Multidisciplinary perspectives on banana (Musa spp.) domestication

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Original multidisciplinary research hereby clarifies the complex geodomestication pathways that generated the vast range of banana cultivars ( cvs). Genetic analyses identify the wild ancestors of modern-day cvs and elucidate several key stages of domestication for different cv groups. Archaeology and linguistics shed light on the historical roles of people in the movement and cultivation of bananas from New Guinea to West Africa during the Holocene. The historical reconstruction of domestication processes is essential for breeding programs seeking to diversify and improve banana cvs for the future.

New multidisciplinary findings from archaeology, genetics, and linguistics clarify the complex geodomestication pathways—the geographical configurations of hybridization and dispersal—that generated the range of modern banana cultivars ( cvs). Although recent molecular research, combined with the outcomes of previous genetic studies, elucidates major stages of banana domestication, such as the generation of edible diploids and triploids, it sheds only partial light on the historical and sociospatial contexts of domestication. The geographic distributions of genotypes involved in banana domestication require human translocations of plants, most likely under vegetative forms of cultivation, across vast regions. Linguistic analyses of (traditional) local terms for bananas reveal several striking regional-scale correspondences between genetic and linguistic patterns. These multidisciplinary findings enable the relative dating of the principal events in banana geodomestication and situate banana cultivation within broader sociospatial contexts. Archaeological findings provide a timeline to anchor and calibrate the relative chronology.

Banana ranks next to rice, wheat, and maize in terms of its importance as a food crop. In addition to being a major cash crop around the world, more than 85% of bananas are grown for local consumption in tropical and subtropical regions (1). The hundreds of cultivated varieties are products of centuries—in some cases millennia—of clonal (vegetative) propagation. Banana fruits can be cooked, roasted, or even brewed (e.g., plantains; East African Highland cvs) or eaten raw (e.g., the yellow Cavendish banana sold in supermarkets globally).

**Musa Genetics and Domestication Thresholds**

The monocotyledon Musaceae family includes the Asian and African genus *Ensete*, the genetically proximal Asian *Musella* genus, and the East Asian genus *Musa*, which is divided into sections with 22 (Eumusa, Rhodochlamys) and 20 chromosomes (Australimusa, Callimusa). Most edible bananas belong to the Eumusa section, and are diploid or triploid hybrids from *Musa acuminata* (A-genome) alone or from hybridization with *Musa balbisiana* (B-genome). A minor cv group, including Fe’i bananas, is confined to the Pacific region and is derived from Australimusa species.

The evolution from wild to edible bananas involved seed suppression and parthenocarpy development. Simmonds (2) proposed the first reconstruction of this complex process in the 1960s. Since then the spectrum of available genetic resources has been greatly expanded, notably with collections from New Guinea (NG), the native area of the *M. acuminata* subsp. *banksi* (3), and through the application of molecular methods to banana diversity analysis (4–7).

In the present study, we present the conclusions of two recent analyses by using simple sequence repeats (8) and DArT (9) markers on the international collection in Guadeloupe (Centre de Coopération Internationale en Recherche Agronomique pour le Développement, France) which assembles more than 400 wild and cultivated accessions covering much of global *Musa* diversity. Analyses here include additional accessions from Cameroon and Nigeria to better represent African cv diversity (Table S1). The results of these analyses were integrated with previous results, including ploidy level and DNA content (10), anthocyanin patterns (11), isozymes (12), nuclear restriction (13) and amplified fragment length polymorphism (14), and chloroplastic and mitochondrial restriction fragment length


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polymorphism (15). The synthesis of these results sheds light upon the two founding events during banana domestication: the transition from wild to edible diploids and the formation of triploids from edible diploids (16) (Fig. S1).

Wild M. acuminata species are diverse and have been differentiated into several subspecies (13, 16). This differentiation is clarified here with the identification of specific nuclear alleles, chromosomal re-arrangements, and chloroplast and mitochondrial patterns. The exclusive natural ranges of the subspecies are also confirmed (Fig. 1).

The key result relevant to domestication history is that edible diploid cv subgroups (AA cvs) derive from hybridizations between different M. acuminata subspecies in island Southeast Asia (SEA; ISEA) and western Melanesia (Fig. 2 and Fig. S2), which could only be brought into contact by human movement and propagation, most probably during the Holocene (i.e., the past 11,700 y). The structural heterozygosity of these hybrid AA cvs, caused by chromosomal re-arrangements between parental subspecies of M. acuminata (17), contributed to genetic sterility (18). This sterility, in association with human selection for pulp enhancement, led to parthenocarpic fruits and edibility.

A further consequence of hybrid status was erratic meiosis in edible AA cvs, thereby occasionally producing diploid gametes (2). The fusion of diploid gametes with haploid gametes generated sterile triploid genotypes. Spontaneous triploidizations involved almost all diploid cvs leading, under human selection via vegetative propagation, to the diversity of modern cultivated triploids, including pure M. acuminata varieties (AAA) and interspecific M. acuminata × M. balbisiana varieties (AAB, ABB) (19).

Molecular phylogenetic analyses have identified the diploid subgroups contributing to modern triploid cvs. Of significance, NG-derived banksii cvs played a major role in the development of several important diploid and triploid cv groups that are now widely dispersed. For example, M. acuminata subsp. zebrina- and subsp. banksii-derived AA cvs contributed to AAA Highland bananas of East Africa. Likewise, subsp. banksii-derived AA cvs with the BB genome contributed to AAB plantains of West Africa and the Pacific. Moreover, in several triploid subgroups, specific accessions within AACvs subgroups have been identified as potential ancestors, suggesting more recent formation (16, 20). For example, the 2N and 4N parentals of the common dessert banana, the AAA “Cavendish,” are genetically close to "Akondro Mainty” of the AAC "Mali" subgroup and “Pisang Pipit” of the AAC "Khai" subgroup, respectively (Fig. 2).

Strict vegetative propagation (i.e., cloning) over long periods of the most popular diploid and triploid varieties led to somaclonal variants, thus amplifying phenotypic diversity (14). The geographical ranges of diploid parents and triploid hybrids point to numerous long-distance movements of either one of the parents before hybridization, or of triploid cvs after hybridization. The geographical dimension of the banana domestication process requires a reconstruction of relevant human movements and interactions—the drivers of the geodomestication process.

**Anchoring Banana Domestication in Time and Place**

Microfossil (phytoliths, pollen) and macrofossil (seeds, pseudostem impressions) remains of bananas have been documented at numerous archaeological and paleoecological sites from Oceania to Africa (21), although their significance varies greatly for understanding the history of banana domestication and cultivation. Within the natural range of Musa, archaeobotanical and paleoecological finds require differentiation to a species’ or subspecies’ level to indicate potential human movement, and also require associated evidence of human exploitation or cultivation. Most identifications are to the genus level and not directly associated with archaeological remains; consequently, they are of limited value for understanding banana domestication because they may solely record wild bananas (21). Outside the natural range of Musa, bananas were exotic, dispersed under cultivation, predominantly sterile, and vegetatively propagated; consequently, an archaeobotanical find of Musa signifies the presence of agriculture.

Predominantly, the Musa genus has been identified in the archaeological record by using phytoliths (21). As a result of parthenocarpy in most cvs, seeds are unlikely to be found in prehistoric agricultural contexts, and usually leaf phytoliths
have been used for identification to the species level, although they are less readily differentiable to the species level than seed phytoliths (22–24). Here, discriminating morphological criteria of leaf and seed phytoliths are reexamined and augmented for reliable interspecific and intraspecific differentiation within *Musa* and between *Musa* and *Ensete* (Figs. S3 and S4 and Tables S2 and S3). These revised discriminatory criteria are applied to assemblages at two key archaeological sites that anchor thresholds of prehistoric *Musa* geodomestication: cultivation of *M. acuminata* at 6,950 to 6,440 calibrated y cal BP at Kuk Swamp in the highlands of PNG and the dispersal under cultivation of sterile AAB plantains by 2,750 to 2,300 cal BP to Nkang, Cameroon.

Abundant Musaceae phytoliths in feature fills associated with agricultural practices and dated to 6,950 to 6,440 cal BP at Kuk are indicative of banana cultivation (25, 26). Identifiable morphotypes with attributes matching the comparative reference samples of *M. acuminata* subsp. *banksii* from NG (Fig. 3 A–C), the only naturally occurring *M. acuminata* subspecies on the island, can be differentiated from other Musaceae grown there (Fig. S3 and Table S2), although archaeobotanical occurrences are rare (Fig. 3D). So, the occurrence of *M. acuminata* morphotypes in an early agricultural context is highly significant and provides a minimum date for the cultivation of subsp. *banksii* derivatives in NG.

Volcaniform leaf phytoliths of *Musa* spp. were reported from two secure archaeological contexts at Nkang in Cameroon: from two horizons within pit 9 (*n* = 20, dated to 2,790–2,300 cal BP) and from a charred deposit adhered to a pottery sherd from pit 7 (*n* = 5, dated 2,750–2,100 cal BP; Fig. 3 E–H) (22, 23, 27). The original morphological criteria used to distinguish *Musa* and *Ensete* phytoliths at Nkang have been revised (Fig. S4 and Table S3) and confirm the phytoliths at Nkang to be *Musa*, as opposed to the native African genus *Ensete*. So, this reevaluation of the Nkang assemblages provides a secure archaeobotanical foundation and minimum date for the cultivation of exotic plantains in West Africa.

This verification of the archaeobotany of *Musa* at Kuk and Nkang is essential to the development of a chronological framework for the domestication phylogeography (from genetics) and dispersal of cvs (from linguistics). Other significant archaeobotanical finds of *Musa* are discussed with reference to other lines of evidence in the subsequent sections. However, differentiation below the genus level has not been possible at most archaeological or paleoecological sites; for example, *Musa* phytoliths date to 4,000 y ago at Kot Diji in Pakistan (28) and have also been associated with the post–3,500-y-old Lapita phenomenon in the western Pacific (21, 29). Exceptions include the identifications of *M. balbisiana* and *M. acuminata* subspecies as in color (in gray for unclassified AAv); clusters of AAcv, identified by the name of a representative accession, are in black. AAcv appeared as hybrids between *M. acuminata* subspecies as illustrated by the clusters from Spiral to Beram collected in PNG, the native area of subsp. *banksii*. If the contribution of the *banksii* genome was still found dominant for the first clusters, it decreased rapidly, balanced by an increasing contribution of zebrinalmicrocarpa genome, in parallel with an increasing heterozygosity. The frequency of *banksii* cytoplasmic type Vp (12) decreased to the benefit of hybrid forms Vp (Vp × Ila) or specifically to the Mala cluster, Ildp (Ildp × Vp). Contributions of these AAcv to triploids, as 2N donor (red arrows) and N donor (blue arrows), are illustrated for some AAA and AAB.

![Phylogenetic relations between AA cvs and wild acuminata subspecies](image-url)

**Fig. 2.** Phylogenetic relations between AA cvs and wild *acuminata* subspecies. Ntree on genetic dissimilarities from 22 simple sequence repeat markers, on 41 AAv and 131 AAcv (also refer to Fig. S2): *M. acuminata* subsp. are in color (in gray for unclassified AAv); clusters of AAcv, identified by the name of a representative accession, are in black. AAcv appeared as hybrids between *M. acuminata* subspecies as illustrated by the clusters from Spiral to Beram collected in PNG, the native area of subsp. *banksii*. If the contribution of the *banksii* genome was still found dominant for the first clusters, it decreased rapidly, balanced by an increasing contribution of zebrinalmicrocarpa genome, in parallel with an increasing heterozygosity. The frequency of *banksii* cytoplasmic type Vp (12) decreased to the benefit of hybrid forms Vp (Vp × Ila) or specifically to the Mala cluster, Ildp (Ila × Vp). Contributions of these AAcv to triploids, as 2N donor (red arrows) and N donor (blue arrows), are illustrated for some AAA and AAB.
is attested in the Philippines with forms **"agutay** and **"kelutay** for wild bananas. Hence, it is likely that the initial reflexes of **"qaRutay** were generated in the Philippines region (Fig. 4C). The linguistic data suggest an initial southward dispersal of **"qaRutay** from the Philippines into Indonesia, with later “ripples” west into mainland Asia and east as far as NG. The initial southward dispersal to Indonesia saw the **"qaRutay** term come into the attested range of **"muku**. Early branches of the **"qaRutay** dendrogram, representing reflexes of **"kalaay** and **"kali**, are distributed east to Melanesia and west to the Asian mainland. An intermediate form is **"kelo**, which is currently attested in multiple languages as far west as the Indian subcontinent and east on NG, but is now almost absent from ISEA. The last of these terminological transformations, **"loka** (from **"kalo** via metathesis), has only recently begun its spread and is restricted to locales across Sulawesi and eastern Indonesia.

The analysis of **"baRat** indicates a probable origin in the Philippines and later spread toward Borneo and SEA (Fig. 4D). Although not widespread, **"baRat** dominates in those areas in which it is found.

In contrast to the phylogenetic depth of **"qaRutay**, the lack of a hierarchy associated with **"punti** reflects a relatively recent and rapid spread with Austronesian languages in ISEA (Fig. 4B) and attests multiple processes of local differentiation.

**Multidisciplinary Consilience on Banana Domestication**

The integrated analysis of genetic, linguistic, and archaeological data enable a coherent reconstruction of the major events in banana domestication, including geographical occurrence, timeline, and cultural associations.

**Generation of Diploid cv Subgroups.** The first crucial step in banana domestication was the hybridization between geographically isolated subspecies of *M. acuminata*, which were brought into contact by people within ISEA and western Melanesia. Ethnobotany supports the human transport of these fertile genotypes because useful parts of banana plants were potentially exploited over millennia for food, fodder, medicine, fiber, domestic uses, or construction materials (39). The term “cultivars” has been coined to denote these potentially pre-domesticated banana plants, namely, “[a]ny

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**Fig. 3.** Ancient banana phytoliths recovered from archaeological excavations at Kuk Swamp, Papua New Guinea (SEM images, A–D), and at Nkang, Cameroon (optical images, E–H). For Kuk: (A and B) dorsal and lateral view of Eumusa seed phytolith recovered from sample S, Kuk; and (D) dorsal view of Eumusa seed phytolith recovered from sample 28, Kuk predating 3,000 cal BP. Morphotypes shown in A–C are specific to *M. acuminata* (Fig. S3 A, B and D). The morphotype with lobate margins shown in D occurs in *M. acuminata* (Fig. S3A) and a similar morphotype occurs in *Musa schizocarpa* (Fig. S3 E and G).

For Nkang: (E–H) multidimensional diagnostics of Musa-type volcaniform phytolith from Pit F9, Horizon 7 at Nkang, dated to 2,750 to 2,100 cal BP; (E) small indentation on left side of crater rim; (F) rectangular base, psilate surface, eccentric cone, and continuous rim; (G) processes along the edge of the base; and (H) processes along the base.

(36). Each distribution is suggestive of different historic processes of dispersal; local diversity of other terminological sets, primarily in NG and near the Himalayas, is suggestive of long-term use of Musaceae.

The distribution of more than 40 surviving reflexes of the protoform **"muku** is concentrated in Wallacea and western NG (34) (Fig. 4A). This “cognate” is attested across a number of unrelated language families. It spreads west from NG across a range of modern Papuan languages in Wallacea, suggesting an early distribution before the purported Austronesian dispersal ca. 4,000 to 3,500 cal BP (34, 37). Reflexes of **"muku** are found in areas (38) where pre-Austronesian linguistic ecologies survive. In areas now dominated by Austronesian languages, **"muku** represents terminological survival and strong resistance to change in the face of radical language shift.

The protoform **"qaRutay** is evident in the Philippines with forms **"agutay** and **"kelutay** for wild bananas. Hence, it is likely that the initial reflexes of **"qaRutay** were generated in the Philippines region (Fig. 4C). The linguistic data suggest an initial southward dispersal of **"qaRutay** from the Philippines into Indonesia, with later “ripples” west into mainland Asia and east as far as NG. The initial southward dispersal to Indonesia saw the **"qaRutay** term come into the attested range of **"muku**. Early branches of the **"qaRutay** dendrogram, representing reflexes of **"kalaay** and **"kali**, are distributed east to Melanesia and west to the Asian mainland. An intermediate form is **"kelo**, which is currently attested in multiple languages as far west as the Indian subcontinent and east on NG, but is now almost absent from ISEA. The last of these terminological transformations, **"loka** (from **"kalo** via metathesis), has only recently begun its spread and is restricted to locales across Sulawesi and eastern Indonesia.

The analysis of **"baRat** indicates a probable origin in the Philippines and later spread toward Borneo and SEA (Fig. 4D). Although not widespread, **"baRat** dominates in those areas in which it is found.

In contrast to the phylogenetic depth of **"qaRutay**, the lack of a hierarchy associated with **"punti** reflects a relatively recent and rapid spread with Austronesian languages in ISEA (Fig. 4B) and attests multiple processes of local differentiation.
Diverse wild *banana* subspecies and subsequent hybrids, *banksii* in the NG AAB | and no. 28 subspecies were probably sub-

...d genome as an A component, PNAS probably followed this or popula-

...c Mandala), B genome in this region. The reverse hybr-

...tnology in the region at approx-

member of a wild population, or its direct fertile derivatives, whether cloned or not, growing outside of the natural habitat, or range, of the species [or subspecies] to which it belongs” (40). Diverse wild *M. acuminata* subspecies were probably subject to predomesticated exploitation in their native regions. In particular, culti-

...wilds derived from subsp. *banksii* in the NG region contributed genetically to numerous cv groups; their antiquity is attested by ar-

...achaeobotanical evidence at Kuk by at least 6,950 to 6,440 cal BP.

Domesticated parthenocarpic diplods resulted from antrhopic translocation of cultiwilds outside of their natural range and subsequent hybridization with local sub-

...species in at least three contact regions (Fig. 5A): between NG and Java (Southern), between NG and the Philippines (Eastern), and among the Philippines, Borneo, and mainland SEA (Northern). Each of these hybridization areas has a clear linguistic association (Fig. 5B).

In the Southern contact area, between NG and Java, initial hybridizations oc-

...urred between subspecies of *banksii* and the *zebrina/microcarpa* complex. This early dispersal can be traced linguistically by the distribution of *muku* reflexes in Wallacea and in western NG (34). This dispersal predates the purported arrival of Austro-

...nsian languages in the region at approx-

...mately 3,500 cal BP. This antiquity would be consistent with the distribution of derived cv AAcvs or AAAcv that are not now found in the area of origin but are widely cultivated in Africa.

The Eastern contact area is genetically evidenced by the contribution of *M. acuminata* subsp. *errans* from Philippines to the cytoplasmon of numerous AAcvs. This Eastern contact area is linguistically at-

...ested by the recent origin inferred by coreference with populations of *M. acuminata* subsp. *banksii*.

Within the Eastern contact area, the southward translocation of *M. balbisiana* is attested by small populations growing along the trail from South China to NG. Although not domesticated for edibility, *M. balbisiana* has been used and moved by people for multiple purposes (e.g., male bud, immature fruit, leaves). Moreover, several AAB and ABB triploid subgroups, with *banksii* genome as an A component, are absent from the northern end of this trail, thereby indicating a southern origin for the contact area and availability of the B genome in this region. The reverse hy-

...osis, a northward translocation of *M. acuminata* subsp. *banksii* and subsequent hybridization with *M. balbisiana* populations, is discounted because no genetic trace of the subspecies is found in the Philippines and further north.

The Northern contact area is hypothe-

...ized for the formation of several AAAcv, which contributed to important commer-

...ial crops. Their genomes represent contributions of *M. acuminata* subsp. *malaccensis* or *microcarpa*, derived from mainland SEA and Borneo, and of sub-

...pecies *errans* from the Philippines. The dispersal of the reflex *baRak* in North Borneo from the prototerm *baRat* in the Philippines clearly corresponds to the genetic hypothesis.

These hybrid AAAcv were widely adopt-

...ted within the primary area of *M. acumin-

...ata* subspecies diversity, where they are still commonly cultivated. Very few dis-

...ered outside this primary area. A striking exception is the AAA cv subgroup, which are remarkable parents of several popular triploid subgroups. Allelic frequencies point to this subgroup being *M. acuminata* subsp. *banksii × zebrina* hybrids, with the Southern contact area as probable origin. Interestingly, this AAA cv subgroup is now only grown along the east coast of Africa and proximal islands (i.e., Madagascar, Zanzigar, Comoros). The isolated occurrence of these cultivated AA diplods far away from the region of pre-

...sumed origin, in which they no longer occur, suggests an ancient transfer across the Indian Ocean.

**Emergence of Triploid cv Subgroups.** A direct consequence of the perturbed gamete formation in hybrid AAAcv was the emergence of triploid genotypes AAA and AAB or ABB by interspeci-

...hizations. Triploidization occurred independently in various contact areas between diplods and from different parental combinations (Fig. 6). Some of the triploids selected for cultivation underwent somaclonal var-

...ation under vegetative propagation to produce the modern phenotypically char-

...terized triploid subgroups. Triploidiza-

...on probably started early after the AAA cv emergence and is certainly still ongoing, as attested by the recent origin inferred for the genome of several AAA in NG.

Of the numerous triploid subgroups, three are remarkable because they are largely cultivated far from their region of generation: the African AAA “Mutika Lu-

...jura,” AAB “African Plantains,” and AAB “Pacific Plantains.” These triploids are not cultivated in Asia, with the exception of a few African Plantain cvs that were probably introduced to South India with the East African slave trade. The antiquity of each subgroup is attested by the extraordi-

...arily large number of cultivated people for multiple purposes (e.g., male bud, immature fruit, leaves). Moreover, several AAB and ABB triploid subgroups, with *banksii* genome as an A component, are absent from the northern end of this trail, thereby indicating a southern origin for the contact area and availability of the B genome in this region. The reverse hy-

...tralized subgroups. Triploidiza-

...on probably started early after the AAA cv emergence and is certainly still ongoing, as attested by the recent origin inferred for the genome of several AAA in NG.
Genetically derived contact areas between $M$. subsp. $zebrina$ and $M$. balbisiana genomes indicate the eastern side of the Southern contact area as origin, where genetically close AAAs are still cultivated.

The AAB African Plantains are a staple crop in the rainforest zone of West and Central Africa. The constitutive A genomes were identified as $banksii$. An AAB similar to African Plantains has been discovered under traditional cultivation by Negrito tribes in the Philippines (44). Another AAB subgroup, Laknau, with analogous morphology and genetic similarity has been documented in the Philippines’ vicinity. These findings suggest a probable origin for the African Plantains in the Eastern contact area between the Philippines and NG, possibly around the Celebes Sea (45).

Two independent introduction events are proposed for these triploid subgroups to Africa: AAA Mutika Lujugira and associated AAcv to East Africa from the South contact area between Java and NG and AAB African Plantains from the East contact area between the Philippines and NG. The arrival of bananas to East Africa is not documented archaeologically; the reported finds at Munsa, Uganda, are problematic, primarily in terms of chronology (46, 47). The generic names for African Plantain are mostly reflexes of the proto-Bantu term *kondo (48), indicating that they arrived in Africa before the expansion of Bantu-associated cultures from ca. 3,000 cal BP (49). The archaeological finds at Nkang (Cameroon) 2,750 to 2,100 BP conform to this timeframe and predate the spread of Austronesian languages from Borneo to Madagascar. Consequently, the mode of dispersal from Asia to Africa is uncertain: terrestrial (42) and maritime routes (48) have been proposed. It is currently unclear how, or if, the banana phytoliths dating to ca. 4,000 y ago at Kot Diji in Pakistan (28) are relevant to understanding the dispersal of bananas to Africa.

AAB Pacific Plantains are spread over the whole Pacific and include the closely related Maia Maoli, Popoulou, and Iholena. Like African Plantains, they are comprised of $M$. balbisiana and $M$. acuminata subsp. $banksii$ genomes. The absence of genetic relationships with Philippine cvs and the persistence in NG of genetically similar AAB forms indicate an origin in the Eastern contact area, but east of and distinct from that of AAB African Plantains. AAB Pacific Plantains potentially originate along the north coast of NG or in the Bismarck Archipelago (29) and were dispersed across the Pacific by Austronesian-speaking colonists (30).

The continual relocation of AAcvs by people contributed to the development of numerous other triploid subgroups.
through hybridization with local diploids. For example, the globally distributed commercial AAAs, “Gros Michel” and “Cavendish,” derive genetically from a 2N gamete of the AAcv Mlali subgroup and an N gamete of the AAcv Khai. The northern origin of these AAA—around the Gulf of Thailand or the South China Sea—implies an earlier northwestward dispersal of Mlali from its original Southern contact zone (Fig. 6). Further westward, the Mlali genome reached India and is found in the Indian AAB cv subgroups “Pome” and the genetically proximal “Nendra Padathi” and “Nadan” (Fig. 6). The long dispersal route of these AA cvs from Wallacea to India is supported linguistically by the continuous series of *qal Rutay reflexes from Indonesia over mainland SEA to India (Fig. 5B).

Conclusions

The integration of archaeology, genetics, and linguistics provides robust insights into the history of banana domestication. Further studies, it allows us to clearly identify several major stages in the domestication history of Musa bananas. Early contacts between different Musa genotypes were created by human interactions, whether by migration or exchange. The resultant interspecific and intersubspecific hybridizations generated both parthenocarpic diploids and triploids. Some of these hybrid cvs, whether by preference or by chance, were widely adopted and dispersed. A small number of triploids, perhaps because of the environmental adaptability conferred by triploidy, have been dispersed by clonal propagation across vast areas.

Research on banana cultivation and domestication is a window on often poorly known human/environment interactions within tropical and subtropical rainforests in the past. Additionally, the dispersals of bananas throughout wet tropical and subtropical regions, including around or across the Indian Ocean, are indicators of interlinked, yet predominantly local, social networks extending from NG to West Africa; these networks are at least 2,500 y old. Research on banana domestication demonstrates how multidisciplinary teams, as well as the application of new methods within each discipline, are essential for unraveling complex social processes in the past.

Bananas have contributed over several millennia to the staple diets of numerous peoples in the tropics and subtropics. Current global production of more than 100 million tons is based on large-scale vegetative propagation of a small number of genotypes, which derive from only a few ancient sexual recombination events. These genetically restricted and inflexible clones are particularly susceptible to diseases, pests, and current ecological changes. The challenge for banana improvement is to produce resistant and sterile polyploid hybrids through genetic recombinations of fertile diploids that meet consumer expectations for each cv type. The required breeding strategy will need to reproduce the sequence of crossings and selections that occurred minimally during the past 6,500 y, while substituting punctually some genitors from closely related genomes selected for their level of resistance to biotic and abiotic stresses. Hence, a prerequisite for banana improvement is to reconstruct as precisely as possible the domestication pathways of the major cv groups.

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