

Supplementary Materials for
**Archaeological findings show the extent of primitive characteristics of maize
in South America**

Flaviane Malaquias Costa *et al.*

Corresponding author: Flaviane Malaquias Costa, flavianemcosta@hotmail.com;
Fabio de Oliveira Freitas, fabio.freitas@embrapa.br; Maria Imaculada Zucchi, mizucchi@sp.gov.br

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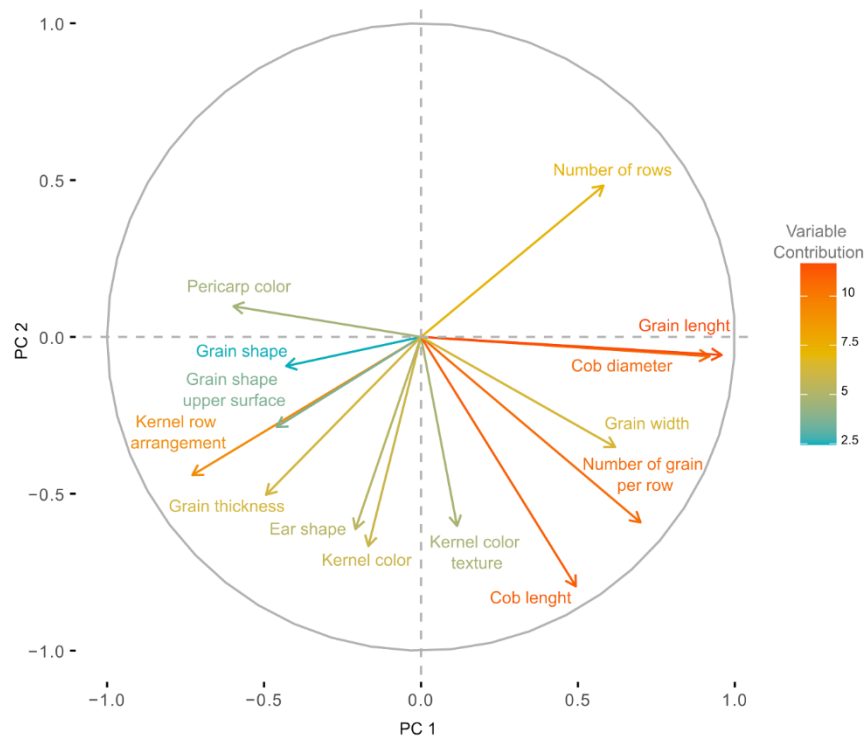
The PDF file includes:

Figs. S1 to S3
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Other Supplementary Material for this manuscript includes the following:

Data S1 to S8

Fig. S1.



Contribution of the variables in the principal component analysis of 22 maize accessions, performed using morphometric descriptors of the maize races. PC 1, first principal component; PC 2, second principal component.

Fig. S2.



Lapa do Boquete, in the Peruaçu Valley, Minas Gerais (MG), Brazil. This is the archaeological site where the largest number of samples was found, including the archeologically characterized ears of maize used for the classification of races in this study. Photos Credit: Fábio de Oliveira Freitas, Embrapa Recursos Genéticos e Biotecnologia.

Fig. S3.



Cave paintings in Peruçu Valley, Minas Gerais (MG), Brazil. In the images, maize and palm (Buriti, *Mauritia flexuosa*) are shown. Photos Credit: Fábio de Oliveira Freitas, Embrapa Recursos Genéticos e Biotecnologia.

Table S1.

Keyword	Archaeological maize			Teosinte		
	Minimum	Average	Maximum	Minimum	Average	Maximum
<i>Cob length (cm)</i>	1.8	6	17	4.5	6.6	11
<i>Base diameter (mm)</i>	0.76	11	32	5.76	11.88	17.7
<i>No. rows</i>	4	12	18	2	4	8
<i>No. grains/row</i>	4	13	40	6	12	27

Minimum, average, and maximum *cob length*, *cob base diameter*, *row number*, and *number of grains per row* characterized from 282 archaeological samples of maize ear/cob fragments from Peruaçu Valley, Minas Gerais (MG), and 22 samples of modern teosinte preserved at the Peabody Museum of Archeology and Ethnology, Harvard University.

Table S2.

<i>Fragment shape</i>	Archaeological maize								Teosinte			
	Integer		Apical		Medium		Basal		Integer		Apical	
	N°	%	N°	%	N°	%	N°	%	N°	%	N°	%
Conical	25	71.43	32	65.31	5	6.41	4	5.33	1	5	1	100
Conical-cylindrical	8	22.86	15	30.61	35	44.87	48	64	9	41	-	-
Cylindrical	2	5.71	2	4.08	38	48.72	23	30.67	12	55	-	-
Total	35	100	49	100	78	100	75	100	22	100	1	100

Frequency of *shapes* estimated from the characterization of 282 archaeological samples of maize ear/cob fragments from Peruaçu Valley, Minas Gerais (MG), and 22 samples of modern teosinte preserved at the Peabody Museum of Archeology and Ethnology, Harvard University. (-): not applicable.

Table S3.

<i>Fragment shape</i>	<i>Major diameter/Apical diameter</i>
Cylindrical	0.75 a 1.25
Conical	2 ou +
Conical-cylindrical	1.25 a 2

Ear/cob shape estimated for the fragments of archaeological samples of maize from Peruaçu Valley, Minas Gerais (MG), and modern teosinte preserved at the Peabody Museum of Archeology and Ethnology, Harvard University, considering preestablished parameters (43, 64).

Table S4.

	Qualitative characteristic	Method	Quantitative characteristic	Method
Cob	<i>Kernel color texture (crown)</i>	Nondestructive	<i>Number of grains per row</i>	Nondestructive
	<i>Kernel crown color</i>	Nondestructive	<i>Cob length (cm)</i>	Nondestructive
	<i>Ear shape</i>	Nondestructive	<i>Cob diameter (cm)</i>	Nondestructive
	<i>Kernel row arrangement</i>	Nondestructive	<i>Number of rows</i>	Nondestructive
	<i>Grain type (endosperm)</i>	Destructive [A representative grain was used to evaluate the endosperm]*		
Grain (kernel)	<i>Pericarp color</i>	Nondestructive	<i>Grain length (mm)</i>	Proposed [A representative grain was used for measurement]*
	<i>Grain shape</i>	Destructive [A representative grain was used for measurement]*	<i>Grain width (mm)</i>	Destructive [A representative grain was used for measurement]*
	<i>Grain shape of the upper surface</i>	Nondestructive	<i>Grain thickness (mm)</i>	Destructive [A representative grain was used for measurement]*

Morphological descriptors used for the characterization of cob and grains and information on the characterization method used for the preservation of archaeological samples from Peruaçu Valley, Minas Gerais (MG). *The detached grains were deposited in an appropriate container, which was duly identified, for conservation along with the original samples.

Table S5.

Date (years BP)	Region of origin	Type of sample	Reference
~ 9.000	Balsas Valley, Southern Mexico	Starch and phytoliths	(5)
~ 7.150	Las Vegas, Ecuador (Pacific Coast)	Phytoliths	(65, 66)
~ 7.000	Panama (Pacific Coast)	Starch	(67)
~ 6.850	Llanos de Moxos, Bolivia (Southwestern Amazonia)	Phytoliths	(25)
~ 6.700	Llanos de Moxos, Bolivia (Southwestern Amazonia)	Phytoliths	(25)
~ 6.700	Paredones and Huaca Prieta, Peru (Pacific Coast)	Ear, grain and straw	(68)
~ 6.500	Rogaguado Lake, Bolivia (Southwestern Amazonia)	Pollen	(26)
~ 6.320	Lake Sauce, Peru (Peruvian Amazonia)	Pollen	(29)
~ 6.000	Ayauch Lake, Ecuador (Western Amazonia)	Pollen and phytoliths	(27)
~ 5.760	Pará, Brazil (Northern Amazonia)	Pollen and phytoliths	(30)
~ 5.300	Ayauch Lake, Ecuador (Western Amazonia)	Phytoliths	(33)
~ 5.300	Upper Madeira River, Rondônia, Brazil (Southwestern Amazonia)	Phytoliths	(31)
~ 4.690 ± 40	Peña Roja and Abejas, Colombia (Western Amazonia)	Pollen	(30)
~ 4.645 ± 40	Araracuara, Colombia (Western Amazonia)	Pollen	(69)
~ 4.190 ± 40	Los Ajos, Rocha, Uruguay (Southeastern Uruguay)	Phytoliths and starch	(34)
~ 3.350	Pará, Brazil (Northern Amazonia)	Pollen	(28)
~ 3.000 to ~ 1.500	Upper Madeira River (Southwestern Amazonia)	Phytoliths and starch	(32)
~ 1.390 ± 40	São Francisco do Sul, Santa Catarina, Brazil (Southern Brazil)	Starch	(35)
~ 1010 ± 60	Peruaçu Valley, Northern Minas Gerais, Brazil (Southeastern Brazil)	Ear, grain and cob	Samples characterized in this study
~ 860 ± 60			
~ 630 ± 60			
~ 570 ± 60			

Date (years before present, BP), region and type of sample in the archaeological records of maize described in the literature for the Americas.

Table S6.

ID	Date (years BP)	Fragment type	Fragment shape	No. rows	No. grains/row	Cob length (cm)
B51	570 ± 60	Integer	Cylindrical	4	8	5.5
B57	570 ± 60	Integer	Conical	4	11	5.3
B1	570 ± 60	Integer	Conical	6	10	4
B31	630 ± 60	Apical fragment	Conical-cylindrical	6	6	3.6
D14	860 ± 60	Apical fragment	Conical	6	6	3
G1	No info.	Apical fragment	Conical	6	10	4.3
H1	No info.	Apical fragment	Conical-cylindrical	6	6	2.3
I4	No info.	Apical fragment	Conical	6	6	2.7
B22	570 ± 60	Middle fragment	Cylindrical	6	7	4.5
J2	No info.	Middle fragment	Conical-cylindrical	6	12	6
E8	1010 ± 80	Basal fragment	Conical-cylindrical	6	8	4.5
I5	No info.	Basal fragment	Conical-cylindrical	6	14	5.3
I6	No info.	Basal fragment	Conical-cylindrical	6	6	2.8
I7	No info.	Basal fragment	Cylindrical	6	4	1.8

Date (years before the present, BP), *fragment type*, *fragment shape*, *number of rows*, *number of grains/row*, and *length of ear/cob fragments* with primitive characteristics from archaeological maize samples from Peruaçu Valley, Minas Gerais (MG). A *number of rows* less than 8 was considered a “primitive” trait.

Table S7.

	Qualitative descriptors		Qualitative descriptors	
Ear	<i>Grain type (endosperm):</i>	Floury	<i>Number of rows:</i>	8/10*
	<i>Ear shape:</i>	Conical/Cylindrical	<i>Number of grains per row:</i>	12
	<i>Kernel row arrangement:</i>	Interlocked/Spiral	<i>Ear length (cm):</i>	7.25
	<i>Kernel color texture (crown):</i>	Plain	<i>Ear diameter (cm):</i>	1.95
	<i>Kernel crown color:</i>	Orange/ Brown		
	<i>Cob color:</i>	Yellow		
Kernel (grain)	<i>Kernel shape:</i>	Flat Oval (38%)/ Orbicular (31%)/ Obovate (15%)/ Trapezoidal (15%)	<i>Kernel length (mm):</i>	5.98
	<i>Kernel shape of the upper surface:</i>	Rounded	<i>Kernel width (mm):</i>	6.53
	<i>Pericarp color:</i>	Brown (69%)/ Dark Brown (23%)/ Orange (8%)	<i>Kernel thickness (mm):</i>	5.21
	<i>Grain color (endosperm):</i>	White		

Qualitative and quantitative morphological descriptors obtained from the characterization of two ears and 12 grains of archaeological maize samples from Peruaçu Valley, Minas Gerais (MG). For the qualitative descriptors, all the variations identified are presented in the table, and for the quantitative descriptors, the average (except for the *number of rows*) is presented. * *Number of rows*: all the identified variations are presented.

Data S1.

Identification code, date (years before present - BP), qualitative and quantitative descriptors for morphological characterization of 282 archaeological samples of maize cob/ear fragments from the Peruaçu Valley-MG. (No Info.) = No information available.

Data S2.

Qualitative and quantitative grain descriptors used for morphological characterization to classify maize races.

Data S3.

Qualitative and quantitative ear descriptors used for morphological characterization to classify maize races. (No Info.) = No information available.

Data S4.

Qualitative and quantitative ear descriptors used for the morphological characterization of 22 samples of modern teosinto (Peabody number: 2001.1.396) conserved at the Peabody Museum of Archaeology and Ethnology, Harvard University. (-) Not applicable

Data S5.

Qualitative and quantitative ear and grain descriptors used for morphological characterization to classify maize races. (No Info.) = No information available. * Maize races from Brazil described in the literature for Lowland South America (Paterniani and Goodman, 1977).

Data S6.

Qualitative and quantitative ear and grain descriptors characterized in order to discuss the evolutionary history of the floury maize races of Lowland South America. (No Info.) = No information available. * Maize races from Brazil described in the literature for Lowland South America (Paterniani and Goodman, 1977).

Data S7.

Passport data for 13 accessions representing maize races used for molecular characterization in this study.

Data S8.

Single nucleotide polymorphisms (SNPs) markers selected for the molecular characterization of 13 maize accessions.

REFERENCES AND NOTES

1. FAO, FAOSTAT statistics database. (Food and Agriculture Organization of the United Nations, Rome, 2020).
2. Y. Matsuoka, Y. Vigouroux, M. M. Goodman, J. Sanchez G., E. Buckler, J. Doebley, A single domestication for maize shown by multilocus microsatellite genotyping. *Proc. Natl. Acad. Sci. U.S.A.* **99**, 6080–6084 (2002).
3. F. O. Freitas, G. Bendel, R. G. Allaby, T. A. Brown, DNA from primitive maize landraces and archaeological remains: Implications for the domestication of maize and its expansion into South America. *J. Archaeol. Sci.* **30**, 901–908 (2003).
4. Y. Vigouroux, J. C. Glaubitz, Y. Matsuoka, M. M. Goodman, J. Sánchez G., J. Doebley, Population structure and genetic diversity of New World maize races assessed by DNA microsatellites. *Am. J. Bot.* **95**, 1240–1253 (2008).
5. D. R. Piperno, A. J. Ranere, I. Holst, J. Iriarte, R. Dickau, Starch grain and phytolith evidence for early ninth millennium B.P. maize from the Central Balsas River Valley, Mexico. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 5019–5024 (2009).
6. J. van Heerwaarden, J. Doebley, W. H. Briggs, J. C. Glaubitz, M. M. Goodman, J. de Jesus Sanchez Gonzalez, J. Ross-Ibarra, Genetic signals of origin, spread, and introgression in a large sample of maize landraces. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 1088–1092 (2011).
7. H. Perales, D. Golicher, Mapping the diversity of maize races in Mexico. *PLOS ONE* **9**, 1–20 (2014).
8. L. Kistler, S. Y. Maezumi, J. Gregorio de Souza, N. A. S. Przelomska, F. Malaquias Costa, O. Smith, H. Loiselle, J. Ramos-Madrigal, N. Wales, E. R. Ribeiro, R. R. Morrison, C. Grimaldo, A. P. Prous, B. Arriaza, M. T. Gilbert, F. de Oliveira Freitas, R. G. Allaby, Multiproxy evidence highlights a complex evolutionary legacy of maize in South America. *Science* **362** (6420), 1309–1313 (2018).

9. L. Kistler, H. B. Thakar, A. M. VanDerwarker, A. Domic, A. Bergström, R. J. George, T. K. Harper, R. G. Allaby, K. Hirth, D. J. Kennett, Archaeological Central American maize genomes suggest ancient gene flow from South America. *Proc. Natl. Acad. Sci. U.S.A.* **117**, 33124–33129 (2020).
10. F. M. Costa, N. C. A. Silva, J. B. Ogliari, Maize diversity in southern Brazil: Indication of a microcenter of *Zea mays* L. *Genet. Resour. Crop Evol.* **64**, 681–700 (2017).
11. E. L. Sturtevant, *Varieties of corn* (USDA Bulletin, Washington, D.C., 1989).
12. T. Á. Kato, C. Mapes, J. A. Serratos, R. A. Bye, *Origen y diversificación del maíz: Una revisión analítica* (Universidad Autónoma de México, Ciudad de Mexico, 2009).
13. N. Yang, Y. Wang, X. Liu, M. Jin, M. Vallebuena-Estrada, E. Calfee, L. Chen, B. P. Dilkes, S. Gui, X. Fan, T. K. Harper, D. J. Kennett, W. Li, Y. Lu, J. Ding, Z. Chen, J. Luo, S. Mambakkam, M. Menon, S. Snodgrass, C. Veller, S. Wu, S. Wu, L. Zhuo, Y. Xiao, X. Yang, M. C. Stitzer, D. Runcie, J. Yan, J. Ross-Ibarra, Two teosintes made modern maize. *Science* **382**, (2023).
14. J. Doebley, Molecular evidence and the evolution of maize. *Econ. Bot.* **44**, 6–27 (1990).
15. J. F. Doebley, H. H. Iltis, Taxonomy of *zea* (Gramineae). I. A subgeneric classification with key to taxa. *Am. J. Bot.* **67**, 982–993 (1980). *evol.* **24**, 98–113 (1992).
16. E. Paterniani, M. M. Goodman, *Races of maize in Brazil and adjacent areas* (CIMMYT, Mexico City, 1977).
17. F. G. Brieger, J. T. A. Gurgel, E. Paterniani, A. Blumenchein, M. R. Alleoni, *Races of maize in Brazil and other eastern South American Countries*. National Academy of Sciences, National Research Council, Washington DC, 1958.
18. F. M. Costa, N. C. de Silva, R. Vidal, C. R. Clement, R. P. Alves, P. C. Bianchini, M. Haverroth, F. de Freitas, E. A. Veasey, Entrelaçado, a rare maize race conserved in Southwestern Amazonia. *Genet. Resour. Crop Evol.* **68**, 51–58 (2021).

19. F. M. Costa, N. C. D. A. Silva, R. Vidal, C. R. Clement, F. De Oliveira Freitas, A. Alves-Pereira, C. D. Petroli, M. I. Zucchi, E. A. Veasey, Maize dispersal patterns associated with different types of endosperm and migration of indigenous groups in lowland South America. *Ann. Bot.* **129**, 737–751 (2022).
20. F. M. Costa, N. C. D. A. Silva, R. Vidal, C. R. Clement, F. De Oliveira Freitas, A. Alves-Pereira, C. D. Petroli, M. I. Zucchi, E. A. Veasey, A new methodological approach to detect microcenters and regions of maize genetic diversity in different areas of lowland South America. *Econ. Bot.* **77**, 345–371 (2023).
21. N. C. De Almeida Silva, R. Vidal, J. Bernardi Ogliari, D. E. Costich, J. Chen, Relationships among American popcorn and their links with landraces conserved in a microcenter of diversity. *Genet. Resour. Crop Evol.* **67**, 1733–1753 (2020).
22. N. C. de Almeida Silva, R. Vidal, J. B. Ogliari, New popcorn races in a diversity microcenter of *Zea mays* L. in the Far West of Santa Catarina, Southern Brazil. *Genet. Resour. Crop Evol.* **64**, 1191–1204 (2017).
23. M. Vallebuena-Estrada, I. Rodríguez-Arévalo, A. Rougon-Cardoso, J. M. González, A. G. Cook, R. Montiel, J. P. Vielle-Calzada, The earliest maize from San Marcos Tehuacán is a partial domesticate with genomic evidence of inbreeding. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 14151–14156 (2016).
24. J. Ramos-Madrigo, B. D. Smith, J. V. Moreno-Mayar, S. Gopalakrishnan, J. Ross-Ibarra, M. T. P. Gilbert, N. Wales, Genome sequence of a 5,310-year-old maize cob provides insights into the early stages of maize domestication. *Curr. Biol.* **26**, 3195–3201 (2016).
25. 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).

26. S. O. Brugger, E. Gobet, J. F. N. van Leeuwen, M. P. Ledru, D. Colombaroli, W. O. van der Knaap, U. Lombardo, K. Escobar-Torrez, W. Finsinger, L. Rodrigues, A. Giesche, M. Zarate, H. Veit, W. Tinner, Long-term man-environment interactions in the Bolivian Amazon: 8000 years of vegetation dynamics. *Quat. Sci. Rev.* **132**, 114–128 (2016).
27. M. B. Bush, D. R. Piperno, P. A. Colinvaux, A 6,000 year history of Amazonian maize cultivation. *Nature* **340**, 303–305 (1989).
28. M. B. Bush, M. C. Miller, P. E. De Oliveira, P. A. Colinvaux, Two histories of environmental change and human disturbance in eastern lowland Amazonia. *Holocene* **10**, 543–553 (2000).
29. M. B. Bush, A. Correa-Metrio, C. H. McMichael, S. Sully, C. R. Shadik, B. G. Valencia, T. Guilderson, M. Steinitz-Kannan, J. T. Overpeck, A 6900-year history of landscape modification by humans in lowland Amazonia. *Quat. Sci. Rev.* **141**, 52–64 (2016).
30. D. R. Piperno, The origins of plant cultivation and domestication in the New World Tropics. *Curr. Anthropol.* **52**, S453–S470 (2011).
31. L. Hilbert, E. G. Neves, F. Pugliese, B. S. Whitney, M. Shock, E. Veasey, C. A. Zimpel, J. Iriarte, Evidence for mid-Holocene rice domestication in the Americas. *Nat. Ecol. Evol.* **1**, 1693–1698 (2017).
32. J. Watling, M. T. Castro, M. F. Simon, F. O. Rodrigues, M. Brilhante de Medeiros, P. E. De Oliveira, E. G. Neves, Phytoliths from native plants and surface soils from the Upper Madeira river, SW Amazonia, and their potential for paleoecological reconstruction. *Quat. Int.* **550**, 85–110 (2020).
33. D. R. Piperno, Aboriginal agriculture and land usage in the Amazon Basin, Ecuador. *J. Archaeol. Sci.* **17**, 665–677 (1990).
34. J. Iriarte, I. Holst, O. Marozzi, C. Listopad, E. Alonso, A. Rinderknecht, J. Montaña, Evidence for cultivar adoption and emerging complexity during the mid-Holocene in the La Plata basin. *Nature* **432**, 614–617 (2004).

35. V. Wesolowski, S. M. F. M. de Souza, K. J. Reinhard, G. Ceccantini, Evaluating microfossil content of dental calculus from Brazilian sambaquis. *J. Archaeol. Sci.* **37**, 1326–1338 (2010).
36. A. Prous, As Muitas Arqueologias das Minas Gerais. *Rev. Espinhaço* **2**, 36–54 (2013).
37. A. Prous, Fouilles de l’Abri du Boquete, Minas Gerais, Brésil. *J. Soc. Am.* **77**, 77–109 (1991).
38. E. Fogaça, A Tradição Itaparica e as indústrias líticas pré-cerâmicas da Lapa do Boquete. *Rev. Mus. Arqueol. Etnol.* **5**, 145–158 (1995).
39. F. O. Freitas, M. J. Rodet, O que ocorreu nos últimos 2000 anos no vale do Peruaçu? Uma análise multidisciplinar para abordar os padrões culturais e suas mudanças entre as populações humanas daquela região. *Rev. Mus. Arqueol. Etnol.* **20**, 109–126 (2010).
40. R. M. K. Bird, M. M. Goodman, The races of maize v: Grouping maize races on the basis of ear morphology. *Econ. Bot.* **31**, 471–481 (1977).
41. E. Anderson, H. Cutler, Races of maize: Their recognition and classification. *Ann. Mo. Bot. Gard.* **29**, 69–89 (1942).
42. F. De María, G. Fernández, G. Zoppolo, *Caracterización agronómica y clasificación racial de las muestras de maíz coleccionadas bajo el proyecto IPGRI. Reunión técnica de la Facultad de Agronomía, Universidad de la República, Uruguay* (1979).
43. N. C. A. Silva, R. Vidal, F. M. Costa, E. A. Veasey, “Clasificación de las razas de maíz de Brasil y Uruguay: Enfoque metodológico y principales resultados” in *Maíces de las Tierras Bajas de América del Sur y Conservación de la Agrobiodiversidad en Brasil y Uruguay*, N. C. A. Silva, R. Vidal, F. M. Costa, E. A. Veasey, Eds. (Ponta Grossa, Atena, 2020), pp. 87–109.
44. M. M. Goodman, W. L. Brown, “Races of Corn” in *Corn and Corn Improvement*, G. F. Sprague, J. W. Dudley, Eds. (American Society of Agronomy, Madison, WI, 1988), 33–79.
45. M. Ridley, *Evolution* (Wiley-Blackwell, Oxford, 2003).

46. N. H. Barton, D. Briggs, J. A. Eisen, D. B. Goldstein, N. H. Patel, *Evolution* (Cold Spring, New York, 2007).
47. M. Nei, Genetic distance between populations. *Am. Nat.* **106**, 283–292 (1972).
48. J. Doebley, The genetics of maize evolution. *Annu. Rev. Genet.* **38**, 37–59 (2004).
49. P. Bommert, N. S. Nagasawa, D. Jackson, Quantitative variation in maize kernel row number is controlled by the FASCIATED EAR2 locus. *Nat. Genet.* **45**, 334–337 (2013).
50. G. M. Janzen, L. Wang, M. B. Hufford, The extent of adaptive wild introgression in crops. *New Phytol.* **221**, 1279–1288 (2019).
51. L. C. R. Pessenda, P. B. Camargo, Datação radiocarbônica de amostras de interesse arqueológico e geológico por espectrometria de cintilação líquida de baixo nível de radiações de fundo. *Quim. Nova* **14**, 98–103 (1991).
52. S. A. Hall, Early maize pollen from Chaco Canyon, New Mexico, USA. *Palynology* **34**, 125–137 (2010).
53. C. Bronk Ramsey, Bayesian analysis of radiocarbon dates. *Radiocarbon* **51**, 337–360 (2009).
54. E. Paradis, K. Schliep, ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* **35**, 526–528 (2019).
55. R Core Team, *R: A language and environment for statistical computing* (R Foundation for Statistical Computing, Vienna, Austria, 2019).
56. A. Kassambara, F. Mundt. Factoextra: Extract and visualize the results of multivariate data analyses. <https://CRAN.R-project.org/package=factoextra> (2020).
57. J. C. A. Gower, A general coefficient of similarity and some of its properties. *Biometrics* **27**, 857–871 (1971).
58. J. Oksanen, G. L. Simpson, F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O’Hara, P.

Solymos, M. H. H. Stevens, E. Szoecs, H. Wagner, M. Barbour, M. Bedward, B. Bolker, D. Borcard, G. Carvalho, M. Chirico, M. De Caceres, S. Durand, H. B. A. Evangelista, R. FitzJohn, M. Friendly, B. Furneaux, G. Hannigan, M. O. Hill, L. Lahti, D. McGlenn, M. H. Ouellette, E. R. Cunha, T. Smith, A. Stier, C. J. F. Ter Braak, J. Weedon, Package “Vegan” Title Community Ecology Package. <https://github.com/vegandevs/vegan> (2022).

59. M. Maechler, P. Rousseeuw, A. Struyf, M. Hubert, K. Hornik, Cluster: Cluster analysis basics and extensions. <https://CRAN.R-project.org/package=cluster> (2015).

60. C. A. Bedoya, S. Dreisigacker, S. Hearne, J. Franco, C. Mir, B. M. Prasanna, S. Taba, A. Charcosset, M. L. Warburton, Genetic diversity and population structure of native maize populations in Latin America and the Caribbean. *PLOS ONE* **12**, 1–21 (2017).

61. J. J. Doyle, J. L. Doyle, Genomic plant DNA preparation from fresh tissue-CTAB. *Phytochem. Bull.* **19**, 11–15 (1987).

62. IBGE, Biomes of Brazil. <https://ibge.gov.br/en/geosciences/maps/brazil-environmental-information/18341-biomes.html?lang=en-GB> (2021).

63. E. Dinerstein, D. Olson, A. Joshi, C. Vynne, N. D. Burgess, E. Wikramanayake, N. Hahn, S. Palminteri, P. Hedao, R. Noss, M. Hansen, H. Locke, E. C. Ellis, B. Jones, C. V. Barber, R. Hayes, C. Kormos, V. Martin, E. Crist, W. Sechrest, L. Price, J. E. M. Baillie, D. Weeden, K. Suckling, C. Davis, N. Sizer, R. Moore, D. Thau, T. Birch, P. Potapov, S. Turubanova, A. Tyukavina, N. De Souza, L. Pintea, J. C. Brito, O. A. Llewellyn, A. G. Miller, A. Patzelt, S. A. Ghazanfar, J. Timberlake, H. Klöser, Y. Shennan-Farpón, R. Kindt, J. P. B. Lillesø, P. Van Breugel, L. Gaudal, M. Vogé, K. F. Al-Shammari, M. Saleem, An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* **67**, 534–545 (2017).

64. C. Senigagliaesi, C. O. Scoppa, D. A. Freggiaro, A. J. Martínez, A. Clausen, O. Polidoro, M. Ferrer, *Catálogo de germoplasma de maíz de Argentina*. (Istituto Agronomico per L'outremare, Firenze, 1997).
65. K. E. Stothert, The preceramic las vegas culture of coastal Ecuador. *Am. Antiq.* **50**, 613–637 (1985).
66. D. M. Pearsall, D. R. Piperno, Antiquity of maize cultivation in Ecuador: Summary and reevaluation of the evidence. *Am. Antiq.* **55**, 324–337 (1990).
67. D. R. Piperno, A. J. Ranere, I. Holst, P. Hansell, Starch grains reveal early root crop horticulture in the Panamanian tropical forest. *Nature* **407**, 894–898 (2000).
68. A. Grobman, D. Bonavia, T. D. Dillehay, D. R. Piperno, J. Iriarte, I. Holst, Preceramic maize from Paredones and Huaca Prieta, Peru. *Proc. Natl. Acad. Sci. U.S.A.* **109**, 1755–1759 (2012).
69. L. F. Herrera, I. Cavelier, C. Rodríguez, S. Mora, The technical transformation of an agricultural system in the Colombian Amazon. *World Archaeol.* **24**, 98–113 (1992).