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Crop biocultural traits shape seed networks: Implications for social-ecological resilience in south eastern Senegal

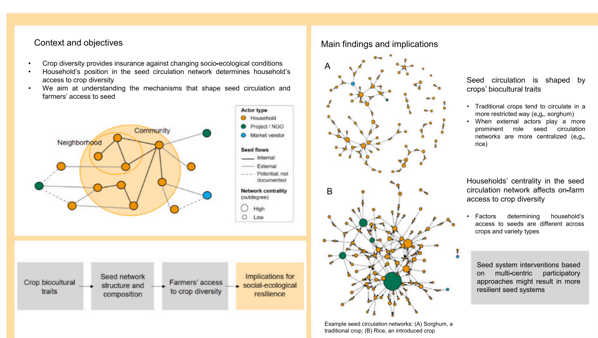
Anna Porcuna-Ferrer [a,b,c,*], Vanesse Labeyrie [b,c], Santiago Alvarez-Fernandez [a], Laura Calvet-Mir [a,d,e], Ndèye Fatou Faye [f], Sarah Ouadah [g], Victoria Reyes-García [a,h,i]

[a] *Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain*
[b] *CIRAD, UMR SENS, F-34398 Montpellier, France*
[c] *SENS, Univ Montpellier, CIRAD, IRD, UPVM, Montpellier, France*
[d] *Institut Metròpoli, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain*
[e] *TURBA Lab, Internet Interdisciplinary Institute (IN3), Universitat Oberta de Catalunya, Av. Carl Friedrich Gauss, 5, Castelldefels, 08860 Barcelona, Spain*
[f] *Institut Sénégalais de Recherches Agricoles, Bureau d'Analyses Macroéconomiques (ISRA-BAME), Route des Hydrocarbures, BP 3120 Dakar, Senegal*
[g] *Université Paris-Saclay, AgroParisTech, INRAE, UMR MIA Paris-Saclay, France*
[h] *ICREA, Institució Catalana de Recerca i Estudis Avançats, Barcelona, Spain*
[i] *Departament d'Antropologia Social i Cultural, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain*

HIGHLIGHTS

- Seed circulation networks mediate farmers' access to crop diversity and agroecosystems' social-ecological resilience.
- We compared the factors mediating seed circulation for six staple crops in a Bassari community, south-eastern Senegal.
- Crop biocultural traits and network actors shape seed circulation, causing differential access to crops and variety types.
- Multi-centric, participatory interventions might strengthen locally adapted crop diversity and seed systems' resilience.

GRAPHICAL ABSTRACT



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ABSTRACT

CONTEXT: Agroecosystems' social-ecological resilience largely depends on the crop diversity generated and maintained by farmers, which provides insurance against changing environmental and socio-economic conditions. In turn, crop diversity generation, maintenance, and distribution is influenced by seed circulation networks. Thus, patterns of seed circulation can support or constrain households' access to crop diversity, affecting on-farm crop diversity.

OBJECTIVE: We aimed at understanding the mechanisms shaping seed circulation and farmers' access to crop diversity by: 1) assessing how crop biocultural traits influence patterns of seed circulation; 2) exploring the connections between household position in the seed circulation network and on-farm crop diversity for different crops.

* Corresponding author at: Institut de Ciència i Tecnologia Ambientals (ICTA), Universitat Autònoma de Barcelona, Cerdanyola del Vallès, Barcelona, Spain.
E-mail address: anna.porcuna@uab.cat (A. Porcuna-Ferrer).

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METHODS: We conducted research in south-eastern Senegal applying crop diversity inventories and a survey to document seed acquisitions for the six local staple crops, which differ in biocultural traits. Household's varietal diversity and household- and community-level network measures calculated for each crop were used to compare seed circulation patterns among crops. Then, we analyzed the association between households' position in the seed circulation networks and households' on-farm crop diversity using generalized linear models.
RESULTS AND CONCLUSIONS: Our research advances two main findings about the importance of seed circulation networks for farmers' access to crop diversity.
First, several seed circulation networks operate in the same community and at the same time. Each species circulated differently, which can be explained by crop's biocultural traits. Socio-cultural traits, like the cultural relevance of a crop, and biological traits, like crop's functional group (e.g., legumes, cereals), affect the patterns of seed circulation. Seed circulation networks that involved external actors, like agricultural extension projects or NGOs, were more centralized than seed circulation networks in which these actors were absent.
Second, household's centrality in the network of seed circulation (indegree and betweenness) was generally associated with higher on-farm varietal diversity. However, the factors that determined household's access to seeds differed among crops and variety types.
SIGNIFICANCE: Farmer-to-farmer seed circulation networks are instrumental for the maintenance and distribution of agrobiodiversity and catalyze the introduction of new diversity in the agricultural system. However, tensions exist between traditional and new (e.g., interventions) mechanisms of seed sharing, resulting in centralized and unidirectional seed distribution, which might affect the social-ecological resilience of the system.

1. Introduction

Crop diversity contributes to farming systems' social-ecological resilience[1] (Cabell and Oelofse, 2012) by providing response diversity to disturbance through a pool of possible adaptations (Altieri and Nicholls, 2017; Labeyrie et al., 2021b; Renard and Tilman, 2019). At the plot and landscape levels, cultivating different species and varieties simultaneously and over time fosters ecological heterogeneity, which helps responding to ecological, social, and economic shocks (Cabell and Oelofse, 2012). Importantly, crop diversity is a direct outcome of biocultural interactions,[2] including farmers' knowledge and practices that allow the generation and maintenance of a constantly evolving biodiversity contributing to farms' long-term social-ecological resilience (Berkes et al., 2000; Folke, 2004; Reyes-García et al., 2014, 2013).

Researchers have investigated the mechanisms affecting the richness and distribution of crop diversity and farmers' access to this diversity (Jarvis et al., 2008; Leclerc and Coppens d'Eeckenbrugge, 2012; Zimmerer et al., 2019). Among the lines explored, scholars have examined the role of social networks in the generation, maintenance, and diffusion of crop diversity and associated knowledge (Calvet-Mir and Salpeteur, 2016; Labeyrie et al., 2021a; Pautasso et al., 2013). Seed circulation networks are shaped by social forms of organization (Labeyrie et al., 2014b; Leclerc and Coppens d'Eeckenbrugge, 2012) and network structure can support or constrain households' access to crop diversity, increasing or decreasing on-farm agrobiodiversity.

Previous research has tested the existence of a relationship between farmers' position in the seed circulation network and on-farm crop diversity levels following two main research lines- e.g., (Abizaid et al., 2016; Calvet-Mir et al., 2012; Díaz-Reviriego et al., 2016; Kawa et al., 2013). Most studies have documented general flows of seeds and information, not allowing to discern differences between crop species and variety types e.g., Calvet-Mir et al. (2012); Díaz-Reviriego et al. (2016); Abizaid et al. (2016), and Kawa et al. (2013). Few studies have considered whether crops and/or varieties might circulate differently depending on their biocultural properties. For example, crop ecology affects seed production and viability and might thus affect seed circulation (Leclerc and Coppens d'Eeckenbrugge, 2012; McGuire and Sperling, 2016). Reproduction type might affect the amount of propagative material that farmers' need or can share – e.g., crops that reproduce vegetatively present a lower multiplication rate and their planting material is less easy to store and transport (McKey et al., 2010); pollination-type might affect out-farm seed acquisition, as gene flows may challenge maintaining the identity of out-crossing varieties over time – e.g., (Allinne et al., 2008) for millet - compared with self-pollinating crops– e.g., rice (Nuijten and Almekinders, 2008). Seed storability can also affect on-farm seed availability (McGuire and Sperling, 2011; Meikle et al., 2002), as seeds sensitive to weather, pests, or other hazards might need faster renewal, which might boost seed circulation. For example, to minimize seed losses during storage, farmers in Haiti sell legume seeds after harvest and buy new ones at sowing time (McGuire and Sperling, 2016). In the same line, the seed stocks of some crops are more susceptible to be used as food in case of shortage than the seeds of other crops. Other factors, such as commercial value, dietary relevance, and the customary exchange value might also be relevant to explain the way different crops circulate (Delêtre et al., 2011; McGuire and Sperling, 2016; Thomas and Caillon, 2016). However, with the exception of a study carried out in the Vanuatu archipelago (South Pacific) (Thomas and Caillon, 2016), we know of no analysis considering the potential simultaneous influence of crops biological and socio-cultural traits in explaining seed circulation patterns.

A different research line has focused on customary rules guiding seed flows. This body of research shows that seed circulation is limited by social factors such as ethnolinguistic boundaries in Kenya (Labeyrie et al., 2016), marriage prohibitions in Gabon (Delêtre et al., 2011), or kinship in the Amazonia (Abizaid et al., 2016). While informative, this literature neglects the role of non-community actors. Seeds and related information circulate through networks involving farmers, but also other actors such as governmental and non-governmental organizations, local markets, the private sector, or local, national, or international institutions (Coomes et al., 2015; McGuire and Sperling, 2016; Pautasso et al., 2013). Research in other fields has shown that the type of actors and the relations between actors impact the resilience and sustainability of social-ecological systems (Bodin, 2017; Bodin et al., 2016), a relation that has yet to be tested in relation to the impact of actor composition on seed exchange networks.

Our work combines research insights from these two research lines to explore how crops biological and socio-cultural traits relate to farmers' access to seeds. Building on the work of Thomas and Caillon (2016), we conceptualize crops as biocultural objects because they embody the interconnectedness of biological and cultural systems. We hypothesize

[1] We adapt the definition of social-ecological resilience - "*the capacity of a system to absorb* disturbance *and reorganize while undergoing change so as to still retain essentially the same function, structure, and identity*" (Walker et al., 2004, p. 3) to agroecosystems by defining agroecosystem resilience as the capacity to produce food despite shocks (Cabell and Oelofse, 2012).

[2] Biocultural interactions refer to the dynamic relationship between biological processes and cultural practices, which are deeply intertwined and mutually influential. For crops, these interactions encompass selection, cultivation, consumption and valuation within specific cultural contexts (Maffi, 2012).

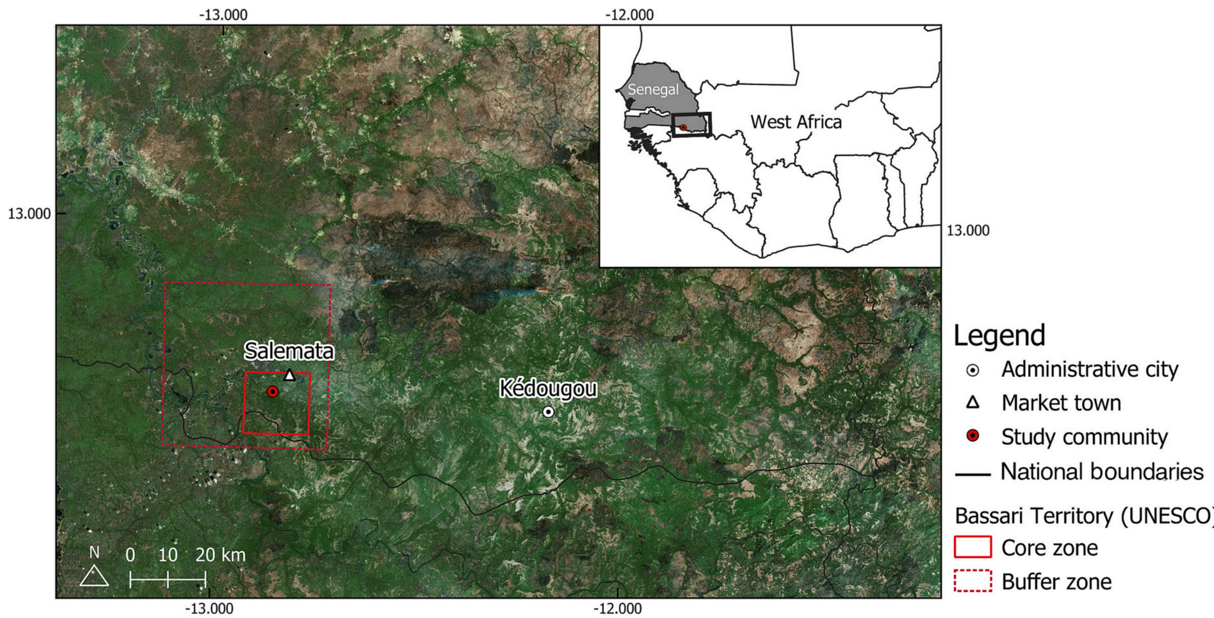

Fig. 1. Map of the study area.

that different crops might circulate differently, with different seed circulation networks operating within the same community. We further hypothesize that the different seed circulation networks can be (at least partly) explained by crops' biocultural traits, including the constellation of actors that intervene in their seed circulation.

We conducted research in south-eastern Senegal, a region where the agricultural system is mostly rain-fed and biodiversity-based. We start by comparing the types of actors involved in seed exchanges and the seed circulation patterns of the six staple crops grown in the area. Then, we analyze the association between households' position in the seed circulation networks and households' crop diversity for each staple crop and their varieties. Finally, we discuss the implications of our results for the social-ecological resilience of smallholder farms.

2. Case-study

2.1. Study site

Data were collected in a Bassari village[3] in south-eastern Senegal (Fig. 1). The altitude in the region varies from 115 to 380 m.a.s.l. and the climate is characterized by a rainy season (approx. May to September) and a longer dry season (ANACIM, 2020). The main administrative centre – Kédougou – and the closest market town – Salemata – are located respectively 90 and 11 km away from the study site. A paved road connects Salemata with Kédougou, but until 2020 access to the administrative city was limited or completely closed during the rainy season. Bassari are the largest ethnic group in the area, where there are also other ethnic groups (e.g., Fula, Coniagui, Dialanké, Malenke). In 2012, UNESCO declared part of the area as a World Heritage site (UNESCO, 2012), called "Bassari territory" in Fig. 1.

The main livelihood activity in the area is rain-fed farming, and the bulk of agricultural activities are concentrated during the rainy season and the beginning of the dry season. In the light of climate change, the rainy season is shortening and the frequency and intensity of dry spells are increasing, challenging local farming activities (Porcuna-Ferrer et al., 2023). Agriculture mostly consists of subsistence-oriented cultivation of cereals (sorghum, rice, maize, fonio) and legumes (peanut, Bambara groundnut). Households also sell excess crops in local markets. Cotton is the main cash-crop, and its cultivation is mostly undertaken through contract-farming arrangements with Sodefitex, a former state-owned company that has been increasingly privatized. Most households are largely self-sufficient foodwise, although there is an increasing dependence on commercial rice. Beyond farming, most households also take part in other income generating and subsistence activities such as wage labour, artisanal work, hunting and gathering, palm wine processing, and harvesting of wild edible plants. Livestock keeping is an important way of capitalization.

Bassari farmers adjust to variable soil conditions by diversifying crops and using different management strategies. *Oxenga* are fields in the hills where farmers mostly rotate peanut, Bambara groundnut, sorghum, cotton, and fonio, using few or no chemical inputs (except for cotton). A typical crop rotation[4] lasts 5–6 years, which requires access to different plots. *Eden* are fields in the floodplains, more fertile and intensively cultivated than in *oxenga*. In *eden* there are no crop rotations, fallow periods are short, and farmers use chemical inputs to sustain production. Farmers' cultivate rice in *eden* fields that get inundated during the rainy season, and maize in the rest. In the past, cultural taboos prohibited agriculture next to the river basins, however cultivation in *eden* is now growing. Contrasting with up-hill lands, land in the lowlands starts to be considered scarce by the Bassari. *Enam* are fields around the houses (generally in the hills), managed quite intensively, without rotations, and maintained largely by using organic fertilizers. They are mostly cultivated with maize and minor crops.

As in other locations worldwide (Garine et al., 2018), seed circulation among the Bassari follows traditional social norms, cultural values, and economic rationales expressed through gender, residence, kinship,

[3] The name of the case-study village is not mentioned to respect anonymity.

[4] A traditional crop rotation would be: a newly-cut field—Field A—is planted with Bambara groundnut and/or peanut. The following year, sorghum is planted in Field A, and a second field— Field B—is planted with Bambara groundnut and/or peanut. In the third year, Field A reverts to Bambara groundnut and/or peanut and Field B to sorghum. This alternation continues until the fields are exhausted, then, new fields are opened and the old fields are cultivated with fonio. Nowadays, in rotations, sorghum is being replaced by cotton and maize, and Bambara groundnut by peanut.

and age-class[5] relations. The Bassari society is generally characterized by sex-opposed spheres of ritual and economic activity (Nolan, 1986). Men and women independently carry out agricultural activities (e.g., seed selection and storage), although they might help each other during specific moments of the crop cycle. Most crops are gender-specific: cotton and sorghum are mostly cultivated by men, and peanut, Bambara groundnut, fonio, and rice are mostly cultivated by women. Maize is cultivated by men and women. Bambara groundnut and sorghum are 'the' gendered crops par excellence and the basis of '*enap*', Bassari staple porridge, which combines women's and men's harvest. Residence is patrilocal (women move to their husband's village), resulting in geographically extensive matrimonial networks. Village residency is a socially structuring factor: age-class system ritual activities (e.g., initiation ceremonies) are performed by groups of neighbouring villages and the organization of communal labour exchange is structured along neighbourhood residency.[6] Indeed, in Bassari language, neighbourhoods are called *andyana*, which translates as "those with whom I work" (Nolan, 1986). Kinship and matrimonial networks are also important in explaining seed circulation: upon a person's death, the Bassari would traditionally transmit seeds to the niece/nephew from sister-side (Gessain, 1975; Nolan, 1986), although this is now changing towards a system in which men inherit their father/grandfather' seeds and women inherit their mother/ grandmother's seeds. Finally, until recently, the age-class was important in structuring Bassari social relationships, tasks, rituals, and communal agricultural work (Nolan, 1986), thus potentially influencing seed circulation.

Besides gender, residence, kinship, and age-class relations, local markets and agricultural extension projects might also shape Bassari seed access. Local markets are mostly attended by women to sell grain or other agricultural or wild-plant products and to buy supplies. Bassari farmers frequent the weekly market in Salemata, and rarely the bigger and permanent market in Kedougou. None of these markets have specialized seed vendors, but seeds are sold by other farmers and resellers who bring seeds from bigger markets. Within the study village, three small shops also sell local peanut seeds during the sowing season. In the last decades, there have also been several NGO- or government-based development projects promoting maize, rice, and peanut cultivation through the provision of seeds, chemical fertilizers, and pesticides (Porcuna-Ferrer et al. in press).

2.2. Biocultural traits and seed management of Bassari staple crops

Bassari current staple crops have different agronomic characteristics, cultivation histories and cultural and symbolic functions in Bassari farming system (Porcuna-Ferrer et al., under review) (Table 1).

Sorghum (*Sorghum bicolor* [L.] Moench) is well adapted to semi-arid agronomic conditions, being resistant to drought and heat (Smith and Frederiksen, 2000). Sorghum is one of the oldest crops cultivated by the Bassari, who rarely renew their seed lot, with most households maintaining the same varieties over decades. Exclusively cultivated by men, sorghum is mostly used for household consumption and particularly for the preparation of sorghum beer, a central product in Bassari ceremonial life (Gessain, 1996).

Bambara groundnut (*Vigna subterranea* [L.] Verdc.), an annual legume with a high nutritional value and tolerance to adverse environmental conditions (Mayes et al., 2019), has also been cultivated by the Bassari for a long time and has a strong symbolic and ceremonial importance. Indeed, sorghum beer and Bambara groundnut seeds are the two only products explicitly forbidden to sell by Bassari tradition. Bambara groundnut is mostly cultivated by women, who renew frequently the seed lots due to the difficult storage and high frequency of pest attacks. Like for sorghum, households maintain the same Bambara groundnut varieties over decades.

Fonio (*Digitaria exilis* Stapf) is a fast-growing cereal well adapted to poor soils and semi-arid conditions (Abrouk et al., 2020). For the Bassari, fonio is a women's crop, introduced at the end of the crop rotation cycle, when the land is exhausted. Fonio is mostly consumed during festivities and, although its sale is not culturally prohibited, economic transactions are rare. Many households only cultivate fonio during the cropping season preceding an important festivity. As a result, seed lots are not stored for a long time within the households. Women typically preserve their seeds by sharing them with other farmers at sowing time and receiving a portion of their harvest afterwards.

Maize (*Zea mays* L.) was introduced in the Bassari territory in the early 1900s by a neighbouring ethnic group (Gessain, 1975). Nowadays, it is strongly promoted by agricultural development projects that supply high yield short-cycle maize varieties and chemical fertilizers. Maize can be cultivated by both men and women, who sow it in fertile and deep soils. Maize is mostly used for household consumption and seems to be replacing sorghum in the Bassari food system, e.g., it has become the main staple in many meals, and its beer is increasingly substituting sorghum beer. Maize seeds are typically stored at home, with granaries predominantly managed by men.

Asian rice (*Oryza sativa* L.) has higher water and nutrient requirements than other local staple crops. Asian rice most likely arrived to the Bassari territory in the 1900s and was initially cultivated in small areas, but its cultivation has increased in the last 20 years, with the arrival of new high yielding varieties initially distributed by the state and later by development projects, which also distribute herbicides and fertilizers. Rice is mostly cultivated by women and nowadays occupies most floodplains in the case-study village. Although women tend to store their own rice seeds, agricultural extension projects are an increasingly important rice seed source.

Peanut (*Arachis hypogaea* L.) is a legume domesticated in South America, initially introduced in the Gambia river basin by Portuguese traders (16th century) and cultivated in small quantities until its large-scale commercial production was promoted by the French colonial government (mid-19th century) and later by post-colonial governments. This promotion entailed the creation of state cooperatives and the distribution of subsidized seeds (Bernards, 2019). Nowadays, although the Senegalese government subsidizes peanut seeds, the Bassari prefer to cultivate their own. Peanuts are mostly cultivated by women for household consumption. Seed lot renewal takes place often, as seeds are very vulnerable to pest attacks. Peanut seeds have important market value and can even be used as an alternative currency.

3. Methods

3.1. Sampling

Data were collected during November 2019 – April 2020 and September 2020–June 2021. Fieldwork was interrupted by the Covid-19 pandemic. As Bassari agricultural activities were not strongly impacted by Covid-19, our data can be considered representative of a 'typical year'. The first author lived in the case-study village during the two

[5] Age-class (also referred to in literature as "age-grade") is a highly-structured hierarchic system in which power is held by the elders. Progression in the age-class system entails conducting a series of tasks and rituals, including agricultural common working days (Nolan, 1986; Gessain, 1975). Traditionally, age-class rituals marked the main agricultural seasons and age-class labour pooling was important to sustain the work-intensive Bassari agricultural system (Nolan, 1986). Age-class progression is gendered and there are rigid rules about men/women's roles in ritual and economic activities.

[6] Bassari neighbourhoods are semi-independent units geographically separated from each other and generally organized according to patrilineal clans. Neighbourhoods have a certain level of independence; each neighbourhood has a chief and neighbourhood boundaries are usually more significant and precise than village boundaries (Nolan, 1986).

Table 1
Crops' characteristics.

	Sorghum	Bambara groundnut	Fonio	Maize	Rice	Peanut
Scientific name	*Sorghum bicolor*	*Vigna subterranea*	*Digitaria exilis*	*Zea mays*	*Oryza sativa*	*Arachis hypogaea*
Biological characteristics						
Functional group	Cereal	Legume	Cereal	Cereal	Cereal	Legume
Type of reproduction	Partially outcrossing	Predominantly self-pollinating	Predominantly self-pollinating	Outcrossing	Predominantly self-pollinating	Predominantly self-pollinating
Storage capacity	High	Low	High	High	High	Low
Socio-cultural characteristics						
Time in the local farming system	Traditional	Traditional	Traditional	Introduced (recently)	Introduced (recently)	Introduced (formerly)
Food use	Staple, traditional dish ("Enap") and sorghum beer	Staple, traditional dish ("Enap")	Staple, mostly for festivities	Staple, modern dish	Staple, modern dish	Sauce, snack
Gendered crop management	Only men	Only women	Mostly women	Women and men	Mostly women	Mostly women
Marketability*	Medium	Low	High	Medium	Medium	High
External support	Low	Low	Low	High	High	Medium

* All crops are mostly cultivated for self-consumption.

periods of data collection, which allowed combining qualitative ethnographic research with systematic data collection.

Our sampling unit was the household,[7] as some agricultural activities are conducted at that level. We defined the limits of the network as that of the studied community and initially included in our sample all Bassari households in our case-study village. We also included households' interactions with actors outside the village, including other households, agricultural extension projects and NGOs, and market vendors.

We visited each household twice, first to conduct a crop diversity inventory and later to conduct a seed exchange network survey. Both interviews were conducted with all available household members who had cultivated an independent plot during the previous cropping season. Some households were not available for interviews, so our final sample includes 117 households (or 95% of a total of 123 households in the village).

3.2. Data collection

3.2.1. Crop diversity inventories of local staple crops

To characterize crop diversity at the village- and household-levels for the six staple crops, we conducted two village focus group discussions, one with men and one with women, and household crop diversity inventories.

Focus group discussions unravelled the local taxonomy of the staple crops and helped us establish a reference list of variety names known by farmers. Because local farmers often replace or mix their seed stock with same-variety seeds from other farmers, we decided to work at two levels: seed lot and variety. Following Louette and Smale, 2000, we use the term "seed lot" to refer to a particular physical batch of seeds of a variety that farmers' maintain through time without mixing it and that they use to produce next season's crops. We use the term 'variety' to refer to the emic categories identified by farmers as a management unit composed by seed lots of the same kind, corresponding to plants with similar phenotypic characteristics according to farmers' perspective (Louette and Smale, 2000). While acknowledging that introduction of crop varieties is a dynamic process and categorization not always exclusive, we adopted the 30 years threshold proposed in the literature to distinguish between variety types (Calvet-Mir et al., 2011; Tardío et al., 2018). We classified varieties in three groups based on farmers' reports about the period and actors introducing them: "farmer varieties", "introduced farmer varieties", and "non-farmer varieties". *Farmer varieties* are varieties selected, reproduced, and kept by farmers and which have been in the local farming system for >30 years (also referred to as "landrace" or "heirloom varieties"[8]). *Introduced farmer varieties* are varieties introduced through farmer-to-farmer seed exchange within the last 30 years. *Non-farmer varieties* refer to varieties developed by professional plant breeders, which have recently arrived to the community through agricultural extension projects. For each variety, during the focus group discussions, we documented the names most frequently used by farmers, the existence of any synonyms, and varieties' characteristics (e.g., maturity cycle, colour, size, uses).

To obtain household's crop diversity inventories, we asked farmers to list all the staple crops they had cultivated during the previous growing season. For each staple crop, we asked them to estimate the surface cultivated in 'cordes' (1 corde = 0.25 ha) and to provide the local names of all the cultivated varieties of each crop. We insisted that respondents listed all varieties grown, including those represented by a very limited number of individual plants. To ensure consistency in naming, we asked follow-up questions about the variety characteristics, which we then compared to our reference lists elaborated during focus groups. When farmers finished listing, we used the reference lists to ensure that we captured all crops or varieties grown in their fields.

3.2.2. Seed network survey

To capture the full diversity of local staple crops cultivated by the household, we conducted a survey with all male and female adults living in the household who had cultivated a plot during the cropping season before fieldwork. For the analyses, individual data (n = 258) were aggregated at household level (n = 117).

The survey had three sections: (1) Farmers' individual information (i.e., age, gender); (2) household information (i.e., number of adults in the household, age and gender of household head(s), cultivated area for each staple crop, number of market assets owned by the household), and (3) source of each cultivated seed lot for: i) the most recent cropping season, ii) the most recent external acquisition (i.e., different than self-produced), and iii) the very first external acquisition (i.e., first time they obtained a particular variety). For each seed lot and variety cultivated, we asked for the number of years since the first acquisition.

For each seed transaction, we also documented: i) its nature (i.e., exchange, purchase, credit, gift/inheritance); ii) seed giver type (i.e.,

[7] We define a household as a group of people (normally belonging to the same extended kin group) pooling resources, including exchanging labour without payment and "eating from the same pot". Among the Bassari, there are monogamous and polygamous households and it is common that several generations live together. Household members can exchange or sell part of their own harvest, but they have to provide part of the harvest for cooking common daily meals. Intra-household seed exchanges are a common way of seed provisioning.

[8] We use the term 'farmer varieties' instead of the most common term 'landraces', to emphasize that our classification is based on farmers' reports.

Table 2
Network-level and node-level measures calculated to describe the seed circulation networks of each of the local staple crops.

	Measure	Definition
Network-level measures	Size	Total number of nodes
	Density	Ratio between the number of existing versus possible links
	Reciprocity	The proportion of mutual connections in a directed graph
	Modularity	The share of internal links in the subgroups from the expected number of links if the distribution was random. Members of the same subgroup (also called 'communities' in social networks' literature) exchange more with other members of the same subgroup than with no-members (compared to what we would expect if seed circulation was random).
	Number of independent components	Number of connected subgraphs where all actors are directly or indirectly connected with other actors of the same subgraph but not with actors belonging to another subgraph.
	Indegree centralization	The sum of differences between each node's indegree and the one having the maximal indegree (normalized by its theoretical version in the case of an in-star graph)
	Outdegree centralization	The sum of differences between each node's outdegree and the one having the maximal outdegree (normalized by its theoretical version in the case of an out-star graph)
Node-level measures	Indegree	The number of incoming ties, which in our case represents the number of seed transactions in which the node was considered as a seed receiver. We classify indegree according to giver type (i.e., seed transactions received from households within the village, households from outside the village, projects/NGOs, and market vendors from outside the village). Indegree is not weighted.
	Outdegree	The number of outgoing ties, which in our case represents the number of seed transactions in which a node was mentioned as seed giver. Outdegree is not weighted.
	Betweenness	Number of times a node is at the shortest path in transactions between two other nodes. The shortest path is calculated based on the number of nodes that separates the different actors. Betweenness is not weighted.

household within the village, household from outside the village, project/NGO, market vendors from outside the village, other). Market vendors from the village were considered as households within the village and market vendors from outside the village were classified as market vendors; iii) the location of the seed giver vs. the receiver (i.e., within neighbourhood, different neighbourhood, outside village, and outside Bassari territory); iv) existing social relation(s) between the seed giver and receiver (i.e., age-class, neighbours, friends, kinship, other).

3.3. Data analysis

3.3.1. Seed circulation networks of local staple crops

Seed transaction events recorded in the seed network survey were aggregated by constructing six seed circulation networks from edge lists, one per crop species. Each edge list contained as many rows as documented seed transactions and two columns: the household that received the seed and the actor who gave the seed. Since our interest was on seed acquisitions outside the household, seed self-production and intra-household seed transactions were excluded from the edge lists.

For each network, we calculated seven network-level measures and three node-level centrality measures (Borgatti et al., 2018). The indegree metric was split into four different metrics according to seed giver type (see Table 2 for details). Data analysis was done using R version 4.1.2 (R Core Team, 2021). All networks were represented and network measures calculated using the R package "igraph" version 1.2.7 (Csardi and Nepusz, 2006). For network visualization, we considered three types of nodes: households, projects/NGOs, and market vendors. Ties between the nodes are directional, not weighted, and represent the different seed transactions. To compare the networks across different crops, we conducted an independence test (Pearson's chi-square test and when not possible, Fisher's exact test) concerning crop species and seed transaction characteristics (i.e., social relationship, actor type, distance to seed sources, and seed transaction type), and post-hoc tests to assess individual frequency deviations. For the social relationship involved in the seed transaction, when seed giver and receiver shared several ties, we only considered the strongest one according to our ethnographic understanding of the case-study area. Analyses were carried out using the package "stats" version 4.21.

3.3.2. Relation between household centrality and varietal diversity

We calculated households' varietal diversity for each main crop using data from the crop diversity inventories. For each household and crop, we generated four variables capturing the total number of cultivated (i) farmer varieties; (ii) introduced farmer varieties; (iii) non-farmer varieties, and (iv) all varieties (i.e., the sum of all types).

The correlation between a households' varietal diversity and position in the seed circulation network was only calculated for households within the case-study village. To estimate the association, we fitted several Poisson generalized linear models (GLM) with a logarithmic link using the "stats" package version 4.1.2 (R Core Team, 2021). Since centrality measures (i.e., indegree, outdegree, betweenness) are not independent, their individual effects might be masked if added in the same model. Therefore, we ran different models for each staple crop (6), variety type (4), and centrality measure (3), adding up to 63 models as sorghum, Bambara groundnut, and fonio did not have 'non-farmer varieties'. In our models, we sequentially used the four varietal diversity variables (i.e., all varieties, farmer, introduced, and non-farmer varieties) as outcome and network measures (i.e., indegree, outdegree, betweenness) as explanatory variables. We ran distinct models for indegree, outdegree and betweenness, while considering as controls several additional factors previously suggested to affect the level of crop diversity grown by the household - i.e., number of adults, percentage of female adults, age of the household head, cultivated surface per main staple crop, and household's economic status (Supplementary material 1). Households with missing data in some explanatory variables were removed from the corresponding models and therefore the sample sizes considered for the final models were smaller than the number of households' actually growing each staple crop.

We conducted a backward model selection process to assess the best models according to the Akaike information criterion (AIC). For each staple crop and variety type, we built 3 complete models, each one including a different centrality measure and all considered explanatory variables (number of varieties and control variables - see Supplementary material 1). The backwards model selection process removed explanatory variables one by one, minimizing AIC values, until we got the best fitted model. Even though initial complete models have the same predictors except the centrality measures, the models after the backwards selection process present different relevant predictors, as all variables without a statistically significant relation with the varietal diversity maintained by the households ($p > 0.1$) were removed from the final model. Final models only include statistically significant relations.

4. Results

4.1. Diversity of local staple crops in Bassari fields

Crop diversity richness and distribution largely varied across households. Peanut, maize, and rice were the most cultivated crops by the 117 households interviewed, often occupying large surfaces. Fonio and sorghum were also cultivated in relatively large surfaces, but by fewer households. Bambara groundnut was cultivated by most households, but in very small surfaces (Table 3).

At the village level, we identified 12 varieties of peanut, 10 of maize, 9 of rice, 6 of sorghum, 4 of fonio, and 4 of Bambara groundnut. On average, households maintained 1–2 varieties for each staple crop, except for peanut, for which most households kept more than two varieties. For sorghum, Bambara groundnut, and fonio, farmer varieties predominated and non-farmer varieties were not reported. Introduced farmer varieties and non-farmer varieties predominated for maize and rice. Peanut non-farmer varieties were rare, and households mostly grew peanut introduced farmer varieties and farmer varieties (Table 3). For each crop, few varieties were cultivated by most households and most varieties were cultivated by only one or two households.

4.2. Networks of seed circulation of local staple crops

4.2.1. Socio-demographic characteristics of seed circulation

We found statistically significant differences among seed transaction characteristics per crop: distance to the seed source (χ-squared = 151.16, df = 30, $p < 0.05$), social relationship (χ-squared = 145.77, df = 35, $p < 0.05$), seed transaction type (χ-squared = 445.26, df = 20, $p < 0.05$), and type of actor mobilized to acquire seeds (χ-squared = 288.05, df = 15, $p < 0.05$). Seed lot and variety age also differed between crop species ($p < 0.05$).

For all crops, most seed acquisitions took place within the case-study village (Fig. 2C). Sorghum seed acquisitions had the lowest geographical spread, with most seed acquisitions taking place within the neighbourhood (70.59%, $p < 0.05$) (Supplementary material 2). Bambara groundnut and peanut seed acquisitions had the widest geographical spread ($p < 0.05$), with seeds flowing in from villages within the Bassari territory, mostly within Senegal (30%), but also from Guinea (7%). Peanut seed acquisitions within the village (but outside the neighbourhood) were larger than for other crops ($p < 0.05$), and acquisitions from outside the Bassari territory were also more frequent than for other crops (3.04% taking place outside the Bassari territory), but this difference was not statistically significant ($p > 0.05$).

Most households mobilized kinship relationships to acquire seeds. However, kinship relations were less important for acquiring maize (46.7% of seeds acquisitions) and rice seeds (39.9%) than for other crops (>60% of seeds acquisitions, $p < 0.05$). For all crops the second and third most important ties mobilized for seed acquisition were neighbours and members of the same age-class. Other types of ties, such as friendship or same group membership (e.g., church, sports, or women groups), were rarely mentioned (Fig. 2A).

Farmers acquired seeds from a diversity of actors. Irrespectively of the crops, most seeds were acquired from other farmers. Other farmers were the predominant providers of Bambara groundnut (100%) and sorghum (96%) seeds, and less dominant in rice seed acquisitions (65.7%, $p < 0.05$). For maize and rice, projects/NGOs played a more significant role as seed providers compared to other crops (19.5% and 33.1% respectively, $p < 0.05$). Peanut was the only network where seed acquisitions from market vendors were important (11.5%, $p < 0.05$) (Fig. 2B).

We found differences in transaction types among crop species. Gifts/inheritance and exchanges were the predominant ways of acquiring seeds for all crops. Seed purchases were reported sporadically (approx. 5% of seed acquisitions) for all crops except for Bambara groundnut, for which no seed acquisitions involving monetary transactions were reported. Conversely, peanut was the only crop for which purchase (from both market vendors and other households) represented 25.7% of seed acquisitions ($p < 0.05$). Maize and rice were the only crops for which credit from projects/NGOs was a common way of sourcing seeds (in 11.36% and 30.6% of seed acquisitions, respectively) (Fig. 2D).

Seed lot renewal rate differed between crop species. Bambara groundnut, peanut, rice, and fonio had the highest seed lot renewal rates (mean seed lot age < 6 years). However, the difference in seed lot age was only statistically significant for Bambara groundnut (mean seed lot age = 2 years; $p < 0.05$). Sorghum seed lots were renewed less often than seed lots from other crops (mean seed lot age = 11 years; $p < 0.05$). Sorghum and Bambara groundnut varieties were the ones kept in the households for the longest time (mean variety age = 28 years; $p < 0.05$) and rice varieties were the most recently acquired ones (mean variety age = 7 years; $p < 0.05$) (Fig. 3).

Finally, we found gendered differences in seed circulation. Women were mostly involved in Bambara groundnut, fonio, rice, and peanut seed circulation, and men played a more prominent role in sorghum and maize seed circulation (Table 4).

4.2.2. Seed network structure and composition

We found different seed circulation patterns among different crops. In terms of network composition, seeds were mostly acquired from households. Projects/NGOs only played an important role in the maize and rice networks. Market vendors were relevant for peanut seed acquisitions (Fig. 4).

Seed circulation networks varied in size among crops, with peanut showing the largest (210 nodes) and fonio the smallest network (61 nodes). All networks had low densities, i.e., low number of connections or ties (from 0.007 for Bambara groundnut to 0.016 for fonio), and low reciprocity (from 0 for maize to 0.063 for peanut), meaning that farmers giving or selling seeds rarely got back seed of the same crop from the same person (Table 4).

All networks presented relatively low indegree centralization indices (from 0.027 for sorghum to 0.053 for peanut), meaning that there was not a single actor concentrating most seed acquisitions. Outdegree centralization indices showed a higher variation among crops (from 0.046 for sorghum to 0.216 for rice), suggesting that seed sourcing is more concentrated for certain crops than for others. For maize, rice, and peanut, projects/NGOs and market vendors were central actors in terms of seed sourcing, whereas for sorghum, Bambara groundnut, and fonio, seed sourcing was less concentrated (Table 4).

In all the networks, we found positive modularity scores (from 0.566 for peanut to 0.832 for sorghum), indicating the presence of subgroups within the networks. Modularity scores were higher for the sorghum, Bambara groundnut, fonio, and maize networks than for the rice and peanut networks (Table 4). Concerning independent components, rice and peanut networks had fewer independent components than networks from other crops, implying that most actors were connected with each other (for both crops the main component comprised >90% of actors).

Table 3
Crop diversity maintained in Bassari fields, per crop.

	Sorghum	Bambara groundnut	Fonio	Maize	Rice	Peanut
Number of households in the case-study village that cultivate the crop (total, %)	79 (67.52)	98 (83.76)	50 (42.73)	115 (98.29)	102 (87.18)	116 (99.14)
Mean surface cultivated per household (in cordes)	0.99	0.52	1.07	1.84	1.55	2.14
Number of varieties (total in the community, mean per household)	6 (1.33)	4 (1.32)	4 (1.02)	10 (1.58)	9 (1.34)	12 (2.53)
Farmer varieties (total, % of households that grow them)	5 (100)	2 (82.98)	3 (85.37)	3 (20)	3 (1.01)	3 (87.93)
Farmer introduced varieties (total, % of households that grow them)	1 (2.74)	2 (37.23)	1 (17.1)	5 (68.69)	4 (69.7)	8 (91.38)
Non-farmer varieties (total, % of households that grow them)	0 (0)	0 (0)	0 (0)	2 (43.47)	2 (55.6)	1 (6.03)

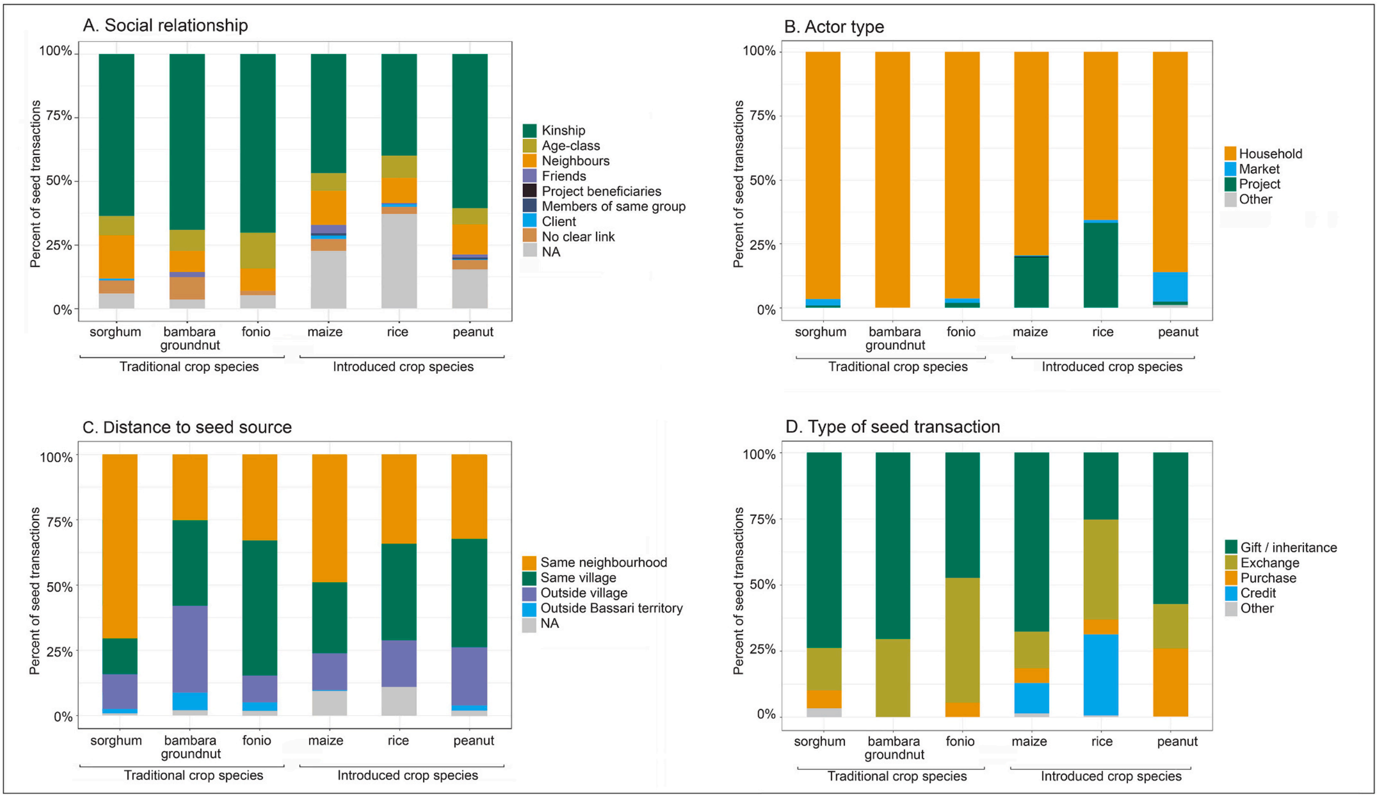

Fig. 2. Seed transactions characteristics (in %), per crop. In A, when giver and receiver shared several ties, only the strongest one was considered. From higher to lower strength: kinship, age-class, friends, neighbours, project beneficiaries, members of the same group, client.

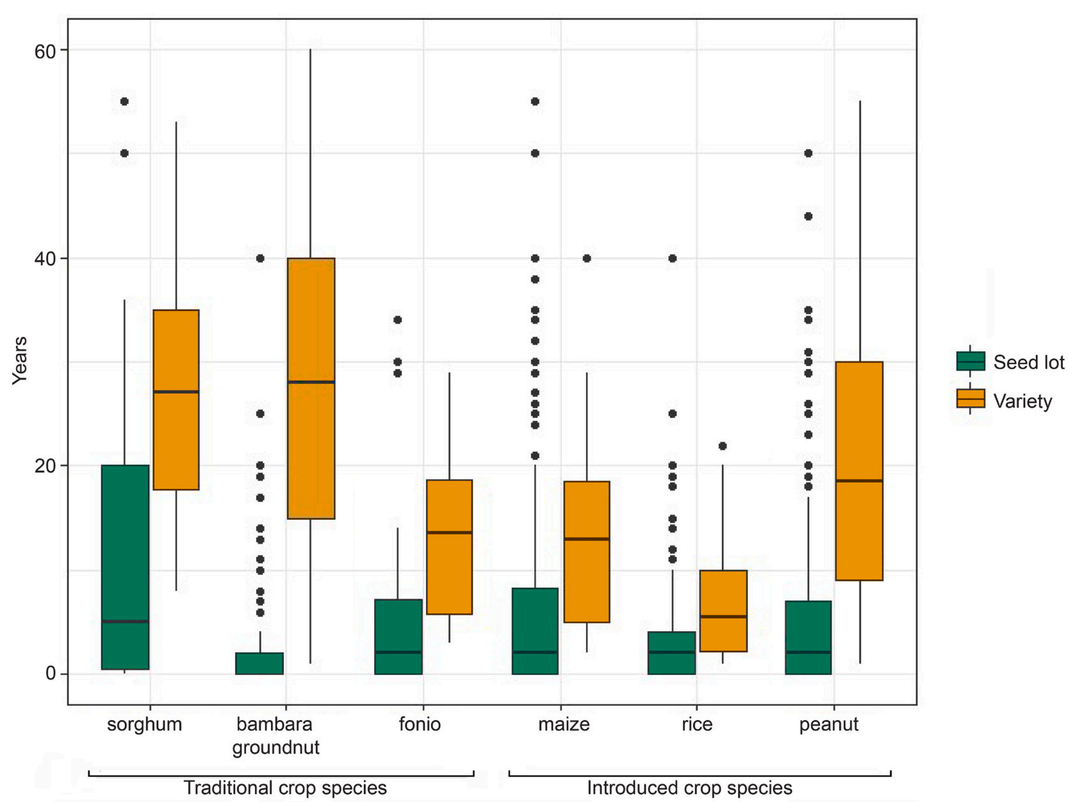

Fig. 3. Number of years that each seed lot and variety has been kept in the household. Calculated based on the most recent seed transaction that each household did to renew a seed lot or to acquire a new variety.

Table 4
Descriptive characteristics of seed circulation networks, per crop. Sample sizes: sorghum ($n = 79$ households), Bambara groundnut ($n = 98$), fonio ($n = 50$), maize ($n = 115$), rice ($n = 102$), peanut ($n = 116$).

	Sorghum	Bambara groundnut	Fonio	Maize	Rice	Peanut
Socio-demographic						
Receivers' age (mean, min-max)	50 (26–76)	45 (16–78)	46 (19–71)	48 (24–86))	43 (12–86)	44 (14–86)
Receivers' gender (% of women)	27.73	99	79.31	39.82	86.33	93.39
Seed circulation network measures						
Size	107	173	61	167	119	210
Density	0.010	0.007	0.016	0.008	0.013	0.010
Reciprocity	0.055	0.010	0.036	0	0.011	0.063
Modularity	0.832	0.767	0.809	0.719	0.630	0.566
Number of independent components	17	17	11	17	3	3
Indegree centralization	0.027	0.034	0.034	0.034	0.038	0.053
Outdegree centralization	0.046	0.063	0.068	0.155	0.216	0.105

The most fragmented network was that of fonio, with 11 independent components, the main one concentrating only 31.15% of network actors, followed by sorghum, Bambara groundnut, and maize, with 17 independent components each, the main one containing 55.14%, 71.67%, and 79.64% of actors, respectively.

4.3. Households' centrality and varietal diversity

Overall, households' varietal diversity was associated to different centrality measures, depending on the crop species and variety type. Across models, household indegree and betweenness most consistently showed statistically significant associations with varietal diversity. Household's outdegree does not appear in the final models because it was not associated in a statistically significant way to varietal diversity for any crop. Cultivated surface, age of the household head, households' economic status, and the number of adults in the household were positively associated with on-farm varietal diversity (Table 5).

4.3.1. All varieties

Household's indegree showed a positive and statistically significant association with the total number of varieties cultivated by a household ('all varieties', Table 5; Supplementary material 3). Household's indegree from households within and outside the village (but not indegree from Projects/NGOs) were significantly related to sorghum, fonio, and peanut varietal diversity. Contrastingly, connections outside the village did not have an important contribution to Bambara groundnut, maize, and rice household's varietal diversity. For these crops, diversity was only related to the indegree from households within the village (Table 5).

4.3.2. Farmer varieties

We found a positive and statistically significant association between the diversity of farmer varieties grown by the household and indegree from households from inside the village for sorghum, Bambara groundnut, and fonio. Only for sorghum the same association was found between households' diversity of farmer varieties and indegree from households outside the village (Table 5). We did not find any statistically significant association between the number of farmer varieties grown and household's indegree in the maize, rice, and peanut networks.

4.3.3. Introduced farmer varieties

Households' diversity of maize, rice, and peanut introduced farmer varieties was associated with household's indegree and/or betweenness. This association was significant when considering indegree from

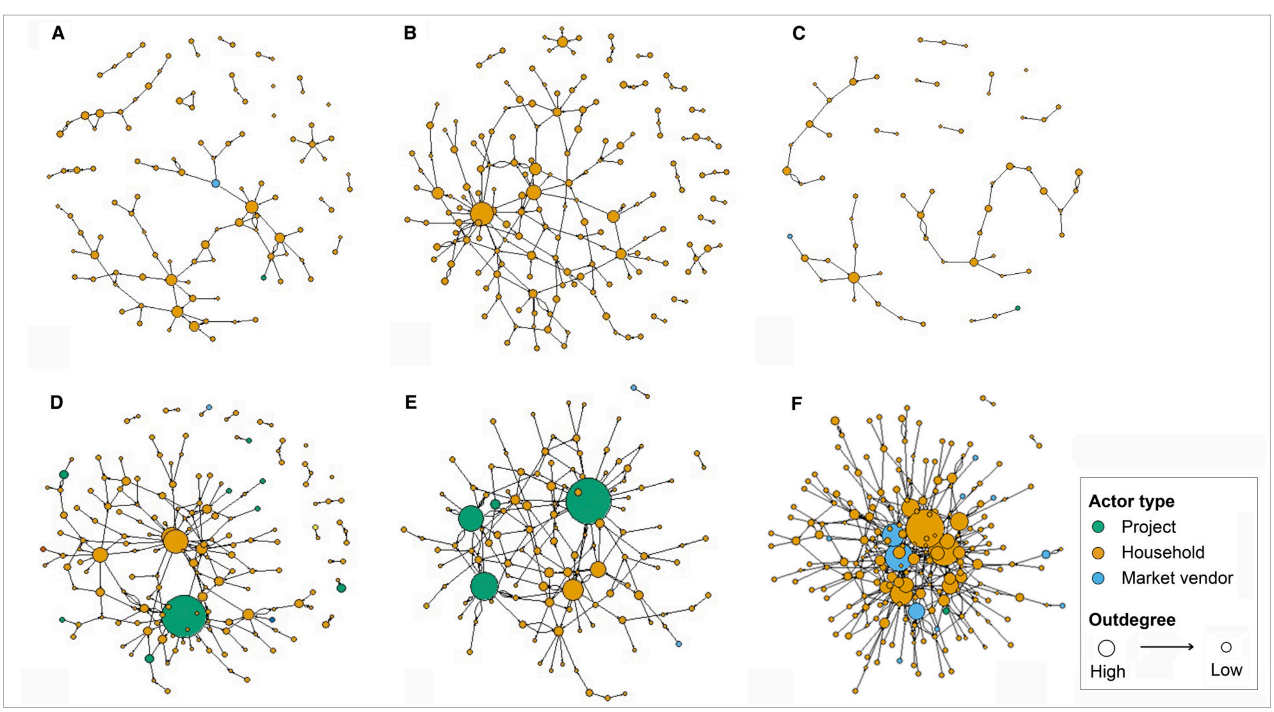

Fig. 4. Seed circulation networks per crop (Fruchterman-Reingold representation). A) Sorghum, B) Bambara groundnut, C) fonio, D) maize, E) rice, F) peanut.

Table 5
Generalized linear model results. Associations between households' centrality in different crop networks and the household's varietal diversity. Only associations statistically significant are shown. Sample sizes: sorghum (n = 79 households), Bambara groundnut (n = 98), fonio (n = 50), maize (*n* = 114), rice (n = 102), peanut (n = 116).

	Crop	Explanatory variables	Outcome variables			
			All varieties	Farmer varieties	Introduced farmer varieties	Non-farmer varieties
Indegree (IN), final models	Sorghum	IN households' village	7.29e-05 ***	0.000215 ***		
		IN households' outside village	0.0502 +	0.080072 +		
	Bambara groundnut	IN households' village	0.0747 +	0.0423 *		
		Cultivated surface			0.0174 *	
	Fonio	IN households' village	0.00706 **	0.0258 *		
		IN households' outside village	0.06935+			
		Cultivated surface			0.043488 *	
	Maize	IN households' village	3.99e-05***		3.83e-05***	
		IN projects / NGOs			0.08508 +	4.59e-05 ***
		Household head age group				0.0248 *
	Rice	IN households' village	0.0521+			0.04485 *
		IN projects / NGOs				0.00315 **
		Cultivated surface	0.0768+		0.04092 *	
	Peanut	IN households' village	3.13e-06 ***		2.54e-06 ***	
		IN households' outside village	0.0946+		0.0562+	
		IN projects / NGOs				1.35e-05 ***
Betweenness (BET), final models	Bambara groundnut	Cultivated surface	0.0295 *	0.000818 ***	0.0174 *	
		Household economic status		0.085400 +		
	Fonio	Cultivated surface	0.0145 *	0.0814 +	0.043488 *	
	Maize	BET			0.0722 +	
		Cultivated surface	0.0707 +			
		Household head age group				0.0394 *
	Rice	BET			0.03969 *	
		Cultivated surface	0.00721 **			0.022007 *
	Peanut	Cultivated surface	0.0425 *		0.0102 *	
		Household economic status				0.0711 +
		Household adults				0.0925 +

p-values: +, *, **, *** at the 0.1, 0.05, 0.01 and 0.001 levels.

households within the village for maize and from households within and outside the village for peanut. For maize and rice, household's varietal diversity of introduced farmer varieties was also associated to household's betweenness.

4.3.4. Non-farmer varieties

Household's diversity of maize, rice, and peanut non-farmer varieties was positively and significantly associated to household's indegree from projects/NGOs. Only for rice, the households' diversity of non-farmer varieties was also associated with household's indegree from other households within the village.

5. Discussion

The main result of our work is that several seed circulation networks operate in the same community and at the same time. This can arguably be explained by differences in the factors determining household's access to and maintenance of seeds of various crops and varieties. This result advances two central arguments about the importance of seed circulation networks for access to crop diversity and, therefore, for the social-ecological resilience of farming communities. First, seed circulation is shaped by crops' and varieties' biocultural traits and second, households' centrality in the seed circulation network is related to on-farm crop diversity. Before discussing the main results, we note that our results suffer from several potential shortcomings.

5.1. Limitations

First, these seed circulation networks aggregate seed transactions taking place at different moments in time and do not consider that the timings of interactions differ across crops. While this method allows us to capture the origin of seeds cultivated nowadays, it could contribute to mask the contemporary mechanisms driving seed circulation (e.g., hampering the identification of seed donor-hubs). Research considering only the most recent seed acquisitions could disclose mechanisms at play that were blurred by our methodological choice. Future research should conduct diachronic analysis to assess how seed circulation changes through time and the possible role of external actors in shaping these changes. Second, we constructed the networks aggregating individual data at household level. However, taking the household as a unit of analysis does not allow to quantitatively assess the importance of some key biocultural variables, such as gender, for seed access and seed network structure. Previous research has shown the importance of intra-household dynamics when studying seed access, highlighting diversity within the household (Wencélius et al., 2016). In this line, future research should look at the relationship between individual farmers' centrality in the seed circulation network and the agrobiodiversity they manage, which might show important factors now masked by our household analysis. Third, the paper has focused on the effect of households' position in seed acquisition networks for cultivated diversity, leaving aside impacts of other factors (included only as control variables). We acknowledge that other variables beyond the ones considered in this study could also influence households' position in the network and on-farm diversity – e.g., diversity of source types and distance to source type. Fourth, our classification of varieties is based on farmers' reports. Previous research has shown that non-farmer varieties provided by extension services are frequently acquired by farmers through peer-to-peer seed circulation (Labeyrie et al., 2014a; Teeken et al., 2012). As a result, these varieties often end up being perceived as farmer varieties by farmers. In our study, this may have led to an underestimation of the number of non-farmer varieties reported, particularly concerning peanut. Despite the long history of peanut variety improvement in Senegal, our inventory only documented one non-farmer variety. Fifth, our analysis treats each crop as independent; however, a more comprehensive approach could adopt a relational perspective that views crops and seed exchange networks as components of a complex system. Future research could explore potential links between the diffusion of different crops and varieties. This could involve investigating whether crops that play a similar role in the agroecosystem (e.g., that occupy a similar position in the crop rotation) circulate together or through the same networks.

5.2. Seed circulation is shaped by crops' biocultural traits

Our findings suggest that seeds from different crops do not circulate in the same way because crops differ on their biocultural traits. Previous work has shown that crops' biological characteristics influence seed production, viability, and availability (Ellen and Platten, 2011). Seed circulation is also shaped by social relations, cultural rules, and symbolic values associated with crops, which guide farmers' practices like selection, management, storage, and uses (Delêtre et al., 2011; Labeyrie et al., 2016; Leclerc and Coppens d'Eeckenbrugge, 2012). Moreover, human history might also affect the type of actors involved in seed circulation and the geographic distribution of crop diversity – e.g., (van Etten, 2006).

Our results add to previous studies highlighting that, even within a village, seed acquisition networks vary across crop species, arguably because of differences in crops' biocultural traits. For example, Bambara groundnut's network is larger, has lower density, lower modularity, and wider geographical spread than other traditional Bassari crops, showing that households participate more actively in exchanging, giving, and acquiring Bambara groundnut than sorghum or fonio seeds. Our ethnographic understanding suggests that this is at least partly related to seed lot renewal rate, which is connected to legume's seed storage qualities. Bambara groundnut (and peanut) seeds are highly vulnerable to pest attacks, which forces farmers to frequent seed lot renewal. However, crop biology alone does not suffice to explain seed network structure, as demonstrated by differences in seed circulation between the two legumes. The peanut seed circulation network was the largest, best connected, most broadly spread, and most reciprocal of all the seed networks studied, which might be related with the specific historical circumstances of cultivation.

The commercial production of peanuts for export was promoted by the French colonial regime in the 19th century and by post-colonial governments after Senegal's independence (year 1960). Although peanuts are no longer the main focus of national policies and nowadays Bassari mostly cultivate peanuts for self-consumption, peanuts continue to be largely acquired through trade and are even used as alternative currency (mostly by women). Peanut abundance in local markets discourages farmers from keeping their own seed, as they know that, in case of need, they will find seed at the market with relative ease. Being widely adopted by the Bassari in the last century, peanuts are less rooted in the local culture than traditional crops and are therefore less subject to cultural rules and norms guiding seed circulation. In contrast, Bambara groundnut seeds bear an important cultural and symbolic value in the local community and circulate in a more restricted way, as shown by the higher number of subgraphs within the seed circulation network. Sorghum provides another good example of how social norms and cultural values restrict the circulation of seeds of traditional crops. Sorghum is an important crop for Bassari ceremonial life and Bassari men's identity. Its seeds circulate mostly within men living in the same neighbourhood, which in the case-study village coincides with members of the same patrilineage, showing the importance of descent and alliance for access to sorghum seeds.

Among the Bassari, the circulation of seeds of traditional crops is particularly embedded in kin, gender and age-class networks. This result is in line with previous research that describes seed circulation as embedded in pre-existing social structures and connected to farmers' social identity (Labeyrie et al., 2014b; Leclerc and Coppens d'Eeckenbrugge, 2012). For example, as in other small-scale societies (Díaz-Reviriego et al., 2016; Howard, 2006), Bassari women play a more important role in household seed provisioning than men, conferring them social status and cultural recognition. They also play an important role in the maintenance of communal social relations, household food security, and generally in caregiving. However, there are also gender-related social differences in seed circulation networks. For example, sorghum seeds are traditionally considered 'the' men crop, and mostly circulate among men.

The actors involved also influence seed flows and seed circulation network structure. Agricultural development agendas and research priorities have historically prioritized the most profitable crops –e.g., peanut production for export during colonial and early post-colonial times – or cereal crops with high yields, important for the country's food security strategy, i.e., rice and maize (Porcuna-Ferrer et al., under review). Consequently, agricultural extension projects, NGOs, and local markets have also made available seeds of these crops. According to our work, when external actors play a prominent role, seed circulation networks tend to have higher centralization indices. For example, for introduced crops (i.e., maize, rice, and peanut), projects/NGOs and market vendors play a relevant role, and fewer actors concentrate more seed sourcing, which risks reinforcing or creating (new) power dynamics and structural inequalities in the local communities.

In the absence of longitudinal data, it is difficult to assess trends in the coexistence of different seed circulation systems. However, based on our data, we interpret the effect of agricultural extension projects and NGOs in seed circulation in two complementary ways. First, projects/NGOs-interventions result in centralized seed diffusion models, which might displace (decentralized) traditional mechanisms / institutions, like kinship or age-class that have secured access to seeds for generations, and create new social networks, increasing the centrality of farmers supported by the projects, NGOs or extension services (Isaac et al., 2021). The substitution of traditional sources by new, institutional sources could lead to overcentralized networks, potentially constraining local communities' social-ecological resilience (Cretney, 2014; Pelling and Manuel-Navarrete, 2011).

Broader socio-economic pressures leading to the rapid transformation of smallholder farming systems and to the weakening of traditional systems of seed sharing also affect how biocultural factors shape seed circulation networks. Local cultivation of sorghum, fonio, and Bambara groundnut is in recession and farmers increasingly rely on projects/NGOs to acquire seeds of newly introduced crops. Market integration, which locally started with the expansion of peanut cultivation in the 1900s and has exploded since the 2000s with the arrival of NGOs and agricultural development projects that promoted maize and rice cultivation have largely contributed to traditional crop abandonment (Porcuna-Ferrer et al., under review). We show that the networks of traditional crops have high levels of fragmentation, small size, and low densities which reflects a high proportion of isolated farmers and a small number of possible seed exchanges. This reduced circulation of seeds increases network fragility, potentially limiting network's capacity to support crop diversity.

A second interpretation of the effect of projects/NGOs in seed circulation refers to their integration in traditional networks. Traditional networks of seed circulation have a high adaptive capacity to channel seeds of new crops. In the theory of change behind the African Green Revolution, farmers' des-centralized seed systems were expected to be gradually replaced by 'formal' centralized ones – e.g., (Scoones and Thompson, 2011; Westengen et al., 2023). However, among the Bassari, as it has been the case in several locations worldwide, linkages and interdependencies between centralized and des-centralized seed systems have developed (Almekinders and Louwaars, 2002; McGuire and Sperling, 2016). Despite being relatively ‘new’ crops in the Bassari farming system and strongly supported by development agendas and the official seed sector, maize and rice substantially circulate household-to-household, suggesting that farmers draw on the strengths of the different seed acquisition systems.

Still, the broader socio-economic dynamics mentioned earlier urge for caution when assessing the benefits of co-existing forms of seed circulation. From an agricultural development perspective, the question is how to improve farmers' access to high-quality adapted seeds without breaking the tightly connected relationships that have traditionally played a pivotal role for the resilience of smallholder farmers (Haider et al., 2020). In this regard, our data supports previous research that emphasizes the importance of moving beyond the dichotomy of ‘formal/centralized’ versus ‘informal/decentralized’ seed circulation in order to effectively understand and support farmers (McGuire and Sperling, 2016; Westengen et al., 2023). It also highlights the need to assess existing seed circulation networks when devising any intervention (Abay et al., 2011).

5.3. Households' centrality in the seed circulation network affects access to crop diversity

Our results show that household centrality in the network of seed circulation is generally associated with on-farm varietal diversity. Previous studies have tested this association, finding contrasting results (Abizaid et al., 2016; Calvet-Mir et al., 2012; Díaz-Reviriego et al., 2016; Kawa et al., 2013). Our results suggest that such contrasting results might just reflect the fact that there is not a single measure of centrality that explains on-farm diversity for all the crops and variety types. Indeed, owing to the specific crop biocultural traits guiding seed circulation, different centrality measures can explain different aspects of access to crop diversity.

As Kawa et al. (2013) and Abizaid et al. (2016), we did not find an association between being an important seed provider (i.e., having a high outdegree) and on-farm varietal diversity. However, we found that the type of actors mobilized for acquiring new seed (indegree types) and the level of household intermediation in the seed circulation network (betweenness) were differently associated with household's varietal diversity, the association depending on the crop and variety type. This finding suggests that household's access to different crops and variety types might depend on its ability to mobilize different types of relations. Access to farmer varieties of traditional crops is best granted through farmers' personal network, whereas households with a higher level of intermediation in the network will hold a more privileged position to access newly arrived varieties, and households that can interact with market-logics and projects/NGOs will probably have better access to non-farmer varieties. Our findings also point to the importance of the socio-economic status of the household for accessing crop and varietal diversity. Specifically, access to land affects cultivated diversity for all crops and most variety types. Household size, age of the household head, and household' financial resources all played an important role favouring access to diversity for certain crops and variety types. These results are in line with previous research that point to wealth as a key structuring factor of seed circulation (e.g., Wencélius et al., 2016).

From a social-ecological resilience perspective, farmer varieties are an important reservoir of biocultural memory, as farmers have selected them over generations for their fit to local natural and management conditions. Seeds often circulate together with knowledge about their characteristics, qualities, and management practices (Calvet-Mir et al., 2012; Reyes-García et al., 2013). Both trait diversity and the associated knowledge are important legacies to help adapt to new conditions (Cabell and Oelofse, 2012; Reyes-García et al., 2014). In turn, access to introduced and non-farmer varieties, particularly to new climate-resilient crops and varieties, can also be an important way for farmers to cope with or adapt to climate change or other stresses (Acevedo et al., 2020), as farmers capacity to change crop species and varieties is a common response to changing climatic conditions (Ruggieri et al., 2021; Schlingmann et al., 2021). Building up on social-ecological resilience theory (Cabell and Oelofse, 2012; Walker et al., 2004), farmers' access to crop and varietal diversity should be ensured through a repertoire of flexible responses (i.e., providing farmers with a wide range of source and crop diversity options), accounting for the trade-offs among these responses. For example, while introducing a cash-crop to the on-farm crop portfolio can work well to meet market demands and farmers' cash needs, the abandonment of drought-resistant subsistence crops can diminish agroecosystem's resilience to other stresses, like climate change (McGuire and Sperling, 2013).

6. Conclusion

This study shows that farmers' access to seeds is conditioned by crop biocultural traits and that farmers' centrality in the seed circulation network affects on-farm crop diversity.

While our findings highlight the instrumental role of farmer-to-farmer seed circulation networks for the maintenance of local crop diversity and for the introduction of new diversity in the agricultural system, they also indicate that new seed sources, such as local markets, agricultural extension projects or NGOs, can offer access to new seeds with adaptive potential. Considering ongoing climate change impacts in the Bassari territory, agricultural interventions need to evaluate trade-offs between responses and medium- and long- term consequences for farmers' social-ecological resilience. The challenge remains on how to enable the coexistence of new and old crops and varieties, and of modern and traditional ways of accessing seeds. In general, there is a certain consensus that horizontal, locally-adapted ways of accessing seeds (e.g., farmer-to-farmer seed circulation) are more sustainable in the long-run than top-down, hierarchical ones (e.g., agricultural extension services), but there is also growing agreement that both strategies should be reconciled for more effective crop diversity conservation (Pautasso et al., 2013; Thomas et al., 2011).

For the Bassari reconciling both approaches would entail that agricultural extension projects and NGOs shift from the current top-down approach to multi-centric participatory approaches that situate farmers' knowledge and practices at the centre. A participatory-based approach would facilitate the broadening of projects' crop-portfolio, including traditional crops like sorghum, Bambara groundnut, and fonio. This would contribute to strengthening locally adapted crop diversity and seed systems, thereby bolstering the social-ecological resilience of smallholder farming communities in the phase of climate and global change.

Declaration of Competing Interest

The authors declare that there is no conflict of interest.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.agsy.2023.103750.

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