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Africa as an evolutionary arena for large fruits

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Summary

- Strong paleoclimatic change and few Late Quaternary megafauna extinctions make mainland Africa unique among continents. Here, we hypothesize that, compared with elsewhere, these conditions created the ecological opportunity for the macroevolution and geographic distribution of large fruits.
- We assembled global phylogenetic, distribution and fruit size data for palms (Arecaceae), a pantropical, vertebrate-dispersed family with > 2600 species, and integrated these with data on extinction-driven body size reduction in mammalian frugivore assemblages since the Late Quaternary. We applied evolutionary trait, linear and null models to identify the selective pressures that have shaped fruit sizes.
- We show that African palm lineages have evolved towards larger fruit sizes and exhibited faster trait evolutionary rates than lineages elsewhere. Furthermore, the global distribution of the largest palm fruits across species assemblages was explained by occurrence in Africa, especially under low canopies, and extant megafauna, but not by mammalian downsizing. These patterns strongly deviated from expectations under a null model of stochastic (Brownian motion) evolution.
- Our results suggest that Africa provided a distinct evolutionary arena for palm fruit size evolution. We argue that megafaunal abundance and the expansion of savanna habitat since the Miocene provided selective advantages for the persistence of African plants with large fruits.

Introduction

The African continent has intrigued ecologists and evolutionary biologists due to its unique history, relatively poor extant biodiversity and threatened ecosystems (Küper *et al.*, 2004; Bonnefille, 2010; Couvreur, 2015; Owen-Smith, 2021). The rainforests of the Afrotropics were labelled the ‘odd man out’ because of their lower vascular plant species richness compared with rainforests in the Neotropics and South-East Asia (Richards, 1973). This low richness could have resulted from high extinction and low speciation rates associated with paleoenvironmental change, such as Miocene cooling and drying (Morley, 2000; Bonnefille, 2010; Hagen *et al.*, 2021). Such paleoenvironmental change may have facilitated the expansion of open, dry, savanna vegetation at the cost of rainforest extent, with effects on diversification, species composition and co-evolutionary dynamics of plants and animals (Kissling *et al.*, 2012; Onstein *et al.*, 2020).

Interestingly, these open ecosystems are home to the largest extant mammals, illustrating that Africa is also unique in its

extant assemblage of megafauna (Owen-Smith, 2021). The Late Pleistocene extinction wave led to the most drastic decline of the largest mammal species in the Americas, Australia and Eurasia, whereas megafauna in mainland Africa remained largely unaffected (Barnosky *et al.*, 2004; Sandom *et al.*, 2014; Stuart, 2015; Smith *et al.*, 2018). The abundance and species richness of African megafauna – including African elephants (*Loxodonta* spp.), giraffes (*Giraffa* spp.) and rhinoceroses (*Diceros bicornis*, *Ceratotherium simum*) – is still largely comparable to (recent) historical conditions (i.e. Pleistocene), especially compared with megafauna on other continents (Stuart, 2015; Faurby *et al.*, 2018). Although several species of megafauna have also persisted in the Asian tropics, range contractions have been strong, and population abundances are low (Mahmood *et al.*, 2021).

The persistence of megafauna (animals > 45 kg; Martin & Klein, 1984) in Africa, or conversely, the extinction of most megafauna elsewhere, may have had cascading effects on biodiversity (Malhi *et al.*, 2016; Galetti *et al.*, 2018). For example, megafauna shape ecosystems by breaking trees, consuming huge amounts of foliage, or by dispersing some of the large seeds of plants with ‘megafaunal’ fruits (fruits > 4 cm; Janzen & Martin, 1982; Guimarães *et al.*, 2008). These fruits, which may have evolved to attract megafaunal animals to maximize effective

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seed dispersal over long distances, are often too large to be handled or swallowed and thus effectively dispersed by small-bodied animals, because gape size constrains which fruits can be ingested (Wheelwright, 1985). Furthermore, fruits (and seeds) represent important functional traits for plants as they influence fitness and survival via effects on dispersal, reproduction and regeneration (Eriksson, 2008; Alzate & Onstein, 2022). Interactions with megafauna have therefore shaped the evolution of interaction-relevant plant traits, such as fruit size (Eriksson, 2008; Dantas & Pausas, 2020; Onstein *et al.*, 2022). Consequently, the theoretical prediction is that vertebrate-dispersed fruits have evolved to be largest in places where megafauna have been abundant throughout geological time, such as in mainland Africa (Mack, 1993).

Nevertheless, eco-evolutionary dynamics, such as ecological sorting or adaptive evolution, can change the occurrences of species and traits over time. For example, large-fruited plants may respond to the extinction of large-bodied interaction partners with co-extinction, or evolution to smaller fruit sizes that allow for dispersal by the remaining smaller-bodied frugivores (Galetti *et al.*, 2013; Onstein *et al.*, 2018). Adaptive evolution to smaller seeds can happen rapidly, for example within decades in an Atlantic Forest palm in response to the local extirpation of large-bodied frugivorous birds (Galetti *et al.*, 2013). This suggests that current distributions of species and their traits may not necessarily reflect long-term historical conditions (Valiente-Banuet *et al.*, 2006; Lawing *et al.*, 2017). However, (pre-)Quaternary legacies – linked to paleoclimate or now-extinct megafugivores – can still be detected in current plant assemblage composition and trait distribution (Blach-Overgaard *et al.*, 2013; Lim *et al.*, 2020; Méndez *et al.*, 2022; Xu *et al.*, 2023). Furthermore, the broad-scale distribution of vertebrate-dispersed fruit sizes often correlates with body or gape sizes of their contemporary animal dispersers (Brodie, 2017; Lim *et al.*, 2020; McFadden *et al.*, 2022). This suggests that the interaction between selection pressures and sorting processes in both the geological past and the present day may have modified fruit size evolution and distribution. An integrated macroevolutionary (i.e. phylogenetic) and macroecological (i.e. assemblage composition) framework may increase our understanding of how deep time and contemporary evolutionary and ecological processes have shaped the evolution and geographical distribution of adaptive functional traits, such as fruit size.

Here, we developed such a framework for palms (Arecaceae), a pantropical, vertebrate-dispersed rainforest family comprising >2600 extant species. Palms show a large range of fruit sizes, of which many display characteristics for ‘megafaunal dispersal’ (Guimarães *et al.*, 2008; Onstein *et al.*, 2017). Palms have been studied extensively phylogenetically, ecologically, biogeographically, and in terms of fruit and seed size evolution and distribution (Dransfield *et al.*, 2008; Couvreur *et al.*, 2011; Kissling *et al.*, 2012, 2019; Onstein *et al.*, 2017, 2018, 2022; Bellot *et al.*, 2020; Lim *et al.*, 2020; Nascimento *et al.*, 2020). For instance, palm fruit size evolution and diversification have likely been influenced by interactions with frugivorous animals (Onstein *et al.*, 2017, 2022), and the occurrence of the largest palm fruits across assemblages is linked to the distribution of the largest extant (global) and Late Quaternary (Neotropical)

frugivorous mammals (Lim *et al.*, 2020). However, whether adaptive evolution has shaped the distribution of those large fruits remains unclear (Ackerly & Monson, 2003), and if so, under which conditions and rates (i.e. rates of stochastic evolution, adaptive selective optima and evolutionary strength towards these optima, Beaulieu *et al.*, 2012). Here, we address these research gaps by: adopting a phylogenetically explicit approach to assess adaptive evolution of palm fruit sizes across biogeographical realms; and null model simulations using stochastic (i.e. ‘neutral’ or ‘random’) fruit size evolution (Maestri *et al.*, 2022).

We hypothesize that the unique conditions in mainland Africa have provided the selective regime, or ‘evolutionary arena’ (Nürk *et al.*, 2020), for the evolution and persistence of large fruits. First, we quantified whether mammalian frugivore assemblages in mainland Africa have changed less in terms of body mass loss (and thus megafauna; i.e. less ‘downsizing’; Donoso *et al.*, 2020) after the Late Quaternary extinctions than elsewhere, as expected from continental-scale differences in downsizing (Barnosky *et al.*, 2004; Sandom *et al.*, 2014; Stuart, 2015; Smith *et al.*, 2018). Second, we evaluated whether mainland Africa has provided a unique selective regime for palm fruit size evolution, with palm lineages in Africa evolving and maintaining larger fruit sizes than lineages elsewhere. Presumably, this selective regime is created by the diversity and abundance of megafauna through geological time, providing consistent temporal co-occurrence between megafauna and large palm fruits, and thus frequent and temporally persistent seed dispersal of large fruits. By contrast, the loss of megafauna elsewhere may have exerted selection pressures for fruit size decrease, leading to smaller optimum fruit sizes outside Africa. Third, we assessed whether variation in the global distribution of the largest palm fruits across assemblages was explained by the interaction between biogeography (Africa vs elsewhere), Late Quaternary downsizing or extant frugivorous mammals, climate and canopy height. If true, this would suggest that the relationship between large palm fruits and its ecological determinants may have followed a different (evolutionary) trajectory in Africa than elsewhere. Finally, we developed a null model to assess whether the role of Africa in the distribution of fruit sizes could have emerged from nondirectional (i.e. neutral and stochastic) evolutionary processes, rather than adaptive evolutionary dynamics.

Materials and Methods

Palm trait and phylogenetic data

For the classification of palms, we followed the World Checklist of Vascular Plants (WCVP; Govaerts *et al.*, 2021), which includes 2641 accepted palm species in 183 genera. We assembled fruit length data – as a proxy for fruit size – from the PALMTRAITS v.1.0 database (Kissling *et al.*, 2019), and used published all-evidence species-level phylogenetic data (Faurby *et al.*, 2016). This led to complete data for 2040 palm species (77.2% of total). To incorporate uncertainty about phylogenetic reconstruction and branch-length variation, we performed all analyses on the maximum clade credibility (MCC) tree and a set of 100 randomly sampled phylogenetic trees from the posterior distribution.

Distribution data

We used the WCVP (Govaerts *et al.*, 2021) to assemble distribution data for all palm species globally at the scale of ‘botanical countries’ (TDWG-3 level). We then grouped species into regional assemblages based on co-occurrence in botanical countries and classified palm species by their distribution in mainland Africa, the Americas, Asia, or elsewhere. Species that occur on multiple continents (22 species, 0.8%) were manually assigned to the continent with the most occurrences on the Global Biodiversity Information Facility (GBIF; Supporting Information Table S1).

Frugivore data

We assembled current and past body size and distribution data for extinct and extant mammals from the PHYLACINE database (Faurby *et al.*, 2018). The PHYLACINE database includes IUCN range maps for the current distribution of mammals and inferred ranges of extant and Late Quaternary extinct species. We focused on ‘primary’ (fruit is main food item consumed) or ‘secondary’ (fruit is of intermediate importance in diet) frugivores based on the MammalDIET data set (Kissling *et al.*, 2014; Lim *et al.*, 2020). Extinct mammals were classified as frugivores when they were from families with a proportion of $\geq 40\%$ frugivores. We additionally included extinct species with missing or poor information from extant clades (e.g. litopternids and toxodons) if available evidence from isotopic and dental microwear suggested that the species was a mixed-feeder or browser (for details see Lim *et al.*, 2020). We calculated the average and maximum 95th percentile body size of frugivore assemblages at the botanical country scale in the present day (extant), and as they were in the Late Quaternary (‘present-natural’ as defined in the PHYLACINE database, including past range maps for extant species in addition to ranges for extinct species). We then calculated the difference in body size between extant and past assemblages as a measure of ‘downsizing’ of mammalian frugivore assemblages. Both the 95th percentile extant mammalian frugivore body mass and the average mammalian frugivore body mass change variables were square root-transformed to approximate a normal distribution of the data.

Environmental data

To account for abiotic environmental effects on the distribution of fruit size, we included global data on annual mean temperature, annual mean precipitation, temperature seasonality, precipitation seasonality (CHELSA v.1.2; Karger *et al.*, 2017) and mean canopy height (Lefsky, 2010) in our models. We used canopy height as a proxy for forest structure and associated factors such as light and moisture availability. These abiotic variables play a crucial role in the geographical distribution and turnover of palms and their traits across assemblages, for example by constraining their environmental niches (Bjorholm *et al.*, 2005; Blach-Overgaard *et al.*, 2013; Méndez *et al.*, 2022).

Downsizing of mammalian frugivore assemblages

First, we evaluated whether African assemblages differed in their decrease in average mammalian frugivore body mass since the Late Quaternary compared with assemblages in the Americas, Asia and elsewhere (H1) using a Kruskal–Wallis test (to account for non-normality in the data) and a *post hoc* Dunn test. We focused on assemblages (botanical countries) that included at least three palm species, to be able to make the connection to palm fruit size evolution and distribution (to be described later).

Africa as a unique selective regime for fruit size evolution

We assessed whether palm fruit lengths have evolved towards distinct adaptive optima in Africa (excl. Madagascar) than elsewhere (H2). Using the palm phylogenies (MCC and posterior sample of trees), we fitted maximum likelihood evolutionary trait models that differ in their assumptions about evolutionary processes, implemented in the ‘OUWIE’ R package (Beaulieu *et al.*, 2016). In total, seven evolutionary trait models were fitted to the log-transformed fruit length data, based on variations of Brownian motion (BM) and Ornstein–Uhlenbeck (OU) processes (Table 1). These models vary in parameters related to the (stochastic) evolutionary rate of fruit length evolution (σ^2), the selective fruit length optimum (θ) and the strength of selection towards this optimum (α). Species in the phylogeny were assigned to discrete selective regime states (Africa vs elsewhere), and ancestral regime states were computed using stochastic character mapping (‘SIMMAP’) in the ‘PHYTOOLS’ R package (Revell, 2012) under an unequal transition rate model. We applied model selection based on the Akaike information criterion for small sample sizes (AICc) to determine the best-fitting underlying process to explain fruit length evolution (Beaulieu *et al.*, 2012). To further explore whether Africa as a selective regime for palm fruit size evolution differs from selection pressures in the Americas and Asia, we repeated the OUWIE model selection for the other biogeographical regions (i.e. Americas vs elsewhere, Asia vs elsewhere), following the same model selection procedure as described for Africa. For more details on model fitting, convergence issues and ancestral regime reconstruction, see Fig. S1 and Methods S1.

Impact of extinction on fruit size evolution

To assess whether (recent) extinctions of large-fruited palms have affected our inferences of distinct evolutionary fruit size optima in Africa vs elsewhere, we ran phylogenetic linear regression models under an Ornstein–Uhlenbeck covariance structure, which accounts for phylogenetic covariance in the model residuals. We assessed how biogeography (Africa vs elsewhere, Americas vs elsewhere, Asia vs elsewhere) affected fruit size variation across species, and how this effect changed after randomly removing 10%, 25%, 50%, 75% and 90% of palm species with megafaunal fruits (≥ 4 cm) from the respective biogeographical regimes. We assessed at which percentage ‘extinction’ the positive effect of the

Table 1 Palm fruit length evolution in mainland Africa and elsewhere.

Model	Description	Explanation	Interpretation
BM1	Single-rate BM model (σ^2)	Fruit size evolves stochastically irrespective of whether species occur in Africa or elsewhere	There is no association between geographical area and fruit size evolution
BMS	Multi-rate BM model allowing σ^2 to differ among lineages in Africa vs elsewhere	Fruit size evolves stochastically, but at different rates for species that occur in Africa or elsewhere	There is an association between geographical area and the rate of fruit size evolution
OU1	Single-optimum OU model	Fruit size evolves towards one optimum value irrespective of whether species occur in Africa or elsewhere	There is no association between geographical area and fruit size evolution
OUM	OU model allowing for distinct trait optima (θ) in Africa vs elsewhere	Fruit size evolves towards distinct optimum values (θ) in Africa vs elsewhere, but under the same stochastic rate (σ^2) and selective force (α) towards this optimum	There is an association between geographical area and the optimum fruit size
OUMV	OU model allowing for distinct θ and σ^2 in Africa vs elsewhere	Fruit size evolves towards distinct optimum values (θ) and under distinct stochastic rates (σ^2) in Africa vs elsewhere, but with the same selective force (α) towards this optimum	There is an association between geographical area and the optimum fruit size and the rate of fruit size evolution
OUMA	OU model allowing for distinct θ and α in Africa vs elsewhere	Fruit size evolves towards distinct optimum values (θ) and under distinct selective forces (α) towards this optimum in Africa vs elsewhere, but with the same stochastic rates (σ^2)	There is an association between geographical area and the optimum fruit size and the selective strength towards this optimum
OUMVA	OU model allowing for different θ , σ^2 and α in Africa vs elsewhere	Fruit size evolves towards distinct optimum values (θ), under distinct stochastic rates (σ^2) and under distinct selective forces (α) towards this optimum in Africa vs elsewhere	There is an association between geographical area and the optimum fruit size, the selective strength towards this optimum and the rate of fruit size evolution

Description, explanation and interpretation on the seven evolutionary trait models assessed in this study. Brownian Motion (BM)-type models describe stochastic evolution of fruit size, while Ornstein–Uhlenbeck (OU)-type models take a selective force that pulls the trait towards optimum values into account. We expected the highest support for the OUM model (in bold), with larger fruits in Africa vs elsewhere, but stochastic rates and selective forces were not necessarily expected to differ between Africa/elsewhere. θ , selective fruit length optimum; σ^2 , evolutionary rate of fruit length evolution; α , strength of selection towards fruit length optimum.

African regime on fruit size would no longer be significant. Phylogenetic regression models were implemented using the ‘PHYLOLM’ R package (Tung Ho & Ané, 2014).

Determinants of the current broad-scale distribution of the largest fruit sizes

To assess whether global variation in assemblage-level fruit sizes is explained by the interaction between biogeography (Africa vs elsewhere), Late Quaternary downsizing, extant megafauna, climate and canopy height (H3), we used linear regression models (LMs). We performed stepwise model selection to evaluate: (1) which biotic and abiotic effects explained variation in the 95th percentile maximum palm fruit lengths (‘maximum palm fruit size’) across assemblages (botanical countries); (2) whether occurrence in Africa (vs elsewhere) explained additional variation in the distribution of maximum palm fruit sizes; and (3) whether interactions between occurrence in Africa and environment (Quaternary downsizing, extant body mass, canopy height and climate) were additionally supported. We considered the decrease in mean mammalian frugivore body size (g) since the Late Quaternary (‘body mass decrease’), 95th percentile maximum extant mammalian frugivore body mass (g) (‘extant body mass’), canopy height (m), mean annual temperature, mean annual precipitation, temperature seasonality and precipitation seasonality as biotic and abiotic effects. We therefore fitted eight models to

the data (Table S2) and used analysis of variance to assess whether adding or removing additive or interaction effects significantly improved model fit (i.e. explained variance). All variables were square root-transformed, except for mean annual temperature, for which a second-degree polynomial transformation fitted better, to achieve a normal distribution of the model residuals during model fitting.

We focused on maximum fruit and mammal body sizes to exclude the influence from smaller-fruited palm lineages that are predominantly dispersed by non-mammalian frugivores (e.g. birds). Furthermore, we used the 95th percentiles (rather than maximum) to reduce the influence of fruit size or body size outliers. We tested for multicollinearity between the predictor variables using Spearman rank correlation (Table S3) and normalized variables to enable a comparison of predictor effects on maximum fruit sizes. Finally, we illustrated the regional variation of trait values of assemblages on a world map.

Spatial autocorrelation

As spatial autocorrelation in response variables in nonspatial LMs can affect outcomes, we additionally fitted spatial autoregressive models (SAR_{err}) that account for spatial autocorrelation in the model residuals using the R package ‘SPATIALREG’ (Bivand & Wong, 2018). Therefore, we assessed Moran’s *I* values and calculated a spatial weight matrix that reflected the minimal distance

to connect each botanical country to at least one other country (i.e. 1423 km). For more details, see Fig. S2 and Methods S1.

A comparison with other angiosperms

We also evaluated whether the unique role of Africa in palm maximum fruit size distribution (H3) was similarly reflected in vertebrate-dispersed angiosperms other than palms. To this end, we assembled fruit width data across angiosperms from the literature and matched these to the TDWG-3 distribution data, focusing specifically on botanical countries that included palms ($n=130$; Govaerts *et al.*, 2021). We included species that are most likely vertebrate-dispersed, based on their fruit type (e.g. fleshy fruits, berries and drupes) or if they came from literature specifically focusing on endozoochorous seed dispersal. This resulted in fruit width data for 4663 angiosperm (excluding palm) species (1074 genera, 173 families); 18% species occurred in Africa. We focused on fruit width (rather than fruit length) because the width of the fruit may represent the same allometry between a single seed and fruit, as is typical for fruit length in palms (where most fruits contain a single or few seeds). We repeated the same stepwise linear model selection as described above for palms, to identify the determinants of variation in the 95th percentile maximum angiosperm (excluding palms) fruit width across global assemblages.

Null model for palm fruit size evolution

To test the degree to which Africa and its conditions have acted as a selective regime for fruit size distribution, we compared the empirical distribution of the largest palm fruits to null expectations under a more 'neutral' or 'stochastic' evolutionary scenario. For this purpose, we simulated palm fruit length evolution under a Brownian motion (BM) process on the palm phylogenetic tree. Evolution under BM is stochastic, and trait values are simply inherited from ancestral to descending lineages with a certain variance. Over time, BM evolution therefore generates interspecific variation in traits across species in a clade, and thus variation of trait values across assemblages, but not as a result of directional (possibly adaptive) evolution. We assumed that the BM process was limited between bounds and could not take negative or infinitely large values (bounded Brownian motion, BBM; Boucher & Démercy, 2016). We took the minimum and maximum observed palm fruit lengths to set these bounds (i.e. log-transformed values of 0.3 and 45 cm). We estimated the required starting parameters from the empirical data under a flat adaptive landscape, including the fruit length inferred at the root of the palm phylogeny ($z_0 = \log(2.78)$) and the stochastic rate of fruit size evolution ($\sigma^2 = \log(1.05)$). The inference creates a matrix with simulated fruit length data for the species at the tips of the phylogeny. Using 100 simulations across the MCC tree, we repeated the same stepwise linear model selection as described above for palms, to identify the determinants of variation in the simulated 95th percentile maximum palm fruit length across global assemblages. More details on the simulations can be found in Methods S1 and Notes S1.

Results

Downsizing of mammalian frugivore assemblages

We found support for the hypothesis (H1) that mammalian frugivore assemblages in mainland Africa have on average lost less body mass since the Late Quaternary extinctions than assemblages in the Americas, but not compared with assemblages in Asia or elsewhere (Fig. 1a; $\chi^2 = 31.47$, $P = 0.0001$). The distribution of assemblages that have experienced increased downsizing revealed to be spatially clustered in the Americas, eastern continental Asia and in two assemblages in sub-Saharan Africa (Fig. 1b). Body size of mammalian frugivore assemblages in those regions declined by between 215 and 999 kg. By contrast, most African assemblages, as well as most assemblages in tropical Asia and the Caribbean, only decreased by between 0.109 and 88.5 kg. Results for relative body mass decrease (i.e. the loss relative to the pre-Quaternary condition) were almost identical to those obtained for absolute decrease (Fig. S3).

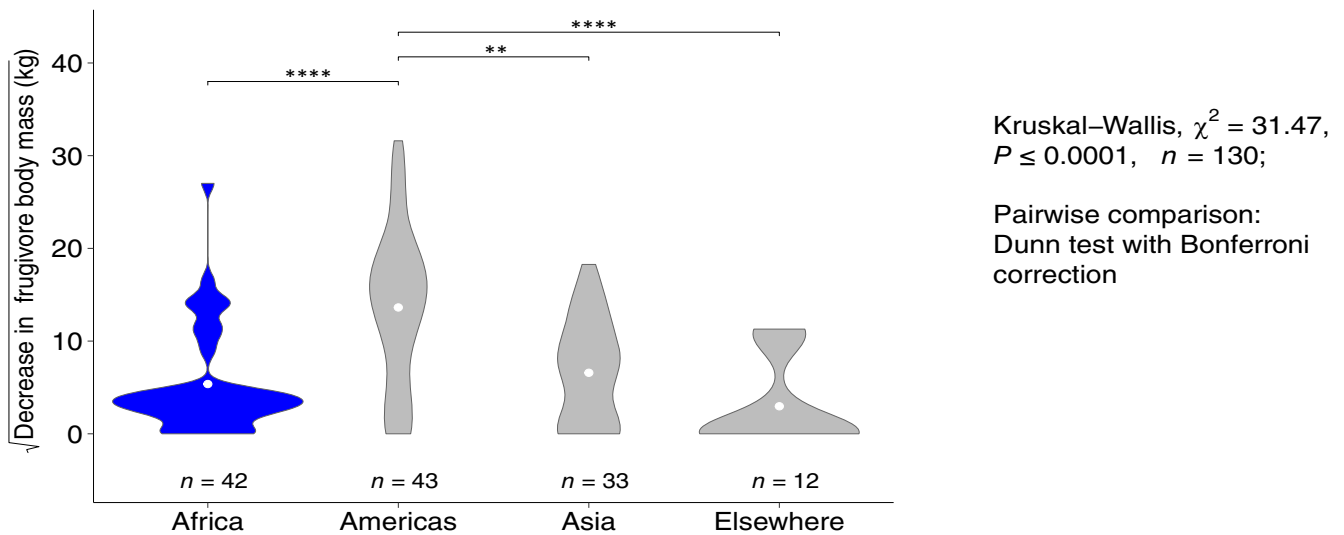
Africa as a unique selective regime for fruit size evolution

We found support for the hypothesis (H2) that mainland Africa has provided a unique selective regime for fruit size evolution, with larger adaptive optimum fruit lengths (θ) in palm lineages evolving in Africa than elsewhere (OUM model selected for 82% of trees, with average AICc weight = 0.71; Fig. S4; Table S4). Optimum fruit lengths in Africa were inferred to be more than twice as large as those elsewhere: $\log(1.19)$ ($\hat{=} 3.26$ cm) in Africa and $\log(0.54)$ ($\hat{=} 1.71$ cm) outside Africa (Fig. 2a; Table S4). In addition, the OUMV model (16% of trees, with average AICc weight = 0.77) inferred different stochastic fruit length evolution rates (σ^2) across the regimes, with rates $c. 1.5$ times higher in Africa than elsewhere. This indicates a stronger constrain on fruit size evolution outside Africa (Fig. 2b; Table S4).

Results for the Americas (primarily Neotropics) and Asia (primarily Indo-Malay region) suggest that these regions have probably also contributed to distinct evolutionary trajectories of palm fruit size evolution, but not to the extent Africa did. Specifically, model selection indicated support for models with different adaptive optima (θ), stochastic evolution rates (σ^2) and selection strengths towards optima (α) (Americas: OUMV = 45% of trees, OUMVA = 38% of trees; Asia: OUMV = 38% of trees, OUMVA = 51% of trees; Fig. S4; Table S4). However, optimum fruit sizes were less extreme than those inferred for mainland Africa (Fig. 2a). The optimum fruit size in the Americas ($c. 2.67$ cm) was only 1.14 times larger than those elsewhere, whereas in Asia, fruits were on average 12% smaller ($c. 2.3$ cm) than elsewhere (Table S4). Although absolute rates of stochastic fruit length evolution (σ^2) in the Americas and Asia were much lower than those in Africa, they were similar in terms of relative estimates (i.e. rates in Americas $c. 1.4$ times higher and in Asia $c. 1.4$ times lower, than elsewhere; Fig. 2b). The inferred strengths of selection were almost identical between regimes (Table S4).

When removing 10–90% of large-fruited species from the analysis, we detected a consistent decrease in the effect size of Africa

(a) Continental differences in downsizing of mammalian frugivores since the late Quaternary



(b) Downsizing of mammalian frugivores since the late Quaternary across tropical assemblages

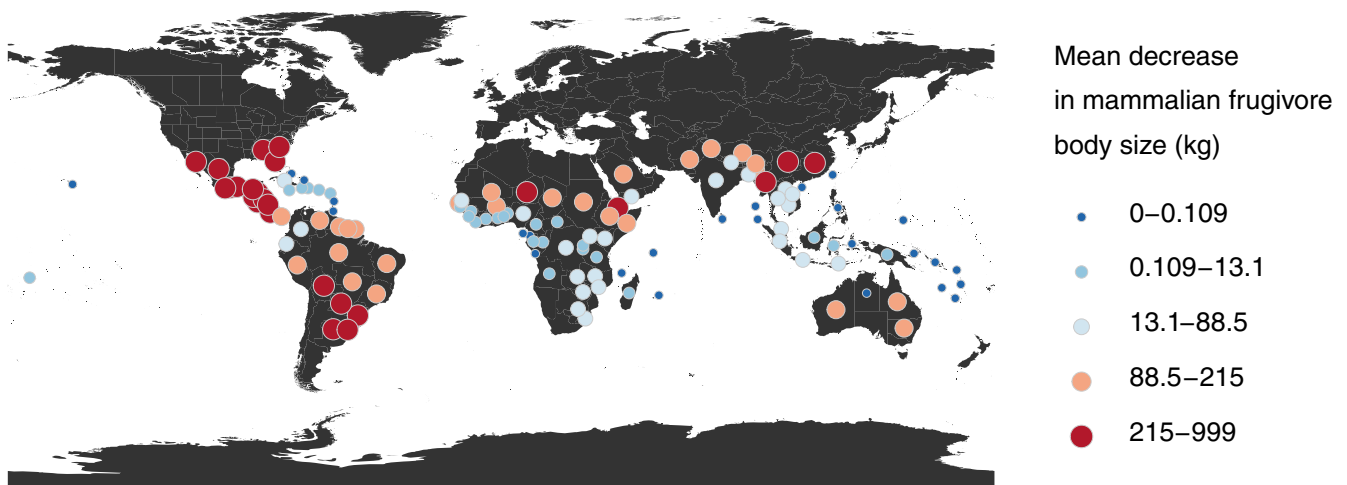


Fig. 1 Downsizing of mammalian frugivore assemblages. Only botanical countries with at least three palm species were included. (a) Difference in the absolute decrease in mammalian frugivore body mass (square root-transformed), between assemblages in mainland Africa, the Americas, Asia and elsewhere. Violin plot shapes illustrate the density of the raw data. Test statistic (χ^2), significance (P) sample sizes (n ; number of botanical countries) and significant differences between groups (****, $P < 0.001$; **, $P < 0.01$) are based on Dunn pairwise comparison tests. (b) Spatial distribution of the absolute degree of downsizing in kilograms (kg) that regional mammalian frugivore assemblages have experienced due to Late Quaternary extinctions and historic range contractions of still extant (persisting) species. Current mammalian frugivore assemblages in mainland Africa are largely similar in their average body masses to Late Quaternary conditions, while most assemblages in the Americas have experienced dramatic turnover from a majority of large-bodied mammalian frugivores towards the predominance of smaller and intermediate-sized mammalian frugivores since the Late Quaternary.

(vs elsewhere) on palm fruit size variation across species (Fig. S5). However, only when removing 90% of African palm species with fruits ≥ 4 cm, African palms had no longer significantly larger fruit sizes than palms elsewhere. This result suggests that recent extinctions of species with large fruits have probably not affected our inference of large palm fruit size evolutionary optima in Africa vs elsewhere. The evolution of biogeographical selective regimes and fruit size on the palm MCC tree is illustrated in Fig. S6.

Determinants of the current broad-scale distribution of the largest fruit sizes

Palm assemblages in Africa produce the largest fruits globally (Fig. 3a; average/SD: Africa 9.9/2.71 cm, Americas 4.49/2.15 cm and Asia 5.35/2.17 cm). This is consistent with patterns from vertebrate-dispersed angiosperms other than palms (Fig. 3b). These patterns deviate from those created under the null model

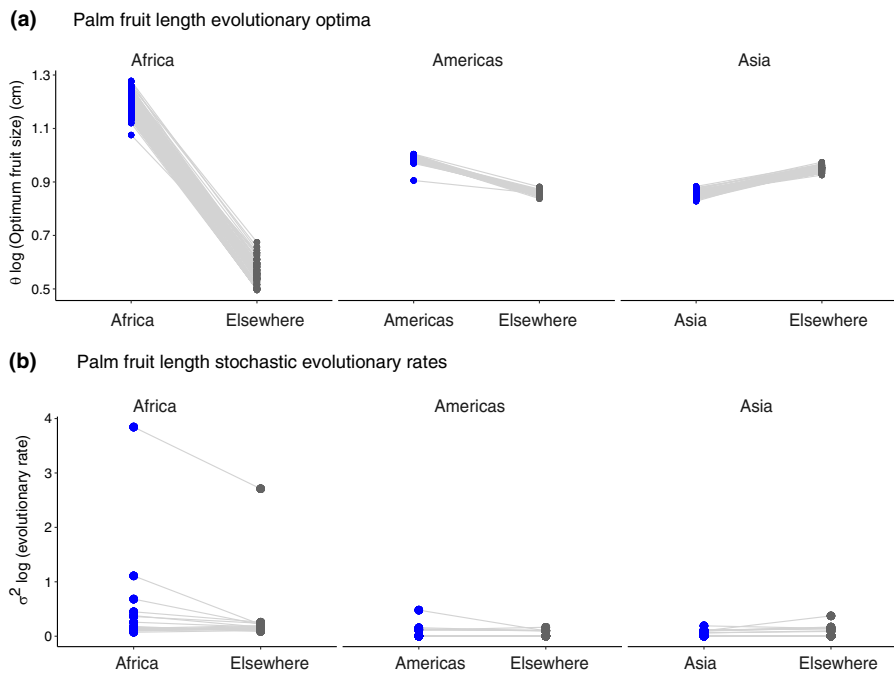


Fig. 2 Palm fruit length evolution across 100 phylogenetic trees in mainland Africa, the Americas and Asia compared with fruit length evolution elsewhere. (a) Inferred optimum fruit length values (θ) under the best Ornstein–Uhlenbeck (OU) models (OUM, OUMV, OUMVA) for empirical palm fruit length evolution. (b) Inferred stochastic evolutionary rates (σ^2) under the best Ornstein–Uhlenbeck (OU) models (OUMV, OUMVA) for palm fruit length evolution. Each dot-line combination represents the parameter estimates from the best-fitting model for a single phylogenetic tree, and only when the model converged. On one phylogeny, much higher stochastic evolution rates were inferred (outlier in b) with $(\log) \sigma^2_{\text{elsewhere}} = 2.7$ and $(\log) \sigma^2_{\text{Africa}} = 3.84$.

of stochastic fruit size evolution, where palm assemblages have smaller maximum fruit sizes and much less variation across assemblages (Fig. 3c). However, comparatively larger fruits are predominantly found in the Americas and mainland Asia, whereas assemblages in Africa have the smallest fruits (Fig. S7).

We found support for the hypothesis (H3) that variation in maximum 95th percentile palm fruit lengths across global assemblages was explained by biogeography (Africa vs elsewhere) as well as the interaction between biogeography and environment. Specifically, the best model (Fig. 4a; Table S2; $F = 42.78$, $P < 0.001$, $df = 111$, $\text{adj. } R^2 = 0.68$) indicated that larger fruits were found in palm assemblages in Africa compared with elsewhere (Fig. 4d; $\beta = 0.5$, $t = 4.43$, $P < 0.001$), with co-occurrence of larger-bodied extant frugivorous mammals (Fig. 4e; $\beta = 0.28$, $t = 23.16$, $P = 0.002$), and in regions with less temperature seasonality ($\beta = -0.38$, $t = -6.09$, $P < 0.001$). Importantly, we found support for an interaction between occurrence in Africa and canopy height (Fig. 4f; $\beta = -0.44$, $t = -2.39$, $P = 0.019$), suggesting that the effect of open canopies (i.e. lower average canopy heights) on large fruits is particularly pronounced in Africa. The best model also included a positive effect of annual precipitation on palm fruit size, but it was no longer significant when the interaction term between Africa and canopy height was included ($\beta = 0.16$, $t = 1.63$, $P = 0.107$). Decrease in Quaternary mammalian frugivore body size (i.e. ‘downsizing’) was a poor predictor of maximum palm fruit sizes.

Results for angiosperms (excluding palms) were similar to those for palms (Fig. 4b; Table S5; $F = 50$, $P < 0.001$, $df = 112$, $\text{adj. } R^2 = 0.68$), except that the effect of extant mammalian frugivore body size on the 95th percentile maximum angiosperm fruit width was not significant, and the negative effect of canopy height on fruit size was similar across biogeographical realms (i.e. no support for an interaction with Africa).

Results from the null model suggest that our empirical findings have not emerged from stochastic fruit length evolution (Notes S1). Specifically, in the best model (Fig. 4c; Table S6; $F = 16.09$, $P < 0.001$, $df = 125$, $\text{adj. } R^2 = 0.32$), biogeography (Africa vs elsewhere), body mass of extant frugivorous mammals and annual precipitation had significant effects on the maximum 95th percentile simulated fruit lengths across assemblages, but the direction of the effects was opposite to the direction detected in the empirical palm model (compare Fig. 4c to Fig. 4a). Furthermore, no effect of canopy height on fruit size was recovered in the null model. Finally, spatial autocorrelation did not affect our results, because both linear and SAR models indicated similar strengths of standardized coefficients of predictor variables on the response (Notes S1; Table S7).

Discussion

The global downsizing of Late Quaternary frugivorous mammals

Downsizing of frugivore communities strongly diminishes ecosystem functioning, such as long-distance seed dispersal by animals (Donoso *et al.*, 2020). Here, we assessed how the dramatic Quaternary extinctions of megafauna on most continents except for Africa (Stuart, 2015) affected the distribution of the largest palm fruits. We expected that the loss of megafauna would have imposed strong selection for large palm fruits to become smaller, or for local extinctions of those large fruits across downsized assemblages due to dispersal limitation (Mack, 1993; Galetti *et al.*, 2018; Onstein *et al.*, 2018). Interestingly, although assemblages in tropical regions outside of Africa – predominantly in the Neotropics – have experienced stronger mammalian downsizing than those in Africa (Fig. 1; Barnosky *et al.*, 2004; Sandom

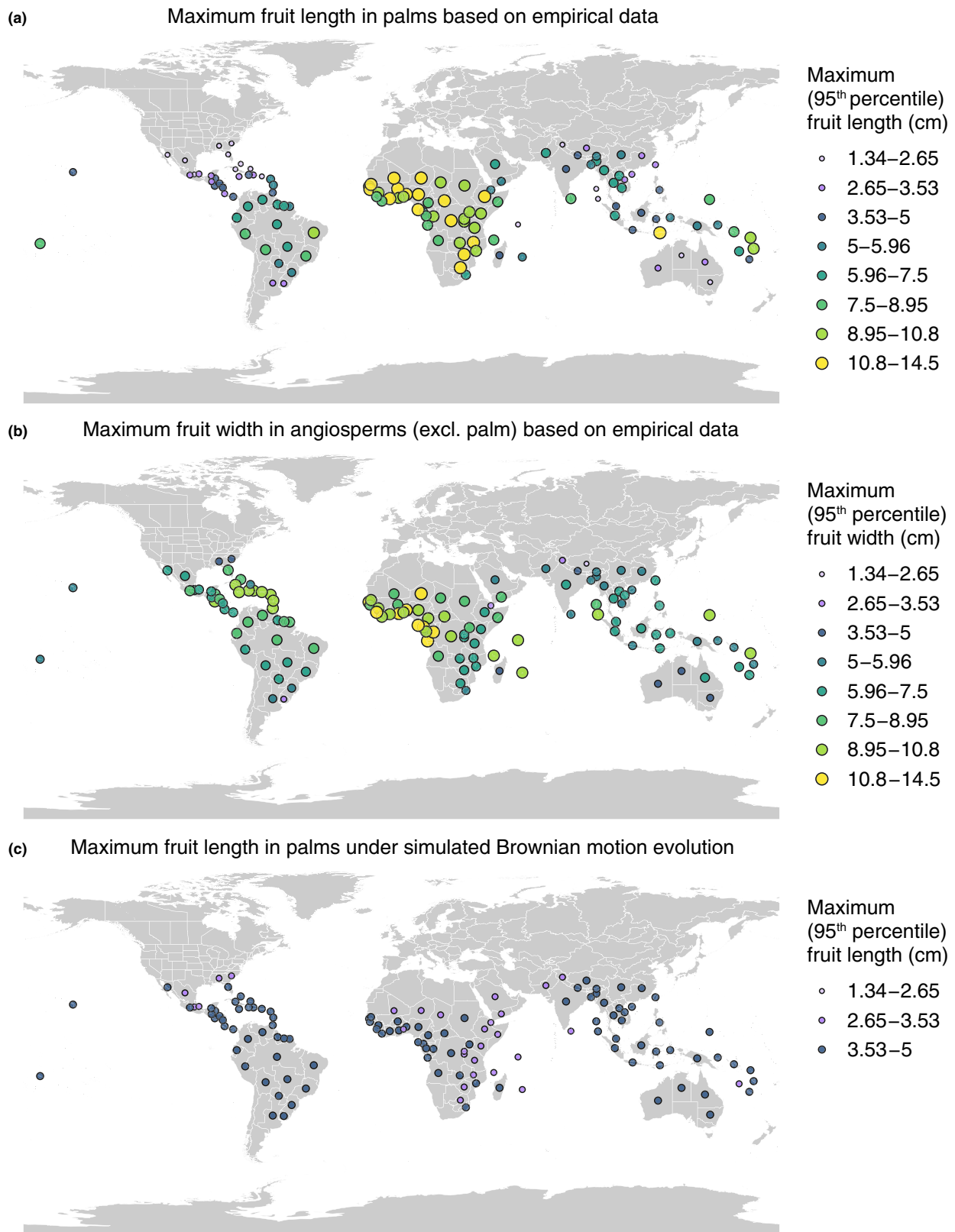
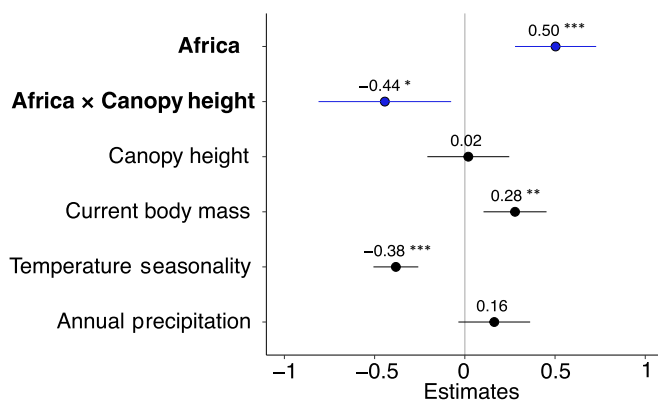
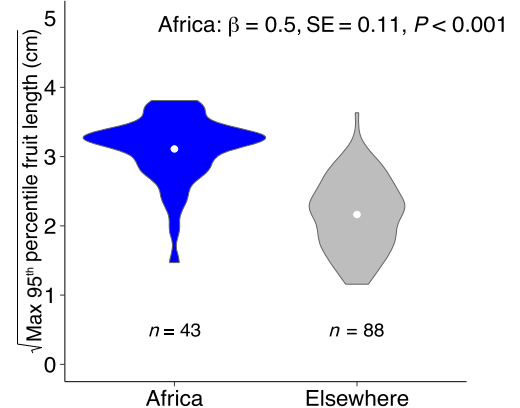


Fig. 3 Global distribution of empirical and simulated palm and angiosperm fruit sizes. Only botanical countries with at least three palm species were included. (a) Palm fruit lengths in centimetres; (b) angiosperm (excluding palm) fruit widths; (c) simulated palm fruit lengths under a null model of bounded Brownian motion evolution. This null model scenario would reflect what the distribution of maximum palm fruits across assemblages could have looked like without directional evolution or selection.

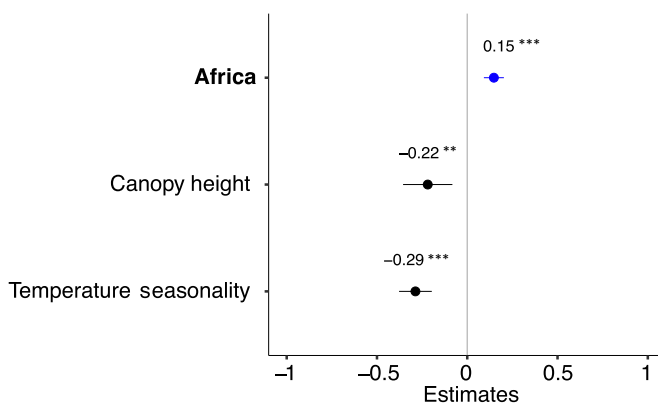
(a) Global determinants of large palm fruits across assemblages



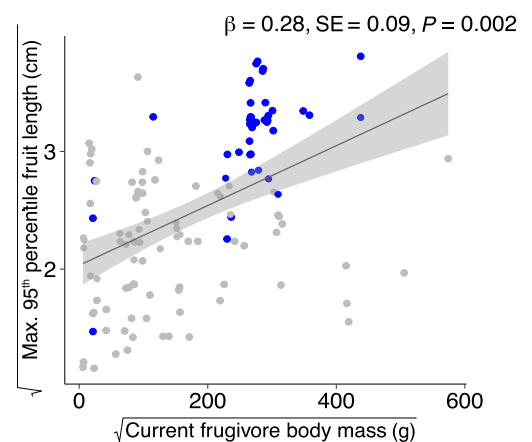
(d)



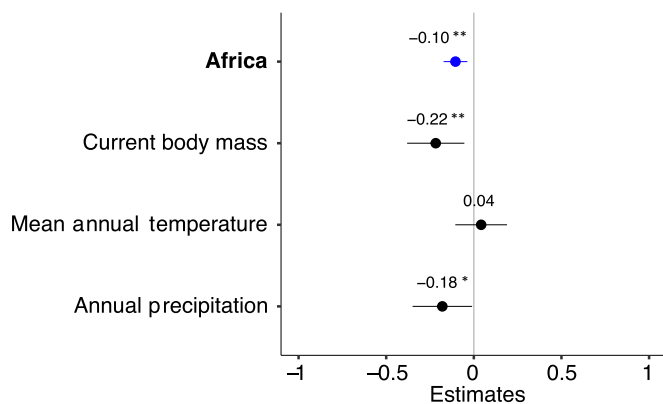
(b) Global determinants of large angiosperms across assemblages



(e)



(c) Global determinants of large palm fruits based on null model simulations under Brownian motion evolution



(f)

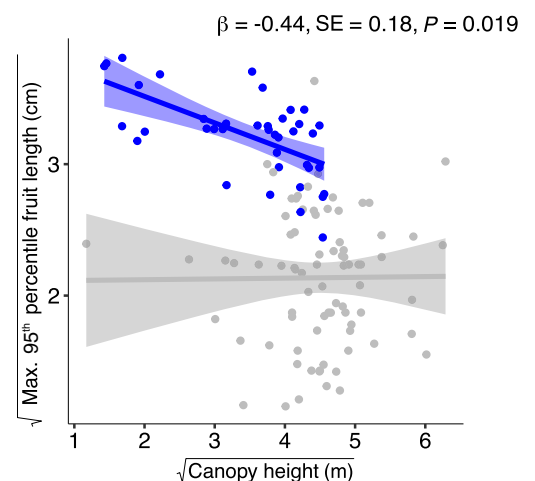


Fig. 4 Determinants of the broad-scale distribution of the largest palm and angiosperm fruit sizes. (a–c) Standardized effects for predictors that were included to explain variation in the maximum 95th percentile fruit sizes across assemblages (botanical countries) from linear models for the empirical palm fruit length data (a), the empirical angiosperm (excluding palm) fruit width data (b) and the null model simulations for palm fruit lengths (c). The effect of the interaction term of canopy height with Africa (a, 'Africa × Canopy height') was relative to palms occurring elsewhere. Before normalization, all variables were square root-transformed. Effects related to Africa are indicated in bold and dark blue; significant effects are indicated with an asterisk: ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$. (d–f) Raw data illustrating relationships between assemblage maximum 95th percentile palm fruit lengths and predictor variables as inferred in (a). Regression lines and GAM-fitted confidence intervals reflect statistically significant relationships supported by the linear model result, where dark blue indicates effects in Africa compared to elsewhere (in grey). The violin plot illustrates the density of the raw data. Model estimate coefficients (β), standard errors (SE) and significance (P) are indicated for each relationship, as well as the sample size (n ; i.e. botanical countries included). max., maximum.

et al., 2014), we did not find that stronger downsizing at the regional (assemblage) level was associated with smaller maximum palm (or angiosperm) fruits (Fig. 4).

Indeed, many palm lineages with very large fruits (e.g. *Astrocaryum*, *Acronomia* and *Mauritia*) have remained in Neotropical ecosystems, even though most Quaternary megafauna (e.g. *Megatherium* (giant sloths), Gomphotheriidae (elephant-like proboscideans)) are extinct (Janzen & Martin, 1982). By contrast, assemblages in the Indo-Malay region still harbour megafauna and have lost relatively little absolute body mass (Fig. 1), but maximum palm (and angiosperm) fruit sizes are overall small (Fig. 3). A possible explanation is that the evolution of (very) large palm fruits has not happened in Asia to the extent it did in Africa and the Neotropics, due to weaker selective pressures for large fruit evolution in Asia (e.g. due to the predominance of seed dispersal by relatively small-bodied birds; Corlett, 2017; McFadden *et al.*, 2022), which is consistent with predictions from stochastic palm fruit size evolution (Figs 3c, S7) and evolutionary models (Fig. 2a).

Nevertheless, the absence of an effect of extinct large fruit-eating animals during the Quaternary on palms contrasts with studies conducted in the Neotropics (Lim *et al.*, 2020) and Madagascar (Méndez *et al.*, 2022). Here, past distributions of now-extinct megafrugivores were still associated with the current distribution of palms, in addition to strong effects of extant frugivores and climate (Méndez *et al.*, 2022). Thus, although there were fewer extinctions of megafauna in Africa compared with the Neotropics and Asia – which may have influenced the differences in fruit sizes between these realms in palms (Figs 2a, 3a) and other vertebrate-dispersed angiosperms (Fig. 3b) – the regional (assemblage) variation in maximum fruit sizes is not explained by regional variation in mammalian downsizing. Instead, it is strongly related to the distribution of present-day megafauna (Fig. 4a; Lim *et al.*, 2020).

Africa as an evolutionary arena

Evolutionary trait models suggested that divergent evolutionary constraints (Futuyma, 2010; Beaulieu *et al.*, 2012) have led to disparate selective regimes for fruit size evolution in Africa compared with elsewhere. Indeed, although palms are relatively species-poor in Africa (excl. Madagascar), with only *c.* 83 species, many (42%) have fruits that are megafaunal in size. The conditions that have determined this African selective regime through geological time, and thus through palm evolutionary history from their origin *c.* 110 Ma onwards (Couvreur *et al.*, 2011), remains unclear, and may have involved a combination of megafauna-related and paleoclimatic selective pressures.

Megafauna, including frugivores, are known to shape the evolutionary trajectory of plant traits (Dantas & Pausas, 2020), including fruit or seed sizes, both on short (Galetti *et al.*, 2013; Onstein *et al.*, 2018) and longer (Eriksson, 2008; Onstein *et al.*, 2022) evolutionary time scales. For example, the expansion of bird and mammal lineages in the Cenozoic may have created opportunities for the evolution of fruit size diversity (Wing & Tiffney, 1987; Eriksson, 2008; Onstein *et al.*, 2022).

Furthermore, it is possible that the availability of very large frugivores (i.e. megafrugivores) lifted the evolutionary constraint on maximum fruit size, allowing fruits to evolve larger over time, consistent with palm selective fruit size optima in Africa being more than twice as large as elsewhere (Fig. 2a). Alternatively, it may be that these large-fruited African palms, which belong to genera *Borassus*, *Raphia*, *Hyphaene*, *Medemia*, *Sclerosperma* and *Elaeis*, already possessed large fruits before the colonization of the African mainland (Fig. S6; Baker & Couvreur, 2013; Bellot *et al.*, 2020). This is consistent with phylogenetic inferences showing that the Cretaceous ancestor of all palms already had very large fruits (Onstein *et al.*, 2022). Consequently, the persistence of megafauna in Africa – including frugivores that are known to frequently feed on large palm fruits (e.g. elephants; Zona & Henderson, 1989) – may have allowed fruits to remain large in Africa, whereas conditions elsewhere led to the evolution of smaller fruits (Galetti *et al.*, 2013; Onstein *et al.*, 2018). This scenario may apply to plant families other than palms, because contemporary species in the Paleotropics (incl. Africa) consistently possess larger fruits than their Neotropical family counterparts (Mack, 1993).

Nevertheless, the less severe extinction of megafauna is not the only feature that makes mainland Africa unique among the continents (Owen-Smith, 2021). Rather, the complex interaction between the abundance of seed-dispersing megafauna and severe climatic changes may have been important for fruit evolution. Drying, cooling and the expansion of savanna vegetation, especially since the Miocene, was more pronounced in Africa than elsewhere (Morley, 2000; Bonnefille, 2010). It is well recognized that changes in vegetation may alter fruit size evolution. For example, the expansion of closed (shady) forests in the early Cenozoic probably led to increases in seed size, and consequently fruit size, because large seeds contain more resources than small seeds, and thereby increase the probability of successful germination in species-rich rainforest understories where competition for light is strong (Tiffney, 1984; Wing & Tiffney, 1987; Eriksson *et al.*, 2000; Eriksson, 2008; Valladares & Niinemets, 2008; Onstein *et al.*, 2022). Conversely, (seasonally) dry or fire-prone environments may also select for thick seed coats that prevent desiccation, and thus possibly larger seeds (and consequently fruits; Westoby *et al.*, 1996). Indeed, many large-fruited African palms occur in dry, open, savanna habitats; the result of rare evolutionary transitions from the rainforest (Cássia-Silva *et al.*, 2019). Strong drying of the African landscape since the Miocene may therefore have favoured the persistence of savanna palms with large fruits, while rainforest palms with large fruits may have experienced increased extinction rates (Pan *et al.*, 2006; Hagen *et al.*, 2021). The fact that open habitats coincide with the occurrence of the largest megafauna in Africa (i.e. the African elephant *Loxodonta africana*), while closed habitats accommodate predominantly smaller mammals and birds, makes it challenging to identify the ultimate drivers of large fruits in Africa.

Finally, our models also inferred a lower stochastic evolutionary rate for palm fruit sizes outside of Africa, thus faster ‘disparification’ (i.e. evolution of fruit size variation across species) in Africa (Fig. 2b). This further suggests that conditions in Africa

lifted constraints on fruit size evolution, possibly because both the largest and smallest fruits were able to persist (Mack, 1993). In addition to the Africa regime, other selective regimes or evolutionary, morphological or developmental constraints related to, for example, fruit colour, defence and island colonizations, have also contributed to palm fruit size evolution, both in Africa and elsewhere (Onstein *et al.*, 2017; Cássia-Silva *et al.*, 2020; Nascimento *et al.*, 2020). This illustrates the complexity of understanding the selective pressures that have shaped the evolution of adaptive, functional traits, such as fruit size.

How Africa shaped large fruits across present-day assemblages

Our linear model results illustrate that Africa stands out by harbouring assemblages that on average produce larger fruits than elsewhere (Figs 3a,b, 4a,b,d; Mack, 1993), and this deviates from what would be expected under a neutral expectation of palm fruit size evolution (Figs 3c, 4c). Furthermore, the largest palm and angiosperm fruits were found in assemblages with low-temperature seasonality and high annual precipitation (i.e. the tropics), illustrating a latitudinal gradient of fruit size (Sinnott-Armstrong *et al.*, 2018). Interestingly, we did not find support for a significant interaction between megafauna and occurrence of the largest fruits in Africa, suggesting that the relationship between the largest frugivorous mammals and the largest palm fruits is similar across biogeographical regions. By contrast, maximum canopy height – as a proxy for forest cover or ‘shadiness’ – interacted with occurrence in Africa, showing that lower average canopy heights (i.e. open habitats) could have strongly influenced the occurrence of the largest palm fruits in Africa, but not elsewhere (Fig. 4f). However, open habitats were associated with the largest angiosperm fruits across biogeographical realms (Fig. 4b). Our results are consistent with large fruit trees in South Africa mostly occurring in open savannas (Bunney *et al.*, 2019), and with Miocene drying and the expansion of savanna vegetation as the ultimate trigger for the evolution and distribution of large palm fruits across African systems (Morley, 2000; Bonnefille, 2010). Large fruits in open habitats may also be a consequence of correlations with traits that maximize herbivory resistance and fire avoidance (e.g. high wood density, early allocation to height and numerous spines), which may be particularly beneficial in savannas (Dantas & Pausas, 2020; Nascimento *et al.*, 2020).

In conclusion, our integrated macroecological and macroevolutionary framework sheds new light on the adaptive dynamics of functional traits (Ackerly & Monson, 2003) – such as fruit size – and suggests that the intricate interaction between drying climate, the establishment of African savannas and the stable availability of frugivorous megafauna for seed dispersal through time, may explain why fruit sizes have evolved and maintained to be larger in Africa than elsewhere. Our results for palms may apply to pantropical vertebrate-dispersed plant taxa more generally, with the parallel evolution of ‘megafaunal’ fruit on the African continent (Mack, 1993). We argue that considering evolutionary processes is essential when identifying the potential

adaptation of functional traits to environments (Ackerly & Monson, 2003).

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Competing interests

None declared.

Author contributions

REO and FJRW designed the study, with input from AC, JYL and WDK. FJRW collected the data and ran analyses with contributions from REO, AC, JYL. FJRW and REO wrote the manuscript with contributions from all authors.

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Data availability

All data and R scripts to carry out the palm analyses are available from GitHub (<https://github.com/FriedaRosa/FruitsAfrica>). Data for angiosperms are provided in the Supporting Information.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Dataset S1 Taxa and sources for angiosperm data.

Fig. S1 Overview of convergence issues.

Fig. S2 Overview of spatial autocorrelation in data.

Fig. S3 Relative decrease in Quaternary mammalian frugivore assemblage body masses.

Fig. S4 Overview of selected evolutionary trait models.

Fig. S5 Extinction effects on evolutionary model parameters.

Fig. S6 Ancestral state reconstruction of geographical area and fruit size.

Fig. S7 Global distribution of simulated palm fruit sizes.

Methods S1 Supplementary details on methods.

Notes S1 Supplementary details on results.

Table S1 Assignment of widespread palm species to realms.

Table S2 Linear model selection for empirical palm data.

Table S3 Spearman's rank correlation coefficients.

Table S4 Parameter estimates from OU_{WIE} evolutionary trait models.

Table S5 Linear model selection for empirical angiosperm data.

Table S6 Linear model selection for simulated palm fruit length data.

Table S7 Results for spatial autoregressive model.

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