Supporting information for the research article:

"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"

Supporting methods

1   **Palm community compositional data**

2   To obtain community compositional data of palm species across Madagascar, we selected the areas in

3   Madagascar that have been intensively sampled for palms, thereby reducing the effect of false

4   absences. We plotted all palm occurrences from the Kew database and used the Biological Records tool

5   from the FSC Tools plugin (https://www.fscbiodiversity.uk/qgisplugin/biorecstool) in QGIS 3.10.8., and

6   created a grid with cells of 0.30 x 0.30 degrees (following a similar approach as was done in

7   Rakotoarinivo et al. 2013). Then, we selected cells with more than 20 palm records, resulting in 40 cells

8   (i.e., assemblages or sites, see Figure S1).

9   **Phylogenetic imputation of palm traits**

10 Because values for the maximum stem height, average fruit length and average fruit width were not

11 available for all the Malagasy palm species (5/190 species missing max stem height, 38/190 species

12 missing average fruit length and 39/190 species missing average fruit width) in the PalmTraits 1.0

13 database (Kissling et al. 2019), we explored phylogenetic data imputation with the R package

14 "Rphylopars" (Goolsby et al. 2017). This technique works best when maximizing number of species and

15 traits, and we thus initially used trait data for all 2557 palm species, and included 12 continuous traits

16   (maximum stem height, maximum stem diameter, maximum leaf number, maximum blade length,

17   maximum rachis length, maximum petiole length, average fruit length, minimum fruit length, maximum

18   fruit length, average fruit width, maximum fruit width, and minimum fruit width) from the PalmTraits

19   1.0 database (Kissling et al. 2019). Species with complete lack of trait data were removed - this included

20   five Malagasy species: *Dypsis lilacina, D. loucoubensis, D. pustulata*, *D. subacaulis* and *Ravenea*

21   *declivium*. The imputation analysis was performed with a set of 100 randomly sampled palm

22   phylogenetic trees from the constrained phylogeny based on the Govaerts et al. (2011) taxonomy

23   available from Faurby et al. (2016). The final species by trait matrix was calculated as the average trait

24   value per species across the 100 imputation matrices, extracting data for the 165 palm species occurring

25   in the 40 assemblages (Table S1).

26   Seed length and seed width data were not available from the PalmTraits 1.0 database, and we

27   therefore extracted these from data provided by Albert-Daviaud et al. (2020). Phylogenetic data

28   imputation was not possible since this provided data for 104 out of 2557 palm species only. For seed

29   size, we therefore focus our fourth-corner analysis on a subset of Malagasy species (those 104 species),

30   assuming that they represent a random subset of seed sizes across Malagasy palms.

31   **Frugivore diet and dispersal-related trait data**

32   Data on extant frugivore body mass, as a proxy for body size, was extracted from Galán-Acedo et al.

33   (2019) for lemurs, Razafindratsima et al. (2018) for bats and rodents, and Sheard et al. (2020) for birds.

34   We selected frugivorous reptiles as listed by Ganzhorn et al. (1999) and gathered body mass data from

35   (Walker et al. 2008, Berg et al. 2017). For extinct megafrugivores, body masses were taken from data by

36   Jungers et al. (2008) for lemurs, and Hansford and Turvey (2018) for elephant birds, in which body

37   masses were inferred based on bone measurements. Frugivory index (i.e., the percentage of fruits in a

38   diet) for extant species was collected from Wilman et al. (2014). For those species with missing data on

39   frugivory index, we approximated it with data from Gainsbury et al. (2018), or assuming consistency of

40   frugivory index within the genus (15 species out of 93 frugivore species, Table S2). Home range data for

41   extant mammals (available for a total of 41/70 mammal species) was extracted from Galán-Acedo et al.

42   (2019) for extant lemurs and for the remaining of extant mammals from Razafindratsima et al. (2018).

43   Hand-wing index of extant birds (HWI; available for 21/22 bird species) was gathered from Sheard et al.

44   (2020). A list of all the frugivores and their traits is provided in Table S2.

45   **Historical distribution ranges of extinct megafrugivores**

46   To reconstruct the historical geographic ranges of extinct megafrugivores in Madagascar, we used a

47   database curated by R.R., with all mammal fossil records from Madagascar, and a modelling algorithm

48   based on co-occurrence records of species across fossil sites (see below for details). Fossil records from

49   elephant birds (4 species) were collected from Hansford and Turvey (2018) and added to the mammal

50   database. Because we are interested in the geographical distribution of extinct giant lemurs and

51   elephant birds, we focused our modelling on co-occurrences of these megafrugivores with other

52   mammalian/avian fossil species with similar ecologies. Thus, from this database, small mammals

53   (rodents, tenrecs) and flying mammals (bats) were excluded because these are not representative to

54   estimate range size of past megafrugivores. *Mesopropithecus dolichobrachion* only had one fossil record

55   in our database, therefore, we decided that modelling its historical distribution would be too unreliable

56   and we deleted this species from further analyses. The final database used to reconstruct the historical

57   distribution of the 13 extinct megafrugivores included in this study, contained a total of 307 fossil

58   records, with 4 orders, 11 families and 55 species (Table S3).

59   To reconstruct the ranges of the nine fruit-eating extinct lemurs and the four elephant birds, we

60   used MInOSSE (Carotenuto et al. 2020), a model-based method that combines a machine learning

61   algorithm and geostatistical approaches, to reconstruct the past ranges of the extinct lemurs and

62   elephant birds, by relying on the distribution of other coeval species (species that are found in the same

63   fossil site) and thus without relying on abiotic environmental predictors. The first step for MInOSSE is to

64   select the species that will be used as predictors to reconstruct the target species historical ranges. For

65   this we used function *minosse.data.* To choose the predictors for each target species, the function uses

66   different strategies. The default is to use a cooccurrence analysis, but when the cooccurrence analysis

67   finds less than 4 predictors, all 55 species are considered. Therefore, in cases where the co-occurrence

68   analysis gave less than 4 predictors (species), we had to use another strategy for predictor reduction.

69   We used the correlation strategy (reduce_covs_by = "corr", covs_th = 0.3) which discards predictors

70   below 0.7 correlation value. We used the maps created with the threshold "MeanProb" which is

71   equivalent to the mean probability of occurrence yielded by the model (see Figure S2 for examples).

72   These maps were then used to extract presence/absence data for each megafrugivore in the 40

73   assemblages in Madagascar.

74   **Palm beta-diversity and trait variation: sensitivity analyses when including frugivores with 80% of**

75   **fruits in their diet (according to Albert-Daviaud et al. 2018).**

76   Since highly frugivorous animals are expected to potentially affect palm composition more strongly so

77   than less frugivorous animals, we repeated all analyses including only frugivores with more than 80% of

78   fruits in their diet, as listed in Albert-Daviaud et al. (2018). From the 28 highly-frugivorous species (20

79   lemurs, three bats and five birds), two lemurs (*Eulemur flavifrons* and *Lemur catta*) did not appear in any

80   of the 40 sites. Also, two bird species (*Hypsipetes madagascariensis* and *Philepitta schlegeli*) appeared in

81   every site and were therefore removed from the distance-based redundancy analysis (dbRDA) and

82   partition of the variation analyses, but were kept for the fourth-corner analysis as their presence may

83   still affect community-median frugivore trait values.

84   dbRDA and partition of the variation. Results were similar as those in the main text, showing that

85   (highly-frugivorous) extant frugivores explained most variation in palm composition, followed by the

86   abiotic environment, the spatial predictors and the extinct megafrugivores. Compared to the main

87   analysis including all frugivores, there were slight differences in the extant frugivores identified to be

88   important for palm beta diversity as inferred by the forward selection approach (*Eulemur rufifrons,*

89   *Eulemur rubriventer, Eulemur macaco, Cheirogaleus medius, Eulemur cinereiceps, Eulemur collaris,*

90   *Eidolon dupreanum, Eulemur albifrons* and *Alectroenas madagascariensis*). Furthermore, the total

91   explained variation by only the extant frugivores (Adj.R^2=0.505, Table S6) and the total explained

92   variation of the model (60%, Fig. S6), was lower compared with the analysis including all frugivores

93   (weighted by thei 'frugivory index', see main text).

94   <u>Fourth-corner analysis</u>. Based on our subset of only highly frugivorous species, we calculated

95   community median body masses for extant only communities (26 species) and past communities (38

96   species), median hand-wing index for extant birds (five species) and median home range of extant

97   mammal species (20 species), to be included in the fourth-corner analysis (together with the eight

98   environmental variables) to assess their relationship with palm dispersal-related trait distributions in

99   Madagascar. Results were slightly different from the analysis including all frugivores (see main text),

100   because effects of past and present frugivore richness and mammal home range size were not

101   significantly affecting any of the traits. Similarly, none of the frugivore traits explained variation in

102   maximum stem heights or seed lengths and widths. Furthermore, we found that larger fruits, specifically

103   fruit length, were found in places where highly frugivorous birds with smaller (rather than larger) hand-

104   wing indices were found (fruit length: Pearson's r= -0.165, P<0.01, fruit width: Pearson's r= -0.126,

105   P<0.05). This suggests that large fruits may benefit from dispersal by less frugivorous (e.g. omnivorous),

106   highly dispersive bird species (as discussed in the main text), but that dispersal limitation by highly

107   frugivorous birds (that depend for >80% on fruits) may still play a role for those larger fruits as well.

108   These results emphasize the importance of omnivores that may only occasionally feed on fruits for the

109   distribution of frugivory-related palm traits across Madagascar.

110   **Palm beta-diversity: sensitivity analysis considering all frugivores as important dispersers**

111   <mark>Since non-specialist frugivores (i.e., omnivores) have been shown to be important seed disperser in e.g</mark>

112   <mark>temperate regions (Dalsgaard et al. 2017)</mark>, we also carried out a sensitivity analysis where the presence

113   absence data of all extant frugivores was not weighted by their frugivory-index, and therefore had

114   presence as ones and absence as zeros.

115   Interestingly, when carrying out the analysis without weighting the presence absence data by

116   the frugivory-index of each frugivore, a similar group of frugivores were found as important predictors

117   of palm composition in Madagascar as when the data was weighted by the frugivory-index. Specifically,

118   we found one difference: instead of the bird *Coua coquereli* we found that *Copsychus albospecularis*,

119   another bird, became a significant predictor of palm beta diversity in Madagascar (in the analysis

120   including all 40 assemblages) (Table S7). For the eastern assemblages, the exact same 11 extant

121   frugivores were recovered (Table 2). For the western assemblages, the global model was not significant,

122   consistent with the analysis presented in the main text, and therefore extant frugivores where not

123   further included here. Results from the variation partitioning where exactly the same as the ones

124   presented in the main text (Figure 2).

125   **Testing direct effects of environment and human impact over frugivore beta-diversity**

126   To test whether environment and human impact variables are also affecting frugivore distributions

127   across Madagascar, and may therefore indirectly affect palms via their effects on frugivores (see

128   discussion in the main text), we implemented a similar approach as the one we used to disentangle the

129   drivers of palm beta-diversity in Madagascar. We therefore used distance-based redundancy analysis

130   (dbRDA) followed by partition of the variation in the same way as explained in the main text, but this

131   time the response variable is the beta-diversity of frugivores across the 40 sites, and we have only two

132   groups of predictor variables: the 12 environmental predictors used for palms, which also include

133   human impact predictors (human footprint from 2009), and the spatial predictors. Both global

134   redundancy analysis models were significant, and after forward model selection, six environmental

135   variables and human footprint were inferred to significantly affect frugivore composition across

136   Madagascar (Table S8). The results show that the environment and human footprint variables together

137   explain a high pure fraction of the variation in frugivore compositional turnover (22%), but most of it

138   was shared with the spatial predictors (58%), that by themselves only explain 2% of the variation (Fig.

139   S4). Interestingly, 'human footprint' (from 2009) was the strongest determinant of frugivore beta-

140   diversity, emphasizing the prominent role of human impact on frugivore populations and species

141   turnover. Soil phosphorus and forest cover had additional strong effects (Table S8). The total explained

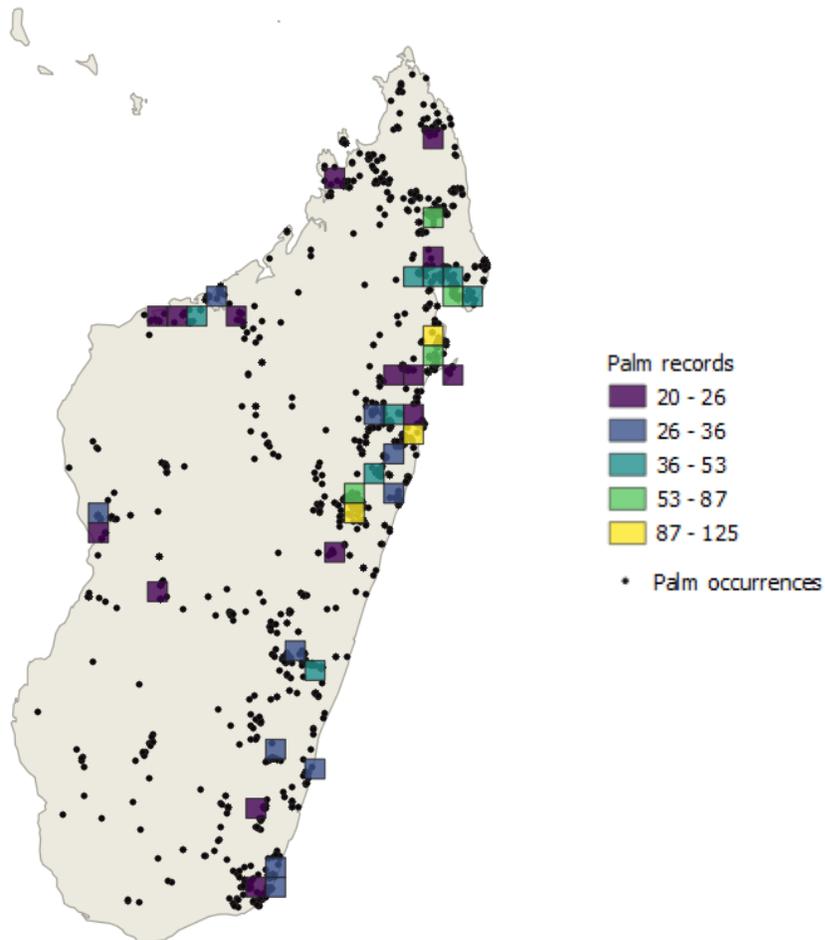142   variation in frugivore beta-diversity was very high, i.e. 82%.

Supporting Figures

Figure S1. Map of Madagascar showing all palm records included in the data base developed by the Royal Botanic Gardens, Kew (small dark dots). A grid of 0.30 x 0.30 degrees was laid on the coordinate records (all grids with less than 20 records were deleted) and it shows higher amount of records with brighter colors and less amount of records with darker colors. We used the 40 cells with at least 20 palm records to generate community-based data.
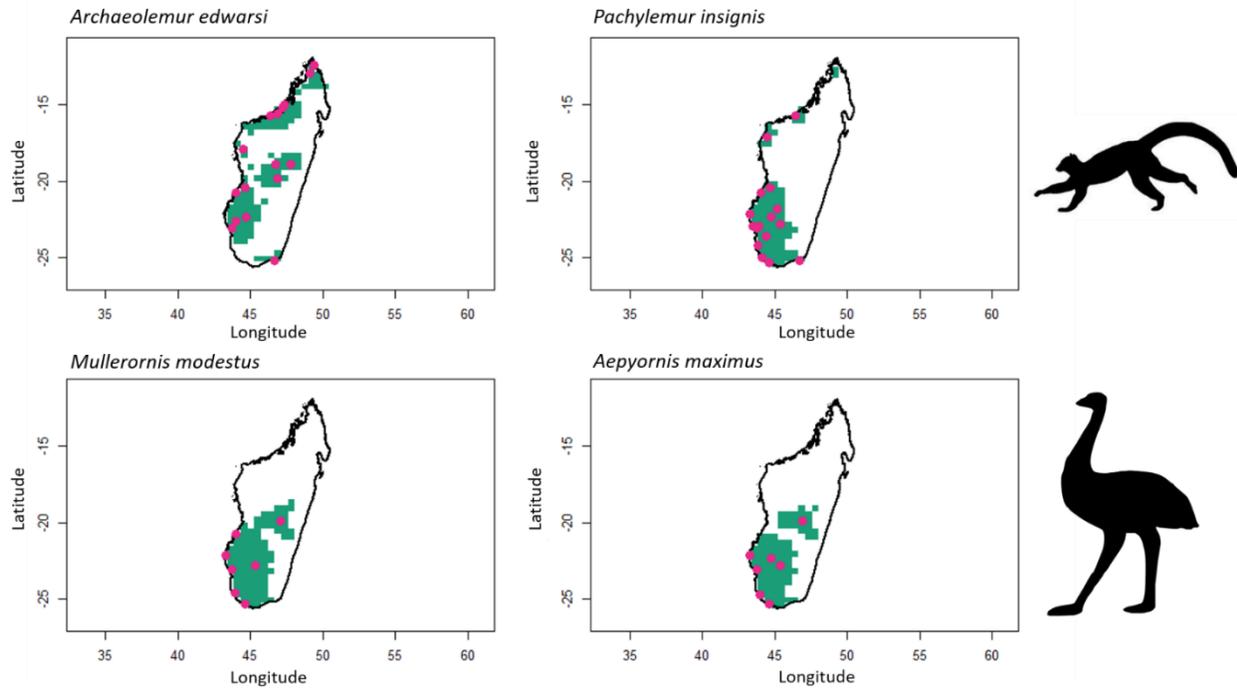
Figure S2. Example maps of the reconstructed distributions of extinct megafrugivores in Madagascar. In green is shown the reconstructed distributions of the extinct megafrugivores and the pink dots show the fossil sites in which fossils of those animals have been found. We show maps for two extinct giant lemurs (*Archaeolemur edwarsi* and *Pachylemur insignis*) and maps for two extinct elephant birds (*Mullerornis modestus* and *Aepyornis maximus*).
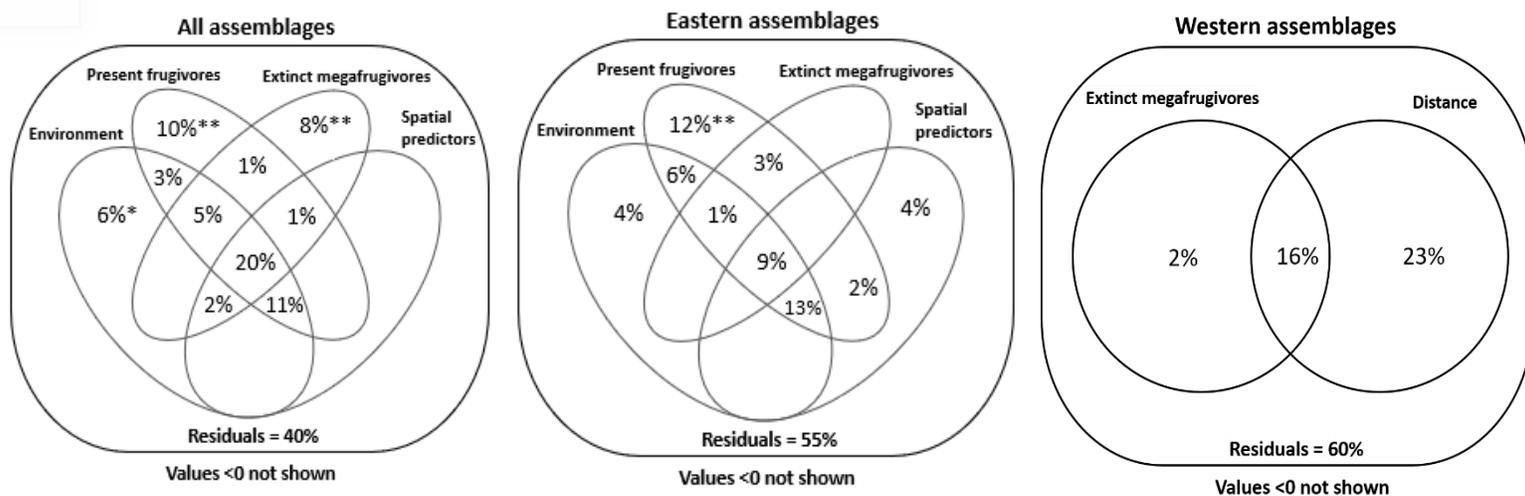
Figure S3. Variation partitioning from the sensitivity analysis including only frugivores with at least 80% of fruit in their diet, as listed by Albert-Daviaud et al. 2018. It shows the individual and shared effects of environment (abiotic/human impact) factors, frugivores and spatial predictors on palm 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 Table S5.

All assemblages

Environmental and human impact variables — Spatial predictors

22%* | 58% | 2%*

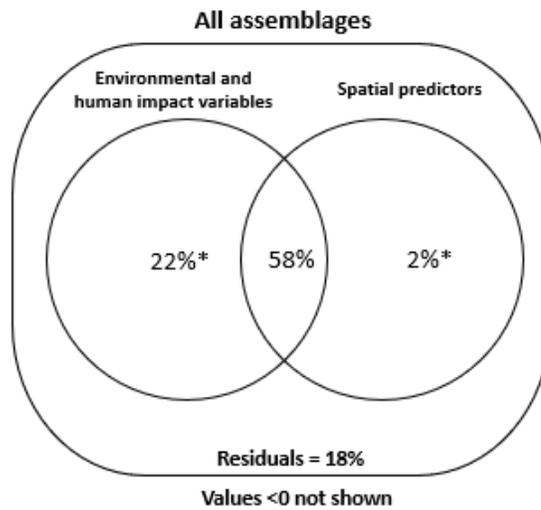Residuals = 18%

Values <0 not shown

Figure S4. Variation partitioning of the drivers of frugivore beta-diversity in Madagascar. It shows the individual and shared effects of environment (abiotic/human impact) factors and spatial predictors on frugivore beta-diversity across 40 assemblages. This was done for all assemblages (40 cells). The rectangular area represents all the variation explained in frugivore beta-diversity across assemblages, and the ovals or circles within that area represent the pure/exclusive effects of the two groups of explanatory variables (abiotic environment/human impact 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 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 S5.

Supporting Tables

Supporting tables S1, S2 and S3 as publicly available data in Dryad Data Repository -

Table S4. Results from the dbRDA models for palm beta-diversity including all frugivores. It shows associated P-values (P) and adjusted R^2 (Adj. R^2) for each palm matrix, **a)** all 40 assemblages, **b)** the 29 eastern assemblages and **c)** the 11 western assemblages for each group of variables: abiotic environment/human impact, present frugivores, extinct megafrugivores and spatial predictors. Frugivores were weighted by their frugivory index (i.e., percentage of fruits in their diet).

a)

Global models for all 40 assemblages					
Environmental variables (12 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	12	8.472	3.287	0.001	0.449
Residual	27	5.798			
Present frugivores (93 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	38	14.140	2.871	0.03	2.263
Residual	1	0.129			
Extinct megafrugivores (12 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	10	6.858	2.683	0.001	0.328
Residual	29	7.411			
Spatial predictors (40 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	2	4.845	9.512	0.001	0.319
Residual	37	9.424			

b)

Global models for the 29 eastern assemblages					
Environmental variables (12 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	12	4.966	1.992	0.001	0.334
Residual	16	3.324			
Extant frugivores (52 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	27	8.161	2.344	0.033	1.496
Residual	1	0.129			
Extinct megafrugivores (10 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	8	3.120	1.509	0.002	0.145
Residual	20	5.169			
Spatial predictors (29 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	2	2.146	4.541	0.001	0.211
Residual	26	6.144			

c)

	Df	Variance	F	P	Adj. R²
Global models for the 11 western assemblages					
Environmental variables (12 variables) - Number of permutations: 999					
Model	10	2.947	-	-	-
Residual	0	0.000			
Extant frugivores (53 variables) - Number of permutations: 999					
Model	10	2.947	-	-	-
Residual	0	0.000			
Extinct megafrugivores (9 variables) - Number of permutations: 999					
Model	7	2.737	5.575	0.011	0.954
Residual	3	0.210			
Spatial predictors (11 variables) - Number of permutations: 999					
Model	2	1.424	3.737	0.007	0.391
Residual	8	1.524			

Table S5. Variation partitioning of palm beta-diversity when including all frugivores and individual models for each pure fraction. Results show the contribution of each group of significant variables (abiotic environmental/human impact variables, present frugivores, extinct megafrugivores and geographical distance), to the total variation of palm beta-diversity across sites on Madagascar and their shared effects for each palm matrix, **a)** all assemblages, **c)** eastern assemblages and **e)** western assemblages. Depending if the global dbRDA model was significant, there are different groups of statistically significant variables per palm matrix. Therefore with four explanatory groups of statistically significant variables (all assemblages, eastern assemblages), the fractions explained uniquely by each of the four groups of significant variables are [a] to [d], joint fractions between two groups of significant variables are [e] to [j], joint fractions between three groups of variables are [k] to [n], and the joint fraction between all four groups of variables is [o]. With two groups of statistically significant variables (western assemblages), the fractions explained uniquely by each of the two tables are [a] and [c], and their joint effect is [b] following Borcard et al. (1992). Figures are provided to help reading the tables. After every variation partitioning analysis, we show the results of the pure fractions of each model and its associated P-values (P) and adjusted R^2 (Adj. R^2) for each palm matrix: **b)** all assemblages, **d)** eastern assemblages and **f)** western assemblages. A summary figure of these results is provided in the main text as Fig. 2, and specific significant variables are shown in Table 2.
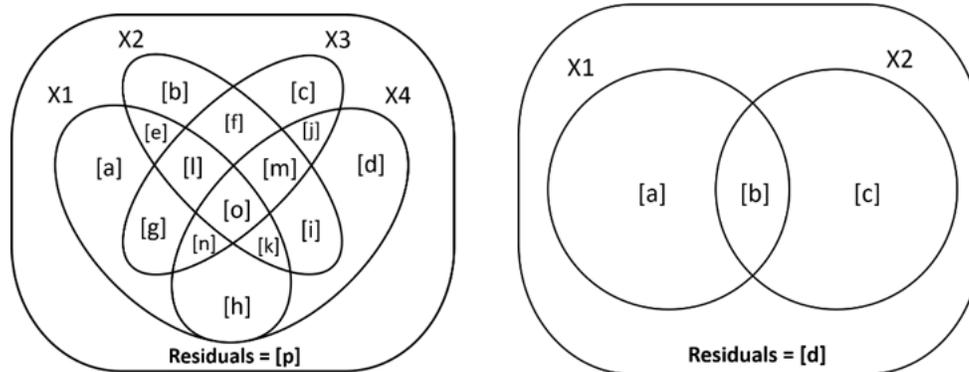
a)

Variation partitioning for all 40 assemblages	
Component	**Adjusted R²**
[aeghklno] = X1 – Environmental variables	0.420
[befiklmo] = X2 – Present frugivores	0.607
[cfgjlmno] = X3 – Extinct megafrugivores	0.305
[dhijkmno] = X4 – Distance	0.318
[abefghiklmno] = X1+X2	0.644
[acefghjklmno] = X1+X3	0.498
[adeghijklmno] = X1+X4	0.413
[bcefgijklmno] = X2+X3	0.626
[bdefhijklmno] = X2+X4	0.594
[cdfghijklmno] = X3+X4	0.413
[abcefghijklmno] = X1+X2+X3	0.698
[abdefghijklmno] = X1+X2+X4	0.637
[acdefghijklmno] = X1+X3+X4	0.496
[bcdefghijklmno] = X2+X3+X4	0.650
[abcdefghijklmno] = All	0.713
Individual fractions	
[a] = X1 | X2+X3+X4	0.063
[b] = X2 | X1+X3+X4	0.216
[c] = X3 | X1+X2+X4	0.075
[d] = X4 | X1+X2+X3	0.014
[e]	0.020
[f]	0.007
[g]	-0.020
[h]	-0.009
[i]	-0.016
[j]	-0.021
[k]	0.101
[l]	0.031
[m]	0.016
[n]	-0.016
[o]	0.232
[p] = Residuals	0.287

b)

Individual models for all the 40 assemblages (after forward selection)					
Purely environmental (6 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	6	1.026	1.427	0.051	0.131
Residual	9	1.078			
Purely extant frugivores (14 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	14	3.363	2.004	0.001	0.319
Residual	9	1.079			
Purely extinct megafrugivores (8 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	8	1.424	1.485	0.021	0.163
Residual	9	1.079			
Geographic distance (40 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	2	0.272	1.136	0.344	-
Residual	9	1.079			

c)

Variation partitioning for the 29 eastern assemblages	
Component	**Adjusted R^2**
[aeghklno] = X1 – Environmental variables	0.276
[befiklmo] = X2 – Present frugivores	0.487
[cfgjlmno] = X3 – Extinct megafrugivores	0.126
[dhijkmno] = X4 – Distance	0.211
[abefghiklmno] = X1+X2	0.519
[acefghjklmno] = X1+X3	0.309
[adeghijklmno] = X1+X4	0.292
[bcefgijklmno] = X2+X3	0.489
[bdefhijklmno] = X2+X4	0.492
[cdfghijklmno] = X3+X4	0.250
[abcefghijklmno] = X1+X2+X3	0.519
[abdefghijklmno] = X1+X2+X4	0.516
[acdefghijklmno] = X1+X3+X4	0.326
[bcdefghijklmno] = X2+X3+X4	0.502
[abcdefghijklmno] = All	0.519
Individual fractions	
[a] = X1 | X2+X3+X4	0.016
[b] = X2 | X1+X3+X4	0.193
[c] = X3 | X1+X2+X4	0.003
[d] = X4 | X1+X2+X3	-0.001
[e]	0.060
[f]	0.031
[g]	0.007
[h]	0.014
[i]	0.017
[j]	-0.002
[k]	0.092
[l]	-0.002
[m]	0.001
[n]	-0.006
[o]	0.095
[p] = Residuals	0.481

d)

Individual models for the 29 eastern assemblages (after forward selection)					
Purely environmental (6 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	4	0.663	1.094	0.334	-
Residual	10	1.515			
Purely extant frugivores (11 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	10	2.555	1.686	0.001	0.229
Residual	10	1.515			
Purely extinct megafrugivores (2 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	1	0.159	1.049	0.414	-
Residual	10	1.515			
Geographic distance (29 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	2	0.297	0.981	0.472	-
Residual	10	1.515			

e)

Variation partitioning for the 11 western assemblages	
Component	**Adjusted R^2**
[ab] = X1 – Extinct megafrugivores	0.174
[bc] = X2 – Distance	0.386
[abc] = X1+X2	0.403
Individual fractions	
[a]	0.017
[b]	0.157
[c] = X2 | X1	0.229
[d] = Residuals	0.596

f)

Individual models for the 11 western assemblages (after forward selection)					
Purely extinct megafrugivores (1 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	1	0.208	1.109	0.349	-
Residual	7	1.315			
Geographic distance (29 variables) - Number of permutations: 999					
	Df	Variance	F	*P*	Adj. R^2
Model	2	0.297	0.981	0.070	-
Residual	7	1.515			

Table S6. Results from the sensitivity analysis dbRDA and forward model selection, only including frugivores with more than 80% of fruits in their diets. Only statistically significant variables (at P < 0.05) are shown, for each palm presence-absence matrix (all, eastern and western assemblages). R2.adj is the R^2 adjusted for the number of predictors in the model. **P<0.001; *P< 0.01

Palm sites matrix	Selected variables	R2.adj
All assemblages	*Cheirogaleus major*	0.622*
	Brachyuromys betsileoensis	0.608*
	Microcebus jollyae	0.591*
	Neodrepanis coruscans	0.576**
	Eidolon dupreanum	0.560**
	Eulemur cinereiceps	0.537**
	Gymnuromys roberti	0.517**
	Propithecus diadema	0.494**
	Cheirogaleus medius	0.470*
	Eulemur collaris	0.444**
	Copsychus albospecularis	0.416**
	Cheirogaleus crossleyi	0.385**
	Eulemur albifrons	0.333**
	Alectroenas madagascariensis	0.260**
Eastern assemblages	*Neodrepanis coruscans*	0.497*
	Eliurus webbi	0.467*
	Fossa fossana	0.441*
	Microcebus murinus	0.410**
	Eulemur rubriventer	0.375**
	Avahi ramanantsoavanai	0.337**
	Avahi meridionalis	0.303**
	Eidolon dupreanum	0.272**
	Propithecus diadema	0.240**
	Cheirogaleus crossleyi	0.201**
	Eulemur albifrons	0.116**
Western assemblages	dbRDA model not significant	

Table S7. Results from the sensitivity analysis dbRDA and forward model selection, over the unweighted presence-absence matrix by the frugivory index, and therefore including all extant frugivores as important seed dispersers. There is only one different predictor from the results shown in the main text: the bird *Copsychus albospecularis.* Only statistically significant variables (at P < 0.05) are shown, for each palm presence-absence matrix (all, eastern and western assemblages). R2.adj is the R^2 adjusted for the number of predictors in the model. **P<0.001; *P< 0.01

Palm sites matrix	Selected variables	R2.adj
All assemblages	*Eulemur rufifrons*	0.515*
	Eulemur rubriventer	0.497**
	Eulemur macaco	0.473**
	Cheirogaleus medius	0.450**
	Eulemur cinereiceps	0.424**
	Eulemur collaris	0.398**
	Eidolon dupreanum	0.366**
	Eulemur albifrons	0.333**
	Alectroenas madagascariensis	0.260**
Eastern-assemblages	*Cheirogaleus major*	0.409*
	Pteropus rufus	0.378*
	Microcebus murinus	0.356*
	Eulemur cinereiceps	0.326*
	Eulemur collaris	0.294*
	Eulemur rubriventer	0.265**
	Eulemur fulvus	0.237**
	Eidolon dupreanum	0.181**
	Eulemur albifrons	0.116**
Western assemblages	dbRDA model not significant	

Table S8. The determinants of palm (Arecaceae) fruit width and seed width across 40 assemblages in Madagascar, including traits from all frugivores. Results for maximum stem height, fruit length and seed length are shown in the main text, Table 2. Fourth-corner analysis results when including all frugivore dispersal-related traits, showing only significant correlations (at P < 0.05) between palm traits and the different predictor variables are shown. Pearson's r indicates the correlation value, Adj. P-value is the P value adjusted for multiple testing.

Predictor	Pearson's r	Adj. P-value
Average fruit width		
Mean annual temperature	0.218	P < 0.01
Community median extant birds' hand-wing index	0.155	P < 0.01
Precipitation of wettest month	0.102	P < 0.01
Temperature seasonality	-0.199	P < 0.01
Soil total phosphorus	-0.118	P < 0.01
Human population density	-0.095	P < 0.01
Average seed width		
Mean annual temperature	0.240	P < 0.001
Precipitation of wettest month	0.104	P < 0.01
Temperature seasonality	-0.217	P < 0.01

Table S9. Determinants of frugivore beta-diversity across Madagascar resulting from the dbRDA and forward selection analyses. Only statistically significant variables (at P < 0.05) are shown. R2.adj is the R^2 adjusted for the number of predictors in the model. **P<0.001; *P< 0.01

Selected variables by forward model selection	R2.adj
Human footprint 2009	0.554**
Soil Total Phosphorus	0.534**
Percentage of forest 2010	0.514**
Solar radiation	0.492**
Minimum temperature of the coldest month	0.440**
Soil Clay	0.395**
Climatic water deficit	0.343**

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