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Tracing ancestor rice of Suriname Maroons back to its African origin

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African rice (*Oryza glaberrima*) and African cultivation practices are said to have influenced emerging colonial plantation economies in the Americas^{1,2}. However, the level of impact of African rice practices is difficult to establish because of limited written or botanical records^{2,3}. Recent findings of *O. glaberrima* in rice fields of Suriname Maroons bear evidence of the high level of knowledge about rice among African slaves and their descendants, who consecrate it in ancestor rituals^{4,5}. Here we establish the strong similarity, and hence likely origin, of the first extant New World landrace of *O. glaberrima* to landraces from the Upper Guinean forests in West Africa. We collected African rice from a Maroon market in Paramaribo, Suriname, propagated it, sequenced its genome⁶ and compared it with genomes of 109 accessions representing *O. glaberrima* diversity across West Africa. By analysing 1,649,769 single nucleotide polymorphisms (SNPs) in clustering analyses, the Suriname sample appears sister to an Ivory Coast landrace, and shows no evidence of introgression from Asian rice. Whereas the Dutch took most slaves from Ghana, Benin and Central Africa⁷, the diaries of slave ship captains record the purchase of food for provisions when sailing along the West African Coast⁸, offering one possible explanation for the patterns of genetic similarity. This study demonstrates the utility of genomics in understanding the largely unwritten histories of crop cultures of diaspora communities.

The forced migration of Africans to the Americas continued for 350 years and included over 35,000 transatlantic voyages with about 12.5 million enslaved Africans⁷. The transatlantic slave trade resulted in many introductions of African plants to the New World. Crops without immediate commercial value for the colonizers were cultivated by enslaved Africans in their dooryard gardens and forest fields, using leftover seeds from slave ship holds^{9,10}. Most research on plantation slavery focuses on the production of export crops, and less attention has been paid to the food regimes on which this enveloping economic system subsisted. Slave traders sailing along the western African coast purchased substantial quantities of locally produced food to feed their human cargoes¹. One of these staples was rice. In Africa, a distinct species is grown, known as African rice (*Oryza glaberrima* Steud.), domesticated in western sub-Saharan Africa 3,500 years ago¹¹ independently from Asian rice (*O. sativa* L.), which was domesticated in China ~9,000 years

ago¹². The introduction of Asian rice to Africa pre-dates the period of slavery¹³ and both species are grown by African farmers¹⁴. Under wet conditions, African rice generally gives lower yields than Asian rice, but it is better adapted to low-input agriculture, drought, poor and acid soils, pests and weeds¹⁵.

The discovery in 2008 of African rice in a Maroon field in Suriname⁷ testifies to the agency of enslaved Africans in the transatlantic distribution of crops and the conservation of cultivation practices by Maroons, descendants of escaped plantation slaves who settled in remote rainforests of Suriname and French Guiana between 1670 and 1860. Here we present the genetic evidence that the Surinamese 'black rice' is *O. glaberrima* and infer its likely origin. This evidence is an incentive to re-examine historical sources to trace the way African rice ended up in the New World and why it was cultivated by enslaved Africans and their descendants.

The records of slave ship captains reveal that rice was frequently bought in West Africa to feed their captives². An example is the recently digitized logbook of the Dutch slave ship *D'Eenigheid* (the Unity), sailing in 1761 from Vlissingen, the Netherlands, which reports purchases of rice in West Africa⁸. Before leaving from Elmina in Ghana with 319 enslaved Africans destined for Dutch plantations in Guyana, the crew of *D'Eenigheid* bought slaves and provisions along the coast of Liberia and Ivory Coast. Besides millet and sorghum, rice was purchased in 'makoeten' (baskets) and 'coffers' (chests of approximately 625 kg) from African merchants approaching the ships by canoe⁸ (Fig. 1).

Leftover rice stock from slave ships was sometimes distributed among plantations¹⁶ or smuggled away by slaves and planted in

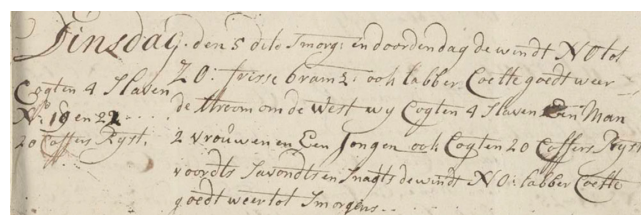


Figure 1 | Logbook entry of the Dutch slave ship *D'Eenigheid*. On 5 January 1762, the crew bought four slaves ('4 slaven') and 20 chests of rice ('20 coffers rijst') near Kwa Kola on the coast of Liberia⁸. Figure reproduced from ref. 8, Zeeland Archives.

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Figure 2 | The Surinamese *Oryza glaberrima* sample (TVA5634) that was propagated to sequence its genome. Seeds still in the husk (left) and dehusked (right). Picture courtesy of C.A. van der Hoeven.

their provision gardens⁹. More than merely a labour force, African knowledge of upland and lowland rice cultivation, harvesting and milling was a key resource for rice cultivation in the Americas, especially in the South Carolina wetlands^{1,2}. *O. glaberrima*, which needs to be dehusked by hand with a wooden pestle in a mortar, was probably the first rice planted in the New World². Evidence for the presence of African rice in the early days of plantation history, however, is only provided by a few written records from the eighteenth century on the red husks of the crop^{2,4} and a single *O. glaberrima* sample collected in 1938 from a Maroon field in French Guiana^{3,17}. In 1955, this sample was considered to be morphologically identical to three *O. glaberrima* landraces grown by Mande-speaking people from the eastern Guinea highlands³.

There is no evidence of commercial, slave-based rice plantations in the Guianas, but in 1718, rice was observed in gardens of enslaved people in Suriname¹⁸. The importance of rice as a staple food for escaped slaves became evident as military expeditions stumbled on extensive rice fields in the refugees' forest camps¹⁹. Maroons have practised slash-and-burn agriculture for centuries in relative isolation from the coastal plantations and maintained much of their traditional language, culture, music and religion²⁰. After slavery was abolished in 1863, Creoles largely abandoned agriculture. Crop cultivars once commonly grown by people of African descent on plantations are now only encountered in Maroon fields⁵.

Rice is the staple food of the Maroons and forms an integral part of their culture²⁰. Dozens of different landraces of upland, rain-fed *O. sativa* have been reported from their fields, including a type of 'black' or 'forest rice' mainly used in rituals^{17,20–22}. Voucher collection, however, has been minimal until 2006, when a small bag of unmilled 'black rice' grains with dark brown husks, long, straight awns and red bran was collected in a Maroon market in Paramaribo⁴ (Fig. 2). This appeared to be the first known *O. glaberrima* collection in the New World after the French Guiana voucher from 1938.

Flowering and fruiting individuals of African rice and additional seeds were collected afterwards in several Maroon villages^{4,5}. Maroons distinguish just one landrace of *O. glaberrima*, which they occasionally consume, but mostly use unprocessed in herbal baths and food offerings to the ancestors. Unmilled seeds are also sprinkled on newly cut fields before burning to ensure a better

harvest^{4,5}. During funerals, bowls of cooked rice from diverse landraces are placed near the graves of the deceased²⁰.

Small-scale farmers across West Africa grow a wide variety of *O. glaberrima* and *O. sativa* landraces, and hybrids between the two species that are either selected by farmers or developed artificially to combine the high yield of Asian rice with the hardiness of African rice¹⁴. Unlike the Maroon rice, African landraces of both species are well represented in germplasm institutes. Recently, the genome sequence of *O. glaberrima* was published²³ and whole genome resequencing SNP maps of 20 diverse samples²³ and 93 West African landraces¹¹ were completed, providing a novel and challenging opportunity to match Suriname rice to its African closest relatives.

The aim of this study was to trace the African ancestry of the Surinamese *O. glaberrima* sample, by assessing its genetic similarity to 109 accessions of the same species across West Africa (Supplementary Table 1), and to ascertain whether this origin coincides with the regions where the Dutch purchased slaves and rice. We also evaluate the degree of genomic divergence of New World African rice that has been grown under traditional Maroon cultivation, likely to have been in close proximity to Asian landraces, for several hundred years.

A single Surinamese sample germinated successfully in the Netherlands. One F_5 was resequenced to 8.3× coverage and aligned to the *O. glaberrima* reference genome AGI 1.1 (ref. 23). We created a set of 1,649,769 SNPs (Supplementary Table 3) and used them in genomic, population genetic and clustering analyses. The Surinamese sample, having been maintained in a limited population size and having been sequenced at the F_5 generation, was surprisingly close to the average heterozygosity at 5.4%, on par with levels in Africa (Supplementary Table 2). For reference, *O. sativa* heterozygosity has been reported to be as high as 15% (breeding centres)²⁴ and as low as 2% (Pakistan rice)²⁵.

Although Maroons sometimes sow African rice on separate fields, the crop often grows in close proximity to Asian landraces. However, there was no apparent introgression between the Surinamese *O. glaberrima* sample and Asian rice.

In an EIGENSTRAT principal component analysis of genomic variation (Fig. 3a and Supplementary Fig. 1), the Surinamese

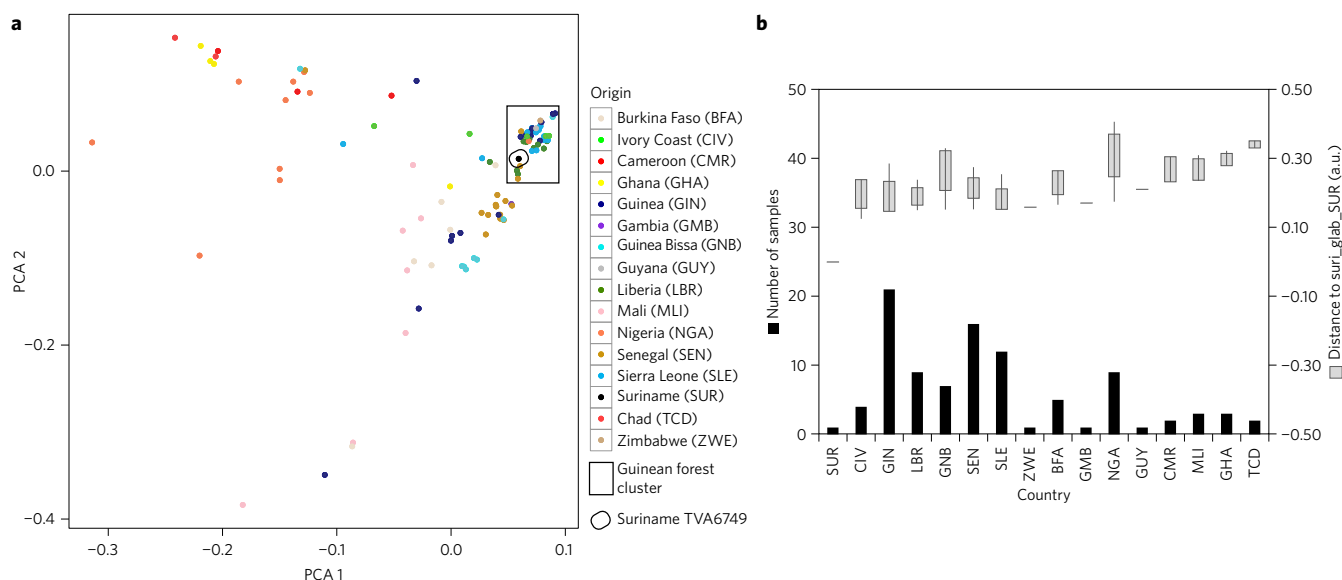


Figure 3 | Comparison of the Surinamese sample with 109 accessions representing *O. glaberrima* diversity across West Africa. a, Principal component analysis (PCA) of the 110 *O. glaberrima* accessions, including the Surinamese sample: two-dimensional plots of the first two principal components. **b**, Accessions grouped according to country. Black bars, the number of samples; grey box and whisker, the minimum, maximum, $\pm$ population s.d. of the clustering distance to the Suriname accession (suri_glab_SUR). Kruskal-Wallis multiple comparison tests (Supplementary Information Table 6) indicated that Nigeria was significantly more distant than Sierra Leone and Guinea.

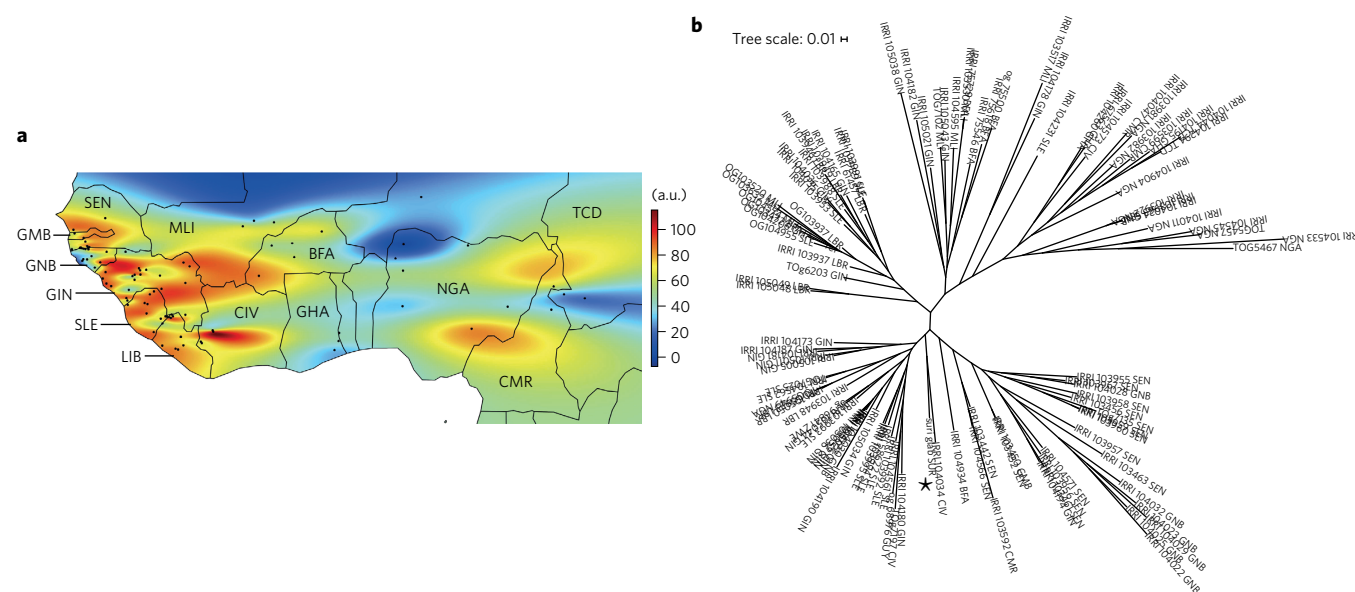


Figure 4 | Heat map of clustering similarity distances to the Surinamese sample, and clustering tree. a, Thin plate spline (TPS) heat map showing the clustering distances from 93 West African *O. glaberrima* samples to the Surinamese sample, interpolated across the West African map. Minimum distance (0.1248, converted to 100, red) and maximum distance (0.40603, converted to 0, blue). **b**, Maximum likelihood (ML) tree showing that the Surinamese sample (suri_glab_SUR, indicated with a star) is sister to IRRI 104034 from the Ivory Coast.

sample clusters near a group largely consisting of Western Guinean forest countries. Genetic distance was calculated using concatenated SNPs following a modified²⁶ methodology, where distances to the Surinamese sample showed that the Western Guinean forest countries were closer than Eastern countries (Fig. 3b and Supplementary Fig. 2). With the only two records of African rice landraces in the New World resembling Guinean forest zone types, it is either the only type brought across the Atlantic, or the only type adequately pre-adapted to the Neotropical rainforest. More specifically, results show the closest kinship between the Surinamese accession and a landrace from the western Ivory

Coast (IRRI 104034), collected in Blolé, a village ~20 km south of the city of Man, and ~300 km from the coast (Fig. 4).

Even though the Surinamese accession is sister to an accession from Ivory Coast, it does not mean that the *O. glaberrima* landrace originated there. More likely, the ancestor of the Surinamese sample came with the people who now inhabit this particular region. Accession IRRI 104034 was collected in 1980 in a Dan-speaking area. Dan is part of the Mande language family, spoken in the north-western Ivory Coast, Senegal, Guinea, Sierra Leone and Liberia, but unrelated to the Volta-Congo languages spoken in the greater part (~75%) of Ivory Coast²⁷ (Supplementary Table 5). Mande speakers

along the Niger River are thought to have participated in domesticating African rice. In the early sixteenth century, they moved southwards to the West African coast, bringing their rice culture with them. The Senegambian coast and the Guinean highlands then became secondary centres of diversification for *O. glaberrima*, during which adaptation to different microenvironments have occurred for millennia^{11,28,29}. Observing the genetic distances calculated across the whole genome (Fig. 4a,b), the Surinamese sample is more similar to the coastal Guinean lowlands and central highlands than to the eastern Guinean highlands, to which the *O. glaberrima* from French Guiana has been previously linked³.

Rice-growing peoples historically inhabit both the Guinea lowlands and highlands: the Atlantic language groups cultivate rice in the brackish coastal swamps, and the Mande-speaking groups grow rain-fed varieties on higher ground²⁷. The six rice accessions most similar to the Surinamese sample were collected from areas dominated by Mande farmers (Supplementary Table 5). Slaveholders in South Carolina preferred Mande-speaking peoples from the 'Rice Coast' (Guinea, Sierra Leone, Liberia and Ivory Coast) because of their rice cultivation skills²⁷. To Dutch slave traders, however, this area was a minor supplier, from which approximately 80,000 people were sent to Suriname. The majority of enslaved Africans in the colony came from Ghana, Benin and Central Africa¹⁰. Nevertheless, Mande-speaking peoples made outsized contributions to Suriname's botanical history. Their knowledge of upland rice cultivation survives in the fields Maroons plant to this day, and words derived from Mande languages frequently appear in Maroon vernacular names for wild plants³⁰.

Slave ship captains may have had little interest in Africa-grown provisions beyond the need to feed their prisoners, but the current ritual importance of African rice in Suriname underscores the deeper significance these staples held for the exiled captives. Maroon agriculture is threatened by large-scale gold mining, migration to the capital and the import of cheap rice. Such developments could lead to the abandonment of labour-intensive crops like rice, and the loss of traditional culture and religion may cause the disappearance of landraces grown for ritual purposes⁵. Modern genomics research on the unique landraces cultivated exclusively by these isolated diaspora communities can reveal the unwritten history of crop movement during one of the largest migrations in human history and offer new insights into African contributions to Atlantic history.

Methods

Between 2006 and 2013, fertile specimens of *O. glaberrima* and seeds kept for sowing material were collected near the Maroon villages Mundje Kreek (5° 10' 21" N–55° 3' 56" W), Mooytiki (4° 7' 38" N–54° 39' 4" W) and Jawjaw (4° 25' 17" N–55° 22' 13" W, Supplementary Fig. 5)^{4,5}. Vouchers in Suriname were collected with permits issued by the Nature Conservation Division of the Suriname Forest Service and deposited at the National Herbarium of Suriname (BBS) and Naturalis Biodiversity Center (L). Rice farmers were interviewed after obtaining their prior informed consent. In 2009, three bags (approximately 60 grams each) of unmilled *O. glaberrima* grains were purchased from Maroon vendors at the Paramaribo Vreedzaam market, the main trading location for medicinal and ritual plants from the country's forested interior³¹. Grains from each sample were sown in 2010 in the greenhouse of the Hortus Botanicus Amsterdam. Only one sample (TVA5634) successfully grew into a fertile individual that produced viable seeds³². In 2014, we made a herbarium specimen with fully developed infructescences (TVA6749) of the fifth generation of this individual and extracted DNA from its fresh leaves, using the Qiagen DNeasy Plant Mini kits (Qiagen). A 300–600 bp genomic DNA paired-end library was constructed using Fragment Library System I with the automated system SPRT-TE (Beckman Coulter) system and sequenced as 2 × 100 bp on an Illumina HiSeq 2500.

Raw paired-end sequence reads from the Suriname sample were used in this study (Supplementary Table 1). This process was repeated for the 93 *O. glaberrima* accessions from Meyer *et al.*¹¹ and for 16 of the accessions from Wang *et al.*²³, obtained from the International Rice Research Institute (IRRI), the United States Department of Agriculture (USDA) and the AfricaRice Genetic Resource Center (GRC). All samples were landraces collected on farms, except og 68976 GUY and og 96841 ZWE (West African landraces grown in rice breeding stations in Guyana and

Zimbabwe). The Suriname reads were trimmed with Sickle³³ (v1.33), aligned to the *O. glaberrima* reference sequence²³, comprising 12 pseudomolecules and 1,939 scaffolds, with Burrows–Wheeler Aligner³⁴ (BWA; v0.6.1) aln and sampe programs, and indexed bam files were created with SAMtools³⁵ (v1.2). Read mate information was updated with FixMateInformation (Picard tools, v1.111) and duplicate reads were marked using MarkDuplicates (Picard tools) and removed from further consideration. Sample alignments were merged using MergeSamFiles (Picard tools) and reads globally realigned around indels using the GATK RealignerTargetCreator/IndelRealigner protocol. SNP calling was performed on the merged alignment using the GATK UnifiedGenotyper. The set of 1,778,594 SNPs was derived from two steps of filtering. First, reads mapping to more than one region of the genome were removed (25% of reads) and base qualities capped at the minimum mapping quality of the read. Then, reads that failed any of the following filters were excluded: mapping quality below 30; depth of coverage greater than 4,987 (about 3.5× higher than the mean depth); Phred-scaled *P* value using Fisher's exact test greater than 399.75; RMS Mapping Quality greater than 61.18; variant confidence/quality by depth <0.32; and Phred-scaled quality score >117,254. Only biallelic variant SNPs from chromosomes were retained, which reduced the SNP set to 1,649,769 SNPs (Supplementary Table 3). Coverage was calculated using the GATK³⁶ (v3.1-1) DepthOfCoverage tool. Heterozygosity was calculated using VCFtools³⁷ (v0.1.12b) '–het'.

Population eigenvectors for principal component analysis (PCA) were obtained using the program EIGENSOFT to run EIGENSTRAT³⁸. Input SNPs were pruned to 1,244,261 SNPs by using settings in PLINK³⁹ (v1.07) '–indep 50 5 1.5'. Eleven PCs were significant to *P* < 0.05 and each accounted for only a small percentage of the variance; variance percentage was included in the PC labels (Supplementary Information Table 4). Two-dimensional PCA plots were made with the top three PCs in R (Supplementary Fig. 1). Clustering distance used in the heat maps (Fig. 4a; Supplementary Fig. 4) and trees (Fig. 4b; Supplementary Fig. 3) was calculated using a modified²⁶ approach with Introgression Browser (vdef67dd) and FastTree²⁴⁰ (v2.1.7). As 99.9% of the polymorphic positions in the genome are excluded by the regular method of deleting positions in which any accession presents either no sequencing coverage, MNPs, InDels or heterozygous SNPs, we decided to keep heterozygous SNPs and regions of no coverage. This increases the number of available polymorphic positions to 1.6 million SNPs. The final clustering distance reported is the pairwise distance calculated from the resulting tree created by FastTree²⁴⁰ as extracted by ETE2⁴¹ (v2.2rev1056). To map clustering distances to geographical coordinates, we conducted a Thin Plate Spline (TPS) regression analysis on all West African accessions using the packages 'fields'⁴², 'raster'⁴³ and 'worldmap'⁴⁴ in R⁴⁵ (v.3.2.3). Samples with low coverage (<5×) were excluded to enhance the quality of the image, leaving 93 accessions available for the analysis. Distances were interpolated across a geographical region from 0° to 20° latitude and –20° to 20° longitude with smoothing parameter lambda set to 0.001. To test whether a different clustering method would produce similar results, we calculated a second genetic distance estimate (Supplementary Fig. 3). This was a neighbour-joining tree from the 110 *O. glaberrima* samples using 494,939 biallelic SNPs, allowing for missing genotypes. Distances were calculated using the equation described earlier^{6,46} and reproduced here:

$$d(X, Y) = \frac{1}{L} \sum_{i=1}^L \left(1 - \frac{1}{2} \max(\delta_{a_i c_i} + \delta_{b_i d_i}, \delta_{a_i d_i} + \delta_{b_i c_i}) \right)$$

Data availability. All *O. glaberrima* collections and associated information from Suriname are digitally available at the collections database of Naturalis Biodiversity Center (<http://bioportal.naturalis.nl>).

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Author contributions

T.R.v.A. conducted the fieldwork in Suriname, and wrote the paper with contributions and input from all co-authors. T.R.v.A. and M.E.S. conceived and guided the research. R.M.H. maintained the living collection of *Oryza glaberrima* from Suriname used in this project. D.C. performed sequencing and assisted with data analysis. R.S.M. and J.M.F. performed alignments, SNP calling, and clustering analyses. S.A.A. and M.A.V. performed phylogenomic and TPS analysis. J.A.C. and H.M. provided background on the geographical and historical aspects of West African rice, slavery and Suriname. R.A.W. and M.D.P. helped to collect the data.

Additional information

Supplementary information is available for this paper. Reprints and permissions information is available at www.nature.com/reprints. Correspondence and requests for materials should be addressed to T.R.v.A. and R.S.M.

Competing interests

The authors declare no competing financial interests.