

Supporting Information

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SI Results

Primate Surveys. We carried out a comprehensive compilation of the population density, biomass density, or any other abundance metric for all diurnal primate species (i.e., excluding night monkeys, *Aotus* spp.) censused during line-transect surveys at 166 Amazonian forest sites (Fig. S1). A total of 86 of these sites (52%) were surveyed by our own standardized, long-term program (1987–2014) of line-transect censuses of forest vertebrates conducted throughout lowland Amazonia (1–6). Data for all other sites were updated from previous compilations (3, 4, 6–8) on the basis of an exhaustive survey of published and unpublished reports of population densities of primate species derived from line-transect censuses. However, we excluded from the final database any survey based on a sampling effort of less than 100 km of line-transect census walks, which was considered to be insufficient.

Environmental perturbations that may or may not be independent from HP, such as selective logging, slash-and-burn agriculture, surface wildfires, and forest fragmentation can lead to marked changes in relative abundances of tropical forest vertebrates (e.g., refs. 9 and 10). This analysis is therefore restricted to survey sites consisting of continuous tracks of primary forest that may have been selectively hunted to varying degrees but otherwise had not been subjected to any form of anthropogenic structural habitat disturbance. However, animal population densities in tropical forests can vary enormously between locations, reflecting baseline differences in habitat structure, forest composition, and primary productivity. In particular, soil fertility profoundly affects the aggregate biomass of vertebrate assemblages in lowland Amazonian forests (11, 12). This analysis is, therefore, designed to at least partly take account of this spatial heterogeneity by restricting comparisons of hunting-effect sizes to geographic clusters of forest sites that had been exposed to a different history of HP, but otherwise shared similar edaphic conditions and belonged to the same major forest type [e.g., terra firme forest on clay soils, terra firme forests on sandy soils, seasonally flooded forests in either black (*igapó*) or white-water (*várzea*) drainages].

All forest sites were either classed as nonhunted ($n = 78$) or assigned to one of three levels of HP—light ($n = 35$), moderate ($n = 27$), and heavy ($n = 26$)—on the basis of: (i) semistructured interviews with hunters who had lived at a given site for at least 2 y before surveys; (ii) present and past human population density and distribution quantified on the basis of the number of households in each study area, either during surveys or revealed by high-resolution (1:250,000) maps (RADAM 1973–1981); and (iii) the number of shotgun blows heard during each census or any other in situ evidence left by hunters (e.g., “waiting” stations, spent shotgun shells). Interviews with hunters were unbiased with respect to fear of disclosing illegal hunting activities, because interviewees in such remote areas were unaware and unsuspecting of legality issues concerning game hunting. To be conservative, this is the most refined resolution afforded by a common HP classification of all sites, given the large variation across studies in the level of details available describing the previous history of hunting, including the duration, intensity and periodicity of game harvest, number of hunters operating in each catchment area, size of catchment areas, hunting techniques and weapons, and prey species, sex, and age-class selectivity of game hunters. Nonhunted sites are defined as those entirely uninhabited by Amerindians, detribalized Amazonians (*caboclos*, *riberieños*, *bush-negros*), and rubber-tappers at the time of surveys, and that offered no enduring evidence of past hunting activity (e.g., axe marks on core hardwoods along perennial

streams; old bark scars on large commercially valuable latex trees). These sites could not be easily reached on foot by hunters, and access by our survey team to many of them was gained with helicopters and small aircraft. The term “nonhunted” as used here is therefore reserved for pristine forests of remote interfluvial basins and headwater regions of Amazonia, rather than areas only rarely visited by hunters (13). Hunting at all hunted sites was carried out primarily with shotguns, because the rapid transition from traditional weapons to firearms has now reached even some of the most remote parts of Amazonia (14). More details on all but the most recently surveyed study areas, site classification in terms of HP, and field procedures used during line-transect censuses and data analysis can be obtained elsewhere (3, 11, 15).

This analysis focuses on a limited set of 16 game and nongame primate species functional groups, from pygmy marmosets (*Cebuella pygmaea*) to the largest atelines (*Ateles* spp. and *Lagothrix* spp.) (Fig. S2). There is considerable variation in the degree to which hunters exercise prey species selectivity across Amazonian forests (14, 16, 17), and not all game species are pursued by hunters at all sites. This analysis is, however, designed to provide a broad assessment of the magnitude of the effect of subsistence hunting across a large number of otherwise undisturbed forest sites, subjected to varying histories of HP. Species are defined here in terms of either single taxonomic species occurring over broad geographic ranges, or functional groups of ecologically analogous congeners (often parapatric species) occurring at different sites (e.g., *Saimiri* spp., *Pithecia* spp., *Lagothrix* spp.).

Spatial Projections of Large Primate Depletion. Levi et al. (18, 19) parameterized and field tested a spatially explicit population model to project the impact of large primate hunting in space and time as a function of the number and spatial distribution of hunters, the frequency of hunts, the spatial distribution of hunting effort, and the efficiency of prey acquisition (kills per encounter). Because central-place hunters are typically limited by the distance that can be walked within 1 d, and must always walk near areas to access distant areas, hunting effort is highly concentrated near human dwellings (20, 21). The impact on wildlife is even more concentrated because the area of concentric annuli centered on a dwelling increases with distance from the central place. Thus, hunters not only expend less effort with distance, but there are many more animals available to reproduce farther from villages, which can compensate for mortality to produce a locally sustainable harvest and steady-state population density beyond some distance interval. We used a steady-state multisettlement model (19) to project the spatial impact of hunting on large primates by the 1,294,435 rural households mapped across the entire Legal Brazilian Amazon (915,877 of which within the phylogeographic boundaries of Brazilian Amazonia), assuming a single hunter per household. Georeferenced households were obtained as disaggregated data from the national census of the rural population throughout all nine states of the Brazilian Amazon (22). The model assumed logistic growth of spider monkeys (*Ateles* spp.) with a maximum intrinsic growth rate of $r = 0.07$, and carrying capacity, $K = 25$ (although this estimate does not influence model results if expressed as a percent of K). Based on previous research (14, 18, 19, 23), we assumed that hunters use firearms (kills per group encounter = 0.9), hunt 40 times per year, and have a spatial spread of hunting effort of $\sigma = 6$ km). This projection results in the spatial impact of unregulated hunting if all rural households hunt primates, but is an overestimate in regions

where taboos prevent hunting of large primates. As part of our mapping steps, we further removed all deforested areas across the Brazilian Amazon (as of 2012) based on a geographic information system mask derived from deforestation data within the phytogeographic boundaries of Brazilian Amazonia, obtained from the Brazilian Space Agency *PRODES* project (24).

Canopy Tree Inventories. We use tree species composition and forest structure data from forest volume surveys carried out by Projeto RADAMBRASIL (1973–1983) that comprehensively mapped forestry resources throughout Brazilian Amazonia (25). This is the largest tropical forest inventory program conducted to date, and represents the best available baseline data on relatively undisturbed Amazonian tree communities because most forest areas had not been subjected to biomass depletion through logging and human population density was very low, thereby being representative of nonhunted forests. The unparalleled coverage of the RADAMBRASIL dataset makes this the most reliable basis for indirect forest biomass estimates across the diverse vegetation types of Brazilian Amazonia (see review in ref. 26). All trees with a CBH ≥ 100 cm (or ≥ 31.8 cm in DBH) were sampled, except for arborescent palms. Woody lianas and hemiepiphytes, such as strangler figs, were also excluded (27). However, given the reverse J-curve in the bole diameter distribution of tropical forest trees, these canopy trees may represent only 8–17% of all trees ≥ 10 cm DBH in a typical Amazonian forest, but account for a disproportionately large contribution to the AGB in closed- and open-canopy forests (65.1–66.4%) (28). Although 2,719 1-ha (20 \times 500 m) tree plots were inventoried using this consistent size and minimum tree size cut-off, we considered data for only 129,720 canopy trees within 2,345 tree plots that contained at least 31 trees per plot (mean \pm SD = 55.32 ± 16.26).

Each plot-scale inventory included species names, tree DBH, the wood volume by species, and a description of the forest ecosystem. The 24 RADAMBRASIL volumes within Legal Amazonia, each of which cover a 4° latitude \times 6° longitude area (~ 29 million ha), contain a ~ 600 -page report describing the vegetation, soils, and other biophysical features; an ~ 700 -page supplement containing tables of wood volumes by species and diameter class for each plot, and a description of the ecosystem; and a packet of six 1:1,000,000-scale thematic maps. A total of 285 genera and 68 families of angiosperm trees, which were identified across all plots, were considered here (genus richness per plot: 25.73 ± 7.2 genera; range = 8–51, $n = 2,345$).

Tree identifications during the in situ execution of RADAMBRASIL forest inventories were made by experienced parobotanists using vernacular names, and later associated with a species Latin binomial or genus. Although most Amazonian forest inventories are based on common names, there are no detailed studies of the reliability of such a posteriori association of species names over the entire Amazon. However, 95% of all tree common names could be correctly identified to the genus level for Guyanan and Surinamese forests (29). Given the higher correspondence between common and genus names, we chose to work at this level of taxonomy. We examined how consistently genus names matched common names within the RADAMBRASIL database for 264 of the 285 tree genera considered in this study; 93% of common names and 88% of all inventoried trees were unambiguously associated with a single genus name. Although differences in botanical knowledge of parobotanists add a further unknown error, 25 forest engineers coordinated the inventories, aided by nine botanists who identified all trees (30). Inventory metadata indicate that each botanist worked in all parts of the region, and that foresters and botanists paired up in different combinations, thereby sharing a common set of tree identification techniques. These procedures tend to harmonize and homogenize species concepts between botanists and reduce spatially

clustered artifacts associated with any remaining idiosyncratic knowledge of each botanist. Genus nomenclature were updated using the Missouri Botanical Garden's Angiosperm Phylogeny (www.mobot.org/MOBOT/research/APweb/), w3Tropicos database (www.tropicos.org/) and the International Plant Names Index (ipni.org/index.html).

Forest Biomass Estimates. Our plot-scale oven-dry AGB estimates are based on tree density, tree size (DBH), and stem-specific wood density or WSG and were calculated using a widely accepted allometric relationship (31), which was later modified by Baker et al. (32). Because our AGB estimates cover a vast area including all major forest types of Amazonia, possible differences in wood density and tree height between subregions are likely (28, 33–35). However, our main intent here is to estimate relative changes in AGB within any given plot across modeled local floristic transitions, rather than absolute AGB values. We used WSG data based on the Global Wood Density database (36), which includes WSG measurements for 2,456 neotropical tree species. These were supplemented by local Amazonian floras in both seasonally flooded (Mamirauá) (34) and upland (terra firme) forests for two large landscapes (Jari, Pará, and Balbina, Amazonas) for which additional WSG data are available (37, 38). For the Balbina landscape, where we have species-specific trait data for 367 tree species ≥ 10 cm DBH (235 and 132 of which bearing fleshy and nonfleshy fruits, respectively), we also examined the relationship between seed mass and wood density (Fig. S4). We calculated mean WSG values for all 264 tree genera corresponding to the RADAMBRASIL database. Genus-level taxonomy in this dataset is highly reliable, whereas the same does not necessarily hold at the species level (27). For 21 (7.4%) genera that included 1,765 of the 129,720 trees sampled (1.36%), for which genus-level data were unavailable, we used the family-level mean WSG values. Like many other plant traits with a strong phylogenetic signal, WSG in neotropical trees tends to be taxonomically conservative and is significantly more variable between species in different genera than within congeners (39), so that the genus to which a tree belongs explains most of the variation in species-specific wood density (32, 40). This finding is supported by independent measurements of WSG values from directly harvested canopy trees of 397 species belonging to 187 genera occurring within a single forest landscape of northeastern Brazilian Amazonia, which shows that WSG is significantly different both at the tree genus and family levels (ANOVA, $P < 0.0001$) but not between congeners [nested ANOVA, $P = 0.96$; our analysis of dataset in ref. 37]. This finding supports the use of genus-level WSG data in this large-scale analysis.

Modeling Floristic Transitions. To estimate long-term changes in AGB (Δ_{AGB}) following extirpation of key dispersal agents of large-seeded trees, we first classified all trees within each plot based on their seed size class and primary abiotic or biotic seed-dispersal vectors, including wind, water, rodent scatter-hoanders, small birds, bats, small primates, large primates, and lowland tapir. A total of 65 of the 285 tree genera in our data are primarily dispersed by: (i) large-bodied, prehensile-tailed ateline primates, including woolly monkeys (*Lagothrix* spp.) and spider monkeys (*Ateles* spp.), but this excludes howler monkeys, which are more folivorous, do not ingest seeds as large as those ingested intact by *Lagothrix* and *Ateles*, and are more tolerant of HP (6); an additional 16 tree genera are primarily dispersed by (ii) tapir (*Tapirus terrestris*), the largest frugivorous ungulate in neotropical forests. These three genera of highly harvest-sensitive large mammals provide highly nonredundant seed dispersal services to many endozoochorous, large-seeded tree species in Amazonian forests (41, 42). This has been shown for large atelines at forest sites across the Brazilian, Peruvian, Bolivian, Colombian, Ecuadorian, and Venezuelan Amazon, and for

central Suriname (41, 43–50); and for lowland tapir wherever they have been studied in neotropical forests (42, 51–54). However, these taxa are consistently driven to local extinction or severely reduced in numbers in overhunted sites (6). Each tree was therefore classified as either “undispersed” or “dispersed” depending on whether they were expected to succumb to dispersal limitation following extirpation of either one or both of these two key functional groups of large-bodied frugivores (see list of plant genera in Table S1). Undispersed tree genera were typically heavy-wooded and highly abundant across the network of undisturbed tree plots, although their stems were no larger in terms of girth than those of dispersed tree genera (Fig. S3). Our floristic transition models based on this form of dispersal limitation assume that these species will become functionally extinct in persistently overhunted forests but are otherwise highly conservative because they do not take into account changes in population density of other midsized to large-bodied vertebrate frugivores that also decline in overhunted forests (6).

On the basis of an abundance-weighted lottery model, we randomly simulated species turnover to produce 1,000 new tree communities for each of the 2,345 forest plots under three different simulation scenarios. In our two large vertebrate extirpation scenarios, we randomly replaced all trees from the subset of species dispersed by either (i) large, prehensile-tailed ateline primates or (ii) both large ateline primates and tapirs with any other tree cooccurring in the same plot, but allocating proportionally higher replacement (gap colonization) probabilities to more abundant tree genera. Finally, in our “control” null-model tree reshuffling scenario, we randomly replaced the same number of trees substituted under scenarios I and II within each plot with any tree withdrawn from the complete cooccurring pool of trees, so that the number of tree replacements within different pairwise model comparisons (extirpation vs. null models) remained the same. Canopy tree plots examined here were highly variable in structure and composition, and contained 55.32 ± 16.26 trees (mean \pm SD; range = 31–153, $n = 2,345$) and a basal area of 11.63 ± 4.45 m²/ha (range = 3.52–47.49 m²/ha). However, plot-scale stem density and basal area are governed by many environmental gradients that range widely across the ~ 5 million km² Brazilian Amazon. When replacing trees within plots, we therefore retained the same number of trees, the same wood volume and the same aggregate basal area of the original plots, but substituted the WSG values of undispersed trees with those of a randomly drawn set of trees (for which the per capita colonization probability was proportional to the abundance of each cooccurring genus within each plot), which were not expected to succumb to dispersal limitation. We then recalculated the total AGB estimates for each of 1,000 simulated tree assemblages in each plot for each simulated extirpation scenario. Finally, we compared the distribution of AGB estimates in the 1,000 communities generated for each plot from each extirpation scenario to that of the random substitution scenario under a null model.

Accounting for Smaller Stems in AGB Estimates. Because the RADAMBRASIL forest inventory program was restricted to trees ≥ 100 cm CBH (≥ 31.83 cm DBH), we investigated the density and size-distribution relationships between this large-tree size class and all trees ≥ 10 cm DBH expected to cooccur within the same plot, because this is the widely standardized minimum size cut-off in tropical forest tree inventories (55). We compiled and analyzed our own AGB estimates for 69,504 stems above 10 cm DBH occurring in 295 plots that we sampled across the Brazilian Amazon, covering a combined area of 104 ha. These plots were widely distributed geographically and included primary forest areas

in seven of the nine Amazonian states in Brazil, a wide variety of soil types, and a proportionally similar composition of forest types as those covered by RADAMBRASIL. Based on those data, smaller trees between 10 and 31.83 cm DBH outnumbered those ≥ 31.83 cm DBH by a mean ratio of 8.41 ± 5.89 to one ($n = 295$ plots). However, the per capita contribution of large trees (≥ 31.83 cm DBH) in terms of aboveground phytomass and carbon storage was overwhelming. For example, the aggregate AGB estimate for the 7,827 large trees ≥ 31.83 cm DBH within our plots was greater than that of the 61,677 trees between 10 and 31.8 cm DBH in the same plots. We therefore calculated the AGB ratio between these two stem-size classes for each plot, which we then used to estimate the missing AGB component in the RADAMBRASIL plots to provide more comparable AGB and carbon storage estimates across this entire network of tree plots. On average, the 295 tree plots we sampled yielded an additional 94.4% (1.5–187.2%, ± 1 SD) in AGB by including the far more numerous but smaller subcanopy trees ≥ 10 cm DBH that were not surveyed by the RADAMBRASIL program. On average, therefore, a more than eightfold increase in tree density only nearly doubled the aggregate AGB in those plots.

Data Analysis. We tested for significant changes in AGB per hectare between the null replacement model at time t_0 and the two large-frugivore extirpation scenarios at time t_1 using paired t tests. In all cases, we use mean AGB estimates calculated for 1,000 randomly generated tree communities under the null replacement model compared with 1,000 communities under each of the two extirpation scenarios. We further correlated plot-scale variation in net changes in AGB [$\Delta_{\text{AGB}} = \text{mean}(\text{AGB}_{t_1} - \text{AGB}_{t_0})$] per plot given both variables describing the structure and taxonomic and functional composition of tree assemblages (mean DBH; stem density; number of tree genera; proportion of basal area contributed by trees bearing fleshy fruits; and mean WSG) and environmental data across the entire Brazilian Amazon that may affect tree species composition [annual rainfall, strength of the dry season (Walsh index), elevation above sea level (SRTM), and a basin-wide metric of soil fertility], and the degree to which large frugivores may have been overhunted (household density within a radius of 10 km of each tree plot). We used a simple information theoretic approach, based on the Akaike Information Criterion to evaluate model performance between simpler and more complex models. All statistical analyses were conducted in the R environment (56).

Areas with higher basal area density of canopy trees primarily dispersed by large primates are at greater risk of species turnover with potential negative changes in AGB and carbon storage. We hypothesized that such areas would be associated with lowland species-rich tree communities on relatively nutrient-rich soils, and that these sites would have higher average per stem wood density (WSG). To assess the characteristics of forest sites with high basal areas of undispersed trees in the large-bodied primate extirpation scenario, we used spatial multiple linear regression implemented with simultaneous autoregression using the *spautolm* function in the R package *spdep*. We used the aggregate basal area per plot of all trees that are primarily large-primate dispersed as the dependent variable and environmental covariates for plot scale WSG, genus diversity, soil fertility (57), strength of the dry season (Walsh index), and elevation above sea level. All variables were standardized before analysis to facilitate interpretation of effect sizes. We ran a separate spatial regression model using the density of human households within 10 km of each 1-ha forest plot to determine if settled areas are nonrandomly associated with sites most at risk for overhunting-induced loss of AGB.

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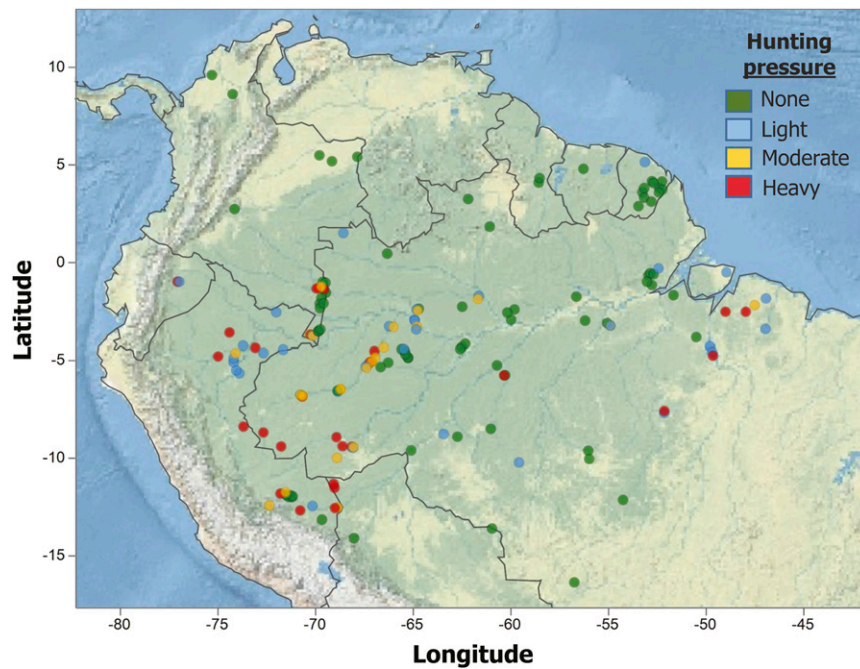


Fig. S1. Geographic location of 166 Amazonian and peri-Azonal forest sites on which forest primate population density estimates considered here are based. Survey sites are distributed across eight of the nine Amazonian countries. Nonhunted forest sites are indicated by green circles; lightly, moderately, and heavily hunted sites are indicated by blue, orange, and red circles, respectively. Overlapping symbols represent more than one spatially independent site within the same forest landscape. All sites had been hunted to varying degrees but were otherwise structurally intact and had not experienced forest habitat disturbance from selective logging, wildfires, and slash-and-burn agriculture, or edge effects from forest fragmentation.

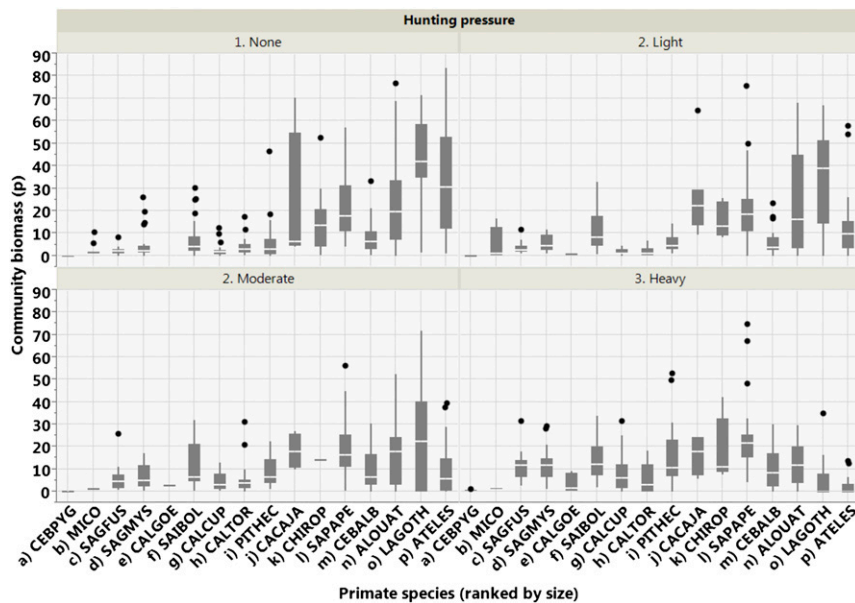


Fig. S2. Boxplots summarizing the proportion of the local community biomass density (kg/km^2) contributed by each of the 16 functional groups of Amazonian diurnal primates (ranked left to right from the smallest to the largest). Vertical bars show means and 50% quartiles; solid dots show outliers. The two large-bodied ateline genera (*Lagothrix* and *Ateles*) clearly dominate the community biomass of nonhunted forests, but are typically driven to local extinction in heavily hunted forests.

Table S1. Checklist of 104 Amazonian plant genera—including trees, high-climbing lianas, understory climbers, and epiphytes—that are hypothesized to succumb to severe seed dispersal limitation under the extinction scenarios proposed in this study

Family	Genera	Plant habit
Anacardiaceae	<i>Spondias, Anacardium</i>	Tree
Annonaceae	<i>Annona, Rollinia, some Duguetia Ephedranthus, Fusaea</i>	Tree
Araceae	<i>Heteropsis, Philodendron, Monstera</i>	Epiphyte
Arecaceae	<i>Socratea, Syagrus</i>	Tree
Bombacaceae	<i>Catostemma, Matisia</i>	Tree
Hippocrateaceae	<i>Cheiloclinium, Peritassa, Tontelea, Salacia</i>	Tree or liana
Chrysobalanaceae	<i>Couepia, several Licania, Parinari</i>	Tree
Convolvulaceae	<i>Lysiostyles, Dicranostyles, Maripa</i>	Liana
Cucurbitaceae	<i>Cayaponia</i>	Climber
Ebenaceae	<i>Diospyros</i>	Tree
Euphorbiaceae	<i>Omphalea</i>	Tree
Flacourtiaceae	<i>Casearia</i>	Tree
Gnetaceae	<i>Gnetum</i>	Liana
Clusiaceae	<i>Calophyllum, Moronobea, Platonina, Rheedia Symphonia, Tovomita</i>	Tree
Humiriaceae	<i>Sacoglottis, Schistostemon, Vantanea</i>	Tree
Icacinaceae	<i>Discophora, Emmotum, Leretia, Poraqueiba</i>	Tree or liana
Lauraceae	<i>Licaria, a few large-seeded Aniba, Nectandra, Rhodostemonodaphne, Ocotea</i>	Tree
Lecythidaceae	<i>Gustavia</i>	Tree
Legum: Caesalpiniaceae	<i>Dialium, some Cassia, Senna, Mora, Dimorphandra, Hymenaea, Peltogyne</i>	Tree
Legum: Papilionaceae	<i>Some Swartzia</i>	Tree
Legum: Mimosaceae	<i>Inga, Enterolobium, some indehiscent Abarema, Stryphnodendron, Zygia</i>	Tree
Loganiaceae	<i>Strychnos</i>	Liana
Melastomataceae	<i>Some large-seeded Mouriri</i>	Tree
Meliaceae	<i>Several Guarea</i>	Tree
Menispermaceae	<i>All Anomospermum, Abuta, Caryomene, Orthomene</i>	Tree
Moraceae	<i>Brosimum, Clarisia, Coussapoa, Helicostylis, Maquira, Naucleopsis, Perebea, Trymatococcus</i>	Tree
Myristicaceae	<i>Osteophloem, some Iryanthera, Virola</i>	Tree
Myrtaceae	<i>Some Eugenia</i>	Tree
Nyctaginaceae	<i>Neea</i>	Tree
Olacaceae	<i>Minquartia, Ptychopetalum</i>	Tree
Passifloraceae	<i>Dilkea, some hard-husked Passiflora</i>	Climber
Polygalaceae	<i>Moutabea</i>	Liana
Quiinaceae	<i>Lacunaria, Quiina</i>	Tree
Rubiaceae	<i>Duroia</i>	Tree
Sapindaceae	<i>Some Paullinia, Talisia</i>	Tree
Sapotaceae	<i>Chrysophyllum, Pouteria, Manilkara, Micropholis, Pradosia, Ecclinusa</i>	Tree
Simaroubaceae	<i>Simaba, Simarouba</i>	Tree
Sterculiaceae	<i>Guazuma, all Theobroma</i>	Tree
Tiliaceae	<i>Apeiba</i>	Tree
Ulmaceae	<i>Ampelocera</i>	Tree
Violaceae	<i>Leonia</i>	Tree