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RESEARCH ARTICLE

Can seed exchange networks explain the morphological and genetic diversity in perennial crop species? The case of the tropical fruit tree *Dacryodes edulis* in rural and urban Cameroon

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Societal Impact Statement

Crop seed exchange networks, shaped by social dynamics, strongly influence the organization and breadth of plant diversity in human-managed environments. Integrating an urban and market perspective, this study explores the diversity dynamics of a socio-economically important Central African fruit tree species, the African plum tree. Tree owners in urban, peri-urban and rural sites use seeds from different origins as their main propagation material, leading to locational variations in genetic diversity and structure. This analysis contributes toward building a framework to inform the research agenda of cultivated African fruit trees, by highlighting the important role of urban centers in safeguarding crop genetic resources.

Summary

- Biocultural factors constrain the dynamics of crop species diversity. Here, we considered different aspects of the social, spatial and temporal dynamics of morphological and genetic diversity in a multi-purpose perennial crop, the African plum tree (*Dacryodes edulis*). We assessed (i) how seed exchange networks were organized along urbanization gradients, and how they influenced the distribution of species diversity; (ii) the temporal dynamic of seed exchange network by characterizing species genetic diversity through time.
- To do so, the study was carried out in Cameroon, where we focused on three urbanization gradients, covering urban, peri-urban and rural areas, corresponding to three different ethnic groups (Bamileke, Bassa, Beti). We combined interviews with tree owners and nuclear microsatellite-based genetic analyses.
- Tree owners from urban and peri-urban sites primarily used distant seed sources, acquired in the market or from their village of origin, as propagation material, whereas tree owners in rural sites relied primarily on village-level seeds. In turn, genetic diversity was not evenly distributed, with rural sites exhibiting their own genetic clusters. On the contrary, the genetic diversity of urban sites was

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enhanced by extensive human-mediated seed flows. Looking at trees from different age classes, we found that genetic diversity was stable over time.

- Overall, this first attempt to combine different levels of diversity for African plum trees in commercially connected areas expands the scope for in situ intraspecific conservation by highlighting the contribution of urbanized areas.

KEYWORDS

agrobiodiversity, crop genetic resources, indigenous fruit, local seed systems, tropical trees

1 | INTRODUCTION

The morphological and genetic variation of crop species are influenced by human actions through the selective pressures they exert, via seed selection for traits of interest or selective removal of undesirable individuals (Gepts, 2004). Genetic diversity is the foundation to ensure crop adaptation to heterogeneous and changing environments (Zimmerer & de Haan, 2017). Understanding the patterns of genetic variation of crop species currently managed in agroecosystems is of paramount importance, as it directly contributes to the quality of human food, to the productivity, resilience, and adaptive capacity of agroecosystems and to the local and global economy (Hajjar et al., 2008; Kahane et al., 2013; Labeyrie et al., 2021; Renard & Tilman, 2019). In contrast to annual crops, whose evolution through domestication is well characterized, long-lived species remain understudied, especially in sub-Saharan Africa.

The effects of cultivation on intraspecific plant diversity are generally demonstrated by comparative studies of wild against cultivated populations. For native perennial species in the tropics, fruits from cultivated populations are often shown to be significantly larger than those from wild stands, although the two population types are not necessarily clearly genetically differentiated (Aguirre-Dugua et al., 2012; Moreira et al., 2017; Rollo et al., 2020). This comparative framework can be complexified, with sampling being carried out from wild populations to more or less intensively managed environments, such as agroforestry systems and monocultures. This thus allows to test the influence of different agricultural contexts or management practices on intraspecific diversity (Cabrera-Toledo et al., 2020; Miller & Schaal, 2006). Contrary to expectations, little differentiation was found by Cabrera-Toledo et al. (2020) between populations from separate compartments. This result was possibly due to exchanges of germplasm among producers, stressing the need of taking the seed exchange network dimension into account in such studies.

Informal seed exchange networks, on which African smallholder farmers rely heavily for their seed supply (Coomes et al., 2015), can promote the maintenance of intraspecific diversity (Pautasso et al., 2013). For orthodox seeds able to conserve their viability after drying to very low moisture content and stored in freezing conditions for a long duration, the temporal evolution of diversity can be tracked through diachronic analyses (Barry et al., 2008; Olodo et al., 2020). For tree species, which are long-lived, but with recalcitrant seeds such as *Dacryodes edulis* (Olayode & Kolawole, 2013), a possible way to monitor diversity through time is to compare genetic diversity for different age classes, and when appropriate to link it with information from owners on their seed sources, as well as evolving management practices. Using this approach on jackfruit trees in Bangladesh, Witherup et al. (2019) found downward trends in diversity over time, as in any selection and breeding process, but which was strong whatever the propagation method used. As for the spatial patterns of diversity, recent studies underlined strong ties between spatial distribution of genetic diversity (“genetic structure” for short) and local patterns of human cultural diversity (Eyzaguirre, 2005; Galluzzi et al., 2010; Jika et al., 2017; Labeyrie et al., 2016; Orozco-Ramírez et al., 2016).

To our knowledge, studies shedding light on the cultural forces affecting plant intraspecific diversity are only seldom conducted for tree species. An investigation on the baobab tree (*Adansonia gregorii*) in northwest Australia, building on genetic and linguistic data, showed congruent patterns of gene flow and borrowed Aboriginal names (Rangan et al., 2015), suggesting that an ancient human use history contributed to the current distribution of the species. Such large coincidence between inferred barriers to gene flow among tree populations and differences in human language was also described in a study carried out on common walnut and sweet chestnut trees in Eurasia (Pollegioni et al., 2020). In both studies though, authors were careful to underline the high spatial autocorrelation between languages and tree genetic variation, as both responded in similar ways to environmental drivers and constraints (Gavin et al., 2013), which could be solved by designing research frames dealing with finer scales.

Urban areas are attracting mounting interest for their potential for biodiversity conservation (Heath et al., 2020), as well as being melting pots of cultural diversity. They are thus interesting places to question the influence of human practices on the genetic diversity of cultivated plants. In sub-Saharan Africa, tree planting in urban areas has been identified since the late 1990s as an activity involving some inter-ethnic co-operation and active seed exchange among inhabitants (Linares, 1996). The relationship between human practices and the intraspecific diversity of useful plants has been rarely approached along urbanization gradients, going from rural to urban areas.

This article thus addresses the distribution of tree morphological and genetic diversity, in relation to the propagation practices of three ethnic groups settled in the urban center of Yaoundé, Cameroon. We chose as our model species the African plum tree (*D. edulis* [G. Don] H.J. Lam), which is native to the tropical rainforests of Central Africa, ranging from Nigeria to Cameroon, Central African Republic, Democratic Republic of Congo, Equatorial Guinea, Gabon and Republic of Congo (Aubréville, 1962; Vivien & Faure, 1985). The species is economically and culturally important, its fruits, the African plums, being largely consumed across the subregion and internationally. They are commonly cooked and eaten as snacks or side dishes (Tabuna & Tanoe, 2009). Endemic to the Gulf of Guinea, African plum trees grow naturally in forested areas of Cameroon, and their presence in Yaoundé before urbanization is suggested by urban toponyms: the pluralized name of African plum in Ewondo (*messa*) is used to refer to several neighborhoods (Ngo Gweth et al., 2015). Although much of the long domestication history of the species is yet to uncover, African plum trees have been gradually cultivated and commercialized within the region. Apart from wild individuals in Central African rainforests (Mboujda et al., 2022), they are now mostly found in home gardens and agroforests from rural up to urban areas (Nguegang Asaa, 2008; Schreckenberg et al., 2002). Reflecting its popularity and socio-economic importance to local people, the species was among those selected for participatory domestication in Cameroon and other countries of the humid lowland of West Africa in the 1990s and early 2000s, whereby its intraspecific variation was characterized and used for agronomic improvement (Franzel et al., 1996; Leakey et al., 2002; Leakey & Simons, 1998; Simons & Leakey, 2004; Tchoundjeu et al., 2002). It is indeed the fruit tree with the highest use-value in cocoa agroforests (Jagoret et al., 2014), as well as one of the most widespread perennials in Yaoundé (Mala, 2009), making it the most suitable native tree species for sampling from rural to urban areas. The species is pollinated by insects from Apoidea taxa in particular (Fohouo et al., 2001), and is predominantly allogamous (Kengue et al., 2002), with selfing possibly occurring in male-hermaphrodite trees (Kengue, 1990). Planting materials propagated by cutting and marcotting are available in some nurseries managed by the National Agricultural Research Institute for Development (IRAD) and the World Agroforestry Centre (ICRAF), as well as in some private nurseries, but in limited quantity (Degrande et al., 2013). Moreover, their use is still limited due to their high price.

This study aimed to explore different aspects of the social, spatial, and temporal dynamic of African plum diversity, furthering previous works on the species (Rimlinger et al., 2021) by (i) comparing the distribution of genetic and morphological diversities in the different sites; (ii) refining our understanding of the uniqueness or not of urban diversity; and (iii) assessing the impact of seed exchanges through time by analyzing the genetic diversity between different trees' cohorts. We thus collected genetic and morphological data on African plum trees from three different ethnic groups present in three production basins to cover the main Cameroonian production area. Further, we characterized the urbanization gradient by adding peri-urban sites, and information on tree age to evaluate the temporal evolution of the diversity. We expect that along the urbanization gradients, seed exchanges are extensive in relation to the rural–urban supply chain, but also favored by exchanges between people from the same ethnic group, with some yet unpredictable variations between ethnic groups. We also expect a stronger genetic structure among rural sites, as these sites are less connected by trade roads, and as exchanges among ethnic groups might be less frequent than exchanges within ethnic groups, driven by kin relationships. Finally, Yaoundé should correspond to a sink of genetic diversity for the species, with planting material sourced from different locations through seeds imported from various rural producing areas, either by buying fruits from the markets or by taking them directly from villages of origin of the city dwellers (Rimlinger et al., 2021). To limit the bias of sampling only one kind of fruit phenotype along the production basins, we considered African plum morphological diversity as well. Overall, we analyzed how management practices, collected through 341 interviews with tree owners, were linked to the distribution of morphological and genetic diversity of cultivated African plum trees.

2 | METHODS

2.1 | Study sites and sample collection

In this study, we extended the methodological framework of Rimlinger et al. (2021) in three ways. Firstly, we included rural as well as peri-urban sites associated with three ethnic groups present in Yaoundé (Bamileke, Beti, and Bassa). This allowed us to test the distribution of genetic diversity between ethnic groups. Secondly, we introduced the intraspecific morphological diversity of fruits, which allowed us to understand if there is a correlation between the level of genetic and morphological diversity. Lastly, the temporal dynamic of seed exchange network was indirectly investigated by characterizing species genetic diversity through time.

In order to characterize the spatial and social dynamics of genetic diversity distribution along the African plums' rural–urban supply chain, tree owners were interviewed, and tree material was sampled for genetic analyses along three urbanization gradients connecting the city of Yaoundé to its main supply areas of African plums. Each urbanization gradient was corresponding to a specific ethnic group (Beti, Bamileke, or Bassa), and was composed of a rural, a peri-urban, and an urban site in different neighborhoods of Yaoundé (Figure 1), allowing to analyze both an urbanization effect and an ethnic group effect. The rural and peri-urban sites were as follows: one in the Centre region (Beti ethnic group), the second stretching to the West region (Bamileke ethnic group), and the third stretching to the Littoral region (Bassa ethnic group). The peri-urban sites were defined as areas whose supply and demand were strongly tied to those of the urban market, due to their paved road connection to the metropolis of Yaoundé (Temple & Moustier, 2004). Rural sites (such as R2) were sometimes located closer to Yaoundé than peri-urban sites (such as PU3), but with poor connections to the city, and thus weaker exchange possibilities. The peri-urban site along the western urbanization gradient had more Beti inhabitants, the predominant ethnic group locally, than Bamileke migrants so a mixed sampling (of both ethnic groups) was adopted. In Yaoundé, we conducted interviews with African plum tree owners from these three ethnic groups in three neighborhoods: one neighborhood from the city center and two from its periphery, as the settlement history and ethnicity of urban dwellers differ between the

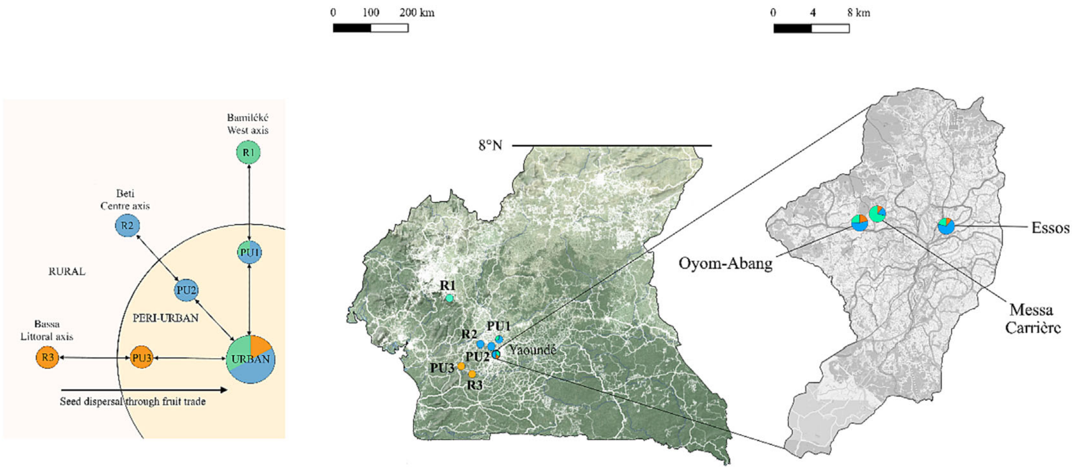

FIGURE 1 Sampling design. On the left, schematic diagram of sampling strategy along the three urbanization gradients, going from urban sites to three rural (R) sites passing through peri-urban (PU) sites, and the distribution of the three ethnic groups in each site (1: Bamileke, 2: Beti, 3: Bassa; the PU1 site including a mixed-sample of Bamileke and Beti tree owners; each group is represented with a color [green, blue, and orange, respectively]). On the right, map of South Cameroon with the rural and peri-urban sites, with a close-up on Yaoundé for the urban sites and the proportion of owners from the different ethnic groups interviewed in each site.

TABLE 1 Summary of the total number of Cameroonian African plum tree owners (N_{TO}) interviewed per site along the urbanization gradient according to their ethnicity; together with the number of trees sampled for morphological characterization (N_{TM}) and for genetic characterization (N_{TG}).

Site type	Urban			Peri-urban			Rural			Total		
Ethnicity	N_{TO}	N_{TM}	N_{TG}	N_{TO}	N_{TM}	N_{TG}	N_{TO}	N_{TM}	N_{TG}	N_{TO}	N_{TM}	N_{TG}
Bamileke	46	51	47	7	12	9	38	99	73	91	162	129
Bassa	23	26	24	36	77	60	29	81	83	88	184	167
Beti	61	82	71	47	89	48	33	75	40	141	246	159
Total	130	159	142	90	178	117	100	255	196	320	592	455

urban core and the outlying areas (Togolo, 2019). Most urban dwellers belonged to the Beti ethnic group in the central site of Essos, whereas urban dwellers from all the three above-mentioned ethnic groups were living in Oyom-Abang and Messa-Carrière sub-counties.

Upon arrival in the different sites, we introduced ourselves to customary chiefs. When possible, we organized a first focus group to meet with African plum tree cultivators of the community, whose reputation was known by people from the chiefdom. Then, interviews, as described in Rimlinger et al. (2021), were based on an opportunistic sampling and a snowballing approach. Before interviews, tree owners were informed of the research intentions and of their right to participate or decline. After interviews, they were given a form stating that the interview had been conducted in accordance with the principles of free and informed consent, which they could sign if they agreed. Summarized information of tree owners' characteristics (gender, age, ethnicity) was added in Supporting Information (Table S1).

In total, we interviewed 341 tree owners (160 women, 181 men) and surveyed 722 African plum trees across these nine sites (one site corresponding to one position on the gradient for one ethnic group, except for the mixed Bamileke-Beti peri-urban site; Table 1 and Figure S1). To characterize the influence of human practices on the distribution of the morphological and genetic diversity of African plum trees, we collected information on the origin of tree planting material, the diversity of fruit morphotypes, and the genetic polymorphism of these individuals. These approaches were developed in the urban, peri-urban, and rural sites. Information on fruit characteristics (see below) was fully available for 592 trees, and information on seed origin used for plantation (see below) was available for 375 trees (Table 1). Geographical coordinates and diameter at breast height (DBH) were collected for each tree. Leaves from 455 of them (from 24 to 83 trees/site) were collected in silica gel for genetic analyses (Table 1).

2.2 | Propagation practices: seed origin and characteristics

We recorded owners' information on the geographic origin of the propagation material (seeds, seedlings, cuttings) used to plant their trees. Taking "situated knowledge" (Nazarea, 1999) in consideration in genetic studies is crucial to accurately understand genetic patterns (Leclerc & Coppens d'Eeckenbrugge, 2012; Gros-Balthazard et al., 2023): this means that local representations and practices, and more broadly, their historical and social underpinnings, are all essential elements to be taken into consideration. Nonetheless, we acknowledge that informants can sometimes provide confusing or inaccurate information (Gros-Balthazard et al., 2020); to avoid this, questions were refined or rephrased to make them as straightforward as possible. When an information could not be obtained or trusted, data were carefully cleaned: missing data were removed, as well as too vague locations, for instance when trees were planted by other relatives or unknown previous owners. From the 722 trees surveyed, a sufficiently precise location could be identified for 375 trees. For these trees, we distinguished four different categories of seed origin: the owner's own field/home garden (category *owner's own trees*; Table 1); outside of the owner's own field/home garden either from the same village (category *same village*) or from a different village (category *different village*); a purchase at the market or in a commercial tree nursery (category *market or nursery*), meaning that the fruit traveled through a commercial exchange network and some might be originating very far from the planting site. For the urban dwellers with a rural background, the seeds could come from their village of origin, which was made explicit with the subcategory *% home village* in the category *different village*. When possible, we calculated the distance between the seed source and the planting location using the R package *geosphere* (Hijmans, 2019).

2.3 | Characterization of fruit morphotypes and tree age classes

For each sampled tree, we first asked African plum tree owners to provide its age, which was often estimated by them based on their life history or that of their family (settlement, births, deaths). They then described the morphological and taste characteristics of its fruits based on an identification sheet (Methods S1) showing different possibilities for fruit size, shape, skin, and pulp color. We chose to use this standardized sampling strategy instead of asking about owners-defined ethnovarieties that are used differently between the three ethnic groups (Lemoine et al., 2023; Rimlinger et al., 2021). To avoid the overrepresentation of fruits with valued qualities, we paid attention, during the interview and sample procedure, not to put emphasis on tasty or large fruits first, and to ask specific questions on small or sour fruits. Based on answers from interviews, we added the extra possibility "fluctuating" for three fruit characteristics (size, pulp color, skin color). It corresponded to fruits with more than one of the different possibilities, either between fruits for a given year or between years. We added the owner description of fruit taste that was later grouped in three categories: (very) good, average, and (very) sour. We assembled four fruit characteristics that were demonstrated as the most important to African plums producers and consumers (fruit size, skin color, pulp color, and taste; Rimlinger et al., 2021) to obtain specific fruit morphotypes. From the initial 722 trees characterized, we retained 592 trees with a complete morphotype corresponding to the four characteristics. We represented the distribution of morphotypes at the regional scale according to their relative frequencies. To check how many new morphotypes were present in each additional site, we also graphed the sampling effort (see Figure S2). Following the study from Jarvis et al. (2008), where an average richness per farm corresponds to the number of traditional varieties per household, we calculated the richness in morphotypes based on the number of trees corresponding to the above targeted characteristics. We estimated the rarefied richness at each site for $N = 25$ trees using the R package *vegan* and measured the evenness (Oksanen et al., 2018). We also applied the Shannon H diversity index at the intraspecific level, as described in Gómez et al. (1998), which takes into account the richness in morphotypes and the distribution of trees among morphotypes in each site, and Pielou's evenness index to see the extent to which some morphotypes were dominant, as presented in Smale et al. (2001). The Shannon H diversity index increases following the number of morphotypes and the evenness of their distribution; Pielou's evenness index is maximal (1) when the distribution is the most even.

Tree age was reported by tree owners for 442 trees (61% of the total number of trees) with ethnoecological methods: specific questions were followed with probe questions when an informant was struggling to remember a specific date or period. When a tree owner was giving an age quickly and swiftly, we estimated it to be trustworthy; when he or she was hesitating, additional questions were asked to help identify it in relation to personal events (birth, wedding, death), local or regional events (fire, flooding, storm), or political events (election, other). The researcher interviewing was here to guide and discuss when the age given seemed implausible. A linear regression of tree age and tree DBH was performed, since DBH is a frequent proxy for age (Lieberman et al., 1985), resulted in an r^2 value of 0.67 (p-value < .001; see Figure S3). We thus used information on trees' DBH to classify them into three age classes, as in previous studies of diversity changes over time (Wehenkel & Sáenz-Romero, 2012; Witherup et al., 2019). Classes were defined as follows: young trees (<15 years old trees; DBH below 20 cm, 97 trees), middle-aged trees (15 to 40 years-old trees; DBH from 21 to 40 cm, 177 trees), and old trees (>40 years old trees; DBH above 41 cm, 168 trees).

2.4 | DNA extraction and genotyping

We extracted DNA from dried leaves corresponding to 455 trees (among which 402 trees with complete fruit morphology are available) following the protocol from Mariac et al. (2006) and genotyped them using 10 out of 21 nuclear microsatellites available for the species, selecting the most polymorphic and unambiguous (DaE-16, DaE-20, DaE-23, DaE-27, DaE-29, DaE-36, DaE-41, DaE-42, DaE-46, DaE-49; Rimlinger et al., 2020). Individuals were genotyped at the CIRAD Genotyping Platform in Montpellier, France, using an ABI 3500 XL sequencer (Applied Biosystem, Foster City, California, USA). Electropherograms visualization and scoring were done with the microsatellite plugin in Geneious 7.1.3 (https://www.geneious.com). Estimations of observed and expected heterozygosity (H_O and H_E), inbreeding coefficient (F_{IS}), the effective number of alleles (*Ne*), the rarefied allelic richness (*Ar*) and null allele frequency (r), and the corrected inbreeding coefficient corrected for the presence of null allele (F_{null}) were obtained for each locus and population using SPAGeDi 1.5 (Hardy & Vekemans, 2002) and INEST 2.2 (Chybicki & Burczyk, 2009).

To compare the distribution of genetic diversity between fruit morphotypes, sites (along the gradient and among ethnic groups), and age classes, we estimated the level of genetic differentiation among sites with the F_{ST} fixation index and tested the genetic structure by using a permutation procedure (5000 iterations) among all individuals and sites with SPAGeDi. Levels of diversity between morphotypes (characteristic by characteristic, in order to see if barriers to gene flow were present between morphotypes), between sites and between age classes, were compared with one-way analysis of variance, controlling for the loci effect. The temporal evolution of genetic diversity through time was investigated by characterizing the level of genetic diversity and structure for the different age classes defined above (young, middle-aged, and old trees).

The pattern of distribution of genetic diversity between the different sites was further characterized by using the Bayesian clustering analysis implemented in STRUCTURE (Pritchard et al., 2000) with admixture ancestry and correlated allele frequencies. Given the global weak genetic structure observed in this study (see Section 3 and Figure S4), we used the LOCPRIOR option, as it facilitates attribution of individuals to a given cluster at a given assignment probability threshold (here of 0.8). K was set from 1 to 10, and each run was replicated 10 times, with a burn-in period of 40,000 followed by 60,000 Markov Chain Monte Carlo repetitions. We first tested the nine sites together, and then ran separate analyses within rural, peri-urban, and urban sites, and within each axis. The optimal number of K was assessed using STRUCTURE HARVESTER (Earl & vonHoldt, 2012).

To determine if planting material exchange is more likely between neighbor tree owners than between distant tree owners, we characterized genetic relatedness between individual trees according to geographical distances. Specifically, we calculated Loiselle's kinship coefficient (F_{ij}; Loiselle et al., 1995) between pairs of individuals for different distance classes using SPAGeDi 1.5 (Hardy & Vekemans, 2002). Spatial genetic structure (SGS) was tested by randomly permutating individuals' position (10,000 iterations). This analysis was carried out separately for urban, peri-urban, and rural sites, with distance classes adjusted to have (i) more than 100 pairwise comparisons for each interval; (ii) a proportion of all individuals represented at least once in the interval superior to 50%; (iii) a coefficient of variation of the number of times each individual was represented inferior to one. For urban trees, we ran the analysis first by urban site, thus mixing tree owners from different ethnicities, second by ethnic group, thus having trees scattered across urban sites. The power of the analysis was good for all groups except for Bassa owners, where the small number of trees was limiting (24 owners, less than 100 pairs of trees per distance interval).

3 | RESULTS

3.1 | Seed origin according to sites

Data on the geographic origin of the seeds used for plantation (use of vegetatively propagated planting material [marcots] was mentioned for less than 0.5% of the trees sampled in this study), as informed by tree owners, indicated that the distance from seed origin to plantation site strongly differed between sites (Kruskal–Wallis test, *p*-value < .001). This resulted in wide variations in mean "origin-to-plantation" (O-P) distance (Table 2). Markets and villages out of Yaoundé accounted for the bulk of seed origins for the trees planted in urban and in peri-urban sites (89% and 75% of them, respectively). Among the *different village* category, the villages of origin of new city dwellers held a special place in urban sites (64% of the seeds from this category) and less so in peri-urban sites (21%). These two "long-distance" categories were significantly less represented (Pearson's Chi-squared test, *p*-value < .001) in rural sites where cultivators used mainly their own seeds or seeds from neighbors and relatives within the same village (73% of the trees). This pattern was observed for all ethnic groups investigated. The mean O-P distance was significantly different between ethnic groups only for urban sites, being highest for Bamileke (Kruskal–Wallis test, *p*-value = .012) and similar for Beti and Bassa (*p*-value = .945).

To visualize the sharp decrease in distance calculated in Table 2, seed origin was mapped separately for urban, peri-urban, and rural sites (Figure 2). The number and spread of the different seed origins was markedly different between peri-urban and urban sites on one hand (Figure 2b,c), and rural sites on the other (Figure 2a). For the former, seeds came from many different localities far away from the plantation locations, whereas for the latter were sourced in few different localities close to the plantation locations.

3.2 | Morphological diversity between sites

The morphotypes were characterized according to three morphological and one taste characteristics (see Figure S5 for distribution of the different characteristics in the sampled sites), with two morphotypes considered different when any of the four characteristics differed. Of all the initial 592 trees, 147 different morphotypes were characterized in total, with an average richness of 41 ± 12 morphotypes per site along the gradient (Table 3). The most common morphotype, with large, blue skin, white pulp and good-tasting fruits, was found for 55 trees (9.3% of the total number of trees; see the rank-abundance distribution in Figure 3). The three most common morphotypes were present in the nine sampling sites, whereas 66 morphotypes were unique to one site. Within each site, the mean number of shared morphotypes (i.e., morphotypes cited by at least two different owners) was 8.9; it ranged from 4 to 19. In percentage of the total number of morphotypes present in each site, it represented in average 15% (ranging from 9% to 19%).

TABLE 2 Mean “origin-to-plantation” (O-P) distance along the three ethnic gradients according to the site type, presenting the data on the geographic origin of the African plum seeds used for plantation in Cameroon. The distance between the location where a seed originated and the one where it was planted was calculated based on geographic coordinates inferred from interviews with tree owners.

		Seed origin (frequency)					O-P distance ± SEM (km)
Ethnic group	Site type[a]	N	Farmer's own trees	Same village[b]	Different village (% home village)	Market or nursery[c]	All origins combined
Bami-leke	Urban (U1)	40	0.03	0.08	0.43 (71%)	0.48	98.5 ± 13.3
	Peri-urban[d] (PU1)	40	0.03	0.28	0.30 (25%)	0.40	40.6 ± 10.2
	Rural (R1)	49	0.14	0.61	0.04	0.20	4.3 ± 1.3
Beti	Urban (U2)	51	0.06	0.06	0.43 (32%)	0.45	31.7 ± 6.7
	Peri-urban (PU2)	39	0.13	0.13	0.21 (12.5%)	0.54	20.8 ± 7.1
	Rural (R2)	54	0.24	0.37	0.22	0.17	7.8 ± 1.9
Bassa	Urban (U3)	18	0.11	0.00	0.44 (88%)	0.44	42 ± 12.6
	Peri-urban (PU3)	37	0.16	0.03	0.43 (25%)	0.38	12.5 ± 2.9
	Rural (R3)	47	0.15	0.68	0.15	0.02	2.5 ± 0.5

Abbreviation: SEM, standard error of the mean.

[a] Sites are codified (U1, PU1, R1, etc.) as in Figure 1;

[b] Same neighborhood in the case of urban sites;

[c] Seeds are bought in markets by purchasing fruits, and in nurseries by purchasing juvenile trees;

[d] Mixed sampling: Beti and Bamileke (see Section 2 for explanation).

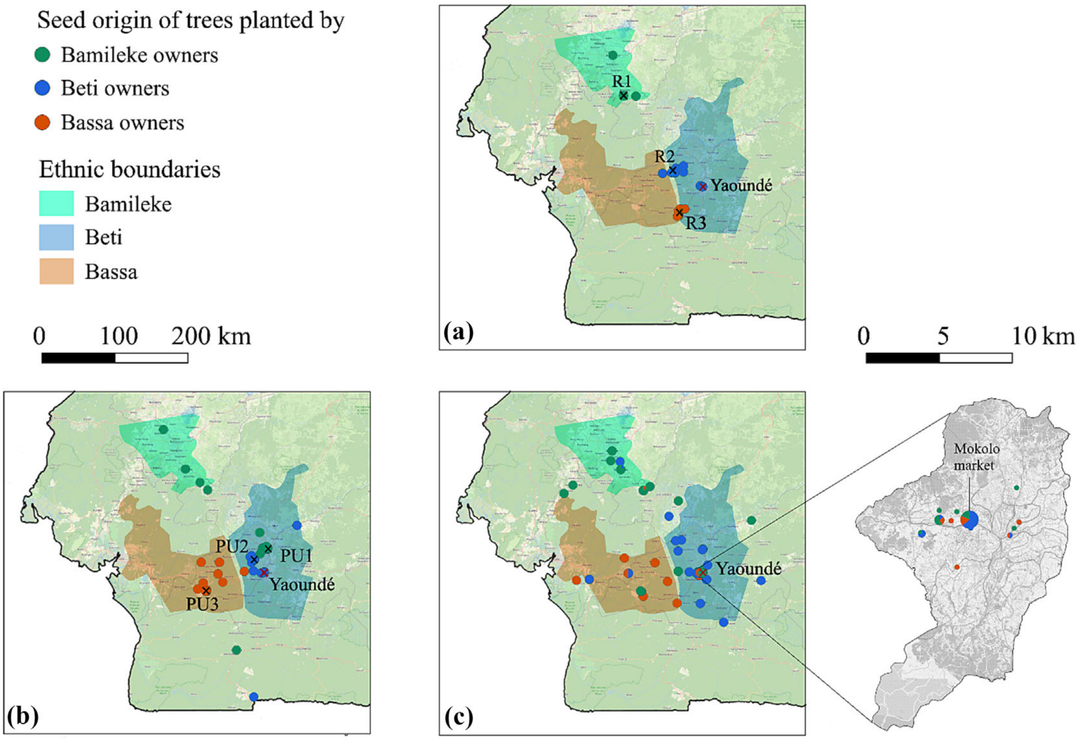

FIGURE 2 Origins of the seeds used to plant *Dacryodes edulis* trees in the different sites in Cameroon: a. rural sites; b. peri-urban sites; c. urban sites, with a close-up on Yaoundé. Details of seed provenances are presented in Table 2. Dots are colored following the ethnic group of the tree owner; rural and peri-urban sites are marked by a black cross and Yaoundé is figured with a red cross. The spatial ethno-linguistic data are taken from Felix and Meur (2001).

The richness was maximal in the Beti peri-urban site when looking at the rarefied morphotypes richness (MR) for $N = 25$ trees, and for the Beti urban and Bassa rural sites when looking at the Shannon index (H). The lowest H value was given for the Bassa urban site, where the smaller number of trees was characterized. The overall evenness was of 0.85, and the rank-abundance distribution (Figure 3) illustrated that only a few morphotypes were represented by many different trees, with almost half of the morphotypes ($N = 64$) characterized only once.

TABLE 3 Indices of richness in *Dacryodes edulis* morphotypes according to sites in Cameroon for the three ethnic groups and site types. Morphotypes were coded based on four characteristics (three morphological, one organoleptic); two morphotypes were considered identical when they shared the same four characteristics.

Ethnic group	Site type[a]	Nb trees	Nb morphotypes	MR	H	Pielou (evenness)
Bamileke	Urban (U1)	51	30	17.4	3.1	0.91
	Peri-urban[b] (PU1)	43	28	18.3	3.1	0.93
	Rural (R1)	99	50	19.2	3.6	0.93
Beti	Urban (U2)	82	53	19.9	3.7	0.92
	Peri-urban (PU2)	58	43	21.3	3.6	0.96
	Rural (R2)	75	46	19.8	3.6	0.94
Bassa	Urban (U3)	26	19	18.4	2.8	0.95
	Peri-urban (PU3)	77	46	19.2	3.5	0.92
	Rural (R3)	81	52	20.5	3.7	0.94
All (nine sites)		592	147	19.5	4.3	0.85

Note: MR: rarefied morphotypes richness calculated for N = 25 trees; H: Shannon index.

[a] Sites are codified (U1, PU1, R1, etc.) as in Figure 1;

[b] Mixed sampling: Beti and Bamileke (see Section 2 for explanation).

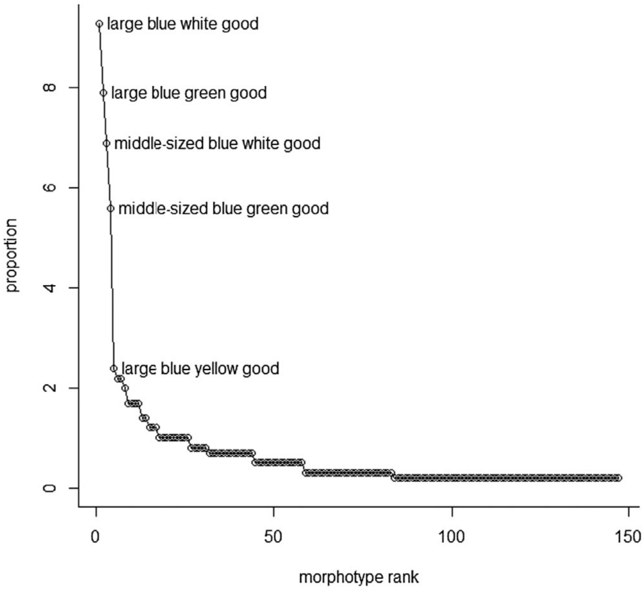

FIGURE 3 Rank-abundance curve displaying the relative morphotype abundance for the fruit of *Dacryodes edulis* trees in Cameroon; the most abundant morphotype is given Rank 1 and the least abundant morphotypes, characterized only once in our case, are given the highest ranks. Characteristics of morphotypes are ordered as follows: fruit size, skin color, pulp color, fruit taste.

3.3 | Distribution of genetic diversity relative to fruit traits

Using the F_{ST} fixation index, we compared the genetic differentiation between trees grouped based on each of their morphological (fruit size, skin, and pulp color) and taste characteristics. For skin and pulp color, and taste, all F_{ST} values from comparisons between pairs among categories were not significantly different from zero, indicating similar allele frequencies, and therefore weak population structure, between them. On the other hand, the F_{ST} between large and small fruits was significantly different from 0 ($F_{ST} = 0.002$; *p*-value = .031).

3.4 | Genetic diversity between gradients

The overall diversity between each gradient differed significantly (*p*-value < .001, Table 4). The mean AR_{15} value (the rarefied allelic richness for k = 15 gene copies) was higher for the Bamileke and Beti gradient (respectively, 7.3 and 7.1) than for the Bassa gradient (6.8). In both the peri-urban and rural areas, the higher AR_{15} was observed for sites from the West/Bamileke axis (rural Bamileke, peri-urban mixed). For the rural area, it was significantly higher than that of the Beti site (*p*-value = .017); for the peri-urban area, it was higher than that of the Bassa site (*p*-value = .015). The comparisons within each axis (Bamileke, Bassa, and Beti separated; except for the peri-urban site of the West axis with a mixed Beti/Bamileke sampling) show a significant difference (*p*-value < .001) for the Centre region/Beti axis only, where the allelic richness of the rural site was lower than that of the peri-urban and urban sites (Table 4). Between sites, the AR_{15} was of 7.2 for both the urban and peri-urban and was of 6.7 for the rural area. The ANOVA controlling for the loci effect confirmed that AR_{15} in rural sites was lower than those of urban and peri-urban sites (*p*-value < .001). Meanwhile, the AR_{15} in those latter sites was similar (*p*-value = .47). Within areas of the gradient, AR_{15} was significantly different among peri-urban sites (*p*-value = .045) and among rural sites (*p*-value = .018) for the three ethnic groups but was equivalent among urban sites (*p*-value = .39; Table 4).

TABLE 4 Genetic diversity indices of Cameroonian African plum trees of the urban, peri-urban, and rural sites for the three ethnic groups. Indices were obtained at the population scale, standard errors of the mean (SEM) are reflecting differences between the 10 microsatellite markers. Population genetics' indices are the following: Np, number of private alleles; Ne, effective number of alleles; AR_{15}, rarefied allelic richness for $k = 15$ gene copies; H_E, expected heterozygosity; H_O, observed heterozygosity; F_{IS}, inbreeding coefficient; values are means ± SEM; F_{null}, estimation of the inbreeding coefficient accounting for null alleles.

Gradient	Ethnic group	Nb trees	Np	Ne	AR_{15}	H_E	H_O	F_{IS}	F_{null}
Urban	Bamileke	47	6	7.7 ± 1.5	7.2 ± 0.7	0.83 ± 0.03	0.72 ± 0.04	0.14 ± 0.05	0.046
	Beti	71	9	7.5 ± 1.1	7.4 ± 0.5	0.84 ± 0.02	0.69 ± 0.04	0.18 ± 0.05	0.034
	Bassa	24	1	6.3 ± 1.0	7.0 ± 0.6	0.80 ± 0.03	0.69 ± 0.05	0.15 ± 0.06	0.031
Peri-urban	Mixed	31	2	7.8 ± 1.0	7.5 ± 0.5	0.85 ± 0.02	0.75 ± 0.04	0.13 ± 0.04	0.065
	Beti	60	3	7.7 ± 1.3	7.2 ± 0.6	0.83 ± 0.03	0.67 ± 0.05	0.20 ± 0.05	0.033
	Bassa	26	5	6.6 ± 1.1	6.9 ± 0.6	0.81 ± 0.03	0.72 ± 0.03	0.11 ± 0.04	0.016
Rural	Bamileke	73	18	7.6 ± 1.2	7.1 ± 0.6	0.84 ± 0.02	0.74 ± 0.04	0.12 ± 0.04	0.014
	Beti	83	4	6.2 ± 0.6	6.5 ± 0.4	0.82 ± 0.02	0.67 ± 0.05	0.18 ± 0.06	0.035
	Bassa	40	2	5.5 ± 0.7	6.6 ± 0.5	0.79 ± 0.03	0.69 ± 0.05	0.12 ± 0.07	0.013
All		455	50	7.3 ± 1.2	7.3 ± 0.6	0.83 ± 0.03	0.71 ± 0.04	0.15 ± 0.05	0.009

TABLE 5 Genetic differentiation between urban, peri-urban, and rural sites of Cameroonian African plum trees for the three ethnic groups. Pairs of sites for which F_{ST} was significantly different from zero (permutation test) are in bold. Cells are colored in gray for similar site types, and in green, blue, and orange for similar ethnic groups (respectively, Bamileke, Beti, and Bassa).

Site type		Urban			Peri-urban			Rural		
	Ethnic group	Bamileke	Beti	Bassa	Mixed	Beti	Bassa	Bamileke	Beti	Bassa
Urban	Bamileke									
	Beti	0.001								
	Bassa	0.005	0.001							
Peri-urban	Mixed	0.0002	0.0004	0.006						
	Beti	−0.005	0.003	0.004	−0.0004					
	Bassa	**0.004**	**0.005**	0.005	0.003	**0.006**				
Rural	Bamileke	**0.008**	**0.009**	**0.017**	**0.007**	**0.006**	**0.015**			
	Beti	**0.011**	**0.015**	**0.023**	**0.015**	0.007	**0.018**	**0.023**		
	Bassa	**0.007**	**0.009**	**0.006**	**0.011**	**0.008**	**0.004**	**0.021**	**0.022**	

3.5 | Patterns of population differentiation between sites

The mean values of F_{ST} varied between −0.0004 and 0.023 (Table 5). F_{ST} values between urban sites were not significantly different from zero. Within peri-urban sites, the Bassa site is the only one presenting a weak and significant genetic differentiation compared to other sites: three pairwise comparisons with other urban or peri-urban sites were significantly different from zero. Rural sites were the most differentiated, having the highest F_{ST} values (from 0.021 to 0.023), all significantly different from zero.

The Bayesian clustering analysis had an optimal value at $K = 3$ (see Figure S6) and attributed rural sites to different clusters (Figure 4). Using an assignment probability threshold of 0.8, each rural site tended to be assigned to one different genetic cluster. This is particularly true for the Bamileke (cluster 1, in green in the Figure 4) and the Bassa sites (cluster 2, in red). The Beti site is more mixed with individuals assigned to the same genetic cluster as the Bassa site or to a third genetic cluster. Individuals from the peri-urban sites are admixed between clusters 1 and 2, except in the Bassa site where they tend to be assigned to cluster 2 (72% of the trees). Individuals from the urban sites are predominantly admixed between clusters 1 and 2. No substructure was detected within similar sites nor within each axis (see Figure S7).

3.6 | Distribution of genetic diversity within sites

A signal of isolation by distance was observed for many sites, with pairwise kinship coefficients decreasing significantly with distance (Figure 5). At the fine scale, the kinship coefficient analysis showed various patterns depending on the type of sites and the ethnic group considered. In the rural sites, a significant spatial structure in distance classes <100 m was detected both in the Bassa and Beti sites (*p*-

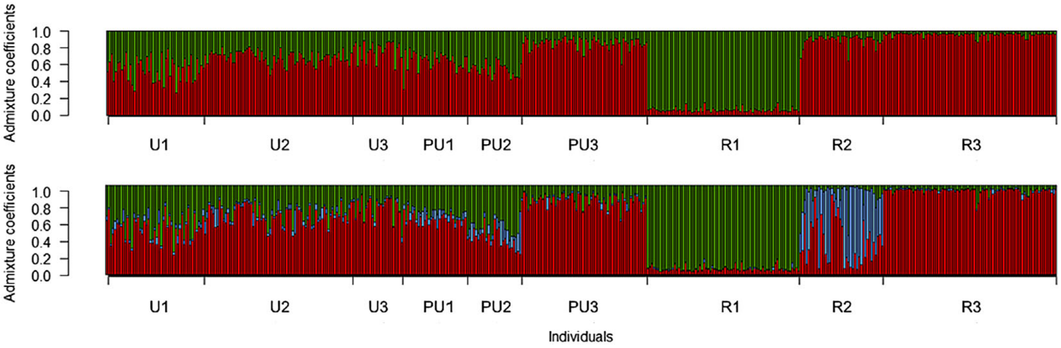

FIGURE 4 Structure of the genetic diversity of *Dacryodes edulis* trees across sites in Cameroon. Output of clustering analysis by STRUCTURE software for two (above, K = 2) and three clusters (below, K = 3) of the total 455 trees across sites. Each individual is represented by a vertical line, which is partitioned into two or three segments depending on K (shown as red, green and blue) that represent the individual's inferred membership in each of the two or three clusters. Individuals, labeled below the figure, are sorted following gradient (U: urban, PU: peri-urban, R: rural) and ethnicity (1: Bamileke, 2: Beti, 3: Bassa; the PU1 site including a mixed-sample of Bamileke and Beti tree owners).

value = .0012 and *p*-value < .001), with F_{ij} values of 0.024 and 0.035 respectively, but was absent in the Bamileke site. For the Bassa rural site, the third distance class (500 m) was also significantly higher than at random (*p*-value = .0096). In the peri-urban sites, the F_{ij} values at short distances were lower than for the rural sites and no spatial structure was detected. The analysis of F_{ij} for the urban sites showed a significant spatial structure found for the first distance class for Bamileke, Bassa, and Beti ethnic group, respectively (*p*-value < .001, *p*-value = .011, and *p*-value = .0016). F_{ij} values presented for each category of sites depending on ethnic groups are added in Figure S8.

3.7 | Temporal evolution of genetic diversity

The rarefied allelic richness for k = 100 gene copies (AR_{100}) for the different tree age classes showed that young trees (*N* = 100 trees), middle-aged trees (*N* = 196), and old trees (*N* = 159 trees) had similar AR_{100} (ANOVA controlling for loci effect, *p*-value = .83), of 15.6, 15.5, and 15.7, respectively. Comparing F_{ST} values among sites in each age class, the trend showed a slightly increasing differentiation through time: the F_{ST} was of 0.007 for old trees, 0.013 for middle-aged trees, and 0.016 for young trees (all values significantly different from 0 as tested with permutations). A similar trend was observed when considering rural sites only, with F_{ST} values of 0.019, 0.022, and 0.041 for old, intermediate, and young trees, respectively. For peri-urban sites, the decreasing trend was not matched, with F_{ST} values of 0.002, 0.019, and 0.008 for old, intermediate, and young trees, respectively.

4 | DISCUSSION

4.1 | Seed sources

Trees from urban, peri-urban, and rural sites strongly diverged with regard to their seed sources, as evidenced by the interview data. Seeds planted in urban and peri-urban sites were for the most part obtained from other rural sites not sampled for the present studies or from city markets, both of which are long-distance seed sources. On the other hand, seeds from rural sites came from short distances, either from cultivators' own fields or from neighbors and relatives in the village. A remarkably high proportion of Bamileke and Bassa urban dwellers reported sourcing their seeds from their home village. The map of peri-urban seed sources also displayed how tree owners of each ethnic group were sourcing most of their seeds within their ethnic boundaries. In the urban area, the higher distance between seed origin and seed plantation for Bamileke reflects that villages from the West region are spread further away than villages where Bassa and Beti are settled. This means that Bamileke urban dwellers used the seeds from their home villages regardless of the distance, which can be explained by the strong linkages they maintained with their rural areas, as recently reappraised in Cameroon by Mainet (2017). Owners' ethnicity is thus an important factor in the African plum seed exchange networks' structure.

On the other hand, African plum trees' owners from urban and peri-urban sites sourced a significant part of their seeds from non-co-ethnic counterparts. An important proportion of the seeds used for planting were obtained from fruits purchased in the city markets, which were the main seed sources in urban and peri-urban sites. Fruits sold on Yaoundé markets come from all production regions, following fructification seasonality (Temple, 2001). Owners sometimes also bought fruits in roadside markets along major road axes connecting different villages and cities while traveling. Moreover, seed flow occurred in adjacent (administrative) regions between two ethnic groups, such as what we observed for the Beti rural site, where owners mentioned a Bassa origin for some of their trees (see Figure 2).

Seed flows along urbanization gradients were mainly from rural sites to urban sites. For rural sites in the Bamileke and Beti axis, 15%–20% of seeds were sourced from markets in nearby cities. In the peri-urban and rural sites on the Beti axis, a few seeds were also sourced in Yaoundé urban markets. Hence, seed flows between rural, peri-urban, and rural areas are not only unidirectional. The role of

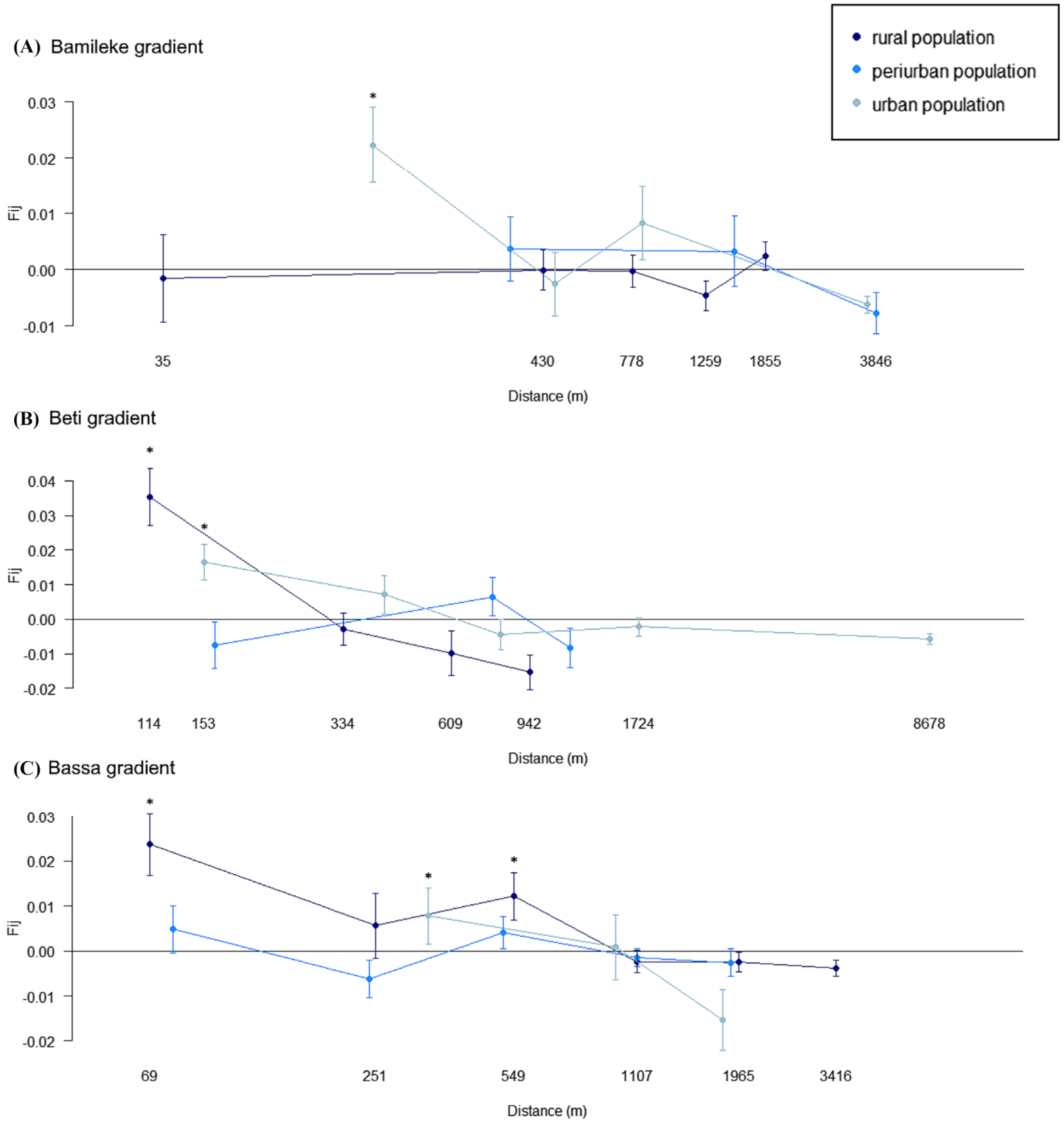

FIGURE 5 Variation of Loiselle's pairwise kinship coefficient (F_{ij}) over distance (m) in *Dacryodes edulis* trees sampled along the Bamileke, Beti and Bassa gradients in Cameroon. Calculations for the different points were made with trees grouped in distance categories (m) on the x axis, from close-by trees on the left side of the graph to wider away trees on its right side. Vertical bars are standard errors of the mean.

urban areas as potential seed sources in rural areas was mentioned for other crops as well, either coming from formal (Latournerie et al., 2005) or informal seed supply networks (Ban & Coomes, 2004).

4.2 | Genetic diversity and its distribution following seed exchange networks

Qualifying the scope of seed exchanges helps to understand genetic patterns. In general, seed dispersal has a great role in shaping spatial distribution of genetic diversity (Hamrick et al., 1993). Together with pollen dispersal, it is indeed responsible for gene flow, a key evolutionary force that leads to a homogenization of genetic diversity among populations (Ellstrand, 2014). Concerning cultivated species, anthropogenic seed dispersal through intentional exchanges between people or through markets allows for long-distance dispersal, which is less common through natural processes (Bialozyt et al., 2006). This is of major importance for population dynamics as it connects otherwise separate distant populations (Cain et al., 2000) and can thus bring new alleles into the local gene pool. The dynamic and structure of seed exchange networks of crop species therefore strongly influence their genetic diversity (Delêtre et al., 2011; Fuentes et al., 2012). For the African plum tree, its natural pattern of diversity based on wild individuals has not been described yet. But in our study, the possibility that we surveyed old (putatively wild) individuals, which had persisted in urban or peri-urban areas, is thin, as we did not collect trees from remnant forests but only from cultivated home-gardens or fields. Moreover, interviews allowed us to demonstrate where seeds used for planting were coming from. We showed how important human-mediated seed dispersal was occurring across large scales: for instance, less than 10% of the trees surveyed in Yaoundé were from within the city. This means that the observed genetic diversity is strongly human-driven: whatever the (unknown) diversity pattern in Yaoundé before urbanization, it plays a minor role in the results obtained.

We further evaluated if the spatial distribution of genetic diversity in African plum tree could be explained to some extent by seed exchanges networks across three urbanization gradients corresponding to three different ethnic groups (Bassa, Beti, Bamileke). Globally, the genetic structure was weak among the sites investigated ($F_{ST} = 0.0097$), but some trends emerge when comparing the different sites along the urbanization gradient (urban, peri-urban, rural). The genetic diversity within sites from the urban and the peri-urban area is homogeneously distributed, whereas a slight genetic structure was observed in rural sites. This is well in line with patterns of seed exchanges that we observed. As people from rural sites predominantly source their seeds locally, this leads to a genetic structure by selection/drift effect. This structure effect is probably offset by the outcrossing sexual reproduction of the species, as well as by new genotypes that might have been introduced into the areas through fruits brought from other sites. It is not possible to tell from our analysis if this structure pattern among rural sites results from fewer exchanges of genetic material among ethnic groups than within ethnic groups, or if this solely corresponds to an isolation by distance pattern. Actually, rural sites investigated were also the most spread out geographically: Bamileke rural site is around 160 km away from Yaoundé, Bassa rural site 80 km away, and Beti rural site 40 km away. We would need to characterize patterns of seed exchanges and associated genetic structure between two ethnic groups at smaller geographical distance to further clarify this pattern, for instance comparing the Beti rural site to a nearby Bassa rural site.

In peri-urban and urban areas, the slight structure observed in rural areas disappeared, in relation to larger seed exchange networks: seeds in these areas were coming from multiple rural villages either through trade roads or through exchanges with relatives located in these (home) villages. Thus, the urban area of Yaoundé acts as a “sink” of genetic resources coming from different sources from the rural area.

We noted that tree owners from the Bassa ethnic group were the one with the fewest seeds estimated to have originated from outside of their cultural area (see on Figure 2). For the three sites along the Bassa axis, we recorded only one occurrence of a seed sourced in the Bamileke region, for a tree that was not attributed to the cluster 3. It was also the only ethnic group whose trees were attributed to the same cluster 3 whatever their location on the gradient.

To date, most studies on seed exchange networks have been centered on communities with limited involvement in the market economy, and thus the contribution of seeds purchased on markets had seldom been incorporated (Garine et al., 2018). The present study was built along African plum trade roads, and therefore included the associated market dynamics. Urban and peri-urban agriculture are known to play a role in maintaining crops' genetic diversity. In our case, by attracting seeds from rural areas, cities and their surroundings can, per se, represent a melting pot of intraspecific diversity cultivated by farmers from the countryside. For the African plum tree, this was done by comparing the levels of genetic diversity observed between a main supply area and a district of Yaoundé (Rimlinger et al., 2021), and by showing that both levels were similar. Adding other rural areas, we demonstrated that the level of genetic diversity in Yaoundé could even be significantly higher than in some rural sites. This observation is well in line with the structuration of the genetic diversity among rural sites according to the seed exchange processes. Altogether, this demonstrates the role played by urban dwellers in the dynamic of genetic resources of crop species.

The downwards trend in F_{ST} values between rural trees following age classes (with the F_{ST} between rural sites being lower for old trees than for young trees) suggests that the populations tend to be more structured than before. This could be caused either by selection and/or genetic drift, leading to more divergent populations through time, without seed flows between rural sites to compensate the reinforcement of the pattern. This seems surprising as the road network might have improved over time, strengthening the connection between the capital city and rural production areas. Such road network would also facilitate the exchange of propagation material, leading to a decrease in genetic structure over time. Nevertheless, our results suggest that the flux of propagation material is predominantly unilateral, from rural areas to urban areas.

4.3 | Bridging morphological and genetic diversity

Three of the four sites containing a rarefied morphotype richness (MR) superior to that of the all-sites mean were the urban, peri-urban, and rural sites on the Beti axis, the fourth being the Bassa rural site. These results must nonetheless be interpreted with caution as the sampling effort varied between sites. The Shannon index is, for instance, lower in urban Bamileke and Bassa and peri-urban mixed sites, which are also the ones with the fewer number of trees. On the other hand, the low MR richness for the Bamileke urban site can be due to the dominance of some morphotypes, as indicated by the comparatively low evenness value. The latter can also reflect more intensive selection practices along this gradient, which also contains one of the most famous African plums production areas for Cameroon (in Makenene).

Genetic differentiation between morphotypes based on comparisons between trees for each trait was weak and did not suggest barriers to panmictic sexual reproduction, suggesting that differences among morphotypes result mostly from genetic drift or selection of non-neutral loci, responsible for morphological characteristics as in Collevatti et al. (2016). We nevertheless observed that the F_{ST} between large plums and small plums was significantly higher than zero.

4.4 | Fine-scale SGS

In natural plant populations, fine-scale SGS is the nonrandom spatial distribution of genotypes, with individuals located closer to one another generally having greater genetic relatedness. A decrease in kinship with geographical distance often results from limited gene dispersal in the species, but local genetic drift and selection can also play a role. Its strength is affected by plant breeding system, life form, and population density (Vekemans & Hardy, 2004). It can also be altered by human management, as was shown for tree species in sylvicultural systems (González-Díaz et al., 2017; Rocha et al., 2020). In this study, trees originated from spontaneous seedling establishment (rarely, a few trees in the category "*owners' own trees*") and predominantly from anthropogenic seed dispersal. In rural sites, the shortest distance class of our kinship analyses (Figure 5) was in general related to trees sampled within the same field, whereas in peri-urban and urban areas, it corresponded to trees from neighboring home gardens. In all areas, fine-scale SGS could arise from owners or neighboring owners using mostly seeds from close-by provenances, although it is more likely to react to trees with family structure. SGS for short distance classes was expectable in rural sites because it is where the proportion of owners planting seeds from their own trees is the highest. It was indeed observed in the Beti and Bassa rural sites but surprisingly not in the Bamileke site, even though most seeds were sourced within the village, like in the two other sites. However, a strong spatial structure at the smallest distance class was observed for all ethnic groups in the urban area. This was rather surprising, given that long-distance seed flow is prevalent in urban sites. In a study on *Ficus racemosa* in Bangalore, India, a fine-scale SGS was also detected despite long-distance pollen flow (Krishnan & Borges, 2018).

5 | CONCLUSION

Intraspecific variation for a given crop species is influenced by its seed exchange network, which is seldom documented in perennial species. In our study, we linked the seed exchanges of African plum trees, an indigenous fruits tree whose seed supply system is mostly informal, with its morphological and genetic diversity. Doing so along urbanization gradients, we showed that the seed system from urban and peri-urban sites was more diversified in terms of geographical origin of seeds than that of rural sites, restricted to mostly intra-village flows. We noted that villages of urban dwellers and their relatives accounted for a large proportion of seeds sourced in Yaoundé urban sites. Genetically, no structure was found for African plum trees from urban and peri-urban areas, but rural sites presented their own genetic clusters. We discussed the possible correlation between these two findings. We also saw that sites with minimum/maximum genetic diversity were not congruent with morphological patterns, also because morphotypes were not genetically structured. Finally, we gained a perspective on the fine-scale structure of trees in the different sites, with positive and somewhat unexpected signals of isolation by distance. Overall, this study shows how urban areas are home to a high African plum tree genetic and morphological diversity, with urban sites attracting multiple pools of diversity and thus exhibiting a higher level of diversity than that of rural areas.

AUTHOR CONTRIBUTIONS

Jérôme Duminil acquired funding and administrated the project. Aurore Rimlinger, Jérôme Duminil, Marie-Louise Avana-Tientcheu, and Stéphanie M. Carrière planned and designed the research. Aurore Rimlinger conducted fieldwork. Aurore Rimlinger and Jérôme Duminil analyzed data. Aurore Rimlinger drafted the manuscript. Jérôme Duminil, Marie-Louise Avana-Tientcheu, and Stéphanie M. Carrière reviewed and edited the manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

RESEARCH ETHICS

Before interviews, researchers explained the reason for the interview, the aim of the research project, and how the data would (anonymously) be used; tree owners were informed of the research intentions and of their right to participate or decline. They consented orally to the interview, which was then conducted. If interviews were completed, respondents were given a form stating that the interview had been conducted in accordance with the principles of free and informed consent, which they could sign if they agreed. The consent form is available upon request.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in OSF at https://osf.io/agwse/?view_only=9bb478afdab24f74a4c746380f28b021.

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