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TROPICAL FOREST

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The extent to which pre-Columbian societies altered Amazonian landscapes is hotly debated. We performed a basin-wide analysis of pre-Columbian impacts on Amazonian forests by overlaying known archaeological sites in Amazonia with the distributions and abundances of 85 woody species domesticated by pre-Columbian peoples. Domesticated species are five times more likely than nondomesticated species to be hyperdominant. Across the basin, the relative abundance and richness of domesticated species increase in forests on and around archaeological sites. In southwestern and eastern Amazonia, distance to archaeological sites strongly influences the relative abundance and richness of domesticated species. Our analyses indicate that modern tree communities in Amazonia are structured to an important extent by a long history of plant domestication by Amazonian peoples.

I ncreasing evidence suggests that the modern floristic composition and structure of Amazonian forests have been influenced by past human activity (1). Seasonal forests and river margins are thought to have been modified more intensively than were wetter and less accessible forests (2, 3). At the basin scale, the magnitude to which pre-Columbian peoples transformed forests is still unclear (4, 5). Humans transformed forests in many ways, through plant cultivation (preceded by cutting and burning), seed dispersal and propagation, and in situ tending of useful resources, such as domesticated plants (6, 7).

Domestication of plant populations is a result of the human capacity to overcome selective pressures of the environment by creating landscapes to manage and cultivate useful species, generating fundamental changes in ecosystems at local and global scales (7). During the domestication of tree populations, initially the "best" individuals were and are managed in situ (6) and only later, if at all, selected and propagated in home gardens and other anthropogenic landscapes. These initial actions of favoring individual trees are referred to as "incidental domestication" (8). The continuation of these activities tends to expand the target populations, both in area and in abundance. Current tending, cultivation, and dispersal of species that occur in high frequency and abundance in anthropogenic landscapes strongly suggest that selective practices have been used in the past (9). Initially, humans cultivate the best variety, selecting individuals with more desirable morphological traits (such as larger fruit size) for future cultivation (10). Selection may lead to the dispersal of plant populations from their original wild habitats to new anthropogenic landscapes (11). This dispersal may give rise to a founder event, which occurs when new populations are based on a small sample of the original population and consequently have less genetic and morphological variability (6). In tree populations, genetic and morphological changes are subtle, especially when managed within forests, and changes may not continue beyond the initial category of incipiently domesticated populations (6). Humans have been domesticating plants since at least 10,000 B.P. (before the present) (12). In Amazonia, plant domestication started earlier than 8000 B.P., mainly in the periphery of the basin (Fig. 1 and fig. S1), where wild populations of domesticated plants have been identified with genetic and morphological analyses (13). Five centuries after the demographic collapse of Amerindian populations (14), domesticated plants persist in Amazonian forests (6), frequently associated with fertile anthropogenic soils (15) and pre-Columbian mounds (16) where human populations were once abundant (1). Here, we used the abundance, richness, and distribution of domesticated plants in forests to assess changes in Amazonian forest composition due to past human activities.

The distribution and abundance of plant species are fundamentally influenced by environmental and evolutionary processes. The synergistic effects of these processes have resulted in distinct plant assemblages across Amazonian regions (17–19). Evolutionary processes operate at all spatial scales and are essential in determining the regional species pool. Environmental filtering (such as geology, soil, or climate) and biotic interactions (such as animal seed dispersal and predation) drive differences among species assemblages across ecological gradients. For example, effective seed dispersal of large-seeded tree species decreases in heavily hunted forests because of the depletion of large vertebrates (20). Composition and dominance patterns of plant assemblages in Amazonian forests differ from one phytogeographical region to another (17, 19); vary along spatial and temporal gradients of rainfall (19, 21, 22), terrain water saturation (23), and

soil fertility (*19*); and may be the result of dispersal limitation (*20*). We evaluated whether the plant domestication process acted together with evolutionary and environmental processes to determine the ecological patterns documented in Amazonian forests.

Using 1170 forest plots of the Amazon Tree Diversity Network (ATDN), ter Steege and coauthors (*17*) identified 4962 species, estimated that about 16,000 woody species occur in Amazonia, and showed that only 227 hyperdominant species dominate Amazonian forests. We used 1091 ATDN plots located in nonflooded lowland Amazonian forests to provide a list of domesticated species on the basis of evidence of at least incipient domestication processes in Amazonia and elsewhere in the Americas. We identified 85 woody species with populations incipiently, semi-, or fully domesticated by pre-Columbian peoples (hereafter, domesticated species listed in database S1). We found that 20 of these 85 domesticated species are hyperdominants: five times higher than the number of hyperdominant species expected by chance.

We then tested whether forests closer to archaeological sites and rivers have higher abundance and richness of domesticated species. Forest composition was evaluated in association with numerous types of archaeological sites, including pre-Columbian habitation sites (with and without anthropogenic soils), earthworks (mounds, causeways, raised fields, and terraces), rock art (paintings and petroglyphs), and identified eco-archaeological regions (fig. S2) (*1*, *24*). We included eco-archaeological regions in the analysis because they indicate environmental settings, with large and abundant pre-Columbian earthworks (*25*). We also used margins of navigable rivers as proxies for pre-Columbian settlements because they are good predictors of anthropogenic soils in Amazonia (*26*). Our analyses also accounted for the effects of different geological regions of Amazonia and for four local environmental conditions: soil cation exchange capacity (CEC), soil pH, rainfall seasonality, and height above the nearest drainage (HAND; a proxy for water-table depth). These variables were selected because they influence forest composition in Amazonia (*19*, *21–23*) and are available for basin-wide analysis.

We found a significantly higher abundance and richness (in absolute and relative terms) of domesticated species in southwestern Amazonian forests, followed by northwestern, southern, and eastern forests, and the lowest values in the Guiana Shield (Fig. 2 and fig. S3). The total number of individuals of domesticated species per hectare (abundance) ranged from 0 to 292, and the total number of domesticated species (richness) ranged from 0 to 19. The relative abundance
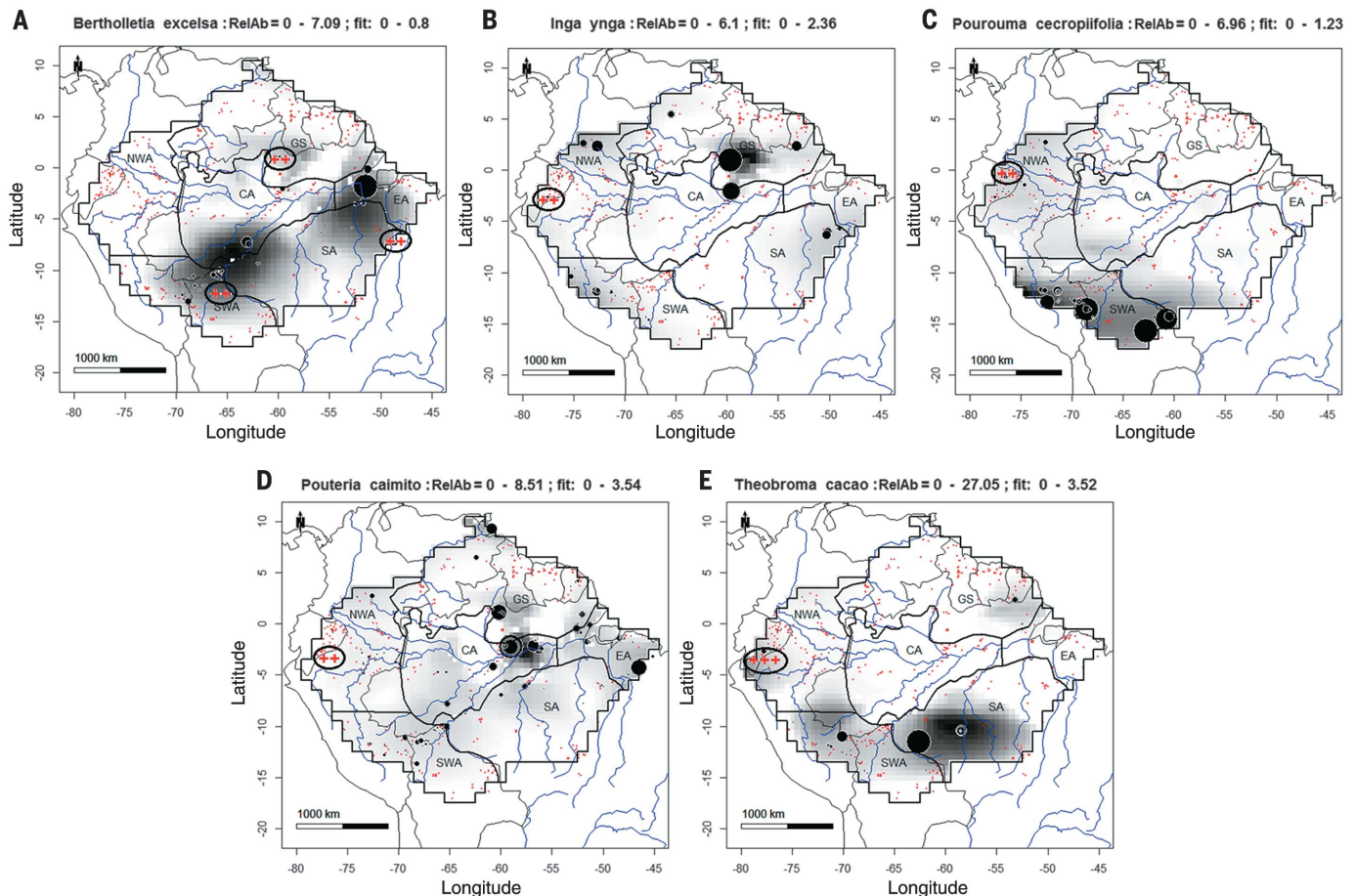
Fig. 1. Distribution maps of five domesticated hyperdominant species in Amazonian forests and their probable origins of domestication. (**A** to **E**) Distribution maps were estimated for five domesticated species that are hyperdominants: (A) *Bertholletia excelsa*, (B) *Inga ynga*, (C) *Pourouma cecropiifolia*, (D) *Pouteria caimito*, and (E) *Theobroma cacao*. The origin of domestication is shown by the symbol "+++" for known origin and by the symbol "++" for hypothetical origin (*13*, *42*). Sizes of black dots indicate the relative abundance of the domesticated species in plots where the species has been recorded. Red dots indicate plots where each domesticated species has not been recorded. Shading shows the interpolated distribution of each species by use of loess spatial interpolation (*17*). The range of relative abundance in plots (RelAb) and the loess spatial interpolation in individual grid cells (fit) are reported in percentage above each map. Maps were created with custom R scripts. Amazonia was divided into six geological regions (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia). [Base map source (country.shp, rivers.shp): Esri (www.esri.com/data/basemaps, copyright Esri, DeLorme Publishing Company.]

ranged from 0 to 61%, and the relative richness ranged from 0 to 19%. Forests with a diverse assemblage of domesticated species tended to have a high abundance of these species (fig. S4). The abundance of all domesticated species was, however, mostly due to 20 hyperdominant species. Domesticated hyperdominant species were more widespread across Amazonian forests than were nondomesticated hyperdominant species. We found that 70% of the 20 domesticated hyperdominant species studied here occur in all Amazonian regions (database S1) versus only 47% of the 207 nondomesticated hyperdominant species (17). Most of the domesticated species that are hyperdominant have incipiently domesticated populations, rather than fully domesticated ones. This finding suggests that humans were probably managing hyperdominant species in forests instead of investing their efforts to fully domesticate populations. Humans may have fully domesticated populations of plant species that were rare in nature and easily adapted to anthropogenic landscapes.

We found that forests closer to archaeological sites had greater abundance and richness (in relative and absolute terms) of domesticated species at the Amazonia-wide level (Fig. 3 and fig. S5). In four of the six Amazonian regions, the relative and absolute richness of domesticated species decreased with distance from archaeological sites or rivers, and in three of these four regions the relative and absolute abundance of domesticated species also decreased with distance from archaeological sites or rivers. These results reveal that forests closer to archaeological sites or rivers within these regions harbor a richer and larger assemblage of domesticated species than forests elsewhere. The relative abundance of domesticated hyperdominant species also decreased with distance from archaeological sites (Fig. 4). In contrast, we tested whether nondomesticated hyperdominant species in three control groups were negatively affected by the distance from archaeological sites, and we did not find a significant negative relation for any control group (Fig. 4). Additionally, nondomesticated hyperdominant species dispersed primarily by primates were more abundant farther from archaeological sites within forests in southern Amazonia and the Guiana Shield (Fig. 4), potentially as a result of heavy hunting around villages (16). Although the absolute and relative abundance of domesticated species in forest plots decreased with distance from navigable rivers in the Guiana Shield, the opposite was observed for the distance from archaeological sites within this region. One possible explanation is insufficient information about the distribution of archaeological sites along tributary rivers, so moving away from a known archaeological site may increase the proximity to other sites that have not been mapped yet. Archaeological surveys into interfluves of major rivers in Central Amazonia documented numerous anthropogenic soils along tributary rivers, showing that these areas were also densely occupied (27).

The map showing the density of archaeological sites in 1°-grid cells (areas of ~110 km^2) indicated large areas of Amazonia without any archaeological site (fig. S6) and revealed that some plots with high values of the relative abundance of domesticated species are located in these grid cells, most likely reflecting the lack of surveys. Although simple regressions showed a pronounced decrease of human impact in forests up to 25 km from archaeological sites and 10 km from rivers (figs. S7 to S11), the strongest human impact was detected in forests located on archaeological sites or within eco-archaeological regions in southwestern and eastern Amazonia. Dominance of domesticated species may, therefore,

Table 1. Mean, median, minimum, and maximum values of all human and environmental variables used in the multiple regression models. Values were calculated at the Amazonia-wide level (All) and region level (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia).

| Region (number of plots)	Values	Distance to archaeological sites (km)	Distance to main rivers (km)	Cation exchange capacity (cmol/kg)	pH	N dry months	HAND
All	Mean	45.65	14.25	12.07	4.49	2.01	37.02
(1091)	Median	25.94	10.52	11.00	4.50	1.00	22.81
	Minimum	0.00	0.00	6.00	3.90	1.00	0.00
	Maximum	349.42	70.58	35.00	5.70	6.00	539.11
NWA	Mean	51.41	9.31	14.36	4.44	1.02	16.67
(197)	Median	32.46	5.40	14.00	4.40	1.00	11.13
	Minimum	0.63	0.00	8.00	4.10	1.00	0.00
	Maximum	196.81	49.73	31.00	5.10	2.00	163.93
SWA	Mean	80.07	14.16	12.57	4.91	2.68	30.77
(158)	Median	59.07	9.23	11.00	4.90	3.00	17.16
	Minimum	0.00	0.07	7.00	4.00	1.00	0.00
	Maximum	219.94	62.94	25.00	5.60	6.00	375.98
SA	Mean	67.35	11.72	9.19	4.54	3.86	39.59
(86)	Median	43.77	5.78	9.00	4.55	4.00	25.55
	Minimum	2.03	0.04	6.00	4.00	2.00	1.06
	Maximum	349.42	46.93	13.00	5.30	6.00	293.89
CA	Mean	20.54	14.79	10.07	4.16	1.99	45.45
(250)	Median	11.64	13.24	10.00	4.10	1.00	47.78
	Minimum	0.62	0.00	7.00	3.90	1.00	0.04
	Maximum	220.35	48.55	18.00	5.10	6.00	119.93
GS	Mean	41.86	19.73	12.78	4.59	1.83	48.57
(317)	Median	32.65	14.39	12.00	4.60	2.00	24.38
	Minimum	0.93	0.09	6.00	4.00	1.00	0.00
	Maximum	127.36	70.58	35.00	5.70	6.00	539.11
EA	Mean	34.18	6.11	11.96	4.51	1.89	24.84
(83)	Median	20.23	2.72	11.00	4.50	1.00	23.38
	Minimum	0.00	0.00	9.00	4.10	1.00	0.62
	Maximum	254.99	52.79	18.00	5.10	6.00	78.72

help predict the occurrence of archaeological sites in Amazonian forests. Guiana Shield plots, for example, with an average of 30% of individuals of domesticated species located close to river margins, but more than 120 km away from an archaeological site, can be used to test this hypothesis and indicate that a widespread survey

of archaeological sites along tributaries in interfluvial areas is critical.

Environmental conditions also controlled the abundance and richness of domesticated species (Fig. 3 and fig. S6) and may have influenced where and how humans shaped forests through time. We found that environmental conditions

explained most (up to 30%) of the variation in the relative abundance and richness of domesticated species in Amazonian regions (Fig. 5), whereas the proxies for past human impacts explained up to 20%. Approximately 70% of the variation remains unexplained by either human or environmental factors in most of the regions.
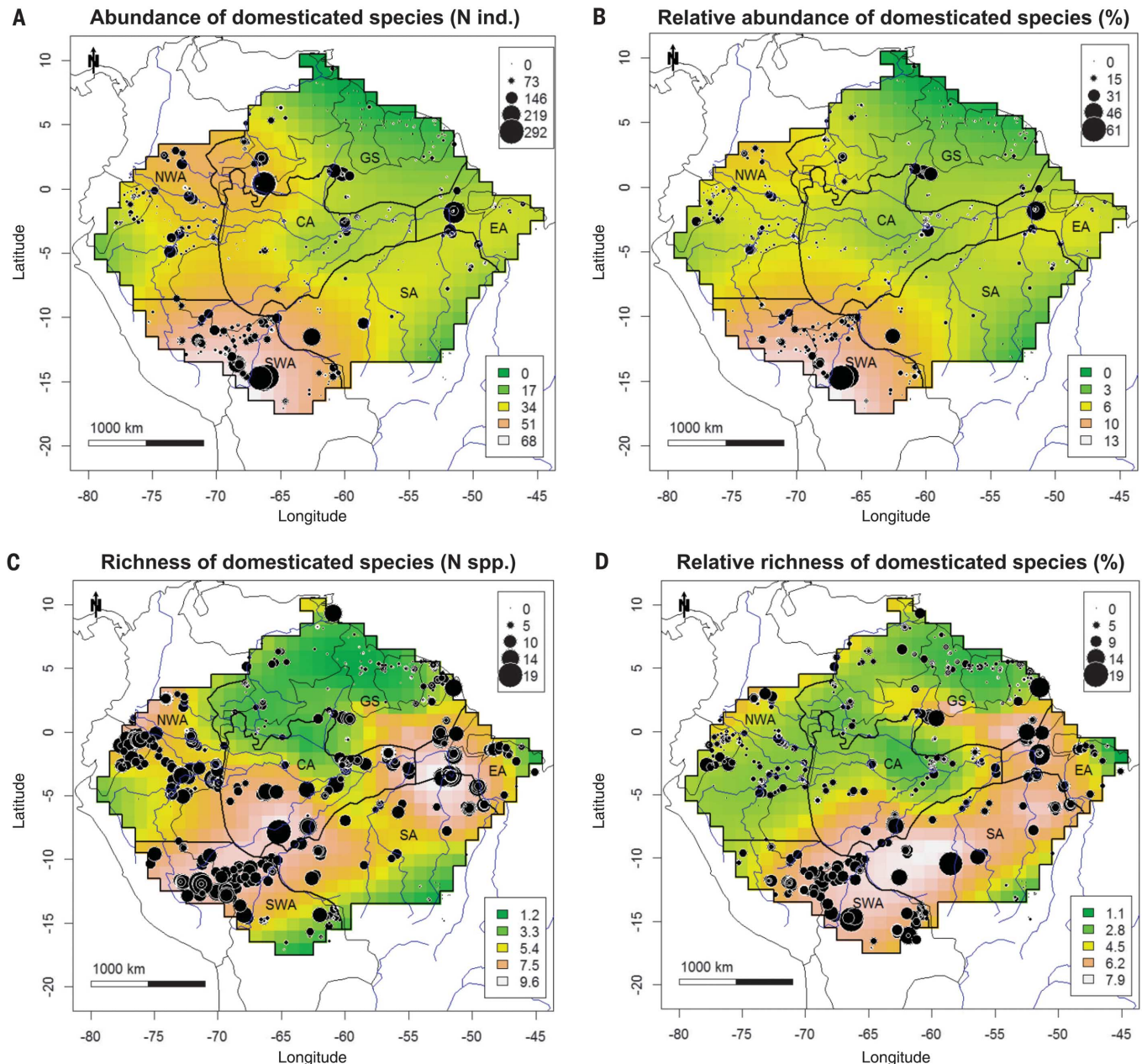
Fig. 2. Spatial variation of 85 domesticated species across Amazonia. (**A** to **D**) Maps showing (A) the spatial variation of the total number of individuals of domesticated species (abundance) per hectare (ha), (B) the relative abundance of domesticated species, (C) the total number of domesticated species (richness) per plot, and (D) the relative richness of domesticated species in lowland plots in six geological regions of Amazonia (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia). Black circles show the observed values of absolute abundance (A) and relative abundance (B), ranging

from 0 to 292 individuals of domesticated species per 1 ha and 0 to 61% of the total number of individuals, and the observed values of absolute richness (C) and relative richness (D), ranging from 0 to 19 domesticated species per plot and 0 to 19% of the total number of species. The white-green background shows the interpolation of the observed values (in percent) in each plot modeled as a function of latitude and longitude on a 1°-grid cell scale by use of loess spatial interpolation (17). Maps were created with custom R scripts. [Base map source (country.shp, rivers.shp): Esri (www.esri.com/data/basemaps, copyright Esri, DeLorme Publishing Company)].
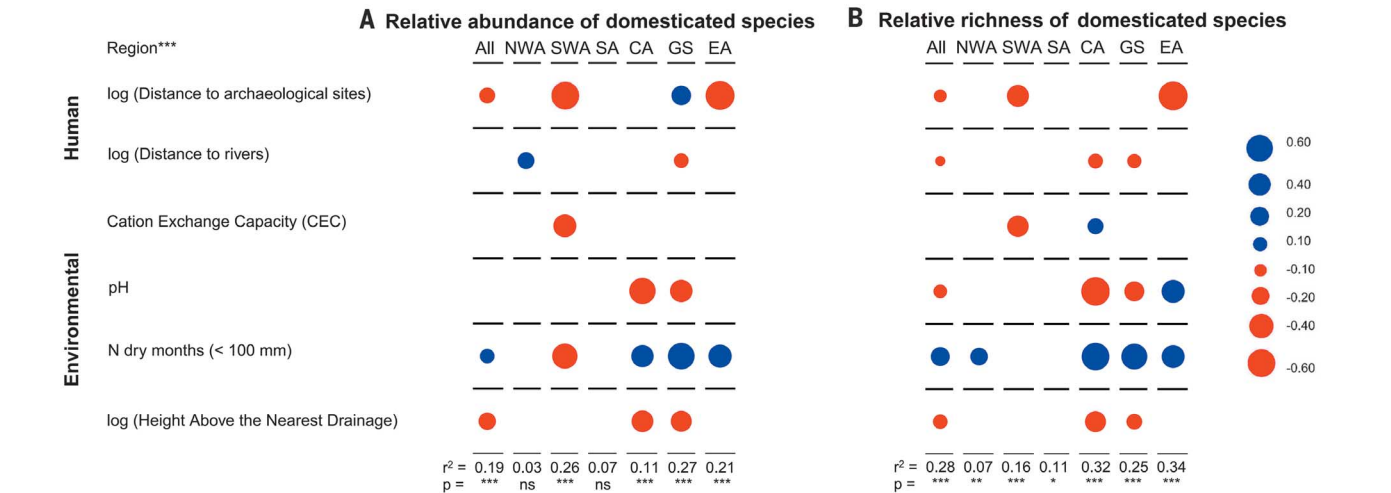
Fig. 3. The relative abundance and richness of domesticated species as a function of human and environmental variables. (**A** and **B**) Standardized regression coefficients for (A) the relative abundance and (B) the relative richness of 85 domesticated species as a function of human factors (distance to archaeological sites and eco-archaeological regions, distance to navigable rivers) and environmental conditions (soil CEC, soil pH, number of dry months, and HAND). Circle size represents the relative contribution of the predictors, shown by standardized coefficients at the Amazonia-wide level (All) and region-level regression models (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia). Red circles indicate negative effects, and blue circles indicate positive effects. Standardized coefficients are presented only for significant relations analyzed in the models ($P \leq 0.05$). Adjusted coefficient of determination (R^2) and significant codes (***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; ns, $P > 0.05$) are presented for the effect of regions at the Amazonia-wide level (All) and all regression models.
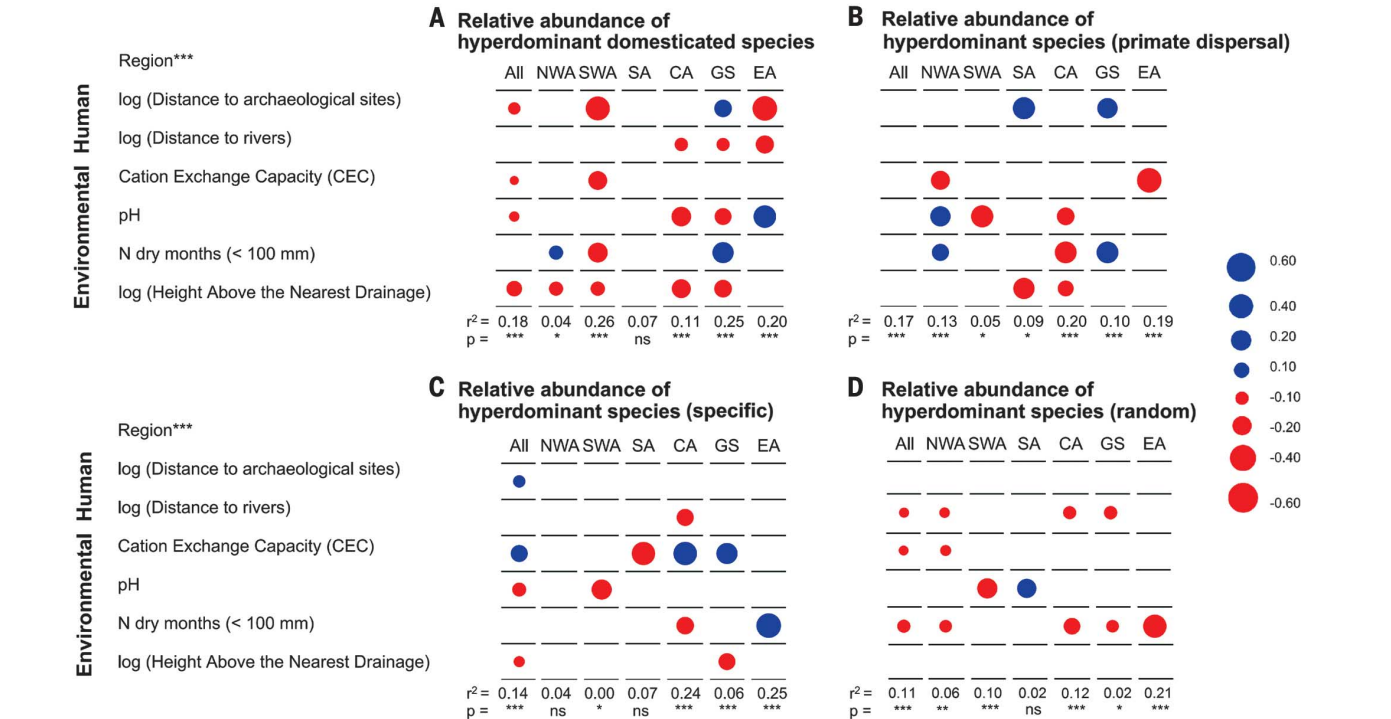
Fig. 4. The relative abundance of hyperdominant species as a function of human and environmental variables. (**A** to **D**) Standardized regression coefficients for (A) the relative abundance of 20 domesticated species that are hyperdominants, (B) the relative abundance of 20 nondomesticated species that are hyperdominants and primarily dispersed by primates, (C) the relative abundance of 20 nondomesticated species that are hyperdominants and not dispersed by primates, and (D) the relative abundance of 20 nondomesticated species that are hyperdominants selected at random, as a function of human variables (distance to archaeological sites and eco-archaeological regions, and distance to navigable rivers) and environmental variables (soil CEC, soil pH, number of dry months, and HAND). Circle size represents the relative contribution of the predictors, shown by standardized coefficients at the Amazonia-wide level (All) and region-level regression models (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia). Red circles indicate negative effects, and blue circles indicate positive effects. Standardized coefficients are presented only for significant relations analyzed in the models ($P \leq 0.05$). Adjusted R^2 and significant codes (***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$; ns, $P > 0.05$) are presented for the effect of regions at the Amazonia-wide level (All) and all regression models.

Fig. 5. Relative contributions of human and environmental variables for explaining variation in relative abundance and richness of domesticated species in Amazonian forests. (**A** and **B**) The partitioning of variation in (A) relative abundance and (B) relative richness of domesticated species exclusively explained by environmental (dark gray) or human factors (light gray), and the variation jointly explained by both (gray). Variance partitioning was conducted over the results of multiple regression analyses presented in Fig. 3. Amazonia was divided into six geological regions (NWA, northwestern Amazonia; SWA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia).
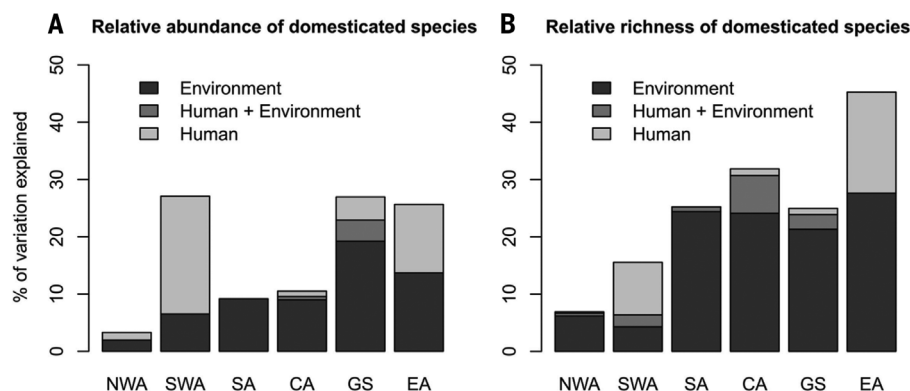
The data available for this broad-scale analysis are based on forest plots and archaeological sites unequally distributed across the study area and on interpolations of environmental conditions. Hence, the data used may not capture the real variation of past human and environmental factors across the basin. Even so, the relative abundance and richness of domesticated species were higher in the southern periphery of the basin (Fig. 2) and increased with rainfall seasonality at the Amazonia-wide level (Fig. 3). Seasonal and open forests in transitional zones were important ecosystems for early humans, who started the domestication of some plants (28), and the longest pre-Columbian occupation sequences have been found either in the southern periphery of the basin or near the estuary of the Amazon River (29). In seasonal forests of southwestern Amazonia, where two major crops most likely originated (manioc, *Manihot esculenta*, and peach palm, *Bactris gasipaes*) (13), plant populations that also responded well to selection and propagation were widely dispersed (13). For instance, sweet manioc was domesticated in southwestern Amazonia before the initial development of small-scale farming societies in the mid-Holocene and expanded widely (28, 30). It was also from the southwestern periphery that two major languages expanded and where the oldest anthropogenic soils have been found, dated from around 4800 B.P. (6, 31). The Arawak language family probably originated in southwestern Amazonia and expanded across Amazonia associated with the early development of farming villages (32). The upper Madeira River is the homeland of the Tupí language family, which also spread widely (33). In southwestern Amazonia, the combination of rainfall seasonality (Table 1), forest-savanna transition (34), high cultural diversity (35), and a long history of forest transformation encompassing landscape engineering by pre-Columbian societies (25) resulted in forests containing diverse and abundant assemblages of domesticated species.

Soil and terrain conditions also determined forest composition (36) and influenced the abundance and richness of domesticated species in forest plots (Fig. 3). We found in some regions higher relative abundance and richness of domesticated species on soils with lower pH. Plots with shallow water tables also concentrated domesticated species. This pattern is driven by dense stands of some species (such as *Mauritia flexuosa, Euterpe oleracea, E. precatoria,* and *Oenocarpus bataua*) on poorly drained soils of Amazonia (37).

Although potential confounding effects of some correlations between human and environmental factors may exist (for example, human settlements located in seasonal forests on poorly drained soils of southwestern Amazonia), we found that human influence is exclusively responsible for about half of the explained variation of the abundance, relative abundance, richness, and relative richness of domesticated species in the southwestern and eastern regions (Fig. 5 and fig. S12). The association between domesticated species and archaeological sites raises a chicken-and-egg question: Did humans enrich forests in southwestern and eastern Amazonia with domesticated species, or did humans choose to live close to forests naturally rich in these species? Our approach cannot demonstrate causality, but the first alternative is most probable, given the sum of other evidence that also supports the influence of past societies in increasing domesticated species abundance and richness in forests. First, numerous archaeological sites were found in all geological regions (fig. S2), which shows that pre-Columbian human societies were distributed across all of Amazonia (1) and created new landscapes for domesticated plants under different environmental conditions (Table 1). Dramatic changes in phytolith assemblages have been found in ancient anthropogenic soils before, during, and after human occupation, indicating that humans transform forest composition once they occupy an area (38). Second, assemblages of up to 19 domesticated species with different geographical distributions and distinct ecological preferences tend to occur in forests close to archaeological sites (Fig. 3 and fig. S5). As an example, we found a set of domesticated species at one forest plot (*Attalea maripa, Astrocaryum murumuru, Bertholletia excelsa, Garcinia macrophylla, Hevea brasiliensis, Oenocarpus bacaba,* and *Theobroma* spp.) that would be unlikely to occur by chance at the same location because of their distinct ecological niches. Third, species domesticated in one particular en-

vironmental setting had wide geographical distributions and tended to be more abundant in locations not associated with their known or hypothetical origins of domestication (Fig. 1 and fig. S1) (13). For instance, cocoa (*Theobroma cacao*) was first domesticated in wet forests on nutrient-rich soils of northwestern Amazonia and is currently more abundant in southwestern and southern forests (39).

Although it is possible that the origin of domestication of some species is not well identified, this is unlikely for species for which extensive morphological and genetic studies have been done (more details in supplementary text, sections 1 to 11). Domesticated species for which information about their origins of domestication exists originated in the periphery of Amazonia (13). Species can have wild populations in one part of Amazonia (where the domestication process started) and incipiently, semi-, or fully domesticated populations in other parts of the basin. Fully domesticated populations show substantial morphological and genetic changes and depend on human management for their long-term survival, whereas incipiently domesticated plants can survive and reproduce without humans, as is the case of most hyperdominant domesticated species. Many domesticated species were dispersed from their origin of domestication to other locations where large pre-Columbian populations lived, and these species eventually accumulated greater intraspecific diversity (13). Our results suggest that plant species that responded well to selection and propagation were widely cultivated and dispersed within and outside their natural range (6, 7) by different societies and at different moments in time. The influence of modern indigenous and nonindigenous societies in the past 300 years on the distribution of some domesticated species may be stronger than the effect of earlier societies. For instance, in the late 17th century, Portugal and Spain stimulated plantations of cocoa trees in Amazonia (40), which—associated with pre-Columbian cultivation—may have increased the abundance of cocoa trees in southwestern Amazonian forests even more.

Our results suggest that past human interventions had an important and lasting role in the distribution of domesticated species found in

modern forests, despite the fact that the location of many archaeological sites is unknown. Almost one fourth of all domesticated species are hyperdominant, and besides their socioeconomic importance, they can also help unravel the human history of Amazonian forests, which is largely overlooked by ecological studies. Detecting the widespread effect of ancient societies in modern forests not only strengthens efforts to conserve domesticated and useful wild-plant populations, which is of critical importance for modern food security (41), but also strongly refutes ideas of Amazonian forests being untouched by man. Domestication shapes Amazonian forests.

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SUPPLEMENTARY MATERIALS

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28 September 2016; accepted 20 January 2017
10.1126/science.aal0157