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Histoire évolutive de l'arbre fruitier *Dacryodes edulis* : implications pour sa conservation et sa gestion durable

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UNIVERSITÉ
DE MONTPELLIER

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Trees are in people. People are in trees.

H.D., HERmione

J'aimerais beaucoup qu'en guise d'introduction à ce manuscrit, il y ait, comme aux premières secondes d'une émission de radio, un jingle. Pour la circonstance, ce serait une accroche de klaxons enjoués et de bribes de dialogues entremêlés, ou de gouttes de pluie sur le toit d'une case de palmes. Puis une voix limpide énumèrerait une liste de choses, les choses de la thèse. Elle dirait qu'en amont, il y a eu une chercheuse-accordeuse, une rencontre en trio, un arbre qui surgit, un sprint concluant. Elle parcourrait ensuite le premier semestre, le temps des folioles découpées et de la centrifugeuse ronflante, du léger vertige à passer de l'autre côté du bureau, pour encadrer travaux pratiques ou dirigés, le temps aussi de la préparation de la mission à venir. Elle s'attarderait sur les mois camerounais, eux qui ont le goût des safous, sonnent de la rumeur des conversations, et sont restés, bel et bien, indélébiles. Puis elle accélèrerait, à mesure que défilent les trimestres et que grimpent les enjeux, s'enrouerait lorsque les rues se vident et que s'éloigne le laboratoire, et deviendrait hachurée, trahie par une connexion capricieuse. Dans un dernier sursaut, elle conclurait, espiègle : « c'étaient donc trois années et demie de thèse sur une anagramme, celle du *safoutier autrefois* ».

Un merci aussi vaste qu'un vieux safoutier, et même un merci immense comme un moabi à vous deux qui avez formé un duo de choc, que dis-je, de rocs, au cours de ces années. Jérôme, pour ton accompagnement attentif, serein et facétieux, ta patience soutenante, ta capacité de dialogue en toutes circonstances, ton souci du bien-être comme du bien-faire. Merci de ta manière de (te) poser des questions, pas seulement sur la science, et d'écouter les réponses. Stéphanie, pour la précision de ton jugement, ton enthousiasme qui porte, ton habileté à voir ou à ajouter de la clarté dans mes tambouilles écrites, tes encouragements aux moments opportuns, tes prises de position avisées. Merci de ce joyeux mélange, ce professionnalisme convivial qui a rendu le chemin plus lumineux.

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Marie-Louise, toute ma gratitude pour la chaleur de l'accueil réservé à mes premiers jours au Cameroun, le suivi attentif de mission en mission et la réactivité d'article en article.

Je reste au Cameroun encore un temps. Merci au personnel de l'IRD, qui a été une équipe efficace et compréhensive pour l'organisation de missions à étudiants multiples. Mohamed Elomo Molo, pour avoir démêlé toutes les situations qui devaient l'être, Colette Essono pour la sérénité devant les modifications de modifications. Joseph Fumtim, pour nous avoir suivis hors Yaoundé, caméra à l'épaule, sourire en bandoulière. Et puis à Alain Fezeu, pour avoir été le meilleur chauffeur-guide-photographe-conteur ! Toujours à la Représentation IRD à Yaoundé, j'ai été heureuse de croiser brièvement Geoffroy de Saulieu – merci pour ce livre des plus utiles – et Christian Seignobos.

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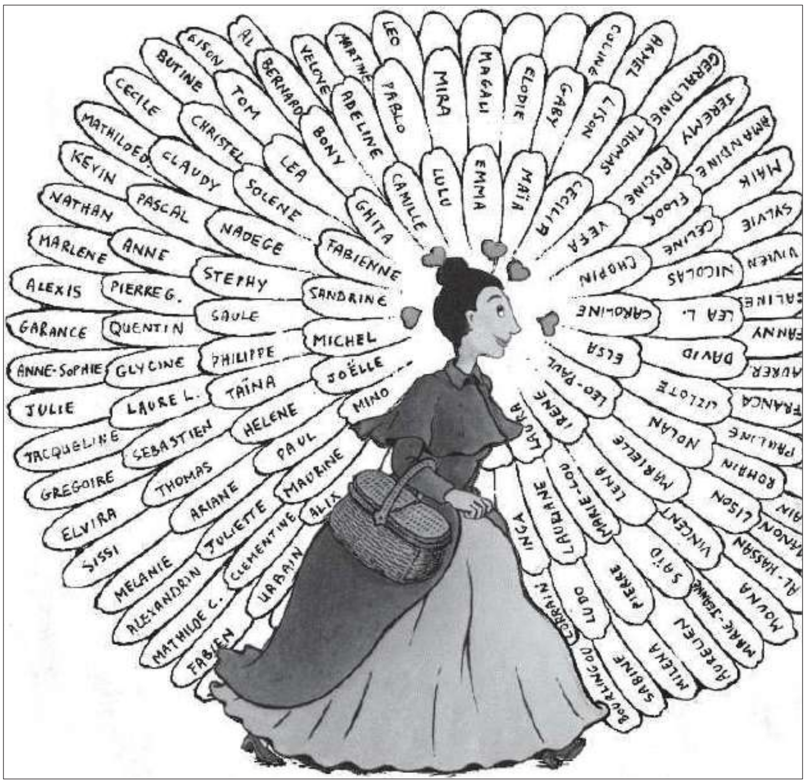
Pour conclure, et puisque cette thèse sans eux compterait pour des prunes, mon dernier mot va à ceux qui ont raconté. En parlant de leurs safoutiers, ils ont déroulé les fils que j'ai tentés de suivre. Pour le temps qu'ils ont dévolu à ces entretiens, aux visites dans les champs, à décrire, à mimer, à faire goûter… Merci infiniment.



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Rimlinger A, Carrière SM, Avana M-L, Nguegang A, Duminil J. 2019. The Influence of Farmers' Strategies on Local Practices, Knowledge, and Varietal Diversity of the Safou Tree (*Dacryodes edulis*) in Western Cameroon. Economic Botany, 73(2):249-264

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Rimlinger A, Marie L, Lemoine T, Meguem F, Avana M-L, Zekraoui L, Mariac C, Carrière SM, Duminil J. 2019. Genetic diversity of the African plum (*Dacryodes edulis*), from Yaoundé home gardens to Cameroonian agroforests. ***Oral**, 4^ème^ Congrès Mondial d'Agroforesterie*, Montpellier

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Rimlinger A, Carrière SM, Avana M-L, Nguegang A, Duminil J. 2018. Interplays between intensification strategies, cultivation practices and varietal diversity of safou tree (*Dacryodes edulis*) in Cameroon. ***Poster**, 2ème Joint Congress on Evolutionary Biology,* Montpellier

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Distinction

2020 2ème édition du prix Jeune chercheur Fondation pour la Recherche sur la Biodiversité – Lauréate, Axe " Conservation de la biodiversité dans les territoires : comment appréhender les dynamiques ?"

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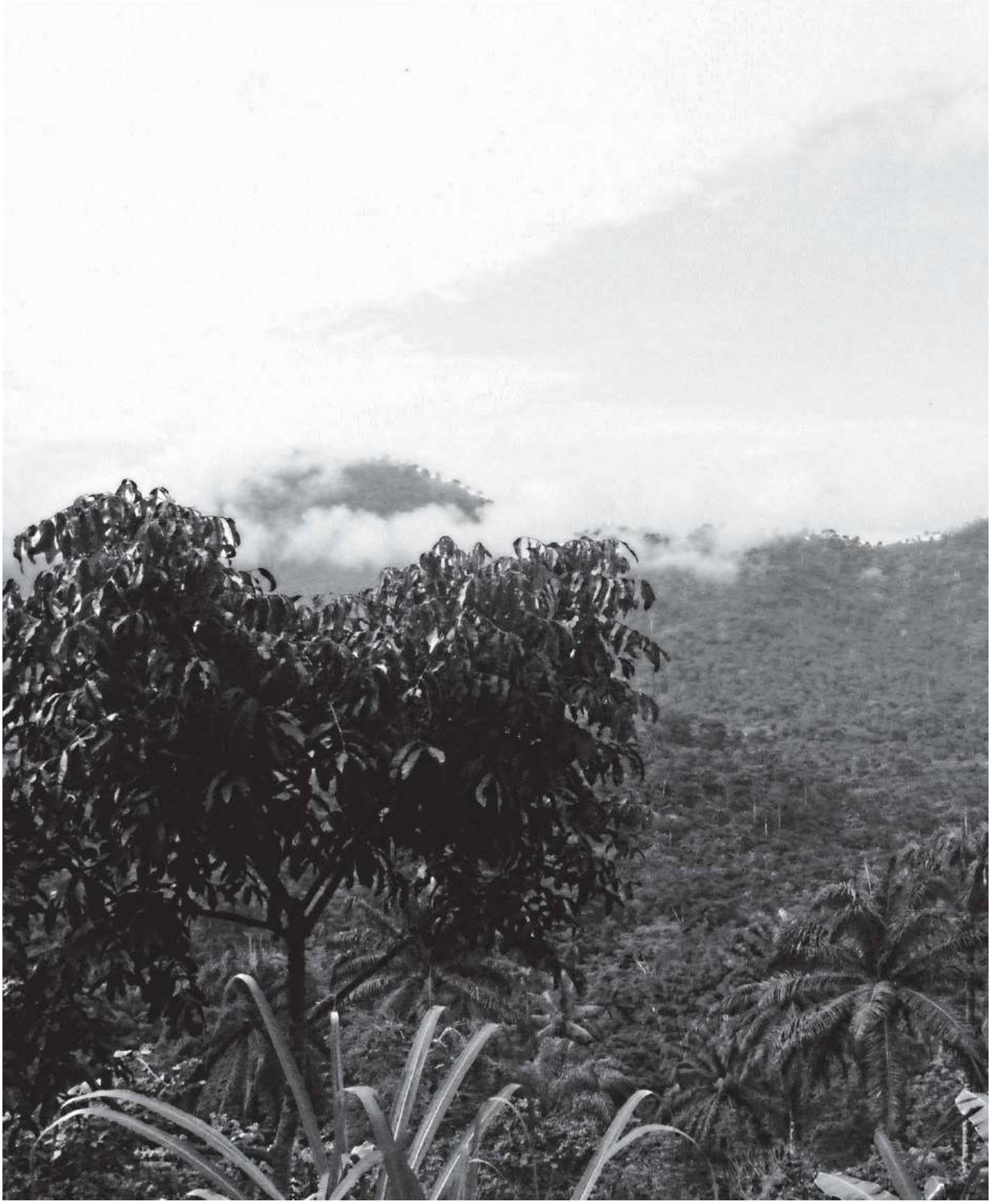
Introduction



La diversité génétique des plantes cultivées est l'une des composantes majeures de la biodiversité et de la part cultivée de l'agrobiodiversité[2] ; elle contribue à la qualité de l'alimentation humaine, et à l'économie locale et mondiale (Labeyrie *et al.* 2021). L'étude de la diversité des plantes cultivées requiert en particulier de bien comprendre la dynamique de son évolution en lien avec son utilisation par les humains. En effet, cette diversité résulte aussi bien de processus évolutifs naturels que de ceux engendrés par des générations de sélection et de mise en culture par les agriculteurs (Brush 2008). La partie cultivée de cette agrobiodiversité est aujourd'hui le socle sur lequel agriculteurs et sélectionneurs s'appuient pour disposer de cultures adaptées à des environnements hétérogènes et changeants (Zimmerer et de Haan 2017).

Mon travail de thèse s'attache à décrire les dynamiques évolutives chez le safoutier (*Dacryodes edulis* [G.Don H.J. Lam), arbre fruitier indigène de la zone forestière humide de l'Afrique centrale et du Golfe de Guinée. Pour les retracer, il aborde aussi bien le domaine de la biologie évolutive que celui de l'ethnoécologie, en prenant en considération les interactions entre cette espèce fruitière arborée et les populations qui l'utilisent, la consomment et la cultivent.

L'introduction énonce le contexte général de ma recherche et introduit les concepts nécessaires à la formulation des questions qui fondent ce travail. Elle présente aussi des éléments généraux sur la biogéographie de la région d'étude et sur la biologie du modèle d'étude, le safoutier. Enfin, elle expose les objectifs et la structure de ma thèse.

A. Dynamiques de la diversité des plantes cultivées

1. Diversité et agrobiodiversité

L'Évaluation mondiale de l'IPBES de la biodiversité et des services écosystémiques[3] (2019) est la production la plus récente rendant compte de la façon dont la biodiversité et les services écologiques fournis par les écosystèmes sont indispensables à la vie humaine. Elle expose en particulier les multiples contributions de la nature aux sociétés[4] (Díaz *et al.* 2018), ainsi que les menaces et les conditions de sa protection. Cette évaluation rappelle aussi que la biodiversité se conçoit à différents niveaux en interaction : diversité des gènes, des organismes et des systèmes écologiques – ces derniers fournissant aux premiers les conditions

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[2] L'agrobiodiversité comprend la biodiversité plantée et la biodiversité associée (Perfecto and Vandermeer 2008)

[3] Les services écosystémiques regroupent l'ensemble des contributions directes et indirectes des écosystèmes à la survie humaine ainsi qu'à sa qualité de vie.

[4] Le terme de contributions de la nature aux populations englobe à la fois les services écosystémiques, mais aussi la manière dont les communautés autochtones et locales perçoivent leur relation avec la nature.

environnementales nécessaires à leur régénération. Puisque la biodiversité concerne ces trois niveaux d'organisation du vivant, elle est de fait un objet de recherche multiscalaire, abordé par de nombreuses disciplines : génétique moléculaire et des populations, biologie évolutive, systématique, écologie des communautés ou encore biogéographie (Blondel 2020).

Composante de la biodiversité, les végétaux sont essentiels à la vie sur terre : ils produisent de l'oxygène, stockent du carbone, contribuent à la formation des sols, à leur stabilité et à l'entretien de leur fertilité, et de manière plus récente contribuent aussi à la vie humaine (alimentation, pharmacopée, matériaux…). L'agrobiodiversité renvoie à la variété et à la variabilité des organismes vivants qui contribuent à l'alimentation humaine et à celle des animaux d'élevage, à l'agriculture dans son sens le plus large, et aux connaissances qui lui sont associées (FAO 2004). Elle inclut à la fois les espèces cultivées et domestiquées, leurs espèces sauvages apparentées, ainsi que toute la variabilité existant au sein de ces espèces (variétés). La sauvegarde de l'agrobiodiversité est primordiale et requiert des stratégies de conservation propres (Jackson *et al.* 2007). En effet l'agrobiodiversité cultivée doit être prise en compte pour son rôle vis-à-vis des différents enjeux de durabilité à l'échelle locale et mondiale (Zimmerer et de Haan 2017) : assurer la sécurité alimentaire (Thrupp 2000), en fournissant une alimentation de qualité (Oduor *et al.* 2019) conforme aux régimes locaux (Jacobsen *et al.* 2015), et au travers de rendements stables permis par une adaptation au territoire (Cleveland *et al.* 1994) ; conserver un maximum de diversité génétique pour maintenir le potentiel adaptatif des espèces, dans la perspective de faire face aux changements futurs (Vigouroux *et al.* 2011) ; favoriser des systèmes agricoles requérant peu d'intrants (Kahane *et al.* 2013) et compatibles avec la diminution des précipitations et la baisse de la recharge des aquifères liées aux péjorations climatiques (Labeyrie *et al.* 2021).

Le plus souvent, les recherches sur l'agrobiodiversité se focalisent sur la diversité des espèces cultivées, avec une attention particulière portée sur les variétés paysannes trouvées dans les champs, les forêts, ou les jardins. Ces variétés gérées localement sont produites en particulier par de petites (< 2ha) exploitations familiales[5], exploitations qui représentent ~80% de l'agriculture au niveau mondial (Lowder *et al.* 2016). Ces exploitations contiennent la richesse spécifique et variétale la plus importante, par rapport aux exploitations de plus grande taille, et

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[5] Les exploitations familiales reposent presque exclusivement sur le travail familial et sur de fortes interrelations entre les familles d'agriculteurs et leur exploitation.

produisent la majeure partie des fruits, légumes secs, racines et tubercules du monde (Ricciardi *et al.* 2018).

Chaque variété porte nécessairement la marque de l'intervention humaine. Du fait de leur évolution dans un contexte écologique et social donné, ces variétés locales correspondent en effet, d'une part, aux attentes du cultivateur vis-à-vis de son système agricole (par exemple en matière d'interactions entre espèces), d'autre part répondent à leurs besoins alimentaires (nourriture) et culturels (goût, modes de préparation). La valorisation de la diversité spécifique et variétale (intraspécifique) à travers les pratiques des cultivateurs a été abondamment mise en évidence dans différents agro-systèmes tropicaux traditionnels (Brush et Meng 1998; Elias *et al.* 2000; Barnaud *et al.* 2007; Brush 2008; Blanco *et al.* 2013; Radanielina *et al.* 2014; Perales et Golicher 2014; Valdivia-Díaz *et al.* 2015). L'intérêt de l'agrobiodiversité tient en partie au fait qu'elle permet aux cultivateurs et cultivatrices d'avoir une réserve de variétés adaptées aux pressions environnementales locales, voire résilientes face aux aléas climatiques ou à la pression des agents pathogènes. À l'échelle de l'exploitation, elle facilite la gestion des risques, dans la mesure où un certain aléa – par exemple un stress hydrique ponctuel, ou un ravageur – peut toucher certaines variétés, mais non leur ensemble.

Puisqu'elle reflète également des préférences culturelles – préparations culinaires exigeant spécifiquement certaines variétés ; variétés médiatrices de relations sociales ou marqueur social (Heckler et Zent 2008) ; lien aux ancêtres (Shen *et al.* 2017) – sa valeur se situe donc aussi spécifiquement à ce niveau (Howard 2010). Depuis le Sommet de la Terre de Rio de Janeiro en 1992, le lien entre savoirs des communautés humaines – quant à la gestion et l'usage des ressources biologiques – et conservation de la diversité biologique, est mieux reconnu et pris en compte. Une prise de conscience s'opère en particulier sur le lien intime entre érosion de la diversité culturelle – qu'il s'agisse des pratiques de subsistance, des habitudes alimentaires, des connaissances et valeurs, des institutions ou des langues – et érosion de la diversité biologique (Pretty *et al.* 2009; Rapport et Maffi 2010).

2. Evolution : théories et concepts

L'un des enjeux historiques de la biologie et de l'écologie vise à décrire et analyser l'évolution des espèces dans leur environnement. Plus largement, il s'agit de comprendre les mécanismes, pluriels et enchevêtrés, contribuant à la diversité du vivant.

La théorie synthétique de l'évolution (ou néodarwinisme) a fait le pont entre la théorie de l'évolution formulée par Darwin et les lois mendéliennes (de Ricqlès et Padian 2009), étendues aux populations par la génétique des populations. Des modèles mathématiques ont servi à appréhender l'évolution des fréquences des gènes au sein des populations. Plus tard, le développement d’outils permettant d’analyser les gènes et les molécules a concouru à l’introduction de concepts nouveaux, tels que les mutations neutres ou la notion d’horloge moléculaire, et à l'acquisition de jeux de données génétiques de plus en plus informatifs, par l’entremise de marqueurs moléculaires, de polymorphismes nucléotidiques simples [SNP] ou sous forme de séquences génétiques complètes (Lefevre *et al.* 2016). Enfin, le développement de modèles simulant l'évolution des populations a facilité l’inférence de paramètres démographiques et historiques à l’origine de cette évolution. Ensemble, marqueurs et modèles permettent de retracer, à différentes échelles évolutives, la démographie et la généalogie des populations étudiées.

La diversité biologique est donc la résultante de processus évolutifs multifactoriels, détaillés ci-dessous, opérant sur un matériel génétique plastique.

a) La diversité génétique

L'information génétique d’un organisme est présente sous plusieurs formes, en fonction du stade de transcription de l’ADN, et dans plusieurs compartiments cellulaires – noyau et mitochondries, ainsi que chloroplastes chez les plantes. La diversité génétique correspond à l'étendue de la variabilité génétique mesurée à l’échelle d’un ou plusieurs individus, populations, ou espèces.

Les effets des forces évolutives détaillées ci-après diffèrent selon l’origine (nucléaire, mitochondriale ou chloroplastique) et la forme de l'information étudiée, et sont autant de paramètres à prendre en compte pour étudier et comprendre les dynamiques de la diversité. Pour s’affranchir autant que possible de leurs effets, les marqueurs privilégiés en génétique des populations sont dits neutres, i.e. leur évolution n'est pas soumise aux contraintes de la sélection. Jusqu’à récemment, l’étude de la diversité génétique était basée sur les techniques de marquage génétique, notamment sur les marqueurs microsatellites (Vieira *et al.* 2016).

A partir des fréquences alléliques fournies par l’utilisation des marqueurs, la diversité génétique peut être calculée de différentes manières. Une première estimation peut faire état de la richesse allélique raréfiée, c’est-à-dire du nombre d’allèles (variants d’un même locus, i.e. une portion d’un gène) présents dans une population, corrigé pour tenir compte de la taille des populations échantillonnées (Hurlbert 1971) :

$$a_g^{(j)} = \sum_{i=1}^{m} 1 - Q_{ijg} \text{ avec } Q_{ijg} = \frac{\binom{N_j - N_{ij}}{n}}{\binom{N_j}{g}}$$

avec N_{ij} le nombre de copies du $i^{\text{ème}}$ allèle dans l'échantillon de la $j^{\text{ème}}$ population ; N_j le nombre total de gènes dans la $j^{\text{ème}}$ population ; m le nombre total d'allèles distincts observés à ce locus et g le paramètre de raréfaction, inférieur à la taille de la plus petite population.

L'indice de diversité génétique de Nei (1973), H_E, correspond à l'hétérozygotie attendue et caractérise le niveau de variabilité des gènes au sein d'une même population, c'est-à-dire qu'il exprime la probabilité que deux allèles obtenus par tirage aléatoire dans une population soient différents :

$$H_E = 1 - \sum_{i=1}^{n} p_i^2$$

avec n le nombre d'allèles au locus considéré et p_i la fréquence allélique pour chaque allèle. La loi d'Hardy-Weinberg est le principe de base qui régit la génétique des populations, décrivant les conditions de l'état d'équilibre des fréquences alléliques. Elle repose sur un certain nombre de prérequis – la population composée d'organismes diploïdes est de grande taille ou de taille infinie, la reproduction se fait par croisement aléatoire (population panmictique), les générations sont non-chevauchantes – avec comme conditionnalité qu'aucune pression évolutive ne s'exerce sur la population. Dans ces situations, il est attendu que la distribution des fréquences alléliques reste identique d'une génération à l'autre à l'échelle de la population.

b) Processus évolutifs

Dans les populations naturelles, les fréquences alléliques ne sont pas toujours constantes, mais évoluent au fil du temps. Les dynamiques évolutives correspondent aux changements génotypiques (ensemble de l'information génétique) et phénotypiques (ensemble des caractères observables) des êtres vivants dans le temps. Dans un premier temps, les principales forces évolutives qui opèrent sur la variation moléculaire sont rappelées.

Encadré 1 : Principales forces évolutives (illustrées Figure 1)

La mutation, conduisant à ce qu'un état différent soit observé à une position donnée du génome entre un individu et ses parents, génère l'apparition de nouveaux allèles. Ces allèles peuvent disparaitre, si l'individu mutant n'a pas de descendance, ou alors être fixés au cours du temps, c'est-à-dire perdre leur caractère transitoire et diffuser dans la population.

La sélection naturelle opère un tri sur ces nouveaux allèles selon qu'ils confèrent un avantage ou un désavantage adaptatif en entraînant des taux de survie et/ou de reproduction différents. À condition que ces taux de survie ou de reproduction soient le fait de différences génétiques héritables d'une génération à l'autre, les mécanismes de sélection dans un environnement donné entrainent une évolution des variants génétiques, favorable aux individus portant des allèles avantageux pour la survie et la reproduction qui se maintiennent et défavorable aux individus portant des allèles délétères qui disparaissent.

La dérive génétique correspond aux changements dans le temps des fréquences alléliques, causés par l'échantillonnage aléatoire d'allèles parentaux, et dépend aussi de la survie et la reproduction fortuites de leur progéniture. Sous ce régime, les fréquences alléliques changent au fil du temps sous le seul effet du hasard. Ce processus est particulièrement déterminant pour les populations de petite taille, où la fluctuation de la fréquence des allèles est plus importante que dans celles de grande taille : les allèles rares ont plus de chance de s'éteindre, et les allèles communs de se fixer. Un cas d'école de dérive est celui de l'effet fondateur, c'est-à-dire lorsqu'une petite population s'individualise, emportant au hasard avec elle une fraction des variants de la population initiale qui vont rapidement se fixer.

La migration (flux de gènes) se caractérise par la circulation des allèles, ce qui conduit à terme, selon son intensité, à une homogénéisation de la variation génétique. Chez les végétaux, les flux de gènes s'effectuent via le pollen et les graines. Les barrières aux flux de gènes peuvent être physiques (rivières, montagnes), en empêchant le pollen ou les graines de se déplacer entre les régions, ou non-physiques (écologiques, reproductives). Des limites sont aussi imposées par la capacité de dispersion de l'organisme. Pour des flux de gènes réduits, la possibilité d'observer une divergence dans les fréquences alléliques, provoquée par la dérive génétique, la mutation et la sélection, est accrue. De ce fait, l'apparition d'une structure génétique distincte entre les populations est favorisée. D'autant qu'une variation dans le succès de certains variants génétiques dû à des différences régionales de sélection génère aussi une variation spatiale des fréquences alléliques.

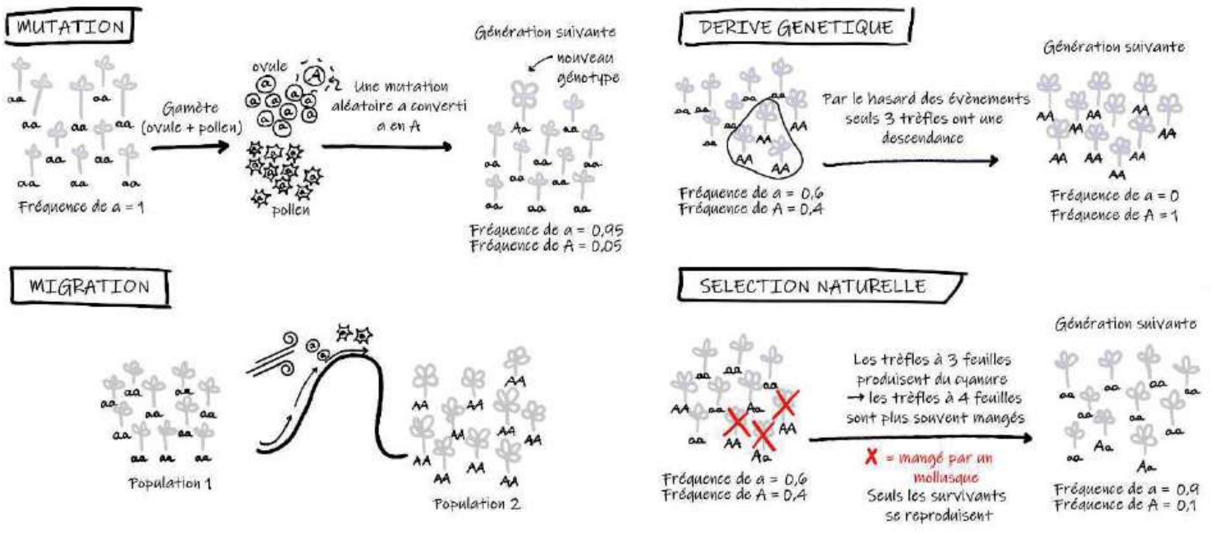

Figure 1. Représentation schématique des principales forces évolutives[6].

La structure génétique correspond à la répartition de la diversité génétique au sein et entre les populations. Des populations partageant la même diversité génétique ne sont pas structurées ; à l'inverse, des populations ayant chacune une diversité génétique spécifique seront fortement différenciées entre elles, c'est-à-dire fortement structurées. L'apparition d'une structure génétique entre populations d'une même espèce, à travers l'espace, résulte principalement de l'action des forces évolutives qui tendent à différencier les populations, à savoir la mutation, la sélection naturelle et la dérive génétique. À ces processus s'oppose l'action homogénéisante de la migration (flux de gènes).

Le fait qu'une structure génétique découle de tout ou partie de ces différents processus signifie que l'observation de la variation spatiale des fréquences alléliques peut être utilisée pour inférer ceux qui l'ont fait émerger.

La différenciation génétique entre populations subdivisées mais connectées est classiquement calculée par les F-statistiques telles que définies par Wright (1951) et unifiées par Weir et Cockerham (1984). L'indice de fixation F_{ST} est appliqué au polymorphisme génétique des populations sur la base d'un modèle en île : la migration s'effectue entre toutes les sous-populations panmictiques de la population subdivisée, sous équilibre migration/dérive. Le F_{ST} peut être interprété comme la part de variance des fréquences alléliques due aux différences entre populations. Il varie entre 0, lorsque les sous-populations présentent les

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[6] adapté de https://www.khanacademy.org/science/ap-biology/natural-selection

mêmes fréquences alléliques, et 1, lorsque chaque sous-population est fixée pour un des allèles présents.

$$F_{\mathrm{ST}} = \frac{H_T - H_S}{H_T}$$

avec H_T l'hétérozygotie attendue pour une population globale en panmixie (les individus de toutes les sous-populations se croisant au hasard) et H_s l'hétérozygotie moyenne attendue pour une panmixie locale (les individus se croisant au hasard à l'intérieur de chaque sous-population).

Les processus évolutifs sont donc induits par les forces évolutives que sont la mutation, la migration, la sélection et la dérive, mais ils peuvent aussi être induits par des actions humaines agissant sur un ou plusieurs de ces processus. C'est le cas en particulier de la domestication, résultante de l'action conjointe de dynamiques biologiques et sociales.

3. Espèces cultivées et domestication : relations entre plantes et sociétés

La domestication des plantes peut être à la fois interprétée dans ses dimensions biologiques et anthropologiques. Elle se réfère : (i) à l'adaptation des espèces domestiquées à l'environnement de mise en culture, et à leur perte d'adaptation à leur habitat d'origine ; (ii) aux changements physiologiques et génétiques produits par différenciation par rapport à une espèce sauvage d'origine ; (iii) à la relation de dépendance qui se construit entre l'espèce domestiquée, les humains et leurs pratiques à l'origine de la domestication (Meyer et Purugganan 2013; Zeder 2015). La domestication étant avant tout un processus, elle peut être décrite selon un continuum de codépendance entre les plantes et les humains. À un pôle du continuum, la relation qu'ont les humains à leur environnement pour leur subsistance est marquée par un faible investissement dans la survie et la production d'espèces de plantes qui se développent sans contraintes (compartiment sauvage). À l'autre pôle, les espèces végétales qui ne peuvent pas se reproduire ou survivre sans l'investissement d'une grande quantité de travail humain (compartiment domestiqué) font l'objet de pratiques visant à améliorer la rentabilité du travail investi (Harris 1989). À son terme, cette dernière relation conduit à l'émergence d'une espèce domestiquée dont la croissance et la reproduction sont conditionnées par le travail de l'espèce domesticatrice, qui en retire en général le bénéfice principal.

Différents modèles ont synthétisé les principales étapes entre les deux extrémités du continuum. Ils n'impliquent pas nécessairement une succession ordonnée et obligatoire des étapes décrites dans le temps, pour conduire à la domestication. Ils sont progressifs uniquement en ce sens que le continuum présente un gradient d'intensification d'apport de travail humain par unité de surface de terre exploitée. Parmi ces modèles, certains mettent l'accent sur le type de relations plantes-humains en jeu, d'autres sur les changements pour les populations sous sélection. Celui de Clement (1999) distingue ainsi cinq types de populations : (1) sauvages, non marquées par l'influence humaine ; (2) ayant fortuitement co-évolué, dans lesquelles des individus s'adaptent à des environnements anthropisés ; (3) nouvellement domestiquées, pour lesquelles les traits des individus sous intervention et sélection humaines sont modifiés, mais sans qu'ils soient encore significativement différents des individus issus des populations sauvages ; (4) semi-domestiquées dans lesquelles coexistent des phénotypes sauvages et de nouveaux phénotypes, résultant de la sélection ; (5) domestiquées, dans lesquelles les nouveaux phénotypes sont uniquement adaptés aux environnements anthropisés. Dans ce dernier groupe, il différencie deux types, les « variétés de pays » (*landraces*), correspondant à des populations cultivées adaptées à leur contexte géographique, et les cultivars modernes, correspondant à des populations fortement sélectionnées adaptées à la monoculture.

4. La domestication et ses processus : perspectives biologiques

L'étude de la domestication est éclairée par les apports de la génétique des populations. Celle-ci s'attache à décrire comment les processus évolutifs, opérant sur des populations soumises à diverses pressions de l'environnement abiotique, modifient la répartition du polymorphisme observé au sein et entre les populations (Hamrick 1982). Ce polymorphisme, i.e. ces variations de la séquence nucléotidique entre individus, est constitutif de la diversité et informatif quant aux différences entre populations. Il est modifié par les flux de gènes qui s'y produisent, ou encore par le régime de reproduction des espèces. Dans le plus simple des cas, la domestication s'opère à partir d'une espèce ancestrale sauvage, au sein de laquelle une fraction est prélevée et mise à l'écart des individus sauvages. Ce goulot d'étranglement initial correspond à une réduction de la diversité génétique parmi les individus fondateurs de la forme cultivée, par rapport à l'ensemble de la diversité trouvée dans le compartiment sauvage. Il touche le génome et ses locus dans leur intégralité, gènes neutres inclus. L'intensité de ce goulot est variable selon les espèces : moins de 4% des populations sauvages ont contribué à la diversité génétique du mil cultivé (*Pennisetum glaucum*, Clotault *et al.*, 2012), contre 40% chez le riz (*O. sativa ssp. japonica*, Zhu *et al.*, 2007), et plus encore chez le maïs (*Zea mays*, Hufford *et al.*, 2012). La diversité génétique résultante est fonction d'une part de l'intensité de la sélection et de la durée de la domestication, de l'autre de la diversité et de la taille de la population originale extraite dans le compartiment sauvage (Lefevre *et al.*, 2016). D'autres paramètres peuvent entrer en jeu dans le processus : de multiples goulots d'étranglement successifs ont pu se produire comme cela a été décrit pour différentes civilisations ou groupes ethniques (Londo *et al.* 2006; Morrell et Clegg 2007) ; le déclin de la diversité a pu avoir lieu indépendamment des effets d'un goulot initial (Allaby *et al.* 2018; Smith *et al.* 2019) ; des transferts de gènes à partir de populations sauvages adjacentes (conspécifiques ou non) ont pu être maintenus voire favorisés, atténuant les effets du goulot d'étranglement (Figure 2 ; Scarcelli *et al.* 2006; Duputié *et al.* 2009). Par ailleurs, l'expansion démographique (i.e. augmentation du nombre d'individus) de la population cultivée tout comme la réduction de la diversité génétique sont ensuite en grande partie conditionnées par les stratégies et les pratiques agricoles ou les techniques de sélections agronomiques (Bellon 1996; Barnaud *et al.* 2007).

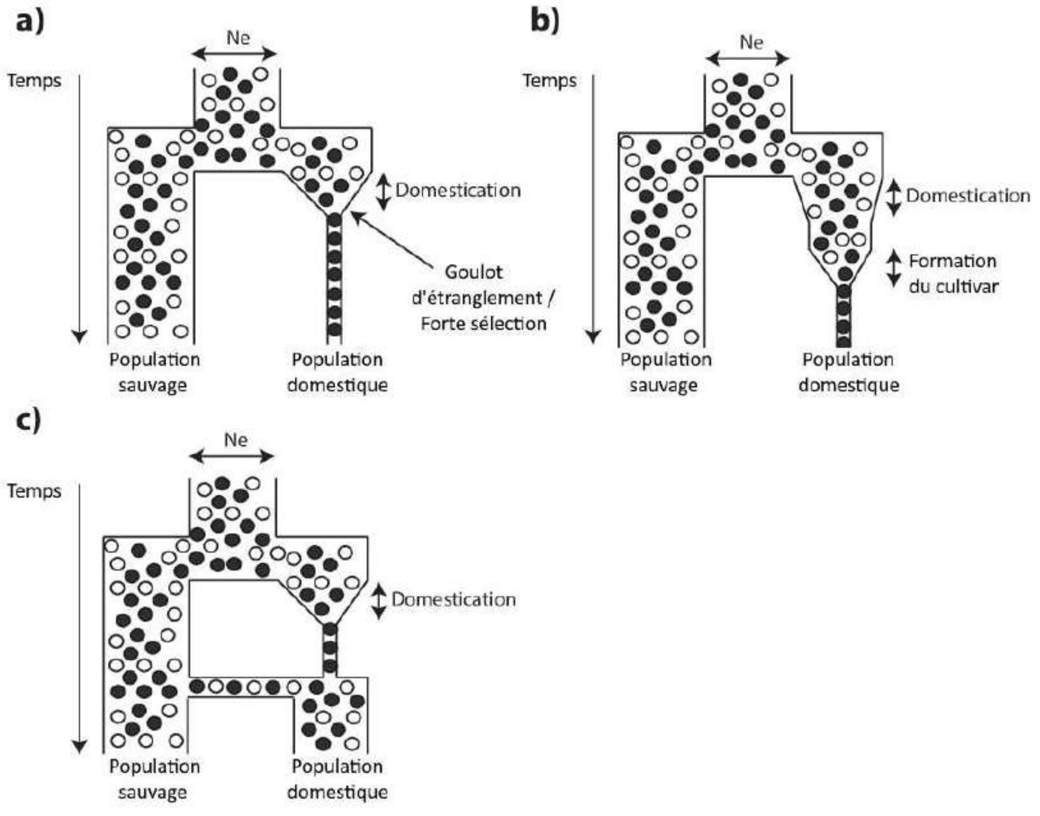

Figure 2. Schéma de différents modèles de domestication et de leur effet sur la diversité génétique. Les ronds noirs et blancs représentent les allèles d'un locus hypothétique dans le génome d'une espèce. N_e est la taille effective de la population : le nombre d'individus reproducteurs dans une population idéalisée

(différente de la taille de la population de recensement). N_e est directement liée à la diversité génétique. Dans ces schémas, la taille de la population augmente et diminue en raison de divers événements (par exemple, des goulots d'étranglement) au fil du temps. Cela a un effet sur la diversité génétique globale, comme pour (a) un modèle de base impliquant un effet fondateur et/ou une forte sélection ; ou pour (b) un modèle impliquant un léger goulot d'étranglement de la domestication et un fort goulot d'étranglement pendant la formation du cultivar. La comparaison avec le modèle (a) montre comment une diversité génétique similaire de la population moderne peut être produite par deux processus différents. On voit dans le cas (c) un modèle représentant l'effet du flux de gènes d'une population sauvage vers une population domestique suite à un goulot d'étranglement, montrant comment la diversité génétique peut augmenter dans la population domestique à la suite du flux de gènes. Figure adaptée de Frantz et Larson (2018).

Ceci pose les facteurs biologiques, écologiques et humains de l'évolution de la diversité qu'il conviendra de prendre en considération.

5. La domestication et ses processus : logiques paysannes

Fruit des interactions à long terme entre les humains et les espèces végétales, l'étude de la domestication interroge aussi bien les sciences biologiques que les sciences humaines et sociales. Les sociétés humaines jouent un rôle sur la façon dont la diversité est structurée à la fois par les pratiques agricoles qu'elles mettent en place et leurs savoirs associés, et les réseaux d'échange de savoirs et de matériel végétal qu'elles déploient. Pour étudier le processus de domestication, il faut donc décrire et comprendre les actions, les pratiques et les savoirs associés, qui agissent sur la biologie de l'espèce ; c'est ce que propose l'approche ethnoécologique (Dounias 2001; Delplancke *et al.* 2012; Garine *et al.* 2018; Bogaard *et al.* 2018). En plus d'identifier, de caractériser et de comprendre les pratiques mises en œuvre lors de la domestication, il s'agit d'expliciter quels sont les apprentissages, perceptions, croyances et représentations sur lesquelles ces pratiques reposent (Barnaud *et al.* 2007; Zent et Zent 2012; de Freitas Lins Neto *et al.* 2013). Une façon d'approcher la question des perceptions et des représentations est de mettre au jour les façons de classer, catégoriser et nommer les plantes utilisées localement (Sadiki *et al.* 2007). Savoir quelles entités sont différenciées, nommées, à quoi ces noms se rapportent, dans quelle mesure ils sont semblables entre eux à l'échelle locale ou régionale et comment ils sont transmis peut permettre d'affiner la compréhension de l'importance locale des espèces et de leur utilisation (Nuijten et Almekinders 2008; Hmimsa *et al.* 2012).

Encadré 2 : Le regard de l'ethnoécologie

Qu'est-ce que recouvre la discipline de l'ethnoécologie ? On propose de s'attarder sur d'autres perspectives (« ethno ») qui traitent du mode de relation entre humains et environnements (écologie). Il s'agit en particulier d'adopter une perspective interdisciplinaire sur la façon dont la nature est perçue par les êtres humains, sur la façon dont la trame des croyances, de la culture et des connaissances définit le lien entre communautés et environnement (Nazarea, 1999).

Qu'est-ce que la perspective ethnoécologique est à même d'apporter ? Historiquement, elle s'est penchée sur la façon dont se formaient les systèmes de savoir relatifs à l'environnement, remettant aussi en perspective la dichotomie nature/culture. L'approche ethnoécologique matérialise le fait apparemment évident que ce que les gens savent sur l'environnement et la façon dont ils classent ces informations auront une incidence sur ce qu'ils font – et ne font pas – à leur environnement.

Les actions humaines qui conduisent à l'uniformisation ou à la diversification des espèces s'exercent sous forme de pressions de sélection, touchant aux choix relatifs à l'environnement de plantation (milieu ouvert, milieu forestier) ; aux choix des nouveaux semis, qui se font (ou non) conformément aux attentes des agriculteurs et consommateurs sur certains critères (régularité de production, durée de conservation, qualité organoleptique, etc.) ; au rejet et à l'abattage des individus indésirables. La sélection peut être consciente, ou « méthodique » selon le terme de Darwin (1868), lorsque les choix sont faits intentionnellement par les cultivateurs et cultivatrices. Ces choix se font en faveur des plantes dont les traits d'intérêt répondent à leurs attentes, et en défaveur des autres. Elle peut aussi être inconsciente, c'est-à-dire sans qu'elle engage la volonté d'agir sur un trait en particulier. Elle est ainsi à l'œuvre quand des plantes sont déplacées de leur milieu naturel vers un milieu anthropisé (Zohary 2004). Ces deux types de sélection correspondent à ce que l'on appelle la sélection artificielle. Deux questions prédominent dans les études sur les processus de sélection artificielle, la première concernant les critères utilisés pour la sélection, la seconde la nature du processus. Enfin, les flux de gènes au sein de l'espèce sont également en partie régulés par les agriculteurs, en particulier via les réseaux d'échanges des semences (organisés entre groupes sociaux, généralisés ou non ; Pautasso *et al.*, 2013; Thomas *et al.*, 2012).

Le cœur de la domestication consiste donc en l'appropriation sociale et culturelle d'un matériel originellement sauvage, puis en un contrôle de sa reproduction (via des actions de sélection), avec pour conséquence un remodelage progressif vers des caractères recherchés, le tout sous l'action concomitante des pressions évolutives « naturelles ». L'étude de la domestication implique alors à la fois de documenter les processus par lesquels elle s'opère – pratiques de cueillette, de transport, de transformation, de semis, de culture, de préparation ; pratiques de gestion (échanges, transferts, règles et normes) ; mécanismes de la sélection artificielle – et ses conséquences sur la morphologie et la génétique des espèces qui en font l'objet.

B. Contextualiser les dynamiques propres au safoutier, un arbre fruitier cultivé d'Afrique centrale

1. Domestication des espèces pérennes longévives

La domestication des espèces cultivées illustre quelques-uns des exemples les plus marqués de transitions évolutives, et a généré un fort intérêt de la part des scientifiques depuis que Darwin s'en est inspiré pour décrire l'évolution des variations phénotypiques, leur transmission, et le pouvoir de la sélection (Olsen et Wendel 2013). L'apparition congruente de certains caractères typiques chez les plantes domestiquées correspond à un ensemble de changements morphologiques et physiologiques favorisés par l'action humaine qui constitue le « syndrome de domestication » (Meyer *et al.* 2012). Les changements phénotypiques sont en général ceux qui rendent la culture plus productive (hypertrophie des organes utilisés, graines plus nombreuses, dormance réduite), la phénologie compatible avec les pratiques culturales (floraison et fructification plus synchronisées, perte de sensibilité à la photopériode), qui facilitent la récolte (non-déhiscence, compacité, port plus érigé, diminution des épines) et la consommation (toxicité réduite ; Olsen et Wendel, 2013). Chez les espèces annuelles, outre la description fine des conséquences morpho-physiologiques, les bases génétiques sous-jacentes sont également de mieux en mieux caractérisées (Lenser et Theißen 2013). Comparée aux espèces annuelles, la domestication des pérennes demeure relativement peu documentée. Son étude concerne principalement des espèces arborées originaires d'Asie (eg le pêcher, Cao *et al.* 2014 ; le pommier, Cornille *et al.*, 2014), de Méditerranée (eg l'olivier, Besnard *et al.* 2018 ; l'amandier, Delplancke *et al.* 2012 ; le palmier dattier, Gros-Balthazard *et al.* 2018) ou d'Amérique latine (eg le parépou, Clement *et al.* 2017 ; la calebasse, Moreira *et al.* 2017 ; le raisin d'Amazonie, Pedrosa *et al.* 2018).

Chez les végétaux, deux grandes catégories de stratégie reproductive sont à distinguer. Les espèces annuelles se reproduisent une fois par an et meurent, alors que les espèces pérennes se reproduisent à de multiples reprises et alternent phases végétatives et reproductives pendant une longue durée, allant de quelques décennies à des siècles (Friedman et Rubin 2015). Tandis qu'espèces annuelles et pérennes doivent opérer une transition entre croissance végétative et floraison, seules les espèces pérennes maintiennent leur croissance une fois la floraison terminée : l'activité du méristème apical étant indéterminée, la croissance végétative peut se poursuivre (Tan et Swain 2006). Toutefois, d'autres caractéristiques sont importantes pour distinguer le processus de domestication des espèces annuelles et pérennes, notamment les différences majeures dans leur mode de reproduction (végétative vs sexuée) et leur stratégie de reproduction (allo- vs autofécondation) (Barrett *et al.* 1996). Les espèces pérennes avec un mode de reproduction sexué fonctionnent majoritairement par allofécondation, c'est-à-dire que leur descendance est issue d'une reproduction croisée avec une autre plante.

Le contraste le plus notable entre les espèces annuelles et pérennes est, pour ces dernières, une longueur importante de la période juvénile (i.e. persistance d'un état végétatif au cours duquel la reproduction n'est pas possible). Cette caractéristique limite drastiquement les possibilités de sélection, puisqu'elle implique que les cultivateurs doivent attendre *a minima* quelques années, voire une ou plusieurs décennies, avant de pouvoir évaluer et sélectionner le plant sur la base de ses premières graines ou de ses premiers fruits (van Nocker et Gardiner, 2014). À la sélection et propagation par semis a été préférée, pour les espèces pérennes le permettant, la propagation clonale. C'est le premier mode de reproduction des espèces fruitières des régions tempérées aujourd'hui et une composante clef du syndrome de domestication de ces espèces (Meyer *et al.* 2012). La multiplication végétative permet en effet de fixer immédiatement dans la descendance des caractères d'intérêt, fixation qui prendrait des générations dans le cadre d'une sélection massale du fait du haut degré d'hétérozygotie et de l'allogamie préférentielle chez la majorité des espèces fruitières.

Pour les arbres fruitiers, le syndrome de domestication s'exprime fortement au niveau de l'augmentation de la taille et de la forme des fruits (Fuller, 2018). Des recherches récentes menées en Amérique du Sud aident à appréhender les types de changements morphologiques ou physiologiques sur certains caractères de sélection, comme l'augmentation marquée de la taille des gousses d'*Inga edulis* (Rollo *et al.*, 2020) et des fruits de *Caryocar brasiliensis* (Sousa Júnior *et al.*, 2018), ou encore une accentuation de la pigmentation des fruits et une apparition de la déhiscence, facilitant la récolte, chez *Bixa orellana* (Moreira *et al.*, 2015).

2. Centres d'origine et foyers de domestication

a) Développement des concepts, évolution des aires ciblées

Historiquement, deux concepts fondamentaux ont traversé au vingtième siècle les réflexions sur la domestication des plantes et les origines de l'agriculture : sa nature "révolutionnaire" et la présence de "centres d'origine". La révolution agricole englobe les conséquences économiques et sociales – sédentarisation, élargissement des groupes sociaux, développement de l'artisanat – engendrées par la capacité des sociétés à produire leur nourriture. La notion de centre d'origine formulée par Vavilov (1926) se réfère aux principaux centres de la domestication des espèces cultivées (Figure 3). Pour une espèce donnée, la région géographique dans laquelle sa variabilité génétique est concentrée est supposée indiquer sa région d'origine, la plante ayant été mise en culture suffisamment longtemps auparavant pour qu'un niveau de diversité élevé ait eu le temps de s'y développer. Ces centres d'origine sont également mis en évidence par la présence d'espèces sauvages apparentées et par le fait qu'ils sont communs à plusieurs espèces cultivées.

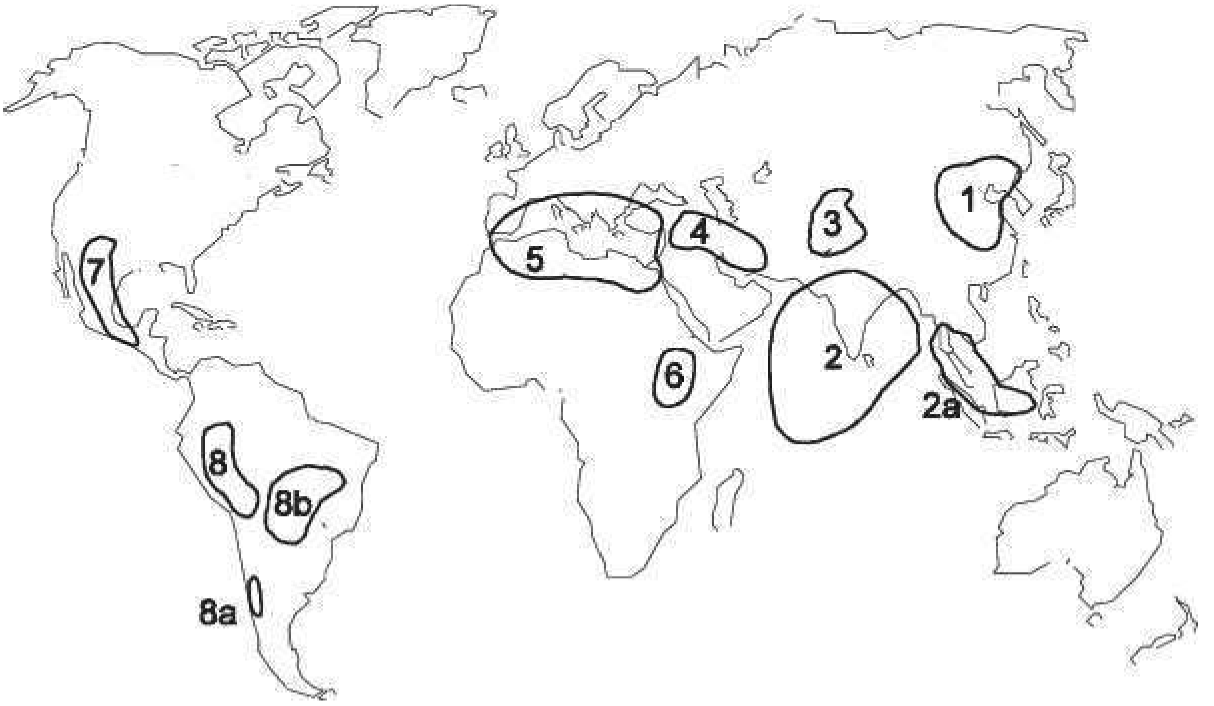

Figure 3. Centres d'origine des espèces cultivées décrits par Vavilov (1926), repris de Borém et Milach (1997). 1. Chine ; 2. Inde ; 2a. Sous centre Indo-malaisien ; 3. Asie centrale (Nord de l'Inde, Afghanistan, Turkménistan) ; 4. Proche-Orient ; 5. Méditerranée ; 6. Éthiopie ; 7. Sud du Mexique et Amérique centrale ; 8. Ouest de l'Amérique du Sud ; 8a. Îles Chiloé et Chili ; 8b. Brésil et Uruguay.

Le modèle défini par Vavilov a depuis été débattu. Harlan (1975) a ainsi remis en cause l'équivalence entre centres de diversité et centres d'origine, remplaçant cette dernière notion par celle de foyer(s) de domestication. À côté des « centres » circonscrits, il a pu mettre en lumière des « non-centres » : des aires diffuses d'origine et de diversification secondaire, pouvant être géographiquement étendues. Des études de synthèse (Purugganan et Fuller 2009; Meyer *et al.* 2012) intégrant notamment des données archéobotaniques ont permis de distinguer plusieurs zones d'origine, indépendantes et de petites tailles, au sein d'espaces qui étaient précédemment considérés comme de grands centres d'origine ; le nombre de foyers de domestication n'est donc pas arrêté, il fluctue et reflète ainsi les avancées sur la connaissance des peuplements humains anciens. Il progresse aussi à mesure que s'affinent les outils méthodologiques à disposition des chercheurs.

b) Domestications sur le continent africain

En Afrique sub-saharienne, Vavilov a identifié un seul centre d'origine : en Afrique centre-orientale (foyer abyssin). Portères (1962), reprenant cette démarche, a, quant à lui, distingué à proximité du foyer nilo-abyssin trois centres de diversification supplémentaires (afro-occidental, afro-oriental, afro-central). Il subdivise le berceau afro-occidental, qui est le territoire d'intérêt de ce travail, en secteurs tropical et sub-équatorial : le premier se caractérise par la prééminence d'espèces céréalières (sorgho, mils et millet, riz africain), le second par ses espèces à rhizomes et à tubercules et ses arbres de forêt « primaire ».

Ces dernières années, les foyers de domestication de plusieurs des espèces citées par Portères ont été précisés à partir de données génomiques : mil à chandelle (*Cenchrus americanus* [*Pennisetum glaucum*], Burgarella *et al.*, 2018), riz africain (*Oryza glaberrima*, Choi *et al.*, 2019; Cubry *et al.*, 2018; Figure 4). Les patrons de domestication d'autres espèces céréalières, notamment le sorgho (*Sorghum bicolor*), ont aussi été affinés grâce à des restes végétaux issus de sites archéologiques (Fuller *et al.*, 2019). Des recherches plus récentes en Afrique de l'Ouest et en Afrique centrale, combinant des approches archéologique, paléobotanique et palynologique, ont permis de montrer que les forêts ont été occupées dès 5000 AP (avant le présent ; fin de l'âge de pierre, Oslisly *et al.*, 2016). Des outils en pierre suggèrent l'exploitation répandue des plantes à tubercules, en particulier plusieurs espèces d'ignames.

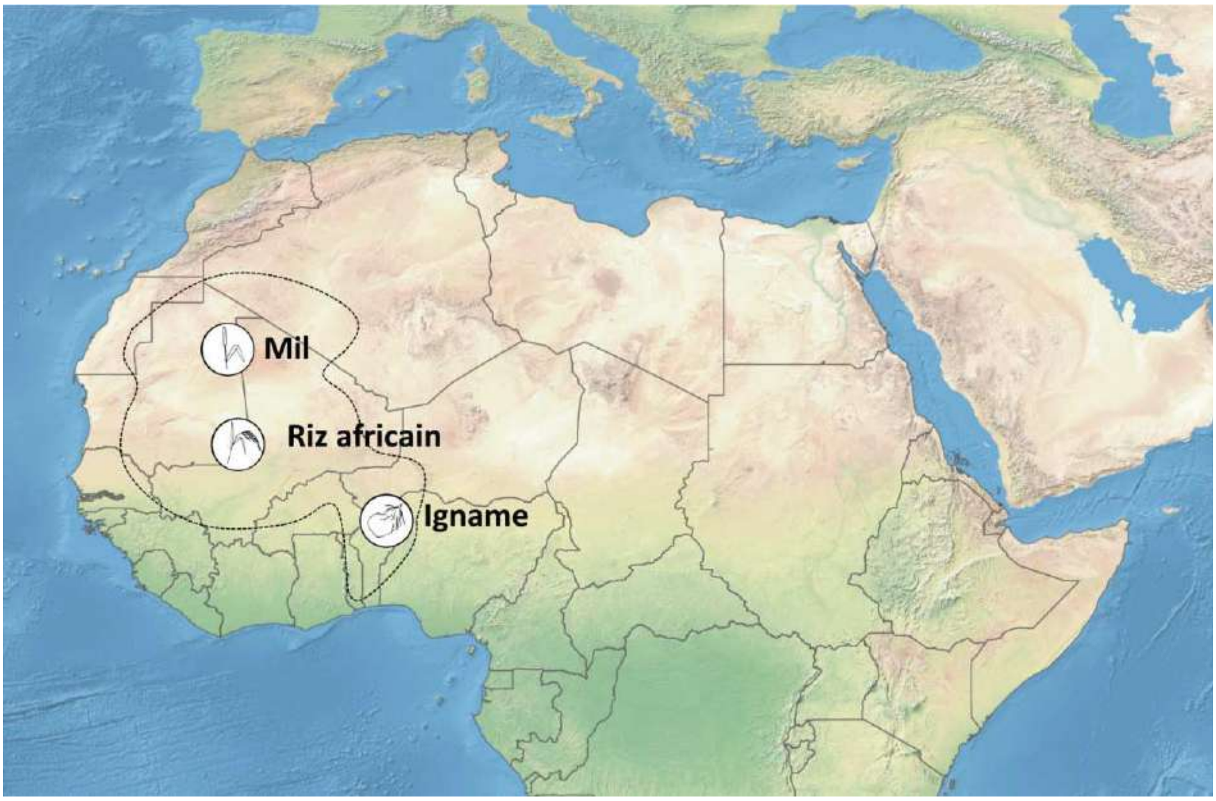

Figure 4. Foyer de domestication dans l'Ouest africain, d'après Scarcelli *et al.* (2019).

Il est probable que des espèces pérennes (palmier à huile, *Elaeis guineensis* ; élémier d'Afrique, *Canarium schweinfurthii*) aient été également utilisées. Pour ces dernières, des restes de péricarpe ont été trouvés dans divers sites archéologiques, à partir de 6100 (±) 250 AP (Oas *et al.* 2015). Initialement, l'usage de ces arbres a pu consister en des collectes régulières, une frontière entre pratique de collecte et pratique de culture (arboriculture, ou du moins protoculture) étant franchie du moment que ces espèces utiles étaient protégées et donc sélectionnées.

L'histoire de l'agriculture de Vansina dans la zone forestière d'Afrique centrale, des premières migrations bantoues à la période coloniale, fournit un point de départ pour comprendre les systèmes agricoles contemporains. Il confirme l'unité essentielle de la culture bantoue occidentale et du mode de subsistance dans cette zone qui englobe le sud du Cameroun, le Gabon, le sud de la République centrafricaine, la Guinée équatoriale, le Congo et le nord du Zaïre.

Le groupe Beti-Bulu-Fang (parfois abusivement appelé "Pahouin") est considéré comme le plus important et le plus étudié des Bantous du Nord-Ouest, dont la population s'étend sur un demi-million de kilomètres carrés (Alexandre 1965). L'agriculture forestière bantoue avant 1500 était probablement basée sur l'igname, la courge ou le melon (*Cucumerops* *edulis*), les haricots, les légumes verts comme l'amarante, les arbres comme le safoutier (*Dacryodes edulis*) et le palmier à huile, ainsi que d'autres cultures mineures (haricots, calebasse, pois Bambara, poivre, légumes verts, figuiers… ; Katz 1998). On retrouve la majorité de ces espèces dans la reconstruction de l'histoire culinaire du groupe bantou à partir de la linguistique historique de Ricquier et Bostoen (2010).

Encadré 3 (début) : Migrations bantoues

L'expansion bantoue se réfère à la diffusion des langues bantoues et des peuples les parlant à travers l'Afrique centrale, de l'Est et du Sud. Les 310 millions de locuteurs bantous sont aujourd'hui présents dans plus d'une vingtaine de pays d'Afrique sub-Saharienne (Patin *et al.* 2017), ce qui en fait l'ensemble linguistique (phylum) avec la plus large distribution dans cette zone. À partir de données de linguistique historique, d'archéologie et de génétique humaine, une chronologie de cette expansion a été proposée (Bostoen 2018). La divergence de la branche bantoue par rapport aux langues bantoïdes, dans une zone située entre le Sud-Est du Nigéria et l'Ouest du Cameroun, aurait pris plus de 2000 ans, à partir de 6000-7000 ans AP et jusque 4000-5000 ans AP.

Encadré 3 (suite) : Migrations bantoues

La diversité des langues bantoues suggère, qu'à une première phase de fragmentation et de mouvement sur de courtes distances, a succédé une seconde phase de rapide dispersion à grande échelle. Leur expansion, d'abord vers le Centre Cameroun, a débuté 3000 à 3500 AP. Les locuteurs bantous ont ensuite, vers 2500 ans AP, atteint simultanément le bassin du Congo, l'Ouest de l'Afrique centrale au sud des forêts tropicales et l'Afrique de l'Est. Cette diffusion remarquablement rapide à travers l'Afrique centrale aurait été facilitée par la nette contraction des forêts tropicales à cette même période (Grollemund *et al.* 2015). Cette réduction du couvert forestier, associée à une érosion intense, suscite un important débat quant à la nature des éléments l'ayant causée. Certaines études démontrent qu'elle est la résultante d'une crise climatique (Giresse *et al.* 2020), tandis que d'autres lui avancent une origine anthropique (Garcin *et al.* 2018). En effet, des traces archéologiques de villages émergent à partir de 3500 ans AP. Elles incluent poteries et outils en pierre polie, fosses dépotoirs, et restes de coques de palmiers à huile et d'élémier d'Afrique. Un peu plus tard, le développement de pratiques agricoles et la maîtrise des techniques de fonte du fer (Neumann *et al.* 2012) auraient permis aux populations bantoues d'avoir un plus grand impact sur leur milieu naturel. La diffusion de la métallurgie date d'environ 2800 AP, coïncidant avec le début de la seconde phase d'expansion (Oslisly *et al.* 2013). Pour ce qui est du développement de l'agriculture, elle a été datée à environ ~2300 AP après la découverte dans la partie Sud du Cameroun de restes de mil, une espèce originaire des régions savanicoles (Kahlheber *et al.* 2009).

3. Patrons évolutifs en Afrique centrale : forêts tropicales humides et espèces pérennes

La distribution actuelle des espèces cultivées est la résultante de processus évolutifs opérant à des pas de temps différents. D'une part, leur histoire récente peut être liée à une diffusion anthropique, favorisant leur dispersion au gré des mouvements des populations qui en ont l'usage et contribuant ainsi à une implantation dans de nouveaux écosystèmes, notamment en limite d'aire de distribution « naturelle ». D'autre part, leur distribution est le fruit de dynamiques de plus long terme : avant d'aborder l'histoire de la domestication en forêt tropicale humide africaine, il faut donc revenir sur le cadre biogéographique de celles-ci et sur les données quant à leur histoire évolutive en relation avec les glaciations du Quaternaire.

Les forêts tropicales africaines, tout comme celles des autres régions situées aux mêmes latitudes, ne sont pas des écosystèmes stables ou stabilisés de longue date (Heaney 1991; Flenley 1998; Mayle *et al.* 2000). L'influence étroite exercée par l'environnement abiotique sur les biomes, et plus spécifiquement la relation entre fluctuations climatiques et distribution des espèces végétales, explique que la biogéographie des communautés végétales présentes en Afrique centrale a amplement évolué au cours des derniers millénaires (Hamilton et Taylor 1991; Maley et Brenac 1998; Malhi *et al.* 2013).

Sur l'ensemble de la zone tropicale, sept pour cent des terres émergées sont couvertes par des forêts tropicales humides, réparties principalement sur le continent africain, les Néotropiques et le sud-est asiatique. Les forêts d'Afrique continentale se retrouvent dans trois centres principaux : l'Afrique de l'Est, la partie méridionale de l'Afrique de l'Ouest, de la Sierra-Leone au Ghana (Haut Guinéen), et, de l'autre côté du Dahomey Gap (« Sillon dahoméen »), l'Afrique centrale, deuxième massif forestier mondial. Une dernière subdivision, basée sur les patrons d'endémisme des espèces animales et végétales (White 1983), distingue au sein de l'Afrique centrale la zone forestière de l'Ouest (Bas Guinéen) et celle de l'Est (Congolia), séparées par les plaines inondables du fleuve Congo (Figure 5).

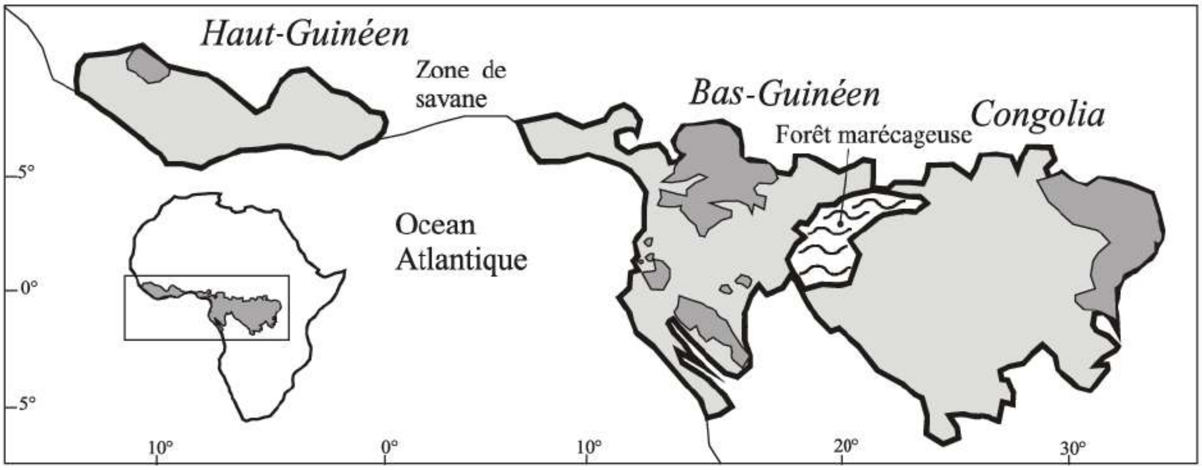

Figure 5. La forêt africaine sempervirente de basse altitude (gris), réparties dans 3 régions, Haut-Guinéen, Bas-Guinéen et Congolia avec en gris foncé les collines et plateaux (adapté de Leal, 2004).

De manière générale, il a été constaté que les forêts tropicales africaines contenaient une diversité spécifique moindre que leurs homologues d'Amérique du Sud et d'Asie du Sud-Est (Couvreur 2015; Slik *et al.* 2015). Une esquisse de l'évolution sur les derniers millions d'années, à partir des reconstitutions (sur bases palynologique, carpologique et paléobotanique), des biomes de la zone d'Afrique centrale indique que, tandis que la forêt tropicale humide couvrait de 22 à 15 millions de km^2 entre 55 Ma (Éocène) et 11 Ma (Miocène), cette superficie est tombée à environ 10 millions de km^2 il y a trois millions d'années (Pliocène). Sa surface actuelle, de 3,4 millions de km^2, est aussi réduite du fait de l'occupation humaine (Malhi *et al.* 2013). Cette tendance générale à la réduction de la superficie des forêts tropicales africaines au fil du temps, beaucoup plus importante en Afrique qu'en Amazonie (Morley 2011; Kissling *et al.* 2012), pourrait expliquer les patrons actuels de diversité des espèces.

La dynamique démographique récente (depuis le Pléistocène) des forêts tropicales africaines peut être reconstituée en synthétisant les résultats d'analyses palynologiques de séquences sédimentaires continentales, d'études de macrorestes végétaux et de phytolithes. De nombreux travaux ont porté sur l'effet des fluctuations climatiques, les modèles de reconstitution climatique montrant une alternance, au cours du Quaternaire, de longues phases de refroidissement (Glaciaires), ou péjorations climatiques, et de phases plus courtes de réchauffement (Interglaciaires - Couvreur *et al.*, 2021; Maley, 1996). Les périodes glaciaires étant caractérisées par un climat à la fois plus sec et surtout plus aride, l'une des hypothèses fortes sur les changements de végétation advenus est que ces périodes (notamment le dernier maximum glaciaire, 18000 AP), marquées par une expansion des zones savanicoles, ont provoqué une contraction du couvert forestier dans des zones refuges (théorie des refuges forestiers ; voir par exemple Robbrecht, 1996; Sosef, 1996). Des controverses existent quant à la localisation de ces zones, distinguées par des données de paléovégétation, et par les patrons actuels de diversité et d'endémisme spécifiques : il s'agirait soit de plusieurs zones refuges discrètes (Maley 1996; Figure 6), soit d'une zone refuge plus continue le long des côtes du Cameroun et du Gabon (Anhuf *et al.* 2006).

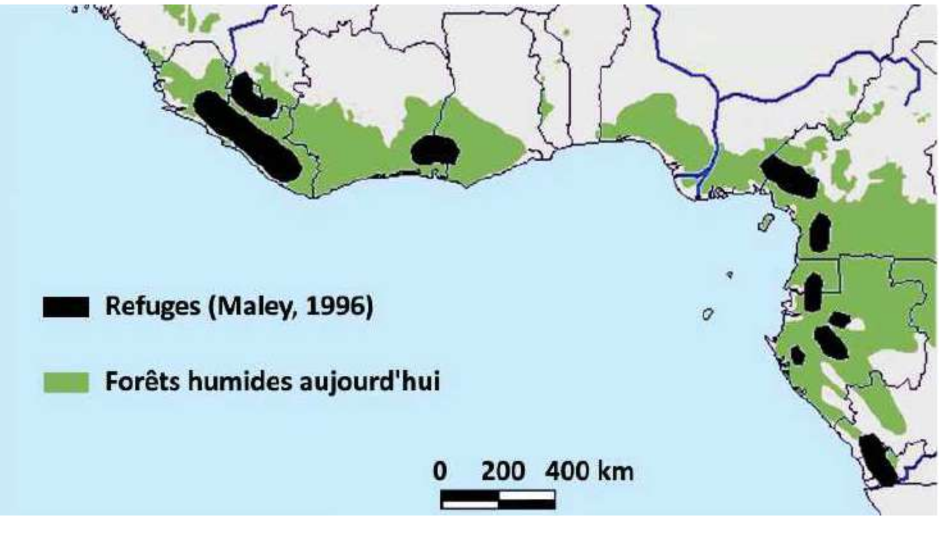

Figure 6. Carte des refuges forestiers selon Maley (1996).

Une hypothèse alternative propose que ces zones aient été peu significatives en tant que refuges, mais que la physionomie des forêts durant les périodes glaciaires aurait effectivement été modifiée (moindre densité des arbres, canopée moins haute ; Cowling *et al.*, 2008).

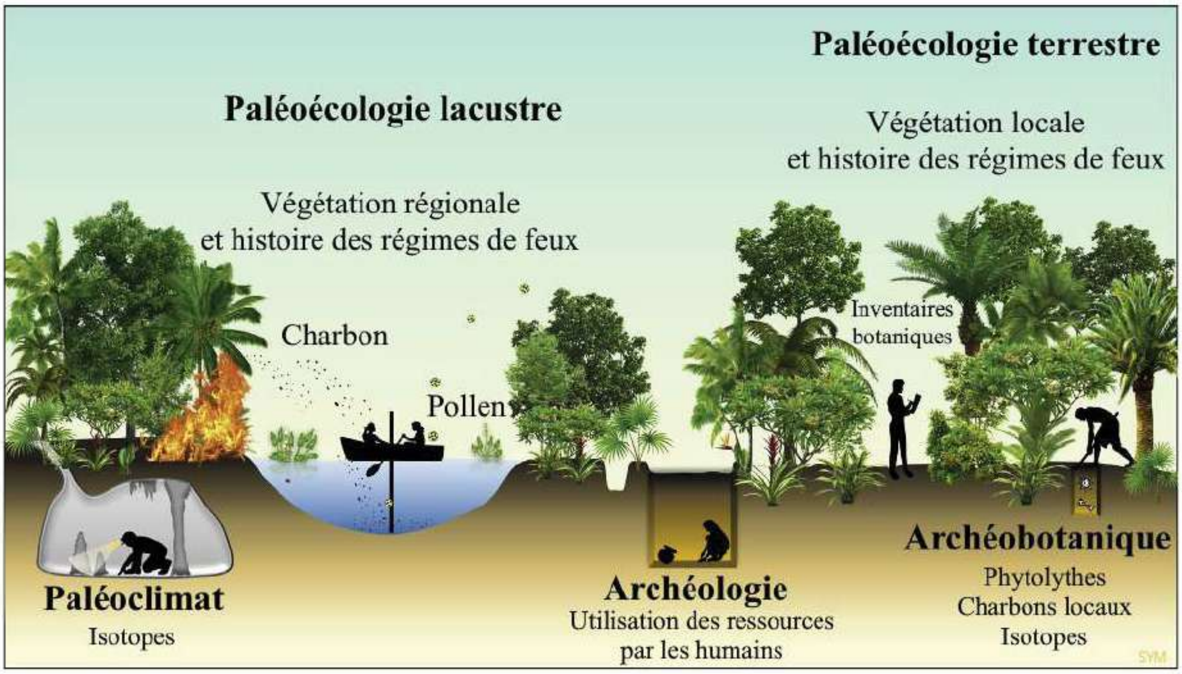

Figure 7. Méthodes employées pour reconstituer les paléoenvironnements (d'après Iriarte *et al.*, 2020).

Outre la reconstitution des paléoenvironnements (Figure 7) et l'étude des patrons d'endémisme et de biodiversité, l'empreinte des changements environnementaux passés peut être appréhendée par la phylogéographie, c'est-à-dire l'étude de la structuration spatiale des variants génétiques au sein des espèces. En se focalisant sur la diversité génétique neutre (non adaptive) des populations, les méthodes de phylogéographie permettent de distinguer les populations plus anciennes de celles nouvellement établies, et donc de faire (ou non) le lien avec les fluctuations climatiques ayant pu participer aux patrons de structuration observés (Hardy *et al.* 2013; Duminil *et al.* 2015). Ces études ont conforté la théorie des refuges forestiers en mettant en évidence l'existence de différents pools génétiques au sein de l'aire de distribution des espèces étudiées, et en datant la divergence entre ces pools génétiques (anciennes barrières aux flux de gènes) aux périodes glaciaires du Quaternaire. Les arbres des forêts tropicales humides (FTH) africaines ont donc gardé une signature génomique des événements démographiques qui ont accompagnés les oscillations climatiques du Quaternaire. Ces études ont principalement porté sur des arbres forestiers utilisés pour leur bois, dont la distribution n'aurait été que très peu affectée par les humains – quoique cette conjecture soit à nuancer. En effet, l'étude des restes archéologiques et de la composition de la végétation en FTH, démontre une influence assez importante des populations sur ces écosystèmes (Vleminckx *et al.* 2014; Biwolé *et al.* 2015; Morin-Rivat *et al.* 2017). Il serait dès lors intéressant de mener des études de phylogéographie sur des arbres alimentaires, possiblement utilisés de longue date par les populations locales, afin d'acquérir des données supplémentaires et de mieux comprendre l'interaction entre les humains et la nature au sein des FTH africaines.

4. Exploitation des produits forestiers non ligneux

Les espèces à usage alimentaire font partie du groupe plus large des produits forestiers non ligneux (PFNL), désignant l'ensemble des biens d'origine biologique autre que le bois, dérivés des forêts ou autres terres boisées et des arbres hors des forêts (FAO 1999). Ces produits font l'objet d'une utilisation ancienne, qu'elle soit alimentaire, médicinale, matérielle ou culturelle. De plus, la vente des PFNL a actuellement un rôle dans le revenu des ménages. La dernière évaluation des ressources forestières mondiales de la FAO (2020) estime ainsi que la valeur de transactions des PFNL a dépassé les sept milliards de dollars en 2015. Dans la mesure où elle ne repose que sur une sélection des espèces les plus commerciales, et ne concerne donc pas l'ensemble des PFNL, cette valeur est une sous-estimation de leur contribution réelle. Cela étant, en Afrique sub-saharienne, des études à l'échelle locale (Ambrose-Oji 2003; Gallois *et al.* 2020) ou régionale (Ingram et Schure 2010) attestent de l'importante contribution des espèces fournissant des PFNL comme moyens de subsistance des populations locales (alimentation / économie des ménages).

Cela est d'autant plus vrai que les modalités d'accès et de gestion de ces ressources sont diversifiées. La revue de littérature de Dawson *et al.* (2014) distingue ainsi trois grandes catégories de PFNL : les produits issus de collectes dans les espaces forestiers (e.g. les « bush mango » ou mangues sauvages, *Irvingia gabonensis*), les produits issus d'arbres intégrés aux systèmes agroforestiers locaux sous une forme semi-domestiquée, et enfin les produits issus d'arbres désormais pleinement intégrés aux systèmes de production commerciaux (caféiers, cacaoyers, huile de palme…). Du fait de leur forte valeur commerciale, le corpus de recherches sur cette dernière catégorie de produits est le plus conséquent. Toutefois, des arbres multi-usages locaux identifiés comme prioritaires pour leur contribution dans les systèmes de subsistance ont fait l'objet à la fin des années 1990 d'une première vague d'études impulsées en particulier par les centres du CGIAR, l'ICRAF et Bioversity International notamment (Eyog-Matig *et al.* 2002; Clark et Sunderland 2004). Ces études ont permis en particulier de préciser les conditions d'une gestion durable des ressources forestières, permettant dans le même temps de pérenniser les stratégies de subsistance qui en dépendent, comme par exemple pour *I. gabonensis* (Vihotogbe 2012) ou pour *Prunus africana* (Vinceti *et al.* 2013).

5. Le safoutier, *Dacryodes edulis*

Le safoutier (*Dacryodes edulis* [G.Don] H.J.Lam) est un arbre fruitier particulièrement important pour la sécurité alimentaire et l'économie des populations de son aire d'origine du bassin du Congo. Il appartient à la famille des Burseraceae, dont les 19 genres et 700 espèces environ sont réparties dans les zones tropicales et subtropicales, avec quelques espèces en zones tempérées chaudes (Daly *et al.* 2011). Les arbres et arbustes de cette famille sont connus pour leurs résines parfumées, et comprennent entre autres les arbres à encens (genre *Boswellia*) et à myrrhe (genre *Commiphora*). Environ 90 espèces sont recensées dans le genre *Dacryodes*. L'Amérique du Sud en compte le plus grand nombre, dont beaucoup décrites récemment (Daly et Martinez-Habibe 2019; Martínez-Habibe et Daly 2019), suivie de l'Afrique (18 espèces) et de l'Asie (16 espèces). Toutes les espèces africaines sauf une (*D. trapnellii*) sont présentes dans les forêts sempervirentes et semi-décidues de la zone guinéo-congolienne. Le Gabon, le Cameroun et la Guinée Equatoriale sont les pays qui comptent le plus grand nombre d'espèces (12, 9 ou 10 et 6 respectivement, voir Onana 2008). Dans la littérature, le safoutier se retrouve aussi sous d'autres dénominations anciennement utilisées, dont les plus fréquentes sont *Pachylobus edulis* G. Don (Don 1832), *Canarium edule* Hook. F (Hooker et Bentham 1849), et *Pachylobus saphu* Engl. (Engler 1896).

a) Traces anciennes et histoire(s) de safoutier

Les traces historiques du safoutier sont peu nombreuses : le péricarpe pulpeux de sa graine charnue ne se conservant pas (Figure 8), il n'est pas identifiable dans les relevés anthracologiques effectués dans la région. Cependant des restes archéo-botaniques provenant d'arbres sont fréquemment retrouvés sur les sites d'occupation humaine du Néolithique : il s'agit des espèces alimentaires *Elaeis guineensis, Canarium schweinfurthii,* plus rarement *Coula edulis* et *Raphia* spp. (Neumann *et al.* 2012; Oslisly *et al.* 2016). Pour le safoutier, il est donc difficile d'avoir des données archéologiques plus précises que celles de la présence du genre *Dacryodes* dans des relevés de pollens effectués en Afrique centrale (Ngomanda *et al.* 2016; Kiahtipes 2018), ce qui n'apporte aucune information quant à l'histoire de son utilisation humaine.

Figure 8. Fruits du safoutier. **a**. point d'insertion du pédoncule ; **b**. fruit entier à maturité ; **c**. coupe longitudinale du fruit sans graine ; **d**. coupe transversale du fruit ; **e**. graine.

On retrouve sa trace dans les textes des premiers explorateurs européens. Il apparaîtrait une première fois dans le journal du marchand néerlandais van den Broecke (La Fleur 2000), qui a visité en 1611 le royaume de Loango au sud-ouest actuel du Congo. Il figurerait ainsi parmi d'autres ressources alimentaires (bananes et plantains, ignames, noix de cola entre autres) sous le nom *masseffes*, qui pourrait correspondre ainsi que le propose une note de traduction, à un emploi d'un préfixe bantu du pluriel *ma* et du suffixe pluriel néerlandais *s*. À la fin de ce même siècle, il est décrit par Cavazzi (1690), un missionnaire italien qui a passé l'essentiel de sa carrière en Angola, mais a séjourné au Congo vers 1666-1667 (Thornton 1979). Etant donnée la brièveté de ses séjours, les informations qu'il fournit sur la faune et la flore ont probablement été compilées à partir de travaux d'autres missionnaires. Parmi les espèces décrites, dont le palmier à huile, il est fait mention du *Zaffo* qui est « à la hauteur et de la grosseur de nos chênes ; il porte un fruit qui ressemble à nos plus grosses prunes et couleur de feu ; rôti sous les cendres chaudes il a une odeur aromatique, et fortifie la tête » (traduction française, 1732).

À partir de cette date, les observations se multiplient, attestant en particulier de la présence de l'arbre aux abords des villages, comme par exemple dans un récit d'expédition en RDC datant du début du XIXème siècle (Tuckey et Smith 1818) :

« Le safu (2) dont M. Lockhart a entendu faire un pompeux éloge par les habitan[t]s, qui le regardent comme le meilleur de leurs fruits, est ordinairement planté à l'entour des villages, depuis Emboma en remontant le fleuve. Les propriétaires apportent le plus grand soin à le défendre contre les attaques des oiseaux. Son importance s'accroît en ce que le fruit mûrit au mois d'octobre, époque à laquelle les vivres sont rares. Il n'y a pas de raison pour douter que cet arbre, dont j'ai fixé la place dans mes remarques sur les amyridés, appartienne originairement à la côte occidentale d'Afrique. (…) (2) C'est sans doute le *zaffo* de quelques anciennes relations du Congo. »

Pour ce qui est de la tradition orale, le safoutier est présent dans un long passage de l'épopée Mɔngɔ, ou « épopée Lianjà-Nsongo », du nom de la fratrie héroïque au centre du récit. Les Mɔngɔ sont une ethnie habitant la cuvette centrale congolaise (actuelle RDC). Plusieurs retranscriptions de ce texte existent, dont celle de Boelaert, qui l'a popularisé (1949). Le passage concernant le safoutier commence au moment où Lianjà est encore dans le ventre de sa mère, Mbombé. Un fruit inconnu d'elle tombe du bec d'un oiseau alors qu'elle est dehors. Le montrant à son mari, il lui apprend que c'est un safou, lui précisant qu'il s'agit d'un fruit comestible. Mbombé le cuisine, le mange et dit qu'il s'agit du seul aliment qu'elle peut encore supporter. Son mari attend le passage de l'oiseau et lui demande la localisation du safoutier pour combler sa femme enceinte. Allant un jour chercher les fruits pour elle, et après diverses péripéties épiques, il sera assassiné par le propriétaire pygmée de l'arbre. Lianjà naît alors miraculeusement adulte, et va venger son père en tuant le propriétaire de l'arbre et en abattant l'arbre qui est cause de sa mort. Il a été proposé que ce récit soit indicatif de la culture du safoutier (Hulstaert 1991). Dans la mesure où les premières parties de l'épopée, dont fait partie cette séquence du safoutier, ont été enregistrées antérieurement (1892) chez d'autres ethnies bantoues de la zone (Vinck 1993), cela indique en particulier que l'espèce était suffisamment répandue et avait une valeur telle qu'elle pouvait prétendre à un rôle symbolique dans la tradition orale.

b) Biologie de la reproduction

La grande majorité des plantes à fleurs, autour de 90% d'entre elles, produisent des fleurs hermaphrodites, qui sont à la fois staminées et pistillées. Environ 10% ont développé une fleur unisexuée, où les organes mâles (androcée formé d'étamines) et femelles (gynécée formé de carpelles) sont portés par des fleurs séparées sur la même plante (monoécie) ou sur des individus séparés (dioécie) (Ainsworth 2000). Ce dernier cas de reproduction, présent chez environ six pour cent des angiospermes, implique la présence d'individus ayant des rôles sexuels différents, soit staminés, soit pistillés, et qui sont respectivement désignés comme des individus mâles et femelles (Renner 2014). Il existe cependant un certain nombre d'autres états sexuels ou systèmes de reproduction, qui peuvent être des formes intermédiaires apparues au cours de l'évolution de l'hermaphrodisme à l'unisexualité complète (Delph 2009). C'est le cas de la gynodioécie, dans laquelle les populations sont composées de plantes femelles et hermaphrodites, ou de l'androdioécie pour des populations d'individus mâles et hermaphrodites.

Lorsqu'une espèce est dioïque, la fécondation est allogame puisque le pollen qui féconde la plante femelle provient forcément d'une autre plante de la même espèce. Le régime de reproduction du safoutier est subdioïque : les individus de *D. edulis* portent soit uniquement des fleurs femelles, soit des fleurs mâles et des fleurs hermaphrodites selon des proportions variées. Concernant ce dernier cas, la proportion de fleurs mâles/hermaphrodites est variable d'une année sur l'autre (Kengue, 1990). Il est essentiellement allogame, même si l'autogamie est possible (Kengue 1990). Comme l'espèce est principalement propagée via ses graines, le caractère allogame de l'espèce implique que la descendance d'un arbre mère présentant des caractères d'intérêt, ne présentera pas obligatoirement ces mêmes caractères.

L'espèce est pollinisée par des insectes (Figure 9). Le complexe de pollinisateurs associé au safoutier compte une vingtaine d'espèces d'apoïdes (abeilles au sens large), avec une prédominance de mélipones, notamment l'espèce *Meliponula erythra* (Fohouo *et al.* 2001). Dans les populations naturelles, les singes, les oiseaux et les mammifères agissent comme des disperseurs de graines, mais la dispersion anthropique des graines est plus importante dans les populations cultivées car les fruits et les graines sont couramment échangés entre parents, voisins et villages (Degrande *et al.* 2013).

Figure 9. Pollinisation d'une inflorescence de safoutier par une abeille.

c) Importance du safoutier et axes de recherche récents

Les noms véhiculaires des fruits du safoutier sont safous ou prunes (Cameroun), *atangas* (Gabon) et *ube* (Nigeria) ; à leur côté, des dizaines de noms vernaculaires existent selon les langues locales. Les safous représentent un aliment de base : ils peuvent être consommés crus, mais l'essentiel de leur consommation se fait après cuisson. Ils sont mangés en snack, ou avec tous types de compléments (Tabuna et Tanoe 2009). Pour ce qui est de son commerce au Cameroun, il se chiffrait en 2002 à près de huit millions de dollars (Awono *et al.* 2002).

L'espèce, identifiée comme l'une des espèces les plus remarquables pour la domestication, a bénéficié de nombreux programmes de recherche. Suite à une thèse pionnière sur sa morphologie et sa biologie (Kengue 1990), les aspects suivants ont en particulier été étudiés :

- l'apport économique de son intégration dans les systèmes agroforestiers (Agwu *et al.*, 2017; Leakey *et al.*, 2002; Schreckenberg *et al.*, 2002 ; Figure 10) ;
- les propriétés biochimiques de ses fruits (Ajibesin, 2011; Ene-Obong *et al.*, 2019) ;
- sa conservation et les traitements post-récolte envisageables (Dossou *et al.*, 2012; Ella Missang *et al.*, 2013; Ndindeng *et al.*, 2012) ;
- son ethnobotanique dans diverses régions (Nigeria, Omonhinmin, 2012 ; Sud-Ouest Cameroun, Egbe *et al.*, 2012) et ses propriétés pharmaceutiques (Omonhinmin et Agbara 2013).

Deux axes de recherche pertinents pour l'étude de la domestication de l'espèce, portant respectivement sur sa diversité génétique et sa diversité morphologique, ont été partiellement investigués.

Les premiers travaux en génétique ont concerné la diversité de l'espèce au Gabon, à Franceville et dans des villages environnants, en lien avec les pratiques de gestion des agriculteurs (Gabeloux 2006). Ensuite, à partir de six marqueurs microsatellites nucléaires développés par Benoit *et al.* (2011), des travaux de biogéographie ont été menés dans le cadre d'une thèse (Todou 2015). Par comparaison à une espèce exclusivement forestière du même genre, *D. buettneri* (Todou *et al.*, 2013a), la diversité intra-population de *D. edulis* était significativement plus élevée. Par ailleurs, l'information génétique a aussi été prise en considération dans la tenue d'essais de reproduction sur un nombre réduit d'accessions identifiées pour constituer des cultivars (Makueti *et al.*, 2015), mais aussi pour comparer accessions sauvages et cultivées (Tchinda *et al.* 2016).

Figure 10. En haut, safoutier présent dans une agroforêt (Kekem, Ouest Cameroun) ; en bas, verger de safoutiers et de manguiers (Koutaba, Ouest Cameroun).

Ces études soulignaient la très faible différenciation des populations échantillonnées, et suggéraient l’existence de flux de gènes (entre sauvage et cultivé ; entre *D. edulis* et *D. buettneri*), et la nécessité de disposer d’un plus grand nombre de marqueurs pour affiner ces résultats. Jusqu’à présent, l’information génétique n’a pas été utilisée pour explorer la question de l’origine de l’espèce. Actuellement, elle est présente sur une grande surface dans la zone forestière humide d'Afrique centrale, notamment au Cameroun, en République centrafricaine, en Guinée équatoriale, au Gabon, au Nigeria, en République du Congo, en République démocratique du Congo (RDC) et à São Tomé (Onana 2008 ; Figure 11).

Son aire d’origine a été avancée, de façon restreinte, au Sud du Nigéria ou au Cameroun (Vivien et Faure 1985; Keay 1989). Certains auteurs proposent plus largement les forêts tropicales du Gabon, Cameroun, Guinée équatoriale, Congo et République Démocratique du Congo (Aubréville 1962). L’optimum écologique de l’espèce, c’est-à-dire sa niche déterminée à partir de spécimens sauvages, correspondrait aux forêts du Gabon et de Guinée équatoriale (Todou *et al.*, 2013). Dans un second temps, l’intérêt des populations pour le safoutier a conduit à ce qu’il soit très souvent planté dans les villages, les jardins de case et les systèmes agroforestiers de type cacaoyère ou caféière ou épargné lors de la mise en culture des champs (Carrière 2003) ; cette mise en culture a pu contribuer à étendre son aire de distribution de l’Ouganda à la Sierra Leone (Troupin 1950). Au Cameroun, l’espèce se retrouve donc dans l’ensemble des zones de forêt tropicale dense humide (provinces du Centre, du Sud, de l’Est, du Nord-Ouest et du Sud-Ouest) et de savane tropicale boisée des provinces de l’Ouest et du sud de l’Adamaoua, qui constitue sa limite écologique (Isseri & Temple, 2002).

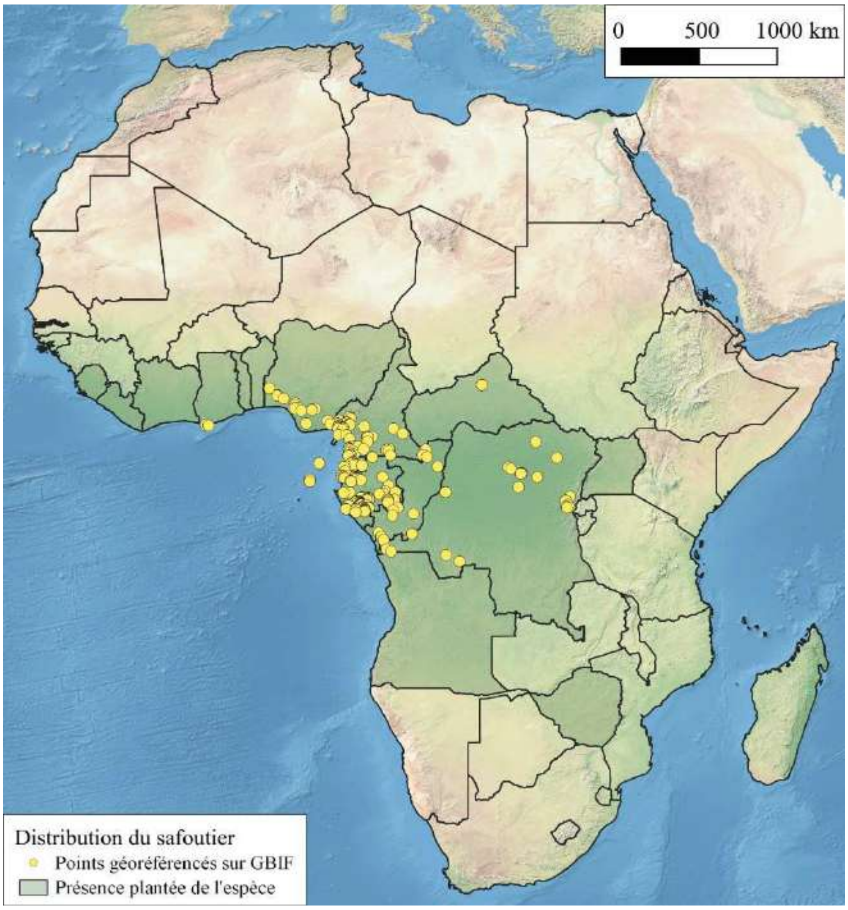

Figure 11. Présence de l'espèce d'après la base de données PROTA (Plant Resources of Tropical Africa) et présence plantée de l'espèce d'après Kengue (2002).

Enfin, la question de la diversité morphologique des safoutiers (Figure 12) a fait l'objet de nombreux travaux. Des classifications ont été proposées en fonction de caractères morphologiques (Okafor 1983) ou morphologiques et biochimiques (Ondo-Azi *et al.*, 2017; Ondo-Azi & Missang, 2013; Youmbi *et al.*, 2010). Les traits des fruits, que ce soient leur taille, leur forme, leur couleur de peau ou de chair, varient de façon importante aussi bien entre les différentes populations et les bassins de production, qu'à l'intérieur d'une même population (Anegbeh *et al.,* 2005; Biloso *et al.*, 2018; Waruhiu *et al.*, 2004). Les connaissances et préférences des cultivateurs n'ont jamais été intégrées à ces classifications, alors que l'existence d'une sélection variétale par les producteurs avait déjà été mise en évidence au Cameroun pour la banane plantain (Mengue Efanden *et al.*, 2003). En revanche, des préférences de consommateurs pour certains types de fruits – fruits de grande taille, à chair épaisse, douce et huileuse – sont attestées (Ndindeng *et al.*, 2012) et se répercutent sur les prix de vente (Leakey *et al.* 2002).

Figure 12. Diversité des tailles, formes et couleurs de peau de safous. Le premier fruit de la première rangée et le dernier de la seconde ne sont pas encore à maturité.

La recherche agronomique menée au Cameroun, par l'IRAD et l'ICRAF notamment, a étudié les possibilités de sélection et d'amélioration variétale (Makueti *et al.*, 2015; Mbeuyo *et al.*, 2013; Tchatchoua *et al.*, 2016) : des marcottes d'arbres (Figure 13) identifiés pour la qualité de leurs fruits sont développées et vendues par l'IRAD. Cela étant, les cultivateurs au Cameroun pratiquent de manière prédominante la propagation de l'espèce par semis, l'usage des variétés améliorées étant encore très marginal (Kuate *et al.* 2006).

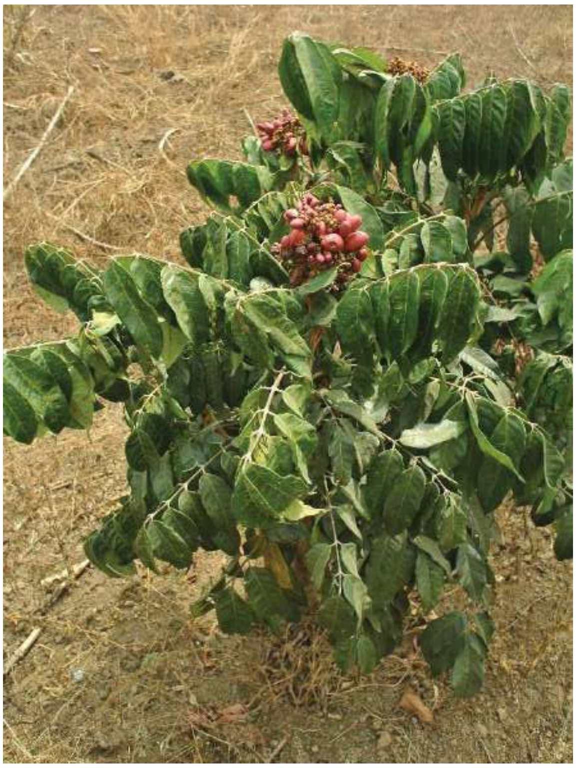

Figure 13. Jeune plant marcotté en fruits, région de Foumbot, Ouest Cameroun

6. Problématique et plan de la thèse

Etant donné les éléments bibliographiques résumés ci-dessus, ce travail vise à apporter de nouveaux éléments de compréhension sur l'histoire évolutive de l'espèce en lien avec les changements climatiques passés, et sur les conséquences des interactions entre les pratiques humaines et sa diversité génétique. Dans ce contexte, les objectifs de mon projet doctoral étaient de :

(I) Mieux comprendre l'histoire évolutive du safoutier en lien avec les glaciations du Quaternaire et son utilisation récente par les humains ;

(II) Caractériser les pratiques culturales et de gestion de l'espèce par différents groupes ethniques du Cameroun ;

(III) Comprendre l'influence de ces différentes pratiques sur la diversité génétique de l'espèce.

(I) Le premier objectif de mon travail de doctorat vise à mieux comprendre l'histoire évolutive de l'espèce à travers son aire de distribution du bassin du Congo, et en particulier quelle a été l'influence des changements climatiques passés sur la répartition de sa diversité génétique. Il s'interroge aussi sur l'histoire de la diffusion de l'espèce, et sur la manière dont la répartition de la diversité génétique entre les safoutiers cultivés dans le Bas Guinéen permet de l'éclairer.

Pour caractériser la répartition de la diversité génétique du safoutier, je me suis appuyé sur deux types de marqueurs moléculaires complémentaires (microsatellites nucléaires, SNP chloroplastiques).

Cet objectif sera développé dans le premier chapitre de ma thèse.

(II) Le second objectif est de caractériser les pratiques de gestion des personnes impliquées dans la culture du safoutier, en fonction de leurs usages et de leurs perceptions de la diversité existante au sein de l'espèce. Il s'articule autour des perceptions des cultivateurs quant à l'organisation de cette diversité, et s'attache à mettre en perspective la façon dont ces perceptions sont organisées en préférences puis mises en pratique vis-à-vis de l'objet diversité. Enfin, il s'intéresse à des bassins de production dont les stratégies de production sont plus ou moins intégrées au marché, afin de voir l'effet de cette intégration sur la diversité des pratiques et des morphotypes de safou.

Cet objectif sera approfondi dans les chapitres deux et trois de ce manuscrit.

(III) Depuis le travail de recherche de Gabeloux (2006), la diversité des pratiques des cultivateurs n'a plus été mise en lien avec la diversité génétique de l'espèce. Le troisième et dernier objectif de mon travail est donc de préciser l'effet des perceptions et des pratiques des cultivateurs appartenant à différents groupes ethniques sur la diversité variétale et la diversité génétique de l'espèce. Mes questionnements portent plus particulièrement sur le lien entre patrons d'échange des semences et diversités du safoutier, en fonction des groupes ethniques et de la localisation le long de la chaine de valeur des safous. Ils visent aussi à évaluer si les patrons de diversité sont congruents entre d'une part l'agrobiodiversité des safoutiers, évaluée à partir de la diversité morphologique de ses fruits, et d'autre part la diversité génétique des arbres échantillonnés.

Cet objectif sera traité dans les chapitres quatre et cinq.

Les chapitres suivants, rédigés en anglais, sont des manuscrits d'article.

Le premier chapitre s'intéresse à la distribution de la diversité génétique du safoutier à travers l'ensemble de son aire de répartition. À travers une approche de phylogéographie j'aborde l'évolution de l'espèce en questionnant l'influence historique des glaciations du Quaternaire ainsi que l'influence beaucoup plus récente de l'utilisation de l'espèce par les populations locales. Je tente en particulier de retracer l'origine géographique de sa mise en culture, et de la propagation de sa culture en Afrique centrale.

Les chapitres suivants (deux à cinq) abordent différents aspects de la culture du safoutier dans les principales zones de production du Cameroun et leurs relations avec la diversité morphologique et génétique de l'espèce.

Le deuxième chapitre a pour cadre l'une des zones rurales du chapitre précédent, l'Ouest Cameroun, où certains bassins de production sont le lieu d'une intensification de la culture du safoutier. Il évalue les liens entre stratégies des personnes impliquées dans la culture des safoutiers, pratiques culturales et diversité variétale.

Le troisième chapitre s'appuie sur trois gradients d'urbanisation, chacun défini par une ethnie dominante, pour montrer comment l'évolution des usages du safou entre zones de production et zones de consommation influence les perceptions, préférences et pratiques des propriétaires de safoutier.

Le quatrième chapitre porte sur la dynamique sociale de la diversité des safoutiers entre milieu rural et milieu urbain, et son effet sur la répartition de la diversité génétique. Il développe plus particulièrement le rôle potentiel des villes dans la conservation.

Le cinquième chapitre reprend le cadre du troisième chapitre, formé de trois gradients d'urbanisation, chacun distingué par une ethnie prédominante. Il met cette fois en relation les pratiques de propagation et la distribution des diversités morphologique et génétique du safoutier.

S'en suit une synthèse des chapitres précédents, complétée par une discussion des différents grands thèmes de cette thèse : la diversité du safoutier, les systèmes de production dont il est une composante, les trajectoires de la domestication dans les agroécosystèmes tropicaux.

Le Tableau 1 reprend les différents axes de recherche, approches et aires géographiques des articles qui composent cette thèse.

Tableau 1. Récapitulatif des différentes approches développées dans cette thèse.

(I) Retracer la phylogéographie du safoutier (*Dacryodes edulis*) : structuration génétique du safoutier	+600 individus 13 microsatellites nucléaires microsatellites 100 individus 697 SNP chloroplastiques	génétique des populations, phylogéographie	diversité et différenciation génétique	Bassin du Congo (Cameroun, Gabon, Congo Brazzaville, RDC en particulier)
(II) Appréhender les processus de domestication en cours : chez le safoutier, perceptions et pratiques entre ville et campagnes, entre ethnies	441 entretiens	ethnoécologie	entretiens	Cameroun (Centre, Ouest)
(III) Comprendre les interactions entre dynamiques biologiques et sociales : échanges de semence, variétés, organisation de la diversité génétique	420 individus, 13 microsatellites nucléaires	ethnoécologie génétique des populations	entretiens, description des variétés, diversité génétique	Cameroun (Centre, Ouest)

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Contexte

Mon projet de recherche doctoral s'appuie et s'insère en grande partie dans le cadre du projet scientifique *Arbopolis : Strengthening African livelihoods, food and nutrition security using indigenous fruit tree species* (financement Agropolis Fondation, 2017 à 2021). Ce projet centré sur l'étude du safoutier vise plus particulièrement à : (i) acquérir une meilleure connaissance de l'espèce en vue de la promotion de sa culture et dans une perspective de gestion durable ; (ii) développer des activités de sensibilisation de la société sur l'important rôle nutritionnel, culturel et économique de cet arbre et sur les interactions qui existent entre les populations et les arbres fruitiers plantés en ville ou à la campagne (Figure 14). Ces activités de sensibilisation ont été menées auprès de mairies et d'écoles maternelles et primaires partenaires du projet. Concernant l'objectif (i), il s'agissait notamment de caractériser : les chaînes de valeur des safous autour de la ville de Yaoundé ; les pratiques de production et de consommation des safoutiers et leurs effets sur la diversité génétique de l'espèce ; les critères de qualité recherchés pour la récolte, la vente et la consommation ; les ethno-variétés de safoutiers ; les descripteurs sensoriels des principales ethnovariétés de safous, leur acceptabilité et les préférences des consommateurs ; et enfin la contribution relative de l'espèce à la couverture des besoins nutritionnels des populations rurales et urbaines.

Ce projet interdisciplinaire était donc centré sur les interactions entre les pratiques agricoles, de gestion et de consommation des safous, et la diversité intraspécifique du safoutier dans les villes et les zones rurales au Cameroun. Partant de la capitale, Yaoundé, ce projet ciblait les sites dans lesquels s'établissent les principales filières vers les zones de production de safous, et ce le long d'un gradient d'urbanisation.

Différents axes de recherche sont développés : l'un d'eux consiste à articuler les pratiques de gestion par les populations le long du gradient et l'organisation des diversités morphologique et génétique du safoutier. Basée sur des entretiens, cette activité permet dans un second temps : (1) la comparaison des logiques de sélection et leur effet sur la diversité des populations de safoutiers dans des contextes écologiques et socio-économiques différents ; (2) la comparaison de la diversité (morphologique, génétique) observée en milieu urbain avec celle de la campagne.

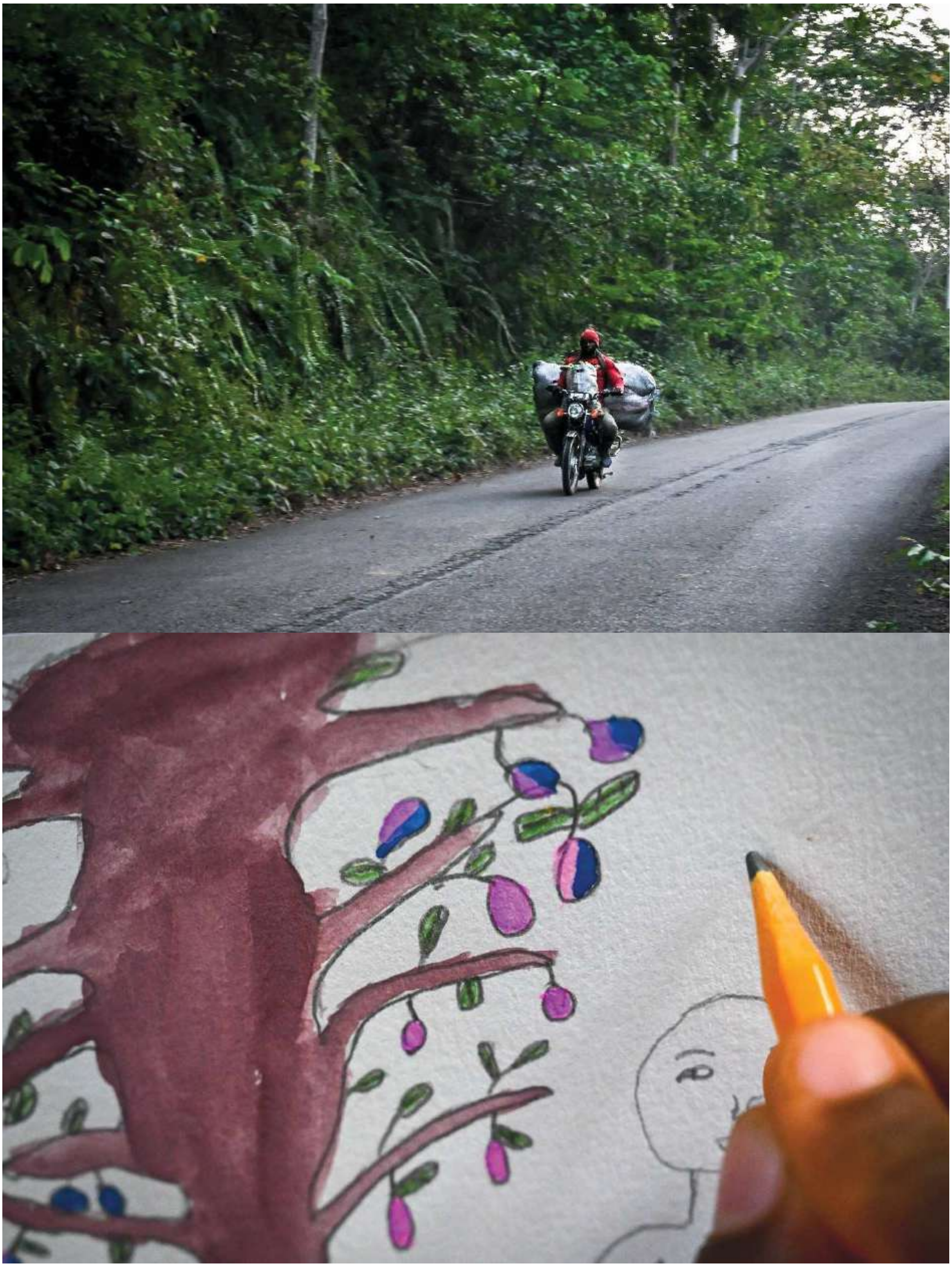


Figure 14. En haut, transport motorisé de safous stockés en filet avant la commercialisation ; en bas, dessin d'enfant de safoutier dans une école à Eseka (Région Centre, Cameroun), représentant des fruits à différents stade de maturation (photographies S. Carrière).

Cette activité était co-supervisée par Stéphanie Carrière (UMR SENS [GRED], écologue et ethnobotaniste à l'IRD) pour la partie interaction sciences humaines et sociales et écologie, et Jérôme Duminil (UMR DIADE, généticien à l'IRD) pour la partie génétique. Une étroite collaboration était aussi engagée avec Marie-Louise Avana (maîtresse de conférences en ethnobotanique et agroforesterie à l'Université de Dschang, Cameroun) pour les aspects scientifiques et pour l'encadrement sur le terrain. Trois étudiants de l'Université de Dschang au Cameroun, deux étudiantes de l'Université de Montpellier et une consultante étaient également impliquées pour la réalisation de cette activité.

Trois binômes ont été constitués par ces étudiants pour mener des entretiens et échantillonner des feuilles et des fruits de safoutiers dans trois sites le long d'un gradient d'urbanisation allant des zones de consommation (ville de Yaoundé) vers les zones de production de safoutiers (Figure 15). Chaque binôme a travaillé en priorité avec un groupe ethnique dominant du Sud-Cameroun : les Bamiléké (binôme 1 ; composé d'Armel Chakocha et moi), les Beti (binôme 2 ; Taïna Lemoine et Mélanie Tsogo) et les Bassa (binôme 3 ; Alexis Gakwavu et Franca Mboujda). Par ailleurs, Lison Marie, étudiante de l'Université de Montpellier, a échantillonné des safoutiers dans un quartier de Yaoundé, en vue de la caractérisation de leur diversité génétique.

Mon implication dans le projet Arbopolis a été l'occasion de coordonner une équipe de cinq étudiants sur le terrain, avec l'intervention ponctuelle d'étudiants supplémentaires. Cette coordination concernait notamment la gestion des aspects administratifs, la logistique des missions de terrain, en lien avec la représentation de l'IRD au Cameroun, ainsi que certaines interventions conjointes. C'est le cas par exemple des *focus groups* de restitution que nous avons effectués ensemble à Yaoundé V et Yaoundé VII.

Les données collectées lors des enquêtes par les trois binômes ont été utilisées dans un premier temps par les étudiants de deuxième année de master dans le cadre de leur mémoire, portant pour chacun sur un gradient d'urbanisation différent et une thématique propre. Lison Marie, après un mois d'échantillonnage à Yaoundé, a fini son stage à l'IRD de Montpellier pour traiter les échantillons de safoutier qu'elle avait récoltés (extraction et génotypage) ainsi que des échantillons de l'Ouest Cameroun que j'avais échantillonnés en 2017. Son mémoire a porté sur la répartition de la diversité génétique entre ces deux zones.

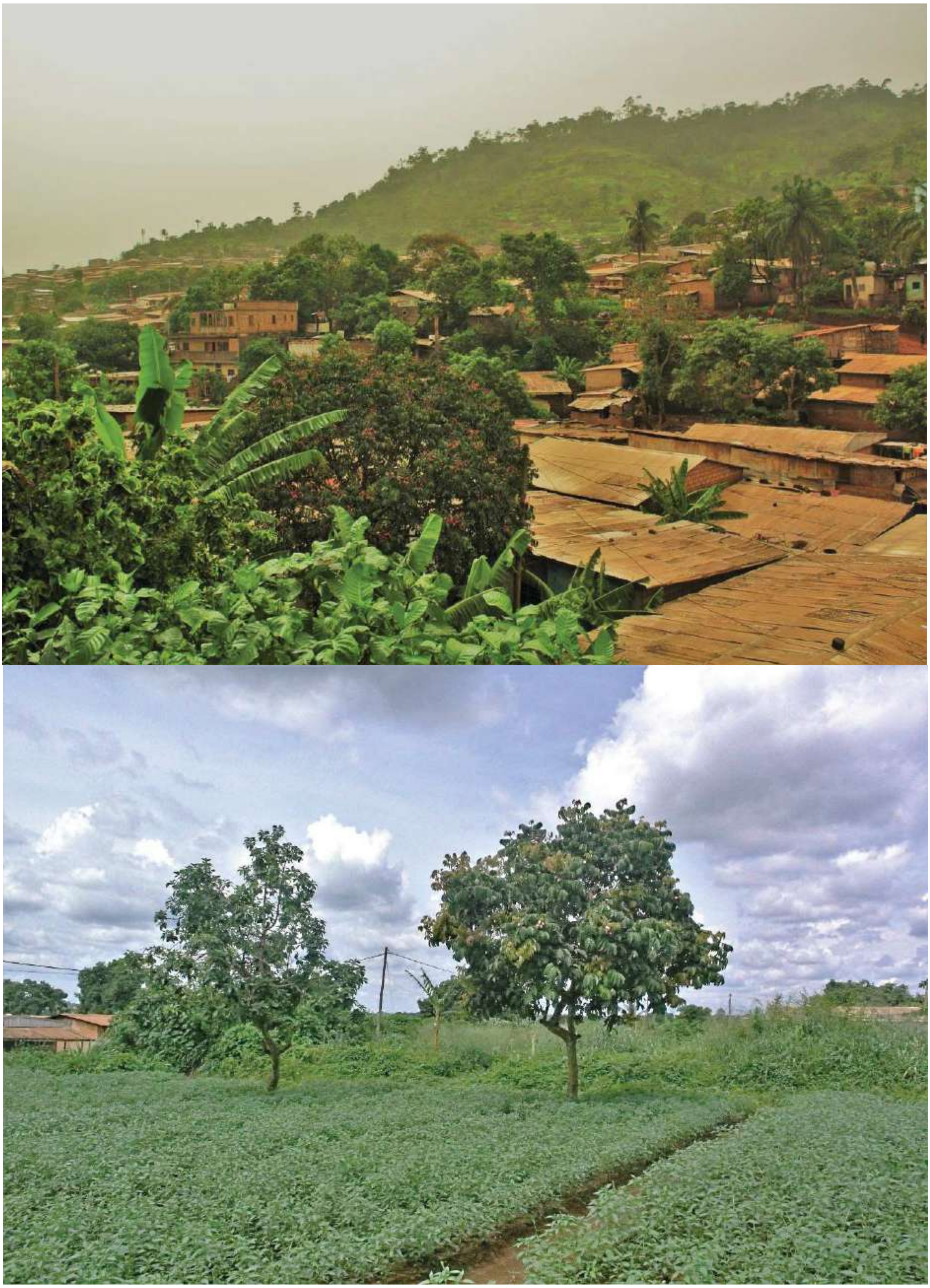


Figure 15. En haut, arbres dispersés entre les constructions à Yaoundé, quartier Messa-Carrière. Au premier plan, à droite d'un bananier, un safoutier est en fruits. En bas, jeune safoutier et jeune avocatier dans un champ maraîcher.

Dans le cadre de mon travail doctoral, j'ai fait une synthèse des données acquises par les trois binômes le long des trois gradients (Figure 16). Elles sont insérées dans les chapitres 3, 4 et 5. Le chapitre 4 s'appuie en particulier sur les données produites par Lison Marie, avec la perspective supplémentaire des échanges de graines entre les zones.

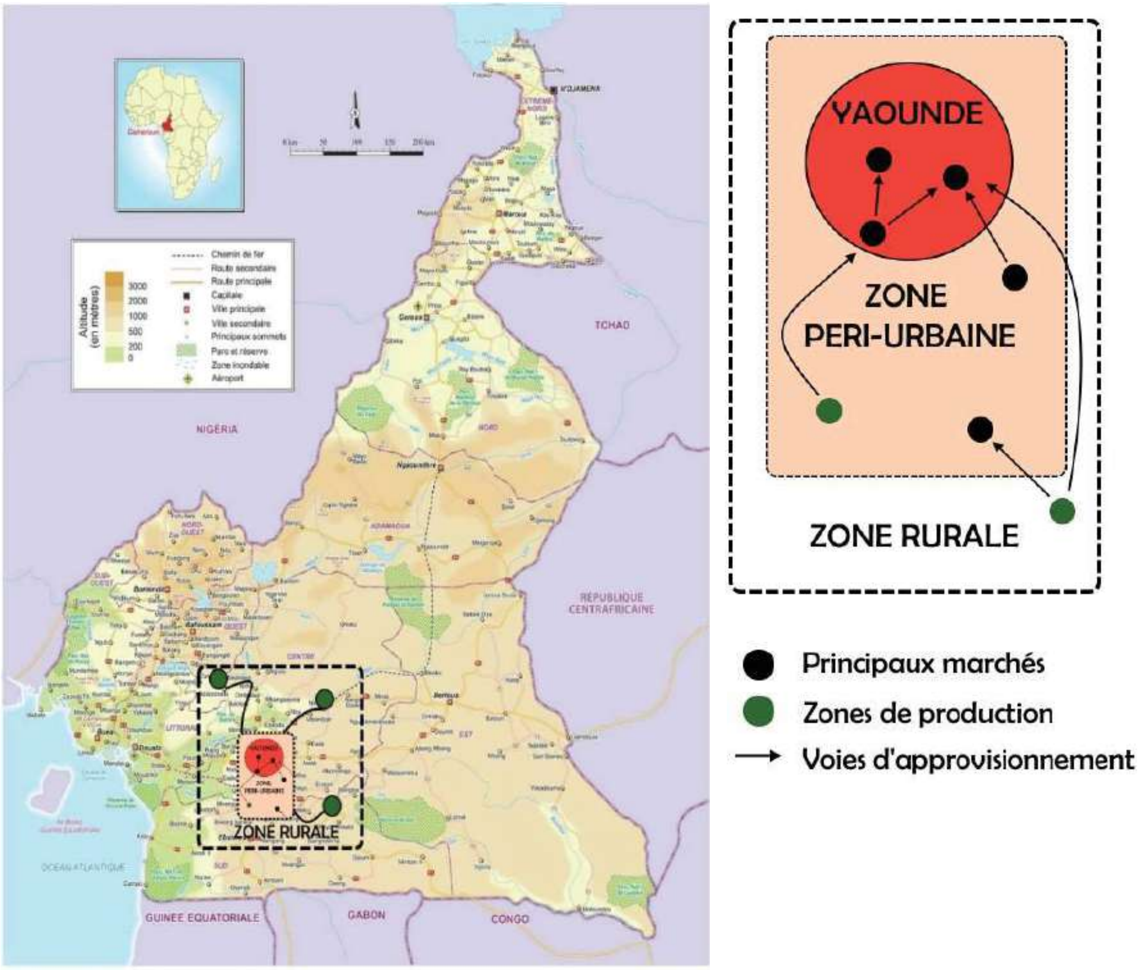
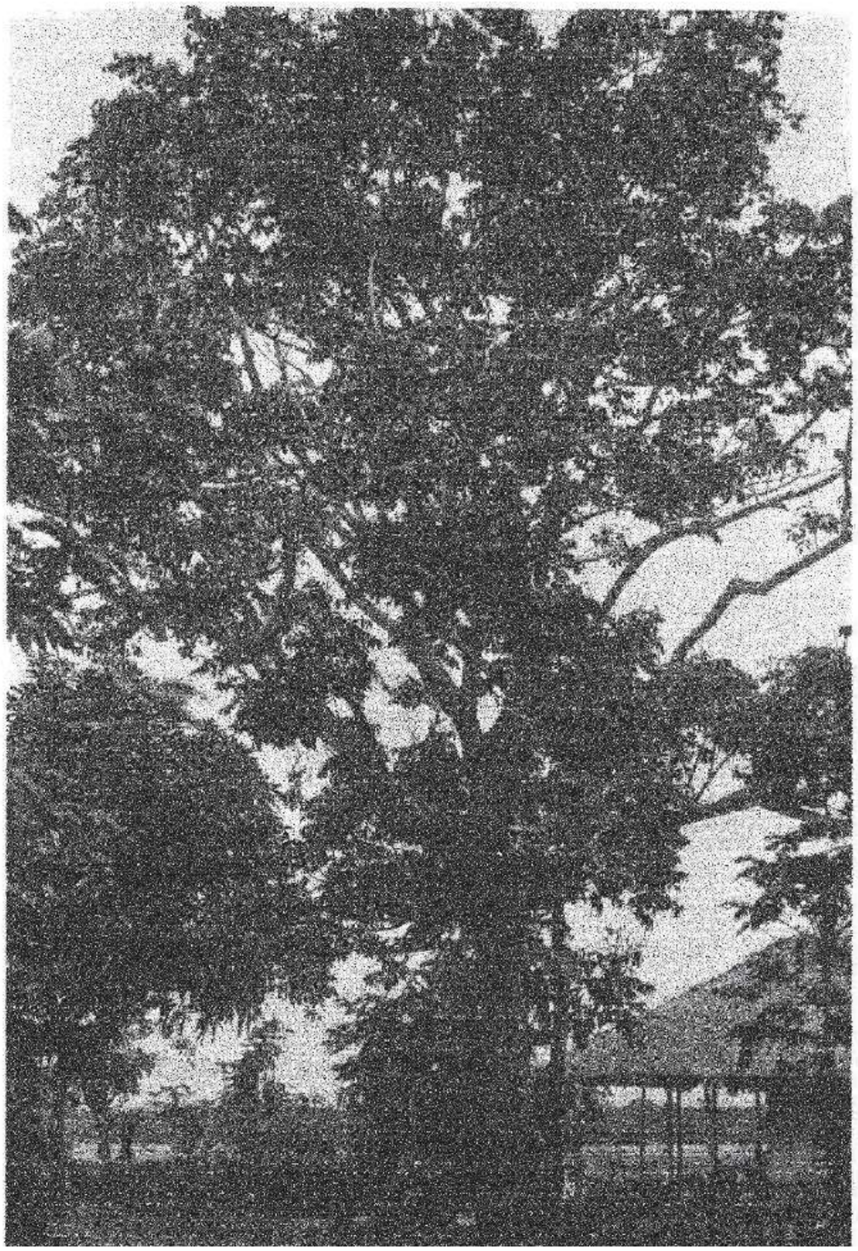


Figure 16. Illustration schématique d'une filière d'approvisionnement en safous, depuis les zones rurales et péri-urbaines jusqu'à Yaoundé où a été investiguée l'influence des pratiques culturales sur la diversité morphologique et génétique des safoutiers.

Chapitre 1

Perspectives génétiques sur les origines du safoutier en Afrique centrale



Safoutier dans les plantations d'Equateurville (actuel Mbandaka, RDC) Franz Thonner, 1898

Genetic perspectives on the origins of an indigenous fruit tree species from Central Africa, *Dacryodes edulis*

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Abstract

Gaining insight into the evolutionary history of African tropical tree species is crucial for the conservation of their genetic resources, especially when local populations rely on them for their nutrition and economy. Here, we investigated the phylogeography of *Dacryodes edulis*, a fruit tree species native to Central Africa using both nuclear and chloroplast DNA polymorphism and focusing on cultivated individuals of the species collected across species' distribution area (Nigeria, Cameroon, Gabon, Central African Republic, Republic of Congo, Democratic Republic of Congo). Estimates of the genetic diversity based on nuclear markers were relatively high for a cultivated species and were the highest in southern Gabon. Using Bayesian genetic clustering methods, three moderately differentiated genetic clusters were recovered in *D. edulis* (pairwise F_{ST}: 0.022 - 0.052): one composed of individuals from Nigeria, one composed of individuals from Democratic Republic of Congo (oriental province) and the last one grouping individuals from Cameroon and northern Gabon. The phylogeographic structure observed with chloroplast DNA was complex, but geographical patterns could be observed with a differentiation cline at the level of the meteorological equator - a pattern commonly observed on rain forest species from the region. Moreover, the presence of haplotypes shared between *D. edulis* and other *Dacryodes* species suggest possible congeneric gene flow. The reconstruction of the cultivation history of the species was not possible with the available information and sampling, but these preliminary results open perspectives for future studies.

Key words: Burseraceae, genetic diversity, phylogeography, rain forests, sub-Saharan Africa, tree species

Introduction

The biogeographic history of African rain forests has long been unknown. Palynological investigations have provided key preliminary information, suggesting notably the influence of past climate change (Dupont *et al.* 2001; Bonnefille *et al.* 2007). During the Pleistocene, climate oscillations caused repeated events of rain forests' demographic contractions and expansions (Maley 1996; Couvreur *et al.* 2021), affecting the intra-specific and inter-specific diversity distribution of species (Hardy *et al.* 2013; Dauby *et al.* 2014; Heuertz *et al.* 2014; Duminil *et al.* 2015; Ley *et al.* 2017; Helmstetter *et al.* 2020). These studies were in line with palynological findings and further suggested major historical barriers to gene flow that were probably corresponding to the expansion of savannah during ice ages. Thus, in the lower Guinea region (sensu White 1983), a divide has been commonly observed on each part of the meteorological equator, roughly corresponding to an old split between forests from Cameroon/northern Republic of Congo and forests from Gabon. Other historical barriers to gene flow were also demonstrated, but were more specific to each species, reflecting idiosyncratic histories/life history traits of the taxa (Dauby *et al.* 2014; Heuertz *et al.* 2014). The savannah corridor in the Dahomey Gap, separating the West African rain forest from that of Central Africa, was also proved to act as an effective barrier to dispersal in some rain forest species (Demenou *et al.* 2018). Other ecological drivers can be at play to explain biogeographic discontinuities, as recently demonstrated for the Central African climatic inversion (Helmstetter *et al.* 2020). These studies are however mainly focused on forest species whose wood is traded worldwide today, but of which local populations probably had only sporadic use in the past. They thus seldom incorporate humans as an influential factor of species' spatial distribution of genetic variation in their analyses.

It is known that major domestication hotspots are located in some regions of sub-Saharan Africa (Portères 1962), alongside with the other old-established centers such as the Fertile Crescent (Brown *et al.* 2009) or the Mediterranean basin (Zeder 2008). Recent genomic studies demonstrated the West African origins of cultivated cereals such as pearl millet (*Cenchrus americanus* [*Pennisetum glaucum*], Burgarella *et al.*, 2018) and African rice (*Oryza glaberrima*, Choi *et al.*, 2019; Cubry *et al.*, 2018) and showed the origin of cultivation of African yams in the Niger River basin (Scarcelli *et al.* 2019). In the rain forests of Central Africa, the picture of agricultural emergence and domestication is barely known, and the extent to which it is associated with the broader historical phenomenon of the Bantu expansion is debated (Diamond and Bellwood 2003; de Filippo *et al.* 2012; Bostoen *et al.* 2015). So far, it is mostly deduced by archaeobotany (Neumann *et al.* 2012; Oas *et al.* 2015; Oslisly and White 2016). Fruit remains of oil palm (*Elaeis guineensis*), common in archaeological sites (Logan and D'Andrea 2012), suggest a long history of human use of forest products. Hard endocarps of *Canarium schweinfurthii*, another species with an oil-rich fruit pulp, are also frequent in archaeobotanical assemblages and its use could be dated back to 11000 years in the Democratic Republic of Congo (Mercader *et al.* 2003).

Although the presence of these archaeobotanical remains indicates interaction between humans and plants in the region, it provides little information *per se* on the development of agriculture. Actually, the degree of management of these forest resources remains unknown. Today, little evidence tells us if they were exclusively gathered from the wild without killing the mother plant, under proto-cultivation (see for instance the notion applied to wild yams' management in Dounias 2001) or incipiently domesticated, with traits of plants in cultivated environments maintained within the range of variation found under natural conditions (Clement 1999). On a broader level, these questions of different intensities of plant use/human intervention pertain to the creation of cultural, or domesticated, landscapes (Clement 2014). By planting or transplanting, tending or weeding, transporting species outside their natural habitats or using fire as a management tool (Erickson 2006), humans indeed imprinted landscapes, even if their signatures (altered plant distribution and cover patterns, enriched soils) in the tropics are not as strong as those left by the spread of agriculture in Eurasia (Iriarte *et al.* 2020). In Central Africa, this concept of a domesticated landscape has been apprehended through the study of forest species composition and archaeobotanical remains. In some localities, data indicated the presence of ancient human settlements as well as human-disturbed environments, with at least a selective retention of useful species (Vleminckx *et al.* 2014; Biwolé *et al.* 2015).

Some complementary information is given by historical linguistic approaches, where vocabulary shared between languages is used to infer shared history. Bostoen (2014) has notably gathered linguistic evidence of the familiarity of early Bantu speech communities to several native fruit tree species, including the oil palm (*Elaeis guineensis*), the bush candle tree (*Canarium schweinfurthii*) and *Dacryodes edulis*. The presence of ancestral "Proto-Bantu" forms that could have given rise to the Bantu names used today, provides an indirect evidence of the exploitation of these plants by Bantu-speaking people, prior to their dispersal into equatorial Central Africa. Further, lexical reconstruction of these food species can help to reconstruct dispersal pathways.

In the present study, we analyzed patterns of genetic diversity distribution of a common indigenous fruit tree species from Central Africa, the African plum tree (*Dacryodes edulis* [G. Don] H. J. Lam). Species distribution stretches over a large area in the humid forest zone of Central Africa including Cameroon, Central African Republic (CAR), Equatorial Guinea, Gabon, Nigeria, Republic of Congo, Democratic Republic of Congo (DRC) and São Tomé (Onana, 2008). A first characterization of the distribution of genetic diversity of *D. edulis*, based on six simple sequence repeats markers (SSRs), suggested the presence of a differentiation pattern between populations from Cameroon and Gabon and highlighted important gene flow between *D. edulis* and its congeneric species *D. buettneri* (Todou *et al.* 2013a).

Using nuclear SSR markers and chloroplast DNA (cpDNA) markers, we aim to examine the spatial patterns of genetic diversity of cultivated African plum tree populations in Central Africa, to gain insight into its evolutionary history. In principle, given their high rate of mutation, SSR markers are particularly useful to characterize spatial patterns of genetic diversity distribution, and to demonstrate (relatively) ancient barriers to gene flow using adequate methodologies (eg Bayesian clustering methods). Given their uniparental mode of transmission and their low mutation rate, cpDNA represent complementary useful markers to unravel biogeographic patterns, which explains their extensive use in the field of phylogeography (Petit and Vendramin 2007; Avise 2009). Interestingly, the joint use of nuclear biparentally-inherited markers and organellar uniparentally-inherited markers further helps to disentangle the demographic history of species, by giving access to genomic signatures at two different time scales and by providing information on inter-specific gene flow (eg chloroplast capture; Duminil *et al.* 2013; Ley and Hardy 2017).

Material and methods

Plant material

Dacryodes edulis is a forest tree species, commonly cultivated in agroforestry systems or home gardens. Taxonomically, it is included in the incense family, Burseraceae. It is a subdioecious species with trees bearing either female flowers only or male and hermaphrodite flowers. It is predominantly outcrossing and pollinated by insects (Kengue *et al.* 2002). Each infrutescence contains a cluster of up to eight fruits (Kengue 1990). Cultivated individuals of the species are mainly propagated by humans that collect and plant seeds from fruits presenting characters of interest, generally dark large-sized fruits with a good taste (Rimlinger *et al.*

submitted). Propagation of the species by vegetative means (marcots) is only recent and still anecdotic. In the wild, its seeds are dispersed by birds and primates (Clark *et al.* 2001).

Sampling and DNA extraction

Leaves or cambium of cultivated *D. edulis* individuals were collected in Nigeria, Cameroon, Gabon, DRC, Republic of the Congo, CAR and São Tomé and Principe (N = 381). Plant material was immediately set in dried in silica gel after sampling to preserve DNA. Samples were also obtained from herbariums, the CIRAD herbarium in Montpellier (N = 17) and the herbarium of the Université Libre de Bruxelles (N = 14), for a total of 412 samples. Total DNA extraction was performed as described in Mariac *et al.* (2006).

Molecular analyses

Two types of complementary markers were used: nuclear microsatellites (SSRs) and single nucleotide polymorphisms (SNPs) from chloroplast DNA (cpDNA).

Genotyping of microsatellites

Among the microsatellites developed in Rimlinger *et al.* (2020), the 13 markers from the multiplexes M3 and M4 were used for amplification and genotyping as described in the paper.

Sequencing of chloroplast DNA and bioinformatic treatment

To prepare and sequence libraries, 100 out of the 647 *D. edulis* available samples were selected to cover species' distribution area. Two individuals from four congeneric species were added (*D. buettneri, D. igaganga, D. osika, D. pubescens*), as well as four samples from species of the family Burseraceae: two *Canarium schweinfurthii* and two *Santiria trimera*.

Approximately 1.5 µg of total DNA extraction for each accession was sheared using a Bioruptor Pico sonication device (Diagenode, Liège, Belgium) to yield ~400-bp fragments. All steps and conditions for genomic libraries preparation (DNA shearing, DNA end repair, adapters ligation, Bst polymerase treatment and real time PCR) followed the protocol of Mariac *et al.* (2014). Libraries were tagged using 6 bp barcodes for multiplexing. The libraries were then generated by performing real-time PCR (optimal cycle number ranging from eight to ten). After clean-up, quantification and qualification using the NanoQuant Plate (Tecan Group Ltd., Männedorf, Switzerland) and QIAxcel (QIAGEN, Valencia, California, USA), respectively, libraries were equimolarly bulked and paired-end sequenced (2 × 150 bp) using Illumina HiSeq 4000 platform at the Novogene U.K. Lab.

Raw reads were first demultiplexed, based on their 6 bp barcodes, using demultadapt (https://github.com/Maillol/demultadapt). Adapters and low-quality bases were removed using cutadapt 1.8 (Martin 2011) with the following options: quality cut-off = 20, minimum overlap = 7 and minimum length = 35. Reads with a mean quality lower than 30 were then discarded using a Perl script[7]. Reads were mapped onto the *Canarium album* reference plastid genome (MN106250) using BWA-mem (Li and Durbin 2009).

SNP calling was performed using Samtools mpileup with options -B and -D (Li *et al.* 2009) as previously described (Scarcelli *et al.* 2016). The VCF file of SNPs was filtered using Varscan 2.3.7 (Koboldt *et al.* 2012) according to the following criteria : remove low quality (<30), remove indels and monomorphs, min var freq 0.15, min freq for hom 0.5 and min coverage of 3. The final set of SNPs in a vcf file was converted into a concatenated sequence alignment of variable positions in fasta format using a custom perl script. Invariant positions were removed, and a concatenated sequence alignment of variable positions was produced.

Genetic diversity analyses

Microsatellites

Only the most readable loci, without duplicate peaks or blurry signals, were kept for diversity analyses, which represented 10 out of the 13 amplified SSR (DaE-16, DaE-20, DaE-23, DaE-27, DaE-29, DaE-36, DaE-41, DaE-42, DaE-46, DaE-49). For the different loci and populations, the observed and expected heterozygosity (H_O and H_E respectively), the inbreeding coefficient (F_{IS}), the effective number of alleles (Ne), the rarefied allelic richness (AR) were estimated using SPAGeDi (Hardy and Vekemans 2002). We also estimated null allele frequency (r) for each locus as well as an estimate of inbreeding coefficient that control for the presence of null alleles (*Fnull*) using INEST 2.2 (Chybicki and Burczyk 2009). The level of population differentiation (as estimated by the F_{ST} fixation index) and the test of genetic structure (permutation of individuals among all populations) were obtained with SPAGeDi.

The presence of intra-specific genetic clusters was tested using the Bayesian assignment approach implemented in the program STRUCTURE 2.3.4 (Pritchard *et al.* 2000). Individuals

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[7] https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_2_Filter_Fastq_On_Mean_Quality.pl

were clustered without using the a priori knowledge of source populations and postulating Hardy-Weinberg and linkage equilibrium among loci. Analyses were done using the admixture model, correlated allele frequencies among populations, and both with and without prior spatial information on the origin of samples. We tested for a number of genetic clusters (K) between K = 1 and K= 10, with 40.000 burn-in, 60.000 iterations, and ten different runs for each K. The most likely number of clusters in the final matrix was identified using the ad hoc ΔK (Evanno *et al.* 2005), as implemented in Structure Harvester (Earl and vonHoldt 2012). The CLUMPP program has been used to permute the 10 runs so that the clusters align across runs (Jakobsson and Rosenberg 2007). An individual was considered as belonging to a given cluster at an assignment probability threshold of 0.80. We visualized the resulting barplot and mapped the proportion of individuals belonging to each of the identified clusters for countries or country regions.

In order to further test for a signal of genetic structure within Cameroon and Gabon (regions of dense sampling), we also led a STRUCTURE analysis on Cameroonian and Gabonese populations only using the same parameters as previous analysis. This analysis covers a sampling corresponding roughly to the one used in Todou *et al.* (2013a).

The TESS3 algorithm, implementing least-squares estimates of ancestry coefficients with a constraint imposed by samples' spatial coordinates, was used on R (package tess3r) as a second approach to further explore the pattern of genetic structure between populations (Caye *et al.* 2016). We set parameters as following; the method used an alternating projected least squares algorithm, a maximum number of iterations of 100.000 and a tolerance of 10^{-10}. The patterns of nuclear genetic diversity of *D. edulis* based on STRUCTURE clusters was finally shown with a principal coordinate analysis (PCoA) using Lynch distance (Lynch 1990), executed with R package POLYSAT (Clark and Jasieniuk 2011).

Chloroplast DNA

Using the chloroplast SNPs of sampled individuals presenting less than 5% of missing data, an haplotype network was built in POPART 1.7 (Leigh and Bryant 2015) using the median-joining network algorithm (Bandelt *et al.* 1999). Due to the important number of haplotypes, related haplotypes were grouped together in 'haplogroups', based on the network topology and the number of mutational steps separating two haplotypes (six substitution steps at least). The geographical distribution of these groups was mapped using QGIS 3.6.1 (QGIS Development Team 2019).

Genetic differentiation between populations can also be informed through haplotypes by comparing G_{ST}, a measure based only on haplotype frequencies, and N_{ST}, which also considers similarities between haplotypes, based on mutation steps between them. When N_{ST} is superior to G_{ST}, it indicates that the contribution of mutations to genetic differentiation is not negligible, and thus a phylogeographic pattern (individuals from haplotypes that are related in the phylogeny are found closer to one another) can be inferred (Pons and Petit 1996). We tested it in the whole sample using the program PERMUT with 10,000 permutations, removing the populations of less than three individuals (Benin, Nigeria and São Tomé), and then replicated it on haplogroups counting enough samples from different populations (haplogroups 1 and 7, see results section).

Results

Genetic diversity and structure revealed with nuclear SSRs

The diversity indices estimated showed an overall high allelic richness, peaking for southern Gabon, and at its minimum in Nigerian and DRC populations, with significant differences between regions or countries as verified with an analysis of variance controlling for the loci effect.

Three clusters were identified as the most likely structure (Figure 2), based on STRUCTURE clustering of nuclear SSRs and the ad hoc ΔK approach (Figure S1). For an attribution threshold of 0.8, the majority of samples (69% of samples) were attributed to these three clusters, outlining a geographic pattern with the DRC and Nigerian populations pertaining to two different clusters (Cluster 1 and Cluster 2, respectively in red and green on Figure 2), and the populations in Cameroon and northern Gabon attributed to Cluster 3. The first split (K=2) separated the Nigerian populations from all other populations.

The STRUCTURE analysis done on Cameroonian and Gabonese populations demonstrated that the populations were largely admixed, but that a sub-structure could be detected with three regions appearing as more original: (i) southern and central Gabon (pops 5 and 6; Table 2); (ii) the Centre-Littoral population of Cameroon (pop 10); (iii) West Cameroon (pop 13) (see Figure S2). Three clusters were identified by the TESS3 algorithm with a threshold set at 0.7, with samples distributed similarly as those of the STRUCTURE analysis but in a more restricted area for Cluster 1 and Cluster 3 (Figure S3). Of the 284 samples attributed over the distribution area for the STRUCTURE analysis, 170 were also attributed in the TESS3 analysis. Cluster 2, represented by the northern population of Nigeria, was similar in both analyses. In the STRUCTURE analysis, Cluster 3 was found in populations from Cameroon, Gabon and CAR, whereas it was restricted to Cameroon with TESS3 computation. Cluster 1 was limited to DRC in TESS3 results, while it also included some individuals from CAR in the STRUCTURE clustering.

The differentiation between the samples from the three clusters given by STRUCTURE was tested, and the F_{ST} was of 0.022 between clusters K1 and K3, of 0.039 for K2-K3 and 0.052 for K1-K3.

This range was similar to that of the F_{ST} from pairwise comparisons between populations (Figure 3). Pairwise F_{ST} values were the highest when computed between the population from northern Nigeria and the other populations.

The structure of genetic variation among the three intra-specific genetic clusters was also visualized with a principal coordinate analysis, based on the Lynch distance between samples. A slight differentiation was observed between the three clusters and the admixed group: the first two eigenaxes of the PCoA accounted for 25 % of the total variance (Figure 4), and overlap was especially important between the cluster 3 and the admixed samples.

Genetic structure revealed with chloroplast SNPs

From the initial 2,302,058 shotgun reads, 109,267 reads were mapped on *Canarium album* cpDNA (Wang *et al.* 2019). The mean proportion of mapped reads was of 2.6% and the mean read depth of 93.6 ± 31×. The alignment of the different individuals led to 1508 SNPs. Excluding outgroup taxa and congeneric species, the number of SNPs detected over all *D. edulis* samples was of 133. Monomorphic and missing sites were removed, as well as individuals with more than 5% missing data. For the final dataset of 112 samples (100 *D. edulis* samples, 9 congeneric samples and three outgroup samples from the Burseraceae family), 697 variable sites were used to build the median-joining haplotype network (Figure 5). This network allowed to see the connections between the 40 distinct chloroplast haplotypes identified in the sample area. They were colored according to seven loosely defined (see Methods) haplogroups (Figure 6).

The haplotypes contained in the six first haplogroups present a relatively restricted distribution in comparison with haplotypes from the haplogroup 7 that was found all over the region: haplogroup 1 (H1.0 to H1.9) was restricted to Gabon, the South of Republic of Congo and the South West of DRC, haplogroup 2 (H2.1 to 2.3) to Gabon, the Republic of Congo and CAR, haplogroup 4 (H4.1 to 4.4) to southern Cameroon and Gabon, haplogroup 5 (H.1 to H.2) to Cameroon and haplogroup 6 (6.1 to 6.3) to DRC and São Tomé. The most common group of haplotypes (H7.0 to H7.9) grouped samples all over *D. edulis* distribution area, from southern Nigeria to DRC. Samples from *Dacryodes* spp. were represented in five of the seven haplogroup, and absent only in haplogroups 2 and 6, which counted few samples. They were either in separate haplotypes (1.8, 3.1, 3.2, 3.3, 5.3) or together with *D. edulis* samples (4.1, 7.2).

G_{ST} and N_{ST} for the whole dataset were not significantly different (respectively 0.067 and 0.032, $p > 0.05$), indicating the absence of phylogeographic structure. For the haplogroups 1 and 7, which comprised enough samples to be tested separately, G_{ST} and N_{ST} were respectively 0.444 and 0.083 (G_{ST} values) and of 0.228 and 0.075 (N_{ST} values), without significant differences between G_{ST} and N_{ST}.

Discussion

Phylogeographic patterns of *D. edulis* in Central Africa

By characterizing the pattern of genetic diversity distribution of **cultivated populations** of the African plum tree (*Dacryodes edulis*), we aimed at deciphering the relative influence of past climate change and cultivation history on its biogeographic history. Genetic discontinuities were demonstrated both with nuclear (SSR) and chloroplast (SNP) molecular markers.

Bayesian clustering methods applied on our whole SSR dataset support the existence of three main genetically distinct groups of cultivated populations of African plum trees: one grouping populations from Nigeria (populations 15 and 16), one corresponding to the population from central DRC (population 3), and the last one grouping populations from Cameroon and central northern Gabon. Contrarily to the previous work of Todou *et al.* (2013a), which indicated a genetic discontinuity between Cameroonian populations and Gabonese populations, the populations from Cameroon and Gabon were not separated in our analyses on the whole dataset. However, our results might not be fully comparable as no samples from the northern half of Gabon were included in Todou *et al.* (2013a) analyses and different SSR loci have been used. If we run our Bayesian clustering analyses only on populations from Cameroon and Gabon our results become more comparable, illustrating the influence of sampling coverage on Bayesian-clustering analyses and the need to interpret results with cautions.

The pattern revealed by the cpDNA analysis is quite complex, with no clear phylogeographic pattern when considering the whole dataset. The North-South divide generally found on each part of the climatic inversion (Hardy *et al.* 2013) is somewhat also present in *Dacryodes edulis*, with some genetic structure apparent at the nuclear level and some specific cpDNA haplogroups present on each part of the inversion (1, 3 and 6 groups in the South; 5 in the North). This North-South genetic differentiation probably corresponds to a genomic signature resulting from Quaternary climate oscillations, with one group of glacial refugia located North of the meteorological inversion and another group located South of it. Given that the cultivation of the species is most probably much more recent than the Pleistocene era, such a genomic signature might mirror the past demographic history of wild populations of the species. We would need to analyse the distribution of cpDNA species in wild *D. edulis* specimens to further interpret this pattern. Intriguingly, whereas six out of seven haplogroups present a certain level of endemism in the region, one is widely distributed across the distribution of the species. There was no strong congruence between the attributions of samples based on SSR and chloroplast SNP, but some patterns can be visible.

To our knowledge, the comparison of these results with those of other cultivated tree species in the region is difficult owing to the scarcity of such studies. Interestingly, and despite the cultivated status of the species, which implies a strong influence of human-mediated gene flow on patterns of genetic diversity distribution (Rimlinger *et al.* 2021), genetic discontinuities observed on *D. edulis* present some similarities with non-cultivated tree species. A genetic isolation of Nigerian samples compared to populations from Cameroon and Gabon was also reported for the useful tree species *Irvingia gabonensis*, as assessed by Ude *et al.* (2006) with amplified fragment length polymorphism. On the other hand, genetic characterization of pan-African samples of *Elaies guineensis* by Bakoumé *et al.* (2015) rather showed that accessions from Cameroon and Nigeria were scattered within the group of West-Central-East Africa.

Cultivation of *D. edulis*: previous insights and prospects

In this study, the patterns of genetic diversity and structure of cultivated *D. edulis* populations were analyzed at the scale of Central Africa. The populations from Gabon, especially in the southern part of the country, exhibited the highest genetic diversity as well as the highest number of private alleles, whereas it was the lowest in the population of central

Nigeria. The high genetic diversity corresponds to the area of ecological optimum of the species, i.e. its niche determined from wild specimens, which was located in the forests of Gabon and Equatorial Guinea (Todou *et al.*, 2013b). Overall, the global estimates of genetic diversity for *D. edulis* were rather high. The expected heterozygosity (0.84) was more similar to that of another widely cultivated species in West Africa, *Parkia biglobosa* (Lompo *et al.* 2018) than to that of timber tree species from Central Africa, which ranged for instance from 0.467 to 0.613 for *Milicia excelsa* (Daïnou *et al.* 2010) and from 0.53 to 0.64 for *Scorodophloeus zenkeri* (Piñeiro *et al.* 2017)**.**

Although it is not possible to localize the origin of domestication of the species from the data we have at hand, we can discuss that the low genetic diversity found within the two Nigerian populations does not support the hypothesis stating that the species' natural range is restricted to the southern part of Nigeria (Vivien and Faure 1985; Keay 1989). On the other hand, the populations in Gabon presented values of allelic richness higher than other countries (Nigeria, CAR) as well as high haplotype diversity within and among populations. We note however, that tracking back the cultivation origin of the species in one specific region relying on estimates of genetic diversity is risky. Indeed, human management practices might have differentially affected levels of genetic diversity from one place to the other, with potentially higher reduction of genetic diversity where selection practices are the strongest, places that can actually correspond to the cultivation origin of the species. Moreover, inter-specific gene flow can influence levels of genetic diversity. The sharing of cpDNA haplotypes between different *Dacryodes* species might indicate pervasive gene flow in this genus, with potential effects on levels of genetic diversity of populations. Gabon has been mentioned as the center of origin of the genus *Dacryodes* based on patterns of species endemism.

The domestication process involves a continuum of phenotypic and genetic changes prompted by selection of traits valued by humans. Between wild and domesticated populations, intermediate steps can thus be observed and defined, such as incipiently domesticated or semi-domesticated populations (Clement 1999). For African plum trees, we do not know yet for how many generations they have been cultivated. Apart from the evidence of a long history of human use inferred from historical linguistic, as addressed in the introduction, the presence of the African plum was attested by the first European who travelled to Central Africa and mentioned the species. It appeared surely with the name "zaffo" in one of the first descriptions of the flora of Congo (Cavazzi 1690) and probably earlier as "masseffes" in a manuscript from the Dutch merchant Peter van der Broecke depicting the kingdom of Loango (now largely in southwestern Congo) he visited in 1611 (La Fleur 2000).

Here, we considered the genetic diversity and structure of cultivated populations. But assessing the degree of domestication requires to compare genetic and phenotypic differentiation between the domestic taxon and its wild progenitor, to see to what extent its area of cultivation stretches outside of the natural range of the species and, if existing, to combine this information to the record of cultivation history (Levis *et al.* 2017). For *D. edulis*, there is thus an especially strong need to compare wild trees in forested areas to cultivated trees, both looking at their morphological and genetic diversity.

Frequent interspecific gene flow between *Dacryodes* spp.?

In the haplotype network, the majority of *Dacryodes* spp. either clustered together in haplotypes with *D. edulis* samples or were in separate haplotypes but with a low number of mutation steps, suggesting the pervasiveness of gene flow between congeneric species. Trees are indeed long-lived plants with overlapping generations and a high reproductive output. Outcrossing is their most common mating system and gene flow in random-mating populations is often high, allowing for slow rates of speciation (Petit and Hampe 2006). This generally favors a high level of genetic diversity and a weak differentiation between populations. The preferentially allogamous mating system of African plum trees and their insect-mediated pollination (Fohouo *et al.* 2001), which fosters outcrossing and hybridization (Goodwillie, Kalisz, and Eckert 2005), facilitate extensive gene flow.

Conclusion

This first study on the large-scale distribution of the genetic diversity of *Dacryodes edulis* sheds light on the genetic relationships among populations of its distribution area. Biogeographic patterns observed here using both nuclear and chloroplast molecular markers, present some commonalities with patterns already observed on tree species investigated in the region. This is notably the case for the historical genetic barrier between Nigerian and Cameroonian populations of the species, and for the historical genetic barrier on each part of the meteorological inversion. This suggests that cultivated populations of *Dacryodes edulis* still contain the mark of the influence of past climate changes in their genome despite extensive human-driven seed-mediated gene flow among populations. The data presented here did not allow to point out to one origin of this cultivated Central African fruit trees species, suggesting a complex history, with possibly important anthropogenic dispersal. The study of wild *D. edulis* populations might bring a new light to the evolutionary history of the species.

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*Chapter cover image: **Thonner F**. **1898**.* Im Afrikanischen Urwald. *Berlin.*

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Figures

Figure 1. Samples of *D. edulis* from its distribution area in DRC (N = 39), Republic of the Congo (N = 27), Central African Republic (N = 22), Gabon (N = 77), Cameroon (N =184), Nigeria (N = 63), Benin (N = 1) and São Tomé (N = 1).

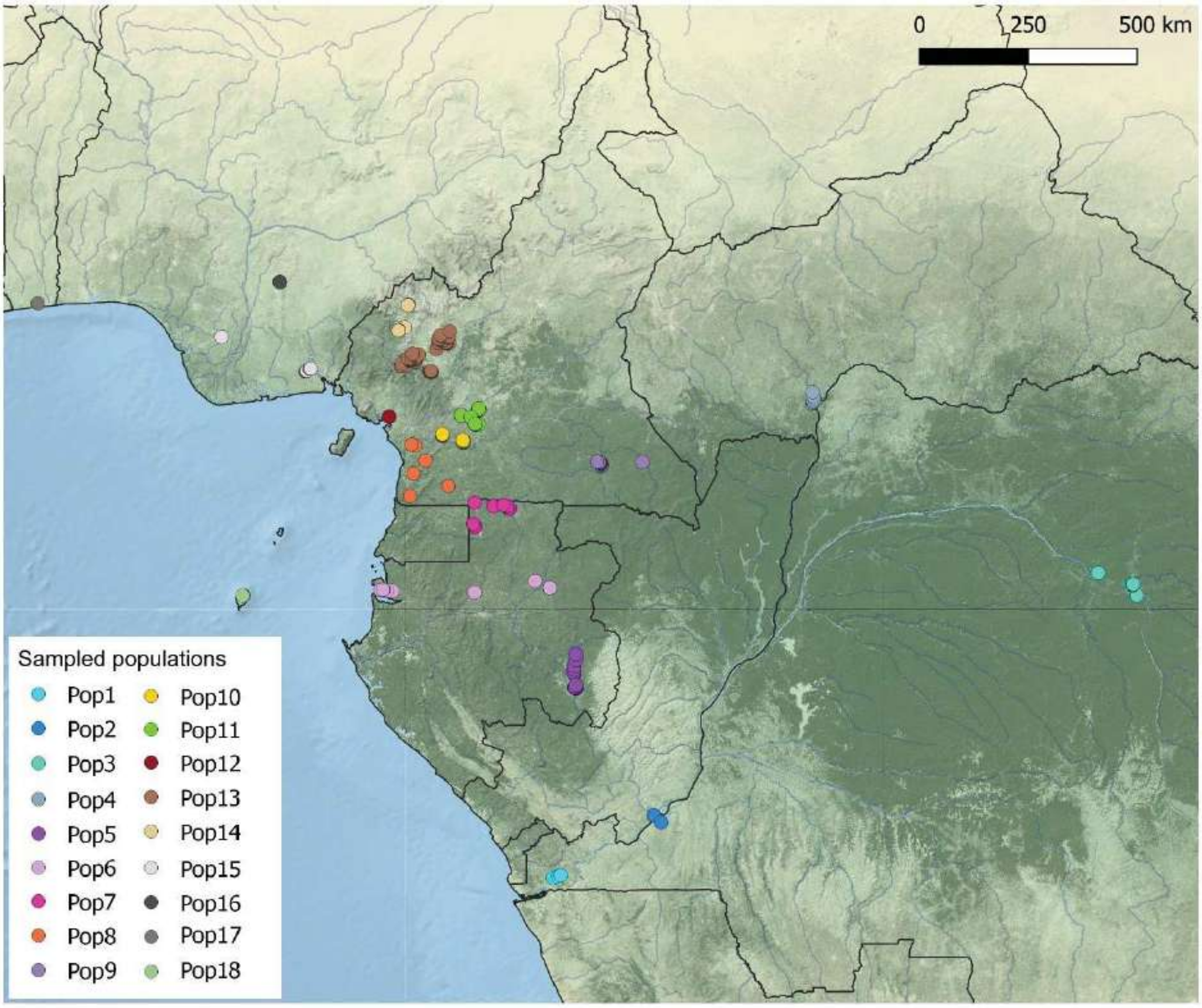


Figure 2. a. Distribution of intra-specific genetic clusters as outlined by the Bayesian clustering analysis inferred in STRUCTURE program, for K = 3 and p > 0.8. **b.** Assignment proportions for each individual to the K = 3 groups are shown on the y-axis. Samples are ordered by populations (indicated above the barplot, with corresponding countries below; details in Table 2).

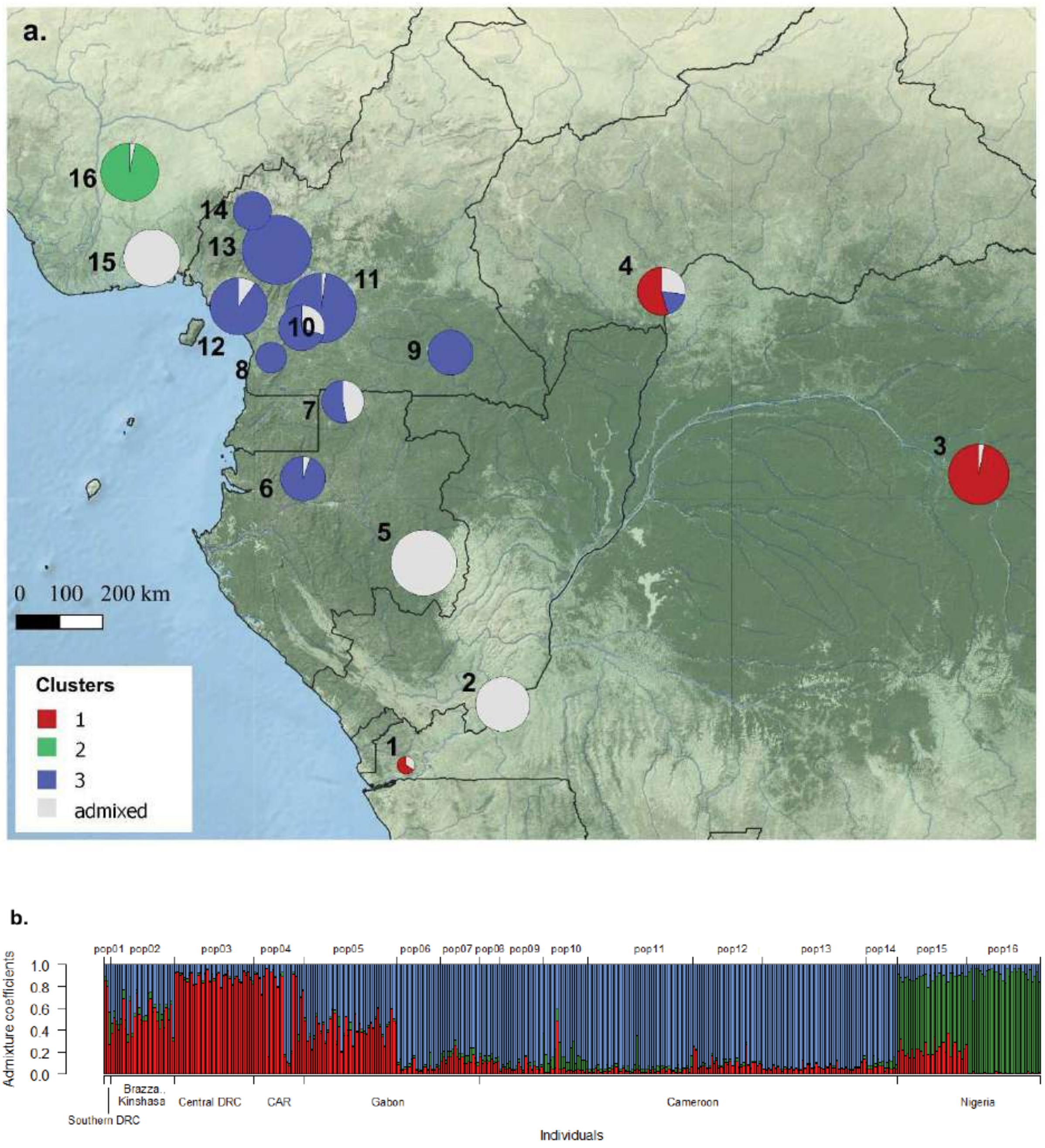


Figure 3. Heatmap based on the F_{ST} between pairs of populations. F_{ST} ranged between -0.0214 (square signalled with *) and 0.0568 (square signalled with **).

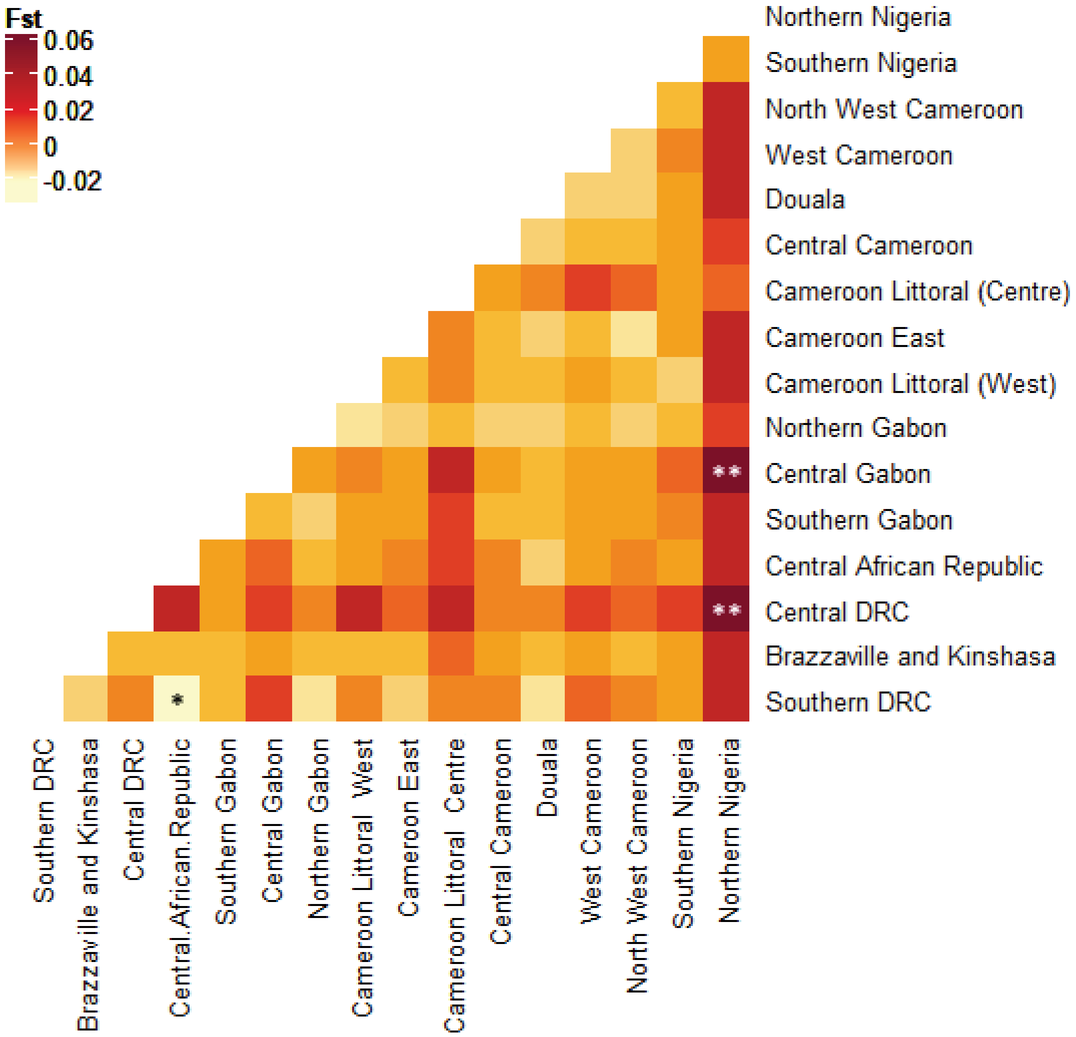


Figure 4. Principal coordinate analysis of genotypes. Individuals are labelled according to the clusters detected by STRUCTURE at K=3.

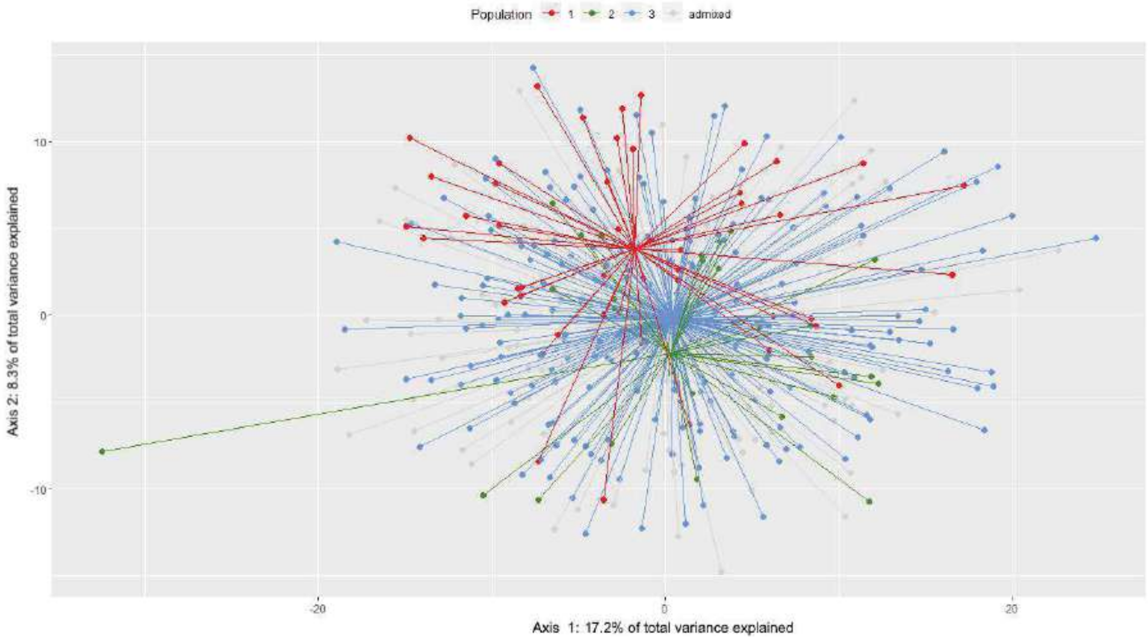


Figure 5. Chloroplast haplotype median joining network of cultivated *Dacryodes edulis* from Central and West Africa based on 697 chloroplast SNPs. Circles represent chloroplast haplotypes colored according to their country of origin (except for green haplotypes that correspond to other species). Circle sizes are proportional to the number of individuals sharing the haplotype. Lines linking haplotypes show how many mutational steps occurred between haplotypes; extinct or unsampled haplotypes are shown with dark circles; the number of mutational steps for pathways connecting *D. edulis* to the reference and the Burseraceae samples are indicated in brackets. Other *Dacryodes* species are noted down below by their corresponding dots as *Db*, *Di*, *Do* and *Dp* standing respectively for *D. buettneri*, *D. igaganga*, *D. osika* and *D. pubescens*.

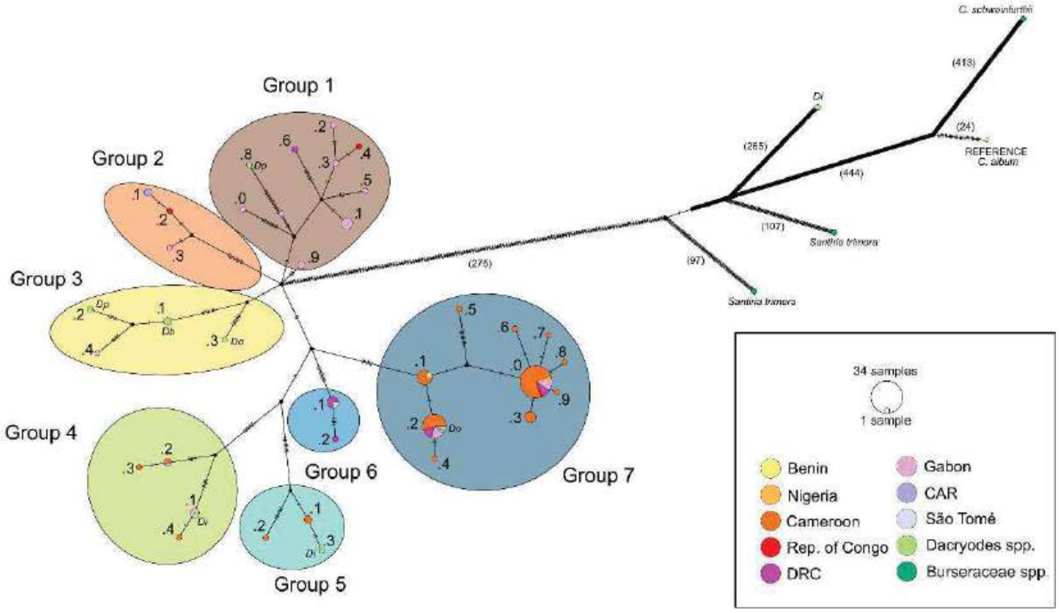
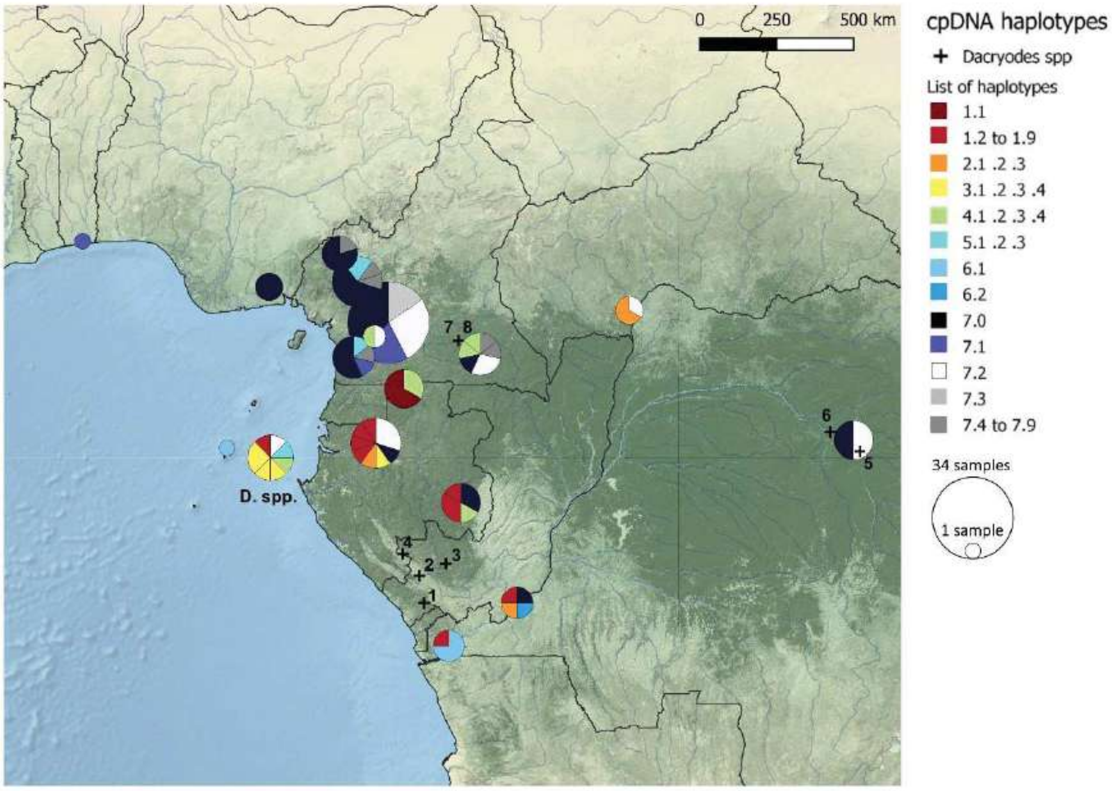


Figure 6. Distribution of *Dacryodes edulis* cpDNA haplotypes across species distribution area. Relatively frequent haplotypes (>0.03) are represented by their own colours; other haplotypes (frequency < 0.03) are represented by a colour corresponding to their haplogroup. Crosses indicate the location of other *Dacryodes spp*. 1: *D. pubescens* (haplotype 1.85); 2&3: *D. buettneri* (3.1); 4: *D. pubescens* (3.2); 5&6: *D. osika* (3.3 and 7.2 respectively); 7&8: *D. igaganga* (5.3 and 4.1 respectively). See Figure S4 for the distribution of the haplogroups.



Tables

Table 1. Number of samples per population. Individuals were arbitrarily grouped in 18 populations according to their geographical coordinates. [A] Number of samples genotyped for nuclear microsatellites. [B] Number of samples sequenced for cpDNA.

Population	Region	N. SSR[A]	N. cpDNA[B]
1	Southern DRC	3	4
2	Brazzaville and Kinshasa	28	4
3	Central DRC	35	8
4	Central African Republic	22	3
5	Southern Gabon	41	7
6	Central Gabon	19	9
7	Northern Gabon	17	6
8	Cameroon Littoral (West)	9	6
9	Cameroon East	19	8
10	Cameroon Littoral (Centre)	20	2
11	Central Cameroon	46	26
12	Douala	31	0
13	West Cameroon	45	10
14	North West Cameroon	14	5
15	Southern Nigeria	31	2
16	Northern Nigeria	32	0
17	Benin	0	1
18	Sao Tomé	0	1
	Total	412	102

Table 2. Genetic diversity indices of the sampled populations of *D. edulis* in 16 populations

Pop	Region	Nb. of samples	Ne	AR	H_E	H_O	F_{IS}	Private alleles
1	Southern DRC	3	4.24	-	0.777	0.583	0.300	0
2	Brazzaville and Kinshasa	28	7.17	5.84	0.834	0.710	0.151	2
3	Central DRC	35	6.02	5.31	0.792	0.633	0.204	3
4	Central African Republic	22	6.04	5.33	0.822	0.632	0.236	2
5	Southern Gabon	41	8.82	6.07	0.845	0.691	0.185	13
6	Central Gabon	19	8.18	5.91	0.835	0.659	0.215	1
7	Northern Gabon	17	7.65	5.89	0.851	0.648	0.244	0
8	Cameroon Littoral (West)	9	6.99	5.45	0.832	0.711	0.154	0
9	Cameroon East	19	7.90	5.71	0.820	0.719	0.126	1
10	Cameroon Littoral (Centre)	20	6.54	5.49	0.791	0.645	0.189	2
11	Central Cameroon	46	7.55	5.89	0.841	0.695	0.175	2
12	Douala	31	7.45	5.84	0.843	0.676	0.202	1
13	West Cameroon	45	7.65	5.79	0.838	0.725	0.136	8
14	North West Cameroon	14	6.58	5.43	0.820	0.621	0.250	0
15	Southern Nigeria	31	6.52	5.40	0.821	0.539	0.348	3
16	Northern Nigeria	32	5.92	5.29	0.797	0.587	0.267	1
All populations		412	8.17	5.98	0.844	0.662	0.216	39

Ne: effective number of alleles, AR: rarefied allelic richness for k=10; H_E: expected heterozygosity; H_O: observed heterozygosity; F_{IS}: inbreeding coefficient.

Supplementary data

Figure S1. Ln likelihood distribution (above) and ΔK output (below) from Structure Harvester showing the rate of change in the log probability of data between successive K values (from 1 to 10). K = 3 was retained as, with K = 7, it maximized ΔK while minimizing the variance of Ln likelihood. Barplot for K = 7 presented below: its substructure is presented in the article when comparing Cameroon and Gabon only.

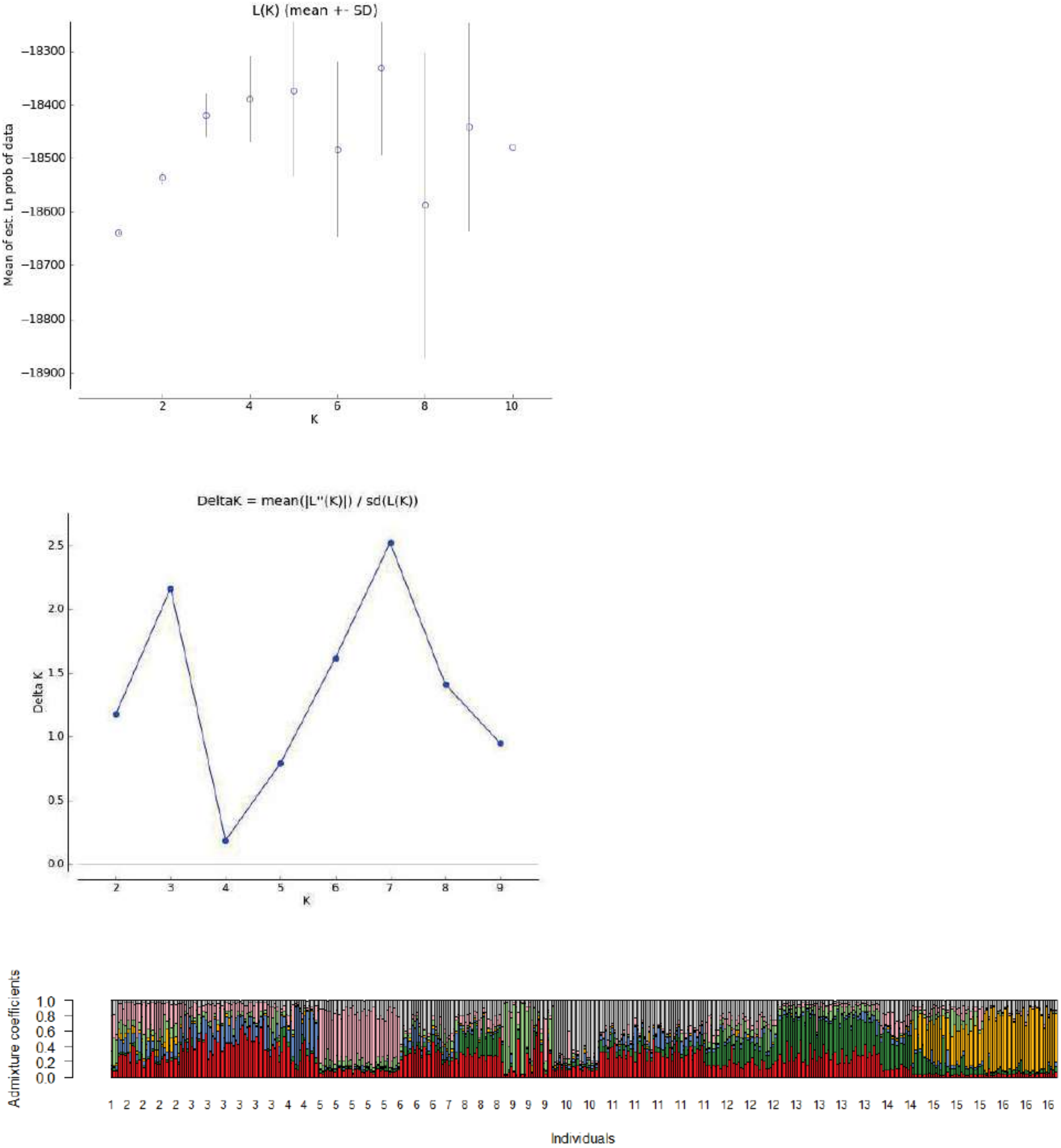


Figure S2. Distribution of intra-specific genetic clusters in Cameroon and Gabon as outlined by the Bayesian clustering analysis inferred in STRUCTURE program, for K = 2 and 3. Populations 5 to 7 are Gabonese, populations 8 to 14 are Cameroonian.

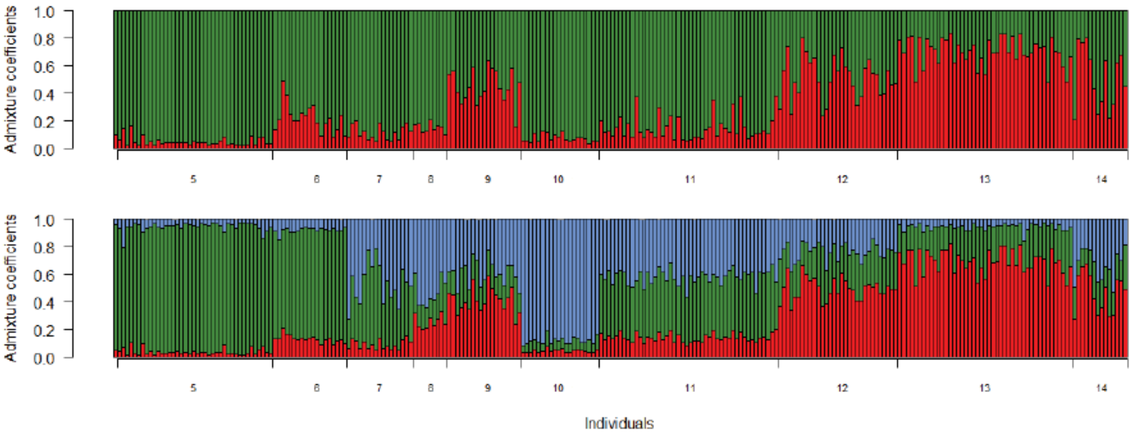


Figure S3. a. Phylogeographic patterns of 412 samples over *D. edulis* distribution area using TESS3, for K =3 and p > 0.8. b. Assignment proportions for each individual to the K = 3 groups are shown on the y-axis. Samples are ordered by populations.

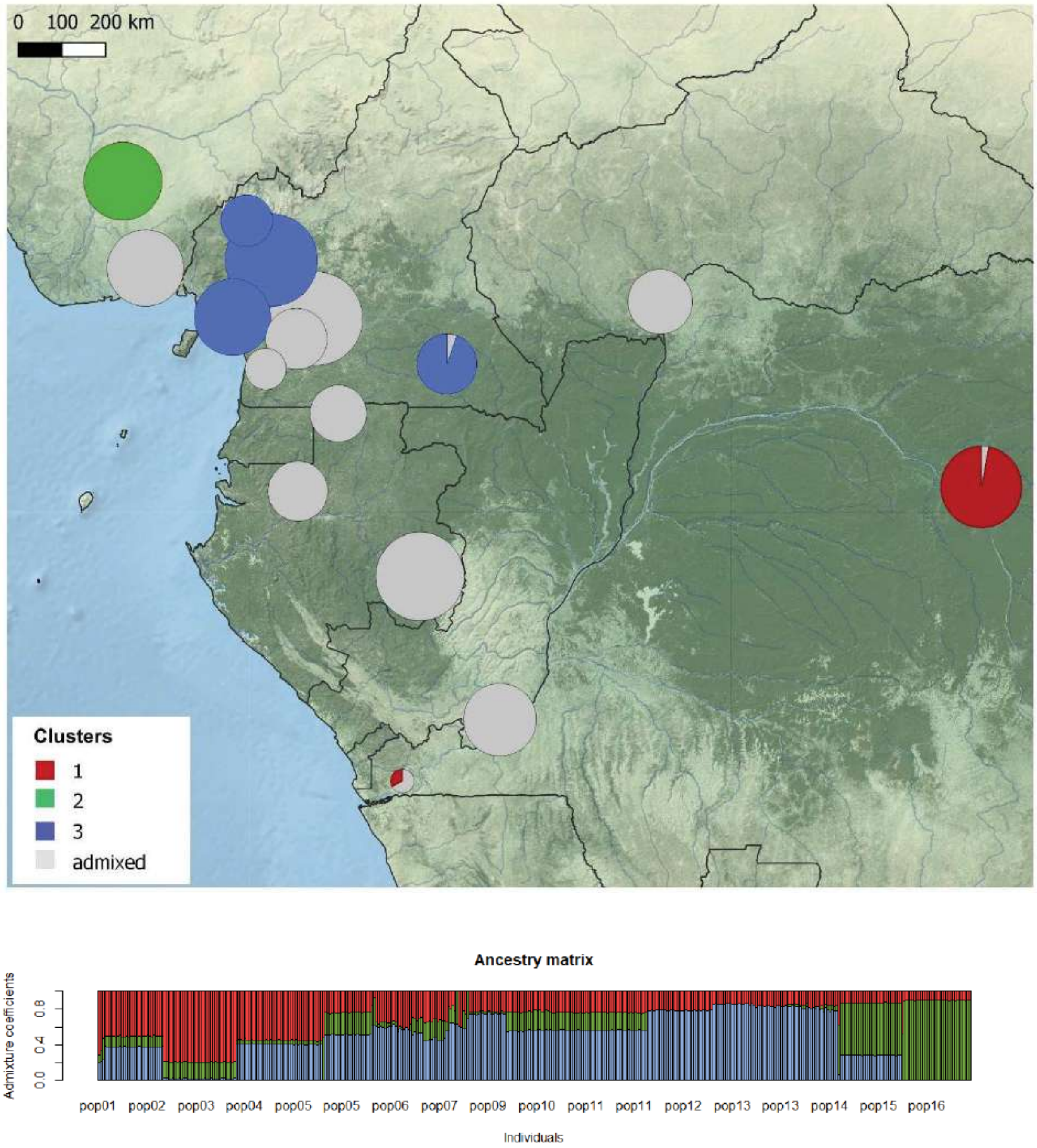
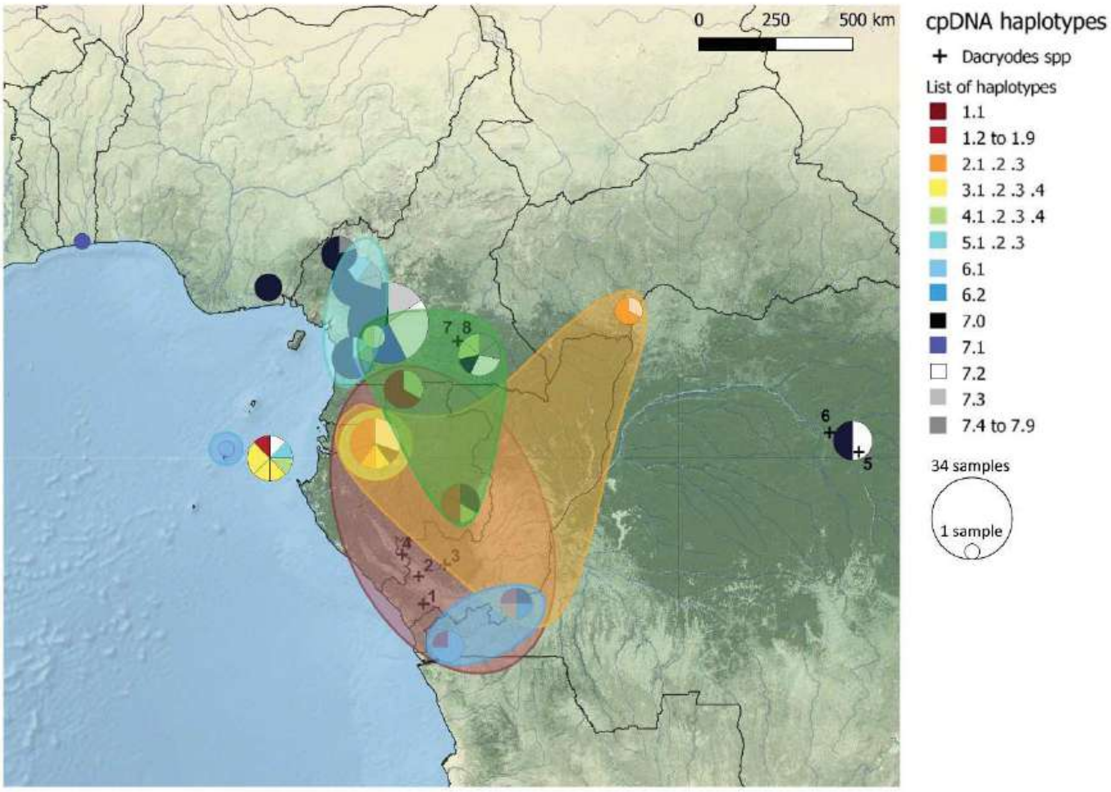


Figure S4. *Dacryodes edulis* cpDNA haplotypes and distribution of regional haplogroups 1 to 6 indicated with shapes. As haplogroup 7 was spread out in the whole distribution area, it was not represented.



Chapitre 2

Stratégies paysannes, leur influence sur les pratiques, les savoirs et la diversité du safoutier dans l'Ouest Cameroun

The Influence of Farmers' Strategies on Local Practices, Knowledge, and Varietal Diversity of the Safou Tree (*Dacryodes edulis*) in Western Cameroon

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Abstract

Highly valued for its edible fruits, the safou tree, *Dacryodes edulis*, is a major component of farming systems in Central Africa. In Cameroon, the species has drawn much attention since the 1990s because of its market potential. Among other fruit tree species, safou trees are integrated within cocoa-coffee agroforests as a means of diversification. In Western Cameroon, farmers' strategies for safou production and commercialization are influenced by a gradient of the species' market integration. Based on semi-structured interviews with farmers and inventories of trees on their farms, this ethnoecological study addresses the relationship between the market integration of production areas, farmers' agricultural practices, and the distribution of local varieties. Interviews revealed that farmers in high-cultivation areas use more diversified planting techniques, but select and use similar planting material. At the local scale, we found a wide range of varieties, defined according to a combination of selected fruit traits. Varieties appearing at multiple sites were also the ones with the most desirable sets of characteristics. The agricultural strategies depicted help us to understand the specificities of the ongoing market integration of indigenous species in the tropics.

Key words: Indigenous tree species, local management strategies, *Dacryodes edulis*, safou, intraspecific diversity, Cameroon, ethnobotany.

Introduction

Timber and non-timber forest products (NTFP) contribute to the livelihoods of most Africans (Timko *et al.* 2010). NTFP are biological products, other than timber, derived from forests, wooded lands, and trees outside forests (Sorrenti 2017). They include food products (fruits, game, mushroom, etc.), fibers, and resins, among others, and can offer medicinal, cosmetic, social, or spiritual value (Mbuvi and Boon 2009). Gathered from the wild, from forest plantations, agroforestry schemes, or from trees outside of forests, they can contribute to people's livelihoods directly or indirectly, through sale in markets. Today, overharvesting or habitat degradation compromise the sustainability of African NTFP species exploitation (Sunderland and Ndoye 2004). This issue is exacerbated by the growing demographic pressure in Central Africa, with the population of sub-Saharan Africa predicted to double by 2050 (Cleland 2013). Ensuring consistent NTFP supply thus requires developing effective resource-use strategies, and can be achieved through the sustainable management of existing NTFP and introduced in local farming systems.

In Cameroon, the wider cultivation of high-value indigenous trees and vegetables (*Prunus africana* [Hook.f.] Kalkman, *Dacryodes edulis* [G. Don] H.J. Lam, *Irvingia gabonensis* [Aubry. Lec. ex O. Rorke] Baill., *Gnetum* spp., *Ricinodendron heudelotii* [Baill.] Pierre ex Heckel]) is regarded as a current attempt at fruit tree domestication (Goldschmidt 2013). This can contribute to local diversified farming systems, relying on crop diversity and complementarity. In the tropics, diversification of cultivated crop species helps yield stabilization and risk reduction by coping with disturbance and change (Altieri *et al.* 2012). Such cultivation practices are used by Cameroon's small-scale farmers, who represent about 90% of the farming community (Molua 2005), and who can partly be sustained by the emergence of NTFP markets and development of corresponding value chains (for bush mango, *Irvingia gabonensis*; or *Gnetum* spp.) (Ingram 2014). When indigenous species become crop commodities, they can be associated with more intensified cultivation systems. In some cases, these systems result in the conversion of natural forests or complex agroforests to monocultural plantations and therefore lead to knowledge loss, resource homogenization, and deforestation. These outcomes are similar to the current state of oil palm cultivation (Mesmin *et al.* 2016) but have not yet occurred in the wider set of indigenous fruit and nut species currently being domesticated. On the other hand, they are frequently integrated into complex tree-based farming systems. They thus benefit the diversity by adding new species in the multifunctional farming system, and benefit the farmer by generating income opportunities (Jamnadass *et al.* 2011; Leakey 2014).

The present study focuses on one key NTFP species, the safou tree, also called bush butter tree or African plum (*Dacryodes edulis*, Burseraceae). Among other indigenous or introduced fruit trees, the safou tree is one with the highest demand in the Congo Basin region. In Cameroon, there are several production areas with different pedoclimatic conditions, cropping systems, and market organizations, making it appropriate for a case study. Originally, safou tree distribution is thought to have been restricted to forest areas, but it is now found throughout the whole forested part of Cameroon, especially in farm land; this extensive range is a consequence of its cultivation for human use (Kengue 1990). Its fruits are especially important in the traditional local diet: their mesocarp, boiled or roasted, is served along with staple foods such as cassava, maize, or plantain. Safou also has numerous benefits in traditional medicine and other associated uses (Ajibesin 2011). Being a multipurpose species, it is abundant in home gardens, agroforestry systems, and as single isolated trees in villages or in fields (Schreckenberg *et al.* 2006). It is the most commonly associated fruit tree in complex multi-storied cocoa agroforestry systems (Jagoret *et al.* 2009; Sonwa *et al.* 2002), where it provides shade in addition to fruits.

Farmers have adopted the species for a long time, keeping existing trees and protecting juveniles in fields and/or home gardens. The cultivation of safou typically involves the elimination of poor quality or poor yielding trees and/or the sowing of seeds from trees with desirable attributes (Leakey *et al.* 2009). Today its importance in Cameroonian trade—annually generating around a million US dollars (Ingram and Schure 2010)—has led some authors (Perez *et al.* 2002) to classify it as a cash crop species rather than a subsistence species. Its cultivation is also motivated by the trend towards the development of “fruit agroforests”, i.e. the diversification of cocoa and coffee farms with fruit trees (Aulong *et al.* 2000). Both elements prompt an expansion of its cultivation and production, especially to meet growing urban centers’ demand for fruit. Such intensification dynamics, prompted by market demand, are still poorly described in studies of West and Central Cameroon (for horticultural production, see Temple *et al.* 2008). Generally, intensification is defined as the combination of an increased number of trees per unit of land area, a higher interest in commercialization, and an increased use of inputs (Rice 2008). These inputs include agrochemical inputs (fertilizers, pesticides) but also farmers’ knowledge and use of improved planting materials (Gockowski *et al.* 2011), even though these are still difficult to access (Takoutsing *et al.* 2012). The effect of intensification on cultivation practices, species knowledge, and intraspecific diversity remains undescribed, although this may be of crucial importance to support of farm conservation and sustainable production strategies.

In this study, we investigated the effect of contrasting agricultural systems, which differ in the ways that safou trees are perceived and grown, along a gradient of market integration in Cameroon's Western Highlands. The objectives and research hypotheses were the following. First we wanted to address whether this gradient was positively related to the intensification of safou tree cultivation, with a more intensively managed system characterized by high-density planting (Rice 2008). Then we aimed to assess whether gender and age affect farmers' ethnobotanical and agronomic knowledge of safou tree ecology and local varietal diversity. This is particularly important because current cultivation practices rely on this knowledge. We posit that older men have accumulated more knowledge about cash crop species (Ayantunde *et al.* 2008; Sunderland *et al.* 2014). As intensification does not automatically decrease varietal diversity in traditional systems (Zawedde *et al.* 2014), our last aim was to provide a preliminary analysis of how local economic and agronomic factors affect safou intraspecific diversity and cultivation practices between sites. All these hypotheses are drawn from the research questions we tested: (1) How are intensification strategies affected by the social status (gender, age) of safou farmers? (2) What was their effect on cultivation practices, associated uses, and knowledge of safou trees? and (3) What comprises farmers' knowledge of safou intraspecific diversity?

Materials and Methods

Model species

The safou tree (*Dacryodes edulis*) is a medium-height, understory forest fruit tree species, reaching up to 40 m when found in its natural forest environment. However, it rarely exceeds 20 m when cultivated. It is mostly cultivated as a fruit and shade tree in coffee-cocoa agroforests and in home gardens (Figure 1). The species is defined as gynodioecious because some individuals present both male and hermaphrodite flowers (with fully developed stamens producing pollen), in varying proportion, while others present only female flowers. The fruits are one-seeded drupes, generally ellipsoid to oblong-ovoid, with high lipid, protein, fiber and vitamin content (Mbofung *et al.* 2002). In Cameroon, flowering peaks at the beginning of the rainy season, between January and May (depending on location), with most fruits maturing from June to September. Early or late flowering and fruiting occur for some trees and considerable inter-annual variation is reported (Kengue 1990). The variability of fruit traits is also considerable, especially for size, shape, mesocarp thickness, epicarp and mesocarp color, taste, and texture (Anegbeh *et al.* 2005; Kengue 2002; Waruhiu *et al.* 2004).

Study area

In order to identify farmers' ethnobotanical and agronomic knowledge, we conducted interviews and field inventories in three study sites (Kekem, Koutaba, and Makenene; Table 1) in the Western Highlands of Cameroon (between 9°46'51.6"–11°00'59.7"E and 4°44'45.2"–5°49'57.3"N, Figure 2). This region is among the most important for fruit production in Cameroon, and ranks first for fruit exportation (Temple 2001). Due to high population densities, the original vegetation, a mixture of semi-deciduous and evergreen tropical forest, has almost totally been converted into a mosaic of agroforestry systems (multi-strata tree-based polycultures) and human settlements where indigenous, cultivated, and exotic plant species occur together (Rivière 2000). Much of the area therefore consists of highly human-modified vegetation with a limited range of tree species interspersed with occasional forest reserves and patches of woodland. Cash crop cultivation (cocoa, coffee) and NTFP exploitation and commercialization are the main economic activities.

The three sites have similar population densities with more than 100 people per km^2 (Institut National de la Statistique 2010), and high rates of immigration from different ethnic groups. Numerically, Bamileke people are dominant in Sites 1 and 3, among other less populous ethnic groups (Mbo, Haoussa, Bakaka, Bamenda), whereas there are more Bamoun people in Site 2. Farmers from the three sites rely on the association of annual crop- and tree crop–based diversified farming systems. The tree crop–based farming systems focus on the production of cash crops, notably cocoa and coffee, but integrate exotic (*Persea americana* Mill., *Mangifera indica* L., *Citrus* spp.) and indigenous species (*D. edulis, Cola acuminata* [P.Beauv.] Schott & Endl., *Canarium schweinfurthii* Engl.). This system of multi-storied tree crop gardens also ensures farmers' subsistence thanks to the addition of other fruit species (banana, pineapple) and root crops (cassava, yam, cocoyam, etc.) interplanted between trees.

The sites were selected for their importance as safou trees cultivation areas. Although all sites produce safou, they can be distinguished by a gradient of integration into Cameroon's market for the species. This gradient comprises two different elements: the road infrastructure and the relative importance of safou trade compared to other crop productions. Site 1 mostly supplies the Littoral region (especially Cameroon's economic and commercial capital Douala), whereas Sites 2 and 3 have good road connections to the Centre region and the capital city of Yaoundé. Crop production from Site 2 is also sent to the Northern Adamaoua region (Garoua, Maroua cities), where the drier climate restricts fruit cropping. The importance of safou trees as a cash crop in the production system of Site 1 is moderate, as it still relies mostly on coffee and cocoa farming, with trade also dominated by maize cultivation. In Site 2, a transition zone from forest to savanna, old coffee stands have been steadily replaced by commercial fruit orchards producing avocado, mango, or safou (Uwizeyimana and Uginet 2003). Finally, Site 3, around Makenene (Centre region, Mbam department), is the main safou production center in Cameroon (Awono *et al.* 2002). Farmers from the West often refer to this as the best zone for the production of high quality fruits. A common name for safou is thus "Makenene's plum." The three study sites are therefore marked by a gradient of interest in safou tree cultivation as a cash crop species. The agronomic factors in each site refer to the production system (field size, associated tree diversity) and the site effect is the combination of economic and agronomic factors.

Informant sampling and data collection

Semi-structured interviews were conducted from January to March 2017 with 131 respondents, all from households owning safou trees. In each site, fieldwork was initiated by a focus group discussion (11–15 people per group), where information was collected about on-farm cultivation practices, and the recognition of different local varieties, classification criteria, and preferences (traits preferred for domestic consumption or market uses). Focus groups were organized with help from Ministry of Agriculture and Rural Development (MINADER) local delegates who were in touch with farmers who had safou trees in their fields. To identify farmers for individual semi-structured interviews, guidance from a local informant was solicited, either a villager selected by the village chief or an agricultural supervisor. The interviews were complemented by snowball sampling. None of the farmers interviewed had been part of participatory domestication programs, although we met with people who were aware of their existence in Makenene (one location where the program was implemented, see Tchoundjeu *et al.* 2006).

Each semi-structured interview recorded the status (gender, age, family and residence status, ethnicity, main activity) and the attributes of the household's fields (field size, number of fruit tree species, and safou trees present in field). Information collected referred to planting/propagation techniques and phytopractices, local uses, and known varieties (examples in Table 2). Special attention was paid to the local farmers' perception of intraspecific variation and to the criteria used to distinguish the different local varieties (i.e., locally-defined types, based on intra-specific differences). When possible, the interviews were conducted with the farmer in the field (agroforest, food crop field, or orchard) or home garden. Field size and fruit tree species associated in the fields were recorded, the latter through a free-listing exercise (Borgatti 1999).

Morphological and ecological characteristics of safou trees (one to ten trees per field) were surveyed during field visits with farmers. Based on the focus group discussions and individual interviews, the sampling was designed to capture varieties' morphological diversity (fruit size, shape, skin, and pulp color) for each individual tree and was guided by farmers' knowledge about trees and fruits. The sampling was based on morphological diversity: farmers were asked to show/describe what they considered their best and worst trees. Depending on field size and on the number of safou trees, one to ten trees were sampled, with a mean of 3.4 trees per farmer. Because it was not the fruiting season, fruit morphology (size and shape) was researched using a template featuring twelve choices (Electronic Supplementary Material 1 [ESM 1]). Four categories were used for size/shape: small (1, 7, and 12), medium (2, 3, and 8), large (5, 10, and 11), and elongated (4, 6, and 9) fruits. Colors were indicated by the farmers. For taste, we recorded whether or not farmers considered fruits to be sour-tasting (safou fruits are sometimes sour like lemon; good fruits are milder in taste). Among the 451 trees sampled, complete data (description of size, taste, skin, and pulp color) were obtained for 248 trees.

Data analysis

The relationship between the different parameters and some selected variables detailed in Table 2 was tested with one-way ANOVA. When differences in means were significant ($p < 0.05$), Tukey's HSD (honest significant difference) tests were computed. In order to see which variables were the most explanatory regarding safou tree density, as well as the number of cited safou varieties, conditional inference trees were used (for a detailed explanation of the method see Delêtre *et al.* 2017). This method allows testing and summarizing of non-parametric regression relationships. It is based on a sequence whereby selected predictor variables (gender, ethnicity, etc.) help partition a response variable, for instance, the number of cited safou varieties. In order to test the dependency or independency of the response variable to its covariates, permutation-based significance tests are used ($p > 0.05$). The trees were built in R 3.2.5 (R Core Team 2015) with the package *partykit* (Hothorn and Zeileis 2015).

Results

Relationship between the integration to safou market and intensification strategies

The low (Site 1), medium (Site 2), and high (Site 3) integration of production sites in safou trade is reflected by the observed on-field density of safou trees (Table 3). Higher densities were found in Site 3 whatever field size category is considered (small, medium, or large); intra-site density was not significantly different for fields of different sizes (Figure 3, Figure 4).

Social factors influencing cultivation practices

Respondents cited several planting techniques they were employing to increase the number of safou trees in their field (spontaneous seedling protection, direct seed sowing in the field or nursery, seedling purchase, or vegetative propagation). The most common phytopractices were tree pruning, trunk notching, fertilizer, and pesticide use. Trees are pruned either to maintain a partial shade cover over cocoa trees or to enhance tree productivity. This latter objective also explains why farmers use trunk notching and fertilizer. Non–species-specific pesticides are used to prevent pests and diseases.

When comparing between genders (Table 4), we observed differences in the number of practices cited for planting techniques and phytopractices. Women also cited fewer fruit tree species than men. The number of uses (useful parts of the trees apart from fruits) known for safou trees and the number of varieties cited by men and women were about the same. All ethnic groups and age categories showed similar cultivation practices associated with safou trees and no difference in practices when separating age category from gender (ESM 2). Knowledge of varieties and uses was also consistent between groups.

Site-specific effects on practices and knowledge of safou diversity

The number of farmers' planting techniques increases from Site 1 to Site 3 (Table 5). When planting relies predominantly on selected seed material (instead of seedlings bought on the market, for example), the use of backyard nurseries is more common in Sites 2 and 3 than in Site 1. According to farmers, they were appreciated as a tool to care for seedlings more easily and as a way to plant more seeds at a time. Although farmers from Site 3 used the highest absolute number of propagation techniques, their use of improved planting materials (such as seedlings from rural nurseries) and of vegetative propagation methods was still scarce.

Regarding the use of agrochemical inputs compared to more traditional low-input phytopractices, pesticides were used by an increasing proportion of farmers along the gradient from Site 1 to Site 3; fertilizer use was similar between sites (Table 5).

Site-specific effects on the varietal diversity of safou trees

The criteria used to distinguish varieties were discussed during focus group discussions (ESM 3). Considering that we were testing the effect of different local market integration on the distribution of varieties found in fields, we focused on fruit characteristics. In total, 44 varieties were mentioned across the three sites (Figure 5), with six trees per variety on average (ESM 4). In Site 3, the lower number of sampled trees was most likely responsible for the smaller number of varieties found.

Generally, varieties appearing at multiple sites displayed characteristics that were appreciated by farmers (Table 6). When farmers talked about the characteristics they valued most, they referred to large-sized fruits, with a white or green pulp (colors farmers commonly identify as appreciated), and oily fruits. On the contrary, fruits with a tanned pulp are often more sour. The varieties represented by the highest number of trees were shared between two or three sites and were all the ones said to taste better. In contrast, sour-tasting varieties accounted for most (in terms of total number of trees) varieties present in one site only. Selective management thus increased and maintained the availability of desirable phenotypes in the population, while less desirable phenotypes were less frequent.

Discussion

Relationship between market integration and intensification strategies

The intensification of safou tree cultivation in Western Cameroon is salient when looking at the number of trees in fields of similar size, farmers' interest in commercialization, and use of farm inputs in three different sites. Along the gradient considered, site comparisons highlighted different trends for these components. Site 1 (Kekem-Manjo) was characterized by rather low safou tree densities (Figure 3): most farmers were keeping fruits for self-consumption (Table 4) and less than a fourth of farmers were using fertilizers or pesticides (Table 4). At the other end of the gradient, farmers in Site 3 (Makenene) managed fields with a high tree density, and close to 80 % of the farmers were selling most of their production. The assumption of intensification is that the higher densities signal a change in agricultural and thus economic strategy, safou trees being seen as a cash crop rather than a subsistence crop (Bikoue *et al.* 2007). However, the direction of causation could be reversed, with higher tree densities resulting in increased yields and a potentially higher willingness to sell most of the harvest. Some farmers (especially Bamoun people from Site 2) with high tree densities/yields reported sending fruits to distant relatives rather than selling them; the fruiting season also matches children's school holidays, when distant family members come back to their village. The household economy component is likely to come into play in these strategies, but was not investigated in this study.

The rationales behind intensification deserve further attention. First, studies on cash crop cultivation strategies have shown that they are affected mostly by land use and market access (Degrande *et al.* 2006). Safou fruit harvest takes place during the rainy season, when vehicle access is impeded. Head-loading is sometimes the only option available for farmers: a too lengthy forest track therefore results in decreased market access. In Site 2, farmers see the new asphalt connection to the Adamaoua region as opening new market opportunities, along with the rise of international trade, with buyers coming from Gabon or Equatorial Guinea. Road access is also a key factor in Site 3, as it is located on a major road connecting Bafoussam to Yaoundé, two urban areas with a high market demand. Safous from Makenene are well known in Cameroon for their good quality; during the fruiting season many people stop to buy fruit to eat and/or to plant seeds from, although this quality might be related to local soil and climatic factors. Altogether, the good fit of safou trees to the soil and climate of Makenene combined with farmers' cultivation strategies has led to the emergence of a high-cultivation area. Some authors (Temple and Nzie 2013) referred to it as a "pre-specialization area" because of converging farmers' choices (Schroth and Ruf 2014) and the use of the region's name to designate the best safous (Makenene safous).

The intensification of safou tree cultivation can eventually be better understood in light of broader agricultural, and more generally subsistence strategies. Economic interests have long placed emphasis on coffee and cocoa farming in Western Cameroon. These crops were monitored by national programs and fostered by state aid. However, as a result of both a steady decrease in the price of coffee and a governmental cut of producer prices and subsidies for cocoa in the early 1990s, farmers have progressively reconsidered the role of cash crops in their agrosystems (Janin 1996; Pédelahore 2014). Since then, compensatory strategies have motivated the development of market garden products and fruit cropping, in a context of increasing urban demand for staple food. With fruit tree cropping (i.e., introduction or reinforcement of fruit tree species in coffee-cocoa-based agroforests), farmers expand their range of production and ensure a year-round source of food and/or possible income and help to cope with economic and climatic uncertainty (Carrière 2003). This diversification applies to tree crop–based systems, but is also true for horticultural crops, with, for instance, the addition of tomatoes, *Solanum lycopersicum* L., to crop fields.

Despite the high economic value and nutritional importance of safou trees, mono-cropping or plantation development of the species is rare. Most farmers reject the strategy of developing specialized orchards due to the scarcity of available land and, above all, the risk associated with fluctuating fruit production. Similar to other fruit tree species, such as grafted *Citrus* species, avocado and mango trees, vegetative propagation trials have been undertaken for safou trees (Mialoundama *et al.* 2002) and market-friendly varieties were identified (Ndindeng *et al.* 2008). However, this type of propagation material is sold by few small-scale nurseries, and often at prohibitive costs (Degrande *et al.* 2013). Nonetheless, the diachronic approach highlights an increase in the number of backyard nurseries set up by farmers. The average frequency of farmers using nurseries at the time of a previous study (Ayuk *et al.* 1999) was 6.5%, as compared to the 62% of farmers interviewed for this study.

Social factors and the way they influence cultivation strategies of safou trees

Variables possibly shaping knowledge and cultivation practices associated with safou trees were tested. We have seen that farmers' age was not a substantial source of variation, neither for planting techniques nor agricultural practices. Age nonetheless shapes farmers' strategies: older farmers may have accumulated capital throughout their lifetime that they are willing to invest in their plantation, whereas younger farmers want to improve their living standards by increasing production and incomes (Chambon and Mokoko 2013). As for the influence of ethnicity, the coexistence of multiple ethnic groups in the area does not seem to prevent knowledge flow. *Mimusops* species in Benin (Sinasson *et al.* 2017) showed the contrary, as uses were different among ethnic groups. Here, the fact that seeds are frequently acquired from neighbors in all three sites suggest that future studies should include specific questions on the presence or absence of ethnic barriers in seed circulation (see for instance Labeyrie *et al.* 2016).

The gender component is more influential. Traditionally, the involvement of women with indigenous fruit trees is important (Kiptot *et al.* 2014). Temple and Nzie (2013) found that generally the number of women involved in crop cultivation within a household was associated with more diversified systems, although their involvement takes place in fields with food crops rather than cash crops. For safou trees, farmers' gender was not shown to influence tree density in the field. The sample of respondents did not allow testing for a difference between male- and female-led households, although in their study on farm trees, Degrande *et al.* (2006) found no gender-related differences. Women's relationship to trees nonetheless differs from men's, being usually restricted to by-products such as branches for fire, leaves for fodder, and fruits for consumption and sale (Kiptot and Franzel 2012). In our interviews, women tend to cite fewer fruit tree species, as they devote less time to their management than men (Gautier and van Santen 2014; Gyau *et al.* 2012). Tree pruning and felling are male-dominated. Fruit harvesting is also a task carried out by men or children, as it often involves tree climbing. For safou trees, the sales system is led by men and women alike now that its demand, commercial value, and production system are closer to those of cash crop species. Small retail trade is still mostly managed by women, while men are in charge of wholesale trade.

Site-specific effects on the varietal diversity of safou trees

The cultivation practices also comprise varietal selection. As shown, variability of safou is high when considering all their possible shapes, color combinations, and pulp tastes. Morphometric studies reported for instance a ten-fold variation for length, width, and pulp thickness among trees (Anegbeh *et al.* 2005; Waruhiu *et al.* 2004), stressing the possibilities for farmers' selection. The fact that numerous varieties, with green or white pulp, are shared among sites reveals the preferences of farmers, who select the seeds they sow. Considering size and taste as targets of fruit selection is common for fruit trees (for baobab, see Assogbadjo *et al.* 2008; for a cactus species, see Parra *et al.* 2012). Biologically, the persistence of varieties with less desired traits is related to the outbreeding nature of the species, favoring a high level of genetic diversity among individuals. Seed selection can therefore be a deceptive process: the selected characteristics from the parent tree are not necessarily found in its progeny. Besides, sex distribution in safou trees is variable, with some individuals bearing fewer female flowers than others, meaning that some seedlings will not turn into highly productive trees. Farmers commonly remove those unproductive safou trees from their fields, having little interest in unprofitable shade trees.

At the varietal level, the decision to fell trees depends on farmers. Some decide to keep only the best varieties, leading to a high tree turnover. Others consider that varieties are complementary, and therefore choose to plant seeds from all different types of fruits in terms of size and taste. For instance, some sour-tasting varieties have advantages (later fructification, longer shelf life, etc.), making them interesting to safeguard. This complementarity is a more general reason why farmers aim to generate intraspecific diversity. Having more trees, they have a better chance of coping with the high inter-annual yield variability. For farmers, this trade-off between keeping trees that are difficult to sell and replacing them thus depends on their priorities (increasing revenue vs. maintaining food security and reducing risk). In Site 3, where trade is more developed, farmers tend to keep fewer of these low quality trees. Safou trees are also multi-purpose trees whose branches, bark, or resin are used; the number of uses should also increase with new industrial applications, e.g., the development of biofuel (Law 2010) or the extraction of oil for food industry (Silou 2012). If we add increased human-driven selection to these considerations, questions about the consequences on the species' diversity must be raised.

Conclusion

This study stressed the heterogeneous strategies associated with the cultivation of safou trees in Western Cameroon, underlined by the huge variation in species density between sites. Contrary to other examples of intensified cultivation, here this strategy is accompanied by more diversified planting techniques. So far, the intensification does not seem to have provoked a decrease in varietal diversity; a wide range of fruit types was found for all sites, with a shared pool of varieties reflecting farmers' preferences. In areas where farmers have a high interest in safou trees as a cash crop species, the combination of a larger number of trees and a limited ability to selectively breed (outcrossing species) could even result in an increase in varietal diversity. This hypothesis will be tested using population genetics to analyze genetic diversity patterns in managed populations and especially in areas where the fruits are commonly traded. The ethnoecological data presented here will help us to understand forthcoming results of genetic analyses. The social component of genetic diversity, including phytopractices and preferences, is indeed critical for understanding crop intraspecific variation (Leclerc and Coppens d'Eeckenbrugge 2011). Such knowledge will also provide key elements to document processes of domestication and to establish criteria for biodiversity conservation, based on local ecological perceptions.

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Figures

Figure 1. Mature safou tree in an agroforest (above left); young tree in an orchard near Koutaba (above right). Farmer collecting safou fruits (below left); fruit varietal diversity (below right).

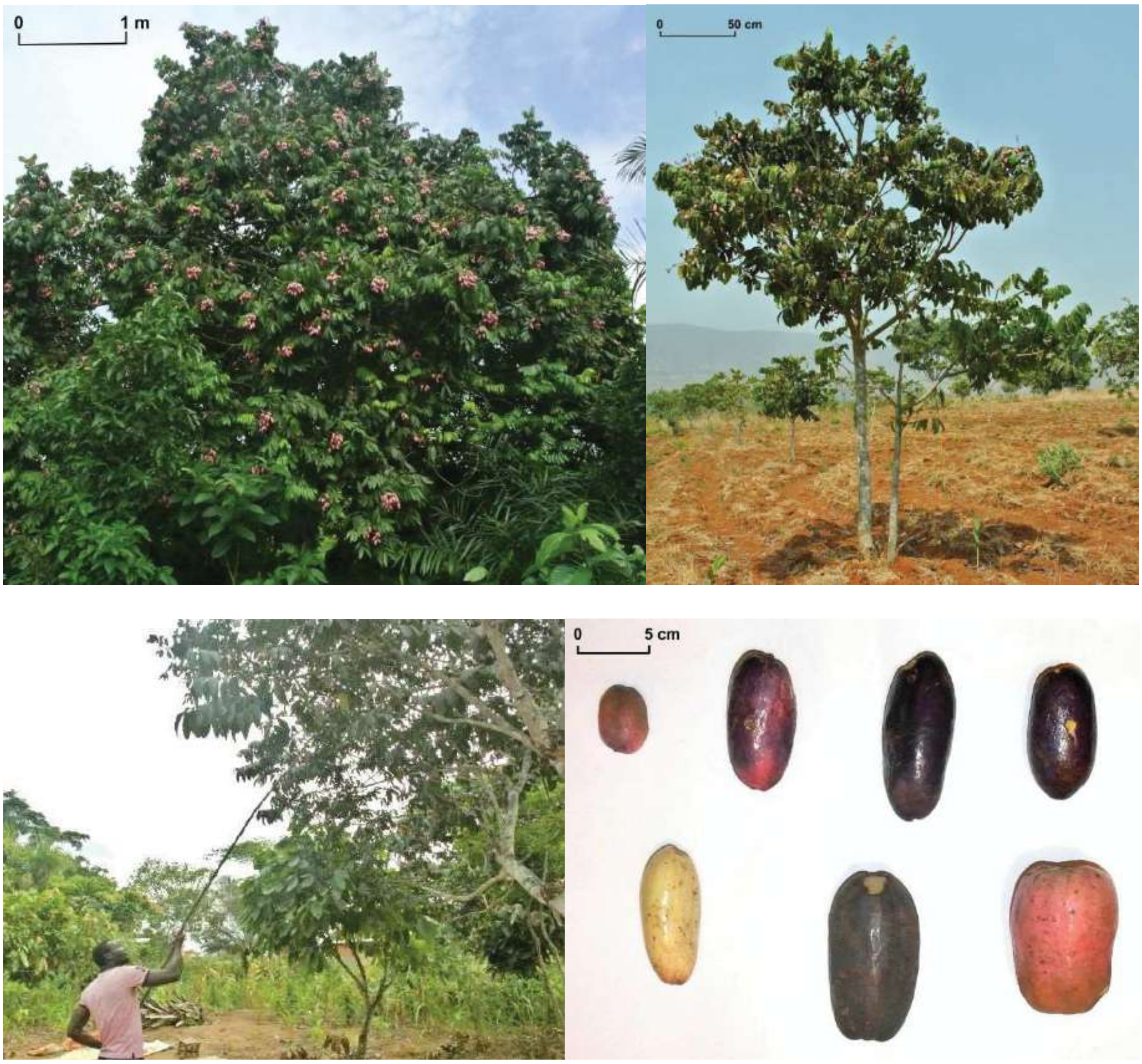


Figure 2. Study sites in Western Cameroon. Site 1 also comprises the localities in Manjo and Bazou.

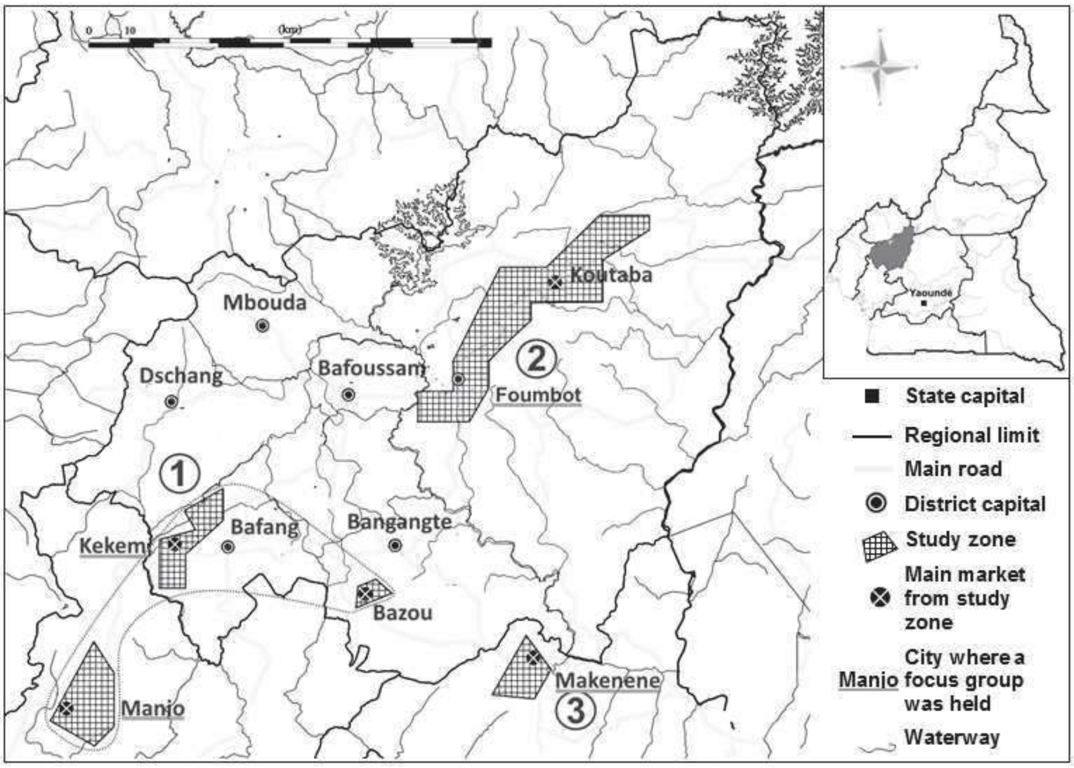


Figure 3. Distribution of safou tree density in fields according to field size classes ([0:2]; [2:4]; [4:12] hectares for small, medium and large fields respectively) for the three study sites. For Sites 1 and 3, fields considered are mixed agroforests. For Site 2, continuous line boxplots include data from both crop fields and orchards. Boxplots showing density in orchards are added in dashed lines for each field size, to show how they participated in raising the mean. Factors considered in relation to density (Figure 4), its partitioning, apart from being site-dependent, were based upon the number of planting/propagation techniques farmers used: farmers owning fields with a higher tree density know more planting/propagation techniques. Furthermore, farmers who have higher safou tree densities sell most of their production.

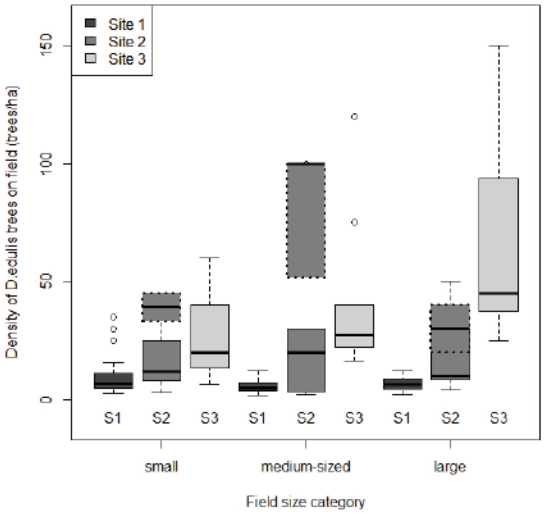


Figure 4. Partitioning of tree density using the conditional inference tree method. Density is positively associated with the number of farmers' planting techniques. Farmers' production aims (MC: mostly consumed; MS: mostly sold; variable: farmers' decision changes from one year to another according to production and price) also allow the partitioning of low density and high density fields.

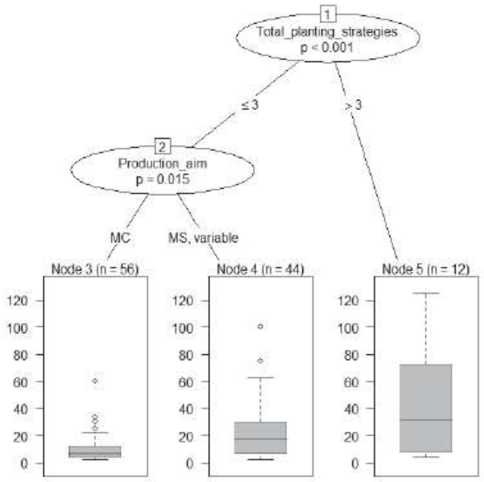
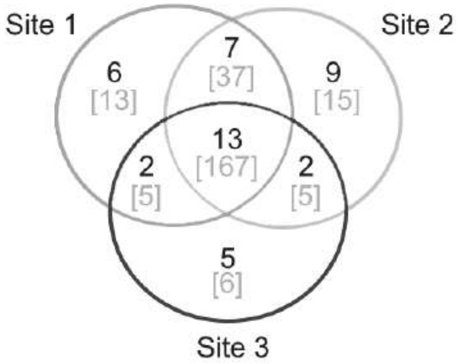


Figure 5. Partitioning of the 44 total varieties sampled in farmers' fields, according to their occurrence in study sites. Thirty percent were shared between the three sites; 25% were found in two of the three sites; the remaining 45% were site-specific. The corresponding number of trees is shown in gray in brackets.



Tables

Table 1. Number and characteristics (gender, age, ethnic group) of the interview respondents conducted in the safou study sites: A: focus group meetings; B: individual semi-structured interviews. Ethnicity is missing for eight people in Site 1.

A. Focus Groups

Study Site	Town, Place	Men	Women	Total
Site 1	Kekem, Village Hall	9	2	11
	Manjo, Agricultural District office	11	0	11
Site 2	Foumbot, Agricultural District office	10	3	13
Site 3	Makenene, local CIG headquarters	13	2	15
	Total	43	7	50

B. Individual Interviews

Study Site	Gender		Age			Total
	Men	Women	<40	40–60	>60	
Site 1	47	28	26	37	12	75
Site 2	22	12	9	20	5	34
Site 3	14	8	6	12	4	22
Total	83	48	41	69	21	131

Study site	Ethnic group					Total
	Bakaka	Bamileke	Bamoun	Mbo	Others	
Site 1	11	42	0	12	2	67
Site 2	0	5	29	0	0	34
Site 3	0	19	1	1	1	22
Total	11	66	30	13	3	123

Table 2. Data recorded and variables tested using one-way ANOVA.

Parameters recorded during interviews with farmers	
Number of safou trees in the field	Field area (ha)
Number of propagation techniques *(e.g., seed directly sown, seed sown in nursery, graft-propagation)*	Number of phytopractices *(e.g., tree pruning, notching, use of fertilizers, use of pesticides)*
Number of different uses for safou trees (*e.g., bark, wood, leaves*)	Number of cited safou varieties (*e.g., oily safou with green pulp, sour safou with red pulp, safou tasting like cocoyam)*
Number of associated fruit trees in the field	
Parameters calculated	
Safou tree density *(number of safou trees in the field/field area*)	Mean distance from field to road (*measured using GPS coordinates*)
Variables tested	
Study site	Age
Gender	Ethnic group

Table 3: Characteristics of farms and trees located in them in the three study sites (± standard error of the mean- SEM). A low, medium, and high safou tree density was expected in Sites 1, 2, and 3, respectively. In columns denoted by 1, values sharing a superscript letter are similar ($P > 0.05$) as analyzed by one-way ANOVA and Tukey's test.

Study Site	**Farm Characteristics**		**Trees on Farm**		
	Mean field size (ha)	Mean distance from field to road (km)^1	Number of associated fruit tree species	Number of safou trees^1	Safou tree density (trees/ha)^1
Site 1	2.6 ± 0.2	5.8 ± 0.5^a	4.8 ± 0.2	18.2 ± 2^b	7.8 ± 0.7^c
Site 2	2.4 ± 0.5	4.5 ± 0.7^{ab}	4.4 ± 0.3	56.4 ± 20^b	21.9 ± 4.2^b
Site 3	2.9 ± 0.3	3.3 ± 0.5^b	5.3 ± 0.4	136 ± 26^a	43.6 ± 6.8^a
All	**2.6 ± 0.2**	**5.1 ± 0.4**	**4.8 ± 0.2**	**49.3 ± 8.3**	**19 ± 2.4**

Table 4. Influence of farmers' gender on cultivation practices associated with safou trees in the study region (mean ± SEM). *Significant test ($P < 0.05$) as analyzed by one-way ANOVA and Tukey's test.

	Women (n = 44)	Men (n = 79)
Field size*	1.75 ± 0.1	3.02 ± 0.3
Density of safou trees (number/hectare)	17.9 ± 3.5	18.7 ± 2.8
Associated fruit trees (number of species)*	3.99 ± 0.3	5.2 ± 0.2
Number of planting techniques*	1.68 ± 0.1	2.36 ± 0.1
Number of phytopractices*	1.23 ± 0.2	1.8 ± 0.1
Number of cited varieties	4.6 ± 0.2	4.6 ± 0.2
Uses	1.79 ± 0.1	1.61 ± 0.1

Table 5. Safou tree planting techniques and phytopractices reported by farmers for each site (means ± SEM). Means in a row without a common superscript letter (a, b, or both) differ (P <0.05) as analyzed by one-way ANOVA and the TUKEY test.

	Site 1 (n = 72)	**Site 2 (n = 33)**	**Site 3 (n = 22)**
Spontaneous	0.26 ± 0.052^{b}	0.52 ± 0.088^{a}	0.27 ± 0.097^{ab}
Seed sown in field	0.65 ± 0.057	0.64 ± 0.085	0.86 ± 0.075
Seed sown in nursery	0.47 ± 0.059^{b}	0.76 ± 0.076^{a}	0.91 ± 0.063^{a}
Seedling bought	0.097 ± 0.035	0.12 ± 0.058	0.045 ± 0.045
Marcotted	0.056 ± 0.027	0.15 ± 0.063	0.045 ± 0.045
Total number of planting techniques	**1.83 ± 0.098^{b}**	**2.39 ± 0.211^{a}**	**2.67 ± 0.232^{a}**
Pruning	0.85 ± 0.044^{a}	0.61 ± 0.097^{b}	0.91 ± 0.063^{a}
Notching	0.14 ± 0.043	0.21 ± 0.072	0.045 ± 0.045
Fertilizers	0.24 ± 0.053	0.42 ± 0.087	0.41 ± 0.11
Pesticides	0.21 ± 0.051^{b}	0.3 ± 0.081^{ab}	0.5 ± 0.11^{a}
Total number of phytopractices	**1.51 ± 0.122**	**1.61 ± 0.206**	**1.9 ± 0.238**
Fruits mostly used for	Self-consumption (64%)	Sale (53%)	Sale (82%)

Table 6. Most common attributes of safou varieties in study sites. Frequencies (%) are displayed in brackets. Detailed distribution of varieties in study sites according to their characteristics in ESM 4.

Varieties' most common attribute	**Site 1**	**Site 2**	**Site 3**	**One site**	**Multiple sites**	**Total**
	101 trees	104 trees	43 trees	34 trees	214 trees	248 trees
Taste	Fine (79.2)	Fine (67.3)	Fine (83.7)	Sour (52.9)	Fine (79.4)	Fine (75)
Color	Green (37.7)	White (30.8)	White (41.9)	Green and red (29.4)	White (35)	Green (36.8)
Size	Medium (30.7)	Large (41.3)	Large (37.2)	Small (38.2)	Large (36.9)	Large (35.9)

Electronic Supplementary Material

Supplementary Material 1. Template provided to farmers for fruit size determination.

Supplementary Material 2. Influence of farmers' age and ethnic group on cultivation practices associated with safou trees in the study region (mean ± SEM). * Significant test (P < 0.05) as analyzed by one-way ANOVA and the Tukey's test.

	Site 1			**Site 2**			**Site 3**		
Age category	**18 - 40 (21)**	**40 - 60 (37)**	**60-84 (12)**	**18 - 40 (8)**	**40 - 60 (19)**	**60-84 (5)**	**18 - 40 (5)**	**40 - 60 (12)**	**60-84 (4)**
Density of safou trees (nb/hectare)	8.28 ± 1.3	7.77 ± 1.0	7.01 ± 0.7	15 ± 3.2	27.5 ± 6.7	11.9 ± 4.5	40.5 ± 5.6	48.3 ± 11.3	33.6 ± 10
Associated fruit trees (nb of species)	4.7 ± 0.5	4.67 ± 0.3	5.5 ± 0.6	3.62 ± 0.7	5.02 ± 0.4	3.28 ± 0.4	4.45 ± 0.5	5.17 ± 0.6	6.5 ± 0.9
Planting techniques	1.9 ± 02	1.86 ± 0.1	1.65 ± 0.2	2.55 ± 0.6	2.32 ± 0.2	2.4 ± 0.5	2.8 ± 0.5	2.67 ± 0.4	2.5 ± 0.3
Phyto-practices	1.57 ± 0.2	1.39 ± 0.2	1.75 ± 0.2	1.75 ± 0.6	1.45 ± 0.2	2 ± 0.3	2.4 ± 0.4	1.83 ± 0.4	1.5 ± 0.3
Varieties	4.27 ± 0.3	4.53 ± 0.2	4.17 ± 0.3	4.88 ± 0.4	5.1 ± 0.4	4.4 ± 0.7	4.8 ± 0.4	4.75 ± 0.3	5 ± 0.9
Uses	1.8 ± 0.2	1.66 ± 0.2	1.96 ± 0.4	1.95 ± 0.3	1.61 ± 0.2	1.2 ± 0.2	0.8 ± 0.2	1.92 ± 0.4	1.25 ± 0.6

	Site 1				**Site 2**		**Site 3**	
Ethnic group	**Bakaka (11)**	**Bamileke (48)**	**Mbo (9)**	**Other (2)**	**Bamileke (4)**	**Bamoun (28)**	**Bamileke (18)**	**Other (3)**
Density of safou trees (nb/hectare)	5.3 ± 0.9	8.41 ± 0.9	7.51 ± 1.2	8 ± 2.7	9.82 ± 3.7	23.6 ± 4.7	46.3 ± 7.7	27.5 ± 5.2
Associated fruit trees (nb of species)	4.09 ± 0.4	5.09 ± 0.3	4.11 ± 0.4	5.5 ± 1.5	4.5 ± 1.3	4.39 ± 0.3	5.46 ± 0.4	4 ± 1.2
Planting techniques	1.82 ± 0.2	1.81 ± 0.1	2.05 ± 0.2	1.5 ± 0.5	1.75 ± 0.5	2.48 ± 0.2	2.83 ± 0.2	1.67 ± 0.3
Phyto-practices	1.05 ± 0.3	1.58 ± 0.1	1.56 ± 0.3	2 ± 0	1.15 ± 0.2	1.68 ± 0.2	2 ± 0.2	1.33 ± 0.9

	Site 1			**Site 2**			**Site 3**		
Age category	**18 - 40 (21)**	**40 - 60 (37)**	**60-84 (12)**	**18 - 40 (8)**	**40 - 60 (19)**	**60-84 (5)**	**18 - 40 (5)**	**40 - 60 (12)**	**60-84 (4)**
Varieties	4.05 ± 0.3	4.55 ± 0.2	4 ± 0.4	4 ± 0	4.25 ± 0.5		5.03 ± 0.3	4.89 ± 0.3	4.33 ± 0.3
Uses	2.27 ± 0.3	1.61 ± 0.1	1.86 ± 0.6	1.75 ± 0	2 ± 0.4		1.58 ± 0.2	1.61 ± 0.3	1 ± 0.6

Supplementary Material 3. Local varietal classification

Two different focuses for varieties definition were evoked. From the producer's point of view, criteria relate to agronomic qualities at the tree level. They are about safou fruit drop (abscission) rate, regularity of fruit production, maturation homogeneity and timing, i.e. all aspects of fruiting "reliability". From the consumer's point of view, fruit characteristics are what matters most. Fruit size was cited by respondents as the most important criterion along with fruit taste, followed by pulp and skin color.

Most often, farmers give names to the different varieties with adjectives referring to size and shape: "le gros costaud" ("the big strong") or "les testicules du mouton" ("the sheep's testicles") indicate the large-sized fruits; small and round varieties are called "la petite bille" ("the small marble"), "le bonbon" ("the lollipop") or "le fruit noir" ("the black fruit"), by reference to the fruits of *Canarium schweinfurthii*. They also make reference to taste attributes: "le meilleur goût" ("the best taste"), "celui qui fait couler les larmes" ("the one that makes you cry") for those that are too sour, or "le légume" ("the vegetable-like"), for a variety whose taste was close to that of a leafy vegetable. Skin color can be evoked, sometimes by analogies to other food products. For instance, white varieties are called "the macabo" when they are large, "the egg" when small. Pulp color and texture are also sometimes used as a descriptor ("the avocado-like", "the yolk-like".) The spectrum of possible variation also includes a wide range of possible shapes, such as conical, heart-shaped or crooked fruits, with additional peculiarities like folds and bumps.

Supplementary Material 4. Distribution of varieties in study sites according to their characteristics (taste, color, size). For each site, relative frequency (Frq.), number of varieties (Nb) and mean number of trees par variety (Tr, in brackets) are displayed. Bold figures are for characteristics with the highest frequency for each category.

Varieties			**Site 1 101 trees**		**Site 2 104 trees**		**Site 3 43 trees**		**One site only 34 trees**		**Multiple sites 214 trees**		**Total 248 trees**	
			Frq. (%)	Nb (Tr)	Frq. (%)	Nb (Tr)	Frq. (%)	Nb (Tr)	Frq. (%)	Nb (Tr)	Frq. (%)	Nb (Tr)	Frq. (%)	Nb (Tr)
Taste	Sour		20.8	10 (2.1)	32.7	14 (2.4)	16.3	6 (1.2)	**52.9**	9 (2)	20.6	9 (4.9)	25.0	18 (3.4)
	Fine		**79.2**	18 (4.6)	**67.3**	17 (4.1)	**83.7**	16 (2.3)	47.1	11 (1.5)	**79.4**	15 (11.3)	**75.0**	26 (7.2)
Col.	Brown	S	0.0	0	1.0	1 (1)	2.3	2 (0.5)	5.9	2 (1)	0.0	0	0.8	2 (1)
	Red	S	10.9	4 (2.8)	9.6	3 (3.3)	4.7	4 (0.5)	14.7	1 (5)	8.4	3 (6)	9.3	4 (5.8)
		F	6.9	2 (3.5)	3.8	2 (2)	9.3	3 (1.3)	14.7	2 (2.5)	4.7	1 (10)	6.0	3 (5)
	Yellow	S	3.0	2 (1.5)	10.6	4 (2.8)	0.0	4 (0)	8.8	2 (1.5)	5.1	2 (5.5)	5.6	4 (3.5)
		F	9.9	3 (3.3)	16.3	4 (4.3)	2.3	4 (0.3)	5.9	1 (2)	12.1	3 (8.7)	11.3	4 (7)
	White	S	2.0	2 (1)	7.7	3 (2.7)	9.3	5 (0.8)	17.6	3 (2)	3.7	2 (4)	5.6	5 (2.8)
		F	29.7	7 (4.3)	23.1	4 (6)	32.6	7 (2)	2.9	1 (1)	**31.3**	6 (11.2)	27.4	7 (9.7)
	Green	S	5.0	2 (2.5)	3.8	3 (1.3)	0.0	3 (0)	5.9	1 (2)	3.3	2 (3.5)	3.6	3 (3)
		F	**32.7**	6 (5.5)	**24.0**	7 (3.6)	**39.5**	12 (1.4)	**23.5**	7 (1.1)	**31.3**	5 (13.4)	**30.2**	12 (6.3)
Size	Elongated		15.8	8 (2)	10.6	6 (1.8)	11.6	3 (1.7)	11.8	3 (1.3)	13.1	6 (4.7)	12.9	9 (3.6)
	Large		29.7	6 (5)	**41.3**	9 (4.8)	**37.2**	8 (2)	29.4	6 (1.7)	**36.9**	7 (11.3)	**35.9**	13 (6.8)
	Medium		**30.7**	7 (4.4)	26.9	10 (2.8)	32.6	8 (1.8)	20.6	6 (1.2)	30.8	7 (9.4)	29.4	13 (5.6)
	Small		23.8	7 (3.4)	21.2	6 (3.7)	18.6	3 (2.7)	**38.2**	5 (2.6)	19.2	4 (10.3)	21.8	9 (6)
	Total		100	28 (3.6)	100	31 (3.4)	100	22 (2.0)	100	20 (1.7)	100	24 (8.9)	100	44 (6.1)

Chapitre 3

Évolution des perceptions, des préférences et des pratiques de culture d'un arbre fruitier local dans les zones rurales et urbaines du Cameroun

Shifting perceptions, preferences and practices in indigenous fruit tree growing in rural and urban Cameroon

(under review - Agriculture and Human Values)

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Abstract

This paper discusses the perceptions, preferences and practices associated with varieties of a native fruit tree species cultivated in Cameroon, the African plum tree (*Dacryodes edulis*). Through interviews and tree surveys with African plum tree owners in urban, peri-urban and rural areas, it examines how they differ along an urbanization gradient and among three ethnic groups (Bamileke, Bassa, Beti), highlighting the links between on-farm decisions, trade, and consumption. Across the three ethnic groups surveyed in the study area, more than 300 different local names of African plums were recorded, which were mostly based on morphological and organoleptic traits, respectively fruit size and skin color, and fruit taste. Preferences of urban dwellers from different ethnic groups were more similar than those of rural dwellers. In rural areas, where African plums are sold as well as self-consumed, owners of the Bassa ethnic group paid more attention to a quantity-related trait (fruit size) than quality-related traits (fruit taste, skin color). These preferences were reflected in the choice of seeds used for planting, while the selective felling of African plum trees mainly targeted unproductive trees. Findings on variations in perceptions and preferences for fruit traits, along the urbanization gradient and among ethnic groups, will help design locally-specific measures to conserve the intraspecific diversity of African plum.

Key words: Farmer selection, fruit traits, ethnovarieties, local knowledge, tree crop, agrobiodiversity conservation, urban homegardens.

Introduction

Profound and rapid changes are currently taking place in global agricultural production and trade. In sub-Saharan Africa, changing eating habits associated with urban growth increase the demand for specific crops and agricultural products (Cockx *et al.* 2019). As such, rural cultivators need to adapt to potential changes in demand from urban dwellers (Satterthwaite *et al.* 2010), particularly for local crops and varieties with valued traits (Tomlins *et al.* 2005; Tsegaye and Berg 2007). Moreover, cultivators also consume a portion of the crops they grow, and their food preferences further guide their choice of cultivated crops and varieties (Gibson 2009). The set of local crops and varieties they manage ultimately reflects demand, i.e. the varieties farmers value, as well as supply possibilities, i.e. the access they have to this set of varieties (Bellon 2004).

Understanding how farmers perceive their environment, and the nature and categorization of ecological perceptions as knowledge, meaning and preferences, is essential to understand the decisions agriculturalists make regarding species and crop varietal management (Nazarea 1999). Local varieties or ethnovarieties, defined as the intraspecific diversity, named and recognized by local users (Rivera *et al.* 2006), are relevant entry points to understand how cultivators perceive and manage their crop diversity (Rival and McKey 2008; Adan *et al.* 2016). Perceptions – or cultural interpretations of sensory and biological information (Ochoa and Ladio 2014) – play a major role in farmers' management decisions. Perceptions of crop traits vary across ethnic groups (Ekue *et al.* 2010; Fandohan *et al.* 2010). Culturally-specific names of local crop varieties reflect these different perceptions to some extent, and provide insight into owners' preferences, whether agronomic, aesthetic, or culinary (Nuijten and Almekinders 2008; Chentoufi *et al.* 2014). Preferences denote positive or negative individual evaluations of the objects under consideration, including comparisons or prioritization, and ranking (Soleri *et al.* 2008). As with perceptions, different ethnic groups often judge differently valued or unvalued traits (Assogbadjo *et al.* 2008; Njukwe *et al.* 2013).

Emphasizing local perceptions and preferences of valued crop species also helps to show how they relate to practices. They include, for example, the link between local varietal knowledge and varietal management practices (Bellon 1991), between cultivator preferences and local variety conservation (Snapp *et al.* 2019), and between cultivator values and on-farm variety persistence (Rana *et al.* 2007).

Changes in cultivators' rationales and related patterns of crop diversity induced by market penetration and increased commercialization have received much attention (Brush 1992; Brush and Meng 1998; Isakson 2011; Wale *et al.* 2012). There is also growing interest in traditional ecological knowledge of urban and peri-urban dwellers (Pradeiczuk *et al.* 2017; Turreira-García *et al.* 2017), and questions about the specificities of urban dwellers' knowledge (Almada 2011; Emery and Hurley 2016). Yet, there is a lack of scholarly attention to changes in knowledge–apprehended here through local perceptions and preferences–and practices, and their link with crop diversity along urbanization gradients, from rural areas where crop species are produced to urban areas where they are sold and consumed in large numbers.

In this study, we aim to document how perceptions, preferences and practices related to a cultivated African fruit tree species vary along the urbanization gradient and among three main ethnic groups involved in its trade in Cameroon. The fruit tree species *Dacryodes edulis* (G. Don) H.J. Lam (Burseraceae), locally known as the African plum tree (French: *safou*), is particularly important for the food security and economy of local populations in its native region in Central Africa (Mollet *et al.* 1995; R. R. B. Leakey *et al.* 2002; Sonwa *et al.* 2002). The species can be found in multiple environments, from agroforestry systems to cities. African plums are a staple food, consumed, once cooked, with all types of side-dishes (Tabuna and Tanoe 2009). Fruit characteristics vary significantly between and within tree populations (Waruhiu *et al.* 2004; Anegbeh *et al.* 2005; Biloso *et al.* 2018; Rimlinger *et al.* 2019). Whereas African plum fruits have been tentatively classified on the basis of morphological traits (fruit size and shape, pulp thickness, branching patterns; Okafor 1983) or morphological and biochemical traits (Youmbi *et al.* 2010; Ondo-Azi *et al.* 2017), cultivators' perceptions of and preferences for the fruit have never been studied. The ubiquity of the tree in urban, peri-urban, and rural areas, where it is the most prevalent indigenous agroforestry tree species (Abada Mbolo *et al.* 2016), makes it a good candidate for contrasting these perceptions and preferences across sites and ethnic groups. Moreover, consumer knowledge, perceptions and preferences for certain types of fruit, the large, thick-fleshed, sweet and oily (Ndindeng *et al.* 2008), are reflected in selling prices (Leakey 2018) and are thus more likely to be valued by producers.

Specifically, we examine how African plum trees owners view and use the species across an urbanization gradient, wherein urban areas are assumed to be predominantly consumption areas, whereas rural areas are predominantly production areas. We then verify how these perceptions are corroborated by local names for the species. Second, we observe how preferences for African plum vary according to fruit use (self-consumption, sale, purchase) and among differentiated groups of tree owners (rural and urban; from different ethnic groups). Finally, we examine patterns of variation in management practices, to see whether they reflect different preferences for the fruit. These perceptions, preferences, and practices are apprehended in a context of rapid market changes along the urbanization gradient, and are ultimately set in relation to the intraspecific diversity of this species.

Methods

Study site

We chose as our study area a region where African plum trees are abundant, both historically and due to a booming commercial production, as the region supplies Yaoundé (3.9 million inhabitants), one of the largest urban markets in Cameroon. Our sampling considered two parameters: (i) the continuous presence of African plum tree populations along an urbanization gradient stretching from urban to peri-urban to rural areas; (ii) the existence of three main ethnic groups (Beti, Bassa, Bamileke) in each of the main production basins supplying Yaoundé, where they are also settled.

Owing to the seasonality of production, the capital's supply of African plum relies on different basins of production, populated by different ethnic groups (Isseri and Temple 2002): the Littoral region (Bassa people), which produces fruit at the beginning of the fruiting season (April, May); the Western region (Bamileke people) and the region around Makénéné, where trees fruit in June and until the beginning of July; and the Central region located around Yaoundé (Beti people), with mature fruit produced from July to October. Study sites thus included: (a) urban sites, with three neighborhoods (Essos, Messa-Carrière, Oyom-Abang) in Yaoundé populated by Beti, Bassa and Bamileke fruit tree owners with moderate housing density and buildings surrounded by small home gardens; (b) peri-urban sites, defined as agricultural spaces in which production systems are oriented towards urban market supply (Temple and Moustier 2004), with three peri-urban towns around Yaoundé sampled, one for each ethnic group; (c) rural sites, more detached from the urban market but still connected to it by trade, with three villages sampled, one for each ethnic group (Figure 1). Our first hypothesis is that production of African plums decreases from rural to urban sites, and its consumption increases due to a higher population density in urban areas.

Data collection

Semi-structured interviews were conducted with 441 tree owners from April to July 2018 (Table 1). We collected information on the status of the *D. edulis* tree owners (age and gender, not used in this study) to keep a good representation of the different age categories and gender. We included in the analysis their ethnicity and their location on the gradient (urban, peri-urban or rural dwellers).

Prior to the interview, tree owners were informed of the research intentions and of their right to participate or decline. At the end of the interview, tree owners 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.

To document perceptions, the interviews focused on two elements. First, we asked tree owners about criteria (including fruit traits) they used to distinguish African plum trees and ethnovarieties. To see if similar traits were used in the local nomenclature of the three ethnic groups, we recorded the local names of African plum trees used by tree owners, their translation, and their description. The described ethnovarieties were then categorized according either to the trait justifying their names, or to other justifications (symbolic, environmental, agronomic). Fruit morphological characteristics were described using an identification sheet [APPENDICE 3] where several choices were proposed for fruit size, shape, skin and pulp color. Fruit taste was also described orally, and later grouped in three categories: (very) good, average and (very) bad. To have the largest pool possible, we recorded both known ethnovarieties (exercise based on the trees the owners remembered, 427 trees in total) and planted ethnovarieties (corresponding to the trees they had in their home garden or field, 806 trees in total).

To document preferences, the interviews focused on the traits tree owners used to rank African plum trees and ethnovarieties. We asked about their criteria for three different types of uses: self-consumptions; sale (which types of fruits are favored to be sold) and purchase (which types of fruits are favored to be bought) of the fruit. We also asked about criteria that negatively affect the appreciation of the fruit (selection criteria).

To document practices, we collected information on how tree owners managed their trees. Some of these practices had a direct impact on the diversity of ethnovarieties (e.g. tree propagation, felling practices). Other practices (e.g. production techniques, traditional practices) were identified to determine whether the practical knowledge of tree owners differed according to their location on the rural-urban gradient and ethnicity.

Data analysis

Differences between quantitative variables and tree owners' groups (Table 2) were tested using a one-way ANOVA (for categories with more than two options) or a Wilcoxon ranking test. To see preferential associations between quantitative variables, cross-tabulation analyses were based on the χ^2 statistic. The χ^2 gives a global diagnosis of the dependence or independence between the variables. In order to visualize the categorical associations, mosaic plots (Hartigan and Kleiner 1981) were plotted: the relative frequencies of the two variables are indicated by rectangles whose area is proportional to the cell value. The rectangles are colored if the residuals derive significantly from the independence hypothesis and are thus informative of the over- or under-representation of the association of some groups (package vcd, option shading_max, Zeileis *et al.* 2007).

To map how fruit traits were related to preferences, Multiple Correspondence Analysis (MCA) was used. It was based on the data set combining the full description of ethnovarieties with fruit size, skin and pulp color, and fruit taste. For each ethnovariety, owners also reported their preference ("valued", "not valued"). MCA is a method of factoring categorical variables (fruit characteristics) and displaying their associations in a two or more dimensional space. Owners' preferences were not used as a variable in the analysis but were displayed within the same space as a supplementary variable.

Results

African plums were predominantly self-consumed, sold and purchased. Food was the main use cited by more than 95% of the tree owners, and fruits were consumed by 100% of owners, even when also commercially sold (78%). Other marginal uses of the trees were cited (medicine and agronomy, as a shade tree in agroforests, accounting respectively for 4% and 2% of the uses). The average number of plum trees per owner was 1.4 ± 0.1, 13.1 ± 2.4 and 26.9 ± 2.8 in the urban, peri-urban and rural sites, respectively. Tree uses varied greatly along the gradient. In the urban sites, the dominant use was consumption or gift (84% of owners), while sale was marginal (16%). In the peri-urban sites, owners using exclusively their fruits for own-consumption accounted for 49% of the total, and 51 % consumed some of the fruits and sold the rest to supply the urban market. In rural sites, most tree owners reported selling their fruits (83%). The proportions of exclusive consumers and sellers were similar in the urban and rural sites for the different ethnic groups, but in the peri-urban sites Beti owners were significantly more engaged in the plum trade (80% of them, p-value = $1.1e^{-06}$), compared to Bamileke and Bassa owners (33% of owners for both). Over the whole gradient, Bassa owned more trees (21.6 ± 3.1) than Bamileke (11.2 ± 2.1) and Beti (7.6 ± 1.1).

Patterns of perceptions along the urbanization gradient and among ethnic groups

More than 10 criteria for distinguishing trees and fruits were recorded (1050 citations in total, Table 3). Overall, the most cited criterion of distinction was taste (29% of the citation). The most cited taste was sourness, with good fruits being perceived as the least sour. The peculiar taste of African plums was expressed by the use of adjectives such as savory, tasty, fragrant. Taste descriptors also referred to texture characteristics: because of its soft/tender/smooth texture, it was compared to other foods, such as buttery avocado or dairy products (butter, cream, cheese). Its floury texture was also mentioned; hence it was compared with tubers (cassava, cocoyam, yam, baked potato). African plums trees were also distinguished by the way trees produce fruits, based on their productivity or their belonging to improved varieties.

The three most common criteria (taste, fruit size and skin color), which accounted for more than 75% of the total responses, were not cited with similar proportions along the gradient. To distinguish plum varieties, rural dwellers cited fruit taste less often, but instead cited fruit size as their first criterion (47.6% of citations by rural dwellers, p-value = 0.008; Figure 2). Differences in the frequencies of traits cited by the three ethnic groups to distinguish plums were mainly found for the rural site. The trait most cited by rural dwellers, fruit taste, was significantly more cited by the Bassa owners, who accounted for 59% of fruit taste citations.

Of all the 1083 trees described, almost half (526 trees) had been given a name by its users. Most names were recorded in rural sites (269 trees), followed by peri-urban and urban sites (126 and 131 names respectively). As regards the distribution by ethnic groups, 303 (58%) of these trees were named by Beti, 124 (24%) by Bassa and 99 (19%) by Bamileke owners in their respective languages. Due to the absence of a common Bamileke dialect, Bamileke names were rarely shared, except at the rural level. Names were not shared between ethnic groups, even in urban sites where ethnic groups cohabit closely. However, the meanings of these names were shared across groups (Figure 3). Ethnovarieties named using these three different traits were cited with similar proportions along the gradient. Among ethnic groups, Bassa owners named significantly fewer varieties based on fruit size, and more based on skin color.

As some names were cited several times (180 were cited by at least two respondents) a total of 346 different African plum tree local names were recorded (N = 219). Regardless of ethnic group, names mainly referred to morphological (size, skin color, shape) and organoleptic (taste, texture) criteria of the fruit (78% of the names), followed by names referring to the history of the tree, including its owner or the place where the tree was planted (Figure 4). Ethnovarieties were most often named based on their fruit size (37% of the names), taste (20%), and skin color (11%), which were also the three most cited traits for distinguishing trees. Some ethnovarieties were recognized and named based on the combination of several criteria.

Patterns of uses and preferences along the urbanization gradient and among ethnic groups

African plum trees owners reported the use of different parts of their trees. The use of fruit as food (self-consumption) was reported by all plum tree owners throughout the gradient, whereas its use as a commodity varied along the gradient: fruit sales increased from urban to rural sites. The second most used part was tree branches (55% of owners), which were collected as fuel wood for cooking. The use of its bark (34% of owners) and leaves (33% of owners) were reported, both for medicinal purpose. The tree as a whole was also reported to be useful by 10% of the owners, for the shade it provided to cocoa and coffee trees in agroforests. Finally, few owners (2%) cited roots as a part of the tree they used, also for medicinal purposes. These uses were unrelated to preferences for most tree owners, but some reported preferences for medicinal uses. These preferences concerned trees bearing rare white fruits ("white plum trees are more used for indigenous remedies; it is also the case with white cola and red corn" Obala, Eton owner, May 2018), the bark and leaves of male trees that never bear fruits (*nèlom sa,* Bassa) to prepare remedies (bark for tuberculosis, leaves for jaundice) or specific age categories of trees (bark and leaves of old trees used to prevent typhoid fever; bark and leaves of young trees used to prepare treatment for snake poisoning).

We recorded the preferences that were associated with the main uses of the fruit. Overall, eight criteria were primarily (99%) cited to describe preferences, whether they were related to self-consumption, purchase or sale. Seven out of these nine criteria were related to fruit traits: taste, fruit size, skin color, pulp texture, pulp color, pulp width and fruit shape. Some tree owners favored the geographic provenance of fruits. Other criteria (smell, seed color, affinity with a seller) accounted for less than one percent of the total citations. Other owners (9%) reported to have no criteria, meaning they liked all fruit types equally.

Globally, tree owners described the ethnovarieties they knew or had planted with four main criteria (pulp and skin color, size and taste of the fruit) and they specified if they liked or disliked them (Figure 5). The valued ethnovarieties were those with a blue, black, white or green skin, a green or white pulp, a medium or big size and a mildly sour taste (elements close to the "valued" preference type). The ethnovarieties that were not valued were those with a pink or a two-colored skin, a red pulp, a very small size, and a very sour taste (elements close to the "not valued" preference type).

Irrespective of whether the fruit was used for self-consumption, purchase or sale, the most valued morphological traits for selecting fruit were taste, fruit size and skin color. The three criteria taken altogether accounted for 94% of preference criteria. Some owners (12%) stated that they had no preference criteria and were eating/buying/selling all types of African plums equally.

The favored criteria for fruit selection varied according to the types of uses (self-consumption, purchase, sale) considered (Figure 6). Taste was the most cited criterion related to self-consumption and purchase of the fruit (64% and 46% of all cited criteria for these use types, respectively). For purchase preferences, taste was followed by the skin color criterion (24%), which was used as a proxy for taste: the darker the African plum, the better the taste. Fruit size was the most cited criterion (50%) of the selling preferences.

As for preferences, the most frequently cited criteria were always the same across ethnic groups for urban sites, but differed significantly across ethnic groups for rural sites (Figure 7). Fruit size was over-represented as the primary preference criterion for the following groups and preference categories: Bamileke owners for self-consumption (35% of Bamileke owners, p-value = $1e^{-04}$); Bassa owners for buying and selling (respectively 64% and 87% of Bassa owners, p-value = $2.2e^{-06}$ and p-value = $1.261e^{-05}$). Beti owners cited fruit taste more often for selling preferences (50% of Beti owners).

Management practices along the urbanization gradient and among ethnic groups

Two categories of management practices (propagation practices, cultivation practices) were recorded. Some of them were aimed at obtaining valued types or getting rid of undesirable trees (propagation, counter-selection), some were related to other aspects of management (production techniques such as pruning of trees, use of fertilizers).

Propagation practices included tree transplanting, direct seeding in the field, or in a backyard nursery and later transplanting the plant into the field. Vegetative propagation was generally not used. Production techniques either targeted individual African plum trees (pruning, heading) or the whole field (natural and chemical manure application, watering, weeding). Overall, more propagation and cultivation practices were cited (one-way ANOVA, $p < 2.98e^{-05}$, Table 4) in rural (4.4) and peri-urban sites (4.2) than in urban ones (3.6). Bamileke owners cited more propagation and cultivation practices (4.9) than owners from other ethnic groups.

Practices that were not linked to the management of tree varietal diversity were also recorded. Traditional practices were used by 14.1% of the owners to manage low production or high fruit drop. The two most common practices were notching the trunk with a sharp object (6.9%) and tying the trunk with lianas or banana leaves (6.3%). Bassa tree owners (19.7%), followed by Bamileke owners (15.3%) cited these practices, whereas Beti owners (10.0%) applied them much less frequently (p-value = 0.038). Urban dwellers also cited far fewer practices (8.7%, p-value = 0.035) than did owners living in peri-urban (17.1%) and rural (17.5%) sites.

As for the seed chosen to be planted, two criteria (fruit taste and fruit size) represented more than 90% of the criteria cited. Some other owners (40%) used no criteria. Urban dwellers took much less account of fruit size (p value = 0.01) than did peri-urban and rural dwellers (Figure 8). In the rural site, Bassa owners cited fruit size (34.8% of the Bassa's first planting selection criteria; p-value = $1.0e^{-06}$) significantly more than Bamileke and Beti owners (7% and 18.3%). They also cited skin color more than the other owners.

Most of the seed selected for planting did not come from the owners' own fields (77% of the 467 trees with information on the seed provenance). They came mainly from trees in the village or city through exchanges with neighbors (14% of seed sources) or from market fruits (local or city market, 37%). Only a few trees from spontaneous regeneration were protected or transplanted (6%). The average distance between the seed source and the planting site was high in urban sites (55.1 ± 5.2 km), intermediate in peri-urban sites (18.9 ± 4.7 km) and low in rural sites (6.7 ± 1.3 km). In urban sites, seeds were brought back from the villages of origins of the tree owners and from regions known for the quality of their fruits (Makénéné market, improved varieties from the IRAD). This distance is underestimated because some seeds were bought at the market and therefore of unknown origin. The average distance is thus much greater in peri-urban and urban sites, where about 40% of the trees originated from market seeds.

Of the 23% of seeds that were coming from the owners' field, owners were asked how they selected which tree to propagate. These trees were mostly (91%) owned by owners in peri-urban and rural sites; urban dwellers stated that they had too little space. The two main selection criteria for these seeds were the taste of the parent tree's fruits, such as mildly or very mildly sour taste (61%) and fruit size (29%), with large fruits being multiplied regardless of their taste. Only five percent of owners cited air-layering as a propagation practice that they knew or used: they were from all ethnic groups, evenly distributed along the gradient.

Undesirable traits further guided selection practices. Not all tree owners selected their seeds; only 230 owners (52% of the total) did. Urban dwellers were significantly less likely to report selection practices (44% of them). Bamileke owners reported selection practices much more often (68% of Bamileke owners, p-value = 0.0002), and Beti owners significantly less (41% of them). A variety of criteria (six major categories of criteria) justified tree selection, some targeting specific undesirable traits. A problem cited by 20% of owners was that the desired traits of the mother tree were not inherited in its offspring, which made selection ineffective for achieving desired traits.

Lack of production (cited by 44% of the selective tree owners) leads to the felling of unproductive trees. This practice was cited more (p-value = $8.9e^{-05}$) by Bassa owners (63% of Bassa owners) than by Bamileke or Beti owners (38% of Bamileke and 36% of Beti owners respectively). Urbanization (15%) and the resulting lack of space for maintaining existing trees led to tree felling. This criterion was significantly (p-value = $4.6e^{-06}$) more cited in urban than in rural sites (representing 27% and 4% of the citations per site respectively). Bad (sour) fruit taste led to the felling of some trees. This criterion was cited by 15.4% of selective owners with similar frequencies among tree owners throughout the gradient and across ethnic groups (18.3, 9.6 and 16.7% for Bamileke, Bassa and Beti respectively). In the peri-urban and rural sites, excessive shade for cocoa trees sometimes resulted in cutting down plum trees (10.6% of respondents). Tall trees (8.1%) were felled because they were difficult and dangerous to harvest. Finally, some trees were felled (7.0%) because of their small fruit size.

Discussion

African plum tree is among the most important indigenous food tree in Central Africa. However, the cultural value of African plum was not manifested through ceremonial gift exchanges, unlike products from other indigenous fruits trees, such as *Garcinia kola* seeds (Egbe *et al.* 2012), *Raphia* wine and products (Mogue Kamga *et al.* 2020), and many others (Ingram and Schure 2010). Nonetheless, some peculiarities distinguishes it from other fruit trees: theft of African plums, as well as that of kola nuts, would be punished by customary code (Laroussilhe *et al.* 1964, in Ndamba 1989). The value of the tree was also expressed through its symbolic use as a living memory. Among the Beti, it was commonly said that plum trees were planted or dedicated to the memory and commemoration of exceptional people. This could be manifested by planting a seed from a parent (especially older or notable people), or by letting a young child plant the seed, leading to an association between the two. This association also exists when a tree is planted for a newborn (Sone 2017). It was also seen in the fact that some trees are named after people, either the cultivator himself or other relatives. In southern Africa as well, fruit trees are often known by individual names, referring to community members (Akinnifesi *et al.* 2010).

Ethnovariety-naming dynamics and evolving perceptions along the urban-rural gradient

A vast number of different names were recorded, in all three ethnic groups surveyed. Given the scarcity of the scientific literature referring to varietal names of fruit trees within the studied area, it is difficult to say how remarkable this result is. Nonetheless, comparison is possible with other fruit tree species in Central Africa. Imported fruit trees, which entered production systems later than indigenous species such as the African plum tree, could also have different names, but in limited number and without symbolic value. This is the case, for example, for mangoes and avocadoes, whose names qualify instead their origin (Ngaoundéré's mango, German mango), their importance in local trade ("Number One" mango; Rey *et al.* 2004) or their texture ("avocado-butter").

For the Beti people in particular, the nomenclature described for the perennial species *Musa* × *paradisiaca* was more expanded than for the previously investigated fruit trees (Mengue Efanden *et al.* 2003), but was not as dense as that reported for the African plum tree. This extensive ethnovarietal nomenclature, which is also found for other African perennial species in East and West Africa (Ouedraogo 1995; Wickens 2008; Gwali *et al.* 2011), expresses the salience of the species (Berlin 1972), and the human involvement around it (Berlin 1992). The great morphological differences between African plums also foster the diversity of local names, with phenotypic boundaries being delineated by cultural preferences (Atran 1998). The names of ethnovarieties shared along the urbanization gradient for Beti owners also indicate the flow of information within communities through learning the general distinctive features of ethnovarieties and their associated names (Boster 1986). This, along with the fact that more than half of the names recorded originated from Beti owners, is quite a puzzle and begs for more investigation on the singular nature of this finding.

Linguistic expressions are indicators of the cultural and social dimensions and value of agricultural resource management: through local names, significant elements of the cultural and economic importance of varieties, and of their commonness, are revealed (Zimmerer 2003). It is thus worth noting the predominance of names referring to size in the local species nomenclature system. With regards to the variation in perceptions of the species (i.e. the way sensory and biological information regarding African plums are interpreted by their owners) along the gradient, the most common fruit traits used to define African plums differed. More rural dwellers cited fruit size as the primary criterion for distinguishing plums, whereas fruit taste was predominantly mentioned by urban dwellers.

Perceptions also differed among ethnic groups in all sites except for urban sites where they were homogeneous. Rozzi (2013) proposed that rural-urban migration, by bringing in cities a diversity of ethnic groups, favors knowledge homogenization. Even if plant knowledge loss is not necessarily occurring in urban areas (Avila *et al.* 2015), the homogenization of knowledge among different cultural groups could be a likely consequence of urbanization, and has already been described regarding plant knowledge in urban markets (Pirondo *et al.* 2011). In our case, the effect of bringing together different ethnic groups in the urban area might be acting on its nomenclature as well. Indeed, the names of ethnovarieties differ from one language to another

(Bamileke, Bassa, Beti), and even within Bamileke, as it is a linguistically fragmented language (Watters 2006). But with the marketing of African plums linking people from different ethnic groups and languages, it would be interesting to see to what extent ethnovarieties that have been given local names are renamed by people specialized in the plum trade. The nomenclature of other food products was simplified in urban markets (Roussel and Woldeyes 2013), with traditional names being adapted to optimize trade and fruit market value (Otieno *et al.* 2015).

A typology of preferences according to sites: from subsistence to market values

Ethnic groups had more similar preferences in urban sites than in rural sites. Regardless of the type of use considered (self-consumption, buying or selling), the fruit preferences criteria were not significantly different between ethnic groups in the urban site. The urban specificity that might come into play is that owners are exclusively consumers, rather than sellers.

The different rationales of consumers and sellers, studied through preferences related to the different uses of plums, showed that preferences changed in the rural, peri-urban and urban sites as a result of the different uses. Fruit taste was valued preferentially through self-consumption preferences and buying preferences, which are those of consumers. On the contrary, fruit size was ranked first in selling preferences. The shift from preferences based on a quality-related trait (fruit taste) expressed by urban dwellers, who are mostly consumers, to preferences based on a quantity-related trait (fruit size) expressed by rural dwellers, who are mostly sellers, shows the strong influence of market-driven logics Although the preferences expressed by consumers ("buying preferences") target fruit taste, the owners prefer to sell large fruits. These fruits are indeed more expensive on the market (Awono *et al.* 2002), and thus more profitable to the sellers. They are also more sought after by *buyam-sellam*, intermediaries who buy crops or non-timber forest products in bulk and then retail in urban markets (Ndoye *et al.* 1997) and who are in charge of a large part of the African plum trade. As they travel to rural areas to buy plums and transfer them to urban markets, their overall standards are less focused on quality (Levai *et al.* 2015).

In rural sites, where most owners are also sellers, the important value of plum size is corroborated by the fact that this trait is also overrepresented for preferences which are categorized as consumer preferences (self-consumption, buying), preferences that are never associated with size in urban sites. But the two uses (as self-consumed food or as a traded commodity) are not necessarily contradictory. Rural Beti owners for instance seem more attached to the criterion of taste than the other ethnic groups and even cite it when expressing their preferences as sellers. Incidentally, this logic is more in line with buying preferences, which are mainly based on fruit taste.

Perceptions and preferences turned into practices

Analyzing the variation in perceptions and preferences is crucial as both reflect cultural or economic values, and influence management practices. Owners indeed aim at increasing the phenotypes producing the desired fruits in the managed tree populations (Sousa Júnior *et al.* 2018). Here, following the valued traits and preferences, practices of rural and urban dwellers also differ. *Dacryodes edulis* is mainly propagated using seeds collected by farmers on trees presenting fruits with desirable traits. Urban dwellers are using the fruit size criterion less often than peri-urban and rural tree owners to select the tree to be propagated. The fruit size criterion is more cited by rural Bassa owners than Beti or Bamileke as a key trait for selecting seeds used to plant their trees. As Bassa owners also cited fruit size as a preferential buying criterion, this shows how preferences may be translated to some extent into planting practices. However, improved planting materials, which would be the best option for obtaining trees with the most valued characteristics, were used by only a few owners. The improved varieties (named cultivars) developed in agronomic centers (Ndindeng *et al.* 2008) were indeed perceived by these owners as having valuable traits: small trees are easy to harvest, and large fruits easy to sell. But the improved cultivars were also described as having non-valued traits, being characterized as fragile and short-lived trees, with fruits whose taste tends to become more and more sour over the years.

Concerning selection practices, Vasquez and Gentry (1989) described some attributes motivating, in the context of commercial trade, the felling of less profitable trees. They were related to: (i) the fruiting phenology of the species (dioecious species with separate male and female trees), (ii) fruit accessibility, and (iii) demand for fruit. As for *D. edulis*, trees bear either female flowers only or a variable ratio of male and hermaphrodite flowers (Kengue 1990). For this latter category, trees presenting a high proportion of male flowers tend to be removed. The African plum trees most likely to be felled are therefore (i) unproductive trees bearing mostly male flowers, (ii) large trees that are difficult to harvest and (iii) trees that bear the fruits least valued on the market (sour fruits, small fruits). But the low percentage (<10%) of owners citing fruit size as a reason for selection also shows that market logic is not the only reason for choosing which trees to keep. Plum trees that bear small fruits are for instance often referred to as "the children's plum tree". In contrast to trees bearing large fruits, often preserved for the market or the family, these trees are used by children to collect the fruits without causing problems. The diversity of plums' morphology and taste thus ensures that the uses and expectations of the species' cultivators complement each other. Its maintenance acts as a strategy to maintain food security or reduce risks (Rimlinger *et al.* 2019). More broadly, the diversity of local varieties can be valued in itself, as an object of pride for cultivators (Caillon and Degeorges 2007; Brush 2008).

Implications for African plum diversity

From our study, two sets of values are coexisting. On the one hand, sellers value a quantity-related trait, and thus express that the increased market accessibility for large-sized plums is a strong incentive for them to grow trees of these varieties. Other studies have highlighted the predominant role played by economic and social drivers in the choices made by individual farmers between local varieties (Dedeurwaerdere and Hannachi 2019). Farmers' management is altered by changing market incentives due to the growing importance of certain products or varieties (King 2007). Farmers' tendency to produce specific crops and varieties that meet market demand is identified as one of many changes underway in sub-Saharan agricultural systems (Houssou *et al.* 2018). On the other hand, consumers value a quality-related trait, taste, which is found in all kinds of different ethnovarieties, and thus express a wide range of preferences. This was also expressed when some owners answered that they had no criteria for the African plums they were planting: all types of ethnovarieties had the same value to them. Indeed, attributes valued by local market dynamics often fail to explain the variation in the number of varieties grown by farmers (Smale *et al.* 2001).

Our findings underscore the need to analyze several levels of knowledge (different ethnic groups, urban and rural dwellers) to obtain a comprehensive picture of the considerations underlying the diversification or erosion of varietal diversity. Urban centers can be important repositories of diversity, as urban owners are less concerned about selecting trees based on fruit size. Urban home gardens thus have multiple potentials as production and conservation areas, all the more as they represent unexpected places to safeguard species' genetic diversity (Rimlinger *et al.* 2020). On the other hand, although more specific criteria are applied to planting material in rural sites than in urban and peri-urban ones, their effect is limited by the predominant allogamy of the species: cross-pollination between trees, combined with high heterozygosity (high genetic variability), prevents the reproduction of targeted maternal traits. As selection practices are rather weak on trees that bear non-valued fruits, pressures on intraspecific plum diversity remains relatively low. The selective retention of these less useful trees in the future might also depend on land pressure, which is increasingly strong along the urbanization gradient.

The value of local varieties is assessed first and foremost by what farmers say and do about them, and is therefore based on their uses and expectations (Zimmerer 1996, Brush and Meng 1998). These uses respond to different needs and constraints, both for cultivators themselves (ecological benefits, consumption qualities, cultural significance) and for use on the market, in order to take advantage of commercial opportunities (Bellon *et al.* 2015). Uses and preferences are functionally related in that different traits valued for local varieties correspond to different uses (Ekue *et al.* 2010; Lunduka *et al.* 2012). In our case, the main uses–self-consumption, sales–are respectively associated with fruit taste and fruit size. These preferences are translated into practices as rural owners who are also sellers are more likely to plant trees using seeds from large fruits. Market integration is expected to change the uses of local varieties, with a shift from subsistence to trade-oriented strategies, and to homogenize the valued traits of varieties (Van Dusen and Taylor 2005). For African plum trees in Cameroon, this risk is mitigated by the current exclusion of fruit crops from government food security policies, which therefore receive neither preferential treatment under subsidized seed dissemination programs nor extensive tree breeding programs. Competition between improved cultivars and traditional seed systems is thus weak. In addition, market development could go hand in hand with the development of new opportunities for local varieties (Keleman *et al.* 2013).

Conclusion

African plums are food products as well as commodities. Urban dwellers use them as the former only, whereas rural dwellers have both uses. Throughout the urbanization gradient, the different ethnic groups investigated here name and classify the existing intra-specific fruit variation using mainly morphological and organoleptic criteria. Interestingly, the most valued fruit criteria vary by use type: taste for self-consumption and purchase, size for sale. They also differ according to the groups of owners. People in rural sites, and especially in the Bassa group, tend to prefer larger fruits. This preference influences the seed selection process, with rural Bassa owners also favoring fruit size over fruit taste.

Divergences between rural and urban dwellers show how choices, preferences and strategies must be understood in a broad economic and social context, in which owners' strategies are underpinned by different logics. Indeed, the choice of ethnovarieties responds to distinct motives along the urbanization gradient: city dwellers have few constraints, apart from lack of space, whereas rural dwellers are driven by demand and market requirements. Some owners are seeking a pool of different varieties, despite the call of market intermediaries for bigger fruits. Our study stresses the need to explore the consumption/production linkage to inform policy decisions. It also suggests that urban areas should be considered not only for the threats they pose to local knowledge (Tang and Gavin 2016), but also for the opportunities they offer as production areas able to foster knowledge exchanges. In the rural sites studied, located within the main production areas for African plum, the fact that some fruit phenotypes are favored could point to a possible negative impact on their diversity. However, the situation is offset by the species being highly outcrossing and by the limited removal of trees whose fruits are not valued. This calls for a methodology formally testing the intensity of varietal selection in commercial areas, and comparing it, along with preferences and propagation practices, in areas further away from commercial networks.

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Figures

Figure 1. On the left, simplified representation of the urbanization gradient, going from urban sites to three rural sites passing through peri-urban sites, and the distribution of the three ethnic groups (Bamileke, Bassa, Beti). On the right, map of Cameroon with the rural and peri-urban sites, with a close-up on Yaoundé for the urban sites.

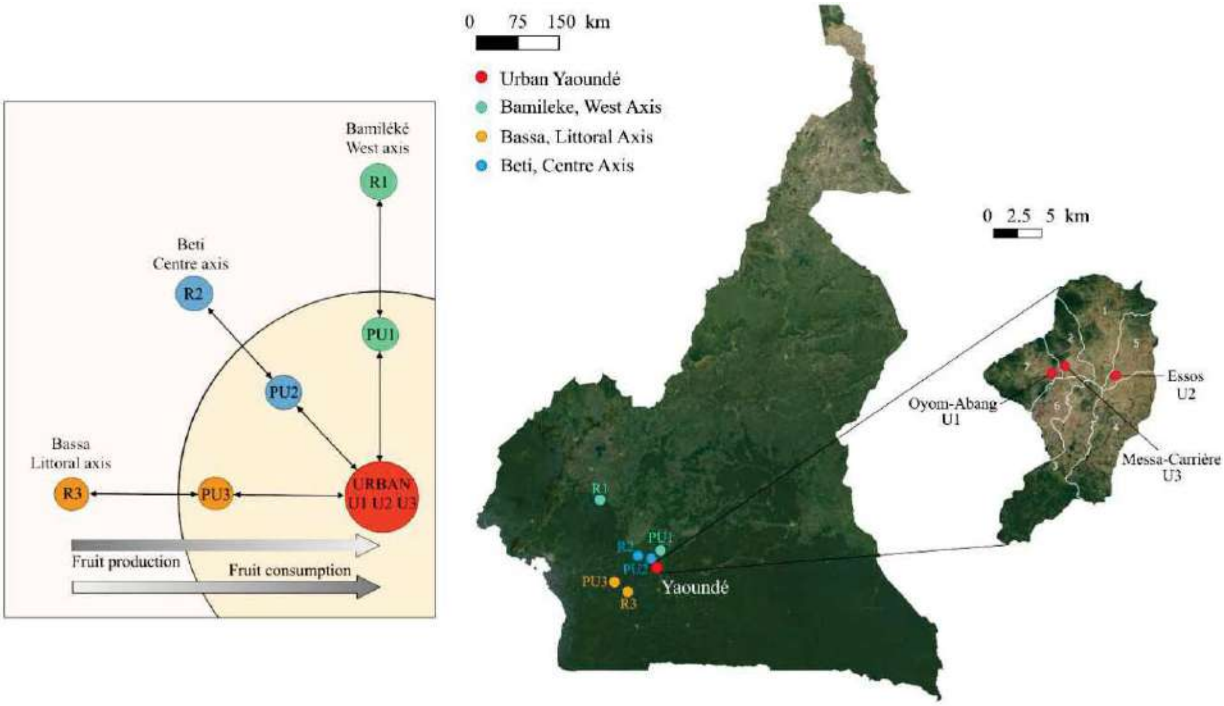


Figure 2. Mosaic plot showing associations between tree owners from different sites (PU=peri-urban) and between different ethnic groups (Bamileke, Bassa, Beti) in rural sites, and the three most cited criteria; T: taste, FS: fruit size, SC: skin color. The color corresponds to Pearson residuals from the χ^2 test: red for the under-represented intersections ($p < 0.05$), blue for the over-represented ones and grey for those that are close to the values expected in the independence hypothesis.

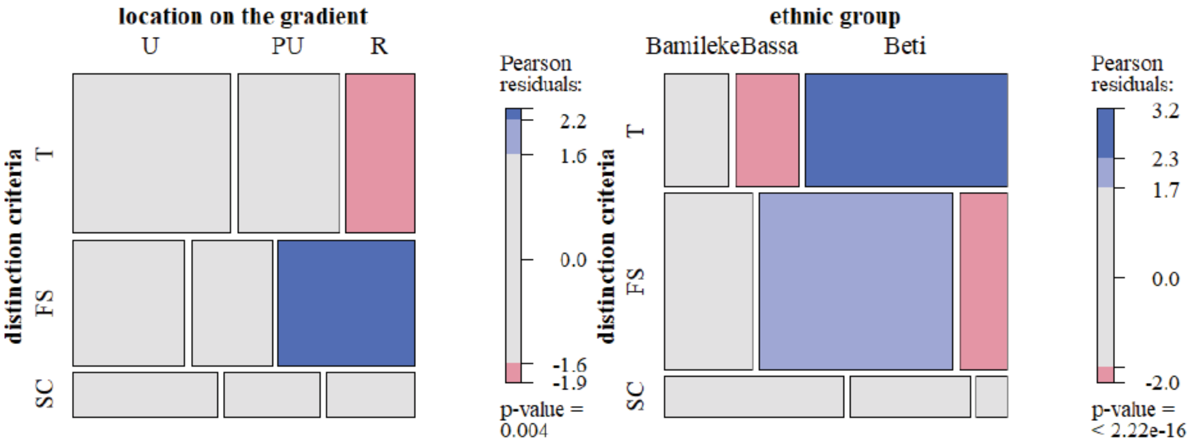


Figure 3. Mosaic plot showing associations between tree owners from different sites and between different ethnic groups (Bamileke, Bassa, Beti) in all the sites combined, and the three criteria mainly used to name ethnovarieties, FS: fruit size, T: taste, SC: skin color.

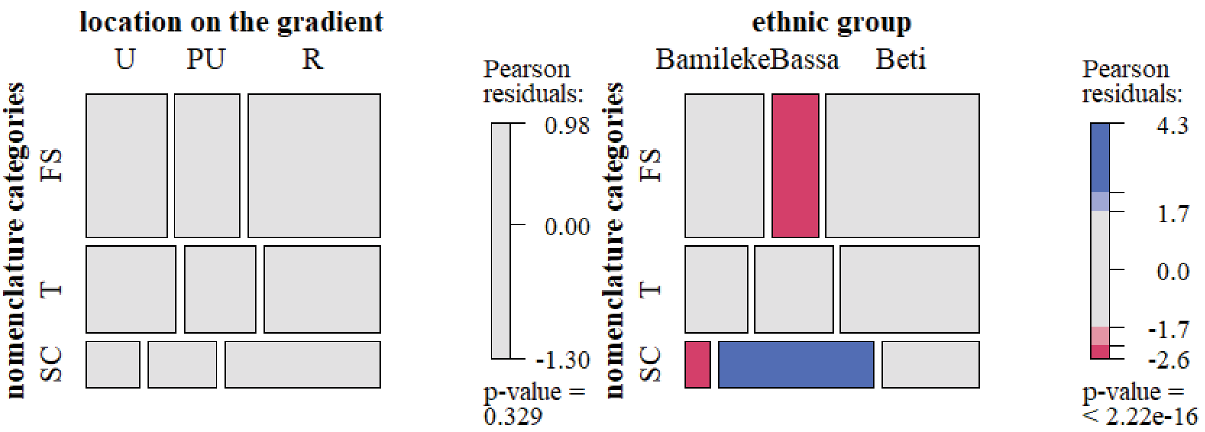


Figure 4. Sunburst graph showing the different categories of criteria (center of the graph) and subcategories (edges of graph) of the nomenclature of African plums. **M**: Morphological, **O**: Organoleptic, **S**: Symbolic, **E**: Environment, **T**: Type of tree ("natural" vs "improved" tree).

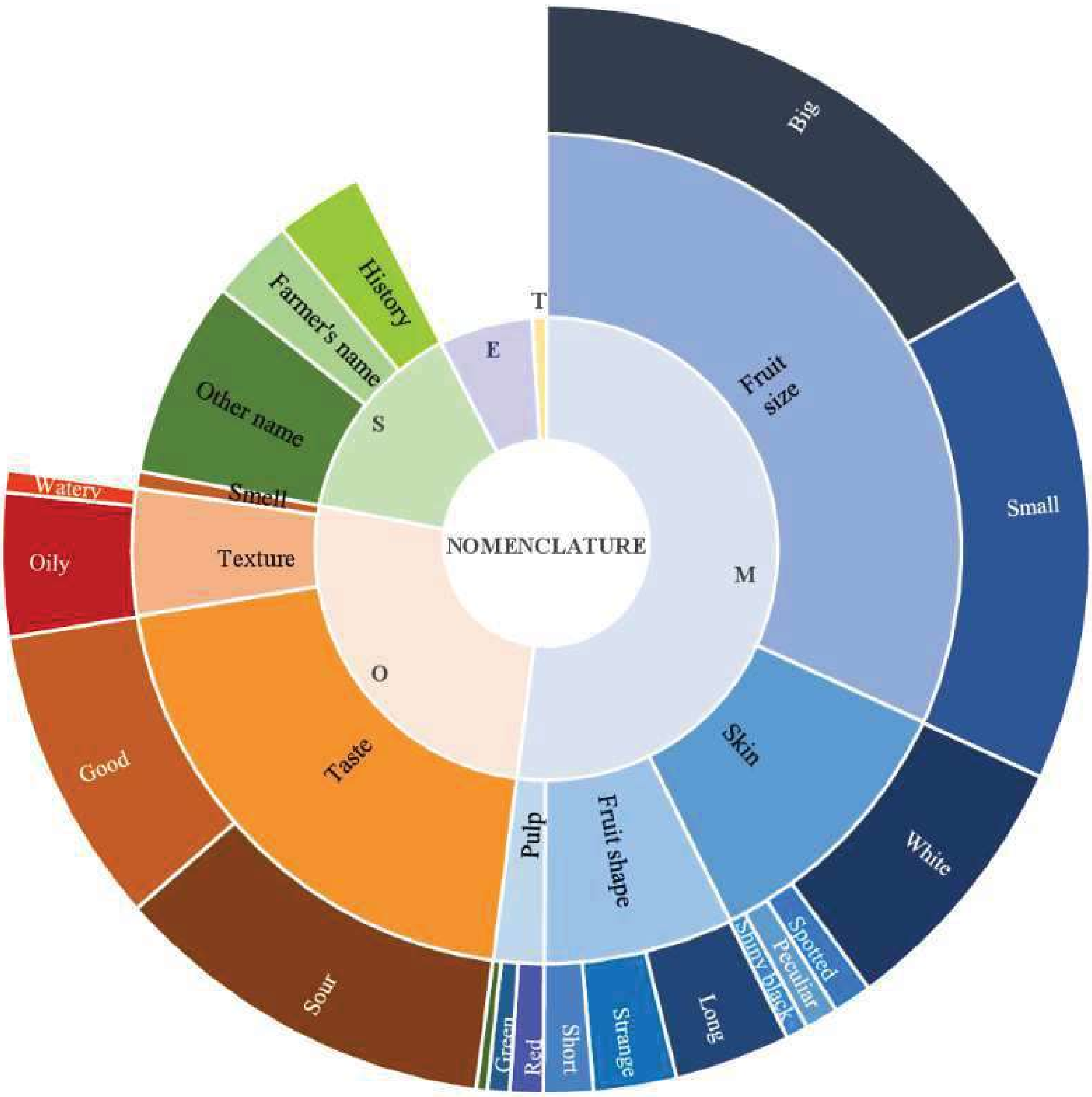


Figure 5. MCA discriminating different groups of ethnovarieties based on pulp and skin color, fruit size and taste, with as a supplementary (inactive) variable the preference criteria relative to the ethnovarieties (those that were and were not valued). Fruit traits on the right side of the graph correspond to the valued ethnovarieties, fruit traits on the left side of the graph correspond to the non-valued ethnovarieties.

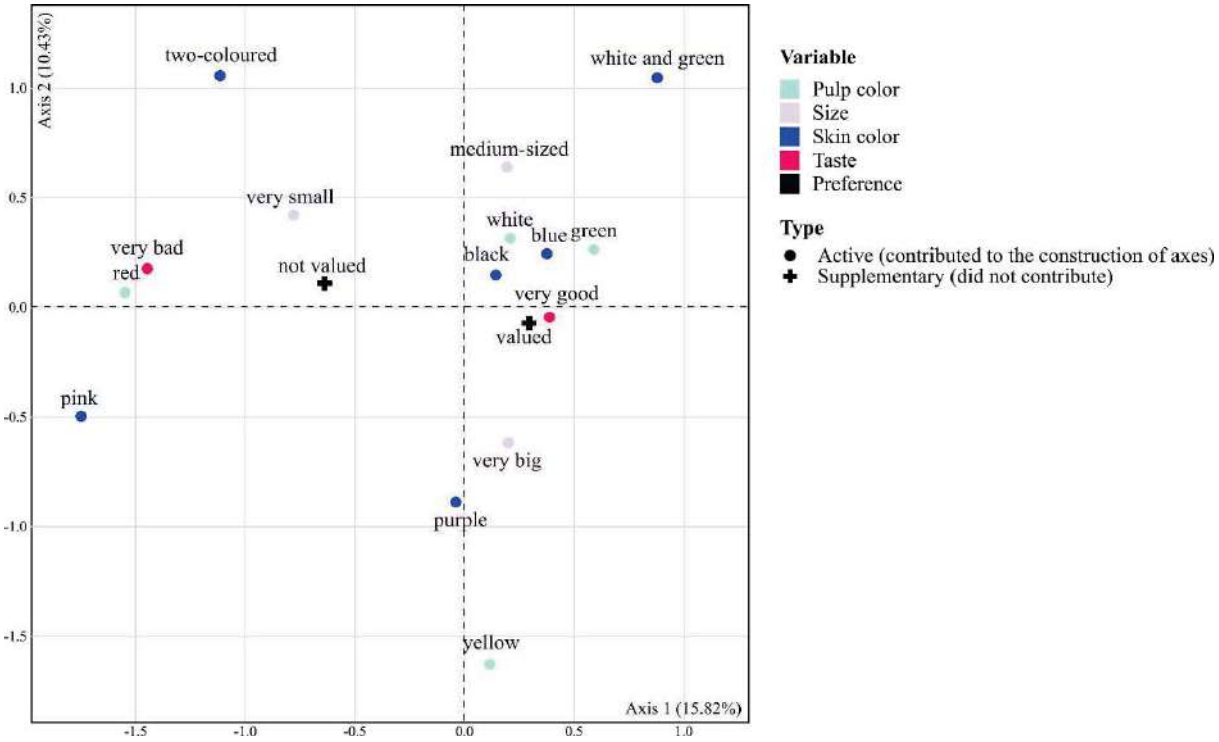


Figure 6. Bar plot showing the relative frequencies of the four most cited fruit criteria depending on the type of use considered. The stars signal criteria that were significantly different between categories of preferences.

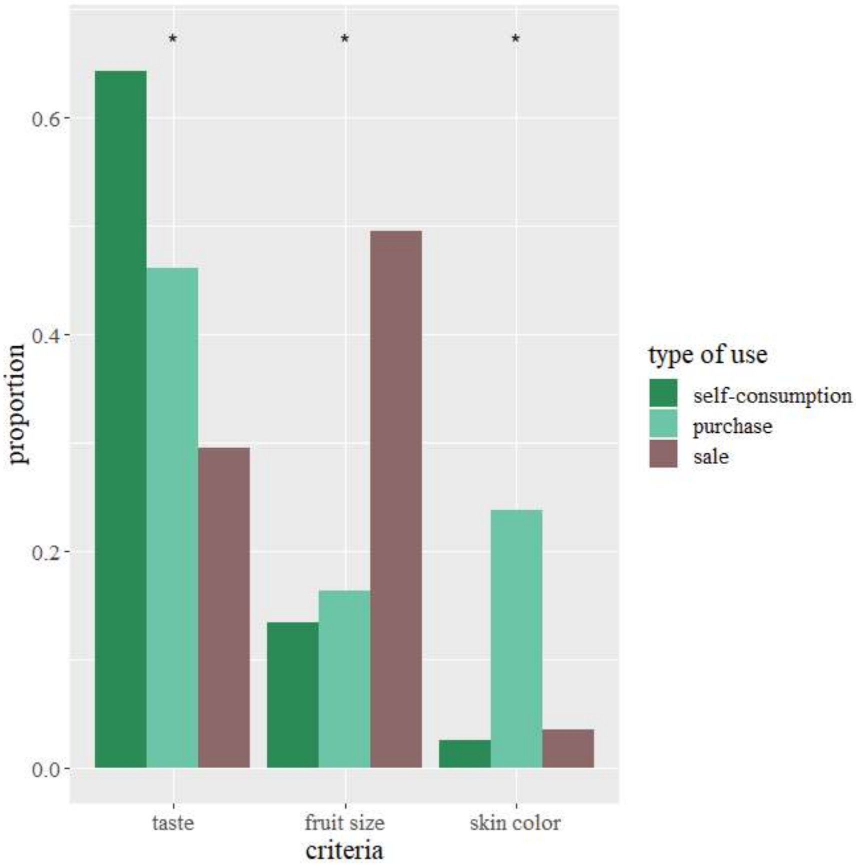


Figure 7. Mosaic plot showing fruit traits (T: taste, SC: skin color, S: fruit size, NC: no criterion) cited by owners from different ethnic groups in rural sites for different types of uses, from left to right: purchase, self-consumption and sale.

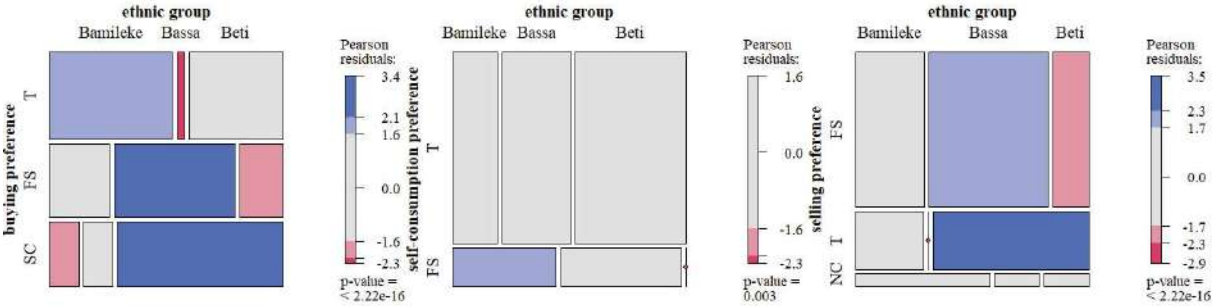
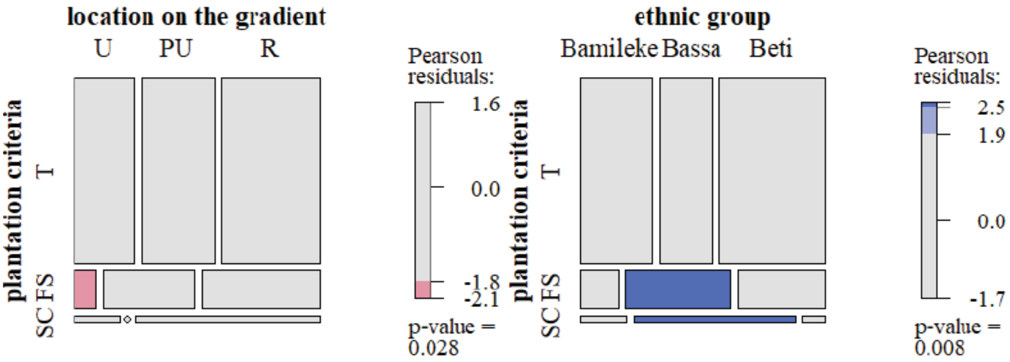


Figure 8. Mosaic plot showing planting choices (T: taste, FS: fruit size, SC: skin or pulp color), according to gradient location and ethnic group in the rural sites.



Tables

Table 1. Summary of *D. edulis* tree owner characteristics along the urbanization gradient.

Gradient Ethnicity	Urban (N = 173)	Peri-urban (N = 127)	Rural (N = 141)	Total (N = 441)
Bamileke (Men/Women)	60 (24/36)	27 (16/11)	48 (34/14)	135 (74/61)
Bassa	37 (10/27)	50 (31/19)	44 (34/10)	131 (75/56)
Beti	76 (37/39)	50 (30/20)	49 (25/24)	175 (92/83)

Table 2. Data recorded during interview with tree owners and variables tested.

Qualitative variables	
• Buying preference criteria • Self-consumption preference criteria	• Selling preference criteria • Planting preference criteria • Selection criteria
Quantitative variables	
• Number of used propagation techniques *(e.g., seed directly sown, seed sown in nursery, graft-propagation)* • Number of traditional practices	• Number of used production techniques *(e.g., tree pruning, notching, use of fertilizers, use of pesticides)*

Table 3. Distinguishing criteria of African plum trees cited by tree owners (N= 350). Criteria in italics do not refer to fruit traits.

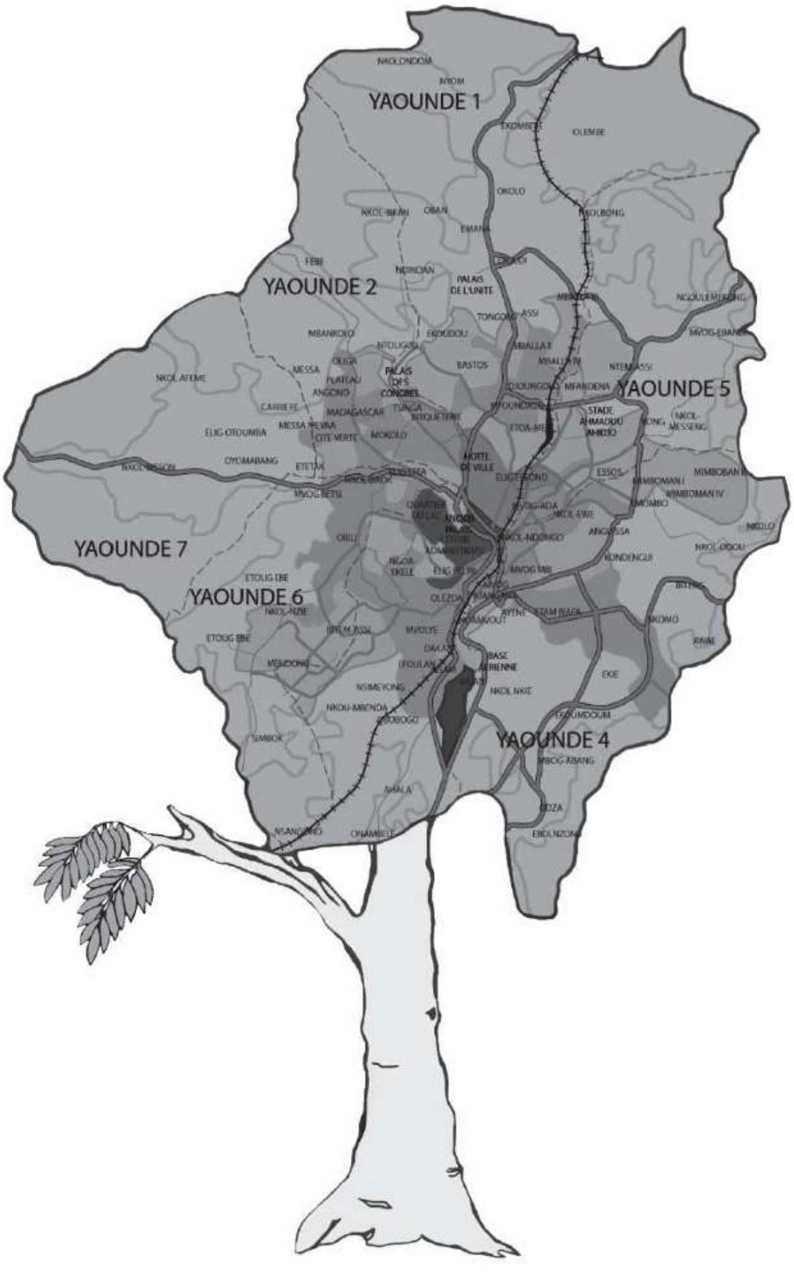
Distinction criteria	Number of citations	Frequence of citations
Taste	250	0.30
Fruit size	231	0.28
Skin color	162	0.19
Fruit shape	80	0.10
Pulp color	60	0.07
Pulp texture	22	0.026
Tree productivity	15	0.018
Pulp width	7	0.008
Skin quality	4	0.005
Leaf size	2	0.002
Others	4	0.005
Total	837	1

Table 4. African plum tree propagation and cultivation practices reported by tree owners of different ethnic groups ("Bami" stands for Bamileke) along the gradient (means ± sem). Means in a row without a common superscript letter (a, b, or both) differ ($p < 0.05$) as analyzed by one-way ANOVA and the Tukey's test.

	Location on the gradient								
	Urban (173)			**Peri-urban (127)**			**Rural (141)**		
Number of propagation practices	1.7 ± 0.07^{a}			2.0 ± 0.08^{b}			$\mathbf{2.2 \pm 0.07^{b}}$		
	Bami	Bassa	Beti	Bami	Bassa	Beti	Bami	Bassa	Beti
	1.9 ± 0.1	1.6 ± 0.1	1.6 ± 0.1	2.0 ± 0.2	2.1 ± 0.2	2.0 ± 0.1	2.1 ± 0.1^{b}	2.6 ± 0.2^{a}	2.0 ± 0.1^{b}
Number of production techniques	1.9 ± 0.1			2.2 ± 0.1			2.2 ± 0.1		
	Bami	Bassa	Beti	Bami	Bassa	Beti	Bami	Bassa	Beti
	2.3 ± 0.2^{a}	1.7 ± 0.2^{ab}	1.6 ± 0.2^{b}	3.0 ± 0.2^{a}	2.0 ± 0.2^{b}	1.9 ± 0.2^{b}	3.6 ± 0.2^{a}	1.6 ± 0.1^{b}	1.3 ± 0.1^{b}

Chapitre 4

Dynamiques sociales d'une espèce fruitière urbaine : implications pour sa diversité génétique



Trees and their seed networks: the social dynamics of urban fruit trees and implications for genetic diversity

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Abstract

Trees are a traditional component of urban spaces where they provide ecosystem services critical to urban wellbeing. In the Tropics, urban trees' seed origins have rarely been characterized. Yet, understanding the social dynamics linked to tree planting is critical given their influence on the distribution of associated genetic diversity. This study examines elements of these dynamics (seed exchange networks) in an emblematic indigenous fruit tree species from Central Africa, the African plum tree (*Dacryodes edulis*, Burseraceae), within the urban context of Yaoundé. We further evaluate the consequences of these social dynamics on the distribution of the genetic diversity of the species in the city. Urban trees were planted predominantly using seeds sourced from outside the city, resulting in a level of genetic diversity as high in Yaoundé as in a whole region of production of the species. Debating the different drivers that foster the genetic diversity in planted urban trees, the study argues that cities and urban dwellers can unconsciously act as effective guardians of indigenous tree genetic diversity.

Key words: urban trees, genetic variability, conservation, indigenous trees, seed exchange network, sustainable management, urban gardens, resilience.

Introduction

Crop seed exchange networks, shaped by social dynamics, have a deep influence on the organization and breadth of plant diversity in human-managed environments. The decisive effect of social organizations, through bonds of kinship, marriage or friendships, has been shown to influence the flows of crop planting materials (Delêtre *et al.* 2011; Labeyrie *et al.* 2014; Jika *et al.* 2017). In turn, crop species' diversity within rural home gardens is influenced by exchanges of planting material (seeds or clonal material) (Ellen and Platten 2011; Díaz-Reviriego *et al.* 2016). In urban environments, although the propagation of plants by humans has been described through the lens of their accidental role in propagule dispersal (Auffret and Cousins 2013; Bullock *et al.* 2018), there are only few studies mentioning intentional seed circulation patterns for crop species, and notably for perennial crop species such as fruit trees. In South America, it was shown that seeds and seedlings from urban home gardens were acquired at local markets, but also through networks of exchanges involving relatives and neighbours (Peroni *et al.* 2016; Sierra-Guerrero and Amarillo-Suárez 2017). Together with the major contribution of natural dispersion and historical plantings in shaping the plant diversity present in urban home gardens, the ones of local nurseries and social networks were also emphasized in the San Juan area, in Puerto Rico (Torres-Camacho *et al.* 2017). In Amazonia, the contribution of rural genetic material to urban gardens has also been demonstrated: the major source of exchanged planting material from urban home gardens is through gifts, which come both from communities and households in the city, and from those in rural areas (WinklerPrins 2002). Conversely, the role of urban centres as sources of planting material has also been exemplified, with rural gardeners purchasing planting material closer to urban centres (Ban and Coomes 2004; Coomes 2010). These different findings highlight the need to understand the extent to which rural-urban bonds may be drivers of crop plant intra- and inter-specific diversity in urban environments.

Trees are a traditional component of urban spaces, mostly planted for ornamental purposes or for their shade. The multi-faceted role of urban trees is now well recognized since they provide ecosystem services critical to urban citizen wellbeing: green places for leisure, noise reduction, climate mitigation, air and water purification, energy savings, habitats for biodiversity, and carbon sequestration (Chen and Jim 2008; Livesley *et al.* 2016; Turner-Skoff and Cavender 2019). In tropical regions, urban trees also contribute to diets (Orsini *et al.* 2013; Sardeshpande and Shackleton 2020). In Kinshasa, fruit production was cited as the main reason why urban dwellers introduced trees around their home, with trees providing additional services (shade, medicine, cash), such as African plum trees, avocado trees and mango trees, being highly valued (Etshekape *et al.* 2018). Among the studies that have characterized urban food-tree species diversity and composition within cities in Central Africa (Bernholt *et al.* 2009; De Lacy and Shackleton 2017; Nero *et al.* 2018; Bolanle-Ojo *et al.* 2020; Chimaimba *et al.* 2020), the origin of planting material is sometimes questioned by separating local (native) and exotic (non-native) trees. But the information on the source of the planting material for local trees is not available. This question matters all the more since the social dynamics of tree planting influence the distribution of tree genetic diversity.

Genetic diversity is the raw material for species adaptation to global changes such as new climates, pests or diseases, or pollution. This fundamental species survival mechanism, that has taken millions of years to develop, is critically threatened by anthropogenic disturbances such as overexploitation, deforestation, land-use change, or climate change. On the other hand, humans can play a positive role in the conservation of species' genetic resources. In particular, research shows that through their traditional practices and local ecological knowledge, tropical smallholder farmers actively participate in safeguarding agricultural biodiversity (Galluzzi *et al.* 2010; Thomas *et al.* 2012; Kull *et al.* 2013; Sthapit 2016). By maintaining many different crops and varieties, farmers retain a range of options for adapting to environmental change and thus promoting resilience in agricultural systems (Frison *et al.* 2011; Lin 2011).

There have been very few studies on the social dynamics of urban fruits trees planting and their influence on species genetic diversity. Our study explored how urban intra-specific diversity can be embedded within human social life (Bennett *et al.* 2017). We developed a multi-disciplinary framework bringing together ethnoecological and genetic data to (i) assess the sources used by urban dwellers to plant new trees; and (ii) evaluate the consequences on the urban intra-specific genetic diversity. Our study examined the seed origins and genetic diversity of an urban population of a major indigenous fruit tree species from Central Africa, the African plum tree (*Dacryodes edulis*, (G. Don) H.J. Lam, Burseraceae), and underlined its specificity by contrasting it with those of a larger rural population.

Materials and Methods

Species description

Dacryodes edulis (G. Don) H.J. Lam (Burseraceae) is a culturally important fruit tree species originating from the Congo Basin. It is mostly cultivated as a fruit and shade tree in coffee-cocoa agroforests (Rimlinger *et al.* 2019), and in home gardens (see pictures in S1 Fig). *Dacryodes edulis* is a predominantly outcrossing species (Kengue *et al.* 2002). It is pollinated by insects, especially Apoidea (Fohouo *et al.* 2001). In natural populations, apes, birds and mammals act as seed dispersers, but anthropogenic seed dispersal is more important in cultivated populations, as seeds and fruits are commonly exchanged between relatives, neighbours, and villages (Degrande *et al.* 2013). The fruits (African plums) are one-seeded drupes. Fruits present a wide range of sizes, shapes, colours (epicarp, mesocarp) and textures (Waruhiu *et al.* 2004; Youmbi *et al.* 2010). They contain more than 50% lipids, but also proteins, fibre and vitamins (Fonteh *et al.* 2005; Stadlmayr *et al.* 2013). Their fleshy, buttery pulp is highly popular, and is consumed with roasted maize, plantain, or tubers. African plums are part of the diet of all cultural groups in tropical Cameroon.

Ethnoecology data collection and analysis

To investigate the social dynamics of urban tree planting, we selected the city of Yaoundé (3.9 million inhabitants), the second largest city in Cameroon. The founding of the city dates back to the late 19th century. Along with most of the large sub-Saharan cities, it has quickly expanded and stretches now over more than 300 km^2. Agricultural activities are carried out both in its urban core and in the surrounding peri-urban areas, ensuring cheap food supplies. Yaoundé's cultural mosaic reflects its urbanization history: because of the destruction and resettlement of neighbourhoods during the colonial era, the city's districts comprise mixed populations coming from different cultural and geographical areas of Cameroon (Bopda 2003; Togolo 2019). *Dacryodes edulis* trees are present throughout the city, especially on its outskirts where the home gardens are mostly bigger, and in low-income neighbourhoods where home gardens contain more useful plant species (Cilliers *et al.* 2013).

We led interviews with tree owners (N=84) in one neighbourhood of Yaoundé, Oyom-Abang, and recorded their cultural origins. This neighbourhood is culturally diverse (different cultural groups are represented, in order of importance in our sampling: Beti, Bassa and Bamileke) and presents a moderate to dense urbanization level, with approximately 105 inhabitants per hectare. Despite urbanization, a network of trees and gardens is interspersed among buildings, with many fruit trees present in backyard home gardens. These home gardens are generally small, located around the family compound, and include mixed crops (fruits, vegetables, tubers). The selection of respondents was based on their ownership of one or more *D. edulis* trees. Prior to the interview, tree owners were informed of the research intentions and of their right to participate or decline. At the end of the interview, tree owners 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.

For comparison with the urban area, the African plum tree planting practices were also recorded with tree owners (N=47) in a rural area. The rural area is located in the West region, one main production area of *D. edulis* fruits in Cameroon (Temple 2001), which supplies the major markets of the two biggest cities in Cameroon, Yaoundé and Douala. Different cultural groups are present throughout the region, the most numerous being Bamileke and Bamoun. Cultivators of this region focus on the production of cash crops, especially cocoa and coffee, but integrate many other fruit trees species in their fields.

We obtained information on the location from where the propagation material (seeds, seedlings) originated for 121 *D. edulis* trees in the urban area. In the rural area, this information was recorded, for trees present in home gardens and fields, in two villages, Manjo and Bandounga (94 trees in total). Four different categories of seed origin were distinguished: the seeds could have been taken directly by the farmer from his own field/home garden (category *farmer's own trees*); the seeds could have been taken outside of the farmer's own field/home garden but still originate from either the same village (category *same village*) or from a different village (category *different village*); or the seeds could have been bought at the market or in a nursery (category *market or nursery*), meaning that the fruit has travelled through a commercial exchange network and possibly originates from far away. For the urban population, the seeds could come from the village of origin of urban dwellers with a rural background, which was made explicit with the subcategory *% coming from the village of origin* in the category *different village*.

Given the high proportion of seeds sown from fruits bought in markets in Yaoundé, the origin of the fruits sold on these markets was traced back through interviews with a total of 89 sellers of African plums, in nine markets of Yaoundé (Emana, Etoudi, Marché des fruits, Mendong, Mfoundi, Mokolo, Mvog Mbi, Nkolbisson, Nsam) from July to September 2017.

Genetic data collection and analysis

To understand the link between urban tree planting behaviours and species genetic diversity characteristics in the city we analysed the level of genetic diversity from the urban population of Oyom-Abang (250 ha) and compared it to that of one rural population stretching over a main production area of *D. edulis* fruits in Cameroon (200,000 ha, Fig 1). In this aim, we sampled 450 trees in Oyom-Abang (164 trees included in the ethnoecological dataset + 286 additional trees sampled only for the genetic characterization) and 399 trees in the rural population (94 trees from the ethnoecological dataset + 305 additional trees), that stretches across the West, Littoral and Centre regions (278, 79 and 42 trees respectively, in a total of fifteen villages).

We extracted the DNA of these 849 urban and rural samples following the protocol of Mariac *et al.* (Mariac *et al.* 2006) (S1 Dataset). The genetic diversity was investigated using fourteen nuclear microsatellite markers amplified in two multiplexes following Rimlinger *et al.* (Rimlinger *et al.* 2020). All the individuals were genotyped using an ABI 3500 XL sequencer (Applied Biosystem, Foster City, California, USA) at the CIRAD Genotyping Platform in Montpellier, France. Electropherograms were visualized and scored with the microsatellite plugin in Geneious 7.1.3 (https://www.geneious.com). For each locus and population, observed and expected heterozygosity (H_O and H_E), inbreeding coefficient (F_{IS}), the effective number of alleles (Ne), the rarefied allelic richness (AR), null allele frequency (r) and the corrected inbreeding coefficient corrected for the presence of null allele (F_{null}) were estimated using INEst 2.2 (Chybicki and Burczyk 2009) and SPAGeDi (Hardy and Vekemans 2002). The level of population differentiation (as estimated by the F_{ST} fixation index) and the test of genetic structure (permutation of individuals among all populations) were obtained with SPAGeDi. Levels of diversity between the urban and rural populations were compared with one-way analysis of variance, controlling for the loci effect. The distribution of the genetic diversity between the two populations was further tested using the Bayesian clustering analysis implemented in STRUCTURE (Pritchard *et al.* 2000) with admixture ancestry, correlated allele frequencies and no prior information about population origin. K was set from 1 to 10, and each run was replicated 10 times, with a burn-in period of 10,000 followed by 40,000 Markov Chain Monte Carlo repetitions. To visualize the distribution of genotypes of the rural and urban populations, a principal component analysis was performed on the microsatellite dataset using the R package adegenet (Jombart 2008).

Results

From the interviews conducted with tree owners on their private land, the geographic origin of the seeds used for plantation indicated wide differences between the rural and urban tree populations (Table 1).

In Yaoundé, 93% of *D. edulis* planted seeds came from beyond the city borders, with half of the seeds used for planting coming from markets, either from Yaoundé markets or from more distant locations known for the quality of their African plums (Makénéné's market for instance, located 200 kms away from Yaoundé). Fruits sold on Yaoundé's markets come from five main areas, located at various distances from the capital, up to 370 km away (S2 Fig). The second most important source of seed is provided by rural villages beyond Yaoundé's border (36%). The main cultural groups present in the sampled urban population are Bamiléké, Bassa and Beti (Fig 1), who originate from different regions (respectively western Cameroon, the Littoral and the central region, an area partly covered by this study, see the Methods section).

Travelling back to their villages is an opportunity for urbanites to bring back fruits and seeds, and the diversity of geographical origins of the cultural groups settled in the city has led to planting seeds from different locations (Fig 2). In contrast, in the rural population, more than 75% of the trees came from the same village territory. These differences of origins translate into wide-ranging differences (Table 1, Wilcoxon signed rank test, p-value < 2.2e-16, effect size = 0.514) in the average distance travelled by seeds.

The level of genetic diversity (rarefied allelic richness for k=300 gene copies) was high and similar (p-value = 0.945, Wilcoxon rank sum test) in the urban and in the rural populations despite large differences in the geographical coverage (250 ha for the urban population, 200,000 ha for the rural one) (Table 2). The genetic composition is largely similar between the two populations as shown by (i) the weak but significant genetic differentiation (F_{ST} = 0.0057 and is significantly different from 0 as measured by an exact G test, p-value <2.2e-16); (ii) the principal component analysis (S3 Fig); (iii) the Bayesian clustering analysis where individuals are attributed to two (weakly differentiated) genetic clusters without relation to their population of origin (S4 Fig).

Discussion

Urban contexts embody a complex socio-cultural nexus where food supply to humans is crucial (Seto and Ramankutty 2016). As shown by this study, similar levels of genetic diversity were observed between the urban and rural tree populations despite large differences in the geographical coverage. The planting practices of urban trees with regards to cultivated fruit trees in the cities can thus generate positive evolutionary dynamics for their diversity. This can be explained by two intertwined processes.

First, big cities are at the heart of market flows and social networks. A vast majority of food produced in rural areas reach cities to be sold in marketplaces. If particularly appreciated, the seed from a good fruit is preserved and planted within the family compound, hence safeguarding its genetic material. This process of fruit exchanges through commercialization from production/rural areas to large cities may account for one of the most important drivers of urban dynamics in favour of the genetic diversity of native fruit trees, whereby most genetic resources of a given valuable fruit species are potentially channelled to cities, being 'attracted' by consumers' demand. Diversity in an urban setting tends to be high not only because there is a lot of inflow of plant material from different surrounding regions but also because seeds used for planting harbour a significant proportion of the genetic diversity of their population of origin given the predominantly outcrossing mating system of the species (Kengue *et al.* 2002).

Second, this large exchange matrix of genetic material is further enhanced by what is known as an 'economy of affection' matrix (Hyden 1983), which refers to the strong affective links shared within a group of people with the same socio-cultural background. For people who migrated to an urban context, this bond includes a relationship with nature and the crops (from species to varieties) from the rural area of origin. Through gift-giving chains, urban dwellers can also have access to wild plants from rural areas (Buchmann 2009). Urban dwellers thus commonly commented that "the best fruits [were] those cultivated in the village of my family". This fits with the more general influence of kinship systems on farmers' seed exchange networks (Delêtre *et al.* 2011; Leclerc and Coppens d'Eeckenbrugge 2012; Labeyrie *et al.* 2016). As big cities attract people from all over the surrounding localities and from various cultural groups, this may be another important factor that determines a concentration of genetic resources from different rural areas in cities.

The way tree planting material is sourced in cities is therefore critical for the current pattern of diversity. The low levels of tree genetic diversity reported in some cities of temperate regions was explained by their reliance on poorly diversified planting material (selected and clonal material) from commercial nurseries (Vanden Broeck *et al.* 2018). The genetic diversity observed in Yaoundé could thus be rooted in the informal seed exchange system, where seeds are loosely selected and planted by urban dwellers.

The diversity of *D. edulis* trees planted in gardens is supported through exchange networks that include kin, friends, and outsiders. The strong reliance on local systems of production and exchange, and the maintenance of rural-urban links, fuel germplasm transfers and lead to unintended positive consequences, such as conservation outcomes and urban sustainability (WinklerPrins 2002). According to traditional conservation perspectives, anthropogenic actions are framed as a major cause of biodiversity erosion (Li *et al.* 2020), or as being deliberately designed to safeguard targeted species and ecosystems (Callicott *et al.* 1999). However, there is a third way where the sum of individual actions contributes to biodiversity conservation: when pursuing other goals, here coping with subsistence needs and maintaining socio-cultural cohesion, they may also maintain genetic diversity of useful crop species (Kirkpatrick 2007). A broader analysis replicating the framework of this study for other crops (Heraty and Ellstrand 2016) and cities pantropically would show how important this serendipitous "safeguarding" of genetic diversity is. Urban home gardens can actually contain a significant proportion of indigenous species (35-60%) which represent additional candidates to test the importance of urban areas for the conservation of species genetic diversity (González-García and Sal 2008; Akinnifesi *et al.* 2010).

According to the United Nations (United Nations 2019), more than two-thirds of the world will live in urban areas by 2050, having major direct and indirect impacts on biodiversity (Grimm *et al.* 2008). It is therefore essential to give to the biodiversity of these anthropogenic landscapes the special attention they deserve (Aronson *et al.* 2014) as well as to promote the contribution of urban trees to human food supply and other ecosystem services. However, with the anarchic urbanization in the rapidly expanding cities of developing countries, these trees are at risk of being wiped out. There is thus an urgent need to identify the main socioeconomic, cultural and political drivers as well as more effective urban biodiversity conservation instruments which may contribute to conserve and further diversify fruit trees in the city (Goddard *et al.* 2010; Aronson *et al.* 2017; Garrard *et al.* 2018). A focus on genetic diversity conservation, promoted by socially desirable measures, can help ensure green, healthy, food provisioning and more resilient cities sheltering crop plant species with a high adaptive potential, in the face of climate change and growing urban populations (McDonnell and MacGregor-Fors 2016; Endreny 2018). Concomitantly with the conservatories and botanical gardens, parks, orchards and individual backyards, which actively support the goal of conserving biodiversity, it is time to better understand, analyse and promote urban home gardens and green spaces as repositories of tree genetic diversity.

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Figures

Figure 1. Map of Cameroon showing the two sample populations. The large rural population on the left (white dots) comprises the two localities where the social dynamic of tree planting was investigated (1, Manjo; 2, Bandounga). The urban population (Yaoundé, orange square) is enlarged on the right, showing the urban trees sampled in the 250-ha area, with information on the ethnic group of the tree owners. Map image was created on QGIS version 3.6.1 (QGIS Development Team 2019). We used OpenStreetMap (www.openstreetmap.org) and shapefiles of Earth with shaded relief and water from Natural Earth (www.naturalearthdata.com/ and of the global tree cover in the area, described in Hansen *et al.* (Hansen *et al.* 2013) and available at glad.umd.edu/Potapov/TCC_2010/. GPS coordinates are stored in the S1 Dataset.

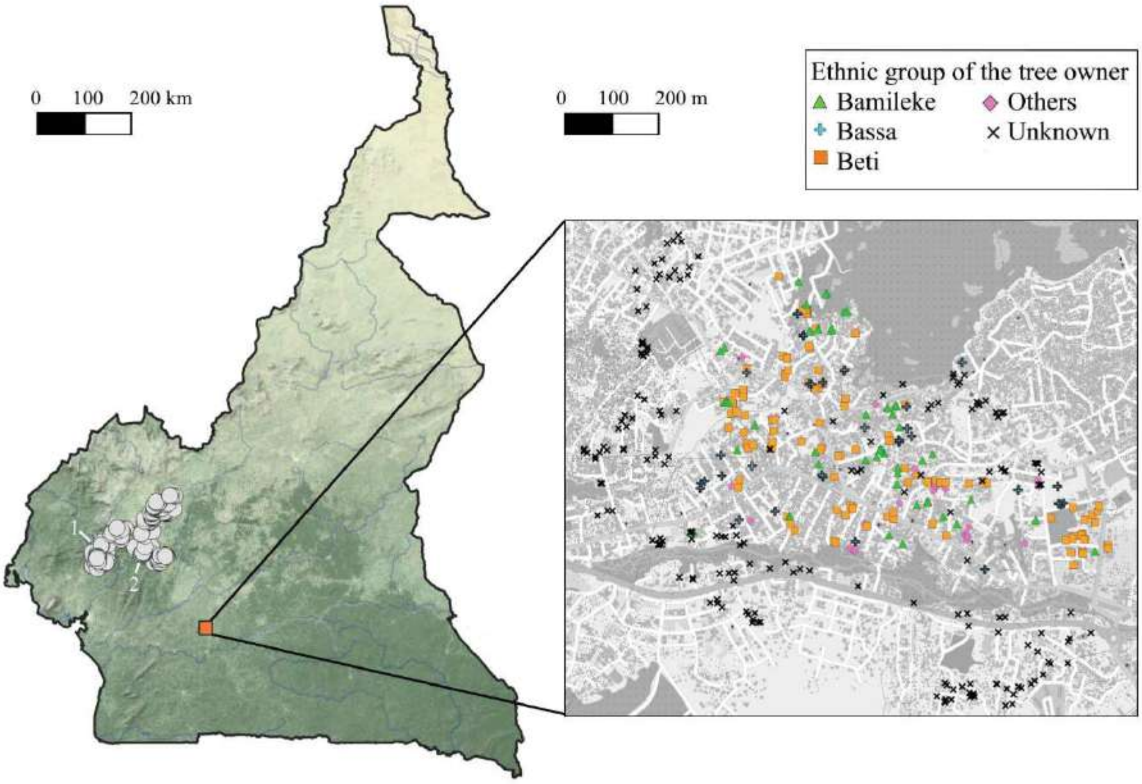
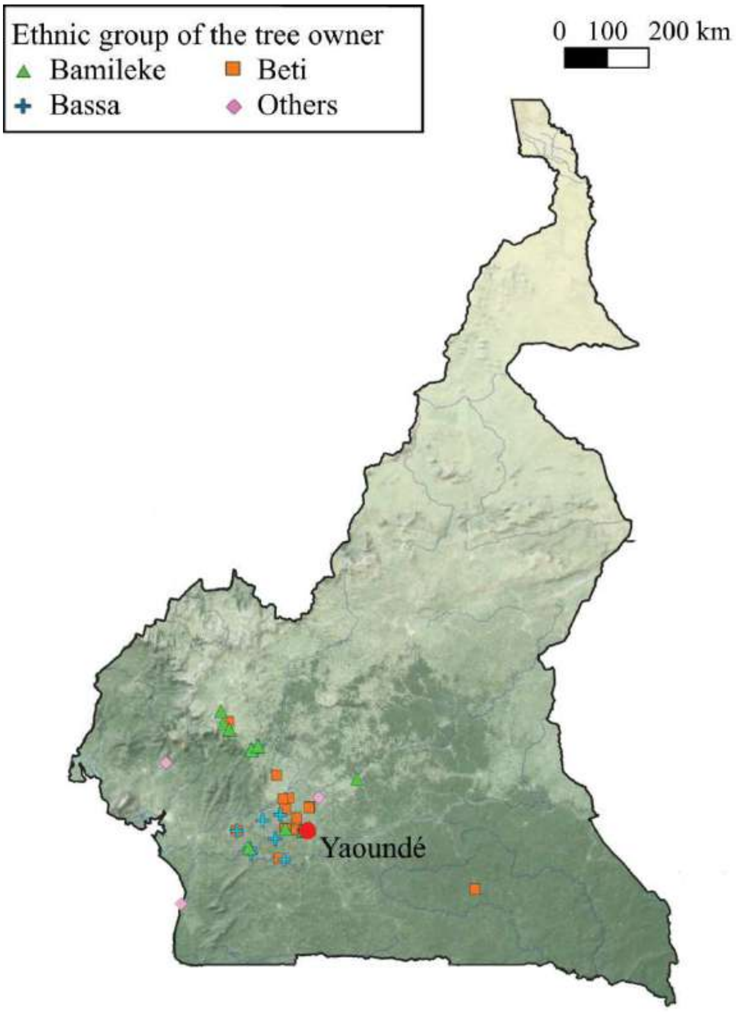


Figure 2. Provenances of the seeds used to plant different urban trees in Yaoundé. The different trees sampled in Yaoundé (n = 121, red dot) are mapped with symbols depending on the ethnic group of the tree owners. Map image was created using the same program and shapefiles as Fig 1. GPS coordinates indicating seed provenance can be found on the OSF repository of the project.



Tables

Table 1. Differences in seed provenance and distance between rural and urban populations of *D. edulis*.

Population	Seed provenance (frequency) *					Seed distance (km) *
	N	Farmer's own trees	Same village	Different village (% village of origin)	Market or nursery	All provenances combined
Urban	121	0.04	0.03	0.36 (81%)	0.57	45.4 ± 5.9
Rural	94	0.30	0.46	0.06	0.18	3.7 ± 0.8

* the seed provenance and seed distance between the two populations are significantly different (as tested respectively with the Pearson's Chi-squared test and Wilcoxon rank sum test; p-value < 2.2e-16).

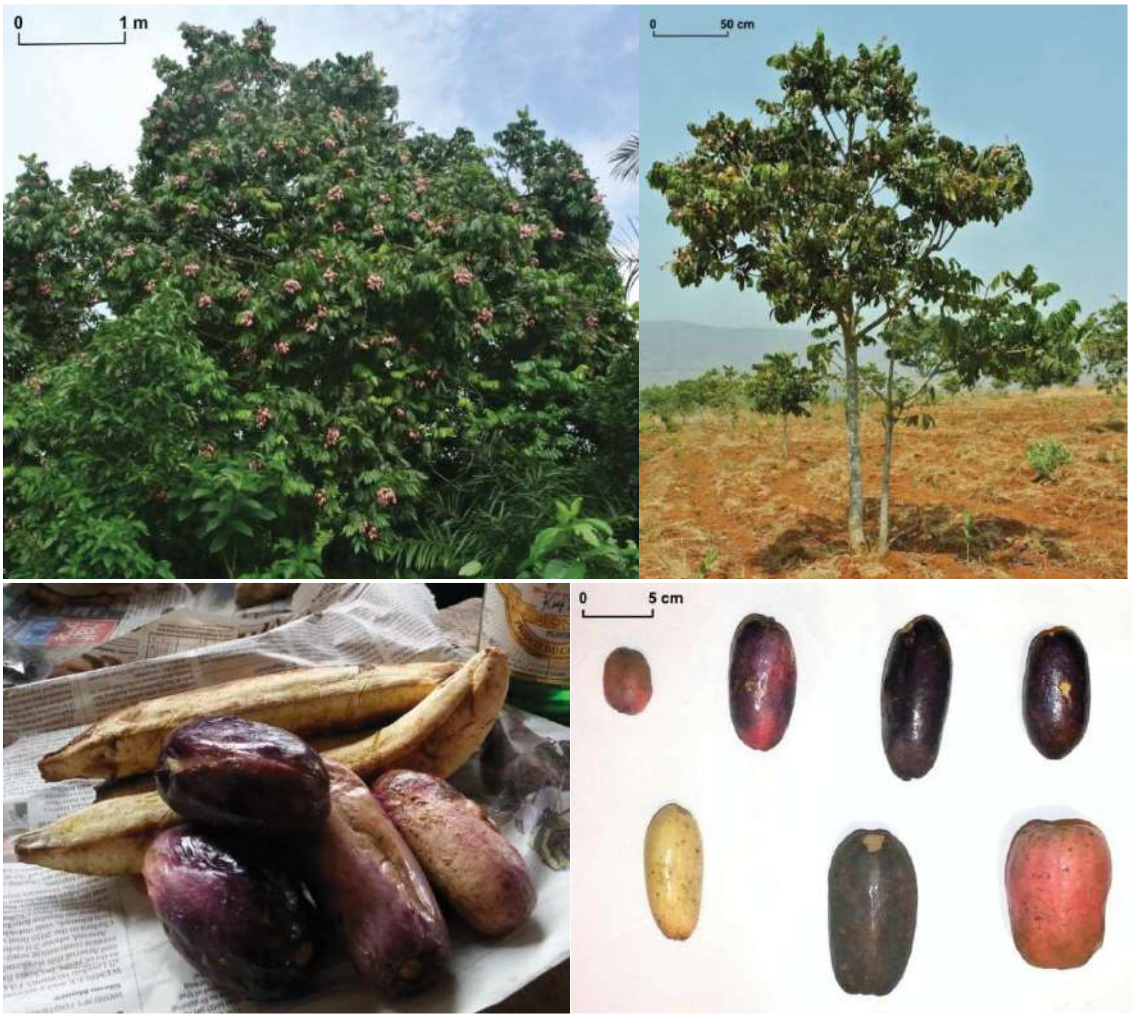
Table 2. Genetic diversity indices of the rural and urban populations of *D. edulis*.

	N	NA	NAe	AR	H_E	H_O	F_{IS}	F_{null}
Urban population	450	18.3 ± 2.9	6.17 ± 1.1	15.7 ± 2.5	0.761 ± 0.039	0.629 ± 0.051	0.181 ± 0.047	0.0201 ± 0.0012
Rural population	399	18.8 ± 2.7	6.40 ± 1.2	16.1 ± 2.3	0.768 ± 0.038	0.659 ± 0.045	0.149 ± 0.036	0.018 ± 0.0014

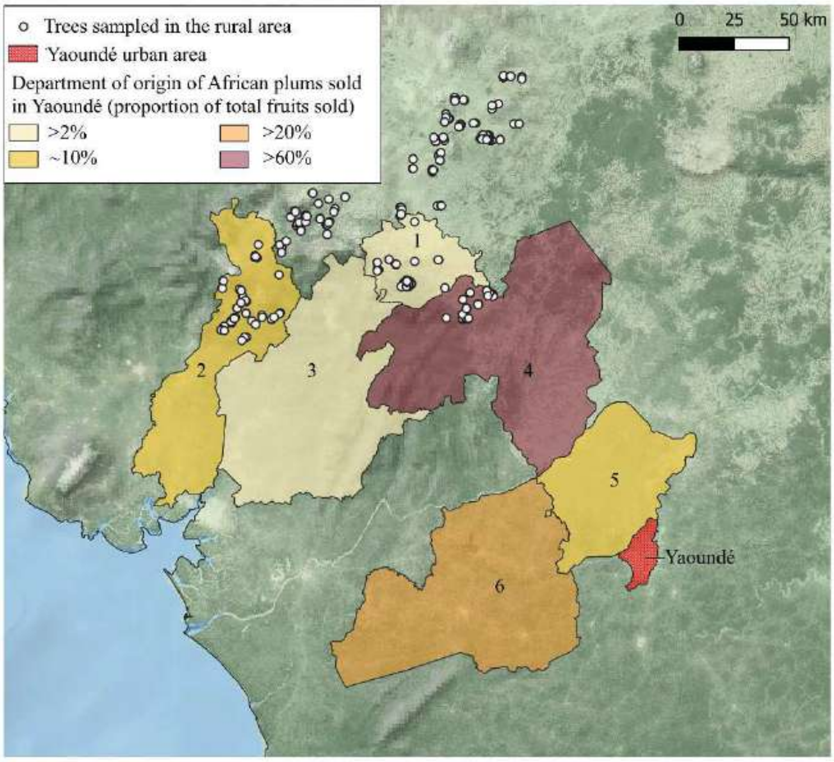
NA: number of alleles; Ne: effective number of alleles, AR: rarefied allelic richness for k=300 gene copies; H_E: expected heterozygosity; H_O: observed heterozygosity; F_{IS}: inbreeding coefficient; F_{null}: inbreeding coefficient corrected for null alleles; values are means ± SEM.

Supporting information

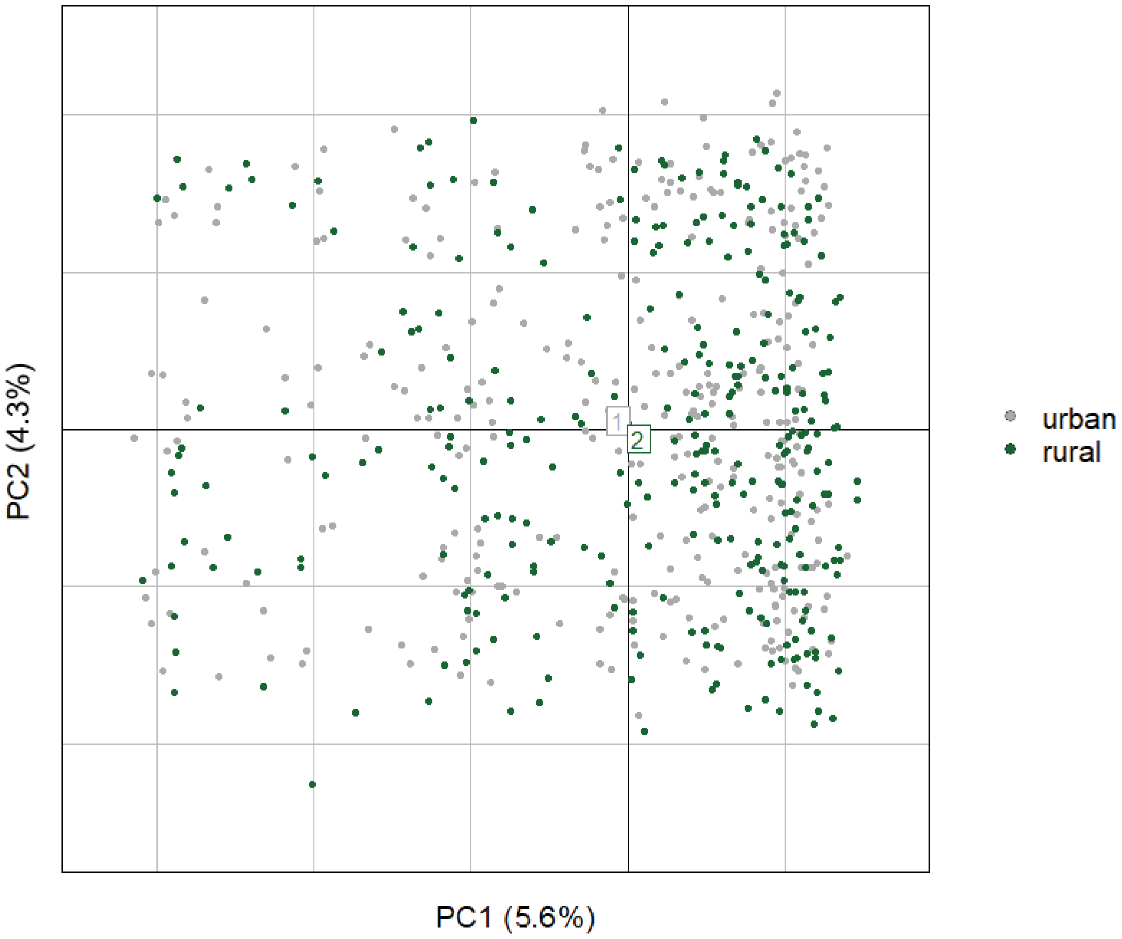
S1 Figure. Pictures of the species. Mature tree in an agroforest (above left); young tree in an orchard near Koutaba (above right). Roasted African plums and plantains sold in the streets (below left); fruit varietal diversity (below right). Pictures from the authors (1, 2, 4: A. Rimlinger; 3: J. Duminil).



S2 Figure. Provenance of fruits sold in Yaoundé markets. Provenance of African plums in Yaoundé main markets, accounting for more than 95% of the total volume of sold fruits reported by the sellers (1: Ndé; 2: Moungo; 3: Nkam; 4: Mbam-et-Inoubou; 5: Lékié; 6: Nyong-et-Kéllé). Dots correspond to the rural trees sampled for the genetic analysis. Administrative boundaries of Cameroon were added using a shapefile available at data.humdata.org/dataset/cameroon-administrative-boundaries. The source of the map data are stored in a database (market_provenance.txt) deposited in the OSF repository of the project.

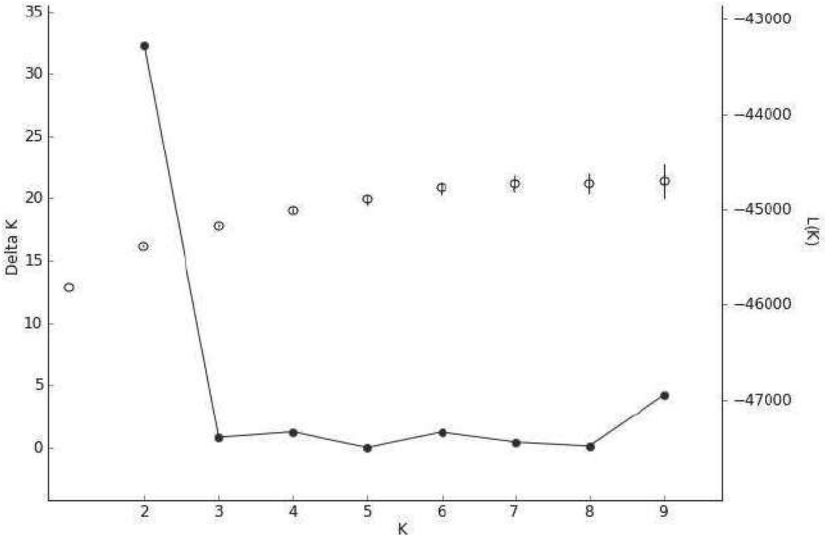


S3 Figure. Principal component analysis (PCA) of Dacryodes edulis microsatellite diversity from the urban and rural populations. The PCA was performed on the allele frequencies of each individual. Genotypes were clustered to show maximal differentiation along the first and second principal component (PC1 and PC2). Individuals do not cluster according to their urban or rural origin, indicating the absence of population structure.

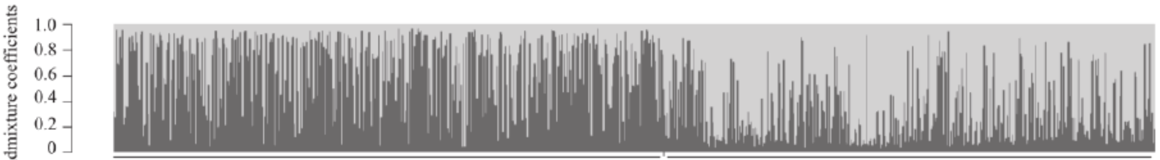


S4 Figure. Bayesian clustering analysis.

S4a: Changes in K values from the mean log-likelihood probabilities (right axis) and plot of mean likelihood L(K) and variance per K value (left axis) from STRUCTURE runs where inferred clusters (K) ranged from 1 to 10.

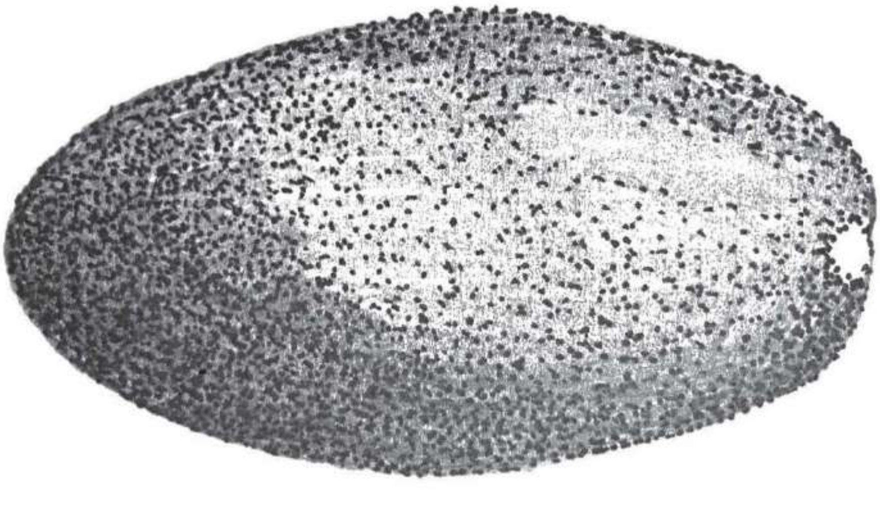


S4b: Output of clustering analysis by STRUCTURE software for two clusters (K=2) of the 849 trees, using fourteen microsatellite markers, grouped by origin (urban trees, rural trees). Each vertical bar represents one individual and shows its inferred cluster membership; black and gray colors correspond each to one cluster. If both colors are present, the haplotype consists of a mixture of markers assigned to both black and gray clusters. The samples from the urban area and rural area were assigned in different proportions to each cluster. Using an assignment probability threshold of 0.8, 41% and 8% of individuals from the urban population were respectively assigned to the black and gray clusters (51% were presenting intermediate genotypes) and 5% and 45% of individuals from the rural population were respectively assigned to the black and grey clusters (50% were presenting intermediate genotypes).



Chapitre 5

Distribution des diversités morphologique et génétique du safoutier suivant différents groupes ethniques le long d'un gradient d'urbanisation



Distribution of morphological and genetic diversity in *Dacryodes edulis* following urbanization gradients in multi-ethnic Cameroon

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Abstract

Biocultural factors can influence the dynamics of crop species diversity. By conducting interviews with tree owners and sampling for genetic analyses, we explored different aspects of the social, spatial and temporal dynamics of diversity in a perennial crop, the African plum tree (*Dacryodes edulis*). The study was carried out in Cameroon, at a geographical scale corresponding to the trade network of the species around the capital city of Cameroon, Yaoundé. We focused on three urbanization gradients corresponding to three different ethnic groups. This involved sampling nine different sites, three in the urban area of Yaoundé, three in the peri-urban area of Yaoundé, and three additional rural sites corresponding to the main African plum production areas that supply the capital. We assessed (i) how seed exchange networks were organized along these 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. We showed that 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 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, which could be due to the relatively closed seed exchange network in rural sites, among other factors discussed. On the contrary, the genetic diversity of urban sites was enhanced by extensive 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 prospects for *in situ* species conservation.

Key words: ethnic groups, population genetics, seed sytems, tree crops, urbanization gradient

Introduction

The morphological and genetic variation of useful plant species are influenced by human actions through the selective pressures they exert, via seed selection practices or selective removal of undesirable individuals (Gepts 2004), and through niche construction, which substantially transforms selective environments (O'Brien and Laland 2012). The effects of cultivation on intraspecific plant diversity are often primarily evidenced by comparative studies of wild against cultivated populations. For 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, as in Barnaud *et al.* (2009) who assessed that the morphological and genetic data in the *Sorghum* complex were congruent with the local taxonomy distinguishing a gradient from wild to domesticated morphotypes. Sampling can also be carried out from wild ecosystems to more or less intensively managed environments, such as agroforestry systems and monocultures, as in Cabrera-Toledo *et al.* (2020), thus allowing to test the influence of different management practices on intraspecific diversity. In their case, contrary to expectations, little differentiation between populations was found in the different compartments. This result was possibly due to high exchanges of germplasm among producers, which stresses the importance of taking the seed exchange dimension into account in studies of this kind.

Informal seed exchange networks, on which smallholder farmers rely heavily for their cultivated species seed supply (Coomes *et al.* 2015), are among the explanatory factors behind the maintenance, or the erosion, of intraspecific diversity (Pautasso *et al.* 2013). The temporal evolution of diversity can be tracked through diachronic analyses for orthodox seeds stored from past collects (Barry *et al.* 2008; Olodo *et al.* 2020). For tree species, which are long-lived, an effective 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. Using this approach on jackfruit trees in Bangladesh, Witherup *et al.* (2019) found downward trends in diversity over time, which was not exacerbated for trees propagated using saplings from nurseries. 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. This was established for instance for sorghum in eastern Kenya, where genetic structure appeared to follow the ethnic partition of cultivators, with social boundaries between neighboring ethnic groups limiting seed exchanges (Labeyrie *et al.* 2014). Similar patterns were observed for maize and pearl millet, despite their highly outcrossing mating system, respectively in southern Mexico and in the Lake Chad Basin (Orozco-Ramírez *et al.* 2016; Jika *et al.* 2017).

To our knowledge, studies shedding light on the cultural forces affecting plant intraspecific diversity were only seldom conducted for tree species yet. An investigation of the baobab (*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, which could be solved by designing research frames dealing with finer scales.

As urban areas are attracting mounting interest in terms of their potential for biodiversity conservation (Heath *et al.* 2020), and are melting pots of cultural diversity, they are interesting new places to question the influence of human practices on the genetic diversity of cultivated plants. In sub-Saharan Africa, crop cultivation in urban areas has been identified as an activity involving some inter-ethnic co-operation and active seed exchange among inhabitants a long while ago (Linares 1996). The relationship between human practices and the intraspecific diversity of useful plants, however, is rarely approached along an urbanization gradient, going from rural to urban areas. This article thus addresses the distribution of tree diversity, morphological and genetic, relative to the propagation practices of three ethnic groups settled in the urban center of Yaoundé, Cameroon. To understand the patterns observed in the urban area, the study is organized around three urbanization gradients, each with the predominance of one ethnic group.

We chose as our model species the African plum tree, *Dacryodes edulis*, which is native to the tropical rainforests of Central Africa. First, the species is economically and culturally important its fruits, the African plums, being largely consumed across the region: once cooked, they are eaten as very common snacks or side dishes (Tabuna and Tanoe 2009). Second, African plum trees have been gradually cultivated and commercialized and are now found in home gardens and agroforests from rural up to urban areas (Schreckenberg *et al.* 2002; Nguegang Asaa 2008). They are the fruit trees 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 them the most suitable native tree species for sampling from rural to urban areas. Third, its pollination by insects, Apoidea in particular (Fohouo *et al.* 2001), and its reproductive biology based on cross-pollination between females and male/hermaphrodite trees is well characterized (Kengue *et al.* 2002).

This study aimed to explore different aspects of the social, spatial and temporal dynamic of African plum diversity. By interviewing with tree owners and conducting sampling for genetic analyses, we analyzed how management practices, specifically propagation practices, and the distribution of morphological and genetic tree diversity were intertwined. The study was carried out along three urbanization gradients corresponding to the involvement of three different ethnic groups on the management of the species. To do so, nine different sites were included, three in the urban area of Yaoundé, three in the peri-urban area of Yaoundé, and three additional rural sites corresponding to main production areas of African plum trees that supply the capital city. Management practices vary between these different areas first, because in urban areas African plums are mostly seen as food, whereas they are also commodities in peri-urban and rural areas, areas linked by value-chains engaged in African plum trade (Rimlinger *et al.* submitted). Second, because the seeds from urban trees are more often sourced outside of the city than those from rural trees (Rimlinger *et al.* 2021). We expect that along the urbanization gradients, seed exchanges are extensive in relation to the rural-urban supply chain but also in relation to favored exchanges between people from the same ethnic group. We also expect a stronger genetic structure among rural sites, as these sites are not connected by trade roads, and as exchanges among ethnic groups might be less frequent than exchanges within ethnic groups. Finally, Yaoundé might correspond to a sink of species genetic diversity receiving planting material from different sources (Rimlinger *et al.* 2021).

Here, we extended this framework in three ways. First, 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. Second, the intraspecific morphological diversity of fruits allowed us to understand if there is a correlation between the level of genetic and the morphological diversity. Last, the temporal dynamic of seed exchange network was indirectly investigated by characterizing species genetic diversity through time.

Methods

Study sites and sample collection

In order to characterize the spatial and social dynamic of genetic diversity distribution along *D. edulis* rural-urban supply chain, interviews of tree owners and sampling of tree material for genetic analyses were set along three urbanization gradients connecting the city of Yaoundé to its main African plum supply regions. 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, Yaoundé (Fig 1), allowing to analyze both an urbanization effect and an ethnic group effect. The rural and peri-urban sites were in production regions supplying the urban area of Yaoundé, 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 site along the West urbanization gradient counted more Beti dwellers, the locally-predominant ethnic group, than Bamileke migrants so a mixed sampling (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 urban core and the outlying areas (Togolo 2019). Most dwellers belonged to the Beti ethnic group in the central site of Essos, whereas urban dwellers from all the three ethnic groups above-mentioned were living in the peripheral Oyom-Abang and Messa-Carrière sites.

In total, we interviewed 323 tree owners and surveyed 1060 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). 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 both in the urban, peri-urban and rural sites. Information on fruit characteristics (see below) was fully available only for 592 trees, and information on seed origin used for plantation (see below) was available only for 375 trees. Leaves from 455 of them (from 24 to 83 trees/site) were collected in silica gel for genetic analyses.

Propagation practices: seed origin and characteristics

We recorded owners' information on the geographic origin of the propagation material (seeds, seedlings) used to plant their trees. Missing data and vague locations were removed, and traceable information was obtained for 375 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 nursery (category *market or nursery*), meaning that the fruit travelled through a commercial exchange network and originates from further away. 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).

Characterization of morphotypes and of tree age classes

We asked African plum tree owners to describe, for each sampled tree, the morphological characteristics of its fruits based on an identification sheet [APPENDICE 3] showing different possibilities for fruit size, shape, skin and pulp color. 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 concatenated four fruit characteristics that were demonstrated as the most important to African plums producers and consumers (fruit size, skin color, pulp color and taste; see Rimlinger *et al.* [submitted]) to obtain specific fruit morphotypes. From the initial 1060 trees characterized, we retained 592 trees with a complete morphotype corresponding to the four characteristics. We observed the distribution of morphotypes at the regional scale by displaying their relative abundance. Following the study from Jarvis and al. (2008), where an average richness per farm corresponding to the number of traditional varieties per household was presented, we calculated the richness in morphotypes based on the morphotypes present at the site scale. 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).

To document the evolution of genetic diversity distribution through time, the diameter at breast height (DBH) of sampled trees was measured during surveys in fields or home gardens. We first verified the strength of the correlation between tree diameter measured in the field and age of the tree as indicated by the tree owner (N= 365, Pearson correlation coefficient = 0.4629; see Figure S1). We arbitrarily grouped trees in different age classes, defined as follows: young trees (DBH below 20 cm, 100 trees), middle-aged trees (DBH from 21 to 40 cm, 196 trees) and old trees (DBH above 41 cm, 159 trees).

DNA extraction and genotyping

We extracted DNA from dried leaves corresponding to 455 trees (among which 402 trees with complete fruit morphology available) following the protocol from Mariac *et al.* (2006) and genotyped them using the same 10 out of 21 nuclear microsatellites available for the species (Rimlinger *et al.* 2020), as already done in our previous study (Rimlinger *et al.* 2021). 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 was 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 (*N*e), the rarefied allelic richness (*A*r) 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 (Hardy and Vekemans 2002) and INEST 2.2 (Chybicki and 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 permuting individuals among all sites using 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 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, correlated allele frequencies and information about site origin (LOCPRIOR) priors. 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. The optimal number of K was assessed using STRUCTURE HARVESTER (Earl and vonHoldt 2012).

To characterize the distribution of genetic diversity at the local level, we calculated the kinship coefficient (Fij) between pairs of individuals for different distance classes using SPAGeDi. 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 is 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.

Results

Seed origin according to sites

Data on the geographic origin of the seeds used for plantation, as informed by tree owners, indicated that the distance from seed origin to plantation site strongly differed between sites (Kruskal-Wallis test, p-value = $1.6e^{-13}$). 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 the trees planted in urban and peri-urban sites 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 (Pearson's Chi-squared test, p-value $<2.2e^{-16}$) less represented 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 = 0.012) and similar for Beti and Bassa (p-value = 0.9455).

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

Morphological diversity between sites

The morphotypes were characterized according to three morphological and one organoleptic characteristics (see S2 for distribution of the different characteristics in the sampled sites), with two varieties 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). All three most common morphotypes were present in the nine sampling sites, whereas 66 morphotypes were unique to one site.

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 (Fig 3) illustrated that only a few morphotypes were represented by many different trees, with almost half of the morphotypes ($N = 64$) characterized only once.

Distribution of genetic diversity relative to fruit traits

Using the F_{ST} fixation index, we compared the genetic differentiation between trees based on each of their morphological (fruit size, shape, skin and pulp color) and organoleptic (taste) fruit characteristics. For pulp color, shape and taste, all F_{ST} values from comparisons between pairs among categories were not significantly different from zero. For skin color, the observed F_{ST} was significantly lower than its expected value ($F_{ST} = -0.004$; p-value = 0.005) between purple and black fruits. On the other hand, the F_{ST} between large and small fruits was significantly different from 0 ($F_{ST} = 0.002$; p-value = 0.031).

Genetic diversity between sites

We summarized the overall diversity for different indices in the nine sites (Table 4). We first verified if the overall diversity between each area of the gradient differed. The mean AR_{15} value (the rarefied allelic richness for k = 15 gene copies) for both the urban and peri-urban areas reached 7.2, 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 = 0.0006), which were similar to each other (p-value = 0.47). We then subset the data, to check first AR_{15} within one area of the gradient (urban only, peri-urban only and rural only) for the three ethnic groups. AR_{15} was significantly different among peri-urban sites (p-value = 0.045) and among rural sites (p-value = 0.018) but was equivalent among urban sites (p-value = 0.39). In both the peri-urban and rural areas, the higher AR_{15} was observed for sites from the West region/Bamileke axis (rural Bamileke, peri-urban mixed). For the rural area, it was significantly higher than that of the Beti site (p-value = 0.017); for the peri-urban area, it was higher than that of the Bassa site (p-value = 0.015). We then compared within each axis, i.e. for similar ethnic groups along the gradient (Bamileke, Bassa and Beti separated; except for the peri-urban site of the West axis with a mixed Beti/Bamileke sampling). The only significant difference (p-value = 0.0002) was observed for the Centre region/Beti axis, where the AR_{15} of the rural site was lower than in the peri-urban and urban sites.

Distribution of genetic diversity between sites

We looked at patterns of population differentiation between sites with the F_{ST} fixation index (Table 5). The mean values of F_{ST} varied between -0.0004 and 0.023. Rural sites were the most differentiated: they had the highest F_{ST} values (from 0.021 to 0.023), as well as observed values of F_{ST} higher than expected at random for all pairs of sites but one, between Beti rural and peri-urban sites. Within peri-urban sites, the one on the Bassa axis stood out, with three pairwise comparisons with other urban or peri-urban sites significantly different from zero. Urban sites had low F_{ST} values that were not significantly different from zero. The lowest F_{ST} was found between the two peri-urban sites with a majority of trees from Beti owners (peri-urban mixed and peri-urban Beti).

The Bayesian clustering analysis, with an optimal value at K = 3, attributed rural sites to different clusters (Fig 4), especially the rural Bamileke and Beti ones. We ran separate analyses to verify if any structure could be found within the admixed samples from the urban and peri-urban sites. We first verified the distribution of diversity within similar sites (samples from the three urban sites, samples from the three peri-urban sites), and second within each axis. Overall, no substructure was detected (see Fig S3).

The samples that were attributed to these three clusters were located exclusively in different rural sites for the two first clusters, K1 and K2. K1 contained all trees from the Bamileke rural site, and K2 half of the trees in the Beti rural site. The third cluster, K3, was neither restricted to rural sites, nor to one ethnic group. It comprised mainly trees from Bassa owners, with all trees from the Bassa rural site but two, 72% of the trees from the Bassa peri-urban site, and half or the trees from the Bassa urban site. More surprisingly, some trees from Beti owners were also attributed to K3: six trees in the Beti urban site and three trees in the Beti rural site.

Distribution of genetic diversity within sites

For all sites, a signal of isolation by distance was observed with pairwise kinship coefficients decreasing significantly with distance. But at the fine scale, the kinship coefficient analysis showed various patterns depending on sites and ethnic groups (Fig 5 and 6). In the rural sites, a strong spatial structure in distance classes <100 m was detected both in the Bassa and Beti sites, with F_{ij} values of 0.0237 and 0.035 respectively. For the Bassa site, the second two short-distance classes (<1 km) were also significantly higher than at random. In the peri-urban sites, the F_{ij} values at short distances were lower than for the rural sites, but still significantly high in the Bassa population for the first distance interval (0-150 m).

For the urban sites, the analysis was first conducted following ethnic groups. The small number of trees from Bassa owners (24) limited the power of the analysis (less than 100 pairs of trees per distance interval). For each ethnic group, significant spatial structure was found for the first distance class. Then, F_{ij} was computed between neighborhoods with mixed ethnic groups. Values for short-distance classes were lower than for ethnic groups, and spatial structure was only assessed for the Oyom-Abang (peripheral) and Essos (central) neighborhoods.

Temporal evolution of genetic diversity

We looked at the rarefied allelic richness for k = 100 (AR_{100}) for the different tree age classes. Young trees (N = 100 trees), middle-aged trees (N = 196) and old trees (N = 159 trees) had similar mean AR_{100} (ANOVA controlling for loci effect, p-value = 0.83), of 15.6, 15.5 and 15.7 respectively. We also verified if there was a trend of increasing or decreasing differentiation through time by comparing F_{ST} values between the nine sites in each age class, and obtained a F_{ST} of 0.016 for young trees, of 0.013 for middle-aged trees and of 0.0067 for old trees (all values significantly different from 0 as tested with permutations). For rural sites only, F_{ST} values were 0.041, 0.022 and 0.019 for young, intermediate and old trees respectively.

Discussion

In this article, we built a comprehensive framework for characterizing the spatial distribution of morphological and genetic diversity of African plum trees in different ethnic groups following three urbanization gradients.

Seed sources

Urban, peri-urban and urban sites strongly diverged with regard to their seed sources. Seeds planted in urban and peri-urban sites were for the most part obtained from other villages 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. What is more, a remarkably high proportion of Bamileke and Bassa urban dwellers who reported taking their seeds from different villages were specifically sourcing them 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 further away than villages where Bassa and Beti are settled. This means that Bamileke urban dwellers used the seeds of their home village regardless of the distance, which can be connected to the strong linkages of urban dwellers with rural areas, as recently reappraised in Cameroon by Mainet (2017). Owners' ethnicity is thus an important factor in the African plum seed exchange networks structuration.

African plum trees' owners sourced a significant part of their seeds from non-ethnic counterparts. An important proportion of the seeds used for planting were actually acquired through market purchase, which was the main seed origin 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 different regions while travelling, which are sold in roadside markets along major road axes. Moreover, seed flow occurred in adjacent 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 seeds (see on Fig 2).

Seed flows along urbanization gradients were mainly oriented 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. Both of these show that seed flows between rural, peri-urban and rural areas are not only unidirectional. The role of 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 network (Ban and Coomes 2004).

Genetic diversity and its distribution following seed exchange networks

Qualifying the scope of seed exchanges helps to understand genetic patterns. In general, unintentional "natural" 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 an 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 was 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 strongly influence their genetic diversity (Thomas *et al.* 2012; Fuentes *et al.* 2012). We 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 different sites investigated ($F_{ST} = 0.0097$), but some trends emerge when comparing the different areas (urban, peri-urban, rural). The genetic diversity among sites from the urban and the peri-urban area is homogeneously distributed, whereas a slight genetic structure was measured among rural sites. This is well in line with patterns of seed exchanges that we observed. Actually, as people from rural sites predominantly source their seeds locally, this leads to a genetic structuration by selection/drift effect. This structuration effect is probably counterbalanced by the outcrossing sexual reproduction of the species, and by some long-distance seed dispersal events when owners buy or bring fruits from other places. It is not possible to tell from our analysis if this structuration 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 measures of 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.

Although not formally demonstrated, we noted that the Bassa ethnic group was the one with the fewest seeds coming from outside of their cultural area (see on Fig 2). For the three sites along the Bassa axis, we recorded only one occurrence of a seed source in the Bamileke region, for a tree that was not attributed to the cluster K3. It was also the only ethnic group whose trees were attributed to the same cluster K3 whatever their location on the gradient.

In peri-urban and rural areas the structuration signal 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 from the village of origin of tree owners. Thus, the urban area of Yaoundé acts as a “sink” of genetic resources coming from different sources from the rural area.

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). Here, as the study was built along African plum value chains, market dynamics were included. Unexpectedly, urban and peri-urban agriculture can have a positive action on the distribution of genetic diversity of crop species. By attracting seeds from rural areas, cities and their surroundings can represent a melting pot of genetic resources cultivated by farmers from the countryside. This was already observed for the African plum tree by comparing the level of genetic diversity observed in one main supplying zone of African plums with that in one neighborhood of Yaoundé (Rimlinger *et al.*, 2021): we had showed that both levels were similar. By extending the framework of this study to additional rural areas, we observed that the level of genetic diversity in the city could even be significantly higher than the level of genetic diversity in some rural sites. This observation is well in line with the genetic structure observed among rural sites and the description of the seed exchange processes. The different genetic clusters that were identified in the rural area are all present in the city. 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 get more structured than they used to. 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.

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. This measure of diversity seemed better suited to our data than the Shannon index, which was biased by the variation in sampling effort: the sites with the fewer number of trees were the ones with the lowest H value (urban Bamileke and Bassa, peri-urban mixed). 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. We propose that for further studies, to have a more adequate assessment and monitoring of agrobiodiversity, we could incorporate plum uses (self-consumption, market) in the chosen index, as for example in Blanco *et al.* (2016).

Genetic differentiation between morphotypes based on comparisons between trees for each trait was weak and did not suggest barriers to panmictic sexual reproduction. We nevertheless observed that the F_{ST} between large plums and small plums was significantly higher than zero.

Fine-scale spatial genetic structure

In natural plant populations, fine-scale spatial genetic structure (SGS) is the nonrandom spatial distribution of genotypes, with individuals closer to one another being genetically more related. Revealed by a strong negative correlation between kinship and distance, it results primarily from limited gene flow, but also from local genetic drift and selection. Its strength is affected by plant breeding system, life form and population density (Vekemans and 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 both from spontaneous seedling establishment (a few trees in the category “*owners’ own trees*”) and from anthropogenic seed dispersal. In rural sites, the shortest distance class corresponded in general 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. 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 (<500 m) 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 of *Ficus racemosa* in Bangalore, India, a fine-scale SGS was also detected despite long-distance pollen flow (Krishnan and Borges 2018).

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 varietal 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 villages of origin of seeds to that of rural sites, restricted to a mostly intra-village flows. We noted that home villages of urban dwellers 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 corroborates the finding of Rimlinger *et al.* (2021) that urban areas host a high African plum tree genetic diversity. What is more, urban sites, by connecting pools of local diversity, can have a diversity superior to that of some rural areas.

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Figures

Figure 1. On the left, schematic diagram of sampling strategy along the three urbanization gradients, going from urban sites to three rural sites passing through peri-urban sites, and the distribution of the three ethnic groups (Bamileke, Bassa, Beti) in each site. 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.

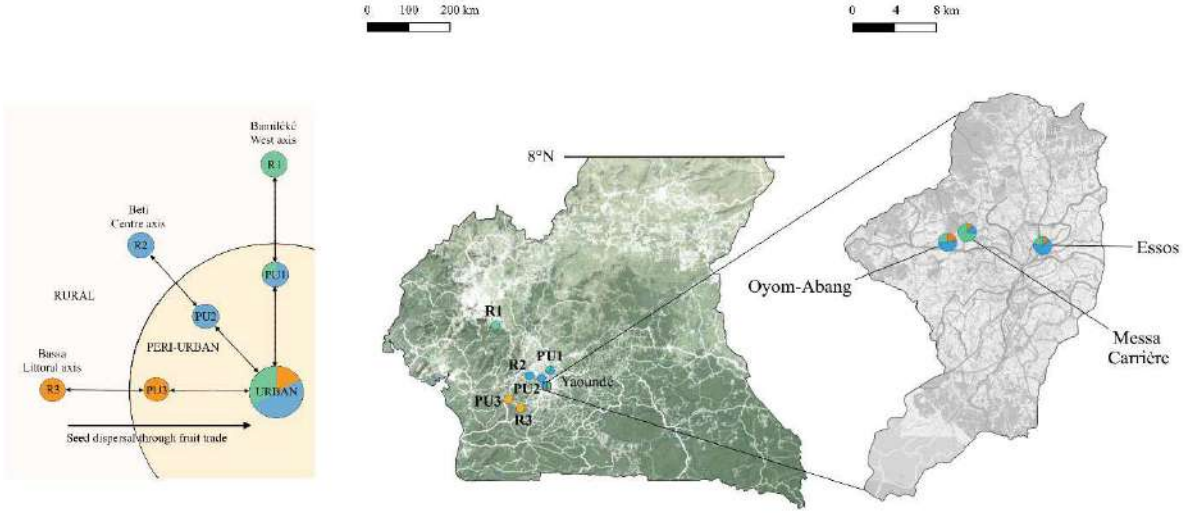


Figure 2. Origins of the seeds used to plant trees in the different sites: **a.** urban sites; **b.** peri-urban sites; **c.** rural sites. The number of seed provenances is presented in Table 2. Dots are coloured following ethnic group of the tree owner; each of peri-urban and rural sites are marked by a black cross and Yaoundé is figure with a red cross. The spatial ethno-linguistic data are taken from Felix and Meur (2001).

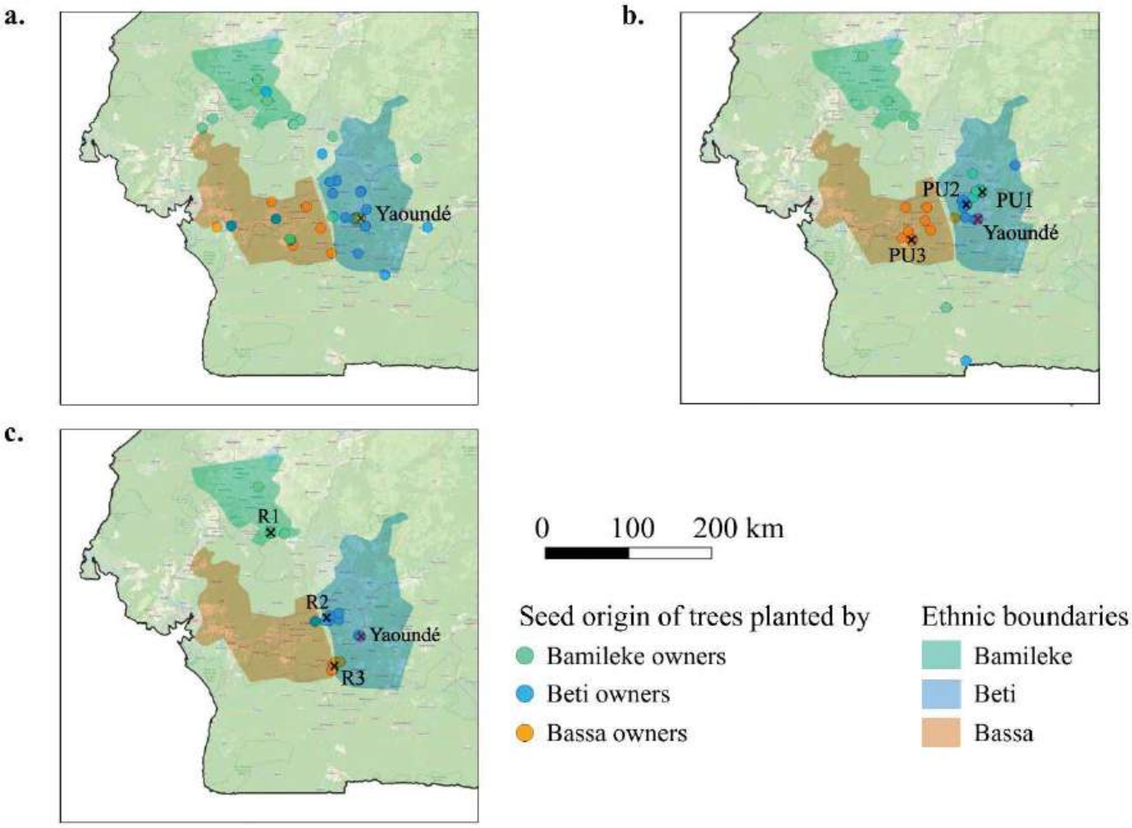


Figure 3. Rank-abundance curve displaying the relative morphotype abundance; the most abundant morphotype is given rank 1 and the least abundant morphotypes, characterized only once in our case, are given the highest ranks. Characteristics of varieties are ordered as follows: size, skin color, pulp color,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

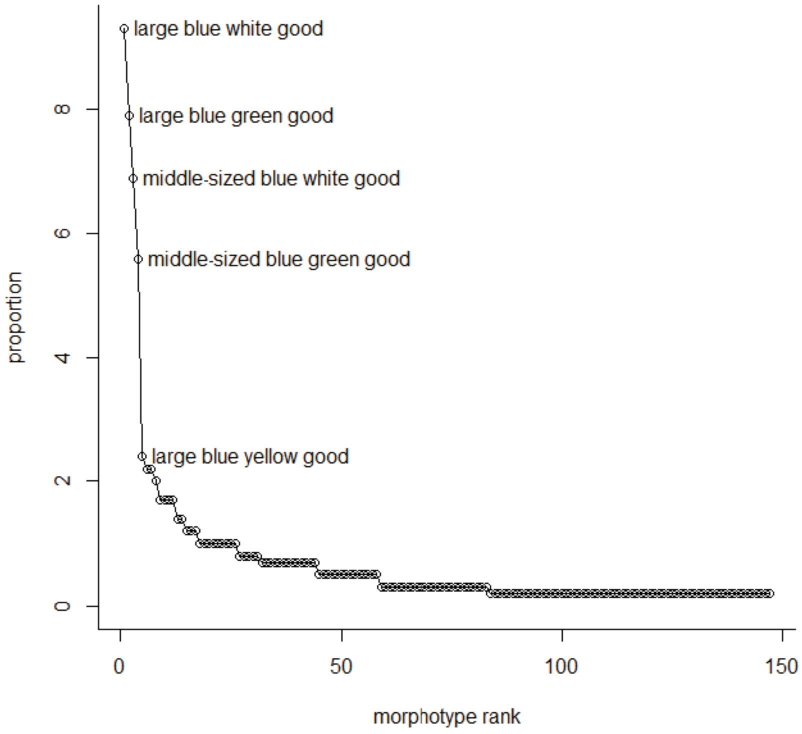


Figure 4. Output of clustering analysis by STRUCTURE software for two and three clusters (K=2 and K=3) of the total 455 trees across sites. Each individual is represented by a vertical line, which is partitioned into two or three segments depending on K (shown as red, green and blue) that represent the individual's inferred membership in each of the two or three clusters. Individuals are sorted following gradient (U: urban, PU: peri-urban, R: rural) and ethnicity, labeled below the figure. Using an assignment probability threshold of 0.8, trees in the rural sites (all Bamileke, all Bassa but two, and half of Beti samples) were assigned respectively to the green (K1), red (K3) and blue (K2) clusters, whereas most of the trees in urban and peri-urban sites were presenting admixed profiles.

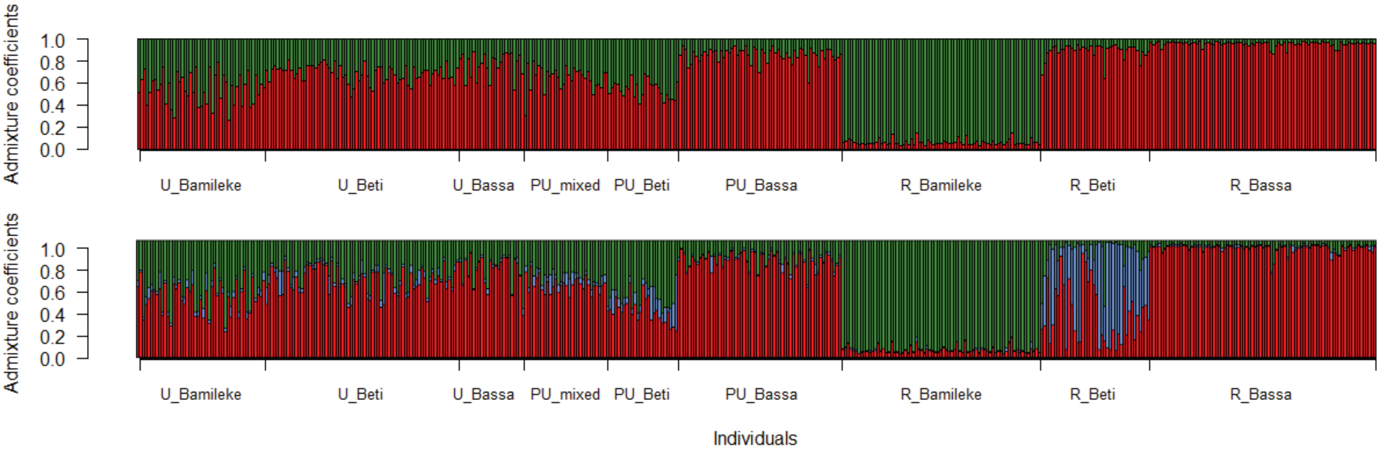
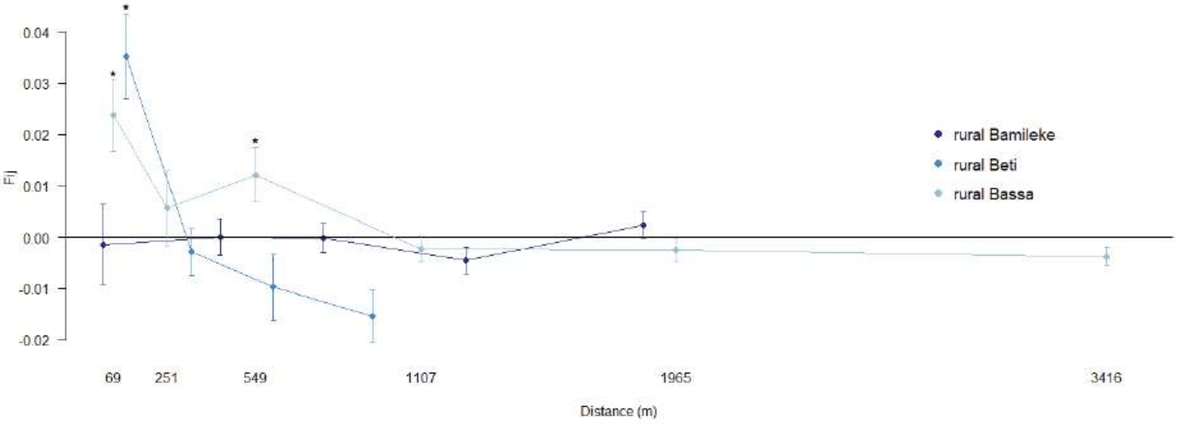


Figure 5. Variation of Loiselle's pairwise kinship coefficient over distance (m) in *D. edulis* trees sampled in the rural (above) and peri-urban (below) sites.



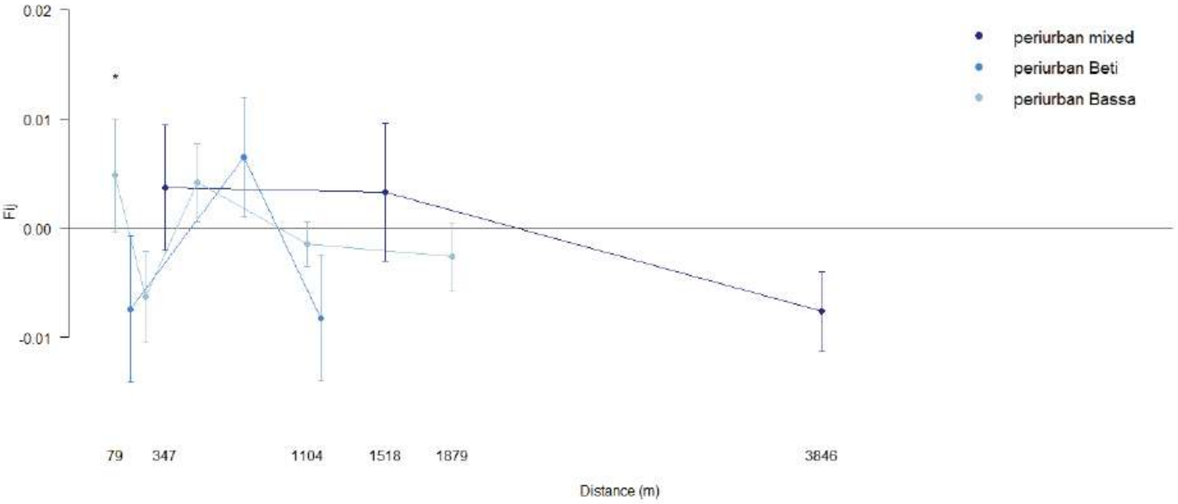
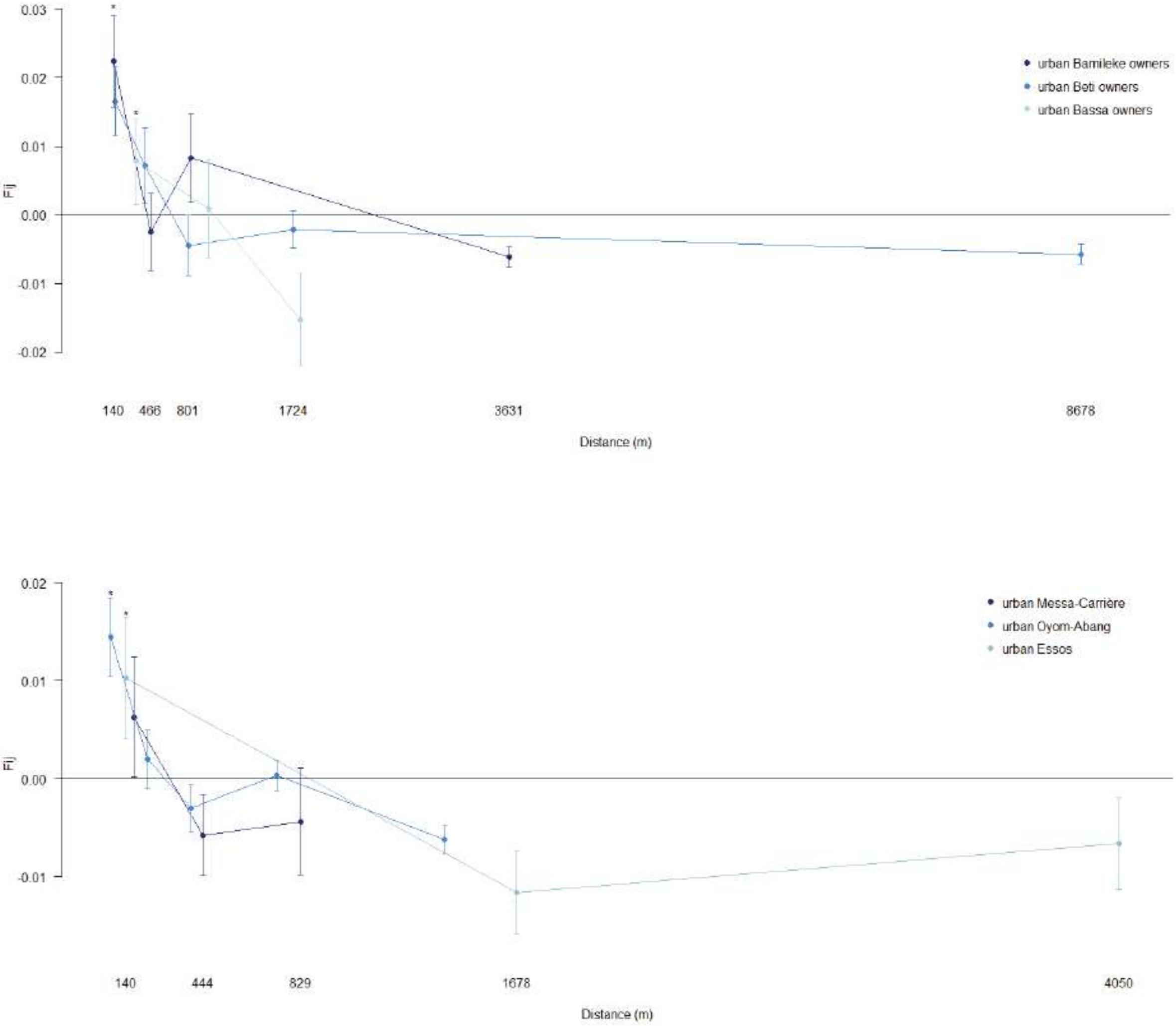


Figure 6. Variation of Loiselle's pairwise kinship coefficient over distance (m) in *D. edulis* trees sampled in the urban sites and pooled by ethnicity of tree owner (above) or by neighborhood (below).



Tables

Table 1. Summary of the number of *D. edulis* tree owners interviewed along the urbanization gradient according to their ethnicity. The number of trees sampled is indicated in brackets (used for morphological characterization [N_{TOT} = 592] – used for genetic characterization [N_{TOT} = 455]).

Gradient Ethnicity	Urban (N = 130)	Peri-urban (N = 92)	Rural (N = 101)	Total (N = 323)
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)

Table 2. Mean "origin-to-plantation" (O-P) distance in urban, peri-urban and rural sites according to the ethnicity of tree owners.

Gradient	Ethnic group	Seed origin (frequency)					O-P distance ± SEM (km)
		N	Farmer's own trees	Same village[1]	Different village (% home village)	Market or nursery[2]	All origins combined
urban	Bamileke	40	0.03	0.08	0.43 (71 %)	0.48	98.5 ± 13.3
	Beti	51	0.06	0.06	0.43 (32%)	0.45	31.7 ± 6.7
	Bassa	18	0.11	0.00	0.44 (88%)	0.44	42 ± 12.6
peri-urban	mixed	40	0.03	0.28	0.30 (25%)	0.40	40.6 ± 10.2
	Beti	39	0.13	0.13	0.21 (12.5%)	0.54	20.8 ± 7.1
	Bassa	37	0.16	0.03	0.43 (25%)	0.38	12.5 ± 2.9
rural	Bamileke	49	0.14	0.61	0.04	0.20	4.3 ± 1.3
	Beti	54	0.24	0.37	0.22	0.17	7.8 ± 1.9
	Bassa	47	0.15	0.68	0.15	0.02	2.5 ± 0.5

[1] same neighborhood in the case of urban sites; [2] seeds are bought in markets by purchasing fruits, and in nurseries by purchasing juvenile trees.

Table 3. Indices of morphotypes richness according to sites for the three urbanization gradients and ethnic groups

Gradient	Ethnic group	Nb trees	Nb morphotypes	MR	H	Pielou (evenness)
urban	Bamileke	51	30	17.4	3.1	0.91
	Bassa	26	19	18.4	2.8	0.95
	Beti	82	53	19.9	3.7	0.92
peri-urban	mixed	43	28	18.3	3.1	0.93
	Bassa	77	46	19.2	3.5	0.92
	Beti	58	43	21.3	3.6	0.96
rural	Bamileke	99	50	19.2	3.6	0.93
	Bassa	81	52	20.5	3.7	0.94
	Beti	75	46	19.8	3.6	0.94
All (nine sites)		592	147	19.5	4.3	0.85

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

Table 4. Genetic diversity indices of African plum trees of the urban, peri-urban and rural sites for the three ethnic groups.

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

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.

Table 5. Genetic differentiation between urban, peri-urban and rural sites of 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.

Gradient		Urban			peri-urban			rural		
	All loci	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**	

Supplementary data

Figure S1. Correlating diameter and age in sampled African plum trees

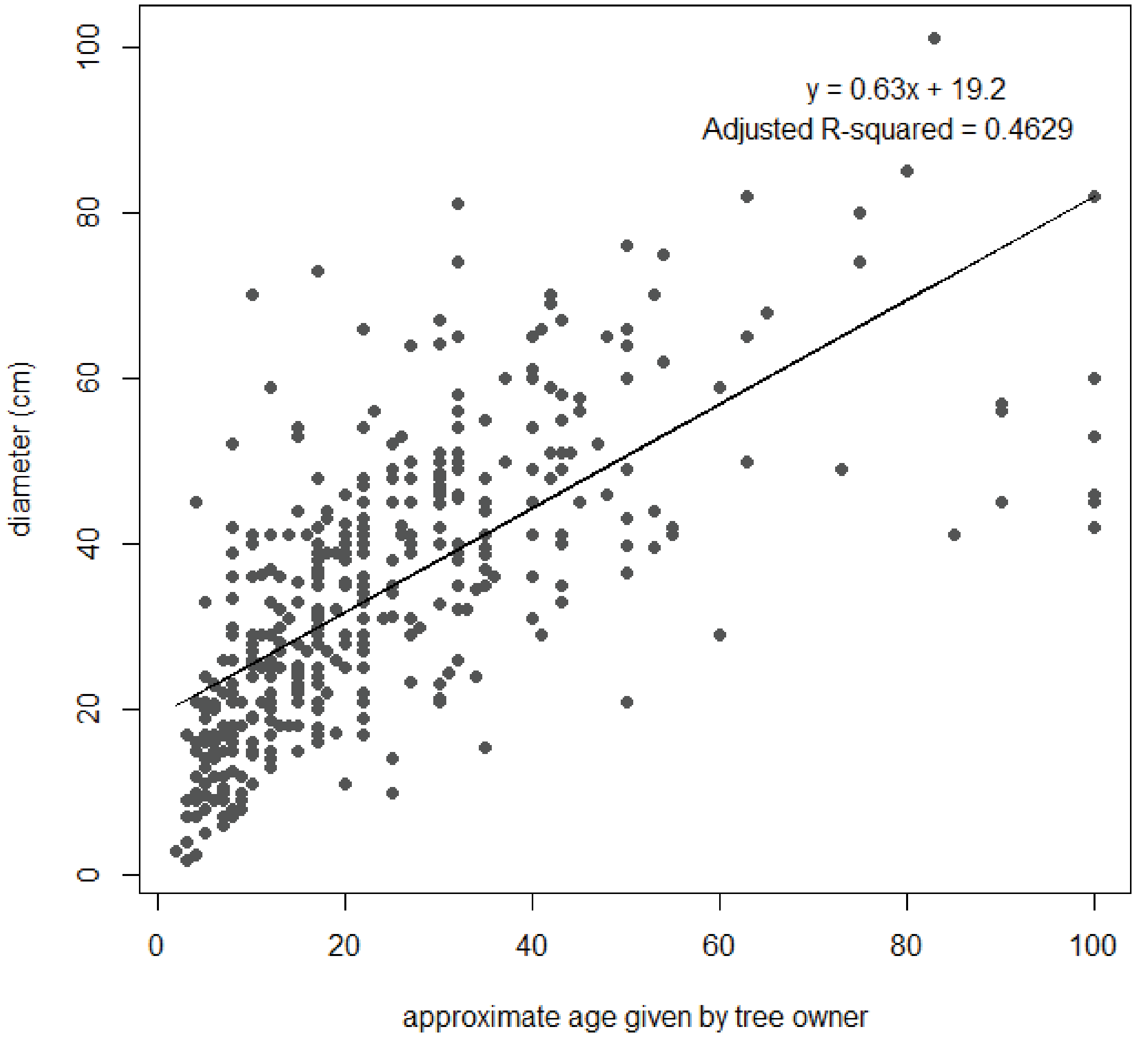
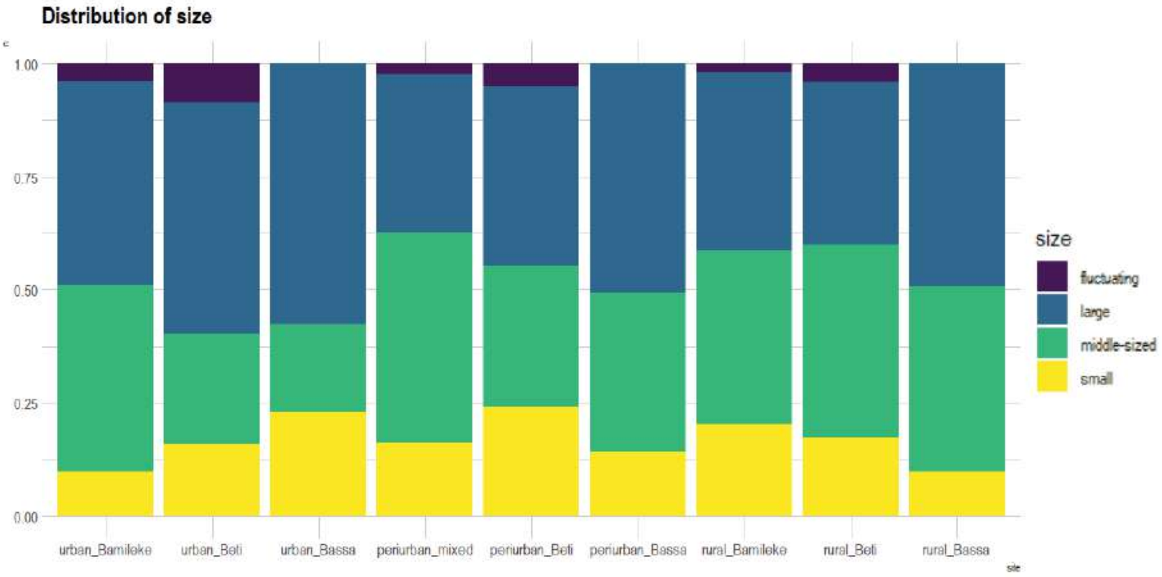
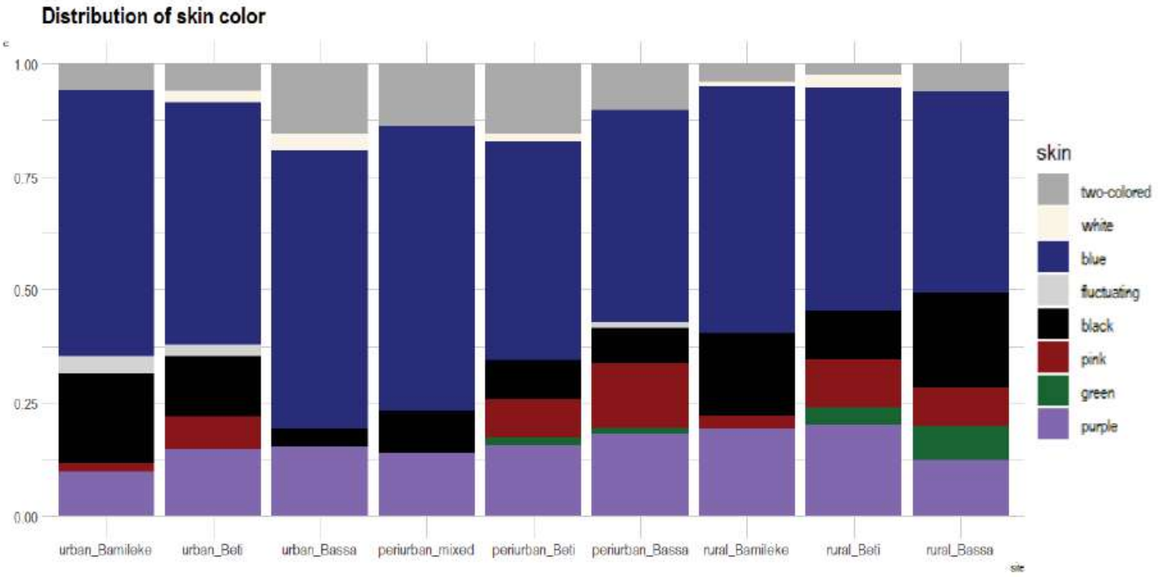
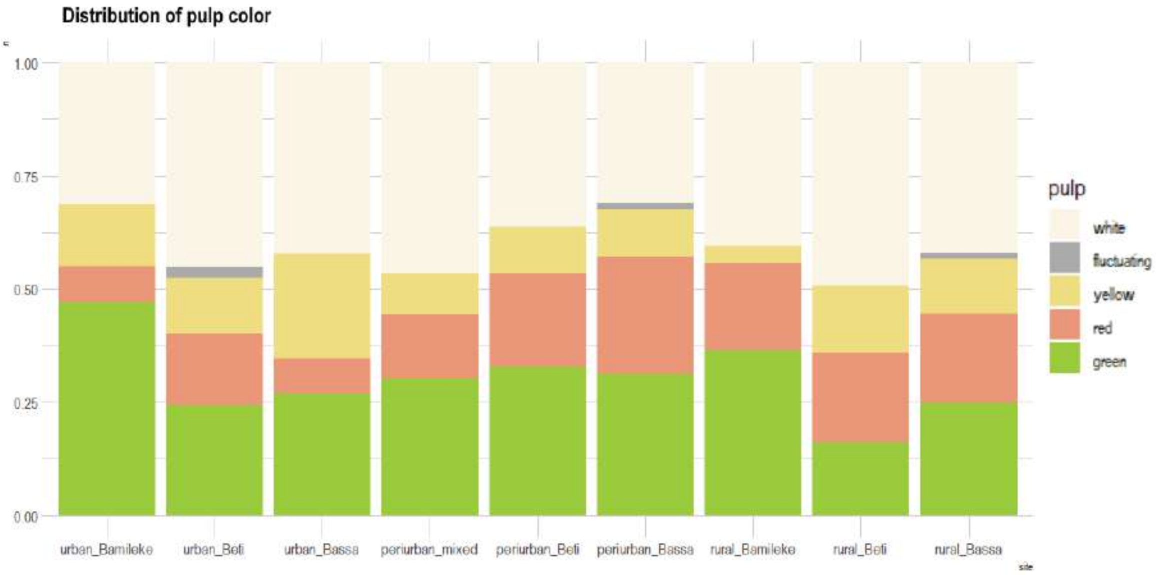


Figure S2. Distribution of fruit characteristics in each site






Distribution of pulp color
1.00
0.75
0.50
0.25
0.00
urban_Bamileke
urban_Beti
urban_Bassa
periurban_mixed
periurban_Beti
periurban_Bassa
rural_Bamileke
rural_Beti
rural_Bassa
site
pulp
white
fluctuating
yellow
red
green

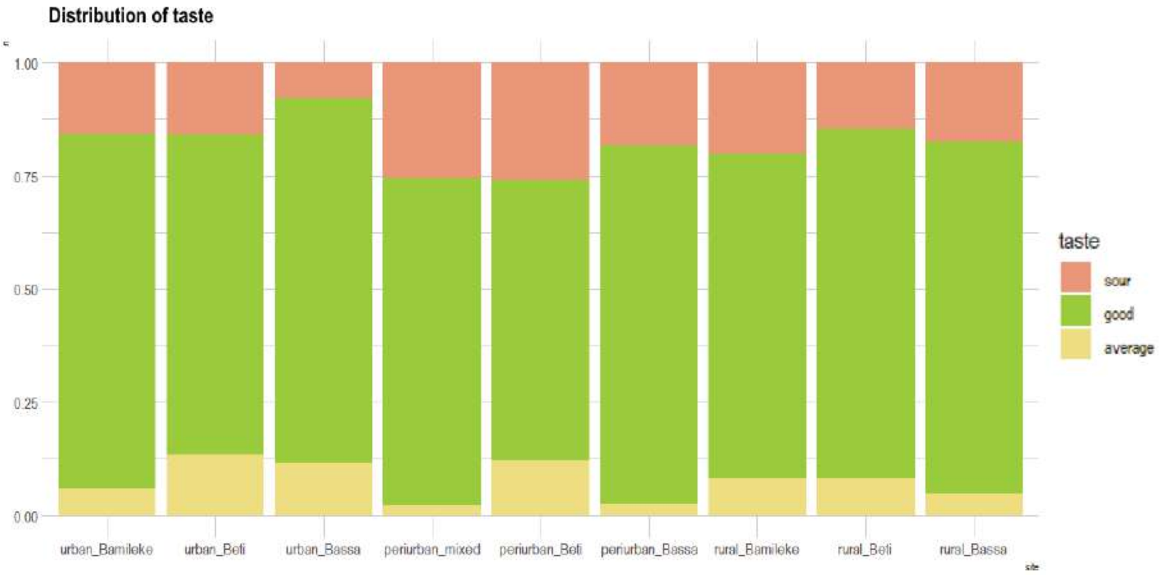
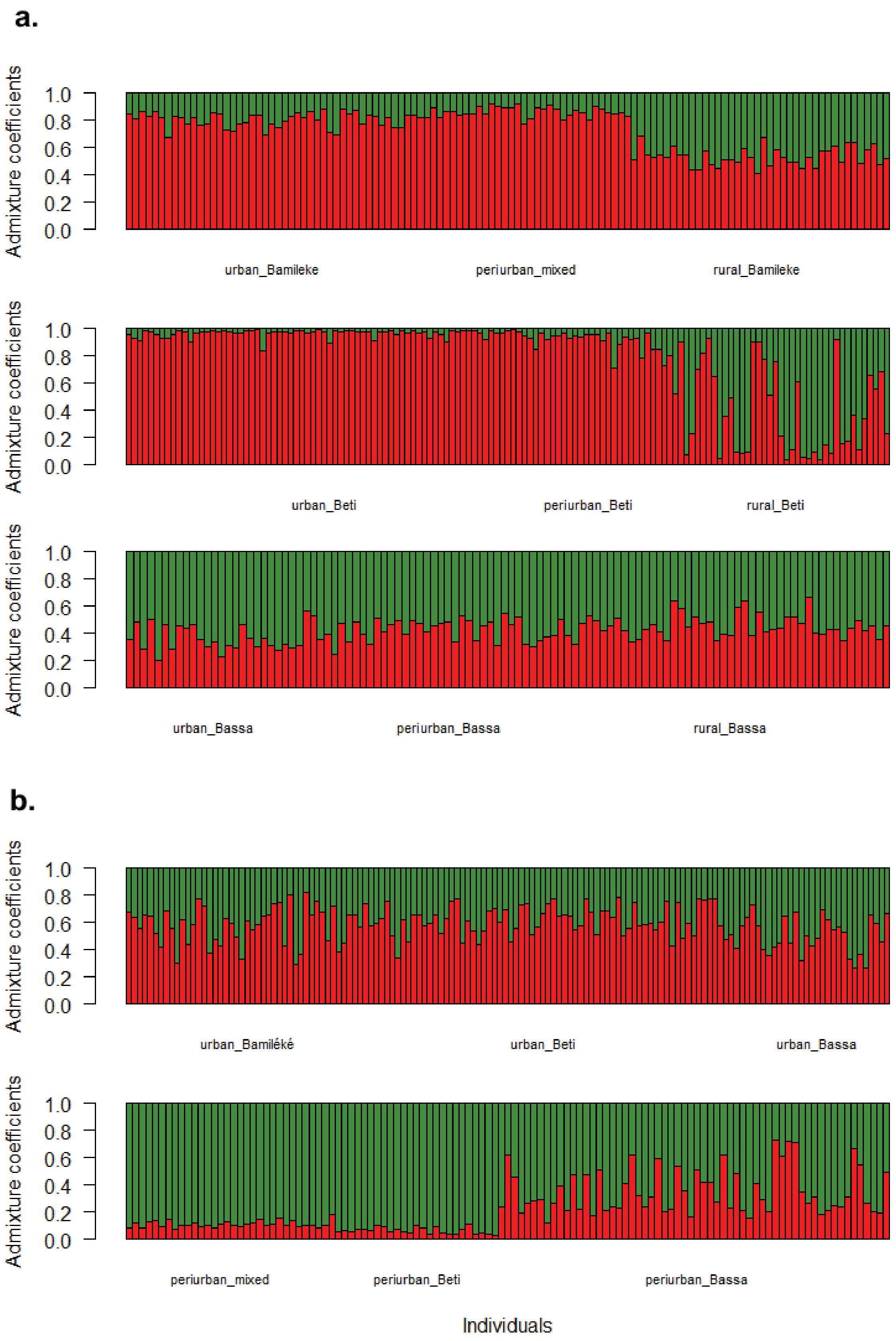

Distribution of taste
1.00
0.75
0.50
0.25
0.00
urban_Bamileke
urban_Beti
urban_Bassa
periurban_mixed
periurban_Beti
periurban_Bassa
rural_Bamileke
rural_Beti
rural_Bassa
site
taste
sour
good
average

Figure S3. Clustering analysis **a.** within each axis (i. West/Bamileke, ii. Centre/Beti, iii. Littoral/Bassa); **b**. among i. urban and ii. peri-urban sites.



Discussion

A. Synthèse des chapitres précédents

Le **chapitre 1** traite de l'histoire évolutive du safoutier dans l'ensemble de son aire de distribution, en se focalisant uniquement sur les populations cultivées de l'espèce. L'utilisation de méthodes bayésiennes sur le jeu de données de marqueurs microsatellites a permis de mettre en évidence une structuration de la diversité génétique en trois groupes principaux : deux groupes de taille restreinte sont localisés aux marges orientales (République Démocratique du Congo) et occidentales (Nigéria) de l'aire de distribution, tandis que le troisième groupe se retrouve sur l'ensemble du territoire du Cameroun et du Nord-Gabon. L'analyse menée à une échelle plus restreinte (Cameroun/Gabon) démontre, malgré un fort taux d'admixture entre les populations étudiées, des pools génétiques secondaires, localisés au Sud Gabon, dans la zone du littoral du Cameroun et dans la région de l'Ouest Cameroun. La structure phylogéographique, renseignée par 697 SNP chloroplastiques, se révèle être peu marquée en dehors d'une différenciation de part et d'autre de l'équateur météorologique, avec des haplogroupes présents uniquement au Nord ou au Sud de l'équateur. Enfin, la présence d'autres espèces du genre *Dacryodes* en sympatrie dans son aire de distribution et le partage d'haplotypes entre ces espèces et *D. edulis* suggèrent la possibilité de flux de gènes entre espèces congénériques.

Le **chapitre 2** se focalise sur les stratégies des cultivateurs dans la région Ouest du Cameroun où l'intégration au marché est la plus forte. Nous avons constaté un nombre plus important de pratiques de propagation des safoutiers dans les sites les plus productifs, même si la propagation par semis y reste prédominante. La diversité des morphotypes, définis à partir d'une combinaison des traits des fruits, est localement élevée. Les morphotypes présents dans plusieurs sites de cette zone sont aussi ceux avec les caractères les plus appréciés. Ces différents aspects sont discutés dans une perspective plus large sur l'évolution des stratégies locales de subsistance.

En suivant un gradient d'urbanisation croissant, de la campagne à la ville (Yaoundé), le **chapitre 3** détaille les différences de perceptions, de préférences et de pratiques agricoles vis-à-vis des safoutiers. Ces différences ont été étudiées pour trois groupes ethniques majeurs du Cameroun, en soulignant les liens entre les décisions de production, la consommation et la commercialisation. L'exploration des perceptions est l'occasion de présenter le système de nomenclature des variétés de safous et les principaux traits autour desquels ce système est structuré pour chacune des ethnies. Les points de correspondance et de divergence quant aux préférences et aux pratiques dépendent en particulier des deux grandes catégories d'usage pour les propriétaires de safoutiers : la consommation ou la vente. L'usage principal des fruits qu'en ont leurs propriétaires influence en effet les caractéristiques des fruits qu'ils privilégient ainsi que leurs choix de plantation et de sélection. Dans les sites ruraux, certains groupes ethniques tendent ainsi à donner davantage de poids à un trait quantitatif (la taille du fruit), plutôt qu'aux traits qualitatifs autrement dominants (goût, couleur de la peau). Dans l'ensemble, ce chapitre informe sur les différences de valeurs accordées par les cultivateurs à cette espèce fruitière et à ses fruits en fonction des usages qui en sont faits.

Retraçant les dynamiques sociales de la diversité du safoutier en milieu rural et urbain dans le **chapitre 4**, nous avons montré pour la première fois que l'importante diversité des safoutiers plantés à Yaoundé, mégalopole africaine, est la résultante d'une circulation intense des graines. Un dense réseau d'échanges de semences relie en effet Yaoundé à son arrière-pays rural, du fait, entre autres, de la vente sur les marchés de la capitale de safous produits dans plusieurs régions du Cameroun. La diversité des safoutiers est aussi renforcée par la circulation des semences transportées par les citadins depuis le village où ils ont leurs racines, reflétant en quelque sorte la mosaïque des groupes ethniques implantés à Yaoundé. Nous avons mis en avant la façon dont ce résultat renouvelait notre perception des espaces fortement anthropisés, en soulignant le rôle potentiellement important des jardins familiaux en zone urbaine comme possibles conservatoires de diversité intraspécifique.

Associant les cadres des chapitres 3 et 4, le **chapitre 5** explore les dynamiques spatiales et sociales de la diversité du safoutier en comparant patrons d'échanges des graines et diversité génétique le long de trois gradients d'urbanisation, pour chacun des groupes ethniques étudiés précédemment (Bamiléké, Béti, Bassa). Il y ajoute une perspective temporelle, en assignant les arbres échantillonnés à trois classes d'âge. Les propriétaires d'arbres des sites urbains et périurbains utilisent principalement des semences d'origines éloignées comme matériel de propagation, alors que les propriétaires des sites ruraux s'appuient principalement sur les semences issues du village. La distribution non uniforme de la diversité génétique, avec des groupes génétiques distincts dans les sites ruraux pourrait indiquer un faible échange de semences entre ces sites. Au contraire, la diversité génétique observée dans les sites urbains est la résultante de flux de semences importants acheminant du matériel génétique issu de différentes provenances du Cameroun. Enfin, en comparant les niveaux de diversité des arbres de différentes classes d'âge, nous avons constaté que la diversité génétique et sa distribution spatiale demeurent inchangées à l'échelle de temps considérée dans cette étude diachronique.

B. Diversité des safoutiers : du morphotype au cultivar, en passant par l'ethnovariété

Les différents niveaux observés de diversité des safoutiers – diversité morphologique, diversité nommée, diversité génétique – demandent une mise en cohérence préliminaire.

Le premier niveau de diversité est celui de la morphologie des fruits. Elle peut se résumer en un *continuum* de variations imbriquées d'au moins quatre dimensions : la taille des fruits, la gamme étendue de couleurs de leur peau et de leur pulpe et leur goût qui conduisent à un foisonnement de types de fruits. Dans les chapitres 2 et 5, le choix de les regrouper en morphotypes correspondant à la combinatoire de quatre critères a permis de donner un aperçu de la façon dont ces morphotypes se distribuaient à travers les sites de production. Les morphotypes ayant les combinaisons de caractéristiques les plus répandues sont fréquents et communs à tous les sites. La question se pose de savoir dans quelle mesure ce mode de classification de la diversité intraspécifique peut avoir du sens par rapport à celui appliqué localement et approché par la nomenclature. La nomenclature des ethnovariétés, i.e. des variétés telles que définies localement, est le résultat des processus d'attribution d'un nom à un arbre par un propriétaire en fonction de sa perception des traits des fruits, et d'autres caractéristiques détaillées dans le chapitre 3. Les catégories de traits utilisées pour définir les ethnovariétés étaient relativement semblables entre les trois ethnies Bamiléké, Béti et Bassa. Parmi les 25 ethnovariétés les plus fréquentes [APPENDICE 4], celles qui se répètent entre les nomenclatures bamiléké, béti et bassa correspondent à des types de fruits aux caractéristiques saillantes : fruits gros et bons, fruits acides, petits fruits ou fruits blancs. Il semble que les variétés les plus désignées avec des noms motivés, c'est-à-dire des noms ayant du sens pour les locuteurs (voir par exemple Grenand 2002), sont celles qui se distinguent du fruit « moyen ». Ainsi, les fruits bleu foncé, communs, ne sont pas nommés d'après leurs caractéristiques, les fruits blancs, plus rares, le sont ; il n'y a pas de désignation de fruits de taille moyenne ou de goût quelconque, mais il y en a bien une pour les petits et les grands fruits, les meilleurs fruits ou les fruits trop acides. En revanche, ces fruits moyens peuvent plus facilement être nommés d'après une personne (noms immotivés ; Lemoine *et al.* en préparation).

À la jonction entre diversité morphologique et diversité génétique, il nous faut évoquer les pratiques agricoles et de gestion qui concernent les safoutiers. Nous avons vu dans les chapitres 2 et 3 que ces dernières avaient en premier lieu pour objectif l'élimination des arbres improductifs. Pour mieux renseigner la conservation du safoutier, l'un des premiers axes à examiner dans l'avenir pourrait être celui de l'évolution de sa biologie reproductive dans des bassins de production où la contre-sélection des individus mâles est particulièrement forte (Makueti *et al.* 2012). En effet, l'élimination systématique dans les plantations des safoutiers à fonction mâle/hermaphrodite (fleurs staminées) pour ne garder que des individus femelles pourrait conduire à terme à une perte de productivité par déficit de pollinisation. Chez d'autres espèces pérennes domestiquées, cette limitation a causé l'évolution des systèmes de reproduction femelles. Pour certaines espèces, elle est associée au développement de la parthénocarpie – c'est-à-dire la production de fruits sans fécondation des ovules, comme c'est le cas chez certains figuiers – ou de l'hermaphrodisme (chez le raisin par exemple ; McKey *et al.* 2010). L'apomixie et le développement de fruits parthénocarpiques ont par ailleurs été observés chez des espèces utiles, de la famille des Burseraceae comme chez la plante médicinale *Commiphora wightii* ou chez *Bursera morelensis* (Daly *et al.* 2011). Chez le safoutier, de nombreux cas de fruits sans graines sont mentionnés par les cultivateurs et rapportés dans la littérature (Anegbeh *et al.* 2005). Les fruits sans graines sont particulièrement fréquents chez les arbres à fructification tardive et concernent près de trois quarts des cas dans l'étude de Kengue *et al.* (2002), mais nous ne savons pas encore si la production de ces fruits sans graine serait un signe de parthénocarpie chez l'espèce. Un autre caractère associé à l'absence de graine est celui d'une chair épaisse (Makueti *et al.* 2012). Que ce soit dans le cas d'arbres fructifiant tardivement ou d'arbres à fruits à chair épaisse, ce sont des traits d'intérêt pour la commercialisation car particulièrement rentables (fruits plus lourds et plus recherchés). Ce sont en tout cas des traits ciblés par la recherche agronomique (Ndindeng *et al.* 2008), et que présentent les plants issus de marcottes qui sont vendus dans les pépinières du secteur formel, mises en place par des institutions de recherche ou de développement (au Cameroun, IRAD, ANAFOR ; Degrande *et al.* 2013).

Le goût fait l'objet de pratiques de gestion chez d'autres espèces cultivées. Pour plusieurs espèces (manioc, Elias *et al.* 2000 ; mangue sauvage ; amandier), c'est la dichotomie entre présence et absence d'amertume qui fait l'objet d'une gestion spécifique. Pour le safoutier, le caractère indésirable n'est pas l'amertume, mais l'acidité. Ce goût a pu surprendre les palais qui n'y étaient pas accoutumés, ainsi que l'atteste Dewèvre (1894) : « Le fruit désigné sous le nom de safu, appartenant à une Térébenthacée, probablement *Canarium edule*, est bien connu sur le territoire du Congo [belge] comme étant l'un des fruits les plus estimés des indigènes. Il constitue même, du 20 décembre au 20 février, leur principale nourriture. Les blancs ne l'aiment pas à cause de sa saveur et de son odeur de térébenthine prononcées ». Mais l'expérience de l'acidité est une composante nécessaire de la dégustation d'un safou : il s'agit plutôt d'atteindre un degré d'acidité optimal c'est-à-dire un juste équilibre entre acidité et douceur. Cela fait l'objet de techniques post-récolte connues des cultivateurs. Les fruits sont souvent laissés à mûrir pendant quelques jours. Dans la mesure où le goût acide est lié à la teneur du fruit en eau (Eyenga *et al.* 2020) et que celle-ci semble se réduire quand le fruit est laissé à mûrir, un safou acide s'adoucit au fil des jours. Selon nos enquêtes, les modes de cuisson prennent aussi cette variable en compte : la cuisson par immersion dans l'eau bouillante est proscrite dans le cas de fruits acides ; celles à la poêle, à la braise ou sous la cendre sont privilégiées.

Par ailleurs, les safous sont à la croisée de plusieurs fonctions et attributions. Le fait qu'ils ne soient pas sucrés les a parfois conduits à être qualifiés de légumes : « Enfin, nous ne pouvons terminer cette énumération des principaux légumes indigènes sans parler du fruit connu sous le nom d'*atanga*. Ce fruit, qui provient d'un arbre de la famille des térébinthacées (*Canarium edule*), a la forme et la grosseur d'une belle datte, la pulpe entoure un noyau oblong assez volumineux. De couleur rouge, d'abord, l'*atanga* devient violet lorsqu'il est arrivé à maturité ; on le mange bouilli à l'eau avec du sel. Sa saveur est légèrement acide, farineuse et aromatique. Beaucoup d'Européens en sont friands » (Duvigneau 1900). Le safoutier est aussi l'un des arbres fournissant un aliment de base, qui peut faire office de repas, comme d'autres espèces telles que l'arbre à pain (*Artocarpus altilis*), le sagoutier (plusieurs espèces de palmiers), le parépou (*Bactris gasipaes*) (Alexandre 2002) – autant d'espèces qui font l'objet de pratiques de gestion spécifiques à travers la ceinture intertropicale.

C. Historique de la culture du safoutier

Pour statuer sur l'historique de la mise en culture du safoutier, un certain nombre de points restent à considérer. Le premier axe à développer pour comprendre l'histoire de la mise en culture du safoutier est d'intégrer à l'échantillonnage le compartiment sauvage, correspondant aux individus présents à l'état spontané dans des zones forestières. De tels arbres sont observés dans les milieux non gérés par les humains, mais leur divergence génétique et morphologique par rapport à la forme cultivée est encore en grande partie inconnue (Tchinda *et al.* 2016). La vérification des patrons de diversité entre les deux compartiments pourra permettre d'une part de vérifier si la mise en culture s'est traduite ou non par un goulot d'étranglement initial depuis le compartiment sauvage vers le cultivé. D'autre part, en comparant la distribution des morphotypes entre formes sauvages et cultivées, le syndrome de domestication mis en avant par Leakey *et al.* (2004) à partir d'une augmentation de la taille des fruits pourra être confirmé ou infirmé. Cela permettra par ailleurs de comparer les niveaux de diversité génétique contenus dans chacun de ces compartiments. Le syndrome de domestication implique généralement un goulot d'étranglement génétique (Doebley *et al.* 2006). Chez les populations cultivées de safoutiers analysées ici, la diversité génétique est relativement élevée, mais que représente-t-elle par rapport à la diversité génétique encore présente dans le compartiment sauvage ? Les safoutiers sauvages sont menacés par la déforestation, et s'ils portent dans leur génome une part importante de diversité génétique non présente dans le compartiment cultivé, il sera important de mettre en place des mesures de conservation adaptées. En effet, ces ressources génétiques forestières représentent une assurance supplémentaire d'adaptation aux changements climatiques, aux maladies, etc. pour le compartiment cultivé (Vincent *et al.* 2019).

La dynamique entre ces deux compartiments est aussi un sujet d'intérêt. Dans les pratiques des populations, leur séparation ne semble pas stricte. Ainsi au Congo, la description d'une gestion conjointe des deux formes est rapportée, l'une étant protégée, l'autre cultivée : « à côté du safoutier sauvage *tanga*, *Pachylobus* [*Dacryodes*] indet. qui pousse en forêt et qui est épargné dans les abattages, existe le *musikha*, *Pachylobus edulis* G. Don. qui est planté dans les villages » (Dupré 1982). Récemment, l'étude de Gallois *et al.* (2020) a mis en évidence dans les zones forestières à l'Est du Cameroun des pratiques de transplantation de jeunes plants de mangues sauvages (différentes espèces de la famille des Irvingiaceae) collectés en forêt et apportés à proximité du lieu de vie. Si on s'arrête à l'étymologie de domestication (du latin *domus*, la maison), c'est bien ce qui est observé ici : le premier jalon d'une possible domestication. D'ailleurs, même si une estimation temporelle du début de la sélection et de la diffusion de l'espèce manque encore, il est probable que l'époque de mise en culture de l'espèce soit trop récente (faible nombre de générations) pour conduire à un isolement reproducteur entre les formes sauvage et cultivée.

A cet égard, lors d'une dernière mission dans l'Est Cameroun, région située hors des principaux circuits de commercialisation du safou (zone de Messok), j'ai tenté de mettre en perspective les résultats obtenus dans les zones de productions principales du safoutier, fortement influencées par la commercialisation de l'espèce. Les résultats de cette mission n'ont pas encore été formellement analysés, mais les observations dans cette zone apportent un certain nombre d'éléments pertinents pour comprendre la gestion safoutier cultivé/safoutier sauvage dans des zones où les deux formes coexistent. Les résultats préliminaires obtenus à partir des enquêtes ethnoécologiques auprès des cultivateurs Nzimé (ethnie bantoue) soulignaient d'abord la faible importance du safoutier, tant au niveau du nombre d’arbres plantés dans les lieux de vie et dans les champs que des connaissances et savoir-faire associés (plantation, entretien, usages). L’appellation de l’espèce, *sa*, était similaire à celle des Béti, et certaines croyances étaient également communes, par exemple l’interdiction de grimper sur les safoutiers pour les neveux (les fils des sœurs, Houseman 2000). Le point important concerne les graines utilisées pour la propagation : même si les cultivateurs connaissent en général bien les safoutiers sauvages et que les fruits de ce dernier sont parfois utilisés pour la consommation, ils ne sont jamais plantés. Les graines plantées venaient d’abord des échanges entre cultivateurs des différents villages mais aussi des marchés locaux (Lomié, Abom-Bang) voire plus lointains (régions Centre, Ouest, Littoral). Cela a pu aboutir à l’introduction de matériel génétique issu d’arbres cultivés qui pourrait être contrasté avec le matériel génétique des arbres sauvages. N’ayant pas d’information sur l’origine géographique des individus sauvages ayant été utilisés historiquement pour la mise en culture, nous ne savons pas s’il s’agirait ici plutôt d’une néo-introduction ou d’une ré-introduction. Dans ce premier cas, le matériel sauvage original proviendrait d’une autre zone géographique, comme par exemple les formations forestières situées entre le Cameroun ou le Nigéria. Dans ce second cas, le matériel sauvage viendrait de cette zone du Sud-Est, et serait réintroduit ici suite à plusieurs générations de sélection relativement intensives dans les zones géographiques plus au Nord-Ouest en lien avec un usage plus important de l’espèce. Pour ce qui est des Baka, aussi présents dans la zone, ils avaient la même dénomination (*sa*) pour les safoutiers, et appelaient les safoutiers sauvages *sa na bene* « safoutiers de la forêt ».

La question de l’isolement reproducteur se pose aussi avec les autres espèces de *Dacryodes*, dont on a vu au chapitre 1 que certaines d’entre elles partageaient des haplotypes communs avec *D. edulis*. Les noms vernaculaires recensés dans la littérature rapprochent quelques fois safoutier et espèce congénérique. *Dacryodes igaganga* est ainsi nommé *assas onone* [safoutier de l’oiseau] chez les Boulou sous-groupe de Béti (Vivien et Faure 1989), un nom qui est parfois repris pour le safoutier. Dans un récit d’exploration de Du Chaillu alors qu’il séjourne chez les Apindjis (Gabon, province de la Ngounié ; 1863), on trouve une intrigante mise en parallèle de deux espèces : « Je vis là le plus gros *ashangou* que j'eusse encore rencontré. Cet arbre portait une quantité de fruits en forme d'olive. Ce fruit est cependant plus gros que nos olives, très-substantiel et d'un rouge foncé quand il est mûr. Agobi me dit que cet arbre et un grand nombre d'autres avaient été plantés par son grand-père : ce qui montre que le droit de propriété est respecté chez ce peuple, au moins depuis deux ou trois générations. Beaucoup de villages sont entourés de bouquets de cette sorte d'arbres. On fait bouillir le fruit ; il acquiert alors une certaine acidité qui le rend à la fois agréable et sain […] Dans les forêts qui avoisinent le littoral, on trouve un arbre qui appartient aussi à la famille des *ashangous* et qu'on appelle *ashafou*. Mais le fruit est moins substantiel et plus acide que celui de l'*ashangou*, et en mûrissant il prend une teinte rose. » D’après les ethnovariétés recensées à Yaoundé, le nom *asa angoun*, proche d’*ashangou* désigne le safou du perroquet, c’est-à-dire le safou dispersé par le perroquet. Dans cet extrait, les caractéristiques attendues semblent inversées entre *ashafou*, proche de safou, espèce sinon sauvage du moins à fruits plus petits et plus acides, et *ashangou*, « safoutier du perroquet », dont les arbres plantés autour des villages portent des fruits plus gros. Au-delà de ces aspects nomenclaturaux et des usages effectués par les différentes populations locales des différentes espèces, la présence d’haplotypes partagés pourrait indiquer la présence de flux de gènes entre espèces proches. Cet aspect doit être approfondi par de nouvelles analyses (collectes dans des zones où plusieurs espèces sont retrouvées en sympatrie, identification des espèces par des botanistes, et confrontation de cette identification avec les données de génétique) afin de mieux comprendre la dynamique évolutive au sein du genre *Dacryodes*, et l’importance des autres espèces de *Dacryodes* dans l’histoire de la mise en culture du safoutier.

D. Dynamiques contemporaines de la culture du safoutier

L’importance alimentaire et économique du safoutier joue un rôle notable dans l’essor actuel de sa culture. Plus largement, cet essor tient aussi à ce que les populations locales présentes dans sa zone de distribution dépendent essentiellement de l’agriculture pour faire vivre leur économie, soumise depuis la fin des années 80 à une crise des produits agricoles de rente sur le marché international (Christensen 2016 ; Janin 1996). La diversification des productions agricoles figure en bonne place parmi les solutions proposées pour amortir cette crise, et est devenue l'une des orientations stratégiques de la politique agricole des décideurs politiques dans la sous-région (Pédelahore 2014). Au cœur de cette stratégie de diversification, une place de choix est dévolue au développement des cultures vivrières et fruitières traditionnelles localement valorisées sur les plans économique et alimentaire (Kehlenbeck *et al.* 2013).

Les safous étaient identifiés comme le premier produit PFNL en valeur et en quantité en 1995 au Cameroun (Ndoye *et al.* 1997). Dans le commerce général des fruits, incluant les produits non-PFNL, sa valeur de production était la troisième plus importante, après celles de la banane et de la noix de cola (Temple 2001). Malgré cela, les acteurs de sa commercialisation sont faiblement organisés, chacun agissant individuellement, ce qui participe à diminuer les prix de vente pour les producteurs (Awono en préparation). Ce faible niveau d'organisation s'explique majoritairement par la rapide dégradation du fruit, qui se garde seulement quelques jours après sa récolte, empêchant le stockage et induisant de très fortes pertes (Dossou *et al.* 2012). Par ailleurs, l'organisation de sa chaine de valeur rend sa vente plus rentable sur le marché régional dans les pays frontaliers du Cameroun, ou sur le marché international à destination de l'Europe, que sur le marché local (Engwali et Mbondji Ntombe 2018). En France et en Belgique, les safous sont ainsi les PFNL les plus importés derrière le *koko* (*Gnetum* spp. ; Tabuna 1999). Les perspectives pour le marché du safou concernent le développement de produits transformés, permettant une plus longue conservation des fruits et de nouveaux débouchés. La fabrication de nouveaux produits (safou séché, pâte de safou, huile et huile essentielle de safou) est menée par de petites unités de production (Tshombe *et al.* 2009).

Cela étant dit, le débouché urbain local, même si moins rentable, reste le plus important en volume d'échanges. L'urbanisation provoque en effet un accroissement des demandes alimentaires, et restructure les systèmes de production en favorisant une intensification des cultures (Temple *et al.* 2008). Elle entraîne aussi l'évolution des pratiques et préférences alimentaires (Cockx *et al.* 2019). Le mode de vie urbain modifie en effet le choix des denrées consommées, les recettes culinaires et les contextes de consommation (Mbarga 2013). Dans un contexte où les consommateurs urbains ont moins de temps pour cuisiner, la facilité et la rapidité de la cuisson des safous en font un aliment adapté au *snacking* (Tabuna et Tanoe 2009). Contrairement à d'autres produits traditionnels associés à un groupe ethnique particulier (Ndonko 1993), les safous sont seulement rattachés à une aire de production (Tabuna et Tanoe 2009) et font donc partie du paysage gastronomique commun dans le Sud du Cameroun. Du point de vue de la sécurité et de la souveraineté alimentaire du Cameroun, la production de safou est donc une aubaine, d'autant que le safou est aussi un fruit à haute valeur nutritionnelle. Il est en effet particulièrement riche en lipides (40% de sa matière sèche) et les teneurs moyennes en fibres et en protéines de sa pulpe sont importantes : une portion moyenne (six fruits) suffit ainsi à couvrir un tiers des besoins alimentaires journaliers en protéines (Icard-Vernière *et al.* 2020).

E. Une vision élargie du contexte de l'émergence de l'agriculture

Pour comprendre l'évolution du safoutier à travers les siècles en lien avec son utilisation par les humains, il est nécessaire de revenir sur l'émergence de l'agriculture en Afrique centrale.

Celle-ci est d'une nature différente de celle de l'agriculture céréalière, requérant d'importantes transformations de l'environnement naturel pour leur mise en culture, présentant des changements morphologiques importants par rapport à leur forme sauvage et s'étant largement diffusées à partir de leur aire d'origine (Zeder 2008). L'agriculture céréalière va aussi de pair avec, d'une part, le stockage des semences, d'autre part la domestication animale pour la fertilisation des terres. L'apparition de l'agriculture en zone intertropicale se fait sans stockage alimentaire, sans nécessité de domestication animale et, dans un premier temps du moins, sans besoin de déboisement massif. Elle repose en effet sur l'utilisation de plantes de lisières (palmier à huile) ou de sous-bois (tubercules) (Vansina 1990). De plus, là où la diffusion de l'agriculture du Moyen-Orient vers l'Europe se faisait plutôt par transplantation d'un modèle en bloc, non-réversible et entraînant la disparition des modes de subsistance de type chasse-cueillette, en Afrique centrale les groupes de chasseurs-cueilleurs et de cultivateurs coexistent sur un même espace sans que l'un n'y devienne exclusif (Ikeya *et al.* 2009; Cummings 2014). Les frontières entre stratégies de subsistance sont quant à elles poreuses ; les groupes sédentaires avec certaines techniques horticoles continuent à pratiquer la chasse, la cueillette, ou la pêche. Par ailleurs, certaines techniques d'exploitation d'espèces sauvages favorisent leur développement : c'est le cas des ignames sauvages, déterrés avec des tarières dont l'usage enrichit le sol dans lequel poussent ces espèces (Dounias 2001). Pour ce qui est des arbres utiles, ils sont épargnés lors du défrichement-abattage de nouveaux champs ; au fur et à mesure que progressent les essars et qu'eux se régénèrent, leur concentration devient plus importante que dans des forêts qui n'auraient pas été sous influence humaine (Carrière 2003). Ce modèle d'émergence agricole progressive, en mosaïque, non homogène à travers le territoire, se retrouve aussi en Amérique du Sud (Iriarte *et al.* 2020) et en Asie du Sud-Est (Hunt et Rabett 2014). Ces premières phases d'association d'horticulture et d'arboriculture, difficiles à repérer, ont pu longtemps être mises au second plan derrière des phénomènes plus tardifs mais plus remarquables, cités dans l'introduction générale : la diffusion dans les forêts tropicales d'espèces céréalières domestiquées, les traces d'activité métallurgique et la découverte de profondes fosses creusées utilisées comme dépotoirs (Saulieu *et al.* 2017).

Pour les arbres fruitiers, Harris (2012) souligne qu'un système de récolte saisonnière des arbres fruitiers – associé à un stockage pour les fruits qui le permettent – était une stratégie plus souple que d'essayer de créer un bosquet domestique en plantant leurs graines. C'est aussi une stratégie efficace, si l'on considère le décalage important entre la durée des générations humaines, la croissance lente des arbres et la faible possibilité de sauvegarder les caractères d'intérêt du fait du mélange génétique au moment de la reproduction. Un dernier point concerne les changements d'usages au cours du temps : des usages répandus par le passé peuvent tomber en désuétude avec le temps, par exemple du fait de l'introduction d'espèces plus performantes et remplissant le même rôle (Raimond et Garine-Wichatitsky 2016). Pour le safoutier, on peut penser que des usages aujourd'hui marginaux, par exemple celui de sa résine inflammable (Omonhinmin 2012), aient été autrefois plus importants.

F. Conservation des ressources génétiques : perspectives actuelles et futures

Le safoutier existe simultanément à l'état cultivé et spontané. La circulation est possible entre les deux au moment du défrichement de nouvelles parcelles, lorsque les plants sont préservés et entretenus. Ces deux niveaux doivent donc être pris en compte pour la conservation des ressources génétiques de l'espèce.

Pour les safoutiers cultivés, il s'agit dans un premier temps d'examiner les facteurs de la dynamique de sa diversité induits par les pratiques humaines. Pour ce qui est de leur propagation, elle se fait majoritairement par semis. En l'absence de dérive/sélection, ce mode de reproduction sexué allogame garantit le maintien de la diversité (Rao et Hodgkin, 2002). En ce qui concerne la sélection, nous avons discuté plus haut de la nécessité de prêter attention à une pression de sélection assez forte constatée chez le safoutier, celle qui pèse sur les individus mâles. Enfin, les pratiques d'échange des semences contribuent à la dynamique de la diversité de l'espèce. Une partie importante des chapitres 4 et 5 est consacrée aux échanges de semences de safoutier dans différentes zones le long de la chaîne de valeur. La figure ci-dessous (Figure 17) reprend les résultats du chapitre 5 pour proposer une mise en relation entre patrons d'échange des semences, à courte ou longue distance, et structuration de la diversité génétique. Ici, les échanges de graines entre régions de production et zones de consommation contribuent aux niveaux de diversité génétique observés localement en zones urbaines et péri-urbaines.

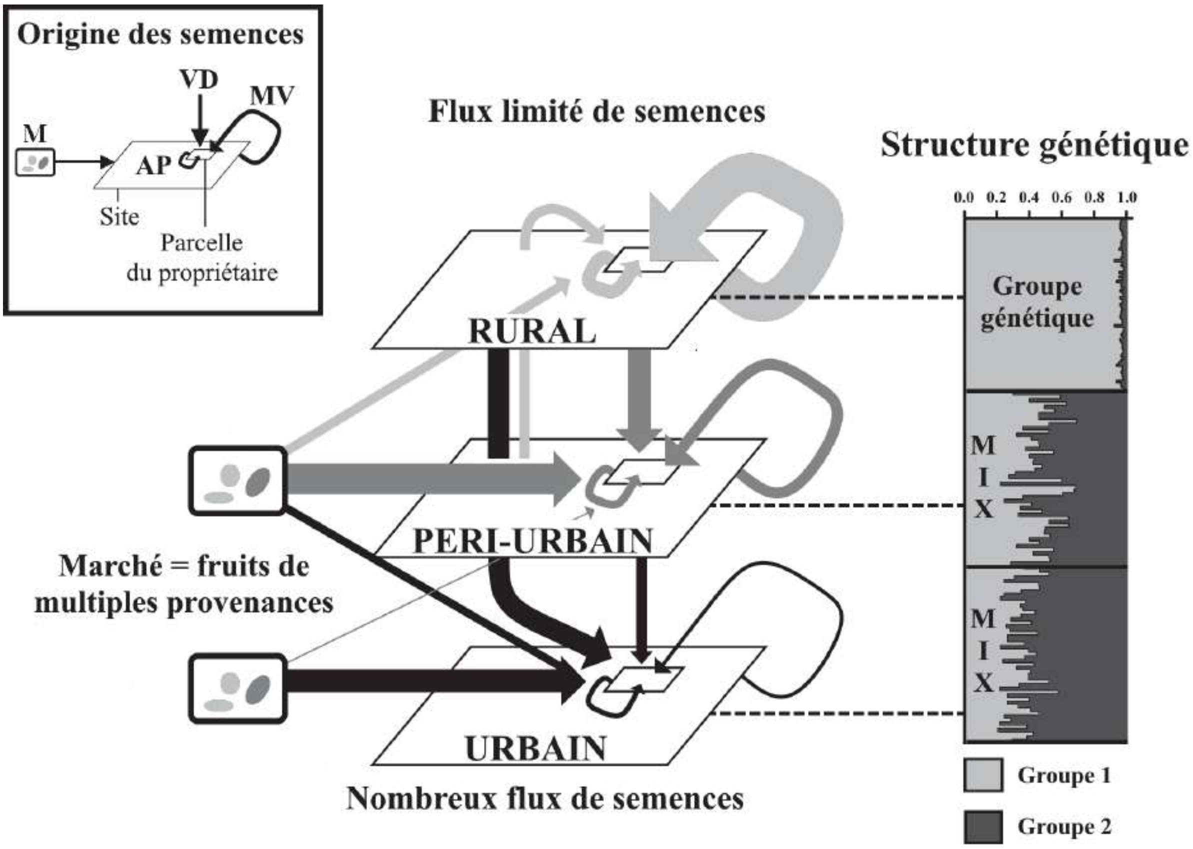


Figure 17. Schéma des échanges des safous le long d'un gradient d'urbanisation et leur effet sur la distribution de la diversité génétique de l'espèce. La largeur des flèches est proportionnelle aux fréquences d'origine des semences dans les sites ruraux, périurbains et urbains, présentées dans le Tableau 2 du chapitre 5. Pour chaque site, la valeur des différentes origines de semences (arbres du propriétaire [AP] ; même village [MV] ; village différent [VD] ; marché ou pépinière [M]) reprend la fréquence moyenne pour les trois groupes ethniques. Les flèches sont colorées en fonction du site, en gris clair, gris foncé et noir pour les échanges de semences alimentant respectivement les sites ruraux, périurbains et urbains. Les fruits présents sur les marchés proviennent de flux (non représentés) à partir des sites ruraux et périurbains du gradient, mais aussi de multiples sites ruraux et périurbains d'autres gradients. Le graphique de droite montre un patron possible de distribution de la diversité génétique entre les sites, avec un plus grand nombre d'individus affectés à un groupe génétique dans le site rural, où les flux de semences provenant de l'extérieur sont limités, et un plus grand nombre d'individus non-attribués (« mix ») dans les sites périurbains et urbains où la plupart des semences proviennent de l'extérieur.

Cela permet de souligner l'intégration au marché comme autre facteur d'évolution de la diversité intraspécifique. Selon les cas, l'intégration d'une espèce dans un circuit commercial peut engendrer des effets positifs ou négatifs. Si l'intégration au marché implique la création et la distribution à large échelle de variétés améliorées, une homogénéisation des variétés se produit à moyen terme (Gatto *et al.* 2021). Or, le système semencier formel du safoutier a pour l'instant une faible pénétration en milieu rural, d'autant que le coût des plants issus de marcottes est prohibitif pour la majorité des cultivateurs (Degrande *et al.* 2013). Par ailleurs, les entretiens conduits ont permis de voir que les cultivateurs qui connaissent les procédés de marcottage en connaissent aussi les désavantages, notamment la plus faible résistance de l'arbre due à l'absence de racine pivot (Asaah *et al.* 2012). À moyen terme, on pourrait imaginer l'émergence d'un système mixte composé de plants issus de semis et de plants issus de multiplication végétative (marcottes, dans le cas du safoutier), tel qu'observé par exemple chez l'amandier (Delplancke et Aumeeruddy-Thomas 2017; Hamadeh *et al.* 2018) ou le figuier (Hmimsa *et al.* 2017). Par ailleurs, la marchandisation n'est pas forcément une source d'uniformisation. Elle peut inciter à remettre certaines espèces ou variétés dans le portfolio variétal des cultivateurs. Pour les produits vivriers marchands, qui suscitent à la fois un engouement dans la consommation locale et font l'objet d'un commerce avec les centres urbains, on n'observe pas systématiquement de forte spécialisation variétale (Raimond et Garine-Wichatitsky 2016).

Mon projet doctoral n'a pas porté sur les safoutiers du compartiment spontané, individus « sauvages » ou descendants d'individus anciennement cultivés présents dans d'anciens peuplements. Comme discuté précédemment, ils doivent être intégrés dans les plans de conservation de l'espèce. Du fait de leur statut, leur conservation dépend plus largement de la conservation de leurs habitats écologiques, fortement menacés par la pression d'anthropisation des espaces (urbanisation, implantation d'équipements, déforestation pour occupation agricole ; Lambin *et al.* 2003). Dans la région Centre du Cameroun (région de Yaoundé), les surfaces de forêt dense ont ainsi été réduites de moitié sur les trente dernières années, et pourraient complètement disparaître d'ici à 2050 (Mesmin *et al.* 2020).

Enfin, nous conclurons sur la stratégie de conservation du safoutier au regard de ces différents éléments. D'abord, la possibilité d'une conservation *ex situ* au sein de banque de graines est problématique pour le safoutier, dont les graines sont récalcitrantes (i.e. qui ne survivent pas à la dessiccation et au froid). Par ailleurs, il n'existe pas de structure centralisée en place au Cameroun pour assurer la conservation du safoutier.

La seconde possibilité classiquement envisagée est celle de la conservation *in situ* : à l'heure actuelle, la quasi-omniprésence de l'espèce dans les agroforêts cacaoyères de la partie Sud du Cameroun est un gage notable du potentiel succès de cette voie. De plus, le mode de propagation dominant actuel par semis en pépinière assure une bonne survie des plantules dans les premiers stades de développement, et l'approvisionnement en graines venant de longue distance favorise le brassage, et donc de hauts niveaux de diversité. Ce sont d'ailleurs dans de telles conditions de culture que l'on observe le maximum de diversité (Khan *et al.* 2020). En outre, l'implantation de safoutiers dans des espaces urbains, intégrés au « verger lâche, à la frondaison discontinue » (Haeringer 1980) que constituent les îlots de verdure des jardins familiaux des villes d'Afrique centrale permet de déciller notre regard sur les nouveaux territoires de la conservation. Amener la biodiversité dans ces lieux de vie redessine les catégories *in* et *ex situ*. À plus grande échelle, c'est aussi ce que l'on observe avec les migrations transnationales, qui favorisent la constitution de réservoirs de biodiversité propices à la conservation en dehors des frontières habituelles (Gladis et Pistrick 2011; Heraty et Ellstrand 2016).

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APPENDICES

APPENDICE 1 : **Rimlinger A**, Marie L, Avana M-L, *et al.* 2020. New microsatellite markers for *Dacryodes edulis* (Burseraceae), an indigenous fruit tree species from Central Africa. Molecular Biology Reports, 47: 2391–2396

APPENDICE 2 : Planche créée dans le cadre de la formation « Ma thèse en bande dessinée », conception G. Bagnolini, M. Ganault, A. Rimlinger

APPENDICE 3 : Fiche des descripteurs du safou utilisés pour la caractérisation morphologique

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Appendice 1

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SHORT COMMUNICATION

New microsatellite markers for *Dacryodes edulis* (Burseraceae), an indigenous fruit tree species from Central Africa

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Abstract

Microsatellites were designed and characterized in the African fruit tree species *Dacryodes edulis* (Burseraceae). The fruits are commercialized throughout Central Africa and the species is present in forested environments as well as cultivated systems. The high variability of these markers makes them suitable to investigate the structure of genetic diversity in this important food tree species from Central Africa. From a genomic library obtained by next-generation sequencing, 21 new polymorphic microsatellite loci were developed. Tested on 95 individuals from four populations coming from three countries of the Congo Basin, the microsatellites displayed two to 20 alleles (mean 7.5; expected heterozygosity 0.003 to 0.937, mean 0.666). The transferability of microsatellites was effective for four other *Dacryodes* species (*D. buettneri*, *D. igaganga*, *D. osika*, *D. pubescens*). This set of newly developed microsatellite markers will be useful for assessing the genetic diversity and differentiation as well as gene flow patterns of *D. edulis* in tropical forests from Central Africa.

Keywords Burseraceae · Microsatellites · Central Africa · Tree crop · *Dacryodes*

Introduction

Dacryodes Vahl (Burseraceae) is a pantropical genus comprising around 90 species [1]. Among African *Dacryodes* spp., *D. edulis* (G. Don) H. J. Lam is a fruit tree species indigenous to tropical forests from the Congo Basin [2]. Its current distribution area is not restricted to tropical forests anymore, since it is an agriculturally significant species now widely cultivated in agroforests and orchards [3]. Six microsatellite markers (Simple Sequence Repeat, SSR) had already been developed [4] and used to study the genetic diversity of *D. edulis* and *D. buettneri* [5]. Given the low number of SSR available, new markers were developed in order to investigate the distribution of its genetic diversity at a local and a supraregional scale, its reproductive biology and to examine the influence of human uses on its genetic diversity. In this aim, we developed 21 polymorphic nuclear microsatellite markers.

Methods and results

Microsatellite development

DNA of one individual collected in the IRAD station in Yaoundé was extracted from a leaf according to the protocol of Mariac et al. [6]. A barcode library from this sample was prepared as described in Mariac et al. [7] and then paired-end sequenced using Illumina MiSeq v2 reagents and 2 × 250 bp at the CIRAD Genotyping Platform

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(Montpellier, France). Demultiplexing based on internal index was performed using the PYTHON script DEMULTADAPT (https://github.com/Maillol/demultadapt) and adapters were removed using CUTADAPT 1.8 [8] with the following parameters: overlap length = 7, minimum length = 35 and quality = 20. Reads with a mean quality lower than 30 were discarded using a freely available PERL script (https://github.com/SouthGreenPlatform/arcad-hts/blob/master/scripts/arcad_hts_2_Filter_Fastq_On_Mean_Quality.pl). The 454 026 total reads were deposited into GenBank SRA under SRA accession PRJNA601870. Paired-end reads were then joined (N = 144 096) using FLASH v1.2.11 [9]. QDD software v3.1.2 [10] was used with default setting to identify nuclear SSR motifs and design primers. From the 1486 SSR identified, 46 loci were selected containing perfect (i.e., not compound) microsatellite dinucleotide motives with at least seven repeats, with primers situated at least 20 bp from the microsatellite region, and with PCR product length between 90 and 300 bp (see Supplementary Material for the 46 primer sequences obtained). One out of four tails with fluorochromes (Q1-6-FAM, Q2-NED, Q3-VIC, Q4-PET; Table 1) was added to the 5′ end of the forward primer of each locus according to locus size in order to allow co-amplification of the loci in multiplex. Having tested the amplification and polymorphism of the 46 loci on six *D. edulis* individuals, we kept the 21 SSR that amplified correctly, displaying clear peak patterns and that were polymorphic. Sequences from these new loci were deposited in GenBank (Table 1).

DNA extraction and PCR conditions

The DNA of 112 individuals (95 *D. edulis*, 5 *D. buettneri*, 3 *D. igaganga*, 4 *D. osika* and 5 *D. pubescens*) was extracted from dried leaves using an adapted version of the protocol of Mariac et al. [6]. The 21 SSR markers were amplified in four multiplex reactions (composition of multiplexes indicated in Table 1). Each multiplex PCR reaction consisted of 0.15 µL for each of the forward primers [10 µM], 0.1 µL of the reverse primers [10 µM], 0.15 µL of each linker (Q1–Q4) [10 µM], 1 µL of DNA (10 ng/µl), 7.5 µl PCR Master Mix (Type-it Microsatellite, Qiagen), and was brought to a total volume of 15 µL with distilled water. PCR were conducted using a thermal cycler Veriti™ 96-Well (Thermo Fisher Scientific) as follow: predenaturation at 95 °C for 3 min then 30 cycles consisting of a denaturation step at 95 °C for 30 s, annealing at 57 °C for 90 s, elongation at 72 °C for 30 s, followed by 10 similar cycles except for the annealing temperature that was set to 53 °C, and a final extension at 60 °C for 30 min. Using 2 µL of PCR product, 10 µL of Hi-Di Formamide (Applied Biosystems, Thermo Fisher Scientific), and 0.12 µL of GeneScan 500 LIZ Size Standard (Applied Biosystems, Thermo Fisher Scientific), the genotypes of all samples were obtained using an ABI 3500 XL sequencer (Applied Biosystem, Foster City, California, USA) at the CIRAD Genotyping Platform in Montpellier. Electropherograms were visualized and scored with Geneious software version 7.1.3 (https://www.geneious.com).

Fifteen loci showed a maximum of two different alleles (diploid pattern). Microsatellites DaE-37 and DaE-46 presented an extra monomorphic band at 165 bp and 227 bp respectively, whereas DaE-5, DaE-10, DaE-13 and DaE-30 showed a pattern of duplicated locus. The two duplicated copies of these loci were thus read independently (see details in Tables 1 and 2). Note however that one of the two copies of DaE-13 was not readable and was not included in the analysis.

For each locus, we determined the number of alleles (*A*), observed heterozygosity (H_o), expected heterozygosity (H_e), inbreeding coefficient (*F*), and null allele frequency (*r*) using INEST 2.2 [11]. Deviations from Hardy–Weinberg equilibrium (HWE) were measured with SPAGeDi [12]. The different parameters were estimated in four populations from three countries: Cameroon (Manjo, Yaoundé), Gabon (Franceville), and Congo (Brazzaville) (Appendix). The transferability of the markers was tested in four species of the genus: *D. buettneri*, *D. igaganga*, *D. osika* and *D. pubescens*.

Microsatellite marker analysis in *D. edulis*

When combining all loci and populations, all the loci were polymorphic, except for the first copy of DaE-10, DaE-10.1 presenting two constant alleles (at 107 and 109 bp). The number of alleles per locus ranged from 2 to 20, with the mean value of alleles per population ranging from 6.5 to 8.4. The mean H_E value per population was very similar between populations (comprised between 0.66 and 0.68; Table 2). Significant deviation from HWE was observed in all populations for three loci (DaE-5, DaE-20, DaE-36), and for seven other loci in one or more populations. This is in great part explained by the presence of null alleles (Table 2).

Cross-amplification in *D. buettneri, D. igaganga, D. osika, D. pubescens*

Transferability of all markers was successful in all four *Dacryodes* species tested (Table 3). Despite low sample numbers, most of the markers were polymorph in these species.

Appendice 1

Table 1 Characterization of 21 microsatellite loci developed for *Dacryodes edulis*

Mix	Micro-satellite marker	Primer sequences (5′–3′)	Fluorescent label[a]	Repeat motif[b]	Allele size range (bp)	GenBank Acc. No
Multiplex 1	DaE-14	F: GGCGGCCATGTTTGTGAAAT R: TACGTAACGGCGATTCAGTTT	Q3-VIC	$(AT)_8$	128–134	MN601769
	DaE-24	F: AGGCGTAGAAATCCCATCCA R: ATCTCCAGGAACGGTTGACT	Q4-PET	$(AT)_8$	157–171	MN601774
	DaE-34	F: TGTGTTTCTTCCGCCTCACA R: ATGAACTGCAGCCTCAAACG	Q3-VIC	$(AT)_7$	172–180	MN601779
Multiplex 2	DaE-5[c]	F: AGGATGTTGGTCTGTTGGTGG R: TGGCAGAGGAGAGGATAAGCA	Q1-6-FAM	$(AT)_8$	100–106 108–140	MN601765
	DaE-7	F: AAGAAGGCAAGGCAACACC R: CAGAGCACACTGTACTGGCA	Q4-PET	$(AG)_8$	111–131	MN601766
	DaE-10[c]	F: ACTTGAGCATGCGTAAATGTCA R: AGGCTGTATGGGATTGGGAAC	Q2-NED	$(AG)_9$	107–109 119–125	MN601767
	DaE-28	F: CAGAGGTGGGAATCTTAAGCCA R: AACACTGCTTCAGCTTTCAGA	Q1-6-FAM	$(AG)_{15}$	153–163	MN601776
	DaE-37[d]	F: ACGTGCTCTTCCTGACACTC R: ACCATGATTTACCCACAGGACT	Q2-NED	$(AG)_{14}$	177–213 (165)	MN601781
	DaE-39	F: ACCCATTTGAGCTCATTTGACA R: TGCCACTGGGAGTAGAAGAGT	Q4-PET	$(AT)_{16}$	172–206	MN601782
Multiplex 3	DaE-13	F: ATGGCCATTCTCACACCTGG R: ACAGTTGATTTCCATTCCACCC	Q2-NED	$(AT)_7$	128–134	MN601768
	DaE-19	F: GCAAGATTGTGGTGTTGCTGT R: GTGACTCGGAGAAAGCGGTT	Q1-6-FAM	$(AAC)_9$	122–147	MN601771
	DaE-27	F: TTCAATATTGTGGCTGGTCCCA R: TCAGCTCTCAGACAAAGGCA	Q4-PET	$(AG)_{15}$	155–199	MN601775
	DaE-30[c]	F: ACACTCCTGCAAGGTCAACA R: AGCACTCCTAATGCCCTCAA	Q3-VIC	$(AT)_{12}$	154–162 164–176	MN601778
	DaE-36	F: TCATTGAGCCACAAGGGAAC R: ACAGAGGAGTGTGATCGAAGA	Q1-6-FAM	$(AT)_{10}$	170–222	MN601780
	DaE-41	F: TGGTTACTTCAAGCACAGAGAC R: CTGCAATATCGATGCCTCTTCT	Q2-NED	$(AT)_{11}$	201–243	MN601783
	DaE-46[d]	F: GCTCCACTTCCACTAGGCTT R: GCCGACCAAGCCTCTTTGAT	Q3-VIC	$(AT)_{10}$	237–291 (227)	MN601785
Multiplex 4	DaE-16	F: CTACTCGTGACTGCTCTTGC R: GGAATGACCGTGTTGTTTGGG	Q3-VIC	$(AG)_{20}$	112–146	MN601770
	DaE-20	F: AGATCCCTCTGAATCCCTGATT R: TCATGTCTTCCCTCTTTAGGCT	Q1-6-FAM	$(AT)_9$	135–185	MN601772
	DaE-23	F: CAGCGAACCCATGTCAAACG R: TCCTCAAAGCTACCCTATCCCA	Q4-PET	$(AG)_{13}$	136–238	MN601773
	DaE-29	F: AGGAGAATCTTGGCACCGAA R: AACTGCAGTTGGTCACCCTC	Q2-NED	$(AG)_{15}$	148–178	MN601777
	DaE-42	F: AAGGAATTGTGGGTGGTGGG R: AGTGGTTATATCGTCCGGTGT	Q3-VIC	$(AT)_7$	206–238	MN601784

The allele size range for each duplicated copy is indicated on two different lines

[a] Q1 = TGTAAAACGACGGCCAGT [13]; Q2 = TAGGAGTGCAGCAAGCAT; Q3 = CACTGCTTAGAGCGATGC; Q4 = CTAGTTATTGCTCAGCGGT (Q2–Q4, after Culley et al. [14])

[b] Number of repeats found in the clone that corresponds to the accession number

[c] Duplicated loci

[d] Loci presenting a monomorphic band, whose size is indicated into brackets

Table 2 Genetic properties of the newly developed 21 polymorphic nuclear microsatellites of *Dacryodes edulis*

Locus	Manjo ($n = 30$)					Yaoundé ($n = 29$)					Franceville ($n = 15$)					Brazzaville ($n = 21$)				
	A	H_e	H_o	F^a	r	A	H_e	H_o	F^a	r	A	H_e	H_o	F^a	r	A	H_e	H_o	F^a	r
DaE-5.1	4	0.67	0.24	0.65***	0.42 ± 0.07	4	0.75	0.20	0.74***	0.43 ± 0.06	4	0.69	0.33	0.53**	0.33 ± 0.16	4	0.68	0.27	0.61**	0.40 ± 0.16
DaE-5.2	14	0.92	0.44	0.52***	0.33 ± 0.07	14	0.92	0.60	0.35***	0.20 ± 0.08	9	0.91	0.42	0.55***	0.36 ± 0.13	13	0.92	0.47	0.50***	0.31 ± 0.11
DaE-7	3	0.34	0.40	-0.18	0 ± 0	4	0.16	0.17	-0.05	0 ± 0	3	0.30	0.20	0.34	0.10 ± 0.10	3	0.33	0.29	0.14	0.04 ± 0.05
DaE-10.1	2	0.18	0.13	0.28	0.07 ± 0.07	2	0.03	0.03	0	0.00 ± 0.00	2	0.07	0.07	0	0 ± 0	2	0.14	0.05	0.66	0.13 ± 0.12
DaE-10.2	4	0.40	0.40	-0.01	0.01 ± 0.03	4	0.51	0.41	0.2	0.05 ± 0.06	4	0.53	0.60	-0.15	0 ± 0	3	0.40	0.29	0.28	0.09 ± 0.07
DaE-13.1	4	0.58	0.48	0.17	0.07 ± 0.04	3	0.60	0.41	0.31	0.20 ± 0.06	3	0.65	0.60	0.07	0.15 ± 0.06	4	0.60	0.52	0.13	0.11 ± 0.05
DaE-14	3	0.51	0.50	0.03	0 ± 0.00	3	0.51	0.59	-0.15	0 ± 0	3	0.59	0.53	0.1	0.07 ± 0.08	3	0.49	0.57	-0.16	0 ± 0
DaE-16	11	0.82	0.83	-0.02	0 ± 0	13	0.88	0.97	-0.1	0 ± 0	7	0.81	0.8	0.02	0.01 ± 0.02	10	0.85	0.81	0.05	0.02 ± 0.04
DaE-19	6	0.66	0.70	-0.06	0 ± 0	5	0.60	0.59	0.03	0.05 ± 0.05	6	0.70	0.73	-0.04	0 ± 0	4	0.62	0.67	-0.08	0 ± 0
DaE-20	13	0.87	0.54	0.39***	0.24 ± 0.08	16	0.84	0.44	0.48***	0.28 ± 0.06	11	0.83	0.57	0.32**	0.15 ± 0.10	14	0.89	0.65	0.28**	0.16 ± 0.08
DaE-23	20	0.91	0.87	0.05	0 ± 0	20	0.80	0.83	-0.03	0 ± 0	15	0.94	0.87	0.08	0.02 ± 0.02	14	0.92	0.76	0.17*	0.08 ± 0.05
DaE-24	4	0.37	0.33	0.11	0.03 ± 0.04	6	0.58	0.62	-0.07	0 ± 0	3	0.35	0.27	0.24	0.07 ± 0.08	3	0.40	0.43	-0.08	0 ± 0
DaE-27	9	0.83	0.80	0.03	0.03 ± 0.03	11	0.85	0.71	0.16	0.05 ± 0.06	10	0.83	0.86	-0.04	0 ± 0	7	0.82	0.86	-0.05	0 ± 0
DaE-28	3	0.40	0.37	0.08	0.02 ± 0.05	4	0.13	0.07	0.49	0.11 ± 0.10	3	0.30	0.33	-0.13	0 ± 0	3	0.52	0.52	-0.01	0 ± 0
DaE-29	8	0.81	0.70	0.14	0.02 ± 0.04	9	0.86	0.86	0	0 ± 0	8	0.82	0.73	0.11	0.01 ± 0.03	9	0.80	0.76	0.05	0 ± 0
DaE-30.1	4	0.59	0.37	0.38	0.14 ± 0.06	5	0.58	0.36	0.39**	0.21 ± 0.07	4	0.49	0.47	0.04	0 ± 0	5	0.67	0.43	0.37	0.16 ± 0.07
DaE-30.2	5	0.48	0.23	0.52*	0.16 ± 0.05	6	0.55	0.28	0.50**	0.17 ± 0.05	3	0.35	0.27	0.24	0 ± 0	6	0.39	0.20	0.50**	0.24 ± 0.12
DaE-34	5	0.72	0.66	0.09	0.07 ± 0.08	4	0.67	0.39	0.42	0.22 ± 0.07	4	0.74	0.14	0.82***	0.66 ± 0.44	5	0.75	0.37	0.52***	0.32 ± 0.09
DaE-36	18	0.92	0.73	0.21**	0.09 ± 0.04	17	0.93	0.36	0.62**	0.32 ± 0.05	12	0.92	0.47	0.50***	0.23 ± 0.06	15	0.89	0.48	0.47***	0.21 ± 0.05
DaE-37	7	0.79	0.77	0.04	0 ± 0	8	0.82	0.79	0.03	0.01 ± 0.03	7	0.80	0.73	0.09	0 ± 0.02	8	0.79	0.71	0.1	0.02 ± 0.04
DaE-39	12	0.90	0.80	0.11	0.06 ± 0.04	10	0.84	0.72	0.14	0.07 ± 0.05	7	0.73	0.46	0.38*	0.22 ± 0.13	10	0.84	0.68	0.19	0.11 ± 0.07
DaE-41	16	0.94	0.93	0	0.01 ± 0.02	16	0.89	0.74	0.17	0.08 ± 0.05	13	0.92	0.57	0.39***	0.21 ± 0.10	14	0.9	0.67	0.26**	0.12 ± 0.06
DaE-42	8	0.75	0.67	0.12	0.02 ± 0.04	8	0.71	0.59	0.18	0.06 ± 0.05	7	0.78	0.69	0.12	0.05 ± 0.07	9	0.84	0.81	0.04	0 ± 0
DaE-46	7	0.71	0.63	0.11	0.00 ± 0.00	10	0.77	0.75	0.03	0 ± 0	7	0.80	0.60	0.26	0.08 ± 0.07	9	0.80	0.86	-0.08	0 ± 0
Multilocus average	7.9	0.67	0.56	0.08	0.07 ± 0.03	8.4	0.66	0.52	0.10	0.10 ± 0.04	6.5	0.66	0.51	0.08	0.11 ± 0.07	7.4	0.68	0.55	0.10	0.10 ± 0.05

A number of alleles sampled, *F* inbreeding coefficient, H_e expected heterozygosity, H_o observed heterozygosity, *n* number of individuals sampled, *r* frequency of null alleles

[a] Significant deviation from Hardy–Weinberg equilibrium at $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Appendice 1

Table 3 Cross-amplification of the 21 new microsatellite loci in four other African *Dacryodes* species (range specified)

Locus	*D. buettneri* ($n=5$)	*D. igaganga* ($n=3$)	*D. osika* ($n=4$)	*D. pubescens* ($n=5$)
DaE-5.1	100–106	100	100	100–106
DaE-5.2	108–138	110–136	110–138	108–136
DaE-7	119–147	113	113–119	113–131
DaE-10.1	128–130	128–130	128–132	126–130
DaE-10.2	119–121	121–125	119–123	119–125
DaE-13.1	128–130	128–132	128–130	126–132
DaE-14	128–148	128–130	128–132	128–134
DaE-16	118–126	122–142	128–150	118–138
DaE-19	134–141	128–137	134–137	128–141
DaE-20	153	149–177	123–157	143–153
DaE-23	146–160	146–200	156–210	146–174
DaE-24	161–167	159–169	159–165	161–169
DaE-27	147–167	161	155–177	127–161
DaE-28	153–167	153	153–177	153–165
DaE-29	156–164	164–180	148–176	156–176
DaE-30.1	154–162	158–162	154–162	154–160
DaE-30.2	164–176	168–170	166–168	164–168
DaE-34	173–192	173–178	173–178	173–175
DaE-36	174–202	198	172–212	168–180
DaE-37	177–189	183–185	183–191	175–189
DaE-39	176–198	184–192	178–192	176–188
DaE-41	213–227	199–223	199–231	199–225
DaE-42	204–206	206–212	206–224	206–218
DaE-46	235–275	239–295	241–245	225–251

n number of individuals tested

Conclusions

In this study, we developed 21 new polymorphic microsatellite markers for the food tree species *Dacryodes edulis*. The study of intraspecific genetic diversity at different geographical scales, as well as the study of species' patterns of gene flow will be facilitated using these markers. The high success rate of transferability to four other *Dacryodes* species will also be helpful for conducting genetic studies within the genus.

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

Appendix

See Table 4.

Table 4 Locality information for the samples used in this study

Species	*n*	Country	Latitude	Longitude	Voucher
Dacryodes edulis	30	Cameroon (Manjo)	4.84343	9.83707	
	29	Cameroon (Yaoundé)	3.87738	11.47541	
	15	Gabon (Franceville)	−1.63520	13.56843	
	21	Republic of the Congo (Brazzaville)	−4.30934	15.20149	
Dacryodes buettneri	1	Cameroon	2.25808	10.54562	
	1	Republic of the Congo	−3.81799	12.55043	
	1	Republic of the Congo	−3.49708	12.30486	
	1	Republic of the Congo	−3.14263	13.09311	
	1	Republic of the Congo	−3.34388	13.24865	
Dacryodes igaganga	3	Cameroon	3.47259	13.46815	
Dacryodes osika	2	Democratic Republic of the Congo	0.29292	25.33752	
	2	Democratic Republic of the Congo	0.76250	24.48694	
Dacryodes pubescens	1	Republic of the Congo	−2.84745	11.81680	
	1	Republic of the Congo	−4.23016	12.42850	
	1	Republic of the Congo	−4.30876	12.45035	
	2	Republic of the Congo	−4.37212	15.17061	ESM1390[a]

[a] Voucher deposited at the BRLU Herbarium and the National Herbarium of Congo, Brazzaville

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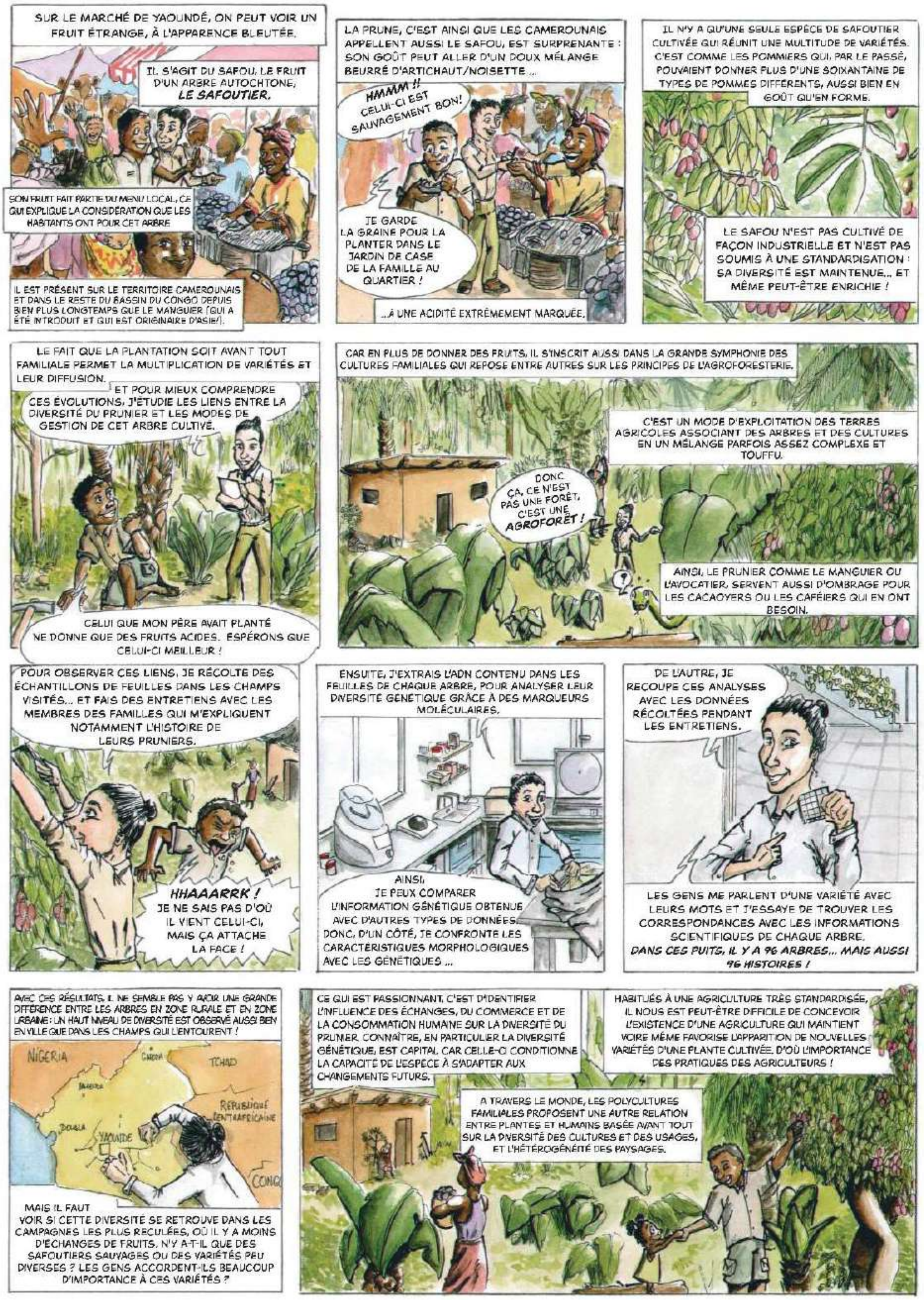
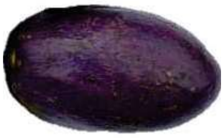
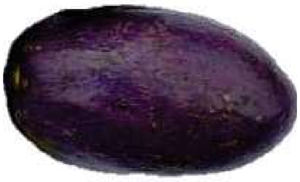

SUR LE MARCHÉ DE YAOUNDÉ, ON PEUT VOIR UN FRUIT ÉTRANGE, À L'APPARENCE BLEUTÉE.
IL S'AGIT DU SAFOU, LE FRUIT D'UN ARBRE AUTOCHTONE, *LE SAFOUTIER.*
SON FRUIT FAIT PARTIE DU MENU LOCAL, CE QUI EXPLIQUE LA CONSIDÉRATION QUE LES HABITANTS ONT POUR CET ARBRE
IL EST PRÉSENT SUR LE TERRITOIRE CAMEROUNAIS ET DANS LE RESTE DU BASSIN DU CONGO DEPUIS BIEN PLUS LONGTEMPS QUE LE MANGUIER (QUI A ÉTÉ INTRODUIT ET QUI EST ORIGINAIRE D'ASIE !).
LA PRUNE, C'EST AINSI QUE LES CAMEROUNAIS APPELLENT AUSSI LE SAFOU, EST SURPRENANTE : SON GOÛT PEUT ALLER D'UN DOUX MÉLANGE BEURRÉ D'ARTICHAUT/NOISETTE ...
HMMM !! CELUI-CI EST SAUVAGEMENT BON!
JE GARDE LA GRAINE POUR LA PLANTER DANS LE JARDIN DE CASE DE LA FAMILLE AU QUARTIER !
...À UNE ACIDITÉ EXTRÊMEMENT MARQUÉE.
IL N'Y A QU'UNE SEULE ESPÈCE DE SAFOUTIER CULTIVÉE QUI RÉUNIT UNE MULTITUDE DE VARIÉTÉS. C'EST COMME LES POMMIERS QUI, PAR LE PASSÉ, POUVAIENT DONNER PLUS D'UNE SOIXANTAINE DE TYPES DE POMMES DIFFÉRENTS, AUSSI BIEN EN GOÛT QU'EN FORME.
LE SAFOU N'EST PAS CULTIVÉ DE FAÇON INDUSTRIELLE ET N'EST PAS SOUMIS À UNE STANDARDISATION : SA DIVERSITÉ EST MAINTENUE... ET MÊME PEUT-ÊTRE ENRICHIE !
LE FAIT QUE LA PLANTATION SOIT AVANT TOUT FAMILIALE PERMET LA MULTIPLICATION DE VARIÉTÉS ET LEUR DIFFUSION.
ET POUR MIEUX COMPRENDRE CES ÉVOLUTIONS, J'ÉTUDIE LES LIENS ENTRE LA DIVERSITÉ DU PRUNIER ET LES MODES DE GESTION DE CET ARBRE CULTIVÉ.
CELUI QUE MON PÈRE AVAIT PLANTÉ NE DONNE QUE DES FRUITS ACIDES. ESPÉRONS QUE CELUI-CI MEILLEUR !
CAR EN PLUS DE DONNER DES FRUITS, IL S'INSCRIT AUSSI DANS LA GRANDE SYMPHONIE DES CULTURES FAMILIALES QUI REPOSE ENTRE AUTRES SUR LES PRINCIPES DE L'AGROFORESTERIE.
C'EST UN MODE D'EXPLOITATION DES TERRES AGRICOLES ASSOCIANT DES ARBRES ET DES CULTURES EN UN MÉLANGE PARFOIS ASSEZ COMPLEXE ET TOUFFU.
DONC ÇA, CE N'EST PAS UNE FORÊT, C'EST UNE *AGROFORÊT !*
?
AINSI, LE PRUNIER COMME LE MANGUIER OU L'AVOCATIER, SERVENT AUSSI D'OMBRAGE POUR LES CACAOYERS OU LES CAFÉIERS QUI EN ONT BESOIN.
POUR OBSERVER CES LIENS, JE RÉCOLTE DES ÉCHANTILLONS DE FEUILLES DANS LES CHAMPS VISITÉS... ET FAIS DES ENTRETIENS AVEC LES MEMBRES DES FAMILLES QUI M'EXPLIQUENT NOTAMMENT L'HISTOIRE DE LEURS PRUNIERS.
HHAAARRK ! JE NE SAIS PAS D'OÙ IL VIENT CELUI-CI, MAIS ÇA ATTACHE LA FACE !
ENSUITE, J'EXTRAIS L'ADN CONTENU DANS LES FEUILLES DE CHAQUE ARBRE, POUR ANALYSER LEUR DIVERSITÉ GÉNÉTIQUE GRÂCE À DES MARQUEURS MOLÉCULAIRES.
AINSI, JE PEUX COMPARER L'INFORMATION GÉNÉTIQUE OBTENUE AVEC D'AUTRES TYPES DE DONNÉES. DONC, D'UN CÔTÉ, JE CONFRONTE LES CARACTÉRISTIQUES MORPHOLOGIQUES AVEC LES GÉNÉTIQUES ...
DE L'AUTRE, JE RECOUPE CES ANALYSES AVEC LES DONNÉES RÉCOLTÉES PENDANT LES ENTRETIENS.
LES GENS ME PARLENT D'UNE VARIÉTÉ AVEC LEURS MOTS ET J'ESSAYE DE TROUVER LES CORRESPONDANCES AVEC LES INFORMATIONS SCIENTIFIQUES DE CHAQUE ARBRE. *DANS CES PUITS, IL Y A 96 ARBRES... MAIS AUSSI 96 HISTOIRES !*
AVEC CES RÉSULTATS, IL NE SEMBLE PAS Y AVOIR UNE GRANDE DIFFÉRENCE ENTRE LES ARBRES EN ZONE RURALE ET EN ZONE URBAINE : UN HAUT NIVEAU DE DIVERSITÉ EST OBSERVÉ AUSSI BIEN EN VILLE QUE DANS LES CHAMPS QUI L'ENTOURENT !
NIGERIA
TCHAD
RÉPUBLIQUE CENTRAFRICAINE
DOUALA
YAOUNDE
CONG
MAIS IL FAUT VOIR SI CETTE DIVERSITÉ SE RETROUVE DANS LES CAMPAGNES LES PLUS RECULÉES, OÙ IL Y A MOINS D'ÉCHANGES DE FRUITS. N'Y A-T-IL QUE DES SAFOUTIERS SAUVAGES OU DES VARIÉTÉS PEU DIVERSES ? LES GENS ACCORDENT-ILS BEAUCOUP D'IMPORTANCE À CES VARIÉTÉS ?
CE QUI EST PASSIONNANT, C'EST D'IDENTIFIER L'INFLUENCE DES ÉCHANGES, DU COMMERCE ET DE LA CONSOMMATION HUMAINE SUR LA DIVERSITÉ DU PRUNIER. CONNAÎTRE, EN PARTICULIER LA DIVERSITÉ GÉNÉTIQUE, EST CAPITAL CAR CELLE-CI CONDITIONNE LA CAPACITÉ DE L'ESPÈCE À S'ADAPTER AUX CHANGEMENTS FUTURS.
HABITUÉS À UNE AGRICULTURE TRÈS STANDARDISÉE, IL NOUS EST PEUT-ÊTRE DIFFICILE DE CONCEVOIR L'EXISTENCE D'UNE AGRICULTURE QUI MAINTIENT VOIRE MÊME FAVORISE L'APPARITION DE NOUVELLES VARIÉTÉS D'UNE PLANTE CULTIVÉE. D'OÙ L'IMPORTANCE DES PRATIQUES DES AGRICULTEURS !
A TRAVERS LE MONDE, LES POLYCULTURES FAMILIALES PROPOSENT UNE AUTRE RELATION ENTRE PLANTES ET HUMAINS BASÉE AVANT TOUT SUR LA DIVERSITÉ DES CULTURES ET DES USAGES, ET L'HÉTÉROGÉNÉITÉ DES PAYSAGES.

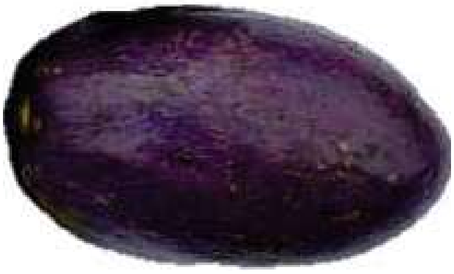
Taille



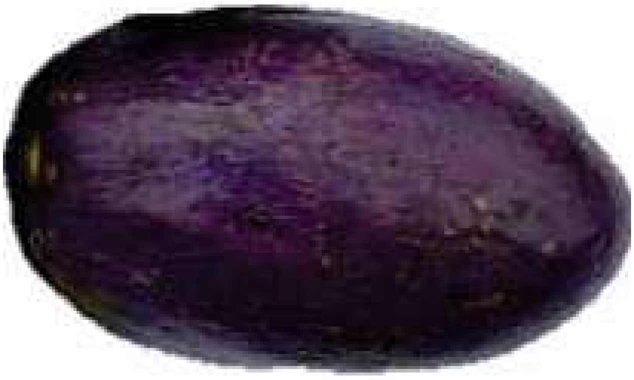
1) Très petit <3 cm



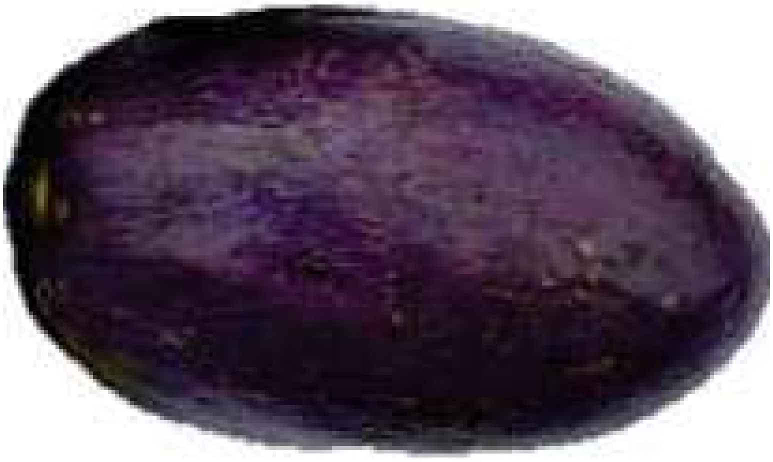
2) Petit 3-5 cm



3) Moyen 5-7 cm



4) Grand 7-10 cm

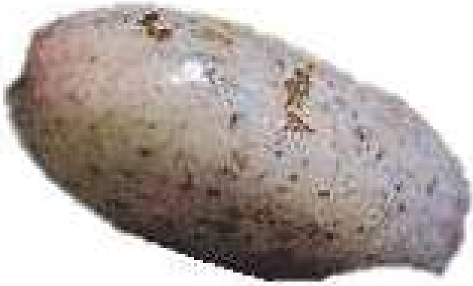


5) Très grand >10cm

Couleur de la peau à maturité

1) Rose, brun rose

2) Blanc, clair

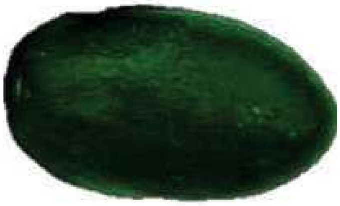


3) Bleu

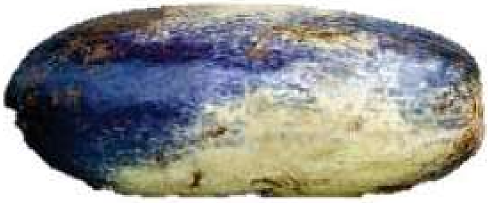
4) Violet

5) Noir

6) Vert


6) Bicolore (une partie du fruit gardant sa couleur non-mature même quand le safou est bon à manger)



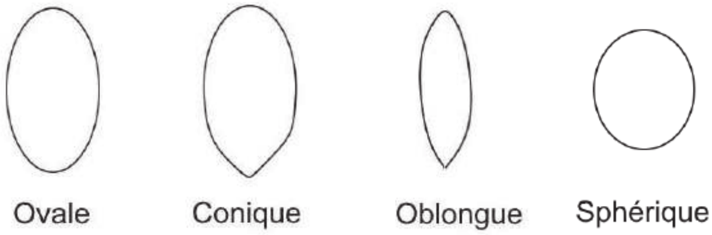

<u>Couleur de la pulpe</u>

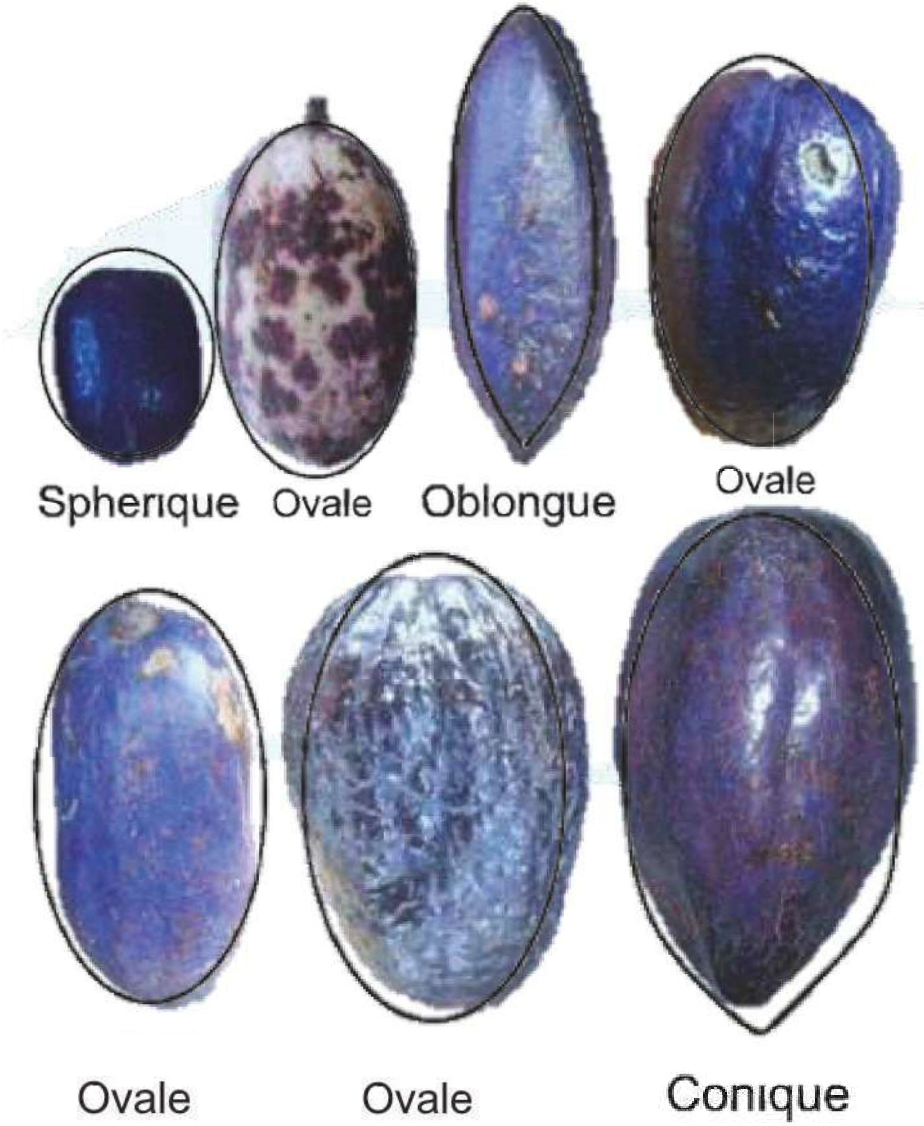
1) Vert 2) Blanc 3) Rouge 4) Jaune

<u>Noyau</u> Présence/absence noyau :

1) Blanc/beige 2) Rouge 3)Vert 4) Marron


<u>Forme</u>



Ovale
Conique
Oblongue
Sphérique


Spherique
Ovale
Oblongue
Ovale
Ovale
Ovale
Conique

<u>Forme</u>

Particularités de forme (creux, renflements, fissures) :

Qualité du fruit

Texture :

Goût : (sur une échelle de 1 à 5, 1 étant le moins bon, 5 le meilleur)

Niveau d’acidité (très acide, moyennement acide, pas acide du tout) :

Présence d’huile : (sur une échelle de 1 à 5, 1 étant le moins huileux, 5 le plus huileux)

Autres critères de définition des variétés

Période de fructification :

Durée de conservation :

	Nom local			Bamiléké (1)		Bassa (2)		Beti (3)		Mixte (N1=60, N2=37, N3=76)	Total
Catégorie	Nom vernaculaire	Traduction	Langue	Rural (n=48)	Périurbain (n=27)	Rural (n=44)	Périurbain (n=50)	Rural (n=49)	Périurbain (n=85)	Urbain	Nombre de citations
Morphologique	Bor kouc	Taro (*Colocasia esculenta*) = fruit grand et bon	Bamiléké	6	0	0	0	0	0	0	6
	Bou Ngop ou bou Ngap	Œuf de la poule	Bamiléké	5	0	0	0	0	0	0	5
	Touc tchueu ou ntou tsoua ou touc dor tchueu	Grand fruit	Bamiléké	11	0	0	0	0	0	0	11
	Sa dor tchueu ou Tsa ndor tshoua	Long (doigt de) fruit	Bamiléké	7	0	0	0	0	0	0	7
	Saha bor keu ou sa'a bonkeu	L’arbre des enfants	Bamiléké	5	0	0	0	0	0	0	5
	Mbam be ou Mba mbe	« fruit noir » (*Canarium schweinfurthii*)	Bamiléké	5	0	0	0	0	0	0	5
	Bom toro ou mbom todo	**Grand fruit**	**Bassa**	**0**	**0**	**1**	**9**	**0**	**0**	**0**	**10**
	Mbey Sa'h ou mbey sa	**Fruit blanc**	**Bassa**	**0**	0	**18**	**7**	**0**	**0**	**2**	**27**
	Abeng	**Beauté Fruit grand et/ou bon**	**Beti**	**0**	**0**	**0**	**0**	**0**	**1**	**4**	**5**

	Nom local			Bamiléké (1)		Bassa (2)		Beti (3)		Mixte (N1=60, N2=37, N3=76)	Total
Catégorie	Nom vernaculaire	Traduction	Langue	Rural (n=48)	Périurbain (n=27)	Rural (n=44)	Périurbain (n=50)	Rural (n=49)	Périurbain (n=85)	Urbain	Nombre de citations
Morphologique	**Asa bio ou djoh ou djoui sa'a**	**Igname, *Dioscorea rotundata* = fruit grand et bon**	**Beti**	**0**	**0**	**0**	**0**	**2**	**3**	**0**	**5**
	Leboack	**Le melon, *Cucumeropsis mannii* = grand fruit**	**Beti**	**0**	**0**	**0**	**0**	**12**	**8**	**4**	**24**
	Itobo	**Grand fruit**	**Beti**	**0**	**0**	**0**	**0**	**5**	**1**	**0**	**6**
	Apouma	**Blanc**	**Beti**	**0**	**0**	**0**	**0**	**0**	**4**	**1**	**5**
	Feu meu	**La chaux (fruit blanc)**	**Beti**	**0**	**0**	**0**	**0**	**1**	**2**	**6**	**9**
	Ebin ntomo ou Ebinin tomo	**Les noyaux du mouton**	**Beti**	**0**	**0**	**0**	**0**	**3**	**11**	**2**	**16**
	Mintongo	**Long fruit**	**Beti**	**0**	**0**	**0**	**0**	**6**	**1**	**0**	**7**
	Mononone ou Mononouane	**Petit oiseau**	**Beti**	**0**	**0**	**0**	**0**	**5**	**20**	**7**	**32**
	Asa'a koss ou asa'a angoun	**Fruit de l'oiseau**	**Beti**	**0**	**0**	**0**	**0**	**0**	**2**	**6**	**8**
Organoleptique	Tshoua mwet	Fruit huileux	Bamiléké	4	0	0	0	0	0	0	4
	Toro mo'o	**Fruit huileux**	**Bassa**	**0**	**0**	**4**	**2**	**0**	**0**	**0**	**6**
	Toro mby	**Fruit acide**	**Bassa**	**0**	**0**	**8**	**5**	**0**	**0**	**0**	**13**
	Asa sang ou osa sang	**Fruit acide**	**Beti**	**0**	**0**	**0**	**0**	**0**	**2**	**2**	**4**

	Nom local			Bamiléké (1)		Bassa (2)		Beti (3)		Mixte (N1=60, N2=37, N3=76)	Total
Catégorie	Nom vernaculaire	Traduction	Langue	Rural (n=48)	Périurbain (n=27)	Rural (n=44)	Périurbain (n=50)	Rural (n=49)	Périurbain (n=85)	Urbain	Nombre de citations
Organoleptique	**Mouno'o mouno'o**	**"huile huile" fruit huileux**	**Beti**	**0**	**0**	**0**	**0**	**0**	**6**	**1**	**7**
	Saang	**Acide**	**Beti**	**0**	**0**	**0**	**0**	**2**	**1**	**5**	**8**
Localisation	Milo'o midouk	Milieu de la cacaoyère	Beti	0	0	0	0	4	0	0	4

Abstract

In tropical forest ecosystems, humans have always benefited from useful plant species, whether as a source of food, fiber, fuel, or medicine. Among these forest products, some of them have been progressively cultivated. This is the case of the African plum tree (*Dacryodes edulis*, Burseraceae), an emblematic fruit tree of Central Africa. This PhD thesis addresses different aspects of the dynamics of the cultivated diversity of African plum trees via an interdisciplinary approach using population genetics and ethnoecology. The first part focuses on the evolutionary history of African plum tree; the second on the cultivation and management practices of the species by different ethnic groups in Cameroon. The third part, bringing together the two disciplines, aims to understand the influence of these different practices on the genetic diversity of the species.

Over its distribution area, the genetic diversity of African plum trees is structured into three main groups. Geographically, the most extensive, which also presents an internal substructure, covers populations of Cameroon and North Gabon. The other two are located at its range margins, in Nigeria and the Democratic Republic of Congo. A historical barrier is suggested on either side of the meteorological equator. These patterns of intra-specific genetic diversity distribution might reflect the impact of Quaternary glaciation events rather than the one of species cultivation. Finally, the sharing of haplotypes between *D. edulis* and other sympatric congeneric species suggests that inter-specific gene flow can occur.

An ethnoecological approach in different African plum production areas in West Cameroon has shown that greater integration into the plum market results in more diversified planting practices and does not have a deleterious effect on varietal diversity in the field. This morphological diversity is also supported by a rich vernacular nomenclature, counting more names for Beti than for Bamileke and Bassa, organized mainly around the morphological and organoleptic criteria of the fruit. Cultivators of African plums show different preferences that diverge according to fruit uses, among which fruit size becomes the most valuable trait for trade producers.

The combination of ethnoecological and genetic approaches allowed to highlight the effects of informal seed exchange networks on the level of genetic diversity and structure. By comparing sites along three urbanization gradients each corresponding to Beti, Bassa or Bamileke, the different seed exchange dynamic between urbanized and rural sites was highlighted. Most seeds used to plant trees in the urban area come from long-distance exchanges, either through markets or not. Consequently, the level of genetic diversity in urban areas is similar or even higher than in rural areas. In addition, the levels of genetic diversity are similar between age classes, suggesting that the species' management practices are not depleting its genetic resources: these practices can be considered sustainable.

In conclusion, we have shown that local knowledge, practices and uses are particularly extensive around the African plum tree. Our results further suggest that local management practices do not, at this stage, impact negatively the species genetic diversity. Nevertheless, this emblematic species, which constitutes a strategic biological model for studying the effect of human practices on genetic diversity in Central Africa, still offers many research questions to be investigated, particularly regarding its cultivation origin and its diffusion history.

Résumé

Dans les écosystèmes forestiers tropicaux, les humains utilisent depuis toujours les espèces végétales utiles, sources de nourriture, de fibre, de combustible ou de médication. Parmi ces produits forestiers, certains d'entre eux ont progressivement été mis en culture. C'est le cas du safoutier (*Dacryodes edulis*, Burseraceae), un arbre fruitier emblématique d'Afrique centrale. Cette thèse aborde différents aspects de la dynamique de la diversité cultivée du safoutier via une approche interdisciplinaire alliant génétique des populations et ethnoécologie. Une première partie porte sur l'histoire évolutive du safoutier ; une seconde s'attache à caractériser les pratiques culturales et de gestion de l'espèce par différents groupes ethniques du Cameroun. Une troisième, faisant converger les approches, vise à comprendre l'influence de ces différentes pratiques sur la diversité génétique de l'espèce.

Sur son aire de distribution, la diversité génétique se structure en trois principaux groupes. Le plus étendu spatialement regroupe les populations du Cameroun et du Nord-Gabon et présente aussi une sous-structuration interne. Les deux autres se situent aux marges de son aire, au Nigéria et en République Démocratique du Congo. Une barrière historique est suggérée de part et d'autre de l'équateur météorologique. Ces patrons de distribution de la diversité génétique au sein de l'espèce semblent résulter des événements de glaciation du Quaternaire plutôt que de la mise en culture de l'espèce. Enfin, le partage d'haplotypes entre *D. edulis* et d'autres *Dacryodes* laisse penser que les flux de gènes sont possibles entre espèces du genre.

Une approche ethnoécologique dans différents bassins de production de safous de l'Ouest Cameroun a permis de montrer qu'une intégration plus forte au marché du safou se traduit par des pratiques de plantation plus diversifiées, et n'a pas d'effet délétère sur la diversité variétale aux champs. À cette diversité morphologique répond une importante nomenclature vernaculaire organisée surtout autour des critères morphologiques et organoleptiques du fruit, et plus étoffée chez les Béti que chez les Bamiléké et Bassa. Les cultivateurs de safous affichent des préférences différentes en fonction des usages du fruit, et une bascule s'opère vers une prédilection pour le critère de taille chez ceux destinant leur production au marché urbain.

Le croisement des approches ethnoécologique et génétique a en particulier permis de mettre en valeur les effets des réseaux informels d'échanges de semences sur la diversité génétique et sa distribution. En procédant par comparaison entre sites le long de gradients à groupes ethniques dominants, les différentes dynamiques entre sites urbanisés ruraux sont soulignées. Les semences utilisées pour planter des arbres en ville proviennent en majorité d'échanges sur de longues distances, transitant ou non par des marchés. En conséquence, des niveaux de diversité identiques, voire supérieurs, sont présents dans les aires urbaines par rapport au milieu rural. Par ailleurs, les niveaux de diversité génétique comparés entre cohortes d'âges sont similaires, suggérant que les pratiques actuelles de gestion de l'espèce n'érodent pas son patrimoine génétique : ces pratiques peuvent être considérées comme durables.

Ces résultats permettent de conclure qu'il existe une grande diversité de connaissances, de pratiques et d'usages autour du safoutier. De plus, les pratiques de gestion locale n'engendrent pas, à ce stade, d'effets néfastes sur sa diversité intra-spécifique. Néanmoins cette espèce emblématique, modèle stratégique pour étudier l'effet des pratiques humaines sur la diversité génétique en Afrique centrale, soulève de nombreuses questions de recherche encore à examiner, notamment vis-à-vis de l'origine de sa mise en culture et de sa diffusion.