



Human diets drive range expansion of megafauna-dispersed fruit species

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Neotropical fruit species once dispersed by Pleistocene megafauna have regained relevance in diversifying human diets to address malnutrition. Little is known about the historic interactions between humans and these fruit species. We quantified the human role in modifying geographic and environmental ranges of Neotropical fruit species by comparing the distribution of megafauna-dispersed fruit species that have been part of both human and megafauna diets with fruit species that were exclusively part of megafauna diets. Three quarters of the fruit species that were once dispersed by megafauna later became part of human diets. Our results suggest that, because of extensive dispersal and management, humans have expanded the geographic and environmental ranges of species that would otherwise have suffered range contraction after extinction of megafauna. Our results suggest that humans have been the principal dispersal agent for a large proportion of Neotropical fruit species between Central and South America. Our analyses help to identify range segments that may hold key genetic diversity resulting from historic interactions between humans and these fruit species. These genetic resources are a fundamental source to improve and diversify contemporary food systems and to maintain critical ecosystem functions. Public, private, and societal initiatives that stimulate dietary diversity could expand the food usage of these megafauna-dispersed fruit species to enhance human nutrition in combination with biodiversity conservation.

human-plant interactions | Pleistocene megafauna | Latin America | plant distribution | plant genetic resources

Neotropical fruit species, once dispersed by Pleistocene megafauna (1, 2), were an important component of human diets in pre-Columbian America (3). Many of those species became underutilized because of the depopulation suffered by Native American cultures and their loss of traditional knowledge after European conquests (3, 4), and also because of diet and cultural homogenization in recent decades (5, 6). Recently, Neotropical fruit species have regained relevance in diversifying food systems to address malnutrition and unsustainable food production (7, 8). Little is known to what extent humans historically have modified the distribution and genetic diversity of Neotropical fruit species. Despite advances in phenotyping, archaeobotany, and DNA techniques, it remains a challenge to distinguish natural populations of fruit-producing species from populations that have been managed and modified by humans (9–12).

Thousands of years of interactions between humans and Neotropical fruit species likely have led to a pool of genetic resources with wide phenotypic ranges in traits of human interest (13). Poor understanding of the historic interactions between humans and fruit species can lead to extirpation of these genetic resources (3, 9, 10). These genetic resources are a fundamental source to improve and diversify contemporary food systems (6, 14) and also to maintain viable populations of fruit species so

that these species can continue fulfilling their ecosystem functions under changing environments (15, 16).

Human effects on the geographic and environmental distribution of fruit species can be assessed by comparing these species vs. species with alternate nonhuman past fruit dispersers, i.e., extinct megafauna. Most Neotropical megafauna became extinct approximately 12,000 y BP, and human impacts strengthened after this time (16). Thus, humans and megafauna may have had different effects on population structure of fruit species over time. We hypothesize that fruit species that were previously dispersed by megafauna but are now not dispersed by humans have smaller geographic and environmental ranges. In contrast, we hypothesize that fruit species previously dispersed by megafauna that are now dispersed by humans have wider geographic and environmental ranges because of human management of these fruit species during the past 15,000 y.

We quantify the role of humans in shaping the distribution of Neotropical fruit species by comparing geographic ranges of extent of occurrence (EOO) and maximum geographic distance (MGD), and climate ranges of annual mean temperature (RAMT) and ranges of annual precipitation (RAP) for 130 identified megafauna-dispersed fruit species in three diet groups:

Significance

Neotropical fruit species once dispersed by megafauna have regained relevance for diversifying human diets to address malnutrition. Little is known about the historic interactions between humans and these fruit species. We quantified the human role in modifying distribution ranges of Neotropical fruit species by comparing the distribution of fruit species that have been part of both human and megafauna diets with fruit species that were exclusively part of megafauna diets. Our results show that human food usage has expanded the distribution of species that would otherwise have suffered range contraction after extinction of megafauna. Our analyses help in identifying range segments of fruit species that may hold key genetic diversity to sustain food systems and to maintain critical ecosystem functions.

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- i) A total of 30 fruit-producing species that were part of megafauna diets but did not become part of human diets. These are fruit species reported to have been consumed by and dispersed by giant sloths and other extinct megafauna in Central and South America (1, 2);
- ii) A total of 61 wild fruit-producing species that have been part of both human and megafauna diets in Central and South America; and
- iii) A total of 39 cultivated fruit-producing species that have been part of both human and megafauna diets in Central and South America.

Distinguishing the geographic ranges and environmental niches from the three diet groups may thus provide insight into the factors structuring the distribution and genetic resources of these fruit species.

Materials and Methods

Species Selection for the Three Diet Groups. A total of 130 Neotropical fruit-producing species were identified as part of megafauna diets in Central and South America, respectively (1, 2). For each species, the New World Fruit Database (nwfdb.bioiversityinternational.org) was used to score whether humans were reported to consume fruit species and nuts from these species. Germplasm Resources Information Network (GRIN) taxonomy was consulted to score whether species are cultivated (<https://npgsweb.ars-grin.gov/gringlobal/taxonomybrowse.aspx>). The three diet groups were further divided between Central and South America according to the region where the extinct megafauna were reported to consume and disperse each of these 130 fruit species (1, 2). Species names were checked and updated according to the Plant List (www.theplantlist.org). The species per diet group and region are listed in Table S1.

Presence Records. Presence records for all 130 species were obtained from herbarium, inventory, and genebank databases stored in the Global Biodiversity Information Facility (<https://www.gbif.org>). Species datasets with fewer than 30 georeferenced presence records were manually georeferenced where possible in Google Earth or with support of www.geonames.org. The final dataset for all 130 species consisted of 51,084 georeferenced presence records.

Species' presence records with inconsistencies between countries as reported in the passport data and at the projected locations outside a border buffer zone of 10 arc minutes were removed following a previous work (17). Coordinates of presence records located in coastal waters within a 10-arc minute buffer zone to the coastline were relocated to the nearest point in the coastline. Presence records with coordinates from country middle points were removed because these points are likely georeferenced at country level with low precision. For each species, duplicate records in the same grid cells with a 2.5-arc minute resolution were removed to reduce sample bias. Outlier presence records with climate values beyond species' niche margins were removed from our dataset because these are likely errors in coordinates or taxonomy. Outliers were removed when the values of five or more of a total of 19 bioclimatic variables were outside a threshold of 2.5 times the interquartile range below the first quartile or above the third quartile. Climate data were derived from the 2.5-arc minute environmental layers of the WorldClim database (18).

Comparison of Species from the Three Diet Groups. To compare the geographic ranges of species from the three diet groups, we calculated three indicators for each species: first, the EOO in millions (M) km² as convex hulls following the guidelines of the International Union for Conservation of Nature (IUCN), possibly including sea cover (19); second, the EOO for land cover only; and third, the MGD between presence records in decimal degrees (DDs). To compare the environmental ranges of species from the three diet groups, we calculated two indicators for each species: first, the range in mean annual temperature (RAMT); and second, the range in annual precipitation (RAP). Climate data were derived from the 2.5-arc minute environmental layers of the WorldClim database (18).

To anticipate possible bias because of the sample size of species' presence records, the geographic and environmental ranges were also calculated for each species by a repeated random subsampling of 20 records without replacement for 100 times. This subsampling technique has been used successfully as an alternative for rarefaction in taxonomic and molecular richness analyses (20). In this subsampling analysis, only 122 species with 20 or more georeferenced records could be included.

One-way ANOVAs between the three diet groups as fixed factor and with Central vs. South America as random factor were calculated with rank data

following ref. 21 because the geographic and environmental data did not follow normal distributions. To reduce the false-positive rate, *P* values obtained were corrected by using the false discovery rate (FDR) method following ref. 22. Box plots were used to visualize differences per diet group and per region.

Comparison of Congeneric Species from the Three Diet Groups. The 130 species included eight genera with congeneric species from two or more diet groups (Table S2). Only three genera included cultivated fruit species and fruit

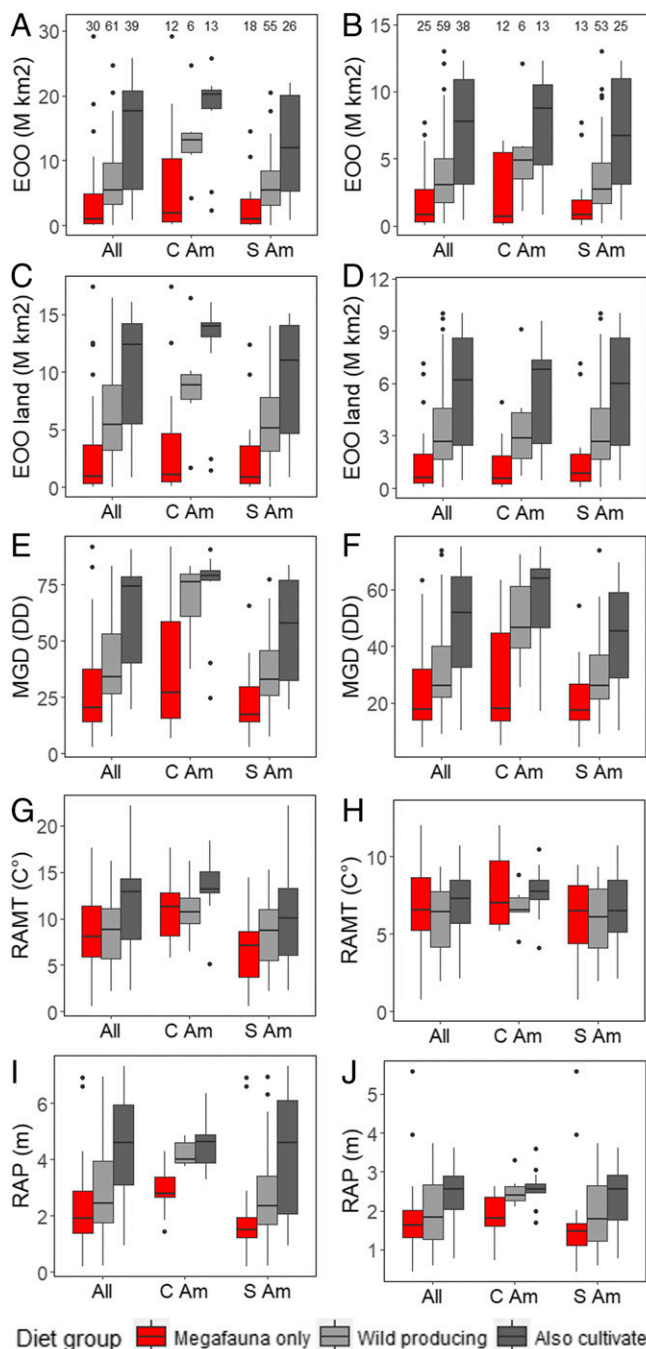


Fig. 1. Comparison of EOO, EOO land (i.e., EOO for land cover only), MGD in DDs, RAMT, and RAP among the three diet groups, fruit species that were exclusively part of megafauna diets (red), wild-producing fruit species (light gray), and cultivated fruit species (dark gray); and between two regions, Central America (C Am), South America (S Am), and both (All). The results in A, C, E, G, and I are calculated with all species' presence records. The results in B, D, F, H, and J are calculated with repeated subsampling without replacement for 100 times (*r* = 20).

Table 1. Mean values of geographic and climatic variables for each of the three diet groups

| Diet groups | EOO, M km ² | EOO for land only, M km ² | MGD, DD | RAMT, C° | RAP, m |
|----------------------------------|------------------------|--------------------------------------|---------|----------|--------|
| Analysis with all data | | | | | |
| Mega fauna only (<i>n</i> = 30) | 4.3 | 3.1 | 29.2 | 8.3 | 2.4 |
| Wild-producing (<i>n</i> = 61) | 6.9 | 6 | 39.3 | 8.6 | 2.9 |
| Cultivated (<i>n</i> = 39) | 14.2 | 10.3 | 61.3 | 11.4 | 4.3 |
| Analysis with subsampling | | | | | |
| Mega fauna only (<i>n</i> = 25) | 2.1 | 1.6 | 24.9 | 6.7 | 1.9 |
| Wild-producing (<i>n</i> = 59) | 3.8 | 3.5 | 31.6 | 6.1 | 2 |
| Cultivated (<i>n</i> = 38) | 7.1 | 5.6 | 48.9 | 7 | 2.5 |

species that were exclusively part of mega fauna diets, whereas six genera included wild-producing fruit species and fruit species that were exclusively part of mega fauna diets.

With only three genera, we were not able to make statistical comparisons between cultivated fruit species and fruit species that were exclusively part of mega fauna diets; we were able to make only a descriptive analysis. With six genera, we were able to carry out one-sided paired *t* tests to compare geographic and climate ranges between congeneric species from wild-producing fruit species and fruit species that were exclusively part of mega fauna diets. Rank data were used, and the *P* values obtained were corrected by using the FDR method as explained earlier for the one-way ANOVAs. If two or more congeneric species were present in one diet group, we used the mean values of their geographic and environmental ranges for the pairwise comparison between the congeneric species from the two contrasting diet groups.

Species Richness Maps. Species richness layers were made for the three diet groups for Central and South America separately by using the presence records of the fruit species that delineate their contemporary geographic ranges. Maps were developed with latitude/longitude projection and WGS84 datum. Each layer had a resolution of 0.5 DD and were made with a circular neighborhood of 2 DD.

Software and Code. All analyses and graph representations were performed in R version 3.3.3 except for the species richness maps, which were made in DIVA-GIS (23). The code and datasets that were used for the analyses are available at https://figshare.com/articles/_/5815878. The R packages that were used are specified in *Text S1*.

Results

The EOO of cultivated fruit species is larger compared with fruit species that were exclusively part of mega fauna diets (Fig. 1 and *Table S3*). The EOO of cultivated fruit species is, on average, 3.3 times larger in the analysis with all data, and

3.4 times larger in the analysis with subsampling (*Table 1*). The EOO of wild-producing fruit species is, on average, 1.6–1.8 times larger compared with fruit species that were exclusively part of mega fauna diets. The EOO of cultivated fruit species is 2.1–1.9 times larger compared with wild-producing fruit species.

The EOO for land cover only of cultivated fruit species is larger compared with fruit species that were exclusively part of mega fauna diets (Fig. 1 and *Table S3*). The EOO for land cover only of cultivated fruit species was, on average, 3.3 times larger in the analysis with all data, and 3.5 times larger in the analysis with subsampling (*Table 1*). The EOO for land cover only of wild-producing fruit species is, on average, 1.9–2.2 times larger compared with fruit species that were exclusively part of mega fauna diets. The EOO for land cover only of cultivated fruit species is 1.7–1.6 times larger compared with wild-producing fruit species.

The MGD of cultivated fruit species is larger compared with fruit species that were exclusively part of mega fauna diets (Fig. 1 and *Table S3*). The MGD of cultivated fruit species is, on average, 2.1 times larger in the analysis with all data, and 2.0 times larger in the analysis with subsampling (*Table 1*). The MGD of wild-producing fruit species is 1.3 times larger in both the analysis with all data and the analysis with subsampling compared with fruit species that were exclusively part of mega fauna diets. The MGD of cultivated fruit species is 1.6–1.5 times larger compared with wild-producing fruit species.

The RAMT of cultivated fruit species and wild-producing fruit species is larger compared with fruit species that were exclusively part of mega fauna diets in only the analysis with all data (Fig. 1, *Table 1*, and *Table S3*). No significant difference is found in the analysis with subsampling. The RAMT of cultivated and wild-producing fruit species also do not differ.

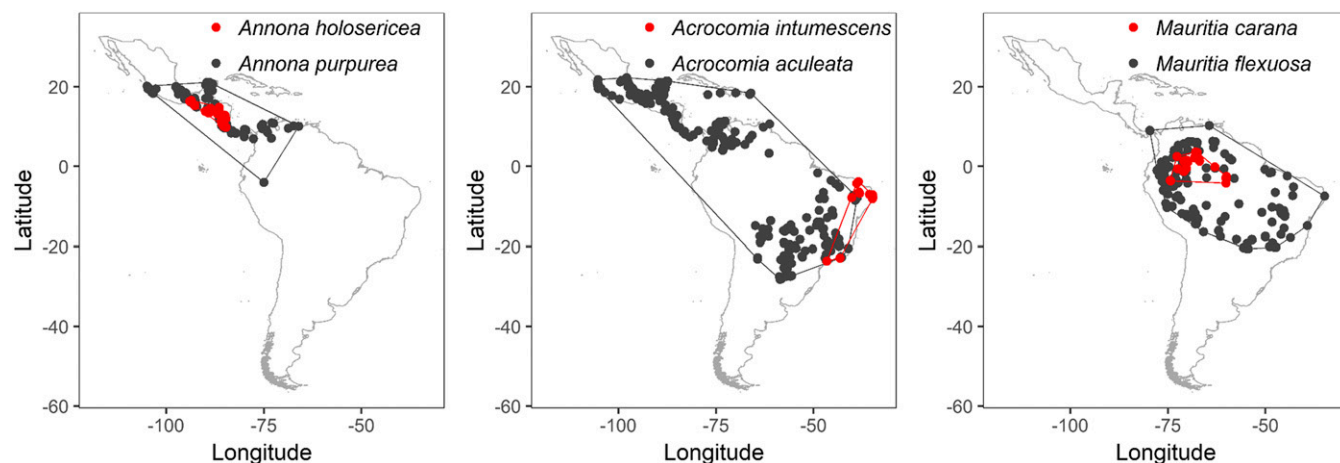


Fig. 2. Comparison of the EOO and distribution of three congeneric species pairs from two contrasting diet groups. Red, fruit species that were exclusively part of mega fauna diets; dark gray, cultivated fruit species.

The RAP of cultivated fruit species is larger compared with fruit species that were exclusively part of megafauna diets (Fig. 1 and Table S3). The RAP of cultivated fruit species is, on average, 1.8 times larger in the analysis with all data, and 1.3 times larger in the analysis with subsampling (Table 1). The RAP of wild-producing fruit species is 1.2–1.1 times larger compared with fruit species that were exclusively part of megafauna diets. The RAP of cultivated fruit species are 1.5–1.3 times larger compared with wild-producing fruit species, but these differences are statistically not significant (Table S3).

Congeneric cultivated fruit species have larger geographic ranges and similar climate ranges compared with fruit species that were exclusively part of megafauna diets (Fig. 2 and Table 2). Similar results were found when we compared congeneric wild-producing fruit species with congeneric fruit species that were exclusively part of megafauna diets (Fig. 3 and Table 2). The differences between congeneric wild-producing fruit species and fruit species that were exclusively part of megafauna diets are not significant in the analysis with all data; these differences are not significant in the analysis with subsampling (Table 2). The genus *Pouteria* stands apart because two *Pouteria* species that were exclusively part of megafauna diets have larger geographic ranges compared with wild-producing *Pouteria* species (Fig. 2).

Seven of the 30 fruit species that were exclusively part of megafauna diets (23%) occur in both Central and South America (Fig. 4). In contrast, 48 of the 99 human-food fruit species (48%) occur in both regions.

In Central America, we identified 12 fruit species that were part of the diets of the extinct megafauna in this region and that did not become part of the human diet (Table S1). Seven of these 12 fruit species (58%) are restricted to the seasonally dry tropical forests on the Pacific coast of Central America (Fig. 4). The other five species (42%) occur also in South America. All six wild-producing fruit species and 13 cultivated fruit species from Central America are spread across Mexico and Central America. All these wild-producing and cultivated fruit species also occur in South America, mostly in Colombia, Venezuela, and Ecuador.

In South America, we identified 18 fruit species that were part of the diets of the extinct megafauna in this region and that did not become part of the human diet (Table S1). Sixteen of these 18 fruit species (89%) occur only in South America (Fig. 4). Their distribution is mostly restricted to the Atlantic coast. Two of these 18 species (11%) also occur in Central America and Mexico. The 55 wild-producing fruit species from South America are widely distributed in this continent, with the greatest species richness in the Amazon. Fifteen of these 55 species (27%) also

Table 2. Comparison of mean geographic and climate ranges of congeneric species from the three diet groups

| Detail | Wild-producing vs. megafauna only | | Cultivated vs. megafauna only | |
|--------------------------------------|-----------------------------------|-------------------|-------------------------------|---------------------|
| | All data | Subsampling | All data | Subsampling |
| No. of congeneric groups | 6 | 4 | 3 | 2 |
| EOO, M km ² | 2.3* | 1.5 ^{NS} | 21.8 ^{NSD} | 12.9 ^{NSD} |
| EOO for land only, M km ² | 2.5* | 1.5 ^{NS} | 17.3 ^{NSD} | 11.2 ^{NSD} |
| MGD, DD | 1.7* | 1.4 ^{NS} | 4.0 ^{NSD} | 3.5 ^{NSD} |
| RAMT, °C | 1.2 ^{NS} | 1.0 ^{NS} | 1.8 ^{NSD} | 1.5 ^{NSD} |
| RAP, m | 1.1 ^{NS} | 1.0 ^{NS} | 2.3 ^{NSD} | 1.6 ^{NSD} |

Values indicate how many times larger the geographic and environmental ranges are on average for respectively wild-producing and cultivated species compared with fruit species that were exclusively part of megafauna diets. NSD, not sufficient data for paired *t* tests; NS, not significant.

**P* < 0.05, one-sided paired *t* tests corrected by FDR method.

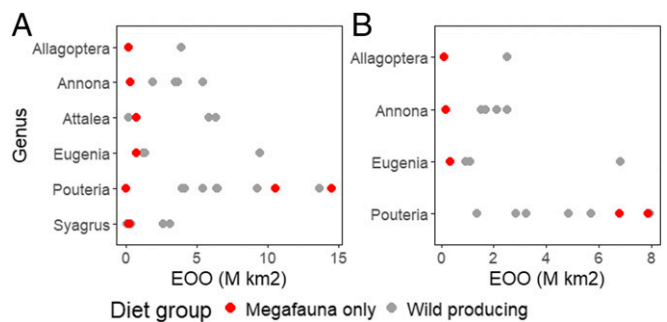


Fig. 3. Comparison of EOO of congeneric species from two contrasting diet groups: red, fruit species that were exclusively part of megafauna diets; light gray, wild-producing fruit species. The EOO values in *A* are calculated with all species' presence records from six genera. The EOO values in *B* are calculated with repeated subsampling without replacement for 100 times (*r* = 20). *B* includes only four genera that have sufficient presence records of species from both diet groups for comparison after subsampling.

occur in Central America and Mexico; 13 species alone occur in Costa Rica. The 27 cultivated fruit species from South America are also widely distributed in South America, with high species richness in northwestern South America. Sixteen of the 27 species (59%) also occur in Central America and Mexico; in Costa Rica alone occur 15 of these 16 species and the same number of species occur in Panama.

Discussion

Our results suggest that humans have been, on average, responsible for 41% of the EOO for wild-producing fruit species and 70% for cultivated fruit species in the Neotropics compared with fruit species that were exclusively part of megafauna diets. In a similar way, human-dispersed fruit species have 51% and 71% larger EOO for land cover only, respectively, and 23% and 51% larger MGDs than fruit species that were exclusively part of megafauna diets. Thus, humans have expanded or maintained the geographic ranges of species that would otherwise have suffered range contraction after extinction of megafauna.

Our results show that humans in the Americas have incorporated high levels of fruit diversity in their diets. Three quarters of the listed fruit species once dispersed by megafauna became part of human diets. Our results therefore suggest that humans have been responsible for the range expansion or maintenance of a large proportion of megafauna-dispersed fruit species.

Half of the fruit species that became part of human diets occur in both Central and South America. High richness of intercontinentally distributed species in Costa Rica, Panama, and Colombia suggests active pre-Columbian exchange and management of Neotropical fruit species by humans between continents. This area in southern Central America and northwestern South America overlaps with an early center of domestication in current Colombia (24) and with the later cultural Chibchan territory (25). In contrast, three quarters of the fruit species that were exclusively part of megafauna diets are restricted to one continent. These results suggest that many megafauna-dispersed fruit species were spread to Central America from South America and vice versa when they had become part of human diets during the past 15,000 y. Thus, after the extinction of giant sloths and other Pleistocene megafauna, humans became important agents of seed dispersal for Neotropical fruit species.

It is difficult to determine to which extent humans actively expanded or maintained the geographic and environmental ranges of these fruit species. Our analyses do not allow identification of the geographic ranges of these species before human influence and their prehuman niches. However, cultivated fruit

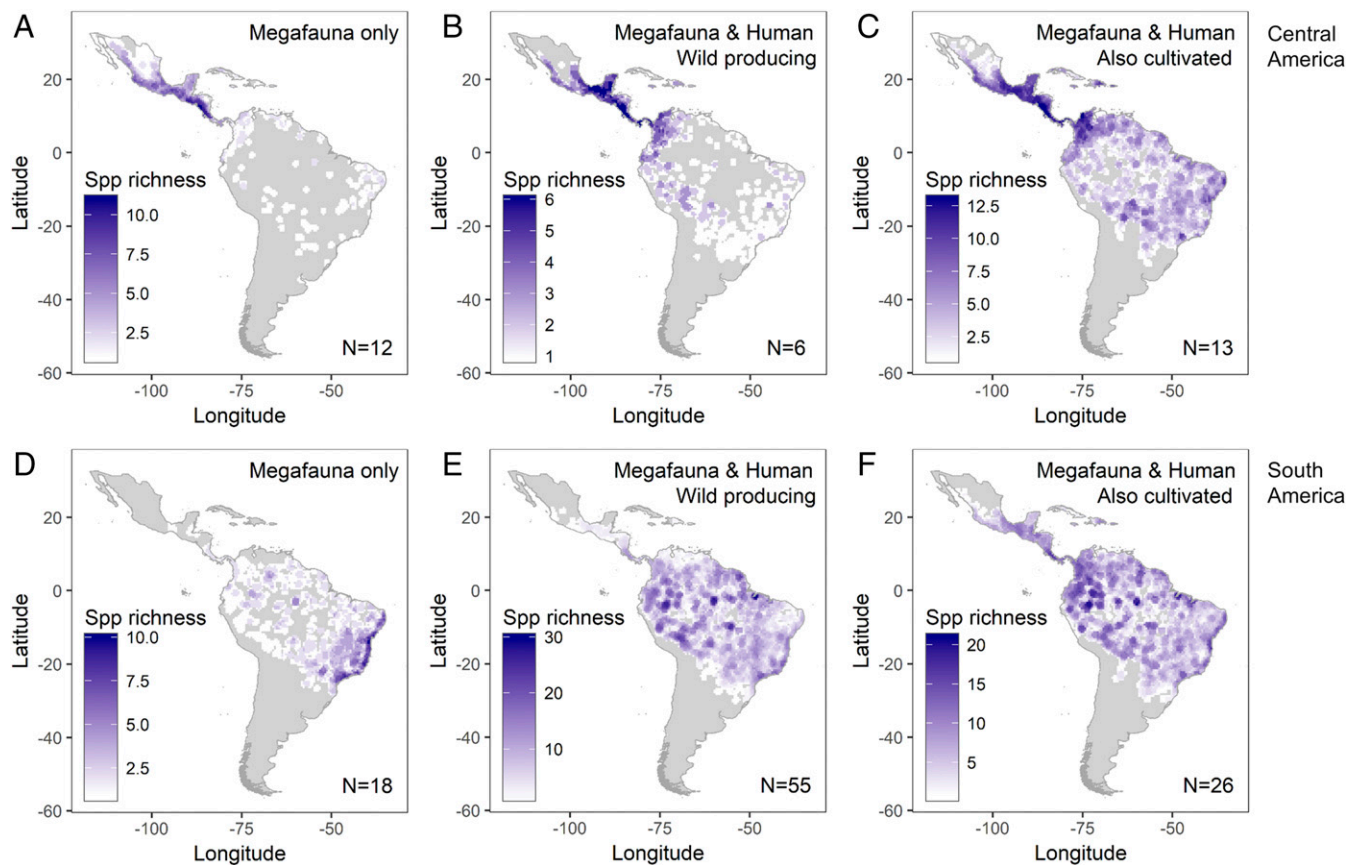


Fig. 4. Sampled richness of the 130 listed fruit species that were part of the megafauna diets in Central America (A–C) and South America (D–F). Comparison of the three diet groups: (i) fruit species that were exclusively part of megafauna diets, (ii) wild-producing fruit species, and (iii) cultivated fruit species.

species have likely expanded distribution ranges beyond their prehuman niches. These dynamics in range expansion have been observed for domesticated cucurbits that spread widely after megafauna extinction, in contrast to the contracted distribution of cucurbit wild relatives, because these species were only consumed and dispersed by megafauna (26). Wild-producing fruit species have likely been more restricted to expand distribution ranges beyond their prehuman niches. Even so, humans could have dispersed these species in new geographic areas and new environmental habitats because of extensive predomestication cultivation in the Neotropics (11, 27).

Indeed, our results show that wild-producing fruit species grow in wider rainfall ranges compared with fruit species that were exclusively part of megafauna diets. This difference suggests that active human management and human dispersal modified the environmental niches of wild-producing fruit species or helped to maintain the prehuman distribution ranges in which these species occurred before the extinction of the megafauna.

Five of the 12 Central American fruit species that were exclusively part of megafauna diets also occurred in South America. These fruit species occur in Central America in seasonally dry tropical forests (1). It could be that these fruit species are currently restricted to isolated patches in two continents because of the contraction of this habitat after approximately 12,000 y BP (28, 29) in combination with reduced dispersal after extinction of megafauna (1, 2). In contrast, cultivated and wild-producing fruit species could have been introduced or maintained in warmer and wetter habitats that became more prevalent in the Holocene (28, 30).

The fact that most congeneric species that were exclusively part of megafauna diets have restricted geographic ranges

according to our analyses further supports the important role of humans in shaping the distribution ranges of Neotropical fruit species. Two *Pouteria* species that were exclusively part of megafauna diets, *Pouteria torta* and *Pouteria venosa*, stand out because they have wider geographic ranges compared with their wild-producing congeneric species. It could be that these species are not consumed anymore by humans, or are still consumed very locally by humans, even though they are not registered in the New World Fruit Database. Humans from the Peruvian Amazon, however, do not prefer to consume *P. torta* compared with wild-producing *Pouteria* species (31). Alternatively, it could be that a few megafauna-dispersed fruit species, such as these two *Pouteria* species, have successfully attracted other dispersers than humans to maintain or expand their distributions. It requires further research to identify successful dispersers other than humans (32), and to identify key characteristics that fruits of megafauna-dispersed species should have to successfully attract humans and other wide-range dispersers.

Our analyses cannot determine when humans shaped the distribution of these fruit species. It is therefore difficult to determine the role of post-Columbian inhabitants of Latin America on the distribution of these fruit species. Post-Columbian inhabitants could have been responsible for substantial range expansion of some Neotropical fruit species in Latin America, such as the suggested recent introduction of araza (*Eugenia stipitata*) from South to Central America (33). For other fruit species, such as cacao (*Theobroma cacao*), post-Columbian colonists may have intensified local planting and distribution (34), but they did not substantially expand the pre-Columbian distribution ranges of these species in Latin America (35, 36). Finally, many fruit species became underutilized in post-Columbian times. Their

reduced food usage could have led to reduced contemporary densities and distribution ranges in Latin America compared with their pre-Columbian distributions (3).

For some fruit species, wide-range genetic and ethnobotanical datasets about their pre-Columbian distribution are available: cacao, cherimoya (*Annona cherimola*), and peach palm (*Bactris gasipaes*) (9, 33, 35, 36). These studies suggest that the pre-Columbian geographic ranges of these fruit species largely overlap with their contemporary geographic ranges in Latin America. We therefore hypothesize that humans expanded most of the geographic and environmental ranges of the megafauna-dispersed fruit species during pre-Columbian times. Further genetic and archaeobotanical studies are required to test this hypothesis. Ethnobotanical and ecological studies about the role of post-Columbian colonists and their cattle on the distribution of fruit species would provide further insights about human–fruit interactions in the Neotropics (33, 34).

Previous studies suggest that the distributions of many Neotropical fruit species have been limited after megafauna extinction, with possible negative implications for ecological functions in tropical ecosystems, such as carbon storage and nutrient transport (15, 16). In contrast, our results suggest that humans may have offset or reversed many of these trends through their diverse food usage. We suggest that research on ecosystem functions of megafauna should take into account past and contemporary interactions between humans and fruit-producing species.

Our results suggest that humans have played an important role in shaping the contemporary genetic diversity of Neotropical fruit

species. Humans have maintained and managed populations of these species in existing locations after the extinction of the megafauna. They also have established and managed populations in new locations. These historic interactions have generated a broad pool of genetic resources for Neotropical fruit species that are maintained in these populations. These genetic resources are a fundamental source to improve and diversify contemporary food systems (6, 14) and to maintain viable populations of fruit species so that these species can continue fulfilling their ecosystem functions under changing environments (15, 16).

Populations of many of these fruit species could be currently threatened because these species have become underutilized in human diets and are not targeted for conservation. Fruit species that were exclusively part of megafauna diets are most vulnerable to range contraction and extirpation, but could have unknown food usages or can be used as gene sources in breeding programs of congeneric species. Public, private, and societal initiatives that stimulate dietary diversity could expand the food usage of megafauna-dispersed fruit species to enhance human nutrition in combination with biodiversity conservation.

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- Janzen DH, Martin PS (1982) Neotropical anachronisms: The fruits the gomphotheres ate. *Science* 215:19–27.
- Guimarães PR, Galetti M, Jordano P (2008) Seed dispersal anachronisms: Rethinking the fruits extinct megafauna ate. *PLoS One* 3:e1745.
- Clement CR (1999) 1492 and the loss of Amazonian crop genetic resources. I. The relation between domestication and human population decline. *Econ Bot* 53:188–202.
- Vietmeyer ND (1986) Lesser-known plants of potential use in agriculture and forestry. *Science* 232:1379–1384.
- Khoury CK, et al. (2014) Increasing homogeneity in global food supplies and the implications for food security. *Proc Natl Acad Sci USA* 111:4001–4006.
- Johns T, Powell B, Maundu P, Eyzaguirre PB (2013) Agricultural biodiversity as a link between traditional food systems and contemporary development, social integrity and ecological health. *J Sci Food Agric* 93:3433–3442.
- Tutwiler A, Padulosi S, Hunter D (2017) Securing sustainable and nutritious food systems through mainstreaming agricultural biodiversity: An interdisciplinary study. *Lancet* 389(Suppl 2):S22.
- Jones AD, Ejeta G (2016) A new global agenda for nutrition and health: The importance of agriculture and food systems. *Bull World Health Organ* 94:228–229.
- Larranaga N, et al. (2017) A Mesoamerican origin of cherimoya (*Annona cherimola* Mill.): Implications for the conservation of plant genetic resources. *Mol Ecol* 26:4116–4130.
- Thomas E, Alcázar Caicedo C, McMichael CH, Corvera R, Loo J (2015) Uncovering spatial patterns in the natural and human history of Brazil nut (*Bertholletia excelsa*) across the Amazon basin. *J Biogeogr* 42:1367–1382.
- Piperno DR (2011) The origins of plant cultivation and domestication in the New World tropics. *Curr Anthropol* 52(suppl 4):S453–S470.
- Braefe S, Dufour D, van Zonneveld M, Rodriguez F, Gonzalez A (2013) Peach palm (*Bactris gasipaes*) in tropical Latin America: Implications for biodiversity conservation, natural resource management and human nutrition. *Biodiversity Conserv* 22:269–300.
- Casas A, Otero-Arnaiz A, Pérez-Negrón E, Valiente-Banuet A (2007) *In situ* management and domestication of plants in Mesoamerica. *Ann Bot* 100:1101–1115.
- Zimmerer KS, de Haan S (2017) Agrobiodiversity and a sustainable food future. *Nat Plants* 3:17047.
- Malhi Y, et al. (2016) Megafauna and ecosystem function from the Pleistocene to the Anthropocene. *Proc Natl Acad Sci USA* 113:838–846.
- Doughty CE, et al. (2016) Megafauna extinction, tree species range reduction, and carbon storage in Amazonian forests. *Ecography* 39:194–203.
- Hijmans RJ, Schreuder M, De La Cruz J, Guarino L (1999) Using GIS to check co-ordinates of genebank accessions. *Genet Resour Crop Evol* 46:291–296.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *Int J Climatol* 25:1965–1978.
- Akçakaya H, Ferson S (2000) Making consistent IUCN classifications under uncertainty. *Conserv Biol* 14:1001–1013.
- Leberg PL (2002) Estimating allelic richness: Effects of sample size and bottlenecks. *Mol Ecol* 11:2445–2449.
- Conover WJ, Iman RL (1981) Rank transformations as a bridge between parametric and nonparametric statistics. *Am Stat* 35:124–129.
- van Zonneveld M, et al. (2015) Screening genetic resources of *Capsicum* peppers in their primary center of diversity in Bolivia and Peru. *PLoS One* 10:e0134663.
- Hijmans RJ, et al. (2004) DIVA-GIS: Sistema de Información Geográfica para el Análisis de Datos de Distribución de Especies. Manual. Version 4, p 91.
- Larson G, et al. (2014) Current perspectives and the future of domestication studies. *Proc Natl Acad Sci USA* 111:6139–6146.
- Hoopes JW (2005) The emergence of social complexity in the Chibchan world of southern Central America and northern Colombia. *J Archaeol Res* 13:1–47.
- Kistler L, et al. (2015) Gourds and squashes (*Cucurbita* spp.) adapted to megafaunal extinction and ecological anachronism through domestication. *Proc Natl Acad Sci USA* 112:15107–15112.
- Hughes CE, et al. (2007) Serendipitous backyard hybridization and the origin of crops. *Proc Natl Acad Sci USA* 104:14389–14394.
- Pennington TR, Prado DE, Pendry CA (2000) Neotropical seasonally dry forests and quaternary vegetation changes. *J Biogeogr* 27:261–273.
- Prado DE, Gibbs PE (1993) Patterns of species distributions in the dry seasonal forests of South America. *Ann Mo Bot Gard* 80:902–927.
- Miller AJ, Knouft JH (2006) GIS-based characterization of the geographic distributions of wild and cultivated populations of the Mesoamerican fruit tree *Spondias purpurea* (Anacardiaceae). *Am J Bot* 93:1757–1767.
- Phillips O (1993) The potential for harvesting fruits in tropical rainforests: New data from Amazonian Peru. *Biodiversity Conserv* 2:18–38.
- Jara-Guerrero A, Escribano-Avila G, Espinosa CI, De la Cruz M, Méndez M (2017) White-tailed deer as the last megafauna dispersing seeds in Neotropical dry forests: The role of fruit and seed traits. *Biotropica* 50:169–177.
- Patiño VM (2002) *Historia y Dispersión de los Frutales Nativos del Neotrópico* (CIAT, Cali, Colombia).
- Bush MB, et al. (2015) Anthropogenic influence on Amazonian forests in pre-history: An ecological perspective. *J Biogeogr* 42:2277–2288.
- Thomas E, et al. (2012) Present spatial diversity patterns of *Theobroma cacao* L. in the Neotropics reflect genetic differentiation in Pleistocene refugia followed by human-influenced dispersal. *PLoS One* 7:e47676.
- Bergmann JF (1969) The distribution of cacao cultivation in pre-Columbian America. *Ann Assoc Am Geogr* 59:85–96.