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RESEARCH ARTICLE

Ethnolinguistic and genetic diversity of fonio (*Digitaria exilis*) in Senegal

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Societal Impact Statement

Fonio (*Digitaria exilis*—Kippist—Stapf) is a neglected cereal crop that plays a crucial role in the food and nutritional security of sub-Saharan populations. Currently threatened with extinction in many countries, fonio, like other minor species, could help give insights into the history of African agriculture and provide clues to past social interactions. Highlighting and preserving genetic diversity that can be used to develop improved varieties improves food security. By recognizing the role of indigenous people and local communities (IPLCs) in agrobiodiversity creation and management, this study provides support for strengthening the rights of rural communities and promoting their food and seed sovereignty as outlined in the United Nations UNDROP Declaration.

Summary

- Fonio (*Digitaria exilis*) is a neglected cereal crop that plays a crucial role in the food and nutritional security of sub-Saharan populations. It is an excellent candidate to diversify agricultural and food systems beyond Africa because of its adaptability and hardiness. However, fonio is threatened with extinction and the factors that organize its genetic diversity remain unknown, despite the fact that this knowledge is necessary to define conservation strategies and uses to achieve sustainable agriculture.
- Here, we combined social anthropology and population genetics analysis of 158 fonio landraces, thereby generating insight into the genetic diversity, population structure and evolutionary history of fonio cultivation in Senegal.
- We noted a spatial structure of genetic diversity at two embedded levels, with the first corresponding to the genetic differentiation between ethnic groups and the

Adeline Barnaud and Claire Billot made equal contributions.

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second to the demographic history of the Mande and Atlantic Congo linguistic families. Selection and seed exchange practices have contributed to shaping fonio genetic diversity at the ethnic level, while the migration of Fulani people over the last 500 years has fragmented the Mandinka kingdom, hence leaving a fonio diversity imprint.

- Our study highlighted that social factors are pivotal in structuring diversity and should be taken into greater consideration in research and conservation projects to dovetail local and regional scales. It also showed that neglected species such as fonio—which are seldom used in breeding and dissemination programmes—are key markers of the history of African agriculture.

KEYWORDS

agrobiodiversity, biocultural diversity, climate change, human migration, neglected and underutilized species

1 | INTRODUCTION

From the early steps of their domestication and diffusion, crops have temporally and spatially evolved through local adaptation evolved (Berger et al., 2011), sometimes beyond the climatic niches of their wild relatives (Abbo et al., 2014; von Wettberg et al., 2018). Studies carried out over the last decade on crop genetic diversity have transformed our understanding of domestication trajectories, while recognizing that social and historical factors have been spatially and temporally shaping genetic diversity (Diamond & Bellwood, 2003; Jobling et al., 2013; Leclerc & Coppens d'Eeckenbrugge, 2011; Vigouroux et al., 2011). Indeed, recent examples have highlighted how the expansion of human farming communities is associated with the co-diffusion of their crops and languages, thereby providing a genetic footprint of this shared history. The dispersal of Bantu farmers from West Africa led to the spread of 'Kafir' sorghum in sub-equatorial Africa, 1000 years BCE (Ehret, 1998). The ancient Persian Empire shaped common walnut (*Juglans regia* L.) diversity between central and eastern Asia (Pollegioni et al., 2015), while the diversity of sweet potatoes (*Ipomoea batatas*) in Polynesia (Oceania) might be explained by their pre-Columbian migration from South America (Roullier et al., 2013). Furthermore, the cultural diversity of farmers also has an impact on crop genetic diversity (Delêtre et al., 2011; Labeyrie et al., 2014; Naino Jika et al., 2017; Orozco-Ramírez et al., 2016). Social ties (kinship systems, bride wealth, filiation, residential and ethnolinguistic homophilies, etc.) promote the dissemination of plant material among farmers within farming communities, while social barriers (marriage prohibitions between kinship systems, social origin, etc.) limit plant material exchanges between farming communities (Leclerc & Coppens d'Eeckenbrugge, 2011). These latter studies suggest that farmers' social identity has contributed to shaping crop genetic diversity.

In this study we focus on fonio (*Digitaria exilis* [Kippist] Stapf), a West African cereal that is cultivated from Senegal to Nigeria. Fonio

(Figure 1b,c) is a small annual herbaceous plant with a highly self-pollinating reproductive system (Barnaud et al., 2017). Extra-early fonio varieties, which are mature within less than 60 days, allow farmers to overcome the risk of food shortages during the lean season (period before the main harvest) (Adoukonou-Sagbadja et al., 2006; Diop et al., 2018; Vodouhe et al., 2003). Fonio is therefore also referred to as 'hunger rice'. Moreover, fonio has a substantial cultural status and plays a key role in ritual ceremonies of many African cultures (Adoukonou-Sagbadja et al., 2006; Blench, 2016). In recent years, fonio has gained popularity within and outside of West Africa due to its nutritional qualities. Yet the fonio crop area has been dramatically reduced in comparison to its original area, hence threatening its diversity (Adoukonou-Sagbadja et al., 2006; Diop et al., 2018).

In Senegal, in the extreme western part of its distribution area, fonio is cultivated by a diverse range of ethnolinguistic groups belonging to the Atlantic-Congo and Mande language families. Atlantic-Congo language speakers (hereafter Atlantic) are represented by Fulani, Balante, Koniagui, Bassari and Bedik ethnic groups, whereas Mande speakers are represented by Mandinka, Malinke and Dialonke ethnic groups (Figure 2). This region thus offers a unique opportunity to gain greater insight into how social, historical and biological factors interact to shape crop genetic diversity. Here, we investigated the links between fonio genetic diversity and ethnolinguistic diversity at different nested scales—from ethnic groups to linguistic families.

This study addressed several questions. Is spatial genetic structure better explained by social factors, by biological or environmental constraints, or by spatial distance? More specifically, does fonio genetic differentiation correspond to ethnic group differentiation, or to linguistic group differentiation? Answers to these questions will help us understand the extent to which social factors are involved in structuring genetic diversity. This is particularly crucial to define the best sampling and conservation strategies for forgotten crops such as fonio.

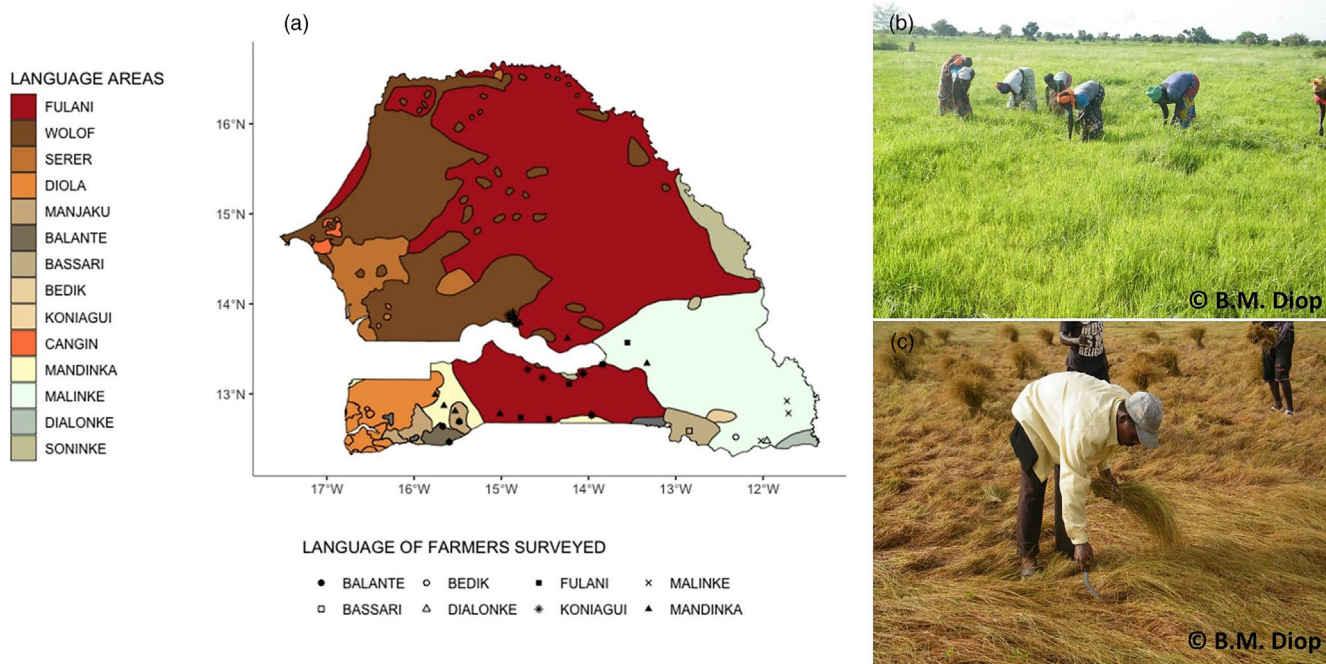


FIGURE 1 Fonio (*Digitaria exilis*) growing areas in Senegal. (a) Fonio sampling location according to the ethnic group map (language data from WLMS 16, www.gmi.org/wlms) and ethnic groups of surveyed farmers. (b) A fonio field during weeding © B.M. Diop–ISRA. (c) A fonio field during harvest © B.M. Diop–ISRA.



FIGURE 2 Classification of languages in Senegal. The upper taxon represents the Mande and Atlantic-Congo language families. The lower taxon represents the Mandinka, Malinke and Dialonke ethnic groups of Mande speakers and the Fulani, Balante, Bassari, Bedik and Koniagui ethnic groups of Atlantic-Congo speakers (source: language data from WLMS 16, www.gmi.org/wlms). The number of fonio accessions sampled according to ethnic groups is indicated in brackets.

2 | MATERIAL AND METHODS

2.1 | Sampling strategy and plant material

Our study area covered the Senegalese fonio production zone (Figure 1a), that is, southern Senegal. The area has a flat relief (24–34 m elevation) except in its southeastern part where the elevation reaches 167 m. Average minimum temperatures ranged from 20.8 to 22.3°C, whereas maximum temperatures were between 35.5 and 36.4°C (Faye et al., 2019). The area lies between isohyets 800 mm in the north and 1200 mm in the south. Our sampling, carried out between October 2013 and March 2014, was focused on the known fonio distribution range, that is, representative of the diversity of the ethnic groups cultivating fonio. Sampling was carried out in 29 villages by an interdisciplinary team, including geneticists, agronomists and linguists. The villages were selected with the assistance of extension agents. In order to be able to consider villages as homogeneous communities, villages located near major roads or markets, as well as large and multiethnic villages, were excluded from the survey. The sampling strategy (see Figure 2) clearly highlighted the representativeness of fonio landraces cultivated by both Atlantic (Fulani, Bedik, Bassari, Koniagui and Balante) and Mandé speakers (Mandinka, Malinke and Dialonke). This information was obtained both from local authorities (regional agricultural development services and village chiefs) and from the farmers concerned.

The geographical position of each village was recorded using a portable Garmin eTrex GPS. One to ten randomly selected farmers were interviewed per village. Social and agricultural data were collected per farmer (Diop et al., 2018). Farmers were also asked, for all landraces grown, whether the seed lot sown in 2013 was of self-produced origin, provided by a neighbour, bought at the market or distributed by a government extension service or NGOs. Farmers were also asked on the uses of each fonio landrace (self-consumption, sale or both). Information on cycle length was collected using complementary approaches, through focus groups, farmer interviews and further phenotyping trials. Two maturing cycle lengths were defined according to farmers' criteria: Early cycles represented <90 days of cultivation and late cycles represented >90 days of cultivation. The robustness of this farmer classification was assessed by common field phenotyping. We found an 84% agreement between the farmers' cycle classification and the cycle lengths obtained from phenotyping (unpublished).

Overall, 158 fonio landraces were collected in bulk or panicles from 144 farmers belonging to different Atlantic and Mandé ethnic groups. This collection is conserved in the national ISRA germplasm collection and in the Biological Resource Center « Seeds Adapted to Mediterranean and Tropical conditions » (CIRAD–INRAE, ARCAD, Montpellier, France).

2.2 | DNA extraction and SSR genotyping

Fresh leaf samples from one plant per accession were collected, and DNA extraction was carried out following the previously described

protocol (Barnaud et al., 2012). Samples were genotyped using the primer 5'-end-M13 tailing procedure, with 14 nuclear microsatellite markers (De04, De05, De06, De07, De08, De14, De15, De17, De19, De24, De25, De34, De37 and De38), according to Barnaud et al. (2012). Positive (three) and negative (one) controls were repeated on each PCR plate to assess the dataset quality. Samples were genotyped on an ABI 3700 sequencer[®] (Applied Biosystems[®]) and sized with GS600LIZ size standard (Applied Biosystems, Foster City, CA). Data were checked for congruence by three different researchers and stored in DataSuds (10.23708/5WDKS1).

2.3 | Data analysis

All statistical analyses were performed using R software (R Core Team, 2018).

2.3.1 | Diversity analysis

Genetic diversity was assessed by estimating the unbiased allelic richness (A_r), the observed (H_o) and unbiased expected heterozygosity (H_e), using `allele.rich` and `basic.stats` functions implemented in the `PopGenReport` R (Adamack & Gruber, 2014) and `hierfstat` R (Goudet, 2005) packages, respectively. These indices were compared between linguistic families, ethnic groups and cycle lengths using pairwise Wilcoxon tests (`pairwise.wilcoxon.test` function) with false discovery rate correction (`stats` R package). The overall and pairwise genetic differentiation among these factors were estimated using the `FST` global fixation index (Weir & Cockerham, 1984). The significant differences were tested using a permutation test (`test.g` function, 1000 permutations). Calculations were carried out using the `hierfstat` R package (Goudet, 2005) at the 5% threshold.

2.3.2 | Genetic structure analysis

Diversity structuring was analysed using: (i) principal component analysis (PCA), (ii) the Bayesian clustering method implemented in `STRUCTURE` (Pritchard et al., 2000), (iii) spatial principal component analysis (sPCA; Jombart et al., 2008), (iv) discriminant analysis of principal components (DAPC; Jombart et al., 2010) and (v) isolation by distance (IBD; Hardy & Vekemans, 2002; Loiselle et al., 1995; Vekemans & Hardy, 2004).

We analysed the population structure using the admixture model with the correlated allele frequencies of the `STRUCTURE` software 2.3.2 (Pritchard et al., 2000). We investigated from $K = 1$ to $K = 10$ ancestral populations. We ran 15 independent replicates per K value of 500,000 burn-in periods followed by 1,000,000 iterations. Outputs were summarized using the `STRUCTURE HARVESTER` package (Earl & vonHoldt, 2012). We evaluated the number of K populations based on Evanno's method (Evanno et al., 2005). For ancestry analysis, we estimated the q parameter according to the simulation with

the highest log probability. We classified individuals in clusters based on an ancestry coefficient of 0.7 or higher.

We also used a model-free method to assess structuring, that is, discriminant analysis of principal components, DAPC (Jombart et al., 2010). We used the `dapc` function of the `adegenet` R package (Jombart, 2008). The `find.clusters` and `k-means` functions were used to determine the number of K clusters (Jombart et al., 2010). The Bayesian information criterion (BIC) was used to identify the optimal cluster number. The number of principal components retained for DAPC analyses was calculated using a cross-validation method implemented in the `xvalDapc` function of the `adegenet` R package (Jombart, 2008).

We first performed sPCA using the `spca` function of the `adegenet` R package to detect and characterize the geographical diversity patterns. The sPCA analyses the genetic diversity spatial patterns considering the spatial autocorrelation. We also assessed the spatial autocorrelation of kinship coefficients between individuals (Loiselle et al., 1995). Mean multilocus kinship coefficient values, F_{ij} , that is, genetic similarity between random individuals in the sample, were regressed according to the linear (d_{ij}) and logarithmic ($\ln [d_{ij}]$) spatial distances between individuals (Hardy & Vekemans, 2002; Loiselle et al., 1995; Vekemans & Hardy, 2004). The geographical distances were calculated as the Euclidean distances. The regression slopes b_d and $b_{\ln d}$ were jointly assessed. Standard errors for the kinship coefficients were estimated using a jackknife procedure over all loci. We tested the significance of the kinship coefficients and the b_d (regression slope of pairwise values on the spatial distance between adjacent individuals) and $b_{\ln d}$ (regression slope of pairwise values on the logarithm of spatial distance) regression slope estimates by comparing the observed values to those obtained after 10,000 random permutations.

Crop genetic diversity is the result of long-term human-environment interactions through crop selection and diffusion, and it can be modelled as a three-way interaction $G \times E \times S$, where S stands for the social differentiation factor (Leclerc & Coppens d'Eeckenbrugge, 2011). We assessed the effect of the environment using the geographical information system (GIS) in DivaGis (<http://www.diva-gis.org/>) to extract 19 climatic variables from the WorldClim database (<http://www.worldclim.org/>). These climate data were summarized using PCA, and axes 1 and 2 were selected for analysis. Permutational multivariate analysis of variance was performed using the `vegan` R package (Oksanen et al., 2013) to assess social (e.g., linguistic family and ethnic group), environmental (e.g., longitude, latitude, and climate) and biological (e.g., cycle length) cofactors in fonio structuring. This nonparametric test involves partitioning the distance matrix in sources of variation (Anderson, 2001). For this analysis, we set 10,000 permutations to estimate the F -statistics and used a significance level of 0.01 to reject the null hypothesis.

3 | RESULTS

The main issue in this study was to investigate whether fonio genetic structure could be better explained by social factors, by biological or

environmental factors, or spatial distance, and more specifically, whether fonio genetic differentiation corresponds to ethnic group differentiation or linguistic group differentiation by testing different nested scales.

3.1 | Genetic diversity

The panel of fonio accessions sampled in this study (158 accessions) is the most exhaustive sampling to date in Senegal. Overall, 132 alleles were detected with 14 nuclear SSR markers, with an average of 9.43 alleles per SSR marker. The number of alleles per marker ranged from 2 (De06) to 43 (De04), with an average of 4% missing data (Table S1). The mean expected heterozygosity (H_e) was 0.43, whereas the mean observed heterozygosity (H_o) was 0.05 (Table 1).

Regarding the genetic diversity, our results revealed no significant differences of expected heterozygosity between the Mande and Atlantic linguistic families (Figure 2), which corresponded to the highest linguistic classification level in our sample (H_e 0.42 vs. 0.40, respectively, MW test, $p = .541$). However, a significant difference was observed regarding allelic richness (7.54 vs. 6.24, respectively, MW test, $p = .024$; see Table 1) and the observed heterozygosity (H_o , 0.07 vs. 0.04, respectively, MW test, $p = .003$), even though H_o was very low (mean 0.05). At the ethnic group level, the average genetic diversity (H_e) of the eight ethnic groups was 0.39 and ranged from 0.29 (Bedik) to 0.47 (Balante). The Balante ethnic group exhibited higher diversity (0.47) as compared to the Bedik (0.29), Dialonke (0.31), Malinke (0.37) and Fulani (0.38) groups (MW test, $p < .05$ for each combination, Mandinka-Bedik, Mandinka-Dialonke, Mandinka-Malinke, Balante-Bedik). Similarly, the Bassari (0.45) had a greater diversity than the Dialonke (0.31) (MW test, $p < .05$). The mean allelic richness was 1.81 (range 1.49–2.01) and was significantly lower in the Bedik, Dialonke and Malinke ethnic groups than in the Balante and Mandinka ethnic groups (MW test, $p < .05$).

Regarding the fonio cycle length, significant differences were observed between late and early-maturing cycles with regard to genetic diversity (mean 0.42; 0.46 vs. 0.38, respectively; MW test, $p = .011$) and to observed heterozygosity (mean 0.05; 0.06 vs. 0.04, respectively; MW test, $p = .014$). But no significant difference was observed for allelic richness (6.71 vs. 6.61, respectively; MW test, $p = .50$).

3.2 | Genetic structure patterns

According to permutational multivariate analysis of variance, the effects of linguistic family, ethnic group and cycle length were significant in structuring fonio genetic diversity, but neither the environment nor the latitude and longitude were significant (Table S2). The comparison of mean sum squares (Anderson, 2001) suggested that social factors (linguistic family 10.5% and ethnic groups 13.5%) had a stronger effect than cycle length (1.3%) in structuring fonio populations (Table S2).

TABLE 1 Summary of the genetic diversity parameters of fonio individuals sampled according to linguistic family, ethnic group and cycle length factors.

	N	Na	F _{is}	Ar	He	Ho
Overall	158	9.43	0.89	8.12	0.43	0.05
Linguistic family						
Atlantic	84	93	0.91	6.24	0.40	0.04
Mande	74	112	0.85	7.54	0.42	0.07
Cycle length						
Early-maturing cycle	93	108	0.85	6.61	0.38	0.04
Late-maturing cycle	65	100	0.94	6.71	0.46	0.06
Ethnic group						
Balante	19	64	0.83	2.01	0.47	0.08
Bassari	6	46	0.31	1.96	0.45	0.27
Bedik	5	25	0.91	1.49	0.29	0.03
Dialonke	7	36	0.96	1.64	0.31	0.02
Fulani	38	68	0.94	1.84	0.38	0.02
Koniagui	21	55	0.9	1.85	0.39	0.03
Malinke	14	51	0.96	1.78	0.37	0.03
Mandinka	48	98	0.88	1.95	0.42	0.05

Note: Ar is an unbiased allelic richness computed for two samples per ethnic group, 62 samples per linguistic family and 44 per cycle length.

Abbreviations: F_{is}, inbreeding coefficient; He, unbiased gene diversity; Ho, observed heterozygosity; N, number of accessions; Na, mean number of alleles.

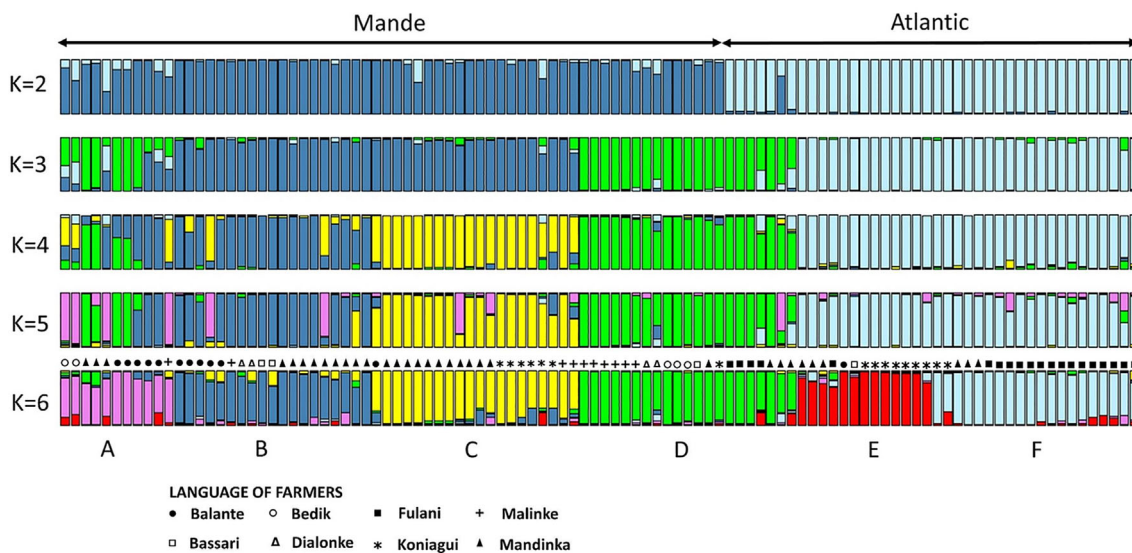


FIGURE 3 Genome plots of each sample in K hypothetical sub-groups obtained using STRUCTURE software (Pritchard et al., 2000). In this study, K ranged from 2 (top) to 6 (bottom). Each accession on the X-axis is represented by K colours ordered by decreasing genome fraction on the Y-axis. For K = 2, the dark blue individuals are located in the Mande language speaking area and the light blue ones in the Atlantic language speaking area. For K = 6: group A encompasses late maturing cycle accessions belonging mainly to the Balante ethnic group, group B late maturing cycle accessions belonging to the Mandinka and Balante ethnic groups, group C early maturing cycle accessions belonging to the Mandinka and Koniagui ethnic groups, group D mainly early maturation accessions (67%) and heterogeneous accessions in terms of ethnic group and spatial distribution, group E early maturation accessions belonging mainly to the Koniagui ethnic group, and group F early maturation accessions belonging to the Fulani ethnic group.

Bayesian analysis showed a successive subdivision of genetic diversity from two to six populations, after which, up to K = 10, no new pertinent group was detected (Figure 3). According to ΔK

statistics (Figure S1), two peaks were noted at K = 2 and K = 5 (Evanno et al., 2005). In the following, we will present the successive groupings with a particular focus on these two values.

The first subdivision obtained by Bayesian assignment (Figure 3, $K = 2$) reflected the differentiation between Mande and Atlantic families. Eighty-five percent of accessions of the first group (59% of all accessions, shown in dark blue in Figure 3 at $K = 2$) were collected among farmers belonging to the Mande family in the eastern and western parts of our study area. Ninety percent of accessions of the second group (38% of all accessions, in light blue in Figure 3 at $K = 2$) were collected among farmers belonging to the Atlantic family in the central part. Three percent of the accessions were of mixed ancestry (i.e., individuals whose ancestry to a given group is below 70%). These results were consistent with the genetic diversity spatial structure obtained via sPCA (Figure 4a), thus reflecting the diversity spatial organization. The F_{ST} calculated between the Mande and Atlantic families was low but significant ($F_{ST} = 0.031$, $p = .001$).

The sPCA revealed a significant ($p = .004$) overall structure, with the first principal component showing a low autocorrelation (Moran's $I = 0.013$). Moreover, no IBD pattern was observed when considering the whole sample ($p = .513$), or within the Atlantic ($p = .261$) and Mande ($p = .136$) families, with low slope values for both regions (bslope-Mande = -1.07×10^{-4} and bslope-Atlantic = -5.17×10^{-4} , respectively) (Figure S2). Similar results were obtained for logarithmic

geographic distances (bslope-Mande = -1.09×10^{-4} and bslope-Atlantic = -1.64×10^{-2} , respectively). This lack of IBD on the spatial organization of genetic diversity (sPCA) suggests that farmers moved with their plants, and also that the adoption of neighbours' crops was not commonplace and that their crop genetic identity had been spatiotemporally maintained.

Subsequent Bayesian analysis subdivisions (Figure 3, $K = 3$ to 6) highlighted diversity patterns related to ethnic groups (corresponding to the lowest classification level in our sample, Figure 2) and cycle length. At $K = 6$, two thirds (104) of the accessions could be assigned to one of the six groups. Group A (11 accessions) and Group B (19 accessions) consisted mainly of late-maturing cycle accessions (91% of Group A, 89% of Group B) from Balante (45% of Group A and 26% of Group B) and Mandinka (47% of Group B). The remaining four groups consisted mainly of early-maturing cycle accessions: group D presented 67% (21 accessions) of early-maturing cycle accessions with no direct link with ethnic groups or geographical origins, while the other three were well differentiated by ethnic origin. Group C included early maturing cycle accessions (20 accessions, 80%) belonging mainly to Mandinka (55%) and Koniagui (30%) ethnic groups. Group E included early maturing cycle accessions (13 accessions,

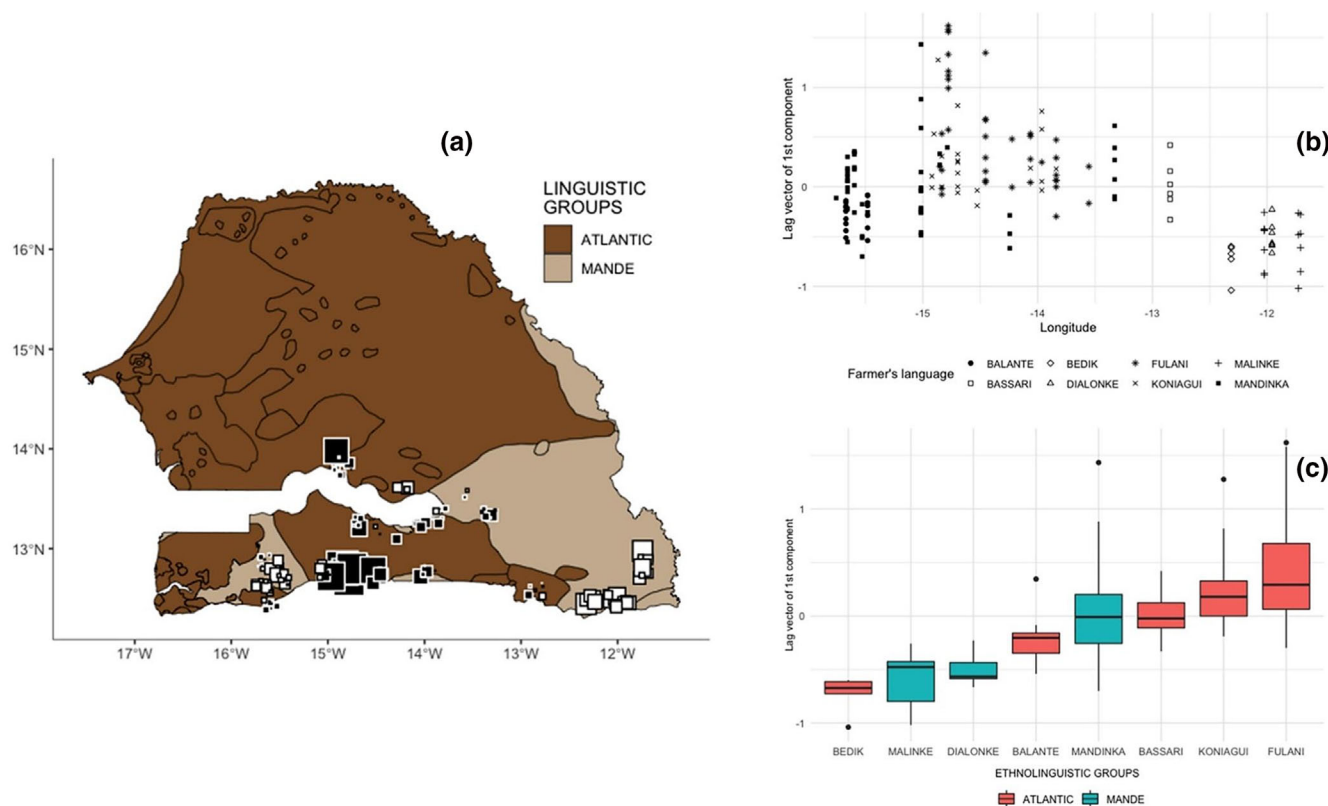


FIGURE 4 Spatial principal component analysis (sPCA) for fonio in southern Senegal. (a) Assignment of individual genotypes to their population of origin. Black and white squares represent individual genotype scores on the first principal component (the only significant PC). Large white squares indicate individuals with highly negative values; large black squares indicate individuals with highly positive local values; and the square dimension is proportional to the degree of differentiation (high for large squares, low for small squares). The base map in light brown corresponds to the distribution area of the Mande linguistic group and the area in dark brown corresponds to the distribution area of the Atlantic linguistic group (source: language data from WLMS16 www.gmi.org/wlms). (b) Distribution of ethnic groups on the first sPCA component according to longitude. (c) Average distribution of ethnic groups on the first sPCA component.

91%) belonging mainly to the Koniagui (61%) ethnic group. And finally, Group F (20 accessions) encompassed all early-maturing cycle accessions belonging mainly to the Fulani (75%) ethnic group. These results suggest that fonio genetic diversity organization has been historically shaped by different farmers' ethnic identities, with, accordingly, the uses of early or late-maturing landraces.

The DAPC scatter plot across all samples revealed overall congruence with the Bayesian assignment at $K = 6$ (chi-squared test, p -values for each group cluster, Group A-Cluster 1 = 0.348, Group B-Cluster 3 = 0.528, Group C-Cluster 4 = 0.295, Group D-Cluster 2 = 0.062, Group E-Cluster 6 = 1, Group F-Cluster 5 = 0.005; Table S3, Figure 5a,b,c). It showed an effect of cycle length and ethnic group on fonio genetic diversity ($Q_{\text{membership}}$, chi-squared, linguistic family = 0.001, ethnic group = 0.0002, cycle = 4.6×10^{-7}). Clusters 1 and 3 were characterized by late-maturing cycle landraces, as opposed to clusters 4, 5 and 6, which were characterized by early-maturing cycle landraces, whereas cluster 2 was more heterogeneous, with a predominance of early-maturing cycle landraces. In terms of social identity, cluster 1 was closely related to the Balante and Malinke ethnic groups, cluster 2 to the Bedik and Malinke, cluster 3 more heterogeneously to the Mandinka, Koniagui and Bassari, cluster 4 to the Dialonke, cluster 5 to the Fulani, and cluster 6 to the Koniagui and Bassari (Figure 4c). Similarly, there were significant

differences (FST, mean 0.054; range -0.038 to 0.18 , Table S4, $p = .001$) between ethnic groups.

Finally, the overall FST calculated between the early- and late-maturing cycles was low but significant (FST = 0.065, $p = .001$). The ethnic group and fonio cycle length contingency table revealed that the Balante were significantly associated with late-maturing cycle landraces (chi-squared residual = 2.48), while the Fulani were associated with early-maturing cycle landraces (chi-squared residual = 1.85), thereby suggesting ethnic group preferences for different cycles.

The sPCA results allowed us to gain further insight into the social and spatial organization of fonio genetic diversity cross-analysis of the lag vector of sPCA and longitude (Figure 4b) showed that Malinke and Dialonke ethnic groups occupied low positions with a strong negative contribution (large white squares on the sPCA map). The Mandinka had variable values but with many in negative positions; the western Mandinka were almost at the same level as Malinke and Dialonke in terms of negative contribution. The Fulani values were in the positive range (large black squares in the sPCA map). Note that as the Mandinka moved closer to Fulani farmers their plants became more heterogeneous and closer to those of the Fulani farmers (Mandinka plants in the Atlantic area were not different from Fulani plants, FST = 0.017, $p = .736$, but were different from Mandinka plants located in the Mande area, FST = 0.039, $p = .032$). Similarly, as the

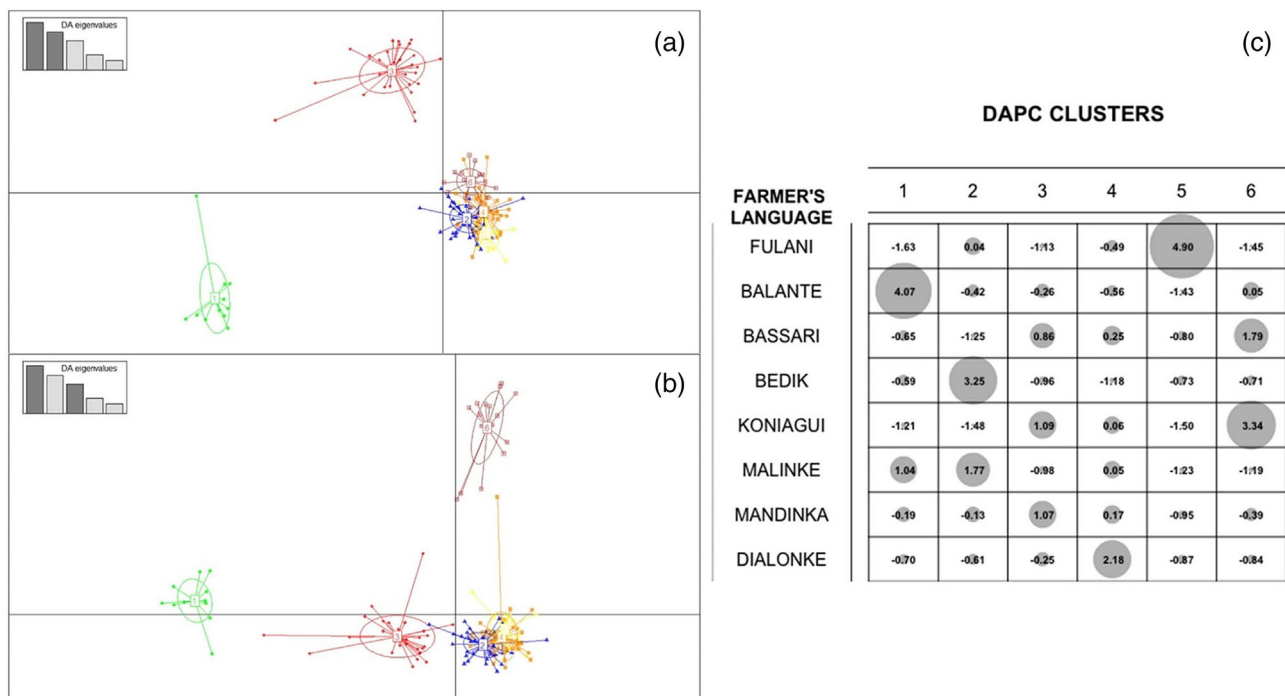


FIGURE 5 Discriminant analysis (DA) of principal component (DAPC) scatter plot of individuals based on 14 SSR markers. Fifty principal components (PCs) and four discriminant functions (dimensions) were retained in the analyses to describe the relationship between clusters. In (a), the first axis separates clusters with late-maturing cycles (clusters 1 and 3) from clusters with early-maturing cycles (clusters 2, 4, 5 and 6), and the second axis separates clusters 1 and 3. In (b), the third axis clearly separates cluster 6 (Koniagui) from other clusters with an early-maturing cycle. Each colour represents a cluster of individuals from the same genetic cluster. (c) shows the chi-squared residual between ethnic groups and clusters from the DAPC. The size of grey circles indicates the strength of association between ethnic groups and the six genetic groups. Balante, Bedik, Dialonke, Fulani and Koniagui ethnic groups were significantly associated with clusters 1, 2, 4, 5 and 6, respectively. Positive (>1.96) or negative (<-1.96) Pearson's residual values allowed us to identify which cells individually contributed to reject the independence (Agregi, 2007; Meyer et al., 2006; Patefield, 1981).

Fulani moved eastwards towards the Malinke and Dialonke areas, they occupied a lower position in the figure. Intermediate or even contradictory positions were noted between the Fulani and Malinke–Dialonke poles. The Bedik were very close to the Malinke–Dialonke, whereas they were expected to be closer to Tenda (Koniagui–Bassari). The boxplot (Figure 4c) shows that the contributions were structured mainly between the Fulani (higher value) and the Malinke (lower value). This could explain the differences between the Atlantic and Mande linguistic families noted with structure at $K = 2$ and sPCA.

4 | DISCUSSION

The main focus of this study was to investigate whether fonio genetic structure is better explained by social factors, biological or environmental factors or spatial distance, and more specifically, to assess the links between fonio genetic diversity and ethnolinguistic diversity at two different nested scales, that is, ethnic group and linguistic family. We found that fonio spatial genetic structure was better explained by social factors than by biological, climatic and spatial distance at local scale.

4.1 | Social boundaries and fonio genetic diversity

Fonio genetic diversity was structured in six genetic clusters, which correspond quite well to ethnic and social groups of farmers. This social organization of diversity has been highlighted in other crops, for example, sorghum (Labeyrie et al., 2014, 2016), maize (Orozco-Ramírez et al., 2016; Perales et al., 2005), cassava (Delêtre et al., 2011) and pearl millet (Naino Jika et al., 2017). The hypothesis is that there are ethnic barriers to seed flow that contribute to the social structuring of genetic diversity. For instance, Naino Jika et al. (2017) found a clear link between the spatial structure of pearl millet populations and boundaries between ethnolinguistic areas, which they explained by the highly symbolic value of pearl millet for different ethnolinguistic groups, thereby probably constituting a strong social constraint to seed exchange. Similarly, Labeyrie et al. (2014) showed that overall sorghum genetic diversity patterns were associated with the ethnic partitioning of farmers in a limited area on the Mount Kenya slope. They argued that ethnic groups preserved different local sorghum varieties, whereas improved varieties were evenly distributed among groups. Orozco-Ramírez et al. (2016) similarly highlighted a relationship between the cultural differentiation of two different adjacent communities in Mexico and maize genetic diversity. They also argued that a lack of seed flow between communities could explain this result.

In the same way, social links and boundaries have shaped the fonio diversity by facilitating or not the circulation of seeds among ethnic groups. For instance, Koniagui and Bassari landraces have the same genetic background. This is not surprising as the two ethnic groups share the same customs and often intermarry (Gessain, 1963). Indeed, seeds are reported to often circulate through existing social

networks such as marriages (see, for example, Garine et al., 2019). Similarly, Malinke domination over the Bedik ethnic group, that is, originally hunter-gatherers (Ndong, 2009), probably resulted in joint adoption of the Malinke surname and fonio landraces, as is the case for other hunter-gatherer populations in agricultural expansion (Downs, 1964), but also through intermarriages (Charest, 1969; Chataigner, 1963). Furthermore, the difference between Balante and Fulani, as shown by the strong association of Balante in cluster 1, the repulsion to Fulani in cluster 5, and vice versa (Figure 5c), could be explained by the fact that the Balante did not tolerate any form of cohabitation before the Mandinka infiltration in the mid-20th century (Pélissier, 1966), and that the Fulani group is characterized by its conservatism and its strong endogamy (Fanchette, 2011; Sow, 2019). Finally, the genetic difference between Balante and Fulani fonio is reinforced by the difference in fonio uses. Balante farmers mainly grow late-maturing landraces while Fulani farmers grow early-maturing landraces. Early-maturing landraces are used for food shortage while late-maturing landraces are used for food and market sale (Diop et al., 2018).

The links between genetic diversity structuring and the social organization of societies are complex and require in-depth knowledge that can only be gained through interdisciplinary approaches. For instance, Balante and Mandinka fonio differ despite the Balante adoption of the Mandinka language. Indigenous peoples sometimes adopt the language of expansionist populations, with little or no cultural exchange (Cavalli-Sforza et al., 1994). This is probably the case for the Balante because the main features and techniques used have remained typically Balante (Pélissier, 1966). These Balante and Mandinka cultural differences may have limited seed flow between farmers' communities, thereby ensuring the genetic differentiation between their crop populations.

The spatial analysis confirmed the social inprint on fonio genetic diversity. Indeed, there was no IBD within genetic groups (Figures 4a, 52). This highlights the role of farmers' seed circulation within ethnic groups in shaping crop genetic diversity. For instance, although Koniagui people were widely distributed (70 km on average), their fonio landraces were found to be more similar to each other than to neighbouring ethnic groups (Figure 5c).

These genetic diversity patterns have been maintained over time until now because they are reinforced by the fonio autogamous reproductive system and seed management practices. In Senegal, almost all of the surveyed farmers (99%) produced their own seeds—each year, they saved the amount of seed necessary for the next sowing. Farmers showed a clear preference for their own landraces (inherited or obtained from their immediate environment), which they considered to be more suitable and reliable. Trust is once again fundamental when it comes to seeds and subsequent food security (Badstue et al., 2006). For the first acquisition, fonio seeds were commonly transmitted vertically from parents to children (for 75% of our farmers), while in times of scarcity, farmers interact with neighbours with the same landraces (10%) to replenish their seed stocks. When this fails, they rely on local markets (12%) and, to a lesser extent, on NGOs (3%) (Diop et al., 2018).

4.2 | Historical human migration shaped the spatial genetic structure of fonio

We have shown the impact of farmer's ethnic identity on fonio diversity organization in the previous section. In our study, historical human migration also shaped fonio genetic diversity on a higher spatiotemporal scale corresponding to the linguistic families (Figures 3 and 4a). These human migrations are probably drivers of the diversification of fonio names. Actually, the Mande roots of fonio indicate a major expansion of the culture around 2000 to 3000 years ago, marked by numerous borrowings of culture names following the establishment of the main (mainly Atlantic) language groups (Blench, 2006). We found an astonishing close correspondence between the spatial genetic structure in two populations and the boundaries of the two linguistic families. Although the presence of fonio is well documented in Senegal since the first millennium AD (400–600 AD at Cubalel in the Senegal River valley) (Gallagher et al., 2018), we no longer find fonio cultivation activities in this zone. Therefore, the expansion of the Mali Empire (Mande linguistic family) into southern Senegal from the 12th century onwards, accompanied by Mandinka, Malinke and Dialonke conquests (Niane, 1989), is mainly responsible for the observed spatial genetic structure. While Malinke and Dialonke migrations stopped in the eastern part of Senegal, Mandinka migrations continued into the western part. In the eastern part, Malinke migrations have, in particular, prevailed over Bedik, Bassari and Koniagui migrations. This domination was such that Bedik had names given according to their social status equivalent to those of Malinke people (Charest, 1969; Ferry, 1967). In the western part, Balante, which are known for their hostility towards foreigners (Ly-Tall, 1984), underwent changes in their social organization after the Mandinka infiltration during WW1 (Pélissier, 1966). In the centre part, Fulani (Atlantic family) fostered conflictual links with Mandinka people. The Fulani are of diverse origins, that is, Macina (Mali), Bundu (Senegal) and Fouta Jalon (Guinea) (Ngaidé, 2012). Their first migrations, probably in search of pasture for livestock (Pélissier, 1966), date back to the 12th century, at the same time as the first Mande migrations (Niane, 1989). Nevertheless, the greatest Fulani migrations were linked to the conquests of Koly Tenguella and his brothers, from the Fouta Jalon massif (Guinea) to Fouta Toro (northern Senegal) at the beginning of the 15th century (Barry, 1988), hence favouring the wide dispersion of Fulani populations across Senegambia. In the mid-19th century and taking advantage of the weakening of the Mali empire, Fulani rebelled and pushed their Mandinka oppressors westwards (Ngaidé, 2012; Niane, 1989). The Mande linguistic family has thus dominated the entire fonio production area since the 12th century, with more or less close relations with other linguistic groups. The observed fonio spatial genetic structure suggests that Fulani migrated with their plants but did not exchange them despite their immersion in a completely different linguistic area (Figures 3 and 4a, $K = 2$). Nevertheless, plants of ethnic groups become more heterogeneous as they move away from their area of origin (Figure 4b). Thus, the spatial structure of fonio genetic diversity is supported by the Fulani ethnic

group in the Atlantic family and by the Malinke ethnic group in the Mande family (Figure 4b) at the border of their area of origin. Combined linguistic and genetic analysis can generate solid insight into the historical and cultural processes (Perrier et al., 2011) involved in fonio evolution, as shown with regard to several other crops worldwide, for example, potatoes in Polynesia (Roullier et al., 2013), banana in the Pacific areas (Perrier et al., 2011), sorghum in Africa (Westengen et al., 2014) and common walnut in Asia (Pollegioni et al., 2015).

5 | CONCLUSION

The main aim of this study was to investigate the links between fonio genetic diversity and ethnolinguistic diversity at different nested ethnic group to linguistic family scales. We showed that the fonio genetic diversity pattern is the result over time of a combination of social (human migration, social barriers) and uses (cycle length) factors, which are constantly coevolving. Crop diversity is often analysed through the lens of individual farmer's choices in response to environmental changes (Lacy et al., 2006), while neglecting social factors such as social organization (Wilkus et al., 2018) and human migration, which are largely involved in seed circulation. Our study highlighted how cultural and social anthropology—through the analysis of human, intermarriage, seed inheritance and exchange practices—and migration can contribute to understanding crop genetic diversity, while also highlighting the need to consider them in the assessment of biocultural diversity for the management of crop genetic resources and farmers' seed sovereignty.

AUTHOR CONTRIBUTIONS

Baye Magatte Diop, Mame Codou Guèye, Adeline Barnaud and Claire Billot designed the research. Baye Magatte Diop, Mame Codou Guèye, Monique Deu, Leila Zekraoui, Justin Raymond Kaly, Omar Diack, Ablaye Ngom, Angélique Berger, Momar Cissé and Marie Piquet contributed to the collection of plants accessions and ethnobotanical data. Baye Magatte Diop, Leila Zekraoui, Carolina Calatayud, Ronan Rivallan and Marie Piquet performed molecular analyses. Baye Magatte Diop, Adeline Barnaud, Christian Leclerc and Claire Billot performed population genetic and anthropological analyses. Baye Magatte Diop, Mame Codou Guèye, Christian Leclerc, Adeline Barnaud and Claire Billot wrote the paper with inputs from Yves Vigouroux, Ibrahima Ndoeye, Khadidiatou Ndir and Ndjido Ardo Kane. All authors have read and approved the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in DataSuds repository (IRD, France) at [10.23708/5WDKS1](https://doi.org/10.23708/5WDKS1). Data reuse is granted under CC-BY licence.

ETHICS STATEMENT

This study was carried out in compliance with the principles of the International Society of Ethnobiology Code of Ethics (International Society of Ethnobiology, 2006), as well as social customs of the ethnolinguistic groups in southern Senegal. The project scope and data collection were clearly disclosed and approved prior to the fieldwork during meetings with village leaders and local administrators. All farmers were individually asked for their oral prior informed consent before all interviews and seed collection operations. A material transfer agreement was signed to frame the exchange of materials and data within the research consortium.

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