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RESEARCH ARTICLE

# Seed Dispersal Anachronisms: Rethinking the Fruits Megafauna Ate

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## Figures



Order	Family
1	Malvaceae
2	Burseraceae
3	Leguminosae
4	Simarubaceae
5	Umbelliferae
6	Convolvulaceae
7	Passifloraceae
8	Convolvulaceae
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49	Convolvulaceae
50	Convolvulaceae

# Abstract

## Background

Some neotropical, fleshy-fruited plants have fruits structurally similar to fruits dispersed by megafauna (mammals >10<sup>3</sup> kg), yet these dispersed by megafauna in South America 10–15 Kyr BP. Anachronistic dispersal systems are best explained by interactions with extinct animals and show impaired dispersal results and dispersal dynamics.

## Methodology/Principal Findings

We introduce an operational definition of megafaunal fruits and perform a principal component analysis of 103 Neotropical fruit species fitting this dispersal mode. We identify two megafaunal fruit types based on previous analyses of elephant fruits: megafaunal fruits with diameter with up to five large seeds, and fruits >10 cm diameter with many small seeds. Megafaunal fruits are well represented in unrelated families (Fabaceae, Solanaceae, Apocynaceae, Malvaceae, Caryocaraceae, etc.) and combine an overbuilt design (large fruit mass and size) with either a few extremely large seeds or many small seeds (usually >100 seeds). Within-genus contrasts between megafaunal and non-megafaunal fruits indicate a marked difference in fruit diameter and fruit mass but less difference in seed mass, with a significant trend for megafaunal fruits to have larger seeds.

## Conclusions/Significance

Megafaunal fruits allow plants to circumvent the trade-off between seed mass and dispersal by relying on frugivores able to disperse enormous seed masses over long distances. Present-day seed dispersal by scatter-hoarding rodents, wind, runoff, flooding, gravity, and human-mediated dispersal allowed some dependent fruit species after extinction of the major seed dispersers. Extinction had several potential consequences, such as a scale shift in dispersal distances, increasingly clumped spatial patterns, reduced genetic diversity, and limited genetic variation and increased among-population structure. These findings could be extended to other plant species dispersed by large vertebrates in defaunated communities.

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## Introduction

The strong evidence that positive density-dependent mortality occurs in both juvenile and adult plants in several different species suggests that this process in plant communities [1], [2]. Fruit traits certainly play a key role in interactions with seed dispersers, affecting the seed dispersal efficiency and negative consequences for plant populations can be expected if this process is absent or impaired (e.g., [4], [5]). Yet, a large fraction of extant species show trait combinations that largely reflect their history of shared adaptations to present-day seed dispersers. In analogy with “ghosts of past mutualisms”, some combinations of fruit traits that can be found in extant species are “ghosts of past mutualisms” [7], [8].

Many ecological studies have identified diverse interactions with different communities, usually ranging from a few to tens of species, on the fruit of a given plant species [9], [10]. Even after recognizing that the interaction can operate on expected traits [11] of fruits, its outcomes and effects on the demography, regeneration and gene flow patterns can be complex. Consequently, some structural patterns in fruits may be associated with assemblages of seed dispersers [12]. In this context, the paradoxical combination of apparent adaptations for the dispersal by some groups of animals that are now extinct, is an interesting topic with deep connections with evolution, ecology and conservation of plant diversity. In fact, the loss of seed dispersers is still ongoing, and current defaunation scenarios have been shown to have serious consequences for plant populations [13]–[16].

Janzen and Martin [7] defined seed dispersal anachronisms as those syndromes with fruit traits and phenological patterns best explained by extinct animals and offered some striking examples of Neotropical species (see also [8], [17]). These “unfit” species share fruit traits and phenological patterns that are at least in part not expected from their interactions with the current seed disperser community, but logically explained if we consider the extinction or loss of their main frugivores. One of the seed dispersal anachronisms, the so-called

syndrome, includes fruits that were likely to be dispersed by now extant megafauna and has been the subject of considerable debate stemming from a lack of precise predictions and definitions [18]–[22]. There is a general consensus of the idea yet, “the ecological and evolutionary assumptions which underlie the megafaunal syndrome need rethinking” so that “an edifying refinement of the turmoil” [18, p. 860]. In this paper we revisit Janzen and Martin’s hypothesis of the traits of megafaunal fruits in a comparative study. We expand their rigorous characterization of the megafaunal syndrome and examine its life-history correlates. Rather than simply redefining it, we aim at identifying conditions under which the hypothesis can be supported, outlining the reasons that it has persisted after loss of frugivores, and discussing the potential demographic and genetic consequences of the megafaunal syndrome.

Janzen and Martin [7] examined the hypothesis that frugivory by large mammals like native horses, gomphotheres, ground sloths, and other Pleistocene megafauna offers an explanation to dispersal-related plant reproductive traits in neotropical lowland forests. In their definition, key traits of megafaunal fruits include: 1) fruit design, with large seeds protected mechanically by thick and hard pericarps and indehiscence, with nutrient-rich pulp and external similarity to fruits dispersed by African mammals; 2) phenological segregation of ripening times through seasonal fruits falling to the ground upon ripening; 3) fruits unattractive or not consumed by arboreal or flying frugivores; 4) a large proportion of the fruit crop rarely being consumed; 5) frugivores include a large coterie of seed predators that consume sporadically as legitimate dispersers; 6) fallen fruits are avidly eaten by extant mammals like horses, pigs, and cattle; and 7) natural habitats of the plant species are forest bottoms on gentle slopes, usually along forest edges with grasslands. The hypothesis of Janzen and Martin [7] was applied to Costa Rican vertebrate species, but subsequent work has suggested that anachronistic dispersal may occur worldwide [see e.g. 8], [22]–[24] and, specifically, megafaunal fruits on different continents [12], [20], [25]–[29]. Janzen and Martin’s idea [7] has been revisited with later analysis [18] and is implicitly assumed in the idea [24] that the Pleistocene extinct megafauna [30], [31] had a central role in the dispersal of angiosperm seeds. On the other hand, many of the species included in the megafauna [7] have been reported to be dispersed by extant frugivores or abiotically (e.g., runoff) [32]. For example, while extremely limited dispersal can be observed for a few species with megafaunal fruits (e.g., *Hymenaea courbaril*), it is well documented dispersal by gravity, water, scatter-hoarding rodents, monkeys, birds or favored by human harvesting. It is important to note that while all the megafaunal fruit species included in our analyses lost *all* their primary dispersers at the megafauna extinction. It is clear that functional dispersal for many species still operates in present-day neotropical communities by means of diverse alternative seed dispersal systems involving other agents such as rodents, tapirs, some primates and even bats [33]–[35]. However, the loss of dispersal by extremely large mammals may imply marked shifts in the consequences of seed dispersal for these plant species. The point ecology of megafaunal fruits can be understood without considering the extinction of their primary dispersers and the dramatic changes in the landscape unfolded by this loss of mutualists. Therefore, we recognize that ma

actually have some legitimate seed dispersers, but we are interested in the extinction of their larger seed dispersers.

Certainly, the post-Pleistocene defaunation of neotropical megafauna. By the end of Pleistocene, the South American fauna had at least 70 mammals from distinct orders with body mass  $\geq 1000$  kg [36], yet no extant megafauna. However, the megafauna is still extant in Africa with 5 genera (*Ceratopithecus*, *Giraffa*, *Hippopotamus*, and *Loxodonta*) and in Asia with 2 genera (*Elephas* and *Rhinoceros*). There is strong evidence that the extinct megafauna from the Pleistocene of South America included fruits in their diet or had mixed diets characteristic of extant elephants, as revealed by isotopic analysis of enamel and bone [37]. Animal-dispersed fruits have been postulated to be bigger in the Palearctic than in the Neotropical [42], but this implies that the extinct megafauna in South America was at least as diverse as the extant megafauna until the end of the Pleistocene [38], [43]. Thus, a proper comparison of fruit species in these areas should include megafauna-related taxa.

In this paper we address the megafaunal syndrome hypothesis by providing a definition and quantification of fruit traits of putative megafauna species in plant communities, comparing them to extant and related species in the same communities, and examining the ecological correlates of the syndrome. Our goal is to operationalize the concept of the megafaunal syndrome, collect evidence on the ecological patterns associated with megafaunal fruits, and hypothesize the consequences for the biology of the set of species involved in this plant-animal interaction. We aim at formulating testable predictions about the potential consequences of the loss of megafauna dispersers assuming that they were important to the evolution of the syndrome. Predictions are based on (1) a rigorous characterization of fruits that is based extensively on large extinct mammals for much of their dispersal architecture, (2) and ecological correlates across fruit species from different plant families. The questions we address are: 1) does the megafauna fruit syndrome exist as a distinct entity in natural communities? 2) what are the life-history and ecological correlates of the survival of megafauna plants in present-day habitats? 3) which potential ecological consequences can be predicted in the absence of the megafauna? and, finally 4) how did plants survive the extinction of their main seed dispersers?

## Definitions

In the subsequent sections we use the following operational definitions.

### Anachronisms.

These are extant interactions between animal frugivores and plant species that do not show strikingly unfit patterns to an extant fauna. Anachronisms are present-day dispersal systems that work on exapted traits [6], [44]. We emphasize them because exapted interactions typically have functional effects on present-day species having evolved out of this functional context. In anachronistic seed dispersal systems the functional role of fruit traits on present-day interactions with frugivores is reduced.

marginal, being replaced in part by abiotic factors (wind, gravity, wa determining secondary seed dispersal [19], [34]. Secondary seed c medium-sized scatter-hoarding rodents might have been fundame of megafaunal fruit species after extinction of their primary seed di [references therein](#)]. Furthermore, interaction with humans has bee extensive maintenance of these species over relatively large geog explored in previous discussions of anachronic dispersal systems. profound changes in seed dispersal patterns are likely to have occ

## Megafauna.

These are faunistic elements (taxa) of the frugivore communities in plant species that characteristically have a large (>1000 kg) body r are using here this restricted definition from Owen-Smith [45], [46] a broad advanced by Martin and Klein [36] (>44 kg) because of its bic America, megafauna include primarily the large terrestrial mammal: extinct xenarthrans, and extinct orders such as Notoungulata)[47]. of large megafauna was driven extinct by human hunting and clima ice age [48]–[51].

## Megafaunal fruits.

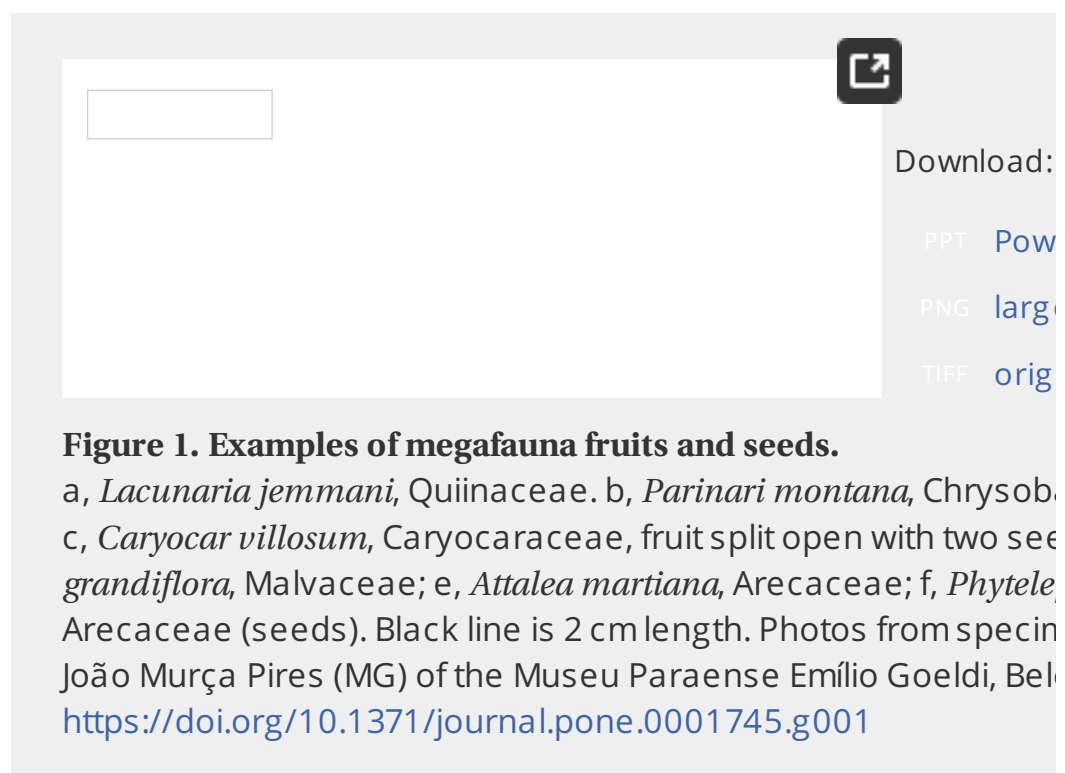
In order to compare megafaunal fruit characteristics with other fruit unambiguous criteria to characterize the syndrome. We used the c African elephant fruits [12], [27], [52]–[58; also see 25,59] and search our own data for Brazilian species that fit this criteria. These specie defined as megafaunal fruit species for subsequent analysis. Eleph considered a useful conceptual model for frugivorous megafauna ( ecomorphology, generalized diet, as well as the quality of the inform dietary habits. Indeed, paleontological evidence based on isotopic extremely similar dietary composition for, e.g., gomphotheres and e defined megafaunal fruits as two fruit types [27]; Type I includes fle: diameter with up to 5 large seeds (generally >2.0 cm diameter), and fruits >10 cm diameter with numerous (>100) small seeds. It is impo definition does not assure that megafaunal fruits will be the larger f community or clade. For example, some palms and Lecythidaceae s large fruits without fleshy pulp [33], [60] and therefore they are not typical rodent-dispersed, nutlike fruits. In addition, by using fruit trai consumption by Paleotropical extant megafauna, these criteria are species sampled so that they can be applied without circularity. Thi and Martin [7] original definition, which is too vague because it inclu fruits which actually have reliable, present-day, main dispersers [17] definition restricts the analysis to megafauna-dependent species a [8], [17], who acknowledges this broad gradient of reliance on meg, among higher plants' fruits. Barlow [8] has termed these fruits 'over likely, the extinct megafauna included a broad range of fruit types i also eaten by other smaller frugivores such as scatter-hoarding roo and birds. We focus here on megafauna-dependent fruit species, a gradient of reliance on megafauna for dispersal can probably be fc

species (moderate, substantial and extreme anachronisms, *sensu* [8]). For these species, the absence of their main seed dispersers from the frugivore communities represent dramatic consequences in terms of restricted dispersal, high mortality of fruits and seeds due to pathogen attack, or severely altered dispersal terms of limited dispersal distance or increased aggregation of the fruits. This narrowed definition is not only consistent with reports of elephant-dispersed fruits [58], [59], [61], but also with other present-day megafauna dispersed fruits [62]–[65]. Therefore, megafaunal fruits are “outlier” fruit species in frugivore communities [8], [17]. They are outliers because of functional lack of fit with present-day dispersal syndromes (suites of fruit traits associated with a particular group of vertebrate frugivores in the community). Here, we provide a morphological-basis for this functional lack of fit. However, we emphasize that lack of fit might be caused by differences in fruit structure, design, size, phenology, life form, microhabitat occupancy, biogeographic provenance, or any other trait that makes the species not particularly associated to a given environment or group of species.

## Results

### Characteristics of megafaunal fruits

We identified 103 megafaunal fruit species (Table 1) fitting our criteria among 1361 fruits out of 1361 sampled species (see Methods). Our definition all included extremely large fruits with many small seeds. However, even some megafaunal fruits have relatively large seeds (e.g., *Hymenaea*, *Theobroma* species, seeds/fruit, and individual seeds >10 g mass) (Fig. 1 and 2).



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**Figure 2. Fleshy fruited megafaunal-dependent species illustrating color variation.**

a, *Attalea speciosa*, Arecaceae; b, *Mouriri elliptica*, Melastomataceae; c, *Stigonocarpa*, Fabaceae; d, *Genipa americana*, Rubiaceae; e, *Salicaria*, Celastraceae; f, *Annona dioica*, Annonaceae. Black reference line. Photos from Fazenda Rio Negro, Pantanal, Brazil; by PJ, MG, and <https://doi.org/10.1371/journal.pone.0001745.g002>



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**Table 1. Relative representation of the megafauna syndrome from different families and summary of fruit trait variation among species.**

<https://doi.org/10.1371/journal.pone.0001745.t001>

Most megafaunal fruits with available data on characteristics (Table 1) are drupaceous (40.1% of the species), berry-like (29.9%) or legumes (12.9%). In all assemblages from different communities, the range of fruit colors is very restricted, predominantly brown, brown-red or brown-green (34.5%) or green-gray (34.5%) or green-yellow (12.9%) or different tones of yellow (21.5%) (Fig. 3; see Figs. 1 and 2). This contrasts markedly ( $\chi^2=408$ ,  $P<0.001$ ) with the distribution of fruit color frequency in different communities worldwide, which is predominantly black-purple or red (Fig. 3), except for New Zealand where blue and white colors are very common. The restricted color pattern is also observed when comparing local sites in south and southeastern Brazil; the combination of orange, brown and green colors in a lowland Atlantic forest site ( $N=174$  species), contrasting with 46% ( $N=54$ ) for Pantanal (Rio Negro) where megafaunal fruits are much more frequent. The relative frequencies of orange, brown and green are 24% and 5%, respectively. Other colors (e.g., yellow, black, and white) are represented in similar proportions. The differences in relative frequencies of fruit colors are highly significant ( $\chi^2=14.16$ ,  $P<0.003$ , d.f.=6).





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**Figure 3. Frequency of megafauna species with different fruit colors compared to the summed frequency in different communities (f**

The available data for Manu (Peru), Monteverde (Costa Rica), Florida, New Zealand [124], and Brazilian Myrtaceae [125] have been pooled to characterize the color distribution pattern in extant communities. <https://doi.org/10.1371/journal.pone.0001745.g003>

Megafaunal fruits are characteristically heavy (Table 1), varying in form from drupaceous designs and elongate legume-like forms up to 50–100 cm. This results in very high seed loads/fruit, with total seed(s) mass/fruit mass (Fig. 4a) ( $R^2=0.9221$ ,  $F=65.12$ ,  $P<0.0001$ , d.f.=2, 11); a trend also comparing intra-familial contrasts (Fig. 4a). The slope of the relation between seed load/fruit and fruit mass (Fig. 4a) does not depart significantly from zero, suggesting seed load is an isometric function of fruit mass for these species; they typically show a larger seed load/fruit relative to non-megafaunal species. The range of seeds/fruit ranges for megafaunal species between 0.2%–97.4% of fruit mass, while the comparable range for non-megafaunal species is 0.01%–1.1%. This is the simple result of increasing total fruit mass, not increasing seed load/fruit (Fig. 4a); thus, there are no differences between megafaunal and non-megafaunal species in seed(s) mass/fruit when accounting for variation in fruit mass ( $F=2.11$ ,  $P=0.17$ , d.f.=2, 11 for the *a posteriori* contrast with fruit mass as



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**Figure 4. Bivariate plots of fleshy fruit traits for megafauna and non-megafauna species.**

Dots, megafauna-fruit species; +, non-megafauna fruited species. (A) total seed(s) mass per fruit and fruit mass. Intrafamilial comparisons are indicated by connecting lines between dots and +s; (B) individual seed mass and total seed(s) mass per fruits.

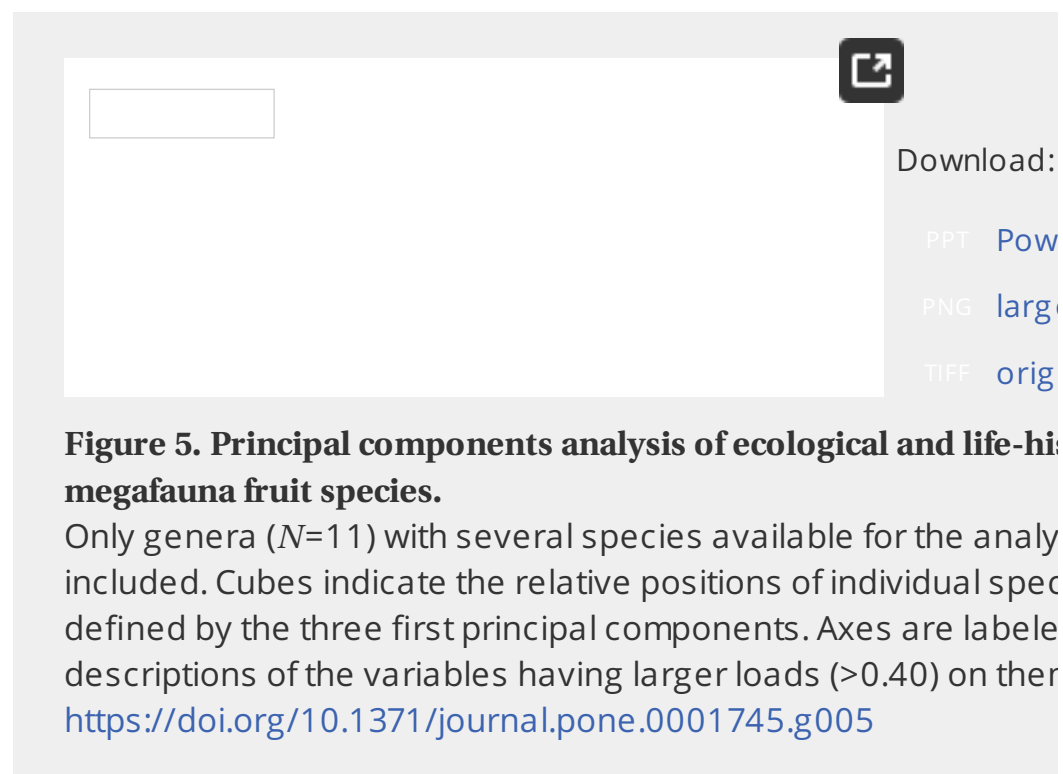
<https://doi.org/10.1371/journal.pone.0001745.g004>

There is also a similar trend in fruit design between megafaunal and non-megafaunal species when comparing the allocation of seed number/fruit and in

expected, a negative trend between both variables is evident in the with individual seed mass decreasing linearly with increasing fruit s  $P < 0.0001$ , d.f.=3, 87). Yet megafaunal species have significantly lar, controlling for variation in seediness ( $F = 8.36$ ,  $P = 0.0048$ , d.f.=1, 89 f slope between megafaunal and non-megafaunal species, Fig. 4b).

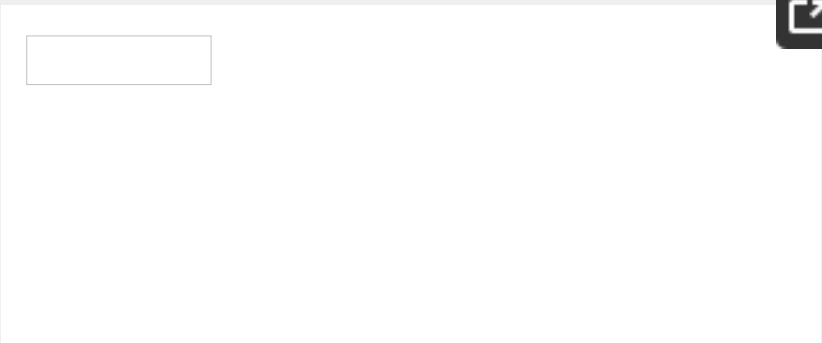
## Ecological and life-history correlates of the megafaunal seed dispersal

Megafaunal species span a wide range of ecological and life-history of their ecological and fruit traits (Fig. 5) revealed characteristic ass related to the taxonomic relatedness. Congeneric species cluster ordination. The PCA with the first three significant components acc total variance. The first component was associated to fruit type anc with increased human use related to multi-seeded fruits with great pulp/fruit (e.g., *Theobroma* spp.). A large group of species chiefly wit legume-like fruits clustered on the positive side (Fig. 5). PCA II was a distribution and geographic range, species with extensive geograp inhabiting cerrado or mixed forest vegetation having positive loads *Syagrus* spp.). Species with Amazonian distribution, associated to cl (e.g., some *Astrocaryum*, *Acrocomia*, *Dipteryx*, *Pouteria* and *Poraqueib on this component. PCA III was associated with fruit color and habit: multi-seeded fruits, chiefly legumes, and dull-colored, brownish pul it; species with bright fruit color, greenish-yellowish, and associated (e.g., some *Syagrus*), had negative loads on it.*



Associations among ecological variables and fruit traits across species randomization (Table 2). Use by humans was significantly correlated with seediness. Geographic range was also positively correlated with seed mass and negatively correlated with seed length (Table 2). All the remaining c

significant. Most, if not all, the megafaunal fruit species share a level ranging from sporadic usage to extensive cultivation. The trends are consistent when examining within-family contrasts for these variables, but sample size limits the analysis. We therefore consider these trends



**Table 2. Correlations between ecological variables (geographic usage) and fruit traits of megafauna species.**  
<https://doi.org/10.1371/journal.pone.0001745.t002>

## The taxonomic and ecological distribution of megafaunal

We analyzed the data available for the  $N=103$  species characterized by any of the external criteria of morphology. Megafaunal fruits appear repeatedly as subsets of species among diverse angiosperm subclades. Megafaunal species represent 10% of the species examined ( $N=1361$  species sampled, including our dataset, the FRUBASE dataset and M. Galetti unpublished data) for Fabales (100%), Arecales (51.2%), and Ericales (36.4%); between 10% and 20% of megafaunal characteristics in Malvales (22.2%), Magnoliales (17.1%), and Solanales (10.7%). Less than 10% of megafaunal species were recorded for Malvales (6.7%), Gentianales (8.4%), Malpighiales (5.9%), Sapindales (4.6%), and Laurales (1.6%). This distribution indicates a widespread presence of megafaunal attributes in these taxa. Families with a high proportion of megafaunal species (Table 1) include Arecaceae, Sapotaceae, Fabaceae, Lecythidaceae, Humiriaceae, Caryocaraceae, some Malvaceae (i.e., formerly Bombacaceae and Sterculiaceae) and Quiinaceae. Among these families, the main genera are *Caryocar* (Caryocaraceae), *Attalea*, *Astrocaryum* and *Syagrus* (Arecaceae), *Andira*, *Dipteryx*, and *Hymenaea* (Fabaceae), *Pouteria* (Sapotaceae), and *Quiina* (Quiinaceae) (Malvaceae).

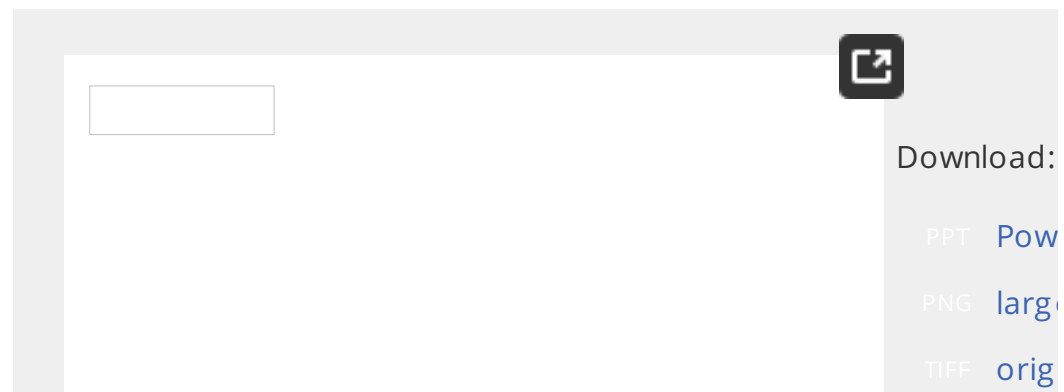
The frequency of megafaunal fruits is not constant across two distinct communities. In a single locality of lowland Atlantic rainforest (Interlago, 13% of the fleshy-fruited tree species ( $N=246$ ) have megafaunal characteristics (e.g., *Pouteria*, *Painari*, *Astrocaryum*), while in a Pantanal site, Fazenda Rio Preto, the frequency of megafaunal species reaches 30% ( $N=147$  species) [35].

In relation to ecological characteristics of the species in our megafaunal dataset, 37.5% are from the Amazonian forest, 13.5% from Atlantic forest, 9.7% from *cerrado* vegetation types, and 28.9% from semideciduous and mixed

(including a variety of formations). The main habitat types represent *terra firme* forest (54.8%) and riverine and swamp forest (16.3%). Most species are restricted to a small region (73.5%) and very few species show a co-distribution (14.3%). Most species are trees (83.3%), frequently showing propagation or vigorous resprouting (84.2%).

## Comparisons between megafaunal fruits and other dispersal syndromes

To account for patterns of phylogenetic relatedness that might bias comparisons, we contrasted the series of fruit phenotypic traits between non-megafaunal species by means of within-family and within-genus contrasts. Within-family contrasts between the two groups of species for the nine traits indicate consistent trends for larger fruit size in megafaunal species of family affiliation. This trend is very marked for fruit diameter and fruit length; for individual seed mass; for all the four traits examined (Fig. 6) with a significant trend for megafaunal fruits to have larger seeds and greater seed mass independently of the general trend for larger fruits (Table 3).



**Figure 6. Within-family contrasts for fruit traits of megafauna and non-megafauna plant species.**

The pattern for fruit length was very similar to fruit diameter and fruit mass. For clarity, each line corresponds to the contrast (difference in mean trait value) between species of the same family with each syndrome.

<https://doi.org/10.1371/journal.pone.0001745.g006>

**Table 3. Summary of the within-family contrasts of fruit traits between megafauna and non-megafauna species.**

<https://doi.org/10.1371/journal.pone.0001745.t003>

The same trend can be confirmed for within-genus comparisons by congeneric species with megafaunal and non-megafaunal fruits. Large megafaunal congeners are encountered in *Spondias* (Anacardiaceae), *Licania* (Chrysobalanaceae), *Garcinia* (Clusiaceae), *Andira* (Fabaceae), *Myrtaceae*, *Pouteria* (Sapotaceae), and *Solanum* (Solanaceae). They are consistently larger for the megafaunal species of *Acrocomia*, *As*. This is not the case for *Attalea*, with *A. dahlgreniana* and *A. dubia* having sized fruits to *A. butyracea*, *A. funifera*, *A. oleifera* or *A. pindobassu*, which are scatter-hoarding rodents. The rodent-dispersed *Attalea* species have fruits with woody pulp. Among the *Eugenia* species, the megafaunal (*E. cambucarana*, *E. klotzchiana*, *E. neoverrucosa*, *E. stipitata*) have fruits with large seeds. Other congeners having mixed disperser coterie with seed-caching rodents and frugivores.

We have less information for within-genus contrasts in seed mass, and *Syagrus* non-megafaunal species have seeds <10 g, contrasting with megafaunal species, with seeds >15 g. Similar trends are observed in *Licania* (<10 g vs >15 g, respectively). The trend is especially evident for drupaceous fruits (data are not available to test for differences in seed mass for berry fruits (e.g., with >10 seeds/fruit). We should expect these species to have large seed mass, only in total fruit size, seediness and, consequently, total seed mass, e.g., Fig. 4b).

## Discussion

The megafauna syndrome hypothesis can potentially provide a broader context to analyze seed dispersal syndromes, resulting in an intellectually rich synthesis advocating an historical component for present-day interactions. Our study and refines the megafaunal seed dispersal syndrome after Janzen [8], [17], aiming at building an operative definition and provide, based on empirical data, a start for the understanding of ecological benefits of seed dispersal and the consequences of megafauna extinction for large-fruited plants.

We distinguished a few fruit attributes that can be used to determine if a fruit is considered dispersed by the extinct megafauna. Being based on the interactions of extant megafauna herbivores and fleshy fruits [27], our approach provides a rigorous framework to analyze the “unfit” neotropical taxa. We identified two distinct lines of fruit-trait variation represented increased dispersal advantages over non-megafaunal species: production of large fruits packaging extremely large individual seeds (*Theobroma*, *Parinari*, *Caryocar*) and production of extremely large fruits with high numbers of moderate-sized seeds.

Our analysis suggests that the megafaunal syndrome is extensive across higher taxa (e.g., Fabaceae, some Malvaceae, Sapotaceae) but other species with megafaunal fruits closely related to species dispersed by frugivores (e.g., Arecaceae, Myrtaceae, Anacardiaceae, Annonaceae). Further research is needed to accurately estimate the frequency of megafaunal

higher taxa and the percentages in our sample should be considered as estimates because they are not based on a systematic sampling of local floras. Our data from different localities indicate that megafaunal fruits can be relatively common (in terms of species) in Pantanal plant formations but with a marked decrease in species richness in the rainforest, where frugivorous birds are common seed dispersers [6].

## The advantages of seed dispersal by megafauna

Megafaunal fruit species represent a wide range of species that show a unique fruit design that cannot be readily interpreted in terms of ongoing interactions with seed dispersers [8], simply because (1) their fruits are intensively dispersed by large mammals when they exist or (2) no extant vertebrate (except primates) can act as seed disperser by endozoochory, due to fruit design limitations. In the case of extremely large frugivores, these fruit species might have escaped the constraints that may keep seed size below a certain threshold value to avoid to compromise dispersal ability. Size/dispersal ability tradeoffs have been widely documented in plant fruits [69]–[71] and are certainly observed in rainforest species. We found that megafaunal species can pack up to 85% seed load per fruit, with a mean of 140 g seed/fruit. Only by relying on large frugivores free of size constraints can plants extensively disperse seeds larger than the 3.5–4.0 cm diameter limit imposed by present-day Neotropical vertebrate frugivores [32], [41], [65], [67]. The 3.5–4.0 cm seed size limit similar to the 2.8 cm limit for ingestion by African forest primates and hominid cephalophines [54]. Very few extant Neotropical dispersers, like tapirs, can handle such seed loads per scat, allowing the dispersal of much larger individual seeds. Seed size, in turn, is a fundamental trait for plant species to survive in peripheral areas, especially on nutrient-poor soils like those of *igapó* forest or floodplain areas with a high frequency of megafaunal-dispersed species. In the Amazon basin, it is that the frequency of megafaunal fruits is higher in a flooded area (Atlantic forest site). Future studies should investigate the regularity and the ecological bases of the variation in number of megafaunal-fruited species across different communities. While dispersal by megafauna might select for specific traits, it is well established that seediness and seed mass are also subject to multiple ecological influences [32], [76]. Our analysis reveals consistent trends for phylogenetic comparisons of fruit mass, seed mass and seediness but we cannot rule out the possibility of evolving in concert with other ecological characteristics.

Large extinct mammals with size not limiting the consumption of megafaunal fruits. Those analyzed here include most of the terrestrial xenarthrans (*Glyptodont*, *Lestodon*-like genera, megalonychids, and megatheriids [77], large sloths (gomphotheres, mammoths, mastodons) [40], and other groups like toxodons and equids [47]. Among the largest ground sloths, *Megatherium* and *Eremotherium*, the cranial traits coupled with the post-cranial ecomorphology point to strongly frugivorous-browser diets related to high browsing. *Eremotherium* was more able to handle softer food [38], [39], [78]. There is also evidence that the megafaunal fruit species interacted with extreme frugivores such as ground sloths [38], gomphotheres, mastodons, and mammoths [39], [40] and smaller-sized but large semi-terrestrial atelines [79]. Evidence of plant-based diets including relatively large fractions of fruit material

remains of fleshy-fruited shrubs and trees come from ecomorphological remains [38]; evidence from coprolite and isotopic analysis [20], [28] well as from studies of present-day large Paleotropical seed dispersers (rhinos, cassowaries) [12], [25]–[29], [42], [54], [56]–[58], [63], [81]. This is not only to sporadic frugivory among megafauna taxa, but also to an exclusive fruit food by these animals. Most of these species were larger than present-day terrestrial megafauna, with the exception of the African elephants. At least 6 families with 13 genera in the Neotropics with body mass >1

A distinct characteristic of megafaunal fruits is that for a given number of fruits pack significantly larger seeds than non-megafauna taxa. This design, combined with large frugivore size, would imply the potential for high numbers of relatively large seeds. Thus, an average-sized terrestrial megamammal could have dispersed thousands of large seeds of a single fruit, scattering them over a sizable area, based on estimates available for modern rhinoceros [27], [54], [81] and extinct megafauna body sizes [38], [39]. Only tapirs, can have large seed loads per scat in the Neotropics [60]. Modern megafaunal fruit species could take advantage of interacting with frugivores dispersing seed loads much larger than those dispersed by extant species, including much larger individual seeds, ultimately entailing increased success in terms of seedling vigor and survival prospects. Besides, large seed loads increase the survival of partial consumption by seed predators [84]. Therefore, megafaunal species were most likely reliable dispersers by providing the dispersal of large quantities of seeds over enormous areas, involving frequent event dispersal.

Additional advantages of the ability to disperse extremely large individuals are related to the possibility that these large mammals acted as long-distance dispersers of these large seeds. No present-day Neotropical frugivore, with the exception of tapirs [62], [85] and introduced species (e.g., feral pigs), is likely to provide services combining reliable consumption and removal of seeds >2. Modern megafaunal potential dispersal on a regular basis (i.e., not sporadic long-distance dispersal recorded by [86]) at scales >10<sup>3</sup>–10<sup>4</sup> m away from the maternal plant. Modern medium- and large-sized gravi-grade species, such as ground sloths, are capable of long-distance dispersal [39]. Dispersal of large-seeded species can be achieved by some present-day frugivores (e.g., large bats, toucans and large crabs) and scatter-hoarding rodents) but most likely with much fewer seeds per event and short-distance events around 10<sup>1</sup>–10<sup>3</sup>m [32], [87]–[89].

## **The survival of megafaunal fruits**

The consequences of disperser extinction are just starting to be understood. In some present-day plant-frugivore interactions [4], [61], [64], [65], [70] the evidence points to three main types of potential bottlenecks that frugivores might cause on plant population viability, and they illustrate analogous consequences of the megafauna extinctions. First, we should expect changes in the quantitative aspects of dispersal, i.e., a significant decrease in the number of seeds successfully dispersed away from the maternal plant, espec

species [65], [67], [72], [92]. Second, the loss of large frugivores may impact on plant demography by severely altering the seed shadow in limitation of dispersal in both distance and area (e.g., [61]). Third, frugivores probably caused parallel effects on population genetic structure and gene flow via seeds.

There is indeed evidence that the loss of large-bodied frugivores, and the large numbers of large seeds over long distances, has caused increased differentiation because of a dramatic loss of potential for gene flow. A molecular analysis of genetic variation and structure of species with large seeds tends to confirm this prediction [93] and several megafaunal fruits in Neotropical vegetation present a similar trend in genetic variability. For instance, *Calophyllum brasiliense*, *Caryocar brasiliensis*, and *Vouacapoua americana* show moderate levels of genetic variability within population but high genetic differentiation among populations, combined with presence of private alleles, reflecting gene flow via seeds [94]–[99].

How to survive 10,000 years without dispersers or with poor dispersers after the mass extinction of megafauna frugivores in South America occurred ~12,000 yr BP, with more recent extinction on islands [51]. This could involve 100–200 generations for some of the tropical species involved, which is highly anomalous [18]. Although we cannot exclude that a few plant species survived extinct after the Pleistocene megafauna extinction, the persistence of these species needs an explanation. Our data suggest most species rely on long-distance dispersal or sporadic primary dispersal by generalist frugivores. While dispersal by endozoochory can be observed in the field for a few species of megafaunal fruits (e.g., *Hymenaea courbaril*, *Duckeodendron cestroides*), it is relatively frequent to record dispersal by gravity, water, scatter-hoarding, or human harvesting, in addition to vegetative propagation [19], [32], [33], [100]–[104]. These are diplochorous systems involving multiple and diverse dispersal vectors [34]. For instance, most megafaunal fruit species from Pantanal were dispersed now by a combination of seasonal flooding and sporadic dispersal by tapirs, cattle, or feral pigs [35]. This impairs their dispersal if we consider the potential effect of extinct megafauna dispersers could have on these species: the removal of large quantities of fruit and extensive dispersal in distance. No extant Neotropical communities has this potential effect of dispersal by endozoochory being now functional in performing dispersal services for megafaunal species.

In addition, interactions with humans (paleoindians and extant Indigenous peoples [105]) have probably been central in the maintenance and dispersal of megafauna species, especially those with multi-seeded fruits. The interactions with humans were probably less pronounced for the large-fruited species, as suggested by the correlation analysis of ecological traits. A significant association of seediness, human usage, and geographical distance in the interactions of megafaunal fruits with humans (see e.g., [105]) might not only affect the local persistence of a number of species, but also their geographical distribution and population sizes. These patterns, however, would require additional studies with a larger number of species.



Finally, environmental influences in some habitat types (e.g., the *Pangloss* formations in Brazil) probably caused secondary seed dispersal as a surrogate disperser for megafaunal species, and this can explain the success of these species associated with flooded areas [17], [19]. The ability to successfully establish in flooded forest relies on dispersal of relatively small seeds and the development of tall seedlings in a short period of time [75] and megafauna is probably central in the successful recruitment of large-seeded species. Recent demographic simulations [35] suggest that the above factors, along with secondary and marginal dispersal, might allow long-term local persistence of some species.

For the smaller-sized fruit species (e.g., Sapotaceae, Anacardiaceae), birds and mammals are the main current frugivores legitimately dispersing them. For a few species, there are mixed disperser assemblages involving birds and mammals. For these, the impact of present-day extinction of the medium-sized frugivorous birds can be as dramatic as the megafauna extinction [14], [15]. Most likely, megafauna species with multi-seeded fruits and small seed size have escaped the pervasive extinction of the large megafauna by a combination of reliance on small frugivores able to handle the seeds, human-mediated dispersal, vigorous sprouting, and increased importance of secondary dispersal by rural mammals. Moreover, some species also are so well-protected against seed predation by parent plants that distance-limited dispersal in present-day scenarios overcomes post-dispersal seed mortality (e.g., large-seeded *Attalea speciosa* [35]). It is clear that megafauna species include a highly heterogeneous assortment of dispersal and ecological characteristics and so we have to consider a diverse range of responses to extinction of their major dispersers. Whether the extirpation of presumably efficient dispersers led to serious disruption of the plant life cycle is probably related to the degree of reliance on megafauna dispersal. A gradient of megafauna-dependence patterns can be envisaged. Most species are expected in extreme megafauna-dependent species.

## Concluding remarks

One of the pervasive consequences of extinction of the major seed dispersers would be a collapse in the natural regeneration cycle, a severe bottleneck in the sequential stages of recruitment, and a shortening of the seed dispersal distance leading to loss of genetic variation. The large post-Pleistocene megafaunal diverse megafauna [48], [106], whether caused by humans or not, has left a dramatic imprint in plant populations in the form of major changes in recruitment patterns, and regional distribution. Certain aspects of the behavior of megafaunal fruit species have been extremely relevant to their survival to the extinction of their major seed dispersers. Many species show vigorous resprouting and vegetative growth following trampling, and this character has certainly favored persistence despite the extirpation of frugivores [4], [35]. In addition, suboptimal dispersal, whether sporadic or due to abiotic factors [18], [19], most likely contributed to a minimum recruitment and population persistence, as suggested by recent numerical simulations.

megafauna fleshy-fruited species considered here rely on present sized mammals such as large primates, tapirs, and introduced feral successful regeneration; many are scatter-hoarded by large rodent situation, the fast-paced extirpation of these large-vertebrate group forest remnants poses a serious threat for the preservation of the p the flora represented by megafauna-dependent plant species [4], [ our data reveal an important role of humans in the maintenance an of the megafaunal species, particularly the large-fruited, multi-seed have been probably more amenable to human use by yielding large relative to their drupaceous counterparts. Anachronistic interaction component of present-day plant-frugivore communities, yet we know they shaped fruit traits and regeneration strategies of the participants. Understanding the functioning of megafaunal fruit species in present can be advanced in the future with the help of comparative analyses communities with and without native megafauna, theoretical model dynamics, and analysis of population genetic variability and spatial areas worldwide are facing fast-paced defaunation [16] it is imperative implications of past extinctions on the population structure of the living predict the effects of ongoing extinction of the seed dispersers.

## Materials and Methods

Data on fruit traits were compiled from the literature and by direct sampling. The area for field samples was located in different major Brazilian vegetation: Pantanal (wetland with dry and gallery forests and cerrado), Caatinga (savanna), Cerrado (savanna-like vegetation) and semideciduous forest. To assign a species to the megafauna group we compared it with Feer's [27] typologies (Type I and II) for elephant fruits, as this provides criteria to evaluate a proper assignment. In total 103 species from 20 genera spanning all Brazilian biomes were sampled (Supplemental dataset is based on references [107]–[116]).

For species included in our survey, data are available for fruit length (cross diameter; DIAM), fresh fruit mass (FRFM), number of seeds per individual seed mass (SEEDM). To assess consistent patterns in fruit traits for megafaunal fruits we compared these characteristics with confamilial species in the large FRUBASE dataset [6] of fleshy-fruit traits of angiosperms including information for 910 species, as well as other non-megafaunal species included in FRUBASE (75 species from Pantanal [35], and 356 from Amazonia Galetti unpubl. data). FRUBASE is a long-term project maintained by the authors of its information derives from literature sources on frugivory and seed dispersal of megafaunal fruits dataset and the list of primary literature used for FRUBASE is available as Supporting Material (Supplementary Table S1), upon request from the authors, or from <http://ebd10.ebd.csic.es/frubase/>.

We first reported the frequency of megafaunal fruits among different taxonomic groups in our datasets by referring the number of megafauna-dependent species within each higher taxa in the reference dataset (the extension of the

database). Here, we were not interested in providing accurate estimates of megafaunal fruits in the Brazilian flora. Rather, our aim was to provide a description of patterns of variation in the frequency of megafaunal taxa. We have investigated if (1) megafaunal fruits are restricted to widespread across many families and orders and (2) megafaunal fruits are more frequent in some taxa than others. When the literature source reported the range of a variable we estimated the midpoint of the range and used it in subsequent analyses. Ecological and life-history information (Supplementary Table S1) was compiled from literature sources [107]–[116] and from unpublished material (P. Guimaraes and P. Jordano, unpubl. data). Disperser types were categorized into three categories: 1) birds, with plant species dispersed predominantly by avian frugivores; 2) mammals, with plant species dispersed predominantly by mammalian frugivores (including those species dispersed by frugivores, mostly large terrestrial rodents) [117]. Thus, categories of increasing participation of mammal frugivores in the seed dispersal of plants (see [6]). Whenever possible we compiled data on life-history traits of plants, including: 1) geographic range, coded in four ranks (restricted, with distribution spanning 2–3 small Brazilian states; regional, 100×10<sup>3</sup> km<sup>2</sup>, spanning a Brazilian region; large, 1,5×10<sup>6</sup>–7×10<sup>6</sup> km<sup>2</sup>, spanning 2–3 Brazilian states; and continental, >7×10<sup>6</sup> km<sup>2</sup>, extending over large areas of Brazil). 2) Use, was coded in four broad categories: no use, if fruits are not consumed; local use, if consumption is recorded locally from wild trees in the human settlements; regional plantation, if cultivation of the plant is recorded; and extended use, if the plant species represents a frequent food item; and extended use, if the plant species is used for other purposes. 3) Fruit type, was coded as drupe or drupaceous, berry-like, or other (including e.g., syconia). 4) Main vegetation type, coded as Amazon forest, semideciduous forest, Cerrado vegetation, Caatinga, Atlantic forest, or other, whenever the species is characteristic of several vegetation types. This information was largely compiled from literature sources and unpublished material (P.R. Guimarães Jr., M. Galetti, and P. Jordano, unpubl. data; Donatti and M.A. Pizo, pers. comm.).

## Statistical analyses

We used randomization tests [119], [120] to assess differences between megafaunal and non-megafaunal species in fruit traits. We used  $N=10000$  resamples for each test and applied the Bonferroni correction when using simultaneous tests on several traits. We used the same approach for differences among disperser type categories for several fruit traits.

In addition to using the raw data for comparisons, we used within-family contrasts for inferring differences between megafaunal and non-megafaunal species without taking into account the patterns of phylogenetic relatedness of data on megafaunal fruits and the irregular distribution of missing data. We used within-family contrasts to partially control the patterns of phylogenetic relatedness (see [6], [121] for a similar approach). We used a binomial test to assess the proportion of positive contrasts (megafaunal fruits with larger values) for each trait. We used 13 within-family contrasts (megafaunal fruits with larger values) for each trait.

compared to non-megafauna confamilial species) exceeded a range of 0.50. For a reduced number of genera we used within-genus comparisons, which were insufficient for a formal test. To test correlations among fruit morphological and ecological variables (geographic range size, and human usage) we used 10,000 resamplings (N=10000). We used a principal component analysis and ordinations of fruit species according to morphological and ecological variables. The PCA was carried out on the transformed variables after using the library `ade4` of the R package [120]. For the ecological and life history variables we used those coded as meristic values (i.e., ordinal scale): fruit color, fruit type (berry and beery-like fruits to legumes and drupaceous fruits), geographic range size, human use, vegetation type (ordered from Amazonian lowland rain forest, mixed, and caatinga and cerrado vegetation) and habitat type (riparian to terra firme forest type). We omitted genera with only one species, and used  $N=11$  genera with two or more species.

Nomenclature and species names follow [122], with modifications for

## Supporting Information

### Table S1.

Fruit characteristics of megafauna-dependent species.

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(0.07 MB XLS)

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## Author Contributions

Conceived and designed the experiments: MG PJ PG. Performed the experiments: MG PJ PG. Analyzed the data: MG PJ PG. Wrote the paper: MG PJ PG.

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