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Trait evolution drives speciation through complex interactions between genome size, adaptation and allometry

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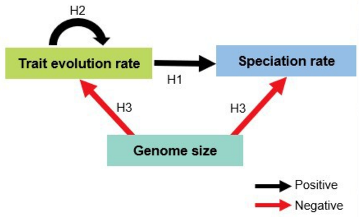
Speciation shapes biodiversity, yet why some lineages diversify faster than others remains unclear. Theory predicts that traits promote ecological speciation through adaptation, but their evolvability (‘trait flexibility’) may be impacted by allometric and genomic constraints. Here we test this by integrating phylogenetic, trait and genome size data for palms (Arecaceae)—a large pantropical family (>2500 species) with 167-fold variation in certain traits (e.g. fruit size) and 60-fold genome size variation. Using structural equation modelling, we test three hypotheses: trait evolution promotes speciation (H1: trait flexibility hypothesis), and speciation and trait evolution rates are constrained by allometry (H2: allometric constraint hypothesis) and genome size (H3: large genome constraint hypothesis). We detected seven major speciation rate shifts during approximately 110-million-years of palm evolution. Tip-derived speciation rates increased with faster evolution in leaf size and plant height, supporting H1, whereas correlated evolution between all traits indirectly influenced speciation, supporting H2. Large genomes were associated with decreased plant height and stem diameter evolution rates supporting H3, but the genome size-speciation association was sensitive to phylogenetic autocorrelation. Our findings illustrate how the interplay between genome size, allometry and trait evolvability affect speciation, emphasizing the importance of holistic approaches for uncovering general mechanisms driving speciation throughout the Tree of Life.

1. Introduction

Speciation, the process by which new species arise, is the primary force shaping biodiversity. Speciation rates vary greatly across the Tree of Life [1,2], yet why some lineages speciate faster than others remain elusive. In plants, morphological traits (hereafter referred to as ‘traits’) and genomic factors are well-established determinants of speciation, as they may respond to selective evolutionary forces [3–5]. However, how these factors interact to influence speciation rate variation across the plant Tree of Life is still not well understood.

Trait evolution or ‘trait flexibility’ [5] (i.e. the evolvability of traits through macroevolutionary time) influences growth, reproduction and survival of



Hypotheses	Predictions	Explanation
H1. Trait flexibility hypothesis: Faster trait evolution ('trait flexibility') leads to faster speciation.	Lineages with the highest trait evolution rates exhibit highest speciation rates.	Divergent evolution of traits can lead to ecological speciation. Hence, lineages with the fastest evolution rates of fruit, leaf, and whole-plant traits can readily adapt to environmental changes, potentially facilitating evolutionary radiation (5, 6).
H2. Allometric constraint hypothesis: Rates of trait evolution are constrained by allometry, which indirectly constrains speciation rates.	Trait evolution rates are statistically correlated.	Allometric constraints impose structural and functional limitations on trait evolution, reducing the extent of possible changes and, consequently, influencing the potential for trait flexibility and speciation (9,18).
H3. Large genome constraint hypothesis: Large genomes impose a negative effect on speciation rate directly, and indirectly by constraining rates of trait evolution.	Genome size shows negative relationships with trait evolution rates and speciation rates.	Genome size sets biophysical constraints and hence sets limits on the minimum size of traits. This restricts the adaptive potential of species, leading to lower rates of trait evolution and speciation (4, 22, 23).

Figure 1. Conceptual framework of hypotheses and predictions on the impact of trait evolution rates and genome size on speciation rates. The diagram illustrates three hypothesized pathways (H1–H3) linking speciation rate, trait evolution rates and genome size. The table summarizes each hypothesis with its corresponding predictions, offering a mechanistic perspective on how these factors may interact to shape speciation dynamics.

species, thereby playing a key role in adaptation, ecological speciation [6] and evolutionary radiation of lineages ('trait flexibility hypothesis') [5,7]. For example, the repeated innovation of key traits (like, zygomorphic flowers, C_4 photosynthesis) in angiosperms allowed them to colonize and diversify in new adaptive zones (*sensu* Simpson [8]) and provided the functional machinery to rapidly adapt to environmental changes in the Cenozoic (last 66 Myr) [5,9]. This pattern is exemplified by the association of angiosperm diversification with seed size [10,11] and plant height [12]. While evolution of individual traits can open new ecological opportunities, single traits seldom act in isolation to shape speciation [7].

Indeed, traits are integrated into coordinated phenotypes across diverse plant lineages because of allometric constraints and trait interdependencies [13,14]. Consequently, changes in one trait, e.g. caused by genetic, developmental or evolutionary/adaptive change, can directly or indirectly influence other structurally or functionally related traits. For instance, fruit size shows an allometric relationship with stem diameter and overall plant architecture [13], stem diameter growth is linked to tree height [15], and tree height and width often show a significant relationship with diameter and lateral spread of roots across trees [16]. Moreover, biomass allocation among roots, leaves and stems often follow predictable allometric rules [17]. Such allometric constraints can limit the evolutionary flexibility of individual traits ('the allometric constraint hypothesis' [18,19]), thereby shaping trajectories of trait evolution and ultimately influencing speciation.

Trait evolution and speciation are further mediated by genomic factors. Genome size (total amount of DNA in a cell's nucleus) imposes biophysical constraints on the minimum size of a cell ('the nucleotypic effect' [20]) which, among other things, can play a role in influencing the evolution of size-related morphological traits (e.g. seed size [21,22]) and hence may influence the overall adaptability and speciation of plants [23] ('large genome constraint hypothesis' [24]). For example, reductions in genome size (genome downsizing) of angiosperms have been linked to their global speciation and rise to dominance during the Cretaceous [25].

Although macroevolutionary associations between traits and speciation [3,5], genome size and speciation [4,26], genome size and traits [21,22], and traits and allometry [15,19] are well established, their interactive effects on speciation remain poorly understood. To capture these multidimensional relationships, we moved beyond the traditional univariate approaches that test for associations between temporal shifts in individual trait evolution and species diversification, and which, therefore, overlook the complex interdependencies among these processes. Instead, we employed a multivariate structural equation modelling (SEM) framework integrating genome size with tip-derived estimates of trait evolution and speciation rates (figure 1). This enabled us to test three key hypotheses within a single analytical model (figure 1, table 1): first, that faster trait evolution leads to faster speciation ('trait flexibility hypothesis', H1); second, that trait evolution is constrained by allometry, thereby reducing speciation rates ('allometric constraint hypothesis', H2); and third, that large genomes constrain trait evolution and speciation rates [24] ('large genome constraint hypothesis', H3)—while capturing both direct and indirect effects.

We tested this framework in palms (Arecaceae), a species-rich tropical plant clade comprising over 2500 species [36], often dominating rainforest floras [27,37]. Anatomical constraints restrict palms largely to subtropical and tropical areas [38,39], reflecting strong niche conservatism [40]. Despite this, palms have persisted through *ca* 110 Myr of climatic change [31], exhibiting remarkable adaptation and extraordinary variations in traits, such as fruit size [11,32], leaf size [27,41] and plant size [12,27,38], that have significant contribution towards their speciation (table 1). For example, palms exhibit 167-fold variation in fruit/seed size (0.3 cm in *Geonoma interrupta* to 50 cm in *Lodoicea maldivica*, the largest seed among angiosperms) and in leaf blade length (0.15 m in *Hydriastele montana* to 25 m in *Raphia regalis*, the largest leaf among angiosperms), and 600-fold variation in plant height (from acaulescent forms, with no or very short stem concealed in the ground, to 60 m in *Ceroxylon quindiuense*) [27,37,38,40,42]. These traits influence dispersal processes mediated by frugivores (i.e. fruit-eating animal), light competition and habitat occupation, promoting niche-driven divergence and ecological speciation (table 1) [11,12,27,38,43]. These traits and their evolution may be influenced by genome size [29,35,44,45], which varies 60-fold across palms, largely independent of polyploidy and chromosome number variations [33,46]. This variation in traits, together with genome size, makes palms an ideal system to understand how these factors may have facilitated or constrained palm speciation, to give rise to their extant diversity.

Table 1. Summary of the ecological and evolutionary relevance of the selected traits and genome size analysed in this study, the predicted relationships under the study hypotheses (H1—H3) and the empirical support for these relationships based on structural equation modelling (SEM) using speciation rates from BAMM, ClaDS and DR, including effect size described as standardized coefficient (std. coeff.).

traits[a]	ecological and evolutionary significance	relevance to hypotheses	results
fruit size[b]	— key to plant–frugivore interactions that influence dispersal distance, gene flow and genetic structure of plant populations, hence directly impacting ecological speciation [12,29]	**H1:** Positive impact of fruit size evolution on speciation	**H1:** No association with speciation detected in any SEM analyses
		H2: Not applicable	**H2:** Not applicable
leaf size[c]	— critical to light capture, gaseous exchange and temperature regulation that impact photosynthesis, respiration and biomass production [19]	**H1:** Positive impact of leaf size evolution on speciation via niche divergence	**H1:** Positive association with speciation supported across all SEM analyses (std. coeff. = 0.145–0.205)
	— influences adaptability to light regimes, especially with limited leaf numbers in palms [31,32], driving vertical niche divergence that could lead to ecological speciation	**H2:** Positive impact of leaf size evolution on fruit size evolution	**H2:** Positive association with fruit size evolution supported across all SEM analyses (std. coeff. = 0.362)
stem diameter	— determines hydraulic efficiency and mechanical stability [33] — mechanical support to crown composed of large leaves and heavy fruits of palms	**H1:** Positive impact of stem diameter evolution on speciation because it aids in the vertical niche differentiation	**H1:** Negative association with speciation supported in two SEM analyses (std. coeff. = −0.156 to −0.159), but not robust after accounting for phylogenetic autocorrelation
	— lack of secondary vascular development and overbuilt trunks early in development, anticipating final height [33], can indirectly influence niche differentiation and speciation	**H2:** Positive influence of stem diameter evolution on fruit size and leaf size evolution	**H2:** Positive association with leaf size evolution supported across all SEM analyses (std. coeff. = 0.313); no association with fruit size evolution detected in any SEM analyses
plant height	— plays a critical role in maximizing light capture and habitat use, especially in absence of branching in palms [32,34]	**H1:** Positive influence of plant height evolution on speciation via niche differentiation	**H1:** Positive association with speciation supported in two SEM analyses (std. coeff. = 0.098–0.130)
	— impacts the position of fruits in forest strata, and hence the dispersal by different frugivore guilds. This can affect plant gene flow, reproductive isolation and speciation [12,13,35] — linked to stem diameter because of lack of secondary vascular development [33]	**H2:** Positive influence of plant height evolution on evolution of fruit size, leaf size and stem diameter	**H2:** Positive association with fruit size (std. coeff. = 0.164–0.167), leaf size (std. coeff. = 0.172) and stem diameter (std. coeff. = 0.313) evolution supported across all SEM analyses
genome size	— imposes biophysical constraint on the minimum size of cells [22,36], thereby limiting the evolution of size-related morphological traits and speciation [26]	**H3:** Negative influence of genome size on speciation rate and evolution of fruit size, leaf size, stem diameter and plant height	**H3:** Positive association with speciation rate supported across all SEM analyses (std. coeff. = 0.186–0.250), but not robust after accounting for phylogenetic autocorrelation Positive association with leaf size evolution (std. coeff. = 0.188) and negative associations with stem diameter (std. coeff. = −0.097) and plant height (std. coeff. = −0.146) evolution supported across all SEM analyses

[a]Trait definitions follow standard palm morphology illustrated in *Evolution and Ecology of Palms* [27] and *Genera Palmarum* [28].

[b]Unpublished seed size data from S. Be. were strongly correlated with fruit size; hence fruit size was used as a proxy for seed size.

[c]Leaf shape can also impact speciation [30]. However, since leaf shape is not influenced by genome size, we did not consider leaf shape in the context of this study.

2. Methods

(a) Palm phylogeny

We used the palm phylogeny of Faurby *et al.* [47] for all analyses. This time-calibrated Bayesian supertree represents a nearly complete (approx. 100% species coverage) species-level coverage of palms [47]. While the species-level phylogeny was reconstructed by integrating both genetic data and taxonomic information, we selected this because alternative phylogenies [48,49] were not available at the species level. This study includes the maximum clade credibility (MCC) tree, which was used for the main analyses, and 1000 posterior-distribution trees, of which 100 were used for sensitivity analysis.

(b) Morphological trait data

We selected 11 size-related traits of palms that likely play a role in ecological speciation and are potentially influenced by the nucleotypic effect of genome size. These traits describe the dimensions of (i) mature fruits (average, maximum and minimum length and width), (ii) fully expanded leaves from mature individuals (maximum lengths of leaf blade, rachis and petiole), (iii) stems (maximum stem diameter), and (iv) overall plant height of mature plants. The traits analysed represent proxies for broader ecological and evolutionary functions in the context of palm speciation (table 1). Other morphological traits were not considered because palms exhibit limited variation in such characteristics, e.g. life history traits, since all palms are 'woody' perennials [28]. Species-level data for these traits were obtained from the PalmTraits v. 1.0 database [37]. The trait values were used to derive trait evolution rates (representing trait flexibility) with no further modification, except in cases where a normalization of the values was needed.

Fruit size and leaf size were represented by multiple categories in the database [37]. While the subsequent analyses using SEM (explained later) allow the testing of multiple variables within a single model, increasing the number of variables greatly raises the number of possible path topologies. This increases the intrinsic dimensionality of the dataset and can introduce type I errors (false positives) into the resulting model [50]. To reduce such errors and avoid the risk of mistaking random statistical patterns for biological relevance, it was essential to include only variables that contribute meaningful value to the model. To identify the relevant variables for fruit size and leaf size, we performed linear regression analyses in R to explore the relationships between the trait categories within these plant parts (see Section 3(a)).

(c) Genome size data

Genome size data (1C-values, in Gbp) were compiled from the prime estimates of the Plant DNA C-values database [46] and from Schley *et al.* [33]. Most estimates in these sources were obtained using flow cytometry with only a small subset in [46] estimated using the Feulgen microdensitometry method. The resulting dataset covers approximately 86% of palm genera (158 out of 184 genera representing all subfamilies) and approximately 17% of palm species (electronic supplementary material, tables S1 and S2). We used D-statistics [51] implemented in the R package 'caper' [52] to test for phylogenetic clustering in the dataset, thereby quantifying potential sampling biases. Four polyploid palms, *Arenga caudata* ($2n = 4\times = 64$), *Jubaeopsis caffra* ($2n = 12\times = 160–200$), *Rhapis humilis* ($2n = 4\times = 72$) and *Voanioala gerardii* ($2n = 38\times = \sim 596$), were considered as outliers because all other palm species are diploids [33]. These species were retained in the dataset but their impact was carefully monitored throughout by sensitivity analyses (explained later).

(d) Taxonomic standardization

Most of our analyses were based on the phylogenetic tree of Faurby *et al.* [47]. Hence, we standardized species names across all data sources using its taxonomy [47]. To ensure clarity, we verified the taxonomy using the World Checklist of Vascular Plants (WCVP) [36], recorded the accepted names (electronic supplementary material, table S2) and removed records that could not be unambiguously assigned to accepted species.

(e) Estimation of speciation rates

We estimated the present-day speciation rates of each species (= tip rates; measured as lineages per Myr) using the MCC phylogenetic tree [47] using three approaches, since consensus on a single best method is lacking. This included two model-based approaches—Bayesian analysis of macroevolutionary mixtures (BAMM) [53] and cladogenetic diversification rate shift (ClaDS) [54]—and one model-free approach—diversification rate statistics (DR) [55]. Each method differs in their assumptions to deduce speciation trajectories. Using Pearson's r correlation, we tested the comparability of these three methods used for speciation rate estimates.

BAMM uses Bayesian statistics to estimate discrete shifts in speciation and diversification rates at nodes of a phylogenetic tree. The *speciation–extinction* parameter simulates posterior distribution based on the prior rate shifts using reversible-jump Markov chain Monte Carlo (MCMC) that implements a compound Poisson process. This allows for rate heterogeneity and random shift distribution along the tree and through evolutionary time [53]. Priors were obtained by the *setBAMMpriors* function in the R package 'BAMMtools' [56] (electronic supplementary material, table S3), which resulted in *expectedNumberOfShifts* parameter to be 1. To check the sensitivity of the assumed priors on the estimated posterior distribution of BAMM speciation rates [57,58], we compared speciation rates deduced from different prior values (see electronic supplementary material, note S1, figure S1) and retained *expectedNumberOfShifts* parameter as 1. MCMC simulation consisted of four independent chains of 300 million generations each, with shift configuration being sampled every 10 000 steps. Run convergence was assessed by the *effectiveSize* function of the R package 'coda' [59]. The initial 10% of MCMC was discarded as burn-in (number of analysed posterior samples = 27 001) and BAMM output was analysed using 'BAMMtools' [56]. Tip rates of speciation were extracted (electronic supplementary material, table S2) using the *getTipRates* function and lineage-specific speciation rates were visualized as phylorate plots by the *plot.bammdata* function [56].

ClaDS uses a Bayesian approach to deduce speciation rate, allowing for small and frequent rate shifts at each branching event of a phylogenetic tree [60]. We used the Julia language [61] implementation of the ClaDS model (ClaDS2) in the PANDA package [62] that uses a constant turnover of extinction rates. The model uses data augmentation with three MCMC chains [54]. Convergence was assessed using Gelman statistics [63] and the chains stopped when the value dropped below 1.05 [54]. To view the speciation rates superimposed on the palm phylogeny, *plot_ClaDS_phylo* from the 'RPANDA' R package was used and the tip rates of each species were extracted (electronic supplementary material, table S2).

DR is a model-free approach that estimates the present-day speciation rate of each species in a phylogeny by making minimal assumptions about the speciation process. It calculates tip rates as a weighted mean of inverse branch lengths under a time-constant, homogeneous model in the absence of extinction [55]. We used R package 'epm' [55] to obtain the tip rates for each species (electronic supplementary material, table S2).

(f) Estimation of trait evolution rates

To estimate trait flexibility (rates of trait evolution), we estimated the present-day rates of trait evolution (= tip rates of traits; measured as changes per Myr), rather than analysing trait values. Rates were derived from the trait values of fruit size, leaf size, maximum stem diameter and maximum plant height using the *phenotypic evolution* parameter implemented in BAMM v. 2.5.0 [53] and the MCC tree [47] as the phylogenetic backbone. The tree was pruned to obtain sub-trees for each trait since data availability varied (electronic supplementary material, table S1) and the BAMM *phenotypic evolution* parameter does not implement sampling fractions [10,64]. The *phenotypic evolution* parameter follows a similar framework to the *speciation-extinction* parameter (see Section 2(e)). Priors were obtained using *setBAMMpriors* in 'BAMMtools' [56] (electronic supplementary material, table S3) that set *expectedNumberOfShifts* to 1. Analyses followed the BAMM speciation rate protocol, tip rates were extracted (electronic supplementary material, table S2), and the lineage-specific trait evolution rates for each trait were visualized as phylorate plots. Palm species are primarily identified based on diagnostic morphological features (e.g. leaflet type, crownshaft structure, endocarp characteristics) [28] that differ from the size-related traits analysed here, and therefore, the trait flexibility inferences (and their association with speciation rates) are unlikely to be strongly biased by species delimitation or cryptic speciation.

(g) Structural equation models

We used SEM to disentangle the direct effects of genome size and trait evolution rates on the speciation of palms, of genome size on trait evolution rates, and among trait evolution rates. All variables were log-transformed and rescaled to 0–1 range to improve normality in model residuals, and to be able to compare standardized effect sizes. SEM was implemented using the R package 'lavaan' [65]. Since the 'lavaan' package does not consider phylogenetic structure, we performed phylogenetic generalized least squares (PGLS) analysis on the final SEM model *a posteriori* (see Section 2(h)). We started with an *a priori* model that included all the hypothesized pathways between the variables (reciprocal paths were not allowed) based on pairwise correlations and theoretical considerations (figure 1, electronic supplementary material, figure S2).

Insignificant relationships were progressively removed until the final model only retained significant pathways ($p < 0.05$), from which the effect sizes expressed as standardized coefficients (std. coeff.) were extracted. The modification indices were checked using the function *modindices* to assess if any previously omitted parameters or covariates were required to improve model fit. Model fit was assessed using multiple indices—p-value of χ^2—tests > 0.05, comparative fit index (CFI) > 0.95, Tucker-Lewis index (TLI) > 0.90, root mean square error of approximation (RMSEA) < 0.05 and standardized root mean square residual (SRMR) < 0.08. Three separate SEM analyses were conducted with speciation rates estimated from BAMM, ClaDS or DR. Most associations between the variables were consistently supported in all models.

(h) Phylogenetic autocorrelation and robustness of results

Effects of trait evolution rates and genome size on speciation may be driven by phylogenetic autocorrelation (i.e. species are not independent due to shared ancestry). Hence, we evaluated whether the main predictors of speciation as detected in the SEMs were also supported when accounting for phylogenetic dependence on the response variable (i.e. speciation rate) using PGLS as implemented in the R 'caper' package [52]. Phylogenetic autocorrelation is accounted for in 'caper' by including a variance–covariance term into the model errors, derived from the shared branch lengths between species and scaled by the λ parameter [66]. λ quantifies the strength of phylogenetic autocorrelation, where $\lambda = 0$ indicates no phylogenetic signal where trait evolution is independent of their phylogenetic relationships, while $\lambda = 1$ indicates trait evolution proportional to phylogenetic relatedness under Brownian motion. We estimated the λ parameter in the PGLS models using maximum likelihood, while fixing the other two scaling parameters (i.e. δ and κ) to one.

A MCC tree is a consensus tree that best represents the overall phylogenetic signal in the data and does not account for the uncertainty of phylogenetic tree topology. This may impact the SEM model correlation estimates since topological changes can influence speciation rates, which can potentially affect the estimates deduced by SEM. To account for the uncertain topology of the palm phylogeny, we deduced speciation rates from 100 randomly sampled posterior-distribution trees [47] using BAMM.

The robustness of the final model estimates was tested by comparing this model with the range of estimates (standardized coefficients) obtained by reiterating the final SEM model 100 times using the variable set of speciation rates derived from BAMM. Coefficients of each correlation were extracted, and their distribution was plotted to check for variation while locating the estimate of the MCC-tree-SEM on the plot. We also checked the significance of p-values for each of the analyses.

To test the effect of outliers, we repeated the SEM analysis using BAMM speciation rates after removing the four polyploid species. To test the influence of large genomes, we repeated the SEM using BAMM speciation rates with two subsets of genome size data: species with genome sizes larger than the median value (i.e. genome sizes larger than 2.64 Gbp/1C) and species with genome size in the 75th percentile range (i.e. genome sizes above the 75th percentile threshold of 4.26 Gbp/1C).

3. Results

(a) Palm speciation is associated with high rates of trait evolution

Substantial speciation rate variation was detected across the palm species, as a result of at least seven evolutionary radiations (figure 2), characterized by lineages with speciation rates (λ_{Sp} = 0.234–0.358 lineages/Myr; range reflects variation across radiations in BAMM) exceeding the background speciation rate in palms (average λ_{Sp} = 0.178–0.260 lineages/Myr; range reflects estimates across 100 phylogenetic trees in BAMM) (for details of all speciation rates, see electronic supplementary material, table S2). Speciation rates estimated using BAMM, ClaDS and DR showed strong correlation (electronic supplementary material, figure S3) indicating that the relative patterns of speciation are robust and well-supported by the underlying data, despite the varying assumptions of each method.

Among the traits, the categories of fruit size and leaf size were found to be positively correlated (electronic supplementary material, figure S4). Hence, the following four traits were chosen for further analysis: fruit size (measured as the average length of fruit, available for 80% of species), leaf size (measured as the maximum length of leaf blade, available for 74% of species), stem diameter (measured as the maximum diameter of stem, available for 76% of species) and plant height (measured as the maximum whole plant height including the crown, available for 78% of species) (electronic supplementary material, table S1). Despite the lower representation of genome size data compared with the traits, we found relatively weak phylogenetic clustering of the genome size data (D-statistics = 0.73; $p < 0.05$ [51]). This indicates that the more limited sampling of genome sizes (approx. 17% of species) across the approximately 86% of palm genera with data was well distributed (figure 2, electronic supplementary material, table S2) and hence unlikely to have a significant influence on the results presented here.

Structural equation modelling tested the relationship between trait evolution rates (regardless of whether trait values increased or decreased) and genome size with the tip-derived speciation rates of palms. Our final SEM model (n = 372 species, figure 3) integrates findings derived from speciation rate estimates from BAMM, ClaDS and DR, which showed largely consistent patterns with model fit indices confirming adequate fit of all models (electronic supplementary material, figures S5–S7). Model robustness was further supported by analyses across 100 posterior distribution trees, with standardized coefficients and p-values showing only minor variation in some cases (electronic supplementary material, figure S8).

Our final model indicates that our combined predictors explain up to 12% variation in speciation rates and up to 19% variation in trait evolution rates across species (figure 3). Rates of leaf size (std. coeff. = 0.145–0.205) and plant height (std. coeff. = 0.098–0.130) evolution showed positive associations with speciation rates (figure 3, table 1), in support of the trait flexibility hypothesis (H1). In contrast, the rate of stem diameter evolution had a negative association with the speciation rate (std. coeff. = −0.156 to −0.159) (figure 3, table 1). However, it is important to note that the stem diameter evolution-speciation association was only supported by SEMs using BAMM and ClaDS (electronic supplementary material, figures S5 and S6), and the plant height evolution-speciation link was only supported in SEMs with ClaDS and DR (dashed lines in figure 3, electronic supplementary material, figures S6 and S7). Fruit size evolution showed no direct relationship with speciation. Phylogenetic autocorrelation (PGLS) analyses showed that speciation rates remained positively associated with leaf size and plant height evolution rates. In contrast, effect of stem diameter evolution rate on speciation may have resulted from phylogenetic autocorrelation, as these were no longer statistically supported in the PGLS. Hence, this relationship should be interpreted with caution (electronic supplementary material, table S4).

(b) Trait evolution is constrained by allometry

In support of the allometric constraint hypothesis (H2), our SEM indicated positive correlations among trait evolution rates (figure 3, electronic supplementary material, figures S5–S7, table 1). Increases in rates of leaf size (std. coeff. = 0.362) and plant height (std. coeff. = 0.164–0.167) evolution were associated with increases in the rate of fruit size evolution. Also, faster rates of evolution of plant height (std. coeff. = 0.172) and stem diameter (std. coeff. = 0.313) were associated with an increased rate of leaf size evolution. A positive association was also found between rates of plant height and stem diameter evolution (std. coeff. = 0.313). Together, the results indicate coordinated evolution among these traits suggesting that their evolutionary association may impact speciation through allometric principles.

(c) Genome size constrains trait evolution and, hence, speciation

In our SEM, we found that large genomes positively associate with speciation rates (std. coeff. = 0.186–0.250) (figure 3, table 1). This contradicts the expectations from the ‘large genome constraint hypothesis’ [24], and rejects H3. This relationship persisted after reanalysing the SEMs excluding four polyploid species to account for the potential impacts of recent polyploidization on speciation (electronic supplementary material, figure S9), and when analysing subsets of species with above-median genome sizes (i.e. larger than 2.64 Gbp/1C, n = 189 species, electronic supplementary material, figure S10) and those above the 75th

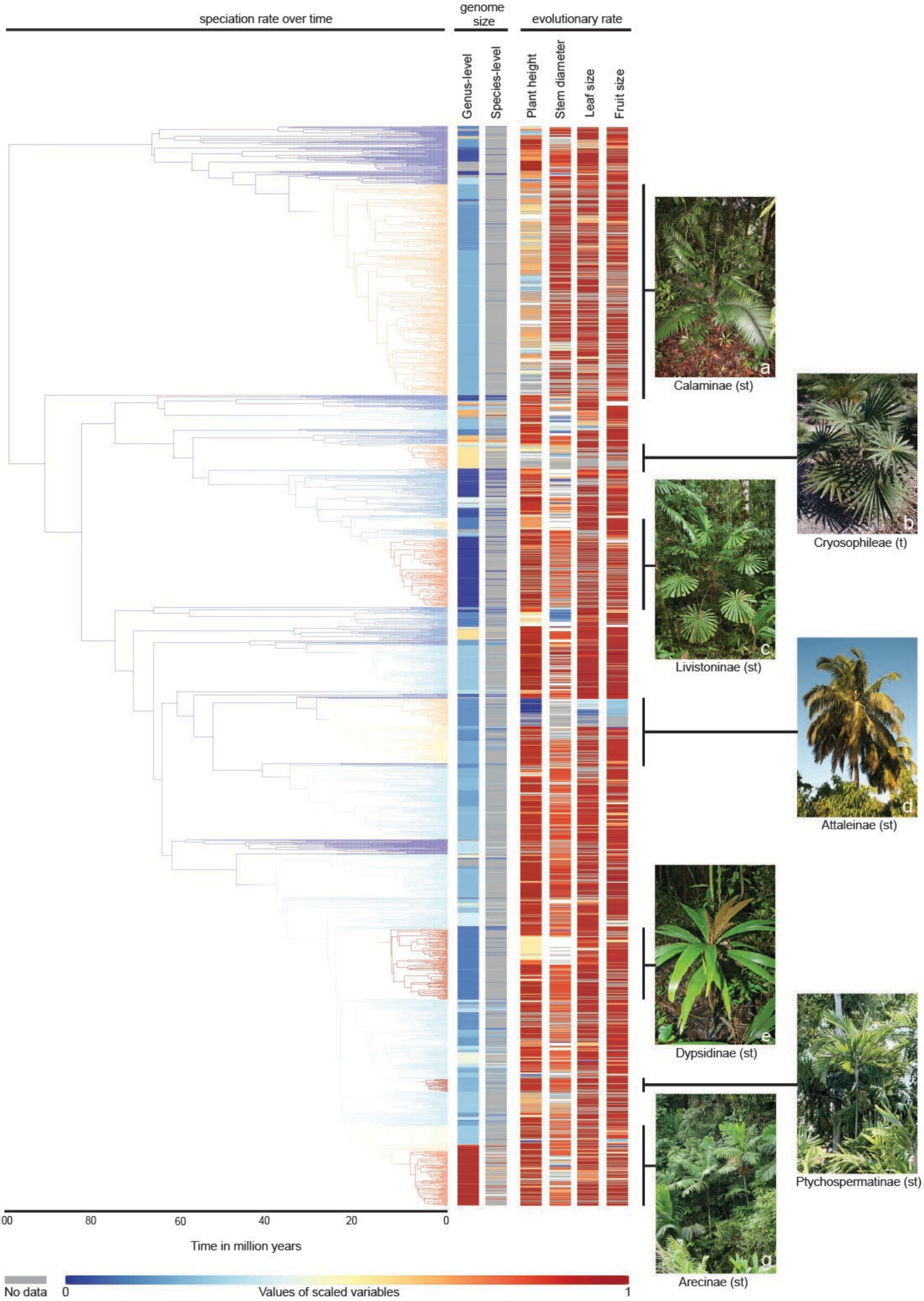


Figure 2. Evolutionary radiations and shifts in speciation rates in palms (Arecaceae). The phylogeny of 2528 palm species showing associated data on genome size and evolutionary rates of plant height, stem diameter, leaf size and fruit size (for details on species names, see electronic supplementary material, figure S12). The phylogeny is colour-coded with speciation rates estimated using BAMM. Evolutionary rates of each trait per species, estimated by BAMM, are indicated alongside the tree. Mean genome size data of each genus (for illustrative purpose only, not used in analyses) and genome size of each species are indicated between the phylogeny and evolutionary rates of traits. Horizontal colour bar at the bottom indicates scaled values of genome size, speciation rate and trait evolution rates, with blue indicating lower values, red higher values, and grey missing data. Vertical black bars on the right highlight lineages exhibiting evolutionary radiations (i.e. speciation rates estimated to be above background speciation rates). Names of these lineages (t: tribes; st: subtribes) are shown below each figure featuring a representative species: (a) *Calamus korthalsii*, (b) *Coccothrinax miraguama*, (c) *Licuala lauterbachii*, (d) *Cocos nucifera*, (e) *Dypsis mocquerysiana*, (f) *Ptychosperma keiense* and (g) *Pinanga rumphiana*. Photos by William J. Baker.

percentile (i.e. genome sizes larger than 4.26 Gbp/1C, $n = 95$ species, electronic supplementary material, figure S11). However, effect of genome size on speciation rate was not supported in the PGLS analysis (electronic supplementary material, table S4).

In terms of trait evolution, genome size showed negative associations with rates of plant height (std. coeff. = −0.146) and stem diameter (std. coeff. = −0.097) evolution but a positive association with the rate of leaf size evolution (std. coeff. = 0.188) (figure 3, table 1). Together, these results suggest that genome size may influence palm speciation rates indirectly, through its effects on trait evolution, providing partial support for the ‘large genome constraint hypothesis’ (H3).

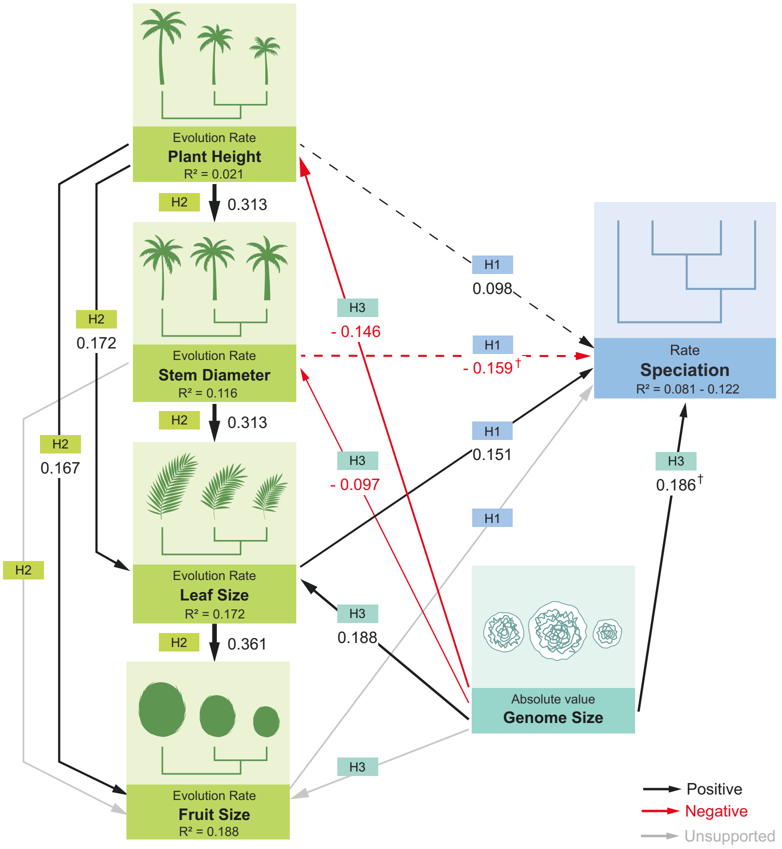


Figure 3. Trait flexibility, allometric constraints and genome size effects on speciation rates in palms (Arecaceae). Structural equation model (SEM) showing the standardized effects of trait evolutionary rates of plant height, stem diameter, leaf size and fruit size on speciation rates (trait flexibility hypothesis, H1), correlations between trait evolution rates (allometric constraint hypothesis, H2) and of genome size on speciation and trait evolution rates (large genome constraint hypothesis, H3) in palms ($n = 372$ species). Speciation rates were derived from BAMM, ClaDS and DR. The effect sizes indicate significant ($p < 0.05$) standardized coefficients. Arrow thickness is proportional to coefficient values, and direction represents the direction of effects. Black arrows denote positive effects, red arrows negative effects. Dotted arrows represent effects that were statistically supported in only two of the speciation rate scenarios derived from BAMM, ClaDS and DR (for details, see electronic supplementary material, figures S5–S7). Coefficient values of BAMM are indicated, or from the respective models if supported only in ClaDS or DR. Grey arrows denote tested but statistically unsupported effects in any of the scenarios. The R^2 values (explained variation based on the combined predictors) are consistent across models (BAMM, ClaDS, DR) for all variables, except for speciation rates, hence the reported range. † indicates relationships not supported in any of the phylogenetic generalized least squares (PGLS) analyses (for either BAMM, ClaDS or DR-derived speciation rates; for details, see electronic supplementary material, table S4).

4. Discussion

Our study identified direct and indirect pathways influencing palm speciation using a macroevolutionary approach, offering an integrated framework to understand the mechanisms behind the extraordinary diversity of this tropical plant family. Although morphological divergence during allopatric and sympatric speciation may be rare when comparing sister species [67], our results suggest that shifts in trait evolution rates as detected among larger clades link to speciation rate shifts, embellishing palms as a model for studying ecological speciation in plants. The strong correlations between variables identified in our study are consistent with and supported by a robust body of evidence indicating causal links among these variables.

(a) Trait flexibility shapes palm speciation through divergent functional evolution

We found seven evolutionary radiations across the palm family. The radiations occurred in three of the four non-monotypic subfamilies, specifically in tribe Calameae (subtribe Calaminae) of subfamily Calamoideae, tribes Cryosophileae and Trachycarpeae (subtribe Livistoninae) of subfamily Coryphoideae, and tribes Cocoseae (subtribe Attaleinae) and Areceae (subtribes Dypsidinae, Ptychospermatinae and Arecinae) of subfamily Arecoideae. Together, these radiations included 24 out of 184 recognized palm genera (figure 2, electronic supplementary material, figure S12 and table S2).

Speciation across the plant Tree of Life has often been linked to morphological evolution [5,9,10,12], and our results suggest that palms follow a similar pattern. We found that rapid rates of leaf size and plant height evolution were associated with higher speciation rates, supporting the 'trait flexibility hypothesis' (H1) (figure 3, electronic supplementary material, figures S5–S7). For example, genera such as *Pinanga* and *Ptychosperma* (tribe Areceae) exhibit high rates of leaf size and plant height evolution alongside fast speciation (electronic supplementary material, figure S12, table S2). These results suggest that divergent trait evolution (flexibility) over macroevolutionary timescales promotes ecological speciation, through enhanced adaptive potential. Leaf size evolution, coupled with variations in leaf shape [30], optimize temperature regulation and light capture under diverse environmental conditions [68]. For example, small-leaved palms of tribe Cocoseae, such as species within *Bactris*, dominate the warm and humid central Amazon, whereas their large-leaved relatives, such as *Attalea*, are more prevalent in the drier northwestern and southeastern Amazon [69]. The ability to adjust leaf size also enhances adaptability to habitats of different light intensity, such as of understorey palms (e.g. *Pinanga coronata*) in shaded habitats [27,70].

Plant height evolution offers biomechanical support to foliar architecture in tall, solitary-stemmed palms, enabling canopy access to light critical for photosynthesis in forest environments [69]. This trait-driven partitioning of vertical space (understorey versus canopy) reduces interspecific competition and facilitates ecological speciation through spatial isolation [71,72]. Vertical stratification also affects seed dispersal dynamics by segregating frugivore communities along vertical gradients, which may influence palm speciation through frugivory-related dynamics [11]. The positive association between plant height and fruit size evolution rates in our study illustrates this. Small-bodied understorey frugivores (e.g. sedentary birds such as cracids (Cracideae)), feeding on small-fruited understorey palms, are often more restricted in movement than larger-bodied canopy frugivores (e.g. strong-flying hornbills (Bucerotidae)) that favour canopy palms with larger fruits [11]. This segregation reduces gene flow among plant populations, enhancing local adaptation, reproductive isolation and ultimately speciation [11,73,74]. Although we did not detect a significant direct relationship between the rate of fruit size evolution and speciation (figure 3), fruit size itself, rather than its rate of evolution, is associated with palm speciation via frugivory-mediated processes [11]. The close link between trait evolution and speciation as detected in our study is consistent with previous work on palms, in which trait-dependent diversification approaches (e.g. state-dependent speciation and extinction (SSE) models) have illustrated that palm speciation is associated with traits, particularly those linked to ecological strategies such as island colonization [11,30,75].

(b) Allometric constraints shape trait evolution and speciation in palms

Our findings support the ‘allometric constraint hypothesis’ (H2) (figure 3). Constraints in palms arise from their unique anatomy, including lack of secondary growth and reliance on a single meristem complex [38]. This structural and developmental rigidity limits the potential functional spectrum of trait combinations [14], restricting phenotypic evolution. For example, rainforest canopy palms maintain allometric relationships between leaf size and plant height to optimize light capture [69]. Similarly, coordination between stem diameter and plant height ensures mechanical and hydraulic stability [15,38,43]. Leaf size is also associated with stem diameter via its leaf base, reflecting coordination of vascular structure required to maintain hydraulic conductance [76]. A notable example of trait integration is found in *Geonoma*, where leaf size, stem diameter and plant height exhibit a strong positive association [77]. Although palms have extensively explored the structural potential of their arborescent monocot architecture [38], their evolutionary trajectories have been constrained by anatomical and physiological trade-offs. These limitations reduce their capacity to fully exploit ecological opportunities, likely restricting speciation.

(c) The complex role of genome size in palm speciation

Genome size has been linked to speciation across angiosperms [24–26], with large-scale analyses suggesting that species with bigger genomes are more constrained in the ability to diversify [78] in support of the ‘large genome constraint hypothesis’ (H3) [24]. In contrast, we found a significant positive association of genome size with speciation rates (figure 3, table 1). However, this effect was not robust to phylogenetic autocorrelation and was only evident in a limited number of radiations (e.g. *Pinanga*), hence not providing strong evidence to either support or refute the ‘large genome constraint hypothesis’ (H3) in the context of evolutionary dynamics of palms. More extensive sampling of palm lineages with broad variations in genome size (e.g. *Calamus*, *Daemonorops*) may uncover more nuanced impacts of genome size on speciation that persist after phylogenetic correction.

Beyond direct effects, genome size may also play a role in influencing speciation indirectly through its nucleotypic effect [20] on anatomical, morphological and physiological traits [22,29,44]. These genome size-trait correlations can play a role in shaping trait evolution, conferring adaptive advantages or disadvantages depending on the ecological context [23], thereby indirectly affecting speciation. Consistent with the ‘large genome constraint hypothesis’ (H3) in this context, we found that genome size constrains the evolution of plant height and stem diameter, and hence speciation (via the plant height evolution–speciation rate relationship) (figure 3). Larger genomes are associated with structural and physiological constraints limiting growth, and thus the evolution of plant height and stem diameter, potentially restricting the adaptation and establishment of large-genomed plants [29,33,45].

Contrary to H3, our data suggest that large genomes can influence palm speciation positively by facilitating, rather than constraining, leaf size evolution. This may be because in stable, hot and humid rainforest climates, where palms predominantly grow, environmental constraints on genome size are relaxed, allowing greater diversity and faster evolution of leaf size, fostering ecological speciation in palms [35,79]. These findings underscore that the influence of genome size on speciation and trait evolution in palms is conditional on the environmental context.

(d) Reliability and limitations of the study

While multiple speciation rate models and SEMs yielded comparable results (electronic supplementary material, figures S3, S5–S8), the explained variance in speciation (12%) and trait flexibility (19%) remains low. The relative contribution of different factors (e.g. trait flexibility, genome size) to speciation, and how their relative importance changes over time and space, also remains unclear. Future work could address this in a more explicit phylogenetic and spatial framework, integrating macroevolutionary and microevolutionary processes along a speciation continuum [80].

The low explained variance in speciation indicates that additional biological and environmental factors contribute to palm speciation, a common outcome in broad-scale evolutionary analyses. Abiotic factors such as climate and soil heterogeneity [39], absolute trait sizes [11,75] and defence-related traits (e.g. spinescence [81]) that mediate species–environment interactions, were not incorporated here but may further refine our understanding of the complex drivers of palm speciation. Furthermore, it would be interesting to include other traits that directly relate to genome size, such as cell size, which could influence physiological processes related to speciation dynamics [82]. Unfortunately, such traits are not yet available for many species, hindering their inclusion in large-scale comparative analyses.

The relationships detected in the SEMs were generally supported across sensitivity assessments (electronic supplementary material, figures S8–S11). However, the associations of speciation rate with stem diameter evolution and genome size showed sensitivity to phylogenetic autocorrelation (electronic supplementary material, table S4). For example, the negative association between stem diameter evolution and speciation rate may represent lineage-specific patterns in some cases, for instance, in *Pinanga* and *Ptychosperma* (tribe Areceae) (electronic supplementary material, figures S5 and S6 and table S2). The negative association may arise from the shared developmental constraint imposed by the possession of a single apical meristem in palms which determines stem diameter size during early ontogeny [34,38] and hence sets limits on its evolutionary flexibility (and hence, speciation).

Genome size sampling across palms was not strongly phylogenetically clustered overall, but the observed phylogenetic autocorrelation between genome size and speciation rate could reflect pseudoreplication [83] caused by partial taxonomic bias towards larger-genome genera. This bias probably represents fewer independent events of genome size variation and therefore may not be representative of the overall palm genome size evolutionary history. For example, species of the large-genome genus *Pinanga* (average genome size = 10.69 Gbp/1C, approx. 30% species with data) are more extensively represented than those of the small-genomed genus *Dypsis* (average genome size = 1.64 Gbp/1C, approx. 4% species with data), even though both lineages exhibit high speciation rates (figure 2, electronic supplementary material, table S2).

Despite these caveats, consistent patterns emerge across the palm phylogeny. Rapid speciation is often associated with fast evolution of plant height (e.g. in *Calamus*, *Attalea* in figure 2) and leaf size (e.g. in *Attalea*, *Pinanga* in figure 2), both relationships being robust to phylogenetic autocorrelation. These findings underscore ecological speciation as a likely dominant process that has shaped palm speciation throughout its evolutionary history [11,27,40,70]. Extending this framework to other plant lineages across clades and evolutionary histories could reveal the extent to which the relationships observed in palms are context-dependent or represent more general principles of plant speciation.

5. Conclusions

Our results highlight that speciation in palms is constrained by the allometric evolvability of morphological traits—leaf size and plant height—and that large genomes may either constrain trait evolution (plant height, stem diameter) or relax it (leaf size) (table 1, figure 3). Our integrated framework confirms that radiations are governed by interacting ecological, morphological and genomic variables rather than single traits or environmental drivers [84,85]. Accordingly, the relative importance and interactions of these factors may vary across clades, evolutionary histories, environmental pressures or abiotic conditions. Such dependencies could be further explored by applying our framework to different lineages grouped by environmental or geographical context (e.g. habitat or geographic range) [86], and/or by investigating deep time evolutionary dynamics in addition to recent dynamics based on tip-rates [87]. Our findings highlight that, across these interacting layers, evolvability, allometry and genomic constraints represent the fundamental dimensions of diversification that deserve broader consideration across ecosystems and the Tree of Life. Although our focus was on palms, the patterns we identified provide a valuable foundation to investigate similar dynamics in other (plant) lineages.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. The data and code used in the manuscript are available at [88]. Supplementary material is available online [89].

Declaration of AI use. We have used AI to improve readability and language of the manuscript.

Authors' contributions. S.Bh.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization, writing—original draft, writing—review and editing; I.J.L.: conceptualization, funding acquisition, resources, supervision, writing—review and editing; S.Be.: conceptualization, resources, writing—review and editing; W.J.B.: conceptualization, resources, writing—review and editing; R.E.O.: conceptualization, formal analysis, funding acquisition, investigation, methodology, software, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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