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Centuries of compounding human influence on Amazonian forests

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Recent evidence suggests that the ecological footprints of pre-Columbian Indigenous peoples in Amazonia persist in modern forests. Ecological impacts resulting from European colonization c. 1550 CE and the Amazonian Rubber Boom c. 1850 to 1920 CE are largely unexplored but could be important additive influences on forest structure and tree species composition. Using environmental niche models, we show the highest probabilities of pre-Columbian and colonial occupation sites, and hence human-induced ecological influences, occurred in forests along rivers. In many areas, the predicted pre-Columbian and colonial distributions overlap spatially with the potential for superimposed ecological influences. Environmental gradients are known to structure Amazonian vegetation composition, but they are also strong predictors of past human influence, both spatially and temporally. Our comparisons of model outputs with relative abundances of Amazonian tree species suggest that pre-Columbian and colonial-period ecological legacies are associated with modern forest composition.

ecological legacy | hyperdominance | Indigenous land use | colonization | tropical forest

The authors declare no competing interest.

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Tropical South America harbors immense biodiversity, including over 85,000 plant species (1). Amazonian rainforests comprise a ca. 6 million km^2 area in tropical South America and are estimated to contain ca. 16,000 tree species and over 390 billion trees (2). Of the 16,000 species, 227 (ca. 1.4%) are termed "hyperdominant" because they comprise half of the 390 billion trees in the forest. Biogeographic variation (Andean vs. Brazilian/Guianan plate material) and precipitation are the main drivers of variation in forest composition on basin-wide scales across Amazonia (3). Drivers of variation in plant communities on more local scales include hydrology and soil characteristics (e.g., refs. 4 and 5).

In the last decades, a growing body of evidence points to the possibility that many Amazonian forests were intentionally modified or indirectly impacted prior to the arrival of Europeans (hereafter, the pre-Columbian period) (6–9). Evidence of large, complex pre-Columbian societies has been uncovered in several regions of Amazonia (9–14). Pre-Columbian Indigenous people have been burning forests, growing crops, and altering the abundances of certain plant species (either intentionally or unintentionally) where they lived for thousands of years (15). The forests that were occupied by pre-Columbian people may still bear some form of imprint, or ecological legacy, on their tree species composition and carbon dynamics (8, 16–18). Pre-Columbian inhabitants are suggested to have increased the richness and abundances of domesticated tree species near archaeological sites (8), and the distribution of known archaeological sites is significantly and positively correlated with the distribution of forest plots that are used to measure tree diversity and abundance (19).

The discussion of ecological legacies of past human activities, however, largely ignores the colonization period (following European arrival) (20–23). The Great Dying of pre-Columbian people in the 1500 and 1600s due to disease, warfare, and enslavement would have resulted in forest regrowth that occurred only a few centuries ago (e.g., ref. 24). Colonial populations began new forms of land management (e.g., plantations), and the period was also characterized by the collapse, displacement, enslavement, and fragmentation of Indigenous populations (20, 25, 26). A particularly formative period for modern Amazonian population distributions was the "Rubber Boom" from approximately 1850 to 1920 (Common Era, CE). During this period, Amazonia became the center of extractive industries for not just rubber (derived from the processing of latex harvested from *Hevea brasiliensis* trees) but also for precious metals, timber, meat, animal skins, and natural oils (27, 28). Immigrants swelled the Amazonian populations, sometimes increasing populations of modern cities such as Belém do Pará, Manaus, and Porto Velho (Brazil) by as much as 400%. At the same time, the Indigenous populations, who constituted the majority of the labor force, were often relocated to meet the demands of the nascent industries (29, 30). Wood-burning ships, new colonists, and unprecedented commercial pressures on the Amazonian landscape led to extensive deforestation in many areas (31–33). Another wave of population decline happened when rubber trees were exported, and many plantations were abandoned. Because of the long lifespan of tropical trees, successional processes are likely ongoing even centuries after forests started to regrow (34, 35).

Wallace and Bates (36), along with other naturalists exploring Amazonia during the 1800s took advantage of the social infrastructure provided by colonists. The naturalists were heavily reliant on Indigenous peoples, guides, boatmen, and collectors (36–38). Many of the collection records of those naturalists are now being georeferenced, digitized, and archived in electronic repositories such as the Global Biodiversity Information Facility (GBIF; https://www.gbif.org). While explorations sometimes strayed quite far beyond colonial settlement sites, the locations of these collection records may represent the general area of collection sites or nearby trading sites because of the dependence of collectors on colonial infrastructure. Either way, these records arguably provide an estimate of the distribution of settlement hubs in Amazonia throughout the colonial history. These settlement hubs likely experienced greater forest alterations due to clearing for cultivation or plantations, construction, wood for steamboat fuel, and the defaunation of large vertebrates for bushmeat and the fur trade (28, 33), than areas farther from settlements.

We use the early GBIF records to create ensemble distribution models (39, 40) that predict the distribution of people across the landscape from early European colonization until the end of the Rubber Boom (i.e., 1600 to 1920 CE; hereafter the colonial period) (Fig. 1*A*). Likewise, we use a database containing over 7,363 georeferenced sites in Amazonia (https://sites.google.com/view/amazonarch/home) to model the distributions of pre-Columbian people (Fig. 1*A* and Dataset S1). We compare the modeled probabilities of pre-Columbian and colonial occupation patterns and compare the model outputs with the relative abundances of 262 hyperdominant and useful tree species recorded in 1,521 forest inventory plots spread throughout lowland Amazonia (2, 41). We hypothesize that: i) the relative abundances of hyperdominant tree species are inversely associated with the

Significance

Amazonian rainforests contain some of the highest biodiversity on Earth, but the extent to which modern forests are shaped by past human actions is unknown. Human activities potentially affect the richness and abundance of many Amazonian species, especially those considered to be useful. For thousands of years, forest management may have cumulatively altered forests that today appear to be completely natural. We generate models predicting the distribution of pre-Columbian Indigenous people (prior to 1550 CE) and the distribution of early colonists across Amazonia (1600 to 1920 CE). We find that certain common and useful plants have had their abundances increased or depleted by past human activities. We highlight the potential role of long-term human–environment interactions in shaping modern Amazonian forests.

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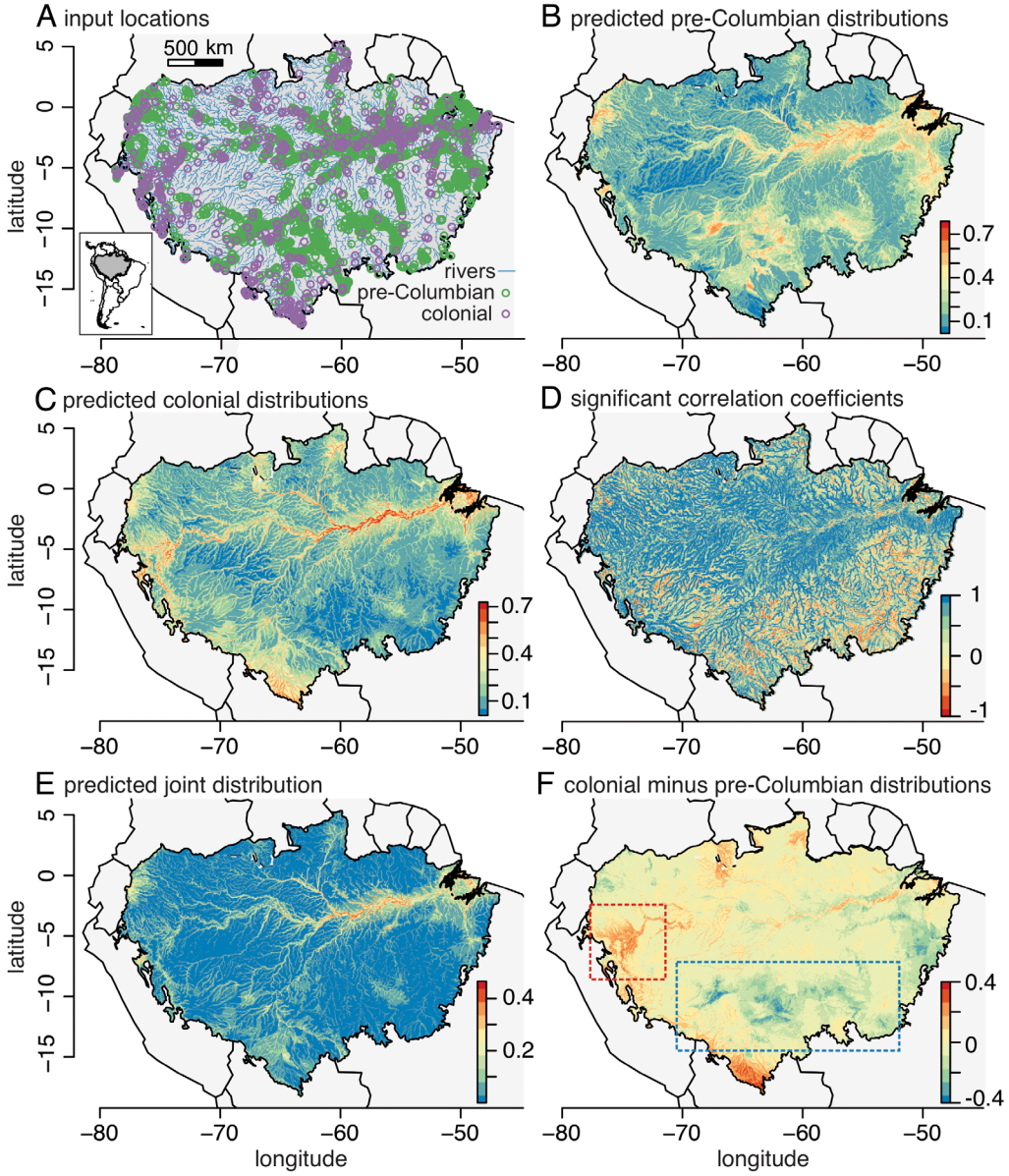

Fig. 1. Occurrence locations and species distribution models of people during the pre-Columbian and colonial periods in Amazonia. (*A*) Spatially filtered (10 km grid cell) occurrence locations of pre-Columbian sites from the AmazonArch database of archaeological sites (N = 6,960), and colonial sites represented by GBIF occurrence locations collected from 1600 to 1920 CE across all biological Kingdoms (N = 1,026). The limits of Amazonia sensu stricto (42) are shown as a gray polygon, and locations of major rivers (>4th order) are shown as blue lines. (*B* and *C*) Probabilities of human occupation during the pre-Columbian and colonial periods based on species distribution models generated using the site locations in panel *A* and a suite of environmental predictors (*Materials and Methods*); (*D*) Local Pearson correlation coefficients between the pre-Columbian and colonial model outputs; (*E*) Joint probability of pre-Columbian and colonial people (e.g., areas that were likely inhabited during both periods); and (*F*) Probability of colonial minus pre-Columbian occupation. Positive numbers indicate areas with higher probabilities of primarily colonial influences (i.e., Iquitos region—red dashed line) whereas more negative numbers indicate areas with primarily pre-Columbian influence (i.e., southern regions—blue dashed line).

probability of colonial influence, ii) the abundances of useful tree species are positively associated with the probability of pre-Columbian or colonial influence, and iii) the relative abundances of early and mid-successional tree species are positively associated with high probabilities of colonial influence.

Results

The ensemble distribution model of pre-Columbian people (Fig. 1*B*) had an AUC value of 0.82 (Dataset S2). Distance from river (*SI Appendix*, Fig. S1) was the most important predictor variable and accounted for 21.5% of the permutation importance in the pre-Columbian model. As with the distribution model of colonial people, settlement probabilities of people were substantially lower at distances >10 km from a fourth-order river (*SI Appendix*, Fig. S2). In both the colonial and pre-Columbian models, elevation (*SI Appendix*, Fig. S1) was the second-most important variable, though it had less than 10% of the permutation importance (Dataset S3) in either model. Given the flatness of Amazonia, elevation is functionally a metric of western (higher) to eastern (lower) geographic placement and thus indicated the higher occupation likelihood of eastern and central Amazonia than the western regions.

The compilation of GBIF data collected during the colonial period and the resulting ensemble distribution model indicated that the highest likelihoods of colonization were along the main Amazon River and its major tributaries (Fig. 1*C*). Probabilities of settlement during the colonial period ranged from 0.006 to 0.75

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and had an AUC value of 0.76 (Dataset S2). Distance from river (*SI Appendix*, Fig. S1) was the most important predictor variable, accounting for 39.5% of the permutation importance in the colonial ensemble model (Dataset S3). Settlement probabilities decreased as distance from river increased, particularly beyond 5 km (*SI Appendix*, Fig. S2).

The modeled distributions of people in the pre-Columbian and colonial periods were positively and significantly correlated (R = 0.56, $P < 0.001$) (Fig. 1*D*). The joint probability model outputs, which reflected the probability of both pre-Columbian and colonial land use, ranged from 0 to 0.47, with the highest values most visible in central and southwestern Amazonia (Fig. 1*E*). Correlations were weaker and even negative in some areas along the periphery of the basin. The calculation of colonial minus pre-Columbian distributions shows that colonial influence was likely stronger than pre-Columbian in the Iquitos region (dashed red line), but the pre-Columbian (and modern) influence was likely stronger in the geoglyph and earthworks region of southern Amazonia (dashed blue line) (Fig. 1*F*).

At the forest inventory plot locations (N = 1,521), the probabilities of colonial human activity ranged from 0.007 to 0.75, compared with probabilities of 0.05 to 0.65 for the pre-Columbian period (Fig. 2). The relative abundances of useful tree species (summed across all categories of use) were significantly and positively correlated with both pre-Columbian and colonial influence (Fig. 2). Summed relative abundances of useful species were highest in plots where the probability of pre-Columbian influence exceeded 0.4, particularly in eastern Amazonia, and the probability of colonial influence exceeded 0.3, particularly in northwestern Amazonia (Fig. 2). Correlation coefficients between abundances and the probabilities of colonial and pre-Columbian settlements did not differ between life strategies (early successional, mid-successional, or late successional) (Fig. 3) or category of use (food, construction, etc.).

Tree species tended to exhibit both pre-Columbian and colonial enrichment, or both pre-Columbian and colonial depletion (Fig. 3). Out of the 262 assessed tree species, the abundances of 133 (51%) were significantly correlated with model predictions of pre-Columbian people, the abundances of 152 species (58%) were significantly correlated with model predictions of colonial distributions, and the abundances of 91 species (35%) were significantly correlated with predictions of overlapping pre-Columbian and colonial distributions (Dataset S1). Of the 152 tree species significantly correlated with probabilities of colonial settlements, 91 had negative correlation coefficients and 61 had positive ones (Dataset S4). Of the 133 species significantly correlated with probabilities of pre-Columbian settlements, 73 had negative and 60 positive correlation coefficients.

Species rarely exhibited colonial enrichment and pre-Columbian depletion (Fig. 3). There were, however, some hyperdominant and useful species, including *Bertholletia excelsa* (Brazil nut), that exhibited pre-Columbian enrichment and colonial depletion. The correlation coefficients between settlement probability and species abundances did not show patterns with the use of the plant (e.g., plants used for construction did not show negative correlation coefficients indicating depletion). Life history strategy also showed no pattern with colonial and pre-Columbian correlation coefficients (Fig. 3).

Discussion

The data supported our hypothesis that useful species abundances were generally higher in plots where probabilities of pre-Columbian and colonial influence were higher (Fig. 2). Our findings, however, did not support the hypotheses that higher probabilities of colonial influence would decrease the relative abundances of hyperdominant species and increase the abundances of early successional species (Figs. 2 and 3). As most forest plots were intentionally placed in structurally mature forests, there were only 15 early successional species in our dataset, and about half were related to pre-Columbian or colonial activity (Fig. 3). Instead, increased abundances of the early successional species are likely related to modern disturbances, including ongoing and continual canopy gap dynamics (e.g., refs. 34 and 43).

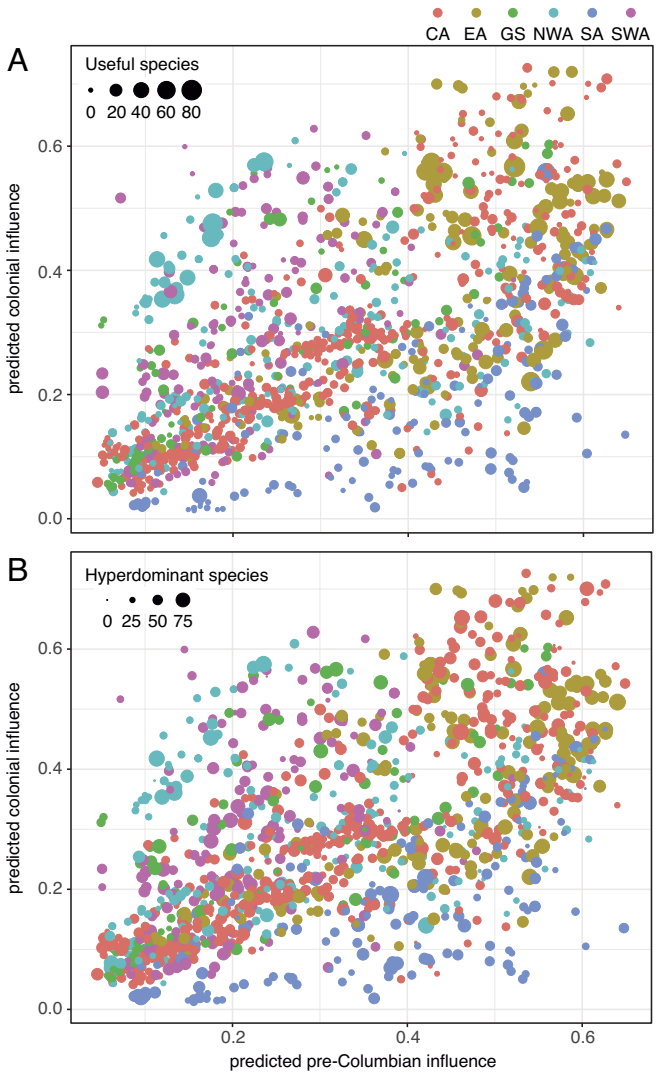

Fig. 2. Predicted probabilities of pre-Columbian and colonial influence at 1,521 Amazonian forest plots (circles). The colors represent the geographic region of the plots (sensu 2): CA = Central Amazonia, EA = Eastern Amazonia, GS = Guiana Shield, NWA = Northwestern Amazonia, SA = Southern Amazonia, SWA = Southwestern Amazonia. The sizes of the circles represent the percentages of (*A*) useful (sensu 75) or (*B*) hyperdominant (sensu 2) species found in the plot.

Spatial Patterns of Pre-Columbian and Colonial Forest Modifications. Previously published models of pre-Columbian population distributions (19, 44, 45) were run with a limited set of (<1,000) occurrence locations based on known archaeological sites. We updated those original models using the AmazonArch database, which contained over 7,000 archaeological sites in the Amazon (before geographic filtering by the model) including ADE and earthworks where most, but not all, were pre-Columbian in

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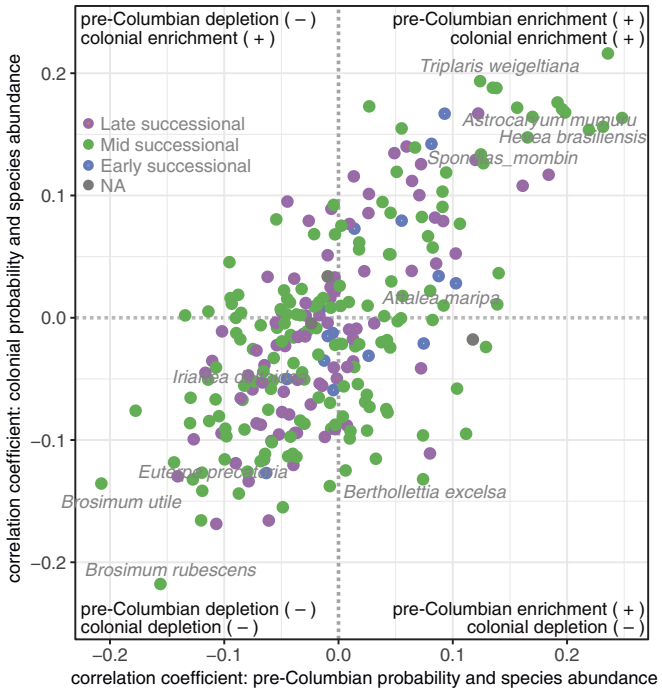

Fig. 3. Correlation coefficients between the relative abundances of 262 hyperdominant and useful Amazonian tree species and model predictions of pre-Columbian and colonial influence. Color indicates whether the species is a pioneer, mid-successional, or late-successional species.

age (Fig. 1 *A* and *B* and Dataset S1). The overall pattern that pre-Columbian human populations congregated around waterways remains a predominant feature in the current and previously published models (19, 44), including those where only material dated in the pre-Columbian period was used (46). The models updated with the AmazonArch sites, however, help the model differentiate probabilities of occupation in interfluvial areas that were more sparsely populated than those close to rivers.

We also used an ensemble modeling approach, which included running the environmental data and occurrence points (model inputs) through a series of algorithms typically used in species distribution models, evaluating the performance of those models, and generating an output based on the weighted average of best-performing models (39). Because the AmazonArch sites extended past the geographical boundaries of the previous dataset, the predicted distribution of pre-Columbian has also expanded. Our updated model (Fig. 1*B*) generated high probabilities for occupation in both the terra preta-rich regions of eastern Amazonia and along the main river channels (44) and the earthwork-rich regions of southwestern and southern Amazonia (9). These probabilities are more realistic than those previously published because of the inclusion of smaller archaeological sites in interfluvial regions.

Europeans began mapping the coastal region of Amazonia in 1499, and the first expedition navigated the length of the Amazon River in 1541 CE (47, 48). Our ensemble distribution model using collection records to predict colonist settlement activity is in broad agreement with historical descriptions and maps of early European expeditions, Jesuit mission locations, and hotspots of the Amazonian Rubber Boom (26, 31–33, 47, 49, 50) (Fig. 1*C* and *SI Appendix*, Figs. S3–S5). Historical records document Jesuit missions and trade networks from 1538 to 1638 CE along the Marañon and Napo Rivers in Ecuador and Peru, the Rio Negro in Brazil, and along the main Amazon River (51) (*SI Appendix*, Fig. S3). Historical maps of South America show that only the main Amazon channel and several of its main tributaries had been explored by colonists by ca. 1700 CE (52, 53) (*SI Appendix*, Fig. S3), but many other tributaries were explored in the next few decades (54, 55) (*SI Appendix*, Fig. S4). Early biological collectors, including Spruce, Wallace, and Bates, traveled through Amazonia before the onset of the Rubber Boom and described how many settlements were located on the main channels (36, 38, 56, 57). During the Rubber Boom (ca. 1850 to 1920 CE), major cities—e.g., Manaus, Belém, Santarém, Porto Velho, and Rio Branco—developed as ports servicing the growing industrial might of Amazonian commerce (31–33, 58, 59) (*SI Appendix*, Fig. S5). At the same time, the Madeira, a white-water river with fertile floodplains, became a center of timber extraction (32) (*SI Appendix*, Fig. S5). With the development of these cities came a high demand for wood and charcoal to fuel boats back to Europe (until the onset of oil-fueled boats in the 1920s). The close agreement between historical maps and the collection locations (Fig. 1*A* and *SI Appendix*, Figs. S3–S5) suggests that GBIF records provide a worthy archive to model the distribution of colonists in Amazonia (Fig. 1*C*).

Rivers form areas of new colonization opportunity (e.g., sandbars) for people and plants. Rivers also determined accessibility, connectivity, and cultural transmission within the forests, and played a large role in structuring the distribution of people during the pre-Columbian and colonial period in Amazonia (44, 60–65) (Fig. 1). The occupants of Amazonia today also commonly settle the riverine environments (22, 66). This consistent dependence on the rivers for accessibility, connectivity, and tradable goods indicates that some riverine forests have undoubtedly been occupied and abandoned multiple times throughout the last several millennia, particularly those located within 10 km of a major river (i.e., a fourth-order river, Fig. 1*E* and *SI Appendix*, Fig. S2) (19, 22). Our models predicted that areas along the main Amazon River channel from Manaus to Belém were likely occupied both during the pre-Columbian and colonial period, as were regions of the Bolivian Beni and western Amazonia (Fig. 1 *D* and *E*). Though it is possible that the dependence on rivers is an artifact of collection of both ecological and archaeological data, it is unlikely. The ATDN dataset includes 391 sites that are >10 km away from a river. In the AmazonArch database, 1,675 out of 7,363 sites were >10 km away from a river. Fire and vegetation reconstructions from charcoal and phytoliths (silica microfossils) found in western and central Amazonian soils show a lighter human footprint in the interfluvial regions compared with locations found within 5 km of a large river (61, 63, 64). Models predicting the distributions of earthworks and Amazonian Dark Earths also suggest that interfluvial areas were more sparsely populated than riverine locations (9, 44). But while sampling is not optimal in either case, it is likely that the same factors driving population distributions today also drove them in the past.

It is important to note that we do not contend that there was no occupation of forests >10 km from rivers by people during the pre-Columbian or colonial period. Some archaeological features, such as the geoglyphs and earthworks in southwestern and southern Amazonia, were created in nonriverine areas during the pre-Columbian period (9, 11, 67, 68). In the colonial period, Indigenous people were displaced and fragmented (69, 70). This displacement, primarily away from rivers and into the terra firme forests also caused changes in the way Indigenous people used the lands that they occupied (69). Further, while the areas that were occupied by the European settlers were primarily along river corridors, the impacts of activities such as hunting likely extended

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further back into terra firme areas (28). In some locations, however, Indigenous people managed to resist colonialism and even impeded efforts of deforestation (71).

Ecological Legacies in Amazonian Forests. Our analyses support hypotheses that past human activities left lasting ecological legacies on modern Amazonian forests that may have been direct or indirect, intentional or unintentional (8, 17–19, 72). Many studies of legacies focus on the enrichment (increase of local abundances and/or enlargement of geographic distributions) of useful species as the primary legacy effect on Amazonian forests (6, 8, 73). Our data show that both pre-Columbian and colonial enrichment happened with some species, such as *Triplaris weigeltiana*, *Astrocaryum murumuru* (Arecaceae), *Hevea brasiliensis* (Euphorbiaceae), and *Spondias mombin* (Anacardiaceae) (Fig. 3). Three of these species are used as either food or construction but *T. weigeltiana* has no known use (Dataset S4). *T. weigeltiana*, however, grows fast and can reproduce vegetatively (is a pioneer) (74) and likely increased during both the pre-Columbian and colonial periods via an increase in forest clearing. This species can even grow as a monodominant on some nutrient poor floodplains (75). *H. brasiliensis* was arguably the most exploited and potentially enriched species in Amazonia during the Rubber Boom (32, 33), but Indigenous people also used the rubber for medicinal and other purposes (76) (Fig. 3 and Dataset S4). *A. murumuru* is used by multiple Indigenous groups (77) and is a successful gap colonizer (78). *S. mombin* is a species in the process of domestication, and is often planted alongside *Theobroma grandiflorum* in agroforestry systems (79).

Depletions of palms such as *Mauritia flexuosa* and *Iriartea deltoidea* have been documented in recent decades (80–82). Our results show that depletions have also likely happened over longer timespans. The relative abundances of several tree species, such as *Brosimum* spp. (Moraceae), *Euterpe precatoria* and *I. deltoidea* (both Arecaceae) were higher in forest inventory plots where the likelihood of pre-Columbian and colonial occupation was lower (Fig. 3). *I. deltoidea* is a palm that is commonly used for construction. Phytolith data from terrestrial soils show that the abundances of phytoliths produced by these genera are higher when other signals of human activity (i.e., fire, cultivation) are low (63, 64, 83). Data from lake sediment records have shown that populations of *I. deltoidea* rebound in the centuries following site abandonment (84).

Ecological legacies are complex. Pre-Columbian people likely enriched some species and colonial people depleted it, but not the other way round. A key example is *Bertholletia excelsa* (Lecythidaceae), known globally as the Brazil Nut (Fig. 3). However, land use (i.e., fire, cultivation, forest opening) can vary across geographic region. *Brosimum* is a mid-succession hardwood genus, whose members are commonly used for construction, medicine, and in some cases food. In our study *Brosimum* spp. were in higher abundances when the probabilities of human influence were lower (Fig. 3).

A significant question arises from these observations: Did people select forests rich in favored species as a homesite, or did people actively enrich or deplete existing forests? This ambiguity between correlation and causation is difficult to resolve, but is perhaps most likely to be correlational, i.e., people selecting a naturally rich area in the cases of long-lived species being targeted for extraction, such as *H. brasiliensis* during the Rubber Boom. Both in the past and even today, people primarily chose to live beside rivers for many reasons, and then likely adapted to using species from riverine settings. Hence, people and a large subset of useful trees tend to co-occur naturally at high densities along rivers. Causal relationships may be inferred when a species is found outside of its natural range (8, 9, 85, 86). A blended pattern in which correlational richness of useful species might trigger the initial settlement choice, but subsequent enrichment occurring as a consequence may shape the history of some forests. For example, in some forest plots in Bolivia >60% of the individuals are domesticated species (8).

Ecological legacies may also result from soil modifications, successional processes following human activities (or site abandonment), or from defaunation of seed dispersers in the landscape (18, 84, 87–89). Up to 84% of Amazonian tree individuals may be useful in some form (90), but the form of plant usage can change across space (i.e., between groups of Indigenous people) and through time, potentially confounding comparisons of usefulness. Our analysis was also limited to Amazonian trees that reach >10 cm diameter at breast height (DBH), and it is likely that many intentionally used plants fall into smaller size classes as they are easier to manage or produce fruit earlier than larger species (91). In many cases, these smaller plants (and cultivated or crop plants) tend to have shorter lifespans, and the legacy effects on modern forests may not be as strong as with the trees that obtain larger sizes and often live more than several hundred years.

Time is important in structuring ecological legacies on vegetation, both the duration of influence and the time since active management or abandonment. The earliest inhabitants were located along the main Amazon River, and began spreading out through the interfluvial regions shortly afterward (14). The pre-Columbian influence in some regions could thus have built over millennia, whereas effects during the colonial period lasted centuries at most. Some regions experienced compounding ecological legacies from both periods. In northwestern Amazonia, for example, the city of Iquitos grew from Jesuit missions, but became a center of power during the colonial era (red dashed line, Fig. 1*F*) (26). Paleoecological data, which were not used to build the model and were completely independent of it, showed that while pre-Columbian people lived in the Iquitos region for millennia, their ecological impact was light until the last few hundred years (92). The paleoecological data also showed that pre-Columbian human activities seemed to be more frequent and intense in some areas along the Napo River in Ecuador compared with northern Peru and Iquitos (63, 64, 93, 94). Not as many colonial records (Fig. 1) were collected from some of the geoglyph-rich regions of southern Amazonia (9), so the pre-Columbian influence on plant communities was likely stronger than the colonial influence (red dashed lines, Fig. 1*F*).

Parsing apart the effects of ecological legacies and environmental gradients poses challenges. Precipitation gradients structure regional patterns of species richness and abundance (3, 4, 95–97), which in turn structure spatial patterns of forest functionality and carbon storage (98, 99). Soil fertility, hydrological gradients, and topographical gradients are responsible for shaping their local patterns (e.g., refs. 4, 5, and 100–103). Forests with lower wood density tend to occur on richer and less well-drained soils such as alluvial floodplains (104). Constant river migrations cause alluvial (riverine) settings to maintain floras rich in early and mid-successional species (101), which also tend to be recognized as useful species (Dataset S4). In the riverine settings where both pre-Columbian and colonial influences were probably highest, ecological legacies added to the array of environmental factors shaping forest vegetation. Future research integrating paleoecological data (i.e., phytolith, charcoal, pollen) with soils and vegetation data measured in both riverine and terra firme forest plots is a promising avenue to comprehensively assess drivers of local plant composition.

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Our data support the suggestion that ecological studies of modern systems should consider the potential lasting impacts of past human activities (e.g., refs. 8, 16, and 105). We show that human impacts in the pre-Columbian and colonial period are potentially important factors to consider if modern vegetation dynamics are to be understood (*SI Appendix*, Figs. S3 and S4). Naturally, the era of modern disturbance cannot be overlooked (22, 88), but it is often so obvious as to be unambiguous and readily recognized. Of more interest to predicting rates of forest change, growth, and their capacity to absorb carbon accurately are the potentially hidden changes that affected forests as recently as 1920 CE (20, 28). Many of the ATDN forest sites are located within a day's walk from villages that were founded during the Rubber Boom. Thus for at least the last 175 y they have experienced direct or indirect effects (e.g., hunting) that may be shaping the current abundance of surveyed trees (106, 107).

Our understanding of Amazonian ecology and carbon budgets obtained from forest inventory plots may largely be a "shifted baseline" (108) if the forests that are considered to be mature in plant surveys are actually still recovering from disturbances that occurred over the last several decades to centuries. At any given time, an old-growth forest is composed of a matrix of various successional states due to gap dynamics (e.g., refs. 34 and 35). Human activity typically increases gap extent and frequency and creates edges and edge effects. At the end of the Rubber Boom period around 1920 CE many of these human-created gaps would have been abandoned and successional regrowth would have begun. Less than 100 y later, in the early 2000s, increased rates of above ground biomass accumulation were documented in Amazonian forest plots that showed no sign of recent disturbance (i.e., are not early successional) (109). Biomass accumulation rates in the plots slowed down a decade later, which was attributed to increased tree mortality (110). Successional trajectories following site abandonment in tropical forests typically show similar biomass accumulation rates that increase for decades but then level off, or slow down, after more than a century of recovery (111), potentially due to the mortality of high abundances of mid-successional trees (112). We suggest that the increases and decreases documented in biomass accumulation rates over the last several decades may be partially driven by colonial era site abandonment and forests being in a state of late succession.

Dated charcoal fragments from Amazonian forest plots show that the time since the last fire ranges from decades to thousands of years (93, 113–115), and some of these recent fires may still be affecting modern soil carbon storage patterns (72, 116). Fire can cause significant changes in forest composition and soil properties (117) and can alter successional trajectories for hundreds of years (18, 35). We recommend an increased effort to obtain estimates of forest age based on dated charcoal fragments and vegetation histories based on plant microfossils such as phytoliths from within forest inventory and recensus plots (83, 93, 113, 115) so that successional stages and trajectories can be considered when predicting how forests respond to global change. Establishing a matrix of reference sites where past human impacts were probably minimal will be critically important for determining the cultural legacies and long-term influence of people on the ecology and carbon sequestration patterns of Amazonian forests.

Materials and Methods

Generating Models of the Distributions of Pre-Columbian and Colonial People. To assess ecological legacies of past human activity on modern forest composition in Amazonia sensu stricto, which includes all lowland areas <500 masl that drain directly into the Amazon River (42), we required three datasets: i) predictions of the distribution of pre-Columbian people, ii) predictions of the distribution of people during the colonial period, and iii) information on the relative abundances of plant species as based on modern botanical inventories. We updated previously published models of the likely distributions of pre-Columbian people (19, 44) using 7,363 locations within Amazonia sensu stricto from the AmazonArch database (https://sites.google.com/view/amazonarch) (Dataset S1). Archaeological site information in the AmazonArch database was compiled, systematized, and georeferenced by a network of archaeologists with a common goal of sharing data. We collated data on biological collections and occurrences from across all biological kingdoms that have been georeferenced to within Amazonia sensu stricto for the colonial period (early colonization through the end of the Rubber Boom, 1600 to 1920 CE; N = 109,438) using data publicly available through the Global Biodiversity Information Facility (https://www.gbif.org). To reduce the effect of sampling bias on predictive models, all occurrence locations falling within the same 10 km^2 grid cell were reduced to a single occurrence location (118). After spatial filtering, 6,960 and 1,026 occurrence points remained (Dataset S5 and Fig. 1) for the pre-Columbian and colonial periods, respectively, and these points were used in subsequent geospatial models.

To generate models predicting the distributions of pre-Columbian and colonial people, we compiled bioclimatic, soil, and terrain-based data layers to use as predictor variables. Bioclimatic variables (N = 19) describe annual averages or extreme values in temperature and precipitation, and were obtained at 30 arc second resolution (ca. 1 km^2) resolution from the WorldClim database (119). Variables of soil characteristics (N = 22) were retrieved at 30 arc second resolution from the Harmonized World Soil Database (120). We performed cross-correlation analyses in each group to reduce the number of predictor variables (44, 121, 122). The Spearman correlation coefficients for all pairwise-comparisons of the bioclimatic (Dataset S6) and soil variables (Dataset S7) were calculated, and variables with correlation coefficients of >0.75 were considered highly correlated. Of the highly correlated variables, we retained those that had the least number of "no-data" values (missing data) or were easiest to interpret ecologically or in the context of human activities. We retained mean annual temperature (BIO1), maximum temperature of warmest month (BIO5), total annual precipitation (BIO12), precipitation of the driest quarter (BIO17) and subsoil percentages of clay, organic carbon, and silt (*SI Appendix*, Fig. S2).

We also generated predictor variables based on terrain and hydrological characteristics. Data on rivers were retrieved from the HydroSheds database (https://www.hydrosheds.org), where rivers were characterized by river order at 15 arc second spatial resolution (123). We used the HydroRivers dataset with 4th order rivers and greater in the models, where 1st order rivers are springs or streams with no tributaries feeding it and the main Amazon River is a 12th order. Fourth-order rivers represent water channels large enough to remain inundated year-round. We then calculated the straight-line distance to the nearest defined river for each Amazonian grid cell at 30 arc second spatial resolution. The resulting raster layer of distance-to-river was used as a predictor variable (*SI Appendix*, Fig. S2). We also used elevation data obtained from Shuttle Radar Topography Mission at 90-m spatial resolution (124) (*SI Appendix*, Fig. S2). Using the elevation data, we also generated a metric of terrain roughness, which is the difference between the maximum and minimum elevation for a given grid cell and its eight neighboring grid cells (125) (*SI Appendix*, Fig. S2). All predictor variables included in the model (N = 10) were generated or resampled from their native resolution to a common resolution of 5 arc minutes (approx. 10 km^2 at the equator) across Amazonia sensu stricto (*SI Appendix*, Fig. S2).

Different distribution modeling algorithms (39, 126, 127) will result in different predictions, so we used an ensemble distribution model based on the weighted averages of the following distribution modeling algorithms: i) a generalized linear model, ii) a generalized boosted regression model (128), iii) a generalized additive model (129, 130), iv) a random forest model (131), and v) a Maxent model (132). Each of these modeling algorithms has been shown to perform well using simulated species with known distributions and empirical data on species–environment relationships (133). For each algorithm, we used the default settings for species distribution modeling using the *ensemble_modelling* function of the "SSDM" package (134) in R (135).

Each model relies on the generation of pseudoabsences to compare the occurrence records with the environmental characteristics, and we used the settings recommended by Barbet-Massin et al. (136). Each model was run with fivefold cross-validation and was then repeated ten times to generate a final model. The performance of each distribution model was evaluated

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using "area under the receiver operating curve" (AUC) scores, which assess the ability of a model to distinguish presence and absence locations compared with random expectation (AUC = 0.5) (127, 137). AUC scores of the models had to exceed 0.6 to be included in the ensemble model. The AUC scores for each model provided the weighting for the final ensemble distribution model so that better-performing models had a stronger influence on the final predicted distribution. Pearson correlation coefficients between the full model and models lacking individual predictor variables were used to assess the relative importance of each of the predictor variables in the ensemble model (138).

We performed ensemble modeling using the occurrence locations for the pre-Columbian and colonial (individually) periods and then assessed correlations between the two model outputs. We calculated the joint probability of pre-Columbian and colonial model outputs to identify areas that were most likely to have been occupied during both periods. We also calculated the local Pearson correlation coefficients across Amazonia using a moving spatial window of 50 km^2 and identified areas that were significantly correlated between the pre-Columbian and colonial models. We also calculated the direction of those correlation coefficients (positive or negative).

Comparing Pre- and Post-Columbian Model Outputs with Forest Inventory Data. We compared the pre-Columbian and colonial model outputs with relative abundance (stems per hectare) estimates for 262 tree species previously categorized as being hyperdominant (2) or useful, respectively (Dataset S4) censused across 1,521 tree inventory plots included in the Amazonian Tree Diversity Network (ATDN) (41, 98) (Dataset S8). The Amazon Tree Diversity Network is a network of botanists, ecologists, and taxonomists who share data across Amazonia and the Guiana Shield regions (https://sites.google.com/naturalis.nl/amazon-tree-diversity-network/homepage). The 1,521 tree inventory plots used in the analyses were collected across studies, years, and regions, and include sites from terra firme forests, varzeas, igapos, and white sand habitats (41). Taxonomic names were standardized and updated for the analysis (41). For each tree species, we also compiled characteristics on the type of use, and we assigned each species into categories of food, construction, food and construction, other (e.g., medicinal use), or nonuseful hyperdominant. We also assigned each species into life history strategy categories of either early successional, mid-successional, or mature forest, which were based on characterizations of genus-level trait data on seed mass and wood density (Dataset S4) (139). Species were characterized as early successional if they had a wood density <0.7 and seed mass category < than five, mid-successional if they had a wood density less than 0.7 but seed mass category ≥5, and mature forest if wood density exceeded 0.7 (139). While this is a simplification, it has been shown to represent most species properly on the pioneer-old growth trait continuum and is necessary to categorize so many species (75, 140, 141).

We extracted the predicted values for the likelihood of pre-Columbian and colonial occupation at each of the 1,521 forest plot locations. Pearson's correlation tests were then used to determine associations between pre-Columbian and colonial model predictions across the plots, and between the model predictions and the relative abundances of each of the focal tree species. We examined the distribution of correlation coefficients between categories of use and life history strategies to test for differential effects of human disturbance on the different groups of tree species.

All analyses were performed in RStudio Version 1.2 (135) using the "raster" (142), "rgdal" (143), "rgeos" (143), "SSDM" (134), and "ggplot" (144) packages.

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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1. K. J. Feeley, M. R. Silman, The data void in modeling current and future distributions of tropical species. *Glob. Change Biol.* **17**, 626–630 (2011).
2. H. ter Steege *et al.*, Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092 (2013).
3. B. G. Luize *et al.*, The biogeography of the Amazonian tree flora. *Commun. Biol.* **7**, 1240 (2024).
4. N. C. A. Pitman *et al.*, Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* **82**, 2101–2117 (2001).
5. R. Montufar, J.-C. Pintaud, Variation in species composition, abundance and microhabitat preferences among western Amazonian terra firme palm communities. *Bot. J. Linn. Soc.* **151**, 127–140 (2006).
6. W. Balée, C. L. Erickson, *Time, Complexity, and Historical Ecology* (Columbia University Press, New York, NY, 2006).
7. P. Roberts, C. Hunt, M. Arroyo-Kalin, D. Evans, N. Boivin, The deep human prehistory of global tropical forests and its relevance for modern conservation. *Nat. Plants* **3**, 17093 (2017).
8. C. Levis *et al.*, Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science* **355**, 925–931 (2017).
9. V. Peripato *et al.*, Over 10,000 pre-Columbian earthworks are still hidden throughout Amazonia. *Science* **382**, 103–109 (2023).
10. M. Heckenberger *et al.*, Pre-Columbian urbanism, anthropogenic landscapes, and the future of the Amazon. *Science* **321**, 1214–1217 (2008).
11. M. Pärssinen, A. Ranzi, S. Saunaluoma, A. Siiriäinen, "Geometrically patterned ancient earthworks in the Rio Branco region of Acre, Brazil: New evidence of ancient chiefdom formations in Amazonian interfluvial terra firme environment" in *Western Amazonia–Amazonia Ocidental*, M. Pärssinen, A. Korpisaari, Eds. (University of Helsinki, Renvall Institute for Area and Cultural Studies, Helsinki, Finland, 2003), vol. 14, pp. 97–133.
12. S. Rostain *et al.*, Two thousand years of garden urbanism in the Upper Amazon. *Science* **383**, 183–189 (2024).
13. A. C. Roosevelt, *Moundbuilders of the Amazon: Geophysical Archaeology on Marajó Island, Brazil* (Academic Press, San Diego, CA, 1991).
14. A. C. Roosevelt, The Amazon and the anthropocene: 13,000 years of human influence in a tropical rainforest. *Anthropocene* **4**, 69–87 (2013).
15. J. R. Oliver, "The archaeology of agriculture in ancient Amazonia" in *The Handbook of South American Archaeology*, H. Silverman, W. H. Isbell, Eds. (Springer New York, NY, 2008), pp. 185–216.
16. W. Balée, "The culture of Amazonian forests" in *Resource Management in Amazonia: Indigenous and Folk Strategies*, D. A. Posey, W. Balée, Eds. (New York Botanical Garden, New York, NY, 1989), pp. 1–21.
17. C. R. Clement *et al.*, The domestication of Amazonia before European conquest. *Proc. R. Soc. B* **282**, 20150813 (**2015**).
18. C. N. McMichael, Ecological legacies of past human activities in Amazonian forests. *New Phytol.* **229**, 2492–2496 (2021).
19. C. N. H. McMichael, F. Matthews-Bird, W. Farfan-Rios, K. J. Feeley, Ancient human disturbances may be skewing our understanding of Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 522–527 (2017).
20. M. N. Nascimento, T. F. Aukes, C. N. McMichael, Indigenous and colonial influences on Amazonian forests. *Plants, People, Planet* **6**, 803–823 (2024).
21. N. H. Witteveen *et al.*, Pre-contact and post-colonial ecological legacies shape Surinamese rainforests. *Ecology* **105**, e4272 (2024).
22. C. N. H. McMichael, K. J. Feeley, C. W. Dick, D. R. Piperno, M. B. Bush, Comment on "Persistent effects of pre-Columbian plant domestication on Amazonian forest composition". *Science* **358**, 6361 (2017).
23. M. M. Arienzo, S. Y. Maezumi, N. J. Chellman, J. Iriarte, Pre-Columbian fire management linked to refractory black carbon emissions in the Amazon. *Fire* **2**, 31 (2019).
24. R. J. Nevle, D. K. Bird, W. F. Ruddiman, R. A. Dull, Neotropical human–landscape interactions, fire, and atmospheric CO_2 during European conquest. *Holocene* **21**, 853–864 (2011).
25. N. D. Cook, *Born to Die: Disease and New World Conquest, 1492–1650* (Cambridge University Press, 1998), vol. 1.
26. M.-E. Reeve, Regional interaction in the Western Amazon: The early colonial encounter and the Jesuit years: 1538–1767. *Ethnohistory* **41**, 106–138 (1994).
27. W. Dean, *Brazil and the Struggle for Rubber: A Study in Environmental History* (Cambridge University Press, 2002).
28. A. P. Antunes *et al.*, Empty forest or empty rivers? A century of commercial hunting in Amazonia. *Sci. Adv.* **2**, e1600936 (2016).
29. R. Santos, *História Econômica da Amazônia (1800–1920)* (TA Queiroz São Paulo, 1980), vol. 3.
30. B. L. Barham, O. T. Coomes, Reinterpreting the Amazon rubber boom: Investment, the state, and Dutch disease. *Lat. Am. Res. Rev.* **29**, 73–109 (1994).
31. S. B. Hecht, *The Scramble for the Amazon and the "Lost Paradise" of Euclides Da Cunha* (University of Chicago Press, 2013).
32. S. B. Hecht, A. Cockburn, *The Fate of The Forest: Developers, Destroyers, and Defenders of the Amazon* (University of Chicago Press, 2010).
33. B. Weinstein, *The Amazon Rubber Boom, 1850–1920* (Stanford University Press, 1983).

Downloaded from https://www.pnas.org by Crystal McMichael on November 17, 2025 from IP address 77.250.87.23.

34. J. Q. Chambers *et al.*, The steady-state mosaic of disturbance and succession across an old-growth Central Amazon forest landscape. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 3949–3954 (2013).
35. R. L. Chazdon, Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* **6**, 51–71 (2003).
36. H. W. Bates, *The Naturalist on the River Amazon* (John Murray, London, UK, 1863).
37. S. S. Renner, *A History of Botanical Exploration in Amazonian Ecuador, 1739–1988* (Smithsonian Institution Press, 1993).
38. R. Spruce, *Notes of a Botanist on the Amazon & Andes: Being Records of Travel On* (Macmillan, 1908), vol. 2.
39. M. B. Araújo, M. New, Ensemble forecasting of species distributions. *Trends Ecol. Evol.* **22**, 42–47 (2007).
40. J. A. F. Diniz-Filho, L. M. Bini, B. A. Hawkins, Spatial autocorrelation and red herrings in geographical ecology. *Glob. Ecol. Biogeogr.* **12**, 53–64 (2003).
41. H. ter Steege *et al.*, Biased-corrected richness estimates for the Amazonian tree flora. *Sci. Rep.* **10**, 1–13 (2020).
42. H. D. Eva *et al.*, *A Proposal for Defining the Geographical Boundaries of Amazonia* (Office for Official Publications of the European Communities, 2005).
43. G. S. Hartshorn, "Tree falls and tropical forest dynamics" in *Tropical Trees As Living Systems*, P. B. Tomlinson, M. H. Zimmerman, Eds. (Cambridge University Press, Cambridge, UK, 1978), pp. 617–638.
44. C. McMichael *et al.*, Predicting pre-Columbian anthropogenic soils in Amazonia. *Proc. R. Soc. B: Biol. Sci.* **281**, 20132475 (2014).
45. C. H. McMichael, M. W. Palace, M. Golightly, Bamboo-dominated forests and pre-Columbian earthwork formations in south-western Amazonia. *J. Biogeogr.* **41**, 1733–1745 (2014).
46. C. N. McMichael, M. B. Bush, Spatiotemporal patterns of pre-Columbian people in Amazonia. *Quat. Res.* **92**, 53–69 (2019).
47. J. Medina, *The Discovery of the Amazon According to the Account of Friar Caspar de Carvajal and Other Documents*, H. C. Heaton, Ed. (American Geographical Society, New York, NY, 1934).
48. A. Vespucci, *The First Four Voyages of Amerigo Vespucci Reprinted in Facsimile and Tr. from the Rare Original Edition (Florence, 1505-6)* (B. Quaritch, 1893).
49. A. Smith, *Explorers of the Amazon* (The University of Chicago Press, Chicago, IL, 1990), p. 344.
50. M. C. Kiemen, The Indian policy of Portugal in America, with special reference to the Old State of Maranhão, 1500–1755. *Americas* **5**, 131–171 (1949).
51. L. Newson, *Cultural Worlds of the Jesuits in Colonial Latin America* (University of London Press, 2020).
52. E. Wells, B. Cole, L. J. Rosenwald, *A New Map of South America, Showing Its General Divisions, Chief Cities & Towns, Rivers, Mountains, etc.*, R. Bonwicke, Ed. (Library of Congress, London, UK, 1700).
53. S. Fritz, *El Gran Rio Marañon, o Amazonas con la Mission de la Compañía de Jesus* (Geograficamente Delineado, Quito, Ecuador, 1707).
54. H. Moll, B. Lens, G. Vertue, *This Map of South America, According to the Newest and Most Exact Observations* (Library of Congress, London, UK, 1712).
55. G. de L'Isle, *Carte de la Terre Ferme, du Perou, du Bresil et du Pays des Amazones. in Chéz l'auteur sur le Quai de l'Horloge a Aigle d'Or* (Library of Congress, Paris, France, 1718).
56. A. R. Wallace, *Narrative of Travels on the Amazon and Rio Negro* (Reeve and Co., London, UK, 1853).
57. J. Thomson, J. G. Menzies, *America*, G. Menzies, Ed. (Library of Congress, Edinburgh, UK, 1813)
58. S. G. Bunker, Modes of extraction, unequal exchange, and the progressive underdevelopment of an extreme periphery: The Brazilian Amazon, 1600–1980. *Am. J. Sociol.* **89**, 1017–1064 (1984).
59. R. P. Miller, P. K. Nair, Indigenous agroforestry systems in Amazonia: From prehistory to today. *Agrofor. Syst.* **66**, 151–164 (2006).
60. M. B. Bush *et al.*, Anthropogenic influence on Amazonian forests in prehistory: An ecological perspective. *J. Biogeogr.* **42**, 2277–2288 (2015).
61. C. McMichael *et al.*, Sparse pre-Columbian human habitation in western Amazonia. *Science* **336**, 1429–1431 (2012).
62. W. M. Denevan, A bluff model of riverine settlement in prehistoric Amazonia. *Ann. Assoc. Am. Geogr.* **86**, 654–681 (1996).
63. D. R. Piperno *et al.*, A 5,000-year vegetation and fire history for tierra firme forests in the Medio Putumayo-Algodón watersheds, northeastern Peru. *Proc. Natl. Acad. Sci. U.S.A.* **118**, e2022213118 (2021).
64. D. R. Piperno *et al.*, Pre-Columbian vegetational and fire history in western Amazonia: Terrestrial soil phytolith and charcoal evidence from three regions. *Quat. Int.* **691**, 40–56 (2024).
65. K. Schillinger, S. J. Lycett, The flow of culture: Assessing the role of rivers in the inter-community transmission of material traditions in the upper Amazon. *J. Archaeol. Method Theory* **26**, 135–154 (2019).
66. C. T. Lloyd, A. Sorichetta, A. J. Tatem, High resolution global gridded data for use in population studies. *Sci. Data* **4**, 170001 (2017).
67. J. Watling *et al.*, Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proc. Natl. Acad. Sci. U.S.A.* **114**, 1868–1873 (2017).
68. D. Schaan *et al.*, New radiometric dates for pre-Columbian (2000–700 BP) earthworks in western Amazonia, Brazil. *J. Field Archaeol.* **37**, 132–142 (2012).
69. M. Livi-Bacci, The depopulation of upper Amazonia in colonial times. *Rev. Indias* **76**, 419–448 (2016).
70. W. Balée, *Sowing the Forest: A Historical Ecology of People and Their Landscapes* (University of Alabama Press, 2023).
71. F. J. Stokes *et al.*, Tropical deforestation and indigenous resistance over the longue durée in South America. *J. Global Hist.* **20**, 121–142 (2025).
72. E. A. de Oliveira *et al.*, Legacy of Amazonian dark earth soils on forest structure and species composition. *Glob. Ecol. Biogeogr.* **29**, 1458–1473 (2020).
73. R. Scoles, R. Gribel, Population structure of Brazil nut (*Bertholletia excelsa*, Lecythidaceae) stands in two areas with different occupation histories in the Brazilian Amazon. *Hum. Ecol.* **39**, 455–464 (2011).
74. J. Brandbyge, A revision of the genus *Triplaris* (Polygonaceae). *Nord. J. Bot.* **6**, 545–570 (1986).
75. H. ter Steege *et al.*, Rarity of monodominance in hyperdiverse Amazonian forests. *Sci. Rep.* **9**, 1–15 (2019).
76. J. A. Duke, R. V. Martinez, *Amazonian Ethnobotanical Dictionary* (CRC Press, 2018).
77. N. Smith, *Palms and People in the Amazon* (Springer, Heidelberg, Germany, 2014).
78. R. Cintra, V. Horna, Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in gaps in Amazonian forest. *J. Trop. Ecol.* **13**, 257–277 (1997).
79. R. M. Alves, A. J. R. Bastos, S. F. d. S. Chaves, J. R. Q. Fernandes, *Spondias mombin* and *Theobroma grandiflorum* in agroforestry system: Productivity implications. *Rev. Bras. Frutic.* **40**, e-061 (2018).
80. C. G. Hidalgo Pizango *et al.*, Sustainable palm fruit harvesting as a pathway to conserve Amazon peatland forests. *Nat. Sustain.* **5**, 479–487 (2022).
81. D. A. Clark, D. B. Clark, R. M. Sandoval, M. V. C. Castro, Edaphic and human effects on landscape-scale distributions of tropical rain forest palms. *Ecology* **76**, 2581–2594 (1995).
82. D. B. Clark, Abolishing virginity. *J. Trop. Ecol.* **12**, 735–739 (1996).
83. B. M. Heijink *et al.*, Holocene increases in palm abundances in north-western Amazonia. *J. Biogeogr.* **47**, 698–711 (2020).
84. C. M. Åkesson *et al.*, Long-term ecological legacies in western Amazonia. *J. Ecol.* **109**, 432–446 (2021).
85. G. H. Shepard, H. Ramirez, "Made in Brazil": Human dispersal of the brazil nut (*Bertholletia excelsa*, Lecythidaceae) in ancient Amazonia. *Econ. Bot.* **65**, 44–65 (2011).
86. C. R. Clement, "Domestication of the pejibaye palm (*Bactris gasipaes*): Past and present" in *The Palm—Tree of Life. Biology, Utilization and Conservation*, M. J. Balick, Ed. (The New York Botanical Garden, New York, NY, 1988), pp. 155–174.
87. C. N. McMichael *et al.*, Ecological legacies of past fire and human activity in a Panamanian forest. *Plants, People, Planet* **5**, 281–291 (2023).
88. C. Levis *et al.*, Pre-columbian soil fertilization and current management maintain food resource availability in old-growth Amazonian forests. *Plant Soil* **450**, 29–48 (2020).
89. K. Redford, The empty forest. *BioScience* **42**, 412–422 (1992).
90. S. D. Coelho *et al.*, Eighty-four per cent of all Amazonian arboreal plant individuals are useful to humans. *PLoS ONE* **16**, e0257875 (2021).
91. F. C. Draper *et al.*, Amazon tree dominance across forest strata. *Nat. Ecol. Evol.* **5**, 757–767 (2021).
92. T. J. Kelly *et al.*, Continuous human presence without extensive reductions in forest cover over the past 2500 years in an aseasonal Amazonian rainforest. *J. Quat. Sci.* **33**, 369–379 (2018).
93. B. M. Heijink *et al.*, Long-term fire and vegetation change in northwestern Amazonia. *Biotropica* **55**, 197–209 (2022).
94. B. M. Heijink *et al.*, Past fire and vegetation change in the hyperdiverse forests of the Ecuadorian Amazon. *Plants* **13**, 2048 (2024).
95. A. H. Gentry, Changes in plant community diversity and floristic composition on environmental and geographical gradients. *Ann. Mo. Bot. Gard.* **75**, 1–34 (1988).
96. N. C. A. Pitman, J. Terborgh, M. R. Silman, P. V. Nuñez, Tree species distributions in an upper Amazonian forest. *Ecology* **80**, 2651–2661 (1999).
97. G. Zuquim, M. M. Jones, O. Ovaskainen, W. Trujillo, H. Balslev, The legacy of human use in Amazonian palm communities along environmental and accessibility gradients. *Glob. Ecol. Biogeogr.* **32**, 881–892 (2023).
98. H. Ter Steege *et al.*, Functional composition of the Amazonian tree flora and forests. *Commun. Biol.* **8**, 355 (2025).
99. S. S. Saatchi *et al.*, Benchmark map of forest carbon stocks in tropical regions across three continents. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 9899 (2011).
100. L. H. Cosme, J. Schietti, F. R. Costa, R. S. Oliveira, The importance of hydraulic architecture to the distribution patterns of trees in a central Amazonian forest. *New Phytol.* **215**, 113–125 (2017).
101. F. Wittmann, J. Schöngart, W. J. Junk, "Phytogeography, species diversity, community structure and dynamics of central Amazonian floodplain forests" in *Amazonian Floodplain Forests*, W. J. Junk, M. T. F. Piedade, F. Wittmann, J. Schöngart, P. Parolin, Eds. (Springer, 2010), pp. 61–102.
102. O. Phillips, P. Hall, A. H. Gentry, S. Sawyer, R. Vasquez, Dynamics and species richness of tropical rain forests. *Proc. Natl. Acad. Sci. U.S.A.* **91**, 2805–2809 (1994).
103. H. Ter Steege *et al.*, Mapping density, diversity and species-richness of the Amazon tree flora. *Commun. Biol.* **6**, 1130 (2023).
104. O. L. Phillips *et al.*, Species matter: Wood density influences tropical forest biomass at multiple scales. *Surv. Geophys.* **40**, 913–935 (2019).
105. M. B. Bush, M. R. Silman, Amazonian exploitation revisited: Ecological asymmetry and the policy pendulum. *Front. Ecol. Environ.* **5**, 457–465 (2007).
106. C. A. Peres, E. Palacios, Basin-wide effects of game harvest on vertebrate population densities in Amazonian forests: Implications for animal-mediated seed dispersal. *Biotropica* **39**, 304–315 (2007).
107. J. Terborgh *et al.*, Ecological meltdown in predator-free forest fragments. *Science* **294**, 1923–1926 (2001).
108. D. Pauly, Anecdotes and the shifting baseline syndrome of fisheries. *Trends Ecol. Evol.* **10**, 430 (1995).
109. T. R. Baker *et al.*, Increasing biomass in Amazonian forest plots. *Philos. Trans. R. Soc. Lond., Ser. B: Biol. Sci.* **359**, 353–365 (2004).
110. R. J. W. Brienen *et al.*, Long-term decline of the Amazon carbon sink. *Nature* **519**, 344–348 (2015).
111. L. Poorter *et al.*, Biomass resilience of neotropical secondary forests. *Nature* **530**, 211–214 (2016).
112. J. Mascaro, G. P. Asner, D. H. Dent, S. J. DeWalt, J. S. Denslow, Scale-dependence of aboveground carbon accumulation in secondary forests of Panama: A test of the intermediate peak hypothesis. *For. Ecol. Manage.* **276**, 62–70 (2012).
113. T. R. Feldpausch *et al.*, Forest fire history in Amazonia inferred from intensive soil charcoal sampling and radiocarbon dating. *Front. For. Glob. Change* **5**, 815438 (2022).
114. A. C. Goulart *et al.*, Charcoal chronology of the Amazon forest: A record of biodiversity preserved by ancient fires. *Quat. Geochronol.* **41**, 180–186 (2017).
115. D. R. Piperno, P. Becker, Vegetational history of a site in the Central Amazon basin derived from phytolith and charcoal records from natural soils. *Quat. Res.* **45**, 202–209 (1996).
116. N. Koele *et al.*, Amazon basin forest pyrogenic carbon stocks: First estimate of deep storage. *Geoderma* **306**, 237–243 (2017).
117. J. Barlow, C. A. Peres, Fire-mediated dieback and compositional cascade in an Amazonian forest. *Philos. Trans. R. Soc. Lond. B, Biol. Sci.* **363**, 1787–1794 (2008).
118. R. A. Boria, L. E. Olson, S. M. Goodman, R. P. Anderson, Spatial filtering to reduce sampling bias can improve the performance of ecological niche models. *Ecol. Modell.* **275**, 73–77 (2014).
119. R. J. Hijmans, S. E. Cameron, J. L. Parra, P. G. Jones, A. Jarvis, Very high resolution interpolated climate surfaces for global land areas. *Int. J. Climatol.* **25**, 1965–1978 (2005).
120. FAO/IIASA/ISRIC/ISS-CAS/JRC, *Harmonized World Soil Database (version 1.1)* (FAO, Rome, Italy/ Laxenburg, Austria, ed. I, 2009).
121. W. Buermann *et al.*, Predicting species distributions across the Amazonian and Andean regions using remote sensing data. *J. Biogeogr.* **35**, 1160–1176 (2008).

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122. C. Merow, M. J. Smith, J. A. Silander, A practical guide to MaxEnt for modeling species' distributions: What it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069 (2013).
123. B. Lehner, K. Verdin, A. Jarvis, *HydroSHEDS Technical Documentation*, WWF US, Ed. (HydroSHEDS, Washington, DC, 2006), https://hydrosheds.cr.usgs.gov. Accessed 5 May 2024.
124. A. Jarvis, H. I. Reuter, A. Nelson, E. Guevara, *Hole-Filled SRTM for the Globe Version 4* (CGIAR-CSI SRTM 90m Database, 2008).
125. M. F. J. Wilson, B. O'Connell, C. Brown, J. C. Guinan, A. J. Grehan, Multiscale terrain analysis of multibeam bathymetry data for habitat mapping on the continental slope. *Mar. Geod.* **30**, 3–35 (2007).
126. M. Marmion, M. Parviainen, M. Luoto, R. K. Heikkinen, W. Thuiller, Evaluation of consensus methods in predictive species distribution modelling. *Divers. Distrib.* **15**, 59–69 (2009).
127. J. Elith *et al.*, Novel methods improve prediction of species' distributions from occurrence data. *Ecography* **29**, 129–151 (2006).
128. J. H. Friedman, Greedy function approximation: A gradient boosting machine. *Ann. Stat.* **29**, 1189–1232 (2001).
129. T. J. Hastie, R. J. Tibshirani, *Generalized Additive Models* (Chapman & Hall, London, UK, 1990), vol. 43.
130. S. N. Wood, Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *J. R. Stat. Soc.: Ser. B (Stat. Methodol.)* **73**, 3–36 (2011).
131. L. Breiman, Random forests. *Mach. Learn.* **45**, 5–32 (2001).
132. S. J. Phillips, R. P. Anderson, R. E. Schapire, Maximum entropy modeling of species geographic distributions. *Ecol. Modell.* **190**, 231–259 (2006).
133. J. Elith, C. H. Graham, Do they? How do they? Why do they differ? On finding reasons for differing performances of species distribution models. *Ecography* **32**, 66–77 (2009).
134. S. Schmitt *et al.*, SSDM: An R package to predict distribution of species richness and composition based on stacked species distribution models. *Methods Ecol. Evol.* **8**, 1795–1803 (2017).
135. R Development Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria, 2025).
136. M. Barbet-Massin, F. Jiguet, C. H. Albert, W. Thuiller, Selecting pseudo-absences for species distribution models: How, where and how many? *Methods Ecol. Evol.* **3**, 327–338 (2012).
137. M. S. Wisz *et al.*, Effects of sample size on the performance of species distribution models. *Divers. Distrib.* **14**, 763–773 (2008).
138. W. Thuiller, B. Lafourcade, R. Engler, M. B. Araújo, BIOMOD–A platform for ensemble forecasting of species distributions. *Ecography* **32**, 369–373 (2009).
139. H. ter Steege, I. Welch, R. Zagt, Long-term effect of timber harvesting in the Bartica Triangle, Central Guyana. *For. Ecol. Manage.* **170**, 127–144 (2002).
140. M. D. Swaine, T. C. Whitmore, On the definition of ecological species groups in tropical rain forests. *Vegetatio* **75**, 81–86 (1988).
141. H. ter Steege, D. S. Hammond, Character convergence, diversity, and disturbance in tropical rain forest in Guyana. *Ecology* **82**, 3197–3212 (2001).
142. R. J. Hijmans, J. van Etten, *raster: Geographic Analysis and Modeling with Raster Data. R Package Version 1* (2012), pp. 9–92.
143. R. Bivand, T. Keitt, B. Rowlingson, *rgdal: Bindings for the Geospatial Data Abstraction Library* (2014). https://CRAN.R-project.org/package=rgdal.
144. H. Wickham, ggplot2. *WIREs Comput. Stat.* **3**, 180–185 (2011).

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