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Temperature predicts leaf shape in palms (Arecaceae)

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Abstract

Leaves display a remarkable variety of shapes, each potentially relevant to the function of these organs and with potential ecological advantages in certain climates. Studies correlating leaf shape with either climate or allometric constraints (how size and shape relate) focus on intraspecific variation or model organisms, and the drivers of leaf shape at a macroecological scale remain poorly known. Here, we determine associations between climatic and allometric factors with the evolution of leaf shape in a lineage with one of the highest diversities of leaf shape known, the palms (family Arecaceae). We apply a Bayesian phylogenetic mixed model to test for associations with leaf shapes (entire, pinnate, palmate, and costapalmate). We further reconstruct the ancestral leaf shape in palms using multistate speciation and extinction models. We find that high mean annual temperature correlates with dissected shapes. The ancestral leaf shape is entire, and pinnate lineages originated multiple independent times after transitions into polymorphism (species with entire or pinnate individuals). Finally, we compared the frequency of shapes with global temperatures through time through the Cenozoic. Although mean annual temperature has a positive effect on leaf dissection, the relative frequency of pinnate lineages increased as global temperatures cooled through time, potentially through colonization of open more seasonal habitats. Dissection could therefore be beneficial at high temperatures, where other leaf shaped lineages would be highly vulnerable under increased global warming. This study contributes to the understanding of leaf shape evolution and its drivers.

Keywords

Climate, dissection, leaf shape, macroecology, MuSSE, temperature.

1. Introduction

Leaves are the engines of nearly all life on land. They capture carbon dioxide from the atmosphere and convert it into readily accessible nutrients that sustain, directly or indirectly, the functioning and health of ecosystems and their biota. The basic functions they carry out – photosynthesis, transpiration and respiration – depend in turn on temperature and water availability. Because they carry out such critical functions for the plants, leaves are most likely under strong natural selection, resulting in morphological adaptations to the environmental conditions.

Throughout the evolution of angiosperms, variation not only in length and width but also in blade dissection (with simple and compound leaves as extremes), margin serration, and contour (e.g. orbicular versus lanceolate leaves) have evolved numerous times independently (Nicotra et al., 2011). Nonetheless, the drivers of leaf shape evolution are poorly known. Research on the evolution and adaptation of leaf shape is often limited to a handful of species (e.g. examples reviewed in Nicotra et al., 2011 and Chitwood & Sinha, 2016; Marcysiak, 2012; Leigh et al., 2017), or to model organisms like *Arabidopsis* (Piazza et al., 2010), which prevents generalization at a larger taxonomic scale.

General expectations regarding functionality can be drawn from examining the leaf adaptations in different environments. Traits like leaf dissection, length and, effective width (diameter of largest circle drawn within a leaf margin; Leigh et al., 2017) potentially change with climate, which affects plant temperature regulation and interacts with water availability (Nicotra et al., 2011; Peppe et al., 2011). For instance, plants in environments with extreme temperatures tend to have small or dissected leaves to prevent leaves from reaching damaging temperatures (Gates, 1986; 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 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 leaf 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 and in arid environments with limited water availability for transpiration, stomata close and high temperatures threaten leaf function. In this case, smaller or deeply dissected shapes reduce overheating and optimize the safety of the leaf (Nardini & Luglio, 2014). Dissection could be beneficial also in species with large and wide leaves that are optimized for high gas exchange, as dissection makes the transportation of water to areas of the blade farthest from the rachis more effective (Givnish, 1979). In contrast, cool climatic conditions may favor entire leaf shapes over dissected shapes, where leaf heating leads to higher temperatures in the leaf compared to the air, which can be beneficial for photosynthesis and growth.

Leaf shape, particularly size, can be tuned to maximize light capture in environments with limited sunlight. This is particularly relevant for monopodial plants (non-branching plants

with a single stem or growth axis) that depend on leaf size or number to increase the total photosynthetic area (Chazdon, 1985; Renninger & Phillips, 2016). However, leaf size is limited by allometry where following Corner's rule, "the larger and sturdy an axis is, the larger and more complicated are its appendages" (Corner, 1949; Tomlinson, 2006). Thus, to produce larger leaves and capture more light, the plant needs to invest significant energy in leaf supporting structures (e.g. petioles and rachis) that are strong enough to resist the stress from wind and rain (Chazdon, 1986). In the forest understory, small leaves with entire shapes could be easier to arrange to maximise light capture than dissected leaves. For very large leaves, dissection allows the leaflets to move independently and reduce the drag produced by strong winds (Niklas, 1992; Vogel, 2009; Blein et al., 2010). 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 1978, 1984; Niinemets, 1998), which states that dissection allows plants to grow rapidly during periods of high light availability by maximizing light capture while investing less in wood density. This association between dissection and growth has been found in Amazonian trees (Malhado et al., 2010). Finally, it has been suggested that dissection has varied ecological roles in herbivory: limiting how effectively herbivores feed (Brown & Lawton, 1991), increasing the chance of herbivory via a correlation with leaf size and growth (Rivero-Lynch et al., 1996), or reducing herbivory by acting like variegated leaves in that patterns of discoloration "distort" the leaf's edges (Givnish, 1990; Campitelli et al., 2008).

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 climatic or phylogenetic constraints, the distribution of leaf shape and their evolution through time should reflect evolutionary processes. In this study, we use palms (Arecaceae) to understand the macroevolutionary drivers of leaf shape variation. Palms are tropical and subtropical, with 80% of the species distributed within a 15-30°C mean annual temperature range (Dransfield et al., 2008), and which exhibit high leaf shape variation compared to other monocots (Horn et al., 2009; Gunawardena & Dengler, 2004). Palms are primarily monopodial (i.e. do not branch) with non-deciduous leaves (Tomlinson, 2006; Dransfield et al., 2008), allowing us to control for the effect of branching strategies over leaf-climate relationships.

Here, we hypothesise that dissection is beneficial in high temperatures. If this is the case, we expect temperature to have a positive effect on the distribution of dissection throughout the palm phylogeny. We also hypothesise that taller species are more likely to have dissected leaves as dissection could allow for large leaves that scale with plant height. In this case, we expect larger plants to be dissected because dissection allows for larger leaves that are more resistant to mechanical damage and that have better weight distribution along the rachis, hence a positive effect of plant height on dissection. We tested these predictions for extant taxa over geological time scale. On the one hand, if our predictions are true, extant variations in climatic conditions across ecoregions should predict the current distribution of palms and leaf shapes. On the other hand, the evolution of leaf shapes through time since the origin of palms should reflect major global climatic changes that occurred since the Late Cretaceous, when palms are thought to have originated (Dransfield et al., 2008). Here, we contribute to the knowledge gap concerning climatic factors and plant allometry. 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 all GLMMs and ancestral trait reconstruction analyses at the species level using a time-calibrated Maximum Clade Credibility tree generated from the tree distribution generated originally by Faurby et al. (2016) and updated by Hill et al. (unpublished). The phylogeny includes 2550 species that were used to annotate leaf shapes, recover coordinate records from the Global Biodiversity Information Facility (GBIF), and estimate species medians for the climatic and allometric variables. We standardized the taxonomic identifications across all data sources using the Kew's World Checklist of Selected Plant Families (WCSP) for Arecaceae (Govaerts et al., 2020). We removed all GBIF records which could not be unambiguously assigned to any of the species accepted by the WCSP.

Leaf shape in palms

Leaf shape variation in palms can be described by three main features: size, plication and dissection. For size, palm leaves can be as small as 15 cm in length (*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). Plication refers to leaf

folding, leaf blades are folded like accordions as they develop, and the type of plication depends on whether the folds are on the upper (induplicate) or lower (reduplicate) ridges. Plication is highly phylogenetically conserved within subfamilies with very 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, palm leaves are either entire or dissected. Dissected leaves usually form from entire blades as they develop and can be pinnate, palmate or costapalmate depending on the length of the leaf rachis and the presence of a costa (an extension of the leaf axis; Dransfield et al., 2008). Interestingly, some palm species are polymorphic (within-species leaf shape variation in which individuals have either entire or dissected leaves), but in such cases, polymorphism only involves entire and pinnate shapes. For the latter, it is worth noting that genomic analyses (e.g. Loiseau et al., 2019) have confirmed that at least some of them represent true polymorphism within populations rather than issues of taxonomy with different taxa currently grouped under one species name being polymorphic.

Based on the information available on Genera Palmarum II (Dransfield et al., 2008) and PalmWeb (<http://www.palmweb.org/>, last consulted in October 2019), we classified all species into “entire”, “pinnate”, “bipinnate”, “palmate” (costapalmate and palmate), and “polymorphic” categories, depending on their leaf shape. We merged the costapalmate and palmate shapes because their leaf blades are highly similar and only differ in the costa. We removed the bipinnate shape category from all analyses because the category includes only 14 out of the 2550 species. Of the species included, the large majority are pinnate (67.7%, Supporting Information Table S1), followed by palmate and entire (22.19% and 5.5% respectively). Only 75 (3.87%) species are polymorphic. They were included in the ancestral state estimation analyses but excluded from the GLMMs because they cannot be assigned to a unique shape category in our models (Supporting Information Table S2).

Palm allometry data

We annotated all species using the data in Palm_Traits v.1 (Kissling et al., 2019) and scored maximum leaf number, maximum petiole length, plant height, and blade length variables. 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 could annotate 47-77% 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 species (465 species, Supporting Information Table S3); the latter removed because their life strategies differ from the rest of palms and their stem height is not readily comparable.

Climatic and ecoregion data

We downloaded 885,130 occurrences of palm species from GBIF (last consulted, January 2019), from which we excluded fossil occurrences and data with missing coordinates. We used the R package *CoordinateCleaner* (Zizka et al., 2019) to remove duplicate coordinates per species, records nearby science institutions, coordinates on bodies of water, and coordinates in city/country centroids, all using a buffer of 5000 m). We further used a custom Python script (https://github.com/mftorres/palm_leaf) and the World Geographical Scheme for Recording Plant Distributions maps (TDWG; Brummitt, 2001) to remove species coordinates falling outside the botanical countries listed as their native areas in the WCSP database. We obtained 56,372 clean coordinate records representing 70% of the species (Supporting Information Table S4), which we used to extract all WorldClim1.4 climatic variables with *dismo* v1.1.4 (Hijmans et al., 2017) and *ade4* v1.7.15 (Dray & Dufour., 2007), both R packages (R Core Team, 2018). We used the extracted WorldClim1.4 data to estimate the de Martonne’s Aridity Index (de Martonne, 1925) for each record as the annual precipitation in mm divided by the mean annual temperature in Celsius + 10. Finally, we estimated the species medians for every climatic variable from which we could extract the information.

After annotating climatic and allometric variables for 1212 to 1439 species out of the 2550 species in the phylogeny (depending on record and data availability), we examined the correlation between variables and chose for the models the variables with a Spearman’s coefficient < 0.7 (Supporting Information Fig. S1). We additionally estimated the variance inflation factor for all variables using the function *vif* and removed those above a threshold of 0.7 (USDM v1.1.18; Naimi, 2015). We chose five climatic and two allometric variables: mean annual temperature ($^{\circ}\text{C}$), temperature seasonality ($\sigma \cdot 100$), annual precipitation (mm); precipitation seasonality ($\sigma \cdot 100$), aridity ($\text{mm}/^{\circ}\text{C}$), maximum leaf number, and plant height (m).

For our palm data, other climatic variables that we do not include in the models (like the maximum and minimum temperature/precipitation of the warmest month) had a high Spearman's correlation coefficient (> 0.7) to one or a few of the variables selected (Supporting Information Fig. S1). Annual precipitation and aridity were highly correlated (Spearman's correlation coefficient = 0.9; Supporting Information Fig. S1); however, because water stress increases the damaging effect of high temperatures and can be a selective pressure for leaf shape, we removed aridity from models that included precipitation and vice versa. Similarly, plant height was highly correlated with the understory/canopy trait and we kept plant height as a proxy for understory/canopy from here on. All variables included in the models were $\log^{10}$ -transformed (with the exception of mean annual temperature) and standardized to have zero mean and a standard deviation of one (Supporting Information Table S4). Finally, we annotated the species ecoregions based on Olson et al. (2001) and as described in Cássia-Silva et al. (2019).

Generalized linear mixed models

We fit a series of GLMMs using all selected variables (except for aridity and annual precipitation, see Results), removing one variable in each iteration, to evaluate the effect. We used logistic regressions to distinguish the variables associated with leaf shape using a series of pairwise comparisons; pinnate (0) vs. palmate (1), entire (0) vs. palmate (1), and entire (0) vs. pinnate (1). All regressions were done using Bayesian phylogenetic logistic regressions 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 of phylogenies generated by Faurby et al. (2016) and updated in Hill et al. (2021), setting them as a random effect. For every model on the 42 phylogenies, we ran two independent chains of 10,000,000 iterations each, with a thinning of 8,000, and a burn-in of 10% of the sampling. Analyses were run at the Chalmers University of Technology cluster through the Swedish National Infrastructure for Computing (SNIC; Gothenburg, Sweden). We ran the models until the chains converged, here defined as effective sampling sizes for all variables higher than 100, and autocorrelation between values lower than 0.2. 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 (Supporting Information Table S5).

Ancestral state estimation

In order 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 ensure we had enough power to estimate parameters: 1) We did not include plication in the analyses due to its high phylogenetic clustering (Fig. 1; but see the discussion about how all folded palmate leaves across plants are similar due to leaf folding inside the bud in Couturier et al., 2011); 2) we created a “polymorphic” category for species exhibiting more than one shape. 3) We excluded all species for which leaf shape information was unavailable from the analyses. This resulted in a dataset containing 2543 species and four character states: palmate (costapalmate + palmate), pinnate, entire and polymorphic. Polymorphism only includes those species that have both pinnate and entire leaves, but never palmate or costapalmate leaves. Hence, when designing the MuSSE models we assumed direct transitions between palmate leaves and polymorphic states (pinnate + entire) to be impossible and therefore constrained the corresponding transition parameters to zero. Because of the large number of parameters for the MuSSE model remaining (18 parameters, Supporting Information Fig. S2), 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). We then proceeded with reducing the model, one constraint at a time until the AIC score did not improve. At each step, all models with one more constraint than the previous (more complex) model 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. Using the best-fitting model as determined above, 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. AIC scores for determining the best MuSSE models stopped improving at the tenth step during the backward model selection procedure, representing 315 models, of which six did not converge.

We used the best-fitting MuSSE model to estimate ancestral states across the tree. Based on this ancestral state estimation we estimated the number and rate of transitions through time as well as the relative frequency of lineages of each leaf type through time. To do so, we sampled states at nodes 100 times, using the relative probabilities of leaf shape estimated for each node as sampling probabilities. 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 happening within a 5 million year sliding window to obtain the number of state transitions through time. We calculated the rate of transition through time by dividing the number of transitions by the sum of branch lengths within each time interval. We repeated the procedure for one iteration out of the 100, but instead of calculating the number of transitions, we calculated the relative frequency of lineages exhibiting each type of 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 extrapolated by Condamine et al. (2020) and based on data from Zachos et al. (2001).

3. Results

Leaf shape and climate

Palms are widely distributed across climatic gradients (except for habitats where extreme frost occurs). However, leaf shapes are not distributed evenly throughout the geographic distribution of the palm family (Figs. 1 and S7-10). The distribution of pinnate and palmate species extends farther from the equator into areas of substantial water scarcity and regular exposure to extreme temperatures. These areas include the tropical and subtropical moist and dry broadleaf forests, temperate forests, grasslands and savannahs, and desert and xeric shrublands (Supporting Information Fig. S10). Meanwhile, the distribution of entire-leaved species is concentrated in tropical areas near the equator where annual temperature and precipitation are more constant. We observe a similar pattern for all climatic variables considered here, in which the species median distributions of pinnate and palmate species are wider than the species median distributions of species with entire leaves (Supporting Information Fig. S3 and Table S6). For mean annual temperatures for example, pinnate species range between 12.8°C and 27.7°C (14.9°C difference), palmates range between 13.8°C and 28.1°C (14.3°C difference), and species with entire leaves range between 14.1°C and 27°C (12.9°C difference). However, the

median of the distribution for mean annual temperatures is higher for palmate (25.1°C), then entire (24.6°C), and lowest for pinnate species (23.7°C).

The GLMMs identified a strong association between temperature and dissection when considering entire and pinnate shapes and a less clear pattern when considering palmate in combination with the other two shapes. When comparing entire versus pinnate shapes, the model including all variables showed a significant positive association between mean annual temperature and pinnate shape ($P = 0.002$). That means that high mean annual temperatures make the pinnate shape more likely. The significance of the positive association persists even when only climatic variables are considered (Figs. 2a and S4). When the model included one climatic and one allometric variable, both had a significant association with pinnate shape. However, when models included only a single variable, the only one that had a significant positive association with pinnate shape was temperature seasonality ($P = 0.001$, Figs. 2c and S4).

When comparing pinnate versus palmate, none of the variables were significant when they were all included in the same model. However, when considering only the climatic variables and none of the allometric ones, mean annual temperature was significant and had a positive association with palmate shapes ($0.018 < P < 0.022$). With this, palmate shape is more likely at high mean annual temperatures, if only climate is considered. When the model included one climatic and one allometric variable, the climatic variable had a significant positive association with palmate shape (and negative with pinnate) if the allometric variable was plant height. Considering one climatic variable together with maximum leaf number resulted in a lack of significant associations (Fig. 2a). Finally, when comparing entire versus palmate shapes, none of the variables had a significant effect regardless of the model (Fig. 2a-c, Supporting Information Table S5).

No significant associations were found with precipitation and aridity unless each was included in the model together with one more variable (Figs. 2a and S4), indicating that the variation in leaf shape they explain is minimal. Precipitation and aridity had a significant and positive effect in models when the other variables are plant height (pinnate versus palmate) and leaf number (entire versus pinnate). However, the Spearman's correlation coefficient between

precipitation and plant height/leaf number, and those between aridity and the same two variables, were small (-0.2 in all cases except between aridity and leaf number, which is -0.3). Finally, for our data and all shape comparisons, the association between shape and temperature was not restricted to annual mean estimates but potentially extends to other variables highly correlated with mean annual temperature including the mean temperature of the coldest month, and the mean temperatures of the driest, warmest, and coldest quarter (Spearman's correlation coefficient = 0.9 for the variables mentioned; Supporting Information Fig. S1).

Allometry and shape

For our data, plant height was highly correlated with growth habit (Spearman's correlation coefficient = 0.8), understory versus canopy (since most palms are found in forested environments); therefore, we did not consider habit explicitly in the models. However, it is worth noting that almost all species with entire leaves live in the understory, while pinnate and palmate species live in both (Supporting Information Fig. S3). Pinnate and palmate species tend to be much larger than species with entire leaves, with median heights of 8.7 m (74.4 m max) in pinnate and 6.6 m (54.9 m max) in palmate species. In contrast, species with entire leaves have a median height of 4.9 m and a maximum height of 39 m, leaf length included in all cases. Regarding leaf number, pinnate and species with entire leaves have a similar median of 10.9 leaves (and a maximum of 55 and 41 respectively) while palmate species tend to have more, with a median of 22 and a maximum of 75 leaves (*Livistona endauensis*; Kissling et al., 2019).

From the GLMMs, we only found a significant association between plant height and shape when comparing entire and pinnate shapes and the direction of the effect changed depending on which other variables were present in the model. Plant height had a significant negative association with pinnate shape when all variables were considered in the model ($P = 0.008$); however, the effect of plant height was a lot smaller than the effect of mean annual temperature (Figs. 2a-b and S4), suggesting that while high mean annual temperatures make pinnate shapes more likely, large plant height make them less likely. Moreover, the directionality of the association between plant height (or maximum leaf number) and pinnate shape varied. The association was negative when models included mean annual temperature, annual precipitation, aridity, and maximum leaf number; the effect was positive when the model included temperature

seasonality or precipitation seasonality (Fig. 2a). Only when the model included plant height and nothing else, did it have a significant positive association with pinnate shape ($P = 0.008$, Fig. 2c).

Ancestral state estimation

The best-fitting model (Supporting Information Fig. S2) 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 of polymorphic species was more than twice higher than that of the others (Supporting Information Fig. S5). Extinction rate for the polymorphic and entire shape lineages was estimated as zero (lineage/unit of time, $\text{l}^{-1}\text{my}^{-1}$). Pinnate lineages had more than twice the extinction rate of palmate lineages, which in turn was higher than the extinction rate for entire lineages. The resulting net diversification for pinnate lineages was close to zero. Palmate lineages followed with a mean net diversification estimated around $0.1 \text{ l}^{-1}\text{my}^{-1}$ and entire lineages 0.2 . Polymorphic lineages clearly had the highest net diversification rate with a posterior distribution averaging around $0.5 \text{ l}^{-1}\text{my}^{-1}$.

Ancestral state estimation based on the best fitting-model inferred entire leaves as the most probable state at the root (Fig. 3). Interestingly, according to our model, pinnate leaf lineages, the most common extant leaf type, originated multiple independent times from entire leaves after polymorphic transition periods. We found that the overall rate of state transitions through time remained relatively constant (Supporting Information Fig. S6). The relative frequency plot (Fig. 4) shows that entire leaves dominated during the early period of diversification, in the Late Cretaceous between 100-80 Million years ago (Mya). However, their relative frequency decreased through time at a steady rate, slowly replaced mainly by pinnate leaves since ca. 80 Mya. The first palmate lineages appeared after the pinnate lineages and their relative frequency remained approximately the same through time, averaging around 0.1 .

4. Discussion

In this study, we explore 1) the associations between leaf shape and climatic and allometric drivers whilst controlling for phylogenetic relationships 2) reconstruct the ancestral leaf shape of palms; and 3) compare shape frequencies and temperature trends through time. We

found that 1) temperature and not plant allometry drives leaf shape; 2) that the ancestor to all palms likely had entire leaves; 3) and that trends in shape frequency do not mirror trends in temperature through time (at least not among the lineages that survived until present day). These findings support the hypothesis that temperature and not allometry explain extant leaf shape distributions in palms and suggest shape as a potential adaptive response to heat.

Leaf dissection and climate

Species with dissected leaves, especially if pinnate, are more frequent where mean annual temperatures are high (Fig. 2a). This is congruent with the wider geographic range of dissected species compared to those with entire leaves; dissected leaf species are distributed throughout the driest and most seasonal ranges where palms are found (Figs. S3 and S8-S10) and dissection is likely an advantageous trait to avoid overheating (Nicotra et al., 2007; 2008; Leigh et al., 2017). These papers note that deeply dissected palm leaves are analogous to compound or dissected leaves in eudicots. The width of each pinnae is often narrower than the width of the whole leaf, and under the same conditions, narrower leaves lose heat to the air faster and reach damaging temperatures more rarely than wider leaves. During water scarcity or in dry environments, avoiding damaging temperatures in the leaf surface is key for protecting the photosynthetic machinery. Here, dissection allows species to withstand temperature extremes, seasonal variation, and water stress (Figs. S3). In areas where water is available, like the moist forest where all shapes occur, dissection is likely less crucial and has less advantage over other shapes.

The association between temperature and dissection is not significant when entire and palmate shapes are compared (Figs. 2 and S4); there are three non-mutually exclusive explanations for this. First, the discrete shape categories in our models might not capture the continuous variation within shapes and could be insufficient for unveiling the climate-shape association. For example, palmate-shape species within *Licuala* and *Saribus* are shallowly dissected and resemble eudicot leaves with toothed margins that are closer to an entire shape. Second, anatomical traits unrelated to shape could be the key adaptations to different environments (Horn et al., 2009). The loss of non-lignified fiber 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). Different

species can evolve different strategies to respond to the same environmental challenges. Third, the correlation between climate and shape are difficult to disentangle from a phylogenetic effect due to a strong geographic structuring of related lineages, particularly in the case of the Coryphoideae subfamily to which the majority of palmate and costapalmate species belong. Models considering continuous variation and data on intra and interspecific variation in dissection depth within palmate shapes are necessary to better understand the relationship between climate and palmate shapes.

Leaf dissection and margin serration have been found to respond quickly to changes in mean annual temperature in the eudicot *Acer rubrum* (Royer et al., 2009). Similar temperature-shape associations have been explored in other eudicots (Nakayama et al., 2014; Chitwood & Shina, 2016); however, research is lacking regarding monocots and the lineage-specific mechanisms behind shape convergence across angiosperms hinders the comparisons between monocots and eudicots (Conklin et al., 2019). A better understanding of the mechanisms by which climate interacts with shape development will come from future studies addressing shape variation quantitatively (Chitwood & Sinha., 2016; Kissling et al., 2018). Quantitative trait data on leaf shape is still lacking for most palms, but data comprising intraspecific variation for some morphological traits like that published in Lenters et al (2021), open the door to more comprehensive analyses. Finally, global temperatures are likely to increase over the coming decades. This could have implications over which palm lineages are able to survive in hotter environments and which could perish. Most palm species that are currently naturalised in areas outside their native distribution are those that originated in open and dry habitats, not in moist forests (Fehr et al., 2020), and all have dissected leaf shapes. Understanding the association between climate and shape and other leaf traits, is necessary to predict potential future homogenization of palm communities in the face of climate change.

Leaf shape and plant allometry

We expected plant height to influence leaf shape via allometry (large plants have large leaves that are likely dissected to avoid mechanical damage; Corner, 1949; Chazdon, 1991b). Regarding allometry, plant height has a negative effect on dissection when pinnate and entire shapes are compared, but the effect is comparatively smaller than that of mean annual

temperature and not observed in other models (Figs. 2 and S4). Tall heights are problematic at extremely high temperatures and water scarcity because water transport and transpiration becomes harder with increased plant height (hydraulic limitation hypothesis; Ryan & Yoder, 1997; Ryan, 2006; Olson et al., 2018). Because pinnate species are more likely at high mean temperatures with potentially high water stress or seasonality in water availability, extremely tall pinnate species are at a disadvantage. However, the positive association between tall heights and dissection only appears when we account for seasonality in temperature or precipitation and nothing else. There might be interactions between mean annual temperature, plant height, and water availability for which we do not explicitly test there. Moreover, traits related with the position, lignification, and structure of cells within the leaf tissue could provide the blade with a resistance to mechanical damage that does not involve shape. This is the case for palmate and cospalmate species, which have veins arranged in a network that provides better leaf support and tolerance to hydraulic disruption (Sack et al., 2008), but data to test such effects systematically across the family are sadly not available.

We also expected plant height to relate to dissection via the rapid growth hypothesis (Givnish, 1978; 1984; Niinemets, 1998; Malhado et al., 2010). Malhado et al. (2010) tested this hypothesis and found an association between dissection and both low wood density and rapid diameter growth. 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). However, most palm species are monopodial and are not under the same selection forces. Moreover, Malhado and coauthors (2010) excluded all palms from their analyses and we cannot directly compare our results with theirs.

Leaf shape evolution

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

According to our model and data available, early crown lineages of palms had entire leaves, while palmate and pinnate shapes appeared later multiple times independently. The

earliest reliably dated and identified leaf fossil known to this day is that of *Sabalites carolinensis* from the Santonian-Campanian (fossil dating from 86-82 Mya), which exhibits a costapalmate shape (Berry, 1914). However, the oldest estimated appearance of palmate and costapalmate lineages occurred between 78-80 Mya and most likely corresponds to the stem of Coryphoideae, slightly more recent than *S. carolinensis*. The earliest pinnate fossil appeared during the Campanian (fossil date 76-70 Mya; Dransfield et al., 2008). According to our ancestral estimation, the first pinnate leaves appeared with the emergence of polymorphic lineages approximately 85 Mya, predating the oldest pinnate fossil. Fossils remain rare and provide at best a minimum age for any taxon or morphological character; the absence of old fossils exhibiting entire shapes is surprising and is explained either by the incomplete nature of the fossil record or by our ancestral state estimation of leaf evolution. We note however that the mismatch between the age of the palmate fossils and the emergence of its shape lineage can result from the uncertainty around the time estimates in the phylogeny we used.

One interesting outcome of our model and ancestral state estimation is the role played by polymorphic lineages. Polymorphism, which only concerns combinations of entire and pinnate shapes, appears as a transitional state between these two shapes forming an evolutionary bridge between ancestral lineages with non-polymorphic leaf shapes. Maximum Likelihood estimates of transition parameters also indicate that there is a strong directionality; the highest transition rates being from polymorphic toward pinnate shapes, the second highest was by transitions from entire shapes towards polymorphism. As a result, polymorphic lineages are maintained in our ancestral state estimation at a constant proportion of about 20% of all palm lineages throughout the history of palm (although extant polymorphic species are around 3%). We also found that pinnate, palmate, and entire lineages do not have significantly different speciation rates but polymorphic lineages have an estimated speciation rate about five times higher than the others. In terms of extinction however, pinnate lineages have the highest rate, followed by palmate and finally entire and polymorphic lineages. These results suggest that the high number of extant pinnate lineages do not result from high diversification rates, but from a high speciation rate of polymorphic lineages combined with a high rate of independent transitions towards pinnate leaves.

Leaf shape through time

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

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

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

are found in dry and seasonal ecoregions such as the Tropical and Subtropical dry forests, temperate regions, savannas, and deserts – all ecoregions in which species with entire leaves are not present (Supporting Information Fig. S10).

Conclusion

We explored the drivers of leaf shape evolution in palms by testing for associations between shape and current climatic and allometric variables, and by reconstructing the evolution of shape throughout palm evolutionary history. We highlight the importance of considering biotic and abiotic factors when studying the evolution of plant traits. In the case of palms, we found that mean annual temperature is associated with leaf dissection. A small negative effect of plant height on dissection may result from the inefficiency of large plant heights in high temperatures due to water transport constraints. The ancestral state to all extant palms is inferred as entire, from which pinnate shapes emerged via polymorphic states (species with both entire and pinnate individuals) and became more frequent. Palmate species emerged from entire states and their frequency remained constant. Palms are important representative taxa of the tropical forests with more than 2,500 species distributed globally. Thus, exploring how its leaf shape diversity emerged contributes to our understanding of shape and its adaptive potential, especially in light of increasing climatic change and temperature extremes.

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Tables

Please see the tables in this shared file:

https://docs.google.com/spreadsheets/d/1QJLNBAhUBWG_Rcqfv2j0Ae_mR_7UaEmn6WvBmBN5yU/edit?usp=sharing

FIGURES

Figures are attached at the end in high resolution

Figure 1. Distribution of leaf shapes at a global scale and throughout the phylogeny of Palms. Left: The maps show the approximate distribution of shapes based on cleaned GBIF records alone and the distribution of species with no coordinate records available is not reflected here. Leaf silhouettes were taken from the illustrations in the Genera Palmarum (Dransfield et al., 2008). **Right:** The calibrated maximum clade credibility tree of 2550 palm species generated by Faurby et al. (2016). 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 color scheme of the maps. **a)** Palmate + Costapalmate, **b)** Pinnate, **c)** Variable within species, **d)** Entire, **e)** Bipinnate. **Cer.**= Ceroxyloideae. **N.**= Nypa.

Figure 2. Results of the Generalized Linear Mixed Models (GLMMs). Leaf shapes show the pair in the models (logistic regression; left = 0, right = 1). **a)** Summarised results from all GLMMs ran; one model per row. Grey boxes represent variables included in each model with non-significant effects, in magenta are the included variables with significant positive effects, and in green the included variables with a significant negative effect. **b)** Distribution of estimates for the most inclusive model (first row in **a**). The colour circle represents the median and the horizontal bars span from the 2.5% to the 97.5% quantiles of the estimated distribution. Results including Aridity instead of Precipitation are similar (Supporting Information Fig. S4). **c)** Summarised results of the models including a single variable, with one model per row. Variables are coded with the same colours as in **b)** and the leaf shapes coded as left = 0 and right = 1. **Temp:** mean annual temperature; **TempS** = temperature seasonality; **Prec** = annual precipitation; **PrecS** = Precipitation seasonality; **LeafN** = Maximum leaf number. Leaf silhouettes were adapted from the illustrations in the Genera Palmarum (Dransfield et al., 2008).

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.

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.

b.

C.