# Title: Over 10,000 Pre-Columbian earthworks are still hidden throughout Amazonia

5

10

15

20

25

30

35

40

Authors: Vinicius Peripato<sup>1</sup>\*†, Carolina Levis<sup>2</sup>†, Guido A. Moreira<sup>3</sup>, Dani Gamerman<sup>4</sup>, Hans ter Steege<sup>5</sup>, Nigel C.A. Pitman<sup>6</sup>, Jonas G. de Souza<sup>7</sup>, José Iriarte<sup>8</sup>, Mark Robinson<sup>8</sup>, André Braga Junqueira<sup>9</sup>, Thiago B. Trindade<sup>10</sup>, Fernando O. de Almeida<sup>11</sup>, Claide de Paula Moraes<sup>12</sup>, Umberto Lombardo<sup>13</sup>, Eduardo K. Tamanaha<sup>14</sup>, Shira Y. Maezumi<sup>15</sup>, Jean P. H. B. Ometto<sup>1</sup>, José R.G. Braga<sup>1</sup>, Wesley A. Campanharo<sup>1</sup>, Henrique L. G. Cassol<sup>1</sup>, Philipe R. Leal<sup>1</sup>, Mauro L. R. de Assis<sup>1</sup>, Adriana M. da Silva<sup>16</sup>, Oliver L. Phillips<sup>17</sup>, Flávia R.C. Costa<sup>18</sup>, Bernardo Monteiro Flores<sup>2</sup>, Bruce Hoffman<sup>19</sup>, Terry W. Henkel<sup>20</sup>, Maria Natalia Umaña<sup>21</sup>, William E. Magnusson<sup>18</sup>, Elvis H. Valderrama Sandoval<sup>22,23</sup>, Jos Barlow<sup>24</sup>, William Milliken<sup>25</sup>, Maria Aparecida Lopes<sup>26</sup>, Marcelo Fragomeni Simon<sup>27</sup>, Tinde R. van Andel<sup>5,28</sup>, Susan G.W. Laurance<sup>29</sup>, William F. Laurance<sup>29</sup>, Armando Torres-Lezama<sup>30</sup>, Rafael L. Assis<sup>31</sup>, Jean-François Molino<sup>32</sup>, Mickaël Mestre<sup>33</sup>, Michelle Hamblin<sup>34</sup>, Luiz de Souza Coelho<sup>35</sup>, Diogenes de Andrade Lima Filho<sup>35</sup>, Florian Wittmann<sup>36,37</sup>, Rafael P. Salomão<sup>38,39</sup>, Iêda Leão Amaral<sup>35</sup>, Juan Ernesto Guevara<sup>40,41</sup> Francisca Dionízia de Almeida Matos<sup>35</sup>, Carolina V. Castilho<sup>42</sup>, Marcelo de Jesus Veiga Carim<sup>43</sup>, Dairon Cárdenas López<sup>44</sup>#, Daniel Sabatier<sup>32</sup>, Mariana Victória Irume<sup>35</sup>, Maria Pires Martins<sup>35</sup>, José Renan da Silva Guimarães<sup>45</sup>, Olaf S. Bánki<sup>5</sup>, Maria Teresa Fernandez Piedade<sup>37</sup>, José Ferreira Ramos<sup>35</sup>, Bruno Garcia Luize<sup>46</sup>, Evlyn Márcia Moraes de Leão Novo<sup>1</sup>, Percy Núñez Vargas<sup>47</sup>, Thiago Sanna Freire Silva<sup>48</sup>, Eduardo Martins Venticinque<sup>49</sup>, Angelo Gilberto Manzatto<sup>50</sup>, Neidiane Farias Costa Reis<sup>51</sup>, John Terborgh<sup>52,29</sup>, Katia Regina Casula<sup>51</sup>, Layon O. Demarchi<sup>37</sup>, Euridice N. Honorio Coronado<sup>53,54</sup>, Abel Monteagudo Mendoza<sup>47,55</sup>, Juan Carlos Montero<sup>56,35</sup>, Jochen Schöngart<sup>37</sup>, Ted R. Feldpausch<sup>57,17</sup>, Adriano Costa Quaresma<sup>36,37</sup>, Gerardo A. Aymard C.<sup>58</sup>, Chris Baraloto<sup>59</sup>, Nicolás Castaño Arboleda<sup>44</sup>, Julien Engel<sup>32,59</sup>, Pascal Petronelli<sup>60</sup>, Charles Eugene Zartman<sup>35</sup>, Timothy J. Killeen<sup>61</sup>, Beatriz S. Marimon<sup>62</sup>, Ben Hur Marimon-Junior<sup>62</sup>, Juliana Schietti<sup>35</sup>, Thaiane R. Sousa<sup>63</sup>, Rodolfo Vasquez<sup>55</sup>, Lorena M. Rincón<sup>35</sup>, Erika Berenguer<sup>64,24</sup>, Joice Ferreira<sup>65</sup>, Bonifacio Mostacedo<sup>66</sup>, Dário Dantas do Amaral<sup>39</sup>, Hernán Castellanos<sup>67</sup>, Marcelo Brilhante de Medeiros<sup>27</sup>, Ana Andrade<sup>68</sup>, José Luís Camargo<sup>68</sup>, Emanuelle de Sousa Farias<sup>69,70</sup>, José Leonardo Lima Magalhães<sup>71,65</sup>, Henrique Eduardo Mendonça Nascimento<sup>35</sup>, Helder Lima de Queiroz<sup>72</sup>, Roel Brienen<sup>17</sup>, Juan David Cardenas Revilla<sup>35</sup>, Pablo R. Stevenson<sup>73</sup>, Alejandro Araujo-Murakami<sup>74</sup>, Bruno Barçante Ladvocat Cintra<sup>75</sup>, Yuri Oliveira Feitosa<sup>76</sup>, Flávia Rodrigues Barbosa<sup>77</sup>, Rainiellen de Sá Carpanedo<sup>77</sup>, Joost F. Duivenvoorden<sup>78</sup>, Janaína Costa Noronha<sup>77</sup>, Domingos de Jesus Rodrigues<sup>77</sup>, Hugo F. Mogollón<sup>79</sup>, Leandro Valle Ferreira<sup>39</sup>, John Ethan Householder<sup>36</sup>, José Rafael Lozada<sup>80</sup>, James A. Comiskey<sup>81,82</sup>, Freddie C. Draper<sup>83</sup>, José Julio de Toledo<sup>84</sup>, Gabriel Damasco<sup>85</sup>, Nállarett Dávila<sup>46</sup>##, Roosevelt García-Villacorta<sup>86,87</sup>, Aline Lopes<sup>88</sup>, Fernando Cornejo Valverde<sup>89</sup>, Alfonso Alonso<sup>82</sup>, Francisco Dallmeier<sup>82</sup>, Vitor H.F. Gomes<sup>90,91</sup>, Eliana M. Jimenez<sup>92</sup>, David Neill<sup>93</sup>, Maria Cristina Peñuela Mora<sup>94</sup>, Daniel P. P. de Aguiar<sup>95,96</sup>, Luzmila Arroyo<sup>74</sup>, Fernanda Antunes Carvalho<sup>18,97</sup>, Fernanda Coelho de Souza<sup>18,17</sup>, Kenneth J. Feeley<sup>98,99</sup>, Rogerio Gribel<sup>35</sup>, Marcelo Petratti Pansonato<sup>35,100</sup>, Marcos Ríos Paredes<sup>101</sup>, Izaias Brasil da Silva<sup>102</sup>, Maria Julia Ferreira<sup>103</sup>, Paul V.A. Fine<sup>104</sup>, Émile Fonty<sup>105,32</sup>, Marcelino Carneiro Guedes<sup>106</sup>, Juan Carlos Licona<sup>56</sup>, Toby Pennington<sup>57,107</sup>, Carlos A. Peres<sup>108</sup>, Boris Eduardo Villa Zegarra<sup>109</sup>, Germaine Alexander Parada<sup>74</sup>, Guido<sup>110</sup>, Vincent Antoine Vos<sup>110</sup>, Carlos Cerón<sup>111</sup>, Paul Maas<sup>5</sup>, Marcos Silveira<sup>112</sup>, Juliana Stropp<sup>113</sup>, Raquel Thomas<sup>114</sup>, Tim R. Baker<sup>17</sup>, Doug Daly<sup>115</sup>, Isau Huamantupa-Chuquimaco<sup>116</sup>, Ima Célia Guimarães Vieira<sup>39</sup>, Bianca Weiss

Albuquerque<sup>37</sup>, Alfredo Fuentes<sup>117,118</sup>, Bente Klitgaard<sup>119</sup>, José Luis Marcelo Pena<sup>120</sup>, Miles R. Silman<sup>121</sup>, J. Sebastián Tello<sup>118</sup>, Corine Vriesendorp<sup>6</sup>, Jerome Chave<sup>122</sup>, Anthony Di Fiore<sup>123,124</sup>, Renato Richard Hilário<sup>84</sup>, Juan Fernando Phillips<sup>125</sup>, Gonzalo Rivas-Torres<sup>124,126</sup>, Patricio von Hildebrand<sup>127</sup>, Luciana de Oliveira Pereira<sup>57</sup>, Edelcilio Marques Barbosa<sup>35</sup>, Luiz Carlos de Matos Bonates<sup>35</sup>, Hilda Paulette Dávila Doza<sup>101</sup>, Ricardo Zárate Gómez<sup>128</sup>, George Pepe Gallardo Gonzales<sup>101</sup>, Therany Gonzales<sup>129</sup>, Yadvinder Malhi<sup>130</sup>, Ires Paula de Andrade Miranda<sup>35</sup>, Linder Felipe Mozombite Pinto<sup>101</sup>, Adriana Prieto<sup>131</sup>, Agustín Rudas<sup>131</sup>, Ademir R. Ruschel<sup>65</sup>, Natalino Silva<sup>132</sup>, César I.A. Vela<sup>133</sup>, Egleé L. Zent<sup>134</sup>, Stanford Zent<sup>134</sup>, Angela Cano<sup>73,135</sup>, Yrma Andreina Carrero Márquez<sup>136</sup>, Diego F. Correa<sup>73,137</sup>, Janaina Barbosa Pedrosa Costa<sup>106</sup>, David Galbraith<sup>17</sup>, Milena Holmgren<sup>138</sup>, Michelle Kalamandeen<sup>139</sup>, Guilherme Lobo<sup>37</sup>, Marcelo Trindade Nascimento<sup>140</sup>, Alexandre A. Oliveira<sup>100</sup>, Hirma Ramirez-Angulo<sup>30</sup>, Maira Rocha<sup>37</sup> Veridiana Vizoni Scudeller<sup>141</sup>, Rodrigo Sierra<sup>142</sup>, Milton Tirado<sup>142</sup>, Geertje van der Heijden<sup>143</sup>, Emilio Vilanova Torre<sup>30,144</sup>, Manuel Augusto Ahuite Reategui<sup>145</sup>, Cláudia Baider<sup>146,100</sup>, Henrik Balslev<sup>147</sup>, Sasha Cárdenas<sup>73</sup>, Luisa Fernanda Casas<sup>73</sup>, William Farfan-Rios<sup>47,118,148</sup>, Cid Ferreira<sup>35</sup>, Reynaldo Linares-Palomino<sup>82</sup>, Casimiro Mendoza<sup>149,150</sup>, Italo Mesones<sup>104</sup>, Ligia Estela Urrego Giraldo<sup>151</sup>, Daniel Villarroel<sup>74,152</sup>, Roderick Zagt<sup>153</sup>, Miguel N. Alexiades<sup>154</sup>, Edmar Almeida de Oliveira<sup>62</sup>, Karina Garcia-Cabrera<sup>121</sup>, Lionel Hernandez<sup>67</sup>, Walter Palacios Cuenca<sup>155</sup>, Susamar Pansini<sup>51</sup>, Daniela Pauletto<sup>156</sup>, Freddy Ramirez Arevalo<sup>23</sup>, Adeilza Felipe Sampaio<sup>51</sup>, Luis Valenzuela Gamarra<sup>55</sup>, Luiz E. O. C. Aragão<sup>1,57</sup>\*

20

5

10

15

\*Corresponding authors. Email: vinicius.peripato@gmail.com; luiz.aragao@inpe.br
†These authors contributed equally to this work;
#deceased 5/Jan./2022; ##deceased 30/Nov./2022

25

30

35

40

#### **Abstract:**

Indigenous societies are known to have occupied the Amazon basin for over 12,000 years, but the scale of their influence on Amazonian forests remains uncertain. Using Light Detection and Ranging information from across the basin, we report the discovery of 24 previously undetected pre-Columbian earthworks beneath the forest canopy. Modeled distribution and abundance of large-scale archaeological sites across Amazonia suggest that 10,272–23,640 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 new archaeological sites around which pre-Columbian societies actively modified forests, a discovery that opens new opportunities for understanding the magnitude of ancient human influence on Amazonia and its current functioning.

### **One-Sentence Summary:**

Amazon-wide LiDAR surveys and predictive models suggest thousands of undocumented archaeological sites across the basin.

### **Main Text**

5

10

15

20

25

30

During the pre-Columbian era, Amazonia was home to dense and complex societies throughout its vast forested area spanning 6.7 million km² (1). These ancient Indigenous societies had a 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 via evidence from on-theground 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 last decade, the use of LiDAR data has revealed the complexity of Mayan civilization by indicating a regionally integrated 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, mainly due to the construction of stone temples in Mesoamerica in contrast to the use of earth 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. Since 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 yet undetected earthworks hidden beneath remote forest landscapes. Based on our predictive model, we estimate the number of undocumented earthworks and identify domesticated tree species associated with earthwork presence.

5

10

15

20

25

Scanning 5,315 km<sup>2</sup> of LiDAR data originally obtained for estimating aboveground biomass throughout the Amazonian forest (22) revealed 24 unreported earthworks in southern, southwestern, central, and northern (the Guiana Shield) Amazonia (Fig. 1[A]) (21). We detected a fortified village in southern Amazonia (Fig. 1[B]), defensive and ceremonial sites in the southwestern (Fig. 1[C-F]), crowned mountains and megalithic structures in the Guiana Shield (Fig. 1[G-I]), and riverine sites on floodplains in central Amazonia (Fig. 1[J-K]).

In southern Amazonia, we found an ancient plaza town located in the Upper Xingu Basin (Fig. 1[B]). This region is known to have supported dense populations in the past, distributed in 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, supporting 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–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–I]). The region holds different types and usages of earthworks: permanent settlements within crowned mountains in French Guiana (26), and ceremonial sites

#### Template revised February 2021

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–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).

5

10

15

20

25

By extrapolating the density of earthworks observed in our LiDAR data (0.0062 earthworks / km²) to the extent of Amazonia (6.7 million km²), we calculated that over 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 earth-building societies were not evenly distributed across the basin (15, 30), more rigorous methods were needed to estimate how many other previously undocumented pre-Columbian earthworks might occur and where. To answer these questions, we used newly developed 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 their adaptation to IPPs is still not available but it might be a welcomed addition to the toolkit of SDM analysis.

This 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. Over 40 variables were considered in the model (table S1), and the selected ones (9 variables) cover gradients of temperature, precipitation, soil structure and fertility, topography, water-table depth, and distance to water bodies (21). Observability 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).

#### Template revised February 2021

Our model predicts the number of yet undiscovered pre-Columbian structures as 10,272 – 23,648, with 95% probability, giving an average of 16,187 new sites (Fig. 2[B]). These estimates suggest that the earthworks already documented in the Amazon to date account for a mere 4 – 9% of the total, and that 91–96% of Amazonian earthworks remain undiscovered.

5

10

15

20

25

30

This predictive model indicated that earthworks are likely concentrated in southwestern Amazonia (Fig. 2[A]) 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-km² rectangle that overlays a significant 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% of predicted probability of earthwork presence for 1-km² cells. These low-probability areas are mostly located in northwestern, northern and central Amazonia, while higher-probability areas ( $\geq 25\%$  of predicted probability that cover 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 of 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 landuse 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–D]). Areas with high soil contents 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

# Template revised February 2021

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).

5

10

15

20

25

As expected, observability covariates indicate that previously reported earthworks are mostly found near roads, which facilitate field research (Fig. 2[C]). 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 in Fig. 2[A], 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 a rapid discovery of new sites across deforested areas (40, 41).

In forested areas, LiDAR surveys guided by our discoveries (e.g., a full coverage of the Fig. 1[B] site) and the probability surfaces in Fig. 2[A] are promising tools for discovering new sites. However, very high probability areas ( $\geq 50\%$  of predicted probability) cover 32,120 km<sup>2</sup>, for which a complete LiDAR survey would require six times more data than has 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 Amazonian forest (42, 43).

We analyzed the relationship between the response (occurrence/abundance) of 79 domesticated tree species identified across 1,676 forest plots (6) and the predicted probability of earthwork presence using generalized linear models to test whether forests with 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 that most significantly increased their response 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,  $\beta = 1.36$ ), based on 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) based on abundance data (fig. S2). The species that most significantly decreased their responses are Erisma japura (p < 0.001,  $\beta = -1.94$ ) based on occurrence data, and E. japura (p < 0.001,  $\beta = -1.7$ ) and Oenocarpus bataua (p < 0.001,  $\beta = -1.7$ ) 0.27) based on abundance data (fig. S2). Although these highlighted species have multiple uses (44), they have been mainly 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 previously archaeobotanical and ethnobotanical data that have already shown that some species (e.g., Bertholletia 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 higher probability of the earthwork occurrence likely prefer habitats where earthworks are usually not found, such as sandy soils with lower fertility (7), or were disfavored due to past practices that might had detrimental effects on some species (45).

5

10

15

20

25

30

The massive extent of archaeological sites and widespread human-modified forests across Amazonia is critically important for establishing a new understanding of interactions between human societies, Amazonian forests and the Earth's climate (37). Ecologically, 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 local areas became depopulated, forests were able to regenerate to a degree that we are still unknown about the structural differences between a pristine and domesticated forest. The forest reclaimed the land, but this is not the case for the Indigenous societies that

# Template revised February 2021

managed these forests and waterbodies and created these large structures. These archeological 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 established within the forest. Today, Indigenous societies require land rights where originally were inhabited by their ancestors, along with the protection of their territories, languages, cultures, heritages, and others. In addition to protecting the natives that remain, the institution of Indigenous lands also collaborates through forest preservation in times of debates on climate change and the search for solutions that minimize impacts on the climate and carbon neutrality.

5

10

15

20

25

30

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 destroying earthworks and fracturing and hampering the identification of pre-Columbian occupation sites which 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 archeological features. Amazonian forests clearly merit protection not only for their ecological and environmental values, but also for their high archaeological, social and biocultural values, which can teach modern society on how to sustainably manage its natural resources.

#### **References and Notes**

20

- 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/10.55161/LXIT5573.
- 2. C. L. Erickson, "8. The Domesticated Landscapes of the Bolivian Amazon" in *Time and Complexity in Historical Ecology*, W. Balée, C. L. Erickson, Eds. (Columbia University Press, 2006), *Studies in the Neotropical Lowlands*, pp. 235–278. https://doi.org/10.7312/bale13562-011.
- 3. E. G. Neves, "Ecology, Ceramic Chronology and Distribution, Long-term History, and Political Change in the Amazonian Floodplain" in *The Handbook of South American Archaeology* (Springer New York, New York, NY, 2008), pp. 359–379. https://doi.org/10.1007/978-0-387-74907-5 20.
  - 4. D. P. Schaan, *Sacred Geographies of Ancient Amazonia* (Routledge, New York, 2016). https://doi.org/10.4324/9781315420530.
- 5. C. de P. Moraes, E. G. Neves, "Earthworks of the Amazon" in *Encyclopedia of Global Archaeology* (Springer International Publishing, Cham, 2019), pp. 1–13. https://doi.org/10.1007/978-3-319-51726-1\_3026-1.
  - 6. C. Levis *et al.*, Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. **355**, 925–931 (2017). https://doi.org/10.1126/science.aal0157.
  - 7. C. Levis *et al.*, How People Domesticated Amazonian Forests. *Front. Ecol. Evol.* **5**, 1–21 (2018). https://doi.org/10.3389/fevo.2017.00171.
  - 8. C. R. Clement, 1492 and the loss of amazonian crop genetic resources. I. The relation between domestication and human population decline. *Econ. Bot.* **53**, 188–202 (1999). https://doi.org/10.1007/BF02866498.
  - 9. U. Lombardo, J. Iriarte, L. Hilbert, J. Ruiz-Pérez, J. M. Capriles, H. Veit, Early Holocene crop cultivation and landscape modification in Amazonia. *Nature*. **581**, 190–193 (2020). https://doi.org/10.1038/s41586-020-2162-7.

- M. J. Heckenberger *et al.*, Amazonia 1492: Pristine Forest or Cultural Parkland? *Science*.
   301, 1710–1714 (2003). https://doi.org/10.1126/science.1086112.
- 11. M. J. Heckenberger, J. Christian Russell, J. R. Toney, M. J. Schmidt, The legacy of cultural landscapes in the Brazilian Amazon: implications for biodiversity. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 197–208 (2007). https://doi.org/10.1098/rstb.2006.1979.
- 12. J. F. Carson *et al.*, Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proc. Natl. Acad. Sci.* **111**, 10497–10502 (2014). https://doi.org/10.1073/pnas.1321770111.

5

10

20

- 13. J. Watling *et al.*, Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proc. Natl. Acad. Sci.* **114**, 1868–1873 (2017). https://doi.org/10.1073/pnas.1614359114.
- 14. C. C. Mann, Ancient Earthmovers of the Amazon. *Science*. **321**, 1148–1152 (2008). https://doi.org/10.1126/science.321.5893.1148.
- 15. J. G. de Souza *et al.*, Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. *Nat. Commun.* **9**, 1125 (2018). https://doi.org/10.1038/s41467-018-03510-7.
- J. Iriarte *et al.*, Geometry by Design: Contribution of Lidar to the Understanding of Settlement Patterns of the Mound Villages in SW Amazonia. *J. Comput. Appl. Archaeol.* 3, 151–169 (2020). https://doi.org/10.5334/jcaa.45.
  - 17. M. A. Canuto *et al.*, Ancient lowland Maya complexity as revealed by airborne laser scanning of northern Guatemala. *Science*. **361** (2018), doi:10.1126/science.aau0137. https://doi.org/10.1126/science.aau0137.
  - 18. A. F. Chase, D. Z. Chase, C. T. Fisher, S. J. Leisz, J. F. Weishampel, Geospatial revolution and remote sensing LiDAR in Mesoamerican archaeology. *Proc. Natl. Acad. Sci.* **109**, 12916–12921 (2012). https://doi.org/10.1073/pnas.1205198109.
  - 19. H. Prümers, C. J. Betancourt, J. Iriarte, M. Robinson, M. Schaich, Lidar reveals pre-Hispanic low-density urbanism in the Bolivian Amazon. *Nature*. **606**, 325–328 (2022). https://doi.org/10.1038/s41586-022-04780-4.
    - 20. C. M. Souza *et al.*, Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. *Remote Sens.* **12**, 2735

(2020). https://doi.org/10.3390/rs12172735.

5

15

- 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, Evaluating spatial coverage of data on the aboveground biomass in undisturbed forests in the Brazilian Amazon. *Carbon Balance Manag.* 14, 11 (2019). https://doi.org/10.1186/s13021-019-0126-8.
  - M. J. Heckenberger, J. B. Petersen, E. G. Neves, Village Size and Permanence in Amazonia: Two Archaeological Examples from Brazil. *Lat. Am. Antiq.* 10, 353–376 (1999). https://doi.org/10.2307/971962.
- 24. M. J. Heckenberger *et al.*, Pre-Columbian Urbanism, Anthropogenic Landscapes, and the Future of the Amazon. *Science*. **321**, 1214–1217 (2008). https://doi.org/10.1126/science.1159769.
  - 25. S. Saunaluoma, M. Pärssinen, D. Schaan, Diversity of Pre-colonial Earthworks in the Brazilian State of Acre, Southwestern Amazonia. *J. F. Archaeol.* **43**, 362–379 (2018). https://doi.org/10.1080/00934690.2018.1483686.
  - 26. G. Odonne, J.-F. Molino, Écologie historique amazonienne, une interdisciplinarité nécessaire. *Les Nouv. l'archéologie*, 11–15 (2018). https://doi.org/10.4000/nda.4162.
  - 27. M. P. Cabral, J. D. de M. Saldanha, Um sítio, múltiplas interpretações: o caso do chamado "Stonehenge do Amapá." *Rev. Arqueol. Pública.* 3, 7 (2015). https://doi.org/10.20396/rap.v3i1.8635797.
  - 28. P. Stenborg, D. P. Schaan, C. G. Figueiredo, Contours of the Past: LiDAR Data Expands the Limits of Late Pre-Columbian Human Settlement in the Santarém Region, Lower Amazon. J. F. Archaeol. 43, 44–57 (2018). https://doi.org/10.1080/00934690.2017.1417198.
- 29. R. Blatrix *et al.*, The unique functioning of a pre-Columbian Amazonian floodplain fishery. *Sci. Rep.* **8**, 5998 (2018). https://doi.org/10.1038/s41598-018-24454-4.
  - 30. 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). https://doi.org/10.1111/jbi.12325.

10

15

- 31. N. A. C. Cressie, "Spatial Point Patterns" in *Statistics for Spatial Data* (John Wiley & Sons, Inc., Hoboken, NJ, USA, 2015), *Wiley Series in Probability and Statistics*, pp. 575–723. https://doi.org/10.1002/9781119115151.ch8.
- 32. G. A. Moreira, D. Gamerman, Analysis of presence-only data via exact Bayes, with model and effects identification. *Ann. Appl. Stat.* **16**, 1848–1867 (2022). https://doi.org/10.1214/21-AOAS1569.
  - 33. R. Valavi, J. Elith, J. J. Lahoz-Monfort, G. Guillera-Arroita, Modelling species presence-only data with random forests. *Ecography (Cop.)*. **44**, 1731–1742 (2021). https://doi.org/10.1111/ecog.05615.
  - 34. S. Y. Maezumi *et al.*, The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nat. Plants.* **4**, 540–547 (2018). https://doi.org/10.1038/s41477-018-0205-y.
  - 35. J. Watling *et al.*, Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. *PLoS One.* **13**, e0199868 (2018). https://doi.org/10.1371/journal.pone.0199868.
  - 36. P. Riris, Spatial structure among the geometric earthworks of western Amazonia (Acre, Brazil). *J. Anthropol. Archaeol.* **59**, 101177 (2020). https://doi.org/10.1016/j.jaa.2020.101177.
  - 37. 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.* **114**, 522–527 (2017). https://doi.org/10.1073/pnas.1614577114.
    - 38. A. M. G. A. WinklerPrins, C. Levis, Reframing Pre-European Amazonia through an Anthropocene Lens. *Ann. Am. Assoc. Geogr.* **111**, 858–868 (2021). https://doi.org/10.1080/24694452.2020.1843996.
- 39. J. Iriarte *et al.*, The origins of Amazonian landscapes: Plant cultivation, domestication and the spread of food production in tropical South America. *Quat. Sci. Rev.* **248**, 106582 (2020). https://doi.org/10.1016/j.quascirev.2020.106582.
  - 40. H. A. Orengo et al., Automated detection of archaeological mounds using machine-

- learning classification of multisensor and multitemporal satellite data. *Proc. Natl. Acad. Sci.* **117**, 18240–18250 (2020). https://doi.org/10.1073/pnas.2005583117.
- 41. A. Bonhage, M. Eltaher, T. Raab, M. Breuß, A. Raab, A. Schneider, A modified Mask region-based convolutional neural network approach for the automated detection of archaeological sites on high-resolution light detection and ranging-derived digital elevation models in the North German Lowland. *Archaeol. Prospect.* **28**, 177–186 (2021). https://doi.org/10.1002/arp.1806.

5

10

15

20

- 42. M. P. Ferreira, M. Zortea, D. C. Zanotta, Y. E. Shimabukuro, C. R. de Souza Filho, Mapping tree species in tropical seasonal semi-deciduous forests with hyperspectral and multispectral data. *Remote Sens. Environ.* **179**, 66–78 (2016). https://doi.org/10.1016/j.rse.2016.03.021.
- 43. M. P. Ferreira, R. G. Lotte, F. V. D'Elia, C. Stamatopoulos, D.-H. Kim, A. R. Benjamin, Accurate mapping of Brazil nut trees (Bertholletia excelsa) in Amazonian forests using WorldView-3 satellite images and convolutional neural networks. *Ecol. Inform.* **63**, 101302 (2021). https://doi.org/10.1016/j.ecoinf.2021.101302.
- 44. S. D. Coelho *et al.*, Eighty-four per cent of all Amazonian arboreal plant individuals are useful to humans. *PLoS One*. **16**, e0257875 (2021). https://doi.org/10.1371/journal.pone.0257875.
- 45. G. Odonne *et al.*, Long-term influence of early human occupations on current forests of the Guiana Shield. *Ecology.* **100**, 1–14 (2019). https://doi.org/10.1002/ecy.2806.
- 46. R. J. W. Brienen *et al.*, Long-term decline of the Amazon carbon sink. *Nature*. **519**, 344–348 (2015). https://doi.org/10.1038/nature14283.
- 47. K. V. Conceição *et al.*, Government policies endanger the indigenous peoples of the Brazilian Amazon. *Land use policy*. **108**, 105663 (2021). https://doi.org/10.1016/j.landusepol.2021.105663.
- 48. G. de Oliveira *et al.*, Protecting Amazonia Should Focus on Protecting Indigenous, Traditional Peoples and Their Territories. *Forests.* **13**, 16 (2021). https://doi.org/10.3390/f13010016.

- C. H. L. Silva Junior, A. C. M. Pessôa, N. S. Carvalho, J. B. C. Reis, L. O. Anderson, L. E. O. C. Aragão, The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nat. Ecol. Evol.* 5, 144–145 (2020). https://doi.org/10.1038/s41559-020-01368-x.
- 50. G. Mataveli, G. de Oliveira, Protect the Amazon's Indigenous lands. *Science*. **375**, 275–276 (2022). https://doi.org/10.1126/science.abn4936.
- 51. V. Peripato *et al.*, Data from: Over 10,000 Pre-Columbian earthworks are still hidden throughout Amazonia. *Zenodo* (2023). https://doi.org/10.5281/zenodo.7750985.

- 52. D. Schaan *et al.*, Construindo paisagens como espaços sociais: o caso dos geoglifos do Acre. *Rev. Arqueol.* **23**, 30–41 (2010). https://doi.org/10.24885/sab.v23i1.286.
- D. Schaan, M. Pärssinen, A. Ranzi, J. C. Piccoli, Geoglifos da Amazônia ocidental. *Rev. Arqueol.* **20**, 67–82 (2007). https://doi.org/10.24885/sab.v20i1.229.
  - 54. D. Schaan, A. Ranzi, M. Parsinen, Arqueologia da Amazônia Ocidental: os Geoglifos do Acre (Universidade Federal do Pará (UFPA), Belém, Brazil, 2008). https://periodicos.ufpa.br/index.php/amazonica/article/view/171/243.
- 55. C. L. Erickson, An artificial landscape-scale fishery in the Bolivian Amazon. *Nature*. **408**, 190–193 (2000). https://doi.org/10.1038/35041555.
  - S. Saunaluoma, Pre-Columbian Earthworks in the Riberalta Region of the Bolivian Amazon. *Amaz. Rev. Antropol.* 2, 106–138 (2010).
     https://doi.org/10.18542/amazonica.v2i1.347.
- 57. C. Erickson, P. Alvarez, S. Calla Maldonado, Zanjas Circundantes: Obras de Tierra Monumentales de Baures en la Amazonia Bolivia. *Proy. Agro-Arqueológico del Beni*, 1–108 (2008). https://repository.upenn.edu/anthro\_papers/11.
  - 58. M. Heckenberger, E. G. Neves, Amazonian Archaeology. *Annu. Rev. Anthropol.* **38**, 251–266 (2009). https://doi.org/10.1146/annurev-anthro-091908-164310.
- 59. M. J. Heckenberger, *The Ecology of Power* (Routledge, 2004), *Critical Perspectives in Ident*. https://doi.org/10.4324/9780203486627.
  - 60. S. Pappas, Mysterious Amazonian Geoglyphs Were Built in Already-Altered Forests. *Live Sci.* (2017). https://www.livescience.com/57775-humans-altered-amazon-rainforests-

geoglyphs.html.

15

- 61. LAStools, Efficient tools for LiDAR processing (2018). https://rapidlasso.com/.
- 62. G. A. Moreira, bayesPO: Bayesian Inference for Presence-Only Data (2021). https://cran.r-project.org/package=bayesPO.
- 5 R Core Team, R: A Language and Environment for Statistical Computing. https://www.r-project.org/.
  - 64. W. Fithian, J. Elith, T. Hastie, D. A. Keith, Bias correction in species distribution models: pooling survey and collection data for multiple species. *Methods Ecol. Evol.* **6**, 424–438 (2015). https://doi.org/10.1111/2041-210X.12242.
- P. J. Diggle, R. Menezes, T. Su, Geostatistical Inference Under Preferential Sampling. *J. R. Stat. Soc. Ser. C Appl. Stat.* 59, 191–232 (2010). https://doi.org/10.1111/j.1467-9876.2009.00701.x.
  - 66. R. M. Dorazio, Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Glob. Ecol. Biogeogr.* **23**, 1472–1484 (2014). https://doi.org/10.1111/geb.12216.
  - 67. OpenStreetMap Wiki contributors, Planet.osm (2023). https://wiki.openstreetmap.org/w/index.php?title=Planet.osm&oldid=2535837.
  - 68. M. C. Hansen *et al.*, High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*. **342**, 850–853 (2013). https://doi.org/10.1126/science.1244693.
- 69. 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). https://doi.org/10.1002/joc.1276.
  - N. H. Batjes, E. Ribeiro, A. van Oostrum, Standardised soil profile data to support global mapping and modelling (WoSIS snapshot 2019). *Earth Syst. Sci. Data.* 12, 299–320 (2020). https://doi.org/10.5194/essd-12-299-2020.
  - 71. G. Zuquim *et al.*, Making the most of scarce data: Mapping soil gradients in data-poor areas using species occurrence records. *Methods Ecol. Evol.* **10**, 788–801 (2019). https://doi.org/10.1111/2041-210X.13178.

- 72. B. Lehner, K. Verdin, A. Jarvis, New Global Hydrography Derived From Spaceborne Elevation Data. *Eos, Trans. Am. Geophys. Union.* **89**, 93 (2008). https://doi.org/10.1029/2008EO100001.
- 73. J.-F. Pekel, A. Cottam, N. Gorelick, A. S. Belward, High-resolution mapping of global surface water and its long-term changes. *Nature*. **540**, 418–422 (2016). https://doi.org/10.1038/nature20584.
  - 74. C. D. Rennó *et al.*, HAND, a new terrain descriptor using SRTM-DEM: Mapping terrafirme rainforest environments in Amazonia. *Remote Sens. Environ.* **112**, 3469–3481 (2008). https://doi.org/10.1016/j.rse.2008.03.018.
- 10 75. ESRI, ArcGIS Desktop 10.5 Spatial Analyst (2016).

5

15

- M. Dudík, S. J. Phillips, R. E. Schapire, "Correcting sample selection bias in maximum entropy density estimation" in *Advances in Neural Information Processing Systems 18*, Y. Weiss, B. Schölkopf, J. C. Platt, Eds. (MIT Press, 2006), pp. 323–330. http://papers.nips.cc/paper/2929-correcting-sample-selection-bias-in-maximum-entropy-density-estimation.pdf.
- 77. J. Elith, M. Kearney, S. Phillips, The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342 (2010). https://doi.org/10.1111/j.2041-210X.2010.00036.x.
- 78. Y. Fourcade, J. O. Engler, D. Rödder, J. Secondi, Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLoS One.* **9**, e97122 (2014). https://doi.org/10.1371/journal.pone.0097122.
- 79. S. J. Phillips *et al.*, Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009). https://doi.org/10.1890/07-2153.1.
- 25 B0. D. I. Warton, L. C. Shepherd, Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *Ann. Appl. Stat.* **4**, 1383–1402 (2010). https://doi.org/10.1214/10-AOAS331.

# Template revised February 2021

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/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).

5

10 Funding: VP and CL were supported by the Coordination of Superior Level Staff Improvement under the Academic Excellence Program (CAPES/PROEX) research grants (1681023, 88887.479608/2020, and 88887.474568/2020); CL was supported by the National Council for Scientific and Technological Development (CNPQ) grants (159440/2018-1, and 400369/2021-4); DG was supported by CNPQ grant (304742/2018-0); AJ was supported by European Research Council (ERC) under an Consolidator Grant (FP7-771056-LICCI); JPO was supported 15 by São Paulo Research Foundation (FAPESP) grant (2017/22269-2) and Airborne LASER Scanning data acquisition by the Amazon Fund grant (14.2.0929.1); HLGC was supported by FAPESP grant (18/14423-4); HtS, VFG, and RS were supported by PVE-MEC/MCTI/CAPES/CNPq/FAPs grant (407232/2013-3); JGS, JI, and MR were supported by Horizon 2020 grant (ERC Cog 616179 and ERC PoC 777845); AMS was supported by CAPES 20 grant (88887.607664/2021); DS, JFM, JE, PP and JC were supported by ANR grant (CEBA 10-LABX-25-01); HLQ, and JLLM were supported by MCT/CNPq/CT-INFRA/GEOMA grant (550373/2010-1, and 457515/2012-0); JLLM were supported by CAPES/PDSE grant (88881.135761/2016-01) and CAPES/Fapespa grant (1530801); EMV were supported by CNPq grant (308040/2017-1); BMF was supported by FAPESP grant (2016/25086-3); BSM, BHMJ 25 and OLP were supported by CNPq/CAPES/FAPS/BC-Newton grant (441244/2016-5), FAPEMAT grant (0589267/2016), and a Royal Society GCRF International Collaboration Award (ICA\R1\180100); TWH was supported by NSF/DEB grant (1556338); LEOCA was supported by 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 30

Template revised February 2021

several Natural Environment Research Council grants to OLP and colleagues (NE/B503384/1, NE/D01025X/1, NE/I02982X/1, NE/F005806/1, NE/D005590/1, NE/I028122/1, NE/S011811/1) and the Gordon and Betty Moore Foundation.

Author contributions: These authors contributed equally: Vinicius Peripato, Carolina Levis.

Conceptualization: VP, CL, LEOCA; LiDAR raw data processing: VP; Earthworks investigation: VP, JGS, JI, MR, LEOAC; Modeling: GAM, DG; Domestication investigation: VP, CL; Writing – original draft: VP, CL, LEOAC; Writing – review & editing: VP, CL, GAM, DG, NP, LEOAC. All of the other authors contributed data, discussed further analyses, and commented on various versions of the manuscript.

**Competing interests:** 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 at Zenodo repository (51).

# **Supplementary Materials**

**Author Affiliations** 

20 Materials and Methods

15

25

figs. S1 to S19

tables S1 to S5

References (52–80)

#### Other Supplementary Materials for this manuscript include the following:

Data S1 and S2 as separate Excel file

Fig. 1

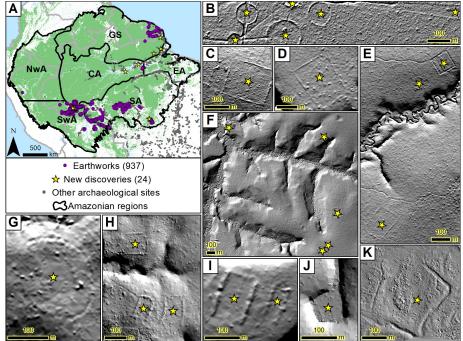


Fig. 1. Geographical distribution of known and newly discovered pre-Columbian geometrical earthworks in Amazonia. (A) Map of previously reported and newly discovered earthworks reported in this study across six Amazonian regions: Central Amazonia (CA); Eastern Amazonia (EA); Guiana Shield (GS); Northwestern Amazonia (NwA); Southern Amazonia (SA); and Southwestern Amazonia (SwA). (B) Newly discovered earthworks in SA. (C-F) Newly discovered earthworks in SwA. (G-I) Newly discovered earthworks in GS. (J-K) Newly discovered earthworks in CA.

Fig. 2

5

10

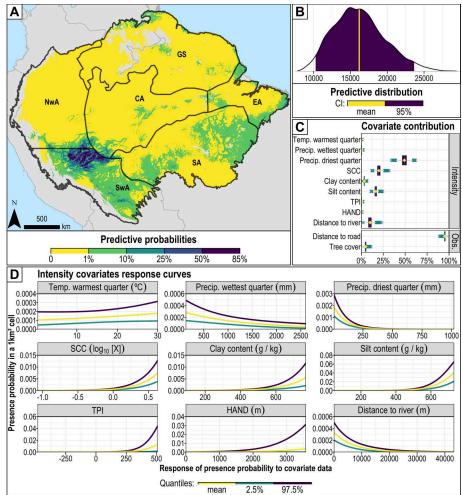


Fig. 2. Probability model of pre-Columbian earthworks across Amazonia. (A) Predicted probability of earthwork presence for 1-km² cells across six Amazonian regions using an Inhomogeneous Poisson Process predictive model: Central Amazonia (CA); Eastern Amazonia (EA); Guiana Shield (GS); Northwestern Amazonia (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. (D) Individual predicted probability of earthwork presence against intensity covariates. SCC, TPI, and HAND are abbreviations for Soil Cation Concentration, Terrain Position Index, and Height Above the Nearest Drainage, respectively. 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

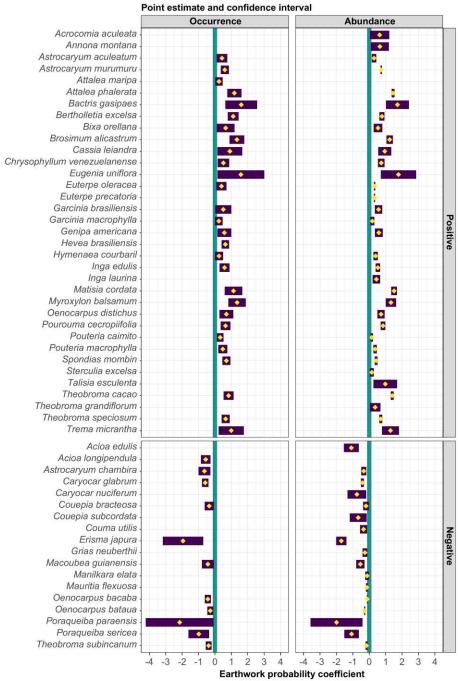


Fig. 3. Significant relationships between the occurrence and abundance of domesticated tree species and the modeled distribution of earthworks in Amazonia. Point estimates and confidence intervals of species significantly associated with predicted probability of earthwork presence, with an overall significance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



# Supplementary Materials for

Over 10,000 Pre-Columbian earthworks are still hidden throughout Amazonia

Vinicius Peripato<sup>1</sup>\*†, Carolina Levis<sup>2</sup>†, Guido A. Moreira<sup>3</sup>, Dani Gamerman<sup>4</sup>, Hans ter Steege<sup>5</sup>, Nigel C.A. Pitman<sup>6</sup>, Jonas G. de Souza<sup>7</sup>, José Iriarte<sup>8</sup>, Mark Robinson<sup>8</sup>, André Braga Junqueira<sup>9</sup>, Thiago B. Trindade<sup>10</sup>, Fernando O. de Almeida<sup>11</sup>, Claide de Paula Moraes<sup>12</sup>, Umberto Lombardo<sup>13</sup>, Eduardo K. Tamanaha<sup>14</sup>, Shira Y. Maezumi<sup>15</sup>, Jean P. H. B. Ometto<sup>1</sup>, José R.G. Braga<sup>1</sup>, Wesley A. Campanharo<sup>1</sup>, Henrique L. G. Cassol<sup>1</sup>, Philipe R. Leal<sup>1</sup>, Mauro L. R. de Assis<sup>1</sup>, Adriana M. da Silva<sup>16</sup>, Oliver L. Phillips<sup>17</sup>, Flávia R.C. Costa<sup>18</sup>, Bernardo Monteiro Flores<sup>2</sup>, Bruce Hoffman<sup>19</sup>, Terry W. Henkel<sup>20</sup>, Maria Natalia Umaña<sup>21</sup>, William E. Magnusson<sup>18</sup>, Elvis H. Valderrama Sandoval<sup>22,23</sup>, Jos Barlow<sup>24</sup>, William Milliken<sup>25</sup>, Maria Aparecida Lopes<sup>26</sup>, Marcelo Fragomeni Simon<sup>27</sup>, Tinde R. van Andel<sup>5,28</sup>, Susan G.W. Laurance<sup>29</sup>, William F. Laurance<sup>29</sup>, Armando Torres-Lezama<sup>30</sup>, Rafael L. Assis<sup>31</sup>, Jean-François Molino<sup>32</sup>, Mickaël Mestre<sup>33</sup>, Michelle Hamblin<sup>34</sup>, Luiz de Souza Coelho<sup>35</sup>, Diogenes de Andrade Lima Filho<sup>35</sup>, Florian Wittmann<sup>36,37</sup>, Rafael P. Salomão<sup>38,39</sup>, Iêda Leão Amaral<sup>35</sup>, Juan Ernesto Guevara<sup>40,41</sup>. Francisca Dionízia de Almeida Matos<sup>35</sup>, Carolina V. Castilho<sup>42</sup>, Marcelo de Jesus Veiga Carim<sup>43</sup>. Dairon Cárdenas López<sup>44</sup>#, Daniel Sabatier<sup>32</sup>, Mariana Victória Irume<sup>35</sup>, Maria Pires Martins<sup>35</sup>, José Renan da Silva Guimarães<sup>45</sup>, Olaf S. Bánki<sup>5</sup>, Maria Teresa Fernandez Piedade<sup>37</sup>, José Ferreira Ramos<sup>35</sup>, Bruno Garcia Luize<sup>46</sup>, Evlyn Márcia Moraes de Leão Novo<sup>1</sup>, Percy Núñez Vargas<sup>47</sup>, Thiago Sanna Freire Silva<sup>48</sup>, Eduardo Martins Venticinque<sup>49</sup>, Angelo Gilberto Manzatto<sup>50</sup>, Neidiane Farias Costa Reis<sup>51</sup>, John Terborgh<sup>52,29</sup>, Katia Regina Casula<sup>51</sup>, Layon O. Demarchi<sup>37</sup>, Euridice N. Honorio Coronado<sup>53,54</sup>, Abel Monteagudo Mendoza<sup>47,55</sup>, Juan Carlos Montero<sup>56,35</sup>, Jochen Schöngart<sup>37</sup>, Ted R. Feldpausch<sup>57,17</sup>, Adriano Costa Quaresma<sup>36,37</sup>, Gerardo A. Aymard C.<sup>58</sup>, Chris Baraloto<sup>59</sup>, Nicolás Castaño Arboleda<sup>44</sup>, Julien Engel<sup>32,59</sup>, Pascal Petronelli<sup>60</sup>, Charles Eugene Zartman<sup>35</sup>, Timothy J. Killeen<sup>61</sup>, Beatriz S. Marimon<sup>62</sup>, Ben Hur Marimon-Junior<sup>62</sup>, Juliana Schietti<sup>35</sup>, Thaiane R. Sousa<sup>63</sup>, Rodolfo Vasquez<sup>55</sup>, Lorena M. Rincón<sup>35</sup>, Erika Berenguer<sup>64,24</sup>, Joice Ferreira<sup>65</sup>, Bonifacio Mostacedo<sup>66</sup>, Dário Dantas do Amaral<sup>39</sup>, Hernán Castellanos<sup>67</sup>, Marcelo Brilhante de Medeiros<sup>27</sup>, Ana Andrade<sup>68</sup>, José Luís Camargo<sup>68</sup>, Emanuelle de Sousa Farias<sup>69,70</sup>, José Leonardo Lima Magalhães<sup>71,65</sup>, Henrique Eduardo Mendonça Nascimento<sup>35</sup>, Helder Lima de Queiroz<sup>72</sup>, Roel Brienen<sup>17</sup>, Juan David Cardenas Revilla<sup>35</sup>, Pablo R. Stevenson<sup>73</sup>, Alejandro Araujo-Murakami<sup>74</sup>, Bruno Barçante Ladvocat Cintra<sup>75</sup>, Yuri Oliveira Feitosa<sup>76</sup>, Flávia Rodrigues Barbosa<sup>77</sup>, Rainiellen de Sá Carpanedo<sup>77</sup>, Joost F. Duivenvoorden<sup>78</sup>, Janaína Costa Noronha<sup>77</sup>, Domingos de Jesus Rodrigues<sup>77</sup>, Hugo F. Mogollón<sup>79</sup>, Leandro Valle Ferreira<sup>39</sup>, John Ethan Householder<sup>36</sup>, José Rafael Lozada<sup>80</sup>, James A. Comiskey<sup>81,82</sup>, Freddie C. Draper<sup>83</sup>, José Julio de Toledo<sup>84</sup>, Gabriel Damasco<sup>85</sup>, Nállarett Dávila<sup>46</sup>##, Roosevelt García-Villacorta<sup>86,87</sup>, Aline Lopes<sup>88</sup>, Fernando Cornejo Valverde<sup>89</sup>, Alfonso Alonso<sup>82</sup>, Francisco Dallmeier<sup>82</sup>, Vitor H.F. Gomes<sup>90,91</sup>, Eliana M.

Jimenez<sup>92</sup>, David Neill<sup>93</sup>, Maria Cristina Peñuela Mora<sup>94</sup>, Daniel P. P. de Aguiar<sup>95,96</sup>, Luzmila Arroyo<sup>74</sup>, Fernanda Antunes Carvalho<sup>18,97</sup>, Fernanda Coelho de Souza<sup>18,17</sup>, Kenneth J. Feeley<sup>98,99</sup>, Rogerio Gribel<sup>35</sup>, Marcelo Petratti Pansonato<sup>35,100</sup>, Marcos Ríos Paredes<sup>101</sup>, Izaias Brasil da Silva<sup>102</sup>, Maria Julia Ferreira<sup>103</sup>, Paul V.A. Fine<sup>104</sup>, Émile Fonty<sup>105,32</sup>, Marcelino Carneiro Guedes<sup>106</sup>, Juan Carlos Licona<sup>56</sup>, Toby Pennington<sup>57,107</sup>, Carlos A. Peres<sup>108</sup>, Boris Eduardo Villa Zegarra<sup>109</sup>, Germaine Alexander Parada<sup>74</sup>, Guido<sup>110</sup>, Vincent Antoine Vos<sup>110</sup>, Carlos Cerón<sup>111</sup>, Paul Maas<sup>5</sup>, Marcos Silveira<sup>112</sup>, Juliana Stropp<sup>113</sup>, Raquel Thomas<sup>114</sup>, Tim R. Baker<sup>17</sup>, Doug Daly<sup>115</sup>, Isau Huamantupa-Chuquimaco<sup>116</sup>, Ima Célia Guimarães Vieira<sup>39</sup>, Bianca Weiss Albuquerque<sup>37</sup>, Alfredo Fuentes<sup>117,118</sup>, Bente Klitgaard<sup>119</sup>, José Luis Marcelo Pena<sup>120</sup>, Miles R. Silman<sup>121</sup>, J. Sebastián Tello<sup>118</sup>, Corine Vriesendorp<sup>6</sup>, Jerome Chave<sup>122</sup>, Anthony Di Fiore<sup>123,124</sup>, Renato Richard Hilário<sup>84</sup>, Juan Fernando Phillips<sup>125</sup>, Gonzalo Rivas-Torres<sup>124,126</sup>, Patricio von Hildebrand<sup>127</sup>, Luciana de Oliveira Pereira<sup>57</sup>, Edelcilio Marques Barbosa<sup>35</sup>, Luiz Carlos de Matos Bonates<sup>35</sup>, Hilda Paulette Dávila Doza<sup>101</sup>, Ricardo Zárate Gómez<sup>128</sup>, George Pepe Gallardo Gonzales<sup>101</sup>, Therany Gonzales<sup>129</sup>, Yadvinder Malhi<sup>130</sup>, Ires Paula de Andrade Miranda<sup>35</sup>, Linder Felipe Mozombite Pinto<sup>101</sup>, Adriana Prieto<sup>131</sup>, Agustín Rudas<sup>131</sup>, Ademir R. Ruschel<sup>65</sup>, Natalino Silva<sup>132</sup>, César I.A. Vela<sup>133</sup>, Egleé L. Zent<sup>134</sup>, Stanford Zent<sup>134</sup>, Angela Cano<sup>73,135</sup>, Yrma Andreina Carrero Márquez<sup>136</sup>, Diego F. Correa<sup>73,137</sup>, Janaina Barbosa Pedrosa Costa<sup>106</sup>, David Galbraith<sup>17</sup>, Milena Holmgren<sup>138</sup>, Michelle Kalamandeen<sup>139</sup>, Guilherme Lobo<sup>37</sup>, Marcelo Trindade Nascimento<sup>140</sup>, Alexandre A. Oliveira<sup>100</sup>, Hirma Ramirez-Angulo<sup>30</sup>, Maira Rocha<sup>37</sup>, Veridiana Vizoni Scudeller<sup>141</sup>, Rodrigo Sierra<sup>142</sup>, Milton Tirado<sup>142</sup>, Geertje van der Heijden<sup>143</sup>, Emilio Vilanova Torre<sup>30,144</sup>, Manuel Augusto Ahuite Reategui<sup>145</sup>, Cláudia Baider<sup>146,100</sup>, Henrik Balslev<sup>147</sup>, Sasha Cárdenas<sup>73</sup>, Luisa Fernanda Casas<sup>73</sup>, William Farfan-Rios<sup>47,118,148</sup>, Cid Ferreira<sup>35</sup>, Reynaldo Linares-Palomino<sup>82</sup>, Casimiro Mendoza<sup>149,150</sup>, Italo Mesones<sup>104</sup>, Ligia Estela Urrego Giraldo<sup>151</sup>, Daniel Villarroel<sup>74,152</sup>, Roderick Zagt<sup>153</sup>, Miguel N. Alexiades<sup>154</sup>, Edmar Almeida de Oliveira<sup>62</sup>, Karina Garcia-Cabrera<sup>121</sup>, Lionel Hernandez<sup>67</sup>, Walter Palacios Cuenca<sup>155</sup>, Susamar Pansini<sup>51</sup>, Daniela Pauletto<sup>156</sup>, Freddy Ramirez Arevalo<sup>23</sup>, Adeilza Felipe Sampaio<sup>51</sup>, Luis Valenzuela Gamarra<sup>55</sup>, Luiz E. O. C. Aragão<sup>1,57</sup>\*

\*Corresponding authors. Email: vinicius.peripato@gmail.com; luiz.aragao@inpe.br †These authors contributed equally to this work; #deceased 5/Jan./2022; ##deceased 30/Nov./2022

#### This PDF file includes:

Author Affiliations Materials and Methods figs. S1 to S19 tables S1 to S5 References

#### Other Supplementary Materials for this manuscript include the following:

Data S1 and S2 as separate Excel file

#### **Author Affiliations**

<sup>1</sup>Remote Sensing Division, National Institute for Space Research (INPE), Av. dos Astronautas, 1758, Jardim da Granja, São José dos Campos, SP, 12227-010, Brazil.

<sup>2</sup>Postgraduate Program in Ecology, Federal University of Santa Catarina, R. Eng. Agronômico Andrei Cristian Ferreira., Trindade, Florianópolis, SC, 88040-900, Brazil.

<sup>3</sup>Centre of Molecular and Environmental Biology, Universidade do Minho, Braga, Portugal.

<sup>4</sup>Departamento de Métodos Estatísticos, Universidade Federal do Rio de Janeiro, Rio de Janeiro, RJ, Brazil.

<sup>5</sup>Naturalis Biodiversity Center, PO Box 9517, Leiden, 2300 RA, The Netherlands.

<sup>6</sup>Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL, 60605-2496, USA.

<sup>7</sup>Department of Humanities, Universitat Pompeu Fabra, Barcelona, Spain.

<sup>8</sup>Department of Archaeology, College of Humanities, University of Exeter, Exeter, UK.

<sup>9</sup>Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona, 08193 Bellaterra, Barcelona, Spain.

<sup>10</sup>Instituto do Património Histórico e Artístico Nacional, Centro Nacional de Arqueologia, Brasília, DF, Brazil.

<sup>11</sup>Departamento de Arqueologia, Universidade Federal de Sergipe, Laranjeiras, SE, Brazil.

<sup>12</sup>Universidade Federal do Oeste do Pará, Santarém, PA, Brazil.

<sup>13</sup>Geographisches Institut, University of Bern, Bern, Switzerland.

<sup>14</sup>Instituto de Desenvolvimento Sustentável Mamirauá, Tefé, AM, Brazil.

<sup>15</sup>Department of Archaeology, Max Planck Institute of Geoanthropology, Jena, Germany.

<sup>16</sup>Postgraduate Program in Geography, Institute of Geography, Federal University of Uberlândia (UFU), Av. João Naves de Ávila, 2121, Santa Mônica, Uberlândia, MG, 38.408-100, Brazil.

<sup>17</sup>School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK.

<sup>18</sup>Coordenação de Pesquisas em Ecologia, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>19</sup>Amazon Conservation Team, 4211 North Fairfax Drive, Arlington, VA, 22203, USA.

<sup>20</sup>Department of Biological Sciences, Humboldt State University, 1 Harpst Street, Arcata, CA, 95521, USA.

<sup>21</sup>Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, 48109, USA.

<sup>22</sup>Department of Biology, University of Missouri, St. Louis, MO, 63121, USA.

<sup>23</sup>Facultad de Biologia, Universidad Nacional de la Amazonia Peruana, Pevas 5ta cdra, Iquitos, Loreto, Peru.

<sup>24</sup>Lancaster Environment Centre, Lancaster University, Lancaster, Lancashire, LA1 4YQ, UK.

<sup>25</sup>Department for Ecosystem Stewardship, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK.

<sup>26</sup>Instituto de Ciências Biológicas, Universidade Federal do Pará, Av. Augusto Corrêa 01, Belém, PA, 66075-110, Brazil.

<sup>27</sup>Embrapa Recursos Genéticos e Biotecnologia, Parque Estação Biológica, Prédio da Botânica e Ecologia, Brasilia, DF, 70770-917, Brazil.

<sup>28</sup>Biosystematics group, Wageningen University, Droevendaalsesteeg 1, Wageningen, 6708 PB, The Netherlands.

<sup>29</sup>Centre for Tropical Environmental and Sustainability Science and College of Science and Engineering, James Cook University, Cairns, Queensland, 4870, Australia.

<sup>30</sup>Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad de los Andes, Conjunto Forestal, 5101, Mérida, Mérida, Venezuela.

<sup>31</sup>Natural History Museum, University of Oslo, Postboks 1172, Oslo, 318, Norway.

<sup>32</sup>AMAP, IRD, Cirad, CNRS, INRAE, Université de Montpellier, Montpellier, F-34398, France.

<sup>33</sup>Institut National de Recherches Archéologiques Préventives, Bègles, France.

<sup>34</sup>Direction des Affaires Culturelles - Guyane, Cayenne, French Guiana.

<sup>35</sup>Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>36</sup>Wetland Department, Institute of Geography and Geoecology, Karlsruhe Institute of Technology - KIT, Josefstr.1, Rastatt, D-76437, Germany.

<sup>37</sup>Ecology, Monitoring and Sustainable Use of Wetlands (MAUA), Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>38</sup>Programa Professor Visitante Nacional Sênior na Amazônia - CAPES, Universidade Federal Rural da Amazônia, Av. Perimetral, s/n, Belém, PA, Brazil.

<sup>39</sup>Coordenação de Botânica, Museu Paraense Emílio Goeldi, Av. Magalhães Barata 376, C.P. 399, Belém, PA, 66040-170, Brazil.

 $^{40} \rm Grupo$  de Investigación en Biodiversidad, Medio Ambiente y Salud-BIOMAS, Universidad de las Américas, Campus Queri, Quito, Ecuador.

<sup>41</sup>Keller Science Action Center, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL, 60605-2496, USA.

- <sup>42</sup>Centro de Pesquisa Agroflorestal de Roraima, Embrapa Roraima, BR 174, km 8, Distrito Industrial, Boa Vista, RR, 69301-970, Brazil.
- <sup>43</sup>Departamento de Botânica, Instituto de Pesquisas Científicas e Tecnológicas do Amapá IEPA, Rodovia JK, Km 10, Campus do IEPA da Fazendinha, Macapá, AP, 68901-025, Brazil.
- <sup>44</sup>Herbario Amazónico Colombiano, Instituto SINCHI, Calle 20 No 5-44, Bogotá, DC, Colombia.
- <sup>45</sup>Amcel Amapá Florestal e Celulose S.A, Rua Claudio Lucio S/N, Novo Horizonte, Santana, AP, 68927-003, Brazil.
- <sup>46</sup>Departamento de Biologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas UNICAMP, CP 6109, Campinas, SP, 13083-970, Brazil.
- <sup>47</sup>Herbario Vargas, Universidad Nacional de San Antonio Abad del Cusco, Avenida de la Cultura, Nro 733, Cusco, Cuzco, Peru.
- <sup>48</sup>Biological and Environmental Sciences, University of Stirling, Stirling, FK9 4LA, UK.
- <sup>49</sup>Centro de Biociências, Departamento de Ecologia, Universidade Federal do Rio Grande do Norte, Av. Senador Salgado Filho, 3000 , Natal, RN, 59072-970, Brazil.
- $^{50}$  Departamento de Biologia, Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 Sentido Acre, Unir, Porto Velho, RO, 76.824-027, Brazil.
- <sup>51</sup>Programa de Pós- Graduação em Biodiversidade e Biotecnologia PPG- Bionorte, Universidade Federal de Rondônia, Campus Porto Velho Km 9,5 bairro Rural, Porto Velho, RO, 76.824-027, Brazil.
- <sup>52</sup>Department of Biology and Florida Museum of Natural History, University of Florida, Gainesville, FL, 32611, USA.
- <sup>53</sup>Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. A. Quiñones km 2,5, Iquitos, Loreto, 784, Peru.
- <sup>54</sup>School of Geography and Sustainable Development, University of St Andrews, Irvine Building, St Andrews, KY16 9AL, UK.

- <sup>55</sup>Jardín Botánico de Missouri, Oxapampa, Pasco, Peru.
- <sup>56</sup>Instituto Boliviano de Investigacion Forestal, Av. 6 de agosto #28, Km. 14, Doble via La Guardia, Casilla 6204, Santa Cruz, Santa Cruz, Bolivia.
- <sup>57</sup>Geography, College of Life and Environmental Sciences, University of Exeter, Rennes Drive, Exeter, EX4 4RJ, UK.
- <sup>58</sup>Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), UNELLEZ-Guanare, Guanare, Portuguesa, 3350, Venezuela.
- <sup>59</sup>International Center for Tropical Botany (ICTB) Department of Biological Sciences, Florida International University, 11200 SW 8th Street, OE 243, Miami, FL, 33199, USA.
- <sup>60</sup>Cirad UMR Ecofog, AgrosParisTech,CNRS,INRAE,Univ Guyane, Campus agronomique, Kourou Cedex, 97379, France.
- <sup>61</sup>Agteca-Amazonica, Santa Cruz, Bolivia.
- $^{62}$ Programa de Pós-Graduação em Ecologia e Conservação, Universidade do Estado de Mato Grosso, Nova Xavantina, MT, Brazil.
- <sup>63</sup>Programa de Pós-Graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.
- <sup>64</sup>Environmental Change Institute, University of Oxford, Oxford, Oxfordshire, OX1 3QY, UK.
- <sup>65</sup>Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amazônia Oriental, Trav. Dr. Enéas Pinheiro s/n°, Belém, PA, 66095-903, Brazil.
- <sup>66</sup>Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Santa Cruz, Santa Cruz, Bolivia.
- <sup>67</sup>Centro de Investigaciones Ecológicas de Guayana, Universidad Nacional Experimental de Guayana, Calle Chile, urbaniz Chilemex, Puerto Ordaz, Bolivar, Venezuela.

<sup>68</sup>Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>69</sup>Laboratório de Ecologia de Doenças Transmissíveis da Amazônia (EDTA), Instituto Leônidas e Maria Deane, Fiocruz, Rua Terezina, 476, Adrianópolis, Manaus, AM, 69060-001, Brazil.

<sup>70</sup>Programa de Pós-graduação em Biodiversidade e Saúde, Instituto Oswaldo Cruz - IOC/FIOCRUZ, Pav. Arthur Neiva Térreo, Av. Brasil, 4365, Manguinhos, Rio de Janeiro, RJ, 21040-360, Brazil.

<sup>71</sup>Programa de Pós-Graduação em Ecologia, Universidade Federal do Pará, Av. Augusto Corrêa 01, Belém, PA, 66075-110, Brazil.

<sup>72</sup>Diretoria Técnico-Científica, Instituto de Desenvolvimento Sustentável Mamirauá, Estrada do Bexiga, 2584, Tefé, AM, 69470-000, Brazil.

<sup>73</sup>Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los Andes, Carrera 1 # 18a- 10, Bogotá, DC, 111711, Colombia.

<sup>74</sup>Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene Moreno, Avenida Irala 565 Casilla Post al 2489, Santa Cruz, Santa Cruz, Bolivia.

<sup>75</sup>Instituto de Biociências - Dept. Botanica, Universidade de Sao Paulo - USP, Rua do Matão 277, Cidade Universitária, São Paulo, SP, 05508-090, Brazil.

<sup>76</sup>Programa de Pós-Graduação em Biologia (Botânica), Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>77</sup>ICNHS, Federal University of Mato Grosso, Av. Alexandre Ferronato 1200, Setor Industrial, Sinop, MT, 78.557-267, Brazil.

<sup>78</sup>Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam, Sciencepark 904, Amsterdam, 1098 XH, The Netherlands.

<sup>79</sup>Endangered Species Coalition, 8530 Geren Rd., Silver Spring, MD, 20901, USA.

<sup>80</sup>Facultad de Ciencias Forestales y Ambientales, Instituto de Investigaciones para el Desarrollo Forestal, Universidad de los Andes, Via Chorros de Milla, 5101, Mérida, Mérida, Venezuela. <sup>81</sup>Inventory and Monitoring Program, National Park Service, 120 Chatham Lane, Fredericksburg, VA, 22405, USA.

<sup>82</sup>Center for Conservation and Sustainability, Smithsonian Conservation Biology Institute, 1100 Jefferson Dr. SW, Suite 3123, Washington, DC, 20560-0705, USA.

<sup>83</sup>Department of Geography and Planning, University of Liverpool, Liverpool, L69 3BX, UK.

<sup>84</sup>Universidade Federal do Amapá, Ciências Ambientais, Rod. Juscelino Kubitschek km2, Macapá, AP, 68902-280, Brazil.

<sup>85</sup>Gothenburg Global Biodiversity Centre, University of Gothenburg, Carl Skottbergs gata 22b, Gothenburg, 413 19, Sweden.

<sup>86</sup>Programa Restauración de Ecosistemas (PRE), Centro de Innovación Científica Amazónica (CINCIA), Jr. Cajamarca Cdra. 1 s/n, Tambopata, Madre de Dios, Peru.

<sup>87</sup>Peruvian Center for Biodiversity and Conservation (PCBC), Iquitos, Loreto, Peru.

<sup>88</sup>Department of Ecology, Institute of Biological Sciences, University of Brasilia, Brasilia, DF, 70904-970, Brazil.

<sup>89</sup>Andes to Amazon Biodiversity Program, Madre de Dios, Madre de Dios, Peru.

<sup>90</sup>Escola de Negócios Tecnologia e Inovação, Centro Universitário do Pará, Belém, PA, Brazil.

<sup>91</sup>Environmental Science Program, Geosciences Department, Universidade Federal do Pará, Rua Augusto Corrêa 01, Belém, PA, 66075-110, Brazil.

<sup>92</sup>Grupo de Ecología y Conservación de Fauna y Flora Silvestre, Instituto Amazónico de Investigaciones Imani, Universidad Nacional de Colombia sede Amazonia, Leticia, Amazonas, Colombia.

<sup>93</sup>Universidad Estatal Amazónica, Puyo, Pastaza, Ecuador.

<sup>94</sup>Universidad Regional Amazónica IKIAM, Km 7 via Muyuna, Tena, Napo, Ecuador.

<sup>95</sup>Procuradoria-Geral de Justiça, Ministério Público do Estado do Amazonas, Av. Coronel Teixeira, 7995, Manaus, AM, 69037-473, Brazil.

<sup>96</sup>Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69067-375, Brazil.

<sup>97</sup>Universidade Federal de Minas Gerais, Instituto de Ciências Biológicas, Departamento de Genética, Ecologia e Evolução, Av. Antônio Carlos, 6627 Pampulha, Belo Horizonte, MG, 31270-901, Brazil.

<sup>98</sup>Department of Biology, University of Miami, Coral Gables, FL, 33146, USA.

<sup>99</sup>Fairchild Tropical Botanic Garden, Coral Gables, FL, 33156, USA.

<sup>100</sup>Instituto de Biociências - Dept. Ecologia, Universidade de Sao Paulo - USP, Rua do Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP, 05508-090, Brazil.

<sup>101</sup>Servicios de Biodiversidad EIRL, Jr. Independencia 405, Iquitos, Loreto, 784, Peru.

<sup>102</sup>Postgraduate program in Biodiversity and Biotechnology Bionorte, Federal University of Acre, Rodovia 364, km 4.5, Distrito industrial, Rio Branco, AC, 69900-000, Brazil.

<sup>103</sup>Postgraduate program in Ethnobiology and Nature Conservation, Federal Rural University of Pernambuco (UFRPE), Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, Pernambuco, PB, 52171-900, Brazil.

<sup>104</sup>Department of Integrative Biology, University of California, Berkeley, CA, 94720-3140, USA.

<sup>105</sup>Direction régionale de la Guyane, Office national des forêts, Cayenne, F-97300, French Guiana.

<sup>106</sup>Empresa Brasileira de Pesquisa Agropecuária, Embrapa Amapá, Rod. Juscelino Kubitschek km 5, Macapá, AP, 68903-419, Brazil.

<sup>107</sup>Tropical Diversity Section, Royal Botanic Garden Edinburgh, 20a Inverleith Row, Edinburgh, Scotland, EH3 5LR, UK.

- <sup>108</sup>School of Environmental Sciences, University of East Anglia, Norwich, NR4 7TJ, UK.
- <sup>109</sup>Dirección de Evaluación Forestal y de Fauna Silvestre, Av. Javier Praod Oeste 693, Magdalena del Mar, Peru.
- <sup>110</sup>Instituto de Investigaciones Forestales de la Amazonía, Universidad Autónoma del Beni José Ballivián, Campus Universitario Final, Av. Ejercito, Riberalta, Beni, Bolivia.
- <sup>111</sup>Escuela de Biología Herbario Alfredo Paredes, Universidad Central, Ap. Postal 17.01.2177, Quito, Pichincha, Ecuador.
- <sup>112</sup>Centro de Ciências Biológicas e da Natureza, Universidade Federal do Acre, Rodovia BR 364, Km 4, s/n, Distrito Industrial, Rio Branco, AC, 69915-559, Brazil.
- <sup>113</sup>Museo Nacional de Ciencias Naturales (MNCN-CSIC), C. de José Gutiérrez Abascal 2, Madrid, 28006, Spain.
- <sup>114</sup>Iwokrama International Centre for Rain Forest Conservation and Development, Georgetown, Guyana.
- <sup>115</sup>New York Botanical Garden, 2900 Southern Blvd, Bronx, New York, NY, 10458-5126, USA.
- <sup>116</sup>Herbario HAG, Universidad Nacional Amazónica de Madre de Dios (UNAMAD), Av. Jorge Chávez 1160, Puerto Maldonado, Madre de Dios, Peru.
- <sup>117</sup>Herbario Nacional de Bolivia, Universitario UMSA, Casilla 10077 Correo Central, La Paz, La Paz, Bolivia.
- <sup>118</sup>Center for Conservation and Sustainable Development, Missouri Botanical Garden, P.O. Box 299, St. Louis, MO, 63166-0299, USA.
- <sup>119</sup>Department for Accelerated Taxonomy, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AE, UK.
- <sup>120</sup>Universidad Nacional de Jaén, Carretera Jaén San Ignacio Km 23, Jaén, Cajamarca, 6801, Peru.

- <sup>121</sup>Biology Department and Center for Energy, Environment and Sustainability, Wake Forest University, 1834 Wake Forest Rd, Winston Salem, NC, 27106, USA.
- <sup>122</sup>Laboratoire Evolution et Diversité Biologique, CNRS and Université Paul Sabatier, UMR 5174 EDB, Toulouse, 31000, France.
- <sup>123</sup>Department of Anthropology, University of Texas at Austin, SAC 5.150, 2201 Speedway Stop C3200, Austin, TX, 78712, USA.
- <sup>124</sup>Estación de Biodiversidad Tiputini, Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito-USFQ, Quito, Pichincha, Ecuador.
- <sup>125</sup>Fundación Puerto Rastrojo, Cra 10 No. 24-76 Oficina 1201, Bogotá, DC, Colombia.
- <sup>126</sup>Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL, 32611, USA.
- <sup>127</sup>Fundación Estación de Biología, Cra 10 No. 24-76 Oficina 1201, Bogotá, DC, Colombia.
- $^{128}\mbox{PROTERRA},$  Instituto de Investigaciones de la Amazonía Peruana (IIAP), Av. A. Quiñones km 2,5, Iquitos, Loreto, 784, Peru.
- $^{129} ACEER$  Foundation, Jirón Cusco N° 370, Puerto Maldonado, Madre de Dios, Peru.
- <sup>130</sup>Environmental Change Institute, Oxford University Centre for the Environment, Dyson Perrins Building, South Parks Road, Oxford, England, OX1 3QY, UK.
- <sup>131</sup>Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7945, Bogotá, DC, Colombia.
- <sup>132</sup>Instituto de Ciência Agrárias, Universidade Federal Rural da Amazônia, Av. Presidente Tancredo Neves 2501, Belém, PA, 66.077-830, Brazil.
- <sup>133</sup>Escuela Profesional de Ingeniería Forestal, Universidad Nacional de San Antonio Abad del Cusco, Jirón San Martín 451, Puerto Maldonado, Madre de Dios, Peru.

<sup>134</sup>Laboratory of Human Ecology, Instituto Venezolano de Investigaciones Científicas - IVIC, Ado 20632, Caracas, DC, 1020A, Venezuela.

<sup>135</sup>Cambridge University Botanic Garden, Cambridge University, 1 Brookside., Cambridge, CB2 1JE, UK.

<sup>136</sup>Programa de Maestria de Manejo de Bosques, Universidad de los Andes, Via Chorros de Milla, 5101, Mérida, Mérida, Venezuela.

<sup>137</sup>Centre for Biodiversity and Conservation Science CBCS, The University of Queensland, Brisbane, QLD, 4072, Australia.

<sup>138</sup>Resource Ecology Group, Wageningen University & Research, Droevendaalsesteeg 3a, Lumen, building number 100, Wageningen, Gelderland, 6708 PB, The Netherlands.

<sup>139</sup>School of Earth, Environment and Society, McMaster University, 1280 Main Street West, Hamilton, Ontario, L8S 4K1, Canada.

<sup>140</sup>Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Av. Alberto Lamego 2000, Campos dos Goytacazes, RJ, 28013-620, Brazil.

<sup>141</sup>Departamento de Biologia, Universidade Federal do Amazonas - UFAM Instituto de Ciências Biológicas ICB1, Av General Rodrigo Octavio 6200, Manaus, AM, 69080-900, Brazil.

 $^{142}\mbox{GeoIS},$  El Día 369 y El Telégrafo, 3° Piso, Quito, Pichincha, Ecuador.

<sup>143</sup>Faculty of Social Sciences, University of Nottingham, University Park, Nottingham, NG7 2RD, UK.

<sup>144</sup>Wildlife Conservation Society (WCS), 2300 Southern Boulevard, Bronx, New York, NY, 10460, USA.

 $^{145}\mathrm{Medio}$ Ambiente, PLUSPRETOL, Iquitos, Loreto, Peru.

<sup>146</sup>The Mauritius Herbarium, Agricultural Services, Ministry of Agro-Industry and Food Security, Reduit, 80835, Mauritius.

<sup>147</sup>Department of Biology, Aarhus University, Building 1540, Aarhus C, Aarhus, 8000, Denmark.

<sup>148</sup>Living Earth Collaborative, Washington University in Saint Louis, St. Louis, MO, 63130, USA.

<sup>149</sup>Escuela de Ciencias Forestales (ESFOR), Universidad Mayor de San Simon (UMSS), Sacta, Cochabamba, Bolivia.

<sup>150</sup>FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, Sacta, Cochabamba, Bolivia.

 $^{151}$  Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Calle 64 x Cra 65, Medellín, Antioquia, 1027, Colombia.

<sup>152</sup>Fundación Amigos de la Naturaleza (FAN), Km. 7 1/2 Doble Vía La Guardia, Santa Cruz, Bolivia.

<sup>153</sup>Tropenbos International, Horaplantsoen 12, Ede, 6717 LT, The Netherlands.

<sup>154</sup>School of Anthropology and Conservation, University of Kent, Marlowe Building, Canterbury, Kent, CT2 7NR, UK.

<sup>155</sup>Herbario Nacional del Ecuador, Universidad Técnica del Norte, Quito, Pichincha, Ecuador.

<sup>156</sup>Instituto de Biodiversidade e Florestas, Universidade Federal do Oeste do Pará, Rua Vera Paz, Campus Tapajós, Santarém, PA, 68015-110, Brazil.

#### **Materials and Methods**

Types of pre-Columbian structures that are referred to as "earthworks" in our study

Pre-Columbian earthworks covered in this research include geometrically patterned enclosures, which have been variously referred to in the literature as: earth structures delimited by trenches (52); geometrically patterned ditched enclosures (53, 54); earthworks (54–56); ringed ditches (55, 57); ditches and sculpted plazas (10, 11, 23, 24, 58, 59); geoglyphs (25, 30, 60); and wells (5). These different types of pre-Columbian anthropogenic structures are all referred to as "earthworks" in this study.

### Light Detection and Ranging (LiDAR) data

In order to identify pre-Columbian earthworks beneath the forest canopy, we used three datasets provided by: (1) the Sustainable Landscapes Brazil project, a technical and financial cooperation agreement between the United States Forest Service (USFS) and the Brazilian Agricultural Research Corporation (EMBRAPA); (2) the Environmental Monitoring via Satellite in the Amazon Biome (MSA) project, funded by the Amazon Fund with resources from Brazil's National Development Bank (BNDES) and overseen by the Center for Science of the Terrestrial System (CCST); and (3) the TRopical Ecosystems and Environmental Sciences (TREES) laboratory research group, located at Brazil's National Institute for Space Research (INPE). The datasets consist of airborne LiDAR obtained along transects across Amazonian forests from 2008 to 2017, see table S3 for airborne LiDAR equipment, parameters and spatial resolution (point density). The full dataset covers 5,315 km², which accounts for 0.08 % of the Amazon forest and represents the largest LiDAR dataset available for Amazonia. All LiDAR data sources are listed in tables S3, and S4, and their spatial distribution is shown in fig. S3[A–C].

The methodology used in these projects differed, which required different parameter settings for LiDAR data processing. We processed the data using the following steps in LAStools software version 180.605 (61): (1) division of LiDAR files (.laz) into tiles to enable multithread processing in the next steps with the lastile tool; (2) noise filtering with the lasnoise tool, using default parameters; (3) first ground classification of the point cloud to acquire sparse control points with the lasground tool; (4) aggregation of points close to the control points (from 1<sup>st</sup> classification) with the lasheight tool; (5) dilution of the point cloud to flag points with lower elevation with the lasthin tool performed three times sequentially; (6) second ground classification, observing only flagged points from the previous step, with the lasground tool; and (7) interpolation of the ground points (from 2<sup>nd</sup> classification) of the Digital Terrain Model (DTM) into a regular grid with the blast2dem tool to create a Digital Elevation Model (DEM) which allowed us to generate products of altimetry, slope, hillshade, and canopy height model, with 0.5 m spatial resolution (see table S5 for parameters).

### Detecting earth-builders' architecture (earthworks)

The first author (VP) searched for earthworks by visual inspection using hillshade data created from the DEM combined, when necessary, with ESRI high spatial resolution imagery. The geolocation was excluded to prevent any bias associated with the viewer's knowledge about the distribution of well-known earthworks, such as the ones that occur on the southern rim of Amazonia. Viewer mental and visual fatigue were minimized by setting a maximum of 50 images to analyze per day. The viewer was trained to search for geometric shapes not congruent with the landscape. Archaeological experts confirmed approximately half of the features flagged by the viewer as evidence of historical human occupation.

Using LiDAR inspected data we identified 24 new earthworks and nine other earthworks that were already cataloged in archaeological databases. Therefore, within the 5,631 km<sup>2</sup> of LiDAR data, we obtained an estimate of 0.0062 earthworks/km<sup>2</sup>. These 33 records were seen on 12 of the 861 LiDAR flight lines. All the identified earthworks hillshade data, elevation, slope, tree cover, location, and a brief description is shown in figs. S4 to fig. S13.

### Modeling earthwork distribution

We performed a statistical analysis based on novel statistical techniques and on an Inhomogeneous Poisson Process (IPP) model (31), using an intensity function based on intensity covariates and thinned by observability covariates (32) to map the potential extent of pre-Columbian earth-building societies across Amazonia. Statistical novelties in our approach include a fully model-based framework for all model components and a data augmentation technique to handle the analytical intractability of the likelihood function of IPPs. Combined with a Bayesian paradigm, these features allow us to analyze the data without model approximations. Quadratic and interaction effects were not included, leaving only linear terms. The IPP model fit was performed using the 'fit\_bayesPO' function of the 'bayesPO' library in R version 4.0.2 (62, 63).

Presence data of earthworks were compiled using our newly-discovered sites (24 sites) together with sites obtained from four datasets provided by: (1) Amazonian Archaeological Sites Network (AmazonArch); (2) Brazilian National System of Archaeological Sites (CNSA); (3) Pre-Columbian Amazon Scale Transformations (PAST) project; and (4) France's National Institute for Preventive Archaeological Research (INRAP). The compilation was carried out by merging data from different datasets within a 500-m radius. This compilation resulted in 937 presence data records. All earthworks data sources are listed in table S4, and their spatial distribution is shown in fig. S3[D–H].

The spatial distribution of earthwork occurrences across the Amazon suffers from a large sampling bias (fig. S14). The current distribution of earthwork sites is skewed towards regions with a higher degree of accessibility and less forest cover (fig. S15). Sampling of all archaeological sites in the Amazon (not only earthworks) follows a similar pattern: a greater number of records in areas with greater accessibility and more intensive research histories. With this biased data collection, the effects of sampling bias in species distribution models (SDMs) applied to archaeological elements throughout the Amazon are always present. However, presence-only data is the only information available. It has become more abundant over the years and, therefore, is a valuable source of information if handled properly (32).

In order to reduce the effects of sampling bias in presence-only datasets, a methodology developed by Moreira & Gamerman (2022) that aims to include components that describe sampling preference was used to develop an appropriate Inhomogeneous Poisson Process (IPP) model (31). Inhomogeneous Poisson processes (IPP) are statistical models for the probabilistic description of occurrences over a region of interest when the intensity of occurrences varies (continuously) over that region. It is also possible to accommodate the effect of explanatory variables on their specification. In addition to these strengths, the IPP approach has an advantage regarding interpretability. Each variable's individual contribution to earthwork presence and observability can be quantified by its respective effect parameter. Thus, the inclusion of observability components, such as the distance from roads and tree cover, as an indication of more favorable locations for the acquisition of samples in the Inhomogeneous Poisson Process

(IPP) model weighted the individual sampling bias of each sample (64–66) and provided better and more satisfactory results in the predictive model.

For observability covariates, the distance to roads was calculated using data from OpenStreetMap (67) data (https://planet.osm.org) and tree-cover was based on global forest change 2000-2018 (68), version 1.6 data (https://glad.earthengine.app/view/global-forest-change). For intensity covariates (environmental layers), we selected over 19 bioclimatic variables from WordClim (69), 12 edaphic variables from SoilGrids (70) and Zuquim et al. (2019) data (71), and 9 topographic variables derived from the elevation data from HydroSHEDS (72) data (https://www.hydrosheds.org), global surface water from JRC (73) data (https://global-surface-water.appspot.com), and water-table depth from AMBDATA (74) data (http://www.dpi.inpe.br/Ambdata/hand.php). All environmental layers used are listed in table S1.

Topographic aspect, roughness, slope, Topographic Position Index (TPI), and Terrain Ruggedness Index (TRI) were derived from elevation data using the 'terrain' function of the 'raster' library in R version 4.0.2 (63). Distance data (distance to nearest river and road) to earthworks location were calculated using the 'gridDistance' function of the 'raster' library in R version 4.0.2 (63). Water accessibility was estimated from elevation, surface water, and slope data using the ArcGIS Spatial Analyst tool (75).

We excluded areas higher than 500 m elevation, because they have bioclimatic and topographic characteristics different enough from Amazonian lowlands that they could skew our model predictions. All data (observability and intensity) were resampled, when necessary, to match the spatial resolution of 30 arc seconds (~ 1 km) and cropped to the extent of the six geological and geographical regions of the Amazon basin (NwA, northwestern Amazonia; SwA, southwestern Amazonia; SA, southern Amazonia; CA, central Amazonia; GS, Guiana Shield; and EA, eastern Amazonia).

None of the intensity covariates included pre-Columbian human occupation density, dating period, or cultural stratification. Those data could be used to refine the analysis of the distribution and occupation of land builders. However, they were not available at a fine enough scale (1 km<sup>2</sup>) to be included in our modeling analysis.

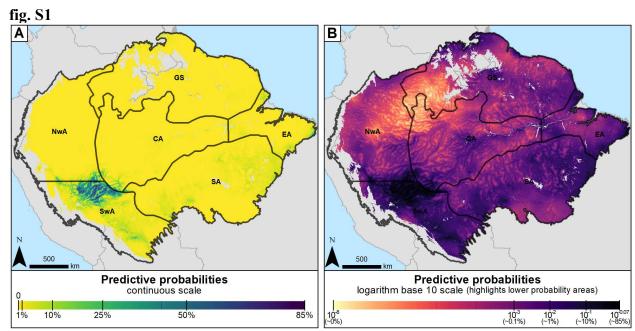
We selected the most informative variables that were not highly correlated with each other (see figs. S16, S17, and S18). Variables retained for the final model were: (1) mean temperature of warmest quarter (Bio 10); (2) precipitation of wettest quarter (Bio 16); (3) precipitation of driest quarter (Bio 17); (4) soil cation concentration; (5) clay content; (6) silt content; (7) Topographic Position Index (TPI); (8) Height Above the Nearest Drainage (HAND); and (9) Distance to nearest river.

We ran a similar distribution model using another presence-only model (MaxEnt) using a sampling probability surface – which regulates the weight of the pseudo-random background data of the model (76–80), created by a Gaussian kernel density map of the presence data – to predict and compare the distribution of earthworks using a pseudo-absence model (fig. S19). We opted for the Inhomogeneous Poisson Process (IPP) model based on the results that are obtained based on probabilistic reasoning, and are provided with their associated measure of uncertainty.

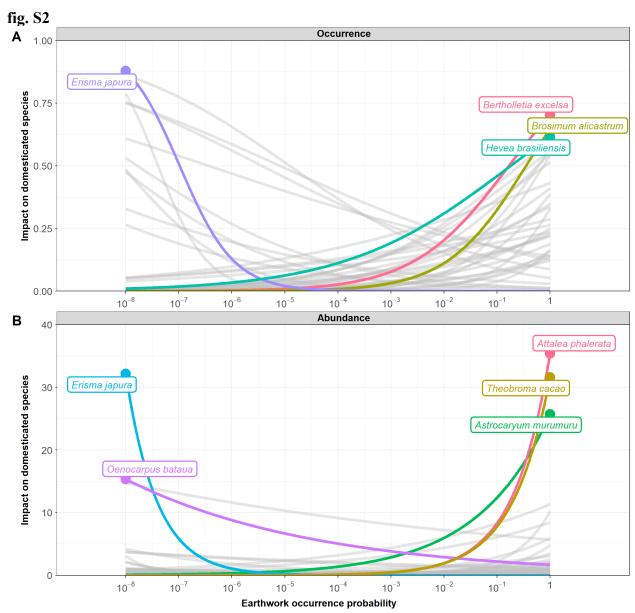
Because the archaeological databases used in this study (AmazonArch, CNSA, INRAP&DAC, and PAST) is constantly being updated, we expect that the incorporation of new data – relevant to describe the distribution of Amazonian earth-building societies – may refine the predicted number of earthworks. Future studies can be done to refine and validate our reproducible and available prediction model (51). Furthermore, the model can also be restricted to specific types of archaeological structures or Amazonian regions.

### <u>Indicators of pre-Columbian domestication and settlements</u>

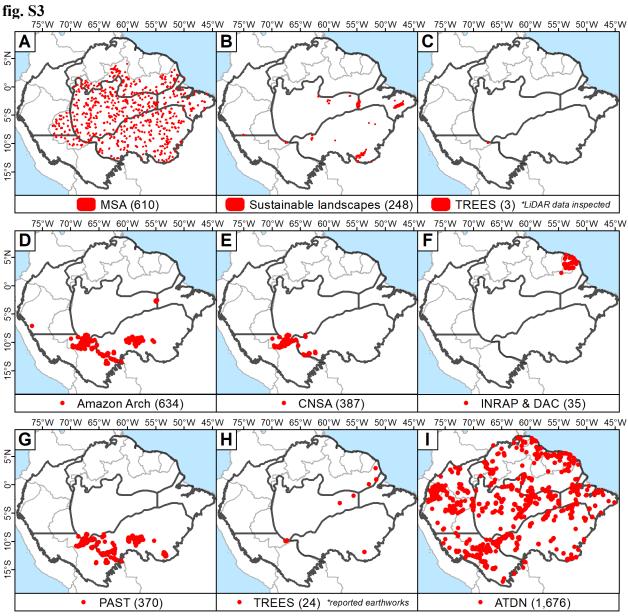
Data from 1,676 forest inventories provided by the Amazon Tree Diversity Network (ATDN) were used to analyze the: (1) occurrence (presence/absence) of domesticated tree species, and (2) abundance (total number of individuals of the same species). We considered "domesticated species" to be 79 arboreal species strongly associated with indigenous management and cultivation practices and with archaeological sites across Amazonia, following Levis et al. (2017). We used a generalized linear model to analyze the relationship between the occurrence and abundance of domesticated species and their individual responses and the probability of earthwork occurrence obtained from the Inhomogeneous Poisson Process (IPP) model on a log-transformed (base 10) scale. We used binomial and Poisson distributions for the occurrence and abundance data respectively. The forest inventory size was used to specify the component fitting. An overall significance level of 0.05 was used as a threshold to identify domesticated species that significantly increased or decreased with the IPP model. The significance level for each species was adjusted based on the desired overall significance (5%) and the total number of species (79). This analysis was conducted using the 'glm' function of the 'stats' library in R version 4.0.2 (63). ATDN data sources are listed in table S4, and their spatial distribution is shown in fig. S3[I].



**fig. S1.** Predicted probability of earthwork presence across Amazonia. (A) Predicted probability of earthwork presence for 1 km2 pixels using an Inhomogeneous Poisson Process predictive model (IPP model) on a continuous scale. (B) Predicted probability of earthwork presence for 1 km2 pixels using IPP model on a log-transformed scale (log10) highlighting the lower probability variation (< 1%) throughout Amazonia. Six Amazonian regions are labeled: 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.



**fig. S2. Impact of earthwork occurrence probability on significant domesticated tree species across Amazonia.** (A) Relationship between occurrence (presence/absence) data and the predicted probability of earthwork presence. (B) Relationship between abundance data and the predicted probability of earthwork presence. Highlighted species are the 10% most significantly (positive or negative) associated with probability of earthwork presence. Other significant species are greyed-out and without names.



**fig. S3. Spatial distribution of the data used within this study.** (A–C) Distribution of processed and inspected LiDAR data in the three datasets compiled for this study. (D–H) Distribution of pre-Columbian earthworks in the five datasets compiled for this study. (I) Distribution of Amazon Tree Diversity Network plot sites.

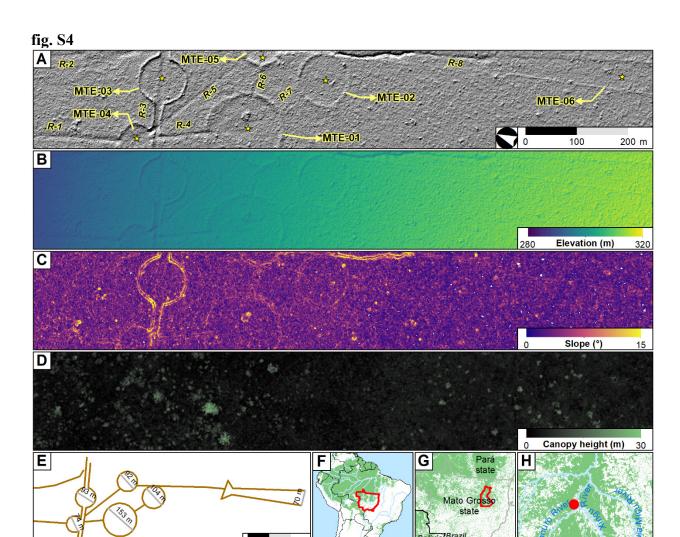
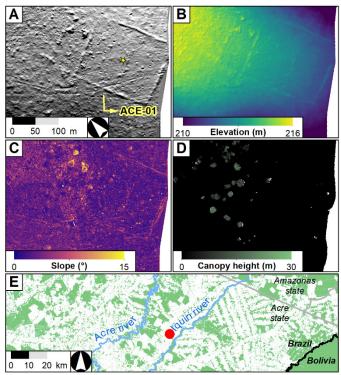


fig. S4. New earthworks discovered using LiDAR in Southern Amazonia (SA). (A) Shaded relief, showing detected earthworks and roads. The digital removal of the forest canopy revealed 5 circular plazas (measuring 70 to 150 m in diameter) and 1 rectangular feature (measuring 1,650 m²) connected by roads. Two of these minor roads (R-1 and R-2) connect to a 200 m long linear path leading to the Iamaçu River. (B) Elevation in meters. (C) Slope in degrees. The Digital Terrain Model (DTM) indicated that all earthworks were located on flat portions of the landscape. (D) Canopy Height Model (CHM), in meters. Near these circular plazas, the Canopy-Height Model (CHM) derived from the LiDAR data revealed an emergent canopy with 35 m tall trees, and palms reaching ~20 m. (E) Schematic design of the detected earthworks. 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. (F) Location of Brazil's Mato Grosso state. (G) Location of the Upper Xingu indigenous resource management area. (H) Location of the earthworks sites.

100 200 m

fig. S5



**fig. S5.** New earthworks discovered using LiDAR in Senador Guiomard, in Acre State, Brazil. (A) Shaded relief, showing detected earthwork. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM), in meters. (E) Location of the earthwork site. The ACE-01 site is located in a pasture.

fig. S6

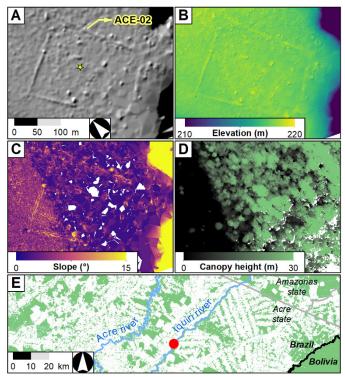


fig. S6. New earthworks discovered using LiDAR in Senador Guiomard, in Acre State, Brazil. (A) Shaded relief, showing detected earthwork. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. (E) Location of the earthwork site. The ACE-02 site is located in a forest edge area, with disturbed vegetation covering a portion of the site.

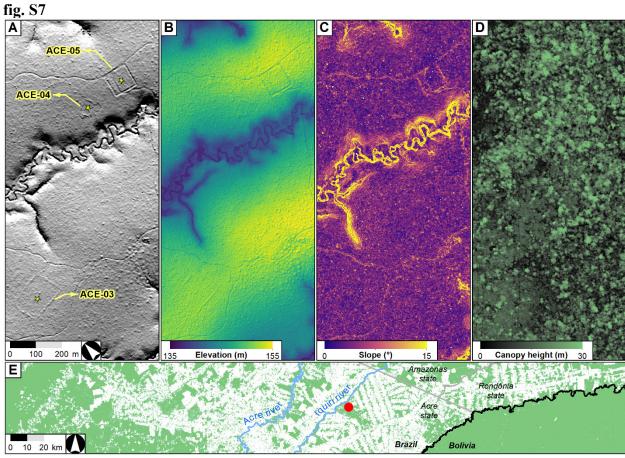
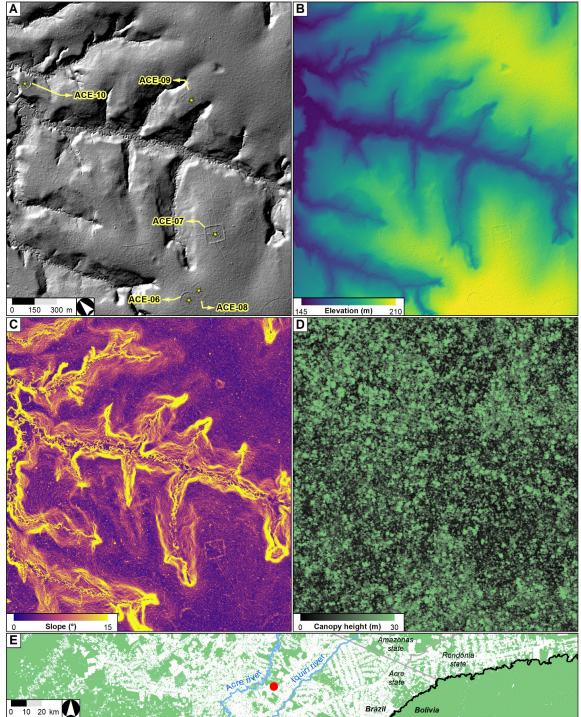


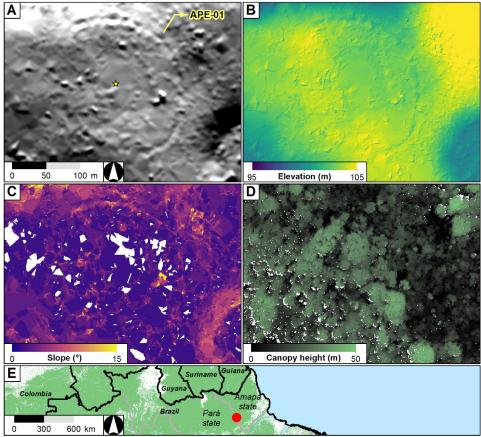
fig. S7. New earthworks discovered using LiDAR in Senador Guiomard, in Acre State, Brazil. (A) Shaded relief, showing detected earthworks. The sites are located beneath the forest canopy, next to a perennial tributary of the Iquiri River. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. The LiDAR data indicated that the landscape around these sites has trees with canopy heights reaching ~22 m. (E) Location of the earthworks sites.



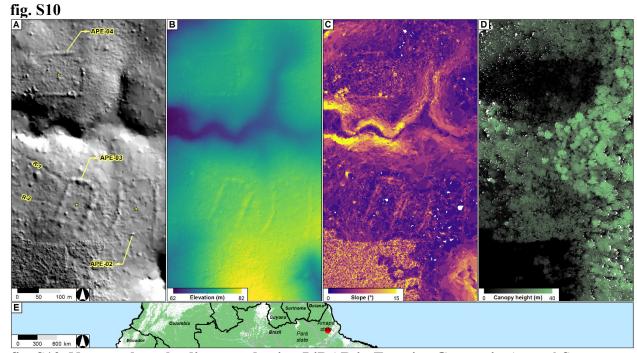


**fig. S8.** New earthworks discovered using LiDAR in Rio Branco, in Acre State, Brazil. (A) Shaded relief, showing detected earthworks. ACE-07 site has prominent road features delimited by embankments, and ACE-06 and ACE-10 have a semi-circular pattern. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. The LiDAR data indicated that the landscape around these sites has trees with canopy heights reaching ~22 m. (E) Location of the earthworks sites.





**fig. S9.** New earthworks discovered using LiDAR in Laranjal do Jari, in Amapá State, Brazil. (A) Shaded relief, showing detected earthwork. The APE-01 site is composed of a rectangular feature surrounded by a circular trench. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. The site is covered by a forest with emergent trees with heights up to 45 m and palms reaching ~20 m. (E) Location of the earthwork site., the site's location on a plateau top, combined with the distinct geometric pattern, suggests that it was once a crowned mountain used as permanent settlement (26).



**fig. S10.** New earthworks discovered using LiDAR in Ferreira Gomes, in Amapá State, Brazil. (A) Shaded relief, showing detected earthworks and roads. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. The sites are surrounded by tall forests (45 m) and are structurally comparable to each other. (E) Location of the earthworks sites. Their proximity to Solstice Archaeological Park (200 km), a location where several pre-Columbian ceremonial sites were found (popularly known as Amazonian Stonehenge), suggests that these features may be formed by megalithic structures (27).



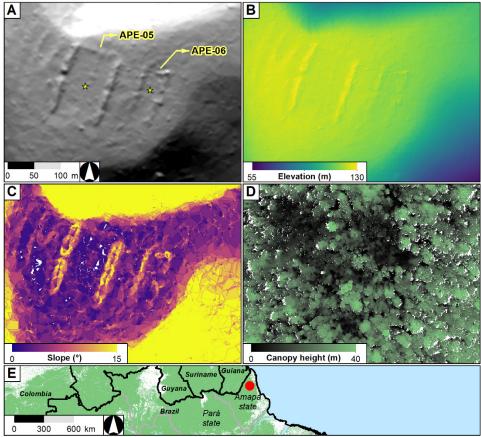
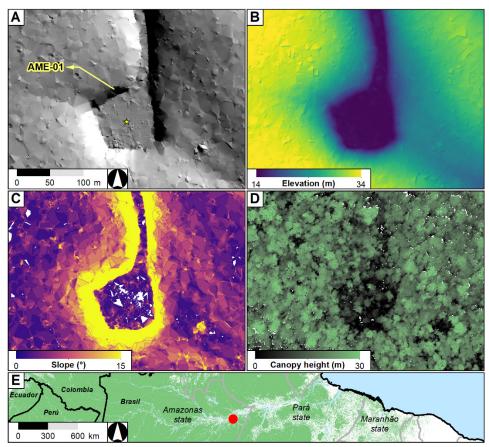


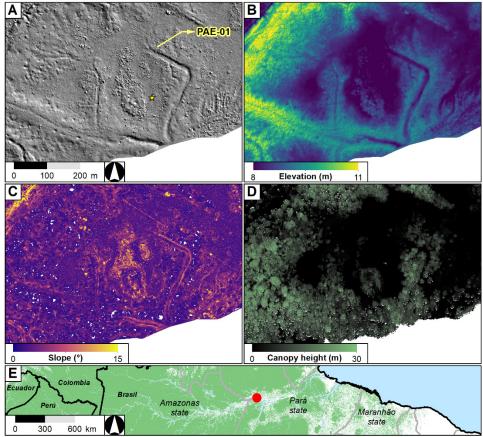
fig. S11. New earthworks discovered using LiDAR in Oiapoque, in Amapá State, Brazil. (A) Shaded relief, showing detected earthworks. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. (E) Location of the earthworks sites. The sites are covered by tall forests (45 m) and are structurally comparable to each other. Their proximity to Solstice Archaeological Park (80 km), a location where several pre-Columbian ceremonial sites were found (popularly known as Amazonian Stonehenge), suggests that these features may be formed by megalithic structures (27).



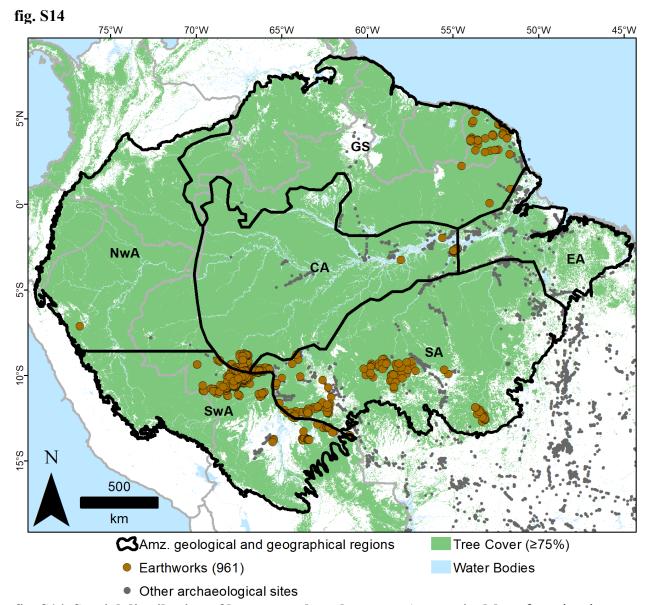


**fig. S12.** New earthworks discovered using LiDAR in Boa Vista do Ramos, in Amazonas State, Brazil. (A) Shaded relief, showing detected earthwork. The geometric-like feature from AME-01 site measures ~100 x 100 m carved 5 m into the ground maintaining a continuous plain terrain of the flooded area. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. (E) Location of the earthwork site.



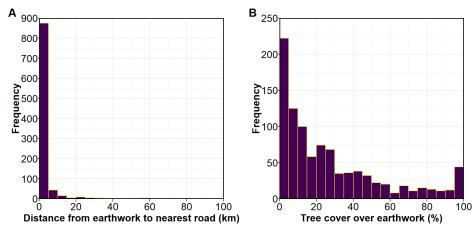


**fig. S13.** New earthworks discovered using LiDAR in Óbidos, in Pará State, Brazil. (A) Shaded relief, showing detected earthwork. It features a linear ditch (~ 0.6 m deep) with one or more 90° angle turns. (B) Elevation in meters. (C) Slope in degrees. (D) Canopy Height Model (CHM) in meters. (E) Location of the earthwork site. The PAE-01 site is located next to the Amazon River.



**fig. S14. Spatial distribution of known earthworks across Amazonia.** Map of previously reported and new earthworks discovered 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). Note the higher concentration of occurrences in the southern regions of the basin.





**fig. S15. Histograms of observability covariates.** (A) Distance from earthworks to nearest road. (B) Tree cover over earthwork. A-B bin width is equal to 5 units.

# **fig. S16**

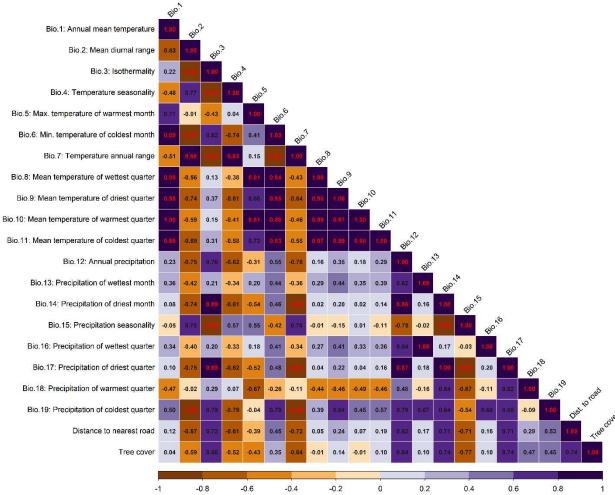


fig. S16. Pearson correlation matrix for bioclimatic variables. Values in red indicate strong correlation (> |0.8|).

fig. S17

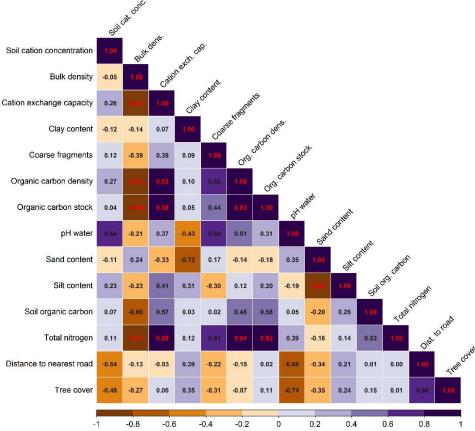


fig. S17. Pearson correlation matrix for edaphic variables. Values in red indicate strong correlation (> |0.8|).



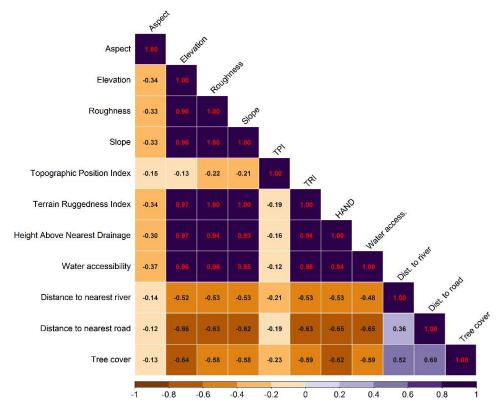
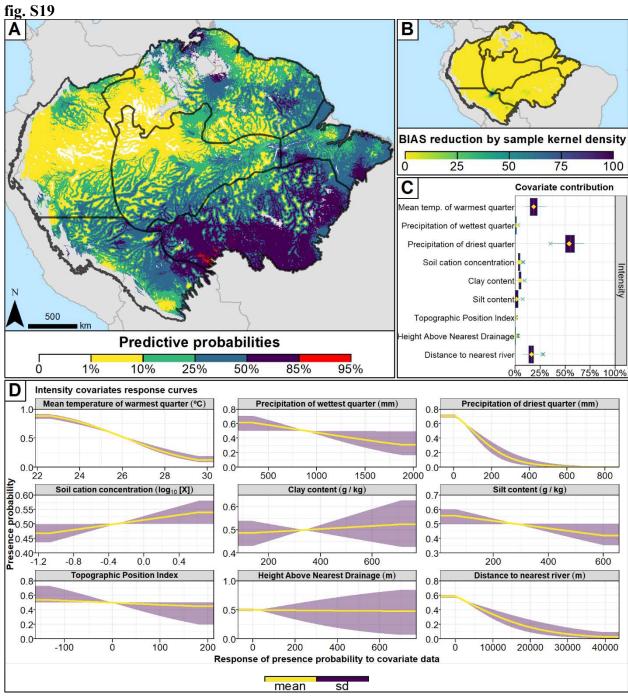


fig. S18. Pearson correlation matrix for topographic variables. Values in red indicate strong correlation (> |0.8|).



**fig. S19.** Maximum entropy model of pre-Columbian earthworks across Amazonia. (A) Predicted probability of earthwork presence for 1-km² pixels across six Amazonian regions. Central Amazonia (CA); Eastern Amazonia (EA); Guiana Shield (GS); Northwestern Amazonia (NwA); Southern Amazonia (SA); and Southwestern Amazonia (SwA). (B) Gaussian kernel density map of the presence data that regulates the contribution of MaxEnt random pseudoabsence (background) data. (C) Boxplot of the individual estimates of covariates' relative contributions, with the yellow diamond indicating mean value. (D) Individual predicted probabilities of earthwork presence plotted against intensity covariates.

# table S1

Type	Variable								
<u> </u>	Bio.1: Annual mean temperature (°C)								
	Bio.2: Mean diurnal range (mean of monthly (max. temp – min. temp))								
	Bio.3: Isothermality ((Bio2/Bio7)*100))								
	Bio.4: Temperature seasonality (Std.Dev. * 100)								
	Bio.5: Max. temperature of warmest month (°C)								
	Bio.6: Min. temperature of coldest month (°C)								
	Bio.7: Temperature annual range (Bio.5 – Bio,6)								
ပ	Bio.8: Mean temperature of wettest quarter (°C)								
Bioclimatic	Bio.9: Mean temperature of driest quarter (°C)								
<u>ii</u>	Bio.10: Mean temperature of warmest quarter (°C)								
[] []	Bio.11: Mean temperature of coldest quarter (°C)								
B	Bio.12: Annual precipitation (mm)								
	Bio.13: Precipitation of wettest month (mm)								
	Bio.14: Precipitation of driest month (mm)								
	Bio.15: Precipitation seasonality (coefficient of variation)								
	Bio.16: Precipitation of wettest quarter (mm)								
	Bio.17: Precipitation of driest quarter (mm)								
	Bio.18: Precipitation of warmest quarter (mm)								
	Bio.19: Precipitation of coldest quarter (mm)								
	Soil cation concentration (log10)								
	Bulk density (cg/cm³)								
	Cation exchange capacity (mmol(c)/kg)								
	Clay content (g/kg)								
.၁	Coarse fragments (cm³/dm³)								
phi	Organic carbon density (dg/dm³)								
Edaphic	Organic carbon stock (t/ha)								
<u> </u>	pH water (ph*10)								
	Sand content (g/kg)								
	Silt content (g/kg)								
	Soil organic carbon (dg/kg)								
	Total nitrogen (cg/kg)								
	Aspect (degrees)								
ల	Elevation (m)								
Topographic	Roughness (m)								
rap	Slope (degrees)								
<b>6</b> 0	Topographic Position Index (TPI) Terrain Ruggedness Index (TRI)								
do]	Height Above the Nearest Drainage (HAND) (m)								
	Water accessibility								
	Distance to nearest river (m)								
Obs.	Distance to nearest road (m)								
Comp	Tree cover (%)								
Comp	1 1100 00 101 (70)								

table S1. Environmental parameters considered as predictors for modeling.

table S2

Probability	Projected area (km²)	Distribution across six Amazonian regions						
threshold		CA	EA	GS	NwA	SA	SwA	
≥ 1%	1,412,738	8%	9%	6%	5%	34%	37%	
≥ 10%	207,915	7%	3%	1%	9%	5%	74%	
≥ 25%	94,713	4%	1%	0%	7%	1%	86%	
≥ 50%	32,120	1%	0%	0%	4%	0%	96%	
≥ 75%	581	0%	0%	0%	0%	0%	100%	

table S2. IPP Model projected area across six Amazonian regions on different probability thresholds.

table S3

D:	ataset	Scanner specification	Scanner frequency	GNSS Specification	GNSS Frequency	IMU Specification	IMU Frequency	Flight altitude	Flight line overlap	FOV	Average point density (last only)
Sustainable Landscapes	2008	LEICA, ALS-50 PHASE II, SN 52	58 - 90 Hz	NOVATEL, OEMV4	2 Hz	IMAR, LN200	200 kHz	805 m	27%	10 - 24°	15 points.m <sup>-2</sup>
	2011	OPTECH INC., ALTM 3100	59.8 Kz	APPLANIX, 09SEN243	5 Hz	LITTON, 413996	100 kHz	850 m	65%	11°	15 points.m <sup>-2</sup>
	2012	OPTECH INC., ALTM 3100	59.8 Kz	APPLANIX, 09SEN243	5 Hz	LITTON, 413996	100 kHz	850 m	65%	11°	16 points.m <sup>-2</sup>
	2013	OPTECH INC., ORION M300	61.4 - 67.5 Hz	APPLANIX, 09SEN243	5 Hz	LITTON, 413996	100 kHz	860 m	65%	10 - 11 °	13 points.m <sup>-2</sup>
	2014	OPTECH INC., ORION M300 * TRIMBLE, HARRIER 68I **	83 Hz * 400 kHz **	APPLANIX, 09SEN243 * APPLANIX, AV510 **	5 Hz * 1 Hz **	LITTON, 413996 * APPLANIX, AV510 **	100 kHz * 200 Hz **	850 m * 500 m **	65%	10 - 12° * 15° **	20 points.m <sup>-2</sup>
	2015	OPTECH INC., ALTM 3100	40 - 55 Hz	OMNISTAR, PGPS16	1 Hz	APPLANIX, AV510	200 kHz	700 m	70%	15°	37 points.m <sup>-2</sup>
	2016	OPTECH INC., ALTM 3100	40 Hz	OMNISTAR, PGPS16	1 Hz	APPLANIX, AV510	200 kHz	750 m	70%	15°	23 points.m <sup>-2</sup>
	2017	OPTECH INC., ALTM 3100	40 Hz	OMNISTAR, PGPS16	1 Hz	APPLANIX, AV510	200 kHz	850 m	70%	15°	15 points.m <sup>-2</sup>
ľ	MSA	TRIMBLE, RIEGL Q680I	5 - 200 Hz	APPLANIX, AV510	1 Hz	APPLANIX, AV510	200 Hz	600 m	0%	22.5°	7 points.m <sup>-2</sup>
T	REES	RIEGL, VUX-1UAV	50 - 550 kHz	APPLANIX, APX15	1 Hz	APPLANIX, APX15	200 Hz	300 m	0%	35°	8 points.m <sup>-2</sup>

table S3. Equipment and parameters in the data collection of each LiDAR database.

table S4

Group Name		Source data	Website
AmazonArch	Amazonian Archaeological Sites Network	Earthwork	https://sites.google.com/view/amazonarch
PAST	Pre-Columbian Amazon Scale Transformations	Earthwork	http://amazoniapast.exeter.ac.uk/
CNSA/IPHAN	Brazilian National System of Archaeological Sites	Earthwork	http://portal.iphan.gov.br/pagina/detalhes/1701
INRAP	National Institute for Preventive Archaeological Research	Earthwork	https://www.inrap.fr/
EMBRAPA	Sustainable Landscapes Brazil	LiDAR	http://www.paisagenslidar.cnptia.embrapa.br/webgis/
CCST	Center of Science of the Terrestrial System	LiDAR	http://www.ccst.inpe.br/projetos/eba-estimativa-de- biomassa-na-amazonia/
TREES	TRopical Ecosystems and Environmental Sciences laboratory	LiDAR	https://www.treeslab.org/
ATDN	Amazon Tree Diversity Network	Domesticated Species	https://sites.google.com/naturalis.nl/amazon-tree- diversity-network/homepage

table S4. LiDAR, Earthwork and Domesticated Species data sources.

table S5

			Values by dataset			
Description	Tool	switches	Sustainable landscapes	MSA	TREES	
Tiles point cloud into a	lastile	-tile_size	400	400	200	
specific size	iasiite	-buffer	50	50	50	
Flags or removes noisy points	lasnoise		tings			
		-step	8	10	8	
Classifies LiDAR points	lasgroun	-stddev	0.5	0.5	0.5	
into ground points	d	-spike	0.5	1	0.5	
		-offset	0.1	0.1	0.1	
Computes height of each point above the ground	lasheight	classify_betwe en	-5 / 1	-10 / 1	-5 / 1	
point doo to the ground		- classify_above	1	1	1	
	lasthin	-step	0.25	0.25	0.25	
	iasinin	-percentile	50 / 1	50 / 1	50 / 1	
Flags only points with the lowest elevation inside a	lasthin	-step	0.5	0.5	0.5	
uniform grid		-percentile	50 / 1	50 / 1	50 / 1	
Ü	lasthin	-step	1	1	1	
	lasthin	-percentile	50 / 1	50 / 1	50 / 1	
		-step	0.85	0.85	0.85	
Classifies LiDAR points	lasgroun	-stddev	0.5	0.5	0.5	
into ground points	d	-spike	0.2	0.2	0.2	
		-offset	0.1	0.1	0.1	
Triangulates the point		-step	0.5	0.5	0.5	
cloud over a continuous Triangular Irregular	blast2de	-hillshade	-	-	-	
Network (TIN)	m	-elevation	-	-	-	

table S5. Filtering parameters in LiDAR data processing.

### Data S1 (separate file).

List of 79 tree species with populations domesticated to different degrees by pre-Columbian peoples in Amazonia according to Levis et al. (2017). The dataset includes the main use of each species, the degree of domestication, origin, local names (in Brazilian Portuguese), and the individual relative significance based on occurrence (presence/absence) and abundance data. Overall significance level of 5% (p < 0.05) with adjusted significance level (p < 0.00065) is also provided. Values highlighted in blue, red, and grey indicate positive, negative, and null significance respectively.

## Data S2 (separate file): Forest plot metadata

ATDNNR: Number in ATDN database Country: country in which plot is located.

Subdivision: Mostly state/province.

Site: site name.

PlotCode: Unique ATDN plot code. Altitude, Latitude, Longitude.

PlotSize: plot size in ha.

PlotType: single: 1 single contiguous area; combi; few plots very close added.

together; pcq: plots built from point center quarter data.

DBHmin: min dbh cut off.

Owner/contact: Owner of plot data.

### References

- 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/10.55161/LXIT5573.
- 2. C. L. Erickson, "8. The Domesticated Landscapes of the Bolivian Amazon" in *Time and Complexity in Historical Ecology*, W. Balée, C. L. Erickson, Eds. (Columbia University Press, 2006), *Studies in the Neotropical Lowlands*, pp. 235–278. https://doi.org/10.7312/bale13562-011.
- 3. E. G. Neves, "Ecology, Ceramic Chronology and Distribution, Long-term History, and Political Change in the Amazonian Floodplain" in *The Handbook of South American Archaeology* (Springer New York, New York, NY, 2008), pp. 359–379. https://doi.org/10.1007/978-0-387-74907-5 20.
- 4. D. P. Schaan, *Sacred Geographies of Ancient Amazonia* (Routledge, New York, 2016). https://doi.org/10.4324/9781315420530.
- 5. C. de P. Moraes, E. G. Neves, "Earthworks of the Amazon" in *Encyclopedia of Global Archaeology* (Springer International Publishing, Cham, 2019), pp. 1–13. https://doi.org/10.1007/978-3-319-51726-1 3026-1.
- 6. C. Levis *et al.*, Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*. **355**, 925–931 (2017). https://doi.org/10.1126/science.aal0157.
- 7. C. Levis *et al.*, How People Domesticated Amazonian Forests. *Front. Ecol. Evol.* **5**, 1–21 (2018). https://doi.org/10.3389/fevo.2017.00171.
- 8. C. R. Clement, 1492 and the loss of amazonian crop genetic resources. I. The relation between domestication and human population decline. *Econ. Bot.* **53**, 188–202 (1999). https://doi.org/10.1007/BF02866498.
- 9. U. Lombardo, J. Iriarte, L. Hilbert, J. Ruiz-Pérez, J. M. Capriles, H. Veit, Early Holocene crop cultivation and landscape modification in Amazonia. *Nature*. **581**, 190–193 (2020). https://doi.org/10.1038/s41586-020-2162-7.
- 10. M. J. Heckenberger *et al.*, Amazonia 1492: Pristine Forest or Cultural Parkland? *Science*. **301**, 1710–1714 (2003). https://doi.org/10.1126/science.1086112.
- 11. M. J. Heckenberger, J. Christian Russell, J. R. Toney, M. J. Schmidt, The legacy of cultural landscapes in the Brazilian Amazon: implications for biodiversity. *Philos. Trans. R. Soc. B Biol. Sci.* **362**, 197–208 (2007). https://doi.org/10.1098/rstb.2006.1979.
- 12. J. F. Carson *et al.*, Environmental impact of geometric earthwork construction in pre-Columbian Amazonia. *Proc. Natl. Acad. Sci.* **111**, 10497–10502 (2014). https://doi.org/10.1073/pnas.1321770111.
- 13. J. Watling *et al.*, Impact of pre-Columbian "geoglyph" builders on Amazonian forests. *Proc. Natl. Acad. Sci.* **114**, 1868–1873 (2017). https://doi.org/10.1073/pnas.1614359114.
- 14. C. C. Mann, Ancient Earthmovers of the Amazon. *Science*. **321**, 1148–1152 (2008). https://doi.org/10.1126/science.321.5893.1148.
- 15. J. G. de Souza *et al.*, Pre-Columbian earth-builders settled along the entire southern rim of the Amazon. *Nat. Commun.* **9**, 1125 (2018). https://doi.org/10.1038/s41467-018-03510-7.
- J. Iriarte *et al.*, Geometry by Design: Contribution of Lidar to the Understanding of Settlement Patterns of the Mound Villages in SW Amazonia. *J. Comput. Appl. Archaeol.* 3, 151–169 (2020). https://doi.org/10.5334/jcaa.45.

- 17. M. A. Canuto *et al.*, Ancient lowland Maya complexity as revealed by airborne laser scanning of northern Guatemala. *Science*. **361** (2018), doi:10.1126/science.aau0137. https://doi.org/10.1126/science.aau0137.
- 18. A. F. Chase, D. Z. Chase, C. T. Fisher, S. J. Leisz, J. F. Weishampel, Geospatial revolution and remote sensing LiDAR in Mesoamerican archaeology. *Proc. Natl. Acad. Sci.* **109**, 12916–12921 (2012). https://doi.org/10.1073/pnas.1205198109.
- 19. H. Prümers, C. J. Betancourt, J. Iriarte, M. Robinson, M. Schaich, Lidar reveals pre-Hispanic low-density urbanism in the Bolivian Amazon. *Nature*. **606**, 325–328 (2022). https://doi.org/10.1038/s41586-022-04780-4.
- 20. C. M. Souza *et al.*, Reconstructing Three Decades of Land Use and Land Cover Changes in Brazilian Biomes with Landsat Archive and Earth Engine. *Remote Sens.* **12**, 2735 (2020). https://doi.org/10.3390/rs12172735.
- 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, Evaluating spatial coverage of data on the aboveground biomass in undisturbed forests in the Brazilian Amazon. *Carbon Balance Manag.* **14**, 11 (2019). https://doi.org/10.1186/s13021-019-0126-8.
- 23. M. J. Heckenberger, J. B. Petersen, E. G. Neves, Village Size and Permanence in Amazonia: Two Archaeological Examples from Brazil. *Lat. Am. Antiq.* **10**, 353–376 (1999). https://doi.org/10.2307/971962.
- 24. M. J. Heckenberger *et al.*, Pre-Columbian Urbanism, Anthropogenic Landscapes, and the Future of the Amazon. *Science*. **321**, 1214–1217 (2008). https://doi.org/10.1126/science.1159769.
- 25. S. Saunaluoma, M. Pärssinen, D. Schaan, Diversity of Pre-colonial Earthworks in the Brazilian State of Acre, Southwestern Amazonia. *J. F. Archaeol.* **43**, 362–379 (2018). https://doi.org/10.1080/00934690.2018.1483686.
- 26. G. Odonne, J.-F. Molino, Écologie historique amazonienne, une interdisciplinarité nécessaire. *Les Nouv. l'archéologie*, 11–15 (2018). https://doi.org/10.4000/nda.4162.
- 27. M. P. Cabral, J. D. de M. Saldanha, Um sítio, múltiplas interpretações: o caso do chamado "Stonehenge do Amapá." *Rev. Arqueol. Pública.* **3**, 7 (2015). https://doi.org/10.20396/rap.v3i1.8635797.
- 28. P. Stenborg, D. P. Schaan, C. G. Figueiredo, Contours of the Past: LiDAR Data Expands the Limits of Late Pre-Columbian Human Settlement in the Santarém Region, Lower Amazon. *J. F. Archaeol.* **43**, 44–57 (2018). https://doi.org/10.1080/00934690.2017.1417198.
- 29. R. Blatrix *et al.*, The unique functioning of a pre-Columbian Amazonian floodplain fishery. *Sci. Rep.* **8**, 5998 (2018). https://doi.org/10.1038/s41598-018-24454-4.
- 30. 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). https://doi.org/10.1111/jbi.12325.
- 31. N. A. C. Cressie, "Spatial Point Patterns" in *Statistics for Spatial Data* (John Wiley & Sons, Inc., Hoboken, NJ, USA, 2015), *Wiley Series in Probability and Statistics*, pp. 575–723. https://doi.org/10.1002/9781119115151.ch8.
- 32. G. A. Moreira, D. Gamerman, Analysis of presence-only data via exact Bayes, with model and effects identification. *Ann. Appl. Stat.* **16**, 1848–1867 (2022). https://doi.org/10.1214/21-AOAS1569.

- 33. R. Valavi, J. Elith, J. J. Lahoz-Monfort, G. Guillera-Arroita, Modelling species presence-only data with random forests. *Ecography (Cop.)*. **44**, 1731–1742 (2021). https://doi.org/10.1111/ecog.05615.
- 34. S. Y. Maezumi *et al.*, The legacy of 4,500 years of polyculture agroforestry in the eastern Amazon. *Nat. Plants.* **4**, 540–547 (2018). https://doi.org/10.1038/s41477-018-0205-y.
- 35. J. Watling *et al.*, Direct archaeological evidence for Southwestern Amazonia as an early plant domestication and food production centre. *PLoS One.* **13**, e0199868 (2018). https://doi.org/10.1371/journal.pone.0199868.
- 36. P. Riris, Spatial structure among the geometric earthworks of western Amazonia (Acre, Brazil). *J. Anthropol. Archaeol.* **59**, 101177 (2020). https://doi.org/10.1016/j.jaa.2020.101177.
- 37. 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.* **114**, 522–527 (2017). https://doi.org/10.1073/pnas.1614577114.
- 38. A. M. G. A. WinklerPrins, C. Levis, Reframing Pre-European Amazonia through an Anthropocene Lens. *Ann. Am. Assoc. Geogr.* **111**, 858–868 (2021). https://doi.org/10.1080/24694452.2020.1843996.
- 39. J. Iriarte *et al.*, The origins of Amazonian landscapes: Plant cultivation, domestication and the spread of food production in tropical South America. *Quat. Sci. Rev.* **248**, 106582 (2020). https://doi.org/10.1016/j.quascirev.2020.106582.
- 40. H. A. Orengo *et al.*, Automated detection of archaeological mounds using machine-learning classification of multisensor and multitemporal satellite data. *Proc. Natl. Acad. Sci.* **117**, 18240–18250 (2020). https://doi.org/10.1073/pnas.2005583117.
- 41. A. Bonhage, M. Eltaher, T. Raab, M. Breuß, A. Raab, A. Schneider, A modified Mask region-based convolutional neural network approach for the automated detection of archaeological sites on high-resolution light detection and ranging-derived digital elevation models in the North German Lowland. *Archaeol. Prospect.* **28**, 177–186 (2021). https://doi.org/10.1002/arp.1806.
- 42. M. P. Ferreira, M. Zortea, D. C. Zanotta, Y. E. Shimabukuro, C. R. de Souza Filho, Mapping tree species in tropical seasonal semi-deciduous forests with hyperspectral and multispectral data. *Remote Sens. Environ.* **179**, 66–78 (2016). https://doi.org/10.1016/j.rse.2016.03.021.
- 43. M. P. Ferreira, R. G. Lotte, F. V. D'Elia, C. Stamatopoulos, D.-H. Kim, A. R. Benjamin, Accurate mapping of Brazil nut trees (Bertholletia excelsa) in Amazonian forests using WorldView-3 satellite images and convolutional neural networks. *Ecol. Inform.* **63**, 101302 (2021). https://doi.org/10.1016/j.ecoinf.2021.101302.
- 44. S. D. Coelho *et al.*, Eighty-four per cent of all Amazonian arboreal plant individuals are useful to humans. *PLoS One*. **16**, e0257875 (2021). https://doi.org/10.1371/journal.pone.0257875.
- 45. G. Odonne *et al.*, Long-term influence of early human occupations on current forests of the Guiana Shield. *Ecology.* **100**, 1–14 (2019). https://doi.org/10.1002/ecy.2806.
- 46. R. J. W. Brienen *et al.*, Long-term decline of the Amazon carbon sink. *Nature*. **519**, 344–348 (2015). https://doi.org/10.1038/nature14283.
- 47. K. V. Conceição *et al.*, Government policies endanger the indigenous peoples of the Brazilian Amazon. *Land use policy*. **108**, 105663 (2021). https://doi.org/10.1016/j.landusepol.2021.105663.

- 48. G. de Oliveira *et al.*, Protecting Amazonia Should Focus on Protecting Indigenous, Traditional Peoples and Their Territories. *Forests.* **13**, 16 (2021). https://doi.org/10.3390/f13010016.
- 49. C. H. L. Silva Junior, A. C. M. Pessôa, N. S. Carvalho, J. B. C. Reis, L. O. Anderson, L. E. O. C. Aragão, The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nat. Ecol. Evol.* 5, 144–145 (2020). https://doi.org/10.1038/s41559-020-01368-x.
- 50. G. Mataveli, G. de Oliveira, Protect the Amazon's Indigenous lands. *Science*. **375**, 275–276 (2022). https://doi.org/10.1126/science.abn4936.
- 51. V. Peripato *et al.*, Data from: Over 10,000 Pre-Columbian earthworks are still hidden throughout Amazonia. *Zenodo* (2023). https://doi.org/10.5281/zenodo.7750985.
- 52. D. Schaan *et al.*, Construindo paisagens como espaços sociais: o caso dos geoglifos do Acre. *Rev. Arqueol.* **23**, 30–41 (2010). https://doi.org/10.24885/sab.v23i1.286.
- 53. D. Schaan, M. Pärssinen, A. Ranzi, J. C. Piccoli, Geoglifos da Amazônia ocidental. *Rev. Arqueol.* **20**, 67–82 (2007). https://doi.org/10.24885/sab.v20i1.229.
- 54. D. Schaan, A. Ranzi, M. Parsinen, *Arqueologia da Amazônia Ocidental: os Geoglifos do Acre* (Universidade Federal do Pará (UFPA), Belém, Brazil, 2008). https://periodicos.ufpa.br/index.php/amazonica/article/view/171/243.
- 55. C. L. Erickson, An artificial landscape-scale fishery in the Bolivian Amazon. *Nature.* **408**, 190–193 (2000). https://doi.org/10.1038/35041555.
- 56. S. Saunaluoma, Pre-Columbian Earthworks in the Riberalta Region of the Bolivian Amazon. *Amaz. Rev. Antropol.* **2**, 106–138 (2010). https://doi.org/10.18542/amazonica.v2i1.347.
- 57. C. Erickson, P. Alvarez, S. Calla Maldonado, Zanjas Circundantes: Obras de Tierra Monumentales de Baures en la Amazonia Bolivia. *Proy. Agro-Arqueológico del Beni*, 1–108 (2008). https://repository.upenn.edu/anthro\_papers/11.
- 58. M. Heckenberger, E. G. Neves, Amazonian Archaeology. *Annu. Rev. Anthropol.* **38**, 251–266 (2009). https://doi.org/10.1146/annurev-anthro-091908-164310.
- 59. M. J. Heckenberger, *The Ecology of Power* (Routledge, 2004), *Critical Perspectives in Ident*. https://doi.org/10.4324/9780203486627.
- 60. S. Pappas, Mysterious Amazonian Geoglyphs Were Built in Already-Altered Forests. *Live Sci.* (2017). https://www.livescience.com/57775-humans-altered-amazon-rainforests-geoglyphs.html.
- 61. LAStools, Efficient tools for LiDAR processing (2018). https://rapidlasso.com/.
- 62. G. A. Moreira, bayesPO: Bayesian Inference for Presence-Only Data (2021). https://cran.r-project.org/package=bayesPO.
- 63. R Core Team, R: A Language and Environment for Statistical Computing. https://www.r-project.org/.
- 64. W. Fithian, J. Elith, T. Hastie, D. A. Keith, Bias correction in species distribution models: pooling survey and collection data for multiple species. *Methods Ecol. Evol.* **6**, 424–438 (2015). https://doi.org/10.1111/2041-210X.12242.
- 65. P. J. Diggle, R. Menezes, T. Su, Geostatistical Inference Under Preferential Sampling. *J. R. Stat. Soc. Ser. C Appl. Stat.* **59**, 191–232 (2010). https://doi.org/10.1111/j.1467-9876.2009.00701.x.
- 66. R. M. Dorazio, Accounting for imperfect detection and survey bias in statistical analysis of presence-only data. *Glob. Ecol. Biogeogr.* **23**, 1472–1484 (2014). https://doi.org/10.1111/geb.12216.

- 67. OpenStreetMap Wiki contributors, Planet.osm (2023). https://wiki.openstreetmap.org/w/index.php?title=Planet.osm&oldid=2535837.
- 68. M. C. Hansen *et al.*, High-Resolution Global Maps of 21st-Century Forest Cover Change. *Science*. **342**, 850–853 (2013). https://doi.org/10.1126/science.1244693.
- 69. 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). https://doi.org/10.1002/joc.1276.
- 70. N. H. Batjes, E. Ribeiro, A. van Oostrum, Standardised soil profile data to support global mapping and modelling (WoSIS snapshot 2019). *Earth Syst. Sci. Data.* **12**, 299–320 (2020). https://doi.org/10.5194/essd-12-299-2020.
- 71. G. Zuquim *et al.*, Making the most of scarce data: Mapping soil gradients in data-poor areas using species occurrence records. *Methods Ecol. Evol.* **10**, 788–801 (2019). https://doi.org/10.1111/2041-210X.13178.
- 72. B. Lehner, K. Verdin, A. Jarvis, New Global Hydrography Derived From Spaceborne Elevation Data. *Eos, Trans. Am. Geophys. Union.* **89**, 93 (2008). https://doi.org/10.1029/2008EO100001.
- 73. J.-F. Pekel, A. Cottam, N. Gorelick, A. S. Belward, High-resolution mapping of global surface water and its long-term changes. *Nature*. **540**, 418–422 (2016). https://doi.org/10.1038/nature20584.
- 74. C. D. Rennó *et al.*, HAND, a new terrain descriptor using SRTM-DEM: Mapping terrafirme rainforest environments in Amazonia. *Remote Sens. Environ.* **112**, 3469–3481 (2008). https://doi.org/10.1016/j.rse.2008.03.018.
- 75. ESRI, ArcGIS Desktop 10.5 Spatial Analyst (2016).
- M. Dudík, S. J. Phillips, R. E. Schapire, "Correcting sample selection bias in maximum entropy density estimation" in *Advances in Neural Information Processing Systems 18*, Y. Weiss, B. Schölkopf, J. C. Platt, Eds. (MIT Press, 2006), pp. 323–330. http://papers.nips.cc/paper/2929-correcting-sample-selection-bias-in-maximum-entropy-density-estimation.pdf.
- 77. J. Elith, M. Kearney, S. Phillips, The art of modelling range-shifting species. *Methods Ecol. Evol.* 1, 330–342 (2010). https://doi.org/10.1111/j.2041-210X.2010.00036.x.
- 78. Y. Fourcade, J. O. Engler, D. Rödder, J. Secondi, Mapping Species Distributions with MAXENT Using a Geographically Biased Sample of Presence Data: A Performance Assessment of Methods for Correcting Sampling Bias. *PLoS One.* **9**, e97122 (2014). https://doi.org/10.1371/journal.pone.0097122.
- 79. S. J. Phillips *et al.*, Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecol. Appl.* **19**, 181–197 (2009). https://doi.org/10.1890/07-2153.1.
- 80. D. I. Warton, L. C. Shepherd, Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *Ann. Appl. Stat.* **4**, 1383–1402 (2010). https://doi.org/10.1214/10-AOAS331.