphological diversity. They are tropical and subtropical, with 80% of the species distributed within a 15-30°C mean annual temperature range (Dransfield et al., 2008), and exhibit wide leaf shape variation (entire, pinnate, palmate, and costapalmate; Dransfield et al.,

2008; Horn et al., 2009). Palms are primarily monopodial with non-deciduous leaves (Tomlinson, 2006; Dransfield et al., 2008), allowing us to control for the effect of branching strategies over leaf-variable relationships.

In this study, we aim at disentangling the contributions of climatic (extrinsic) and allometric (intrinsic) factors on leaf shape by testing four specific hypotheses: **H1:** Climate, and in particular temperature, contributes more to leaf shape than allometry. If dissection is advantageous at high temperatures, pinnate- and palmate-leaved species should be distributed in areas with high mean or extreme temperatures. **H2:** Plant height is correlated with dissection via Corner's rule, in which case we expect tall plants to have large and dissected leaves. We test H1–H2 by comparing a) extant dissected and non-dissected shaped species and b) all shapes in a pairwise manner. **H3:** The plant's height in relation to forest canopy height (a proxy for light availability) is correlated with longer rachises, particularly when considering pinnate- and palmate-leaved species. The low light availability in the understorey and the need to maximise light capture should favour species with long over those with short rachises. We test H3 by comparing all shapes in a pairwise manner. **H4:** If climate is a stronger contributor to leaf shape evolution through time, this should be reflected in a temporal congruence between major global climatic changes and leaf shape shifts, since the Late Cretaceous, when palms are estimated to have originated (Dransfield et al., 2008).

Understanding the evolution of leaf shape through past and current environmental conditions provides a context for predicting plant responses to changing climates (Chitwood & Sinha., 2016).

2. Methods

We conducted Generalised Linear Mixed Models (GLMMs) and ancestral trait estimation analyses at the species level using a time-calibrated Maximum Clade Credibility tree generated from the tree distribution in Faurby et al. (2016) and updated by Hill et al. (2021). The phylogeny included 2550 species that were used to annotate leaf shapes, recover geographic records from the Global Biodiversity Information Facility (GBIF), and estimate species medians for the climatic and allometric variables. We standardised the taxonomy across all data sources

using Kew's World Checklist of Selected Plant Families (WCSP) for Arecaceae (Govaerts et al., 2020) and removed records that could not be unambiguously assigned to accepted species.

Leaf shape in palms

Leaf shape variation in palms can be described by three features: size, plication and dissection. Palm leaves can be as short as 15 cm (*Chamaedorea tuerckheimii,* Dransfield et al., 2008), as wide as 8 m (in the cospalmate *Corypha umbraculifera*; Tomlinson, 2006), and as large as 25 m in length (*Raphia regalis*; Hallé, 1977). Blades are folded like accordions during development and the type of plication depends on whether the folds are on the upper (induplicate) or lower (reduplicate) ridges. Plication is phylogenetically conserved within subfamilies with few exceptions; the only induplicate subfamily is Coryphoideae (except for the tribe Trachycarpeae, Fig. 1), whereas Calamoideae, Nypoideae, Ceroxyloideae, and Arecoideae are all reduplicate (Dransfield et al., 2008). Finally, leaves are either entire or dissected. Dissected leaves can be pinnate, palmate, or costapalmate depending on the length of the rachis and the presence of a costa (an extension of the leaf axis; Dransfield et al., 2008). Some species are polymorphic where intraspecific variation in leaf shape is present, but in such cases, polymorphism only involves entire-leaved and pinnate shapes. Genomic analyses (e.g. Loiseau et al., 2019) have confirmed that some of them represent true polymorphisms within populations rather than different taxa currently grouped under one species name.

Based on Genera Palmarum II (Dransfield et al., 2008), additional information on the PalmWeb (https://palmweb.org/, last consulted May 2022), and herbarium specimens (access through GBIF), we classified all species as "entire", "pinnate", "bipinnate", "palmate" (costapalmate and palmate), or "polymorphic". We merged the costapalmate and palmate shapes because the only difference between them is the presence of a costa. We removed the bipinnate category from all analyses because it includes only 14 out of 2550 species. Of the species included, the majority are pinnate (66.18 %; Table S1, Supplementary Material), followed by palmate (21.26 %) and entire (5.12%). Only 75 (6.76 %) species are polymorphic and while they were included in the ancestral state estimation, they were excluded from the GLMMs because they cannot be assigned to a unique shape category (Table S2).

Palm allometry data

We annotated species with all traits available in the Palm_Traits v.1 (Kissling et al., 2019) but considered only those relevant to our hypotheses: maximum petiole length (m), plant height (m), blade length (m), and maximum rachis length (m). We calculated plant height by adding the variables 'MaxStemHeight_m', 'Max_Petiole_length_m', and 'Max_Blade_Length_m', with 'MaxStemHeight_m' set to zero for acaulescent species. We estimated an additional index that measures plant height controlled by canopy height ("height over canopy") as a proxy to the Understorey/Canopy variable in Kissling et al. (2019). The index differentiates between e.g. two tall species, one occurring in a high canopy and another in a low canopy forest. To calculate it, we divided the palm height species value by the height extracted at the coordinate point from the Global Vegetation Height layer (Simmard, 2011). All calculations and code are available at https://figshare.com/s/b3a5fb5fd9abc5eeb485. We annotated 61-100% of the species in the phylogeny depending on the variable. Species without annotations were either not annotated in Palm_Traits v.1 or were climbing or had both climbing and no-climbing habits. (479 species, Table S3); the latter were removed from the GLMM analyses because their life strategies differ from other palms and their stem height is not comparable.

Climatic data

We downloaded 994,084 raw occurrences from GBIF (last consulted in April 2022) and excluded fossils and records without coordinates, we kept observations, living and preserved specimens, and material samples. We used the R package (R Core Team, 2018) *CoordinateCleaner* (Zizka et al., 2019) to remove duplicate coordinates per species and records nearby science institutions, bodies of water, and city/country centroids, using a buffer of 5000 m and 10000 m for centroids and cites respectively. We used a Python script (https://figshare.com/s/b3a5fb5fd9abc5eeb485) and the World Geographical Scheme for Recording Plant Distributions maps (TDWG; Brummitt, 2001) to remove records falling outside their native botanical countries according to the WCSP. We obtained 124,703 clean records representing 61.56% of the 2550 species in the phylogeny (Table S4), which we used to extract all Chelsa v2.1 bioclim variables (Karger et al., 2017; Karger at al., 2018) with a python script (https://figshare.com/s/b3a5fb5fd9abc5eeb485). Finally, we estimated the species medians for every variable from which we could extract the information (Table S4).

We determined correlations between variables and chose those with a Spearman's coefficient < 0.7 (Fig. S1). We additionally estimated the variance inflation factor for all variables using python's statsmodels library (Seabold and Perktold, 2010) and kept those with values below two. We kept five climatic and three allometric variables: mean annual temperature (°C*100), temperature seasonality (standard deviation °C*100), annual precipitation (kg m-2); precipitation seasonality (standard deviation kg m-2), aridity index (mean annual precipitation/mean annual potential evapotranspiration; kg m-2/time unit), plant height (m), rachis length (m), and height over canopy. Temperature seasonality and mean annual precipitation, and plant height and height over canopy were correlated (Spearman's correlation coefficient = -0.8 and 0.73 respectively; Fig. S1); and thus, assessed in separate models (Fig. 2). All variables used were $\log_{10}$-transformed and standardised to have zero mean and a standard deviation of one (Table S4).

Generalised linear mixed models

We fit a series of GLMMs for each of the first three hypotheses with logistic regressions to distinguish the variables associated with leaf shape using pairwise comparisons; entire (0) vs. dissected (1), pinnate (0) vs. palmate (1), entire (0) vs. palmate (1), and entire (0) vs. pinnate (1); these were implemented in the R package *MCMCglmmRAM (*Hadfield, 2015). For computational constraints, we ran every model on 42 (Adams, 1979) phylogenies randomly selected from the distribution, setting each as a random effect. For every model, we ran four independent chains of 10,000,000 iterations each, a thinning of 5,000, and 8000 burn-in. Analyses were run on a HPE Cray OS computer through the Swedish National Infrastructure for Computing. We estimated effective sampling sizes (ESS) and evaluated chain convergence with a python script (https://figshare.com/s/b3a5fb5fd9abc5eeb485). Chains converged and effective sample sizes scored higher than 200. We evaluated the significance of the effects for every predictor variable based on whether the 2.5 and 97.5% quartiles of the estimated density overlapped zero (Table S5).

Ancestral state estimation

To select an appropriate model for the ancestral trait estimation, we first used the Multi-State Speciation and Extinction (MuSSE) model from the R package *diversitree* (FitzJohn, 2012) to compare speciation, extinction, and transition rates between leaf shapes. We adjusted the leaf shape dataset to avoid over parametrization of our models: 1) excluded plication due to high phylogenetic clustering (Fig. 1; but see Couturier et al., 2011); 2) used a "polymorphic" category for species exhibiting more than one shape; 3) excluded all species with missing data for leaf shape. This resulted in 2543 species in the dataset and four character states: palmate (costapalmate + palmate), pinnate, entire, and polymorphic. As polymorphism only includes pinnate and entire-leaved shapes, we assumed direct transitions between palmate and polymorphic states (pinnate + entire) to be impossible and therefore constrained the corresponding transition parameters to zero.

Given the large parameter number remaining (18 parameters), we selected the best-fitting model using a backward model selection procedure on the maximum clade credibility tree only. We started fitting a model in which all remaining parameters were unconstrained, using maximum likelihood estimation (ML; see the list and values of the parameters in the Supplementary Material). We then proceeded with reducing the model, one constraint at a time until the AIC score stopped improving. At each step, all models with one more constraint (less complex) than the previous model (more complex) were fitted and ranked according to their AIC scores. The model with the lowest AIC score was retained as the base model for the next step, providing it was significantly lower ($\Delta AIC > 2$) than the best model from the previous step. AIC scores for determining the best MuSSE models stopped improving at the tenth step during backward model selection, representing a total of 297 models fitted, of which 22 reported problems of convergence. Using the final best-fitting model, we performed an MCMC analysis to compare posterior distributions of parameters. We ran the MCMC for 10,000,000 generations, sampling every 8,000 generations and a burnin of 1,100. We used the ML parameter estimation as starting points for the MCMC. In addition, we performed ML estimations of the best-fitting model for 100 trees randomly sampled from the posterior distribution to account for phylogenetic uncertainty.

We used the best-fitting MuSSE model to estimate ancestral states, the number and rate of transitions through time, and the relative frequency of leaf shape through time by sampling the relative probabilities of shape estimated for each node 100 times. For each iteration, at each branch where a state transition occurred we sampled a random timing from a uniform distribution for the event along that branch. Finally, for each iteration, we counted the number of transitions within a 5 million year sliding window and calculated the rate of transitions through time by dividing the number of transitions by the sum of branch lengths within each time interval. We repeated this procedure for 100 trees randomly sampled from the posterior distribution, but instead of calculating the number of transitions, we calculated the relative frequency of lineages exhibiting each leaf shape through time. Finally, we compared the relative shape frequency through time with the global temperature change scale computed for an ice-free ocean (Zachos et al. 2001; Condamine et al., 2020).

3. Results

Leaf shape and variable distributions

Based on the species' annotations for allometric variables, we observed that pinnate and palmate species tended to be much larger than entire-leaved species, with median plant heights of 7.39 m (1 m min - 68 m max; Table S5) in pinnate and 7 m (1 m min - 49 m max) in cospalmate and palmate species. In contrast, entire-leaved species had a median height of 3.8 m (1 m- 28 m max), leaf and petiole length included in all cases. When considering dissected shapes together, their mean plant height was twice the mean height of non-dissected species (7 m and 3.7 m respectively). Regarding maximum rachis length as the trait distinguishing pinnate and palmate leaves, their median lengths were similar (2.9 m and 2.4 m respectively) but their maximum rachis lengths differed (19 m and 8 m respectively). Regarding height over canopy (plant height/canopy height), the median index for species with pinnate leaves was $4e^{+10}$, for species with palmate leaves was $7e^{+10}$, and for species with entire-leaved species was $1.3e^{+10}$. Values of height over canopy are high for tall species occupying areas with low canopies, close to one for species with the same height as the canopy, and small for short species under high canopies.

Palms were widely distributed across climatic gradients (except for habitats where soil temperatures fall below -2°C for a long period of time). However, leaf shapes were not distributed evenly throughout the geographic distribution of the family (Fig. 1 and Fig. S5-6). Pinnate and palmate species were distributed farther from the equator with wider climatic seasonality or into areas where water scarcity and exposure to extreme temperatures are possible. Meanwhile, the distribution of entire-leaved species was concentrated in tropical areas near the equator where annual temperature and precipitation are more constant. We observed a similar pattern for most climatic variables used, in which the species median distributions of pinnate and palmate species were wider than that of entire-leaved species (Fig. S2 and Table S5). Such is the case for the aridity index, annual precipitation, and precipitation seasonality. For annual mean temperature and temperature seasonality, the ranges were wider for pinnate- then entire-leaved species and narrower for palmate-leaved species. For mean annual temperatures, pinnate species ranged between 1.7°C and 28.7°C (Δ 26°C), palmate ranged between 4.4°C and 27.4°C (Δ 22.9°C), and entire-leaved species ranged between 3.8°C and 28.4°C (Δ 24.5°C). However, the median of the distribution for mean annual temperatures was higher for palmate (25.1°C), then entire-leaved (24.6°C), and lowest for pinnate species (23.7°C).

Generalised Linear Mixed Models

When disentangling the effects of allometry and climate on leaf shape, results from the GLMMs showed a significant positive association between plant height and shape when comparing entire-leaved versus pinnate-leaved species (P or proportion of samples above or below zero=0.99; Fig. 2 and Table S6) and entire-leaved versus dissected species (pinnate and palmate species; P=0.99). The association was consistent across models regardless of which climatic variables were included; for the model including annual precipitation instead of annual temperature seasonality, annual precipitation showed a positive and almost significant association with pinnate species when compared to entire-leaved species (P=0.951), but not when comparing dissected and entire-leaved shapes (P=0.89). Nevertheless, the effect of plant height is an order of magnitude larger than the effect of precipitation (Table S6, Supplementary Material). For models comparing pinnate and entire-leaved shapes in which height over canopy was included instead of plant height (these two variables showed high correlation and could not be included in the same model), only height over canopy was almost significantly and positively

associated with pinnate shapes (P=0.953) but the significance was lost if the model did not account for annual precipitation (Fig 2, Table S6). No climatic variables were consistently found to be significantly associated with leaf shape (0.35<P< 0.94; Fig. 2 and Table S6).

When disentangling the effects of rachis length, height over canopy, and climate, we found a significant positive association between rachis length and pinnate shapes when compared to entire-leaved species; plants with longer rachises are more likely to be pinnate. In addition to rachis length, annual precipitation had a significantly positive association with pinnate species and height over canopy was almost significant (P=0.99 and P=0.968, respectively). Here, the effect of rachis length was an order of magnitude larger than that of precipitation and height over canopy, which had similar effects. The models resulted in no association between rachis length and shape when comparing pinnate- versus palmate-leaved species (0.34< P<0.5; Fig. 2 and Table S6).

Ancestral state estimation

The best-fitting model (Fig. 4a) had nine parameters and resulted from 1) merging the speciation rates for palmate, pinnate, and entire shapes; 2) merging the extinction rates for entire and polymorphic shapes; and 3) constraining six transition parameters. The resulting speciation rate (lineage/unit of time, $l^{-1}my^{-1}$) of polymorphic species was more than twice higher than that of the others (Fig. S3). The extinction rate for the polymorphic and entire-leaved lineages was much lower than that of pinnate and palmate lineages. The resulting net diversification for pinnate lineages was close to zero. Palmate lineages followed with a mean net diversification estimated around 0.09 $l^{-1}my^{-1}$ and 0.2 $l^{-1}my^{-1}$ for entire-leaved lineages. Polymorphic lineages had the highest net diversification rate with a posterior distribution averaging around 0.45 $l^{-1}my^{-1}$. The most frequent transitions happened from entire to polymorphic to pinnate shapes.

The ancestral state estimation resulting from the best-fitted model on the MCC tree inferred both entire-leaved and polymorphic shapes as the most probable state at the root (Fig. 4b). Analyses across 100 trees also supported entire-leaved and polymorphic shapes as the most probable root state. The outcomes of the transition rate parameters are frequent transitions from entire-leaved to pinnate shapes after a polymorphic transition phase. We found that the overall

368 rate of state transitions through time remained relatively constant. The relative frequency of
369 shapes through time remained relatively stable with some fluctuations (Fig. 4c). The first
370 palmate lineages appeared around 80 My ago and their relative frequency remained
371 approximately the same through time, averaging between 15 to 20%. Despite being the most
372 probable ancestral states, entire-leaved and polymorphic shapes were rapidly replaced by
373 pinnate, representing on average 10-20% each.
374
375 **4. Discussion**
376 In this study, we aimed at disentangling the contributions that plant allometry and climate
377 have on leaf shape by testing whether **H1)** climate, and more specifically temperature,
378 determines leaf shape; or **H2)** leaf shape is constrained by plant height, or **H3)** rachis length,
379 climate, or height over canopy determine leaf shape; in addition to whether **H4)** the frequency of
380 leaf shape through time reflects global temperature fluctuations through time. Our results suggest
381 that taller plants are more likely to have dissected leaves and, regarding climate, only annual
382 precipitation matters and makes species more likely to have pinnate-shaped leaves (Fig. 2).
383 Moreover, longer rachises make pinnate shapes more likely, but in entire-leaved species and not
384 palmate-shaped ones. In congruence with our results, we observed a lack of correspondence
385 between leaf shape frequency and temperature fluctuations through time. Our models of
386 ancestral trait estimation revealed that the ancestor of all palms likely had entire and/or
387 polymorphic leaves.
388
389 *Leaf dissection and climate*
390 Contrary to our first hypothesis, neither mean annual temperature nor temperature
391 seasonality had an effect on leaf shape (Fig. 2 and Table S6). We expected that plants exposed to
392 extremely high temperatures would have dissected leaves as a strategy to avoid overheating their
393 leaves faster (Nicotra et al., 2007; 2008; Leigh et al., 2017). Similarly, we expected that a high
394 aridity index –a proxy for a lack of water in the environment– would favour pinnate leaves over
395 other shapes. Our results showed no significant associations between climate and leaf shape for
396 most of the models and only the effect of annual precipitation was significant when comparing
397 pinnate and entire-leaved species, thus rejecting **H1**. According to our models, species that
398 experience high annual precipitation are more likely to be pinnate than entire-leaved when

controlling for plant height. Tall heights are problematic at extremely high temperatures and water scarcity because water transport becomes harder with increased plant height (hydraulic limitation hypothesis; Ryan, 2006; Olson et al., 2018). It is likely that species growing in higher annual precipitation have more water available and can grow taller, ultimately resulting in longer leaves and a higher probability of having pinnate leaves.

The association between climate and palmate-leaved shapes is not significant and only precipitation is associated with pinnate shapes (Figs. 2 and S4); three non-mutually exclusive hypotheses could explain the general lack of associations. First, the discrete shape categories in our models might not fully capture interspecific variation in dissection depth and could be insufficient for unveiling the climate-palmate associations. Second, leaf traits unrelated to shape could be key adaptations to different environments (Horn et al., 2009). For example, the loss of non-lignified fibre bundles in the leaf mesophyll or the presence of bridge-like veins connecting the adaxial and abaxial layers of the leaf are traits thought to be advantageous in dry environments (Kenzo et al., 2007; Horn et al., 2009). Third, in the case of palmate and costapalmate species, the correlation between climate and shape is difficult to disentangle from a phylogenetic effect due to the strong geographic structuring of related lineages, particularly in the Coryphoideae subfamily to which the majority of palmate and costapalmate species belong.

Research is lacking regarding monocots and the lineage-specific mechanisms behind shape convergence across angiosperms hinder the comparison between monocots and eudicots (Conklin et al., 2019). A better understanding of the mechanisms by which climate interacts with shape development will come from studies addressing shape variation quantitatively (Chitwood & Sinha., 2016; Kissling et al., 2018).

Leaf shape and plant allometry

We expected plant height to influence leaf shape via allometry so that large plants would have large leaves that are more likely dissected to avoid mechanical damage (Corner, 1949; Chazdon, 1991b). We found that plant height has a positive effect on dissection such that taller plants are more likely to have pinnate leaves (Fig. 2 and Table S6). Our results were consistent when comparing dissected –pinnate and palmate together– and pinnate species against species

with entire-leaved shapes, thus supporting **H2**. Only when comparing palmate- versus entire-leaved species, all effect estimates were not significant (Fig. 2). This suggests that the association between plant height and dissection is primarily driven by the number of pinnate species (66.18% versus 21.26% species with palmate leaves) and that other factors are involved when palmate species are considered (as discussed in the section above).

Following the "rapid growth hypothesis" (Givnish, 1984; Niinemets, 1998), we expected plant height to relate to dissection. Malhado et al. (2010) tested this hypothesis in Amazonian species (except palms and species with a mix of simple and compound leaves), and found an association between dissection and both low wood density and rapid diameter growth. They argue that dissection is adaptive under favourable light conditions because producing compound or dissected leaves is physiologically less expensive than branching and thus promotes rapid vertical growth (Malhado et al. 2010). The rapid vertical growth could be a particularly beneficial strategy for palms considering that most species are monopodial and do not branch. We found a positive association between height over canopy –calculated as plant height divided by canopy height– and pinnate shapes when these are compared to entire-leaved species (Fig. 2 and Table S6), although the association was marginally significant. Large height over canopy values result when plants are taller than the canopy and values close to zero result from canopies taller than plants. Palmate-leaved species had the highest median height over canopy, closely followed by pinnate-leaved species, and entire-leaved species had the lowest median. We explain this trend in median height over canopy by the tendency of pinnate and palmate species to be equal or taller than the canopy, whereas entire-leaved species are rarely tall enough to approach the forest canopy and they do not occur in open habitats. The significance of this association, however, should be interpreted carefully as height over canopy values are derived from, and correlated with, plant height.

The lack of association between height over canopy when comparing pinnate and palmate-leaved species further suggests that pinnate and palmate species occupy similar spaces around the canopy and there would not be much difference in the overall light availability conditions. Malhado et al., (2010) excluded palms from their analyses and testing whether rapid growth or light capture optimisation better explains dissection in palms is not possible with the

data in our study; a deep look at species-level measurements of growth rates and light capture efficiency could shed a light on this question.

Finally, we expected that the probability of having pinnate versus palmate-leaved species would be driven by rachis length via light capture optimisation. Pinnate leaves are essentially palmate or costapalmate leaves but their pinnae are distributed throughout a longer plane. On one hand, the elongated rachis of pinnate-leaved species could be a strategy for maximising light capture when living under the canopy. Investing in longer rachis and leaves has the additional advantage of increasing blade surface whilst reducing mechanical damage and self-shading. On the other hand, species with palmate and costapalmate leaves in which the leaflets are arranged radially, are more associated with open habitats (Dransfield et al., 2008) where light availability is high compared to the understory. However, we found no association between rachis length and the probability of pinnate- versus palmate-leaved species, thus rejecting **H3** (Fig. 2 and Table S6). This result is consistent with a lack of association between height over canopy and leaf shape when comparing pinnate versus palmate-leaved species, meaning that neither the plant's position with respect to the canopy nor the rachis length explain leaf shape. The association between rachis length and shape is only significant when comparing pinnate- versus entire-leaved species, which can be explained by Corner's rule: large plants have large leaves which necessarily have longer rachises.

Leaf shape evolution

We found that dissected leaf shapes evolve frequently during the history of palms (Fig. 3), a result consistent with previous research. Using 178 taxa with pinnate or palmate species only, Horn et al. (2009) concluded that shape is homoplasious and changes between states are frequent.

Our analyses indicated that entire, pinnate and polymorphic leaf shapes appeared during the early stages of palm diversification (Fig. 4c), and the only leaf shapes that clearly evolved at a later stage were palmate and costapalmate between 70-80 Mya and correspond to the stem of Coryphoideae. Our results suggest that palmate shapes emerged more recently than the age of the costapalmate fossil *Sabalites carolinensis* (Santonian, 86.3-83.6 Mya; Berry, 1914), commonly cited as the earliest palm leaf fossil. However, uncertainty as to the stratigraphic assessment of

492 the formation from which *S. carolinensis* was reported calls for the reassessment of the fossil's
493 age to be Campanian (83.6-72.1 Mya; Greenwood et al., 2022). If that is the case, the oldest
494 costapalmate (here merged with palmate) fossil would postdate the older Coniacian–early
495 Campanian "pinnate-entire" *Phoenicites imperialis* (Dawson) emend. Greenwood et Conran
496 comb. nov. (89.8 to approximately 80 Mya; Greenwood et al., 2022) and be contemporaneous to
497 the mid-Campanian "undivided" *Plicatophyllum* (81-76 Mya; Crabtree 1987; Greenwood et al.,
498 2022) –a scenario that is consistent with our results–. Macrofossils remain rare and provide at
499 best a minimum age for any taxon or morphological character; the absence of older fossils is
500 likely explained by the incomplete nature of the fossil record and its identification.

501 One interesting outcome of our model and ancestral state estimation is the role played by
502 polymorphic lineages. Polymorphism, entire-leaved and pinnate shapes only, appears as a
503 transitional state between these shapes forming an evolutionary bridge between lineages with
504 non-polymorphic leaf shapes (Fig. 3). Maximum Likelihood estimates of transition parameters
505 also suggest a strong directionality; the highest transition rates being from polymorphic toward
506 pinnate shapes and the second highest was transitions from entire-leaved shapes towards
507 polymorphism (Fig. 4a and S3). As a result, polymorphic lineages are maintained in our
508 ancestral state estimation throughout time despite that only 3% of extant species are
509 polymorphic. Pinnate-, palmate-, and entire-leaved lineages do not have significantly different
510 speciation rates but the speciation rate for polymorphic lineages is more than twice higher.
511 Regarding estimated extinction, however, pinnate lineages have the highest rate, almost two
512 times higher than palmate and costapalmate. Extinction is almost null for entire-leaved and
513 polymorphic lineages. Thus, according to our best model, the high number of extant pinnate
514 lineages might not result from high diversification rates, but from a high speciation rate of
515 polymorphic lineages combined with a high rate of independent transitions towards pinnate
516 leaves.
517
518 *Leaf shape through time*
519 We found no clear relationship between temperature variations and changes in the
520 relative frequency of leaf shapes, thus we reject **H4** (Fig. 4c). The late Cretaceous and early
521 Eocene were periods of high global temperatures, with ever-wet tropical areas distributed
522 towards high latitudes. Palms thrived during these periods forming the Palmae Province,

523 becoming ecologically dominant in South America, Africa and India (Pan et al., 2006). During
524 the Eocene, global temperatures decreased at a relatively fast pace (Zachos et al., 2001) and kept
525 declining towards the present, except during the Mid-Miocene climatic optimum. As
526 temperatures decreased, the frequency of pinnate lineages increased and that of palmate lineages
527 remained constant, and we did not identify any global temperature change that drove major
528 evolutionary changes in leaf configuration.
529
530 One interesting outcome of the ancestral state estimation is the fact that polymorphic
531 states might have been found already since the early period of palm diversification and remained
532 in fairly constant proportions (Fig. 4c). Polymorphism is widespread across palms, but it does
533 not appear as an evolutionary innovation specific to a single group but rather as a property that
534 may have been retained over time across many lineages. The conserved ability to produce both
535 types of leaves may explain why shifts from one type to another occurred so frequently. This is
536 even more striking when considering the absence of a repeated appearance of costapalmate-
537 shaped leaves, that are effectively not part of the polymorphism syndrome. However, these
538 results should be interpreted with caution since validating them would require a comprehensive
539 taxonomic sampling beyond Arecaceae.
540
541 **Conclusion**
542 We explore the drivers of leaf shape evolution in palms by disentangling the associations
543 between shape, climate, and allometric variables related to plant height, and by reconstructing
544 the evolution of shape throughout their evolutionary history. We highlight the importance of
545 considering biotic (intrinsic) and abiotic (extrinsic) factors when studying the evolution of traits.
546 Regarding palms, tall plants are more likely to be dissected and, specifically, to have pinnate-
547 shaped leaves. High annual precipitation increases the likelihood of having pinnate leaves when
548 controlling for plant height, likely because water transport is more challenging for tall plants and
549 taller heights are possible under high water availability. Palms are important representative taxa
550 of the tropical forests with more than 2,500 species distributed globally. Exploring how their leaf
551 shape diversity emerged contributes to our understanding of shape and its adaptive potential to
552 future climate conditions.
553

Author contributions

M.F.T.J. conducted data curation, trait annotations at the species level, formal analyses, visualisation, and writing of the original draft as well as reviewing and editing. N.C. conducted data curation, formal analyses, visualisation, and contributed with writing, critical review and commentary. T.E. contributed to the conceptualisation and with critical review and commentary of the manuscript. J.U.F. contributed to the conceptualisation and with critical review and commentary of the manuscript. A.A. contributed with the critical review and commentary of the manuscript. S.F. contributed to the conceptualization and methodology, and with critical review and commentary of the manuscript. C.D.B. contributed to the conceptualization and with critical review and commentary of the manuscript.

Acknowledgements

We acknowledge the logistic and computational support provided by the Swedish National Infrastructure for Computing via the allocated projects SNIC2020-7-61 and 2020-8-85. MFT and CDB acknowledge financial support from the Swedish Research Council (2017-04980). This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001 to TE. AA acknowledges financial support from the Swedish Research Council (2019-05191), the Swedish Foundation for Strategic Research (FFL15-0196), and the Royal Botanic Gardens, Kew. SF is funded by the Swedish Research Council (2017-03862). The research presented in this paper is a contribution to the strategic research area Biodiversity and Ecosystems in a Changing Climate, BECC.

Data Availability Statement

All data generated during this study and the coding scripts for analysing it are available as Supplementary Material in the following repository: https://figshare.com/s/b3a5fb5fd9abc5eeb485.

REFERENCES

Adams, D. (1979). The Hitchhiker's Guide to the Galaxy. London, UK: Pan Books.

Berry, E. W. (1914). The upper Cretaceous and Eocene floras of South Carolina and Georgia (No. 84). US: US Government Printing Office.

Brummitt, R. K. (2001). World Geographical Scheme for Recording Plant Distributions, Edition 2. *Biodiversity Information Standards (TDWG)*, http://www.tdwg.org/standards/109

Chazdon, R. L. (1991a). Effects of leaf and ramet removal on growth and reproduction of *Geonoma congesta*, a clonal understorey palm. *The Journal of Ecology* **79**(4):1137-1146.

Chazdon, R. L. (1991b). Plant size and form in the understory palm genus *Geonoma*: are species variations on a theme? *American Journal of Botany* **78**(5): 680-694.

Chitwood, D. H., & Sinha, N. R. (2016). Evolutionary and environmental forces sculpting leaf development. *Current Biology* **26**(7): R297-R306.

Crabtree, D.R., (1987). The early Campanian flora of the Two Medicine Formation, northcentral Montana. University of Montana. USA.

Condamine, F. L., Silvestro, D., Koppelhus, E. B., & Antonelli, A. (2020). The rise of angiosperms pushed conifers to decline during global cooling. *Proceedings of the National Academy of Sciences* **117**(46): 28867-28875.

Conklin, P. A., Strable, J., Li, S., & Scanlon, M. J. (2019). On the mechanisms of development in monocot and eudicot leaves. *New Phytologist* **221**(2): 706-724.

Corner, E. J. H. (1949). The durian theory or the origin of the modern tree. *Annals of Botany* **13**(52): 367-414.

Couturier, E., Du Pont, S. C., & Douady, S. (2011). The filling law: a general framework for leaf folding and its consequences on leaf shape diversity. *Journal of Theoretical Biology* **289:** 47-64.

Dransfield, J., Uhl, N. W. , Asmussen, C. B., Baker, W. J., Harley, M. M. , & Lewis, C. E. (2008). *Genera palmarum, the evolution and classification of palms*. Richmond, Surrey UK: Royal Botanic Gardens, Kew.

Faurby, S., Eiserhardt, W. L., Baker, W. J., & Svenning, J. C. (2016). An all-evidence species-level supertree for the palms (Arecaceae). *Molecular Phylogenetics and Evolution* **100**: 57-69.

FitzJohn, R. G. (2012). Diversitree: comparative phylogenetic analyses of diversification in R. *Methods in Ecology and Evolution* **3**(6): 1084-1092.

the Global Biodiversity Information Facility. GBIF Occurrence Download https://doi.org/10.15468/dl.w8djyx retrieved on 26 April 2022.

Givnish, T. J. (1979). On the adaptive significance of leaf form. Topics. In: O.T. Solbrig, G.B. Jain, G.B. Johnson and P.H. Raven eds. *Plant Population Biology.* New York, US: Columbia University Press, 375-407.

Givnish, T. J. (1984). Leaf and canopy adaptations in tropical forests. In: E. Medina, H.A. Mooney and C. Vásquez-Yánes eds. *Physiological ecology of plants in the wet tropics. Tasks for vegetation Science, vol 12*. Dordrecht, Netherlands: Springer, 51–84.

Givnish, T. J. (1987). Comparative studies of leaf form: assessing the relative roles of selective pressures and phylogenetic constraints. *New phytologist* **106**: 131-160.

Givnish, T.J., (1988). Adaptation to sun and shade: a whole-plant perspective. Functional Plant Biology, 15(2): 63-92.

Greenwood, D.R., Conran, J.G. & West, C.K., (2022). Palm fronds from western Canada are the northernmost palms from the Late Cretaceous of North America and may include the oldest Arecaceae. Review of Palaeobotany and Palynology, **301**: 104641.

Govaerts, R., Dransfield, J., Zona, S., Hodel, D. R., & Henderson, A. (2020). *World Checklist of Arecaceae.* Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; http://wcsp.science.kew.org/ Retrieved 25 February 2020

Gurevitch, J., & Schuepp, P. H. (1990). Boundary layer properties of highly dissected leaves: an investigation using an electrochemical fluid tunnel. *Plant, Cell & Environment* **13**(8): 783-792.

Hadfield, J. D. (2015). Increasing the efficiency of MCMC for hierarchical phylogenetic models of categorical traits using reduced mixed models. *Methods in Ecology and Evolution* **6**(6): 706-714.

Hallé, R. (1977). The longest leaf in palms? *Principes* **21**: 18.

Hill, A., Torres Jimenez, M. F. , Chazot, N., Cássia-Silva, C., Faurby, S., & Bacon, C. D. (2021). Fruit colour and range size interact to influence diversification. *bioRxiv*. 10.1101/2021.10.26.465838.

Horn, J. W., Fisher, J. B., Tomlinson, P. B., Lewis, C. E., & Laubengayer, K. (2009). Evolution of lamina anatomy in the palm family (Arecaceae). *American Journal of Botany* **96**(8): 1462-1486.

Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, P., & Kessler, M. (2017). Climatologies at high resolution for the Earth land surface areas. Scientific Data. 4-170122.

Karger D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E, Linder, H.P., & Kessler, M. (2018). Data from: Climatologies at high resolution for the earth's land surface areas. EnviDat. https://doi.org/10.16904/envidat.228.v2.1

Kenzo, T., Ichie, T., Watanabe, Y., & Hiromi, T. (2007). Ecological distribution of homobaric and heterobaric leaves in tree species of Malaysian lowland tropical rainforest. *American Journal of Botany* **94**(5): 764-775.

Kissling, W. D., Balslev, H., Baker, W. J., Dransfield, J., Göldel, B., Lim, J. Y., Onstein, R. E., & Svenning, J. C. (2019). PalmTraits 1.0, a species-level functional trait database of palms worldwide. *Scientific Data* **6**(1): 1-13.

Kissling, W. D., Walls, R., Bowser, A., Jones, M. O., Kattge, J., Agosti, D., Amengual, J., Basset, A., Van Bodegom, P. M., Cornelissen, J. H., & Denny, E. G. (2018). Towards global data products of Essential Biodiversity Variables on species traits. *Nature Ecology & Evolution* **2**(10): 1531-1540.

Leigh, A., Sevanto, S., Close, J. D., Nicotra, A. B. (2017). The influence of leaf size and shape on leaf thermal dynamics: does theory hold up under natural conditions? *Plant, Ccell & Eenvironment* **40**(2): 237-248.

Loiseau, O., Olivares, I., Paris, M., de La Harpe, M., Weigand, A., Koubínová, D., Rolland, J., Bacon, C. D., Balslev, H., Borchsenius, F., & Cano, A. (2019). Targeted capture of hundreds of nuclear genes unravels phylogenetic relationships of the diverse Neotropical palm tribe Geonomateae. Frontiers in Plant Science **10**:864.

Malhado, A. C., Whittaker, R. J., Malhi, Y., Ladle, R. J., tTer Steege, H., Phillips, O., Aragão, L. E. O. C., Baker, T. R., Arroyo, L., Almeida, S., & Higuchi, N. (2010). Are compound leaves an adaptation to seasonal drought or to rapid growth? Evidence from the Amazon rain forest. *Global Ecology and Biogeography* **19**(6): 852-862.

Nardini, A., & Luglio, J. (2014). Leaf hydraulic capacity and drought vulnerability: possible trade-offs and correlations with climate across three major biomes. *Functional Ecology* **28**(4): 810-818.

Nicotra, A. B., Cosgrove, M. J., Cowling, A., Schlichting, C. D., & Jones, C. S. (2008). Leaf shape linked to photosynthetic rates and temperature optima in South African *Pelargonium* species. *Oecologia* **154**(4): 625-635.

Nicotra, A. B., Hermes, J. P., Jones, C. S., & Schlichting, C. D. (2007). Geographic variation and plasticity to water and nutrients in *Pelargonium australe*. *New Phytologist* **176**(1): 136-149.

Nicotra, A. B., Leigh, A., Boyce, C. K., Jones, C. S., Niklas, K. J., Royer, D. L., & Tsukaya, H. (2011). The evolution and functional significance of leaf shape in the angiosperms. *Functional Plant Biology* **38**(7): 535-552.

Niinemets, Ü. (1998). Are compound-leaved woody species inherently shade-intolerant? An analysis of species ecological requirements and foliar support costs. *Plant Ecology* **134**(1): 1-11.

Niklas, K. J. (1992). Petiole mechanics, light interception by lamina, and "economy in design". *Oecologia* **90**(4): 518-526.

Olson, M. E., Soriano, D., Rosell, J. A., Anfodillo, T., Donoghue, M. J., Edwards, E. J., León-Gómez, C., Dawson, T., Martínez, J. J. C., Castorena, M., & Echeverría, A. (2018). Plant height and hydraulic vulnerability to drought and cold. *Proceedings of the National Academy of Sciences* USA **115**(29): 7551-7556.

Pan, A. D., Jacobs, B. F., Dransfield, J., & Baker, W. J. (2006). The fossil history of palms (Arecaceae) in Africa and new records from the Late Oligocene (28–27 Mya) of north-western Ethiopia. *Botanical Journal of the Linnean Society* **151**(1): 69-81.

Peppe, D. J., Royer, D. L., Cariglino, B., Oliver, S. Y., Newman, S., Leight, E., Enikolopov, G., Fernandez-Burgos, M., Herrera, F., Adams, J. M., & Correa, E. (2011). Sensitivity of leaf size and shape to climate: global patterns and paleoclimatic applications. *New phytologist* **190**(3): 724-739.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Renninger, H. J., & Phillips, N. G. (2016). Palm physiology and distribution in response to global environmental change. In: Goldstein G., Santiago L. eds. *Tropical tree physiology*. Cham, Switzerland. Springer, 67-101

Ryan, M. G., Phillips, N., & Bond, B. J. (2006). The hydraulic limitation hypothesis revisited. *Plant, Cell & Environment* **29**(3): 367-381.

Seabold, S. & Perktold, J., (2010). Statsmodels: Econometric and statistical modelling with python. In Proceedings of the 9th Python in Science Conference **57**(61): 10-25080.

Simard, M., Pinto, N., Fisher, J.B. & Baccini, A., (2011). Mapping forest canopy height globally with spaceborne lidar. Journal of Geophysical Research: Biogeosciences, **116**(G4).

Tomlinson, P. B. (2006). The uniqueness of palms. *Botanical Journal of the Linnean Society* **151**(1): 5-14.

Tsukaya, H. (2006). Mechanism of leaf-shape determination. *Annual Review of Plant Biology* **57**: 477-496.

Valladares, F., Skillman, J.B. & Pearcy, R.W., (2002). Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. American journal of Botany, 89(8): 1275-1284.

Vogel, S. (2009). Leaves in the lowest and highest winds: temperature, force and shape. *New Phytologist* **183**(1): 13-26.

Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Díaz, S., Gallagher, R. V., Jacobs, B. F., Kooyman, R., Law, E. A., & Leishman, M. R. (2017). Global climatic drivers of leaf size. *Science* **357**(6354): 917-921.

Zachos, J., Pagani, M., Sloan, L., Thomas, E., & Billups, K. (2001). Trends, rhythms, and aberrations in global climate 65 Ma to present. *Science* **292**(5517): 686-693.

Zizka, A., Silvestro, D., Andermann, T., Azevedo, J., Duarte Ritter, C., Edler, D., Farooq, H., Herdean, A., Ariza, M., Scharn, R., & Svantesson, S. (2019). CoordinateCleaner: Standardized cleaning of occurrence records from biological collection databases. *Methods in Ecology and Evolution* **10**(5): 744-751.

Figures

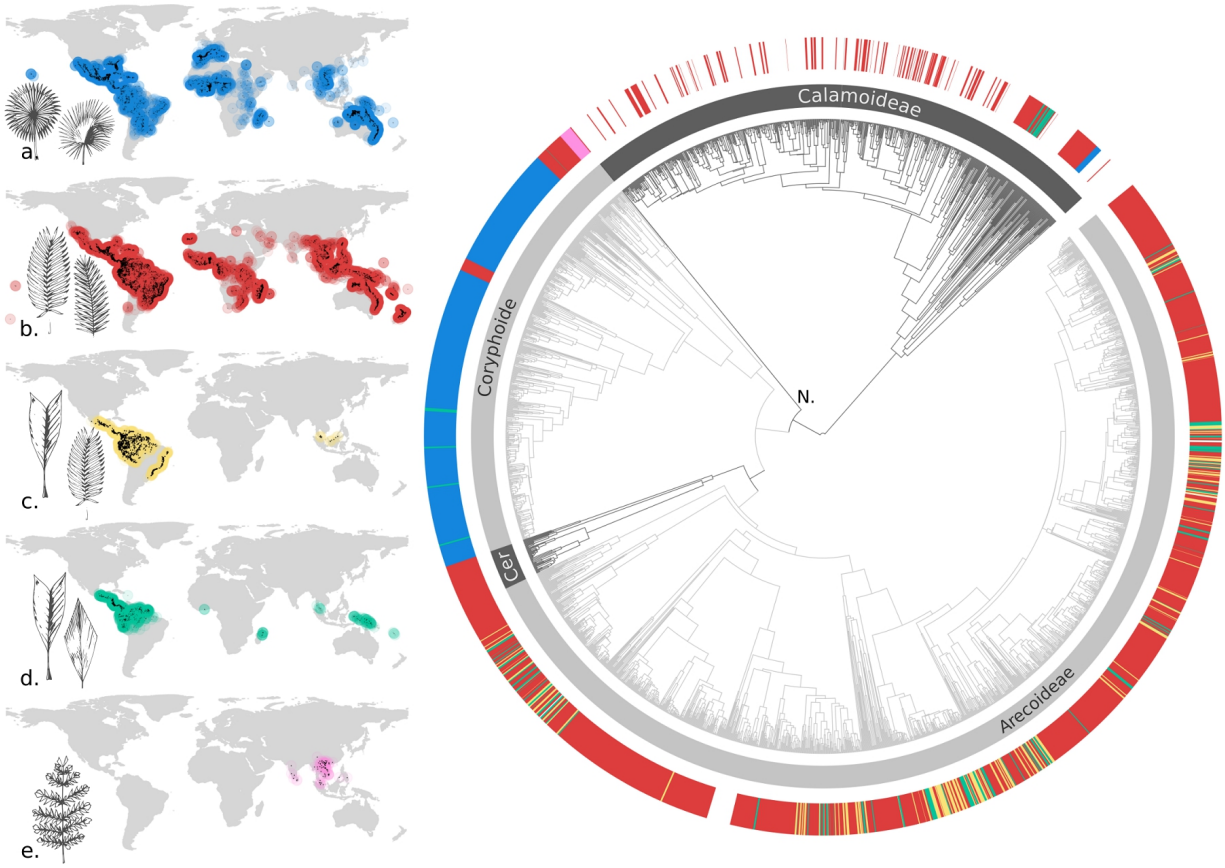


Figure 1. Leaf shape distribution at a global scale and throughout the Palm phylogeny. **Left:** The maps show the approximate distribution of shapes based on cleaned GBIF records (see Methods). Leaf silhouettes were modified from the illustrations in the Genera Palmarum (Dransfield et al., 2008). **Right:** The calibrated maximum clade credibility tree of 2550 palm species (Faurby et al., 2016; Hill et al., 2021). Dark and light greys are used to distinguish between subfamilies. The outermost ring shows the distribution of leaf shapes across the phylogeny and follows the same colour scheme in the maps. Species with no leaf shape colours are climbing and were removed from the Generalised Linear Mixed Models. **a)** Palmate + Costapalmate, **b)** Pinnate, **c)** Polymorphic, **d)** Entire, **e)** Bipinnate. **Cer.**= Ceroxyloideae. **N.**=Nypa.

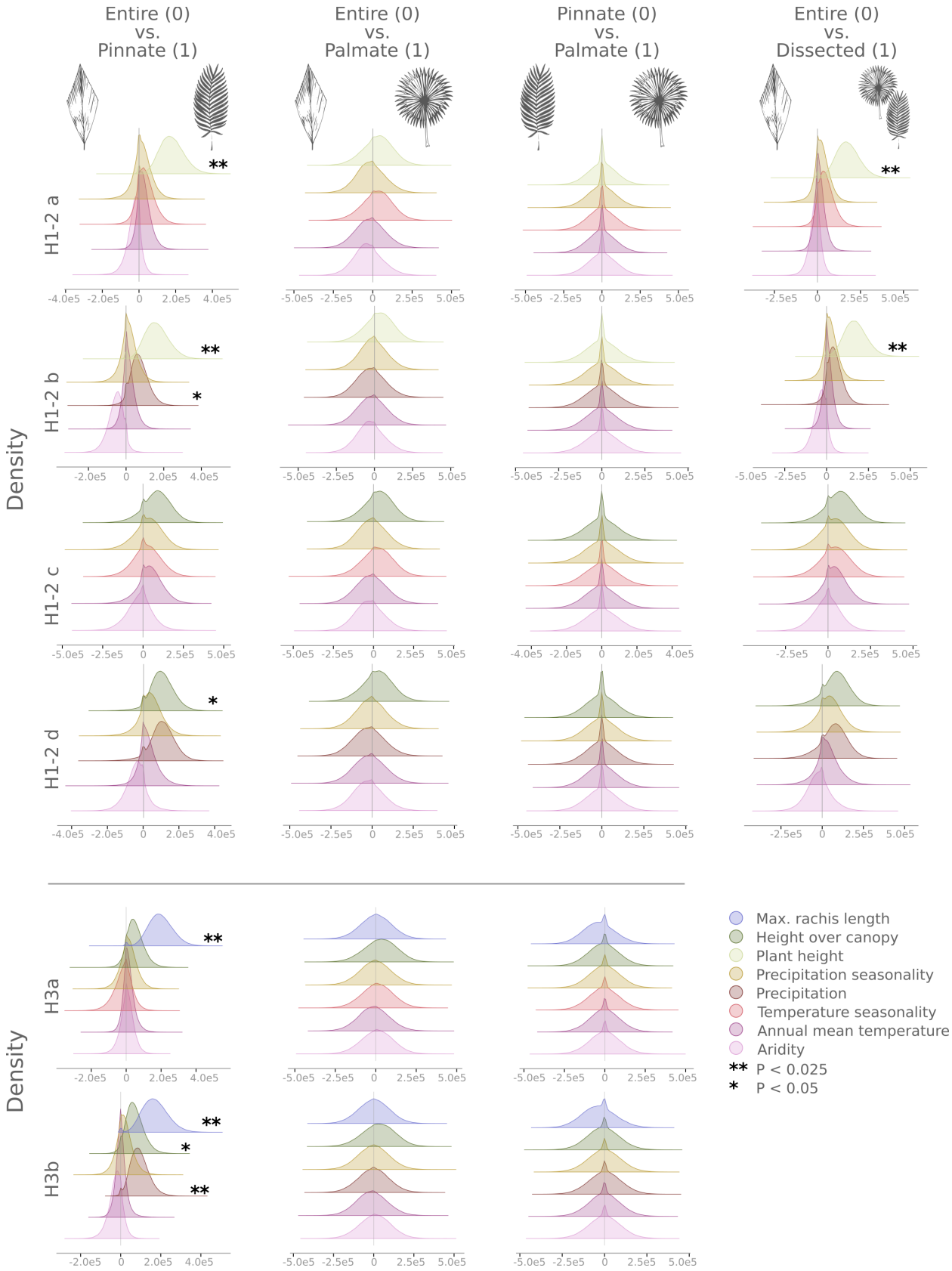

Entire (0) vs. Pinnate (1)
Entire (0) vs. Palmate (1)
Pinnate (0) vs. Palmate (1)
Entire (0) vs. Dissected (1)
Density
H1-2 a
H1-2 b
H1-2 c
H1-2 d
H3a
H3b
**
*
-4.0e5 -2.0e5 0 2.0e5 4.0e5
-5.0e5 -2.5e5 0 2.5e5 5.0e5
-2.5e5 0 2.5e5 5.0e5
-2.0e5 0 2.0e5 4.0e5
Max. rachis length
Height over canopy
Plant height
Precipitation seasonality
Precipitation
Temperature seasonality
Annual mean temperature
Aridity
** P < 0.025
* P < 0.05

Figure 2. Effect estimate distributions from the Generalised Linear Mixed Models (GLMMs). Leaf shapes show the pair compared in the models (logistic regression; left=0, right=1). Each row shows the results from the models concerning hypotheses H1-3. Palmate = (costapalmate+palmate). We tested hypotheses H1-2 for each shape separately and for entire versus dissected (palmate + costapalmate + pinnate), H1-2a, H1-2b, H1-2c, and H1-2d correspond to the models including either plant height or height over canopy, or temperature seasonality or precipitation. Hypothesis H3 was tested for each shape separately and H3a and H3b correspond to the models including either temperature seasonality or precipitation. Leaf silhouettes were modified from the Genera Palmarum (Dransfield et al., 2008).

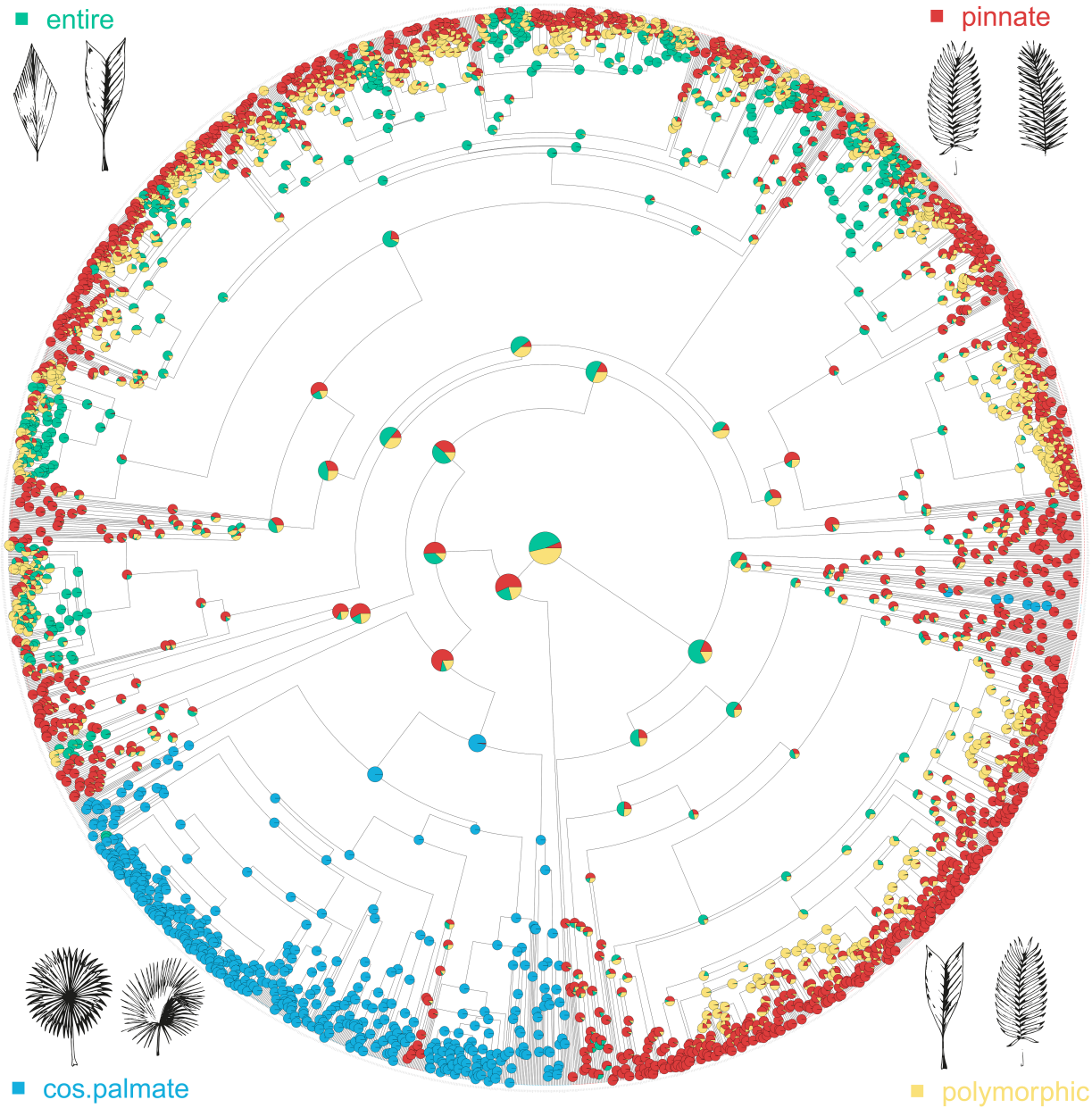


Figure 3. Ancestral state estimation of leaf shape across palms (Arecaceae) using the calibrated maximum clade credibility tree (Faurby et al., 2016; Hill, et al., 2021). The pie charts show the probability of each state at the given node. States are colour-coded as follows: Blue: Palmate (costapalmate+palmate); Red: Pinnate; Green: Entire; Yellow: Polymorphic (where individuals of the same species have either entire or pinnate leaves). Leaf silhouettes were modified from the Genera Palmarum (Dransfield et al., 2008).

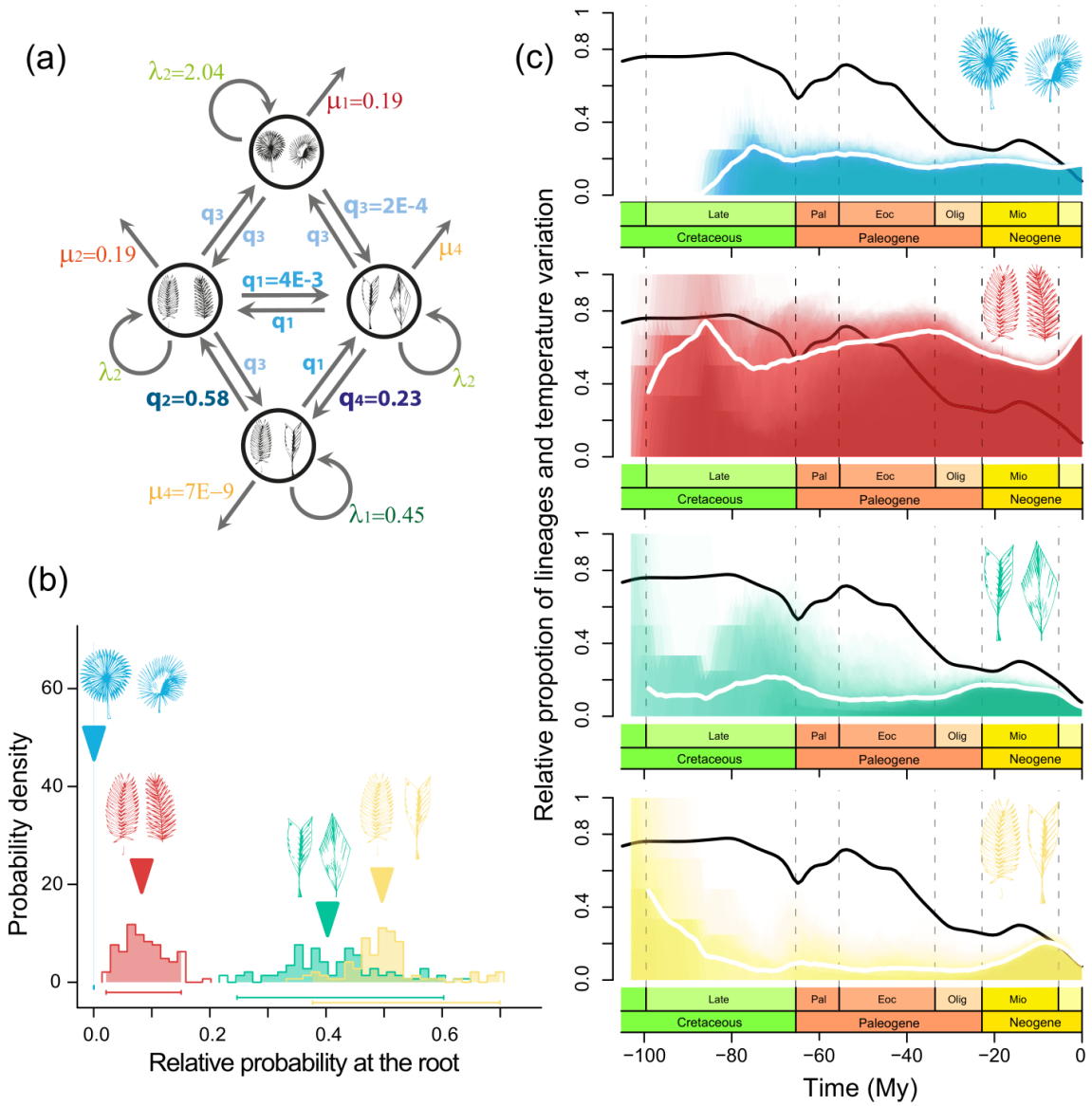
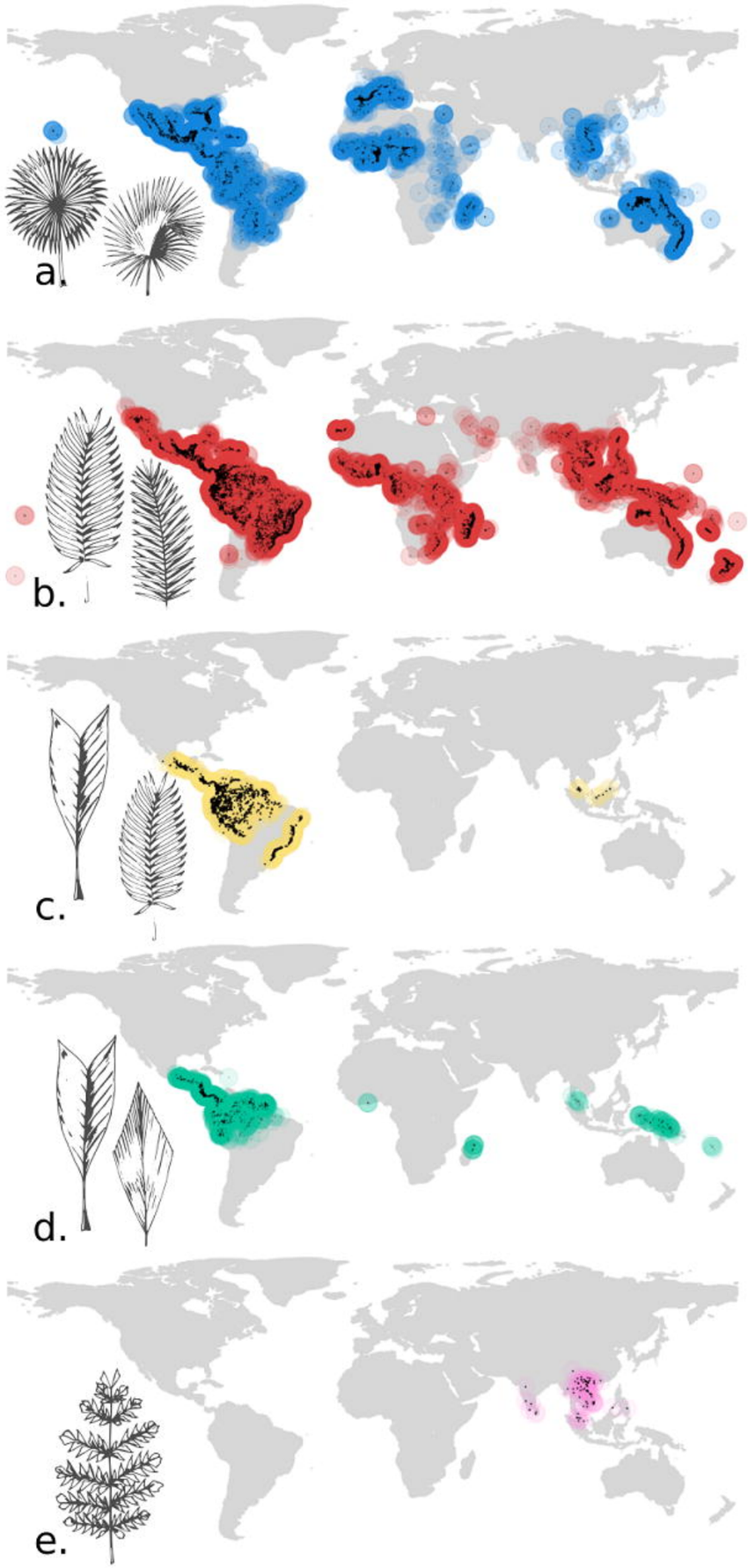
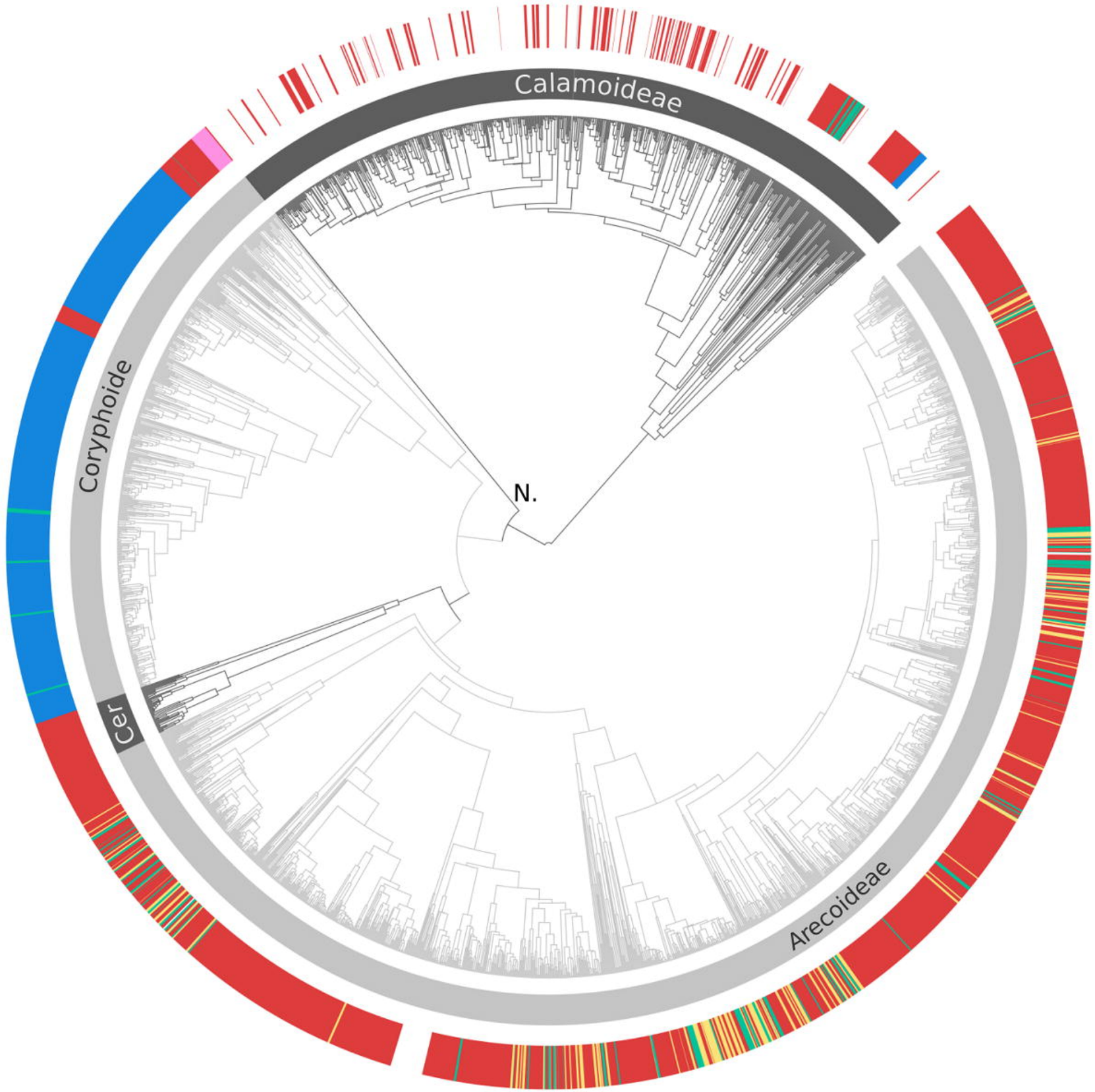
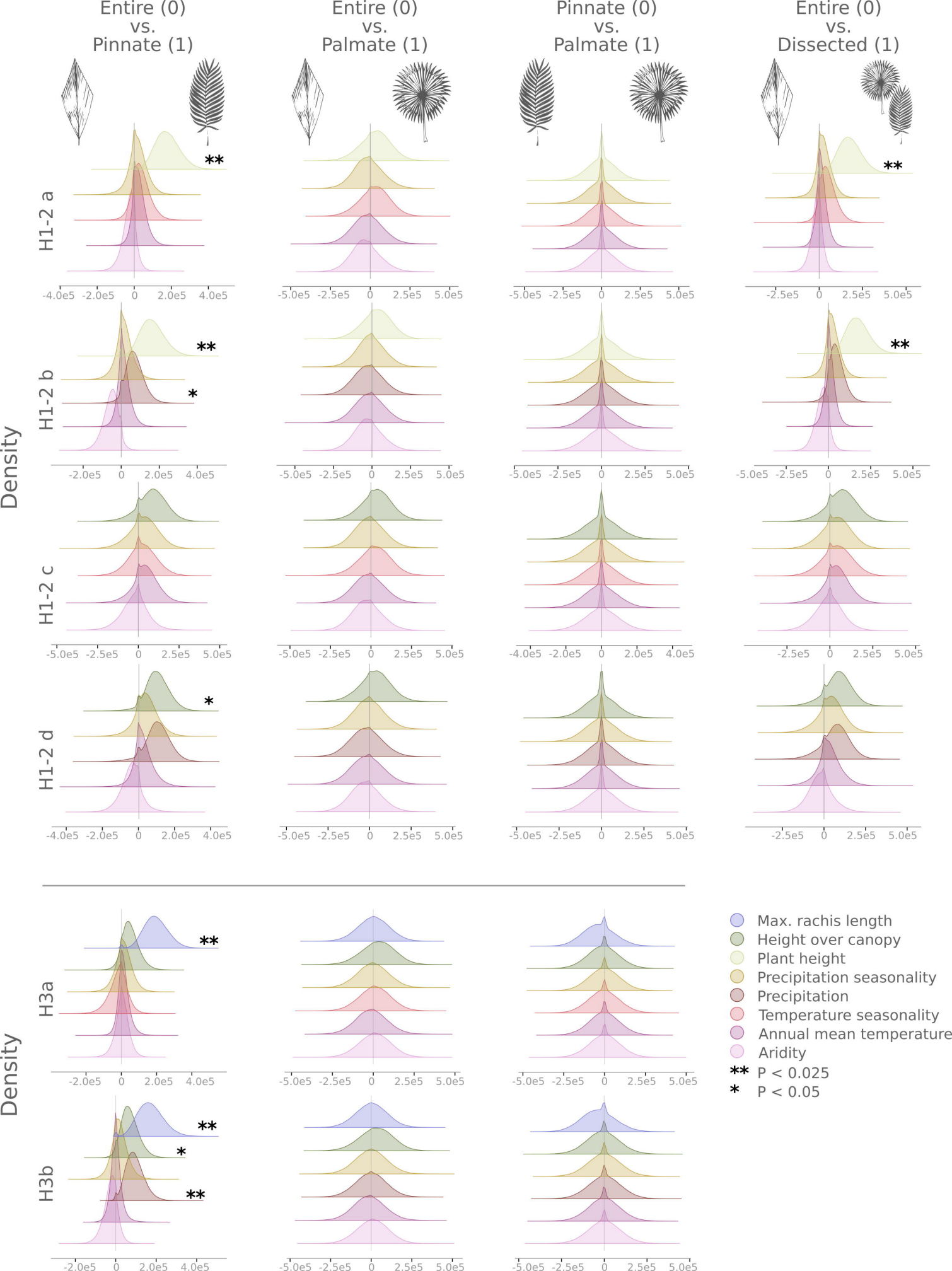
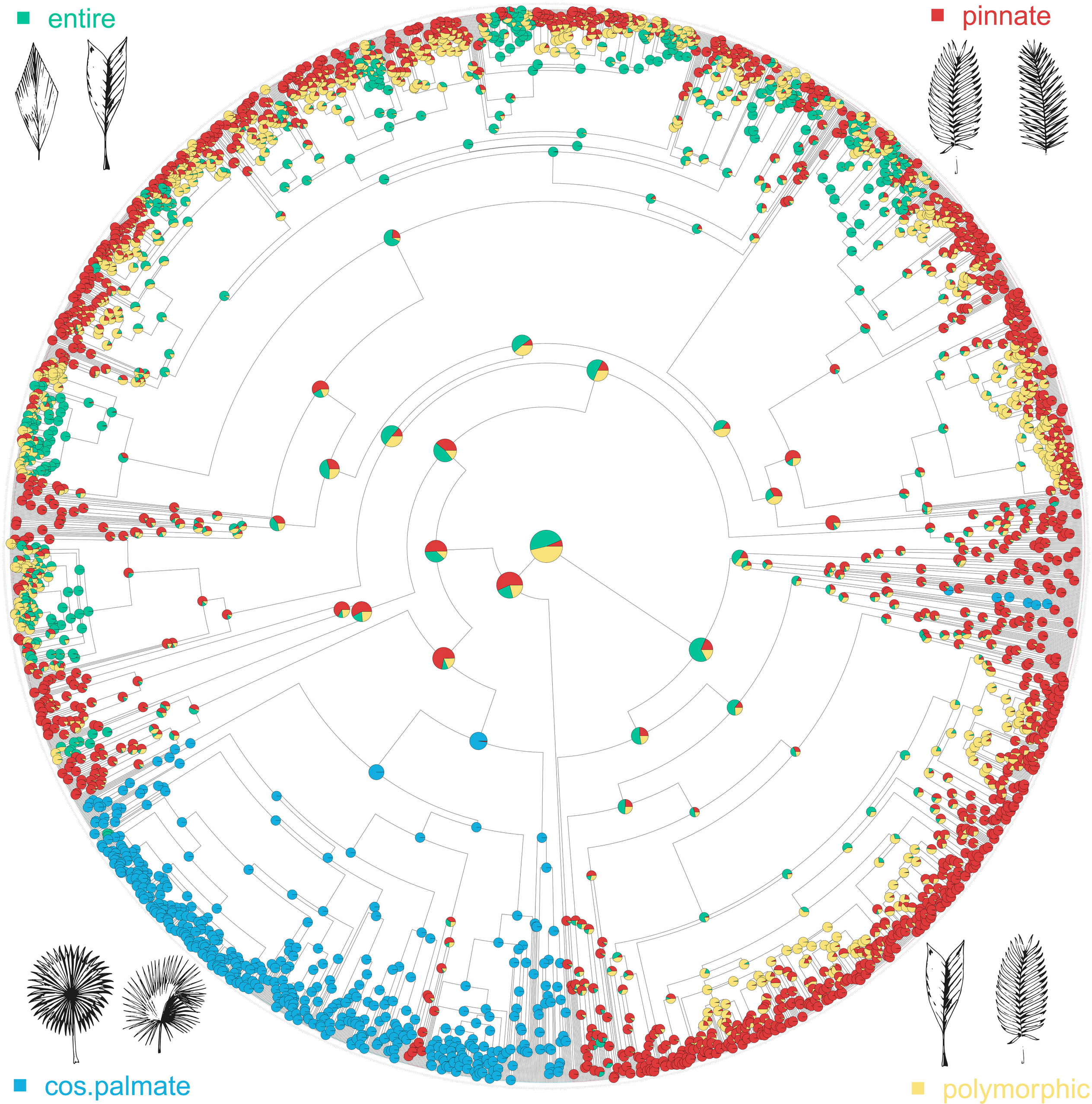


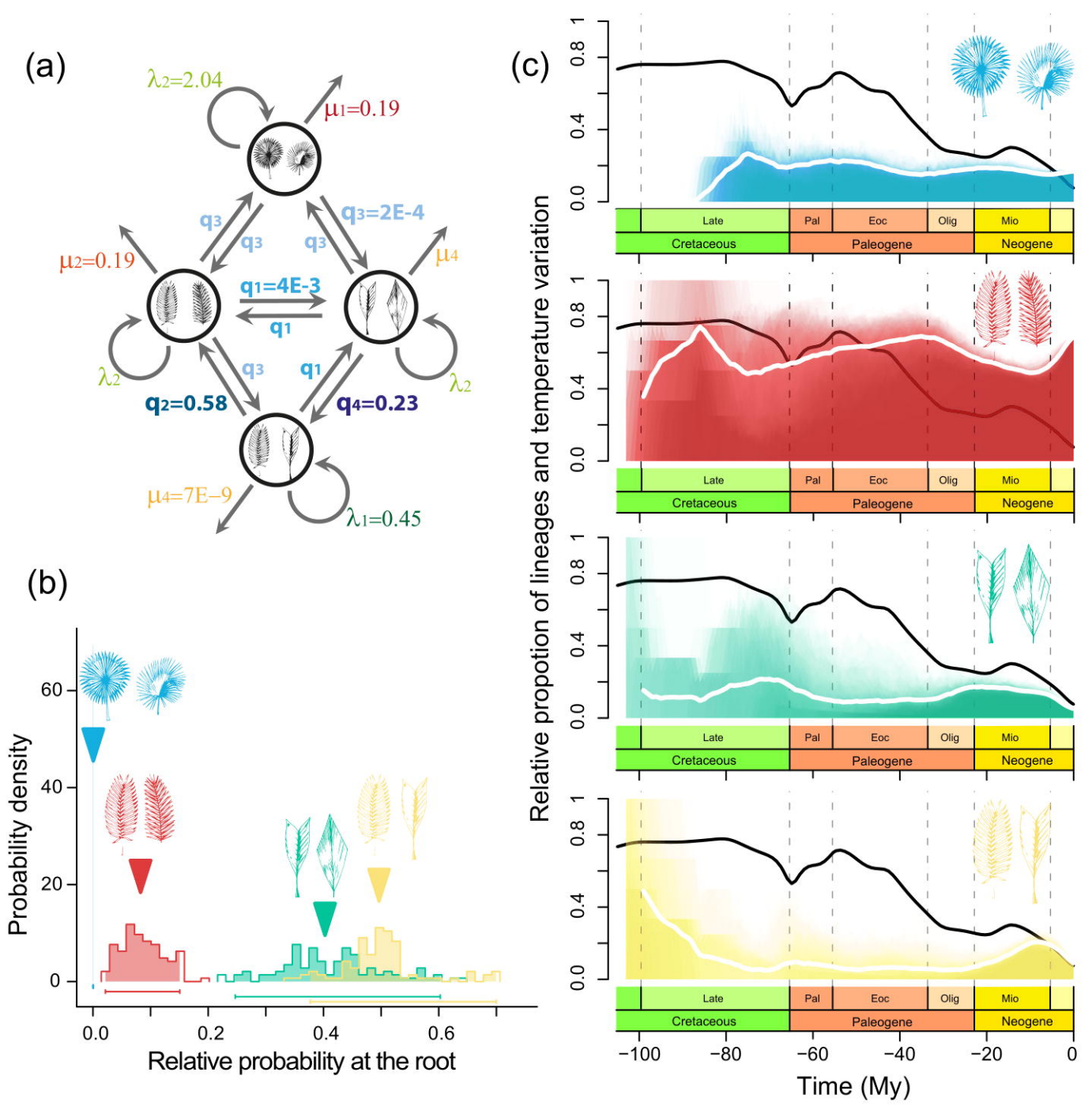
Figure 4. Palm leaf shape through time. (a). Parameters of the best-fitting MuSSE model used to estimate ancestral states; variables with the same colour have the same value. Lambda (λ) is the speciation rate parameter for each state, *q* is the transition rate between states, and mu (μ) is the extinction rate parameter. **(b)** Relative probability of the ancestral state at the root of Arecaceae across 100 random trees sampled from the posterior distribution of the MCMC. States are colour-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). **(c)** Proportion of lineages with each leaf shape compared to global temperature variation through time. The white lines show the average proportion and the coloured lines show the relative proportion sampled from the 100 ancestral state estimations. States are colour-coded as in (b). Leaf silhouettes were modified from the Genera Palmarum (Dransfield et al., 2008).


a.
b.
c.
d.
e.


Calamoideae
Coryphoide
Cer
N.
Arecoideae


Entire (0) vs. Pinnate (1)
Entire (0) vs. Palmate (1)
Pinnate (0) vs. Palmate (1)
Entire (0) vs. Dissected (1)
Density
H1-2 a
H1-2 b
H1-2 c
H1-2 d
H3a
H3b
**
*
-4.0e5 -2.0e5 0 2.0e5 4.0e5
-5.0e5 -2.5e5 0 2.5e5 5.0e5
-2.5e5 0 2.5e5 5.0e5
-2.0e5 0 2.0e5 4.0e5
-4.0e5 -2.0e5 0 2.0e5 4.0e5
Max. rachis length
Height over canopy
Plant height
Precipitation seasonality
Precipitation
Temperature seasonality
Annual mean temperature
Aridity
** P < 0.025
* P < 0.05


entire
pinnate
cos.palmate
polymorphic


(a)
λ2=2.04
μ1=0.19
q3
q3
q3=2E-4
q3
μ2=0.19
μ4
q1=4E-3
q1
λ2
λ2
q3
q1
q2=0.58
q4=0.23
μ4=7E−9
λ1=0.45
(b)
Probability density
Relative probability at the root
(c)
Relative propotion of lineages and temperature variation
Late
Pal
Eoc
Olig
Mio
Cretaceous
Paleogene
Neogene
Time (My)