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## Research

### Megafrugivores as fading shadows of the past: extant frugivores and the abiotic environment as the most important determinants of the distribution of palms in Madagascar

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The extinction of all Madagascar's megafrugivores ca 1000 years ago, may have left its signature on the current distribution of vertebrate-dispersed plants across the island, due to the loss of effective seed dispersal. In this study, we dissect the roles of extinct and extant frugivore distributions, abiotic variables, human impact and spatial predictors on the compositional turnover, or beta-diversity, of palm (Arecaceae) species and their dispersal-related traits across 40 assemblages in Madagascar. Variation partitioning showed that palm beta-diversity is mostly shaped by the distribution of extant frugivores (eight lemur, three bird, two rodent and one bat species) and the abiotic environment (e.g. forest cover, slope and temperature), and to a lesser extent by the distribution of extinct megafrugivores (several giant lemur and elephant bird species). However, the contribution of these variables differed between dry western assemblages and wet eastern assemblages, with a more prominent role, albeit still small, of extinct megafrugivores in the west. These results suggest that palm distributions in the dry west of Madagascar, where megafrugivores were probably most abundant in the past, still show signatures of past interactions. With a fourth-corner analysis we observed that the distribution of palm species with relatively large fruits and seeds was negatively associated with frugivore richness of both past and present communities and home range sizes of extant mammalian frugivores. This suggests that palm species with relatively large fruits tend to occur in places with fewer, small-ranged mammalian frugivores, which may indicate dysfunctional seed dispersal. Nevertheless, our results also indicate that several wide-ranging bird species with high dispersal ability (large hand-wing index) that also occasionally feed on fruits may compensate for this potential dispersal loss. Our study sheds new light on dispersal anachronisms in Madagascar, and how defaunation and past species interactions may underlie current plant distributions.

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Keywords: abiotic environment, Arecaceae, beta-diversity, dispersal limitation, frugivory, megafrugivore extinction, plant–animal interaction

## Introduction

Tropical ecosystems harbour more plant species than any other ecosystem in the world (Kier et al. 2005). Identifying what drives this diversity and particularly the factors determining the variation in species composition among sites (i.e. beta-diversity) in such species-rich communities, remains a central question in ecology (Ricklefs 2004). The underlying drivers of beta-diversity have traditionally been studied in relation to geographical distance (Nekola and White 1999) and environmental gradients (Jankowski et al. 2009), whereas fewer studies have assessed how biotic interactions, such as the distributions of mutualistic interaction partners (e.g. seed dispersers), affect beta-diversity (Kemp et al. 2017). The distribution of fruit-eating and seed-dispersing animals (frugivores) may play an important role in the beta-diversity of plants in tropical rainforests, because up to 90% of tropical woody plants depend on frugivores for their seed dispersal (Jordano 2000). Large-bodied seed dispersers, such as ‘megafrugivores’ (i.e. subset of largest species having fruit as the main part of their diet in a given ecosystem; Moleón et al. 2020) may be especially important, as they generally have relatively large home-ranges and large gape widths which allows them to handle, ingest and disperse large seeds across long distances (Pires et al. 2018). The role of megafrugivores in tropical plant beta-diversity remains, however, poorly known.

Until the arrival and settlement of humans on the island of Madagascar around 1000 years ago, large-bodied vertebrates roamed the island, especially in the west (Crowley 2010, Crowley et al. 2011). Since then, Madagascar lost at least 17 large-bodied vertebrate genera, including megafrugivores, such as giant lemurs (e.g. species in genera *Archaeolemur*, *Pachylemur*) and elephant birds (e.g. species in genera *Aepyornis*, *Vorombe*) (Burney et al. 2004, Crowley 2010). This may explain the existence of dispersal anachronisms, that is plant species bearing traits (such as large fruits) that seem to be maladapted to the extant frugivore community (Janzen and Martin 1982, Guimarães et al. 2008). Currently, lemurs are thought to be the most important seed dispersers of Malagasy plants (Albert-Daviaud et al. 2018), but most of them are also threatened with extinction (IUCN 2020), which may lead to dysfunctional dispersal of fleshy-fruited plants (Albert-Daviaud et al. 2020). Understanding the consequences of frugivore extinctions for plant distribution is essential for the successful conservation of plants across Madagascar and many other tropical ecosystems (Johnson et al. 2017).

In this study, we aim to identify whether (mega-)frugivore extinctions have affected beta-diversity of palms (Arecaceae) and their dispersal-related traits (stem height, fruit size and seed size) across Malagasy sites. Madagascar is a ‘hotspot’ for palms, with more than 200 species, of which 98% are endemic to the island and 83% are

threatened with extinction (Dransfield and Rakotoarinivo 2012, Rakotoarinivo et al. 2014). At least 94% of the extant palms in Madagascar are dispersed by animals (Albert-Daviaud et al. 2018), such as birds and lemurs (e.g. *Alectroenas madagascariensis*, *Eulemur macaco*; Birkinshaw 1999). Importantly, palms are the most represented family among anachronistic species in Madagascar (Albert-Daviaud et al. 2020). The largest palm fruits found in Madagascar are those of *Borassus madagascariensis* (average length of 30 cm; Dransfield and Beentje 1995), which is an endemic species found in the dry western part of the island, and has already been identified as anachronistic (Albert-Daviaud et al. 2020). Other species have been identified as likely suffering from dysfunctional dispersal due to the size of their seeds and fruits (*Lemurophoenix halleuxii*, *Orania longisquama* and *Satranala decussilvae*; Albert-Daviaud et al. 2020).

To quantify whether megafrugivore extinctions have affected palm beta-diversity, we first disentangled the effects of abiotic environment, human impact and the past and present distributions of extant and extinct frugivores on compositional variation (beta-diversity) of palm communities across sites in Madagascar. We hypothesize that dispersal limitation resulting from frugivore extinctions has reduced the connectivity and occupancy of many palm species, thus leading to high compositional turnover. We expect a particularly strong signal of extinct megafrugivores on palm beta-diversity in the western part of Madagascar, where these animals were mostly occurring in the past (Crowley et al. 2011), assuming that the current distribution of palm species has not been reshaped by other factors such as changing environments and human impact. In addition, we expect water-related variables, temperature and edaphic conditions to influence palm beta-diversity, because drought, low temperatures and the availability of clay and aluminium have all been shown to limit palm distributions in different parts of the world (Svenning 2001, Tripp and Dexter 2006, Blach-Overgaard et al. 2010). Finally, human impact and proximity to settlements may additionally influence beta-diversity, for example by causing habitat fragmentation and local frugivore extinctions that may lead to decreased connectivity between palm populations and communities.

Second, we assessed whether dispersal-related palm traits are predominantly associated with dispersal-related frugivore traits, or alternatively, the abiotic environment or human impact. Since the evolution and distribution of dispersal-related traits in palms have been shown to be shaped by frugivore distributions and their ecological traits (Onstein et al. 2017, 2018, 2020, Lim et al. 2020), as well as abiotic conditions such as water-related variables, temperature and soil variables (Bollen et al. 2005, Gödel et al. 2015), we also expect the distribution of palm traits in Madagascar to be

affected by both biotic and abiotic factors. Last, human population density may negatively affect the distribution of relatively large palms and large fruits and seeds, because humans use palm stems and leaves for construction (Bussmann et al. 2015) and may affect large-seeded plants by causing defaunation of their large-bodied frugivorous dispersers (Laurance et al. 2006).

## Material and methods

### Palm distributions and assemblages

We assembled occurrence data for palms in Madagascar from records provided by the Royal Botanic Gardens, Kew ( $n=2606$  georeferenced occurrences for 203 species), and our own sampling ( $n=386$  coordinate records for 10 species). Palm species only known from cultivation (*Dyopsis*

*plumosa* and *D. albofarinosa*), or introduced species (*Cocos nucifera*, *Elaeis guineensis*, *Phoenix dactylifera*), were excluded from the dataset. The final dataset contained 2531 occurrence records for 190 species of Malagasy palms. To obtain community compositional data, we selected areas in Madagascar that have been intensively sampled for palms, thereby reducing the effect of false absences, resulting in 40 assemblages or sites (Supporting information). From these 40 sites, we obtained a presence/absence site-by-palm species matrix. From the 190 species, 25 species were not occurring in any of the sites, resulting in a final matrix containing  $n=165$  species of Malagasy palms across 40 sites.

To be able to disentangle the effects of biotic and abiotic factors in areas where megafugivores have mostly occurred in the past (dry west) versus areas where megafugivores were probably scarce (wet east), we assigned assemblages to ecoregions, focusing on ‘Madagascar humid forest’ (as classified in the Ecoregions2017 map by Dinerstein et al. 2017) as the ‘eastern’

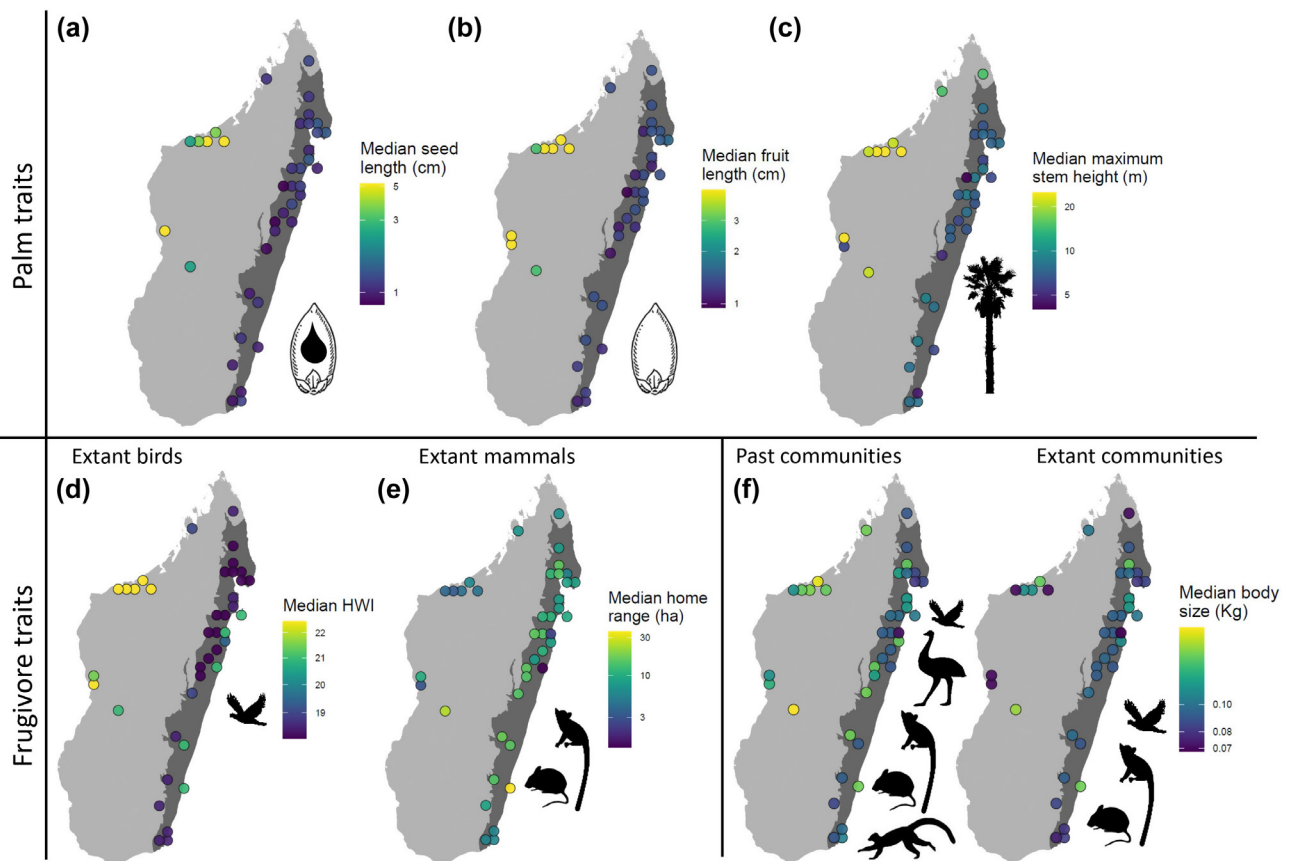


Figure 1. The distributions of palm (Arecaceae) dispersal-related traits and frugivore dispersal-related traits of extinct megafugivores and extant species in Madagascar across 40 assemblages. In dark grey the wet ‘Madagascar humid forest’ ecoregion is shown, which was used to select the eastern assemblages (29 sites) and belongs to the larger ‘Tropical & Subtropical Moist Broadleaf Forests’ biome. The rest of the sites were indicated as western assemblages (11 sites), mainly distributed in the dry west ecoregions and mostly belonging to the ‘Tropical & Subtropical Dry Broadleaf Forests’ biome. Maps show all median values of (a) present palm average seed length per assemblage, (b) present palm average fruit length per assemblage, (c) present palm maximum stem height per assemblage, (d) extant birds (21 species) hand-wing index (HWI), (e) extant mammals (41 species) home range and (f) body size for past communities (including both extant and extinct frugivores) and only extant communities. Circles represent the location of the centroid of each  $0.3 \times 0.3$  degrees cell, with brighter colours representing higher values.

assemblage group (29 sites,  $n = 159$  species) which belongs to the larger 'Tropical and Subtropical Moist Broadleaf Forests' biome, and the remaining assemblages, belonging to several other, drier ecoregions, as the 'western' assemblage group (11 sites,  $n = 32$  species), which mostly belong to the 'Tropical and Subtropical Dry Broadleaf Forests' biome (Fig. 1).

### Palm dispersal-related traits

Stem height, fruit size and seed size have been considered as important traits underlying seed dispersal ability in plants. These traits are especially relevant for the foraging activity by frugivores, depending on their gape width, body size constraints and activity in certain forest strata (Jordano 1995, Muller-Landau et al. 2008, Thomson et al. 2011). We therefore collated maximum stem height and average fruit length and width from the PalmTraits 1.0 database (Kissling et al. 2019), and average seed length and width from Albert-Daviaud et al. (2020). Because stem height and fruit size values were not available for all the 165 Malagasy palm species from the PalmTraits 1.0 database, we imputed the missing data by phylogenetic data imputation with the R package 'Rphylopar' (Goolsby et al. 2017). Phylogenetic data imputation was not possible for seed sizes because of missing data for the majority of palm species, resulting in seed size data for  $n = 104$  Malagasy palm species only. More details about the phylogenetic imputations can be found in Supporting information.

### Frugivore distributions and assemblages

We collated distribution data for extant and extinct frugivores in Madagascar, and selected all animals which have fruit in their diet as stated in Razafindratsima et al. (2018). We also included three species of potential reptilian seed dispersers (Ganzhorn et al. 1999). For extinct species, we included all elephant birds following the species delimitation by Hansford and Turvey (2018) (four species), and lemurs that were inferred to have a diet of 'mixed fruits' based on dental use wear (nine species, Godfrey et al. 2004). For all extant fruit-eating animals, we obtained current polygon ranges from the International Union for Conservation of Nature, ver. 2020-2 (IUCN 2020). To reconstruct historical geographic ranges of the extinct megafrugivorous lemurs and elephant birds, we compiled fossil records of extinct mammals, including lemurs, from 34 sources (Supporting information). Fossil records of elephant birds were collected from Hansford and Turvey (2018). We used MInOSSE (Carotenuto et al. 2020a), a model-based method that reconstructs the past ranges of extinct fauna, by relying on the distribution of other coeval species (i.e. species found in the same fossil site) and without using environmental predictors. This approach is implemented in the R package 'Ecopast' (Carotenuto et al. 2020b). More details on this method are provided in the Supporting information. Based on the distribution maps, we extracted presence-absence data of extant and extinct frugivores in the 40 sites, resulting in the present and potential past co-occurrence of palms with 105 (93 extant and 12

extinct) frugivores. This was done using R packages 'raster' (Hijmans 2020), 'rgdal' (Bivand et al. 2021) and 'sp', with functions *over* and *extract* (Pebesma and Bivand 2005).

### Frugivore traits

We collated the most comprehensive collection of functional trait data for Malagasy mammals and birds to date, which includes traits related to their seed dispersal ability. This included body mass for extinct and extant frugivores (all 105 species), frugivory-index (i.e. the percentage of fruits in their diets) for extant animals (all 93 species), hand-wing index (HWI) – a proxy for dispersal ability – for extant birds (21 species) and home range size for extant mammals (41 species). To understand the contribution of frugivore traits to explaining palm trait composition, we calculated the median of the selected frugivore traits for each of the 40 'past' (all extant and extinct frugivores) and 'present' (only extant frugivores) assemblages (Fig. 1). More information on data sources and a list of all the frugivores and their traits is provided in the Supporting information.

### Abiotic variables and human impact across assemblages

A set of climatic, topographic and soil related variables known to be associated with palm distributions (Svenning 2001, Tripp and Dexter 2006, Blach-Overgaard et al. 2010) and their traits (Gödel et al. 2015), was obtained from MadaClim (<<https://madaclim.cirad.fr/>>) for climate and topographic conditions (average data for the years 1970–2000) and from the International Soil Reference and Information Centre (<<http://data.isric.org>>) for soil variables. Human-related variables were taken from the maps in Venter et al. (2016). Average values for the 40 assemblages were extracted from each  $0.30 \times 0.30$  degrees grid cell using function *extract* of package 'raster' (Hijmans 2020).

After checking for strong correlation (Pearson's  $r > 0.7$ ) between all variables, we kept 12 variables to assess their effect on palm beta-diversity: five climatic and topographic variables (minimum temperature of the coldest month, annual climatic water deficit, slope, solar radiation and percentage of forest in the year 2010), five soil variables (clay content, cation exchange capacity, extractable aluminium, total nitrogen and total phosphorus) and two human impact variables (human population density for the year 2010 and human footprint for 2009). To assess which environmental variables affect palm trait distributions, we focused on a subset of variables that have been shown to be important for the distribution of plant traits, in particular palm traits (Gödel et al. 2015): annual mean temperature, temperature seasonality, annual mean precipitation and precipitation of the wettest month, percentage of forest, total nitrogen, total phosphorus and human population density. We scaled the abiotic variables by converting them to standardized z-scores, by subtracting each environmental variable from their mean and dividing it by the standard deviation (mean = 0, SD = 1).

## Abiotic, human and frugivory determinants of palm community composition

To disentangle the relative importance of abiotic, biotic and human impact factors for explaining palm beta-diversity, we used a variation partitioning approach (Borcard et al. 1992, Legendre and Legendre 2012). In addition to the abovementioned predictors, we also considered the spatial location (latitude and longitude) of assemblages to account for potential spatial gradients (called 'spatial predictors' hereafter) in palm beta-diversity across sites.

We used distance-based redundancy analysis (dbRDA; Legendre and Andersson 1999) to model community composition, using the R function *capscale*. Beta-diversity was calculated by the Sørensen index of dissimilarities between assemblages (Sørensen 1948) with function *vegdist* setting `binary=TRUE` and method 'bray'. Using dbRDA models, we partitioned the variation explained by four groups of predictors: abiotic environment (including human-related variables), extinct megafrugivores, extant frugivores and spatial predictors. We first evaluated which variables within each group of predictors were significantly related to palm beta-diversity by performing forward model selection based on adjusted  $R^2$  and p-values, as implemented in function *ordiR2step* (Blanchet et al. 2008). Only the statistically significant variables were then retained for the variation partitioning analysis. We partitioned the variation explained by each group of predictors into their pure and shared fractions using the function *varpart*, which is based on the partition of adjusted  $R^2$  values (Peres-Neto et al. 2006). All functions used are included in the R package 'vegan' (Oksanen et al. 2020).

To explore whether highly frugivorous animals are more important for palm community composition than frugivores that also feed on other food items, we weighted the presence/absence matrix of frugivores in the community by their frugivory-index, calculated as the proportion of fruit in their diet. For example, *Alectroenas madaagascariensis* is known to only feed on fruits (i.e. frugivory-index = 1), whereas *Coua serriana* has 70% of fruits in its diet (frugivory-index = 0.7). Still, because non-specialist frugivores (i.e. omnivores) may be as important for seed dispersal as specialist frugivores (e.g. in temperate regions, Dalsgaard et al. 2017), we assessed sensitivity of palm compositions to the frugivory level by comparing an analysis that included only highly frugivorous dispersers (i.e. with at least 80% of fruits in their diet, as listed in Albert-Daviaud et al. 2018), with another that included a presence-absence matrix unweighted by frugivory-index. Finally, in addition to a Madagascar-wide analysis with all assemblages included, we also performed variation partitioning separately for the western and eastern assemblages to assess whether the relative importance of the determinants of palm beta-diversity differed between the west and east of the island. More details of the approach are provided in Supporting information.

## Abiotic, human and frugivory determinants of palm fruit size composition

To investigate the link between dispersal-related palm traits (maximum stem height, fruit length and width, seed length and width) and the environment (abiotic, human and frugivores) in Madagascar, we used a fourth-corner analysis (Legendre et al. 1997). This method correlates environmental and trait variation by linking species presence/absence (matrix L; palm species  $\times$  cell), environment (matrix R; cells  $\times$  abiotic/human/frugivore variables) and species traits (matrix Q; palm species  $\times$  palm traits) across sites, to estimate the fourth link – that between environment and palm traits (Dray and Legendre 2008, Dehling et al. 2014). We included eight environmental and human impact variables as well as the assemblage-median frugivore traits (see above and Fig. 1) as explanatory variables in the model. Again, we also evaluated how results were affected when only considering community-median traits of highly frugivorous dispersers.

The fourth-corner analysis was conducted with package 'ade4' (Dray and Dufour 2007) and function *fourthcorner*, with permutation model number 6 (49 999 permutations), which permutes values of sites and values of species. We used the false discovery rate method (fdr; Benjamini and Hochberg 1995) to adjust p values for multiple testing, following Dray et al. (2014). All data analyses for this study were performed using R 3.6.1 (<[www.r-project.org](http://www.r-project.org)>).

## Results

### Effects of abiotic environment, human impact and frugivory on palm beta-diversity

All the dbRDA global models showed a significant effect of environment (abiotic and human), the distribution of extinct and extant frugivores, and spatial predictors on palm beta-diversity across the 40 assemblages (Table 1; Supporting information). Individual variables that came out as significant for each palm matrix (all palms, east and west) after forward selection are shown in Table 1. Together, all the significant predictors explained 71% of the total variation in palm composition in the Madagascar-wide analysis, 52% in the east, and 40% in the west (Fig. 2; Supporting information). The proportion of compositional variation explained across the entire island was highest for the extant frugivores (Adj. $R^2$  = 0.607), followed by the abiotic/human environment (Adj. $R^2$  = 0.420), the spatial predictors (Adj. $R^2$  = 0.318) and the extinct megafrugivores (Adj. $R^2$  = 0.305). Most of this variation was explained by the shared influence of the four groups of variables, but significant fractions of variation were also explained by some exclusive effects. Both extant frugivores and extinct frugivores uniquely explained significant fractions of variation (22% and 8%, respectively), whereas the variation uniquely explained by the environment was not significant (Fig. 2, Supporting information). The

Table 1. The determinants of palm (Arecaceae) beta-diversity across 40 assemblages in Madagascar. Only statistically significant variables (at  $p < 0.05$ ) are shown, which were selected by forward selection from each dbRDA significant model (abiotic environment/human impact, extinct megafrugivores and present frugivores) for each palm presence-absence matrix (all, eastern and western assemblages).  $R^2$ .adj is the  $R^2$  adjusted for the number of predictors in the model. \*\*\* $p < 0.001$ ; \*\* $p < 0.01$ .

Palm sites matrix	Abiotic environmental/human impact factors		Extinct megafrugivores		Extant frugivores			
	Selected variables	$R^2$ .adj	Selected variables	$R^2$ .adj	Selected variables	$R^2$ .adj		
All assemblages	Forest cover (percentage of forest)	0.412*	<i>Archaeolemur majori</i>	0.314*	<i>Cheirogaleus major</i> <i>Brachyuromys betsileoensis</i> <i>Microcebus jollyae</i>	0.622*		
							0.608*	
	Slope	0.397**	<i>Aepyornis maximus</i> <i>Palaeopropithecus ingens</i>	0.295*	<i>Neodrepanis coruscans</i> <i>Eidolon dupreanum</i> <i>Eulemur cinereiceps</i>	0.576**		
		0.370**		0.274*		0.560**		
	Solar radiation	0.318**	<i>Aepyornis hildebrandti</i>	0.252**	<i>Gymnuromys roberti</i>	0.517**		
	Climatic water deficit	0.253**	<i>Archaeolemur edwarsi</i>	0.225**	<i>Propithecus diadema</i>	0.494**		
					<i>Cheirogaleus medius</i>	0.470*		
					<i>Vorombe titan</i>	0.182**	<i>Eulemur collaris</i>	0.444**
					<i>Coua coquereli</i>	0.416**		
					<i>Cheirogaleus crossleyi</i>	0.385**		
		<i>Pachylemur insignis</i>	0.126**	<i>Eulemur albifrons</i>	0.333**			
		<i>Babakotia radofilai</i>	0.091**	<i>Alectroenas madagascariensis</i>	0.260**			
Eastern assemblages	Total soil nitrogen	0.279*	<i>Archaeolemur majori</i>	0.128**	<i>Neodrepanis coruscans</i> <i>Eliurus webbi</i> <i>Fossa fossana</i>	0.497*		
						0.467*		
	Slope	0.254**			<i>Microcebus murinus</i> <i>Eulemur rubriventer</i>	0.410** 0.375**		
	Solar radiation	0.194**	<i>Aepyornis hildebrandti</i>	0.064**	<i>Avahi ramanantsoavanai</i>	0.337**		
<i>Avahi meridionalis</i>					0.303**			
<i>Eidolon dupreanum</i> <i>Propithecus diadema</i>					0.272** 0.240**			
Minimum temperature of the coldest month	0.100**			<i>Cheirogaleus crossleyi</i> <i>Eulemur albifrons</i>	0.201** 0.116**			
Western assemblages	dbRDA model not significant		<i>Pachylemur jullyi</i>	0.176*	dbRDA model not significant			

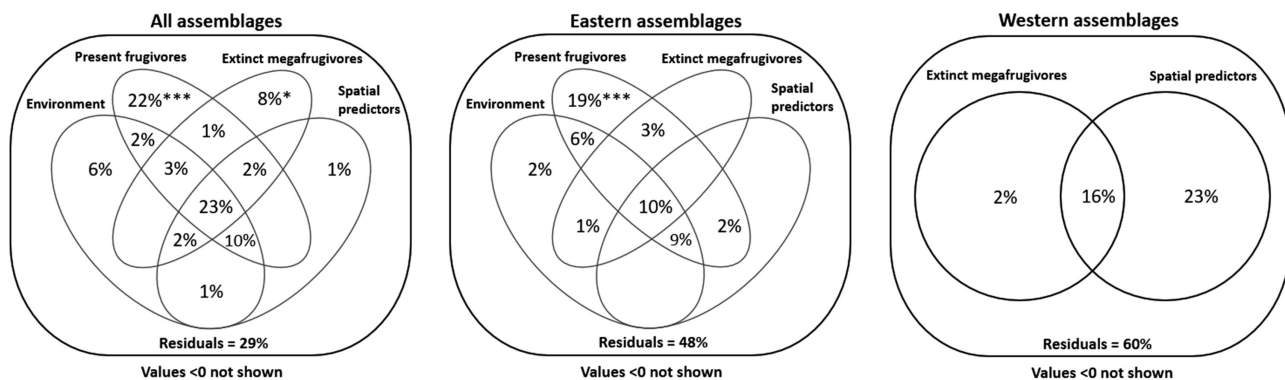


Figure 2. Variation partitioning of the individual and shared effects of environment factors (abiotic/human impact), frugivores and spatial predictors on palm beta-diversity across 40 assemblages. This was done for all assemblages (40 cells), wet eastern assemblages (29 cells) and drier western assemblages (11 cells). The rectangular area represents all the variation explained in palm beta-diversity across assemblages, and the ovals or circles within that area represent the pure/exclusive effects of the four groups of explanatory variables (abiotic environment/human impact, present frugivore distributions, extinct megafrugivore distributions and spatial predictors) and their joint effects (overlapping parts of the ovals or circles). Numbers inside the ovals indicate the percentage of explained variation, which are adjusted  $R^2$  values. The residual variation (variance that was not explained by the chosen groups of explanatory variables) is reported for each matrix as 'Residuals'. Values  $< 0$  are not shown. \*\*\* $p < 0.001$ , \* $p < 0.01$ . For more details on the results from the variation partitioning analyses see Table 1 and Supporting information.

most important abiotic variables associated with palm beta-diversity were forest cover, slope, minimum temperature of the coldest month, solar radiation and annual climatic water deficit. For the frugivores, 14 extant frugivores (eight lemurs, three birds, two rodents and one bat) and eight extinct megafrugivores (five giant lemurs and three elephant birds) were inferred to be significantly associated to palm composition (Table 1). Human impact variables were not significant.

For the eastern assemblages, similar to the Madagascar-wide analysis, most variation in palm composition was explained by extant frugivores (Adj.R<sup>2</sup>=0.487), followed by the environment (Adj.R<sup>2</sup>=0.276), spatial predictors (Adj.R<sup>2</sup>=0.211) and the extinct megafrugivores (Adj.R<sup>2</sup>=0.126), with the only significant pure fraction explained by extant frugivores (19%, Fig. 2). Fewer environmental factors, extant frugivores (11 species) and extinct megafrugivores (two species) were inferred to be important for palm composition in the east compared with the Madagascar-wide analysis (Table 1).

For the western assemblages, the global dbRDA models with the environmental/human impact variables and the extant frugivores as predictors were not significant. Therefore, the variation partitioning was performed with the extinct megafrugivores and spatial predictors only. Spatial predictors explained more variation (Adj.R<sup>2</sup>=0.386) than the extinct megafrugivores (Adj.R<sup>2</sup>=0.174), with (non-significant) pure fractions of 23% (spatial predictors) and 2% (megafrugivores, i.e. the species *Pachylemur jullyi*) (Fig. 2, Table 1).

When only including highly frugivorous dispersers, results were similar to the Madagascar-wide analysis, except that palm beta-diversity explained by the extant frugivores was lower (nine significant frugivores, Adj.R<sup>2</sup>=0.505), and

therefore the total amount of variation explained by the model also decreased (60%). In addition, different frugivores were identified as important, although lemurs were still predominant. When we did not weight the presence-absence data by the frugivory-index, results were almost identical to the initial Madagascar-wide analysis, except that *Cooua coquereli* was replaced by *Copsychus albospecularis* (both bird species) as a significant predictor of palm beta diversity. All detailed results are provided in Supporting information.

### Effects of abiotic environment, human impact and frugivory on dispersal-related palm traits

Communities with the largest average palm fruits, seeds and maximum stem heights are found in the western part of Madagascar, as are the largest extinct megafrugivores and birds with the highest dispersal ability (largest hand-wing index), whereas the communities with the largest extant frugivores and mammals with the largest home range sizes are in the east (Fig. 1). Since correlation values between fruit widths and lengths as well as seed widths and lengths are very high ( $r > 0.8$ ), we only report results for fruit length and seed length here (but see Supporting information for results for the other traits). The fourth corner analysis identified several correlations between palm traits and environmental and human impact variables (Table 2). Specifically, fruit and seed lengths were larger in places with higher mean annual temperatures and maximum precipitation of the wettest month, and smaller in climates with more temperature seasonality and higher total soil nitrogen. In addition, fruit lengths were larger on soils with lower total phosphorus and in areas with lower human population densities. Maximum stem

Table 2. The determinants of palm (Arecaceae) dispersal-related traits across 40 assemblages in Madagascar. Fourth-corner analysis results with only significant correlations (at  $p < 0.05$ ) between palm traits and the different predictor variables are shown. Since fruit lengths and widths and seed lengths and widths are highly correlated, we are showing here only results for fruit length and seed length. See Supporting information for results on fruit and seed widths. Pearson's  $r$  indicates the correlation value, Adj.  $p$ -value is the  $p$  value adjusted for multiple testing. HWI=hand-wing index.

Dispersal-related traits	Predictor	Pearson's $r$	Adj. $p$ -value
Maximum stem height	Soil total phosphorus	-0.183	$p < 0.01$
Average fruit length	Mean annual temperature	0.292	$p < 0.001$
	Median extant birds HWI	0.209	$p < 0.01$
	Precipitation of wettest month	0.137	$p < 0.01$
	Temperature seasonality	-0.258	$p < 0.001$
	Soil total nitrogen	-0.180	$p < 0.01$
	Present communities' frugivore richness	-0.177	$p < 0.001$
	Past communities' frugivore richness	-0.161	$p < 0.001$
	Soil total phosphorus	-0.128	$p < 0.01$
	Median extant mammals' home range	-0.119	$p < 0.01$
	Human population density	-0.106	$p < 0.01$
Average seed length	Mean annual temperature	0.284	$p < 0.001$
	Median extant birds HWI	0.181	$p < 0.01$
	Precipitation of wettest month	0.127	$p < 0.01$
	Temperature seasonality	-0.256	$p < 0.001$
	Soil total nitrogen	-0.164	$p < 0.01$
	Median extant mammals' home range	-0.136	$p < 0.01$
	Present communities' frugivore richness	-0.179	$p < 0.01$
	Past communities' frugivore richness	-0.175	$p < 0.001$



heights were also larger in places with low soil phosphorus. In relation to dispersal-related frugivore traits, fruit and seeds lengths were larger in places where mammal home ranges were smaller, but where the hand-wing index of birds was higher, and where total richness of past and extant frugivores was lower. Stem height did not show any significant correlation with frugivore traits (Table 2).

When only including highly frugivorous animals in the analysis, results were comparable to those presented above, but we found that larger fruit lengths coincided with highly frugivorous birds with a smaller hand-wing index, contrary to results including traits from all frugivorous birds (Supporting information).

## Discussion

The continued defaunation of large-bodied animals in Madagascar and many other parts of the globe affects important ecosystem dynamics such as seed dispersal of plants by animals. In this study, we assessed the effects of extant and extinct (mega-)frugivores and the abiotic environment on the beta-diversity and dispersal-related trait variation of a keystone tropical plant family – palms – in Madagascar (Fig. 1). In contrast to our expectation, we show that beta-diversity is only moderately explained by the past distribution of megafrugivores, whereas the distribution of extant frugivores, forest cover, slope, temperature and climatic water deficit, contribute much more to palm compositional variation in Madagascar (Fig. 2, Table 1). Fruit and seed size variation among species and assemblages was associated with multiple frugivore traits and richness, climate and soil variables (Table 2), suggesting that unique biotic and abiotic selective pressures and community assembly processes may have contributed to the distribution of large palm fruits and seeds in Madagascar.

### Extant frugivores as the strongest predictor of palm beta-diversity in Madagascar

Our results indicate that the distribution of extant frugivores is the strongest predictor of the variation in the composition of palms across Madagascar, and particularly so in the eastern part of the island (Fig. 2). Several of the most important frugivores (Table 1) that could explain this pattern are frequently observed to feed on palm fruits (*Eulemur macaco*: Donati et al. 2007; *Eulemur cinereiceps*: Ralainasolo et al. 2009, *Alectroneas madagascariensis*, *Eulemur fulvus* and *Cheirogaleus medius*: Bollen et al. 2004b). Both the high proportion of variation exclusively explained by extant frugivores and the observed frugivory interactions suggest that palm beta-diversity is predominantly the result of seed dispersal by animals, and not just the result of co-occurrences driven by abiotic and trophic niches. It is well recognized that ongoing habitat fragmentation, deforestation and hunting in Madagascar are threatening frugivore populations. Extant lemur populations have been massively reduced and have increasingly smaller range

sizes (Barrett and Ratsimbazafy 2009, Schwitzer et al. 2014). Although we did not detect a direct effect of human population density or human footprint on palm beta-diversity, the human impact may be indirect, via impacts on environmental drivers and frugivore distributions. Indeed, human footprint, which is a variable summarizing all human impact variables (Venter et al. 2016), was the strongest predictor of frugivore beta-diversity in Madagascar (see the results of a dbRDA in Supporting information).

### Abiotic determinants of palm species assemblage composition across Madagascar

We show that palm communities in Madagascar have also been shaped by the abiotic environment, especially by forest cover, slope, minimum temperature of the coldest month, solar radiation and climatic water deficit. Yet, most of the variation explained by the abiotic environment was shared with the frugivore distributions and spatial predictors, suggesting that marked, spatially autocorrelated environmental gradients across the island explain the joint distribution of palms and extant frugivores. For example, the steep environmental gradients that divide east and west co-vary with both palm and frugivore distributions. This climatic boundary provides a first filter for palm composition and turnover: the east is dominated by humid forest ecoregions (lowland humid forest and subhumid forests) and the west by arid open ecoregions (dry forest, succulent woodlands, savannas, spiny thickets). This explains why water-related factors (annual climatic water deficit) and forest cover became non-significant when analysing eastern assemblages alone. Some of the environmental effects on palm beta-diversity could be explained by palm richness differences driven by temperature and precipitation across Madagascar (Rakotoarinivo et al. 2013). Paleoclimate, which has been shown to have shaped mainland African palm distributions (Blach-Overgaard et al. 2013), could also explain some of the unexplained variation (up to 29%, Fig. 2) of palm beta-diversity in our analyses.

### Extinct megafrugivores and the composition of palms across assemblages in Madagascar

Extinct megafrugivore distributions explained a small but significant pure fraction of beta-diversity of palms in Madagascar (8%, Fig. 2). However, this result may have been mostly driven by western assemblages, where extinct megafrugivores came out as an important driver of palm beta-diversity (explaining 18% of the variation, albeit only a small pure fraction of 2%). Consistently with their historical distributions towards the west of Madagascar, this suggests that megafrugivores could have left their signature in palm community composition we see today in the dry west of the island. These megafrugivores may have typically occupied drier niches in more open habitats than their extant sister taxa nowadays (Crowley et al. 2011). Alternatively, the larger megafrugivore imprint in the west might still be visible due to less disturbance (e.g. human activity) and/or environmental change than in the east.

Other factors could also contribute to explain the faded imprint of megafrugivores in Madagascar. Besides potential biases in frugivore fossil data, palm species may have adapted to the extinction of megafrugivores by evolving smaller fruits, thereby erasing any potential effect of dispersal limitation by the extinction of past megafrugivores (Galetti et al. 2013, Onstein et al. 2018). Alternatively, palm species may have responded to the extinction of potential past interaction partners by readjusting their distributions. Unfortunately, there are not much data available of past distributions of palms in Madagascar due to their poor macrofossil record, thus limiting our understanding of the significance of past frugivores for seed dispersal of Malagasy palms. Nevertheless, fossil pollen of large-fruited *Hyphaene* and *Bismarckia* in the northwest (Lake Mitsinjo) in the Late Holocene (Matsumoto and Burney 1994), and *Dypsis* (probably *D. lutescens* and *D. saintelucei*) in the southeast (SM-matrix, Mandena, Virah-Sawmy et al. 2010), suggests that past palm distributions are consistent with the current range and may not have been entirely readjusted after the megafrugivore extinctions.

### Determinants of palm traits across assemblages in Madagascar

We show that low species richness of extant and past frugivore communities is associated with the distribution of palm species with relatively large fruits and seeds across Madagascar. Furthermore, we show that these large-fruited palms co-occur with small-ranged extant mammal communities. Both observations suggest that palm species with large fruits may be suffering from seed dispersal limitation – either because the available frugivores may not be able to disperse the fruits over long distances, or because they are simply not available. Nevertheless, although frugivore species richness is low, it is unclear whether abundance of extant frugivores is also lower in communities with relatively large palm fruits. Furthermore, several wide-ranging bird species with high dispersal ability (large hand-wing index, Sheard et al. 2020) co-occur with palm species with relatively large fruits and seeds. These birds (e.g. *Agapornis canus*, vasa parrots – *Coracopsis* spp., *Alectroenas madagascariensis*) may be important for the occasional long-distance dispersal of palms and other plants across Madagascar (Bollen et al. 2004a). Furthermore, some of these birds, such as parrots, have been shown to be effective dispersers of megafaunal palm fruits in other parts of the world (e.g. South America; Blanco et al. 2019). Finally, increased human population density, and its potential link to defaunation, was negatively associated with palm fruit length, suggesting that large-fruited species are rarer in proximity to human settlement, and possibly threatened by human impact.

Abiotic environmental variables were overall more important for explaining variation in palm dispersal-related traits than frugivores (Table 2). Higher temperatures, higher precipitation in the wet season and soils poor in nutrients were associated with larger fruits and stems. This result is

consistent with those found in continental Africa, where climatic factors played the most prominent role in explaining palm fruit sizes (Lim et al. 2020). Furthermore, temperature and precipitation, rather than the historical distributions of megafauna, explained the distribution of megafaunal fruits in southern Africa (Bunney et al. 2019). It should be noted that the association between frugivore and plant traits and their co-distributions may also be explained by plant or frugivore characteristics that we did not include in this study, such as fruit scent and colour or spinescence (Nevo et al. 2018, Nascimento et al. 2020, Onstein et al. 2020), or frugivore dispersal distance.

### The future of species with anachronistic fruits in Madagascar

Remarkably, the distribution ranges of some big-fruited palms in Madagascar, such as *Hyphaene coriacea* and *Bismarckia nobilis* are surprisingly large. How these ‘anachronistic’ species have managed to keep these large ranges is an open question. Possibly, abiotic dispersal mechanisms such as barochory or water-mediated dispersal (e.g. rain water run-off, streams, rivers) may compensate for the dispersal limitation caused by the extinction of megafrugivores in Malagasy plants (Devey et al. 2013, Buerki et al. 2015). This idea is supported by our results, since communities with higher precipitation of the wettest month (e.g. wet season in the west, which often leads to water run-off and small rivers in these otherwise dry, open landscapes), positively correlated with palm fruit size. Nevertheless, water-mediated seed dispersal and the potential for buoyancy of large Malagasy palm fruits has obtained little empirical evidence so far, with the exception of the fruits of a rare southern Malagasy palm, *Ravenea musicalis* (max 2.3 cm in length), which are known to float and even germinate underwater (Dransfield and Beentje 1995). Whether other Malagasy palm fruits are able to float, disperse and germinate after extensive time in water needs further investigation.

Alternative dispersers could also have taken up the dispersal role for large-fruited plants, such as small rodents, livestock or humans, as shown more prominently in the Neotropics (Guimarães et al. 2008, Blanco et al. 2019). In Madagascar, Razafindratsima (2017) found that rodents in the rainforest of Ranomafana had a limited role in secondary seed dispersal of *Abrahamia thouvenotii* (Anacardiaceae) and *Cryptocarya crassifolia* (Lauraceae), and our results also provide some evidence that the Betsileo short-tailed rat (*Brachyuromys betsileoensis*) and the voalavoanala (*Gymnuromys roberti*) are important for turnover of palm species across Malagasy communities (Table 1).

In summary, we show that the distribution of extant seed dispersers is the best predictor of palm compositional variation across Madagascar, and our study therefore provides important insights into the persistence of potentially anachronistic plant species, and the adjustment of geographical distributions of Malagasy plants, in response to past and ongoing environmental change.

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### Author contributions

**Laura Méndez:** Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (equal); Visualization (lead); Writing – original draft (lead). **Duarte S. Viana:** Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **Adriana Alzate:** Formal analysis (equal); Methodology (equal); Writing – review and editing (equal). **W. Daniel Kissling:** Conceptualization (equal); Writing – review and editing (equal). **Wolf L. Eiserhardt:** Conceptualization (equal); Writing – review and editing (equal). **Roberto Rozzi:** Data curation (equal); Writing – review and editing (equal). **Mijoro Rakotoarinivo:** Data curation (equal); Writing – review and editing (equal). **Renske E. Onstein:** Conceptualization (lead); Investigation (equal); Supervision (lead); Formal analysis (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (lead).

### Transparent Peer Review

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### Data availability statement

Supporting information for this study, palm species list and palm and frugivore traits with imputed data (Supporting Tables S1, S2, and S3) are openly available on Zenodo: <<https://doi.org/10.5281/zenodo.5844407>>. All the data used, including environmental, edaphic and human variables per assemblage, is openly available on the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.v41ns1rwr>>, and R scripts to conduct all the analyses are published at Zenodo: <<https://doi.org/10.5281/zenodo.5840921>>.

### Supporting information

Any supporting information associated with this article is available from the online version.

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