

## ANTHROPOLOGY

# More than 10,000 pre-Columbian earthworks are still hidden throughout Amazonia

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Indigenous societies are known to have occupied the Amazon basin for more than 12,000 years, but the scale of their influence on Amazonian forests remains uncertain. We report the discovery, using LIDAR (light detection and ranging) information from across the basin, of 24 previously undetected pre-Columbian earthworks beneath the forest canopy. Modeled distribution and abundance of large-scale archaeological sites across Amazonia suggest that between 10,272 and 23,648 sites remain to be discovered and that most will be found in the southwest. We also identified 53 domesticated tree species significantly associated with earthwork occurrence probability, likely suggesting past management practices. Closed-canopy forests across Amazonia are likely to contain thousands of undiscovered archaeological sites around which pre-Columbian societies actively modified forests, a discovery that opens opportunities for better understanding the magnitude of ancient human influence on Amazonia and its current state.

During the pre-Columbian era, Amazonia was home to dense and complex societies throughout its vast forested area spanning 6.7 million km<sup>2</sup> (1). These ancient Indigenous societies had profound knowledge of earthmoving, riverine dynamics, soil enrichment, and plant and animal ecology, which allowed them to create domesticated landscapes that were more productive for humans (2–4). With earthmoving techniques, Indigenous peoples created a wide variety of earthworks (i.e., ring ditches, geoglyphs, ponds, and wells), mostly between 1500 and 500 years before present, with social, ceremonial, and defensive functions (5). Around these earthworks, they also managed hundreds of tree species, some of which show evidence of domestication (6–9), and effected long-lasting changes in forest composition (10–13). The scale and intensity of that landscape transformation remain unknown, in part because there has never been a comprehensive inventory of pre-Columbian sites across the basin.

Domesticated landscapes in Amazonia have mostly been discovered by means of evidence from on-the-ground surveys (5, 14). Earthworks can be detected by orbital optical satellites with very high spatial resolution (15), but that technique is mostly suitable for deforested areas (16). Airborne light detection and ranging (LIDAR) data—a remote sensing technique that can map microtopography beneath the forest canopy—has substantially changed our understanding of the magnitude of pre-Columbian urbanism in Mesoamerica (17, 18) and South America (19). Over the past decade, the use of LIDAR data has revealed the complexity of Mayan civilization by indicating a regionally inte-

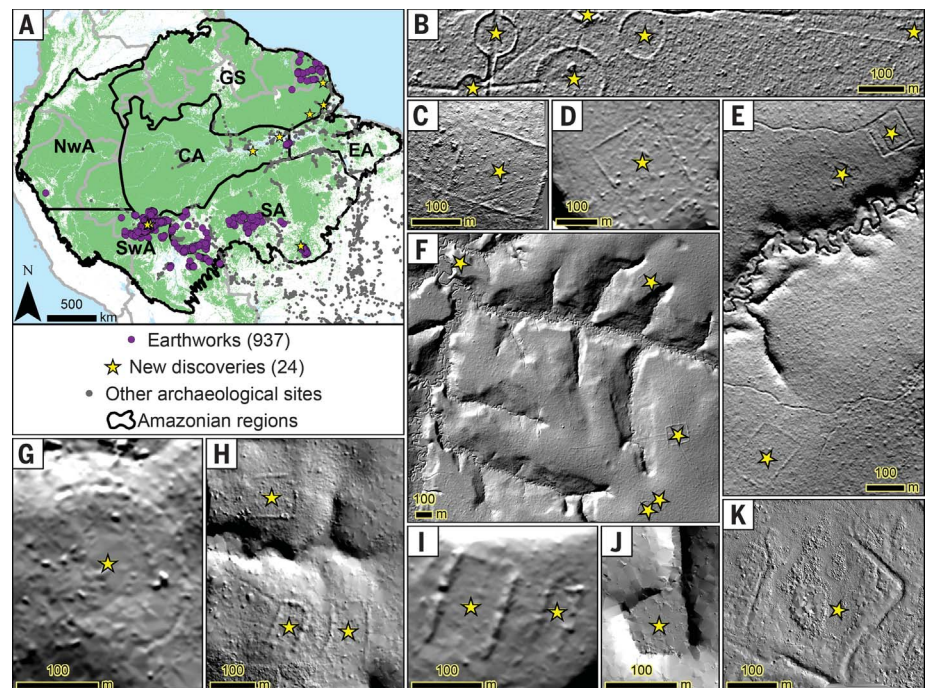
grated urban-rural community network in Mesoamerica (17). More recently, LIDAR enabled the detailed mapping of two monumental pre-Columbian settlements in an intensively domesticated landscape hidden under forest in southwestern Amazonia (19). Although Mesoamerican archaeological sites feature very different types of structures—stone construction as opposed to the use of earth, as in Amazonia—

LIDAR technology has substantially improved our spatial understanding of archaeological sites in forested landscapes by enabling the visualization of ancient large-scale earthworks (18, 19) beneath the forest canopy. Because deforestation in Amazonia has removed about 17% of the natural vegetation cover to date (20), LIDAR has the potential to reveal many more discoveries in the remaining 83% of the basin that is opaque to other remote sensing approaches.

Here, we report a large number of previously undocumented pre-Columbian earthworks with geometrically patterned enclosures in an Amazon-wide LIDAR dataset covering 0.08% of the basin (21). We combine these newly discovered sites with a comprehensive dataset of existing archaeological sites (ring ditches, geoglyphs, ponds, and wells) to model areas likely to harbor as yet undetected earthworks hidden beneath remote forest landscapes. On the basis of our predictive model, we estimate the number of undocumented earthworks and identify domesticated tree species associated with earthwork presence.

## Archaeological discoveries beneath the canopy

Scanning 5315 km<sup>2</sup> of LIDAR data originally obtained for estimating aboveground biomass throughout the Amazonian forest (22) revealed



**Fig. 1. Geographical distribution of known and newly discovered pre-Columbian geometric earthworks in Amazonia.** (A) Map of previously reported and newly discovered earthworks (purple circles and yellow stars, respectively) reported in this study across six Amazonian regions: central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GS), northwestern Amazonia (NwA), southern Amazonia (SA), and southwestern Amazonia (SwA). (B) Newly discovered earthworks in SA. (C to F) Newly discovered earthworks in SwA. (G to I) Newly discovered earthworks in GS. (J and K) Newly discovered earthworks in CA. Scale bars, 100 m.

24 unreported earthworks in southern, south-western, central, and northern (the Guiana Shield) Amazonia (Fig. 1A) (27). We detected a fortified village in southern Amazonia (Fig. 1B), defensive and ceremonial sites in southwestern Amazonia (Fig. 1, C to F), crowned mountains and megalithic structures in the Guiana Shield (Fig. 1, G to I), and riverine sites on floodplains in central Amazonia (Fig. 1, J and K).

In southern Amazonia, we found an ancient plaza town located in the Upper Xingu Basin (Fig. 1B). This region is known to have supported dense populations in the past, distributed throughout plaza villages interconnected by road networks and surrounded by domesticated landscapes with a diverse array of terrestrial and aquatic resources (10, 23). It is also clear that the earthworks in this region extend beyond the sampled area of the 200-m-wide LIDAR transect, restraining their full identification. The layout of these earthworks is similar to that of other fortified villages documented in this region, which supports the idea that these structures were built before European contact (10, 15, 24).

In southwestern Amazonia, we found a combination of rectangular and circular features, known as geoglyphs, without detectable interconnecting roads occurring on flat terrain close to water bodies (Fig. 1, C to F). Documented defensive and ceremonial earthworks in this region were built around two millennia ago and are dispersed across the well-drained plateaus of the tributaries of the Purus and Madeira rivers (25).

In the Guiana Shield, we detected a combination of rectangular and circular features on plateaus near water bodies (Fig. 1, G to I). The region holds different types of earthworks with different usages: permanent settlements within crowned mountains in French Guiana (26) and ceremonial sites featuring megalithic structures arranged in circular clusters found along the coast of Amapá, Brazil (27).

In the floodplains of central Amazonia, a hotspot of pre-Columbian riverine settlements (3, 23, 28), we identified two other earthworks (Fig. 1, J and K). We considered these sites to be anthropogenic because of their straight edges, although the geometry of these sites is distinct from that of the earthworks found in upland forests. Constant sedimentary deposition over the centuries, through periodic floods, may have buried smaller features, preserving only the observed structures, which elsewhere have been associated with pre-Columbian fisheries management (29).

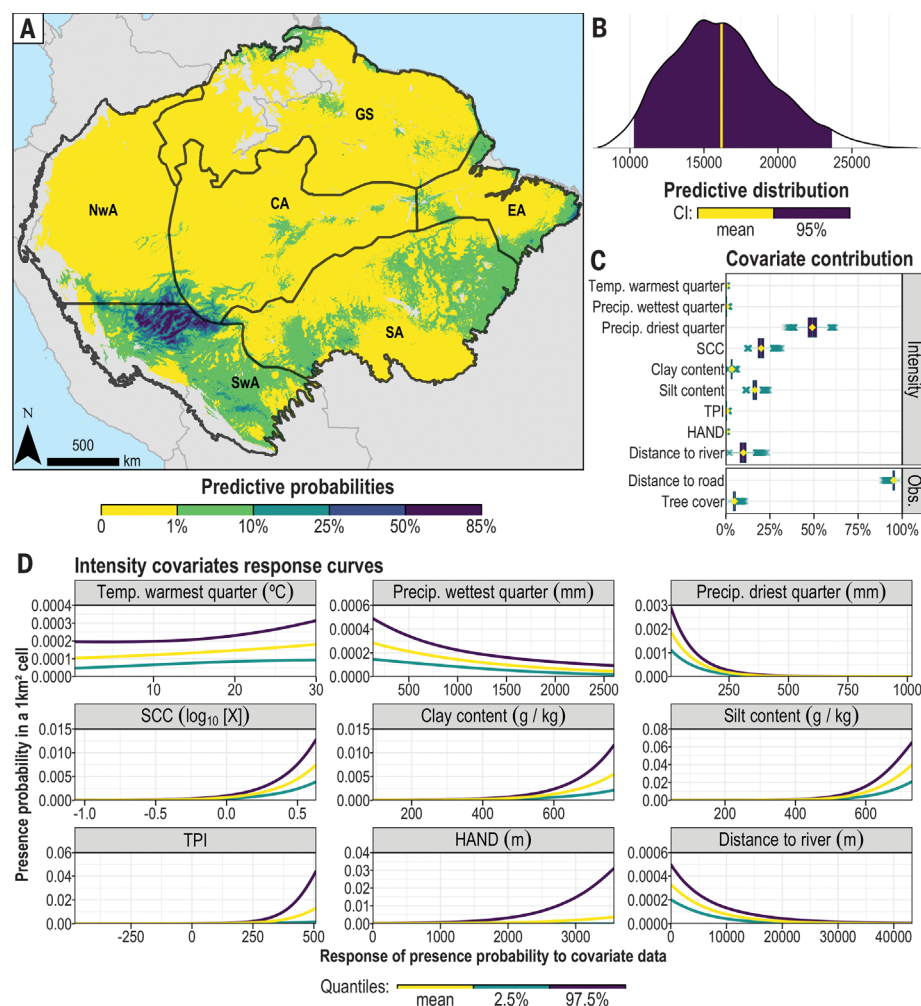
### Modeling basin-wide distribution of earthworks

By extrapolating the density of earthworks observed in our LIDAR data (0.0062 earthworks/km<sup>2</sup>) to the extent of Amazonia (6.7 million km<sup>2</sup>), we calculated that >41,000 earthworks may occur throughout the forest. However, given

that our LIDAR data covered only 0.08% of the total area of Amazonia and that earth-building societies were not evenly distributed across the basin (15, 30), more-rigorous methods were needed to estimate how many other as yet undocumented pre-Columbian earthworks might occur and where. To answer these questions, we used newly developed Bayesian statistical techniques and an inhomogeneous Poisson process (IPP) model (31), with an intensity function using intensity covariates and thinned by observability covariates (32). Recently, the use of other machine learning techniques such as random forests have become popular for species distribution models (SDMs). There is still

some uncertainty about this use (33), and the implementation of random forests to IPPs is still not available, but it might be a welcome addition to the toolkit of SDM analysis.

The aforementioned statistical analysis was based on the records of 937 known earthworks complemented by our discoveries (24 earthworks), with three bioclimatic, three edaphic, and three topographic variables as intensity covariates. More than 40 variables were considered in the model (table S1), and the selected ones (nine variables) cover gradients of temperature, precipitation, soil structure and fertility, topography, water-table depth, and distance to water bodies (27). Observability



**Fig. 2. Probability model of pre-Columbian earthworks across Amazonia.** (A) Predicted probability of earthwork presence for 1-km<sup>2</sup> cells across six Amazonian regions using an inhomogeneous Poisson process predictive model: central Amazonia (CA), eastern Amazonia (EA), Guiana Shield (GS), northwestern Amazonia (NwA), southern Amazonia (SA), and southwestern Amazonia (SwA). Areas not modeled (NA) are greyed out. (B) Predictive probability function for the number of as yet undetected earthworks; the dark area under the curve represents the credibility interval (CI) of the probabilities associated with each number. (C) Boxplot of the estimated relative contribution of each covariate; the yellow diamond indicates the mean value. SCC, soil cation concentration; TPI, terrain position index; HAND, height above the nearest drainage. (D) Individual predicted probability of earthwork presence against intensity covariates. For projected areas across each Amazonian region on different probability thresholds, see table S2, and for the IPP model on continuous values, see fig. S1.





**Fig. 3. Significant relationships between the occurrence and abundance of domesticated tree species and the modeled distribution of earthworks in Amazonia.** Point estimates and confidence intervals of species significantly associated with predicted probability of earthwork presence, with an overall significance level of 5%. Positive species are more likely to occur and be abundant where predicted probability of earthwork presence is high, whereas negative species are less likely to occur and be abundant there.

covariates were used to describe the dataset sample preference by indicating the most favorable location for sample acquisition (32). The effect of sample selection bias was individually weighted for each sample (21).

Our model predicts the number of as yet undiscovered pre-Columbian structures at be-

tween 10,272 and 23,648, with 95% probability, giving an average of 16,187 sites (Fig. 2B). These estimates suggest that the earthworks already documented in the Amazon to date account for a mere 4 to 9% of the total, and that 91 to 96% of Amazonian earthworks remain undiscovered.

This predictive model indicated that earthworks are likely concentrated in southwestern Amazonia (Fig. 2A) and corroborated previous studies that found this region to be a hotspot of earth-building societies (13, 15, 34). In addition, nearly all the highest-probability cells ( $\geq 25\%$  predicted probability) occur in a 94,713-km<sup>2</sup> rectangle that overlays a substantial portion of the Brazilian state of Acre. Indeed, southwestern Amazonia contains the earliest plant cultivation and domestication (9, 35), the oldest anthropogenic soils (35), low-density urbanism (19), and now a much higher density of earthworks. The underlying spatial data distribution may offer valuable information about pre-Columbian practices before European contact (36).

Our analysis also suggests that pre-Columbian societies engaged in earthwork construction in all other regions, covering a broader area than previously thought. However, earthworks are heterogeneously distributed across Amazonian regions. Almost 80% of the basin has a 0 to 1% predicted probability of earthwork presence for 1-km<sup>2</sup> cells. These low-probability areas are mostly located in northwestern, northern, and central Amazonia, whereas higher-probability areas ( $\geq 25\%$  predicted probability, covering 1.41% of the basin) are located in southwestern Amazonia. Earth-building societies were very common in some parts of the basin, but they may not have occupied all of Amazonia (6, 15, 30, 37). Other types of domesticated landscapes, such as Amazonian dark earths, are widespread [see maps in (37–39)] in regions (e.g., central Amazonia) where the earthworks analyzed in our study (ring ditches, geoglyphs, ponds, and wells) are not commonly found. Given the diversity of pre-Columbian societies and their land-use practices over 12,000 years of ancient Amazonian history, forests were likely modified at varying intensities by different Indigenous populations through time (7, 38).

Forests modified by earth-building societies are more likely to occur in locations with high temperature and low precipitation during the wettest and driest quarters (Fig. 2, C and D). Areas with high soil content of clay and silt and high cation concentrations also show high probabilities of earthwork presence. In addition, earthworks tend to be located on plateaus with deep water tables, yet close to water bodies. This combination of environmental conditions probably facilitated the construction of earthworks by offering periods with less precipitation and higher temperature, and soils with a better texture for earthmoving. In addition, the presence of a drier season facilitates burning, which could help remove the vegetation for building earth structures (12), while higher soil cation concentrations could attract settlements for the development of diversified food production systems with plants

managed and domesticated to different degrees (15, 30).

As expected, observability covariates indicate that previously reported earthworks are mostly found near roads, which facilitate field research (Fig. 2C). Tree cover, however, has no effect on the current distribution of earthworks. Thus, new earthworks can still be found even in deforested areas. The use of conventional very-high-resolution remote sensing data, guided by the probability surfaces produced here (Fig. 2A), is likely to reveal more previously undetected earthworks in both closed-canopy and deforested areas of Amazonia. In addition, the rise of machine learning techniques applied to archaeological site detection may lead to rapid discovery of new sites across deforested areas (40, 41).

In forested areas, LIDAR surveys guided by our discoveries (e.g., full coverage of the Fig. 1B site) and the probability surfaces in Fig. 2A are promising tools for discovering new sites. However, very-high-probability areas ( $\geq 50\%$  predicted probability) cover 32,120 km<sup>2</sup>, for which a complete LIDAR survey would require six times more data than have been collected to date in the Amazon. Thus, other approaches, such as mapping the distribution and abundance of domesticated species associated with earthwork presence, may help locate new sites within the Amazonian forest (42, 43).

### Relationships with domesticated species

We analyzed the relationship between the response (occurrence and abundance) of 79 domesticated tree species identified across 1676 forest plots (6) and the predicted probability of earthwork presence using generalized linear models to test whether forests with a higher probability of earthwork presence have a higher frequency and abundance of domesticated species (21). The occurrence and/or abundance of 35 domesticated species increased with the predicted probability of earthwork presence, while those of 18 species decreased. In total, the occurrence and/or abundance of 53 of the 79 domesticated species showed significant association with the predictive model of earthwork distribution (Fig. 3).

The species whose responses increased the most significantly along with the probability of earthwork occurrence are *Bertholletia excelsa* ( $P < 0.001$ ,  $\beta = 1.13$ ), *Hevea brasiliensis* ( $P < 0.001$ ,  $\beta = 0.65$ ), and *Brosimum alicastrum* ( $P < 0.001$ ,  $\beta = 1.36$ ), on the basis of occurrence data, and *Astrocaryum murumuru* ( $P < 0.001$ ,  $\beta = 0.71$ ), *Attalea phalerata* ( $P < 0.001$ ,  $\beta = 1.42$ ), and *Theobroma cacao* ( $P < 0.001$ ,  $\beta = 1.43$ ), on the basis of abundance data (fig. S2). The species whose responses decreased the most significantly are *Erismia japura* ( $P < 0.001$ ,  $\beta = -1.94$ ), on the basis of occurrence data, and *E. japura* ( $P < 0.001$ ,  $\beta = -1.7$ ) and *Oenocarpus bataua* ( $P < 0.001$ ,  $\beta = -0.27$ ), on the basis of abundance data

(fig. S2). Although these highlighted species have multiple uses (44), they have mainly been used for their edible fruits and nuts in Amazonia, with the exception of *H. brasiliensis*, which has been used intensively for latex production (data S1). Species that are more frequent and abundant in forests with higher probability of earthwork occurrence were probably favored by a combination of interacting past Indigenous management practices and ecological processes (6). These results confirm previous archaeobotanical and ethnobotanical data that have already shown that some species (e.g., *B. excelsa*, *Astrocaryum* spp., and *Attalea* spp.) are more abundant on and near archaeological sites across Amazonia (8, 14, 36). Species that are less frequent and abundant in areas with a higher probability of earthwork occurrence likely prefer habitats where earthworks are usually not found, such as sandy soils with lower fertility (7), or were disfavored by past practices that might have had detrimental effects on some species (45).

### Social-ecological implications

The massive extent of archaeological sites and widespread human-modified forests across Amazonia is critically important for establishing an accurate understanding of interactions between human societies, Amazonian forests, and Earth's climate (37). Considering the widespread extent of locations modified by pre-Columbian management and cultivation practices, Amazonia can be viewed as an ancient social-ecological system, with long-term responses to climate change (46), more similar to old secondary forests than pristine climax ecosystems (10).

The discovery of earthworks hidden beneath dense forest canopies also indicates that, given sufficient time after these sites became depopulated, forests regenerated over the centuries. It is still unknown, however, the scale of structural and floristic differences between pristine and domesticated forests across Amazonia. The forest reclaimed the land, but this is not the case for the Indigenous societies that managed these forests and waterbodies and that created these large structures. These archaeological legacies can play a role in present-day debates around Indigenous territorial rights. They serve as tangible proof of an ancestor's occupation, way of life, and their relationship with the forest. Today, Indigenous peoples struggle to recognize their right to land originally inhabited by their ancestors, along with the protection of their territories, languages, cultures, and heritages. In addition to protecting the native peoples that remain, the institution of Indigenous lands also collaborates with forest conservation in times of debates on climate change and the search for solutions that minimize impacts on the climate and promote carbon neutrality.

These human-modified landscapes harbor an impressive archaeological heritage. Of the

24 earthworks newly reported in our study, 50% are located in areas with some degree of legal protection. When all 937 known earthworks are considered, however, only 9% are located inside Indigenous lands and protected areas. To date, most pre-Columbian earthworks have been discovered after deforestation. The highest density of known earthworks in Amazonia is, therefore, outside protected areas and mostly located in the region with the highest historical and current rates of deforestation, called the "Arc of Deforestation." Protected areas and Indigenous territories can act as barriers against illegal activities that promote the degradation and destruction of Amazonia's natural and cultural heritage, but their implementation and expansion depend on strong government policies and law enforcement (47, 48).

Ironically, modern-day deforestation is removing the very evidence of pre-Columbian land-use strategies that were able to transform the landscape without causing large-scale deforestation (13). Today, Amazonia is experiencing expansion of agriculture and cattle ranching (49, 50), especially where earthworks are concentrated in the southern and southwestern regions, risking the destruction of earthworks and fracturing and hampering the identification of pre-Columbian occupation sites that provide direct evidence of ancient Indigenous territories. Our data on earthwork probability, suitable environmental conditions, and associated domesticated species should narrow the search for Indigenous heritage sites, enhanced by optical and LIDAR sensing to identify, monitor, and help conserve archaeological features. Amazonian forests clearly merit protection not only for their ecological and environmental value but also for their high archaeological, social, and biocultural value, which can teach modern society how to sustainably manage its natural resources.

### REFERENCES AND NOTES

1. E. G. Neves et al., "Chapter 8: Peoples of the Amazon before European colonization" in *Amazon Assessment Report 2021* (UN Sustainable Development Solutions Network, 2021); <https://doi.org/10.5516/LXIT5573>.
2. C. L. Erickson, in *Time and Complexity in Historical Ecology: Studies in the Neotropical Lowlands*, W. Balée, C. L. Erickson, Eds., Historical Ecology Series (Columbia Univ. Press, 2006), pp. 235–278.
3. E. G. Neves, in *The Handbook of South American Archaeology*, H. Silverman, W. H. Isbell, Eds. (Springer, 2008), pp. 359–379.
4. D. P. Schaun, *Sacred Geographies of Ancient Amazonia: Historical Ecology of Social Complexity* (Routledge, 2016).
5. C. de P. Moraes, E. G. Neves, in *Encyclopedia of Global Archaeology*, C. Smith, Ed. (Springer International Publishing, Cham, 2020), pp. 3491–3503.
6. C. Levis et al., *Science* **355**, 925–931 (2017).
7. C. Levis et al., *Front. Ecol. Evol.* **5**, 171 (2018).
8. C. R. Clement, *Econ. Bot.* **53**, 188–202 (1999).
9. U. Lombardo et al., *Nature* **581**, 190–193 (2020).
10. M. J. Heckenberger et al., *Science* **301**, 1710–1714 (2003).
11. M. J. Heckenberger, J. C. Russell, J. R. Toney, M. J. Schmidt, *Philos. Trans. R. Soc. London Ser. B* **362**, 197–208 (2007).
12. J. F. Carson et al., *Proc. Natl. Acad. Sci. U.S.A.* **111**, 10497–10502 (2014).



13. J. Watling *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **114**, 1868–1873 (2017).

14. C. C. Mann, *Science* **321**, 1148–1152 (2008).

15. J. G. de Souza *et al.*, *Nat. Commun.* **9**, 1125 (2018).

16. J. Iriarte *et al.*, *J. Comput. Appl. Archaeol.* **3**, 151–169 (2020).

17. M. A. Canuto *et al.*, *Science* **361**, eaa0137 (2018).

18. A. F. Chase, D. Z. Chase, C. T. Fisher, S. J. Leisz, J. F. Weishampel, *Proc. Natl. Acad. Sci. U.S.A.* **109**, 12916–12921 (2012).

19. H. Prümers, C. J. Betancourt, J. Iriarte, M. Robinson, M. Schaich, *Nature* **606**, 325–328 (2022).

20. C. M. Souza Jr. *et al.*, *Remote Sens.* **12**, 2735 (2020).

21. Materials and methods are available as supplementary materials.

22. G. Tejada, E. B. Görgens, F. D. B. Espírito-Santo, R. Z. Cantinho, J. P. Ometto, *Carbon Balance Manag.* **14**, 11 (2019).

23. M. J. Heckenberger, J. B. Petersen, E. G. Neves, *Lat. Am. Antiq.* **10**, 353–376 (1999).

24. M. J. Heckenberger *et al.*, *Science* **321**, 1214–1217 (2008).

25. S. Saunaluoma, M. Pärssinen, D. Schaaf, *J. Field Archaeol.* **43**, 362–379 (2018).

26. G. Odomne, J.-F. Molino, *Les Nouv. archéologie* **152**, 11–15 (2018).

27. M. P. Cabral, J. D. M. Saldanha, *Rev. Arqueol. Pública* **3**, 7–13 (2015).

28. P. Stenborg, D. P. Schaaf, C. G. Figueiredo, *J. Field Archaeol.* **43**, 44–57 (2018).

29. R. Blatrix *et al.*, *Sci. Rep.* **8**, 5998 (2018).

30. C. H. McMichael, M. W. Palace, M. Golightly, *J. Biogeogr.* **41**, 1733–1745 (2014).

31. N. A. C. Cressie, in *Statistics for Spatial Data*, Wiley Series in Probability and Statistics (John Wiley & Sons, Inc., revised ed., 2015), pp. 575–723.

32. G. A. Moreira, D. Gamerman, *Ann. Appl. Stat.* **16**, 1848–1867 (2022).

33. R. Valavi, J. Elith, J. J. Lahoz-Monfort, G. Guillera-Aroita, *Ecography* **44**, 1731–1742 (2021).

34. S. M. Maezumi *et al.*, *Nat. Plants* **4**, 540–547 (2018).

35. J. Watling *et al.*, *PLOS ONE* **13**, e0199868 (2018).

36. P. Riris, *J. Anthropol. Archaeol.* **59**, 101177 (2020).

37. C. N. H. McMichael, F. Matthews-Bird, W. Farfan-Rios, K. J. Feeley, *Proc. Natl. Acad. Sci. U.S.A.* **114**, 522–527 (2017).

38. A. M. G. A. WinklerPrins, C. Levis, *Ann. Am. Assoc. Geogr.* **111**, 858–868 (2021).

39. J. Iriarte *et al.*, *Quat. Sci. Rev.* **248**, 106582 (2020).

40. H. A. Orengo *et al.*, *Proc. Natl. Acad. Sci. U.S.A.* **117**, 18240–18250 (2020).

41. A. Bonhage *et al.*, *Archaeol. Prospect.* **28**, 177–186 (2021).

42. M. P. Ferreira, M. Zortea, D. C. Zanotta, Y. E. Shimabukuro, C. R. de Souza Filho, *Remote Sens. Environ.* **179**, 66–78 (2016).

43. M. P. Ferreira *et al.*, *Ecol. Inform.* **63**, 101302 (2021).

44. S. D. Coelho *et al.*, *PLOS ONE* **16**, e0257875 (2021).

45. G. Odonne *et al.*, *Ecology* **100**, e02806 (2019).

46. R. J. W. Brien *et al.*, *Nature* **519**, 344–348 (2015).

47. K. V. Conceição *et al.*, *Land Use Policy* **108**, 105663 (2021).

48. G. de Oliveira *et al.*, *Forests* **13**, 16 (2021).

49. C. H. L. Silva Junior *et al.*, *Nat. Ecol. Evol.* **5**, 144–145 (2021).

50. G. Mataveli, G. de Oliveira, *Science* **375**, 275–276 (2022).

51. V. Peripato *et al.*, Data from: Over 10,000 Pre-Columbian earthworks are still hidden throughout Amazonia, version 1.0.0, Zenodo (2023); <https://doi.org/10.5281/zenodo.7750985>.

ACKNOWLEDGMENTS

This paper is the result of the work of hundreds of different scientists and research institutions in the Amazon over the past 80 years. Without their hard work, this analysis would have been impossible. We thank members of the following projects and groups for providing data and support: Sustainable Landscapes Brazil project; Center for Science of the Terrestrial System; TRopical Ecosystems and Environmental Sciences; Amazon Tree Diversity Network; Amazonian Archaeological Sites Network; Pre-Columbian Amazon-Scale Transformations; Biodiversity Research Program in Western Amazon Center for Integrated Studies of Amazonian Biodiversity (PPBio-AmOc/INCT-CENBAM); and the Brazilian Space Agency (AEB). **Funding:** V.P. and C.L. were supported by the Coordination of Superior Level Staff Improvement under Academic Excellence Program (CAPES/PROEX) research grants (1681023, 88887.479608/2020, and 88887.474568/2020); C.L. was supported by National Council for Scientific and Technological Development (CNPQ) grants (159440/2018-1 and 400369/2021-4); D.Gam. was supported by a CNPQ grant (304742/2018-0); A.B.J. was supported by the European Research Council (ERC) under a Consolidator Grant (FP7-771056-LICCI); J.P.H. B.O. was supported by a São Paulo Research Foundation (FAPESP)

grant (2017/22269-2) and Airborne LASER Scanning data acquisition by the Amazon Fund grant (14.2.0929.1); H.L.G.C. was supported by a FAPESP grant (18/14423-4); H.T.S., V.H.F.G., and R.S. were supported by a PVE-MEC/MCTI/CAPES/CNPq/FAPs grant (407232/2013-3); J.G.d.S., J.L., and M.Rob. were supported by Horizon 2020 grants (ERC Cog 616179 and ERC PoC.777845); A.M.d.S. was supported by a CAPES grant (88887.607664/2021); D.S., J.-F.M., J.E., P.P., and J.C. were supported by an ANR grant (CEBA 10-LABX-25-01); H.L.d.Q. and J.L.L.M. were supported by MCT/CNPq/CT-INFRA/GEOMA grants (550373/2010-1 and 457515/2012-0); J.L.L.M. was supported by a CAPES/PDSE grant (88881.135761/2016-01) and a CAPES/Fapespa grant (1530801); E.M.V. was supported by a CNPq grant (308040/2017-1); B.M.F. was supported by a FAPESP grant (2016/25086-3); B.S.M., B.H.M.-J., and O.L.P. were supported by a CNPq/CAPES/FAPS/BC-Newton grant (441244/2016-5), a FAPEMAT grant (0589267/2016), and a Royal Society GCRF International Collaboration Award (ICAR\180100); T.W.H. was supported by an NSF/DEB grant (1556338); L.E.O.C.A. was supported by a CNPQ/PQ grant (314416/2020-0). Floristic identification in plots in the RAINFOR forest monitoring network and plot data management by ForestPlots.net have been supported by several Natural Environment Research Council grants to O.L.P. and colleagues (NE/B503384/1, NE/D01025X/1, NE/I02982X/1, NE/F005806/1, NE/D005590/1, NE/I028122/1, and NE/S011811/1) and the Gordon and Betty Moore Foundation. **Author contributions:** Conceptualization: V.P., C.L., and L.E.O.C.A. LIDAR raw data processing: V.P. Earthworks investigation: V.P., J.G.d.S., J.L., M.Rob., and L.E.O.A.C. Modeling: G.A.M. and D.Gam. Domestication investigation: V.P. and C.L. Writing – original draft: V.P., C.L., and L.E.O.A.C. Writing – review & editing: V.P., C.L., G.A.M., D.Gam., N.C.A.P., and L.E.O.A.C. All of the other authors contributed data, discussed further analyses, and commented on various versions of the manuscript. **Competing interests:** The authors declare that they have no competing interests. **Data and materials availability:** Data from publicly available sources are cited in the supplementary materials. Other data and computer codes used in the analysis are publicly available in Zenodo (51). **License information:** Copyright © 2023 the authors, some rights reserved; exclusive licensee American Association for the Advancement of Science. No claim to original US government works. <https://www.science.org/about/science-licenses-journal-article-reuse>

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## SUPPLEMENTARY MATERIALS

[science.org/doi/10.1126/science.ade2541](https://doi.org/10.1126/science.ade2541)

Materials and Methods

Figs. S1 to S19

Tables S1 to S5

References (52–80)

MDAR Reproducibility Checklist

Data S1 and S2

Submitted 16 September 2022; accepted 31 August 2023  
10.1126/science.ade2541