



UNIVERSITY OF LEEDS

This is a repository copy of *Persistent effects of pre-Columbian plant domestication on Amazonian forest composition*.

White Rose Research Online URL for this paper:  
<http://eprints.whiterose.ac.uk/114745/>

Version: Accepted Version

---

**Article:**

Levis, C, Costa, FRC, Bongers, F et al. (150 more authors) (2017) Persistent effects of pre-Columbian plant domestication on Amazonian forest composition. *Science*, 355 (6328). pp. 925-931. ISSN 0036-8075

<https://doi.org/10.1126/science.aal0157>

---

© 2017, American Association for the Advancement of Science. This is an author produced version of a paper published in *Science*. Uploaded in accordance with the publisher's self-archiving policy.

**Reuse**

Unless indicated otherwise, fulltext items are protected by copyright with all rights reserved. The copyright exception in section 29 of the Copyright, Designs and Patents Act 1988 allows the making of a single copy solely for the purpose of non-commercial research or private study within the limits of fair dealing. The publisher or other rights-holder may allow further reproduction and re-use of this version - refer to the White Rose Research Online record for this item. Where records identify the publisher as the copyright holder, users can verify any specific terms of use on the publisher's website.

**Takedown**

If you consider content in White Rose Research Online to be in breach of UK law, please notify us by emailing [eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk) including the URL of the record and the reason for the withdrawal request.



[eprints@whiterose.ac.uk](mailto:eprints@whiterose.ac.uk)  
<https://eprints.whiterose.ac.uk/>

## 1 **Domestication shapes Amazonian forests**

2  
3 Carolina Levis,1,2 Flávia Costa,3 Frans Bongers,2 Marielos Peña-Claros,2 Charles R.  
4 Clement,4 André B. Junqueira,5 Eduardo G. Neves,6 Eduardo K. Tamanaha,6,7 Fernando  
5 O.G. Figueiredo,1 Rafael P. Salomão,8 Carolina V. Castilho,9 William E. Magnusson,3  
6 Oliver L. Phillips,10 Juan Ernesto Guevara,11,12 Daniel Sabatier,13 Jean-François  
7 Molino,13 Dairon Cárdenas López,14 Abel Monteagudo Mendoza,15 Nigel C.A.  
8 Pitman,16,17 Alvaro Javier Duque Montoya,18 Percy Núñez Vargas,19 Charles Eugene  
9 Zartman,3 Rodolfo Vasquez,15 Ana Andrade,21 José Luís Camargo,21 Ted R.  
10 Feldpausch,22,10 Susan G.W. Laurance,23 William F. Laurance,23 Timothy J. Killeen,24  
11 Henrique Eduardo Mendonça Nascimento,3 Juan Carlos Montero,25,20 Bonifacio  
12 Mostacedo,26 Iêda Leão Amaral,3 Ima Célia Guimarães Vieira,8 Roel Brienem,10 Hernán  
13 Castellanos,27 John Terborgh,17 Marcelo de Jesus Veiga Carim,28 José Renan da Silva  
14 Guimarães,28 Luiz de Souza Coelho,3 Francisca Dionízia de Almeida Matos,3 Florian  
15 Wittmann,29 Hugo F. Mogollón,30 Gabriel Damasco,11,9 Nállarett Dávila,31 Roosevelt  
16 García-Villacorta,32,33 Euridice N. Honorio Coronado,34,10 Alberto Vincentini,1 Thaise  
17 Emilio,35,1 Diogenes de Andrade Lima Filho,3 Juliana Schietti,1 Priscila Souza,1 Natalia  
18 Targhetta,36 James A. Comiskey,37 Beatriz S. Marimon,38 Ben-Hur Marimon Jr.,38  
19 David Neill,39 Alfonso Alonso,40 Luzmila Arroyo,41 Fernanda Antunes Carvalho,1  
20 Fernanda Coelho Souza,1 Francisco Dallmeier,40 Marcelo Petrati Pansonato,1 Joost F.  
21 Duivenvoorden,42 Paul Fine,11 Pablo Roberto Stevenson Diaz,43 Alejandro Araujo-  
22 Murakami,41 Gerardo A. Aymard C.,44 Chris Baraloto,45,46 Dário Dantas do Amaral,8  
23 Julien Engel,47 Terry W. Henkel,48 Paul Maas,49 Pascal Petronelli,45 Juan David  
24 Cardenas Revilla,20 Juliana Stropp,50,51 Doug Daly,52 Rogerio Gribel,53 Marcos Ríos  
25 Paredes,54 Marcos Silveira,55 Raquel Thomas-Caesar,56 Tim R. Baker,10 Jerome  
26 Chave,57 Naara Ferreira da Silva,36 Leandro Valle Ferreira,8 Carlos A. Peres,58 Miles R.  
27 Silman,59 Carlos Cerón,60 Fernando Cornejo Valverde,61 Anthony Di Fiore,62 Eliana M.  
28 Jimenez,63 Maria Cristina Peñuela Mora,64 Marisol Toledo,25 Edelcilio Marques  
29 Barbosa,3 Luiz Carlos de Matos Bonates,3 Nicolás Castaño Arboleda,14 Emanuelle de  
30 Sousa Farias,65 Alfredo Fuentes,66,67 Jean-Louis Guillaumet,68 Peter Møller  
31 Jørgensen,67 Yadvinder Malhi,69 Ires Paula de Andrade Miranda,20 Juan Fernando  
32 Phillips,70 Adriana Prieto,71 Agustín Rudas,71 Ademir R. Ruschell,72 Natalino Silva,73  
33 Patricio von Hildebrand,74 Vincent A. Vos,75,76 Eglée L. Zent,77 Stanford Zent,77 Bruno  
34 Barçante Ladvoat Cintra,36 Marcelo Trindade Nascimento,78 Alexandre A. Oliveira,79  
35 Hirma Ramirez-Angulo,80 José Ferreira Ramos,3 Jochen Schöngart,29 Rodrigo Sierra,81  
36 Milton Tirado,81 Geertje van der Heijden,82,83 Emilio Vilanova Torre,80,84 Corine  
37 Vriesendorp,16 Ophelia Wang,85 Kenneth R. Young,86 Claudia Baidier,87,79 Angela  
38 Cano,43 William Farfan-Rios,59 Cid Ferreira,20 Bruce Hoffman,88 Casimiro  
39 Mendoza,89,90 Italo Mesones,11 Armando Torres-Lezama,80 Maria Natalia Umaña  
40 Medina,91 Tinde R. van Andel,92 Daniel Villarreal,41 Roderick Zagt,93 Miguel N.  
41 Alexiades,94 Henrik Balslev,95 Karina Garcia-Cabrera,59 Therany Gonzales,96 Lionel  
42 Hernandez,97 Isau Huamantupa-Chuquimaco,19 Angelo Gilberto Manzatto,98 William  
43 Milliken,99 Walter Palacios Cuenca,100 Susamar Pansini,101 Daniela Pauletto,102 Freddy  
44 Ramirez Arevalo,103 Neidiane Farias Costa Reis,104 Adeilza Felipe Sampaio,101 Ligia  
45 Estela Urrego Giraldo,18 Elvis H. Valderrama Sandoval,105,103 Luis Valenzuela  
46 Gamarra,15 César I.A. Vela,106 Hans ter Steege,92,107,8

- 47  
48 1Programa de Pós-graduação em Ecologia, Instituto Nacional de Pesquisas da Amazônia -  
49 INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
50  
51 2Forest Ecology and Forest Management Group, University of Wageningen, Lumen,  
52 building no.100, Droevendaalsesteeg 3, Wageningen, 6708 PB, Netherlands  
53  
54 3Coordenação de pesquisas em Biodiversidade, Instituto Nacional de Pesquisas da  
55 Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
56  
57 4Coordenação de Tecnologia e Inovação, Instituto Nacional de Pesquisas da Amazônia -  
58 INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
59  
60 5Department of Soil Quality, Wageningen University, Droevendaalsesteeg 3, Wageningen,  
61 PO Box 47, 6700AA, The Netherlands  
62  
63 6Museu de Arqueologia e Etnologia da USP, Universidade de São Paulo, Av. Prof.  
64 Almeida Prado, 1466, São Paulo, SP, 05508-900, Brazil  
65  
66 7Laboratório de Arqueologia, Instituto de Desenvolvimento Sustentável Mamirauá, Estrada  
67 do Bexiga, 2584, Fonte Boa, Tefé, AM, 69553-225, Brazil
- 68 8Coordenação de Botânica, Museu Paraense Emílio Goeldi, Av. Magalhães Barata 376,  
69 C.P. 399, Belém, PA, 66040-170, Brazil  
70  
71 9EMBRAPA – Centro de Pesquisa Agroflorestal de Roraima, BR 174, km 8 – Distrito  
72 Industrial, Boa Vista, RR, 69301-970, Brazil  
73  
74 10School of Geography, University of Leeds, Woodhouse Lane, Leeds, LS2 9JT, UK  
75  
76 11Department of Integrative Biology, University of California, , Berkeley, CA, 94720-  
77 3140, USA  
78  
79 12Museo Ecuatoriano de Ciencias Naturales, Av. Río Coca E6-115 e Isla Floreana, Quito, ,  
80 Ecuador  
81  
82 13UMR AMAP, Institut de Recherche pour le Développement (IRD, UMR AMAP), TA A-  
83 51/PS2, Bd. de la Lironde, Montpellier Cedex 5, 34398, France  
84  
85 14Herbario Amazónico Colombiano, Instituto SINCHI, Calle 20 No 5-44, Bogotá, DF,  
86 Colombia  
87  
88 15Jardín Botánico de Missouri, , Oxapampa, Pasco, Peru  
89

90 16Science and Education, The Field Museum, 1400 S. Lake Shore Drive, Chicago, IL,  
91 60605-2496, USA  
92  
93 17Center for Tropical Conservation, Duke University, Nicholas School of the Environment,  
94 Durham, NC, 27708, USA  
95  
96 18Departamento de Ciencias Forestales, Universidad Nacional de Colombia, Calle 64 x Cra  
97 65, Medellín, Antioquia, 1027, Colombia  
98  
99 19Herbario Vargas, Universidad Nacional de San Antonio Abad del Cusco, Avenida de la  
100 Cultura, Nro 733, Cusco, Cuzco, Peru  
101  
102 20Coordenação de Biodiversidade, Instituto Nacional de Pesquisas da Amazônia - INPA,  
103 Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
104  
105 21Projeto Dinâmica Biológica de Fragmentos Florestais, Instituto Nacional de Pesquisas da  
106 Amazônia - INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
107  
108 22College of Life and Environmental Sciences, University of Exeter, , Exeter, EX4 4RJ,  
109 UK  
110  
111 23Centre for Tropical Environmental and Sustainability Science, College of Marine and  
112 Environmental Sciences, James Cook University, Cairns, Queensland, 4870, Australia  
113  
114 24Agteca-Amazonica, , Santa Cruz, , Bolivia  
115  
116 25Instituto Boliviano de Investigacion Forestal, Universidad Autónoma Gabriel René  
117 Moreno, Km 9 Carretera al Norte, El Vallecito, FCA-UAGRM, Santa Cruz, Santa Cruz,  
118 Bolivia  
119  
120 26Facultad de Ciencias Agrícolas, Universidad Autónoma Gabriel René Moreno, Santa  
121 Cruz, Santa Cruz, Bolivia  
122  
123 27Universidad Nacional Experimental de Guayana, Calle Chile, urbaniz Chilemex, Puerto  
124 Ordaz, Bolivar, Venezuela  
125  
126 28Instituto de Pesquisas Científicas e Tecnológicas do Amapá - IEPA, Av. Feliciano  
127 Coelho, 1509. Trem, Macapá, Amapá, 68901-025, Brazil  
128  
129 29Biogeochemistry, Max Planck Institute for Chemistry, Hahn-Meitner Weg 1, Mainz,  
130 55128, Germany  
131  
132 30Endangered Species Coalition, 8530 Geren Rd., Silver Spring, MD, 20901, USA  
133  
134 31Biologia Vegetal, Universidade Estadual de Campinas, Caixa Postal 6109, Campinas,  
135 SP, 13.083-970, Brazil  
136

137 32Institute of Molecular Plant Sciences, University of Edinburgh, Mayfield Rd, Edinburgh,  
138 EH3 5LR, UK  
139  
140 3320a Inverleith Row, Royal Botanic Garden of Edinburgh, , Edinburgh, EH3 5LR, UK  
141  
142 34Instituto de Investigaciones de la Amazonía Peruana, Av. José A. Quiñones km. 2.5,  
143 Iquitos, Loreto, Peru  
144  
145 35Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond,  
146 Surrey, TW9 3AB, UK  
147  
148 36Coordenação de Dinâmica Ambiental, Instituto Nacional de Pesquisas da Amazônia -  
149 INPA, Av. André Araújo, 2936, Petrópolis, Manaus, AM, 69060-001, Brazil  
150  
151 37Inventory and Monitoring Program, National Park Service, 120 Chatham Lane,  
152 Fredericksburg, Virginia, 22405, USA  
153  
154 38Departamento de Ciências Biológicas, Universidade do Estado de Mato Grosso, , Nova  
155 Xavantina, MT, Brazil  
156  
157 39Ecosistemas, Biodiversidad y Conservación de Especies, Universidad Estatal  
158 Amazónica, Km. 2 1/2 vía a Tena (Paso Lateral), Puyo, Pastaza, Ecuador  
159  
160 40Center for Conservation Education and Sustainability, Smithsonian Conservation  
161 Biology Institute, National Zoological Park, MRC 0705, Washington, DC, 20013-7012,  
162 USA  
163  
164 41Museo de Historia Natural Noel Kempff Mercado, Universidad Autónoma Gabriel Rene  
165 Moreno, Avenida Irala 565 Casilla Post al 2489, Santa Cruz, Santa Cruz, Bolivia  
166  
167 42Institute of Biodiversity and Ecosystem Dynamics, University of Amsterdam,  
168 Sciencepark 904, Amsterdam, Noord Holland, 1098 XH, The Netherlands  
169  
170 43Laboratorio de Ecología de Bosques Tropicales y Primatología, Universidad de los  
171 Andes, , Bogotá, DF, Colombia  
172  
173 44Programa de Ciencias del Agro y el Mar, Herbario Universitario (PORT), UNELLEZ-  
174 Guanare, , Guanare, Portuguesa, 3350, Venezuela  
175  
176 45UMR Ecologie des Forêts de Guyane, Institut National de la Recherche Agronomique  
177 (INRA), Campus agronomique, Kourou Cedex, 97379, French Guiana  
178  
179 46International Center for Tropical Botany (ICTB), Florida International University, 11200  
180 SW 8th Street, OE 167, Miami, FL, 33199, USA  
181  
182 47UMR Ecologie des Forêts de Guyane, CNRS, , Kourou Cedex, , French Guiana  
183

184 48Department of Biological Sciences, Humboldt State University, 1 Harpst Street, Arcata,  
185 CA, 95521, USA  
186  
187 49Taxonomy and Systematics, Naturalis Biodiversity Center, Darwin building, Darwinweg  
188 4, Leiden, 2300 AA, The Netherlands  
189  
190 50Land Resource and Management Unit, Joint Research Centre of the European  
191 Commission, Via Enrico Fermi 2749, TP 440, Ispra, VA, I-21027, Italy  
192  
193 51Institute of Biological and Health Sciences, Federal University of Alagoas, Av. Lourival  
194 Melo Mota, s/n, Tabuleiro do Martins, Maceio, AL, 57072-970, Brazil  
195  
196 52New York Botanical Garden, 2900 Southern Blvd, Bronx, New York, NY, 10458-5126,  
197 USA  
198  
199 53Diretoria de Pesquisas Científicas, Instituto de Pesquisas Jardim Botânico do Rio de  
200 Janeiro, , Rio de Janeiro, RJ, Brazil  
201  
202 54Servicios de Biodiversidad EIRL, , Iquitos, Loreto, Peru  
203  
204 55Museu Universitário, Universidade Federal do Acre, , Rio Branco, AC, 69915-559,  
205 Brazil  
206  
207 56Iwokrama International Programme for Rainforest Conservation, , Georgetown, , Guyana  
208  
209 57Laboratoire Evolution et Diversité Biologique, CNRS and Université Paul Sabatier,  
210 UMR 5174 EDB, Toulouse, 31000, France  
211  
212 58School of Environmental Sciences, University of East Anglia, , Norwich, NR4 7TJ, UK  
213  
214 59Biology Department and Center for Energy, Environment and Sustainability, Wake  
215 Forest University, 1834 Wake Forest Rd, Winston Salem, NC, 27106, USA  
216  
217 60Escuela de Biología Herbario Alfredo Paredes, Universidad Central, Ap. Postal  
218 17.01.2177, Quito, Pichincha, Ecuador  
219  
220 61Andes to Amazon Biodiversity Program, , Madre de Dios, Madre de Dios, Peru  
221  
222 62Department of Anthropology, University of Texas at Austin, SAC 5.150, 2201 Speedway  
223 Stop C3200, Austin, TX, 78712, USA  
224  
225 63Grupo de Ecología de Ecosistemas Terrestres Tropicales, Universidad Nacional de  
226 Colombia Sede Amazonía, , Leticia, Amazonas, Colombia  
227  
228 64Universidad Regional Amazónica IKIAM, Km 7 via Muyuna, Tena, Napo, Ecuador  
229

230 65Laboratório de Ecologia de Doenças Transmissíveis da Amazônia (EDTA), Instituto  
231 Leônidas e Maria Deane, Fiocruz, Rua Terezina, 476, Adrianópolis, Manaus, AM, 69057-  
232 070, Brazil  
233  
234 66Herbario Nacional de Bolivia, Universitario UMSA, Casilla 10077 Correo Central, La  
235 Paz, La Paz, Bolivia  
236  
237 67Missouri Botanical Garden, P.O. Box 299, St. Louis, MO, 63166-0299, USA  
238  
239 68Departement EV, Muséum national d'histoire naturelle de Paris, 16 rue Buffon, Paris,  
240 75005, France  
241  
242 69Environmental Change Institute, Oxford University Centre for the Environment, Dyson  
243 Perrins Building, South Parks Road, Oxford, England, OX1 3QY, UK  
244  
245 70Fundación Puerto Rastrojo, Cra 10 No. 24-76 Oficina 1201, Bogotá, DF, Colombia  
246  
247 71Instituto de Ciencias Naturales, UNAL, Universidad Nacional de Colombia, Apartado  
248 7945, Bogotá, DF, Colombia  
249  
250 72Embrapa Amazonia Oriental, Trav. Dr. Enéas Pinheiro s/nº, Belém, PA, Brazil  
251  
252 73Universidade Federal Rural da Amazônia, , Belém, PA, Brazil  
253  
254 74Fundación Estación de Biología, Cra 10 No. 24-76 Oficina 1201, Bogotá, DF, Colombia  
255  
256 75Universidad Autónoma del Beni, , Riberalta, Beni, Bolivia  
257  
258 76Regional Norte Amazónico, Centro de Investigación y Promoción del Campesinado, C/  
259 Nicanor Gonzalo Salvatierra N° 362, Riberalta, Beni, Bolivia  
260  
261 77Laboratory of Human Ecology, Instituto Venezolano de Investigaciones Científicas -  
262 IVIC, Ado 20632, Caracas, Caracas, 1020A, Venezuela  
263  
264 78Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Av.  
265 Alberto Lamego 2000, Campos dos Goyatacazes, RJ, 28013-620, Brazil  
266  
267 79Instituto de Biociências - Dept. Ecologia, Universidade de Sao Paulo - USP, Rua do  
268 Matão, Trav. 14, no. 321, Cidade Universitária, São Paulo, SP, 05508-090, Brazil  
269  
270 80Instituto de Investigaciones para el Desarrollo Forestal (INDEFOR), Universidad de los  
271 Andes, Conjunto Forestal, C.P. 5101, Mérida, Mérida, Venezuela  
272  
273 81GeoIS, El Día 369 y El Telégrafo, 3° Piso, Quito, Pichincha, Ecuador  
274  
275 82Department of Biological Sciences, University of Wisconsin-Milwaukee, , Milwaukee,  
276 WI, 53202, USA

277  
278 83Smithsonian Tropical Research Institute, Apartado Postal 0843-03092, Panama City, ,  
279 Panama  
280  
281 84School of Environmental and Forest Sciences, University of Washington, , Seattle, WA,  
282 98195-2100, USA  
283  
284 85Environmental Science and Policy, Northern Arizona University, , Flagstaff, AZ, 86011,  
285 USA  
286  
287 86Geography and the Environment, University of Texas at Austin, 305 E. 23rd Street, CLA  
288 building, Austin, TX, 78712, USA  
289  
290 87Agricultural Services, Ministry of Agro-Industry and Food Security, The Mauritius  
291 Herbarium, , Reduit, , Mauritius  
292  
293 88Amazon Conservation Team, Doekhieweg Oost #24, Paramaribo, , Suriname  
294  
295 89FOMABO, Manejo Forestal en las Tierras Tropicales de Bolivia, , Sacta, Cochabamba,  
296 Bolivia  
297  
298 90Escuela de Ciencias Forestales (ESFOR), Universidad Mayor de San Simon (UMSS), ,  
299 Sacta, Cochabamba, Bolivia  
300  
301 91Department of Biology, University of Maryland, , College Park, MD, 20742, USA  
302  
303 92Biodiversity Dynamics, Naturalis Biodiversity Center, Darwin building, Darwinweg 4,  
304 Leiden, 2300 AA, The Netherlands  
305  
306 93Tropenbos International, Lawickse Allee 11 PO Box 232, Wageningen, 6700 AE, The  
307 Netherlands  
308  
309 94School of Anthropology and Conservation, University of Kent, Marlowe Building,  
310 Canterbury, Kent, CT2 7NR, UK  
311  
312 95Department of Bioscience, Aarhus University, Building 1540 Ny Munkegade, Aarhus C,  
313 Aarhus, DK-8000, Denmark  
314  
315 96ACEER Foundation, Jirón Cusco N° 370, Puerto Maldonado, Madre de Dios, Peru  
316  
317 97Centro de Investigaciones Ecológicas de Guayana, Universidad Nacional Experimental  
318 de Guayana, Calle Chile urbaniz Chilemex, Puerto Ordaz, Bolivar, Venezuela  
319  
320 98Departamento de Biologia, Universidade Federal de Rondônia, Rodovia BR 364 s/n Km  
321 9,5 - Sentido Acre, Unir, Porto Velho, Rondônia, 76.824-027, Brazil  
322



323 99Comparative Plant and Fungal Biology, Royal Botanic Gardens, Kew, Richmond,  
324 Surrey, TW9 3AE, UK  
325  
326 100Herbario Nacional del Ecuador, Universidad Técnica del Norte, , Quito, Pichincha,  
327 Ecuador  
328  
329 101Programa de Pós-Graduação em Desenvolvimento Regional e Meio Ambiente PGDRA,  
330 Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 - Sentido Acre, Unir,  
331 Porto Velho, Rondônia, 76.824-029, Brazil  
332  
333 102Instituto de Biodiversidade e Floresta, Universidade Federal do Oeste do Pará, Rua  
334 Vera Paz, Campus Tapajós, Santarém, PA, 68015-110, Brazil  
335  
336 103Facultad de Biología, Universidad Nacional de la Amazonia Peruana, Pevas 5ta cdra,  
337 Iquitos, , Peru  
338  
339 104Programa de Pós-Graduação em Desenvolvimento Regional e Meio Ambiente PGDRA,  
340 Universidade Federal de Rondônia, Rodovia BR 364 s/n Km 9,5 - Sentido Acre, Unir,  
341 Porto Velho, Rondônia, 76.824-028, Brazil  
342  
343 105Department of Biology, University of Missouri, , St. Louis, MO, 63121, USA  
344  
345 106Facultad de Ciencias Forestales y Medio Ambiente, Universidad Nacional de San  
346 Antonio Abad del Cusco, San Martín 451, Puerto Maldonado, Madre de Dios, Peru  
347  
348 107Ecology and Biodiversity Group, Utrecht University, Padualaan 8, Utrecht, ,  
349 Netherlands  
350  
  
351  
352

353 **Mounting evidence from different disciplines shows that pre-Columbian societies**  
354 **altered their living environment and domesticated plant populations in Amazonia<sup>1,2</sup>.**  
355 **Seasonal forests and river margins are thought to have been modified more**  
356 **intensively than wetter and less accessible forests<sup>3</sup>, but the extent to which pre-**  
357 **Columbian peoples transformed Amazonian forests is still debated<sup>1-5</sup>. We provide the**  
358 **first broad-scale analysis of the distribution of 85 domesticated woody species**  
359 **in 1091 lowland forest plots across Amazonia, and show that one-fourth are**  
360 **hyperdominant species<sup>6</sup>. We found that soil fertility, rainfall seasonality and shallow**  
361 **water tables strongly influence the relative abundance and richness of domesticated**  
362 **species in Amazonian forests. In south-western and eastern forests, the proximity to**  
363 **archaeological sites is also positively correlated to the relative abundance and richness**  
364 **of these domesticated species. Moreover, the current distribution of many**  
365 **domesticated species is not associated with their known or hypothesized origin of**  
366 **domestication<sup>7</sup> suggesting human-assisted dispersal in lowland forests. Our analyses**  
367 **show that Amazonian forests, especially in south-western and eastern regions, result**  
368 **from an interplay between environmental conditions and long-term plant**  
369 **domestication by Amazonian peoples.**

370

371 Tropical rainforests may seem untouched at first glance, yet an increasing amount of  
372 evidence posits that the floristic composition and structure of Amazonian forests have been  
373 influenced by past human activities and domestication processes<sup>2</sup>. Humans transformed the  
374 composition of forests in many ways, including plant cultivation (preceded by cutting and  
375 burning), seed dispersal and propagation, and in situ tending of useful resources, such as  
376 domesticated plants<sup>8,9</sup>. Domesticated plants vary from incipiently to fully domesticated  
377 populations caused by selection of traits useful for humans (e.g., large and sweet fruits),  
378 followed by propagation of these specific phenotypes<sup>8</sup> (see Methods and Supplementary  
379 Information for definition of domesticated species). Incipient domestication starts when  
380 humans propagate plant populations with particular phenotypes outside their natural  
381 environment and tend, cultivate, and disperse them.

382 Humans have been domesticating plants since at least 10,000 BP<sup>10</sup>. In Amazonia, plant  
383 domestication started earlier than 8,000 BP, mainly in the periphery of the basin (Fig. 1 and  
384 Supplementary Fig. 1), where wild populations of domesticated species have been

385 identified by genetic and morphological analysis<sup>7</sup>. South-western Amazonia is one region  
386 where important crop domestication occurred<sup>7,10</sup>, and from which crops were dispersed to  
387 other parts of the basin<sup>2</sup>. Five centuries after the demographic collapse of Amerindian  
388 populations<sup>11</sup>, domesticated plants still persist in Amazonian forests<sup>8</sup>, generally in areas  
389 where human populations were once abundant<sup>2</sup>. Well-known examples are high  
390 concentrations of domesticated trees and palms strongly associated with fertile  
391 anthropogenic soils<sup>12</sup> and pre-Columbian mounds<sup>13</sup>.

392 The distribution and abundance of plant species, however, is fundamentally influenced  
393 by ecological and evolutionary processes. The synergistic effects of evolutionary and  
394 ecological processes, such as environmental filtering (e.g. geology, soil, climate), have  
395 resulted in distinct plant assemblages across Amazonian regions<sup>6,14,15</sup>. Evolutionary  
396 processes operate at all spatial scales and they are essential in determining the regional  
397 species pool. At smaller spatial scales environmental filtering and biotic interactions (e.g.,  
398 animal seed dispersal and predation, competition) drive differences among species  
399 assemblages across ecological gradients. For example, effective seed dispersal decreases in  
400 heavily hunted forests because of the depletion of large vertebrates<sup>16</sup>. Composition and  
401 dominance patterns of plant assemblages in Amazonian forests differ from one  
402 phytogeographical region to another<sup>6,15</sup>, vary along spatial and temporal gradients of  
403 rainfall<sup>15,17,18</sup>, terrain water saturation<sup>19</sup> and soil fertility<sup>15</sup>, and may be the result of dispersal  
404 limitation<sup>16</sup>.

405 Using the Amazon Tree Diversity Network (ATDN) database containing 1170 forest  
406 plots, ter Steege and co-authors<sup>6</sup> estimated that about 16,000 woody species occur in  
407 Amazonia and showed that only 227 species dominate Amazonian forests. In the ATDN  
408 plots, we identified 85 woody species with some evidence of domestication by pre-

409 Columbian peoples (hereafter domesticated species), 20 of which are hyperdominant  
410 species (24% of 85 domesticated species listed in Supplementary Table 1). We then tested  
411 the hypothesis that the hyperdominance of domesticated species in Amazonian forests  
412 could be partly explained by the intensity of human occupation and transformation of  
413 landscapes in the past<sup>6</sup>.

414 We analysed the proportion of domesticated species in 1,091 ATDN forest plots located  
415 in non-flooded lowland forests across Amazonia to test if forests closer to archaeological  
416 sites and rivers have higher abundance and richness of domesticated species. Forest  
417 composition was evaluated in association with numerous types of archaeological sites  
418 encompassing different kinds of past human activities in the landscape<sup>2</sup> (see Methods and  
419 Supplementary Fig. 2). We also considered margins of navigable rivers as proxies for pre-  
420 Columbian settlements, because they are good predictors of anthropogenic soils in  
421 Amazonia<sup>20</sup>. To evaluate the effect of historical human factors on the abundance and  
422 richness of domesticated species in forests, our analyses accounted for the effects of  
423 different geological regions of Amazonia and for four local environmental conditions: soil  
424 cation exchange capacity (CEC), soil pH, rainfall seasonality, and terrain height to the  
425 nearest drainage (HAND, a proxy for water table depth).

426 We found a significantly higher relative abundance of domesticated species in south-  
427 western Amazonian forests, followed by southern, north-western and eastern forests, and  
428 the lowest values in the Guiana Shield (Fig.2, Supplementary Fig. 3). The relative richness  
429 of domesticated species is also higher in south-western forests, followed by southern and  
430 eastern forests, and lower in the Guiana Shield. The relative abundance of domesticated  
431 species in forest plots ranges from 0 to 61%, relative richness from 0 to 19%, and total  
432 number of domesticated species from 0 to 19 species (Fig. 2, Supplementary Figs 3 and 4).

433 Forests with a diverse assemblage of domesticated species tend to have a high abundance of  
434 these species (Supplementary Fig. 5). The abundance of all domesticated species is,  
435 however, mostly due to 20 hyperdominant species. Domesticated hyperdominant species  
436 are more widespread across Amazonian forests than non-domesticated hyperdominants (see  
437 Supplementary Information). Although domesticated species are widely distributed, their  
438 abundances across Amazonia are heterogeneous, probably because of the interaction  
439 between environmental heterogeneity and distinct human histories in different Amazonian  
440 regions.

441 We found that all domesticated species were more abundant in forests closer to  
442 archaeological sites at the Amazonia-wide level, and within south-western and eastern  
443 regions (Fig. 3a). Domesticated species that are hyperdominant also decreases with distance  
444 from archaeological sites (Supplementary Fig. 6). In contrast, hyperdominant non-  
445 domesticated species of all groups tested were not significantly affected by distance to  
446 archaeological sites at the Amazonia-wide level (Supplementary Fig. 6). Additionally, non-  
447 domesticated species dispersed primarily by primates were more abundant farther from  
448 archaeological sites or rivers within forests in southern and eastern Amazonia and the  
449 Guiana Shield (Supplementary Fig. 6), either resulting from heavy hunting around  
450 villages<sup>16</sup> or because non-domesticated species tend not to be favored by humans in forests  
451 closer to archaeological sites or rivers.

452 In four of the six Amazonian regions, the relative richness of domesticated species  
453 decreases with distance from archaeological sites or rivers (Fig. 3b), indicating that forests  
454 closer to archaeological sites or rivers concentrate a richer assemblage of domesticated  
455 species. Although the relative richness of domesticated species in plots decreased with  
456 distance from navigable rivers in Central Amazonia and the Guiana Shield, this was not the

457 case for the distance from archaeological sites. One possible explanation is the insufficient  
458 information about the distribution of archaeological sites along secondary rivers, so moving  
459 away from a known archaeological site may represent getting closer to another site that has  
460 not been mapped yet.

461 Environmental conditions also influence the abundance and richness of domesticated  
462 species (Fig. 3), and probably constrain where and to what degree humans have shaped  
463 forests through time. We found that environmental conditions drive most of the explained  
464 variation of the relative abundance and richness of domesticated species in Amazonian  
465 forests (Fig. 4). The relative abundance and richness of domesticated species is higher in  
466 the southern periphery of the basin (Fig. 2) and increase with rainfall seasonality at the  
467 Amazonia-wide level (Fig. 3). Seasonal and open forests in transitional zones were  
468 important ecosystems for the early humans who started the domestication of some plants<sup>21</sup>,  
469 as the longest pre-Columbian occupation sequences have been found either in the periphery  
470 of the basin or near the estuary<sup>22</sup>. In these regions, the combination of rainfall seasonality,  
471 forest-savanna transition<sup>23</sup>, high cultural diversity<sup>24</sup> and a long history of forest  
472 transformation encompassing landscape engineering by pre-Columbian societies probably  
473 resulted in forests containing diverse and abundant assemblages of domesticated species.

474 Soil and terrain conditions also determine forest composition<sup>25</sup> and influence the  
475 abundance and richness of domesticated species in forest plots (Fig. 3). We found higher  
476 relative abundance and richness of domesticated species on soils with greater cation  
477 exchange capacity. Plots with shallow water tables also concentrate domesticated species.  
478 This pattern reflects the existence of dense stands of some species (e.g., *Mauritia flexuosa*,  
479 *Euterpe oleracea*, *E. precatoria* and *Oenocarpus bataua*) on poorly-drained soils of  
480 Amazonia<sup>26</sup>.

481 Although potential confounding effects of some correlations between human and  
482 environmental factors may exist (e.g., human settlements located in seasonal forests on  
483 fertile soils of south-western Amazonia) we found that the human influence is uniquely  
484 responsible for about half of the explained variation of the relative abundance of  
485 domesticated species in the south-western and eastern regions (Fig. 4). The correlation  
486 between domesticated species and archaeological sites raises a chicken-and-egg question:  
487 did humans enrich forests with domesticated species in south-western and eastern  
488 Amazonia or did humans choose to live close to forest already rich in these species? The  
489 approach used here cannot demonstrate causality, but the first alternative is most probable.  
490 Firstly, archaeological sites were found in all geological regions (Supplementary Fig. 2),  
491 which shows that humans were distributed across the whole Amazon Basin and created  
492 new ecosystems for domesticated plants in different environments and regions<sup>2</sup>. Secondly,  
493 assemblages of up to 19 domesticated species with different geographical distributions and  
494 distinct ecological preferences tend to be more abundant in forests close to archaeological  
495 sites (Fig. 3 and Supplementary Fig. 5). For instance, we found a set of domesticated  
496 species at one forest plot (*Attalea maripa*, *Astrocaryum murumuru*, *Bertholletia excelsa*,  
497 *Garcinia macrophylla*, *Hevea brasiliensis*, *Oenocarpus bacaba* and *Theobroma* spp.) that  
498 would be unlikely to occur by chance at the same location. Thirdly, species domesticated in  
499 one particular environmental setting have wide geographical distributions and tend to be  
500 more abundant in other locations, which are not associated with their hypothetical origin of  
501 domestication<sup>7</sup> (Fig. 1 and Supplementary Fig. 1). For instance, the cocoa tree (*Theobroma*  
502 *cacao*) was first domesticated in wet forests on nutrient-rich soils of north-western  
503 Amazonia, and is currently more abundant in south-western and southern forests, or the  
504 valuable açai palm (*Euterpe oleracea*) domesticated in the floodplain forests of the Amazon

505 Estuary<sup>8</sup>, where large açai groves occur, is currently abundant in terra-firme plots of  
506 southern Amazonia (for more details, see Supplementary Information).

507 While it is possible that the origin of domestication of some species is not well  
508 identified, this is unlikely for species for which morphological and genetic studies have  
509 been done (details in Supplementary Information). Our results suggest that human groups  
510 started selecting locally a suite of useful species<sup>7</sup> and species that responded well to  
511 selection and propagation were widely cultivated and dispersed within and outside their  
512 natural range of distribution<sup>8</sup>. More detailed studies are needed to fully disentangle the  
513 cause-and-effect relationships between historical human factors, environmental drivers and  
514 the distribution of Amazonian trees. Genetic analyses of populations of domesticated  
515 species in forest plots should be combined with paleoecological and archaeobotanical data  
516 to reconstruct changes in their genetic diversity and abundance across spatial and temporal  
517 gradients. We also need historical data to comprehend the interplay between human and  
518 environmental factors at different moments in time. The influence of modern societies in  
519 the last 300 years on the distribution of some domesticated species may be stronger than the  
520 effect of earlier societies. For instance, in the late 17th century the Portuguese and Spanish  
521 crown stimulated plantations of cocoa trees in Amazonia<sup>28</sup>, which - associated with pre-  
522 Columbian cultivation - probably increased the abundance of cocoa trees in south-western  
523 Amazonian forests even more.

524 Our results suggest that past human interventions likely have had an important and  
525 lasting role in the distribution of domesticated species found in modern forests, including  
526 hyperdominant domesticated species, as has been shown for Brazil nut (*Bertholletia*  
527 *excelsa*)<sup>29</sup>. Dominance of domesticated species may help to predict the occurrence of  
528 archaeological sites near forest plots. Guiana Shield plots, for example, with an average of



529 30 % of individuals of domesticated species but located more than 120 km away from a  
530 known archaeological site can be used for testing this hypothesis. More surveys of  
531 archaeological sites are needed, especially in north-western and southern Amazonian  
532 forests, and along tributaries in interfluvial areas, to fully understand the effect of past  
533 human intervention on the vegetation. More research on forests shaped by humans will also  
534 strengthen efforts to conserve the genetic diversity of domesticated and wild plant  
535 populations, which are critical to ensure food security for modern Amazonian peoples<sup>30</sup>.

## 536 **Methods**

### 537 Data collection: floristic data

538 We used 1091 forest inventory plots of the Amazon Tree Diversity Network (ATDN)  
539 database distributed across Amazonia (Supplementary Fig. 2). Only lowland (terra firme  
540 and white-sand podzol) plots were included in the analysis; wetland plots, as defined in ref  
541 by ter Steege et al.<sup>6</sup>, were excluded. Plots cover a wide range of soils and topographies  
542 (Supplementary Table 2). Most plots (N = 827) measure 1 ha; others vary from 0.1 to 9 ha.  
543 In each plot, ATDN scientists inventoried all woody species with  $\geq 10$  cm diameter at  
544 breast height; almost all individuals were identified to the species level (95 % of plots have  
545 less than 5 % of individuals without botanical identification). Plots with more than 25 % of  
546 unidentified trees to species were excluded from the analysis of the relative richness of  
547 domesticated species. Although identification problems exist in Amazonian tree  
548 inventories, domesticated species are widely used and cultivated, and are therefore better-  
549 known to botanists and local parataxonomists.

### 550 List of domesticated species in ATDN plots

551 We created a list of woody species with some evidence of selection and propagation by  
552 humans in Amazonia that we call domesticated species (for more details about

553 domestication, see Supplementary Information). First, we considered the list of  
554 domesticated species at European contact compiled by Clement<sup>8</sup>, excluding herbs and  
555 species identified to the genus level (e.g., *Hevea* spp.). To this, we added two species with  
556 evidence of past human selection that have been studied by Clement's group (*Euterpe*  
557 *precatoria* and *Caryocar brasiliense*) and one species considered to be the wild progenitor  
558 of a species with domesticated populations (*Bixa urucurana*)<sup>31</sup>.

559 We then conducted a bibliographical search for recent articles on domesticated plants  
560 using "domestication in Amazon\*" and "domestication in Brazil\*" (and all other  
561 Amazonian countries) as keywords in Web of Science and "domestication in Amazon\*" in  
562 Google Scholar. Three palm species (*Attalea phalerata*, *Phytelephas macrocarpa* and  
563 *Astrocaryum chambira*) were incorporated in the list based on two recent papers<sup>32,33</sup>.

564 We also used Mansfeld's World Database of Agricultural and Horticultural Crops<sup>34</sup>  
565 (<http://mansfeld.ipk-gatersleben.de/apex/f?p=185:3>) to add new species to the list. First,  
566 from this database we obtained a list of cultivated species in all Amazonian countries.  
567 Then, information about wild geographical distribution, cultivation, uses and domestication  
568 was obtained for all cultivated species that occur in any lowland forest plot to classify the  
569 degree of domestication (DD) of each species. Cultivation is defined here as the process of  
570 growing plants and plant domestication involves not only cultivation, but also selection and  
571 propagation of specific phenotypes by humans. The degree of domestication of cultivated  
572 species was based on the following indicators adapted from Clement<sup>8</sup>, Dempewolf et al.<sup>35</sup>  
573 and Hammer & Khoshbakht<sup>36</sup>:  
574 (A) Any degree of phenotypic differentiation between the domesticated taxon and its wild  
575 progenitor (evidence of phenotypic variation; DD = 2).

576 (B) The extent of cultivation in terms of geographical area (if the geographical area of  
577 cultivation is outside its natural range of distribution within the Americas - North, Central  
578 and South America; DD = 1).

579 (C) Evidence of cultivation since 1492 AD (DD = 1) and before 1492 AD (DD = 2), both  
580 suggesting a long history of mass selection.

581 All species with a summed degree of domestication  $\geq 2$  from Mansfeld's World  
582 Database (10 species) were included in the new list, resulting in a list with 85 domesticated  
583 species. Finally, we validated all names with the Taxonomic Name Resolution Service  
584 using the Tropicos® database (accessed in May, 2015). We cross-checked all scientific  
585 names of domesticated species with the list of all species present in ATDN plots.

#### 586 Data collection: historical human factors

587 To quantify the gradient of historical human influence, we measured the distance from each  
588 forest plot to the nearest archaeological site and to the nearest river margin (Supplementary  
589 Fig. 2). Distance from rivers was chosen as a proxy of pre-Columbian settlements because  
590 this is a good predictor of the probability of finding sedentary pre-Columbian occupation  
591 sites in Amazonia<sup>20</sup>, which probably reflects peoples' preferences for living along rivers to  
592 have access to resources and easy transportation. Distance from the river is not strongly  
593 correlated with any of the environmental variables we tested (Supplementary Fig. 7), which  
594 allows using all variables in the analysis. The river network was obtained from the  
595 HydroSHEDS dataset (available at <http://hydro.sheds.cr.usgs.gov>)<sup>37</sup>. 'Upcell' values are  
596 features of the HydroSHEDS dataset that represent the maximum flow accumulation at any  
597 location in the river network. We used rivers with upcell values greater than 15000, the  
598 same values used to define perennial and navigable rivers in a previous study<sup>20</sup>. For larger  
599 rivers (more than 1 km wide) we used river polygons obtained from ANA/BRASIL<sup>38</sup>. The

600 distribution of archaeological sites was obtained from a recent database of 3318  
601 archaeological sites in lowland South America that includes pre-Columbian habitation sites  
602 (with and without anthropogenic soils), earthworks (mounds, causeways, raised fields,  
603 terraces) and rock art (paintings and petroglyphs)<sup>2</sup>. All archaeological sites are places  
604 where material remains of past human activities are still visible in the landscape.

#### 605 Data collection: regional and local environmental data

606 To account for the effect of regional environmental conditions we used the geological  
607 regions delimited according to ter Steege et al.<sup>6</sup>, who showed that six different geological  
608 regions are dominated by different suites of tree species. To account for the effect of local  
609 environmental conditions, soil fertility (Cation Exchange Capacity), soil pH, rainfall  
610 seasonality and the Height Above the Nearest Drainage (HAND) were included in the  
611 analyses. Cation Exchange Capacity (CEC) and soil pH were obtained from SoilGrids 1 km  
612 for all plots using the mean values from 5 to 15 cm of soil depth<sup>39</sup>; rainfall seasonality was  
613 calculated as the maximum cumulative number of months with < 100 mm of rainfall using  
614 the monthly data from 1998 to 2004 of the Tropical Rainfall Measuring Mission (TRMM)  
615 satellite product 3B43 V6 at a 0.25° resolution (about 28 km at the equator)<sup>40</sup>; HAND was  
616 obtained from the Ambdata database<sup>41</sup>. All variables are presented in the Supplementary  
617 Table 2.

#### 618 Data collection: control groups of hyperdominant non-domesticated species

619 To understand whether non-human primates may promote dominance of certain tree  
620 species in forests closer to archaeological sites and rivers, we analysed the effect of  
621 distance from archaeological sites and rivers on the proportion of non-domesticated species  
622 that are dispersed by primates and probably by other vertebrates. Although all vertebrates

623 disperse forest seeds, large non-human primates have similar fruit preferences as humans  
624 and their actions in the forest can be compared with human behaviour<sup>3</sup>. We identified 20  
625 non-domesticated species with estimated population sizes comparable to those of the 20  
626 hyperdominant domesticated species, and that are primarily dispersed by non-human  
627 primates. We also selected two control groups of non-domesticated species: the first group  
628 consists of 20 hyperdominant species based on specific criteria and the second of 20  
629 hyperdominant species selected at random. The criteria used to select the first control group  
630 are: 1) species with estimated population sizes comparable to those of the 20  
631 hyperdominant domesticated species; 2) species that belong to the same botanical families  
632 as the 20 hyperdominant domesticated species; 3) species that are not mainly dispersed by  
633 primates. The lists of the control groups of hyperdominant species are presented in the  
634 Supplementary Table 3.

#### 635 Data analyses

636 All analyses were conducted in the R environment<sup>42</sup>. We used a spatial loess model to  
637 produce distribution maps for 12 domesticated species for which there is reasonably good  
638 information about their origins of domestication (Fig. 1 and Supplementary Fig. 1). Using  
639 the same approach as ter Steege et al.<sup>6</sup>, Amazonia was divided into 1° latitude and  
640 longitude grid cells, and their interactions were used as variables in the loess regression  
641 models. The model was used to estimate average density of individuals in each grid cell and  
642 compare it to the origin of domestication predicted by previous studies<sup>2,7</sup> (see  
643 Supplementary Information for the origin of domestication of each species). These studies  
644 have analyzed the geographic distribution of genetic and morphological diversity found in  
645 cultivated and wild populations of domesticated species. Higher genetic diversity often

646 indicates the location of the origin of domestication, in which the genetic variability found  
647 in cultivated populations is a subset of the genetic variability found in wild populations.

648 We used the list of domesticated species to quantify three domestication measures<sup>43</sup>: (1)  
649 the relative abundance of domesticated species in the plot (the number of individuals of  
650 domesticated species divided by the total number of individuals found in the plot); (2) the  
651 relative richness of domesticated species in the plot (the number of domesticated species  
652 divided by total number of species found in the plot); and (3) the relative abundance of  
653 hyperdominant domesticated species in the plot (the number of individuals of domesticated  
654 species that are hyperdominants divided by the total number of individuals found in the  
655 plot). The lists of hyperdominant non-domesticated species (control groups) were used to  
656 quantify (4) their relative abundance in the plot as described above.

657 We calculated the spatial variation of the relative abundance and the relative richness of  
658 domesticated species to understand how the proportion of domesticated species varies  
659 across Amazonia. We also used a loess regression model to interpolate the measures of  
660 domestication for the entire Amazon. The model was used to estimate the relative  
661 abundance and the relative richness of domesticated species for each grid cell (Fig. 2). We  
662 used an exponential model to fit the relationship between the relative abundance of 85  
663 domesticated species and the relative richness of 85 domesticated species in forest plots  
664 presented in the Supplementary Fig. 5.

665 To evaluate the relationship between the measures of domestication and the measures of  
666 abundance for control groups (response variables) and historical human and environmental  
667 conditions (explanatory variables) we used mixed-effects models and multiple regressions.  
668 In the Amazonia-wide model, geological regions were incorporated as random factors and  
669 explanatory variables as fixed factors in mixed-effects models. Within each geological

670 region, we analyzed the effects of environmental and human factors on the response  
671 variables using separate multiple regression models. Mixed-effects and multiple regression  
672 models were implemented with the lmer and lm functions, respectively, of the R lme4<sup>44</sup> and  
673 R sjstats packages<sup>45</sup>. Results of the hyperdominant domesticated and non-domesticated  
674 species are presented in the Supplementary Fig. 6. We included all explanatory variables in  
675 the models, because they are not strongly correlated (Supplementary Fig. 7). Simple  
676 scatterplots of the response variables against distance from archaeological sites and rivers  
677 are presented in Supplementary Fig. 8-11.

678 We used variation partitioning to determine how much of the variation in the response  
679 variables can be explained by historical human factors, by environmental conditions and by  
680 human and environmental factors together. The fractions of variation were based on the  
681 results of three multiple regression models (adjusted  $R^2$ ): a model with only human factors  
682 included as predictors; a model with only local environmental predictors; and a human +  
683 environment model, including both sets of predictors. Variation partitioning was  
684 implemented using the varpart function of the R vegan package<sup>47</sup>.

## 685 **References**

- 686 1. Tollefson, J. *Nature* **502**, 160-162 (2013).
- 687 2. Clement, C. R. et al. The domestication of Amazonia before European conquest. *Proc. R.*  
688 *Soc. Lond., B, Biol. Sci.* **282**, 20150813 (2015).
- 689 3. Bush, M. B. et al. Anthropogenic influence on Amazonian forests in pre-history: An  
690 ecological perspective. *J. Biogeogr.* **42**, 2277-2288 (2015).
- 691 4. Stahl, P. W. Interpreting interfluvial landscape transformations in the pre-Columbian  
692 Amazon. *Holocene* **20**, 1598-1603 (2015).

- 693 5. Piperno, D. R., McMichael, C. & Bush, M. B. Amazonia and the Anthropocene: What  
694 was the spatial extent and intensity of human landscape modification in the Amazon Basin  
695 at the end of prehistory? *Holocene* **25**, 1588-1597 (2015).
- 696 6. ter Steege, H. et al. Hyperdominance in the Amazonian tree flora. *Science* **342**, 1243092  
697 (2013).
- 698 7. Clement, C .R., de Cristo-Araújo, M., Coppens D'Eeckenbrugge, G., Alves Pereira, A. &  
699 Picanço-Rodrigues, D. Origin and domestication of native Amazonian crops. *Diversity* **2**,  
700 72-106 (2010).
- 701 8. Clement, C. R. 1492 and the loss of Amazonian crop genetic resources. I. The relation  
702 between domestication and human population decline. *Econ. Bot.* **53**, 188-202 (1999).
- 703 9. Boivin, N. L. et al. Ecological consequences of human niche construction: Examining  
704 long-term anthropogenic shaping of global species distributions. *Proc. Natl Acad. Sci. USA*  
705 **113**, 6388-6396 (2016).
- 706 10. Purugganan, M. D. & Fuller, D. Q. The nature of selection during plant domestication.  
707 *Nature* **457**, 843-848 (2009).
- 708 11. O'Fallon, B. D. & Fehren-Schmitz, L. Native Americans experienced a strong  
709 population bottleneck coincident with European contact. *Proc. Natl Acad. Sci. USA* **108**,  
710 20444-20448 (2011).
- 711 12. Junqueira, A. B., Shepard Jr, G. H. & Clement, C. R. Secondary forests on  
712 anthropogenic soils in Brazilian Amazon conserve agrobiodiversity. *Biodivers. Conserv.*  
713 **19**, 1933-1961 (2010).
- 714 13. Erickson, C. L. & Balée, W. in *Time and Complexity in Historical Ecology: Studies in*  
715 *the Neotropical Lowlands* (eds. Erickson, C. L. & Balée, W.) 187–233 (Columbia  
716 University Press, 2006).



- 717 14. Hoorn, C. et al. Amazonia through time: Andean uplift, climate change, landscape  
718 evolution, and biodiversity. *Science* **330**, 927-931 (2010).
- 719 15. ter Steege, H. et al. Continental-scale patterns of canopy tree composition and function  
720 across Amazonia. *Nature* **443**, 444-447 (2006).
- 721 16. Peres, C. A., Emilio, T., Schiatti, J., Desmoulière, S. J. & Levi, T. Dispersal limitation  
722 induces long-term biomass collapse in overhunted Amazonian forests. *Proc. Natl Acad. Sci.*  
723 *USA* **113**, 892-897 (2016).
- 724 17. Esquivel-Muelbert, A. et al. Seasonal drought limits tree species across the Neotropics.  
725 *Ecography* **39**, 001-012 (2016).
- 726 18. Bush, M. B., & McMichael, C. N. Holocene variability of an Amazonian  
727 hyperdominant. *J. Ecol.* (2016).
- 728 19. Schiatti, J. et al. Vertical distance from drainage drives floristic composition changes in  
729 an Amazonian rainforest. *Plant Ecol. Divers.* **7**, 241-253 (2014).
- 730 20. McMichael, C. H. et al. Predicting pre-Columbian anthropogenic soils in Amazonia.  
731 *Proc. R. Soc. Lond., B, Biol. Sci.* **281**, 20132475 (2014).
- 732 21. Piperno, D. R. The origins of plant cultivation and domestication in the New World  
733 Tropics: patterns, process, and new developments. *Curr. Anthropol.* **S4**, 453-470 (2011).
- 734 22. Roosevelt, A. C. The Amazon and the Anthropocene: 13,000 years of human influence  
735 in a tropical rainforest. *Anthropocene* **4**, 69-87 (2013).
- 736 23. Mayle, F. E. & Power, M. J. Impact of a drier Early–Mid-Holocene climate upon  
737 Amazonian forests. *Proc. R. Soc. Lond., B, Biol. Sci.* **363**, 1829-1838 (2008).
- 738 24. Crevels, M. & der Voort, H. in *From Linguistic Areas to Areal Linguistics* (ed.  
739 Muysken, P.) 151–179 (John Benjamins Press, 2008).

- 740 25. Quesada, C. A. et al. Basin-wide variations in Amazon forest structure and function are  
741 mediated by both soils and climate. *Biogeosciences* **9**, 2203–2246 (2012).
- 742 26. Emilio, T. et al. Soil physical conditions limit palm and tree basal area in Amazonian  
743 forests. *Plant Ecol. Divers.* **7**, 215-229 (2014).
- 744 27. Thomas, E. et al. Present spatial diversity patterns of *Theobroma cacao* L. in the  
745 neotropics reflect genetic differentiation in Pleistocene refugia followed by human-  
746 influenced dispersal. *PLoS One* **7**, e47676 (2012).
- 747 28. Alden, D. The significance of cacao production in the Amazon region during the late  
748 colonial period: An essay in comparative economic history. *Proc. Am. Philos. Soc.* **120**,  
749 103-135 (1976).
- 750 29. Thomas, E., Alcázar-Caicedo, C., McMichael, C. H., Corvera, R. & Loo, J. Uncovering  
751 spatial patterns in the natural and human history of Brazil nut (*Bertholletia excelsa*) across  
752 the Amazon Basin. *J. Biogeogr.* **42**, 1367-1382 (2015).
- 753 30. Esquinas-Alcázar, J. Protecting crop genetic diversity for food security: political,  
754 ethical and technical challenges. *Nat. Rev. Genet.* **6**, 946-953 (2005).
- 755 31. Moreira, P. A., Lins, J., Dequigiovanni, G., Veasey, E. A. & Clement, C. R. The  
756 domestication of Annatto (*Bixa orellana*) from *Bixa urucurana* in Amazonia. *Econ. Bot.*  
757 **69**, 127-135 (2015).
- 758 32. Sosnowska, J., Walanus, A. & Balslev, H. Asháninka palm management and  
759 domestication in the Peruvian Amazon. *Hum. Ecol.* **43**, 1-16 (2015).
- 760 33. García, N. et al. Management of the palm *Astrocaryum chambira* Burret (Arecaceae) in  
761 northwest Amazon. *Acta Bot. Bras.* **29**, 45-57 (2015).
- 762 34. Hanelt, P. *Mansfeld's Encyclopedia of Agricultural and Horticultural Crops: Except*  
763 *Ornamentals* (Springer Science & Business Media, 2001).

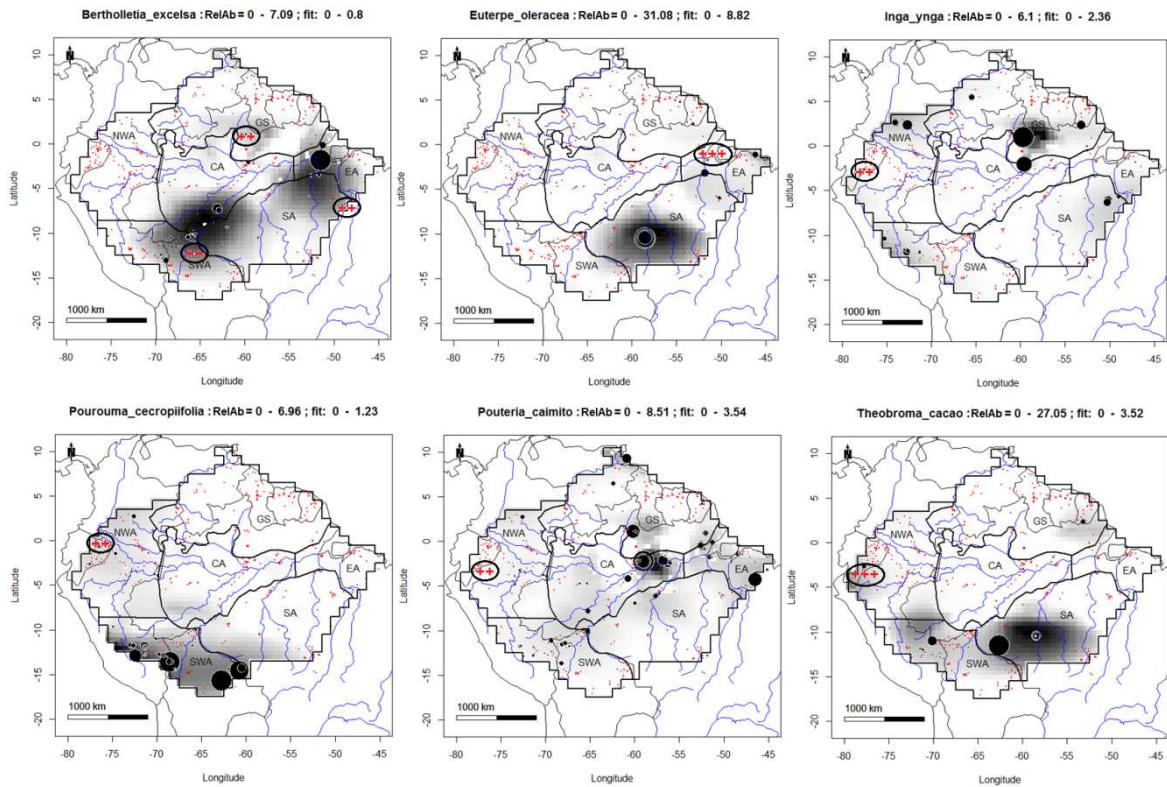
- 764 35. Dempewolf, H., Rieseberg, L. H. & Cronk, Q. C. Crop domestication in the  
765 Compositae: a family-wide trait assessment. *Genet. Resour. Crop Ev.* **55**, 1141-1157  
766 (2008).
- 767 36. Hammer, K. & Khoshbakht, K., A domestication assessment of the big five plant  
768 families. *Genet. Resour. Crop Ev.* **62**, 665–689 (2015).
- 769 37. Lehner, B., Verdin, K. & Jarvis, A. New global hydrography derived from spaceborne  
770 elevation data. *Eos, Trans. Amer. Geophys.* **89**, 93-94 (2008).
- 771 38. BRASIL. Manual de Construção da Base Hidrográfica Ortocodificada (Brasília: ANA,  
772 SGI, 2007).
- 773 39. Hengl, T. et al. SoilGrids1km-Global Soil Information based on automated mapping.  
774 *PLoS One* **9**, e105992 (2013).
- 775 40. Kummerow, C., Barnes, W., Kozu, T., Shiue, J. & Simpson, J. The Tropical Rainfall  
776 Measuring Mission (TRMM) sensor package. *J. Atmos. Ocean Tech.* **15**, 809–817 (1998).
- 777 41. Nobre, A. et al. Height above the nearest drainage - a hydrologically relevant new  
778 terrain model. *J. Hydrol.* **404**, 13-29 (2011).
- 779 42. R Development Core Team. R: A Language and Environment for Statistical  
780 Computing. (Vienna, Austria: the R Foundation for Statistical Computing, 2011).
- 781 43. Levis, C. et al. Historical human footprint on modern tree species composition in the  
782 Purus-Madeira interfluve, central Amazonia. *PLoS One* **7**, e48559 (2012).
- 783 44. Pinheiro J., Bates D., DebRoy S., Sarkar D. & R Core Team. nlme: Linear and  
784 Nonlinear Mixed Effects Models. R package version 3.1-128. [http://cran.r-](http://cran.r-project.org/package=nlme)  
785 [project.org/package=nlme](http://cran.r-project.org/package=nlme) (2016).
- 786 45. Lüdecke D. sjPlot: Data Visualization for Statistics in Social Science. R package  
787 version 2.0.1. <https://cran.r-project.org/package=sjPlot> (2016).

788 46. Legendre, P. Studying beta diversity: ecological variation partitioning by multiple  
789 regression and canonical analysis. *J. Plant Ecol.* **1**, 3-8 (2008).

790 47. Oksanen, J. et al. '*vegan*': Community ecology package. R package version 2.4-0.  
791 <https://cran.r-project.org>, <https://github.com/vegandevs/vegan> (2016).

792 **Acknowledgements** This work were supported by CRC Conselho Nacional de  
793 Desenvolvimento Científico e Tecnológico (CNPq) projects (Proc. 303851/2015-5);  
794 INREF Terra Preta Program, NUFFIC;

795 **Figures**



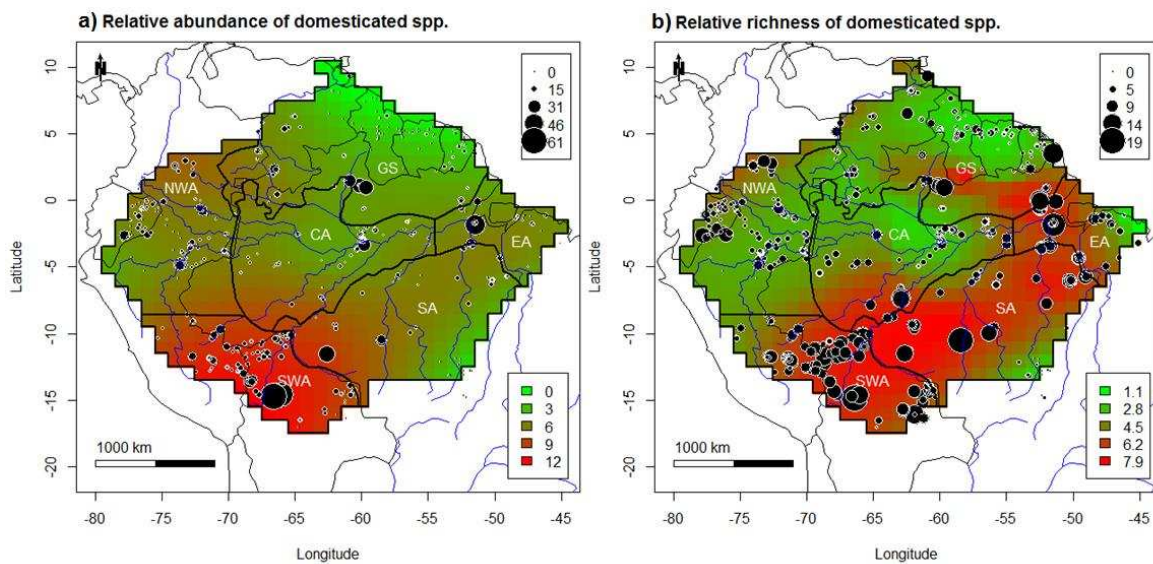
796

797 **Figure 1. Distribution maps of 6 hyperdominant domesticated species in Amazonian**  
798 **forests and their probable origins of domestication<sup>7,29</sup>.** The origin of domestication is

799 shown by the symbol (+++) for known origin and by the symbol (++) for suspected origin.

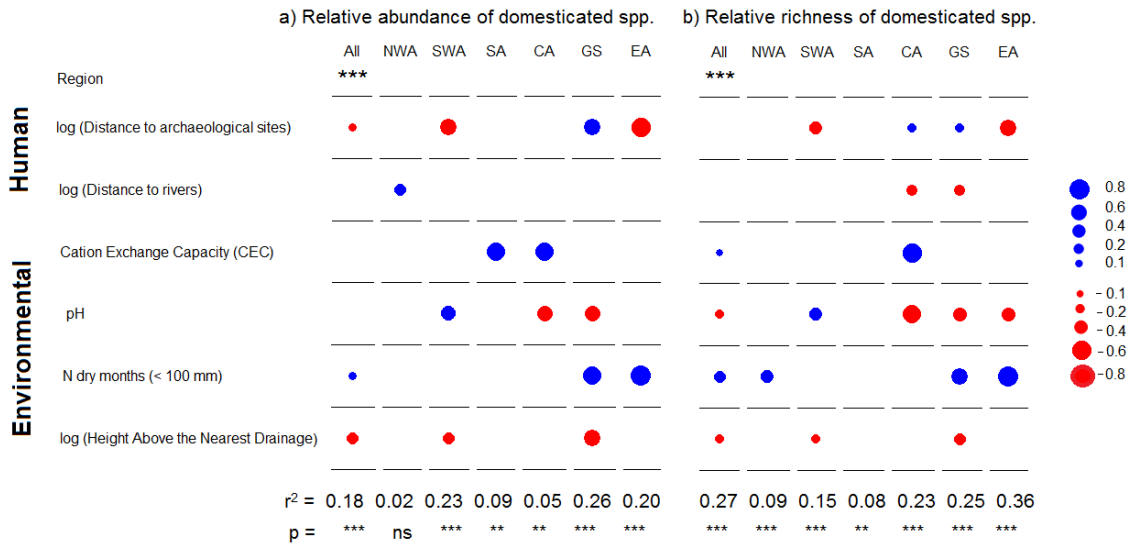
800 Sizes of black dots indicate the relative abundance of the species in the plots where the

801 species has been recorded. Red dots indicate plots where the species has not been recorded.  
 802 Shading shows the interpolated distribution of each species using loess spatial  
 803 interpolation<sup>6</sup>. The range of relative abundance in plots (RelAb) and the loess spatial  
 804 interpolation in individual grid cells (fit) are reported in percentage above each specific  
 805 map. Maps created with custom R script. Amazonia was divided in six geological regions  
 806 (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern Amazonia;  
 807 CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Base map source  
 808 (country.shp, rivers.shp): ESRI (<http://www.esri.com/data/basemaps>, © Esri, DeLorme  
 809 Publishing Company).



810 **Figure 2. Spatial variation of domesticated species across Amazonia.** Maps showing the  
 811 spatial variation of (a) the relative abundance of 85 domesticated species and (b) the  
 812 relative richness of 85 domesticated species in lowland plots in six geological regions of  
 813 Amazonia (NWA, north-western Amazonia; SWA, south-western Amazonia; SA, southern  
 814 Amazonia; CA, central Amazonia; GS, Guiana Shield; EA, eastern Amazonia). Black  
 815 circles show (a) the observed values of relative abundance of domesticated species in each  
 816 plot, ranging from 0-61%, and (b) the observed values of relative richness of domesticated  
 817

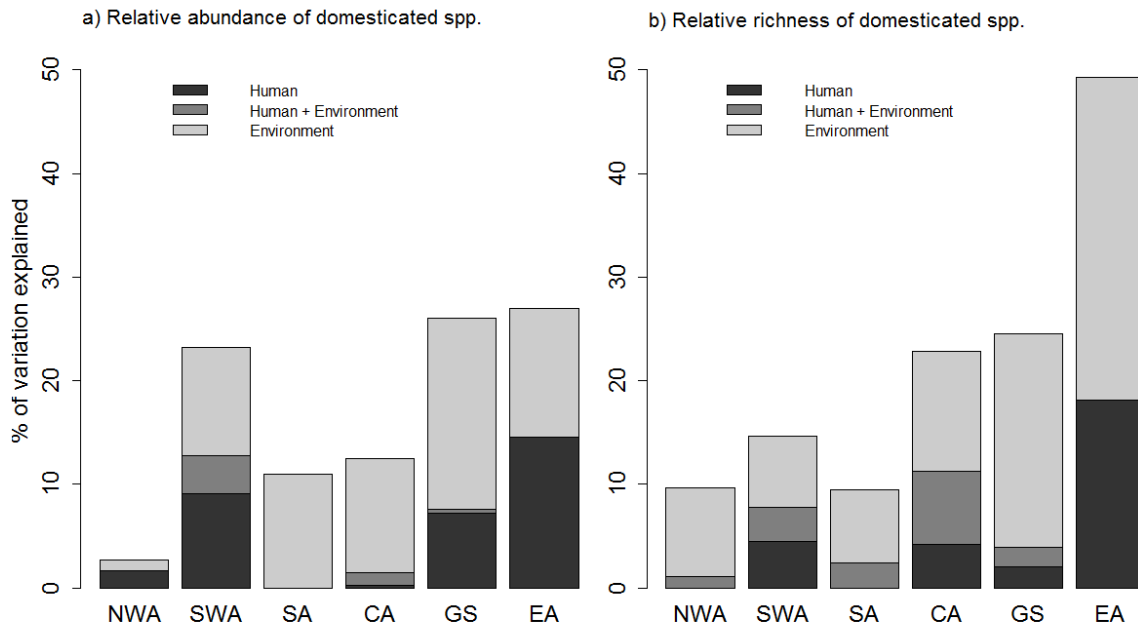
818 species in each plot, ranging from 0-19%. The red-green background shows the  
 819 interpolation of the observed values (in %) in each plot modelled as a function of latitude  
 820 and longitude on a 1°-grid cell scale using loess spatial interpolation<sup>6</sup>. Maps created with  
 821 custom R script. Base map source (country.shp, rivers.shp): ESRI  
 822 (<http://www.esri.com/data/basemaps>, © Esri, DeLorme Publishing Company).



823

824 **Figure 3. The relative abundance and richness of domesticated species as functions of**  
 825 **human and environmental variables.** Standardized regression coefficients for (a) the  
 826 relative abundance of domesticated species, (b) the relative richness of domesticated  
 827 species as a function of human factors (distance to archaeological sites, distance to  
 828 navigable rivers) and environmental conditions (soil Cation Exchange Capacity, soil pH,  
 829 number of dry months and Height Above the Nearest Drainage). Circle size represents the  
 830 relative contribution of the predictors, shown by standardized coefficients at the Amazonia-  
 831 wide level (All) and region-level regression models (NWA, north-western Amazonia;  
 832 SWA, south-western Amazonia; SA, southern Amazonia; CA, central Amazonia; GS,  
 833 Guiana Shield; EA, eastern Amazonia). Red circles indicate negative effects and blue  
 834 circles positive effects. Standardized coefficients presented only for the significant relations

835 analysed in the models ( $p < 0.05$ ). Adjusted  $r^2$  and significant codes ( $p$  values):  $< 0.001$   
836 ‘\*\*\*’  $< 0.01$  ‘\*\*’  $< 0.05$  ‘\*’  $> 0.05$  ‘ns’ are presented.



837

838 **Figure 4. Relative contributions of human and environmental variables for explaining**  
839 **variation in abundance and richness of domesticated species in Amazonian forests.**

840 The figure shows the partitioning of variation in relative abundance (a) and relative  
841 richness (b) of domesticated species uniquely explained by environmental (light gray) or  
842 human factors (dark gray), and the variation jointly explained by both (gray). Variance  
843 partitioning was conducted over the results of multiple regression analyses presented in  
844 Figure 3. Amazonia was divided in the six geological regions (NWA, north-western  
845 Amazonia; SWA, south-western Amazonia; SA, southern Amazonia; CA, central  
846 Amazonia; GS, Guiana Shield; EA, eastern Amazonia).