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BRIEF REPORT

Towards conservation and sustainable use of an indigenous crop: A large partnership network enabled the genetic diversity assessment of 1539 fonio (*Digitaria exilis*) accessions

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Social Impact Statement

The use of neglected and underutilized species (NUS) in agrosystems is a potential solution to the challenges arising from global change. These species could contribute to the equitable diversification of agricultural systems. Providing knowledge on their genetic diversity and fostering access to data and results is essential for the development of strong collaborative future research. The study addressed these issues by assessing the diversity of the largest fonio (*Digitaria exilis*) collection existing to date. Associated with a user-friendly Shiny application (<https://shinyapps.southgreen.fr/app/foniodiv>), our results reinforce research efficiency and broaden the prospects for all actors involved in enhancing fonio and indigenous crops as valuable resources for the future.

Adeline Barnaud and Claire Billot contributed equally.

For affiliations refer to page 7.

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KEYWORDS

climate change, diversification, millets, neglected and underutilized species, Shiny application, West Africa

1 | INTRODUCTION

Agrobiodiversity conservation is a key concern for agriculture, food and human health (FAO, 2020). However, agrobiodiversity has declined considerably with the agriculture intensification thrust that prevailed in the 20th century. Although thousands of wild plants and crop species have been used throughout human history, only a few dozen of them currently represent a major food supply to sustain humankind. Overreliance on a limited number of genetically uniform high yielding crops makes food supply vulnerable and increases the risk of micronutrient deficiencies (Beal et al., 2017). There is thus growing consensus that agriculture diversification is key in the quest to build sustainable agrosocio-systems with enhanced productivity and resilience to increasing environmental hazards (Hertel et al., 2023).

Smallholder farming systems worldwide are still based on a diverse range of local crops and landraces, with farmers serving as agrobiodiversity custodians (Bellon & Brush, 1994; Ricciardi et al., 2021). This is particularly the case for neglected and underutilized species (NUS) that are critically important genetic resources. Although these species received limited attention from global research, which explain why they are referred to as 'neglected', they have the potential to play numerous roles in improving food production and quality, especially in harsh environments (Hunter et al., 2019; Stamp et al., 2012; Ulian et al., 2020). They are often of socio-cultural importance, while representing valuable sources of livelihood and income for both men and women, particularly marginalized groups. Current attention on these locally adapted crops is increasing, but they are still largely understudied and untapped. Providing knowledge on these genetic resources could foster their wider use in national and local food systems, while over-exploitation must be avoided to best conserve this agrobiodiversity and avoid threatening smallholder farming systems.

White fonio (*Digitaria exilis* [Kippist] Stapf) is a small domesticated cereal that is cultivated in West Africa (Figure 1). It is a crucial food resource for smallholder farmers located in arid and semi-arid areas. Fonio feeds several million people and contributes to food security at local and regional levels throughout a region stretching from Senegal to Nigeria (Vodouhe et al., 2007). The origin and history of this crop remain unclear. Based on areas of varietal diversification and linguistic roots of vernacular names, fonio cultivation is thought to have emerged around the Inner Niger delta before spreading eastward to Nigeria (Blench, 2016; Portères, 1976). But the oldest fonio archaeobotanical remains were recovered in central Nigeria and are dated to the early first millennium AD (Champion et al., 2023). Despite its importance, the low yields and post-harvest difficulties (e.g., dehusking) associated with fonio have sometimes led farmers to replace it with other staple or

cash crops such as maize and cotton (Dansi et al., 2010). While these high-yield crops require relatively fertile soils, fonio cultivation is adapted to marginal land, drought and sandy soils (Vodouhe et al., 2007). Plus, fonio plays a crucial role during the hunger season, with short flowering cycle varieties being harvested before major food crops have reached maturity. Fonio is hence otherwise known as 'hungry rice'. Described as a 'treasure' by Vodouhe et al. (2007), the taste of small-grained fonio is very appreciated, while the seeds contain high levels of essential sulphur-containing amino acids, with almost twice the amount of methionine compared with maize, sorghum or rice (Cruz et al., 2016; Jideani & Jideani, 2011). Beyond its agronomic and nutritional value, fonio often has high social value in local communities, playing numerous roles in ritual ceremonies (Adoukonou-Sagbadja et al., 2006; Diop et al., 2018). Large-scale characterization of white fonio genetic resources—given the contribution of this staple crop to food and nutrition security in West Africa—is essential to ensure its conservation and sustainable use.

Yet few studies have focused on fonio genetic diversity. The first genetic studies relied on dominant markers, including random



FIGURE 1 A cultivated fonio field in Guinea (top), inflorescences of white fonio showing panicles bearing racemes (bottom left) and white fonio racemes with ready to harvest seeds (bottom right). Adeline Barnaud ©.

amplified polymorphic DNA (RAPD) (Hitu et al., 1997), and amplified fragment length polymorphism (AFLP) (Adoukonou-Sagbadja, 2010; Adoukonou-Sagbadja et al., 2007, 2010) markers. The recent development of simple sequence repeat (SSR) markers, single nucleotide polymorphism (SNP) markers and other genomic resources has paved the way for better characterization of fonio genetic diversity (Abrouk et al., 2020; Barnaud et al., 2012; Ibrahim Bio Yerima et al., 2021; Olodo et al., 2019; Sarah et al., 2017; Wang et al., 2021). Fonio was shown to feature a highly self-pollinating system (Barnaud et al., 2017) and to be geographically structured to a great extent by ecological and social factors (Abrouk et al., 2020; Ibrahim Bio Yerima et al., 2021).

However, genetic analyses have never considered the full geographical distribution of fonio in West Africa. Among the 157 white fonio landraces analysed by Abrouk et al. (2020), only a few accessions were sampled in some countries, while two key countries, namely Nigeria and Senegal, which are at the edge of the fonio distribution area, were not considered at all. Then Ibrahim Bio Yerima et al. (2021) assessed the genetic diversity of 259 fonio accessions from six countries, but accessions from Senegal, Côte d'Ivoire, Ghana and Togo were overlooked. Hence, so far, no full-scale assessment of fonio genetic resources has been carried out. Moreover, the challenges with regarding agrosystem diversification are not only to produce knowledge and resources but also to create innovative approaches to foster connections between national and international stakeholders involved in promoting fonio as a valuable potential contributor to agriculture sustainability. In this paper, we used SSR markers to evaluate the genetic diversity of the largest fonio collection available so far, consisting of 1539 accessions from the entire fonio distribution area in West Africa. We also developed an application using Shiny R scripts to interactively explore the genetic diversity of our dataset, thereby boosting prospects for future academic and non-academic collaboration to make effective and sustainable use of the adaptive potential of fonio genetic resources.

2 | MATERIALS AND METHODS

2.1 | Plant material

A total of 2372 fonio accessions representative of the entire crop range were collected or shared between 1977 and 2021 in the framework of different research projects involving multiple collaborations between French and African research institutions. This seed collection is preserved in Montpellier (GAMeT Resource Center, ARCAD and IRD France) and in national genebanks (e.g., GBioS/UAC Benin).

2.2 | DNA extraction and SSR genotyping

For each of the 2372 accessions, 10 individuals were germinated under greenhouse conditions. Total genomic DNA was extracted from

ground fresh leaf tissue from one to seven plants per accession according to the modified CTAB protocol (Doyle & Doyle, 1990). A total of 14 polymorphic and easily scorable SSR loci were selected from previous studies (Barnaud et al., 2012). The forward primer of each SSR was 5'-end-labelled using the M13 tailing procedure (Schuelke, 2000). Genotyping was performed according to the methods described by Barnaud et al. (2012). PCR fragments were separated on an ABI PRISM 3730 DNA Analyzer (Applied Biosystems, Foster City, Calif., USA) and sized compared to the GS600LIZ size standard (Applied Biosystems, Foster City, CA). Genotyping data were scored automatically and verified manually using GeneMapper version 3.7 (Applied Biosystems, Foster City, CA.). We performed double reading of the profiles and used negative and positive controls. Individuals having more than two missing genotypes among the 14 SSR markers were removed. Clones were also removed for population genetic structure analyses. We thus focused on a total of 1539 unique and high-quality genotyped individuals spanning the entire current *D. exilis* distribution range. Among these 1539 individuals, 1352 were associated with geographical coordinates.

2.3 | Population genetic structure

For each locus, we assessed the level of genetic diversity with the adegenet v2.1.5 R package (Jombart, 2008) by computing the number of alleles, the observed and expected heterozygosities (H_o and H_e), the F_{IS} value and the proportion of missing data.

We first assessed population genetic structure via principal component analysis (PCA) using the dudi.pca function implemented in the ade4 v.1.7-19 R package (Dray & Dufour, 2007). Missing data were replaced by the mean allele frequencies using the scaleGen function in the adegenet v.2.1.5 package (Jombart, 2008). The population genetic structure was then described using the individual-based Bayesian genetic assignment method implemented in STRUCTURE v.2.3.4 (Pritchard et al., 2000). We ran 15 independent runs per K value, ranging from 1 to 12, using a burn-in period of 20,000 steps followed by 100,000 Markov Chain Monte Carlo iterations, with admixture and correlated allele frequency models. Outputs were processed with CLUMPP v.1.1.2 (Jakobsson & Rosenberg, 2007) in order to find the best alignment among each replicate run. The resulting matrices and barplots were displayed using the pophelper v2.3.1 R package (Francis, 2017). We determined the most-likely number of genetic clusters (K) with Evanno's method implemented in the *evannoMethod-Structure* function in the pophelper v2.3.1 package, which identifies the optimal K based on the rate of change in the log likelihood between successive K values (Evanno et al., 2005). We then used the *ggts3Q* function of the tess3r R package (Caye et al., 2016) to interpolate ancestry coefficients of the 1352 georeferenced accessions. Finally, we co-analysed the inferred fonio genetic diversity structure with *WorldClim* v2.1 bioclimatic variables that represent extreme, annual and quarter trends related to temperature and precipitation (<https://www.worldclim.org/data/bioclim.html>). WorldClim data correspond to a set of global climate layers (climate grids) with a spatial

resolution of 2.5 arc minutes (approximately 5×5 km) that were obtained through interpolation of climate station records from 1970 to 2000. We performed PCA on the 19 bioclimatic variables extracted for the 1352 georeferenced accessions, followed by a multivariate analysis of variance (MANOVA) on the first two principal components, with the genetic structure inferred at $K = 6$ as the grouping variable for non-admixed accessions (membership coefficients >0.65).

2.4 | Interactive application

We developed an open-access and web-based Shiny application to provide users an interactive way to explore and view the dataset and results. We used the open-source JavaScript library leaflet (<https://rstudio.github.io/leaflet/>) associated with the Plotly R open source graphing library (<https://plotly.com/r/>). This application returns an interactive map and PCA plots in which points can be selected and viewed on the map. Passport information on the selected points are returned in a data table. This tool may be accessed at: <https://shinyapps.southgreen.fr/app/foniodiv>.

3 | RESULTS

The aim of this paper was to evaluate, using SSR markers, the genetic diversity of the largest fonio collection available so far, consisting of 1539 *D. exilis* landrace accessions from the entire distribution area. We investigated the extent to which our results corroborate and specify the previous knowledge on the fonio population structure.

3.1 | Genetic dataset

All 14 SSRs were polymorphic and revealed a total of 195 alleles, with an average of 1.88% of missing data (Table 1). The mean observed heterozygosities (H_o) were much lower than the expected heterozygosities (H_e), so the F_{IS} values were close to one for all markers.

3.2 | Population structure

The first PCA axis (1.95% of the total variance) revealed three main groups (Figure 2b): Nigeria and Togo, Ghana, and Guinea and Central West Africa (Mali, Burkina Faso, Niger). The majority of the accessions from Central West Africa clustered at the middle of the plot and differed from most accessions from Ghana (negative PCA 1 values) and from accessions from southern Togo and Nigeria (positive PCA 1 values, Figure 2b; Figure S1). The second axis (1.62% of the total variance) differentiated this last group from the Guinean accessions.

Otherwise, the application can display the second and third components of the PCA. By selecting accessions with higher PC3 values, landraces cultivated at the northern limit of the fonio distribution range were highlighted (Figure S2).

Evanno's criteria (ΔK) of the STRUCTURE analysis indicated that our dataset could be best described with six genetic clusters (Figure S3), although a structuring in three genetic groups was almost equally supported, as observed with the PCA (Figures S3 and S4). Considering higher K values did not reveal any clear new cluster (Figure S5). The barplots at $K = 6$, associated with the interpolation map of ancestry coefficients (Figure 2c,d), showed a strong spatial pattern of genetic diversity. Accessions from Nigeria and southern Togo belonged to the same genetic cluster (purple). The majority of Ghanaian accessions clustered together with a few individuals from Burkina Faso, Benin and Togo (Figures 2c,d and S6). Accessions originating from western and eastern Guinea belonged to different genetic groups (blue and yellow, respectively), with the latter more related to southern Mali and Senegal. Niger accessions mainly grouped in one cluster (grey) that also contained accessions from central Mali, while the light blue cluster around the Dogon region and northern Burkina Faso made a discontinuity between Niger and Mali. However, while we detected a strong geographical pattern, some geographically close accessions from the same country or not belonged to distinct genetic groups (Figures 2c and S6).

The PCA performed on the 19 bioclimatic variables revealed many correlations between the variables (Figure S7a). We found a significant effect of the genetic groups inferred by STRUCTURE at $K = 6$ on the values of these variables, represented by the two principal components (MANOVA, $F = 115.78$, $p < .001$). Raster maps of four bioclimatic variables associated with PC1 and PC2 are represented in Figure S7b.

TABLE 1 Names and genetic diversity parameters listed for the 14 microsatellite loci used to genotype the entire fonio (*Digitaria exilis*) collection. Summary statistics were computed on the 1539 *D. exilis* accessions successfully genotyped and further used in population structure analyses.

Locus	#N	H_o	H_e	F_{IS}	% NA
De_05	11	0.044	0.623	0.929	0.004
De_07	6	0.012	0.165	0.925	0.010
De_15	7	0.016	0.129	0.873	0.012
De_17	4	0.013	0.187	0.930	0.012
De_22	3	0.003	0.060	0.956	0.014
De_24	12	0.060	0.659	0.909	0.007
De_25	14	0.086	0.763	0.888	0.016
De_34	7	0.017	0.172	0.900	0.015
De_36	3	0.022	0.349	0.938	0.010
De_37	47	0.113	0.953	0.882	0.027
De_38	7	0.038	0.507	0.925	0.010
De_04	53	0.120	0.964	0.875	0.118
De_08	10	0.055	0.526	0.896	0.003
De_29	11	0.016	0.486	0.968	0.004

Abbreviations: F_{IS} , inbreeding coefficient; H_e , expected heterozygosity; H_o , observed heterozygosity; #N, number of alleles; %NA, proportion of missing genotype.

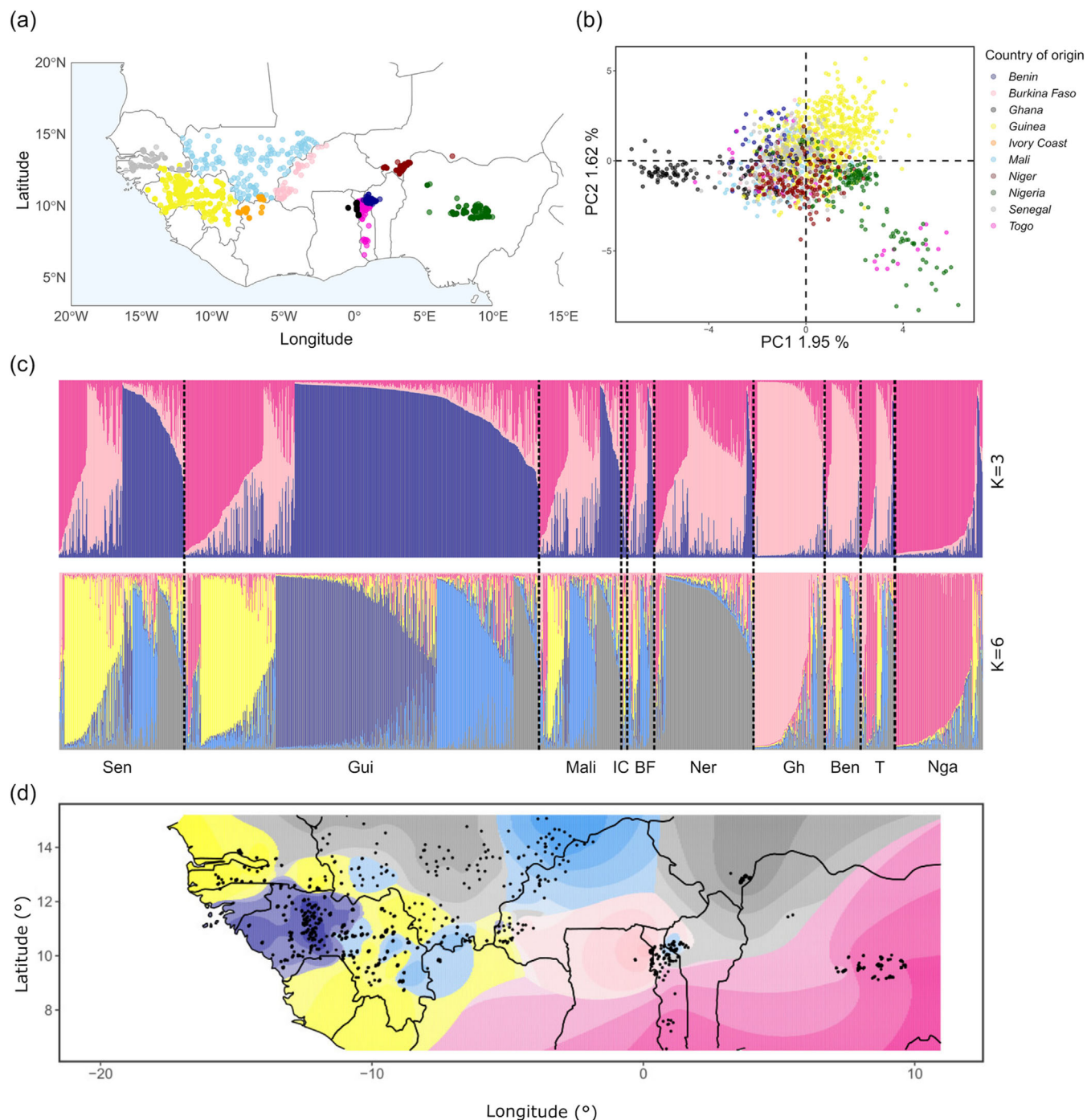


FIGURE 2 White fonio collection and genetic structure assessed for 1539 individuals distributed throughout the fonio cultivation range. (a) Map of West Africa showing the *Digitaria exilis* georeferenced accessions from the whole collection. (b) Principal component analysis carried out on the allelic matrix of the 1539 white fonio individuals successfully genotyped with 14 microsatellites markers, and projected on the first and second components. (c) Barplots of the population structure ($N = 1539$ individuals) inferred with STRUCTURE for $K = 3$ (top) and $K = 6$ (bottom). Each individual is represented by a vertical bar, partitioned into K segments representing the proportion of genetic ancestry from the K clusters. (d) Map representing the interpolation of ancestry coefficients coloured according to their population inferred with STRUCTURE at $K = 6$. Sen = Senegal; Gui = Guinea; IC = Ivory Coast; BF = Burkina Faso; Ner = Niger; Gh = Ghana; Ben = Benin; T = Togo; Nga = Nigeria.

4 | DISCUSSION

In this study, we characterized the genetic structure of *D. exilis*, a crucial minor staple crop for food and nutrition security in West Africa. We

used the largest white fonio collection existing to date. Our results enhanced the prospects for conservation and sustainable use of fonio cultivated diversity. We developed the open-access Shiny application for this purpose and to enable different actors to readily query the data.

4.1 | Geographical pattern of fonio genetic diversity

The use of an unprecedented number of genotypes of white fonio landraces encompassing its current distribution range revealed that its infra-specific diversity was spatially structured in six distinct genetic clusters. This corroborates the previous results obtained by Abrouk et al. (2020) where a similar geographical structure was identified. At a narrower scale, we retrieved the three genetic clusters obtained by Wang et al. (2021), differentiating accessions from southern Mali, central Mali near the Burkina Faso border and Niger. While these studies used high throughput sequencing techniques, our results showed that SSRs markers are still appropriate for characterizing the genetic structure of populations. Moreover, the integration of new countries in our study extended and specified the fonio genetic diversity range. While the southern Togo accessions previously formed a clearly distinct population (Abrouk et al., 2020), our results showed that they shared close genetic relationships with accessions from Nigeria. We evidenced that accessions from Niger clustered with accessions from central Mali, despite being geographically isolated. We improved the distinction between eastern Guinea and the Fouta Djallon highlands. Finally, the accessions from Ghana widened the range of the fonio genetic diversity.

This genetic structure pattern could have resulted from several processes. First, the highly selfing reproductive system of fonio (Barnaud et al., 2017) increases genetic drift and limits gene flow between populations, so geographical structure could be expected. Spatial population structuring has also been noted for other typical West African crops such as African rice (*Oryza glaberrima* Steud; Veltman et al., 2019) and pearl millet (*Pennisetum glaucum* [L.] R. Br.; Rhoné et al., 2020). While the former is autogamous, the latter features a high outcrossing rate that allows gene flow between different pools of wild relatives, which partially explain the observed geographical structure pattern (Burgarella et al., 2018). Second, crop genetic diversity is the result of long-term genetic environmental human interactions through crop selection and diffusion. 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, 2012). Social factors are particularly important in smallholder farming systems. For instance, the maintenance of crop genetic differentiation among sorghum landraces cultivated in eastern Kenya is due to the centripetal orientation of seed exchanges among three ethnolinguistic groups, despite the fact that they are geographically close to each other (Labeyrie et al., 2016). Concerning fonio, this study showed that the large-scale fonio genetic structure was significantly associated with climatic variables, as already demonstrated in addition to the ethnolinguistic factors (Abrouk et al., 2020). At the national scale, the two geographically and genetically distinct fonio producing zones in Togo could be explained by different agro-ecological growing conditions, but also by different introduction events in places where the agricultural practices of farmers belonging to distinct sociocultural groups have maintained the genetic differences (Adoukonou-Sagbadja et al., 2006). Similarly, Diop et al. (in press) highlighted that the genetic

differentiation of fonio observed in the central part of Senegal was associated with the expansion of the Fulani into this region. Our analyses demonstrated relationships between this region, central Mali and Niger, perhaps reflecting large scale human migration histories and the spread of their fonio landraces. Such historical population movements might also explain the particularity of accessions from Ghana. Further research is however needed to gain further insight into the interaction of social, environmental and historical factors at different spatial scales.

4.2 | Challenges for sustainable uses and conservation of fonio genetic resources

The growing concern about diversifying agriculture and food has generated interest in the use of indigenous crops to build resilient agricultural systems (Cantwell-Jones et al., 2022; Hunter et al., 2019; Padulosi et al., 2011; Ulian et al., 2020). The significant genotyping effort in this study provided the first view of fonio genetic structure throughout its entire cultivation area. This overview of the fonio genetic resources offers critical information to geneticists and breeders establishing core collections. This will boost the understanding of the adaptive potential of this crop.

As for other crops, conservation and new collections are of high priority for fonio. Indeed, limited collections are available and the two main fonio producers, that is, Guinea and Nigeria, do not have major landrace collections. The largest collection available is the one analysed in this study, which encompasses over 2000 accessions of *D. exilis* accessions resulting from a collective effort between national and international institutions. Moreover, there are no wild fonio (*Digitaria longiflora*, *Digitaria* sp.) collections apart from herbariums despite the growing evidence that these resources are pivotal for the future (Burgarella et al., 2019; Pironon et al., 2019). Nevertheless, ex situ collection should be associated with on-farm conservation initiatives. This is all the more important as fonio cultivation is under pressure and the crop is becoming scarcer in many regions where unique genetic diversity prevails (Diop et al., 2018, in press; Saidou Sani et al., 2018). Better integration of ex situ and in situ conservation will ensure that breeders and farmers be able to take advantage of the available diversity to obtain crops adapted to environmental changes (Antonelli, 2023; Dempewolf et al., 2023).

4.3 | Towards an integration process: Stakeholders and scales

The wide network of partners involved in this study enabled to unveil the complete population genetic structure of white fonio. Combined with a user-friendly tool enabling the community to retrieve the data and associated results, our study represents a first step before going further with appropriate sampling and high-throughput sequencing methods to answer deeper questions linked to the fonio domestication history and its signatures of local adaptation. With regard to

climate issues, assessment of the fonio adaptive potential should be coordinated with a diverse range of stakeholders through participatory bottom-up processes. In fact, even though the role of scientists and breeders is to characterize the full extent of genetic diversity to produce and select adapted varieties, farmers are the stewards of the associated knowledge and practices on how to use them in agrosystems. Moreover, participatory approaches (e.g., in farmer field research units; community biodiversity management) are often conducive to novel adoptions of fonio cultivation while ensuring transmission of the associated knowledge to future generations (Sidibé et al., 2020). To achieve this goal, co-constructing agricultural strategies with smallholder farmers and increasing their access to cultivated diversity is key (Louafi et al., 2021).

Finally, regional collaborations between producing countries should certainly be developed to promote the circulation of landraces that might be adapted to conditions that prevail in distant regions in the near future (Rhoné et al., 2020). Although a major sampling effort was made for this study, some geographic discontinuities remain in our data. Further prospections have to be carried out to understand why fonio is or is not cultivated in certain areas, and potentially contribute to its introduction in new regions. There is therefore a need to increase coordination between different countries and actors to ensure effective management of the cultivated diversity. From this standpoint, we hope that the development of the open-access Shiny application will boost interest and future interactions and collaborations between the different actors involved so as to collectively promote greater diversity in the field and in diets.

AUTHOR CONTRIBUTIONS

Adeline Barnaud, Claire Billot, Christian Leclerc, Jean-Louis Noyer and Jean-Louis Pham designed the study and trained the partners for sampling collection and associated data. Enoch G. Achigan-Dako, Charlotte Adje, Emmanuel Sekloka, Joseph Adjebeng-Danquah, Richard Y. Agyare, Samuel K. Bonsu, Abdul R. Issah, Doris K. Puzoaa, Theophilus K. Tengey, Tely Diallo, Mamadou B. Barry, Baye M. Diop, Monique Deu, Mame C. Gueye, Abdou R. Ibrahim Bio Yerima, Ndjido A. Kane, James Kombiok, Yeremakhan Keita, Louise Akanvou, Yacoubou Bakasso, Ablaye Ngom, Happiness O. Oselebe, Marie Piquet, Soukeye Conde, Edak A. Uyoh, Solomon Abraham, Sani Saidou, Suleiman D. Abdul, Stephen N. Dachi, Adeline Barnaud and Claire Billot collected the accessions. Sandrine Causse, Sylvie Vancoppenolle, Caroline Calatayud, Marie Couderc, Tely Diallo, Baye M. Diop, Ablaye Ngom, Katina Olodo, Marie Piquet, Ronan Rivallan and Leila Zekraoui generated the data. Thomas Kaczmarek, Adeline Barnaud, Claire Billot, Yves Vigouroux and Christian Leclerc performed the analyses. Thomas Kaczmarek, Adeline Barnaud, Claire Billot, Yves Vigouroux and Christian Leclerc wrote the manuscript. Thomas Kaczmarek developed the Shiny application. All the authors revised on the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The passport and SSR data that support the findings of this study are openly available in the DataSuds repository (IRD, France) at [10.23708/TX5DE2](https://doi.org/10.23708/TX5DE2). Data reuse was granted under CC-BY licence.

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