THÈSE EN CO-TUTELLE POUR OBTENIR LE GRADE DE DOCTEUR

En Biologie et Amélioration des plantes

Ecole Doctorale « Société et Environnement de l'Université Quisqueya, Haïti
et École doctorale GAIA Université de Montpellier, France

Unité de recherche DIADE

Characterizing coffee genetic resources and agrobiodiversity in Haitian coffee-based agroforestry systems

Caractérisation du patrimoine génétique des caféiers et de l'agrobiodiversité des systèmes agroforestiers caféicoles haïtiens

Présentée par Claude Patrick MILLET
Le 10 Décembre 2024

Sous la direction de Valérie PONCET et Evens EMMANUEL
Et co-encadré par Clémentine Allinne, Wesly Jeune et Pierre Marraccinni

Devant le jury composé de

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« Ce que nous sommes ? Si c'est une question, je vais te répondre : eh bien, nous sommes ce pays et il n'est rien sans nous, rien du tout. Qui est-ce qui plante, qui est-ce qui arrose, qui est-ce qui récolte ? Le café, le coton, le riz, la canne, le cacao, le maïs, les bananes, les vivres et tous les fruits, si ce n'est pas nous, qui les fera pousser ? Et avec ça nous sommes pauvres, c'est vrai, nous sommes malheureux, c'est vrai, nous sommes misérables, c'est vrai. Mais sais-tu pourquoi, frère ? A cause de notre ignorance : nous ne savons pas encore que nous sommes une force, une seule force : tous les habitants, tous les nègres des plaines et des mornes réunis. Un jour quand nous aurons compris cette vérité, nous nous lèverons d'un point à l'autre du pays et nous ferons l'assemblée générale des gouverneurs de la rosée, le grand coumbite des travailleurs de la terre pour défricher la misère et planter la vie nouvelle. »

Jacques Roumain, *Gouverneurs de la Rosée* (1944)

Summary (English)

Haitian Coffee-based agroforestry systems (CAFS) are important contributors to rural livelihoods and provide several ecosystem services, despite facing significant challenges. They contribute to households' economic resilience and food security, but also to the maintenance of natural processes and biodiversity conservation. There has been little scientific study of these systems and the genetic composition and variety mixtures of their coffee plots. To that end, we sought to characterize the agrobiodiversity and genetic resources of historically important coffee growing regions of northern and southern Haiti.

We sampled 28 CAFS to capture the local diversity of cultivated coffee and performed KASP-genotyping of SNP markers and HiPlex multiplex amplicon sequencing for haplotype calling. By comparing field samples to reference specimens from international collections using genetic structure analyses, we assigned them to one of five varietal groups, both traditional and more recent. We also identified inter-varietal hybrids. Our analyses revealed considerable genetic diversity in Haitian farms, higher in fact than many farmers realized.

We then compared this diversity (also using KASP genotyping) to that found across coffee-growing regions of Guadeloupe, as well as their respective bioclimatic contexts, and investigated the historical determinants of the islands' genetic resources. By contrast to Haiti's complex varietal mixtures, only two Arabica groups occurred in Guadeloupe. The traditional Typica variety is still present on both islands, growing across a variety of climatic environments. We also found *C. canephora* on both islands, with multiple likely origins, and identified *C. liberica var. liberica* in Guadeloupe. Overall, Guadeloupe experienced fewer, but older introductions of non-Typica coffee while several recent introductions took place in Haiti, driven by local and global factors and reflecting the history of Arabica varietal development and spread.

We also characterized the broader agrobiodiversity of 39 Haitian farms (including the genotyped ones). To that end, CAFS typologies were established using variables pertaining to coffee genetic diversity, plot structure and injury profiles, shade tree and associated crop diversity, bioclimate, and delivery of ecosystem service related to coffee performance, species and nutritional diversity, tree uses, carbon storage, and nitrogen availability. Associations between typologies were investigated. Surveyed coffee plots were generally varietally diverse, aging, and subject to pest and diseases. Most CAFS occurred on a spectrum of farm regeneration (old to renewed coffee plots) tied to the adoption of "modern" coffee varieties, with implications for ecosystem services. We described 3 distinct ecosystem service bundles delivered by CAFS, focused on maximizing subsistence, coffee performance, and tree utility, respectively.

Over the course of this thesis, we thus studied coffee farms through the lens of genetic diversity, history, ecosystem services, and the interrelation of their components. The resulting view of Haitian CAFS is one of diversified, complex, and dynamic systems. This raises several

interesting questions which are discussed in the manuscript, and may *in fine* contribute to more productive, sustainable and resilient systems.

Common language summary

Haitian coffee agroforestry systems are crucial to rural livelihoods and local biodiversity. They face significant problems which, to be solved, require better knowledge of their agrobiodiversity (i.e. diversity of living beings in agricultural systems). We studied farms in two Haitian coffee (*Coffea arabica*) growing regions. Using genetic analyses, we assigned field samples to five varietal groups (plus inter-varietal hybrids). We found considerable, yet under-recognized, genetic diversity in these farms. We then compared this diversity to that of Guadeloupe, and investigated the factors that shaped them during their shared, then divergent histories. Guadeloupe experienced fewer, but older variety introductions than Haiti. We also found other coffee species on the islands. Finally, we described the broader agrobiodiversity of Haitian farms. We described farm typologies based on coffee, shade tree and associated crop diversity, and the ecosystem services they support. We investigated associations between them. Our studies of Haitian farms paint a picture of diverse, complex, and dynamic systems.

Résumé (français)

En Haïti, les systèmes agroforestiers à base de caféiers (SAFC) contribuent de manière importante à la subsistance, résilience, et sécurité alimentaire des communautés rurales, ainsi qu'au maintien de nombreux processus naturels et à la conservation de la biodiversité. Cependant, ils sont confrontés à de nombreux problèmes. Le manque de connaissances scientifiques sur ces systèmes et leur agrobiodiversité étant un frein à leur revitalisation, nous avons œuvré à les caractériser durant cette thèse. Nos travaux se sont portés sur des SAFC diversifiés de deux régions historiquement importantes pour la caféiculture haïtienne, dans les départements du Nord et de la Grande-Anse.

Tout d'abord, la diversité génétique et les mélanges variétaux des caféiers (*Coffea arabica* L.) de 28 parcelles ont été étudiés dans par des méthodes moléculaires : le génotypage (KASP) de SNP et le séquençage ciblé d'amplicons (Hi-Plex) pour appel d'haplotypes. En comparant les échantillons de terrain à des individus de référence issus de collections internationales, notamment par des analyses de structure de population, nous avons procédé à l'assignation variétale des caféiers haïtiens. Cinq groupes variétaux (traditionnels ou plus récents), y ont été détectés, ainsi que des hybrides inter-variétaux. Nous avons démontré que les SAFC haïtiens présente une diversité génétique considérable et souvent sous-estimée.

Nous avons ensuite comparé cette diversité (à nouveau par génotypage KASP) avec celle présente dans les régions caféicoles de Guadeloupe, et caractérisé leurs contextes bioclimatiques respectifs. Nous avons aussi recherché les facteurs historiques qui ont impacté les ressources génétiques actuelles des îles. Contrairement aux mélanges variétaux complexes d'Haiti, seuls 2 groupes d'Arabica sont présents en Guadeloupe. La variété Typica, historique et patrimoniale, est encore cultivée dans les deux îles, dans des contextes bioclimatiques variés. Nous avons également identifié des Robusta (*C. canephora*) d'origines diverses dans les deux îles, et *C. liberica* var. *liberica* en Guadeloupe. Les ressources génétiques de ces îles reflètent leur histoire, d'abord communes, puis divergentes. Elles découlent d'introductions moins fréquentes et plus anciennes en Guadeloupe qu'en Haïti.

Nous avons également caractérisé l'agrobiodiversité plus large de 39 SAFC haïtiens (dont les 28 génotypés). Pour ce faire, des typologies ont été établies sur la base de variables décrivant la diversité génétique des caféiers, la structure des parcelles, et les profils de dégâts biotiques de celles-ci, ainsi que la diversité des arbres de couvert et cultures associées. Nous avons aussi caractérisé les services écosystémiques fournis, en lien avec la santé et productivité des caféiers, la diversité spécifique et nutritionnelle représentée, la multiplicité d'usages des arbres, le stockage de carbone ou encore la disponibilité de l'azote. Les interactions entre ces typologies ont été décrites. Les SAFC se placent sur un gradient de renouvellement (des fermes âgées aux parcelles regénérées), lié à l'adoption de certaines variétés, avec des conséquences sur la fourniture de services. Trois tendances ont été identifiées pour cette dernière, avec un focus sur la maximisation des services liés à la subsistance, la production caféière, et l'utilité de la strate arborée, respectivement.

Durant cette thèse, nous avons étudié les SAFC à travers le prisme de la génétique, de l'histoire, ou encore de l'interrelation entre leurs différentes composantes. La vision des SAFC qui en émerge est celle de systèmes diversifiés à plusieurs niveaux, complexes et dynamiques. Nous avons discuté des nombreuses questions que soulèvent nos résultats, qui pourraient *in fine* contribuer à l'amélioration de la productivité et de la résilience de ces systèmes, et de leur capacité à répondre aux besoins socio-économiques et écologiques des communautés qui les gèrent.

Résumé vulgarisé

Les systèmes agroforestiers caféicoles d'Haiti sont importants pour le bien-être des communautés locales et la biodiversité. Cependant leur agrobiodiversité (la diversité des être vivants faisant partie des systèmes agricoles) est encore méconnue. Nous avons étudié des parcelles de deux régions caféicoles haïtiennes. Par des analyses génétiques, nous avons assigné les caféiers (*Coffea arabica*) échantillonnés à cinq groupes variétaux et avons déterminé que la diversité de ces parcelles est considérable, mais sous-estimée. Nous l'avons comparée à celle, plus faible, des régions caféicoles de Guadeloupe, et avons décrit comment les histoires, d'abord partagée, puis divergentes, de ces îles les ont façonnées. Enfin, nous avons décrit plus largement l'agrobiodiversité des fermes haïtiennes, que nous avons catégorisées selon la diversité de leur végétation, leur climat, et les services écosystémiques qu'elles fournissent. Nous avons décrit les associations entre ces typologies. Nos études démontrent que les systèmes caféicoles d'Haiti sont complexes et dynamiques.

Rezime (Kreyòl)

An Ayiti, sistèm agroforestyè ki baze sou kafe (SAFK) gen anpil enpòtans pou sibzistans, rezistans, ak sekirite alimantè kominote riral yo, ansanm ak konsèvasyon pwosesis natirèl yo. Yo ede pwoteje biyodivèsite natirèl peyi a, ak biyodivèsite kiltive (agwobiyodivèsite) tou. Sepandan, yo fè fas ak anpil pwoblèm. Mank konesans syantifik sou sistèm sa yo (epi sou agwobiyodivèsite ki reprezante anndan sistèm sa yo) se yon obstak pou relans ak ranfòsman sistèm sa yo. Pandan tèz sila a, nou travay pou karakterize agwobiyodivèsite SAFK nan de rejyon ki te jwe yon wòl enpotan nan listwa kilti kafe ayisyen, nan depatman Nò ak Grandans.

Premyèman, nou dekri divèsite jenetik ak melanj varyete pye kafe (*Coffea arabica* L.) nan 28 SAFK ak de metòd molekilè: jenotipaj sible makè SNP (KASP), ak sekansanj anplikon (Hi-Plex) pou fè apèl aplotip. Nou konpare echantiyon jaden yo ak plizyè echantiyon referans ki soti nan koleksyon entènasyonal, sitou atravè analiz estrikti popilasyon, pou nou kapab fè idantifikasyon varyetal pye kafe ayisyen yo. Nou idantifye senk gwoup varyete (tradisyonèl oswa pi resan), ak plizyè ibrid entè-varyetal. Nou demontre ke SAFK ayisyen yo posede yon divèsite jenetik konsiderab, ki pi wo ke sa nou te atann.

Dezyèmman, apre karakterizasyon kafeye ayisyen yo, nou konpare divèsite yo ak sa ki prezan sou zile Gwadloup yo gras ankò ak jenotipak SNP KASP, epi nou karakterize kontèks biyoklimatik ansanm rejyon detid yo. Nou chèche faktè istorik ki kapab eksplike strikti ak divèsite resous jenetik aktyèl ki prezan sou zile yo. Okontrè de melanj varyete konplèks nou jwen nan jaden Ayiti yo, nou jwenn sèlman 2 gwoup Arabika an Gwadloup. Varyete istorik « Typica » a toujou prezan nan de zile yo, nan kontèks biyoklimatik diferan. Nou rive idantifye tou espès kafe « Robusta » (*C. canephora*, de divès orijin) nan tou de zile yo, ak yon twazyèm espès Gwadloup : *C. liberica var. liberica*. Resous jenetik de zile sa yo reflete istwa yo, ki te pataje pandan lontan, men ki devye anpil nan de denye syèk yo. Ayiti te gen plis entwodiksyon diferan varyete Arabika (men mwens entrodiksyon lòt espès) pase Gwadloup, epi yo pi resan.

Twazyèmman, nou karakterize agwobiyodivèsite (nan yon sans pi laj) 39 SAFK ayisyen (pami yo, 28 jaden ki te echantiyone pou karakterizasyon jenetik yo). Pou fè sa, nou etabli plizyè tipoloji sou baz diferan varyab ki dekri divèsite jenetik pye kafe yo, estrikti ak pwofil atak byotik (maladi, pichon ak bèt ki atake pye kafe yo) bouke kafe yo, osi byen ke divèsite pyebwa ak lòt kilti ki prezan nan jaden yo. Nou karakterize tou sèvis ekosistemik SAFK yo bay an relasyon ak sante epi pwodiktivite pye kafe yo, divèsite espesifik ak nitrisyonèl ki prezan nan jaden yo, diferan itilizasyon ki kapab fèt de pyebwa yo, epi estokaj kabòn ak disponiblite azòt nan sistèm yo. Nou dekri plizyè entèraksyon ant diferan tipoloji sa yo. SAFK yo pozisyone sou yon gradyan renouvèlman (Soti jaden ki ansyen rive nan jaden rejenere) ki korespon ak adopsyon sèten varyete modèn (tankou « Catimor »), epi ki gen konsekans sou sèvis ekosistèm jaden yo bay. Nou idantifye twa tandans nan jaden yo, ki konsantre sou maksimize sèvis sibzistans, pwodiksyon kafe, ak sèvis piblik kouch pye bwa a, respektivman.

Pandan tèz sila a, nou anplwaye metòd jenetik, istorik, epi sitemik pou nou etidye SAFK yo, ak entè-relasyon ki genyen ant diferan eleman sistèm sa yo. Vizyon SAFK ki soti de travay sa montre ke jaden sa yo se de sistèm ki konplèks ak dinamik. Nou diskite sou anpil kesyon rezilta nou yo soulve, ke nou espere ap kapab kontribye nan amelyore pwodiktivite ak

rezilyans sistèm sa yo, ak kapasite pou yo satisfè diferan bezwen sosyo-ekonomik ak ekolojik kominote yo.

Rezime senplifye

Sistèm agroforestyè ki baze sou kafe yo gen anpil enpòtans pou byennèt kominote lokal yo ak konsèvasyon espès ak pwosesis natirèl yo. Sepandan, gen yon mank konesans sou agwobiyodivèsite yo (kidonk, divèsite èt vivan ki fè pati sistèm agrikòl yo). Nan kad tèz sa a, nou etidye plizyè jaden nan de rejyon peyi d'Ayiti kote kafe pouse. Nou itilize analiz jenetik, pou kategorize echantiyon pye kafe (*Coffea arabica*) ayisyen yo an senk gwoup varyete. Nou demontre genyen anpil divèsite nan jaden sa yo. Nou konpare resous jenetik Ayisyen yo ak sa yo ki prezan sou zile Gwadloup nan kontèks Istwa de zile sa yo (ki te pataje nan kòmansman, men ki devye anpil depi de syèk) . Finalman, nou dekri agwobiyodivèsite (nan sans laj) jaden ayisyen yo, ke nou kategorize dapre divèsite vejetasyon yo, klima yo, ak sèvis ekosistèm yo bay yo. Nou dekri asosyasyon ki egziste ant tipoloji sa yo. Etid nou yo montre jaden kafe ayisyen yo konplèks ak dinamik.

List of publications

The following articles have been produced in the cours of this PhD thesis

With the doctoral candidate as first author

(published) **Millet, Claude Patrick, Clémentine Allinne, Tram Vi, Pierre Marraccini, Lauren Verleysen, Marie Couderc, Tom Ruttink, Dapeng Zhang, William Solano-Sanchéz, Christine Tranchant-Dubreuil, Wesly Jeune, Valérie Poncet**. 2024. "Haitian Coffee Agroforestry Systems Harbor Complex Arabica Variety Mixtures and Under-Recognized Genetic Diversity." *PLOS ONE* 19 (4): e0299493. https://doi.org/10.1371/journal.pone.0299493.

(published) **Millet, Claude Patrick, Boris Delahaie, Frederic Georget, Clémentine Allinne, William Solano-Sànchez, Dapeng Zhang, Wesly Jeune, Lucile Toniutti, and Valérie Poncet.** 2024. "Guadeloupe and Haiti's Coffee Genetic Resources Reflect the Crop's Regional and Global History." *Plants, People, Planet*. DOI: 10.1002/ppp3.10584

(submitted) **Millet, Claude Patrick, Wesly Jeune, Jephthé Samuel Guervil, Luc André St Armand, Jean Fritzner Amazan, Guerlande Duval, Reuben Bersonly Jean Louis, Brunet Robert, Valérie Poncet , and Clémentine Allinne.** Ecosystem service bundles associated with agrobiodiversity in Haitian coffee-based agroforestry systems. Submitted to *Ecosystem Services*

As co-author

Valérie Poncet, Piet Van Asten, Claude Patrick Millet, Philippe Vaast, Clémentine Allinne. **2024**. Which diversification trajectories make coffee farming more sustainable? *Current Opinion in Environmental Sustainability* **68**: 101432.

Conferences

(Oral presentation) **Millet, Claude Patrick, Clémentine Allinne, Tram Vi, Pierre Marraccini, Lauren Verleysen, Marie Couderc, Tom Ruttink, Dapeng Zhang, William Solano-Sanchéz, Christine Tranchant-Dubreuil, Wesly Jeune, Valérie Poncet. 2024**. Characterizing and explaining diversification in Haitian Coffee agroforestry systems. *XX International Botanical Congress (IBC) Symposium*: Plant Diversity, Biogeography and Evolution in the Tropics for Conservation, Restoration and Sustainable Use (session 1). Madrid, Spain.

(Oral presentation) **Millet, Claude Patrick, Clémentine Allinne, Wesly Jeune, Valérie Poncet. 2024**. Caractérisation du patrimoine génétique des caféiers et de l'agrobiodiversité des systèmes agroforestiers caféicoles haïtiens. Journées Scientifiques PITAG, Port-au-Prince, Haiti.

(Electronic Poster) **Millet Claude Patrick, Allinne Clémentine, Vi Tram, Marraccini Pierre, Verleysen Lauren, Ruttink Tom, Zhang Dapeng, Solano Sânchez W., Tranchant Christine, Jeune Wesly, Poncet Valérie. 2023.** Unexpected coffee varietal diversity in Haitian coffee agroforestry systems. In : *Book of abstracts of the 29th conference ASIC 2023*. ASIC, VAAS. Hanoï : ASIC, p. 191. ASIC Conference on Coffee Science. 29, Hanoï, Viet Nam

(Poster) **Millet Claude Patrick, Allinne Clémentine, Vi Tram, Marraccini Pierre, Verleysen Lauren, Ruttink Tom, Zhang Dapeng, Solano Sânchez W., Tranchant Christine, Jeune Wesly, Poncet Valérie. 2023**. « Les caféiers dans les systèmes agroforestiers haïtiens: mélanges variétaux complexes et diversité génétique dynamique ». Journées Scientifiques PITAG, Port-au-Prince, Haiti.

Index

Synthèse des travaux

1. Contexte

L'agrobiodiversité est l'ensemble des organismes qui contribuent au sens large à l'agriculture et au fonctionnement des agroécosystèmes. Elle constitue un levier important d'amélioration de la durabilité des systèmes de culture, et de leur capacité à faire face ou à s'adapter aux chocs climatiques, biotiques, ou encore socio-économiques. Elle s'organise à plusieurs échelles, des mosaïques de paysages aux mélanges variétaux d'une même culture. Elle contribue à l'amélioration variétale et donc des rendements, mais aussi au contrôle des maladies et ravageurs. De plus, elle sous-tend la fourniture de nombreux services écosystémiques et peut aider à réduire les besoins des agrosystèmes en intrants chimiques. De ce fait, elle est au cœur de nombreux systèmes traditionnels tels que les systèmes agroforestiers, qui combinent cultures pérennes et annuelles sous une strate arborée, souvent composée d'arbres utiles. Dans la République d'Haïti, les systèmes agroforestiers diversifiés sont au centre des questions de subsistance, de résilience et de sécurité alimentaire des communautés rurales. De plus, ils jouent un rôle crucial dans la conservation de la biodiversité et la délivrance d'autres services écosystémiques dans ce pays qui fait face à une forte dégradation de ses écosystèmes naturels. Cette thèse s'intéresse en particulier aux systèmes agroforestiers à base de caféiers (SAFC).

En Haiti, les caféiers cultivés appartiennent principalement à l'espèce Arabica (*Coffea arabica* L.) ? Cette espèce amphidiploïde, allotétraploïde (2n = 4x = 44), et largement autogame est originaire des hauts plateaux d'Afrique de l'Est (principalement l'Ethiopie), mais est aujourd'hui cultivée à travers les régions tropicales et constitue 60% de la production de café. Son proche parent, le caféier Robusta (*C. canephora* Pierre ex Froener), diploïde (2n=22) et allogame, est également largement cultivé. De l'Ethiopie, l'Arabica a d'abord été introduit au Yémen, qui a conservé le monopole de sa culture jusqu'au XVIIème siècle, où l'espèce a été acquise par les puissances coloniales européennes. Sa diffusion par ces dernières a conduit à de nombreux goulots d'étranglement successifs qui ont diminué la diversité génétique des Arabica cultivés, mais aussi à la création de nombreuses variétés appartenant principalement à deux grandes lignées, Typica et Bourbon. La lignée Typica a été introduite en Haiti (alors la colonie française de Saint Domingue) en 1726. La culture des caféiers a vite pris son essor sur cette île, et a continué à jouer un rôle central dans l'économie et la production agricole d'Haiti suite à son indépendance en 1804. Cependant, au fil de son histoire et particulièrement durant les XXème et XXIème siècles, la caféiculture haïtienne s'est confrontée à de nombreuses crises : des marchés internationaux volatiles, un manque de gouvernance locale et d'appui aux agriculteurs, de nombreux aléas climatiques, ou encore l'émergence de maladies devastatrices telles que la rouille des caféiers (*Hemileia vastatrix*) ou le scolyte des baies (*Hypothenemus hampei*). La production haïtienne a donc fortement diminué au cours des dernières décennies.

2. Objectifs de la thèse

C'est dans ce contexte de déclin d'une culture patrimoniale, et qui fait partie intégrante de systèmes diversifiés d'importance socio-économique et écologique majeure, que nous avons réalisé cette thèse. Elle avait pour but principal de pallier aux nombreuses lacunes dans la connaissance scientifique des SAFC (principalement, mais pas uniquement, en Haïti). Elle s'organise en trois chapitres dont les objectifs étaient : i) la caractérisation des mélanges variétaux et de la diversité des caféiers des SAFC haïtiens, ainsi que des perceptions locales de celles-ci, ii) la comparaison des ressources génétiques (ainsi que des contextes bioclimatiques) des caféiers d'Haiti et de la Guadeloupe, et l'identification de leurs déterminants historiques, et iii) la caractérisation de l'agrobiodiversité au sens plus large des SAFC haïtiens et de la fourniture de services écosystémiques qu'elle sous-tend.

3. Sites d'étude principaux de cette thèse

Cette thèse s'inscrit dans le cadre général d'une tentative de relance de la caféiculture, et plus particulièrement dans celui du Programme d'Innovations Technologiques pour l'Agriculture et l'Agroforesterie (PITAG) financé par de nombreux bailleurs internationaux, piloté par le ministère Haïtien de l'agriculture (MARNDR) et mis en œuvre par un consortium d'ONG, d'universités, de centres de recherche et d'acteurs du secteur privé. Le projet PITAG a réalisé en 2021 un diagnostic préliminaire d'environ 122 SAFC de deux départements (Nord et Grande-Anse) d'Haiti, puis un diagnostic approfondi d'une quarantaine. Ces diagnostics ont mené à la création d'une base de données à partir de laquelle 28 parcelles présentant diverses compositions variétales suspectées de *C. arabica* ont été sélectionnées, 14 dans le département du Nord et 14 dans la Grande-Anse, réparties sur plusieurs communes. Ces 28 parcelles ont été échantillonnées pour les études génétiques décrites dans les deux premiers chapitres de la thèse. Le troisième chapitre, quant à lui, concerne la caractérisation de l'agrobiodiversité de l'ensemble des SAFC visités lors du diagnostic approfondi.

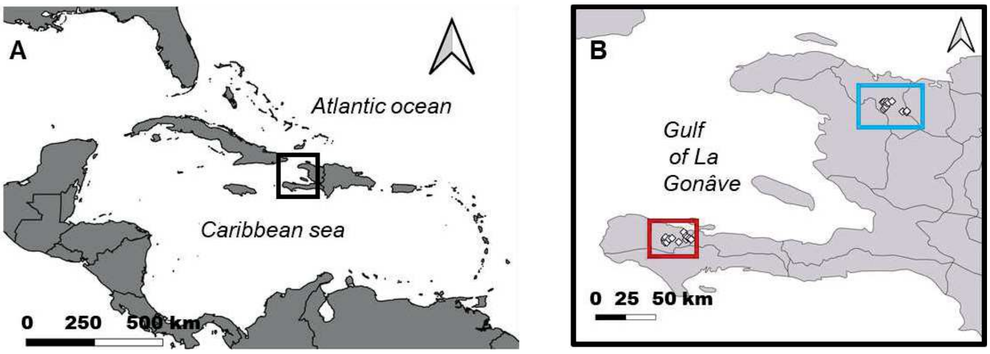


Figure 1. Emplacement des sites d'étude A. Haiti (encadré noir) dans le bassin Caribbéen. B. Sites d'études dans le Nord (encadré bleu) et la Grande-Anse (au sud, encadré rouge)

4. Caractérisation génétique des caféiers Haïtiens

Le premier chapitre concerne principalement la caractérisation génétique et des mélanges variétaux de caféiers Arabica dans les SAFC étudiés. En effet, la composition de ceux-ci était encore mal connue, car si de nombreuses introductions variétales avaient été reportées par des projets de développement agricole, leur diffusion n'avait pas été suivie. De plus, l'état actuel de la variété Typica, à grande valeur historique et considérée comme la composante principale de la caféiculture haïtienne, n'avait jamais été déterminé par des méthodes génétiques.

La collecte d'échantillons pour la caractérisation variétale par génotypage a été réalisée fin 2021. Les connaissances des fermiers sur leurs parcelles ont été mobilisées pour effectuer des prélèvements (1) sur les variétés cultivées majoritairement (recherche de diversité) et si possible (2) sur les caféiers « atypiques », présentant des traits les distinguant des autres. L'identification faite par les acteurs locaux a été notée. Ces « catégories vernaculaires » constituent une représentation du savoir local. Plusieurs accessions de référence (n = 96, dont des accessions sauvages, commerciales, et hybrides) ont été acquises de la collection internationale d'Arabica conservée au CATIE (Costa Rica). Des feuilles ont également été collectées d'autres espèces de *Coffea* (*C. canephora, C. liberica* et *C. congensis*) des serres de l'IRD pour servir de références extérieures (*outgroups*).

Le génotypage ciblé (méthode KASP) de 96 marqueurs SNP (Zhang *et al.*, 2021) initialement développés pour discriminer un large ensemble de variétés (dont celles du CATIE) a été réalisé sur nos échantillons par LGC BioSearch Technologies (Middlesex, UK). Nous avons également obtenu les génotypes sur ces mêmes marqueurs pour une dizaine d'accessions de référence supplémentaires issues du HARC (Hawaii, USA).

4.1. Assignation variétale et composition génétique des parcelles haïtiennes

La diversité génétique globale et sa distribution géographique ont été estimées avec des statistiques descriptives et des calculs au niveau des parcelles, communes et département (logiciel GenAlEx v. 6.51b2 ; Peakall et Smouse 2012). Les statistiques de diversité génétique montrent une forte hétérogénéité au sein des parcelles haïtiennes, mais aussi un niveau de diversité à l'échelle du pays comparable à celui de l'ensemble des accessions de référence. Cette diversité n'est pas significativement structurée à l'échelle des départements (p = 0.431) ni des communes (p = 0.141), mais plutôt des fermes (p = 0.001) (testé avec le package R Hierfstat v. 0.5-11 Goudet 2005). Cela a été confirmé par un calcul de F_{ST} par paires.

Une ACP a été réalisée sur les échantillons haïtiens et de référence (packages R LEA v. 3.10.2, tidyverse v. 2.0.0 et ggplot; Frichot et François 2015; Wickham et al. 2019), confirmant l'importance relative et le manque de structuration à grande échelle de la diversité haïtienne.

Une analyse de structure de la diversité a été réalisée avec la fonction sNMF du package r LEA (K = 1-10, 100 répétitions) sur les Arabica. Pour celle-ci, un seuil de 80% de contribution d'une population ancestrale a été retenu pour caractériser des groupes variétaux. Un seuil de 40% de contribution a aussi été défini pour la sous-catégorisation d'individus admixés. Des F_{ST} par paires entre groupes variétaux génétiques ont été calculés dans GenAlEx. Une valeur de K = 6 a été retenue pour l'analyse de structure réalisée sur les Arabica haïtiens et de référence.

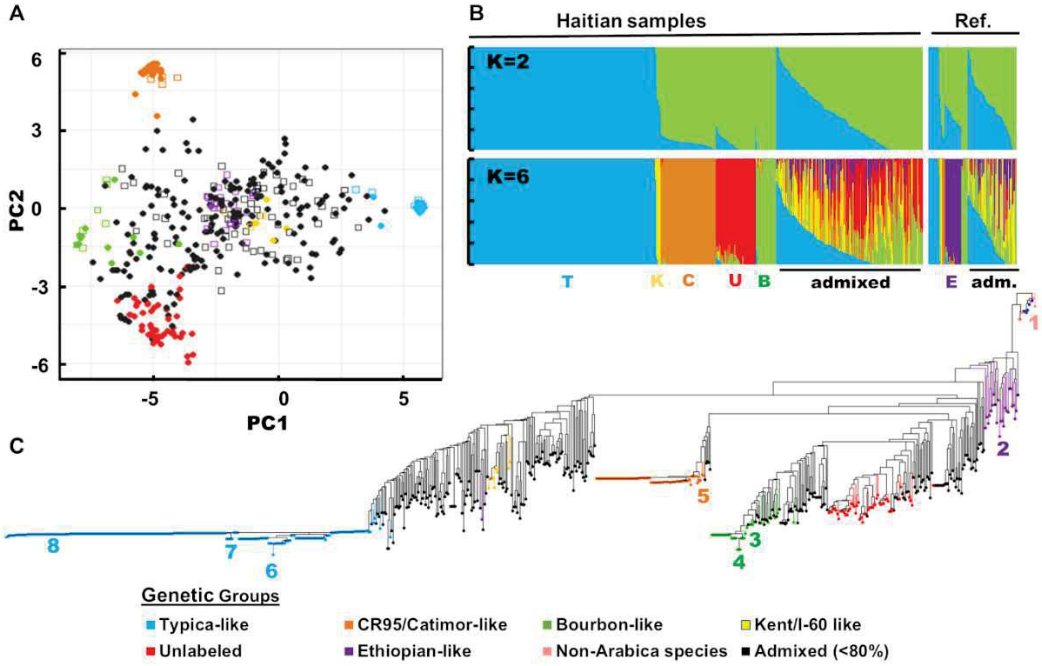


Figure 2. Structure et diversité génétique des caféiers haïtiens par rapport à celles des caféiers de collections internationales. A. Analyse des composants principaux réalisée sur les échantillons haitiens (●) et de référence (□) ; deux premiers axes (46,89% et 11,26% de la variance, respectivement). B. analyse de structure de population des *C. arabica* pour K = 2 (haut) et K = 6 (bas). C. Dendrogramme (*Unweighted neighbor-joining*) des individus haitiens et de référence, coloré selon les groupes génétiques identifiés. Les individus de référence suivants sont indiqués à titre d'illustration 1) GUI2 *C. canephora* 2), T.02731 Jimma Galla Sidamo, 3) T.02542 Caturra, 4) Ku042 Red Bourbon, 5) T.08867 CR-95, 6) T.03427 Cera, 7) Ku214 Jamaica Blue Mountain, 8) T.00989 Guadeloupe.

Six groupes variétaux génétiques ont donc été identifiés (Fig. 2). Ils ont été nommés en fonction des individus de référence avec >80% d'assignation :

Typica-like ($n_{\text{Total}} = 263$, $n_{\text{Haiti}} = 248$). La variété historique traditionnelle est encore cultivée et les fermes monovariétales, typiquement plus difficiles d'accès, en sont des conservatoires.

Bourbon-like ($n_{\text{Total}} = 35$, $n_{\text{Haiti}} = 27$) : Il pourrait s'agir du Bourbon traditionnel ou de variétés plus modernes comme le Caturra (Ester, 1978). Très apparentées, elles ne sont pas différenciées par l'analyse de structure.

CR95/Catimor-like ($n_{\text{Total}} = 77$, $n_{\text{Haiti}} = 73$): Les Catimors (Caturra x Hybride de Timor) ont beaucoup été propagés pour leur résistance à la rouille du Café. (Queneherve 2015)

Kent/I-60-like ($n_{\text{Total}} = 9$, $n_{\text{Haiti}} = 7$). Le Kent est une ancienne variété Indienne, autrefois résistante à la rouille et très populaire au début du XXème siècle. Il pourrait s'agir d'une introduction plus ancienne (Haarer, 1923)

Un groupe composé uniquement d'individus haïtiens (« *Unlabeled* », $n_{\text{Total}} = n_{\text{Haiti}} = 52$). Ils ne peuvent pas être identifiés avec certitude, mais il pourrait s'agir de variétés résistantes colombiennes introgressées par l'hybride de Timor (Tabi, Castillo), dont l'introduction en Haïti est attestée, mais qui sont absentes des collections du CATIE. Nos références les plus apparentées sont les Sarchimor, aussi issus de l'hybride de Timor.

Les accessions d'Ethiopie ($n_{Total} = 23$, $n_{Haiti} = 1$), quasi-uniquement de référence.

Au total 407 individus haïtiens et 52 de référence ont été assignés selon un seuil de 80% d'appartenance, et 194 haïtiens et 65 références sont considérés comme admixés. Un dendrogramme (*unweighted neighbor-joining tree*) a été construit à partir d'une matrice de distance (1000 bootstraps, DARwin v. 6.0.21, Perrier et Jacquemoud-Collet 2006)L'ACP, le dendrogramme et l'analyse de structure ont tous donné des résultats cohérents.

Tous les groupes génétiques (hormis les *Ethiopian-like*) ont été identifiés dans les deux départements. La composition variétale des parcelles était hétérogène et cohérente avec les tendances identifiées par les statistiques de diversité (Fig . 3), avec quatre parcelles monovariétales (Typica), deux bi-variétales, et 22 parcelles présentant 2 à 5 groupes génétiques ainsi que des individus admixés. Parmi les individus admixés avec une contribution significative de groupes génétiques donnés (seuil de 40%), 68.2% ont été trouvés dans une parcelle contenant tous les groupes parentaux ayant contribué. Compte tenu de la grande proportion d'individus admixés présents dans les parcelles contenant également les groupes variétaux contributeurs, certains de ces individus sont probablement issus de croisements entre variétés cultivées dans une même parcelle, avec germination de la banque de graines du sol puis conservation des individus. La vaste répartition des individus admixés suggère que certains pourraient aussi être propagés par des réseaux d'échanges.

Certains échantillons d'une parcelle du Nord ont aussi été identifiés comme appartenant à l'espèce *C. canephora* (Robusta), qui n'a jamais été reportée en Haïti auparavant.

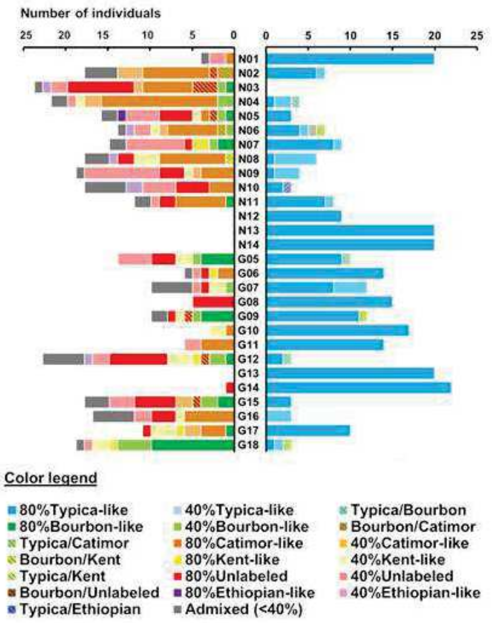
4.2. Comparaison de jeux de marqueurs

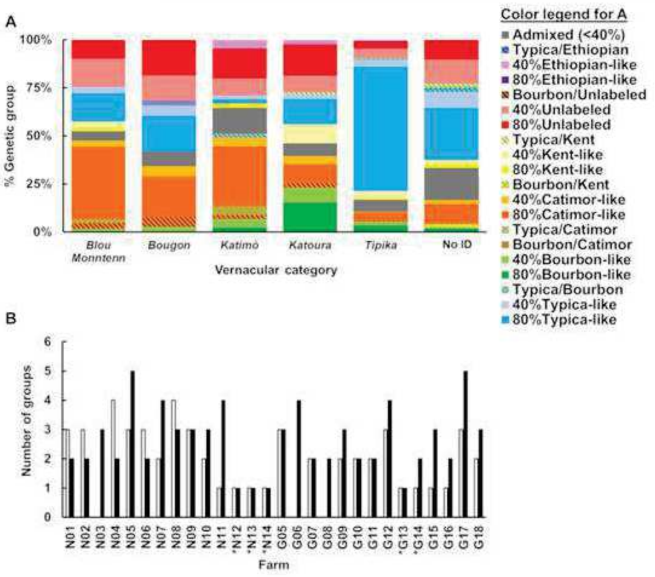
En parallèle, nous avons réalisé le séquençage ciblé d'amplicons (méthode HiPlex) de 400 régions du génome contenant des marqueurs SNP discriminant les deux lignées, Typica et Bourbon. Un pipeline bio-informatique (alignement et appel de variants) suivant un script développé par Bawin (2022) a permis de définir des haplotypes composés d'ensembles de SNP d'une région-cible donnée, traités comme des génotypes de marqueurs multi-alléliques.

L'ACP, le dendrogramme et l'analyse de structure ont aussi été réalisés à partir des données d'haplotypes HiPlex pour comparaison. Un test de Mantel réalisé sur les matrices de distances basées sur les données SNP et Haplotypes respectivement a démontré qu'elles sont significativement corrélées ($p = 0.001$, $R^2 = 0.19$). De plus une relation quasi-linéaire a été observée entre les niveaux de diversité génétique (H_e) calculés pour les deux jeux de marqueurs ($y = 1.13x+0.01$, $R^2 = 0.99$). Cependant, des différences dans les résultats d'analyse de structure et les dendrogrammes ont été observées, probablement dues au biais d'assignation des marqueurs (en particulier le jeu HiPlex, particulièrement sensible aux différences Typica-Bourbon).

4.3. Perceptions locales de la diversité des caféiers

Cinq catégories vernaculaires ont été enregistrées sur le terrain, correspondant toutes à des noms de variétés commerciales (Fig . 4A): *Tipika* ("Typica", ou "Vieux café"), *Katoura* ("Caturra"), *Katimò* ("Catimor"), *Bougon* ("Bourbon") et *Blou Monntenn* ("Blue Mountain"). Les caféiers Robusta, présents dans une seule parcelle, étaient appellés *Kafe Brezil* (« Café Brésil »). Malgré un manque de correspondance entre les catégories vernaculaires et les groupes variétaux identifiées, des tests de χ^2 de Pearson ont révélé une association significative entre les catégories vernaculaires et les groupes génétiques (χ^2, $p = 2.2e^{-16}$). Le nombre de groupes génétiques identifiés dans les parcelles n'était pas corrélé au nombre de variétés déclarées par les cultivateurs ($P = 0.314$, Fig. 4B). Cependant, une corrélation a été trouvée entre la perception par les cultivateurs du statut mono- ou multivariétal des parcelles et la présence d'un ou plusieurs groupes génétiques dans celles-ci ($p = 1.995^{e-7}$). En général, les cultivateurs distinguent assez bien la variété traditionnelle des variétés modernes introduites, et les parcelles homogènes des parcelles diversifiées. Cependant, ils ont tendance à sous-estimer la diversité de leurs caféiers, et ne prennent pas en compte les croisements. Les incohérences dans la nomenclature pourraient être dus à l'élaboration d'une classification vernaculaire basée sur des critères spécifiques, mais aussi à l'introduction de variétés sous des noms trompeurs ou à la propagation d'erreurs d'identification dans les réseaux d'échanges.





(A gauche) **Figure 3. Contribution des groupes génétiques et des individus admixés à la composition des parcelles.** Nombre de *C. arabica* par parcelle présentant une contribution significative de la variété Typica (à droite) et des autres variétés (à gauche). Les pourcentages dans la légende correspondent aux seuils d'assignation. Les individus hachurés sont ceux présentant >40% de contribution de deux groupes variétaux. Les individus en gris ont <40% de contribution de tous les groupes.

(A droite) : **Figure 4. Identifications vernaculaires et génétiques des caféiers haïtiens**. A. composition (en %) des catégories vernaculaires en individus de chaque groupe génétique assigné. B. Nombre de variétés (vernaculaires) reportées par les cultivateurs et de groupes génétiques identifiés. Toutes les parcelles sauf celles marquées d'un * présentaient aussi des individus admixés.

5. Caractérisation et comparaison des ressources génétiques de caféiers de la Guadeloupe et d'Haiti

Le second chapitre concerne l'étude comparée du patrimoine génétique des caféiers haïtiens et guadeloupéens. Cette comparaison est intéressante au vu de l'histoire de la caféiculture caribéenne, et du rôle qu'ont joué ces deux îles dans la diffusion des caféiers en Amérique. Le caféier Arabica, a d'abord été introduit en Martinique en 1723 à partir de semences issues du plant offert au roi de France par les hollandais. De là, il a été diffusé à d'autre îles des Antilles, dont la Guadeloupe et Saint-Domingue (l'actuelle Haiti) en 1726. De ces îles, ainsi que du Suriname, les caféiers ont été propagés à travers l'Amérique tropicale. L'introduction des caféiers en Amérique a constitué le dernier des goulots d'étranglement principaux subis par la lignée Typica, et dont l'impact sur la diversité génétique actuelle des caféiers cultivés s'observe encore. Haiti et, dans une moindre mesure, la Guadeloupe, ont toutes deux bénéficié à une époque de leur histoire d'une filière caféicole importante, qui est aujourd'hui fortement affaiblie.

La comparaison de ces deux îles se justifie également par leur histoire géopolitique initialement partagée, puis fortement divergentes à partir du XIX^{ème} siècle. En effet, elles étaient jusque-là toutes deux des colonies françaises à l'économie basées sur un système de plantation. Cependant, après l'indépendance d'Haiti en 1804, ces îles ont suivi des trajectoires fortement différentes : tandis qu'Haiti échappa à l'emprise directe des puissances coloniales, mais se confronta à de nombreuses crises politiques et économiques, la Guadeloupe demeura une colonie française jusqu'à sa départementalisation en 1946. Tandis que la caféiculture continua d'occuper une place centrale dans l'économie Haïtienne jusqu'à la fin du XXème siècle, son importance en Guadeloupe diminua progressivement dès le XIXème siècle jusqu'à devenir vestigiale, sans toutefois perdre son importance patrimoniale.

A l'heure actuelle, des efforts de relance des secteurs caféicoles d'Haiti et de la Guadeloupe sont en cours. Cependant, comme dans le cas d'Haiti, les ressources génétiques des caféiers guadeloupéens sont encore peu caractérisées et donc mal connues. Le second chapitre de cette thèse avait donc pour but de déterminer la structure et la diversité génétique des caféiers de la Guadeloupe et d'Haiti, et notamment de l'état actuel de l'intégrité génétique des peuplements de caféiers Typica (répétant ainsi dans le cas d'Haiti la caractérisation effectuée durant le premier chapitre afin d'en comparer les résultats). De plus, partant du principe énoncé par McCook (2017) que la composition des parcelles caféicoles (ainsi que leur structure) est façonnée par des processus historiques, aussi bien à l'échelle locale et mondiale, nous avons cherché à identifier les facteurs historiques ayant impacté le patrimoine génétique actuel de ces îles antillaises. Enfin, nous avons cherché à caractériser leurs enveloppes climatiques.

5.1. Sites d'étude et stratégie d'échantillonnage des caféiers pour la caractérisation génétique

Les données de génotypage ciblé KASP des caféiers Haïtiens obtenues dans le cadre du premier chapitre de la thèse ont été réutilisées. A celles-ci se sont ajoutées des données issues d'un échantillonnage en Guadeloupe. Celui-ci a été réalisé dans le cadre d'un projet RITA (*Réseau d'Innovation et de Transfert Agricole*) et a eu lieu en 2022 en Basse-Terre, sur l'étendue actuelle de la culture du café sur l'île, particulièrement au niveau de la Cote Sous-le-Vent. Son but principal était de maximiser la diversité des caféiers représentés. Au total, 33 sites ont été échantillonnés, dont plusieurs anciennes plantations caféières reconverties en systèmes agroforestiers ou de polyculture. Au total, 145 échantillons ont été collectés, dont un de la Terre de Bas de l'archipel des Saintes.

5.2. Jeux de données génétiques

Les données issues des individus de référence décrits dans le premier chapitre ont également été réutilisées. A celles-ci se sont ajoutées des données issues du génotypage KASP d'accessions de référence supplémentaires, mais aussi des données de *C. canephora* de groupes génétiques publiés dans Mérot-L'Anthoene et al. (2019). Au total, 123 individus de référence ont été inclus. Les marqueurs ayant été choisis principalement pour leur capacité de discrimination sur l'espèce Arabica, les individus d'autres espèces présentaient un nombre plus important de données manquantes. Afin de maximiser l'utilité des données génétiques, trois jeux de données à finalités différentes (sous-ensembles de marqueurs) ont été définis:

Le « jeu Arabica » constitué d'individus de l'espèce C. arabica avec 80 locus et 834 individus de C. arabica ($N_{Guadeloupel}$=111, N_{Haiti}=601, et $N_{références}$=122).

Le « jeu Liberica » (40 locus) constitué d'individus de *C. liberica* guadeloupéens putatifs (N=6), ainsi que de 2 représentants de chaque (sous)espèce de caféiers disponibles (ainsi que les 2 sous-espèces de Liberica).

Le « jeu Robusta » (58 locus) constitué d'individus de *C. canephora* guadeloupéens putatifs (N=17), des Robusta haitiens identifiés dans le premier chapitre (N=6), et des individus de référence (N=11) des groupes génétiques A, D (Afrique de l'Ouest), E, R (centrale) et O (de l'Est) issus de Mérot-L'Anthoene et al. (2019).

5.3. Analyses génétiques et caractérisation variétale

La caractérisation variétale des caféiers Arabica a été réalisées à partir du jeu de données « Arabica » selon la méthode décrite dans le premier chapitre, avec les mêmes outils. Les statistiques de diversité génétique de la Guadeloupe, ainsi que des deux départements haïtiens, ont été calculées. Une ACP, ainsi qu'un dendrogramme (*unweighted neighbor-joining tree,* Fig. 4) ont été réalisés, suivis d'une analyse de structure de la diversité. Cette fois, un seuil de 75% de contribution d'une population ancestrale a été retenu pour caractériser des groupes variétaux, en-dessous duquel les individus étaient considérés comme admixés.

Une valeur de K = 8 a été retenue pour l'analyse de structure réalisée sur les Arabica haïtiens, guadeloupéens, et de référence. Huit groupes variétaux génétiques ont donc été identifiés. Les six groupes précédemment décrits dans le chapitre 1 ont été confirmés par cette nouvelle analyse : Typica-like (N_{Gl}=91, N_{Ht}=247 and N_{ref}=14), Bourbon/Caturra-like (N_{Ht}=29, N_{ref}=14), CR-95/Catimor-like (N_{Ht}=72, N_{ref}=4), Kent/I-60-like (N_{Ht}=8 and N_{ref}=3), un groupe Ethiopian-like (N_{Ht}=1, N_{ref}=24) et un groupe sans individus de référence (Unlabeled, NHaïti=49). Un deuxième groupe « unlabeled », (U2, NHaïti=25) a aussi été identifié, ainsi qu'un groupe SL/Kenyan-like (N_{Gl}=11, N_{ref}=4). Ce dernier regroupe plusieurs échantillons guadeloupéens ainsi que 4 accessions de référence historiquement développées ou présentes au Kenya. Seuls ce groupe et celui des Typicas ont été identifiés en Guadeloupe. Plusieurs individus admixés (principalement en Haiti) ont de nouveau été identifiés (N_{Gl}=9, N_{Ht}=168, N_{ref}=59).

L'ACP et le dendrogramme (Fig. 5) sont généralement en accord avec les résultats de l'analyse de structure, hormis dans le cas du second groupe « unlabeled ». Ce dernier se compose d'individus qui avaient été considérés dans le chapitre précédent comme admixés, et qui n'ont pas été regroupés sur le dendrogramme. Nous suggérons donc que ce dernier pourrait être dû à un artéfact de la méthode employée. Ces analyses ont permi de démontrer une forte homogénéité au sein du groupe variétal Typica partagée par les deux îles ainsi que les individus de référence d'autres provenances.

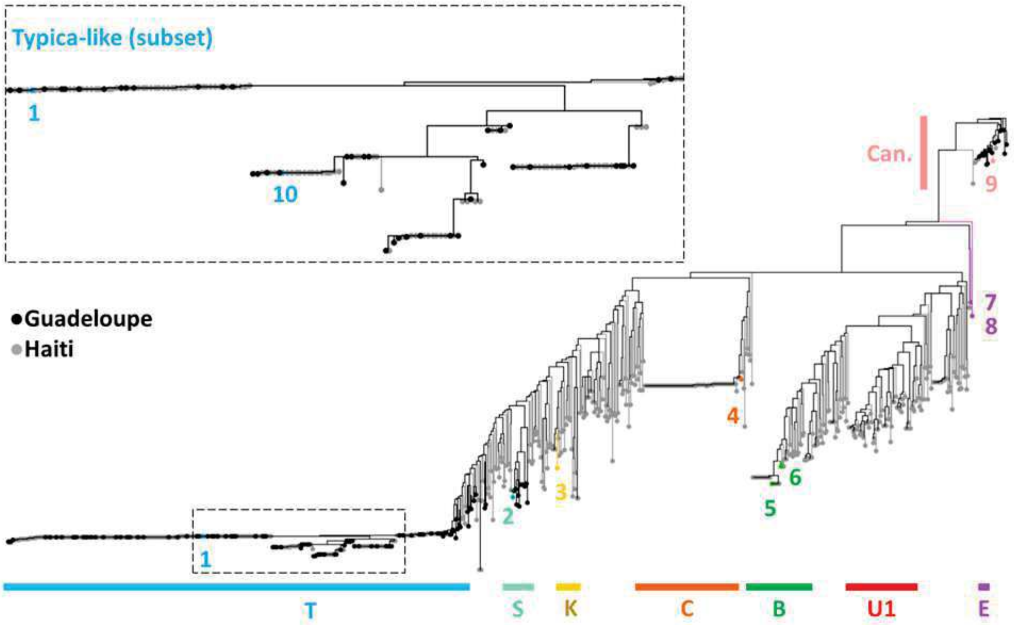


Figure 5. Dendrogramme (UNJ) des caféiers de guadeloupe (●) et d'Haïti (●). Les barres colorées représentes les groupes variétaux identifiés par une analyse de structure de population (sNMF) : C= CR95/Catimor-like, K= Kent/I60-like, T= Typica-like, B= Bourbon-like, E= Ethiopian-like, S= SL/Kenyan-like U1= Unlabeled1, Can.=Canephora (*outgroups*.) Une partie de la branche des Typica est agrandie dans le cadre. Les numéros désignent l'emplacement de certains individus de référence : 1. (Ku214) Typica/Jamaica Blue Mountain, 2. (T.04313) SL28, 3. (T.04268) Kent, 4. (T.08667) CR95, 5. (Mw264) PR6791/Bourbon Select, 6. (T.02542) Caturra, 7. (T.04667) E-160, 8. (T.04290) Jimma Kaffa, 9. (GUI2) Guinean *C. canephora*, 10. (T.00990) Surinam.

Des dendrogrammes basés sur une matrice de distance (méthode « *simple matching* ») ont également été construits à partir des jeux « Liberica » et « Robusta ». Ils ont permis d'assigner les Liberica guadeloupéens à la sous-espèce *C. liberica var. liberica*, et de démontrer que les Robusta haïtiens et guadeloupéens présentent des contributions de groupe génétiques différent et sont probablement admixés. Les Robusta semblent plus largement répandus en Guadeloupe qu'en Haïti (Fig. 6).

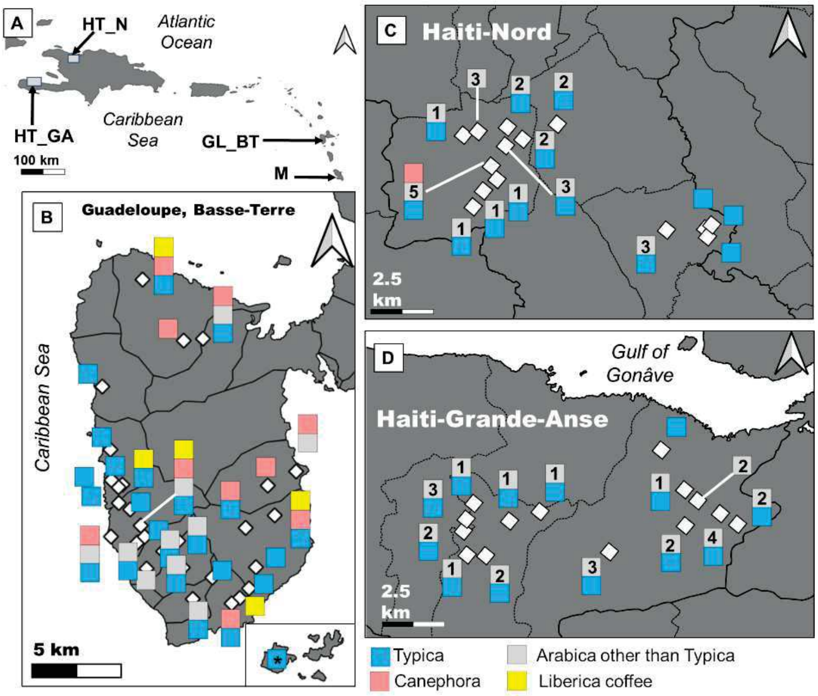


Figure 6. Sites échantillonnées et distribution des groupes génétiques de caféiers guadeloupéens et haïtiens. A. Emplacement des départements du Nord (HT_N) et de la Grande-Anse (HT_GA) en Haiti, de la Basse-Terre de Guadeloupe (GL_BT) et de la Martinique, lieu d'introduction du caféier dans les Antilles. B. Guadeloupe, y compris les Saintes (encadré, * désignant un Typica au phénotype « Moka »). C. Nord, Haïti, D. Grande-Anse, Haïti. Les numéros désignent le nombre de groupes variétaux (hormis Typica) présents dans les fermes haïtiennes. Cartographié dans QGIS v. 3.30 avec des données de Natural Earth (naturalearthdata.com) et de Hijmans and UC Berkeley (2015a,b), Patterson and Kelso (2012).

5.4. Enveloppes climatiques

Des données bioclimatiques (19 variables bioclimatiques standard basées les tendances de température et de précipitation) et d'altitude ont été téléchargées pour les sites d'échantillonnage de la base de données WorldClim (v 2.1, résolution de 30s). Une ACP a été réalisées sur celles-ci (fonction prcomp de R) afin de décrire les enveloppes climatiques pour les régions suivantes : les 3 ensembles paysagers de Basse-Terre en Guadeloupe Nord Basse-Terre / Côte au Vent; Sud Basse-Terre and Côte sous-le-Vent ; Région Guadeloupe & DEAL Guadeloupe, 2011) et le département du Nord, la partie Est du département de la Grande-Anse, et la partie Ouest de la Grande-Anse en Haiti. Elle a permis de qu'elles se différenciaient de manière considérable. Cela pourrait potentiellement justifier la considération d'effets de terroir.

5.5. Facteurs historiques déterminants de la diversité génétique des caféiers

Une recherche bibliographique itérative a été entreprise afin d'identifier les facteurs historiques ayant impacté la composition et diversité actuelle des îles, à la fois dans des sources historiques (monographies, rapports, manuels…) et contemporaines (articles, historiographies). Nous avons ainsi pu proposer un historique de l'évolution des ressources génétiques des caféiers sur les deux îles, et le mettre en relation avec des mutations dans la caféiculture (Fig. 7).

Dans le cas de la Guadeloupe, le déclin de la caféiculture, enclenché assez tôt dans l'histoire de celle-ci, a mené à la préservation de la variété Typica (et notamment à l'absence significative de la variété Bourbon ou de son descendant, Caturra). Cependant, des tentatives de relance ou de renforcement de cette filière se sont traduites par l'introduction du groupe variétal des SL/Kenyan-like des caféiers Arabica, mais aussi des espèces Liberica et Robusta. Ces dernières, mises en cultivation à la fin du XIXème et au début du XXème siècle, respectivement, ont été propagées dans les colonies Européennes suite à l'émergence d'épidémies sévères de la rouille du caféier en Asie, puis en Afrique. Les variétés plus modernes, telles que les Catimors développés durant la seconde moitié du XXème siècle en réponse à la rouille et notamment à son arrivée dans les Amériques, sont absente de la Guadeloupe car celle-ci avait alors presqu'entièrement délaissé la caféiculture au profit d'autres cultures telles que la banane. Ainsi, malgré la présence de plusieurs espèces de caféiers, les Arabicas de Guadeloupe présentent peu de diversité génétique. Cependant, la prédominance des Typica pourrait constituer un levier de valorisation d'un produit patrimonial et qualitatif.

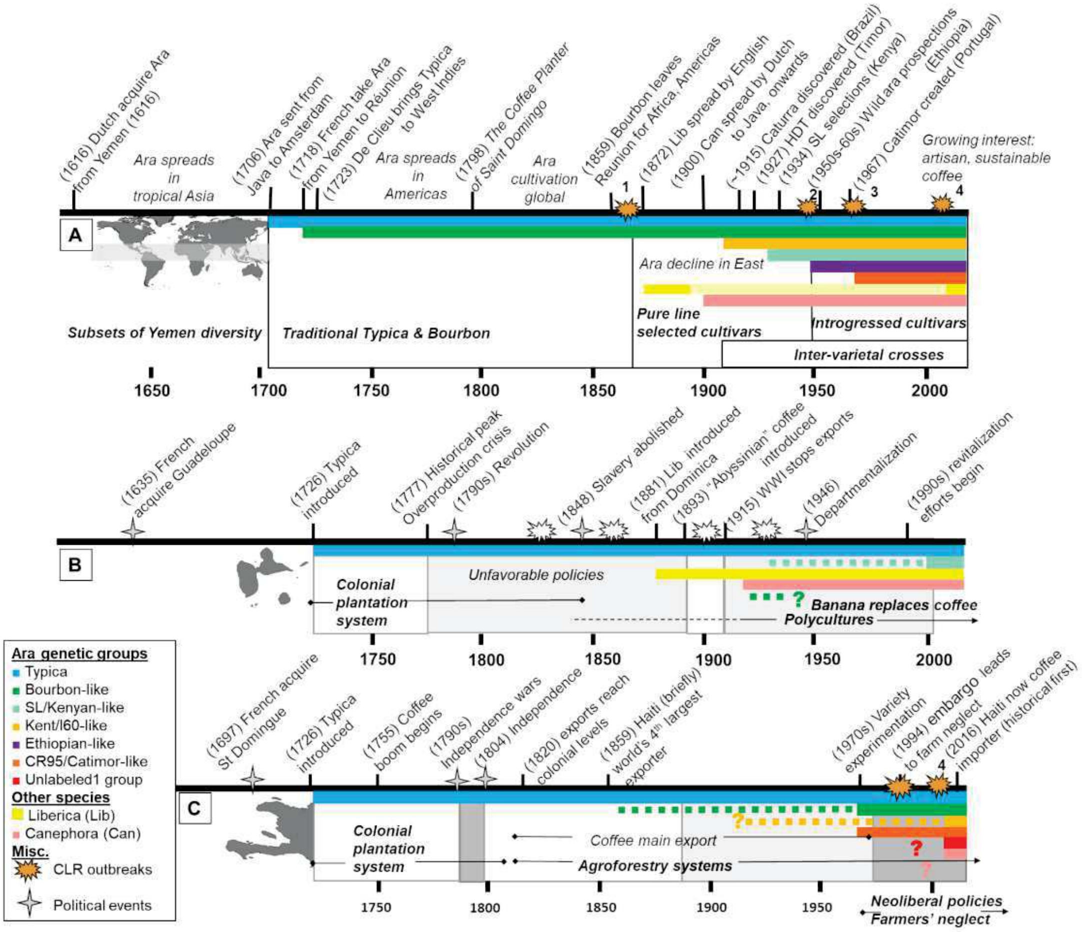


Figure 7. Chronogramme des déterminant historiques des ressource génétiques des caféiers, A. à l'échelle mondiale (avec dans les cadres les principales innovations variétales chez Arabica), B. en Guadeloupe (avec les explosions blanches représentant des crises phytosanitaires) et C. en Haiti. Les plages blanches et grises représentent de périodes de croissance et de déclin de la culture des caféiers, respectivement. Certaines étapes clé de l'avancée de la rouille du caféier (CLR) sont représentés : 1. Sa découverte près du lac Victoria (Afrique, 1861) et son apparition dans les plantations d'Asie du sud (1869), 2. Sa propagation en Afrique de l'Ouest (1950-1960), 3. Son arrivée en Amérique (Brésil, 1970) et 4. La « Big Rust », épidémie dévastatrice en Amérique Latine (2008-2013). (Morris, 1881; Nicholls,

1881; Ukers, 1922; Haarer, 1923; Kopp, 1929; Lalanne, 1934; Robert, 1935; Moral, 1955; Hoy, 1962; Sylvain, 1972b; Ester, 1978; Amaya *et al.*, 1999; Lafleur, 2006; McCook, 2006, 2017; Avelino *et al.*, 2015; McCook & Vandermeer, 2015; Harvey *et al.*, 2021; Muñoz-Pajares *et al.*, 2023; McCook & Montero-Mora, 2024)

Dans le cas d'Haiti, les introductions d'autres espèces semblent avoir été plus limitées (absence de Liberica) et plus tardive (rareté du Robusta). Cela est probablement dû au fait qu'Haiti n'était plus une colonie de puissances européennes au moment de leur diffusion. Cependant, de nombreuses introductions variétales ont eu lieu durant le XXème siècle, issues de plusieurs vagues de développement variétal, comme par exemple le Caturra issu d'une phase de sélection massale (identification d'hybrides au champs), le Kent initialement propagé depuis l'Inde pour sa résistance (aujourd'hui perdue) à la rouille, ou encore les Catimors et autres descendants de l'hybride de Timor, promus à partir des années 1970 et aujourd'hui encore en réponse à l'arrivée de la rouille dans les Amériques. Certaines de ces introductions sont le produit de tentatives de technification, c'est-à-dire de transformation des systèmes caféicoles passant notamment par le remplacement des variétés traditionnelles et leur intensification, qui n'ont pas abouti en Haiti, menant ainsi à des parcelles multi-variétales à la diversité complexe et dynamique identifiée lors du premier chapitre.

6. Caractérisation de l'agrobiodiversité et des services écosystémiques associés dans les SAFC Haïtiens

Les ressources génétiques des caféiers haïtiens ayant été caractérisées, et leurs déterminants historiques identifiés, nous nous sommes intéressés aux contextes dans lesquels elles évoluent. En effet, les caféiers haïtiens font partie d'une agrobiodiversité plus large qui contribue à la subsistance des communautés rurales, à leur résilience, et à la fourniture de services écosystémiques importants. La caractérisation de l'agrobiodiversité et des services qu'elle sous-tend, nécessaire à la conception de SAFC plus durables, performants, et à même de satisfaire les besoins des cultivateurs, a été entreprise dans le cadre du troisième chapitre de cette thèse.

6.1. Base de données utilisée

Les données utilisées pour l'étude décrite dans ce chapitre proviennent principalement du diagnostic approfondi réalisé de Février à Mars 2021 sur 39 SAFC haïtiens, précédemment mentionné. Ce diagnostic à donné lieu à une base de données décrivant les parcelles de caféiers (âge, densité…), l'incidence de maladies et ravageurs, le couvert arboré et les cultures associées. La collecte de ces données s'est basée sur le décompte et le phénotypage de caféiers, le décompte et la mesure du diamètre (dbh) des arbres de couvert dans un quadrat de 1000m2, et de décomptes de cultures associées dans des quadrats de 100m2. Trente-trois taxons d'arbres, appartenant à au moins 28 genres, dont plus de la moitié indigène, ont été recensés, ainsi que sept cultures annuelles associées aux caféiers.

Certaines variables génétiques issues du premier chapitre ont également été incorporées à la base de données : présence de chaque groupe génétique, le nombre de groupes génétiques par parcelle, le pourcentage d'individus admixés, et l'hétérozygotie attendue (diversité génique). Les données d'altitude et les variables bioclimatiques les plus pertinentes (Bio01-Annual temperature, Bio02-Diurnal range, Bio04-Temperature seasonality, Bio12-Annual precipitation et Bio15-Precipitaiton seasonality) de WorldClim (v2.1) ont également été incoporporées.

6.2. Caractérisation des SAFC

Ces différentes catégories de variables ont été utilisées pour construire les typologies de CAFS suivantes :

Une typologie basée sur les variables de diversité génétique des caféiers (Gen) a été construite à partir d'une analyse factorielle pour données mixtes (FAMD), suivie d'une analyse de clustering hierarchique (HCPC) dans FactomineR v 2.8 (Francois Husson, Julie Josse, Sebastien Le, Jeremy Mazet 2006). Trois catégories ont ainsi été définies : Gen1 avec une diversité génétique et variétale faible, Gen2 avec une diversité génétique forte et la présence de Catimors, et Gen3 avec une diversité génétique forte et l'absence de Catimors.

Des typologies basées sur la composition et la densité d'arbres de couvert (Tree) et de cultures associées (Crop), respectivement, ont été établies à partir d'un calcul de distances de Bray-Curtis entre les parcelles (ecodist v 2.1.3 ; Goslee and Urban 2006) suivies d'une analyse de cluster hierarchique (hclust, méthode Ward, avec option cuttree k=3 ; package ade4 v.1.7-22, Dray and Dufour 2007). Trois catégories ont été définies pour chaque typologie. Pour les arbres, les catégories étaient : Tree1 avec une forte densité d'arbres, Tree2 avec une faible densité d'arbres plus petits, avec *Inga vera* pour légumineuse principale, et Tree3 avec une faible densité d'arbres plus grands, avec *Samanea saman* comme légumineuse principale. Pour les cultures associées, les catégories étaient : Crop1

Des typologies basées sur l'altitude et le bioclimat (Clim), la structure des bouquets de caféiers (CPS), et les profils de dégâts de maladies et ravageurs (IP), respectivement, ont été établies à partir d'une ACP suivie d'une HCPC dans FactomineR, avec 2 catégories chacune. En général Clim1 regroupait les parcelles de climats plus chauds et secs et de plus basse altitude que Clim2, et CPS1 regroupait les parcelles plus jeunes et moins denses que CPS2. La catégorie IP1 regroupait les parcelles avec des incidences plus élevées d'œil-de-poule (*Mycena citricolor*) et de scolyte des baies, et IP2 les parcelles avec des incidences plus élevées de rouille, d'anthracnose (*Colletotrichum sp.*) et de mineuses des feuilles (insectes).

Des tests de Fisher ainsi qu'une analyse de correspondance (Fig. 8) réalisés à partir de tables de contingence croisant ces différentes typologies a permis de mettre en évidence des associations entres celles-ci. En particulier, un gradient de régénération des parcelles a été identifié, opposant d'une part les parcelles plus veilles, sans Catimors et plus impactées par la rouille, et d'autre part les parcelles plus jeunes, donc régénérées plus récemment avec des Catimors (en réponse à la pression de la rouille) et présentant une incidence d'œil-de-poule plus élevée.

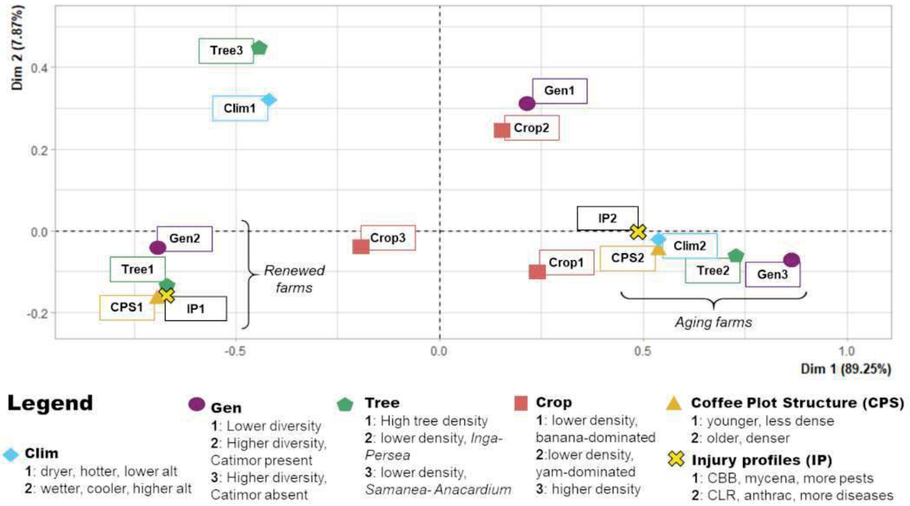


Figure 8. Analyse de correspondance montrant les associations entre les différentes typologies de CAFS établies : diversité génétique des caféiers (Gen), arbres de couvert (Tree), cultures associées (Crop), bioclimat (Clim), structure des bouquets de caféiers (CPS) et profils de dégâts (maladies et ravageurs, IP). Abréviations : CBB= scolyte des baies, CLR= rouille du caféier, anthrac= anthracnose, alt= altitude.

6.3. Caractérisation des services écosystémiques fournis par les SAFC

De nombreuses variables indicatrices du niveau de fourniture de service écosystémiques ont également été calculées et incorporées à la base de données. Les services priorisés sont principalement ceux qui bénéficient de manière directe aux cultivateurs et aux communautés rurales. Ainsi ont été calculées un indice de production des parcelles (en kg.ha-1) à partir d'informations données par les cultivateurs), la biomasse aérienne des arbres de couvert (indice de séquestration de carbone, à partir d'équations allométriques (package BIOMASS v. 2.1.11, Réjou-Méchain *et al.*, 2016), la proportion de légumineuses ($\varnothing_{legumes}/\varnothing_{total}$), les indices de diversité Shannon et Simpson indicateurs de la diversité des arbres et cultures associées (package R 'vegan' v. 2.6-4chili r, Oksanen et al. 2001), un score d'utilité de la strate arborée calculé à partir d'usages reportés dans la littérature (Koohafkan & Lilin, 1989; Timyan, 1996; Diazgranados *et al.*, 2020) , le pourcentage d'espèces indigènes (selon Kew Plants of the World Online, https://powo.science.kew.org), ou encore un score de la contribution des CAFS à la diversité alimentaire des foyers (HDDS, (Swindale & Bilinsky, 2006; Kennedy *et al.*, 2011).

Nous avons comparé les valeurs de ces variables entre les catégories de chaque typologie de CAF présentées ci-dessus (ANOVAS ou tests de Kruskall-Wallis) pour déterminer comment la structure et la composition des CAFS sous-tendent la fourniture de services écosystémiques. Par exemple, nous avons identifié des différences significatives de pourcentage de défoliation (indicateur de la santé des caféiers) au sein des typologies basées sur les arbres de couvert (Tree), le bioclimat (Clim), la structure des bouquets de caféiers (CPS) et les profils de dégâts (IP), indiquant un impact potentiel du couvert arboré et de la structure des fermes sur l'incidence des maladies et, *in fine*, les pertes de rendement.

Nous avons également calculé une matrice de corrélation entre ces différents services afin d'identifier des synergies et/ou compromis entre eux. Ainsi, nous avons par exemple trouvé une corrélation positive entre la production caféière des parcelles et la proportion de légumineuses, et une corrélation négative entre la production caféière et plusieurs variables de diversité.

Certains indicateurs de services comme le pourcentage d'espèces indigènes et la biomasse aérienne n'étaient corrélés à aucuns autres, indiquant potentiellement une absence de compromis qui suggèrent des leviers d'amélioration de la délivrance de certains services.

Enfin, nous avons établi une nouvelle typologie à 3 catégories basée sur les variables indicatrices de services (SE) à partir d'une ACP suivie d'une HCPC dans FactomineR (Fig. 9). Nous avons ensuite croisé cette typologie avec les précédentes par une analyse de correspondance (Fig. 10).

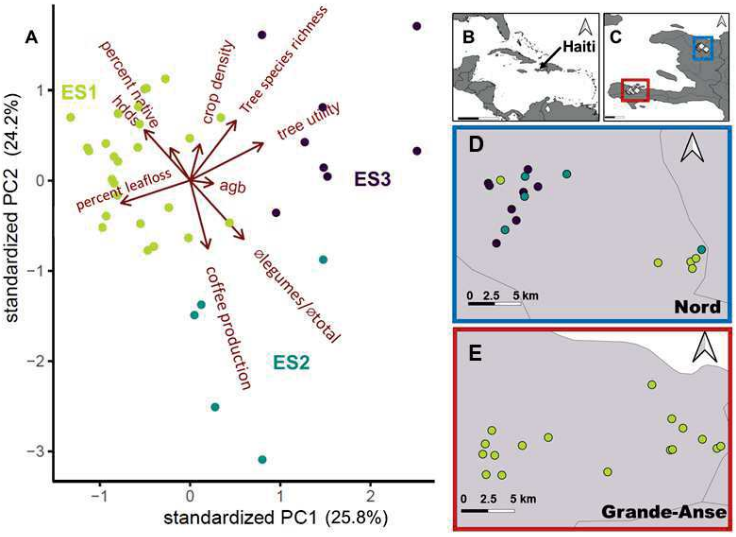


Figure 9. Tendances dans la fourniture de services écosystémiques. A. ACP et cercle de corrélation des indicateurs de services (deux premiers axes). B. Haïti et la Caraïbe (barre d'échelle : 250 km), C. Emplacement des sites en Haïti (barre d'échelle : 25 km), D. Dans le Nord et E. dans la Grande-Anse. Pour A, D et E, Les couleurs correspondent à des catégories dans la typologie de services écosystémiques établie par une analyse de cluster

La catégorie SE1 regroupe les parcelles fournissant des services basés sur la subsistance : elles produisent moins de café et stockent moins de carbone, mais contribuent à une diversité nutritionnelle plus importante. Cette catégorie est la seule présente dans la Grande-Anse, et concerne principalement les fermes vieillissantes (cf. gradient de régénération). Elle regroupe donc probablement les parcelles dont les caféiers ont été endommagés par des aléas climatiques ou des stress biotiques, ou dont l'importance à diminué en raison des difficultés rencontrées par la filière caféicole. La catégorie SE2 regroupait les fermes (exclusivement au Nord) se focalisant sur la fourniture de services liées au café, notamment la production et la mobilisation de la strate arborée par l'augmentation de la proportion d'arbres de service (légumineuses) au détriment de la richesse spécifique et de l'utilité de la strate arborée. Enfin, la catégorie SE3 (aussi exclusive au Nord) regroupait les fermes se focalisant sur la fourniture de services liées à la strate arborée, dont l'accumulation de biomasse, la diversité et la multiplicité des usages des arbres. Les catégories ES2 et ES3 concernent généralement les parcelles caféières renouvelées (cf. gradient de régénération).

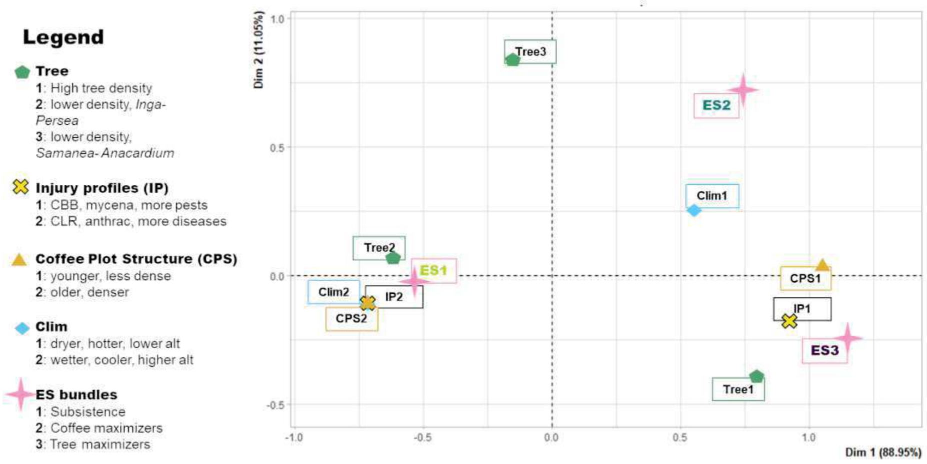


Figure 10. Analyse de correspondance montrant les associations entre les différentes typologies de CAFS établies : arbres de couvert (Tree), cultures associées (Crop), bioclimat (Clim), structure des bouquets de caféiers (CPS) et profils de dégâts (maladies et ravageurs, IP) et celle basée sur les services écosystémiques (ES). Abbréviations : CBB= scolyte des baies, CLR= rouille du caféier, anthrac= anthracnose, alt= altitude.

Ces résultats nous ont permis de suggérer des stratégies de mobilisation de services par l'identification de voies d'amélioration potentielles des CAFS selon des trajectoires réalistes et réalisable dans les conditions actuelles, mais dont la réalisation ne pourra se faire qu'en co-construction avec les cultivateurs, dans le respect de leurs priorités, mais aussi du cadre de contraintes engendrées par **celles-ci.**

7. Discussion générale

Les travaux réalisés durant cette thèse ont cherché à décrire les SAFC à travers le prisme de la génétique, de l'histoire, ou encore de l'interrelation entre leurs différentes composantes. La vision des SAFC qui en émerge est celle de systèmes diversifiés à plusieurs niveaux et dynamiques, bien que soumis à de nombreux problèmes.

Nous avons démontré que les SAFC haïtiens présentent des mélanges variétaux complexes, ainsi qu'un brassage génétique conséquent. Ainsi, ils constituent à la fois des conservatoires de variétés historiques (particulièrement Typica) et des générateurs de nouvelle diversité. Nos travaux sont les premiers, à notre connaissance, à caractériser les caféiers haïtiens par des méthodes moléculaires, et font partie des rares études décrivant leur contexte de culture. La diversité des caféiers haïtiens est souvent méconnue, et sous-estimée, même par ses cultivateurs. Elle résulte de la convergence de nombreux facteurs historiques : la mondialisation de la filière caféière, l'émergence de grandes épidémies, les travaux de développement variétal, les politiques de développement internationale, l'abandon en Haïti du système colonial et de ses modes de production agricoles, ou encore la marginalisation du milieu rural dans ce pays.

La vision des ressources génétiques des SAFC haïtiens que nous proposons soulève de nombreuses questions : sont-elles soumises à des processus d'évolution et en particulier d'adaptation ? Par quels filtres écologiques doivent-elles passer ? Et quelles conséquences phénotypiques résultent de leur diversité ? Quelles implications agronomiques engendrent-elles ? Et peuvent-elles constituer un levier d'amélioration de la caféiculture haïtienne ? Pour y répondre, il serait nécessaire de poursuivre les études de ces systèmes. En particulier, le phénotypage au champ, mais aussi la description des qualités organoleptiques des caféiers génotypés, et particulièrement des individus admixés, devraient être entrepris. Certains de ces travaux étaient prévus dans le cadre de cette thèse, mais n'ont pas pu être réalisés en raison de la situation socio-politique actuelle en Haïti.

Notre caractérisation des systèmes caféiers renforce la notion proposée par les travaux en sciences humaines que la diversification des parcelles, leur résilience, et leur contribution à l'autonomie alimentaire et économique des foyers est une priorité des cultivateurs, qui organisent leurs fermes de manière à pouvoir bénéficier de nombreux services écosystémiques. Se pose donc la question : Comment la caractérisation de l'agrobiodiversité peut-elle conduire à la conception de systèmes plus performants, plus résilients et plus à-même de satisfaire les besoins des communautés rurales ? Nous proposons que la typologie des services fournis par les SAFC peut servir de base à l'identification de voies d'amélioration des SAFC, et à leur co-construction. Cependant, là encore, les travaux scientifiques sur ces systèmes sont trop peu nombreux et méritent d'être approfondis. Quelle que soit les solutions envisagées pour régénérer la caféiculture haïtienne, la dimension culturelle, socio-économique, mais aussi écologique des SAFC, ainsi que leur agrobiodiversité, doivent être prises en compte.

Prologue

Ask any Haitian which local product they are fondest of, and they are likely answering *Kafe*, coffee. As a plant, crop, and beverage, coffee is deeply intertwined with the Haitian landscape, culture and identity. Its history there is long and complicated, as will be discussed in the following pages. Some of it is dark, as was that of enslaved people toiling on colonial coffee farms. But it is also a history of resilience as coffee, having fared better than most cropped during the turmoil of Haitian independence wars, quickly became a lynchpin of the burgeoning nation's economy. It has been an instrument of exploitation, as when urban elites and global traders exploited smallholder farmers through unfair markets. It has also been an instrument of empowerment: after independence, farmers distanced themselves from any system resembling that of a plantation and instead established diversified cropping system, weaving coffee into a broader tapestry of agrobiodiversity. Nearly two centuries ago, the crop was taken out of plantation monocultures conducted under the scorching Caribbean sun, and brought under the shade of agroforestry systems, alongside a host of plants bearing edible fruits, roots and tubers, medicine, and materials to build and cook with. Many coffee trees can still be encountered there today.

But at present the country is struggling, and the crop alongside it. And so, a question is being asked: *can coffee-growing agroforestry systems still play a part in strengthening Haiti's agriculture and rural communities, while helping to protect its environment? And if so, how?* Though this is too complex a question for any one study to answer, this doctoral thesis aims to contribute to the scientific knowledge needed to do so. In its course, we have sought to characterize the diversity of Haitian coffee genetic resources, and that of the systems in which they are grown and managed, by using multidisciplinary methods and viewing the subject through the lens of population genetics, history, and ecosystem services. I can only hope that other studies will build upon it.

General Introduction

At the time of writing this manuscript, the Integrated Food Security Phase Classification (IPC), a multi-stakeholder (including United Nations agencies) initiative aimed at monitoring global food security, warns that half of Haiti's population faces high food insecurity, with several regions reaching a "emergency"-level of severity (4/5), and most others in "crisis" (3/5). This is the result of acute gang violence and economic, political and social chaos in recent years, limiting imports, transportation and exchanges between cities (IPC, 2024). This situation makes evident the need for Haitian communities to become more resilient and food-secure. Strengthening Haitian agriculture, a sector upon which the majority of the population relies (De Salvo *et al.*, 2018), will undoubtedly be a central part of this undertaking. Particular attention should be given to diversified cropping systems which can be managed sustainably, require few inputs, and can satisfy many of the farmers' needs. This thesis focuses on coffee-based agroforests which are, or have the potential to become, just such systems. Over the course of this introduction, we will first explain the important role of agroforestry for Haiti, but will also consider how it, and diversification in general, can help advance the global quest for a more sustainable and adaptable agriculture. We will then focus on this thesis' main organism of interest, coffee trees, before presenting the study aims, questions and main hypotheses that have guided this work. At the core of this thesis (as of that of agroforestry) is the concept of **agrobiodiversity** (also known as agricultural biodiversity). The FAO describes it thusly: "*the variety and variability of animals, plants, and micro-organisms on earth that are important to food and agriculture which result from the interaction between the environment, genetic resources and the management systems and practices used by people [including] genetic, species and agro-ecosystem diversity*" (FAO, 1991). The many benefits of agroforestry systems are achieved by harnessing agrobiodiversity, which will be further explained in the following sections.

1. Agroforestry and other diversified cropping systems, in Haiti and Beyond

1.1. What are agroforestry systems?

Agroforestry systems are, in a broad sense, agricultural systems in which crops are grown, or livestock raised, under a layer of trees. These systems are found all over the world, and can display a wide range of characteristics. Nair (1985) offered a framework for classifying agroforestry systems based on combinations of their three main possible components, namely perennial woody vegetation (trees, a requisite for consideration as agroforestry), crops (generally herbaceous), and animals. The main types of system are thus Agrisilvicultural systems (Trees and crops—or tree crops), Silvopastoral systems (Trees and livestock or pastures), and Agrosilvopastoral (Trees, crops, and pastures/animals). For the purpose of this manuscript, we will henceforth only consider agrisilvicultural systems, to which coffee agroforests generally belong (Toledo & Moguel, 2012). Often, agroforestry is combined with other forms of land use such as pasture or open cropland within a broader system of agricultural production (Sinclair, 1999).

Agroforestry systems comprise a considerable proportion of coffee farming in the Republic of Haiti (fig. 1). There, Arabica coffee (*Coffea arabica* L.) is mainly grown under shade in diversified, traditional systems known as *jaden* (or “jardins” in French, gardens in English, sometimes *jaden kreyòl* or *jaden lakou*), with virtually no chemical inputs (Amaya *et al.*, 1999; Rodriguez *et al.*, 2011; Vital, 2014)

Figure 1. Agroforestry system in Northern Haiti. Shade trees are mango (*Mangifera indica*, foreground), breadfruit (*Artocarpus altilis*, left midground) and saman (*Samanea saman*), while pictured crops are coffee (*Coffea arabica*) and bananas (*Musa sp.*). Photo credit: Claude Patrick Millet

1.2. Haitian agroforestry is crucial to rural livelihoods…

Accurate and up-to-date statistics on Haiti’s agricultural sector are hard to find, but Arabica cultivation is estimated to contribute to the livelihood of 200,000 families (Institut National du Café d’Haïti, 2015). Moreover, the importance of Haitian agroforests goes well beyond the production of coffee. In order to fully grasp it, it is necessary to consider how the social and environmental contexts of Haiti are intertwined, and the crucial the role played by agroforestry systems in both dimensions.

Attempts to intensify agroforestry systems have generally ended is failure. Efforts to increase cultivation of mango (*Mangifera indica*), another Haitian cash crop of great importance, provide a good illustration of this, and shine a light on the value placed by farmers on traditional, diversified agroforestry systems (Steckley & Weis, 2016; Jayaram, 2018). Haitian mango exports rose steadily between the 1960s-1990s, even as traditional crop exports declined. However, they eventually stagnated, despite repeated attempts at increase by development projects. Though this is partly due to changes in global mango trading, as well as policy-based changes in Haiti's trade relations, Steckley and Weiss (2016) identify "Peasant balances" as another major reason for this stunted market growth. By this concept, they refer to the value placed by '*Peyizan*' (smallholder farmers) on the autonomy and resilience of their cropping system over intensification in service of greater mango production. Farmers are quoted in their study as being unwilling to rely on any single crop, nor on global commodity markets, as both are prone to volatility, instability, and failure.

By contrast, diversified agroforestry systems can more reliably uphold rural livelihoods by maintaining access to a variety of resources (Fig. 2). Despite their importance to Haitian farmers, these systems have received insufficient scientific attention. The study by Jean-Denis *et al.* (2014) ranks among the most comprehensive of them. It recorded 69 useful plant species in Haitian agroforestry systems, enabling a great variety of uses. Many perennial tree species such as avocados (*Persea americana*), mangoes, breadfruit (*Artocarpus altilis*), coconut (*Cocos nucifera*), citrus trees (*Citrus spp.*), papaya (*Carica papaya*), guava (*Psidium guajava*), cacao (*Theobroma cacao*), *kenèp* (or Spanish lime, *Melicoccus bijugatus*), *zabriko* (or "apricot", *Mammea americana*), and annual species such as bananas and plantains (*Musa spp*), cassava (*Manihot esculenta*), sweet potatoes (*Ipomea batatas*), yams (*Dioscorea spp*) and taro (*Colocasia esculenta*) are cultivated both for subsistence (consumption by the household) and for sale in local markets. In addition, these systems contain several species that are used for timber, fuelwood and/or animal feed (e.g. *Cedrela odorata, Simarouba glauca, Catalpa longissimi, Swietenia mahagoni, Roystonea sp.*), medicinal uses (e.g. palma christi, *Ricinus communis*, although most species can be used in traditional medicine according to Timyan, 1996), and artisanal uses (e.g. bamboo, *Bambusa vulgaris* and *kalbas* or calabash, *Crescentia cujete*). In structure, composition, and multiplicity of uses, these systems resemble traditional homegardens widespread in the tropical world (see the book by Kumar & Nair, 2006 for a variety of examples). Owing to their important agrobiodiversity, Haitian agroforestry systems provide food security and necessary resources to rural communities (Temple *et al.*, 2014; Steckley & Weis, 2016), but also contribute to alleviating Haiti's environmental problems.

Figure 2. Diversification of a Haitian coffee-based agroforestry system. Photograph of a study site, farm GA05, showing coffee trees (Coffea arabica), associated crops (Yams, *Dioscorea sp*. and bananas and/or plantains, *Musa sp*.), and shade trees (including *Roystonea borinquena*, *Inga vera* and *Mangifera indica*). Through diversification of their cropping system and incorporation of permanent tree cover, farmers are able to access several ecosystem services. Photo credit: Claude Patrick Millet

1.3. …And to the Haitian environment

Indeed, Haiti is infamous for the extent of its environmental degradation (Fig.3, 4). Despite being part of the Caribbean Islands Biodiversity Hotspot, with a high level of animal and plant endemism owing to its biogeographical history and mountainous topography (Carmona *et al.*, 2010; Anadón-Irizarry *et al.*, 2012), Haiti has lost over 99% of its primary forest (Hedges *et al.*, 2018). This situation is undoubtedly concerning, as mass extinction of the country's considerable biodiversity is underway (Maunder *et al.*, 2008). Furthermore, deforestation can severely impact ecosystem service delivery, and is associated with increased soil erosion and desertification (Laurance, 1999; Chakravarty *et al.*, 2012). Modeling studies have shown that deforestation in Haiti threatens water supply and therefore agricultural production (Mompremier *et al.*, 2022) and exacerbates flooding risks (Jean Louis *et al.*, 2024). This loss of ecosystem function leaves the Haitian population vulnerable, threatening livelihoods and indeed lives.

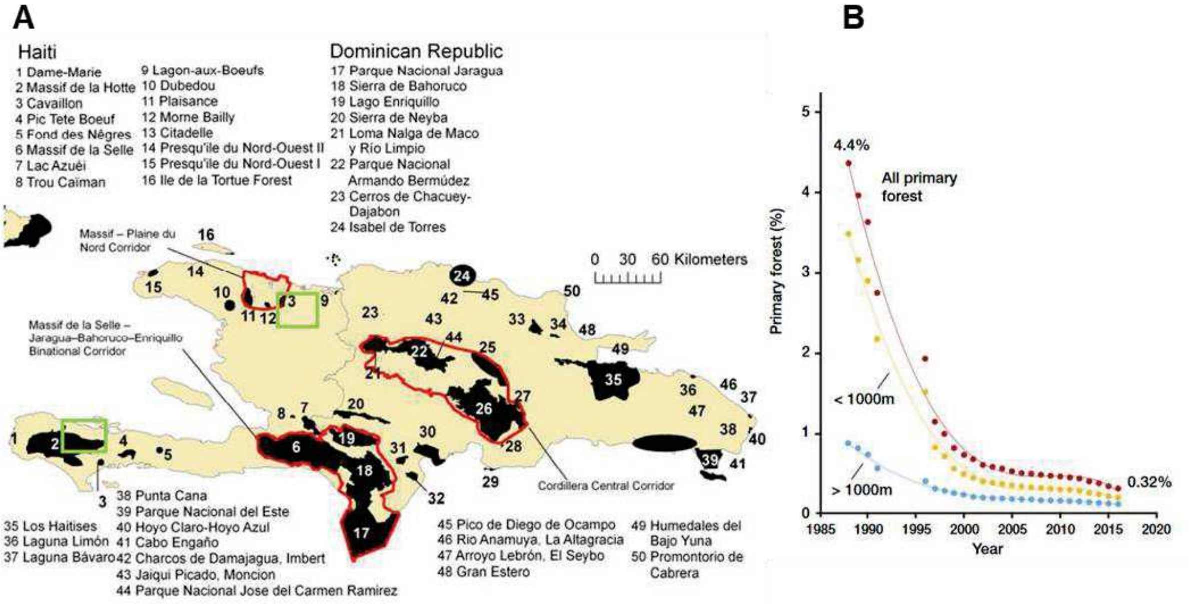


Figure 3. Biodiversity under threat in Haiti. A. Hispaniolan key biodiversity areas and corridors (red boundaries). Image source: Critical Ecosystem Partnership Fund. Added green frames represent the present thesis' study areas. **B. Primary forest cover loss in Haiti, 1985-2018**. Colored lines represent forest above 1000m altitudes, below 1000m, and all forests, respectively. Taken from Hedges *et al.* (2018)

Despite this, there have been increasing calls to challenge longstanding assumptions that Haiti's social, political, cultural and economic attributes condemn it to a state of barrenness and ecological failure, accusing these narratives of being counterproductive (Tarter, 2016; Stork & Maertens, 2017). Recent remote sensing studies have estimated the standing tree cover to be between 20 % (Pauleus & Aide, 2020) and 30 % (Churches *et al.*, 2014). While some local (Salomon *et al.*, 2021) and national-scale (Pauleus & Aide, 2020) studies have found a reduction in tree cover in recent decades, others have reported an overall increase (Rodrigues-Eklund *et al.*, 2021). Decades of scholarship and field expertise have concluded that the Haitian rural population has developed strategies to meet many of their tree-based needs, mostly through silviculture and agroforestry practices (Murray, 1987; Tarter *et al.*, 2018). As a result, managed agrosystems constitute a main form of standing forest cover in Haiti (Feller *et al.*, 2006; Fig. 4).

In particular, woodlots of fast-growing exotic species such as "Bayawonn" *Prosopis juliflora* are widely grown and harvested for charcoal use, with evidence pointing to at least some areas being sustainably managed (Tarter *et al.*, 2018). Other woodlots incorporate timber trees, native or introduced, and particularly those belonging to species that were introduced by reforestation projects. These practices, which have been called a form of "domestication of wood" (Murray, 1987), have allowed people to continue meeting their needs. Still, it is important to note that these systems offer limited benefits to biodiversity conservation. It has been suggested that they could contribute to the regeneration of native tree species through ecological facilitation (improvement of local conditions for the establishment of seedlings) and by attracting seed dispersers such as birds and bats (Smucker & Timyan, 1995). However, they cannot compensate the massive loss of endemic and endangered species that is contained in primary forests, which remain a great conservation concern (Hedges *et al.*, 2018, 2019).

Traditional diversified agroforestry systems, such as those in which coffee is cultivated, are another common form of forest cover (fig. 4), and one that is of potentially higher value for biodiversity. Relatively little is known of the conservation value of agroforestry systems in Haiti. However, studies have shown that these systems can provide important habitat for birds, including species of conservation interest, even when embedded within unsuitable habitat such as urbanized spaces (Exantus *et al.*, 2021). These same systems were found to provide important habitats for pollinating insects as well, owing to their lack of heavy agrochemical use. In fact, peri-urban agroforestry systems were found to contain greater insect order richness than comparable remnant forest sites (Beaujour & Cézilly, 2022). The importance of Haitian agroforests to biodiversity conservation is consistent with scientific understanding of these systems (Bhagwat *et al.*, 2008; Wurz *et al.*, 2022). It is also consistent with (admittedly anecdotal) observations, made throughout several years of living in Haiti, of the presence of several arthropods, reptiles, amphibians, migratory and sedentary birds, as well as native woody and herbaceous flora (pers. obs.) in such systems. This conservation value is largely tied to the presence of mature trees which provide habitat for several other species, including pollinators and epiphytic flora (Jezeer *et al.*, 2019; De Leijster *et al.*, 2021). While agroforestry systems cannot provide the same biodiversity value as natural forests (e.g. Kessler *et al.*, 2012), they can provide an important, attainable, and context-appropriate improvement over highly-degraded open landscapes, which remain common in Haiti.

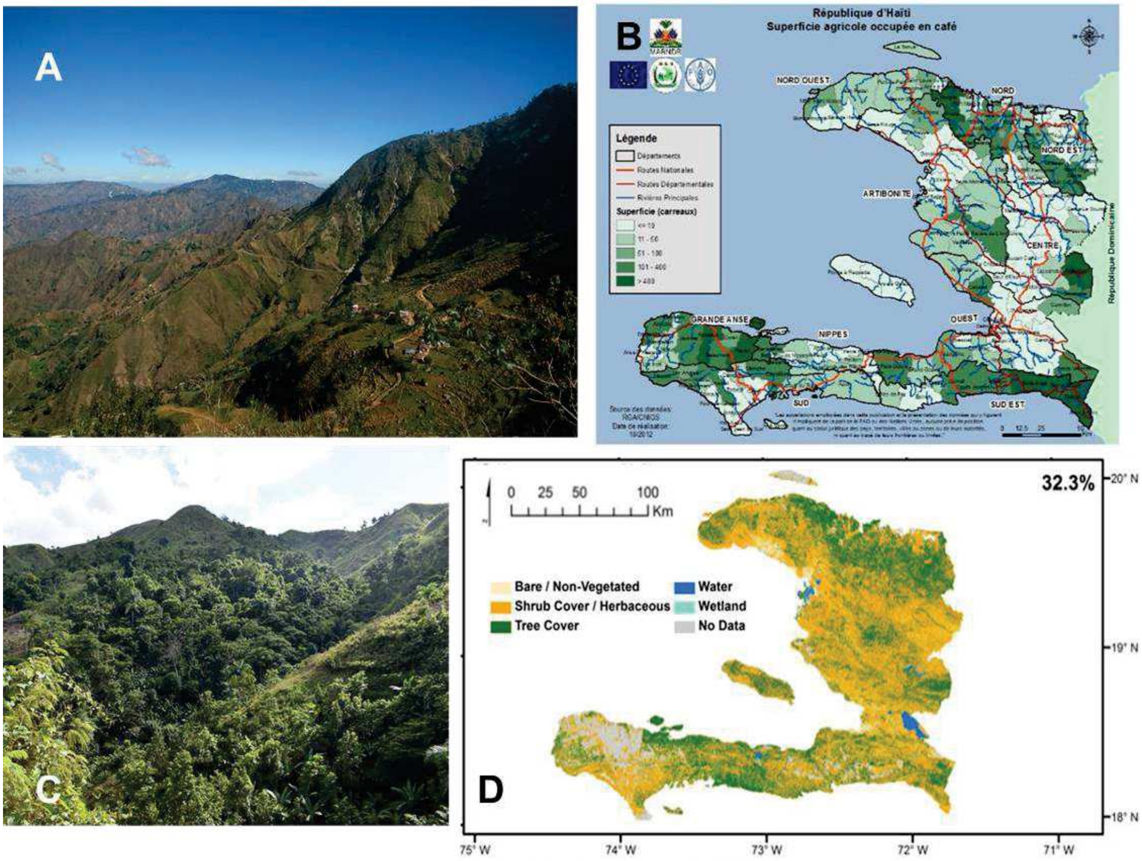


Figure 4. The importance of coffee-based agroforestry systems to Haiti's environment. A. Deforested mountains (In the Ouest department). B. Heatmap of municipalities colored according to total surface under coffee cultivation (source: MARDNR, Haiti) C. Mountains covered in agroforestry systems in Grande-Anse, Haiti. D. Land cover map of Haiti taken from remote sensing study (Churches *et al.*, 2014). *Note the overlap between forest cover and coffee cultivation in B. and D.* Photo credit (A, C): Claude Patrick Millet

2. A broader conversation around agriculture

The primary concern of this thesis is describing, characterizing, and improving the understanding of Haitian coffee agroforestry systems, with the hope that the produced knowledge may, in some way, contribute to strengthening agricultural production, ecosystem service provision, and rural livelihoods. However, in doing so, it touches upon a question that is central to a broader discussion, one that is being had the world over: how can agricultural productivity be sustained in a way that is less environmentally damaging, more resilient, and adaptable to changes?

2.1. Diversification and agrobiodiversity as possible answers to the problems of modern Agriculture

Agriculture can be broadly understood as the management of ecosystems, and the genetic resources contained therein, for the purpose of satisfying human needs and wants (Meyer & Purugganan, 2013; Purugganan, 2019; Stetter, 2020). This generally results in the simplification of structure and diversity (genetic and taxonomic) of these systems. As plants were brought into cultivation and spread to other regions, they experienced a series of genetic bottlenecks, so that cultivated plants are less diverse than their wild counterparts (Olsen & Wendel, 2013; Shi & Lai, 2015). Their cultivation also entailed a modification of natural ecosystems, often leading to habitat loss, fragmentation, displacement of biodiversity, and breakdown of ecosystem function (Gámez-Virués *et al.*, 2015; Feit *et al.*, 2019), though there are exceptions. Indeed, studies suggest that some traditional forms of land use were/are compatible with maintaining high levels of habitat and biological diversity, such as swiddens in Bhutan (Siebert & Belsky, 2014), Pre-Columbian forest management in the Amazon (Heckenberger *et al.*, 2007), or diversified pastures in Europe (Peyraud *et al.*, 2012; Gaujour *et al.*, 2012).

While the process of simplification began with the domestication of crop species many thousands of years ago, it greatly accelerated with the Green Revolution of the 1960s (Pinstrup-Andersen & Hazell, 1985). This has caused the homogenization of agricultural landscapes and crop varieties grown in them, and the intensification of management practices (Altieri, 2002; Bonnin *et al.*, 2014) in many parts of the world, though admittedly to a much more limited extent in the principal study area of this thesis, the Republic of Haiti. While the aforementioned developments have allowed global agricultural production to increase greatly, they have also brought about severe negative consequences, and have proven unsustainable. As a result, plant scientists, breeders, and agronomists are paying increasing attention to something already known to ecologists, and to many traditional farmers before them: that diversity can enhance the resilience of cropping systems, and that it is an important ally in facing the issues that challenge them (Altieri, 1999; Østergård *et al.*, 2009; Renard & Tilman, 2021). Diversification and simplification now appear as two paths offered to farmers, policymakers, and societies as a whole; the former being better suited to addressing extant and emerging challenges (Petersen-Rockney *et al.*, 2021; Labeyrie *et al.*, 2021).

This increase in awareness of the importance of agrobiodiversity has popularized concepts such as agrobiodiversity and **agroecology**. Since being coined in the 1930s, agroecology has been subject to a variety of definitions (Wezel *et al.*, 2009). However, Malézieux (2017) identifies its three core principles: 1) agricultural production founded on ecosystem function, 2) maximization of functional biodiversity and 3) strengthening of biological regulations in agroecosystems. These principles serve as basis for the "ecological intensification" of cropping system through a variety of actions aiming to base production and resilience on functional diversity and complementarity, maintain fertility through soil cover, manage the balance between facilitation and competition between plants, regulate pests through trophic interactions and biopesticides, and establish processes mimicking ecological processes such as using fallow as analogue to succession after disturbances (Malézieux, 2012). Agroecology and agrobiodiversity have also become more prevalent in institutional discourse and decision-making, with agricultural planning incorporating ecological intensification, and conservation planning paying attention to agricultural as well as "wild" biodiversity. For instance, included among the 23 targets adopted by the COP15 of the Convention on Biological Diversity is the following:

> “*Ensure that areas under **agriculture**, aquaculture, fisheries and forestry are managed sustainably, in particular through the **sustainable use of biodiversity**, including through a substantial increase of the application of biodiversity friendly practices, such **as sustainable intensification**, **agroecological** and other innovative approaches contributing to the resilience and long-term efficiency and productivity of these production systems and to food security, conserving and **restoring biodiversity and maintaining nature’s contributions to people, including ecosystem functions and services***”

(CBD Target 10, https://www.cbd.int/article/cop15-cbd-press-release-final-19dec2022, emphasis added).

2.2. The ecosystem services framework

The main reasons to diversify cropping systems at any level is the same: to enhance agroecosystem function and, *in fine*, the benefits provided by ecosystems to people. A useful framework to study the value of diversified systems is that of **Ecosystem Services**. This concept arose from the growing recognition in recent decades of the central role played by ecosystems in permitting and enhancing human well-being (Daily, 1997; Salzman, 1997). While exact definitions vary, ecosystem services can be broadly defined as the benefits (“services”) provided to humans, directly or indirectly, by ecosystems and the processes involved in their function. The concept of ecosystem services gained particular prominence after the publication of the United Nations-commissioned *Millenium Ecosystem Assessment* (Millenium Ecosystem Assessment, 2005). The latter proposes the most widely-used typology of services (see sidebar 1). More recently, a framework was proposed by The Economics of Ecosystems and Biodiversity study (Kumar, 2012) integrating ecosystem services and biodiversity with human well-being by connecting them with economic and political considerations (Fig. 5).

Diversity underlies ecosystem function and resulting services by participating in various processes such as nutrient cycling and trophic interactions, including in agroecosystems (Altieri, 1999). For farmers, the main benefits will be those that support farm production. Diversity can increase yields and/or yield stability through processes such as ecological facilitation, increase in pollinator abundance (Figueroa *et al.*, 2020), or resource use efficiency. Multi-crop systems in particular allow farmers to “diversify their portfolio” and lessen the impact of crop failure (Vandermeer *et al.*, 1998; Paut *et al.*, 2019). Diversification of cropping systems can also reduce pest and disease pressure by reducing the proportion of susceptible species or genotypes, and by promoting the presence of biocontrol agents (Altieri & Nicholls, 2002; Grab *et al.*, 2018). Some practices can also help maintain or restore soil fertility (e.g. by incorporating nitrogen-fixing legumes in cropping systems; Herridge *et al.*, 2008; Lüscher *et al.*, 2011; Rodriguez *et al.*, 2020) and control erosion (e.g. by maintaining perennial soil cover; Blanco Sepúlveda & Aguilar Carrillo, 2015). Through all of these effects, diversification can also improve the cost efficiency of farming, by reducing the need for agrochemicals. Agricultural diversification has also been shown to support biodiversity (Perfecto & Vandermeer, 2008; Chateil *et al.*, 2013; Strobl, 2022).

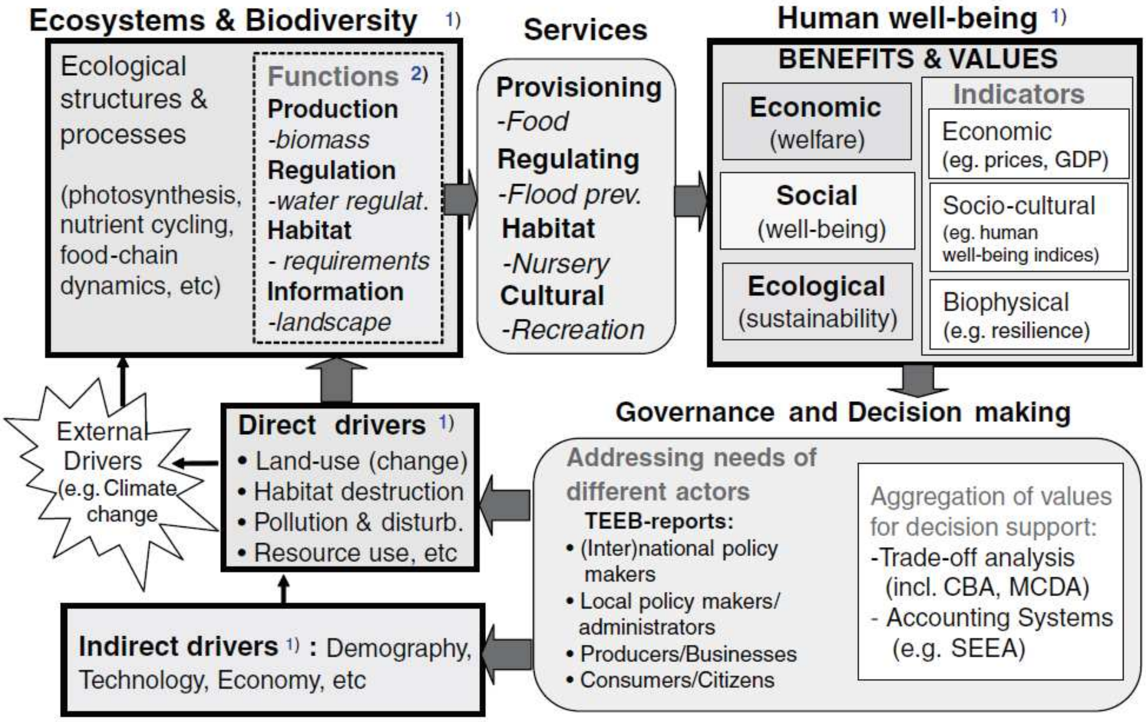


Figure 5. TEEB conceptual framework linking ecosystems and biodiversity with human well-being. Notes 1) bolded lines coincide with Millenium Ecosystem Assessment framework. 2) Subset of ecosystem processes and components directly involved in service provision. (Taken from de Groot *et al.*, 2012)

Sidebar 1. Typologies of Ecosystem Services

The following classification (and figure) is proposed by the Millenium Ecosystem Assessment (2005):

Provisioning services concern the supply of necessary or desirable material goods such as food, water, wood and fiber, or medicine

Regulating services concern processes that regulate the environment (e.g. climate and diseases) to make it more hospitable

Cultural services are those that provide spiritual, aesthetic, educational or recreational value, and contribute to an individual and collective sense of identity

Supporting services concern the natural processes and cycles that underly ecosystem functioning and make possible the delivery of other services, such as primary production and nutrient cycling.

The MEA also proposed a categorization of the constituents of human well-being enabled by ecosystem services:

Security: including personal safety and secure access to resources

Basic materials for good life, including nutrition, livelihood, and shelter

Health, including through access to clean air and water

Good social relations, particularly those enabled by cultural services

Freedom of choice and action, which emanates from the previous four.
This classification has been modified or adapted in other frameworks such as that of The Economics of Ecosystems and Biodiversity, which proposes a more general classification of the benefits of ecosystem services for human well-being: **Economic** (welfare), **Social** (well-being) and **Ecological** (sustainability)

Ecosystem functioning is generally the result of a complex web of interactions and processes, often including human intervention. As a result, ecosystem service delivery is similarly complex: there can be considerable variation in the nature and level of services, and both synergistic and antagonistic (trade-off) effects between services can occur (De Bello *et al.*, 2010; Lavorel & Grigulis, 2012; Rapidel *et al.*, 2015). The links between service delivery and ecosystem diversity have been abundantly explored, yet remain insufficiently known. In particular, it is necessary to identify and develop appropriate ecosystem service indicators that can adequately serve to evaluate delivery by ecosystems. Van Oudenhoven et al (2018) propose several key criteria for developing suitable ecosystem service indicators, based on four necessary conditions. Indicators must indeed be **1. credible**. They must constitute a valid representation of the subject, be accepted by the scientific or expert community and backed by scientific literature, and must be quantifiable. They must be **2. useful and relevant for stakeholders and decision makers,** and **3. be perceived as legitimate and politically fair by them**. They must answer a need for information, be scalable and transferable across spatial scales and areas, and useful for monitoring change over time. They must be understandable and should be selected through an inclusive, transparent process. Finally, it must be **4. feasible**, logistically and economically, to develop, measure, quantify and, if need be, revisit and update them.

Studies have looked at various aspects of diversity and their role in ecosystem service delivery, from taxonomic (Hooper *et al.*, 2005) to functional (Díaz & Cabido, 2001; De Bello *et al.*, 2010; Lavorel & Grigulis, 2012) and even genetic (intraspecific, Strobl, 2022). In fact, these different levels of diversity are all implicated in ecosystem function, and often interdependent (Vellend & Geber, 2005; Cadotte *et al.*, 2011). Owing to their central role in ecosystem service delivery, the multiple components of diversity can be (and have been) harnessed to improve the productivity, sustainability and adaptability of cropping systems. At the genetic level, diversity can be used to improve crop while specific or functional diversity can be enlisted for agricultural system diversification to face many present and future challenges.

2.3.Diversity can help make better crops…

In the first half of the XXth century, Soviet scientist Vavilov first proposed the concept of "Centers of origin" for cultivated crops, which hold greater genetic diversity which could be harnessed for improving crops through breeding (Harris, 1990). Later reconceptualized as "**centers of diversification**", the usefulness of their genetic resources for crop improvement is now well established (Harlan, 1951, 1965, 1971). The **Gene Pool** concept was proposed by Harlan and de Wet (1971) to provide a practical framework for incorporating formal taxonomy and cultivated plant classification through genetics. Both the wild relatives of cultivated species (Crop Wild Relatives) and the many crop varieties that were developed (see Sidebar 2) through farmer-mediated selection have the potential to contain genetic variation that can help respond to emerging pressures (Akem *et al.*, 2000; Lopes *et al.*, 2015; Zhang *et al.*, 2017; Dempewolf *et al.*, 2017; Bohra *et al.*, 2022). As such, they are of conservation concern, particularly in light of modern agriculture's tendency towards homogenization (Harlan, 1975; Khoury *et al.*, 2022). Attention is increasingly paid to the need for characterizing, evaluating and conserving these resources (Meilleur & Hodgkin, 2004; Castañeda-Álvarez *et al.*, 2016).

This understanding has led to the establishment of germplasm collections, which are ex situ repositories of multiple varieties and accessions, with an aim towards conserving the available **genetic diversity** of both wild and cultivated germplasm. Such collections have been established for a variety of annual (e.g. soybean—Perry & McIntosh, 1991; durum wheat—Pecetti *et al.*, 1992; cucumber—Shetty & Wehner, 2002; peanut—Holbrook & Dong, 2005; rice, *Oryza spp*—Yan *et al.*, 2007; maize—Yang *et al.*, 2011; tomato—Mata-Nicolás *et al.*, 2020) and perennial crops (e.g. cacao—Bekele *et al.*, 2006; Arabica coffee—Engelmann *et al.*, 2007; olives—Haouane *et al.*, 2011; grapes—Emanuelli *et al.*, 2013; Robusta coffee—Verleysen *et al.*, 2023), and have proven of great value for varietal development.

However, there exist limitations to the usefulness of germplasm collection. On a basic level, they may not be representative of the total diversity of the crop, depending on sampling bias, and misidentification of accessions is also an issue (Pruvot-Woehl *et al.*, 2020). Furthermore, by taking crops out of their cultivation context, germplasm collections effectively "freeze" the processes of artificial and natural selection that allow crops to adapt to environmental pressures and farmers' needs (Brush, 2000). Finally, in sexually propagated species, particularly short-lived annuals, genetic erosion by loss of alleles can occur as a result of genetic bottlenecks experienced across sowing cycles, as was shown in beans *Phaseolus vulgaris* (Negri & Tiranti, 2010). Therefore, it has been proposed that the more dynamic **in-situ management of crop genetic resources** be encouraged as a complementary approach (Thomas *et al.*, 2012; Borg *et al.*, 2018). Studies in temperate cereal crops such as bread wheat (*Triticum aestivum*) have shown that farmer selection leads to locally-adapted crops which require fewer inputs (Enjalbert *et al.*, 2011).

Sidebar 2. Defining crop varieties: a surprisingly complex endeavor

In order to appropriately study, assess, and plan for agricultural diversification, it is necessary to understand intraspecific crop diversity. The concept of variety is one that is therefore useful to consider, since it is the unit or level of crop diversity most often used, despite the term being difficult to define. Appropriately enough, there can be a great variety of meanings and concepts behind it. Depending on context, "variety" can be used interchangeably with a wide range of terms, such as "subspecies", "line", "cultivar", or "landrace". Other workers nest several of these terms within each other, as in the hierarchical classification proposed by Harlan and de Wet (1971): species-subspecies-race-subrace-cultivar-line/clone/genotype. In the taxonomic sense, the term "variety" has been used interchangeably with others such as "subspecies" as a subdivision of the "species" taxon (Hamilton & Reichard, 1992), referring to wild populations. The term is however also widely used in agronomic contexts.

A **landrace**, also known as local, traditional, folk, or farmer's variety, is a locally-adapted population of a certain crop, which display varying levels of genetic and phenotypic diversity or integrity, while still remaining identifiable (Zeven, 1998; Villa *et al.*, 2005; Saxena & Singh, 2006; Berg, 2009). They typically result from a mix of natural and artificial selection for yield stability, but have not been subject to formal breeding programs. The term "population-variety" has also been used to refer to freely-breeding, relatively diverse, often traditional crop varieties (Thomas *et al.*, 2012; Massias *et al.*, 2020).

Plants that do result from breeding programs are typically called **"modern", "elite" or "improved" varieties** or cultivars, often developed with the aim of maximizing yields (Tripp, 1996; van de Wouw *et al.*, 2010). From the 20th century onwards, their development also focused on genetic homogeneity to facilitate standardization and efficiency of their (often intensive) cultivation and marketing. **Cultivars** are generally understood to be derived from the selection of a limited number of plants, and propagated by means that preserve a high level of genetic uniformity (the term "inbred line" may also be used, e.g. Lai *et al.*, 2010). Furthermore, many cultivars are propagated through vegetative means and are therefore clones (Pringle, 1975), though they may undergo diversification through somatic mutations (McKey *et al.*, 2010; Achtak *et al.*, 2010). The term "cultivar" is occasionally used to refer to modern, improved varieties, by opposition to landraces (Villa *et al.*, 2005), but is also used to refer to ancient varieties, such as for grapevine (Ucchesu *et al.*, 2015). The concept of homogeneity as part of varietal definition has become particularly prevalent as questions arose over intellectual property rights, and the emergence of institutional frameworks to define the concept. For instance, the criteria for attaining varietal status defined by the International Union for the Protection of New Varieties of Plants include homogeneity and stability as well as novelty (UPOV, 2010).

To complicate matters, farmers may also use culturally-informed plants classifications (dubbed "**Folk taxonomy**"), which have their own logic that may not always correspond to biological classification (Berlin *et al.*, 1966; Sambatti *et al.*, 2001; Bizuayehu, 2008; Gros-Balthazard *et al.*, 2020). The naming of plant varieties can run into additional sources of confusion, particularly it is associated with trademarks or **geographic origin labels** (Marie-Vivien, 2008). Measuring or calculating genetic (dis)similarity can help distinguish varieties, but this requires that appropriate thresholds be defined (Noli *et al.*, 2013). Even then, matters will remain complicated due to the various cladistic levels at which varieties are defined.

2.4. …And make better systems

Agricultural diversification can also be applied at multiple scales, and to various ends (Beillouin *et al.*, 2019a; Zabala *et al.*, 2023). At the **national** level, it has been found to stabilize agricultural production and limit years of sharp losses (Renard & Tilman, 2019). At the **landscape** level, it can be achieved through increasing heterogeneity in land use (Tscharntke *et al.*, 2005). There is evidence that even simple mosaics of different monocultures, can have a positive impact on farm productivity (Burchfield *et al.*, 2019). On the **farm** level, diversification can take many forms, of varying degrees of complexity. Intercropping is a traditional practice of growing two or more crops together. In particular, cereal-legume intercropping has received much attention due to its ability to improve yields (at least for cereals) and/or decrease the amount of fertilizer needed (Machado, 2009; Ren *et al.*, 2014; Li *et al.*, 2021). Intercropping has also been found effective for weed suppression (Gu *et al.*, 2021) and improve resource use efficiency (Evers *et al.*, 2019). Similarly, non-crop species may be incorporated within farms for the benefit of the crop, for instance through incorporating shade trees (Almeida & Valle, 2007; Jha *et al.*, 2011; Tscharntke *et al.*, 2011), or hedges as windbreaks (Forman & Baudry, 1984). Temporal diversification of monocultures can also be achieved through crop rotation, with positive effects on yield (Zhao *et al.*, 2020; Shah *et al.*, 2021). Some systems are also constructed with the aim of maximizing diversity, such as traditional homegardens (Kumar & Nair, 2006b). These agroforestry systems combine a wide variety of perennial and annual, woody and herbaceous useful species and can be extremely diverse, with several dozen species in a single farm (Wezel & Bender, 2003; Kehlenbeck & Maass, 2004).

Diversification can also occur at the species level, namely through **intraspecific diversity** and **varietal mixtures** (Reiss & Drinkwater, 2018). While having fewer overall benefits than more complex forms of diversification (Beillouin *et al.*, 2021), mixtures of varieties can lead to improved yields and lower pest and disease pressures (Barot *et al.*, 2017; Borg *et al.*, 2018; Cissé *et al.*, 2022). Traditionally, cropping systems contained "population-varieties" or landraces which had some amount of genetic diversity, favoring the stability of yield and its adaptability to changing conditions over its maximization. Diversified crops can in turn generate diversity through sexual reproduction and genetic mixing (e.g. Elias & McKey, 2000 for an example in Cassava, *Manihot esculenta*).

Despite its many benefits, there remain several difficulties to implementing agricultural diversification. Meynard *et al.*(2018) identify several such obstacles in France, placing them all under the umbrella of "socio-technical lock-in". This term refers to a lack of agronomic, economic and political conditions, including appropriate genetic material for "minor" crops, unfavorable value chains, and lack of coordination among actors in a given sector. Similarly, Morel *et al.*, (2020) identify 46 different obstacles to diversification in Europe with most falling under socio-technical barriers, such as lack of technical and economic knowledge and references, low agronomic performances of such systems (real or perceived), need for further technological investments, market uncertainties, or lack of communication between value chain actors. In their discussion of how genetic engineering is systemically favored over agroecological innovations in agricultural research aiming to solve current issues, Vanloqueren and Baret (2009) identify several factors that disadvantage agroecology, including the focus on short-term, small-scale improvements to agricultural productivity, the political value placed on competitiveness, the priorities of powerful private sector actors, as well as several cultural and cognitive biases against in favor of more "technical" solutions. This may be because the agroecological movement has not achieved the same level of perceived legitimacy as industrial food systems among the broader public (Montenegro De Wit & Iles, 2016). Other workers have identified several exogenous factors, including institutional barriers, hindering diversification and strategies for pursuing food sovereignty in poorer regions of Latin-America (Chappell *et* *al.*, 2013) while in Haiti, attention has been called to the fact that decision-makers tend to favor intensification, in opposition to farmers' preference for diversification (Steckley & Weis, 2016; Jayaram, 2018).

One big challenge to ecological intensification and diversification of cropping systems is that the standards by which agroecology is compared to conventional farming are inherently disadvantageous to the former (Vanloqueren & Baret, 2009). While several metrics have been proposed for the evaluation of these systems (such as the land equivalent ratio for comparing the productivity of mixed crops to that of monocultures; reviewed by Smith *et al.*, 2017), there have yet to be universally accepted methods that incorporate both ecological and socioeconomic dimensions (Dumont *et al.*, 2016, 2021). As such, there remain significant knowledge gaps in the implementation of diversification (Duru *et al.*, 2015; Borg *et al.*, 2018) and the management of trade-offs between the different ecosystem services it promotes (Rapidel *et al.*, 2015). The effects of diversification of farmers' income was cited among the identified gaps in scientific literature on the topic (Beillouin *et al.*, 2019b), which is surprising given that it arguably ranks among the greatest incentives for its adoption. The benefits of diversification are known to be highly context-specific, which may further hamper planning and implementation (Beillouin *et al.*, 2021; Poncet *et al.*, 2024).

Having gotten an overview of the broader conversation around modern agriculture's impacts and challenges, and the quest for a path forward, we may now turn our attention to the present thesis' crop of interest: **Coffee trees**. As we will demonstrate over the course of this thesis, this plant is an important component of many traditional Haitian agroforests, with a rich local history. It occurs in a variety of contexts which provide opportunities for the study of both intraspecific diversity and system-wide diversification, both in a local and global context.

3. Coffee

3.1. The genus Coffea

The genus *Coffea* belongs to the family Rubiaceae. Following its merging with *Psilanthus*, and recent description of new members, its species number increased from 104 to 131 (as of 2024, powo.science.kew.org), and its previously African-only distribution was extended to tropical Asia and Australasia (Davis *et al.*, 2011; Davis & Rakotonasolo, 2021; Stoffelen *et al.*, 2021). These perennial, woody trees and shrubs inhabit a wide range of habitats, from moist tropical forest to dry savanna, including islands such as Madagascar and the Mascarenes (Chevalier, 1946; Davis *et al.*, 2006; Anthony *et al.*, 2010). Despite their taxonomic diversity, only a handful of species are cultivated (Fig. 6), with the main ones being *C. arabica* L. ("**Arabica coffee**", ~60% of total production), *C. canephora* Pierre ex Froehner ("**Robusta** coffee", ~40%), and, to a much lesser extent, *C. liberica* W. Bull (Ferreira *et al.*, 2019; International Trade Centre, 2021). Interestingly, these species display other exceptional characteristics: *C. arabica* is the only tetraploid (2n = 4x = 44) among otherwise diploid species, and one of the few considered to be autogamous, while *C. canephora* and *C. liberica* have the broadest natural distributions of any *Coffea* species.

Figure 6. Photographs of notable coffee species. Clockwise from top left: *Coffea eugenioides*, a progenitor species of Arabica; *C. canephora* or Robusta, also a progenitor species of Arabica; *C. liberica liberica*, or Liberian coffee; *C. liberica dewevrei*, or Excelsa coffee; *C. stenophylla*, or Highland coffee, and wild *C. arabica*, Arabica coffee.

3.2. Arabica, the first and foremost cultivated coffee

Of the main economic species, Arabica (Fig. 6, 10A) is likely the first to have been cultivated, and certainly the first to have been established outside of its region of origin. The species originates from the Highlands of Ethiopia, South Sudan and Kenya, and is derived from the hybridization of two ancestral species *C. canephora* and *C. eugenioides* (Anthony *et al.*, 2002). Genomics studies have determined this hybridization and resulting polyploidization to have resulted from a single event, which took place fairly recently (Scalabrin *et al.*, 2020; Salojärvi *et al.*, 2024). As a result, Arabica is an **allotetraploid** (2n = 4x = 44), but also amphidiploid species, meaning that its two subgenomes do not recombine. The species also displays a relatively **low level of genetic diversity**, exacerbated by its (facultatively) **autogamous** mating system ("selfing").

3.3. A history of Arabica cultivation

The early history of Arabica use and cultivation is steeped in legend and uncertainties. William Ukers (editor of the Tea and Coffee Trade Journal)'s 1922 book "All about Coffee" is particularly informative on this topic. One oft-relayed tale is that of Kaldi the young goat herder who, upon observing unusually high levels of activity among his flock, traced their boundless energy to a wild coffee plant which they had grazed on. He eventually shared his discovery with a monk, who discovered how to brew a hot beverage from coffee beans, setting the stage for one of History's most important drinks (Ukers, 1922). It has been in fact argued that coffee's place in the culinary practices and oral traditions of Ethiopia's Oromo people far predate this legend (Bacha *et al.*, 2019). Outside of its native range, coffee cultivation was first established in Yemen (confirmed through genetic studies by Silvestrini *et al.*, 2007; Montagnon *et al.*, 2021), though the date of this initial spread is uncertain (anywhere between the VIth and XVth centuries). Coffee was shipped from Yemen through the port of Mokka, a name that is still associated with the beverage to this day. Though jealously protective of their monopoly, Yemeni growers were not able to retain it: legend tells of a Muslim pilgrim, Baba Budhan, who smuggled seeds to Mysore, India, where he was able to grow and propagate the crop. Still, it was in the near East (supplied by Yemen) that Europeans first came to know about coffee in 1528, the specific epithet *arabica* bearing the legacy of this encounter (Ukers, 1922).

Europe was then in the process of its colonial expansion, a political, economic and cultural enterprise in which botany was enlisted to help the subjugation of peoples and lands (Sangwan, 1983; Baber, 2016). Agricultural expansion and establishment of new crops were important components of colonialism, to which Arabica coffee was soon incorporated (Fig. 7). The Dutch acquired seeds of this precious plant in the early 1600s, introducing them to the East Indies, and eventually to Suriname via the greenhouses of Amsterdam (Ukers, 1922; De Bivar Marquese, 2022). They also gifted French King Louis XIV a young coffee tree in 1714. Its offspring were given to Gabriel De Clieu, a naval officer, who transported them to Martinique in 1723. This voyage has been recounted with perhaps some romanticization, the plants reportedly surviving pirate attacks, attempted destruction by an envious passenger, and dangerous lack of water (Ukers, 1922). From Martinique and Suriname, coffee was spread to plantations throughout the Caribbean and tropical Americas. This wave of dispersal gave rise to the **Typica** lineage, one of the most historically significant varietal groups Arabica. Around the same period (1708-

1718), the French acquired Arabica from Yemen and established the crop on Réunion Island, then known as Bourbon. This resulted in the **Bourbon** lineage, which did not leave the island until the 1860s, but was widely and quickly adopted on many farms in Africa and the Americas (World Coffee Research, 2019).

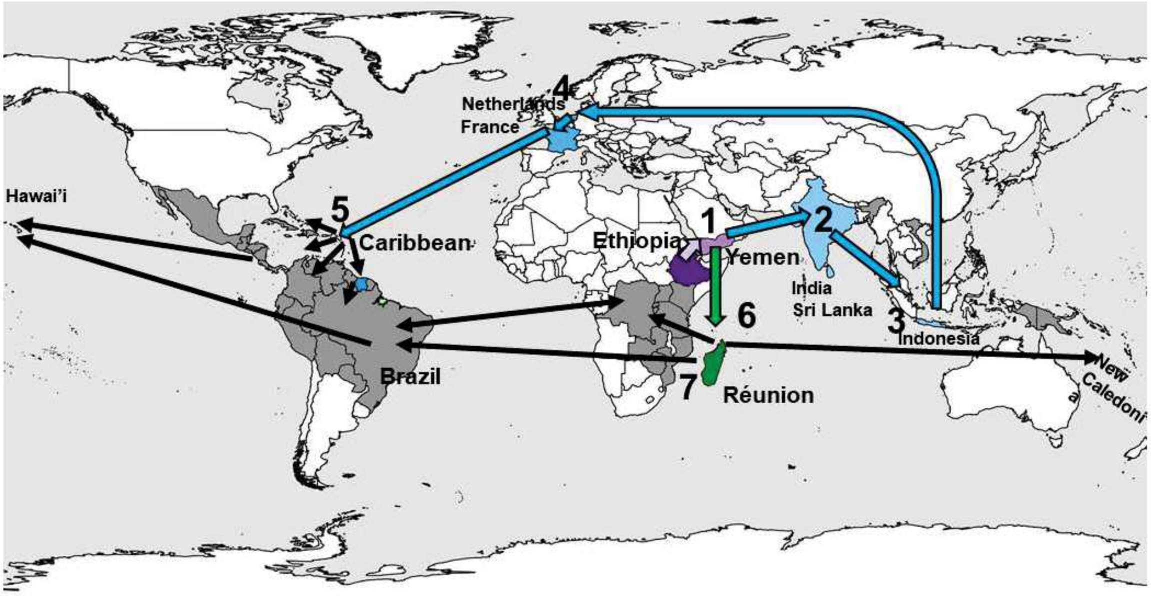


Figure 7. Historical spread of Arabica. Blue and green arrows represent the steps that led to the Typica and Bourbon lines, respectively. 1. Arabica originates from Ethiopia, taken to Yemen, possibly as early as 6th century CE. 2. The Dutch introduce coffee to Ceylon (Sri Lanka) in 1658 while, according to tradition, Baba Budan smuggles seven seeds to India, 1965. 3. The Dutch introduce Arabica to Java (1699), then to other "East Indies". 4.Coffee plants are taken to Amsterdam from Java in 1706, and soon after gifted by the Dutch to the French. 5. The French bring Arabica (Typica) to Martinique in 1723, from which it will spread to the Caribbean and South America, then Central America and, over the following centuries, to other places including East Africa. 6. In 1723, the French acquire Arabica from Yemen and introduce it to Bourbon Island (Réunion). 7. Starting 1856-1859, Bourbon coffee is introduced from Réunion to New Caledonia, East Africa, and eventually the Americas, where it and its derived varieties eventually replace Typica in most parts. Figure based on Salojärvi *et al.*, 2024 (extended data figure), with modifications based on the work in Chapter 2 of the thesis. Maps created in QGIS v. 3.30.1 using Natural Earth (Free vector and raster map data @ naturalearthdata.com) and shapefiles from Hijmans and UC Berkeley (2015a,b) and Patterson and Kelso (2012).

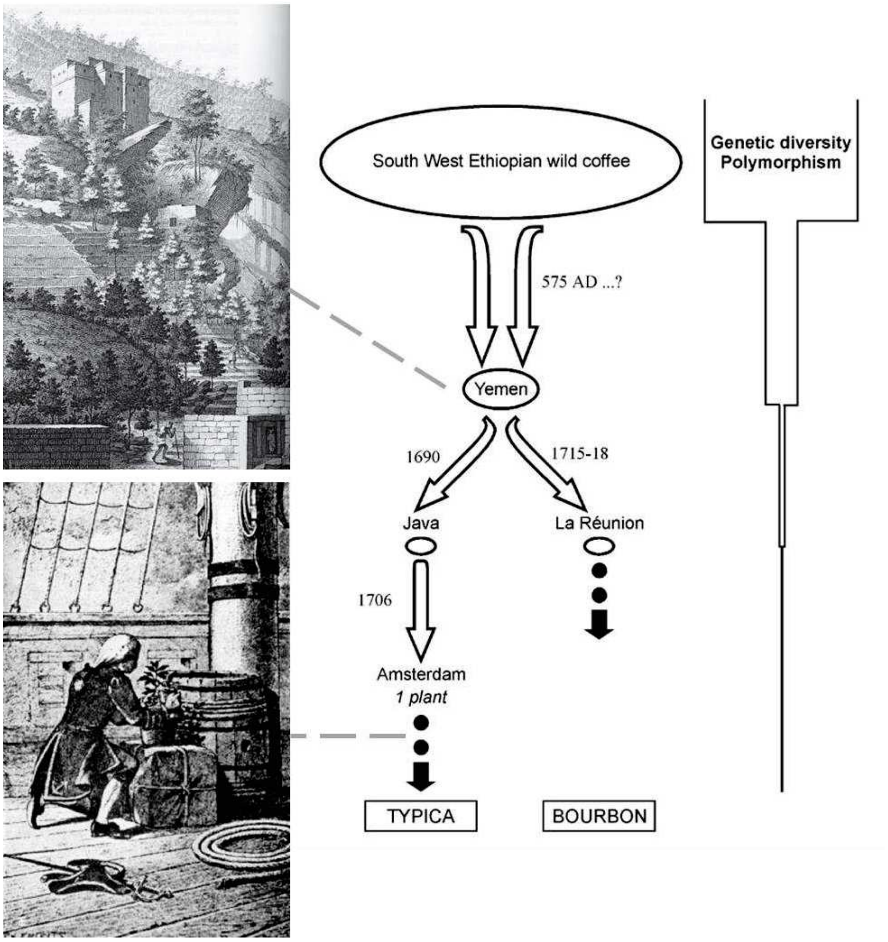


Figure 8. Successive historical reductions in genetic diversity experienced by the main cultivated lines of *Coffea arabica*. A. Timeline and associated population bottlenecks, taken from Anthony *et al.*, 2002. B. Yemeni coffee cultivation on terraces, by G.V. Baurenfeind, engraved by G. Haas, 1774. Taken from Friis, 2015. C. Illustration of De Clieu tending to a coffee plant on his 1723 voyage to Martinique, taken from Ukers, 1922.

Owing to the strong **successive population bottlenecks** experiences by both the Typica and Bourbon lineages (Fig. 8), the majority of coffee farms were established from a very narrow genetic basis (Anthony *et al.*, 2002). Nevertheless, several cultivars were developed (Fig. 9) from these, initially through a process of massal selection and propagation of mutant strains. While this process occurred in plantations worldwide (e.g. ‘Erecta’ and ‘Laurina/Bourbon pointu’ Bourbon mutants were found in Indonesia and Réunion Island, respectively), many such mutants were discovered in Brazil, such as Maragogipe (1870), Amarella (1871) and Cera (1935) from Typica, or **Caturra** in 1915-18 from Bourbon (Haarer, 1923). The latter, a dwarf mutant, has proven extremely important, both as a parent variety for breeding and as a crop itself (World Coffee Research, 2019), being cultivated until present (e.g. Cerda *et al.*, 2020). As the XXth century advanced, solving issues caused by biotic and abiotic pressures became a focus of breeding, both in pure Arabica and through use of hybrids. In particular, the **Timor hybrid**, a spontaneous *C. arabica x C. canephora* cross discovered in 1927 (Bettencourt, 1973), was heavily used for its resistance to **coffee leaf rust**, *Hemileia vastatrix* (Lashermes *et al.*, 2000b,a). In the 1950s and 1960s, prospections of wild Arabica from Ethiopia took place, which led to the establishment of several accessions into germplasm collections (Engelmann *et al.*, 2007). This was spurred by the realization that wild genetic resources were both of interest for breeders, and endangered by habitat loss (Charrier & Berthaud, 1990). Several field genebanks were established worldwide, such as those of the *Centro Agronómico Tropical de Investigación y Enseñanza* (CATIE) in Costa-Rica, *Centro Nacional de Investigaciones de Café* (CENICAFE) in Colombia*, Instituto Agronômico de Campinas (IAC) in Brazil,* National Agricultural Research Organisation (NARO) in Uganda, the Ethiopian Biodiversity Institute (EBI) or the Western Highlands Agriculture and Forestry Science Institute (WASI) in Vietnam (Vi *et al.*, 2022). In recent years, coffee breeders have begun focusing on these accessions as potential parents for elite, highly-performing F1 clones (Breitler *et al.*, 2022; McCook & Montero-Mora, 2024). Increasingly, breeding of Arabica has focused on coffee quality, with several studies focusing on understanding the genetic basis of organoleptic qualities (Leroy *et al.*, 2006; Montagnon *et al.*, 2012). Still, pest and disease resistance also remain a central aim of breeding efforts, as does adaptability to climate change (van der Vossen *et al.*, 2015). These and further developments are discussed in the second chapter of the present manuscript, which considers the history of Coffee breeding and its impacts on the extant genetic resources of Haitian and Guadeloupean coffee. In this chapter, particular importance is also given to coffee leaf rust and its devastating impacts.

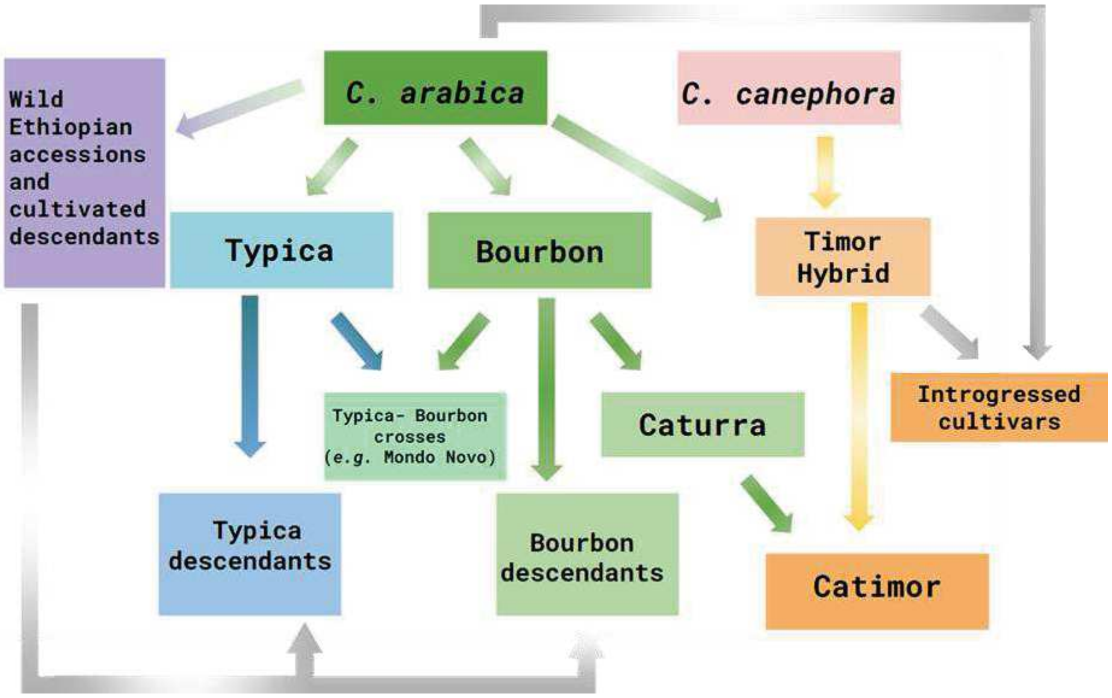


Figure 9. Main historically significant cultivated lines of *Coffea arabica*. Made based on World Coffee Research (2019)

3.4. Arabica cultivation today

Arabica continues to dominate world coffee production, owing to its reputation as the species with the best cup quality and thus greatest market value (Ferreira *et al.*, 2019; International Trade Centre, 2021). Suitable conditions for Arabica cultivation are found at altitudes of 700-2200m, mean annual rainfall of 1200-1800 mm and temperatures between 18-21°C, up to 23°C, though some sources report broader ranges, and microclimate can compensate for improper macroclimate to an extent (De Camargo & Pereira, 1994; DaMatta & Ramalho, 2006; International Trade Centre, 2021). Though cultivated throughout the tropics, the bulk of Arabica coffee is now produced in the Americas and its native East Africa (International Trade Centre, 2021).

In addition to leaf rust, Arabica is prone to several diseases, primarily of fungal (e.g. American leaf spot *Mycena citricolor*, Coffee berry disease *Colletotrichum kahawae*, or leaf spot *Cercospora coffeicola*), but also of bacterial and viral origin, as well as several pests, chief among which are the coffee berry borer *Hypothenemus hampei* (Coleoptera), leaf miner *Leucoptera spp* (Lepidoptera) and root-knot nematodes *Medoigyne spp*. (International Trade Centre, 2021). Furthermore, Arabica cultivation is increasingly threatened by global climate change, which is expected to reduce suitable cropping area and require farmers to adapt their cropping systems, or risk losing them (Jaramillo *et al.*, 2011; Davis *et al.*, 2012; Bunn *et al.*, 2015; Jawo *et al.*, 2023).

3.5. Robusta, a strong second

In comparison to the long, storied history of Arabica coffee, Robusta (*C. canephora,* Fig. 6, 10B) has only been known to the world at large for less than two centuries (Fig. 11), though local populations from its area of origin were known to make use of spontaneous trees in local forests (Haarer, 1923; Chevalier, 1929) and to cultivate it at small scales in the actual Gabon, Angola, Uganda and Democratic Republic of Congo from the XIXth century (Chevalier, 1929; Montagnon *et al.*, 1998a). As mentioned above, *C. canephora* has the broadest distribution of all coffee species, being found throughout the African equatorial rainforest, from Uganda to Guinea. Botanists have long debated the subclassifications of the species, and genomic studies have determined the species to be structured in 8 genetically and geographically distinct genetic groups (Mérot-L'Anthoene *et al.*, 2019), with a deeper separation of groups along the Dahomey gap between Guinean and Congolian forests (Gomez *et al.*, 2009). These genetic groups have different agronomic and chemical characteristics (Montagnon *et al.*, 1998a). Unlike Arabica, *C. canephora* is an obligate **allogamous diploid** ($2n=2x=22$). The species has greater resistance to the main Arabica diseases, coffee leaf rust and berry disease, though it is susceptible to others (Do Ceu Silva *et al.*, 2006).

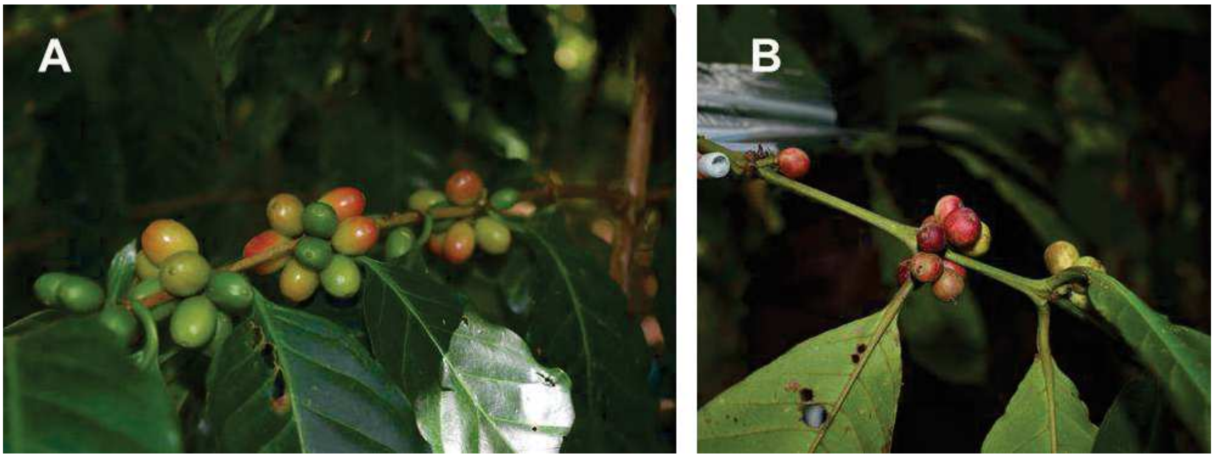


Figure 10. Fruiting coffee trees. A. Arabica cherries B. Robusta cherries

In the early XXth century, Robusta was first introduced and selected in Java in response to a rust epidemic having devastated Arabica plantations, while other varieties were selected from West African accessions (e.g. Gabonese 'Kouillou' or 'Conilon' coffee) and introduced to various countries (Montagnon *et al.*, 1998a). Following a process of massal and recurrent selection, whereby strains of agronomic interest were identified or created, respectively, exceptional specimens were clonally propagated, and these 'elite' clones widely distributed (Montagnon *et al.*, 1998b). However, and despite its greater tolerance to drought and temperature shocks than Arabica (DaMatta & Ramalho, 2006), Robusta cultivation is also increasingly threatened by climate change (Bunn *et al.*, 2015). For instance, studies in Vietnam, the leading Robusta producer, have shown that coffee stand aging and genetic vulnerability to climate change are of increasing concern (Vi, 2023). Robusta is generally considered to be of lower quality than Arabica, with higher caffeine and lower sugar content giving it a stronger (harsher, some may say) flavor (Leroy *et al.*, 2006; International Trade Centre, 2021). Nevertheless, as for Arabica, there have been efforts to understand the genetics of Robusta organoleptic quality in order to improve it via breeding (Leroy *et al.*, 2011).

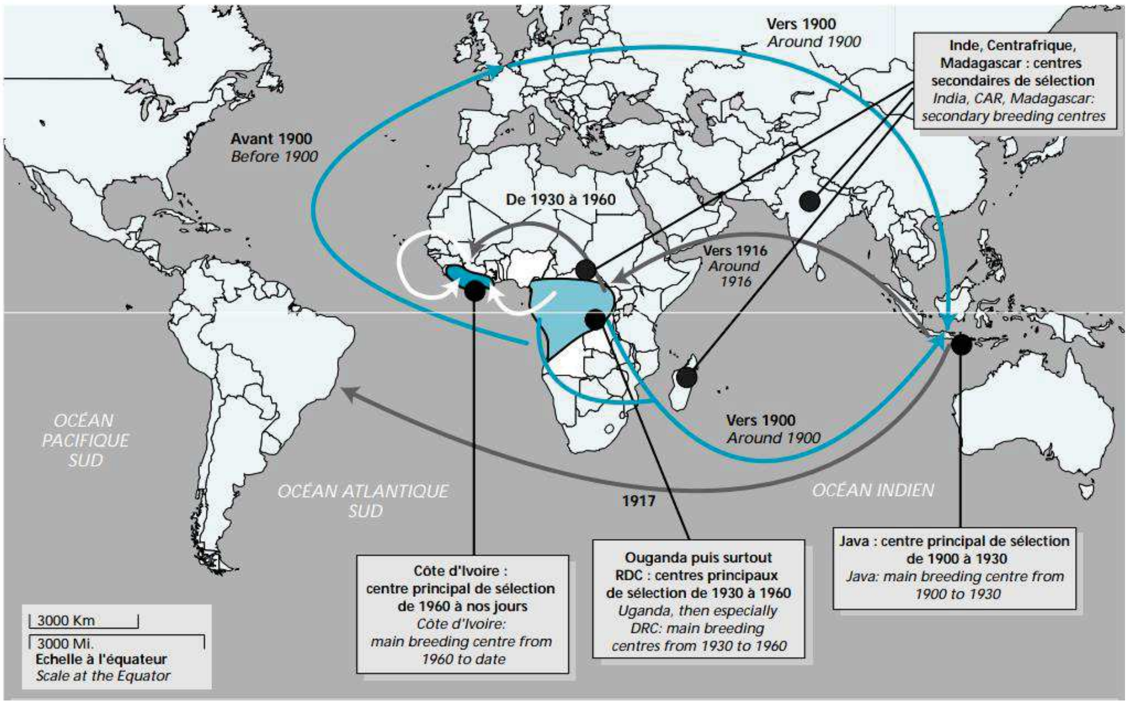


Figure 11. Historical spread of Robusta. Taken from Montagnon *et al.*, 1998b

3.6. Other cultivated *Coffea* species

Despite its current marginal status, **Liberica coffee** (*C. liberica*) in fact has been cultivated longer than Robusta coffee. Its native range stretched from Guinea to Uganda and North Angola (Chevalier, 1929; Davis *et al.*, 2006). Two or three Liberica allopatric sub-species are accepted: *C. liberica liberica, C. liberica dewrevei*, and possibly *C. liberica dewrevei f. bwanbensis* (Davis *et al.*, 2006), though some genetic analyses suggest the former two at least may merit full species status (N' Diaye *et al.*, 2005). Discovered in the forests of Liberia in the late 1800s, the nominate subspecies was noted for its large size, large grains, robustness and adaptability, and was introduced to several countries in Asia and the Americas (Morris, 1881; Nicholls, 1881;

Davis *et al.*, 2022). It enjoyed a brief period of success, but was overtaken by Robusta (Haarer, 1923; Chevalier, 1929).

Other species have been occasionally cultivated at small scales in the past two centuries, only to be largely forgotten until now. Indeed, in recent years, renewed scientific and agronomic attention has been paid not only to Liberica coffee (particularly the *dewevrei* subspecies, also known as Excelsa coffee), but also to the likes of *C. stenophylla* and *C. congensis* (Davis *et al.*, 2020, 2022; Bertrand *et al.*, 2023). This is driven in large part by the predicted harmful effects of climate change on currently cultivated species.

3.7. The legacy of Coffee genetic studies

The present thesis is in large part based on the characterization of Haitian agroforest coffee genetic resources through genotyping. As such, it is preceded by important studies by a great many workers to develop the knowledge base of coffee genetics. It also benefits from a legacy of genotyping methods and marker development. We will here list several such markers used by genotyping studies in the past seven decades. The information presented is mostly taken from the review by Schlötterer (2004)**,** but some examples on the use of these markers to study coffee is also included (see also Vi *et al.*, 2022).

Allozyme markers (from 'allelic variants of enzymes') were the first true molecular markers. The principle is as follows: different alleles of a same gene may result in enzyme proteins with different sizes and charge due to amino acid substitution, which can be visualized through electrophoresis and used to assess genetic variation between samples. In the late 1970s, these were used by Berthou et al (1980) to assess intra- and interspecific diversity in several *Coffea* species (though not Arabica). These markers were limited by low polymorphism.

Restriction Fragment Length Polymorphism (RFLP) markers were developed following the 1960s discovery of restriction endonucleases and allowed for the study of DNA directly, therefore displaying higher polymorphism. Using these markers, Berthou et al. (1983) investigated taxonomic relationships between *Coffea* species and hypothesized that *C. arabica* was likely descended from an ancestral *C. eugenioides*. Later, these markers allowed Lashermes et al. (1999) to demonstrate that *C. arabica* was descended from diploid progenitors species *C. canephora* and *C. eugenioides*.

The invention of PCR greatly facilitated molecular studies by allowing the amplification of DNA regions that may otherwise be insufficient for marker-based studies. **Simple sequence repeat (or microsatellites)** markers (i.e. DNA regions of 1-10 nucleotides long sequences repeated multiple times in a short often <100 base pair interval; Richard *et al.*, 2008) were a particularly important development. Other, albeit less-reliable PCR-amplified length-based markers were also developed, such as **Randomly Amplified Polymorphic DNA (RAPD)** utilizing short primers of arbitrary nucleotide sequences to reveal polymorphism (Williams *et al.*, 1990), or **Amplified Fragment Length Polymorphism (AFLP)** combining RFLP markers with PCR amplification.

Using these markers, DNA fingerprinting, i.e. using genotype information to assign individuals to a particular taxon or genetic group, became more common (Nybom *et al.*, 2014), as did the study of genetic variation within species. Combinations of SSR, AFLP and RAPD markers were used to demonstrate the low level of genetic diversity of *C. arabica*, identify Ethiopia as its center of diversification (Lashermes *et al.*, 1996; Anthony *et al.*, 2001, 2002), and investigate Robusta introgression in Timor Hybrids (Lashermes *et al.*, 2000a). AFLP markers (Poncet et al. 2005) were also used to assess the genetic differentiation between *C. liberica liberica* and *C. liberica dewevrei* (N' Diaye *et al.*, 2005), while Poncet et al (2007) developed SSR markers for *C. canephora* which could also be used to genotype other species. SSR markers in particular remain useful tools that have been used in various countries to assess local coffee genetic resources, and those of international germplasm collections (Silvestrini *et al.*, 2007; Baltazar & Fabella, 2020; Pruvot-Woehl *et al.*, 2020; Sánchez *et al.*, 2020; Kiwuka *et al.*, 2021; Benti *et al.*, 2021).

Particularly with the advent and development of sequencing technology (see below for more information), and especially in recent years, **Single Nucleotide Polymorphisms (SNP)** have become an increasingly popular type of marker used in genetic studies. Alleles at loci with SNP differ by a single nucleotide, are typically abundant within genomes, and have low mutation rates. However, because SNP markers used in genotyping studies are typically biallelic, each individual locus has a very limited information content. SNP markers have been variously used to investigate the origin of *Coffea arabica* (Scalabrin *et al.*, 2020) and its cultivation history (Salojärvi *et al.*, 2024), the structure of wild *C. canephora* populations across their range (Mérot-L'Anthoene *et al.*, 2019) and at country-level or their vulnerability to climate change (de Aquino *et al.*, 2022; Tournebize *et al.*, 2022). Associations between SNP and organoleptic qualities of coffee have also been studied (Tran *et al.*, 2018; José Luis *et al.*, 2022).

3.8. DNA sequencing and targeted genotyping

Parallel to the discovery of new useful markers, methods for acquiring genotype data also evolved, particularly with the advent of sequencing, i.e. the description of nucleotide sequences within a given interval (Heather & Chain, 2016; Hu *et al.*, 2021). The first generation of sequencing methods such as "Sanger sequencing" (Sanger *et al.*, 1977) were slow and time-intensive, as only one sequence could be analyzed at a time. Later technological developments allowed for significant increases in the speed and efficiency of sequencing by mass-sequencing multiple DNA strands in parallel. So-called "second generation" sequencing methods (such as the well-known Illumina Platform) produced short (250–800 bp) reads which then had to be reassembled into genomes of varying levels of completeness by using bioinformatic tools. A combination of first- and second-generation sequencing data were used to assemble the *C. canephora* reference genome (Denoeud *et al.*, 2014). Recently, a genome assembly for *C. arabica* (in part) using second generation sequencing was published by Salojärvi *et al.* (2024). The "Third generation", such as on Oxford Nanopore Technology (ONT) and Pacific Biosciences (Pacbio) platforms, encompasses methods which allow for the sequencing of significantly longer reads (upwards of 10 kb). Salojärvi et al (2024), Scalabrin *et al.* (2024) concurrently published Arabica genome assemblies using (totally or in part) long read sequencing.

The availability of reference genomes permitted by sequencing greatly improved the identification of polymorphic regions that could be used to assess diversity. By sequencing a variety of samples (often called “resequencing”) and aligning their reads on the reference genome, variant sites can be identified and used to generate genotype data. To that end, a variety of bioinformatic tools have been proposed for alignment, such as the BWA-MEM algorithm (Li, 2013), and variant calling, such as the GATK toolkit (McKenna *et al.*, 2010).

This increased knowledge also allowed the development of methods for targeted genotyping. By focusing on the most polymorphic, and therefore informative regions, it is possible to genotype a large number of samples in a more efficient and less costly manner.

Some of these methods rely on targeted sequencing, such as the HiPlex deep amplicon sequencing technology: DNA is barcoded (to identify sample of origin) and amplified by PCR in the presence of target-region specific primers which are then sequenced with high read depths, i.e. multiple copies of the same sequence (Nguyen-Dumont *et al.*, 2013). Through bioinformatic pipelines, these sequences can be aligned onto a reference genome for variant calling and genotyping. Hi-Plex targeted amplicon sequencing was used in the present study, as described in Chapter I.

Other technologies rely on allele detection for direct genotyping of samples. For instance, DNA chip arrays are one such technology: these are solid surfaces on which strands of synthesized DNA corresponding to targeted regions are fixed. Once added, sample DNA hybridizes with strands corresponding to complementary target loci, producing a signal indicative of genotype (Kockum *et al.*, 2023). Mérot-L’anthoene et al. (2019) developed a 8.5K SNP array informative for both Arabica and Robusta, and used it to demonstrate that the easternmost *C. canephora* genetic group is closely related to the “Canephora” subgenome of *C. arabica*. Kompetitive Allele Specific PCR (KASP) assays are another method which, while similar in principle, do not require chip structures. Sample DNA is amplified by PCR in the presence of allele-specific primers with fluorescence-emitting components that directly emit a signal upon binding with the appropriate target DNA sequence. This method was employed in the present study (detailed in Chapters I and II), with targeted loci corresponding to up to 96 core markers particularly informative of Arabica diversity (Zhang *et al.*, 2021), selected among those identified by Mérot-L’anthoene et al. (2019).

3.9. Coffee cropping systems

Beyond characterization of coffee genetic resources, this thesis also aims to describe and characterize the agroecological context in which coffee trees are grown in Haiti. As such, it is important to consider the ways in which coffee cropping systems are organized and managed. Coffee is cultivated in a broad range of agronomic contexts and management intensity. Toledo and Moguel (2012) have proposed the following, widely accepted, typology of Coffee-growing systems (Fig. 12), ranging from highest to lowest complexity:

- **A. Traditional rustic system**: in these systems, coffee plants are planted in the understory of native forest, as a complement or substitute for the naturally-occurring lower strata. This system has the lowest impact on natural vegetation, and closely mimics the traditional form of Arabica coffee management in the specie's native range.

- **B. Traditional Polyculture** (Coffee garden): These systems retain the appearance and complex, multi-strata structure of natural forests, but their composition is determined by farmer choice to a considerably higher degree. They are composed of diverse assemblages of useful species, with coffee being one of many crops.
- **C. Commercial Polyculture**: In these systems, coffee is grown under a somewhat diversified layer of trees chosen for their compatibility as shade species, and other uses
- **D. Shaded monoculture**: these consist in simplified, two-strata systems in which coffee is grown under a monospecific shade layer, generally with added agrochemical inputs
- **E. Full sun**: These intensive monocultures, grown without shade, are supported by high inputs of fertilizer, pesticides, and labor. This remains the major form of coffee production worldwide, especially in large producers such as Vietnam and Brazil (Poncet *et al.*, 2024).

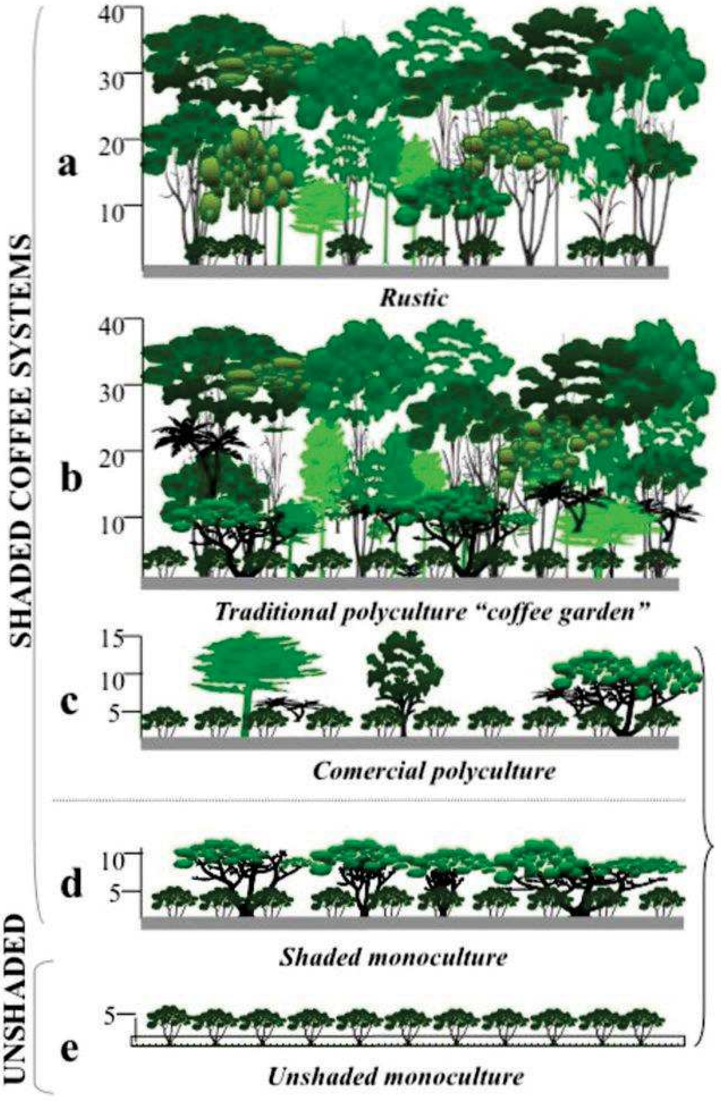


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Figure 12. Typology of coffee-growing systems, by Toledo & Moguel (2012)

With the exception of Full-sun coffee, these systems all fall under the umbrella of Agroforestry, despite the deep differences between them. The concept of agroforestry is ancient and traditional, but is also increasingly the focus of scientific attention as a potential tool to address the problems of modern coffee cultivation (Poncet *et al.*, 2024), and indeed agriculture as a whole.

As a form of agriculture that is inherently based on diversification, agroforestry offers good opportunities to incorporate ecological intensification and increase ecosystem service delivery through mobilization of genetic, specific and functional diversity (Rapidel *et al.*, 2015; Poncet *et al.*, 2024; Isaac *et al.*, 2024). Much research has been done on ecosystem service delivery by coffee-based agroforestry systems, especially in Latin-American shaded coffee farms, and particularly on the role of shade and diversification on coffee productivity and pest regulation (Kumar & Nair, 2006b; Garrity *et al.*, 2010; Jha *et al.*, 2011; Cerda *et al.*, 2020). Studies have shown that while topo-climatic variables such as altitude and rainfalls are the main factors determining pest and disease profiles (or injury profiles) in agroforestry systems (Allinne *et al.*, 2016), microclimatic and ecological effects of the tree layer can have a significant impact on various biotic stresses such as leaf rust (Avelino *et al.*, 2004, 2007; Cerda *et al.*, 2017a), American leaf spot (Avelino *et al.*, 2007) or coffee berry borer (Bagny Beilhe *et al.*, 2020).

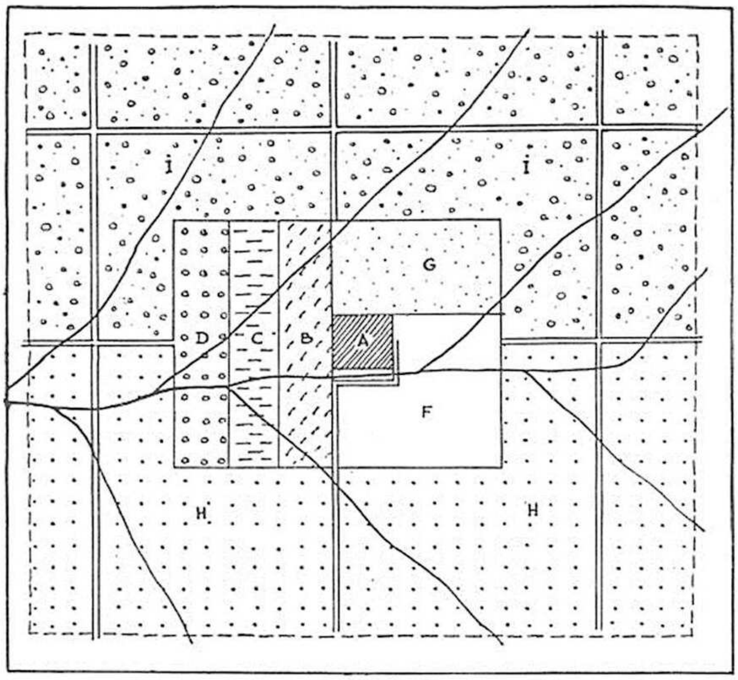
A major focus of research is the study of potential trade-offs between different ecosystem services delivered by coffee agrosystems, with an aim to minimizing them (Rapidel *et al.*, 2015). It has been shown that the benefits of diversification can be reaped without compromising on coffee yield under certain management conditions (Meylan *et al.*, 2017; Cerda *et al.*, 2020), but not others (Campanha *et al.*, 2004). In addition to the aforementioned topo-climatic variables, management intensity, the resulting nature and extent of shade, and the complex ecological interactions in the system can all affect coffee performance in agroforestry (Avelino *et al.*, 2004, 2007; Allinne *et al.*, 2016; Durand-Bessart *et al.*, 2020). For instance, incorporating legume trees such as *Erythrina poeppigiana* can enhance coffee tree growth through increased Nitrogen availability in less intensive systems, but only when properly trimmed to avoid over-shading (Haggar *et al.*, 2011; Sauvadet *et al.*, 2019).

The genetic identity of coffee trees must also be considered, as not all coffee cultivars are suitable for cultivation under higher levels of shade (Koutouleas *et al.*, 2022). Because coffee cultivation has historically (and even recently) trended towards intensification, varietal development has typically focused on producing varieties that could perform well in monocultures or intensive agroforestry. As discussed in Chapter II, only recently have breeders begun to attempt developing varieties specifically adapted to smallholder agroforestry (Breitler *et al.*, 2022). This has been deemed a paradigm shift, in which coffee is expected to adapt to extant farm conditions, rather than vice-versa (McCook & Montero-Mora, 2024).

As for any ecosystem, the study of ecosystem service delivery by coffee agroforestry systems require identifying appropriate and useful indicators (Van Oudenhoven *et al.*, 2018). For instance, given that these systems are primarily oriented towards production, it is often necessary to appropriately quantify yield and yield losses (Wang *et al.*, 2015; Cerda *et al.*, 2017b). Several such indicators have been proposed (Nutter *et al.*, 1993; Lobell *et al.*, 2009, see Cerda *et al.*, 2017b for coffee) such as potential yield (theoretical yield that can be expected from a given genotype given perfect growing conditions), attainable yield (a site-specific value of yield that can be expected using all available production techniques and pest-control measures, given local environmental conditions), actual yield (the measurable yield that is actually obtained from farms), or yield gap (the difference between the former and the latter). It is often necessary to measure or calculate proxies for ecosystem service delivery, as the actual value is prohibitively difficult to obtain. For instance, aboveground biomass is often used as a proxy for the carbon sequestration service (e.g. Redondo-Brenes & Montagnini, 2006; Van Den Berge *et al.*, 2021), though it is also more directly indicative of other services such as timber provision. As actual biomass measures are destructive and difficult to perform, allometric equations have been proposed for estimation using easily-measurable traits such as diameter at breast height (Chave *et al.*, 2014; Andrade *et al.*, 2022). Similarly, since it is virtually impossible to survey the entirety of a system's biodiversity, many studies focus on measuring the diversity of one (e.g. butterflies, in Jezeer *et al.*, 2019) or multiple (e.g.trees, lianas, terrestrial herbs, epiphytic liverworts, birds, butterflies, lower canopy ants, lower canopy beetles, dung beetles, bees, wasps, parasitoids, in Kessler *et al.*, 2012) taxonomic or functional groups of interest.

4. A Short History of Haitian coffee

Coffee has long played an important role in Haiti's agricultural history, starting from the colonial era. The French colony of Saint-Domingue, which would become Haiti following independence in 1804, was a plantation economy powered by the institution of slavery, and in which sugarcane was the main product. However, following its introduction in 1726, Arabica coffee proved a very attractive crop for newer planters seeking to settle the mountainous island's abundant lands at higher altitudes (Moral, 1955; Trouillot, 1982; De Bivar Marquese, 2022). Coffee farms were started on cheaper land, required lower financial investments to establish, and required less labor than did sugarcane fields. Coffee was grown in monocultures under full sun after cutting and burning down forestland (Laborie, 1798), with little regard for soil conservation and therefore long-term sustainability (McCook, 2017). The colony's coffee sector grew prodigiously even as sugarcane began to stagnate. In the later years of the XVIIIth century, Slave rebellions and the wars of the Haitian Revolution laid waste to Saint-Domingue's plantations and severely diminished crop yields, though coffee was able to fare better than other export crops due to the crop's tolerance of neglect (Lundahl, 1984): By 1820, the island had practically re-attained its colonial yield levels (Moral, 1955). The country's position as a small, newly free state surrounded by colonial powers left it unable to escape the global commodity trade, and export crops continued to be the main driver of its economy, coffee chief among them. They were also part of the heavy payment required of France to Haiti after Independence, as "compensation" for the loss of its most valuable colony (Oliver-Smith, 2010). The importance of coffee continued well into the XXth century. Ukers (1922) wrote "For well over a century Haiti has been shipping tens of millions of pounds of coffee annually; and the product is the mainstay of the country's economic life. In all that time, however, shipments have maintained much the same level."



— Plan d'une caféterie coloniale (reproduction d'une planche de Laborie, ouvr. cit.). — A - Maison d'habitation et bâtiments d'exploitation. — B, C, D - Jardins. — F - Terres des esclaves. — G - « Savanes ». — H - Plantations de caféiers. — I - Bois debout.

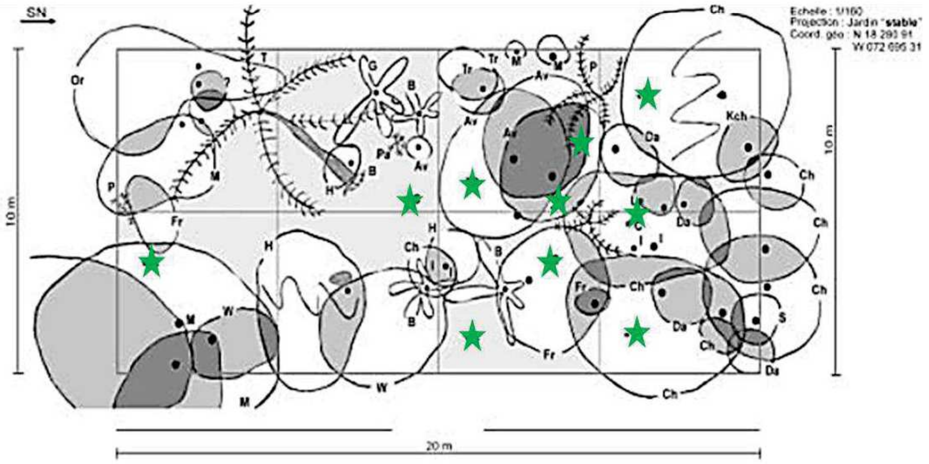


Figure 13. Transformation of coffee-growing systems from St Domingue's colonial plantations to Haiti's diversified agroforests. Top: diagram showing XVIIIth century full-sun coffee monoculture plantation (H) and adjacent woodland (I), taken from Moral (1955) based on Laborie (1798). Bottom: diagram showing a "typical" mature Haitian diversified agroforestry system with coffee trees indicated by stars. Taken from Jean-Denis *et al.* (2014)

The continued importance of Haitian coffee cultivation belies the radical change that occurred in the way it was conducted (Fig. 13): following Independence, the plantation system was abandoned in favor of small, highly fragmented, diversified homegardens and agroforestry systems (Moral, 1955). Furthermore, farmers benefitted little from the wealth generated by coffee production, being subject to exploitation by speculators and the elite class which exported the commodity (Plummer, 1984). The vitality of the coffee sector, and indeed that of the agricultural sector as a whole, diminished throughout the XXth and into the XXIth century as socio-political crises plagued the country (Fig. 14, 15). This decline can be traced through the following statistical snapshots:

- Coffee's share of commodity export earnings fells from 48% (25800 metric tons) in 1960-1962 to 32% (21300 t) in 1974-1976.
- By the late 1980s, while the crop was still central to the livelihood of roughly half of its rural population, Coffee only accounted for 6% of Haiti's GDP (Lopez & Dorsainville, 1990) and 18% of its total exports (Vital, 2014), with Haiti accounting for a mere 0.6% of world production (Dupuy, 1989).
- Coffee exports decreased 13-fold in volume between 1984 and 2004, and earnings decreased ninefold between 1980 and 2010 (Vital, 2014). Coffee cropping area also decreased steadily during this time (Agricultural Risk Management Team, 2010).

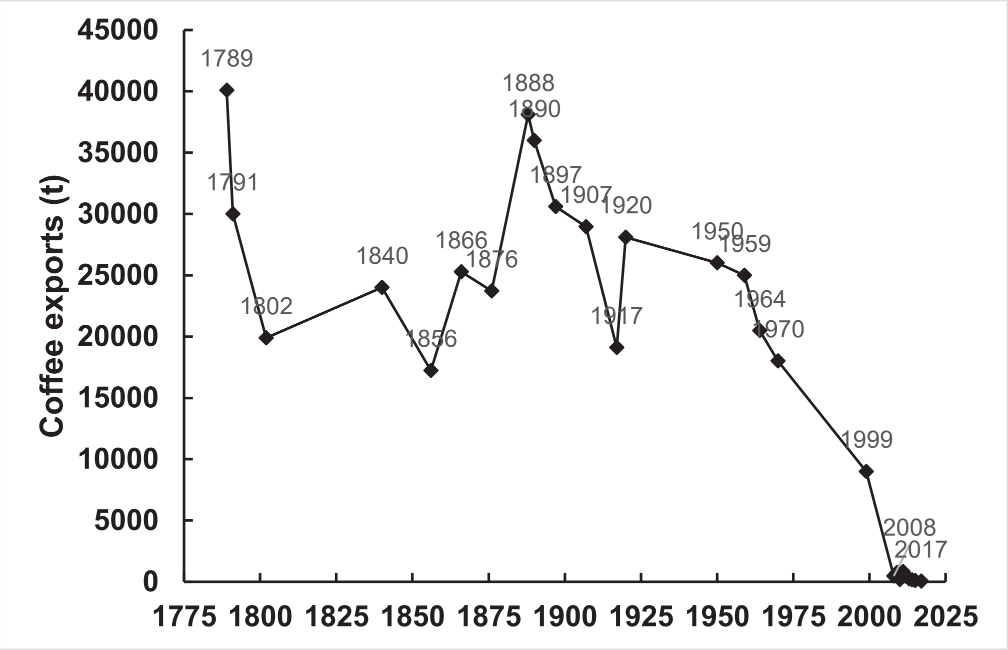


Fig. 14. Approximate coffee exports (in metric tons) by Haiti, 1789-2017, based on consulted literature (Data sources: Ukers, 1922; Moral, 1955; Sylvain, 1972; Lundahl, 1984; Amaya *et al.*, 1999, INCAH; https://www.incah-haiti.gouv.ht/)

Though some of this decrease in exports was due to an increase in both local consumption and clandestine trade of coffee across the border to the neighboring Dominican Republic (Amaya *et al.*, 1999; Rodriguez *et al.*, 2011), the main culprit was a drop in production. This situation led to a still-ongoing proliferation of development projects funded by international agencies and non-governmental organizations (NGOs), each proposing, and ultimately failing, to sustainably strengthen the agricultural sector (Tarter *et al.*, 2016). Starting the in the 1970s, these programs began importing and distributing modern coffee varieties, with little control over their spread. These projects did not succeed in curtailing this decline in the following decades, and in 2016 Haiti became a net coffee importer for the first time in its history (Josselin, 2018).

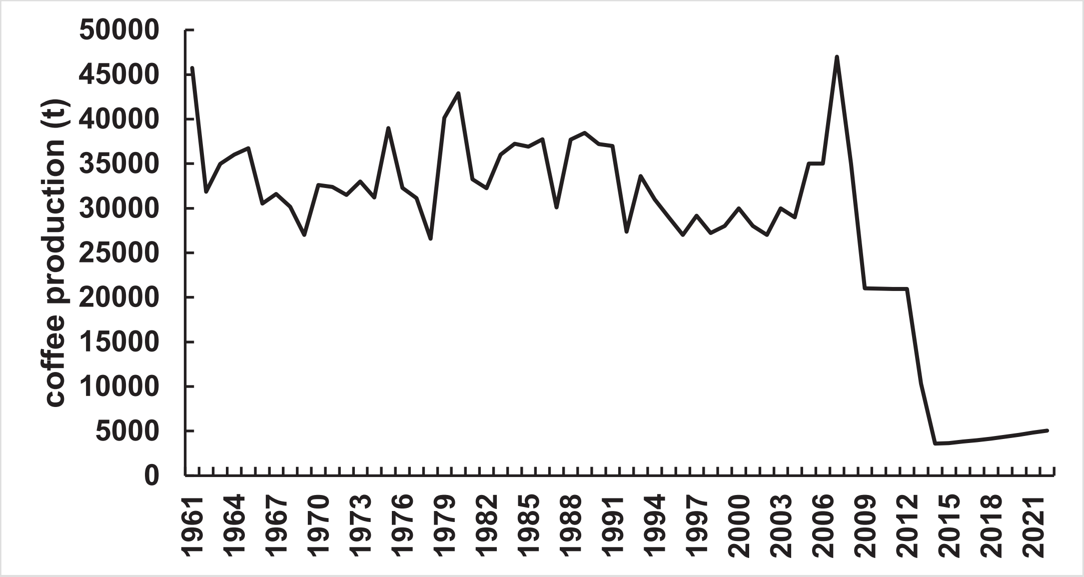


Fig. 15. Approximate green coffee production (in metric tons) by Haiti, 1961-2022 (Data source: FAO stat, https://www.fao.org/faostat/en/#data)

Historically and presently, there have been many major contributing factors to this decline: coffee pests and pathogens (such as leaf rust and the coffee berry borer), extreme weather events, and worsening soil erosion and fertility loss (Lopez & Dorsainville, 1990; Vital, 2014). These were exacerbated by a chronic lack of involvement from the public sector, insufficient scientific research on Haitian coffee-growing systems, insufficient support to farmers, and a periodically volatile global market causing prices to fluctuate. These obstacles and pressures caused farmers to increasingly turn away from coffee in favor of other crops such as beans and cereals, and to coffee stand aging due to lack of farm regeneration, with an estimated 70% of trees older than 20 years (Vital, 2014; Queneherve *et al.*, 2015). In addition, coffee cultivation in Haiti is increasingly threatened by global climate change, with an expected reduction in suitable areas in the future (Eitzinger *et al.*, 2013). While there were an estimated 400,000 Haitian Coffee growers in 1984 (Zimmermann, 1986), this number was halved only three decades later (Vital, 2014).

Nevertheless, coffee is still cultivated on all mountain chains in the country, but primarily in the following departments: Nord (especially in the municipalities of Plaisance and Dondon), Centre (Baptiste, Savanette), Sud-Est (Thiotte) and Grande-Anse (Beaumont, Roseau, Jérémie, Pestel), generally in localities between 300 and 1500 m of elevation (Amaya *et al.*, 1999; Rodriguez *et al.*, 2011; Vital, 2014). Despite the many difficulties discussed above, some growers' cooperatives (particularly in Thiotte and Baptiste) are able to access North-American, European and Japanese niche markets under Gourmet and Fair-Trade labels, as well as the 'Haitian Bleu' trademark, fetching higher prices than on local markets.

5. Research questions and objectives

The challenges facing Haiti in general, and the Haitian coffee sector in particular, as well as the broader considerations around agricultural diversification and sustainability, all constitute the context in which this thesis is embedded. It was conducted as part of the PITAG project (Sidebar 3), which aims to promote the development and adoption of innovative, sustainable methods for agriculture and agroforestry. One important challenge facing the implementation of such projects is the lack of scientific information available for Haitian systems. Therefore, this thesis aimed (i) **to improve scientific understanding of agrobiodiversity and associated ecosystem services in Haitian coffee-based agroforestry systems** and (ii) to **identify pathways for improving them through mobilization of these resources.**

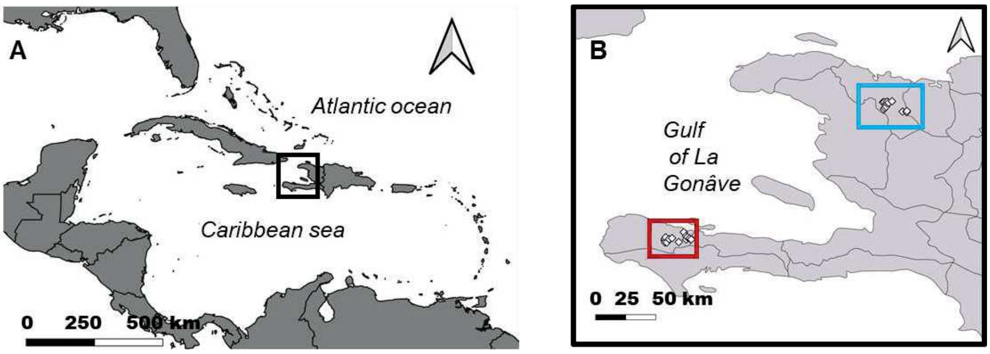


Figure 16. Study location in the Caribbean (A) **and Haiti** (B) with the departments of Nord (blue) and Grande-Anse (southern, in red) framed

Sidebar 3. PITAG at a glance

Name: Projet d'Innovation Technique en Agriculture et Agroforesterie (Agricultural and Agroforestry Technological Innovation Program)

Dates: started 2018, ends: September 2024

Funders: Interamerican Development Bank, Global Agriculture and Food Security Programme, and Haitian government

Coordination : Ministère de l'agriculture, des ressources naturelles, et du développement rural (Haitian Ministry of Agriculture, MARNDR)

Implementing consortium : Agriculteurs et Vétérinaires Sans Frontières (AVSF, France), Centre de coopération internationale en recherche agronomique pour le développement (CIRAD, France), Centro Agronómico Tropical de Investigación y Enseñanza (CATIE, Costa Rica), Ayitika (private sector company, Haiti), American University of the West Indies, American University of the Caribbean (Haiti), Université Chrétienne du Nord d'Haiti, with support from Institut de Recherche pour le Développement Durable (IRD, France)

Sub-projects: Coffee agroforestry, Cacao-based agroforestry, Market gardening, Legume-cereal intercropping, sweet potato-cassava-yam-taro, rice-cropping systems

To that end, we have conducted the following studies, organized in three chapters, each with their distinct research questions, but all geared towards the thesis' aforementioned aims. We have approached the three chapters with a theoretical framework focused on the interconnectedness of the various factors, biotic and abiotic, human and non-human, past and present, that have shaped, and continue to shape these systems (Fig. 17). As such, we also strove to mobilize a variety of data sets and sources to address this interconnectedness.

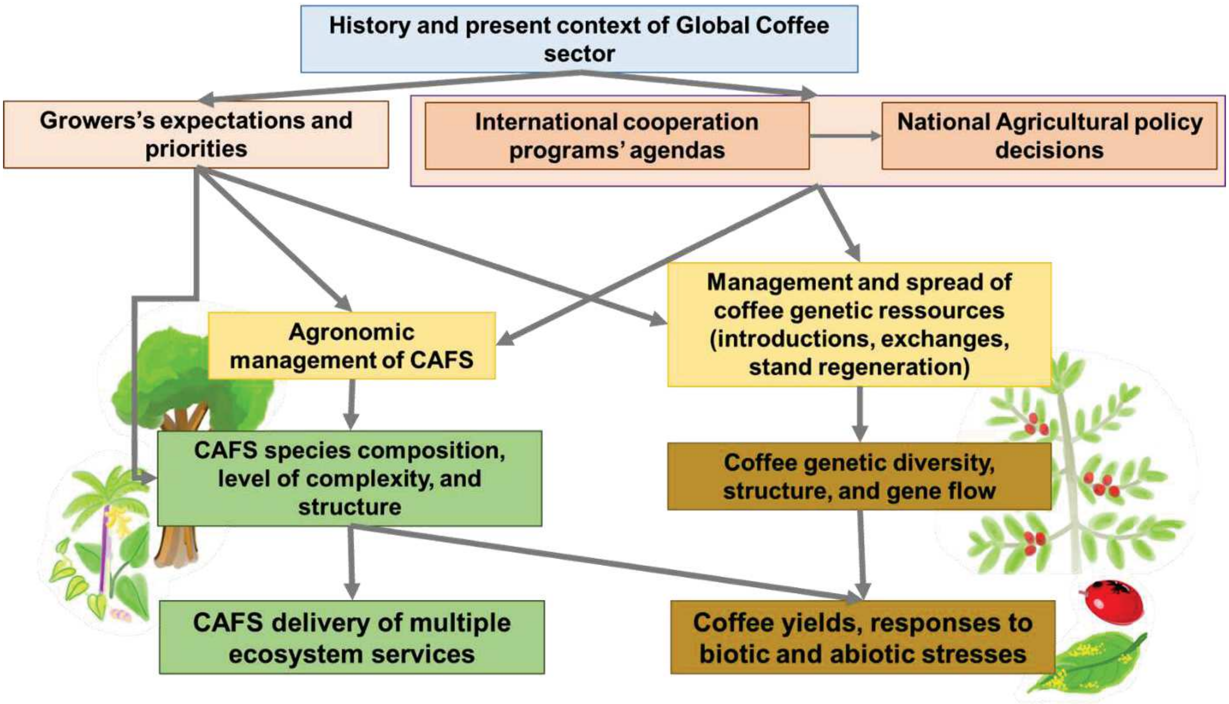


Figure 17. Representation of the theoretical framework describing interconnectedness of human and non-human factors affecting coffee-based agroforestry systems. This framework was developed at the beginning of this thesis and updated iteratively over its course.

The first chapter **(I)** consists in the characterization of genetic and varietal diversity within Haitian agroforestry systems using targeted genotyping methods, and was structured around the following research questions:

Q1.1 What is the genetic diversity of coffee trees in Haitian agroforestry systems, and how is it structured?

Q1.2 Is this diversity subject to evolutionary processes?

Q1.3 How does this genetic diversity fit within local knowledge and understanding of coffee resources?

The chapter addressing these questions was published in PlosOne under the title *Haitian coffee agroforestry systems harbor complex Arabica variety mixtures and under-recognized genetic diversity*.

***

***The second chapter* (II)** aimed to characterize the genetic and varietal diversity of coffee in Guadeloupean agroforestry systems, reconfirm that which was described for Haiti, and compare the two. These comparisons were interpreted through a historical lens, considering Haiti and Guadeloupe's initially similar, then greatly divergent histories, as well as that of coffee breeding and cultivation in general. It also sought to characterize and compare the bioclimatic environment in which these genetic resources exist. The research questions were as follows:

Q2.1 What is the genetic diversity of coffee trees in Guadeloupean agroforestry systems, and how is it structured?

Q2.2 How do they compare to that of Haiti, and what historical factors have shaped these differences and similarities?

Q2.3 What bioclimatic environment(s) do these resources (particularly the historical Typica variety) occur in? Is there variation in these environments, potentially being a source of differentiation for coffee produced on these islands?

The chapter addressing these questions was published in Plants People Planet under the title *Guadeloupe and Haiti's Coffee genetic resources reflect the crop's regional and global history.*

***

***The third chapter* (III)** aimed to take a broader view of the agroforestry systems in which Haiti's coffee genetic resources occur, to characterize their agrobiodiversity and consider the ways it contributes to delivery of ecosystem services. This was done using a database describing agroforestry systems' bioclimatic environment, coffee stands (and associated pests and diseases), shade trees and associated crops. We used multivariate analyses to classify farms into typologies based on several variable classes (including ecosystem service proxies), and investigated associations between them, in keeping with the following questions:

Q3.1 What is the diversity and structure of the various components (coffee, trees and associated crops) of Haitian coffee-based agroforestry systems?

Q3.2 What associations exist between this agrobiodiversity and the delivery of ecosystem services by agroforestry systems?

Taken together, these studies aim to elucidate the diversity dynamics at play in Haitian agroforestry systems, and provide a solid scientific basis for efforts to revitalize these cropping systems which are socially, ecologically, culturally and historically important to Haiti and its populations. In fine, we aim for our results to elucidate ways of mobilizing the agrobiodiversity of CAFS at all levels in order to optimize them. The main findings, limitations, and perspectives of this thesis will be discussed following these chapters.

Figure 18. Photograph of the Citadelle Laférrière, Haiti's most iconic monument, surrounded by woodland and agroforestry systems, taken on the way to field sampling. Agroforestry systems contribute several ecosystem services to Haiti, particularly through maintaining forest cover and strengthening food security. As historically-significant anthropic landscapes, they also provide aesthetic and cultural services. Photo credit: Claude Patrick Millet

Transition to Chapter I

(And methodological notes)

In order to successfully improve and better manage coffee-cropping systems, and to support the valorization of local genetic resources (particularly heritage varieties such as Typica), it is necessary to understand the genetic resources contained therein. The first step in this thesis was thus to characterize the genetic diversity and structure of coffee in Haitian agroforestry systems. To our knowledge, this endeavor had not yet been undertaken, or in any case published in the scientific literature. Several reports on the topic of coffee had been produced from public and multilateral institutions, generally agreeing that most trees were of the Typica variety, though others were also grown. While the somewhat idiosyncratic way in which coffee stands are allowed to regenerate from the seed bank had been noted, there was virtually no discussion of possible gene flow within them. There was thus a need to genotype Haitian coffee stands and describe their varietal composition, as well as investigate possible processes of genetic mixing.

The methodology used in this chapter is well-established. The development of robust, reliable and efficient markers for coffee genotyping has already been expounded in the general introduction. The field of **population genetics** offers tools and metrics to describe the diversity and structure of organism populations from genotyping data, provided adequate sampling. The basis of many such statistical tools is the Hardy-Weinberg Equilibrium (HWE) principle (Weinberg, 1908; Hardy, 1908), which predicts allelic frequencies for panmictic populations in which there is no sub-structure, total allogamy, truly random mating, and infinitely large population size). One retrospective states it as such: "*if the alleles are A and a with frequencies p and q (=1-p), then the equilibrium gene frequencies are simply p and q and the equilibrium genotypic frequencies for AA, Aa and aa are p2, 2pq and q2*" (quoted from Mayo, 2008). These frequencies can be compared to those observed in the sample genotype data to identify deviations from HWE, which point to structuring forces such as nonrandom mating, inbreeding, autogamy or even cloning. Statistics based on deviation from HWE are widely used in population genetics to compare genetic diversity (e.g. using expected heterozygosity or gene diversity, H_e), assess inbreeding within (F_{is}) or differentiation between sub-populations (F_{st}), and other uses (Kanaka *et al.*, 2023).

Several tools have also been proposed to determine **population structure** by reconstructing between 2 and *K* hypothetical ancestral populations from samples' genotype data, then assigning to each sample a probability of contribution from each population (e.g. François, 2016). These have been widely used in genetic studies of crops in order to identify distinct genetic groups, cultivars, or species, as well as admixture between groups. By incorporating reference specimens of relatively certain identity (see chapter for discussions on potential identification errors) in these analyses, varietal identification of field samples can be done by assigning field samples to the varietal group that shares high probabilities of contribution from the same population as them. Population structure analyses are often used in conjunction with dendrograms based on pairwise distance between individuals, such as neighbor-joining trees (Saitou & Nei, 1987), and principal component (or coordinate) analyses (PCA or PCoA), in order to visualize the positioning of individual samples within the broader diversity, as well as clustering of related individuals. For instance, combinations of two or more of these methods have been used in the study tree crops such as apples (*Malus domestica*, Cornille *et al.*, 2012), apricots (Herrera *et al.*, 2021), date palms (Gros-Balthazard *et al.*, 2020), and olives (Zunino *et al.*, 2024), cereals such as fonio *(Digitaria exilis*, Kaczmarek *et al.*, 2023) and durum wheat (*Triticum turgidum ssp. durum*, Baloch *et al.*, 2017; Negisho *et al.*, 2021), or the largely clonally-propagated cassava (Rabbi *et al.*, 2015). This methodology has also been used to characterize coffee genetic resources at various scales (Mérot-L'Anthoene *et al.*, 2019; Kiwuka *et al.*, 2021; Vi *et al.*, 2023). We used it successfully in the two following chapters for varietal characterization of field coffees, and identification of admixed individuals. As I had recorded the putative identification of sampled coffee trees based on local knowledge, we also had the opportunity to compare them to the genetic results. This is also an important step to understand how genetic resources are perceived by their stewards, and to identify discrepancies which must be considered in future planning.

How it happened:

Prior to my involvement, PITAG had conducted in-depth agronomic and socio-economic surveys of several coffee farms. On this basis, study sites were selected by Clémentine Allinne and Valérie Poncet, who also devised the sampling protocols along with Pierre Marraccinni. At the beginning of this thesis (November and December 2021), I obtained the necessary materials and conducted the field sampling, with the logistical support of Wesly Jeune and PITAG consortium team members (cf. acknowledgements). I then travelled with the samples to IRD (Montpellier, France) where I performed the DNA extractions for Hi-Plex sequencing with the support of Marie Couderc and others. KASP genotyping was done by LGC Biosearch and Hi-Plex sequencing by Kurt Lamour of Floodlight Genomics LLC (Knoxville, TN, USA). The Hi-Plex data were processed in parallel by Lauren Verleysen under the supervision of Tom Ruttink, and by myself using a different pipeline, modified from Tram Vi, with the support of Christine Tranchant-Dubreuil (in the end, the former was incorporated in the analyses for the paper). I then conducted the analysis of the genotype data (both KASP SNP and HiPlex haplotypes), under the supervision of Valérie Poncet and Clémentine Allinne. Following the varietal characterization I reported the results to PITAG (written reports and oral presentations), and produced individualized reports to be distributed to each farmer, explaining the varietal composition of their farm and a few agronomic characteristics of each varietal group.

Chapter

I

Chapter I

Haitian coffee agroforestry systems harbor complex Arabica variety mixtures and under-recognized genetic diversity

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Abstract

Though facing significant challenges, coffee (*Coffea arabica*) grown in Haitian agroforestry systems are important contributors to rural livelihoods and provide several ecosystem services. However, little is known about their genetic diversity and the variety mixtures used. In light of this, there is a need to characterize Haitian coffee diversity to help inform revitalization of this sector. We sampled 28 diverse farms in historically important coffee growing regions of northern and southern Haiti. We performed KASP-genotyping of SNP markers and HiPlex multiplex amplicon sequencing for haplotype calling on our samples, as well as several

Ethiopian and commercial accessions from international collections. This allowed us to assign Haitian samples to varietal groups. Our analyses revealed considerable genetic diversity in Haitian farms, higher in fact than many farmers realized. Notably, genetic structure analyses revealed the presence of clusters related to Typica, Bourbon, and Catimor groups, another group that was not represented in our reference accession panel, and several admixed individuals. Across the study areas, we found both mixed-variety farms and monovarietal farms with the historical and traditional Typica variety. This study is, to our knowledge, the first to genetically characterize Haitian *C. arabica* variety mixtures, and report the limited cultivation of *C. canephora* (Robusta coffee) in the study area. Our results show that some coffee farms are repositories of historical, widely-abandoned varieties while others are generators of new diversity through genetic mixing.

Keywords

Agrobiodiversity, Arabica coffee, Haiti, Agroforestry systems, Variety mixtures

1. Introduction

1.1. Diversity and resilience of agrosystems

Agricultural systems are faced with various stressors, both biotic (pests, diseases) and abiotic (droughts, nutrient deficiencies, temperature shocks, etc.). Modern agricultural practices for responding to these pressures are increasingly called into question for their unsustainable nature, especially as these issues are exacerbated by global climate change (Burgess et al., 2022). There is thus ever-growing urgency to improve the resilience and sustainability of crop systems and the various services they provide. Crop diversity in farming systems can help this endeavor by supporting the delivery of ecosystem services without compromising on productivity (Beillouin et al., 2021; Tamburini et al., 2020). Diversification of cropping systems can be achieved at the farm scale by combining multiple species (Li et al., 2021), but varietal diversity at the crop level can also contribute to crop productivity and resilience (Wuest et al., 2021). For instance, there is evidence that intraspecific diversity can suppress pests and pathogens by increasing spatial and genetic heterogeneity and decreasing the proportion of susceptible individuals (Gibson and Nguyen, 2021; Hajjar et al., 2008). It can also increase yield stability, particularly under stress (Reiss and Drinkwater, 2018). Consequently, there is increased scientific interest in the effect of varietal mixtures, particularly for annual crops such as cereals (e.g. Fletcher et al., 2019; Giunta et al., 2020).

1.2. Agroforestry systems

The benefits of agrobiodiversity are particularly well-mobilized in diversified agroforestry systems, especially smallholder farms and homegardens in tropical regions. These often-traditional systems feature considerable botanical richness, combining several cash and subsistence crops with fuelwood, timber, medicinal and culturally important species (Fernandes and Nair, 1986; Huai and Hamilton, 2009). As such, they are important providers of several ecosystem services such as food security, farmer economic resilience, pest and disease regulation, nutrient cycling, soil conservation, preservation of local knowledge and traditions, as well as conservation of natural biodiversity and crop genetic diversity (Rapidel et al., 2015; Sharma et al., 2022).

This role is of even greater importance in countries such as Haiti, which is faced with the heavy degradation of its natural ecosystems and their biodiversity, and therefore the risk of losing associated ecosystem services (Hedges et al., 2018; Roc, 2008). In fact, most of the country's remaining forested areas are primarily agroforestry systems (Feller et al., 2006). Furthermore, Haiti is a Least Developed Country whose population is primarily rural. The economic resilience provided by diversified agroforestry systems is therefore valued by farmers (Steckley and Weis, 2016; Tarter et al., 2016). These so-called "Creole Gardens" combine fruit, timber and charcoal trees with perennial crops such as coffee, cacao, banana and plantain, as well as annual crops such as yam and taro (Jean-Denis et al., 2014). Ensuring the continued social, economic and ecological viability of these systems is thus of prime importance. The present study focuses on Haitian Coffee Agroforestry Systems (hereafter "CAFS").

1.3. *Coffea arabica*: biology and domestication

***Coffea arabica* L. (Rubiaceae)** is an allotetraploid (2n = 4x = 44), amphidiploid, mainly autogamous, fairly recent (665,000 years ago) natural hybrid of diploid ancestors species *C. canephora* and *C. eugenioides* (Lashermes et al., 1999; Scalabrin et al., 2020). It is the most important species for the global coffee beverage market (Ferreira et al., 2019) representing about 60% of the global production (ICO, 2019).

Though originating from the mountains of Ethiopia, *C. arabica* was first cultivated in Yemen, and became widespread in tropical regions in the XVII-XVIIIth centuries as it was introduced to various European colonies. Two main lineages of *C. arabica* were cultivated outside of Yemen: the Typica and Bourbon lines, which both experienced strong successive genetic bottlenecks leading to a much narrower genetic diversity compared to natural populations (Anthony et al., 2002; Salojärvi et al., in press).

Despite this low diversity, several cultivated varieties were developed in the XXth century onwards, taking advantage of mutations in the two main lines. These "modern" varieties were later crossed with Ethiopian accessions or the Timor Hybrid (a spontaneous hybrid of *C. arabica* and *C. canephora* (Bettencourt, 1973; Cramer, 1957) to introduce traits of agronomic interest such as pest and disease resistance (Montagnon et al., 2012). Currently, *C. arabica* is grown in a variety of agricultural systems ranging from full-sun intensive monoculture to shaded, botanically and structurally complex agroforestry systems (Toledo and Moguel, 2012). As for many crops, global climate change is expected to severely and negatively affect Arabica coffee cultivation (Bunn et al., 2015; de Sousa et al., 2019) but increasing the proportion of shade-grown coffee (and therefore CAFS) can mitigate that impact (Gomes et al., 2020).

1.4. Opportunities provided by coffee genetic diversity

As adaptation to environmental changes and stresses can be achieved through mobilization of crop genetic diversity, germplasm collections are an important contributor to the continued vitality of the coffee sector. The CATIE international collection is one of the better-known Arabica collections (Dulloo et al., 2021; Engelmann et al., 2007), with a total of 1975 accessions, including Ethiopian wild materials, traditional and modern varieties, as well as more recent hybrid lines bred for quality, productivity, and disease resistance. However, *ex-situ* conservation of genetic resources can have certain drawbacks: it effectively freezes the process of natural and farmer selection, preventing adaptation to changing conditions in the field (Brush, 2000). At the same time, collected accessions are not truly static either, but may lose their genetic integrity over time through outcrossing or identification errors (Pruvot-Woehl et al., 2020; Verleysen et al., 2023). The more dynamic *in-situ* (farm-based) conservation of genetic diversity can therefore serve as a beneficial complementary approach. Leveraging diversity for adaptation and improvement of coffee yield, quality and resilience has been made easier through the increasing availability of marker-based methods of molecular characterization of coffee plant genotypes (Anthony et al., 2002; Lashermes et al., 1999; Mérot-L'Anthoene et al., 2019; Scalabrin et al., 2020). Due to *C. arabica* being a relatively recent species with low genetic diversity made even lower in cultivated accessions by successive bottlenecks, its genome displays a low level of polymorphism. Therefore, targeted genotyping of regions with known polymorphisms, and particularly Single Nucleotide Polymorphisms (SNPs) has shown promise as a cost-effective and efficient way to characterize and identify the genetic identity, diversity and population structure of Arabica coffee (Scalabrin et al., 2020; Sousa et al., 2017; Zewdie et al., 2022; Zhou et al., 2016)

1.5. Coffee in Haiti

Coffee cultivation on Haitian soil dates back to the French colonial era, when the Typica line was introduced and established on the mountainous island in 1735 (Trouillot, 1982). By the end of the XVIIIth century, the then-colony of St-Domingue had become the first coffee producer in the world, accounting for half of the global supply (De Bivar Marquese, 2022; Ferreira et al., 2019). When Haiti became independent in 1804, *C. arabica* 'Typica' remained an important agricultural resource, though multiple crises throughout the country's history reduced its productivity and contribution to the nation's economy (Dupuy, 1989; Lundahl, 1984). Examples include a lack of financial and technical support to farmers, world market volatility, coffee pest (e.g. the coffee berry borer, *Hypothenemus hampei*) and disease (e.g. Coffee Leaf Rust, *Hemileia vastatrix*) outbreaks, soil erosion and nutrient loss, and coffee stand aging (Vital, 2014).

In the present day, these issues are still ongoing, but Haitian coffee retains the potential to be attractive on smaller-batch, specialty markets. Indeed, Creole Gardens are the main type of coffee-cropping systems and receive virtually no agrochemical inputs (Amaya et al., 1999). They can produce ethical and environmentally-friendly shade coffee, which is of high quality (Koutouleas et al., 2022). Some growers' cooperatives are able to sell their harvest on North-American, European and Japanese gourmet markets at high prices (Amaya et al., 1999; Vital, 2014), and local workshops with growers suggest a renewed interest in reviving this once-important culture (Eitzinger et al., 2019). The Haitian context makes clear that any effort to revitalize local coffee production must do so in a way that safeguards the ecological value of diversified CAFS and their contribution to the socioeconomic resilience and food security of local communities.

1.6. Study aims

With few publications about Haitian coffee in the scientific literature, reports from multilateral development and NGO projects remain the main source of information. These suggest that Typica remains the main variety grown in Haitian fields, but that from the 1970s onwards new varieties were introduced by several agricultural development programs (Amaya et al., 1999; Ester, 1978; Queneherve et al., 2015). The distribution and dissemination of coffee varieties in Haitian CAFS is poorly documented. The revitalization of diverse agroforestry systems is of economic, social, cultural and ecological importance. Therefore, there is a need to better understand the genetic diversity contained therein, as well as its structure, in order to assist in the decision-making of farmers and policy actors and to help conserve coffee genetic resources.

This study therefore aimed to characterize the genetic diversity and genetic structure of Arabica coffee cultivated in Haitian CAFS. We focused on collecting data from two administrative departments of development priority: Nord and Grande-Anse, in northern and southern Haiti, respectively. In each department, 14 farms were selected to collect leaf samples for genetic analysis and information on the coffee tree was recorded through farmer surveys. The objectives were: (i) to determine varietal diversity and its distribution over the territory using SNP target markers and a set of Arabica diversity reference accessions, (ii) to compare local knowledge of this diversity based on farmer survey to genetic variety classification; (iii) to draw up guidelines for the dynamic conservation and development of this varietal diversity.

2. Materials and Methods

2.1. Selection of study sites

The present study took place in two administrative departments, Nord and Grande-Anse, in northern and southern Haiti, respectively. These regions were historically important coffee producers since the colonial era (De Bivar Marquese, 2022), but now struggle to sustain production. Sampling sites were selected on the basis of a preliminary survey of 122 Non-intensive, diversified CAFS, of which 43 were subsequently surveyed in-depth. These surveys were conducted in 2021 by the multilaterally-funded Agricultural and Agroforestry Technological Innovation Program (*PITAG*) implemented by *Agronomess et Vétérinaires Sans Frontières* and the Haitian Ministry of Agriculture. Twenty-eight of the surveyed CAFS (14 per department) were selected on the basis of farmer-reported varietal diversity for inclusion in the present study. Selection of study sites took into account geographical spread, range of farmer-reported (expected) varietal composition, and inclusion of several municipalities in order to attain good representation of diversified Haitian CAFS in the two administrative departments. Selected gardens were thus spread across five municipalities (*communes*): Bahon, Dondon and Grande Rivière du Nord (Nord); Beaumont and Pestel (Grande-Anse) (Table S1). After in-person explanation of the study aims, signatures on Prior Informed Consent (PIC) forms were gathered from all farmers. Material transfer agreements (MTAs) and export permits for the collected samples were obtained from the Haitian Ministry of Agriculture, Natural Resources and Rural Development (MARNDR).

2.2. Sampling strategy and local knowledge collection

Coffee leaf samples were collected in November-December 2021. In order to capture the diversity present in the surveyed gardens, farmers were asked to identify the various (putative) coffee varieties growing in their field. At each site but one, a minimum of 20 plants were sampled, taking care to include all putative varieties in similar quantities. In addition, farmers were asked to point out any and all coffee plants that seemed atypical to them, for example in their health, vigor, productivity, or lack thereof. When such coffee trees were identified, they were sampled as well. Therefore, our sampling covered a wide range of coffee tree ages, phenotypes and putative varieties. Four healthy, mature leaves from plagiotropic axes of the coffee trees were collected, when possible from the third fully-grown pairs from the apex, and preserved in silica gel.

In addition to the Haitian field samples, a panel of varieties and wild accessions (n=96) was obtained from the CATIE international coffee germplasm collection (Turrialba, Costa-Rica) with additional samples (n=15) from the HARC collection (Hawaii, USA) which were provided by USDA-ARS, SPCL (Beltsville, MD, USA) to serve as references for varietal assignment. Finally, wild *C. arabica* (n=6), as well as *C. canephora* (n=5), *C. liberica* (n=3) and *C. congensis* (n=2) were sampled from the IRD collection (Montpellier, France) as outgroups (Table S2).

2.3. Vernacular names

Any work taking advantage of Haitian coffee diversity will need to understand how its stewards perceive and categorize it in order to maximize the effectiveness of farmers' participation. Putative varietal identification of collected field samples were recovered from surveys. These came primarily from farmers, although in some cases this was impossible and the identification came from local agronomists instead. Taken together, these identifications (hereafter "vernacular categories") were considered to provide an indication of local knowledge. To avoid confusion, vernacular category names were written with the Haitian creole spelling. When no clear identification could be provided, a "No ID" record was made for that sample.

2.4. Molecular methods

2.4.1. KASP SNP genotyping

A set of 96 SNPs were first genotyped by KASP assay. Mérot-L'Anthoëne et al. (2019) developed a DNA array of 8580 biallelic SNP from *C. canepho*ra and *C. arabica* sequencing, 945 of which were designed specifically to be informative for *arabica* diversity assessment. From the latter, Zhang et al. (2021) selected a set of 96 core SNPs found to be polymorphic and discriminant across a panel of commercial and wild accessions of *C. arabica*, including many of our reference samples from the CATIE international collection. Selective genotyping by KASP assay targeting these core markers was conducted by LGC Biosearch Technologies (Middlesex, UK). Raw genotyping data (coded as A/B, biallelic markers) was filtered to exclude loci with missing data in <30% of samples, and individuals with <30% missing genotype data. Genotyping error rates were calculated using three duplicate samples included for genotyping, as percent difference in genotype calls between duplicates across all called SNP sites.

2.4.2. HiPlex amplicon sequencing

In parallel, genotyping data was obtained on the same sample set using highly multiplex amplicon sequencing (HiPlex) of 400 regions (110-120 bp each) selected to be variable between the Typica and Bourbon varieties (Bawin, 2022). DNA was extracted from Haitian and reference samples using a protocol with MATAB+DTT lysis buffer following a sorbitol wash of the material (adapted from Bawin, 2022). Amplicon libraries were prepared by Floodlight Genomics LLC (Knoxville, TN, USA), and were sequenced by Admera Health (South Plainfield, NJ, USA). Obtained reads were mapped onto each of the two subgenomes of the *C. arabica* reference genome sequence v0.6 of the accession ET-39 (Salojärvi et al., in press) using a customized script by Bawin (2020), available on GitLab (https://gitlab.com/ybawin/sequence-data-processing-tetraploids). After filtering, read-backed haplotyping was conducted based on SNPs in the HiPlex read data using the SMAP software package v4.2.0 (Schaumont et al., 2022). The full pipeline description can be found in supplementary notes. Genotype tables were then filtered to exclude loci with missing data in >30% of Arabica samples specifically, then individuals of all *Coffea* species with >30% missing data. Variant calling error rates were calculated using 12 duplicate samples included for sequencing.

2.5. Genetic analyses and varietal characterization

Full genetic analyses were carried out on the targeted SNPs genotyped with the KASP assay, since they were optimized to reveal intra-Arabica (both between cultivated and wild accessions) diversity. Then, the results were compared with HiPlex haplotype data designed to distinguish Typica and Bourbon varieties and their potential hybrids.

Global genetic diversity and its geographical distribution were estimated by using descriptive statistics and genetic differentiation pairwise F_{ST} values (with corresponding p-values at 999 bootstraps) calculated at the farm, municipality and department levels using GenAlEx software package v. 6.51b2 (Peakall and Smouse, 2012). For the latter, values were calculated both per locus within groups and per group across all loci. The significance of each hierarchical level was tested using the varcomp.glob, as well as test.between, test.within and test.between.within (1000 permutations each) function in the R package Hierfstat v. 0.5-11 (Goudet, 2005)

Varietal and farm composition characterization were carried out in several steps. Principal component analyses (PCA) was performed on Haitian and reference samples (both including and excluding reference samples) using the R packages LEA v. 3.10.2 (Frichot and François,

2015) and Tidyverse v. 2.0.0 (Wickham et al., 2019) ggplot function. Unweighted neighbor-joining dendrograms were made from a simple-matching distance matrix with 1000 bootstrap replicates using the software DARwin v. 6.0.21 (Perrier and Jacquemoud-Collet, 2006) in order to visualize the diversity of Haitian coffee plants in relation to that of reference samples. In addition, an analysis of population structure using the sNMF function (K=1-10, 100 repetitions) of the R package LEA v. 3.10.2 was conducted. A threshold of 80% membership to a sNMF population was used to assign samples to a varietal group (hereafter "genetic group"), which was labeled according to the reference samples in that group. Samples with <80% membership in any group were considered to be admixed. In order to infer putative intervarietal crosses and more fully describe the sampled coffee diversity, we used a threshold of 40% membership from one or more genetic groups to sub-categorize admixed individuals. Pairwise F_{ST} (and p-values at 999 bootstraps) were calculated between genetic groups (including and excluding reference samples) with GenAlEx v. 6.51b2.

The results obtained with the targeted KASP SNP genotyping data were then compared with those obtained with HiPlex amplicon sequencing haplotype data designed to distinguish Typica and Bourbon varieties and their potential hybrids. In addition to the above analyses, a Mantel test of correlation was performed on the HiPlex haplotype and KASP SNP genotyping data distance matrices using GenAlEx v. 6.51b2. Allele counts for *C. arabica*-only (field and reference) HiPlex haplotype data were extracted using the adegenet R package v. 2.1.10 (Jombart, 2008) and a sNMF analysis of population structure was conducted with the same parameters as for the KASP SNP genotyping data. Genetic groups were again defined using an 80% membership threshold.

For subsequent analyses and discussion of the results, the KASP-based genetic groups were retained as they were determined on the basis of markers selected using a broader panel of Arabica accessions (Zhang et al., 2021), and more accessions were represented in the reference samples for the present study.

2.6. Vernacular and genetic identification comparison

We investigated the degree of correspondence between local *C. arabica* vernacular category names and their genotypic makeup from the KASP SNP genotyping data by testing for correlation between the sizes of the sNMF-determined genetic groups (with admixed individuals lumped together as one group, as well as sub-categorized according to the 40% membership threshold) and those of the vernacular categories (including the "No ID" group). We also tested for correlation between the number of varieties grown on farms (as reported by farmers) and the number of varietal clusters identified for that field, excluding admixed individuals. For all these analyses, we used a series of Pearson's χ^2 tests of independence in R.

Farms were categorized based on the local perception of their diversity (with "diverse" farms having more than two reported vernacular categories and "less diverse" farms having one or two) and their genetic group diversity (again, with "diverse farms" having more than two genetic groups and "less diverse" farms having one or two). We tested the correlation between locally-perceived and genetic group diversity. The genetic diversity categories were the same regardless of whether the admixed individuals were sub-categorized. Another test was performed, this time categorizing farms as either “monovarietal“ (only one group) or “multi-varietal” (two or more groups), again according to vernacular category and genetic group diversity. Pearson’s χ^2 tests of independence were again used for all these analyses.

3. Results

3.1. Genetic diversity analyses

After filtering, KASP SNP genotyping data were obtained for 724 individuals (including 117 *C. arabica*, five *C. canephora* and one *C. congensis* reference sample) at 87 loci. There were no differences over all loci for the three duplicated samples.

Over all Haitian samples, expected heterozygosity (or gene diversity, H_e) was 0.33, only slightly lower than among all Arabica references in the *ex-situ* collections (H_e=0.37). Across farms, H_e ranged from 0.02 (*Ka Gous,* farm code G13) to 0.34 (*Bertin,* farm code N07). Mean H_e and marker polymorphism were lower across farms (0.23 and 66.7% respectively) than across municipalities (0.28 and 83.9%) and departments (0.32 and 89.7%). In all but the lowest diversity farms, observed heterozygosity (H_o) was consistently lower than H_e, as expected for autogamous species. The inbreeding coefficient (F_{IS}) of farms ranged from 0.38 to 0.85, with an intermediate value across Arabica reference accessions (F_{IS}=0.62). These statistics, which are detailed in supplementary materials (Table S3, S4 and S5), indicate that there is considerable diversity across Haitian samples, but that farms exhibit great variability in the genetic makeup of their germplasm.

Statistical tests of the effect of different geographic levels on coffee genetic structure in Hierfstat revealed a non-significant impact of the department (p=0.431) and municipality (p=0.141) levels, which is also apparent in pairwise F_{ST} comparisons (Table S6). However, the municipality of Bahon (containing four farms) was notable in that it harbored less diversity (H_o= 0.043) than the single farm in the adjacent municipality of Grande Rivière du Nord (H_o= 0.067). The farm level was found to have a significant impact (p=0.001) on genetic structure of sampled Haitian Arabica. Therefore, within- and between farm heterogeneity was the main source of variation in the genetic structure of coffee tree stands (Table S7).

The lack of genetic structure at department and municipality levels was also seen in the scattered distribution of Haitian samples along the main axes of the PCA (Fig. 1.A). Reference samples of *ex-situ* collections were also quite scattered, suggesting that a good proportion of global *C. arabica* diversity was represented in our reference panel. Despite this, some Haitian samples did not cluster with any reference individuals.

3.2. Varietal assignment

Varietal assignment and characterization were carried out using a genetic structure analysis performed on both Haitian and reference samples with KASP SNP genotyping data. Cross-entropy for the sNMF structure analysis was lowest between K=5-8. Increasing the number of clusters starting from K=2 and up to K=6 (Fig. 1.B) allowed for the identification of distinct varietal clusters labeled according to reference samples included therein. These were: a Typica-like (n=263, including n_H=248 Haitian samples), Bourbon-like (n=35, n_H=27), CR95/Catimor-like (n=77, n_H=73), Kent/I-60-like (n=9, n_H=7), and Ethiopian-like (n=23, n_H=1) group, as well as a sixth group exclusively composed of Haitian samples (n=52). The Ethiopian-like group was made up of collection accessions from *C. arabica*'s natural distribution range, with only one Haitian sample assigned to it.

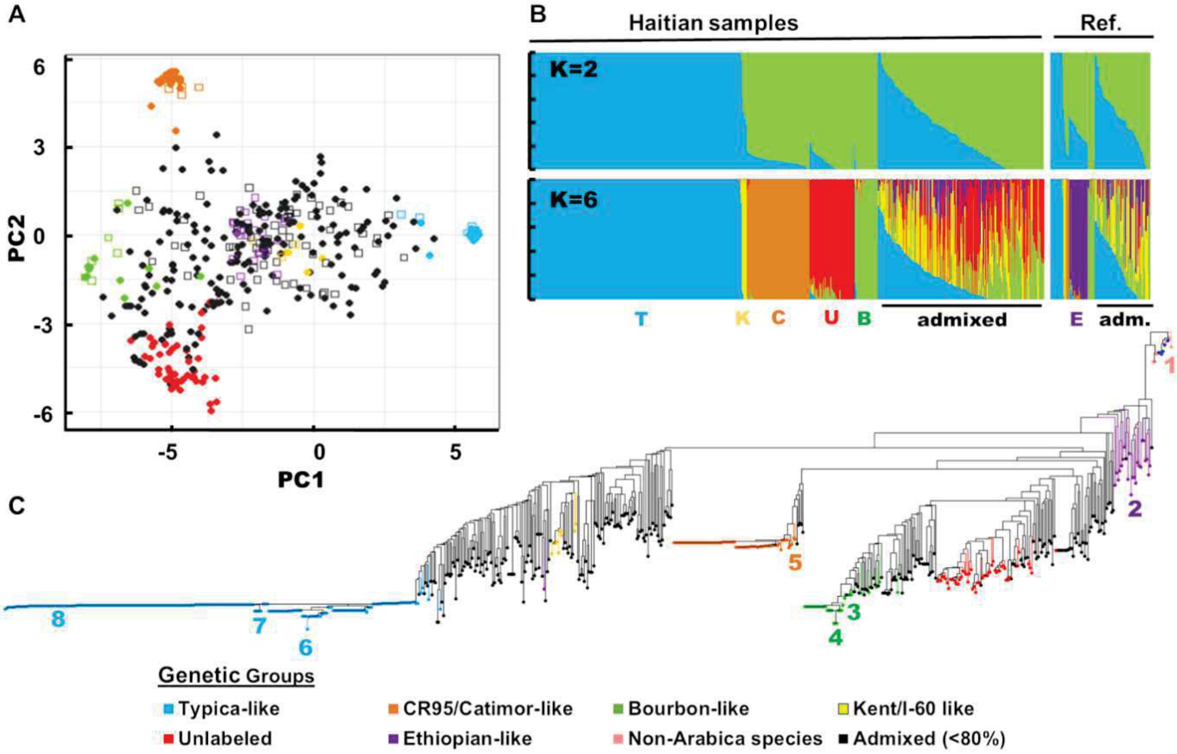

Figure 1. Genetic structure and diversity of Haitian Coffee in relation to reference samples from international collections, based on SNP genotyping data. A. Principal Component Analysis performed on Haitian (filled circles) and reference (open squares) *C. arabica* samples showing the first two axes (46,89% and 11,26% of variance explained, respectively). **B.** *C. arabica* population structure analysis at K=2 (top) and K=6 (bottom) for Haitian and reference (Ref.) samples. Initials at bottom correspond to genetic groups defined in the legend, with only the Ethiopian-like and admixed (adm.) reference individuals labeled. **C.** Unweighted neighbor-joining dendrogram of reference and Haitian coffee samples (with non-*C. arabica* species in pink at the root) based on simple matching distance matrix. Numbers represent select reference individuals for illustrative purposes: 1) GUI2 *C. canephora*; 2) T.02731 Jimma Galla Sidamo; 3) T.02542 Caturra; 4) Ku042 Red Bourbon; 5) T.08867 CR-95; 6) T.03427 Cera; 7) Ku214 Jamaica Blue Mountain; 8) T.00989 Guadeloupe. Sample color code was based on 80% membership threshold in one ancestral population at K=6 from population structure analysis.

Pairwise F_{ST} values between the six genetic groups, considered as distinct varietal groups, showed them to be well-differentiated, whether calculated using only Haitian samples (Fig. 2.A) or including reference accessions. Overall, mean genetic distance between individuals in the same group was 0.016 ± 0.037 SD. The genetic group with the highest similarity between individuals was Typica (0.010 ± 0.022, mean ± SD) and the genetic group with the highest mean genetic distance between individuals was the Ethiopian-like group (0.196 ± 0.057 SD) (Fig. 2.B).

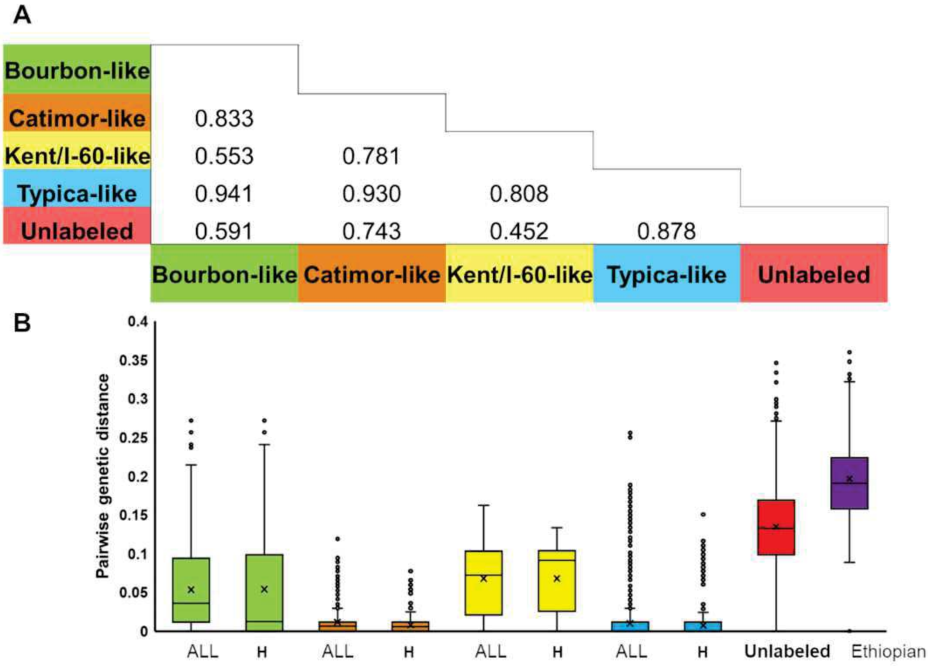

Figure 2. Genetic differentiation between and within genetic groups. A. Pairwise F_{ST} between identified *C. arabica* genetic groups calculated on Haitian samples (N=406) from data based on SNP genotyping data. All p-values <0.001 at 999 repetitions. **B.** Boxplot of pairwise simple matching genetic distances within genetic group for reference + Haitian (« All ») and Haitian-only (« H ») individuals. Colors correspond to those used for group labels in panel A. Only one Haitian sample was assigned to the Ethiopian-like group. The « Kent/I-60-like », « CR95/Catimor-like » and « Ethiopian-like » group names have been shortened for legibility.

Using the 80% membership threshold, 407 Haitian and 52 reference samples were assigned to a variety. 194 Haitian samples were considered to be admixed, with 128 of them having >40% membership from one genetic group, 20 samples from two groups (and always at least one of the two traditional lineages, Typica or Bourbon), and 46 samples never reaching 40% membership from any genetic group. 65 reference accessions were considered to be admixed.

The distribution on the PCA axes, and the clustering of individuals on the neighbor-joining dendrogram (Fig. 1.C) were consistent with results of the structure analysis. The first axis of the PCA primarily separated the Typica from the Bourbon groups, while the second axis primarily differentiated the CR-95 like and the "Unlabeled" groups (Fig. 1.A). The group of "Unlabeled" coffee trees were those which did not cluster with any reference sample in the PCA, confirming the absence of their representation in the CATIE international collection. The clustering of individuals on the neighbor-joining dendrogram was consistent with that of the structure analysis (Fig. 1). The dendrogram showed Ethiopian accessions to be the most basal among *C. arabica* samples, and separated the other cultivated varieties in two main groups consistent with the historical Typica and Bourbon lineages and their derived varieties.

3.3. Comparison with HiPlex haplotype data

After filtering, 691 samples (including 94 *C. arabica*, three *C. canephora*, one *C. congensis*, and two *C. liberica* reference samples) and 225 multi-allelic haplotype markers were obtained from the HiPlex amplicon sequencing data. Mean variant call error rate was 1.4% (min = 0.2%, max = 3.6%). Among *C. arabica* samples, we obtained SNP calls from KASP SNP genotyping data and HiPlex haplotype calls for 684 individuals (590 field and 94 reference samples). Genetic distance matrices per marker set were significantly correlated (p=0.001, R^2=0.19). Likewise, there was a fairly linear relationship between the expected heterozygosity (gene diversity) calculated from both sets of markers at the farm (y=1.01x+0.03, R^2=0.71) and municipality (y=1.13x+0.01, R^2=0.99) levels (Fig. S1).

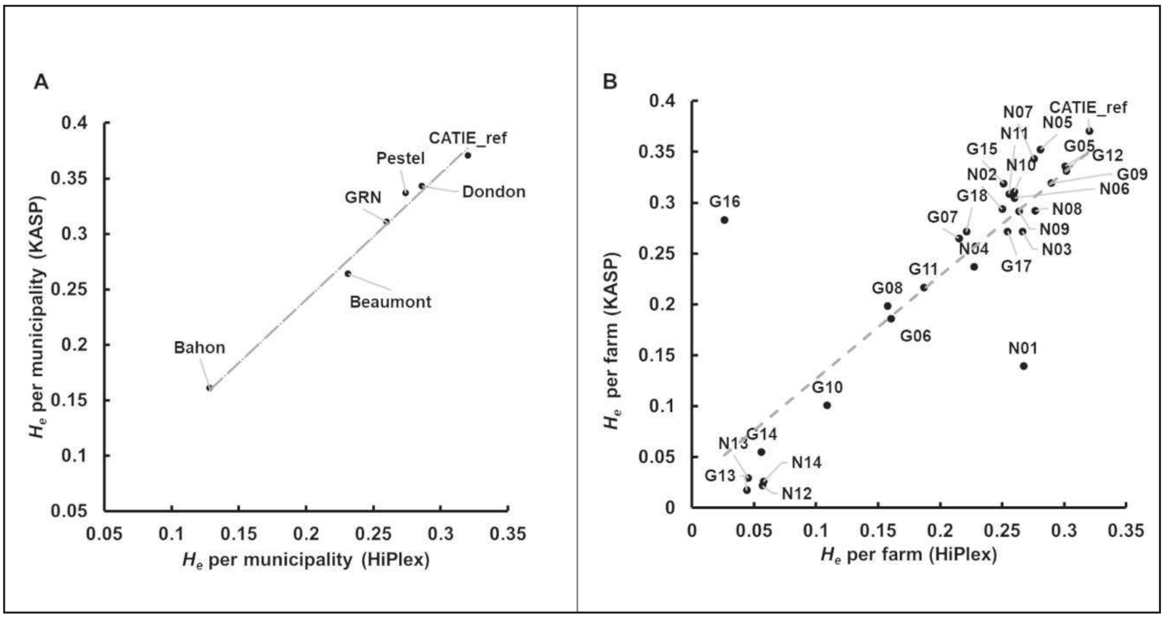

Figure S1. Expected heterozygosity (H_e) calculated on HiPlex haplotype genotyping *versus* KASP SNP genotyping. A. Plot of HiPlex- *vs.* KASP-based H_e values for sampled municipalities (*communes*) in Haiti (« GRN » refers to Grande Rivière du Nord, trend line in grey: y=1.13x+0.01, R^2=0.99). **B.** Plot of HiPlex- *vs.* KASP-based H_e values for sampled farms in the Nord (N) and Grande-Anse (G) departments (trend line in grey: y=1.01x+0.03, R^2=0.71). In both plots, H_e value calculated on reference samples from the CATIE international collection (N=96) are included for comparison.

Population structure analysis for HiPlex haplotype data displayed low cross-entropy starting at K=6, with a cluster of Ethiopian samples appearing at K=7 (vs. K=6 for the KASP SNP data). The accessions assigned to a genetic group with the KASP SNP data set were assigned to a corresponding HiPlex-based genetic group with a high frequency, although with a higher proportion for the large Typica groups (78.57%) than for the smaller Bourbon groups (46.88%), and the Kent/I-60-like group with only eight accessions could not be assigned with certainty with HiPlex haplotype data (Table S8). The additional cluster detected from HiPlex haplotype data appears to be mostly made up of admixed individuals. The corresponding neighbor-joining dendrogram shows that relationships between the samples were generally conserved, although it split the Typica and Bourbon lines at a more basal position, before the Ethiopian-like group differentiation (Fig. S2).

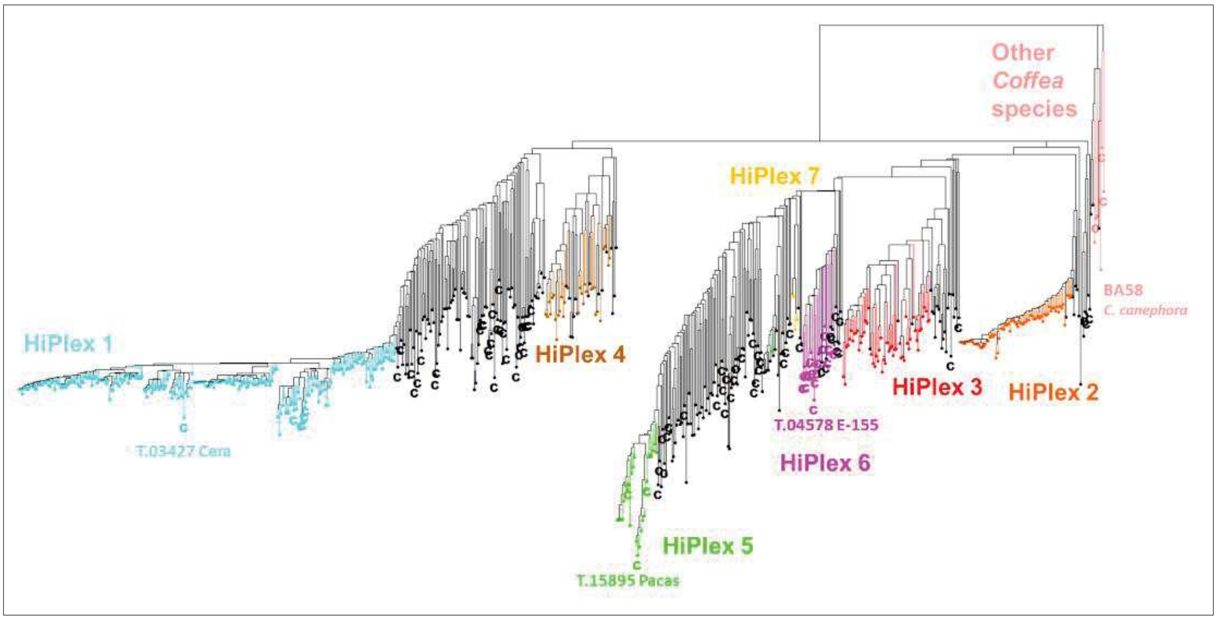

Figure S2. Unweighted neighbor-joining dendrogram of Haitian coffee samples and reference samples from collections ("C") based on SNP data from HiPlex haplotype data. Individuals were colored according to a 80% threshold of membership in ancestral populations identified by population structure analysis (K=7). All samples are *Coffea arabica* except where indicated at the root of the dendrogram. Select reference individuals are labeled for illustrative purposes.

3.4. Identification of Robusta coffee trees among Haitian samples

Several sampled individuals from one farm (N05) in northern Haiti, locally identified as a distinct variety, were suspected to belong to a different *Coffea* species based on visual aspect of the leaves and fruits and the lower genotyping success using Arabica-targeting markers. Using a subset of the 57 most complete markers across *Coffea* species, and thus recovering *C. congensis* and *C. liberica* samples which had been excluded from prior analyses, we calculated distance matrices and generated neighbor-joining dendrogram that suggested these individuals belonged to *C. canephora* (Fig. S3).

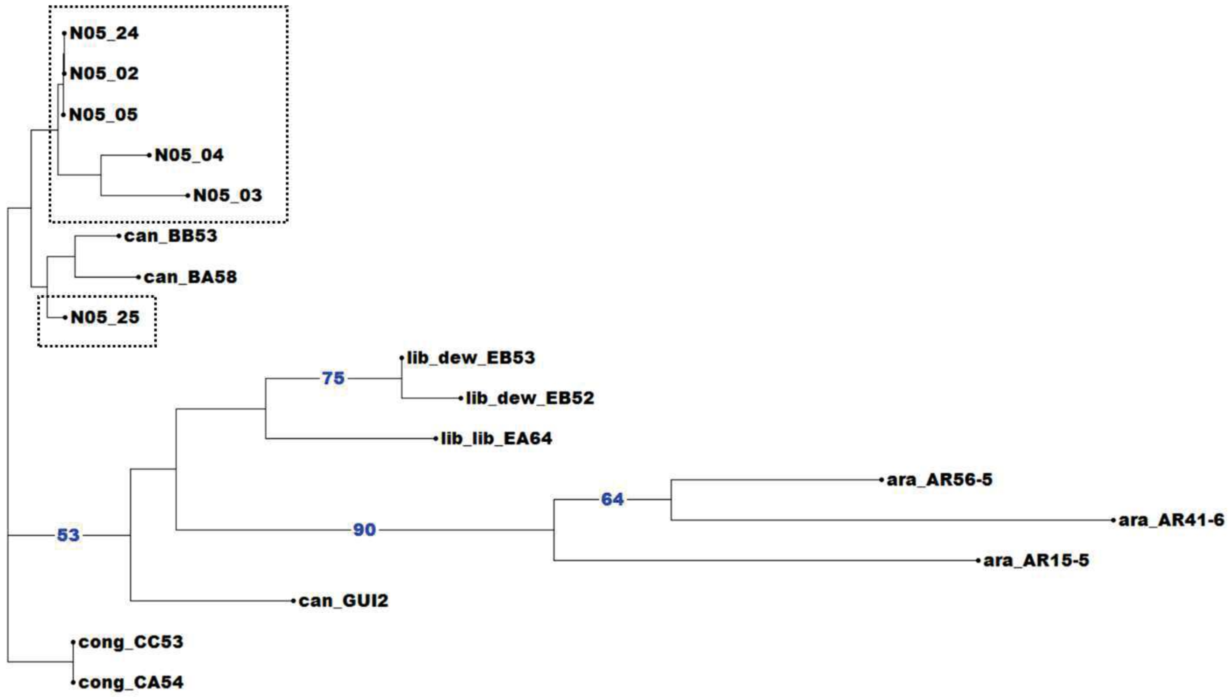

Figure S3. Unweighted neighbor-joining dendrogram of Haitian Robusta coffee trees and reference samples. Haitian samples are in dotted frames**.** The tree was built from a simple-matching distance matrix calculated from KASP SNP genotyping data. Prefixes in reference sample names refer to their species: can = *Coffea canephora*, lib_lib = *C. liberica liberica*, lib_dew = *C. liberica dewevrei*, ara = *C. arabica* and cong = *C. congensis*. Bootstrap values (1000 repetitions) are shown when >50.

3.5. Farm composition

All genetic groups but the Ethiopian were identified in both departments (Fig. 3). The Kent/I-60-like group was absent from two municipalities, Bahon and Grande Rivière du Nord, although Bahon only had one muti-varietal farm and Grande Rivière du Nord was only represented by a single (albeit multi-varietal) farm. The Bourbon-like group was also absent from the Grande Rivière du Nord farm. The composition of farms varied considerably. There were four monovarietal farms, which invariably consisted of the Typica genetic group, and had no admixed individuals. Two farms had individuals from the Typica and "Unlabeled" groups, and no admixed individuals. The 22 remaining farms had between two and five genetic groups, as well as admixed individuals of varying genetic backgrounds. Of the 148 admixed individuals with contribution from at least one genetic group at the >40% membership threshold, 68.2% co-occurred with plants from all contributing genetic groups. A further 4.7% had contribution from two genetic groups but co-occurred with plants from only one of those contributing groups. Finally, 40 out of the 148 admixed individuals (27.0%) were not cultivated on the same farms as any plant from the contributing genetic groups (Fig. 4).

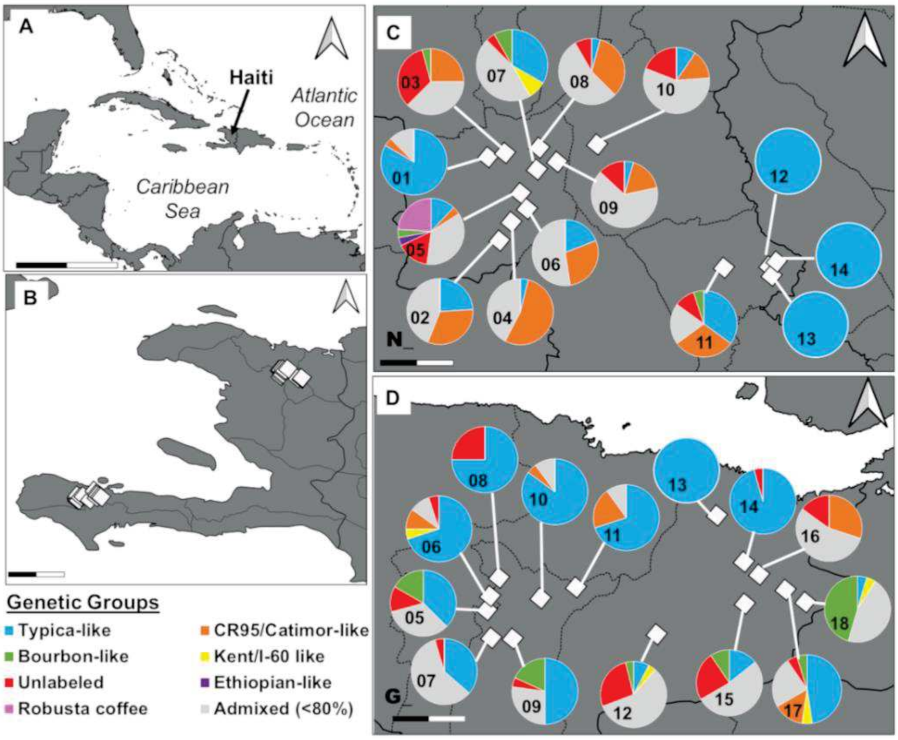

Figure 3. Location and coffee genetic group composition of sampled farms in Haiti, based on SNP genotyping data. **A.** Geographic location of the Republic of Haiti in the Caribbean region. Scale bar ticks represent a distance of 250 km. **B.** Study area in the Nord (N, northern) and Grande-Anse (G, southern) departments. Scale bar ticks represent 25 km. **C.** Farm location and genetic group composition in the Nord department and **D.** in the Grande-Anse department. Scale bar ticks in 3.C and 3.D. represent 2.5 km.

Note: one farm (N05- *Bernice*) contained « Robusta coffee » (*C. canephora*) in addition to *C. arabica.* All other Haitian samples are *C. arabica*.

Maps created in QGIS v. 3.30.1 using Natural Earth (Free vector and raster map data @ naturalearthdata.com) and shapefiles from Hijmans and UC Berkeley (2015 a,b) and Patterson and Kelso (2012).

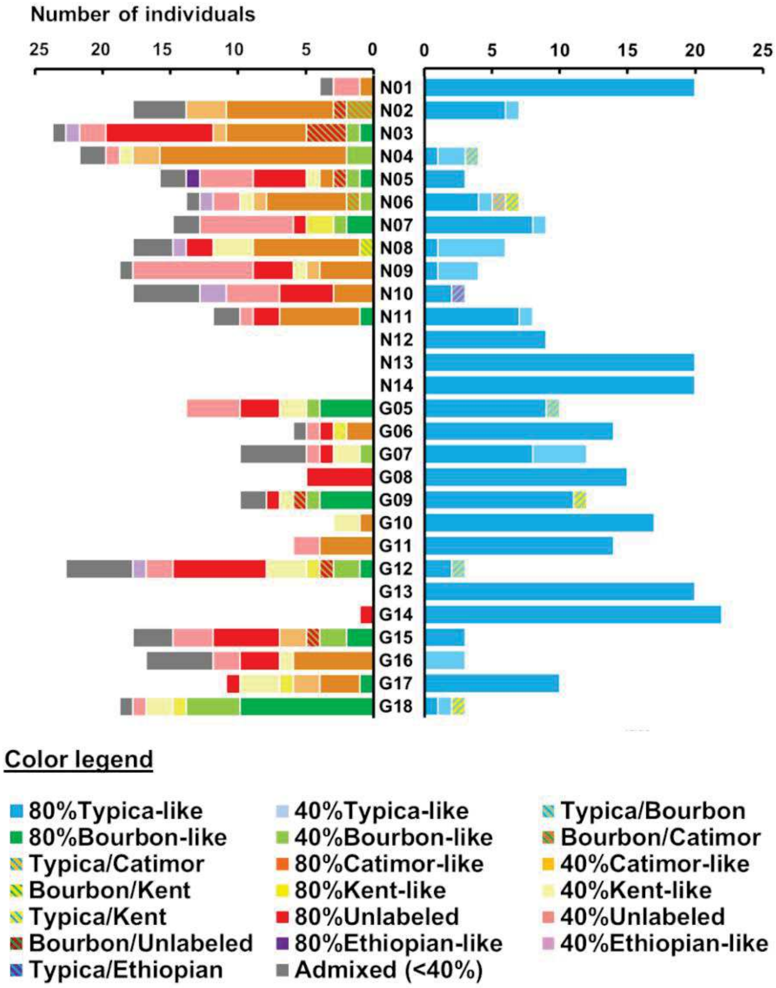

Figure 4. Contribution of genetic groups and admixed individual to farm composition. Number of *C. arabica* samples per farm with contribution from the historical Typica variety (right) and other genetic groups based on SNP genotyping data (left). Percentages in the legend refer to contribution thresholds. Hatched colors correspond to samples with >40% membership from two genetic groups. Admixed samples in grey never reached 40% membership from any genetic group. The « Kent/I-60-like» and « CR95/Catimor-like » group names have been shortened for legibility. Farms are noted Nx for the Nord (northern) and Gx for Grande-Anse (southern) departments, respectively.

3.5. Local knowledge of variety mixtures

Five main vernacular category names were recorded during sampling, and all correspond to conventionally-used coffee varieties. The vernacular categories in Haitian creole were: *Tipika* (for "Typica", also called "Vieux café"), *Katoura* ("Caturra"), *Katimò* ("Catimor"), *Bougon* (for "Bourbon") and *Blou Monntenn* ("Blue Mountain"). A sixth name, *Kafe Brezil* ("Brazil Coffee"), was used to refer to the phenotypically distinct *C. canephora* individuals. 48 individuals could not be identified, and therefore were not assigned to a vernacular category.

Pearson's χ^2 test revealed significant correlation between vernacular category and genetic group membership, whether considering hybrids as one category or sub-categorizing them ($p=2.2e^{-16}$ in both cases). To illustrate the overlap between local knowledge and genetic identification, the percent representation of genetic groups in each vernacular category was plotted (Fig. 5.A). Despite the correlation found, vernacular categories were shared among samples belonging to various genetic groups, with some counterintuitive associations. For instance, "Blue Mountain" coffee generally refers to Jamaican Typica trees, which is consistent with the clustering of most reference Blue Mountain samples in the Typica genetic group. However, 31% of plants identified as *Blou Monntenn* were found to belong to the CR95/Catimor-like group. In fact, CR95/Catimor-like plants were more likely to be identified as *Blou Monntenn* (31.5%) than as *Katimò* (19.2%). Likewise, no plant assigned to the Bourbon-like genetic group was identified as *Bougon*, though 51.9% of them were identified as *Katoura*. The Caturra variety is a dwarf mutant of Bourbon coffee, and the structure analysis assigned Caturra reference samples to the Bourbon-like genetic group. 83.0% of samples from the Typica genetic group were identified as *Tipika*, and made up 64.1% of the latter. Of the 48 samples which had no clear vernacular category, 47.9% were admixed individuals and 27% were assigned to the Typica genetic group.

The number of varieties reported by farmers was not significantly correlated with the number of genetic groups (p=0.314), nor was there a significant correlation between local perception of diversity and genetic group diversity (p=0.1199) (Fig. 5.B). However, there was a significant association between farms' monovarietal or multi-varietal status as perceived locally and as determined by genetic group composition ($p=1.995e^{-7}$).

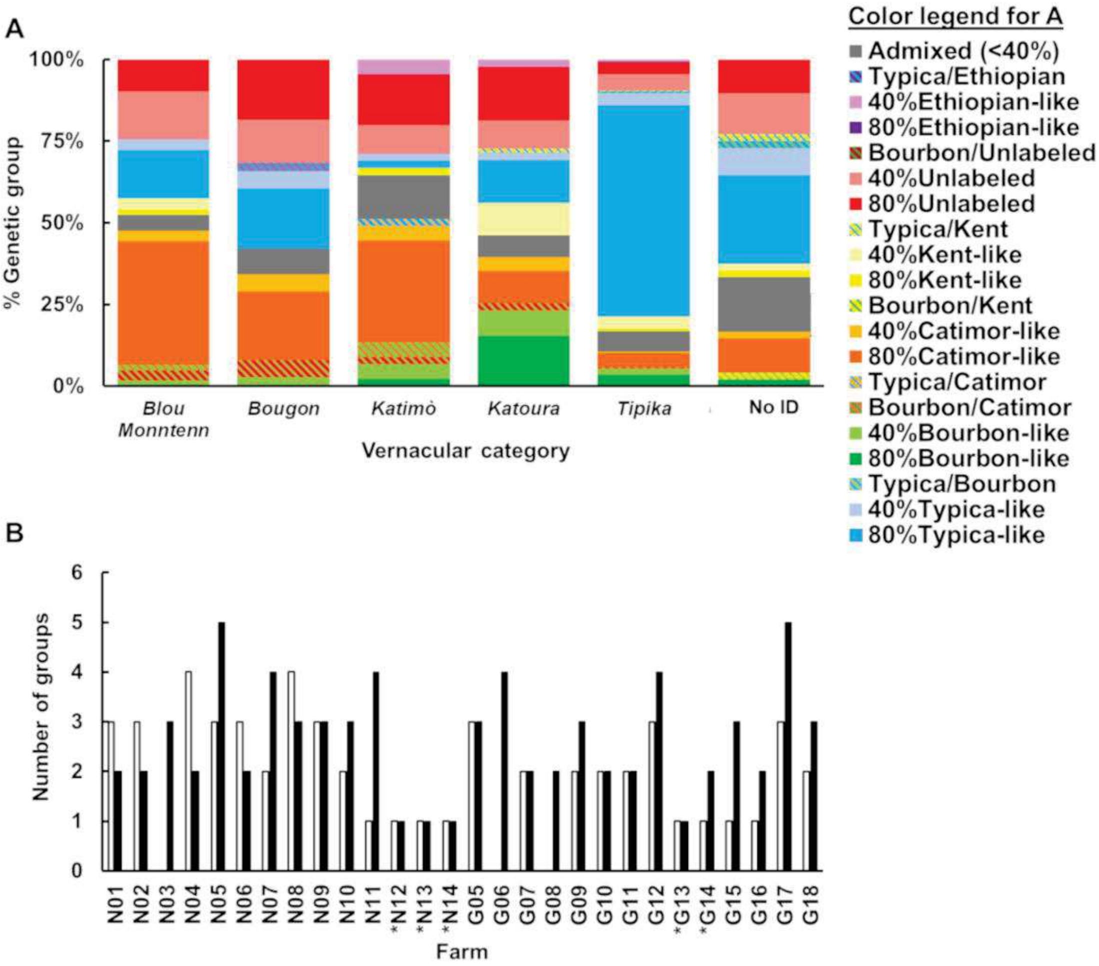

Figure 5. Vernacular identification of Haitian *C. arabica* samples in relation to their assigned genetic groups based on SNP genotyping data. **A.** Percent representation of each genetic group (and admixed individuals) in vernacular categories based on local knowledge. Color legend represent genetic composition, with hatched colors representing admixed individuals with >40% membership from two genetic groups. Admixed samples in grey do not reach 40% membership from any genetic group. The « Kent/I-60-like» and « CR95/Catimor-like » group names have been shortened for legibility. **B.** Number of vernacular varieties reported by farmers at time of sampling (open bars) and genetic groups identified by SNP genotyping (filled bars) in the Nord (Nx) and Grande-Anse (Gx) departments. Farms also had admixed individuals, except those marked with *. Where farmers were unsure of their farm's vernacular variety composition, no data is shown.

4. Discussion

4.1. Two sets of markers for different genetic background signals

Cultivated Arabica coffee varieties originate mostly from two main lineages, Typica and Bourbon, as well as from crosses between them and with Ethiopian accession and the Timor Hybrid (Montagnon et al., 2012). As such, we sought to distinguish between putative varieties using a set of markers (KASP SNP genotyping) designed for cultivated and wild accession diversity (Mérot-L'Anthoene et al., 2019; Zhang et al., 2021). However, given the recorded historical introduction in Haiti of Typica and the early global spread of Bourbon, we also aimed to differentiate the two lineages using a multiplex amplicon sequencing assay (HiPlex) designed to discriminate the two varieties with variety-specific haplotypes (Bawin, 2022).

Results acquired from both HiPlex haplotype and KASP SNP markers showed similar levels of genetic diversity across farms and municipalities, and both distances matrices were correlated. There were considerable similarities, but also notable differences between the structure analyses (sNMF results): the most likely cluster number was K=7 for the HiPlex haplotype data whereas it was K=6 for the KASP SNP data, as these were the values at which Ethiopian-like genetic groups were identified. In both analyses, however, genetic groups were identified for major varieties, Typica-, Bourbon-, CR95/Catimor-like samples and the "Unlabeled" Haitian cluster with comparable level of assignation.

These overall differences may result from differences in the KASP and HiPlex marker assay design objectives. The KASP SNP marker set was developed to discriminate a broad panel of wild and commercial accessions while the HiPlex marker set was developed to maximize polymorphism between the two main cultivated varieties and identify crosses between them. In particular, by emphasizing the differences between Typica and Bourbon, these markers seem to introduce a level of ascertainment bias and erase the trace of the Ethiopian origin of these varieties (Ethiopian accessions are no longer basal on the tree). While we decided to focus on the KASP SNP genotyping data for varietal identification, the HiPlex haplotype assay may be useful in identifying further structuring in admixed individuals, when focusing on Typica x Bourbon hybrids, and are thus likely best used to infer intra-varietal structure.

Our study revealed considerable Arabica coffee diversity in Haitian CAFS. Five main varietal genetic groups were identified encompassing the two main cultivated Typica and Bourbon Arabica lineages. In fact, some farms had levels of gene diversity (H_e) only slightly lower than that measured across all reference *ex-situ* collection accessions, consistent with the PCA showing considerable overall between global Arabica diversity (as determined from our reference accessions) and that present in Haitian samples. Farm composition was also quite variable: lower-diversity farms had up to two genetic (varietal) groups and little to no evidence of admixture, whereas high-diversity farms had two to five genetic groups as well as admixed individuals of varying genetic backgrounds.

4.2. Haitian farm diversity

Coffee genetic diversity showed no significant structure at the level of departments or municipalities suggesting that all varietal groups have been introduced or exchanged across both departments. Genetic variability was therefore highest within and between farms, with an overall lack of regional specificity or North-South divide. Nevertheless, there is a pattern of monovarietal farms being situated in more remote locations away from the main roads and larger cities. This is notably the case in the Bahon municipality in the North: the town is smaller and further away from the main northern city of Cap-Haitien, and the three monovarietal farms were in remote mountains accessible by foot or motorcycle, but not by car. The monovarietal farm in Grande-Anse was also the farthest from the main road. These farms have thus remained out of the reach for the many development projects that are involved in the introduction and spread of newer varieties.

4.3. Notes on varietal identification

Varietal identification by clustering of samples (as was done in the present study) can be complicated by the diversity of criteria used for defining a variety or accession (Berg, 2009; Montagnon et al., 2012; Villa et al., 2005). Organoleptic properties, growth habits and other phenotypic traits, as well as geographic origins all factor in the concept of varieties in a way that could not be captured by our genetic methods. For instance, "Jamaican Blue Mountain" reference accessions were not genetically differentiated from other references in the Typica group, and "Caturra" and "Bourbon"-named reference accessions clustered together. The history of varietal naming in *C. arabica* is also complex. In the XXth century particularly, an abundance of new varieties and accessions were described from homozygote mutants and their outcrossing progeny (Haarer, 1923). Haarer (1923) gives the example of "Typica amarello" (*sic*), a yellow-fruited mutant of Typica, which was crossed with Bourbon to yield "Bourbon amarello", showing how nomenclature can obscure parentage. Indeed, in our study Typica Amarillo and Bourbon Amarillo references clustered together as admixed individuals. The matter is further complicated by recent genetic studies that have shed light on issues in mislabeling and maintenance of genetic integrity in coffee accessions worldwide (Pruvot-Woehl et al., 2020; Verleysen et al., 2023). Nevertheless, our methodology allows for the assignment of coffee plants to genetic groups that can be used to reconstruct pedigree relationships, infer cultivation history, predict agronomic performance, evaluate diversity and identify diversification processes in coffee farms.

4.4. Local perceptions of coffee varieties and diversity

Comparisons of the genetic and vernacular identification of sampled coffee plants revealed them to be correlated. Nevertheless, there were inconsistencies between the two categorizations. Montagnon (2022) reported similar discrepancies between genetic and vernacular categorization of Arabica in traditional Yemeni farms, though by contrast to the latter study all vernacular categories recorded in Haiti corresponded to commercially-used varietal names. Overall, local knowledge is apt at distinguishing monovarietal stands from diversified ones, but the level of diversity is often underestimated, with some genetic groups and processes of admixture being overlooked. This is consistent with other studies comparing farmer-reported with genetically-determined varietal diversity (e.g. Asfaw et al., 2021; Gros-Balthazard et al., 2020).

Discrepancies may be in part due to farmers developing their own ways of categorizing plants based on practical concerns or phenotypic observations independent of plants' genetic parentage (Hunn, 1982), even as the names used may be repurposed. For instance, plants from the Catimor-like genetic group had a similar likelihood of being assigned to the "*Katimò*" and "*Blou Monntenn*" vernacular categories. Speaking with farmers during sampling, it became apparent that *Blou Montenn* is often used to identify compact plants with shorter internodes. As generally understood, Blue Mountain coffee refers to Typica plants grown in the eponymous Jamaican mountains (WCR, 2019). The attribution of this label to non-Typica plants in Haiti may originate from development projects mislabeling imported material, as one report referred to the implementation of varietal replacement in participating farms, whereby "the "Typica" coffee variety was substituted by the "Blue Mountain" variety, which was rust tolerant" (De Salvo et al., 2018). The high proportion of admixed individuals could also be blurring the distinctions between varieties. Still, vernacular category names can provide insight to aid in interpreting genetic analyses. For instance, though neither market set distinguished Caturra from their Bourbon relatives, the presence of the *Katourra* vernacular category suggests that at least some of the genetic Bourbon-like Haitian samples could be Caturra. While one might expect this distinction to be easily resolvable through phenotypic observation, given Caturra's characteristic compact, "dwarf" growth form, the matter becomes considerably more complicated in the reality of Haitian fields. Indeed, stand ageing and lack of pruning has led to older plants acquiring tall, complex and extremely variable architectures that were quite different from those occurring in more diligently managed coffee stands.

4.5. Persistence of the historical Typica-like group

Plants in the Typica group were found in all farms except two. This group also made up the coffee stands in all four monovarietal farms, with two more being composed exclusively of plants from the Typica and Unlabeled group. Typica was thus the most widespread variety in the surveyed areas, which was expected, as this variety was the first to be introduced from a limited number of original clones and became widespread both during and after the colonial era. This variety is the traditional "*Vieux café*" from Haiti, and our analysis confirms that despite the genetic mixing taking place in Haitian CAFS, it has retained its genetic integrity both in northern and southern Haiti. Typica have very good potential for quality but display low yields and high susceptibility to disease (World Coffee Research, 2019).

The Typica cluster was found to have the least diversity, which is consistent with the strong population bottleneck that resulted from the introduction of this lineage to the Neotropics, the first instance of coffee being grown in the Americas. This group had the most overlap between genetic groups and vernacular categories, and local farmers were more likely to describe plants from other genetic groups as "*Tipika*" than they were to ascribe plants from the Typica-like genetic group to other vernacular categories. This suggests a high degree of familiarity with the *Vieux Café*, and that Typica is still seen as the "quintessential" Haitian coffee variety. Anecdotally, during sampling, most farmers described their fields as "*Vieux Café / Tipika*" stands, supplemented in many cases by other varieties acquired more recently from cooperatives, nurseries or development projects.

4.6. Varietal groups beyond Typica established in Haitian CAFS

4.6.1. Bourbon-like group

Individuals assigned to the Bourbon-like genetic group were found on ten farms. Notably, none of the vernacular "*Bougon*" were assigned to this group, though many "*Katoura*" were. We could not determine whether the Bourbon-like group came from historical or more recent introductions. The Bourbon variety has been cultivated in the Neotropics since the XVIIIth (Haarer, 1923) or mid-XIXth century (World Coffee Research, 2019), though we found no record of early introduction to Haiti. Seeds from varieties named Bourbon (H33) and Caturra (T2308) were imported to Haiti in the 1970s from Turrialba, Costa-Rica (Ester, 1978). Caturra was noted to have an especially vigorous growth, with monovarietal fields being established in

Southeast Haiti. Despite their genetic closeness, Bourbon has better cup quality potential and lower nutrition requirements but also lower yields than Caturra, making further investigation into the Haitian plants' identity important. Both are susceptible to coffee leaf rust and other diseases.

4.6.2. CR95/Catimor-like group

Over half of the surveyed farms contained individuals that clustered with CR95 reference accessions: ten in the North and five in Grande-Anse. CR95 is part of the coffee leaf rust tolerant Catimor group originating from a cross between Caturra and the Timor Hybrid, though loss of resistance has been reported. These are high-yielding plants with lower quality potential and high nutrition requirements (World Coffee Research, 2019). Trials of the then-experimental Catimor variety (T5159) were conducted in Haiti as early as 1977 (Ester, 1978), and it was widely disseminated in Haiti by various agricultural development projects in the 1990s (Queneherve et al., 2015). As previously discussed, Catimors may have been disseminated under other names through distribution networks.

4.6.3. Kent/I-60-like group

Only five farms (just one in the North) were found to contain Kent/I-60-like trees, though almost half of them (13 farms) had plants with <40% membership from Kent/I-60-like ancestors. The Kent variety originated in 1911 on an eponymous estate in Mysore, India. At the time, it boasted (now-lost) resistance to coffee leaf rust, leading to its widespread cultivation in India and East Africa (Haarer, 1923). Though to our knowledge no record exists of its introduction in Haiti, Haarer (1923) makes clear that it enjoyed a great reputation, deeming it the best choice should seed be imported from another country. The relative rarity of Kent/I-60-like Haitian individuals and the widespread presence of admixed individuals is consistent with an old introduction of this variety.

4.6.4. Unlabeled group

Population structure analyses identified a varietal cluster containing no reference individuals, making its identification difficult. It was present in 17 of the sampled farms. The closest reference sample was a Sarchimor (Villa Sarchi Bourbon mutant x Timor Hybrid, WCR) with 50.0% likelihood of contribution from this group. The "Unlabeled" plants could potentially belong to Timor Hybrid-introgressed Colombian varieties Tabi and Castillo, which are known to have been used in trials in both departments starting in 2013 (Queneherve et al., 2015). However, no farmer reported growing them, and they are absent from the CATIE international collection. This group's widespread presence on sampled farms suggest that they are readily spread through distribution networks, though seemingly without a specific vernacular name.

4.6.5. Inter-varietal individuals

Admixed individuals between two genetic groups were at least twice more likely to be found in farms where at least one, and more often two of their contributing parental varieties were represented, suggesting that at least some were the result of genetic mixing within their farm. Renewal of coffee stands occurs primarily through germination of the seed bank, though some farmers also source their trees from nurseries or development programs (Amaya et al., 1999; Queneherve et al., 2015). While *C. arabica* is considered to be mainly autogamous, its rate of allogamy has been estimated at >10% (Carvalho and Krug, 1949) and significantly more in some cases (Berecha et al., 2014), allowing gene flow and recombination between individuals (Pruvot-Woehl et al., 2020). Furthermore, pollinators can increase the seed set of *C. arabica* (Klein et al., 2003), and are more numerous in agrosystems with more diversity and lower use of chemical inputs (Centeno-Alvarado et al., 2023), potentially favoring outcrossing. The within-farm production of admixed individuals could therefore result from *in-situ* outcrossing and subsequent recruitment from the seed bank. Very little scientific attention has been paid to the varietal mixtures and genetic mixing in *C. arabica* fields outside of the Ethiopian accessions in the species' geographic area of origin (Benti et al., 2021; Berecha et al., 2014). While our analyses agreed with previous reports of considerable diversity in Ethiopian accessions, our results highlight the potential role of non-intensive, no-input CAFS in generating diversity from cultivated accessions under appropriate conditions. As Haitian CAFS are recovering from the severe 2012 rust epidemic, which impacted much of the Neotropical region (Avelino et al., 2015; Queneherve et al., 2015), natural selection may have favored admixed individuals with greater resistance to the disease. This could explain the high proportion of admixed individuals with contribution from the CR95/Catimor-like group and perhaps also the "Unlabeled" group.

Two alternate or complementary explanations for inter-varietal individuals could be proposed. Firstly, there are reports of the Mondo Novo variety being introduced to Haiti, though it is said to have failed to establish in the fields (Eitzinger et al., 2019). Survival of this cross between the Typica and Bourbon varieties may account for some of the admixed individuals in Haitian farms. As such individuals were present in all diversified farms, their production may also be taking place in nurseries or in certain specific farms from which they are spread through networks of seed and seedling exchange. These processes might be strengthened by aforementioned inaccuracies in local assessment of farm varietal composition.

Six admixed samples were identified as having >40% membership from the Ethiopian-like group (in addition to a single individual from Haiti assigned to that genetic group). One possible source is the Geisha variety, which is known for its high cup quality potential. It was reportedly used in trials in the 1970s (Ester, 1978), though mentions of it are all but absent from subsequent sources. The Geisha sample in our reference panel was itself considered admixed, with 46.8% contribution from the Ethiopian-like genetic group.

4.7. Robusta coffee: an unreported crop in Haitian CAFS

One farm in the North was also found to contain *C. canephora*, a species whose presence in Haiti had not been previously recorded to our knowledge. *C. canephora*, or "Robusta coffee", is the second most economically important *Coffea* species (Ferreira et al., 2019). In Haiti, it was identified as *Kafé Brezil* ("Brazil Coffee"), potentially pointing to an introduction from this country where it is widely cultivated. A report from the South of Haiti also makes mention of "Brazil Coffee", referring to it as a new, rust-resistant but less productive "variety" (Eitzinger et al., 2019) rather than another species altogether. The cultivation of Robusta is more recent, and its expansion since the end of the XIXth century is linked, among others, to the increase in demand for coffee worldwide, the susceptibility of *C. arabica* to coffee leaf rust, despite its lower potential cup quality (Verleysen et al., 2023). A recent trend towards increased cultivation of this species in Latin American countries, where only Arabica was previously grown, has also been noted (Harvey et al., 2021). This is due to Robusta's attractive qualities of greater rust resistance but also to the fact that it is more resilient to the effects of climate change. Cultivation of *C. canephora* appears to be relatively rare in Haiti at present.

4.8. Maintenance and generation of diversity in Haitian CAFS: specificity, implications and future directions

Harvey et al. (2021) noted a trend of widespread replacement of thousands of hectares of traditional varieties in Latin America, by disease-resistant (and especially rust-resistant) cultivars such as Catimors and Sarchimors, derived from Timor Hybrids. A rise in the intensification of cultivation was also observed, albeit with a concurrent increase in the area of coffee cultivated under voluntary sustainability standards. By contrast, disease-resistant varieties have been introduced to Haitian CAFS in the North and Grande-Anse departments, but have not replaced traditional varieties and indeed appear to have mixed with them under consistently low-intensity management. This complicates varietal identification and variety-specific management in the field, but also allowed for the generation of considerable genetic diversity, as revealed by our analyses.

In addition to resistant cultivars, F1 hybrids bred for heterosis from traditional varieties and more distant Ethiopian accessions have been developed (van der Vossen et al., 2015). These hybrids are increasingly promoted as a response to concerns over quality, productivity, disease resistance, and the need for ecologically sustainable shade-adapted coffee plants. In a study of acceptance by Central American farmers, these hybrids, when available, were found to be attractive (Turreira-García, 2022). However, they come with the caveat that the vast majority of them do not breed true, and must therefore be propagated clonally or purchased. This is important given the economic context and management system in Haitian CAFS. Indeed, any prospect of importing such hybrids must consider that the dynamic process of genetic mixing and seedling recruitment taking place in Haitian CAFS might lead to unexpected outcomes.

The considerable Arabica genetic diversity found in Haitian CAFS may contribute to the coffee sector's continued survival despite the considerable challenges it faces by providing potential for adaptation to biotic and abiotic stressors. Furthermore, given the process of genetic mixing among genetic groups in Haitian CAFS, this environmental pressure could promote processes of natural selection and adaptation. This likelihood is increased by the presence in various farms of rust-resistant cultivars such as Catimor (and possibly the "Unlabeled" group). In addition, this process could be supplemented by human-mediated selection of select, agronomically attractive plants to conserve, propagate and exchange (Elias and McKey, 2000). Measures of the production potential and pest and disease burden at the plant and farm level in Haitian CAFS are needed to test these hypotheses. In addition, admixed individuals should be investigated for their potential agronomic performances and organoleptic qualities in the search for genotypes of interest. Finally, propagation networks should also be studied to better understand the processes of genetic diversification in Haitian CAFS.

4.9. Leveraging Haitian coffee diversity

Increased understanding of the diversity and varietal composition identification of Haitian CAFS can better support farmers' decision-making and inform field management, as varieties differ in their agronomic characteristics and requirements (World Coffee Research, 2019). For instance, farmers interested in accessing specialty coffee markets may choose to focus on varieties with higher cup quality or historical-cultural value such as the Typica *Vieux Café* despite lower yields and higher pest and disease pressure. By contrast, those interested in producing dry-processed coffee beans for local markets may instead value higher-yielding genotypes that are more resistant to disease such as Catimor, and those for whom coffee is not a priority crop in their diverse CAFS may focus on plants tolerant of neglect. Furthermore, given that potential coffee cup quality is partially genetically determined (Leroy et al., 2006; Montagnon et al., 2012; Sobreira et al., 2016), increased accuracy in the knowledge of farms' standing diversity and varietal makeup can help inform the commercialization of harvested coffee beans by better describing the varietal blends produced at a farm or regional level. Finally, this knowledge can allow CAFS to function as *in-situ* conservatories of the country's coffee germplasm resource (Brush, 2000), as well as sources for their propagation and dissemination. This can occasion a shift of farmers' perceived role from mere purveyors of economic product to active participants in the management of the country's genetic resources.

4.10. Conclusion

Our results indicate that Haitian coffee farms act not only as repositories of heritage varieties, but as generators of new genotypic combinations. This study is among the first to study *in-situ* coffee variety mixtures in general and to characterize that of Haitian coffee farms in particular. The Haitian coffee sector would benefit from further studies, including phenotypic characterization which may help identify genetic material that is particularly well adapted to the local ecological and agronomic conditions. Future directions may also include the establishment of a Haitian germplasm conservation center. This genetic heritage contributes to the potential for renewal of the Haitian coffee sector which may in turn help maintain the provision of crucial ecosystem services by agroforestry systems. Shade-grown coffee could thus help safeguard Haitian biodiversity and improve community resilience and food security.

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Data availability statement

All relevant data are available within the manuscript and its Online Resource files. The passport and genotyping (KASP SNP genotypes and HiPlex amplicon sequencing haplotypes) data that support the findings of this study are available in the DataSuds repository (IRD, France) at https://doi.org/10.23708/T6YZML.

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Supporting Information

Table S1. Name, location and number of samples for each study site. The municipality Grande-Rivière-du-Nord is abbreviated as GRN.

Farm ID	**Department**	**Municipality**	**Locality name**	**Latitude**	**Longitude**	**Number of plants sampled**
G05	Grande-Anse	Beaumont	Belance	18.4672105	-73.97903	24
G06	Grande-Anse	Beaumont	Bois Misquette	18.4763379	-73.976884	20
G07	Grande-Anse	Beaumont	Bois Lacombe	18.4490638	-73.976122	22
G08	Grande-Anse	Beaumont	Fonds Cochon	18.4883196	-73.97104	20
G09	Grande-Anse	Beaumont	Bois Pin	18.4485387	-73.962085	22
G10	Grande-Anse	Beaumont	Labondance	18.4749466	-73.943939	20
G11	Grande-Anse	Beaumont	Savane Zidor	18.4821107	-73.920777	20
G12	Grande-Anse	Pestel	Tozia	18.451436	-73.868033	26
G13	Grande-Anse	Pestel	K-Gous	18.5289797	-73.828653	20
G14	Grande-Anse	Pestel	Mabilai	18.4987137	-73.811	23
G15	Grande-Anse	Pestel	Desriveaux	18.4713702	-73.810397	21
G16	Grande-Anse	Pestel	Billard Dépôt	18.490385	-73.801059	20
G17	Grande-Anse	Pestel	Jeanbellune	18.480481	-73.783794	21
G18	Grande-Anse	Pestel	Mentor	18.4723964	-73.77081	22
N01	Nord	Dondon	Grand Chemin	19.5459768	-72.269341	25
N02	Nord	Dondon	Fleury	19.4915679	-72.261885	24
N03	Nord	Dondon	Clément	19.5487275	-72.258205	24
N04	Nord	Dondon	Matador	19.5037206	-72.254102	26
N05	Nord	Dondon	Bernice	19.5224983	-72.248129	25
N06	Nord	Dondon	Bellevue	19.5123115	-72.243898	24
N07	Nord	Dondon	Lanneau	19.5339873	-72.23641	24
N08	Nord	Dondon	Michel	19.5520965	-72.235948	24
N09	Nord	Dondon	Bois Rouge	19.542891	-72.224254	23
N10	Nord	GRN	Vieux Cayes	19.5542768	-72.198133	21
N11	Nord	Baron	Muscady	19.4739142	-72.11539	20
N12	Nord	Baron	Cadette	19.4748559	-72.085731	9
N13	Nord	Baron	Mompoint	19.4687234	-72.084296	20
N14	Nord	Baron	Grenier	19.4778762	-72.08105	20

Table S2. **List of sample accessions used as references in the study**. List of reference samples by code and accession name, country and region of origin (when this information is known to the authors), and name of the holding institution whose collection the sample was acquired from. Also mentioned is whether the accession was used in the study that selected the core SNP panel used in the KASP SNP genotyping assay (Zhang et al., 2021), and what genetic group the sample was assigned to with sNMF population structure analysis using KASP SNP data (at K=6) and HiPlex haplotype data (at K=7). Genetic groups are abbreviated as follows: Typ = Typica-like, CR = CR95 (Catimor)-like, BBN = Bourbon-like, Kent = Kent/I-60-like, Ethio = Ethiopian-like, Admix = admixed assignment. "N/A" in either column indicates that the sample was not represented in the corresponding dataset.

Sample Code	**Accession**	**Country of origin**	**Region of origin**	**used by Zhang et al., 2021**	**Holding institution**	**Assign KASP K=6**	**Assign HiPlex K=7**
AR 56_5	*C. arabica*	Ethiopia			IRD, France	Ethio	HiPlex6
AR15_5	*C. arabica*	Ethiopia			IRD, France	Ethio	Admix
AR22_5	*C. arabica*	Ethiopia			IRD, France	Ethio	HiPlex6
AR41_6	*C. arabica*	Ethiopia			IRD, France	Ethio	HiPlex6
BA58	*C. canephora*	Ivory Coast			IRD, France	N/A	N/A
BB53	*C. canephora*	CAR			IRD, France	N/A	N/A
CA54	*C. congensis*	CAR			IRD, France	N/A	N/A
CC53	*C. congensis*	Congo			IRD, France	N/A	N/A
CTR	Caturra	CATIE collection			IRD, France	Admix	Admix
EA64	*C. liberica var. liberica*	Ivory Coast			IRD, France	N/A	Admix
EB52	*C. liberica var. dewevrei*	CAR			IRD, France	N/A	N/A
EB58	*C. liberica var. dewevrei*	CAR			IRD, France	N/A	N/A
GUI2	*C. canephora*	Guinea			IRD, France	N/A	N/A
HA_13	*C. arabica*				IRD, France	N/A	N/A
T.00977	Blue Mountain	Guatemala	La Aurora	Yes	CATIE, Costa-Rica	Typ	N/A
T.00989	Guadeloupe	El Salvador	La Libertad	Yes	CATIE, Costa-Rica	Typ	HiPlex1
T.00990	Surinam	El Salvador	La Libertad	Yes	CATIE, Costa-Rica	Typ	HiPlex1
T.01993	Goiaba	Brasil	Campinas	Yes	CATIE, Costa-Rica	Kent	HiPlex1
T.02147	Murta	Guatemala	La Aurora	Yes	CATIE, Costa-Rica	BBN	Admix
T.02246	Jimma-1	Ethiopia	Jimma	Yes	CATIE, Costa-Rica	Ethio	HiPlex5
T.02249	Dessie	Ethiopia	Dessie	Yes	CATIE, Costa-Rica	Admix	HiPlex6
T.02251	Batie	Ethiopia	Dessie	Yes	CATIE, Costa-Rica	Admix	Admix
T.02254	Jimma-6	Ethiopia	Jimma	Yes	CATIE, Costa-Rica	Ethio	Admix

T.02257	Lekemti	Ethiopia	Lekemti	Yes	CATIE, Costa-Rica	Admix	HiPlex6
T.02298	Coorg	Kenya	Ruiru	Yes	CATIE, Costa-Rica	Typ	Admix
T.02299	Laurina	Costa Rica	Cartago	Yes	CATIE, Costa-Rica	Admix	Admix
T.02394	Mocha Java	Puerto Rico	Mayaguez	Yes	CATIE, Costa-Rica	BBN	Admix
T.02395	Erecta	Puerto Rico	Mayaguez	Yes	CATIE, Costa-Rica	Typ	Admix
T.02542	Caturra	Brasil	Campinas	Yes	CATIE, Costa-Rica	BBN	Admix
T.02676	Laurina	Camerun	Dschang	Yes	CATIE, Costa-Rica	Admix	Admix
T.02702	Mibirizi	Congo	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.02727	Dalle	Kenya	Sidamo	Yes	CATIE, Costa-Rica	Ethio	Admix
T.02731	Jimma Galla Sidamo	Kenya	N/A	Yes	CATIE, Costa-Rica	Ethio	Admix
T.02741	Erecta	Kenya	N/A	Yes	CATIE, Costa-Rica	BBN	HiPlex6
T.02742	Dilla Alghe	Ethiopia	Sidamo	Yes	CATIE, Costa-Rica	Admix	HiPlex5
T.02744	Rume Sudan	Kenya	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.02758	Barbuk Sudan	Sudan	Barbuk	Yes	CATIE, Costa-Rica	Admix	N/A
T.03081	Carrizal	Costa Rica	Alajuela	Yes	CATIE, Costa-Rica	Admix	Admix
T.03214	Geisha	Tanzania	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.03215	K-7	Kenya	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.03427	Cera	Brasil	Campinas	Yes	CATIE, Costa-Rica	Typ	Admix
T.03443	Ceilan	Puerto Rico	Mayaguez	Yes	CATIE, Costa-Rica	Typ	HiPlex1
T.03469	Bourbon Salvadoreno	El Salvador	La Libertad	Yes	CATIE, Costa-Rica	BBN	HiPlex1
T.03491	Lejeune 08	Ethiopia	Bada Buna	Yes	CATIE, Costa-Rica	Ethio	Admix
T.03507	Lejeune 12	Ethiopia	Bada Buna	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.03645	Cumbaya				CATIE, Costa-Rica	Typ	HiPlex6
T.04007	Loulo	Ethiopia	Sidamo	Yes	CATIE, Costa-Rica	Admix	N/A
T.04060	Murta	Isla Reunión	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.04076	Typica Amarillo	Colombia	Caldas	Yes	CATIE, Costa-Rica	Admix	Admix
T.04078	Caturra Variegata	Colombia	Caldas	Yes	CATIE, Costa-Rica	BBN	Admix
T.04250	Goiaba	Colombia	Caldas	Yes	CATIE, Costa-Rica	Admix	HiPlex5

T.04253	Maragogipe	Colombia	Caldas	Yes	CATIE, Costa-Rica	Admix	Admix
T.04258	Bourbon Mayaguez	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04259	Jackson 2	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04268	Kent	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Kent	Admix
T.04271	Kent	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04273	Kabare	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04278	Babaca Kaffa	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04281	Lignee-M	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Admix	Admix
T.04286	Wondo Sidamo	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Ethio	Admix
T.04290	Jimma Kaffa	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Ethio	Admix
T.04292	Wush Wush Kaffa	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.04294	Mocha de Tahiti	Congo	Ruanda Urundi	Yes	CATIE, Costa-Rica	Typ	HiPlex6
T.04308	Dalle mixed	Malawi	N/A	Yes	CATIE, Costa-Rica	Ethio	HiPlex1
T.04310	Mocha	Malawi	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.04313	SL28				CATIE, Costa-Rica	Admix	Admix
T.04314	SL34				CATIE, Costa-Rica	Admix	Admix
T.04317	I-60	Malawi	N/A	Yes	CATIE, Costa-Rica	Kent	Admix
T.04375	Bourbon Amarillo	Venezuela	Monajas	Yes	CATIE, Costa-Rica	Admix	Admix
T.04479	E-301	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Admix	N/A
T.04539	E-293	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	N/A
T.04570	E-147	Ethiopia	Illubabor	Yes	CATIE, Costa-Rica	Ethio	N/A
T.04573	E-150	Ethiopia	Illubabor	Yes	CATIE, Costa-Rica	Ethio	Admix
T.04578	E-155	Ethiopia	Illubabor	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.04583	E-325	Ethiopia	Illubabor	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.04599	E-341	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	Admix
T.04610	E-352	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	Admix
T.04667	E-160	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.04681	E-167	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	N/A

T.04688	E-174	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	HiPlex6
T.04692	E-178	Ethiopia	Kaffa Jimma	Yes	CATIE, Costa-Rica	Ethio	N/A
T.05175	IHCAFE 90				CATIE, Costa-Rica	Admix	HiPlex6
T.05199	Cioiccie I	Colombia	Caldas	Yes	CATIE, Costa-Rica	Admix	Admix
T.05267	Catuai	Costa Rica	San José	Yes	CATIE, Costa-Rica	Admix	Admix
T.05268	Catuai	Costa Rica	San José	Yes	CATIE, Costa-Rica	Admix	Admix
T.05283	Cioiccie S-6	Brasil	Campinas	Yes	CATIE, Costa-Rica	Admix	Admix
T.05314	Hibrido_041				CATIE, Costa-Rica	Admix	HiPlex6
T.05325	Catuai	Costa Rica	Alajuela	Yes	CATIE, Costa-Rica	Admix	Admix
T.08867	CR 95				CATIE, Costa-Rica	CR	Admix
T.11723	Garnica	Mexico	Veracruz	Yes	CATIE, Costa-Rica	BBN	N/A
T.11948	Hibrido_101				CATIE, Costa-Rica	Admix	Admix
T.11950	Clon 7355	Ethiopia	N/A	Yes	CATIE, Costa-Rica	Admix	Admix
T.12534	Clon 7357	Ethiopia	N/A	Yes	CATIE, Costa-Rica	Typ	Admix
T.12837	Hibrido_055	Mexico	Veracruz	Yes	CATIE, Costa-Rica	Admix	Admix
T.12841	Catimor	Mexico	Veracruz	Yes	CATIE, Costa-Rica	Admix	Admix
T.12842	Catimor	Mexico	Veracruz	Yes	CATIE, Costa-Rica	Admix	Admix
T.12846	Hibrido_089	Mexico	Veracruz	Yes	CATIE, Costa-Rica	Ethio	Admix
T.12851	Garnica	Mexico	Veracruz	Yes	CATIE, Costa-Rica	Admix	Admix
T.14718	Sarchimor				CATIE, Costa-Rica	Admix	Admix
T.14723	Icatu	Brasil	Campinas	Yes	CATIE, Costa-Rica	Admix	Admix
T.14724	Catimor				CATIE, Costa-Rica	Admix	Admix
T.15895	Pacas	El Salvador	La Libertad	Yes	CATIE, Costa-Rica	BBN	Admix
T.16636	Cavimor				CATIE, Costa-Rica	Kent	HiPlex5
T.16651	Cavimor				CATIE, Costa-Rica	Kent	Admix
T.16742	Mundo Novo	Brasil	Minas Gerais	Yes	CATIE, Costa-Rica	Admix	Admix
T.16762	Mundo Novo	Brasil	Minas Gerais	Yes	CATIE, Costa-Rica	Admix	Admix
T.16764	Catuai	Brasil	Minas Gerais	Yes	CATIE, Costa-Rica	Admix	Admix

T.19878	Arabusta				CATIE, Costa-Rica	Admix	Admix
T.19943	Arabusta				CATIE, Costa-Rica	Admix	Admix
T.03617	Blue Mountain				CATIE, Costa-Rica	Admix	Admix
S15_2	*C. canephora*	Guinea			IRD, France	N/A	N/A
SBIL4	*C. canephora var. maclaudi*				IRD, France	N/A	N/A
Ku041	Red_bourbon				HARC, Hawaii, USA	BBN	N/A
Mw235	Pink_bourbon				HARC, Hawaii, USA	BBN	N/A
Mw264	Bourbon Select PR_6791				HARC, Hawaii, USA	BBN	N/A
Ku117	Typica_Guatemala				HARC, Hawaii, USA	Typ	N/A
Ku118	Typica_Guatemala				HARC, Hawaii, USA	Typ	N/A
Ku132	Typica_San_Ramon				HARC, Hawaii, USA	Typ	N/A
Ku214	Jamaica Blue_Mountain				HARC, Hawaii, USA	Typ	N/A
Ku215	Jamaica Blue_Mountain				HARC, Hawaii, USA	Typ	N/A
Ku085	8667				HARC, Hawaii, USA	CR	N/A
Ku086	8667				HARC, Hawaii, USA	CR	N/A
Ku143	Kents				HARC, Hawaii, USA	TK	N/A
T.08667	CR95				CATIE, Costa-Rica	CR	N/A
T.04271	Kents_198				CATIE, Costa-Rica	Admix	N/A
T19844	Hibrido_038				CATIE, Costa-Rica	Kent	N/A
T.05296	Sarchimor				CATIE, Costa-Rica	Admix	N/A

Table S3. Haitian *Coffea arabica* diversity statistics calculated on SNP genotyping data for the sampled departments of Nord (N) and Grande-Anse (G), and both combined (N+G): sample size, observed heterozygosity (**H_o**), expected heterozygosity (=gene diversity, **H_e**), Fixation index (as **F_{IS}**) and percent marker polymorphism (% P). Values calculated from reference *C. arabica* individuals (Arabica ref.) are included as a comparison. Where applicable, data is presented as Mean ± SD.

Department	**Nb. of samples**	**H_o**	**H_e**	**F_{IS}**	**% P**
N	300	0.072 ± 0.01	0.332 ± 0.02	0.761 ± 0.03	0.908
G	301	0.093 ± 0.01	0.309 ± 0.02	0.666 ± 0.04	0.885
Overall (N+G samples)	601	0.083 ± 0.01	0.325 ± 0.02	0.724 ± 0.03	0.908
Arabica ref.	110	0.140 ± 0.01	0.373 ± 0.01	0.620 ± 0.03	0.989

Table S4. Haitian *Coffea arabica* diversity statistics calculated on SNP genotyping data for the sampled municipalities (*communes*) in the Nord (N) and Grande-Anse (GA) departments: sample size (N), observed heterozygosity (**H_o**), expected heterozygosity (=gene diversity, **H_e**), Fixation index (as **F_{IS}**) and percent marker polymorphism (% P). Values calculated from reference *C. arabica* individuals (Arabica ref.) are included as a comparison. "GRN" = Grande Rivière du Nord. Where applicable, data is presented as Mean ± SD.

***Commune* (municipality)**	**Nb. of samples**	**H_o**	**H_e**	**F_{IS}**	**% P**
N-DONDON	210	0.082 ± 0.01	0.338 ± 0.02	0.740 ± 0.03	0.908
N-GRN	21	0.067 ± 0.01	0.311 ± 0.02	0.784 ± 0.03	0.793
N-BAHON	69	0.043 ± 0.02	0.161 ± 0.01	0.757 ± 0.04	0.793
G-BEAUMONT	148	0.081 ± 0.02	0.264 ± 0.02	0.705 ± 0.04	0.828
G-PESTEL	153	0.105 ± 0.01	0.337 ± 0.02	0.632 ± 0.04	0.874
Arabica ref.	110	0.140 ± 0.01	0.373 ± 0.01	0.620 ± 0.03	0.989

Table S5. Haitian *Coffea arabica* diversity statistics for the sampled farms in the Nord (N) and Grande-Anse (G) departments, based on SNP genotyping data: sample size (N), observed heterozygosity (**H_o**), expected heterozygosity (=gene diversity, **H_e**), Fixation index (as **F_{IS}**) and percent marker polymorphism (% P). Values calculated from reference *C. arabica* individuals (Arabica ref.) are included as a comparison. Where applicable, data is presented as Mean ± SD.

Farm	**Nb. of samples**	**H_o**	**H_e**	**F_{IS}**	**% P**
N01	24	0.045 ± 0.02	0.139 ± 0.01	0.678 ± 0.05	0.759
N02	25	0.043 ± 0.01	0.294 ± 0.02	0.804 ± 0.05	0.828
N03	24	0.075 ± 0.02	0.272 ± 0.02	0.713 ± 0.04	0.690
N04	26	0.096 ± 0.01	0.237 ± 0.02	0.584 ± 0.04	0.851
N05	19	0.099 ± 0.02	0.335 ± 0.02	0.677 ± 0.04	0.885
N06	21	0.102 ± 0.01	0.305 ± 0.02	0.618 ± 0.04	0.839

N07	24	0.098 ± 0.01	0.343 ± 0.02	0.693 ± 0.03	0.759
N08	24	0.083 ± 0.01	0.292 ± 0.02	0.667 ± 0.04	0.839
N09	23	0.095 ± 0.01	0.292 ± 0.02	0.615 ± 0.04	0.770
N10	21	0.067 ± 0.01	0.311 ± 0.02	0.784 ± 0.03	0.793
N11	20	0.062 ± 0.01	0.309 ± 0.02	0.747 ± 0.04	0.793
N12	9	0.036 ± 0.02	0.022 ± 0.01	-0.569 ± 0.09	0.046
N13	20	0.036 ± 0.02	0.029 ± 0.01	-0.188 ± 0.10	0.069
N14	20	0.036 ± 0.02	0.026 ± 0.01	-0.209 ± 0.10	0.069
G05	24	0.087 ± 0.01	0.336 ± 0.02	0.727 ± 0.04	0.805
G06	20	0.075 ± 0.02	0.186 ± 0.02	0.581 ± 0.05	0.759
G07	22	0.138 ± 0.02	0.265 ± 0.02	0.532 ± 0.04	0.793
G08	20	0.046 ± 0.02	0.198 ± 0.02	0.746 ± 0.05	0.632
G09	22	0.103 ± 0.01	0.319 ± 0.02	0.633 ± 0.04	0.782
G10	20	0.073 ± 0.02	0.101 ± 0.01	0.399 ± 0.05	0.678
G11	20	0.032 ± 0.02	0.217 ± 0.02	0.852 ± 0.05	0.724
G12	26	0.153 ± 0.02	0.331 ± 0.02	0.552 ± 0.04	0.828
G13	20	0.034 ± 0.02	0.017 ± 0.01	-1.000 ± 0.00	0.034
G14	23	0.036 ± 0.02	0.055 ± 0.01	0.774 ± 0.06	0.506
G15	21	0.095 ± 0.01	0.319 ± 0.02	0.687 ± 0.04	0.805
G16	20	0.113 ± 0.01	0.283 ± 0.02	0.542 ± 0.04	0.747
G17	21	0.133 ± 0.02	0.272 ± 0.02	0.510 ± 0.04	0.759
G18	22	0.159 ± 0.01	0.272 ± 0.02	0.377 ± 0.03	0.839
Arabica ref.	110	0.140 ± 0.01	0.373 ± 0.01	0.620 ± 0.03	0.989

Table S6. Pairwise F_{ST} values between Haitian *Coffea arabica* sampled in municipalities (*communes,* M) of two departments (D), calculated from KASP SNP genotyping data. "GRN" refers to Grande Rivière du Nord. p-values above diagonal, based on 999 permutations, are as follows: * = p≤0.05, **= p≤0.01, ***= p≤0.001

D		**Grande-Anse**		**Nord**		
	M	**Beaumont**	**Pestel**	**Dondon**	**GRN**	**Bahon**
Grande-Anse	**Beaumont**			***	***	***
	Pestel	0.045		***	***	***
Nord	**Dondon**	0.118	0.028		*	***
	GRN	0.204	0.063	0.020		***
	Bahon	0.043	0.146	0.225	0.388	

Table S7. Pairwise F_{ST} values between Haitian *Coffea arabica* sampled in farms (F) from five municipalities (M) and two departments (D), calculated from KASP SNP genotyping data. "GRN" refers to Grande Rivière du Nord. p-values above diagonal, based on 999 permutations, are as follows: * = p≤0.05, **= p≤0.01, ***= p≤0.001, ns= not significant.

D			Grande_Anse														Nord													
	M		Beaumont							Pestel							Dondon									GRN	Bahon			
		F	G05	G06	G07	G08	G09	G10	G11	G12	G13	G14	G15	G16	G17	G18	N01	N02	N03	N04	N05	N06	N07	N08	N09	N10	N11	N12	N13	N14
Grande_Anse	Beaumont	G05		**	**	***	ns	***	**	**	***	***	*	***	**	***	***	***	***	***	ns	**	ns	***	***	***	*	***	***	***
		G06	0.151		*	ns	**	ns	ns	***	***	*	***	***	ns	***	ns	***	***	***	***	***	***	***	***	***	***	*	**	**
		G07	0.080	0.038		*	ns	***	ns	***	***	***	***	***	ns	***	**	***	***	***	***	***	***	***	***	***	**	***	***	***
		G08	0.123	0.000	0.046		*	*	ns	***	***	*	***	***	*	***	ns	***	***	***	***	***	***	***	***	***	***	ns	***	***
		G09	0.008	0.080	0.029	0.073		***	ns	***	***	***	***	***	ns	***	***	**	***	***	**	*	ns	***	**	***	ns	***	***	***
		G10	0.262	0.013	0.121	0.051	0.168		ns	***	*	ns	***	***	***	***	ns	***	***	***	***	***	***	***	***	***	***	ns	**	**
		G11	0.121	0.000	0.017	0.018	0.040	0.040		***	***	**	***	***	ns	***	ns	***	***	***	***	**	***	***	***	***	**	*	***	***
	Pestel	G12	0.053	0.294	0.178	0.260	0.103	0.410	0.250		***	***	ns	***	***	***	***	***	***	***	ns	***	**	***	***	*	***	***	***	***
		G13	0.380	0.118	0.240	0.155	0.296	0.034	0.169	0.518		ns	***	***	***	***	*	***	***	***	***	***	***	***	***	***	***	ns	**	*
		G14	0.331	0.062	0.185	0.087	0.244	0.000	0.113	0.475	0.003		***	***	***	***	ns	***	***	***	***	***	***	***	***	***	***	ns	***	*
		G15	0.046	0.302	0.177	0.270	0.104	0.429	0.260	0.000	0.546	0.499		***	***	***	***	***	*	***	ns	***	*	***	**	*	**	***	***	***
		G16	0.126	0.339	0.217	0.338	0.149	0.471	0.276	0.036	0.596	0.550	0.058		***	***	***	**	**	**	***	**	***	**	*	ns	*	***	***	***
		G17	0.064	0.025	0.012	0.049	0.005	0.111	0.000	0.167	0.248	0.195	0.178	0.182		***	*	**	***	***	***	**	**	***	***	***	ns	**	***	***
		G18	0.161	0.452	0.338	0.442	0.194	0.553	0.399	0.148	0.663	0.624	0.150	0.199	0.304		***	***	***	***	***	***	***	***	***	***	***	***	***	***
Nord	Dondon	N01	0.214	0.000	0.074	0.015	0.126	0.000	0.006	0.360	0.056	0.012	0.376	0.417	0.071	0.512		***	***	***	***	***	***	***	***	***	***	ns	***	**
		N02	0.100	0.204	0.106	0.237	0.089	0.336	0.146	0.109	0.461	0.417	0.108	0.057	0.085	0.250	0.282		***	*	***	ns	***	ns	***	**	ns	***	***	***
		N03	0.133	0.410	0.286	0.387	0.207	0.532	0.360	0.042	0.634	0.595	0.036	0.057	0.269	0.194	0.482	0.145		***	**	***	***	***	***	***	***	***	***	***
		N04	0.199	0.375	0.271	0.402	0.211	0.505	0.308	0.157	0.622	0.581	0.166	0.064	0.218	0.270	0.454	0.041	0.138		***	**	***	**	***	***	**	***	***	***
		N05	0.021	0.269	0.163	0.228	0.087	0.404	0.229	0.008	0.527	0.477	0.000	0.088	0.150	0.163	0.350	0.115	0.041	0.180		***	*	***	***	**	***	***	***	***
		N06	0.071	0.183	0.094	0.207	0.062	0.313	0.126	0.080	0.449	0.400	0.090	0.045	0.062	0.232	0.259	0.000	0.128	0.044	0.093		***	ns	***	**	ns	***	***	***
		N07	0.015	0.188	0.100	0.164	0.019	0.288	0.145	0.051	0.409	0.364	0.044	0.107	0.077	0.132	0.247	0.110	0.132	0.197	0.041	0.077		***	**	**	*	***	***	***
		N08	0.110	0.289	0.177	0.306	0.126	0.417	0.231	0.089	0.535	0.493	0.082	0.053	0.158	0.211	0.364	0.022	0.094	0.047	0.103	0.020	0.112		***	**	*	***	***	***
		N09	0.101	0.299	0.194	0.279	0.129	0.420	0.246	0.047	0.538	0.493	0.058	0.031	0.159	0.231	0.370	0.113	0.082	0.138	0.075	0.073	0.061	0.097		ns	**	***	***	***
	GRN	N10	0.079	0.280	0.159	0.265	0.102	0.409	0.225	0.018	0.531	0.484	0.023	0.000	0.143	0.201	0.353	0.062	0.051	0.112	0.047	0.046	0.063	0.053	0.005		*	***	***	***
	Bahon	N11	0.053	0.134	0.064	0.157	0.027	0.261	0.076	0.082	0.404	0.351	0.089	0.050	0.020	0.231	0.207	0.002	0.146	0.078	0.087	0.000	0.049	0.038	0.064	0.038		**	***	***
		N12	0.297	0.056	0.168	0.090	0.214	0.008	0.100	0.439	0.037	0.000	0.458	0.509	0.174	0.587	0.017	0.378	0.559	0.550	0.431	0.358	0.325	0.452	0.454	0.441	0.311		ns	ns
		N13	0.382	0.121	0.252	0.175	0.302	0.088	0.188	0.519	0.148	0.084	0.547	0.595	0.261	0.659	0.094	0.460	0.634	0.621	0.525	0.448	0.408	0.534	0.538	0.531	0.405	0.067		ns
		N14	0.374	0.109	0.238	0.158	0.291	0.051	0.169	0.513	0.057	0.037	0.540	0.588	0.246	0.653	0.068	0.453	0.628	0.615	0.519	0.441	0.402	0.527	0.531	0.524	0.396	0.000	0.025	

Table S8. Correspondence between genetic groups defined on KASP SNP data or HiPlex haplotype data. Genetic groups were determined for Haitian and reference samples of *Coffea arabica* based on an 80% threshold of membership in ancestral populations determined by population structure analyses at K=7 and K=6 for HiPlex and KASP genotyping, respectively. Data is presented as number of samples from any KASP group that is assigned to a HiPlex group, and percentage so that the sum of percentages for each KASP group amounts to 100%.

		KASP SNP data						
	Group	**Typica-like (N=252)**	**CR95/ Catimor-like (N=72)**	**« Unlabeled » Haitian samples (N=51)**	**Bourbon-like (N=32)**	**Ethiopian-like (N=20)**	**Kent/I-60-like (N=8)**	**Admixed (N=249)**
HiPlex haplotype data	**HiPlex1 (N=241)**	**198 (78.6%)**	9 (12.5%)	6 (11.8%)	6 (18.8%)	-	0.0	22 (8.8%)
	HiPlex2 (N=71)	9 (3.6%)	**50 (69.4%)**	1 (2.0%)	-	-	**2 (25.0%)**	9 (3.6%)
	HiPlex3 (N=51)	4 (1.6%)	1 (1.4%)	**31 (60.8%)**	1 (3.1%)	-	0.0	14 (5.6%)
	HiPlex4 (N=30)	1 (0.4%)	-	2 (3.9%)	1 (3.1%)	-	0.0	26 (10.4%)
	HiPlex5 (N=26)	5 (2.0%)	1 (1.4%)	-	**15 (46.9%)**	-	0.0	5 (2.0%)
	HiPlex6 (N=17)	-	-	-	-	**15 (75.0%)**	0.0	2 (0.8%)
	HiPlex7 (N=4)	-	2 (2. 8%)	-	-	-	**2 (25.0%)**	0.0
	Admixed (N=244)	35 (13. 9%)	9 (12.5%)	11 (21.6%)	9 (28.1%)	5 (25.0%)	**4 (50.0%)**	**171 (68.7%)**

Supplementary Note: HiPlex read processing bioinformatics pipeline

HiPlex reads were mapped onto each of the two subgenomes of the *C. arabica* reference genome sequence v0.6 of the accession ET-39 (Salojärvi et al., in press) using the BWA-MEM algorithm in BWA v0.7.17 (Li, 2013) with default settings. To correctly classify reads to the respective *C. arabica* subgenomes, a genome read categorization approach was applied using a customized script by Bawin (2020), available on GitLab (https://gitlab.com/ybawin/sequence-data-processing-tetraploids). After filtering out ambiguously mapped reads, new 'categorized' read mapping (BAM) files were created with only high quality (subgenome-specific) mapped reads. These BAM files were indexed with Samtools v1.10 (Li et al., 2009), and read groups were added with Picard v2.18.25 (Picard Toolkit, 2019). Single nucleotide polymorphisms (SNPs) were called with GATK (Genome Analysis Toolkit) Unified Genotyper v3.7.0 (McKenna et al., 2010). SNPs were filtered using the following parameters: min-meanDP 30, mac 4, and minQ 20, and multi-allelic SNPs were removed with GATK. The remaining SNPs were then subjected to further filtering with the following parameters: minDP 10, minGQ 30, minQ 30, min-alleles 2, max-alleles 2, and maf 0.05 using VCFtools v0.1.16 (Danecek et al., 2011). Read-backed haplotyping was conducted based on SNPs in the HiPlex read data using module *SMAP haplotype-sites* of the SMAP software package v4.2.0 (Schaumont et al., 2022, https://gitlab.ilvo.be/genomics/smap) with mapping_orientation ignore, partial exclude, no_indels, min_read_count 10, min_distinct_haplotypes 2, min_haplotype_frequency 5, discrete_calls dosage, frequency_interval_bounds 10 10 90 90, dosage_filter 2, and completeness 30. Genotype tables were then filtered to exclude loci with missing data in >30% of Arabica samples, then individuals of all species with >30% missing genotype data.

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Transition to Chapter II

(And historical notes)

The uncovering of unexpectedly high levels of coffee genetic and varietal diversity (higher in fact than most farmers recognize) in Haitian agroforestry systems raises the question of why and how this diversity came to be. We were therefore interested in understanding how historical forces might have shaped the composition and structure of this diversity. This provided an opportunity to link population genetics with **environmental history**. There is a well-established, robust tradition within the field of History to study natural resources and the social, political, cultural and ecological forces that have shaped them (Cronon, 1993). In fact, historians have taken much interest in coffee's cultivation, trade and ethnobotany (Ukers, 1922; McCook, 2006, 2017; Friis, 2015). For their part, geneticists have taken an interest in historical changes in crops as revealed through genetic analyses (Bonnin *et al.*, 2014; Pont *et al.*, 2019; Balfourier *et al.*, 2019).

I gained access to data from a Guadeloupean coffee genotyping study done using (mostly) the same KASP genotyped SNP markers, generated during a project on Guadeloupean coffee, and with it, to the opportunity to compare the genetic resources of Haiti and Guadeloupe. Guadeloupe and Haiti share similarities in their history: both lands were acquired by France following the colonization and subjugation of native populations, and were developed into plantation economies through the labor of enslaved people. The native populations were thus replaced by European colonists, imported Africans, and their descendants, giving rise to creole cultures that retain similarities in present day. However, starting in the XIX^th^ century, Guadeloupe and Haiti went down very different historical paths. This similarity and subsequent divergence in histories provided the chance to consider the past and present factors that shaped the diversity and structure of their coffee trees in a comparative manner. The second chapter discusses these differences in history as pertains to coffee genetic and varietal composition. However, it is interesting to gain a better understanding of the history of Guadeloupean coffee cultivation and trade more generally, as a parallel to that of Haiti, which was explained in the general introduction. Therefore, I will here provide a somewhat more detailed historical account.

A short history of Guadeloupean coffee

After France acquired Guadeloupe in 1635, it began producing crops such as sugarcane and cotton, but entered a phase a great crop diversification in the 1720s (Kopp, 1929; Hoy, 1962). Coffee cultivation thus began on the island in 1726 and quickly grew to historic highs in that century. Indeed, 3000t were exported from the island in 1777. However, the global market became unable to absorb these quantities, leading to an overproduction crisis which, combined with agricultural policies that favored sugarcane over coffee, greatly reduced the latter's area of cultivation. The XIXth century brought additional political instability in metropolitan France as well as the colonies (Lafleur, 2006), with the French revolution, slave revolts, English incursions into Guadeloupe, as well as the eventual abolition of slavery further diminishing the island's coffee production. As another wave of French colonialism expanded into Africa, coffee plantations were started there in the 1830s and began competing with Caribbean coffee. In fact, because Antillean coffee was subject to more advantageous tariffs, African coffee was often transported there before being reexported to Europe, while agricultural policies continued to cause a reduction in export crops (save the sacrosanct sugarcane) and the polarization of farm sizes towards large plantations and small family-worked farms. Finally, XIXth century coffee growers also had to contend with pests and pathogens which relentlessly attacked their trees (Lafleur, 2006).

The XXth century was also one of turmoil for coffee growers. Guadeloupean coffee enjoyed an excellent reputation which caused reportedly “inferior” coffee from Brazil and Haiti to be exported through the island under false designation of origin (Lafleur, 2006). The fame of Guadeloupean Arabica coffee came in part from the traditional and idiosyncratic institution of the *bonifierie*, in which the beans were processed (Dulcire, 2005). Guadeloupe coffee exports rose in the early XXth century, but this rebound was short-lived. The two World Wars greatly hindered coffee exports, while major hurricanes in 1921 and 1928 damaged the farms, so that in 1929 Guadeloupe produced only one-fifth of the amount it exported in 1777 (Lafleur, 2006; Desarthe, 2020). That year, the coffee farms were described thusly: they were small, mostly concentrated on Basse-Terre’s Windward coast, and suffering from improper management and lack of labor supply (Kopp, 1929). Repeated periods of price drops in the global coffee stock exchange, as well as the departmentalization of Guadeloupe by France (and accompanying wage raises) further reduced coffee’s profitability and therefore the sector’s vitality. The rise of banana as a major export crop around the 1930s also competed with coffee (Lalanne, 1934). By 1962, Guadeloupe’s agriculture was mainly centered around sugarcane and banana as export crop, as well as subsistence crops in homegardens. By 2005, Guadeloupe only exported 20-30t of coffee grown on about 100-120 ha. This decline has not weakened the cultural importance of the crop to the island’s inhabitants as evidenced by the festivals, museums, and oral recollections of the crop’s glorious past (Dulcire, 2005; Lafleur, 2006; Breton, 2017). Coffee still contributes to rural livelihoods in Guadeloupe, and, as in Haiti, many growers express a desire to see the crop revitalized (Dulcire, 2005; Kiki, 2015; Chaumeil, 2023; Mazardin & Saj, 2023).

How it happened:

The Haitian data generated for Chapter I was reused, while the Guadeloupe data was generated by Lucile Toniutti and Frédéric Georget for a RITA project which the former chaired. As a result of prior concertation between Lucile Toniutti, Valérie Poncet and Dapeng Zhang (who defined the markers), the Haiti and Guadeloupe genotyping targeted (almost entirely) the same marker set, and KASP SNP genotyping of Guadeloupean samples was also conducted by LGC BioSearch. I then took charge of combining the data (removing non-corresponding markers), generating the three sub-datasets used in Chapter II, and performing the genetic analyses. I also conducted the bioclimatic envelope analyses, as well as the search for historical information to produce the history and chronogram of coffee resources on the island, with support from the co-authors of the article.

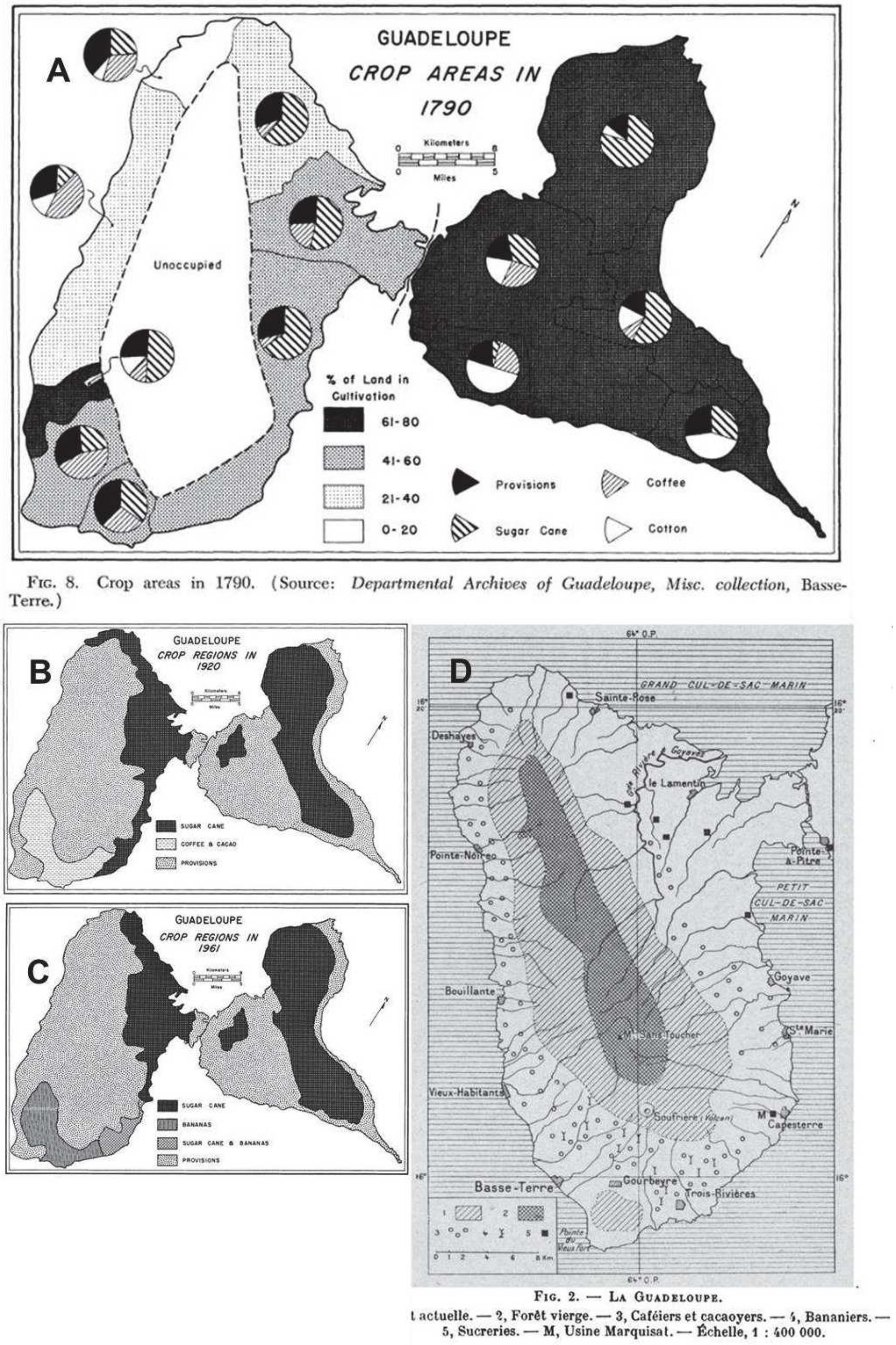

Figure 1. Place of coffee in Guadeloupe's agriculture, 1790-1961. A. Crop areas of Guadeloupe, with Coffee as lighter hatched surfaces in pie charts. B. Crop regions of Guadeloupe, 1920, with coffee as lighter grayed surface. C. Crop regions of Guadeloupe, 1961, showing near complete replacement of coffee by banana. A-C taken from Hoy (1962). D. Map of Basse-Terre, Guadeloupe *circa* 1929, showing coffee farms (open circles). Taken from Kopp (1929).

Chapter
II

Chapter II

Guadeloupe and Haiti's Coffee genetic resources reflect the crop's regional and global history

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Summary

- The West Indies, particularly former French colonies like Haiti and Guadeloupe, were central to the spread of coffee in the Americas. The histories of these Islands are shared until the XIXth century, where they diverged significantly. Still, both Islands experienced a strong decline in their coffee sector. Characterizing the genetic and varietal diversity of their coffee resources and understanding historical factors shaping them can help support revitalization efforts.

- To that end, we performed KASP-genotyping of 80 informative SNP markers on field samples from across main coffee-growing region of Guadeloupe, and two historically important ones in Haiti, as well as 146 reference accessions from international collections. We also compared bioclimatic variables from sampled geographic areas, and searched for historical determinants of present coffee resources.

- At least 5 *Coffea arabica* varietal groups were found in Haiti, versus 2 in Guadeloupe, with admixed individuals in both. The traditional Typica variety is still present in both islands, growing across a variety of climatic environments. We also found *C. canephora* on both islands, with multiple likely origins, and identified *C. liberica var. liberica* in Guadeloupe.

- These differences are explained by the Islands' respective histories. Overall, Guadeloupe experienced fewer, but older introductions of non-Typica coffee. By contrast, several recent introductions have taken place in Haiti, driven by local and global factors and reflecting the history of Arabica varietal development and spread. Diversity on these islands is dynamic, and our results reveal opportunities and limits to the future of Guadeloupean and Haitian Coffee.

Keywords: Agrobiodiversity, Arabica, Coffee, Guadeloupe, Haiti, Historical determinants, Typica, Varietal diversity

Societal Impact statement

Despite strong historical declines, Guadeloupe and Haiti's coffee sectors remain important to rural communities' livelihood and resilience. Coffee also holds value as part of the islands' historical legacy and cultural identities. Furthermore, it is often grown in agroforestry systems providing important ecosystem services, which will become more important as these vulnerable islands work to adapt to a changing climate. Current efforts to revitalize coffee farms and target strategically-important specialty markets would benefit from understanding existing genetic resources and the historical factors that shaped them. Our study reveals the rich history reflected in current coffee stands on the islands.

Societal Impact statement (French version)

Malgré un fort déclin historique, les filières caféières guadeloupéenne et haïtienne font partie intégrante de la vitalité économique des communautés rurales, de l'identité culturelle et du patrimoine historique de ces îles. De plus, les caféiers y sont généralement cultivés dans des systèmes agroforestiers fournissant de nombreux services écosystémiques, et qui seront des leviers d'adaptation aux changements climatiques. La caractérisation des ressources génétiques caféières de ces îles (et des facteurs historiques les ayant façonnées) appuieront les tentatives de revitalisation de la caféiculture. Cette étude met en lumière les nombreuses mutations historiques qui se reflètent dans la composition des peuplements de caféiers actuels.

1. Introduction

The history of agriculture is also that of the management and spread of plant genetic resources. Cropping systems shape crop genetics, and are in turn shaped by them. As such, cultivated plant genetic diversity and structure can both reveal and be explained by cultivation history (e.g. Magris et al. 2021; Costa et al. 2022; Helmstetter et al. 2020). This has proven true for Coffee, a major perennial crop (Fig. 1). Ethiopian Highlands are the center of origins of Arabica coffee (*Coffea arabica* L., Rubiaceae) but cultivation and trade was mostly developed by Yemen before the XVIIth century (hence the species name, (Ukers, 1922; Friis, 2015). From there, it spread worldwide along two main routes, giving rise to two major cultivated lineages (Anthony *et al.*, 2002). The first passed through Tropical Asia to eventually reach the Americas, producing the Typica lineage, and the second through Bourbon (Reunion) Island to produce the Bourbon lineage, later widely spread. Each step led the crop trough important genetic bottlenecks, resulting in a loss of diversity (Anthony *et al.*, 2002; Salojärvi *et al.*, 2024). Another species, *C. canephora* Pierre ex. Froehner or "Robusta", has a wide wild distribution in African rainforest, and was spread beyond its center of diversity in the XXth century as a response to pathogen pressures on Arabica (Montagnon *et al.*, 1998; Verleysen *et al.*, 2023). Today, Arabica makes up 60% of world coffee production, with Robusta accounting for much of the rest (International Trade Centre, 2021). A third species, *C. liberica* Hierns, is farmed in modest proportions (Ferreira *et al.*, 2019) though its cultivation predates that of Robusta by decades (Morris, 1881; Ukers, 1922). Today, coffee trees are pantropical, and grown in varied systems ranging from complex, diversified and shaded agroforestry systems (such as traditional homegardens), to full-sun, intensively-managed commercial monocultures (Toledo & Moguel, 2012; Poncet *et al.*, 2024). This economically vital crop is increasingly threatened by global climate change (Bunn *et al.*, 2015; de Sousa *et al.*, 2019; Tournebize *et al.*, 2022) and faces concerns over the agricultural commodity system's human and ecological costs, creating a need for greater resilience, adaptability and sustainability of coffee cultivation (Poncet *et al.*, 2024).

1.1. Arabica Coffee: history in the West Indies

As the entry point of coffee in the Americas, the Caribbean region played an important role in the process of Coffee's circumtropical spread. Despite prior unsuccessful attempts, the history of coffee in the West Indies definitively began in 1723 when the naval officer De Clieu introduced *C. arabica* to Martinique, from the offspring of a tree gifted by the Dutch to the French king (Ukers, 1922). From there, it was propagated to other French colonies, including Guadeloupe and to Saint-Domingue (now Haiti) in 1726. From these and Suriname, where it had been introduced in 1718 by the Dutch, it would spread throughout the Neotropics, eventually becoming a crop of global importance. While they are no longer major players in the global coffee trade, the West Indies were once important centers of production. As the final, drastic bottleneck experienced by the Typica lineage, the genetic legacy of the crop's introduction to the region has left its mark on modern Arabica diversity. Nevertheless, little work has been done on the genetic resources of coffee present in these regions, particularly in the former French colonies which were historically so important to the global coffee trade.

1.2. Guadeloupe and Haiti: common, then divergent histories

Guadeloupe and Haiti (hereafter "the Islands", despite Haiti being only part of Hispaniola Island) both played a major role in the early cultivation and spread of coffee in the Americas. They also share similarities in their socio-political history: both were French colonial, Slave labor-powered plantation economies. Both Islands' native populations were replaced by European colonists, enslaved Africans, and their descendants, giving rise to similar creole cultures. However, the Islands' fates diverged significantly in the XIXth century. Guadeloupe remained a colony until antiimperialist efforts led to full status of French Overseas Department in 1946. By contrast, a successful Slave rebellion in Saint-Domingue led to the Republic of Haiti becoming an independent nation in 1804, escaping direct colonial rule (though not foreign powers' spheres of economic and geopolitical influence). Since then, the history of Haiti has been marked by socio-political instability, pervasive inequalities and rampant poverty, even during periods of relative agricultural vitality, and worsening environmental crises. Therefore, despite socio-economic issues of its own, Guadeloupe enjoys greater political stability and human development than Haiti. The Islands' social, economic and political histories, first shared, then divergent, are reflected in the history of their agricultural sector. As such, they have shaped the various aspects of coffee cultivation on the Islands.

Coffee cultivation began on Guadeloupe in 1726 and quickly grew to historic highs (3000t exported in 1777, harvested from >8 million trees), followed by an overproduction crisis (Kopp, 1929; Lafleur, 2006). Since that time, the extent and productivity of coffee farms has mostly receded from various causes such as XIXth-century political upheavals, unfavorable policies, frequent biotic attacks, XXth-century turmoil (World Wars, economic crises), major hurricanes (e.g.1921, 1928) and the rise of banana cultivation (1930s) as a main export crop (Kopp, 1929; Hoy, 1962; Lafleur, 2006). By 2005, Guadeloupe only exported 20-30t of coffee grown on about 100-120 ha (Lafleur, 2006). Still, Guadeloupean coffee has historically enjoyed an excellent reputation. It is known as *Café bonifieur*, in reference to the *bonifieries* which are traditional coffe-processing establishments unique to Guadeloupe.

Coffee was also introduced to Saint Domingue in 1726 and thrived in the island's abundant mountains. Farms were established as full-sun monocultures, to the detriment of forest and soil health (Ukers, 1922; Trouillot, 1982; De Bivar Marquese, 2022). The colony quickly became the major coffee producer until the 1790s Haitian Revolution laid waste to plantations. Though production recovered and exports continued to be the main driver of newly independent Haiti's economy (Lundahl, 1984), coffee systems transitioned to small, highly fragmented, diversified farms. Peasant farmers were vulnerable to global and local economic and political inequities, as well as pests, pathogens, extreme weather events, and soil erosion (Moral, 1955; Plummer, 1984; Dupuy, 1989; Amaya *et al.*, 1999). The sector's vitality diminished throughout the XXth into the XXIth century. A proliferation of internationally-funded development proposed, and failed, to strengthen Haitian agriculture (Ester, 1978; Eitzinger *et al.*, 2019).

1.3. The present state of the coffee in the Islands

Despite its precipitous decline, Guadeloupean coffee remains an appreciable supplement to rural livelihoods (Dulcire, 2005), and still holds cultural importance to its inhabitants (Dulcire, 2005; Lafleur, 2006; Breton, 2017). In recent years, there has been renewed interest in expanding coffee cultivation in Guadeloupe. With crop diversification being a potential response to the growing need for greater sustainability in Banana cultivation, greater integration of coffee's part in these systems has been suggested (Tarsiguel *et al.*, 2023). These initiatives, started by growers' cooperatives, have gained support from several stakeholders such as local government, scientific and private sector institutions. However, the viability of this undertaking is still debated, and the various growers themselves have contrasting views and priorities

(Dulcire, 2005). Similar efforts exist in Haiti, and are also faced with considerable difficulties. While some growers are able to export their coffee for the niche, gourmet market under the label “Haitian Blue”, most farms, including in historical strongholds, struggle to maintain production (Amaya *et al.*, 1999; Agricultural Risk Management Team, 2010). Most Haitian coffee farms have a low management intensity, with coffee stand regeneration happening mostly through spontaneous seed bank germination. Such systems are crucial to maintaining Haiti’s forest cover (Feller *et al.*, 2006) and rural livelihoods (Steckley & Weis, 2016).

1.4. The need to characterize the local structure and diversity of coffee, and their determinants

From similar beginnings, the histories of Guadeloupe and Haiti’s coffee sectors unfolded in drastically different ways. In the present, these Islands share a common desire for the crop’s revitalization through agroforestry, though these efforts will unfold in highly contrasted economic, social, governmental and cultural contexts. These factors entail a need for greater knowledge of the Islands’ coffee genetic resources, but also of their historical determinants and environmental context. The agrobiodiversity contained in traditional systems can be leveraged to help achieve these goals, and there is a need for greater scientific understanding of this topic. Development and greater availability of genetic study methods has promoted the study of local diversity for Arabica (e.g. Zewdie et al. 2022; Anthony et al. 2001) and Robusta (Vi *et al.*, 2023) alike. In particular, targeted genotyping of known polymorphic regions is a cost-effective and useful way to study Coffee diversity (Verleysen *et al.*, 2023; Millet *et al.*, 2024).

There is much value to characterizing crop genetic diversity: by taking stock of existing resources, it can inform their management and decision-making to improve agrosystems. Furthermore, it provides an opportunity to consider the historical forces that have shaped them (Bonnin *et al.*, 2014). Writing about Latin American coffee cultivation, the historian McCook (2017) explains: “The structure of any coffee farm at any given moment is intensely historical and encompasses both local and global processes”. This can be expected of West Indian coffee farms as well, and particularly of their genetic resources. To what extent has the diversity of coffee in the Islands changed over time, and what is the present-day status of the historical Typica? In addition, understanding the bioclimatic context of these resources is of value, as such environmental conditions can affect quality (Bertrand *et al.*, 2012), and serve to differentiate products. In short, knowledge of history and of local environmental specificities not only provides lessons for planning the crop’s future, but can increase the commodity’s market attractiveness and value, including through labelling efforts.

Therefore, the present study aims to use targeted genotyping to the following aims: i) to determine the present genetic structure of the historically significant Typica variety in Guadeloupe and Haiti, ii) to characterize the overall local coffee tree genetic and varietal diversity, iii) to compare Arabica diversity between Islands, and to that held in international collections, iv) to interpret genetic data through a historical lens, and v) to characterize and compare the crop’s bioclimatic environments across study areas. The past and present determinants of the Islands’ coffee genetic resources will thus be discussed, as will the implications they hold for the crop’s future in the region.

2. Materials and Methods

2.1. Materials and Sampling

In Guadeloupe, sampling took place in 2022 in Basse-Terre, across the present extent of coffee cultivation, particularly along the southern part of *Côte Sous le Vent* (Leeward —western— coast). In total, 33 farms were prospected as part of a RITA project (*Réseau d'Innovation et de Transfert Agricole*). These were mostly historic coffee plantations that have been abandoned or reconverted into agroforests and polycultures, under organic or conventional management (Fig. S1). One sample was also obtained from a farm on a satellite island (Terre de Bas, Les Saintes) south of Basse-Terre. In total, 145 Guadeloupean samples were collected. We also used Haitian field sample data from Millet et al (2024), acquired in 2021 from the Nord (North) and Grande-Anse (Southern peninsula) departments. These historically important coffee regions (De Bivar Marquese, 2022) have since experienced severely diminished yields. 14 farms per department were visited with Haiti's Agricultural and Agroforestry Technological Innovation Program (PITAG). These were agroforests of varying levels of complexity and coffee stand age, with virtually no chemical inputs. 620 Haitian samples were thus included in the study. The larger sampling size in study areas of Haiti is reflective of their much greater geographic extent.

Figure S1. Photographs indicative of the cultivation context of Coffee (*Coffea*) in Guadeloupe. A. Banana-Coffee polyculture system. **B.** Young coffee (potentially "Mocha"-type Typica) germinating naturally in agroforest in Caillou Lamentin, Guadeloupe **C.** Coffee agroforest on Basse-Terre, Guadeloupe

Sampling on both Islands was done in collaboration with farmers, and aimed to maximize represented diversity in the study areas, including all putative (reported) varieties. Healthy, mature leaves were collected from plagiotropic axes, dried and preserved in silica gel before conditioning for DNA extraction.

2.2. Reference samples

Leaf samples were obtained for reference individuals of commercial and wild coffee from the CATIE international coffee germplasm collection (Turrialba, Costa-Rica) and IRD (Montpellier, France). In addition, genotype data was acquired from HARC collection (Hawaii, USA) provided by USDA-ARS, SPCL (Beltsville, MD, USA), and from studies by Mérot-L'Anthoëne et al. (2019). Finally, sequencing data was obtained for the Arabica lectotype (Linnaean herbarium sample BM000558021), as well as a Costa Rica 95 specimen, from a recent study (Salojärvi *et al.*, 2024).

In total, the reference sample set contained 123 *C. arabica* individuals encompassing several wild accessions, historical and modern commercial varieties, F1 hybrid cultivars, in addition to the Linnean sample. Also included were 18 *C. canephora* from several geographically-determined genetic groups, *one C. liberica var. liberica*, two *C. liberica var. devrewei* and two *C. congensis* (Table S1).

2.3. Genotyping

We applied the genotyping sequencing method to genotype the accessions at 80 core SNP selected by Zhang et al. (2021) from the Mérot-L'Anthoene et al. (2019) array on the basis of their ability to discriminate across several commercial and wild *C. arabica* accessions.Mérot-L'Anthoene et al. (2019) previously produced a DNA array for Coffea in which 945 biallelic SNP were specifically selected to assess diversity within *C. arabica*. Of these, Zhang et al. (2021) identified a core set of markers polymorphic across a panel of commercial and wild Arabica accessions, including many references included in the present study. The marker information and sequences are provided in Table S2. Processing of field and reference leaf samples, from DNA extraction to selective KASP assay genotyping of target markers, was performed using a proprietary protocol by LGC Biosearch Technologies (Middlesex, UK). 27 Arabica and 2 Liberica (one of each subspecies) were repeatedly genotyped as duplicates. Duplicate reference samples were compared to exclude a few loci with >1 difference between repeats. Genotype information from duplicate samples were then combined into "consensus" samples with fewer missing data (with the few loci having divergent calls considered missing data).

Because the markers were primarily designed for Arabica, other species had more missing data. Still, they were also informative for related species. Three marker subsets were selected to minimize trade-offs between individual data completeness and maximal inclusion of samples from all species to more fully characterize sampled diversity. We thus used three species-specific genotype sets.

In addition, genotype information at target loci were obtained for the Arabica and Robusta references from previously generated sequencing data. Target marker sequences were blasted onto the *C. arabica* reference genome sequence v0.6 of the accession ET-39 (Salojärvi *et al.*,

2024) to obtain positions which were used to extract genotype information from the Linnean and CR95 sequencing data from a VCF file.

2.3.1. “Arabica dataset”

All genotyped Arabica samples were combined, and loci missing in >30% of samples, then individuals with >26% missing genotypes were filtered out to produce the final dataset (field and reference samples, hereafter the “arabica dataset”). After all filtering steps, the “arabica” dataset contained genotype information at 80 loci for 834 individuals (Table S2) from Guadeloupe (N_{Gl}=111), Haiti (N_{Ht}=601) and international germplasm collections (N_{ref}=122).

2.3.2. “Liberica dataset”

There are two cultivated subspecies of *Coffea liberica*, which are quite genetically distinct (N’ Diaye *et al.*, 2005). To determine which ones were present in the study areas, after preliminary identification, putative Liberica field samples from Guadeloupe (N_{Gl}=6) were combined with *C. liberica* var. *liberica* (N_{ref}=1) and *C. liberica var. dewrevei* (N_{ref}=2) reference individuals, as well as two representatives from each other available species including *C. congensis* (outgroups), and a subset of markers with <30% missing data across these samples (40 in total) was selected to form the Liberica dataset.

2.3.3. “Robusta dataset”

We also sought to identify the possible origins of field *C. canephora* samples by comparing them to references from known geographic-genetic groups as defined in (Mérot-L’Anthoene *et al.*, 2019)9. References from groups A, D (West African), E, R (Central) and O (East) were combined with putative Haitian and Guadeloupean Robusta field samples into a Robusta-only dataset (34 samples: N_{Gl}=17, N_{Ht}=6 and N_{ref}=11). We used a subset of 58 markers available with <40% missing data across this sample group, this more permissive threshold increasing the chances of retaining informative loci for *C. canephora*..

2.4. Genetic analyses

We described each island’ coffee resources in terms of both diversity and varietal composition. Descriptive genetic diversity statistics were calculated on the Arabica dataset for North and Southwest Haiti, Guadeloupe, and across reference accessions using GenAlEx software v. 6.51b2 (Peakall & Smouse, 2012).

A Principal component analysis (PCA) was then performed on field and reference samples using the R packages LEA v. 3.10.2 (Frichot & François, 2015) and Tidyverse v. 2.0.0 (Wickham *et al.*, 2019) ggplot function to visualize the Islands’ coffee diversities in relation to that represented by reference accessions.

Varietal characterization of field samples was then carried out using a population structure analysis run with sNMF function (K=1-10, 100 repetitions) of the R package LEA v. 3.10.2. Varietal groups were defined using a 75% threshold of contribution from ancestral populations reconstructed at the most appropriate K value, and labeled according to reference samples assigned therein. Individuals with <75% contribution were considered admixed or of unclear varietal assignment.

An unweighted neighbor-joining dendrogram was constructed from a simple-matching distance matrix (1000 bootstrap replicates) calculated on the Arabica dataset Using DARwin v. 6.0.21 software (Perrier & Jacquemoud-Collet, 2006). Robusta individuals (N=26) were added to the tree as outgroups. This was then repeated by including the Linnaean sample and Costa-Rica 95 (Salojärvi *et al.*, 2024) in order to see the former's positioning in relation to the arabica diversity considered in this study.

Simple-matching distance matrices were independently calculated, and neighbor-joining trees constructed from the Liberica and Robusta datasets respectively, using DARwin v. 6.0.21.

2.5. Bioclimatic variables

In order to characterize the climatic contexts in which Guadeloupe and Haitian coffee grows, climate data (1970-2000 average) for the 19 standard Bioclimatic variables based on temperature and precipitation patterns, and elevation data were downloaded from Worldclim (version 2.1) at 30s resolution. Data at sampled coordinates was extracted with R package Raster (v 3.6-20). A PCA was performed (R function prcomp) and plotted with package *ggbiplot* (v. 0.55) to describe the climatic envelopes of the six following geographic zones: Basse-Terre's three *Ensembles Paysagers* (Nord Basse-Terre / Côte au Vent; Sud Basse-Terre and Côte sous-le-Vent, (Région Guadeloupe & DEAL Guadeloupe, 2011) and Haiti's Nord, western Grande-Anse and eastern Grande-Anse.

2.6. Search for historical determinants of genetic structure

In order to interpret local genetic diversity through a historical lens, the results of the varietal characterization were used to guide iterative searches for sources providing historical insight regarding their introduction and cultivation on the Islands, primarily using Google Scholar (scholar.google.com), the Internet Archive (archive.org) and the Manioc digital library (manioc.org). We sought out contemporary scholarly work on both plant science and history, but also historical accounts, manuals, monographs, and development project reports.

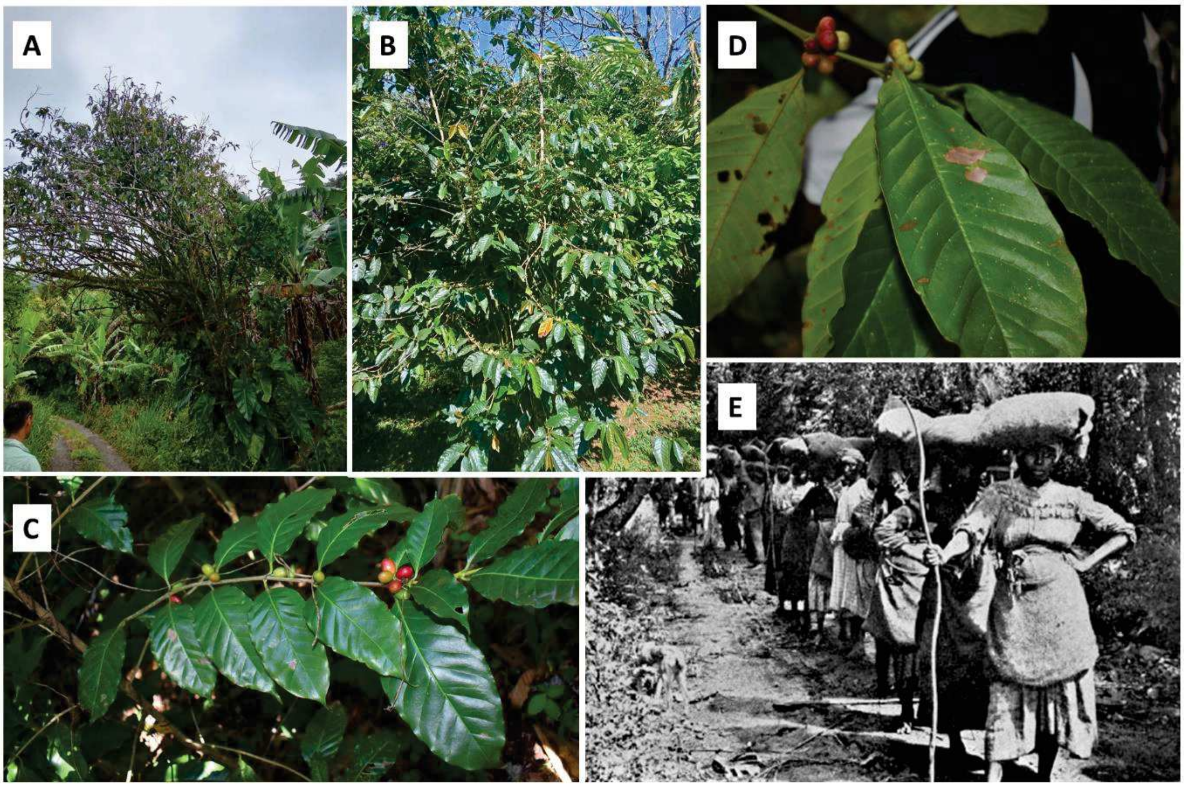

Figure 1. Photographs of Coffee in Guadeloupe and Haiti. A. old (>60 years) Typica (*Coffa arabica*) tree in a coffee-banana polyculture in Matouba, Guadeloupe. **B.** SL/Kenyan-like Arabica in Matouba, Guadeloupe. **C.** Cherries on low-yielding Typica branch in Northern Haitian agroforest. **D.** Robusta (*C. canephora*) cherries and leaves in Northern Haitian agroforest. **E.** Guadeloupean coffee pickers returning from the field circa 1920s, taken from Ukers (1922) and digitized by the Gutenberg Project (https://www.gutenberg.org/). Photo credits: A. and B. Lucile Toniutti, C. and D. Claude Patrick Millet.

3. Results

3.1. Arabica diversity analyses

We described and compared the levels of diversity of Guadeloupe and Haiti, and to that represented in international collections. Gene diversity (as expected heterozygosity, He) was highest for reference individuals (H_e= 0.384 ± 0.014 SE), slightly lower for North (H_e=0.340 ± 0.02) and Southwest (H_e=0.317 ± 0.02) Haiti, and lowest by far for Guadeloupe (H_e=0.093 ± 014, see also Table S3). This is consistent with the PCA plot, with references having the widest distribution, followed by Haitian samples (Fig. 2A, B).

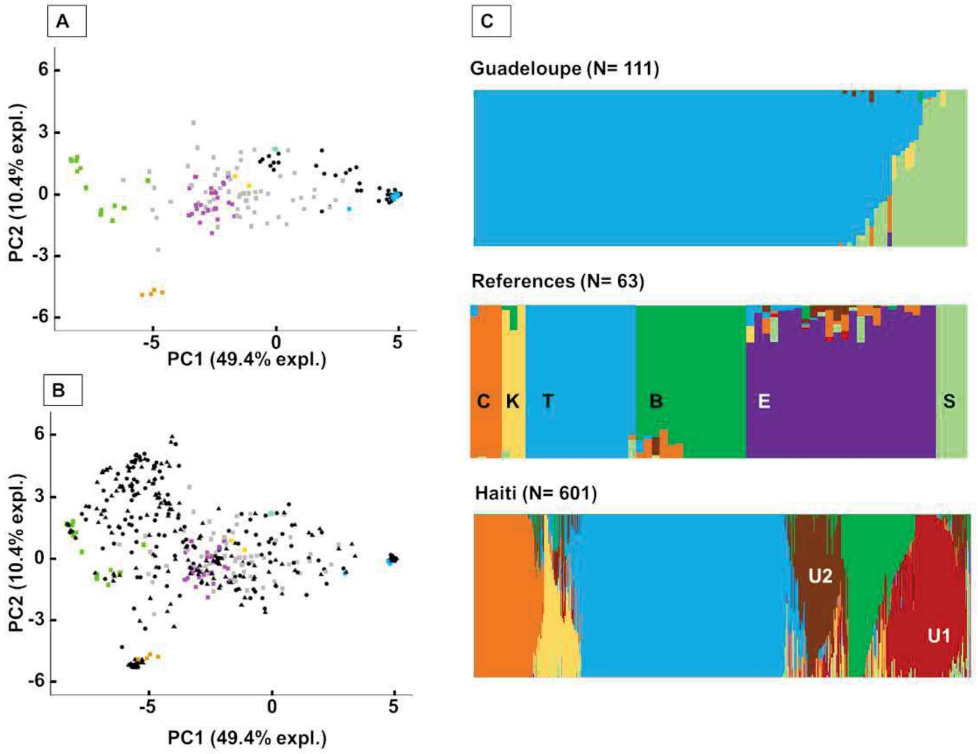

Figure 2. **Genetic structure and diversity of *Coffea arabica* from Guadeloupe and Haiti in relation to reference samples from international collections. A.** Plot of Guadeloupean (in black) and reference samples (all others) along the first 2 axes of a Principal Component Analysis performed on Guadeloupean, Haitian and reference samples. **B.** Plot of Haitian (in black) and reference (all others) samples along the first 2 axes of the same PCA. **C.** *C. arabica* population structure analysis at K=8 showing results for Guadeloupe (top), reference (middle) and Haiti (bottom) samples. Only references with >75% contribution from any one group are shown. Groups are labelled according to references assigned therein: C= CR95/Catimor-like, K= Kent/I60-like, T= Typica-like, B= Bourbon-like, E= Ethiopian-like, S= SL/Kenyan-like. Two groups were composed of only Haitian samples (U1= Unlabeled1 and U2=Unlabeled2). The reference individuals on the PCA plots (A. and B.) are colored according to the genetic groups described in C., with all references with <75% contribution from any group shown in gray.

Table S3. ***Coffea arabica* diversity statistics calculated on SNP genotyping data for the sampled regions of Basse-Terre Guadeloupe and Haiti (Nord and Grande-Anse departments)**: sample size, observed heterozygosity (H_o), expected heterozygosity (=gene diversity, H_e), Fixation index (as F_{IS}) and percent marker polymorphism (% P). Values calculated from reference *C. arabica* individuals (Arabica ref.) are included as a comparison. Where applicable, data is presented as Mean ± SD.

Group	**N samples**	H_o	H_e	F_{IS}	**% P**
Guadeloupe	111	0.050 ± 0.02	0.093 ± 0.01	0.570 ± 0.06	63.75%
Nord-Haiti	300	0.075 ± 0.01	0.340 ± 0.02	0.757 ± 0.04	93.75%

Grande-Anse, Haiti	301	0.097 ± 0.01	0.317 ± 0.02	0.660 ± 0.04	91.25%
Arabica ref.	122	0.152 ± 0.01	0.384 ± 0.01	0.588 ± 0.03	100.00%

3.2. Arabica varietal characterization

We assigned field samples to varietal groups using a population structure analysis on the arabica dataset. The latter had its lowest cross-entropy between 7 and 10, and increasing values up to K=8 allowed for the identification of distinct varietal clusters labeled according to reference samples included therein. Six of these groups included reference individuals and could thus be associated with known varieties, but two of them were composed of Haitian field samples exclusively and were thus unlabeled (Fig. 2C). The 8 arabica genetic varietal groups identified were as follows: a Typica-like group (N_{Gl}=91, N_{Ht}=247 and N_{ref}=14, Figs. 1.A; S2.A), a Bourbon-like group (N_{Ht}=29, N_{ref}=14), a CR-95/Catimor-like group (N_{Ht}=72, N_{ref}=4, Fig. S2.B), a Kent/I-60-like group (N_{Ht}=8 and N_{ref}=3), a SL/Kenyan-like group (N_{Gl}=11, N_{ref}=4, Fig. 1.B), an Ethiopian-like group (N_{Ht}=1, N_{ref}=24), and two unlabeled, Haiti-only groups (N_{Ht}=49 and 25 respectively). Several individuals (N_{Gl}=9, N_{Ht}=168, N_{ref}=59) had <75% contribution from all groups, and were thus considered admixed. These groupings are also consistent with the distribution of individuals on the PCA plot (Fig. 2).

The clustering of samples on the “Arabica” neighbor-joining dendrogram is also in agreement with the population structure analysis (Fig. 3). Using *C. canephora* samples as outgroups, wild Ethiopian individuals are basal, and followed by the split of cultivated Arabica into two main lineages with Typica and Bourbon individuals, respectively. The dendrogram shows correct sample clustering according to their assigned varietal groups, with the exception of one of Haitian Unlabeled group (hereafter “Unlabeled2”). “Unlabeled2” individuals were split across the two main branches of cultivated Arabica. Guadeloupean SL/Kenyan-like samples clustered together and with references from that group. Pairwise F_{st} between genetic groups show them to be well-differentiated (Table S4).

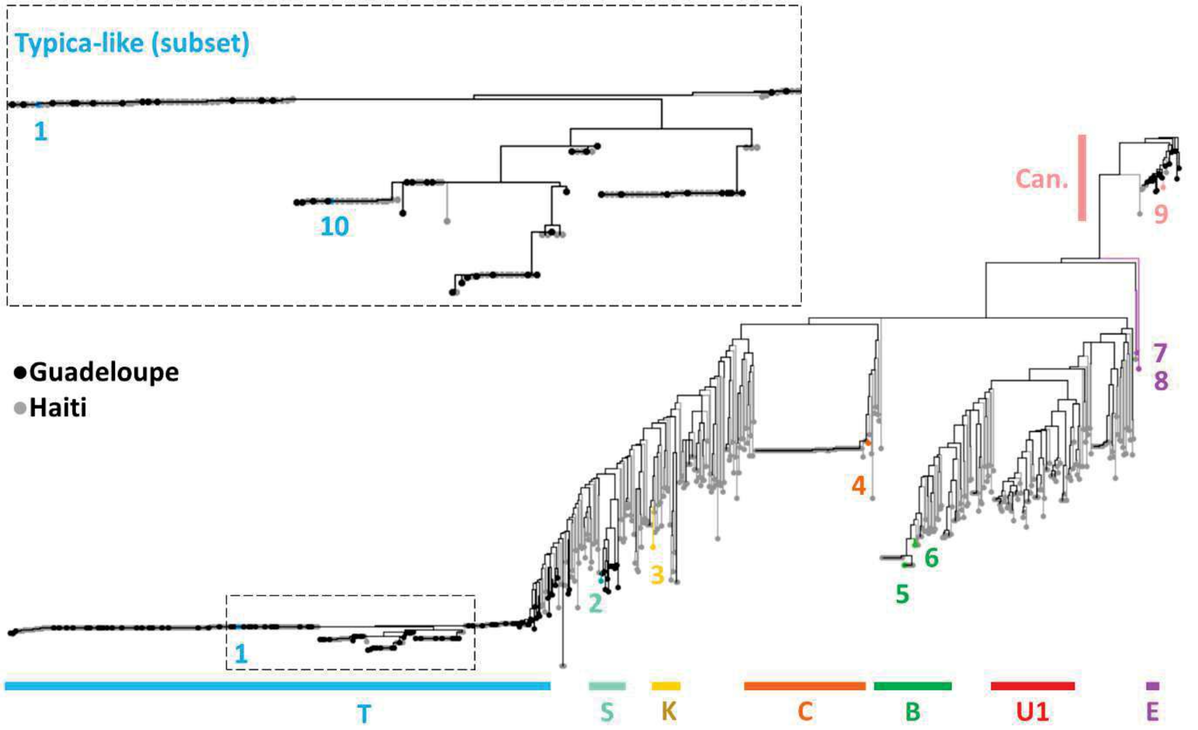

Figure 3. Unweighted Neighbor-joining dendrogram of Guadeloupe (in black)**, Haitian** (in grey) and **reference** (in color) ***C. arabica* and *C. canephora* individuals**. Calculated from simple-matching distance matrix. Colored bars represent varietal groups identified by sNMF population structure analysis: C= CR95/Catimor-like, K= Kent/I60-like, T= Typica-like, B= Bourbon-like, E= Ethiopian-like, S= SL/Kenyan-like U1= Unlabeled1 (Haiti-only) group, plus Can.=Canephora outgroups. A portion of the Typica branch is magnified (in frame). To aid legibility, a few representative reference individuals are included, colored according to their assigned varietal group (excluding Canephora) as identified by sNMF population structure analysis. These are: 1. (Ku214) Typica/Jamaica Blue Mountain, 2. (T.04313) SL28, 3. (T.04268) Kent, 4. (T.08667) CR95, 5. (Mw264) PR6791/Bourbon Select, 6. (T.02542) Caturra, 7. (T.04667) E-160, 8. (T.04290) Jimma Kaffa, 9. (GUI2) Guinean *C. canephora*, 10. (T.00990) Surinam.

Typica-like individuals clustered together indiscriminately of origin. In fact, identical genotypes at all loci were found across several locations in Haiti (both departments) and Guadeloupe, as well as among reference individuals of different origins. The dendrogram including the sequenced samples (Fig. S3) shows the correct placement of the Costa-Rica 95 control, and the Linnaean sample being closest to the Typica cluster.

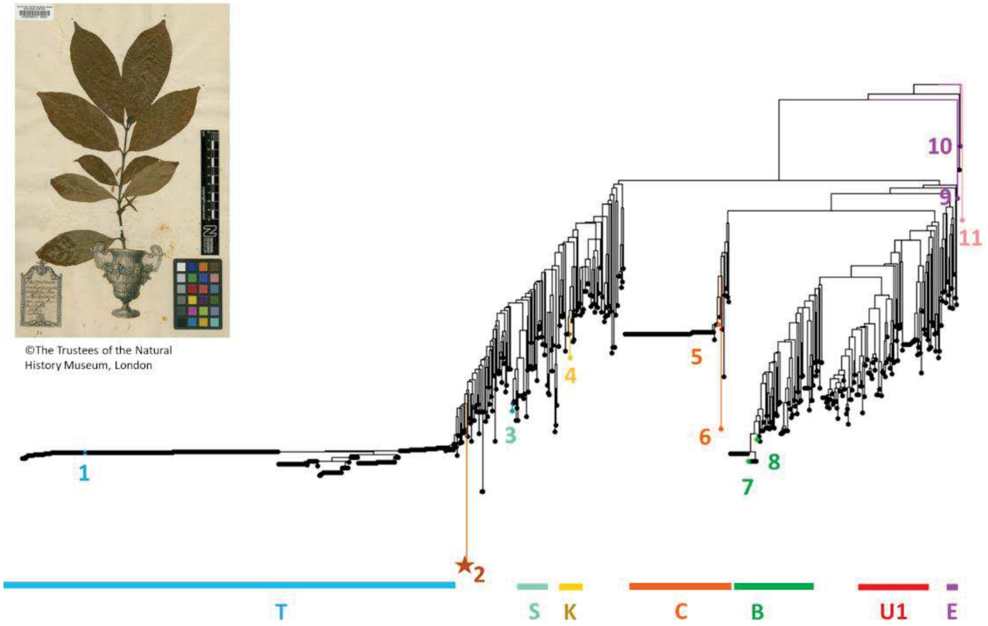

Figure S3. Unweighted Neighbor-joining dendrogram of field (in black) **and collection** (in color) ***C. arabica* with “Linnaean” sample (Arabica lectotype,** star symbol**)**. Calculated from simple-matching distance matrix. Colored bars represent varietal groups identified by sNMF population structure analysis: C= CR95/Catimor-like, K= Kent/I60-like, T= Typica-like, B= Bourbon-like, E= Ethiopian-like, S= SL/Kenyan-like U1= Unlabeled1 (Haiti-only) group. Reference individuals are colored according to their assigned varietal group (excluding Canephora) as identified by sNMF population structure analysis, and are the following: 1. (Ku214) Typica/Jamaica Blue Mountain, 2. Linnean *C. arabica* lectotype (LINN32) 3. (T.04313) SL28, 4. (T.04268) Kent, 5. (T.08667) CR95, 6. CostaRica95 (Salojärvi *et al.*, 2023) 7. (Mw264) PR6791/Bourbon Select, 8. (T.02542) Caturra, 9. (T.04667) E-160, 10. (T.04290) Jimma Kaffa, 11. (GUI2) Guinean *C. canephora* (outgroup). Image insert is the Linnaean BM000558021 lectotype, released under the CC BY 4.0 DEED license by the Trustees of the Natural History Museum, London.

Table S4. Genetic differentiation between varietal groups. Pairwise F_{ST} between identified *Coffea arabica* genetic groups calculated on Guadeloupe, Haitian and Reference samples based on a 75% threshold of inclusion (N=598). All p-values ≤0.001 at 999 repetitions.

	Bourbon-like	**CR95-like**	**Ethiopian-like**	**Kent/ I60-like**	**SL/Kenyan-like**	**Typica-like**	**Unlabeled 1**
Bourbon-like							
CR95-like	0.805						
Ethiopian-like	0.646	0.754					
I60/Kent-like	0.503	0.736	0.355				
SL/Kenyan-like	0.721	0.871	0.541	0.331			
Typica-like	0.923	0.919	0.850	0.758	0.822		
Unlabeled1	0.612	0.771	0.579	0.460	0.637	0.885	
Unlabeled2	0.654	0.699	0.401	0.312	0.547	0.836	0.479

Our results show there is less diversity and fewer varietal groups in Guadeloupe than in Haiti, but both Islands share the historical Typica variety, which is widespread in all coffee-growing regions.

3.3. Identification of Robusta genetic groups of origins

On the “Robusta-only” dendrogram, field individuals did not all cluster together with references from any single genetic group, nor were samples from the same island or indeed the same farm grouped together (Fig. S4). Field samples clustered with references from groups D (Upper Guinean), A (“Conilon”, Congo-Brazza), E/R (RDC), and O (Ugandan) but were often positioned more basally, suggesting admixture with contribution from several geographically-determined genetic groups. Robusta samples were found on only one (Northern) Haitian farm, but were present throughout Basse-Terre in Guadeloupe

3.4. Identification of Liberica samples to subspecies level

On the “Liberica” dataset dendrogram (Fig. S5), Guadeloupe field samples clustered with *C. liberica* subspecies *liberica* but not *C. liberica dewrevei*. These samples originated from locations across the study area. No Haitian sample belong to either subspecies.

3.5. Islands coffee composition

Nearly all Arabica varietal groups were present and widely distributed in Haiti, with farms ranging from one to five varietal groups, but Robusta was found on only one farm, and Liberica is absent. By contrast, only the Typica and SL-like groups were present in Guadeloupe, but both Robusta and Liberica were found across coffee-growing areas of the island (Fig. 4). The historical Typica variety is present in all six geographic zones.

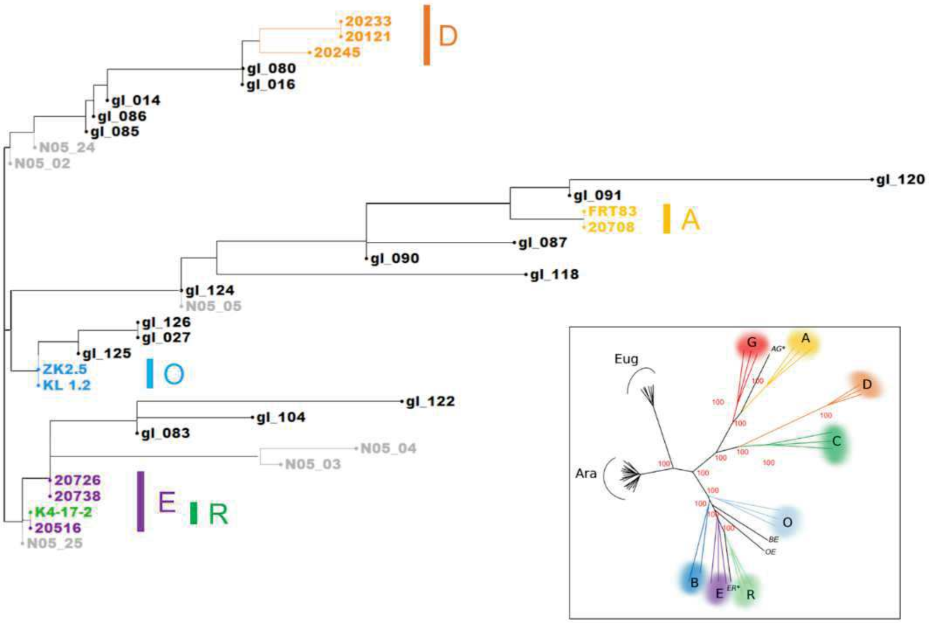

Figure S4. Unweighted neighbor-joining dendrogram of *Coffea canephora* field and reference samples. Calculated on a simple-matching distance matrix. Guadeloupe (gl) samples are in black, Haitian samples (N=Nord department) in grey. Colored points represent reference samples taken from Mérot-L'Anthoene et al. (2019) representing different geographically-determined genetic groups of wild Canephora (indicated by the colored bars). **Framed:** Neighbour-joining tree based on Euclidian distances showing reproduced from Mérot-L'Anthoene et al, 2019 released under CC BY 4.0 DEED license) showing relationships between the Canephora genetic groups). The same color scheme is reused in main tree. *N.B.* KL 1.2 is an admixed (O+E) individual.

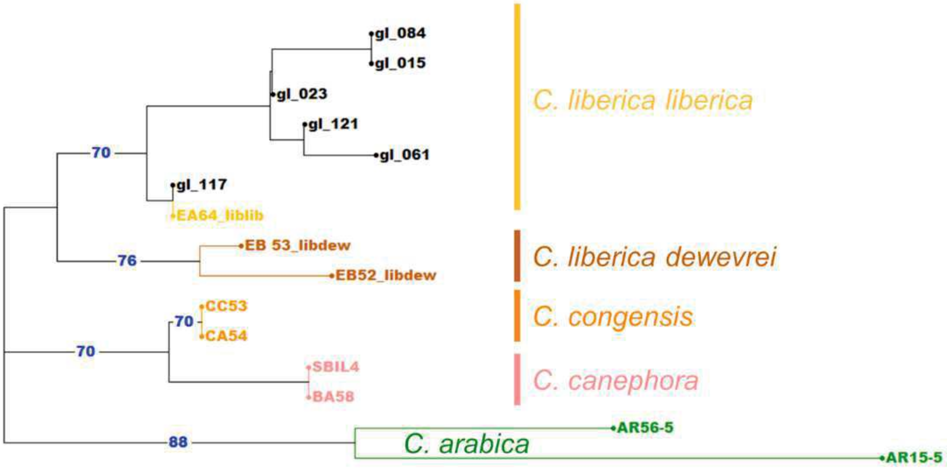

Figure S5. Unweighted neighbor-joining dendrogram of field (gl, Guadeloupe, black) **and reference** (colored) **samples.** Calculated on a simple-matching distance matrix from 40 markers set designed to minimize missing data in *Coffea liberica* samples. Colored bars indicate the represented species. Bootstrap values ≥ 70 shown.

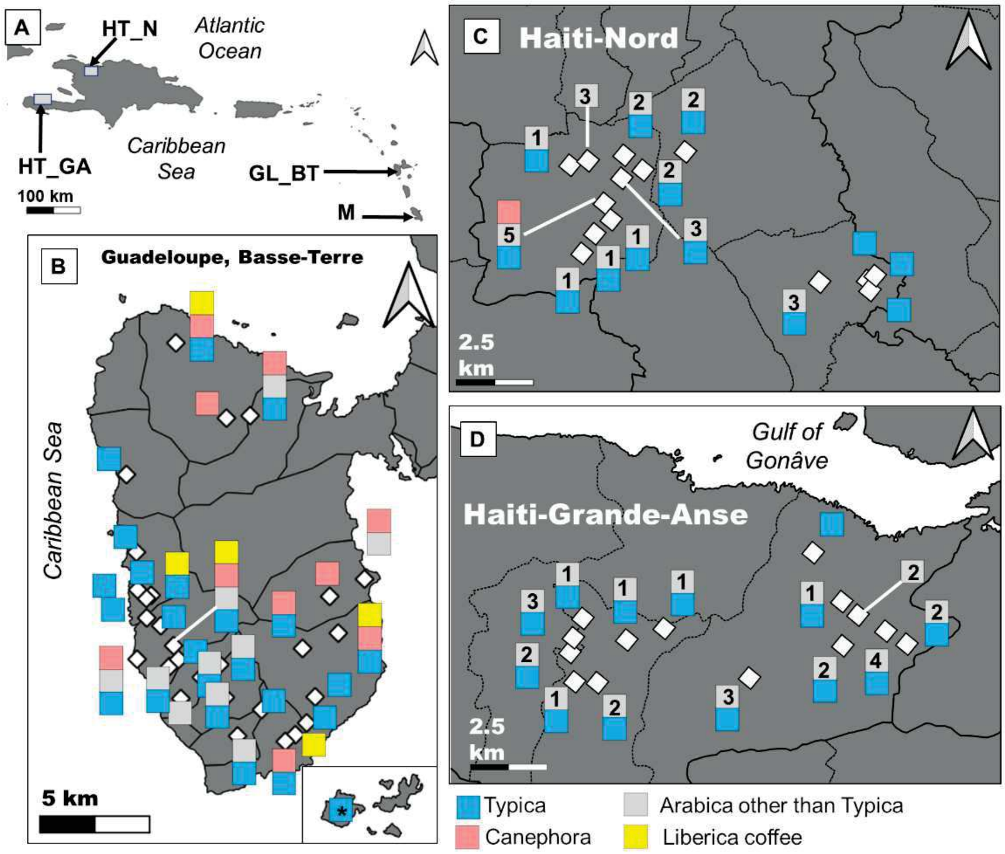

Figure 4. Sampling locations and Coffee genetic group distribution in Guadeloupe and Haiti. A. Location of study areas in the West Indies (HT_N= Haiti Nord department, HT_GA= Haiti Grande-Anse department, GL_BT= Guadeloupe, Basse-Terre) with Martinique (=M) also shown (first Coffee introduction in West Indies). **B.** Sampling locations and their genetic resources in Basse-Terre, Guadeloupe, with Les Saintes in the insert (* Typica sample corresponded to small-seeded "Moka" phenotype) **C.** Nord department in North Haiti and **D.** Grande-Anse department in Southwest Haiti. Stacked squares indicate presence of a Coffee category in samples. Grey squares represent all C. arabica with >75% contribution from Typica-like group, including other varietal groups (counts indicated for Haitian sites, always 1 — SL/Kenyan like — in Guadeloupe) and admixed individuals. Maps created in QGIS v. 3.30.1 using Natural Earth (Free vector and raster map data @ naturalearthdata.com) and shapefiles from Hijmans and UC Berkeley (2015a,b) and Patterson and Kelso (2012).

3.6. Climatic envelopes

The Climatic envelopes of the six geographic zones were characterized and show a clear separation of Haiti and Guadeloupe's zones along a spectrum of high-to-low altitude and precipitation, and low-to-high temperature (Fig. S6). There were also gradual differences between Southern and Northern Haiti, and between Basse-Terre (Guadeloupe)'s two coasts. Overall, Guadeloupe's East coast is warmest and driest with lower elevation, while Southeast Haiti is cooler, wetter and higher in elevation (Fig. S7).

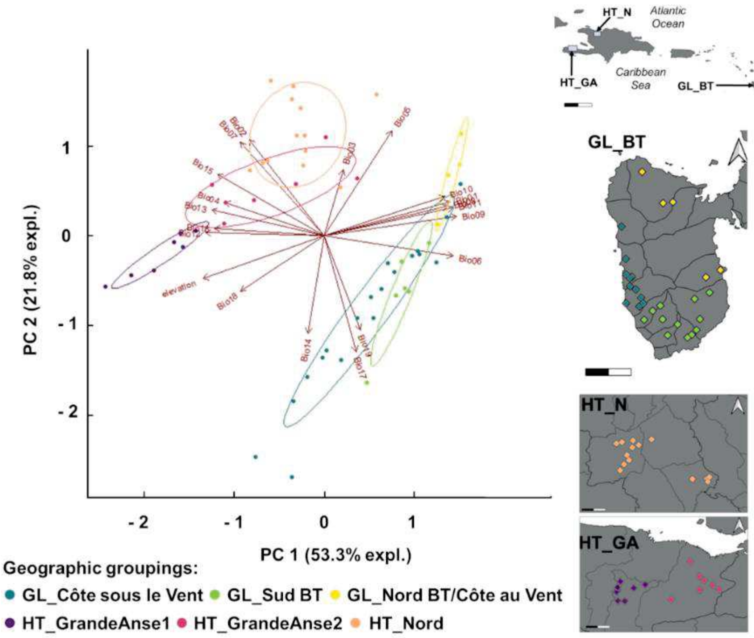

Figure S6. Principal component analysis calculated on 19 standard Bioclimatic variables and elevation data for sampling locations in Guadeloupe and Haiti. Ellipses drawn and points colored based on geographic grouping of sample locations. For Guadeloupe (GL), locations are grouped according to *Grands Ensembles Paysagers* (Landscape units) representing the Leeward (Côte sous le Vent), Windward (+ Northeastern, Nord/Côte au Vent) and Southern (Sud) coasts of Basse-Terre (BT), respectively. For Haiti, locations in the *Nord* department are grouped together, while those in the Grande-Anse department are separated into a western (1) and eastern (2) cluster. Bioclimatic variables (historical average for 1970-2000) and elevation data at 30s resolution were used, downloaded from WorldClim (www.worldclim.org). Maps show location of geographic groupings (GL_BT= Guadeloupe (GL): Basse-Terre, HT_N = Haiti: (HT) Nord Department, HT_GA = Haiti: Grande-Anse department

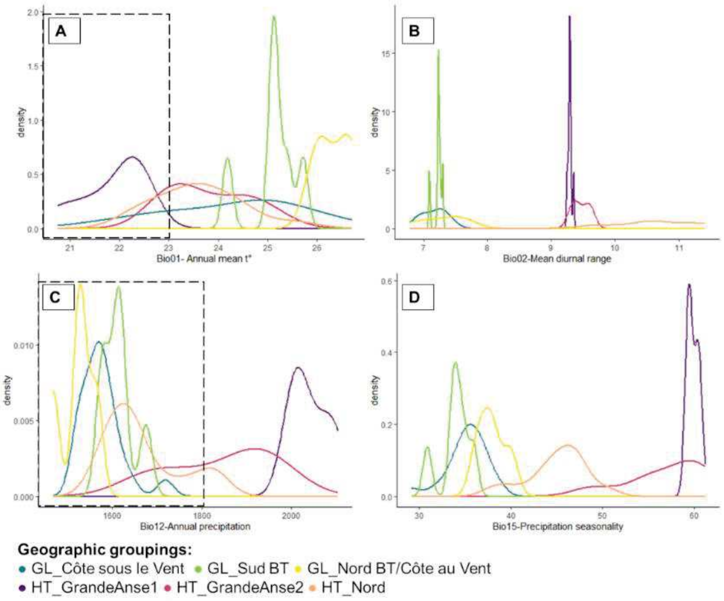

Figure S7. Density estimates calculated on standard Bioclimatic variable data for 6 sampling location groups in Guadeloupe and Haiti. A. Bio01: Annual mean temperature (°C). Dash-lined frame represents suitable range for *Coffea arabica* (De Camargo & Pereira, 1994). **B.** Bio02: Mean diurnal range of temperature (°C). **C.** Bio12: Annual precipitation (mm). Dash-lined frame represents optimal range for *C. arabica* (Alègre, 1959 in DaMatta and Ramalho 2006). **D.** Bio15: Precipitation Seasonality. For Guadeloupe (GL), locations are grouped according to *Grands Ensembles Paysagers* (Landscape units) representing the Leeward (Côte sous le Vent), Windward (+ Northeastern, Nord/Côte au Vent) and Southern (Sud) coasts of Basse-Terre (BT), respectively. For Haiti, locations in the *Nord* department are grouped together, while those in the Grande-Anse department are separated into a western (1) and eastern (2) cluster. Bioclimatic variables (historical average for 1970-2000) at 30s resolution were used, downloaded from WorldClim (www.worldclim.org).

3.7. Historical determinants of genetic structure

Global and local historical factors shaping the genetic composition and structure of the Islands' coffee resources were identified and used to generate timelines representing the various historical and geographic scales (Fig. 5). Though a comprehensive history was outside of our study's scope, the generated timelines include all major determinants, to the best of our knowledge. In some cases, it was possible to trace the introduction of species (e.g. Liberica in Guadeloupe, Nicholls 1881) or varieties (e.g. Catimor in Haiti, Ester 1978) through contemporary books and reports. In other cases, monographs, reports and personal accounts testified to their presence on the Islands at a particular time (e.g. of Robusta in 1920s Guadeloupe, Ukers 1922 and of Caturra in 1970s Haiti, Ester 1978) or testified to the status of certain varietal groups during a particular time (e.g. of Kent's popularity in the 1910s-20s, Haarer 1923). Certain historians have also produced works identifying major historical drivers of varietal development, such as the global progressive spread of Coffee Leaf Rust (McCook, 2006, 2017), as well as works relating the history of coffee in Haiti (Moral, 1955; De Bivar Marquese, 2022) and Guadeloupe (Hoy, 1962; Lafleur, 2006).

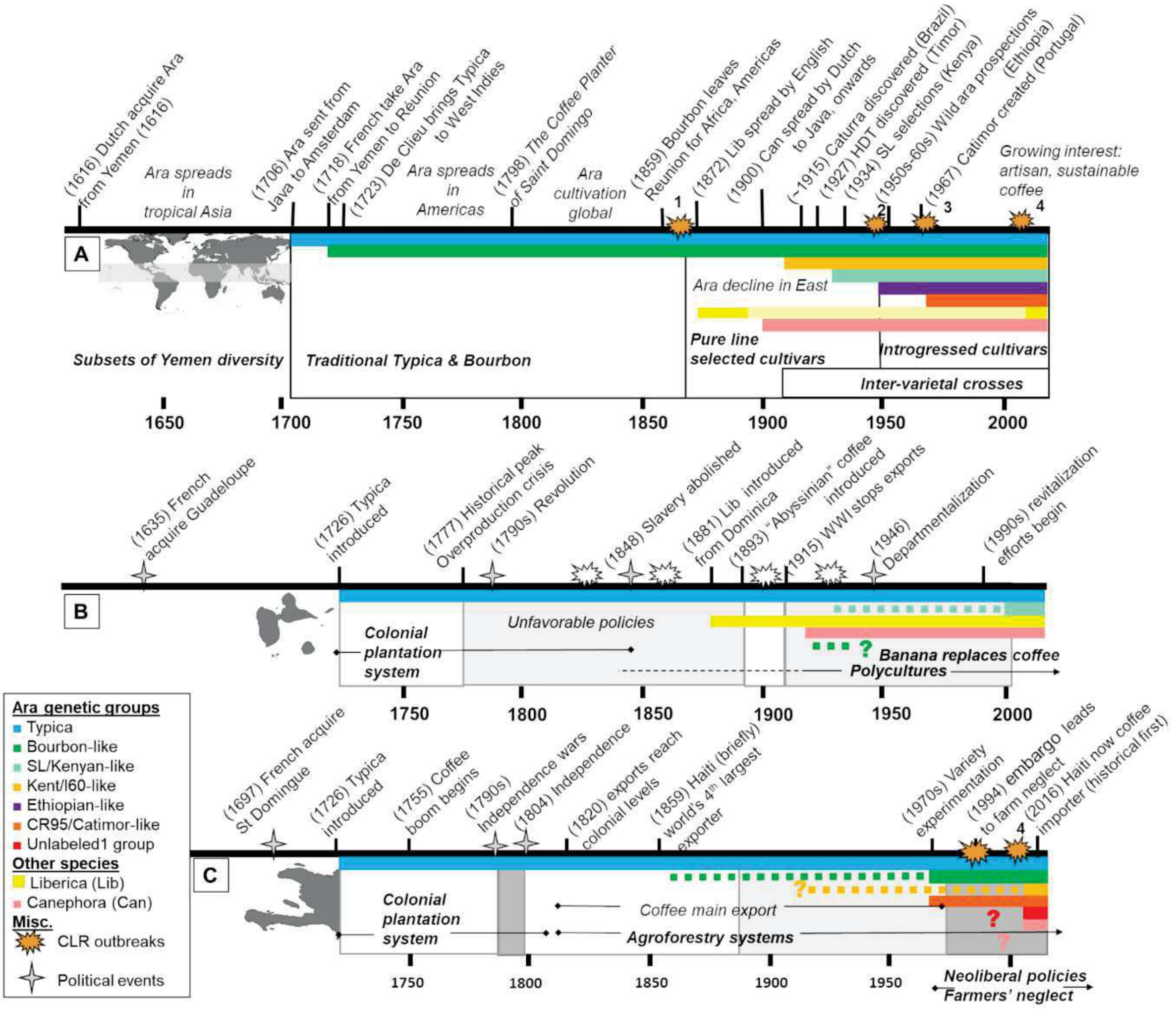

Figure 5. Historical timeline of events affecting Guadeloupe and Haiti coffee genetic resources. A. Global timeline. Boxes below timeline represent major developments in the genetic profile of cultivated Arabica worldwide. **B.** Timeline showing major events affecting the composition and vitality of the coffee sector in Guadeloupe and **C.** in Haiti. For B. and C., Boxes underneath timelines represent periods of coffee sector positive (empty) and negative (greyed) growth. For all timelines, Ara= *Coffea arabica*, Lib= *C. liberica*, Can.=*C. canephora*. Ticks represent historical events in coffee cultivation, and colored lines represent period of cultivation for genetic groups identified in this study (uncertainties represented by dashed lines). Coffee Leaf Rust (CLR, *Hemileia vastatrix*) events represented: 1. CLR discovery near Lake Victoria (East Africa, 1861) and first big outbreak in Ceylon (Sri Lanka) and South India (1869), beginning its spread in tropical Asia and Pacific islands, 2. CLR spread through Western African farms (1950-60s), 3. Arrival in Americas (Brazil, 1970) and spread through the 80s, and 4. The Big Rust (2008-2013) epidemic in Latin America. For B., white explosions represent various (often unspecified) waves of coffee illness reported for Guadeloupe, Insufficient data for Haiti (Morris, 1881; Nicholls, 1881; Ukers, 1922; Haarer, 1923; Kopp, 1929; Lalanne, 1934; Robert, 1935; Moral, 1955; Hoy, 1962; Sylvain, 1972b; Ester, 1978; Amaya *et al.*, 1999; Lafleur, 2006; McCook, 2006, 2017; Avelino *et al.*, 2015; McCook & Vandermeer, 2015; Harvey *et al.*, 2021; Muñoz-Pajares *et al.*, 2023; McCook & Montero-Mora, 2024).

4. Discussion

4.1. A shared history reflected in the Typica variety

Our analyses of Guadeloupean Arabica have revealed that the heritage Typica variety is still widespread on the island, being found across all sampled coffee regions (Fig. 1.A; Fig. 4). The same is true in Haiti where it persists in large stands in multi-varietal farms, and in monovarietal systems.

There was little genetic diversity in the Typica varietal group regardless of origin: identical genotypes across all markers were found in individuals from all sampled regions, as well as collection references, including the prestigious Jamaican Blue Mountain coffee (Fig. 3) as well as references labelled "Suriname" (T.00990) and "Guadeloupe" (T.00989). This is consistent with historical accounts and genetic studies confirming that Typica originated from a very limited number of individuals (Anthony *et al.*, 2001; Salojärvi *et al.*, 2024), themselves resulting from successive genetic bottlenecks along its global spread. Indeed, after the Dutch acquired Arabica from Mocha, Yemen, the crop was introduced to India, Sri Lanka, Java around 1696-1699, Amsterdam, and eventually the Americas (1718-1726, Ukers 1922). This originated the **Typica** lineage, which was established both in the Suriname fields and De Clieu's plantation in Martinique.

The globalization of tropical crops being a key part of European colonialism, Guadeloupe and Saint-Domingue (Haiti) were deeply impacted by this process. In these Islands, coffee was first cultivated in unshaded monocultures (Laborie, 1798; Moral 1955), though agroforestry eventually came to predominate as Guadeloupean coffee receded (Hoy, 1962; Lafleur, 2006) and Haitian independence did away with plantations (Lundahl, 1984). This shift was permitted by Typica's ability to perform well under shade. The plant would spread from the early XVIIIth century onwards to Brazil from the Guyanas, and to Central America from the West Indies (Ukers, 1922; Herrera & Charles Lambot, 2017).The position of the Linnaean lectotype close to the Typica cluster on the dendrogram (Fig. S3) suggests that it was related to the plants that were introduced to Suriname by the Dutch and the Caribbean by De Clieu, perhaps being or sharing a common progenitor.

4.2. Guadeloupean "Moka": a phenotypically distinct form of Typica

One Guadeloupean individual from the Saintes satellite Islands, assigned to the Typica group, was observed to have consistently small-sized cherries. Arabica with this trait are generally called *Ti café* ("small") or "Moka" in Guadeloupe (Lafleur, 2006) and enjoy the best reputation for quality. Our markers do not differentiate these Moka from other Typica. The Moka phenotype may originate from punctual mutations in Typica, similar to Caturra being a dwarf mutant of "tall" Bourbon (WCR), also indistinguishable with our markers. The term "Mocha" was historically used for Yemeni coffee, which was described as small-beaned and of superior quality, (Ukers, 1922; Haarer, 1923) but is genetically diverse (Montagnon *et al.*, 2021). Guadeloupean Moka is not likely closely related to Yemeni accessions. Therefore, the name "Mocha" should not be taken to have genetic meaning, but may rather be used to describe plants with similar traits.

4.3. Old East African accessions provide a modest increase to Guadeloupean coffee diversity

While Typica forms the core of Guadeloupean coffee resources, several other Arabica belong to the “SL/Kenyan-like” varietal group (Fig. 1.B), which does not appear to be present in Haiti. This varietal group was not identified by Millet et al (2024). SL/Kenyan-like references (N_{ref}=4) included T.04313-SL28, T.04314-SL34, and T.02742- “Dilla Alghe”, which are all Eastern African accessions. SL selections were developed in the 1930s in Kenya by the Scott Agricultural Laboratories by breeding trees from various collections in Eastern Africa: SL28 for drought tolerance, and SL34 for cup quality. The Dilla Alghe accession was collected in Ethiopia and introduced to Kenya in 1942 (USDA, 1958; Sylvain, 1958).

To our knowledge, the origin of SL/Kenyan-like coffee to Guadeloupe is not attested in the literature. Our genetic study corroborates that already carried out in 2017 by WCR using other types of molecular markers (SSR), which also revealed the presence of SL-type coffee plants in Guadeloupe (L. Toniutti, pers. obs.). The Guadeloupean samples were fairly spread out, though predominantly on the Western coast. When asked, farm owners could not identify or recall the origin of the SL/Kenyan-like plants (pers. comm.). Several Guadeloupean samples were identified as admixed, with varying levels of Typica and SL/Kenyan-like contribution. These elements suggest a relatively old introduction of this varietal group, and subsequent interbreeding with local Typica.

Discrepancies exist between historical accounts and our genetic results. Documents from 1930s describe four coffee “species” on Guadeloupe: “Arabica” (ie. Typica), the rare but productive “Roy” or “Bourbon”, the sensitive “Abyssinica”, and the recently introduced “Liberica” (Lalanne, 1934; Robert, 1935). We did not identify the Bourbon-like varietal group in Guadeloupe. If it had indeed been introduced, it is either still rare, or no longer present. In the 1930s, “Abyssinica” referred to coffee from south-eastern Ethiopia (Roussel & Verdeaux, 2007), and these trees had apparently been imported to Guadeloupe in 1898 (Lafleur, 2006), predating SL selections by decades. This could be explained by the replacement of “Abyssinian” coffee by Kenyan-derived trees, or perhaps by common ancestry between the two (especially given “Dilla Alghe”’s inclusion in the SL/Kenyan-like group).

4.4. Haitian Arabica diversity reflects a global legacy of coffee breeding

While some genetic diversity is provided by the SL/Kenyan-like varietal group to the otherwise homogeneous, Typica-dominated Guadeloupean Arabica, it is far below that observed in Haiti. Multiple varietal groups of commercial or historical importance have been identified there, including Bourbon-like, Kent/I60-like, and CR95/Catimor-like groups. We also identified two unlabeled, exclusively Haitian groups. One was identified in previous work(Millet *et al.*, 2024), and was hypothesized to be related to Timor hybrid-introgressed Colombian cultivars such as Tabi and Castillo, reported in Haiti (Queneherve *et al.*, 2015) but absent from our reference collections. The Unlabeled 2 group, unrecognized by the dendrogram, therefore appears dubious and may be an artefact of admixture. Indeed, varietal groups have experienced considerable genetic mixing in Haiti, as evidenced by the large number of individuals with <75% contribution from any one group (see also Millet *et al.*, 2024).

The varietal diversity of Haitian coffee is a legacy of the genetic history of Arabica since the XVIIIth century. Soon after the Typica line was established, a second wave of Arabica dispersal also started from Yemen, from where the French introduced coffee into Bourbon Island (called today "La Réunion") around 1708-1718 (Ukers, 1922; Haarer, 1923). This introduction gave rise to the **Bourbon** Arabica lineage, which did not leave the island until its propagation to Africa and the Americas in the 1860s (World Coffee Research, 2019). Over time, and despite Arabica's narrow genetic base, a process began of varietal diversification of the main lines through massal selection and propagation of mutant strains. Starting in the late XIXth century, it led to several varieties such as Maragogipe (Typica mutant from Bahia, Brazil, first identified in1870) and Caturra (Bourbon dwarf mutant from Minas Gerais, Brazil, ca. 1915-1918, Haarer 1923). The Caturra variety would eventually be introduced to Haiti in the 1970s (Ester, 1978).

In parallel, as coffee spread, so too did its pests and pathogens, and particularly the Coffee Leaf Rust (CLR, *Hemileia vastatrix*, Fig. S2.C). Originating around Lake Victoria in Eastern Africa, Rust quickly spread to South and Southeast Asia in the 1860s (McCook, 2006). Notably, this initial spread of Rust may have been exacerbated by the adoption in the Eastern Hemisphere of the "West Indian" coffee cultivation system (full-sun monoculture), of which an early, influential proponent was the Saint-Domingue planter P.J. Laborie (Laborie, 1798; McCook, 2017). CLR then spread in Africa in the 1920s, and finally the Americas in the 1970s (McCook, 2006).

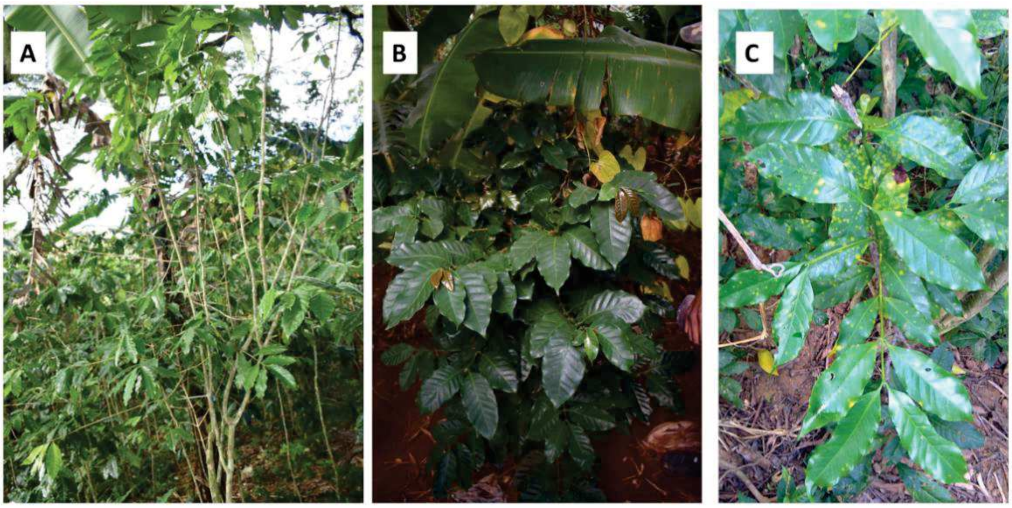

Figure S2. Photographs of *Coffea arabica* illustrating some genetic groups present in Haiti. **A.** traditional "tall" *C. arabica* variety (Typica) vs **B.** "modern", compact, Timor hybrid-introgressed variety (CR95/Catimor-like) in Haitian agroforests. **C.** Coffee Leaf Rust (*Hemileia vastatrix*)-stricken Typica plant in Northern Haiti. CLR was a strong biotic pressure leading to abandonment of traditional varieties worldwide in favor of introgressed cultivars.

The impact of biotic aggressors was exacerbated by the low genetic diversity of cultivated Arabica (Anthony et al, 2002). These epidemics led to the widespread abandonment of older varieties, which were highly susceptible to the disease. With growing biotic pressures, growers sought new, more resistant Arabica varieties such as "**Kent's coffee**", which was identified in

India in 1911 (Haarer, 1923). Displaying (since-lost) CLR resistance, it was widely spread, particularly to Eastern Africa. The introduction to Haiti of the Kent-like group is likely to have taken place a long time ago (Millet *et al.*, 2024) , possibly as early as the first half of the XXth century, when it enjoyed great popularity, and Haiti's coffee sector greater vitality.

There were also efforts to make Arabica coffee more resistant through hybridization with other species. The spontaneous Timor Hybrid (HDT), (*C. arabica x canephora*) identified in Timor in 1927 (Bettencourt, 1973), gave rise to HDT-introgressed varieties such **Catimors** (crossed with Caturra; such as the CR95 cultivar Fig. S2.B), Sarchimors (with Villa Sarchi) and Colombian varieties (Muñoz-Pajares *et al.*, 2023). Indeed, in the mid-XXth century, there was a shift from simply fixing mutations to generating new, better-yielding genetic combinations through institutional breeding (Carvalho *et al.*, 1962; McCook, 2017). In the 1970s, as the major pests and diseases had reached much of Latin America, national and international agencies like USAID (US Agency for International Development) implemented agricultural "technification" projects in developing countries, aiming to offer "technical packages" consisting in improved varieties and/or agronomic intensification through agrochemical control of pests and pathogens (McCook & Vandermeer, 2015; McCook & Montero-Mora, 2024).

Many such projects came to Haiti, occasioning introductions of varieties such as Caturra and the then-new Catimor (Sylvain, 1972a; Ester, 1978; Amaya *et al.*, 1999). However, these projects failed to consider Haitian agroforestry's long history, which arose as a repudiation of the plantation system and out of need for resilience and risk management in the face of longstanding instability, and was incompatible with these technical packages. This explains the abundant genetic mixing in Haitian coffee farms.

4.5. Guadeloupe and Haiti's divergent histories reflected in their contrasted Arabica resources

As previously discussed, many Arabica varietal introductions took place in Haiti in the XXth century, brought about by global and local changes in policymaking, coffee breeding, and pathogen pressures. A more severe wave of CLR outbreaks nicknamed "The Big Rust" again ravaged Latin-American farms between 2008-2013, exacerbated by socio-economic, ecological, agronomic and meteorological factors (Avelino *et al.*, 2015; McCook & Vandermeer, 2015). As global markets experienced increased volatility from 1990s onwards, many farmers in Central America reduced investment in labor and inputs during periods of very low coffee prices and reverted to less intensive (and investment-hungry) production methods (McCook & Montero-Mora, 2024). This relaxed pressure on pathogens played a role in the Big Rust of the 2010s (Avelino *et al.*, 2015; McCook & Montero-Mora, 2024). Haiti was among the countries impacted, and again development projects responded by introducing resistant varieties such as Colombian introgressed cultivars (Queneherve *et al.*, 2015; Jean-Denis, Sardou & Roesch, Katia, 2017), further increasing local diversity.

By contrast, and despite mentions of a "Rust" or even "*Hemileia*" attacking Guadeloupean coffee prior to the 1940s, (Lalanne, 1934; Lafleur, 2006), this disease is neither widespread nor particularly problematic in Guadeloupe today, possibly due to coffee's limited extent on the island. Furthermore, Guadeloupe, being a French department and having largely shifted from coffee to banana exports, was less concerned with XXth and XXIst century developments in global coffee, such as technical package adoption. This may explain the absence of otherwise widespread varieties such as HDT-introgressed Catimors which were increasingly prioritized following rust outbreaks. In fact, the abandonment of coffee for banana cropping began even before the development of introgressed Catimors, having been greatly promoted by a severe 1928 hurricane which laid waste to a quarter of Guadeloupe's coffee stands. This caused farmers to increasingly turn towards bananas (which had primarily been a subsistence crop until then), which had shorter production cycles and thus earlier marketability (Lafleur, 2006; Desarthe, 2020).

The lack of coffee farm revitalization also permitted the continued persistence of Typica in Guadeloupe, and today it, along with Haiti, is among the few countries still cultivating Typica (WCR). The historically important variety has been abandoned throughout the world due to low yields and high susceptibility to Rust. The Big Rust devastated Haitian farms, but did not cause the abandonment of Typica. Haiti's neighboring country, the more prosperous Dominican Republic, is an interesting case: many of its farms are traditional, diversified agroforests with Typica-dominated coffee stands, and reported varietal (Typica-Caturra) interplanting, but technification has been increasing there as throughout Latin America (Siegel & Alwang, 2004). In response to pressure from CLR, the Dominican Coffee Council has recommended that farmers shift to Introgressed varieties, and has supported this enterprise through distribution of seed material (Consejo Dominicano del Café, 2017).

Today, many farms in Latin America consist in pure-line or Introgressed cultivars grown in full sun or simplified, carefully-managed shade systems, often with agrochemical inputs, with a trend towards intensification despite increasing consciousness of issues in sustainability (Perfecto *et al.*, 2019; Cerda *et al.*, 2020; Harvey *et al.*, 2021). These transformations occurred in neither Guadeloupe, where coffee was simply not a priority crop, nor Haiti. In the case of the latter, this is likely due to the fact that Haitian farmers tend to prioritize autonomy, limited reliance on markets, and "bet-hedging" through diversification (Steckley & Weis, 2016). Furthermore, the partial failure and unintended consequences of technification in Haiti is also tied to institutional weakness, and the broader pattern of failure by foreign intervention and international aid to attain their development objectives (Ramachandran & Walz, 2015; Schöneberg, 2017).

4.6. Divergent histories also reflected in introduction of other species to the Islands

Concerns over coffee pathogens coincided with colonial efforts in Africa, and its forests were prospected for resistant species which could be cultivated. Thus "**Liberian**" *C. liberica* and "**Robusta**" *C. canephora* coffee began supplementing or replacing Arabica in various parts of the world, the latter especially gaining prominence over the course of the XXth century (Ukers, 1922; Chevalier, 1929; Cramer, 1957).

While most sampled Guadeloupe coffee trees were Arabica, several belonged to *C. canephora*. This diploid, obligate allogamous species is native to much of equatorial Africa. Wild populations display a geographically-determined genetic structure, with 8 groups identified (Mérot-L'Anthoene *et al.*, 2019). Though *C. canephora* was previously used by local populations, its global spread was initiated when it was introduced it to Java in 1900 to replace CLR-stricken Arabica (Haarer, 1923; Chevalier, 1929; Cramer, 1957). Strains developed there were quickly spread to other Rust-affected countries. Twenty years later, Robusta was reported from Guadeloupe (Ukers, 1922). Today, it is the second-most commercially important Coffee species, (approximately 40% of global production), though considered of lesser cup quality (International Trade Centre, 2021). It is not harvested for export in Guadeloupe, being restricted to local consumption.

Some Haitian Robusta individuals were also found (Fig. 1.D), all on the same farm in Northern Haiti. The species seems a more recent arrival to Haiti, as to our knowledge it is unattested in historical literature, and appears to have a limited distribution. In a report on a PITAG farmers' workshop, Eitzinger (2019) writes: "New varieties (e.g., the "Brasil" [*sic*] variety) are more resistant [to CLR than Typica], but have less production". *Brazil* is the name given by locals to the sampled Haitian *C. canephora*. The latter were already growing on the farm when the owner purchased it in 2014 (pers. com.), and their origins are thus unclear. Our results suggest that both Islands' Robusta samples are related to several genetic groups, and may be of mixed origins (Fig. S4). "Conilon" (group A)-type *C. Canephora*, which is widely cultivated in Brazil, appears to be only one several contributors, and references from this group were closer to some Guadeloupe samples than to any Haitian one. This points to possible introductions of either multiple Robusta of different origins, or of admixed individuals from Robusta breeding programs.

Six Guadeloupe samples belonged to the subspecies *Coffea liberica var. liberica,* and none to *C. liberica var. dewevrei*. This tall-growing, large-leaved, diploid, obligate allogamous species originates from Western and Central Africa (Davis *et al.*, 2022). First found by botanists near Monrovia, it was first exported by the British. Sent to Kew Gardens in 1872, it spread to British colonies worldwide (Morris, 1881), arriving in Dominica in 1874 (Nicholls, 1881). The plant was particularly appreciated for its vigor, productivity, and resistance to the "White fly" (Coffee leaf-miner, *Cemiostoma coffeellum*) which damaged Arabica farms (Nicholls, 1881, Kew bulletin). By 1881, Liberica was propagated from Dominica to Guadeloupe (Nicholls, 1881). It enjoyed a relatively fast growth on the market in the early 1900s, but was quickly supplanted by Robusta (Haarer, 1923; Chevalier, 1929). Like Robusta, Liberica is not harvested for export in Guadeloupe.

Our results are consistent with the known history. Ukers (1922) writes that Liberica and Robusta were planted extensively in Guadeloupe to replace aging Arabica stands, but no similar mention is made for Haiti. This may be due to colonial administrations' roles in this dispersal at a time Haiti was no longer part of the colonized world.

4.7. Additional considerations

In this study, we characterized Guadeloupe and Haiti's coffee genetic resources, and identified historical determinants of their structure. As such, we focused on events and processes directly affecting them: plant breeding and varietal introductions, evolution of biotic pressures that required genetic innovations, and incorporation of new species in cropping systems. However, it is important to note that these processes occurred within the broader context of the global coffee trade. The history of world coffee trade has been marked by periods of instability, transformations, and unpredictability. A comprehensive account of these is beyond the scope of this paper, but a the XXth century deserves particular mention. Its first half was characterized by boom and bust cycles, in which Brazil (emerging as dominant producer in the wake of the Haitian Revolution) loomed especially large (Schurz, 1922; Topik, 2019). Efforts by the international community followed to regulate the coffee trade through treaties such as the 1962 International Coffee Agreement (Bilder, 1963). After the latter ended in 1989, another period of acute farmer vulnerability and price volatility began (contributing to farm neglect and, eventually, to the CLR crises (Ponte, 2001; Avelino *et al.*, 2015). However, changes in consumer values also led to demand for more socially and ecologically sustainable coffee, and development of various certification schemes (and ensuing debates over their efficacy; Ponte, 2001; Grabs, 2020; Harvey *et al.*, 2021). This political-economic history was interrelated with that of coffee genetic innovations, affecting actors' willingness, incentives, pressures, and resources to develop, adopt, spread and manage new genetic material.

Pushes to revitalize the Islands' coffee sectors must be understood in this global context as well local ones. These efforts must be pursued in a manner that is ecologically and economically sustainable, resilient to climate change, and adapted to local needs and priorities. Local genetic resources can be harnessed to advance those goals, but this is contingent on understanding their limitations.

4.8. Despite compromises, Typica may remain a cornerstone of the Islands' Coffee sector

In Guadeloupe, Arabica diversity is low, but historically notable. The Typica variety particularly justifies the reputation afforded to Guadeloupean coffee, and its cultivation could be maintained for supply on niche, gourmet markets with low volumes, with a focus on historical and cultural importance (Dulcire, 2005). This also creates opportunities for further development of agro-tourism based on this patrimonial resource (Breton, 2017). Typica also retains potential in Haiti, which has in recent decades established itself on small-batch, quality-oriented markets and where the Typica variety continues to dominate despite significant diversification. Its persistence is due in part to its historical importance and status, attested by its local names of "Bonifieur" and "Café Créole" in Guadeloupe, and "Vieux Café" in Haiti. These vernacular names suggest that coffee agro-forests deliver not only provisioning and regulating ecosystem services, but also cultural ones.

The Typica variety is well-adapted to agroforestry systems, including both Islands' traditional *jardins creoles*: the same rusticity that allowed Coffee stands to survive the Haitian revolutionary wars (Lundahl, 1984) also allowed it to persist in present systems and through continuing sociopolitical instability. It can also serve to diversify Guadeloupean banana farms and make them more resilient. However, Typica is low-yielding and biotic aggressor-sensitive, cannot satisfy expectations of competitive, high volume productivity, and is likely to leave farmers vulnerable to pests and diseases. Insights can be gleaned from another Typica-growing West-Indian nation: Jamaica. Owing to the prestige and reputation of its Blue Mountain coffee, which is historically Typica (consistent with our genotyping results), the variety persists through intensive cropping methods, agrochemical use, and encouragement from a well-organized network of cooperatives, private sector firms, public actors, and an industry board that work to maintain its profitability. Despite this, production is decreasing, and several Jamaican farmers struggle with economic and biotic pressures and institutional barriers. They also express interest in varietal diversification through growing adoption of CLR-resistant Geisha and other varieties (Guido *et al.*, 2020; Willis & Johnson, 2020; Birthwright, 2023).

Since the XVIIIth century, Haitian coffee has been unfavorably compared to Martinique and Guadeloupe's Coffee (Ukers, 1922; Moral, 1955; Lafleur, 2006) due to post-harvest treatment: Haitian coffee has long had the issue of its beans being processed improperly (Moral, 1955; Arias *et al.*, 2006). However, both Guadeloupean and Haitian Typica coffees retain a very high cup quality potential provided adequate post-harvest processing. In the case of Guadeloupe, low profitability owing to high production costs is an issue, which can be alleviated by crop diversification and labelling or certification to increase value (Mazardin & Saj, 2023). However, this process is hindered by a relative lack of institutional structuring of the coffee sector, insufficient capacity building and lack of integration of its actors (Dulcire & Ribeyre, 2003; Dulcire, 2005; Kiki, 2015; Chaumeil, 2023) .

The potential effect of environment must also be considered: Typica has persisted for centuries in a variety of bioclimatic conditions on the Islands, but some areas may not allow for its quality and production potential to be best expressed. Indeed, our analyses revealed a clear bioclimatic differentiation of Guadeloupe and Haiti (fig S6), as well as revealing internal regional differences. Most regions were within the appropriate reported range of mean annual rainfall (1200-1800mm) and slightly above that for annual temperature (18-21, up to 23°C) for Arabica, though microclimate and agroforestry conditions can compensate for improper macroclimatic conditions (De Camargo & Pereira, 1994; DaMatta & Ramalho, 2006). Locations on Guadeloupe's *Côte au Vent* (Windward) coast were warm and low in elevation, consistent with its historical status as marginal coffee land, where coffee could only grow in moist ravines (Jean Gottmann, 1945; Lafleur, 2006). Environment and microclimate can affect coffee quality, potentially producing a *terroir* effect to differentiate the otherwise genetically homogeneous Typica (Bertrand *et al.*, 2012), and further justifying labelling (or certification of geographic origin) efforts. Organoleptic testing is required to confirm this effect.

4.9. Legacy of diversification in Haiti and Guadeloupe must be considered

In Guadeloupe, the SL/Kenyan-like and Moka varieties identified in our genetic analysis could also be considered to create a niche cluster of excellence with high added value, but with the same agronomic limitations as the Typica variety, particularly in regards to CLR susceptibility. The genetic homogeneity of these coffee stands would need to be assessed to support labelling or marketing efforts. These limitations also apply to many of the varieties introduced to Haiti.

Farms with introgressed varieties may be less affected by CLR, but these varieties may be more susceptible to other pathogens such as *Mycena citricolor* (Ribeyre & Avelino, 2012). Furthermore, some countries have reported loss of CLR resistance in Catimors (Cabral *et al.*, 2016). Compact, "modern" varieties such as Caturra and Catimor also have higher nutritional requirements than traditional ones, and may therefore require fertilizer or manure application to perform well (World Coffee Research, 2019). Anecdotally, several Haitian farmers participating in the present studies remarked that compact varieties were very productive in their first 5-6 years, after which their yields dropped, while production lasted longer in Typica. This may be due to nutrient limitations in compact varieties, or possibly lack of adequate pruning to rejuvenate vegetative organs (Somarriba & Quesada, 2022). In diversified systems in which coffee is but one crop among many, and in which farmers may be uninterested in increasing their management intensity, or unable to do so due to lacking necessary resources (labor, money, or technical knowledge), traditional varieties are thus better suited.

Regarding other *Coffea* species, the role of Robusta in Guadeloupe seems unlikely to change, but Liberica has re-emerged as a trendy species in specialty shops, albeit to a limited extent (Davis *et al.*, 2022) and may help diversify production, especially on the Windward coast. The continued presence of these species suggests that farmers are open to cultivating coffee trees other than Typica if they can be incorporated into relevant food networks, including household economies. In Haiti, “Brasil coffee” (Robusta) adoption has been slow, and its future is uncertain. However, it may be well-suited to the local market, where quality expectations are lower.

4.10. Appropriateness of varietal introductions depends on local contexts

With traditional varieties being low-yielding and CLR-sensitive, and Introgressed varieties requiring intensification (and potentially losing CLR tolerance), questions could be raised on the appropriateness of maintaining a purely conservative approach to Arabica cultivation. The advent of modern genetics, with increasing availability of marker-based genotyping, has greatly facilitated the study and valorization through breeding of coffee diversity. In the 1950s-60s, realizing the value of crop diversity and the untapped genetic potential of crop wild relatives, scientists had prospected **wild Ethiopian accessions** and put them in germplasm collections along with commercial accessions (Engelmann *et al.*, 2007). In the 1990s, this collected diversity began to be channeled into F1 “hybrid” clone lines combining pest and disease resistance, agronomic performances (vigor, yield, adaptation to shade), good organoleptic qualities (Breitler *et al.*, 2022) and climate change adaptation (Kahsay *et al.*, 2023). This development has been called a paradigm shift (McCook & Montero-Mora, 2024), in which coffee breeding adapts to local farm systems (rather than farms adapting to Coffee trees’ requirements), though it arguably continues the process of inter-varietal crosses stretching from 1943’s Mondo Novo (Typica x Bourbon, WCR). To date, this development of new resilient varieties in the world has impacted neither Haiti nor Guadeloupe.

Importing modern varieties or even F1 hybrid clones to Guadeloupe could be an option to bypass the traditional varieties’ limitations, provided the chosen material is adapted to farming systems. Guadeloupe is equipped with scientific institutions that can greatly help their adoption. However, doing so entails the foregoing of traditional varieties and the historical value and narrative they provide. The decision is ultimately in the hands of coffee growers and of politics. Another possible avenue is the prospection of admixed Typica-SL/Kenyan-like trees to identify possible traits of interest via phenotyping. If found, such trees could benefit from the narrative of being “purely” from Guadeloupe.

As for Haiti, History has shown that farmers are attached to traditional farming systems, and that new genetic material is absorbed into existing systems rather than replacing them. Newer varieties like F1 clones are un-adapted to local field management practices that result in dynamic genetic diversity within Coffee stands (Millet *et al.*, 2024). However, this history has yielded a high Arabica diversity that should be also explored to identify potential phenotypes of interest and adaptation mechanisms (if any) resulting from various socio-economic and ecological filters to which it is subjected. This could lead to new cultivars that can be spread to other similar cropping systems.

Both Islands have had prior, ultimately unsuccessful attempts at relaunching their coffee agriculture, and current ones are taking place in the context of a changing climate working against them (Bunn *et al.*, 2015; de Sousa *et al.*, 2019). Growing interest in sustainable and niche coffee (ICO, 2023) provides opportunities for these marginal producers. Knowledge of standing genetic resources and their historical determinants can help inform their research, management and marketing for better, more resilient coffee farming systems.

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Author contributions (CRediT)

Claude Patrick Millet: Conceptualization, Formal Analysis, Investigation, Methodology, Writing – Original Draft Preparation, Review & Editing; **Boris Delahaie**, Supervision, Writing – Review & Editing Writing – Review & Editing, **Frédéric Georget**: Conceptualization, Investigation, Methodology, Supervision, Writing – Review & Editing, **Clémentine Allinne**: Conceptualization, Funding Acquisition, Methodology, Supervision, Writing – Review & Editing, **William Solano-Sánchez**: Resources, **Dapeng Zhang**: Methodology, Resources, **Wesly Jeune**: Project Administration, Funding Acquisition, Supervision, **Lucile Toniutti**: Conceptualization, Funding Acquisition, Investigation, Methodology, Project Administration , Supervision, Writing – Review & Editing, **Valérie Poncet**: Conceptualization, Funding Acquisition, Methodology, Supervision, Writing – Review & Editing

Data availability statement

The data and related documentations that support the findings of this study are available on request in DataSuds repository (IRD, France) at https://doi.org/10.23708/MRPVHL.

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Conflict of Interest statement

The authors declare no competing interest.

Supporting Information

The following supporting information were directly included within the chapter text for better legibility

Table S3. *Coffea arabica* diversity statistics calculated on SNP genotyping data for the sampled regions of Basse-Terre Guadeloupe and Haiti (Nord and Grande-Anse departments)

Table S4. Genetic differentiation between varietal groups

Figure S1. Photographs indicative of the cultivation context of Coffee (*Coffea*) in Guadeloupe

Figure S2. Photographs of *Coffea arabica* illustrating some genetic groups present in Haiti

Figure S3. Unweighted Neighbor-joining dendrogram of field and collection *C. arabica* with "Linnaean" sample (Arabica lectotype)

Figure S4. Unweighted neighbor-joining dendrogram of *Coffea canephora* field and reference samples

Figure S5. Unweighted neighbor-joining dendrogram of field and reference samples (Liberica dataset)

Figure S6. Principal component analysis calculated on 19 standard Bioclimatic variables and elevation data for sampling locations in Guadeloupe and Haiti

Figure S7. Density estimates calculated on standard Bioclimatic variable data for 6 sampling location groups in Guadeloupe and Haiti

The following supporting information are shown below:

Table S1. **List of sample accessions used as references in the study**

Table S2. Flanking sequences for each SNP marker, and diversity statistics per locus calculated over all *C. arabica* samples

Table S1. **List of sample accessions used as references in the study**. List of reference samples by code and accession name, country and region of origin (when this information is known to the authors), and name of the holding institution whose collection the sample was acquired from. Also mentioned is whether the accession was used in the study that selected the core SNP panel used in the KASP SNP genotyping assay (Zhang et al., 2021, indicated as [1] in the "Citation" column) or in other published works ([2] Millet et al, 2024 or [3] Mérot-L'Anthoène et al, 2019), and what genetic group the sample was assigned to with sNMF population structure analysis (at K=8). Genetic groups are abbreviated as follows: Typ = Typica-like, CR = CR95 (Catimor)-like, BBN = Bourbon-like, Kent = Kent/I-60-like, Ethio = Ethiopian-like, SL/K = SL/Kenyan-like. This latter column only concerns samples with >75% likelihood of belonging to groups.

Sample	**Accession**	**Country of origin**	**Region of origin**	**Citation**	**Holding institution**	**Assign sNMF K=8**
MS-1	*C. arabica*				IRD	Ethio
AR 56_5	*C. arabica*	Ethiopia		[2]	IRD	Ethio
AR15_5	*C. arabica*	Ethiopia		[2]	IRD	Ethio
AR22_5	*C. arabica*	Ethiopia		[2]	IRD	
AR41_6	*C. arabica*	Ethiopia		[2]	IRD	Ethio
BA58	*C. canephora*	Ivory Coast		[2]	IRD	
BB53	*C. canephora*	CAR		[2]	IRD	
CA54	*C. congensis*	CAR		[2]	IRD	
CC53	*C. congensis*	Congo		[2]	IRD	
PM3	Caturra				IRD	BBN
EA64	*C. liberica var. liberica*	Ivory Coast		[2]	IRD	
EB52	*C. liberica var. dewevrei*	CAR		[2]	IRD	
EB58	*C. liberica var. dewevrei*	CAR		[2]	IRD	
GUI2	*C. canephora*	Guinea		[2]	IRD	
HA_13	*C. arabica*			[2]	IRD	Ethio
T.00977	Blue Mountain	Guatemala	La Aurora	[2]; [1]	CATIE	Typ
T.00989	Guadeloupe	El Salvador	La Libertad	[2]; [1]	CATIE	Typ
T.00990	Surinam	El Salvador	La Libertad	[2]; [1]	CATIE	Typ
T.01993	Goiaba	Brasil	Campinas	[2]; [1]	CATIE	
T.02147	Murta	Guatemala	La Aurora	[2]; [1]	CATIE	BBN
T.02246	Jimma-1	Ethiopia	Jimma	[2]; [1]	CATIE	Ethio
T.02249	Dessie	Ethiopia	Dessie	[2]; [1]	CATIE	
T.02251	Batie	Ethiopia	Dessie	[2]; [1]	CATIE	
T.02254	Jimma-6	Ethiopia	Jimma	[2]; [1]	CATIE	Ethio
T.02257	Lekemti	Ethiopia	Lekemti	[2]; [1]	CATIE	
T.02298	Coorg	Kenya	Ruiru	[2]; [1]	CATIE	

T.02299	Laurina	Costa Rica	Cartago	[2]; [1]	CATIE	
T.02394	Mocha Java	Puerto Rico	Mayaguez	[2]; [1]	CATIE	BBN
T.02395	Erecta	Puerto Rico	Mayaguez	[2]; [1]	CATIE	Typ
T.02542	Caturra	Brasil	Campinas	[2]; [1]	CATIE	BBN
T.02676	Laurina	Camerun	Dschang	[2]; [1]	CATIE	
T.02702	Mibirizi	Congo	N/A	[2]; [1]	CATIE	
T.02727	Dalle	Kenya	Sidamo	[2]; [1]	CATIE	
T.02731	Jimma Galla Sidamo	Kenya	N/A	[2]; [1]	CATIE	Ethio
T.02741	Erecta	Kenya	N/A	[2]; [1]	CATIE	BBN
T.02742	Dilla Alghe	Ethiopia	Sidamo	[2]; [1]	CATIE	SL/K
T.02744	Rume Sudan	Kenya	N/A	[2]; [1]	CATIE	
T.02758	Barbuk Sudan	Sudan	Barbuk	[2]; [1]	CATIE	
T.03081	Carrizal	Costa Rica	Alajuela	[2]; [1]	CATIE	
T.03214	Geisha	Tanzania	N/A	[2]; [1]	CATIE	
T.03215	K-7	Kenya	N/A	[2]; [1]	CATIE	
T.03427	Cera	Brasil	Campinas	[2]; [1]	CATIE	Typ
T.03443	Ceilan	Puerto Rico	Mayaguez	[2]; [1]	CATIE	Typ
T.03469	Bourbon Salvadoreno	El Salvador	La Libertad	[2]; [1]	CATIE	BBN
T.03491	Lejeune 08	Ethiopia	Bada Buna	[2]; [1]	CATIE	Ethio
T.03507	Lejeune 12	Ethiopia	Bada Buna	[2]; [1]	CATIE	Ethio
T.03645	Cumbaya				CATIE	Typ
T.04007	Loulo	Ethiopia	Sidamo	[2]; [1]	CATIE	
T.04060	Murta	Reunion Island	N/A	[2]; [1]	CATIE	BBN
T.04076	Typica Amarillo	Colombia	Caldas	[2]; [1]	CATIE	
T.04078	Caturra Variegata	Colombia	Caldas	[2]; [1]	CATIE	BBN
T.04250	Goiaba	Colombia	Caldas	[2]; [1]	CATIE	
T.04253	Maragogipe	Colombia	Caldas	[2]; [1]	CATIE	
T.04258	Bourbon Mayaguez	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04259	Jackson 2	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04268	Kent	Congo	Ruanda Urundi	[2]; [1]	CATIE	Kent
T.04271	Kent	Congo	Ruanda Urundi	[2]; [1]	CATIE	

T.04273	Kabare	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04278	Babaca Kaffa	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04281	Lignee-M	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04286	Wondo Sidamo	Congo	Ruanda Urundi	[2]; [1]	CATIE	
T.04290	Jimma Kaffa	Congo	Ruanda Urundi	[2]; [1]	CATIE	Ethio
T.04292	Wush Wush Kaffa	Congo	Ruanda Urundi	[2]; [1]	CATIE	Ethio
T.04294	Mocha de Tahiti	Congo	Ruanda Urundi	[2]; [1]	CATIE	Typ
T.04308	Dalle mixed	Malawi	N/A	[2]; [1]	CATIE	
T.04310	Mocha	Malawi	N/A	[2]; [1]	CATIE	
T.04313	SL28			[2]	CATIE	SL/K
T.04314	SL34			[2]	CATIE	SL/K
T.04317	I-60	Malawi	N/A	[2]; [1]	CATIE	Kent
T.04375	Bourbon Amarillo	Venezuela	Monajas	[2]; [1]	CATIE	
T.04479	E-301	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04539	E-293	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04570	E-147	Ethiopia	Illubabor	[2]; [1]	CATIE	Ethio
T.04573	E-150	Ethiopia	Illubabor	[2]; [1]	CATIE	Ethio
T.04578	E-155	Ethiopia	Illubabor	[2]; [1]	CATIE	Ethio
T.04583	E-325	Ethiopia	Illubabor	[2]; [1]	CATIE	
T.04599	E-341	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04610	E-352	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04667	E-160	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04681	E-167	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04688	E-174	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.04692	E-178	Ethiopia	Kaffa Jimma	[2]; [1]	CATIE	Ethio
T.05175	IHCAFE 90			[2]	CATIE	
T.05199	Cioiccie I	Colombia	Caldas	[2]; [1]	CATIE	
T.05267	Catuai	Costa Rica	San José	[2]; [1]	CATIE	
T.05268	Catuai	Costa Rica	San José	[2]; [1]	CATIE	
T.05283	Cioiccie S-6	Brasil	Campinas	[2]; [1]	CATIE	
T.05314	Hibrido_041			[2]	CATIE	
T.05325	Catuai	Costa Rica	Alajuela	[2]; [1]	CATIE	
T.08867	CR 95			[2]	CATIE	CR

T.11723	Garnica	Mexico	Veracruz	[2]; [1]	CATIE	BBN
T.11948	Hibrido_101			[2]	CATIE	
T.11950	Clon 7355	Ethiopia	N/A	[2]; [1]	CATIE	
T.12534	Clon 7357	Ethiopia	N/A	[2]; [1]	CATIE	Typ
T.12837	Hibrido_055	Mexico	Veracruz	[2]; [1]	CATIE	
T.12841	Catimor	Mexico	Veracruz	[2]; [1]	CATIE	
T.12842	Catimor	Mexico	Veracruz	[2]; [1]	CATIE	
T.12846	Hibrido_089	Mexico	Veracruz	[2]; [1]	CATIE	
T.12851	Garnica	Mexico	Veracruz	[2]; [1]	CATIE	
T.14718	Sarchimor			[2]	CATIE	
T.14723	Icatu	Brasil	Campinas	[2]; [1]	CATIE	
T.14724	Catimor			[2]	CATIE	
T.15895	Pacas	El Salvador	La Libertad	[2]; [1]	CATIE	BBN
T.16636	Cavimor			[2]	CATIE	
T.16651	Cavimor			[2]	CATIE	
T.16742	Mundo Novo	Brasil	Minas Gerais	[2]; [1]	CATIE	
T.16762	Mundo Novo	Brasil	Minas Gerais	[2]; [1]	CATIE	
T.16764	Catuai	Brasil	Minas Gerais	[2]; [1]	CATIE	
T.19878	Arabusta			[2]	CATIE	
T.19943	Arabusta			[2]	CATIE	
T.03617	Blue Mountain			[2]	CATIE	SL/K
S15_2	*C. canephora*	Guinea		[2]	IRD	
SBIL4	*C. canephora var. maclaudi*			[2]	IRD	
Ku041	Red_bourbon			[2]	HARC	BBN
Mw235	Pink_bourbon			[2]	HARC	BBN
Mw264	Bourbon Select PR_6791			[2]	HARC	BBN
Ku117	Typica_Guatemala			[2]	HARC	Typ
Ku118	Typica_Guatemala			[2]	HARC	Typ
Ku132	Typica_San_Ramon			[2]	HARC	Typ
Ku214	Jamaica Blue_Mountain			[2]	HARC	Typ
Ku215	Jamaica Blue_Mountain			[2]	HARC	Typ
Ku085	8667			[2]	HARC	CR
Ku086	8667			[2]	HARC	CR
Ku143	Kents			[2]	HARC	
T.08667	CR95			[2]	CATIE	CR

T.04271	Kents_198			[2]	CATIE	
T19844	Hibrido_038			[2]	CATIE	Kent
T.05296	Sarchimor			[2]	CATIE	
20233	*C. canephora* group D	Ivory Coast	Fouroubankoro	[3]		
20121	*C. canephora* group D	Ivory Coast	Gbapleu	[3]		
20245	*C. canephora* group D	Ivory Coast	Marahoue	[3]		
FRT83	*C. canephora* group A			[3]		
20708	*C. canephora* group A	Togo	Niaouili	[3]		
ZK2.5	*C. canephora* group O	Uganda	Zoka	[3]		
KL1.2	*C. canephora* (O x E)	Uganda	Kibale	[3]		
20726	*C. canephora* group E	Congo	SouankeGabon	[3]		
20738	*C. canephora* group E	Congo	Impfondo Dongou	[3]		
20516	*C. canephora* group E	CAR	Yombi	[3]		
K4-17-2	*C. canephora* group R	DRC	Niaouili	[3]		

Table S2. Flanking sequences for each SNP marker used in the study, and diversity statistics per locus, calculated over all *C. arabica* (field + reference) **samples** (N=834)**.** I= Shannon's Information Index, H_o= Observed heterozygosity, H_e= Expected heterozygosity and F= Fixation index (=1-H_o/H_e)

Marker	Sequence	I	H_o	H_e	F
Ca0195	CACATGTCAAACCAAAACAAAATACAGCCAAAGTAGCACTACACAAAAATGTAATAAGCC**[A/G]**TTTTCTAGACGAAATTGACTTGTTTTTGATTAAGGTCACTAATCTTGCTCTTGTTCAAC	0.324	0.033	0.183	0.817
Ca0241	TTGGTAGAATTTAGACCGTGCTTTTTTTGTTTCTGCACGACTTAGGGCATTGAAGGTTGA**[A/T]**GACCAAGATGGATAAGAGTGCACGCTCTTTAATCTTGGCTCCATTGCTCACAGACGTAAA	0.193	0.034	0.117	0.562
Ca0360	TGCTTATTTAGCCAATCAGAAAAAAGGCAGGACAAAAATTTCATGAACCAACAATATAAC**[C/G]**CTGAATTAGAGAAAATCGTTCAAAACATTTTTTCGTCCTTCACTTTTAAAATTGTTGTTT	0.603	0.084	0.417	0.811
Ca0462	TAGCTTGGTCCCATCAAAATGTCACATTTAAGTGGTTTGCTTCAAAAAATTCAGACGAGT**[A/G]**TGTTGTGCACTCGTTTTGTCTGGTGGTGATTCAGTCCCTTCCGGATTATCCCTGGGCCAC	0.427	0.065	0.279	0.824
Ca0471	TCAAGAAGAAAATGAAGGCATAAATGCGTTTGATGCGTTTTTTTTTCCCTTTTTTTTTTT**[A/C]**CTTTTAGTTTTTCTGGTATATTTATCGGGGATTTGTGTGATATGCATGAAAATTCTAAAA	0.550	0.089	0.370	0.767
Ca0516	GCAAATATCAGAAACCTCAGGGGAGGTTTCTGCAATTATCCTTTGATTCTATTGACAAGG**[T/C]**AAAAACCTCCTTTTCTGAGTTGGAAAGTTGGATTGACTACTGATATGGCCGCAGCATTGA	0.592	0.084	0.406	0.803
Ca0557	ATATCAAATACGACTACGCTTACTATATTGCGTTGTATCATTCGCTCATATTTGGCGAGT**[A/C]**CTCACTATAAAAATGATTAACAGACTACCCACATACTGCTACGACTACGAGCATCCGAGT	0.570	0.097	0.386	0.753
Ca0935	TTGACAGATTATATACACACATAAGTGAAACGGTCATACAATAGCAGTTTATAATTTAAA**[T/C]**GATTGAAAACGGTAAAAAATAATTTAAAACGGTAAAAAACGACATTGAGGCCAAAAGAAT	0.080	0.012	0.044	0.723
Ca0938	AAATCTTCAAACAGGAATTACTAAGAATAAATTCCAATCAATCATTAAAAAAGATACTAC**[A/G]**AAAAATCCTTCTCAACTTCTTACTAAACCTATGGTTATTAGACAAGAAACCCAGTCAACT	0.083	0.010	0.046	0.777
Ca0999	ATATAATTTGGCAAATAATTCACAATCCACGAAATGTATTCATTAGCGGAGCAATAGACT**[T/G]**TTTGAAAGTTTAGGATGTGTATGAATTGCATTTTTCGTCATTTTTTATGGAAAATGCCTT	0.122	0.011	0.073	0.617

Ca1205	TGGTTATCATGTTCAAGTGAAGAGATTTGAAACGGAAGTATTTTGTTTGTATTGAATCCT**[T/C]**TATCTTCACTTGACGCATATGGGATTAGCGAAGTGACAACTGGCTAATAACAAGTGCATA	0.657	0.766	0.465	-0.640
Ca1209	ATATAATGTTGTTGTCTTTTCATACTTTTGCAGATTCAAGCAATGGTTTCAAGAAATGGA**[T/C]**AGTTAGTGTAGCCAATAACAGAACTGCATGAATAGAAAGTATCTCTGTCATGTCTTTAAG	0.161	0.029	0.101	0.899
Ca1299	CTGGAACCGAAGAAGGTGGTTTTTGAAAATATTAAGGTGAAGTCGACACTGTTGGATCAA**[A/G]**TTAAAGAGGGTCAAGTGAAGGACCCAATGGTGCAAAAGTGGGTGGAAAAGGTGAAGAAAG	0.457	0.057	0.316	0.813
Ca1320	GAGAGGATAAATCTTGACAGATCATCTTAATCTTGCCTTGATTTAGTAAGAAATCAACAA**[T/G]**AACCACAAATCTAGTCCGAACAAAGGTGCAACAAGGTGATAAGGAAGCTTGAGGTCGAGT	0.137	0.022	0.073	0.749
Ca1405	ACAATTCGAAAAGAAACTCAAGTTCCATCAAGGAACTCCATAAAAGAGAACAACTCACTC**[T/G]**AAATTTTATTAGTTTTCTCTAAAAAAACGCTGCAAGGACTATATTTATAGCCTTATAAGA	0.112	0.024	0.064	0.544
Ca1546	AAGCACTATCTATCACCACCCATTTGAAGATGATCAGCCTCCACAGATAGATAGTGGAGC**[T/C]**AATGCAATGCACCAGGAGTTGCCTCCACCATTTACTTGACTTCTCTAGTAACTTGTCTTC	0.477	0.072	0.334	0.785
Ca1807	TTTTTCCAAAAAATTTTTTCTAATAAAAGAAGAGTGGAATTTGGAAAGCACAGAAGAGAT**[A/T]**GGAAGATTATAATCCACGACCTCTAATTTCTTTTCTAAAAAGAAAGTACCCTAGTGATGA	0.611	0.063	0.425	0.864
Ca1866	CCAATAAAGATTTAGTCAATAATAACCAGCCGGAACAGATTGTGTCATGAGCTCACCGCC**[A/C]**AAAAACCGGCATCAATCAACAACAAATGGACCAAATTTACAGAATTGTCCACCTACTTCA	0.523	0.077	0.369	0.842
Ca2002	AAAATTTCCTTCTTTTTCCTTTCTTTTTTTTCCCCTTTTTCTTTTCTTTTCTTTACTCTT**[A/C]**TTTTTCCTCCCTCTCTATTGATCACTTGTCGATTATTAGCACCGCTGTCACCAGTACCTT	0.499	0.073	0.342	0.720
Ca2024	GATATTCTGCTTTTACAGTGCCAAAAACGACGCTCCACTTGTTAGTAGGCTATAAGAGCT**[A/C]**AAAAATGAGTGATCATACGTACATTATACTTTATACACACGGAATATGAAATCCCTACCA	0.466	0.064	0.323	0.800

Ca2034	CCATATAATTTCCGTTTTGGGTGCCAAAAAAGCCACCCACTATCATTCCAAAGTCGAGTA**[C/G]**CACTGGATTATACTCCTTAAAGAAAAACATGACCAGAAAATCTATTAAAATGTAACTGAT	0.470	0.072	0.328	0.780
Ca2044	TTATGCTCACAAAATAGGGAACAAATAAGCGCAGTAATGCCACTGCCTTCTCTTGTCTCC**[A/G]**CACATTAATTCCAAAGAACTTTCAACCGAAACACTACGGTAGAAGCTGGTGAACTCACCA	0.359	0.069	0.227	0.529
Ca2247	CTGCTCGGTGGAGAACTTGGCCGCCTGAAATTTCACCGCAGAGCTCACCAGCTGGCTGAG[**A/G]**GCCTCGGTGTCCAAGTCCCCTGGATAGGGGTCGGAGTCGACCTCCCCGACCTTTCACACA	0.523	0.077	0.363	0.789
Ca2285	CTAAACTTCCTTCATCTGCTTGGGGACATGCTGTATTACATATAACAACACTTGTGAGGA**[T/C]**TAGGCCGACAAGTTATCATACTTATTCTCCGCTACAATTGACTTTTGATTATGAGCCAAA	0.572	0.079	0.394	0.835
Ca2349	CCTTCTACTCGGGTTGAGTGTGGTACATGCTACCGCTCAGCACTTACAAGTCAAGTACAA**[A/G]**ATTTCAAGTAGTATTCAAGTTATAAACATGTATATCAAGTCAATAATAACCAGTAAACAG	0.210	0.007	0.129	0.932
Ca2606	AAATTCAAATTTCCCTGAAAAAATTTGTTAGAAGGTGCGTAGATATACACATCCGTTTGG**[T/G]**TAGGTGGTGATTTAATCCCTTCCGAATTTTCCTTGGGACCTTTTTAGATCCTCGCTTCCC	0.313	0.043	0.193	0.739
Ca2987	CATACAAGTGCTATATTTGGATCATTGAATACTACATCTAGGCTAGCTATGGTGTAATTT**[T/C]**CTTATGTATTCGAATCTTACTTTCGTAGTTAATCAATTATACTTATAACTAATCCATACC	0.250	0.042	0.141	0.684
Ca3164	TCCTAGTTTGAGCTGAAGTTTTAAAAGCTATCTTTATTAGTAGAGTATTTAGTTAAGAAA**[A/C]**AAAGGATGTTATCTTTTGTACTTTCCTGTTCCACTTAGGAGTTTATTTTTAGAGCGAATT	0.421	0.335	0.264	-0.215
Ca3165	ATAATTTTTATCCTTGGAACCTAGGGATCTACCACATTTCAGGCGTGCTTTAGATTCATT**[A/G]**GCACGTGCATTCGTCCTTCTAGTATATCAATTTTAATTGAAACATTTTTAGTATGAATAT	0.581	0.094	0.405	0.737
Ca3177	TAATTCACACTATTATCAACCAATATATCATGGCTTTCTTTTTGCCAATAATTTCTAATT**[C/G]**TATGATTGCCAATGTATTCATCCATCCCACAAGTACCAACAATTTCTGTAATATTCTCAT	0.577	0.091	0.399	0.753
Ca3218	ATTCTTTTTTATGTATAACAAACTAAAATTTATTTCAGATCAGAAAAAGCATAAAATACT**[T/G]**TTTCTTTCACTTTAAGAAAAAATGGTGAATTGGGCGACTGCGATGTGAATGGATAAGATA	0.086	0.012	0.039	0.766

Ca3220	CTATTTATGAGGTGTCTTAGTCCAATAACTTCTACCCAGAATACAAATGAAACAGATGAT**[A/C]**ATGCTCTATCCTTAGAGCCACTTGAATATAAGGCAATCAGTGCCAATTGCCAACCTCCCG	0.111	0.016	0.054	0.740
Ca3400	TACTTCACTATGCCCTTGATATGCATTCATCATGTAGATTGACTTTTTAGAAGTTTGTTT**[T/G]**GCCATGTATGCCAATGGAAATTATAGCTTTCCAATTAAATGGAAGTATCCTTGTATCTTT	0.033	0.015	0.014	-0.030
Ca3457	TTAGTCCCTCATATTTCCTTTTCAATATTTTATGACTTATGCTTCTAAACTTATGGGATT**[A/T]**CAGACTTGATCTAGCAATTCGGACAGCGAATCGGTATATAAGTGCGTCTGATGAATAAGA	0.452	0.065	0.311	0.774
Ca3594	GATAAGGGCAAGGCTGGCCCCTTGACATCCACACTACCACCTCCACCTCATGATATGCAT**[T/C]**CTCAGTGAAAAAGGCTCATGAAAGATATTTGTTTCATGGAGGCATACGTAGTGGAGTGTT	0.482	0.057	0.338	0.829
Ca3700	GCTCAAATACAACAAATAAGGATCCGGTAAAATCAGAAAGACCGTCATCTTTGGGTAGGT**[T/G]**GTTTGAACTTTACATAAACCAACTCTGTGAAAAAAAATATCAACACGGATTCTTGATACC	0.540	0.067	0.379	0.818
Ca3701	TCTTTCATCTAATCGTCTCTTCCCTAAGAAGATGGACTACGGTATCAATCTTATTCCATT**[T/G]**TTTTTCTGCTTTGCTATATTGAGAGTCAAATGATTTGCAATCGAATTTTATTTGCATTAT	0.398	0.077	0.250	0.720
Ca3769	AAGAGAAGAATACATTAACCATATACTATAGTTTTTTCTTGGAGTTGTTTTTGTTGTTAT**[T/C]**AGAGATTTTTTTTTCAATAGCCGATAGTTAGTAGACATTTTTGCCAGTAAAGTATAGTTT	0.329	0.261	0.196	-0.179
Ca3794	TGGAGGCAAAGTTGGAAGAAACAAGACGCAAGGAGAAAATGATGAAATTGTTGCTGTTTG**[T/C]**AGCGTTTGTTTTCGTAGTGCAGAATTTGTTGAGCAAATATTGAGTTGTAACAAGCATTTG	0.507	0.066	0.357	0.613
Ca3795	TAGACAGTCTCTTTGTTTGTTCTTGAGAAGTTGTTGTAGCTGGTGGCTCATCTGGTTATC**[T/G]**CCTTCTTATCTTCTTTGGCCGGCCAGGAAGCTTGATGGTTTCAGGTGGCAAAACAAGCCC	0.505	0.057	0.355	0.630
Ca3838	GCAACGTCTTCAGCAGATCCACCTCGATGCAAATGCGAGCTACACTCGGTCGTGGCACAG**[T/C]**AAGAGTGGCCGCATCCACTAGTAATGGCAGACCCACGCATGATAGAATCTGAAAAAACAC	0.454	0.066	0.312	0.802
Ca3940	TATGGATAGAACGAAAATGCATCTCCAGCTGAGAACCTGTTGTTCCGGCTAGCTCCAAGA**[A/C]**AAGCTTCAAATTTTGATAACGTTGGGTTGGGCTGAACTTTAGGAACTAAATATTAATCTA	0.495	0.064	0.351	0.816

Ca3970	GAAAAAATAGTTATTTTGAAATATCAAATCTAGATATGGAACTAGCTAATTATACTCCTC**[A/C]**TCATCCCCTCTCTGTGAATAGGCATATACCTATTATAGTTAGTGCTCCTGTTATATCTTA	0.460	0.080	0.307	0.729
Ca4029	TCACACCGGAAGATGCATCCTCTTTAGCTATTTCTACTCTTCCATTAGACAAAACTTTCG**[A/G]**GACCGTTGGGCTCATCCCAGAATGCTTAAGATACCATCTAAATATTGGAAAACCATTAAA	0.468	0.073	0.320	0.590
Ca4219	TTCATACTTTATTTCATTGATCATTTGATTCTTGAAATCTTCGCAAGCAAGTAAGTGACA**[T/C]**GAAGAATGTTTTTACTACTAGTAAATTAGTTGAACGTGGGACAAGAAAAATTGATGTGAA	0.555	0.063	0.380	0.850
Ca4223	ATTCTTGAAAAATGAGAATTTCACCATCGGAAGAAAATTTAAGACTCGTTCAGATTGTGA**[C/G]**TTTTTCAGGATTTTTTTGAAATATTTCTTGAACATATTTTCTAATTACCTTTTTTTTTTT	0.625	0.661	0.434	-0.496
Ca4233	AATACTCTTTTTTGGAGTTATGGAGGTGGCTCATTTGCAGGAACAGGCTCTCAGGTTACA**[A/T]**GGAAGGACAGTCAAAGATGGCAACAAGGTGATGGCTGAACCAAAGTTTGGGATGTACAGG	0.559	0.064	0.386	0.849
Ca4257	CCCGCTTACGAAATACGATGAATGACACAGGCAAGGACAACAGCAGGACATGTACCAAAC**[A/C]**AAGTCGTATGCCCAGAAAAGTGATGCCTTCTAAAAAGAATCCTTAAAATGTAATTTTTTC	0.551	0.074	0.369	0.814
Ca4373	GCTTGGCTCGAGCTACTTGCGAGCGGCTCGATTCGTTTGCAGCCCTAGTTTCAACACGCT**[T/C]**TTAGAGAAGAAAGAAGTGGAAGTGCTATTTCAACACACTTAAAAGAGAAGGAAAAAGACT	0.522	0.048	0.364	0.898
Ca4856	TCCAGCCTTGGAGTACTTGACACAGTATGTAAATCAGGTCATGACTAAGGCTACACAAAT**[A/C]**AAAAATTAGCATGATTTGTGGCGTTGAAAACTAGATTCGAAGTAATAAAAATCATGAGAA	0.334	0.017	0.207	0.921
Ca4929	ATCTTCTTACCGACACCCCAACGACAAGAAAGTGTCCAGTAGAGGTGCAATCGGGTCGGG**[T/G]**TCGGGTTGACGGGTCGGGTTGGGCTTAAGTATAGCAAAGAACCTGCTGAATCGAATCCGA	0.496	0.073	0.344	0.844
Ca4998	ATTTTAAAAGCCAAAGCAAACATTTTGAAACTTGTAAATAGCACCTTAATTTATTTATGA**[T/C]**ACATGGATAATGTGTTTGCCAGAATCTATTACAGATGGTGAATCTGACAACTACTTGTGC	0.624	0.572	0.436	-0.284
Ca5014	TATTAACAACGATGTCCAACTTTTGATTCGGAAATTTCAATCCGTGGAAGAATTTTGGCT**[C/G]**TAAAATATTATTGTGCGACTTGATTTTATTTCATTGTCATCTTTAATTTCTTATGACTGA	0.268	0.174	0.153	-0.132

Ca5065	ACAACAATGCTATAGTGGACGGAATTGTGATCTATTATGACTGTTAGCAGTTTATCAAGT**[A/T]**GTTAGTTAATATTCTGTGTGAAACTGAATGCAGGTTTTAGCATTAGTTGGTGATCAGCTT	0.331	0.053	0.204	0.726
Ca5137	TCCTTGCCATTTGTAAATAAACTTGGACATGGCCTCAGAATTCCAATTCCCAAAAGTAAA**[A/T]**TTTTTTTAATGTTCGCGTTCAATTTTAGACCAGTTCTTTATAAAGAAATCGTAGACCAGT	0.516	0.070	0.354	0.843
Ca5198	AGTGAGTAAAAGAAAAAACAAAGCAAAATAAAGAAAAGAAAATGAATGAACCACATGTCA**[A/G]**AGTGAGAGAGATTCACTTGACAATCGTTGGCATTGATATAACAACTCCACTTTTTCTTA	0.605	0.026	0.420	0.925
Ca5205	GTGGTCATCACCCTCTTTGGTGATACTGGAAGTTAGGGTTCTACCCTTGCCTCTCTCAAA**[T/C]**TTGCCACAATATGTGATTGGTCTTAGTTGACCATCTCCTCTTACCCCTTTCCCCTAGATT	0.546	0.093	0.363	0.753
Ca5273	TTAGATTAACACTCAGAAATAAGCGAAATTCTGGTACAAAGCACAAGCTAAGGTAGAGCC**[T/C]**ATAAGCCAATACCATCCAACTAATTAATAACTGAAAGTGCGACTGAAAACCTTAAATCCA	0.338	0.033	0.194	0.795
Ca5293	TTGTGGATTGTCTTTGGCTCTAGGGATGCAGAAGAAGAAGATGCCAAAACTGTGGTTTTT**[T/C]**TGGGAACAACTAGCAGGAAAACTTGATTGATGGCTAATTTTGCAACCCAATAGAATATTA	0.579	0.160	0.395	0.624
Ca5304	GCACCATTAGTGTGAGTAAGATTAATATGTAAAAGTTACATGTCCAAGTCATGATTGAAT**[T/G]**ACAGGTAACAATTCAAATTTAAGAGAATGCCAATTAAGTGCATGTGTTCAAAGTAGAAAA	0.305	0.212	0.182	-0.165
Ca5432	ACTTCCATAGCCTTTCGTGATAAACAACGGTTAAATTTACTTAGATTCGGAAGAACCAGC**[T/C]**GGTTCAATCATTAACCCATTAAACCAAAATGAGTTTTAAAGAACTCGCCAGCTCAATTAA	0.569	0.080	0.384	0.801
Ca5511	CTATTACAAACTAATGGATCCCGATATGGTTGCATTGTGTGTGTGCTATAATAGTGATAG**[A/T]**CTTGCTATCTAAGGACAATTAGCATAAGAAATACCAACAAATGACTAAATATTAAAAAAT	0.471	0.081	0.324	0.551
Ca5549	GCTAACCATGACAATGAAATCATACTTGGTACCTCCTATTGAGTAAGTTTCGAGCAAAAC**[A/C]**ACACGTATTGATTTCTGAAATTTGCACTGTTTCGATATCGAAATACTACCTTCTTTACAT	0.464	0.073	0.314	0.827
Ca5578	GTAGCCACTATGCCGGACTATTCAAAACATTCGGATGGTGCTCAGGGATTTACATGCTAC**[A/G]**CTGGAATATACCTTTAGGGAAGGGAATACGATGGTGGTCACCCTTGCGTCTGCGCATTTG	0.431	0.067	0.293	0.740

Ca5588	GCAGTAAGGCCACAATTAAACAGCGTCTGATTAAAATCCTCCATATTTCGTGCATTCGGT**[A/G]**GTGCCCCCCCAAGCCTTTCTGACGCCTCCGCGATGATATTAAAATCCCCAGCCAACATCC	0.067	0.015	0.029	0.545
Ca5643	GGTCGAGGCCATGTACTACTCTTTTTTTTTTTTTTCCCAAACGATAAGAGAGAGGCCATG**[A/T]**ACTACTTGTTCAAATCGGATTTGAACTTAAGAGTTTTTACTCAATCAAACTCGAATAACA	0.569	0.069	0.386	0.843
Ca5810	AGACATAAATAAGGATCAGGCCATATCTTTAATCATGTACAAACAGAAAGAGAGAGGGCA**[C/G]**TTATGAACAGACAGAAACATTATAAATGCAACAGCCAACAGAACAAGAATTGATTGTTGG	0.585	0.110	0.399	0.741
Ca5818	CAAGGGAAATTTTTAGCACAGGTACAAATTTATCGTTTTCTTTCTTTCTATTCCTTTTGC**[T/C]**TCACAGGCTAAATCCATTCAAATGTTGAAACTTAAGAGATTGTAGAACTACTTGTCCTAA	0.562	0.151	0.377	0.607
Ca5821	CTCTCGACTCTCTCCCCAGCCTCCTCTACTTGTGTGCGTGGCCTTGGGCTTTGTCTAATC**[A/T]**CTCTCGACCGAATCGGATAACGCCTACGCCGTCTCCTCTTCGCTTCTTTGTTTTTTCGCC	0.594	0.172	0.408	0.595
Ca6081	CCGACTTTGAGTTCTCCTCCCCCTCCTCTTCCTTCAACATTGAGTTCTCCACCACCTCCT**[T/C]**CACCAACACCAACTTCGAGCCCTCCACCACCTATGCCTAGTCTGCCACCAAAAGTATCTG	0.502	0.063	0.353	0.617
Ca6117	ATTTACTCTCTAAAATATATATTGCAAAAATGATAGAGCAATTATTGAGCATATTTTGCG**[T/C]**TGTTATTCTATCTTCATTTTGGTTACTTACTGTGCTATATTGAGATTTTGCTCATATTTG	0.492	0.063	0.348	0.814
Ca6219	TGGATCTAGATTTGGTCTAAATCATAGAAAATCATACCCTGCCTAAATCAATGATTCTCT**[T/C]**ATTGGGTAGGATTTAAGTTGACAAATTAAATTCAAATTCTACCTAAGTATATTGTATCTA	0.406	0.090	0.260	0.705
Ca6249	TTTTAACCTACACACCTCAAAAATCTAATACCTCAAAAATTTTGAACAAAAAATCTAATA**[T/C]**ACAAAAAAATTTGTTCCAACCCACCACTCCAACCACCACCTCTCCTGGCGCCGCCGGTCA	0.097	0.037	0.051	0.150
Ca6268	TCGGGGCCCGCCTCTTATGAGGCTTGGAACCTGATGACTCAGATAGATTAGGTTTTTCG**[A/G]**AGCCATGTAAGGGCAAAGATGTCAATAACAAAGGCACAGAGCCGACAAGAAAACACCAAA	0.594	0.051	0.408	0.873
Ca6385	TGAAAAGATAGAAGGCAGATTAAAAGTTGTGTACACCTTTAGCAGCAAAGGCACTCTGGC**[A/C]**TTTCCACACCAAATTCCACATCGATTCTCGGGGAGGTTAAGGGTTAGGTTATTAATTTTC	0.495	0.072	0.350	0.792
Ca6387	CTCTCATCCAGTTCATTTTGCATGGCAGTGCAGAAATTCTGATTACATATGCTTTTGTAT**[A/C]**TACAATCGGTTCTGAAAATTGCTAATGTCACCTCTAAGTGATTTGTTTCTCTATTGAACT	0.564	0.054	0.381	0.872

Ca6811	GGGTTTTAATAAAATAAGATGAGAGCCGGTTTAGGATTATTTGGTTGGGTATCGGAGATG**[T/G]**GCCTTGGTTTTTTTGGGGTTTTCCGATTGGCTTGAGAGGGTCAAACCCACTCCCTTTGGT	0.142	0.021	0.079	0.830
Ca6828	TTAATTGTTAATCAACAAAAGACGGATTCTTATCTACAAAGTATGAGGAATCAATTGGGC**[T/C]**AGATATAAGAAATACAAAGTCAGATGAGTCAGATGGCAGTGGCAATCAACCGCCTAGAAT	0.118	0.016	0.067	0.715
Ca6840	GTGAACAAGATAAATGGCTACACAAGCTTCAGTAAAACAAGTGCTTGGGGCACCAAGAAC**[T/C]**TCGAAAACAACTTCAAAAGACTCACTTTTGAAGATAATAGTTCATCCTGATAACTTCTGC	0.518	0.088	0.365	0.575
Ca6849	CTGAAGAGTCAACTAGTTGTTGGGAGTATCAGACGTCCGGTACTTCCGATACTCGCGTCC**[A/G]**ACAGTGGGCAGTGAGCTTGAAGAATCTTCTTTAATTCTTTCTCATTTTATTTTCACTTGA	0.512	0.071	0.367	0.807

Transition to Chapter III

(And methodological notes)

The previous chapters were focused on coffee genetics, and the varietal diversity and mixtures found in agroforests. However, these genetic resources do not exist in a vacuum, but within the context of complex, diversified cropping systems. These have been presented at length in the general introduction, with particular attention given to the ecosystem services they provide. The ecosystem service framework is arguably of particular importance in countries such as Haiti where so much of the land is subject to anthropic management and use. This chapter aims to characterize agrobiodiversity in agroforestry systems, as well as the ecosystem services they underly. Haitian CAFS are interesting in light of the historical absence of agrochemical intensification in these systems. They can be seen as a laboratory for experimenting with agroforestry system optimization beyond the issues and compromises entailed by transition from intensified farms. With diversity at their core, they also offer opportunities to consider how the different levels of diversity can be mobilized and organized spatially (and perhaps temporally) to improve these systems and strike the necessary balance between their three dimensions: economic, social, and ecological.

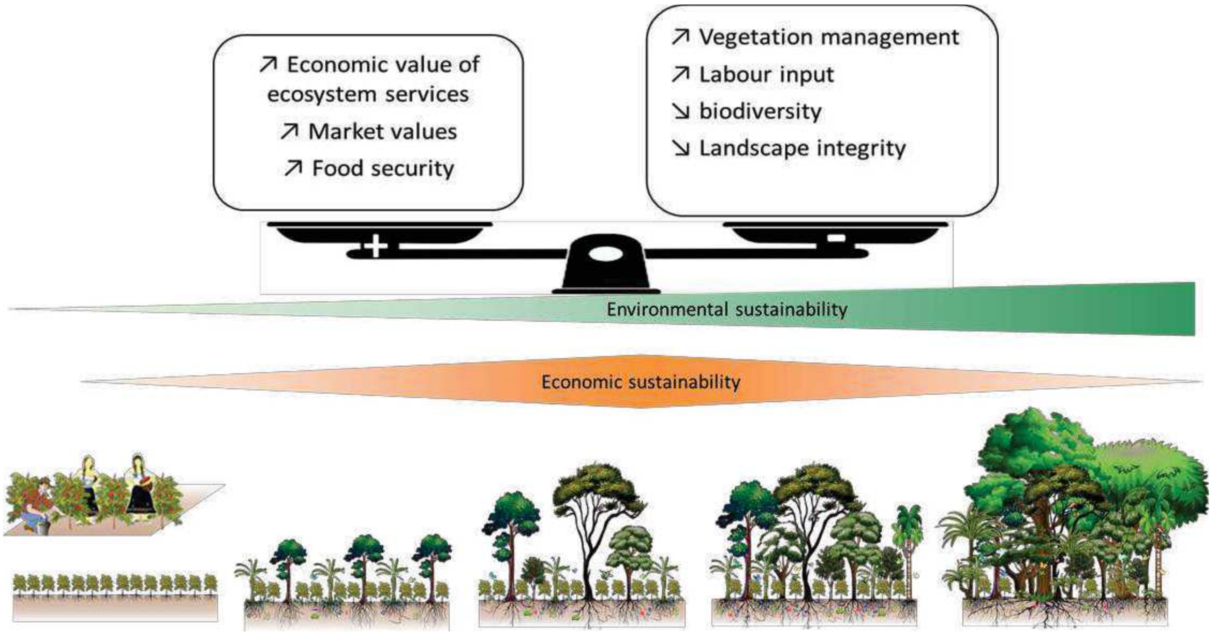

Figure 1. Gradients of socio-economic and ecological sustainability of coffee cropping smallholder systems. A balance between these two dimensions may be reached through management of agrobiodiversity. Adapted from Poncet *et al.* (2024).

We applied the lens of **Systemic agroecology** which aims to take a broad view of Agroecosystems and the interactions between their components (Rapidel et al, 2015) as opposed to, say, functional ecology approaches which may seek to describe direct interactions between individual components of the system (Diaz & Cabido, 2001). Rather than explain processes within the system, our approach was diagnostic, seeking to identify links between agrobiodiversity and service provision in order to potentially elucidate pathways for improving service provision (see Cerda et al, 2020 for a good examples of this approach). The study of ecosystem services delivered by agroecosystems, even when focusing on crop-specific services such as pest and disease regulation, is necessarily **multi-dimensional** and must find ways to incorporate the system's complexity. Indeed, unlike in experimental conditions, crops are subject to a variety of environmental factors in even the simplest agroecosystems (for instance, a combination of biotic aggressors). In some cases, simple univariate tests such as Analysis of Variance (ANOVA) or Kruskal-Wallis tests can be useful for investigating specific effects or associations within the broader agrosystems. For instance, testing for **synergies or trade-offs between ecosystem services** can be done by simply testing for correlations, positive or negative, between quantitative, continuous indicator variables, for instance with Pearson's product-moment correlation tests or bivariate linear regressions (Cerda *et al.*, 2020). However, **multivariate and multifactorial statistical approaches** are often needed to investigate the structure of agroecosystems (Bianconi *et al.*, 2013).

These approaches can be rather complex, for instance using structural equation modeling (SEM). However, this approach ideally requires a strong preliminary conceptual model of the different interactions within the system, as well as a process of refinement to increase the goodness of fit. Nevertheless, SEM have been useful in describing interactions between various components of coffee agroforests, including indirect ones (Durand-Bessart *et al.*, 2020). However, it is also possible to investigate complex systems by itemizing their components, and using processing techniques that reduce complex data into more manageable ones. Principal Component Analysis (PCA), Factor analyses and Multiple correspondence analyses (MCA) are particularly useful in that regard. Through such methods, data from multiple variables, including of different types (e.g. categorical or continuous) or expressed in different units, can be "reduced" to a set of coordinates used to project samples in a multidimensional space. Hierarchical clustering can then be applied on this data to describe variable clusters, which can represent the components of the system. Associations between clusters can then be investigated using relatively simple analyses such as Pearson's X^2 test of independence, Fishers' exact tests. This approach has often been used successfully in studies that involve describing pest and disease clusters, or injury profiles (Savary *et al.*, 1997; Allinne *et al.*, 2016; Bhattarai *et al.*, 2017). For this chapter, we have used this methodology, which previous studies have proven robust.

How it happened:

The data used in the following chapter mostly originates from the in-depth surveys conducted by PITAG teams in coffee and cacao-growing agroforestry systems in 2021, with the scientific input of partners from CIRAD (Fig. 2). The data collection phase was primarily overseen by Wesly Jeune and members of the two universities in the PITAG consortium, UCNH and AUC, which are co-authors of the resulting article. Clémentine Allinne and I performed quality control on the data and selected those that were of higher quality and relevance. We then devised a list of additional variables to be calculated and/or obtained, and a workflow for data analysis. I selected genetic diversity variables from the study detailed in Chapter I to include in the database. I assembled the final database and, finally, performed the analyses under the supervision of Clémentine Allinne and Valérie Poncet.

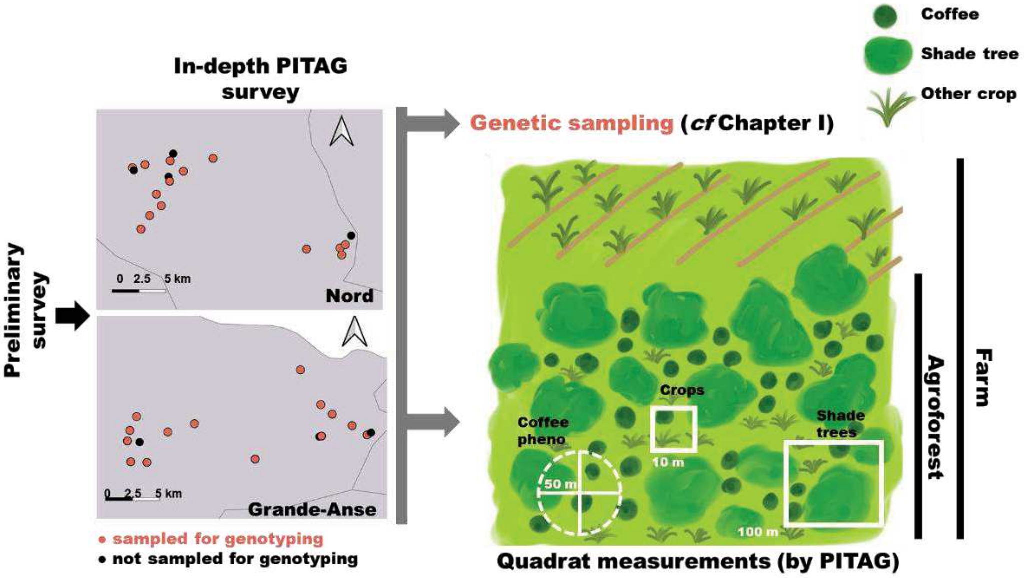

Fig 2. Diagram representing the data acquisition strategy for Chapter III of the thesis. Note that we focused only on the Agroforestry component of the farms, which could also include other cropping systems such as full-sun mono- or poly- cultures.

Chapter
III

Chapter III

Ecosystem service bundles associated with agrobiodiversity in Haitian coffee-based agroforestry systems

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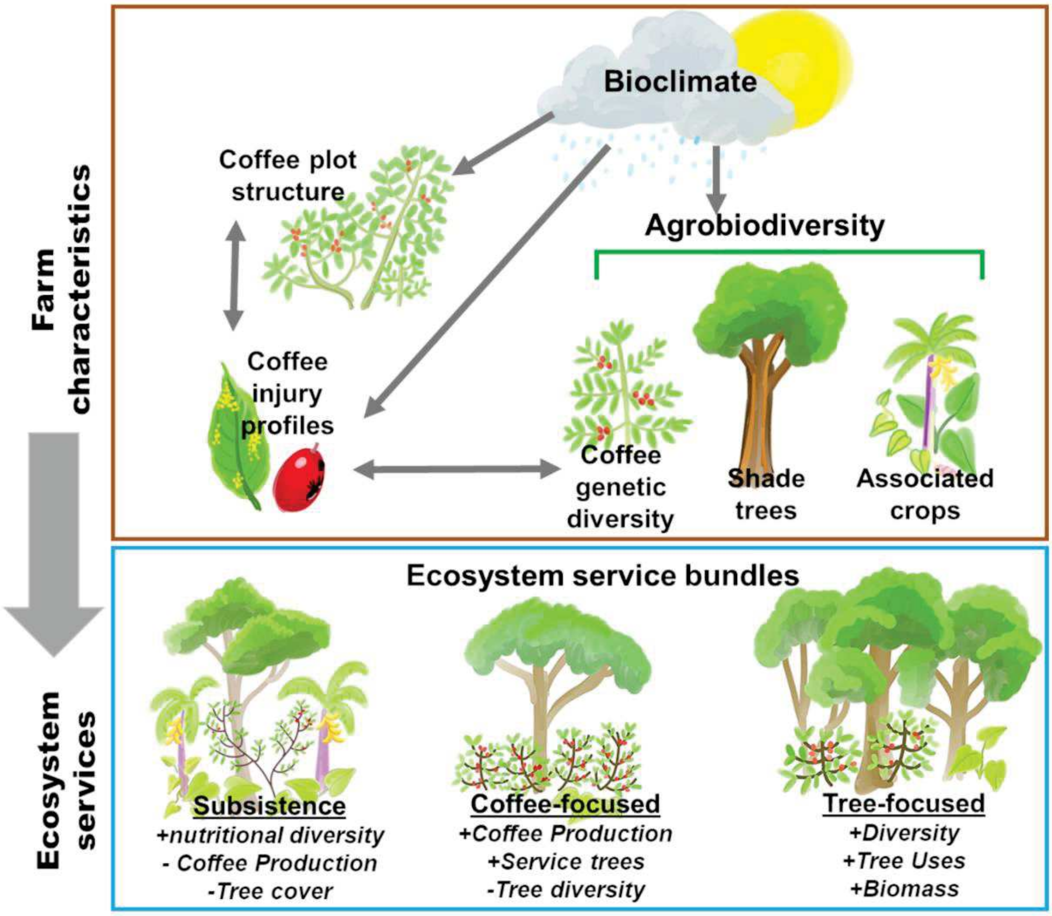
Abstract (and graphical abstract)

Smallholder Coffee agroforestry systems (CAFS) deliver multiple ecosystem services (ES) crucial to farmer livelihoods, resilience of rural communities, maintenance of natural processes, and biodiversity conservation. Their importance is likely greatest in countries with vulnerable populations such as Haiti. Nevertheless, little is known about ES delivery by Haitian CAFS. Therefore, we characterized the biodiversity and structure of 39 representative farms in two coffee-growing regions of Haiti (North and Southwest), and the multiple services they support. To that end, CAFS typologies were established from variables pertaining to coffee genetic diversity, stand structure and injury profiles, shade tree and associated crop diversity, and bioclimate. Associations between typologies were investigated. We also established a typology based on delivered ES related to coffee performance, species and nutritional diversity, tree uses, carbon storage, and nitrogen availability. Surveyed coffee plots were generally varietally diverse, aging, and subject to pest and diseases. Most CAFS occurred on a spectrum of farm regeneration (old to renewed coffee plots) tied to the adoption of “modern” coffee varieties, with implications for ES delivery. Furthermore, we described 3 distinct ES bundles delivered by CAFS, focused on maximizing subsistence, coffee performance, and tree utility, respectively. Finally, our results highlight the importance of the tree strata for ES, including conservation of native species. Overall, our study contributes to the still-limited knowledge of Haitian CAFS agrobiodiversity. Trade-offs between certain ES, and absence of trade-offs between others, signal possible CAFS improvement pathways.

Graphical abstract



Keywords: Agrobiodiversity, agroforestry systems, coffee, Haiti, ecosystem service bundles

Highlights

- High but variable agrobiodiversity structure, composition in Haitian coffee farms
- Coffee plots have complex varietal diversity but face aging, pests and diseases
- Farms have diverse strata of introduced and native useful tree and crop species
- Three service bundles focused on coffee, trees, and subsistence were identified
- Service bundles differ by coffee farm typologies and between North and Southwest

1. Introduction

Biodiversity underlies or enhances the delivery of several key ecosystem services upon which human and non-human communities rely (Daily 1997). This is true for agricultural systems as well as natural ones (Altieri 1999). The former rely largely on agrobiodiversity, which can be defined as the diversity of organisms that contribute in a broad sense to food production and agriculture, and are associated with cropping and livestock raising within ecological complexes (Jackson et al. 2013). Agrobiodiversity can be promoted by several diversification practices, from crop-specific ones such as variety mixtures (Wuest, Peter, and Niklaus 2021; Reiss and Drinkwater 2018) to system-wide approaches such as intercropping (Li et al. 2021; Machado 2009). Beyond the main provision service of crop yields, agrobiodiversity can support pest and disease regulation (e.g. by reducing their incidence and/or impact on the host plant) and enhance nutrient availability (e.g. when incorporating nitrogen-fixing legumes into cropping systems). It can also reduce soil erosion (when increasing the proportion or duration of vegetation cover), and buffer against shocks to production systems and the communities that manage them (e.g. by stabilizing yields and mitigating failure of one crop through harvest of another, Jose 2009; Renard and Tilman 2021).

Diversification if often at the core of agroforestry systems. In fact, some agroforestry systems such as traditional homegardens rank among the most diversified cropping systems, combining timber, fuelwood and fruiting trees, annual and perennial subsistence and cash crops, and even medicinal or culturally- significant plants (Fernandes and Nair 1986; Sharma, Mina, and Kumar 2022). As such, they are central to the livelihood and resilience of many rural communities, and to the conservation of natural biodiversity in the face of ecological degradation, particularly in impoverished countries.

The Republic of Haiti exemplifies this important role of agroforestry systems: the country is faced with several economic and socio-political challenges that have left its mostly-rural population vulnerable. Furthermore, it has experienced a history of severe deforestation and natural habitat loss stretching from the time of European colonization, putting the delivery of ecosystem services at risk (Mompremier et al. 2022; Jean Louis et al. 2024; A. M. Tarter, Freeman, and Sander 2016). Agroforestry systems have helped mitigate this by providing farmers' needs for food, fuel, cash, and ability to manage risks (Steckley and Weis 2016; A. M. Tarter, Freeman, and Sander 2016; Sabin et al. 2022). This role has become more crucial in recent years, as widespread insecurity and instability has led to food shortages throughout the country (IPC 2024), which national and foreign-imposed policies have rendered dependent on food imports (Cohen 2013; Steckley and Weis 2017). Furthermore, agroforestry systems represent a major part of Haiti's forest cover, and therefore also provide important habitat for several wild species and help protect soils and watersheds (Feller et al. 2006).

Historically and even today, coffee (*Coffea arabica* L.) has been a central component of many Haitian smallholder agroforestry systems. Introduced in 1726 to the then-French colony of Saint-Domingue, the crop proved well-suited to the mountainous terrain, and its cultivation spread to the point of Saint-Domingue becoming the main coffee producer globally in the second half of the XVIIIth century (De Bivar Marquese 2022; Trouillot 1982). Coffee was then grown in full-sun monocultures, though this form of cultivation did not survive long following Haitian independence as farmers, eager to dismantle the oppressive plantation system, converted to diversified coffee-growing agroforestry systems (CAFS, Moral 1955). These systems continued to support the Haitian economy for two centuries, as coffee remained the main agricultural export well into the 1970s. However, faced with pest and disease (particularly the coffee leaf rust, *Hemileia vastatrix,* hereafter "Rust") outbreaks, government neglect, soil degradation, natural disasters and stand aging, Haitian CAFS have seen their yields severely reduced (Amaya et al. 1999; Vital 2014; Arias, Brearley, and Damais 2006). Despite this, Haitian coffee remains potentially attractive to specialty markets as an ethical, environmentally-friendly shade coffee provided proper post-harvest processing, especially as the historically significant, high-cup quality Typica variety is still prevalent (Millet et al. 2024; (in press)).

Haitian CAFS typically have low management intensity and negligible (if any) agrochemical use. While Typica is the main cultivated variety, several farms feature multiple Arabica variety mixtures, considerable genetic mixing, and dynamic generation of diversity, enabled by plant material exchange networks and regeneration of coffee plots by germination from the seed bank (Millet et al. 2024). Therefore, these systems display diversity at several levels, from CAFS-wide species diversity (with multiple crop and shade tree species) to intraspecific coffee genetic and varietal diversity. However, agrobiodiversity (at any level) in Haitian CAFS has been little studied (but see Jean-Denis et al. 2014; Millet et al. 2024), and its implication in the delivery of ecosystem services merits scientific attention.

Indeed, CAFS can vary greatly in the structure and complexity of their plant communities, influenced by farmer choices and management and in turn influencing them, with implications on service delivery. They range from rows of coffee grown under one or two carefully selected shade tree species to forest-like systems with hundreds of species (Toledo and Moguel 2012). This leads to a diversity of ecological interactions that can generate synergies as well as trade-offs between coffee yields, pest and disease regulation, and other services (Allinne, Savary, and Avelino 2016). There exists a complex interplay of different components of CAFS structure such as coffee plot characteristics, shade extent and shade tree identity, and pest and disease assemblages (Durand-Bessart et al. 2020). For example, shade provided by the tree strata can have both direct and indirect, positive and negative effects on coffee disease incidence (Durand-Bessart et al. 2020; Motisi, Papaïx, and Poggi 2022). Furthermore, this diversity of coffee-cropping systems exists on a spectrum of socio-economic and ecological sustainability, and so trajectories towards greater system resilience are highly context-specific (Poncet et al. 2024). However, there exists methodological frameworks to adequately characterize the different CAFS components and the ecosystem (dis)services they underly (Allinne, Savary, and Avelino 2016; Bianconi et al. 2013), and indeed to propose pathways for CAFS improvement through identification of "model" farms in which tradeoffs between services are minimized (Cerda et al. 2020). To our knowledge, no such studies have been conducted in Haiti, despite the strong reliance of Haitian farmers on the services delivered by agroforestry systems.

Understanding the role of diversity in the provision of ecosystem services in local contexts is important to identify appropriate diversification trajectories in order to maximize the resilience and benefits of these systems, minimize trade-offs, and better address local communities' needs and priorities (Teixeira et al. 2022; Rapidel et al. 2015; Poncet et al. 2024). To this end, we studied a range of diversified CAFS in historically important coffee growing regions of northern and southwest Haiti with the objectives to i) characterize coffee, crop, and shade tree diversity and structure within Haitian CAFS, ii) determine how this diversity and structure supports delivery of major ecosystem services, iii) identify associations between services and iv) propose ways to increase service delivery through insight from the better-performing farms.

2. Materials and Methods

2.1. Selection of study sites

A preliminary survey of 122 Non-intensive, diversified smallholder CAFS took place in 2021 in two administrative departments, Nord and Grande-Anse (northern and southern Haiti, respectively). These were conducted by the multilaterally-funded Agricultural and Agroforestry Technological Innovation Program (PITAG) implemented by Agronomes et Vétérinaires Sans Frontières and the Haitian Ministry of Agriculture. Of these, 39 were subsequently surveyed in-depth (Feb-Mar. 2021), selected to represent a diversity of elevation and biophysical ranges, and farm owner demographics (age, gender…). Data on variable categories relating to coffee management and injury profiles (pests and disease), tree cover and associated crops were measured in the field, and farmer-reported information about the farms and their productivity were recorded. KoboToolbox software (https://www.kobotoolbox.org/) was used for all field surveys. 28 of these farms (14 per department) were also sampled for genotyping studies aimed at characterizing their genetic diversity (Millet et al. 2024). Farms ranged from 0.04 to 5.5 ha (0.9 ha on average). The selection of CAFS for genotyping studies was done on the basis of geographic spread, diversity of farmer-reported (expected) varietal composition, and inclusion of several municipalities to be representative of diversified CAFS in the two regions. In total, five municipalities (communes) were included: Bahon, Dondon and Grande Rivière du Nord in the Nord; and Beaumont and Pestel in Grande-Anse.

2.2. Data Acquisition

2.2.1. Coffee tree phenotyping and injury profiles

On each farm, 14 to 16 coffee trees were phenotyped in the following manner: in a 1000m^2 survey quadrat (starting from the center), four trees were randomly selected in each of the cardinal directions. For each tree, the number of vertical axes and number of primary branches on the three main vertical axes. On three primary branches per tree (located in the upper, middle and lower third of the coffee tree crown, respectively), the number of nodes and standing leaves per branch were counted. These were used to calculate percent defoliation rates in coffee trees (hereafter "% leaf loss"). This indicator is taken to represent leaf losses due to pests, diseases, senescence, and nutritional deficiencies, and therefore to indicate the overall healthiness of the tree. On all coffee trees, visible diseases and evidence of pest activity were recorded (as presence/absence). Farm-wide incidence of recorded pests and diseases (as proportion of affected trees) and percent pest and disease-free trees were then calculated.

2.2.2. Non-coffee trees and crops

To survey cover trees, a 1000 m^2 representative square quadrat was established on each CAFS, and the tree identity and diameter at breast height (dbh) of all major axes (trunks) were recorded. Associated crops were also surveyed by establishing representative $100m^2$ square quadrats, and recording the identity and number of each species therein.

2.2.3. Coffee genetic diversity variables

In the 28 genotyped CAF, a minimum of 20 coffee plants (save one farm with fewer individuals) were sampled for genotyping, for a total of 607. As this took place during a different phase of the PITAG project, these were not necessarily the same trees on which the previously described measurements were taken. The main objective of the genotyping study was to characterize the genetic and varietal diversity of CAFS in the study area, and so sampling aimed at maximizing diversity by choosing plants of contrasting appearance, as well as by enlisting farmers' knowledge and impressions. The genetic diversity data used in the present study was generated in Millet et al, 2024. Sampled plants were assigned to five varietal groups using targeted genotyping of 87 biallelic SNPs via comparison to a panel of reference accessions from international collections. For the present study, we used varietal group presence/absence data, total number of varietal groups represented per farm, and gene diversity (expected heterozygosity, H_e). We also calculated the proportion of admixed individuals per farm, defined as individuals having <80% contribution from any one varietal group, thereby likely resulting from inter-varietal genetic mixing.

2.2.4. Bioclimatic variables

Worldwide data for the 19 standard Bioclimatic variables (1970-2000 average) and elevation were downloaded at 30s resolution from Worldclim (version 2.1). Data at sampled coordinates was then extracted with R package Raster (v 3.6-20, Hijmans 2010). The five most relevant bioclimatic variables for coffee cultivation (Bio01-Annual temperature, Bio02-Diurnal range, Bio04-Temperature seasonality, Bio12-Annual precipitation and Bio15-Precipitaiton seasonality) were retained for analyses and checked for non-redundancy.

2.2.5. Ecosystem Service indicators

In studies of ecosystem service delivery, consideration must be given to the appropriate choice of indicators (Van Oudenhoven et al. 2018). We chose to focus on indicators which were relevant to the Haitian context, in which CAFS play a crucial role in the material well-being of the communities that manage them. As such, we prioritized proxies for services that are directly beneficial to farmers, though some are also relevant for biodiversity conservation and other environmental concerns

2.2.6. Coffee Farm productivity

Farmers were asked how they would describe the average coffee productivity of their farm over the past three years, in the commonly-used local unit of *marmite* which corresponds to approximately 2.7 kg of Coffee (a *marmite* is a standard n° 10, ~110 oz tin can, universally used as a measuring cup for retail in local markets). This was used along with reported farm surface area to calculate an indicator of Coffee production, defined here as the actual yield accessed by farmers (coffee harvest).

2.2.7. Carbon sequestration and Nitrogen cycling services

A conservative estimate of Above-Ground Biomass (AGB) was calculated from the tree cover quadrat data. Using the R package BIOMASS v. 2.1.11 (Réjou-Méchain et al. 2016), wood density estimates were obtained at the lowest possible taxonomic level and used along with the dbh to calculate AGB according from allometric equations which do not require height data (Chave et al. 2014). In addition, we calculated AGB using the allometric equation for fruit trees proposed by Andrade et al (2022) and verified that both estimates were strongly correlated. We also calculated an indicator of the relative importance of nitrogen fixing species in the cover tree strata (total dbh of Fabaceae/total dbh of all trees, per farm, hereafter $\varnothing_{legumes}/\varnothing_{total}$). While nitrogen fixation by legumes does not always translate to high availability for crops (Sauvadet et al. 2021; Palm 1995), this can be considered an indicator of potential contribution by trees to nitrogen entry in the agrosystem (Herridge, Peoples, and Boddey 2008).

2.2.8. Tree and crop diversity

Mean abundance of associated crops per 1000 m^2 was calculated and combined with tree cover data to calculate species richness and Shannon and Simpson diversity indices per CAFS (excluding coffee) using the R package 'vegan' v. 2.6-4chili r (Oksanen et al. 2001). These indices were also calculated exclusively on tree data and on associated crop data, respectively.

2.2.9. Tree usefulness

In order to assess the usefulness to farmers of non-coffee trees in the CAFS, we described potential uses for each tree using associated categories reported in the Royal Botanic Gardens Kew World useful plant species checklist (Diazgranados et al. 2020). We retained six categories of direct material importance to farmers ("Human food", "Invertebrate food", "Animal food", "Materials", "Medicine" and "Fuel") and omitted the other four either because of redundancy with our other indicators ("Environmental use", "Gene source"), or because their uses can be so context-specific and culturally-determined that they may not apply to our systems ("Poisons", "Social use"). In some cases, the Kew checklist did not list uses which could be reasonably expected of a species (such for fuelwood), and which were included in other sources specific to Haiti (Timyan 1996; Koohafkan and Lilin 1989). In others, the Kew checklist reported uses as "Human food" for species for which we could find no mention of this use by Haitians in the literature. In such cases, modifications were made to the species' usage lists. We then calculated a utility score per farm (as number of individuals of a species per farm × number of uses for its species, summed across all species)

2.2.10. Percent native species

As an indicator of biodiversity conservation, we calculated for each farm the percentage of species which are native to Haiti in relation to the total species richness. Native status was determined according to the Kew Plants of the World Online database (https://powo.science.kew.org/).

2.2.11. Household Dietary Diversity Score (HDDS)

A Household Dietary Diversity Score (Swindale and Bilinsky 2006; Kennedy, Ballard, and Dop 2011) was calculated for each farm by tallying the number of food groups represented in each farm's crop and tree data; only trees with reported "Human food" use were considered. Among the food groups listed in the HDDS calculator, the following were applicable: "Roots, tubers and starches", "vegetables", "Fruits", "Pulses, legumes, nuts", and "Sugar/honey". Some species belonged to two food groups: e.g. *Anacardium occidentale* being both a fruit and a nut, and were counted twice.

2.3. Statistical analyses

When unspecified, the analyses were performed using R Stats base package.

2.3.1. CAF typologies

We sought to describe farm characteristics of CAFS and classify them according to associations between their components using multivariate analyses. To that end, we established a typology of CAFS according to variable categories describing different components (after Savary et al. 1997 and Allinne, Savary, and Avelino 2016), including three components of CAF diversity Coffee genetic diversity ("Gen"), Tree cover ("Tree"), and Associated Crops ("Crop"); as well as three additional system descriptors: Coffee plot structure (hereafter CPS), Bioclimatic environment ("Clim"), and Injury profiles (hereafter IP; see Tables 1-6 for the list of variables used to establish typologies). For CPS, Bioclimatic and IP, we reduced the variables using PCA (excluding farms with missing data), then performed cluster analyses on resulting coordinates using the HCPC function in the R package FactomineR v 2.8 (Francois Husson, Julie Josse, Sebastien Le, Jeremy Mazet 2006). The same methodology was done for the Coffee genetic diversity variables, using a factor analysis for mixed data (FAMD) instead of PCA. The number of clusters retained for each variable category were determined after preliminary data exploration by aiming to define a small number of contrasting clusters while considering inertia gain at each K value. For the Tree and Associated Crop data, Bray-Curtis distance matrices were calculated using the R package ecodist v 2.1.3 (Goslee and Urban 2006) and used to cluster farms using the hclust (using Ward method) and cutree functions of the ade4 package (Dray and Dufour 2007). We then investigated associations between variable clusters: we built contingency tables between clusters for each pair of variable categories, and applied Fisher's exact tests. We also tested for associations between the presence or absence of each varietal group (Typica-, CR95/Catimor-, Bourbon/Caturra-, Kent/I-60-like and Unlabeled) and the CPS and IP categories, and for associations between the farm typologies and the Department (Nord or Grande-Anse) the farms are in. We finally constructed a contingency table summarizing significant associations between the six typologies and performed a correspondence analysis in FactomineR.

2.3.2. Ecosystem services proxies: patterns of associations and interactions

We sought to describe patterns of ecosystem service delivery in Haitian CAFS. Firstly, we compared service delivery among the CAF typologies for each variable category in the following manner: for each ecosystem service indicator, a Levene test of equality of variables was performed, followed by an Analysis of Variance (ANOVA) and subsequent Shapiro-Wilk test of normality of the ANOVA residuals and, when appropriate, a Tukey post-hoc test. When either the Levene or Shapiro-Wilk tests revealed that conditions for ANOVAs were not met, a Kruskal-Wallis (hereafter KW) test was used instead, followed by Dunn-Bonferroni post-hoc test when appropriate.

In order to test for associations and trade-offs between services, a pairwise correlation matrix was also calculated on the service variables using Pearson's product-moment correlation tests. This was done using all available service indicators. Tree density (trees.ha^{-1}) was not considered as a service indicator, but we tested for correlations between it and the service variables as well. To evaluate potential competition between CAFS vegetation components, we also tested for pairwise correlation between the density of Coffee trees, Shade trees, and associated Crops.

In addition, we sought to describe patterns of associations between multiple ecosystem service indicators when considered as a whole. For this, we chose the most relevant indicator variables, reduced them using PCA, and performed hierarchical clustering (k=3) of farms based on service delivery with FactomineR. For this analysis exclusively, farms with missing data were not excluded, but values were inputed for missing variables by FactoMiner's default method (considering group averages). Thus, another CAFS typology, "ES", was established. We avoided redundant variables (e.g. Species richness and Shannon Index). HDDS was strongly correlated to Crop diversity (as trees contributed fewer points to the score), and was considered to incorporate it. Coffee diversity (H_e) was not included to build the typology as it was used to construct the Gen typology. Associations between the ES typology and the CAFS component variables typologies were investigated using Fisher's exact tests, and another correspondence analysis was performed.

We also aimed to identify the farms that were able to provide multiple services, and could provide insights on pathways to improving CAFS. We applied k-means clustering (with k=3) on each ES indicator variable independently in order to categorize farms with lower, intermediate or higher levels of delivery of a particular service. We then calculated an overall ecosystem service delivery score according to the equation 1:

$$\frac{\text{nb.higher}\times 3+\text{nb.intermediate}\times 2+\text{nb.lower}\times 1}{\text{nb.higher}+\text{nb.intermediate}+\text{nb.lower}} \qquad (1)$$

where "nb.higher", "nb.intermediate" and "nb.lower" referring to the number of times a farm was categorized in the corresponding ES delivery tier. We then tested for differences in ecosystem service scores between ES typology clusters (KW).

Finally, we investigated how CAFS have impacted Haitian tree diversity by testing the relationships between the native status of the different taxa represented in the tree strata (this time using a native or pre-Columbian versus colonial or postcolonial introduction dichotomy) and their commonness (percent and number of farms present), abundance (mean number per farm) and number of reported uses using KW and Dunn-Bonferroni tests.

3. Results

3.1. Common patterns of CAFS diversity

Overall, surveyed CAFS were quite diverse, with an average of 7.9 ±2.3 SD recorded species (a range of 4-13), corresponding to a mean system-wide Shannon diversity index of H'= 0.97 ±0.36 SD (range: 0.12 to 1.60).

Coffee farms had on average 2.6 ±1.1 Arabica varietal groups (range: 1-5), 30.4% admixed individuals (range: 0.0-65.2%), and a mean gene diversity (H_e) value of 0.23 ±0.11 (range: 0.017-0.343). The most commonly encountered coffee variety across sampled farms was Typica (>92% farms), followed by an unlabeled varietal group (of uncertain assignment due to lack of proximity to reference individuals from international collections, see Millet et al 2024). The Rust-tolerant CR95-like Catimor variety was present in 50% of surveyed farms, and was considerably more common in the Nord department (10 out of 14 farms) than in Grande-Anse (5/14 farms, fig.1A).

Thirty-three shade tree taxa were recorded, representing at least 28 genera, some of which were represented by multiple species (e.g. *Citrus, Annona, Artocarpus,* fig. 1B). Over half (55%) of tree taxa were native to Haiti, and 16% were introduced by indigenous peoples during the pre-Columbian period. The most common tree species (>50% farms) were mangoes (*Mangifera indica*), *Inga vera* and *Citrus* trees, particularly the sweet *C. x sinensis* and bitter *C. x aurantium* oranges. While non-native/pre-Columbian trees were present in more farms and in greater numbers per farm than native species, these differences were not significant (Kruskal-Wallis *p*=0.07-0.08 in all cases, fig. S1). However, they did have significantly more reported uses (*p*=0.01). Seven taxa of associated crops were recorded in surveyed CAFS, with the most common being yams (*Dioscorea sp.*) and bananas and plantains (*Musa spp*), found in >50% of systems, often in the highest densities (Fig. 1C). Farms had on average 2.3 associated crop species ± 1.0 SD.

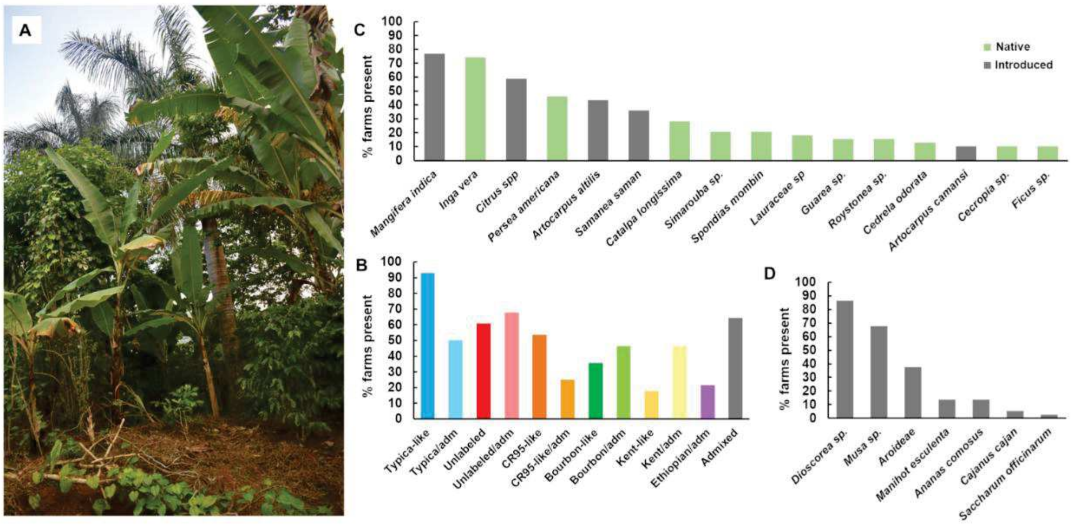


Figure 1. Patterns of diversity in Haitian coffee agroforestry systems: commonness (as % of farms in which a taxon is represented) of A. main tree species (>10% farms present), B. Coffee varietal categories, and C. associated crops

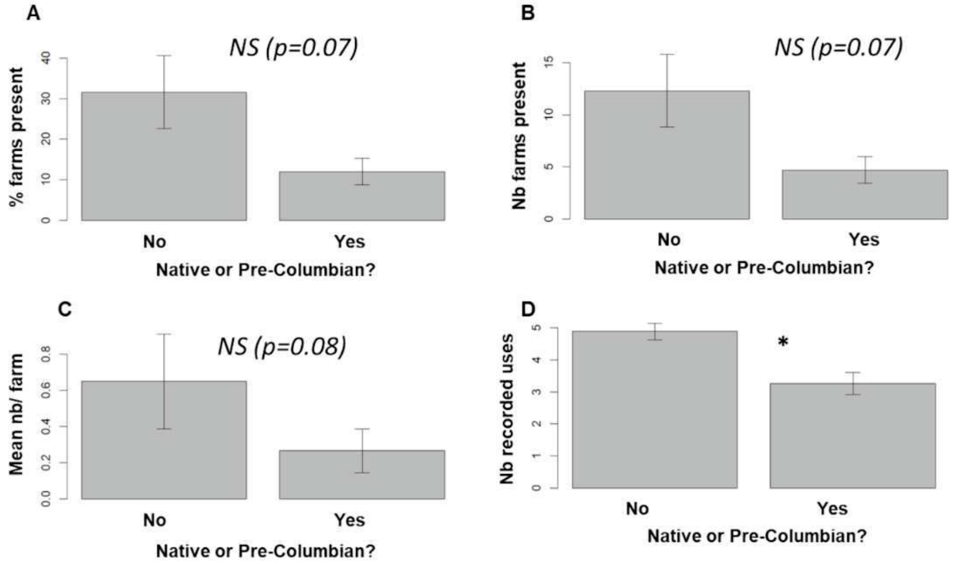


Figure S1. Commonness and usefulness of trees in Haitian Coffee agroforestry systems of different origins. Native or Pre-Colombian trees were compared with those introduced during or after the Colonial era to highlight changes in species composition. A. Percentage and B. Number of farms in which the categories are present, C. Mean number per farm of trees of each category. D. Mean number of recorded uses for trees in each category. *NS*= not significant. *: *p*-value <0.05

3.2. CAFS typologies

Using hierarchical clustering, we established CAF typologies based on coffee genetic and varietal diversity ("Gen"), shade tree composition and abundance ("Tree"), and associated crop ("Crop") composition and abundance, respectively, with 3 classes (clusters) each, and based on Bioclimate and elevation ("Clim"), CPS and IP, respectively, with 2 classes each.

The Coffee genetic typology (table 1, fig. S2A) clustered together farms that had low genetic and varietal diversity (including monovarietal Typica farms, Gen1), farms with higher diversity and the presence of CR95-like Catimor plants (Gen2), and higher-diversity farms in which the latter group was absent (Gen3). Overall, Gen2 was mostly present in the Nord Department, while Gen3 was mostly in Grande-Anse (Fishers' test p=0.032).

Table 1. Description of clusters in the Coffee genetic and varietal diversity typology, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Abbreviations used as follows: Nb var: Number of varietal groups present, % adm: percent admixed individuals, H_e: expected heterozygosity (gene diversity). Group labels with the format "*variety*/Adm" denote admixed individuals with <40% contribution from one varietal group, while those with "*variety*/*variety*" have <40% contribution from 2 varietal groups. Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001

Coffee Genetic & Varietal Diversity	**Cluster**	**Gen1**	**Gen2**	**Gen3**	**ALL farms**
	N	**9**	**12**	**7**	**28**
Nb var* **	Mean	1.56	3.17	3.14	2.64
	SD	0.53	1.11	0.69	1.13
% adm* **	Mean	3.61	41.46	45.87	30.40
	SD	5.46	16.76	11.97	22.60
H_e* **	Mean	0.09	0.28	0.31	0.23
	SD	0.08	0.04	0.03	0.11
Typica-like	% presence	100.00	83.33	100.00	92.86
Typica/Adm* **	% presence	0.00	66.67	85.71	50.00
Bourbon/ Caturra -like**	% presence	0.00	33.33	85.71	35.71
Bourbon/Adm* **	% presence	0.00	50.00	100.00	46.43
Unlabeled*	% presence	22.22	75.00	85.71	60.71
Unlabeled/Adm**	% presence	22.22	83.33	100.00	67.86
Ethiopian/Adm	% presence	0.00	41.67	14.29	21.43
Admixed ***	% presence	11.11	91.67	85.71	64.29
CR95/ Catimor_like* **	% presence	33.33	100.00	0.00	53.57
CR95/Adm*	% presence	0.00	50.00	14.29	25.00
Kent/I-60-like	% presence	0.00	16.67	42.86	17.86
Kent/Adm*	% presence	11.11	58.33	71.43	46.43

The Tree typology (table 2, fig. S2B, S3A) broadly separated farms with high tree density (Tree1), those with lower tree densities dominated by *Inga vera* and Avocado (*Persea americana*, Tree2), and those with lower densities which have *Samanea saman* replace *Inga vera* as main legume tree (Tree3). The Tree1 and Tree3 clusters predominated in the North, and Tree2 in Grande-Anse (Fishers' test p<0.001). Crop clusters (table 3, fig. S2C, S3B) separated Banana and Plantain (*Musa spp*)-dominated farms with lower crop densities (Crop 1), Yam (*Dioscorea sp.*)-dominated farms with lower densities (Crop2), and those with higher crop densities (Crop 3). There was no significant association between Crop typologies and Departments.

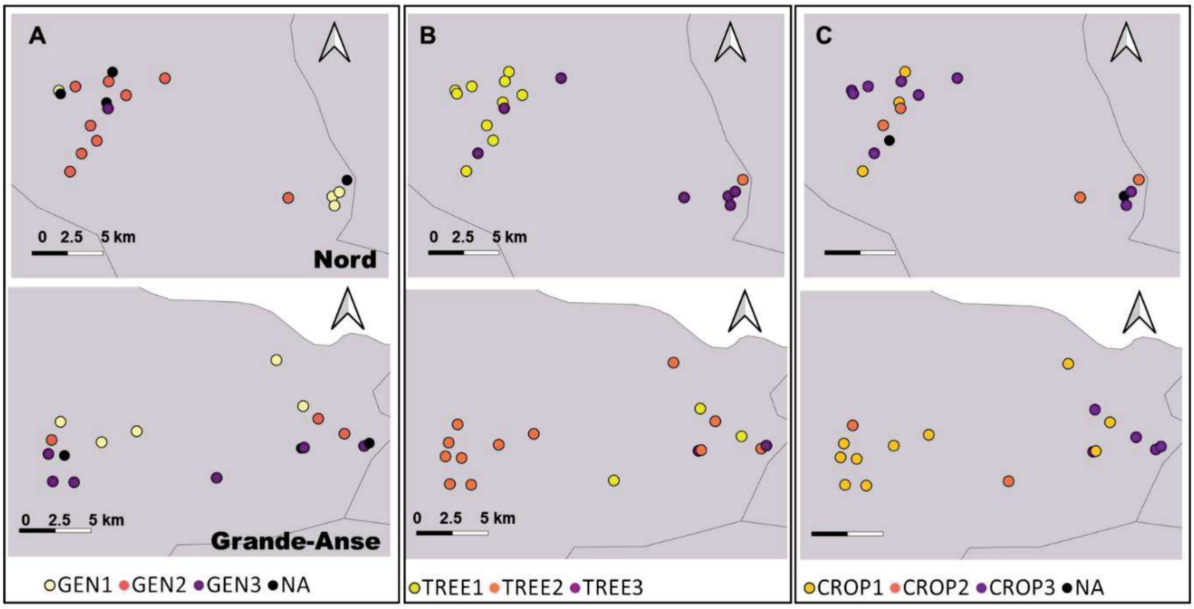


Figure S2. Variation in agrobiodiversity among Haitian coffee-based agroforestry systems. Surveyed farms in the Nord (top) and Grande-Anse (bottom) departments colored according to the typology cluster to which they were assigned by hierarchical clustering performed on A. coffee genetic and varietal diversity variables (Gen), B. Shade tree composition (Tree) and C. Associated crop composition (Crop).

Typologies are as follows:

●GEN1-Lower coffee diversity; ●GEN2- Higher diversity, Catimor present; ●GEN3- Higher diversity, Catimor absent

●TREE1- High tree density; ●TREE2- lower density, has more *Inga* and *Persea*; ●TREE3- lower density, has more *Samanea and Anacardium*

●CROP1- lower density, banana-dominated; ●CROP2- lower density, yam-dominated; ●CROP3- higher density

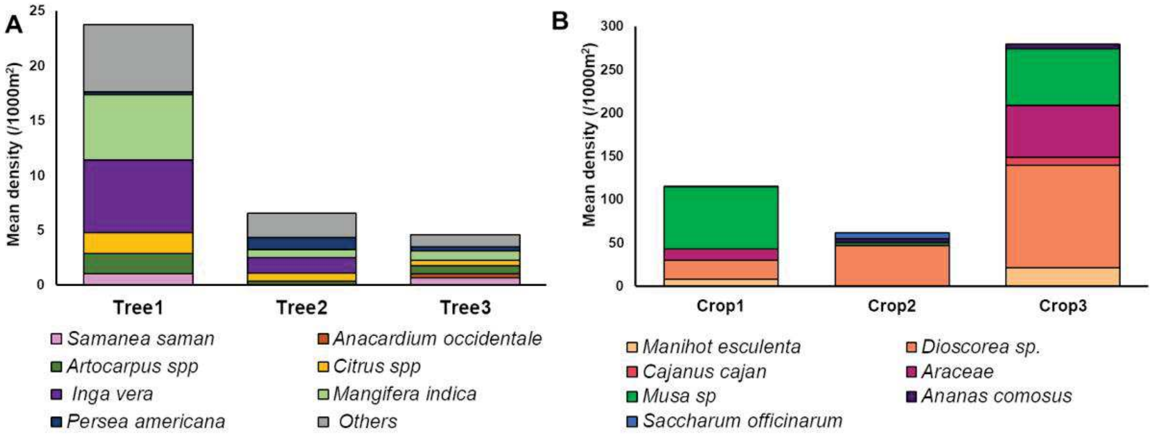


Figure S3. Tree and crop composition and abundance data. A. Mean density (per $1000m^2$ quadrat) of trees in farms belonging to the three clusters of the Tree data-based typology. B.

Mean density (per 1000m^2 quadrat) of coffee agroforestry system-associated crops in farms belonging to the three clusters of the crop data-based typology

Table 2. Description of clusters in the Tree layer typology, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001. Note: tree counts for species in the genera *Annona, Artocarpus* and *Citrus* respectively were combined (calculated at the genus level) for the PCA and HCPC.

Trees		**Cluster**	**Tree1**	**Tree2**	**Tree3**	**ALL farms**
		N	13	17	9	39
Samanea saman*		Mean	1.00	0.00	0.67	0.49
		SD	1.00	0.00	0.50	0.76
Anacardium occidentale		Mean	0.00	0.00	0.33	0.08
		SD	0.00	0.00	0.50	0.27
Annona spp	*A. muricata*	Mean	0.08	0.18	0.00	0.10
		SD	0.28	0.53	0.00	0.38
	A. reticulata	Mean	0.15	0.00	0.00	0.05
		SD	0.55	0.00	0.00	0.32
***Artocarpus spp ***	*A. altilis*	Mean	1.31	0.35	0.56	0.72
		SD	1.89	0.70	0.53	1.26
	A. camansi	Mean	0.54	0.00	0.11	0.21
		SD	1.13	0.00	0.33	0.70
	A. heterophyllus	Mean	0.00	0.00	0.11	0.03
		SD	0.00	0.00	0.33	0.16
Calophyllum brasiliense var. antillanum		Mean	0.00	0.00	0.11	0.03
		SD	0.00	0.00	0.33	0.16
Catalpa longissima*		Mean	1.77	0.00	0.22	0.64
		SD	1.79	0.00	0.44	1.31
Cecropia schreberiana		Mean	0.00	0.35	0.00	0.18
		SD	0.00	0.79	0.00	0.60
Cedrela odorata		Mean	0.31	0.12	0.00	0.15
		SD	0.63	0.33	0.00	0.43
Chrysophyllum cainito		Mean	0.23	0.00	0.00	0.08
		SD	0.44	0.00	0.00	0.27
Citrus spp*	*C. maxima*	Mean	0.00	0.29	0.00	0.13
		SD	0.00	0.59	0.00	0.41
	Citrus sp.	Mean	0.77	0.18	0.22	0.41
		SD	1.54	0.39	0.44	0.99
	C. x aurantium	Mean	0.77	0.18	0.22	0.38
		SD	0.83	0.39	0.44	0.63
	C. x sinensis	Mean	0.38	0.06	0.00	0.15
		SD	1.12	0.24	0.00	0.67

Terminalia sp (*T. buceras* or *T. tetraphylla*)	Mean	0.00	0.06	0.00	0.03
	SD	0.00	0.24	0.00	0.16
Ficus sp.	Mean	0.15	0.18	0.00	0.15
	SD	0.55	0.39	0.00	0.49
*Guarea sp. (*likely *G. guidonia)*	Mean	0.15	0.29	0.00	0.18
	SD	0.38	0.59	0.00	0.45
Inga vera*	Mean	6.62	1.41	0.00	2.85
	SD	6.31	0.62	0.00	4.51
Mangifera indica*	Mean	6.00	0.76	0.89	2.54
	SD	6.32	0.90	0.33	4.38
Unidentified	Mean	0.08	0.00	0.00	0.03
	SD	0.28	0.00	0.00	0.16
Lauraceae sp (likely *Ocotea* or *Nectandra*).	Mean	1.31	0.18	0.11	0.56
	SD	4.13	0.39	0.33	2.41
Persea americana*	Mean	0.23	1.12	0.33	0.67
	SD	0.60	0.86	0.50	0.84
Psidium guajava	Mean	0.15	0.00	0.00	0.05
	SD	0.55	0.00	0.00	0.32
Roystonea sp.	Mean	0.15	0.41	0.00	0.26
	SD	0.55	0.71	0.00	0.64
"Bwa lèt" (possibly *Sapium jamaicense*)	Mean	0.08	0.00	0.00	0.03
	SD	0.28	0.00	0.00	0.16
Simarouba sp. (likely *S. glauca* or *S. berteroana)*	Mean	0.69	0.29	0.11	0.38
	SD	1.49	0.59	0.33	0.96
Spondias mombin	Mean	0.31	0.12	0.33	0.23
	SD	0.63	0.33	0.50	0.48
Swietenia mahagoni	Mean	0.23	0.00	0.00	0.08
	SD	0.60	0.00	0.00	0.35
Terminalia catappa	Mean	0.00	0.00	0.11	0.03
	SD	0.00	0.00	0.33	0.16
"Bois de Soie" (likely *Trema micranthum* or *Mutingia calabura*)	Mean	0.00	0.00	0.11	0.03
	SD	0.00	0.00	0.33	0.16
Trophis racemosa	Mean	0.15	0.00	0.00	0.05
	SD	0.55	0.00	0.00	0.32
Piper amalago	Mean	0.08	0.00	0.00	0.03
	SD	0.28	0.00	0.00	0.16
Trichilia hirta	Mean	0.08	0.00	0.00	0.03
	SD	0.28	0.00	0.00	0.16

Table 3. Description of clusters in the Agroforestry-associated crops typology, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001

Associated Crops	**Cluster**	**Crop1**	**Crop2**	**Crop3**	**ALL farms**
	N	14	7	16	37
Manihot esculenta	Mean	7.86	0.00	21.46	12.25
	SD	20.49	0.00	50.57	35.94
Dioscorea sp*	Mean	21.43	46.67	117.92	67.93
	SD	21.83	12.17	85.30	72.58
Cajanus cajan	Mean	0.00	0.00	9.58	4.14
	SD	0.00	0.00	29.41	19.59
"Malanga" Aroideae	Mean	13.81	0.00	59.79	31.08
	SD	17.29	0.00	109.68	76.09
Musa sp*	Mean	71.19	2.86	65.42	55.77
	SD	51.30	4.05	81.72	66.44
Ananas comosus	Mean	0.95	5.24	5.00	3.51
	SD	3.56	12.45	16.78	12.32
Saccharum officinarum	Mean	0.00	7.14	0.00	1.35
	SD	0.00	18.90	0.00	8.22

The bioclimate and altitude typology (Clim, table 4) opposed farms from generally warmer, dryer and lower-altitude environments (Clim1, including all farms from the North and a few from Grande-Anse) to those from cooler, wetter, higher altitude environments in Grande-Anse (Clim2).

Table 4. Description of clusters in the typology based on Bioclimatic variables and elevation data, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001

Bioclimatic and Elevation data	**Cluster**	**Clim1**	**Clim2**	**ALL farms**
	N	21	18	39
Bio01- Mean annual temp (°C)***	Mean	23.69	22.40	23.09
	SD	0.89	0.94	1.11
Bio02-Mean diurnal range (°C)***	Mean	10.42	9.35	9.93
	SD	0.66	0.09	0.72
Bio04-Temp seasonality (°C)***	Mean	123.27	139.87	130.93
	SD	4.58	2.78	9.21
Bio12-annual precipitation (mm)***	Mean	1676.38	1996.44	1824.10
	SD	78.79	72.75	178.22
Bio15-Precipitation seasonality ***	Mean	46.14	59.03	52.09
	SD	4.12	2.01	7.29
Altitude (m)***	Mean	386.64	578.84	475.35

	SD	158.92	172.30	189.73

The coffee plot structure variables (CPS, table 5) opposed farms with younger, less dense coffee plots (CPS1) to those with older, denser and more complex plots (CPS2).

Table 5. Description of clusters in the Coffee Plot structure typology, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001

Coffee Plot Structure	**Cluster**	**CPS1**	**CPS2**	**ALL farms**	
	N	13	14	multiple	
Coffee crop age (years)* **	Mean	11.77	52.50	34.97	*over N=39*
	SD	10.87	25.89	27.82	
Coffee crop density (per ha)* **	Mean	1471.52	7004.86	3683.06	*over N=33*
	SD	1704.96	3893.90	3978.06	
% replanted* **	Mean	28.69	2.92	15.57	
	SD	22.08	5.44	24.40	
% immature plants	Mean	21.55	23.22	18.74	
	SD	19.58	11.08	16.17	
% productive plants	Mean	68.55	62.07	65.29	
	SD	20.73	17.58	21.57	
% senescent plants	Mean	6.63	11.29	13.24	
	SD	9.76	10.93	19.02	
Mean number axes* **	Mean	1.52	2.72	2.23	*over N=33*
	SD	0.59	0.87	0.89	
mean number primary branches* **	Mean	7.33	58.73	38.29	
	SD	11.99	15.19	30.71	

Finally, from the pest and disease incidence variables we identified two Injury Profiles (IP, table 6), characterized by higher incidences of American Leaf Spot (ALS, *Mycena citricolor*) and Coffee berry borer (CBB, with more pests but fewer diseases overall; IP1), or by higher Rust, Anthracnose and Leaf Miner incidence (and more diseases but fewer pests overall; IP2), respectively. The Clim, CPS and IP typologies were all strongly associated with the Departments and thus farm location (Fishers' test p<0.001 for all).

Table 6. Description of clusters in the Coffee pest and disease injury profile typology, constructed from a Principal Component Analysis and subsequent Hierarchical clustering of Principal Components using the variables represented (rows). Variables that significantly contributed to the hierarchical clustering are in bold, with level of significance: *<0.05, **<0.01, ***<0.001

Pest and disease Injury profiles	**Cluster**	**IP1**	**IP2**	**ALL farms**
	N	13	19	32
Coffee Leaf Rust* (*Hemileia vastatrix*)	Mean	0.63	0.85	0.76
	SD	0.39	0.19	0.30
American leaf spot (*Mycena citricolor*) **	Mean	0.25	0.01	0.11
	SD	0.35	0.03	0.25
Cercospora sp	Mean	0.05	0.16	0.12
	SD	0.16	0.30	0.25
Anthracnose (*Colletotrichum sp*)***	Mean	0.03	0.76	0.46
	SD	0.12	0.33	0.45
Dieback (*Colletotrichum sp)*	Mean	0.01	0.02	0.02
	SD	0.05	0.03	0.04
Percent disease-free trees**	Mean	0.20	0.00	0.08
	SD	0.25	0.01	0.18
Coffee Berry borer (*Hypothenemus hampei)* ***	Mean	0.88	0.10	0.42
	SD	0.25	0.10	0.42
Leaf miner*	Mean	0.03	0.32	0.20
	SD	0.09	0.38	0.32
Percent pest-free trees***	Mean	0.09	0.57	0.37
	SD	0.20	0.35	0.38

Our dependences analyses based on Fisher's tests reveal the following significant association between typologies (table S1): Gen-Clim, Gen-CPS, Gen-IP, Tree-Crop, Tree-Clim, Tree-CPS, Tree-IP, Clim-CPS, Clim-IP, and CPS-IP. These patterns are also apparent in the correspondance analysis. In particular, the first axis of the latter (fig. 2) was highly explanatory (89.25% of inertia). It opposed farms with higher tree densities, younger, less dense coffee plots containing CR95-like Catimors, affected by the ALS and CBB-dominated injury profile (Tree1, CPS1, Gen2, IP1, hereafter "Renewed farms") to those with lower tree densities and older, denser but genetically diverse coffee plots particularly affected by Rust, and generally found at higher altitudes (Tree2, CPS2, Gen3, IP2, Clim2, hereafter "Aging farms"). The second axis (7.87% of inertia) further separated the Tree2 from Tree3, Crop1 from Crop2, and Gen1 from Gen3.

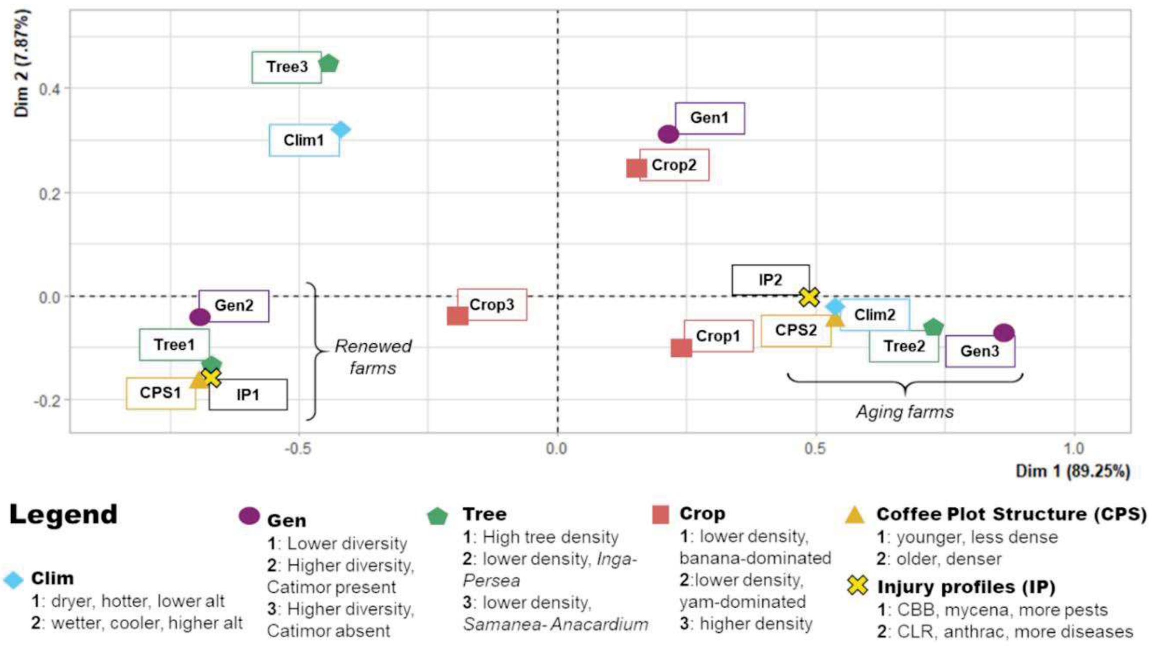


Figure 2. Correspondence Analysis plot showing associations between clusters from typologies based upon components of agroforestry system diversity (Gen: coffee genetic and varietal diversity; Tree: tree composition; Crop: Associated crop composition, in red) and **other system characteristics** (Clim: Bioclimatic and elevation data; CPS: coffee plot structure; IP: pest and disease injury profiles, in blue). Abbreviations used are as follows: catimor: CR95-like catimor coffee variety, CBB: Coffee Berry Borer (*Hypothenemus hampei*), mycena: *Mycena citricolor*, CLR: Coffee Leaf Rust (*Hemileia vastatrix*), anthrac: Anthracnose (*Colletotrichum sp*). Tree2, Tree3 are labelled according to their dominant legume tree, Crop1 and 2 to their dominant crop species

Farms with presence of Catimors were more likely to belong to the CPS1 ($p<0.001$) and IP1 clusters. No significant association was detected between either the CPS or IP typologies and any of the other varietal groups.

3.3. Interactions between ecosystem services

We performed pairwise correlation tests between the various ecosystem service indicator variables. Several correlations were found that reflected expected overlaps between the service indicators (such as between Shannon indices and species richness values, table S2). However, we also found significant correlations that were indicative of synergies or trade-offs between services delivered by CAFS. For instance, Coffee production was positively correlated to the relative abundance of leguminous trees ($\varnothing_{legumes}/\varnothing_{total}$), but negatively correlated with several diversity variables. Coffee tree % leaf loss was negatively correlated to both Tree species richness and abundance of Legumes. Notably, we found no correlation between Coffee productivity and coffee % leaf loss. Furthermore, neither AGB nor the proportion of native trees were correlated with any other service indicator. However, non-native trees did have significantly more reported uses than native ones ($p=0.01$). There were no correlations between number of reported uses of a species and its occurrence (in % farms present), nor its abundance (mean number per farm). Tree densities were only positively correlated to Tree species richness ($p<0.001$, correlation coefficient 0.64), Tree utility score ($p<0.001$, cor 0.99), and System-wide species richness ($p=0.003$, cor 0.48), and negatively to % leaf loss ($p<0.001$, cor 0.61). No pairwise correlation was found between the densities of Coffee plants, shade trees and associated crops (individuals/ha).

A PCA was performed on the indicator variables to identify trade-offs between services, and subsequently perform hierarchical clustering to establish a typology. The PCA was constructed following the pairwise correlation tests, with the most relevant variables retained (fig.3A). The first dimension (25.79% of variance) was most determined by %leaf loss (contribution: 25.78%) and tree utility score (28.75%). The second (24.24% of variance) was most shaped by Coffee production (25.15%), Tree Species Richness (19.33%) and $\varnothing_{legumes}/\varnothing_{total}$ (18.60%). The 3rd dimension (12.71% of variance) was mostly shaped by AGB (57.02%), then crop density (22.04%); and the 4th (11.50% of variance) by % native species (57.45%) and crop density (25.40%). This is consistent with coffee health being correlated with tree diversity, and coffee production with legume tree proportion, and also with the independence of AGB, % native species, and crop density with most or all other variables.

The ES typology resulted in 3 clusters (table 7, fig. 3A): ES1 had lower coffee health (higher % leaf loss) and productivity, $\varnothing_{legumes}/\varnothing_{total}$, tree utility scores, and AGB, and higher-than-average % native tree species and HDDS scores. This cluster included some farms in the Nord department, and all farms in Grande-Anse. ES2 had higher-than-average productivity and $\varnothing_{legumes}/\varnothing_{total}$, but lower tree species richness and proportion of native species, and lower HDDS. ES3 has higher-than-average tree species richness and utility scores, as well as lower % leaf loss. The ES2 and ES3 clusters were exclusive to the Nord department (fig. 3 D, E). Pearson's correlation tests showed significant correlations between the service delivery scores and axes 1 and 2 of the ES-variables PCA, but not axes 3 and 4, consistent with these axes being mostly explained by few variables (AGB and % Native trees, respectively). The ES clusters had significant differences in their overall service delivery scores (ANOVA $p<0.001$). Tukey post-hoc test revealed the ES3 cluster has the highest scores (1.91±0.19 SD), while the other two had lower scores that did not differ significantly from each other (ES1: 1.52±0.23, ES2: 1.57± 0.25).

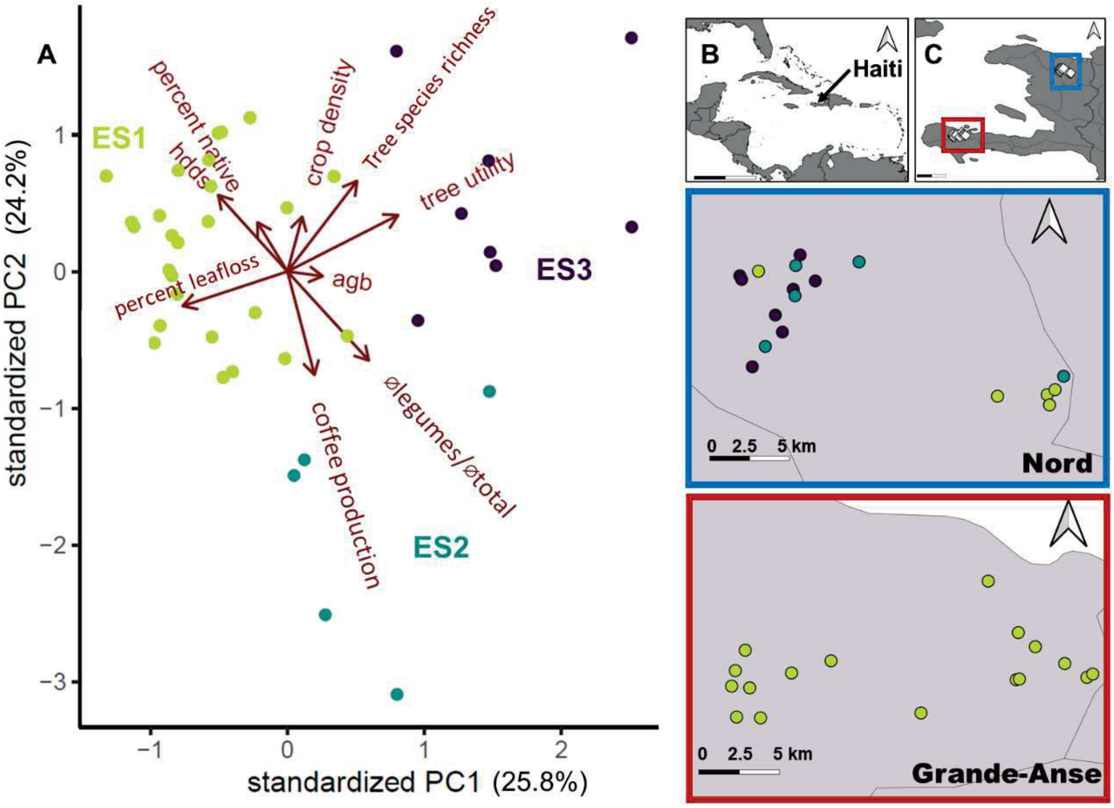


Figure 3. Ecosystem service delivery patterns across Haitian Coffee Agroforestry Systems. A. Plot of farms and variable correlation circle along the first 2 axes of a Principal Component Analysis based on ecosystem service indicators. B. location of Haiti in the Caribbean (scale bar ticks =250 km). C. Study locations in the Nord (North, blue) and Grande-Anse (South, red) departments (scale bar ticks= 25 km). In A., D. and E., farms a. D. Surveyed farms in the Nord and E. Grande-Anse departments colored according to the ecosystem service typology (ES) cluster to which they were assigned by hierarchical clustering. Maps created in QGIS v. 3.30.1 using Natural Earth (Free vector and raster map data @ naturalearthdata.com) and shapefiles from Hijmans and UC Berkeley (2015a,b) and Patterson and Kelso (2012)

Table 7. Variation in ecosystem service delivery indicators (rows) across clusters of the ES typology. Underlined variables were used in the Principal Component Analysis and subsequent Hierarchical Clustering on Principal Components used to define the clusters. Presented as means (M) and standard deviation (SD), along with the significance level of the parametric (ANOVA "aov") or nonparametric (Kruskal-Wallis, "kw") test (as appropriate). Letters above the p values correspond to significant differences among clusters as identified by post-hoc tests (Tukey for aov, Dunn-Bonferroni for kw). Abbreviations used are as follows: spRich: Species richness. H': Shannon diversity index, HDDS: Household dietary diversity score, AGB: Above-ground biomass, ⌀legumes/⌀total: ratio of the sum of diameter at breast height of all legume trees on the farm to that of all trees.

Service Clusters			**ES1: Subsistence**	**ES2: Coffee productivity-favoring**	**ES3: Tree service-favoring**
Coffee	**Productivity (kg. ha-1)**	**Mean**	**105.71**	**1148.07**	**137.19**
		SD	**105.26**	**551.76**	**81.86**
			a	**b**	**ab**
		p	**** (kw)**		
	% Leaf Loss	**Mean**	**64.73**	**62.17**	**40.31**
		SD	**9.80**	**3.57**	**7.69**
			a	**a**	**b**
		p	***** (aov)**		
Tree diversity	$\text{spRich}_{\text{trees}}$	**Mean**	**5.27**	**3.60**	**8.38**
		SD	**1.71**	**1.52**	**1.85**
			a	**a**	**b**
		p	***** (aov)**		
	H'_{trees}	**Mean**	**1.58**	**1.11**	**1.79**
		SD	**0.33**	**0.26**	**0.30**
			a	**b**	**a**

		p	**** (aov)**		
	% Native species	**Mean**	**0.56**	**0.25**	**0.49**
		SD	**0.23**	**0.28**	**0.13**
			a	**b**	**ab**
		p	*** (aov)**		
	Tree utility score	**Mean**	**32.23**	**37.00**	**107.25**
		SD	**16.51**	**42.99**	**55.86**
			a	**a**	**b**
		p	***** (kw)**		
Crop diversity	**$\text{spRich}_{\text{crops}}$**	**Mean**	**2.56**	**1.60**	**1.71**
		SD	**0.92**	**0.89**	**0.76**
		p	*** (kw)**		
	H'_{crops}	**Mean**	0.71	0.29	0.43
		SD	0.42	0.41	0.43
		p	. (aov)		
HDDS		**Mean**	**3.84**	**3.00**	**3.29**
		SD	**0.62**	**0.00**	**0.49**
			a	**b**	**ab**
		p	**** (kw)**		
System-wide diversity	**$\text{spRich}_{\text{system}}$**	**Mean**	**7.92**	**5.20**	**10.00**
		SD	**1.96**	**1.64**	**2.16**
			a	**b**	**c**
		p	***** (aov)**		
	$\text{H'}_{\text{system}}$	**Mean**	**1.04**	**0.55**	**1.04**

		SD	**0.31**	**0.35**	**0.37**
			a	**b**	**a**
		p	*** (aov)**		
Carbon sequestration and Nitrogen cycling	**AGB (Mg.ha^{-1})**	**Mean**	**84.56**	**179.05**	**212.79**
		SD	**14.65**	**14.28**	**16.14**
			a	**ab**	**b**
		p	**** (kw)**		
	$\varnothing_{legumes}/\varnothing_{total}$	**Mean**	**0.18**	**0.62**	**0.43**
		SD	**0.15**	**0.25**	**0.20**
			a	**b**	**b**
		p	***** (aov)**		

3.4. Ecosystem service delivery along CAFS typologies

We investigated ecosystem service delivery across the various CAFS typologies (table S3). Notably, no significant differences in coffee productivity nor % leaf loss were detected between clusters in the coffee genetic (Gen) typology. Similarly, neither coffee plot structure (CPS), nor Injury profile (IP) categories differed in their productivity (though p-values for the latter two were ~0.076). However, CPS and IP typologies clusters did have significant differences in % leaf loss (as did the Tree clusters).

Tree typology clusters differed significantly in some tree-related indicators (such as species richness, % native species, utility scores, HDDS and AGB), but not in others (notably $\text{Shannon}_{\text{trees}}$ and $\varnothing_{\text{legumes}}/\varnothing_{\text{total}}$). Crop typology clusters did not differ in any of the crop-related indicators, nor indeed any indicator except coffee productivity.

Fishers's tests revealed significant association of the ES typology to the Tree, Clim, CPS and IP ($p<0.001$ for all), but not Gen nor Crop typologies (table. S4). In the correspondence analysis combining ES delivery clusters with the CAFS typologies, ES1 was associated with "Aging farm" clusters, and ES3 with "Renewed farm" clusters, albeit more loosely, on the first dimension (88.95% inertia) (fig. 4). The second dimension (11.05% inertia) further separated ES2 (coffee production-focused services) from the other clusters. Despite ES2 and ES3 clusters being overwhelmingly comprised of diverse coffee plots with CR95-like Catimors (Gen2), Fisher tests revealed no significant association to the Coffee genetic typology.

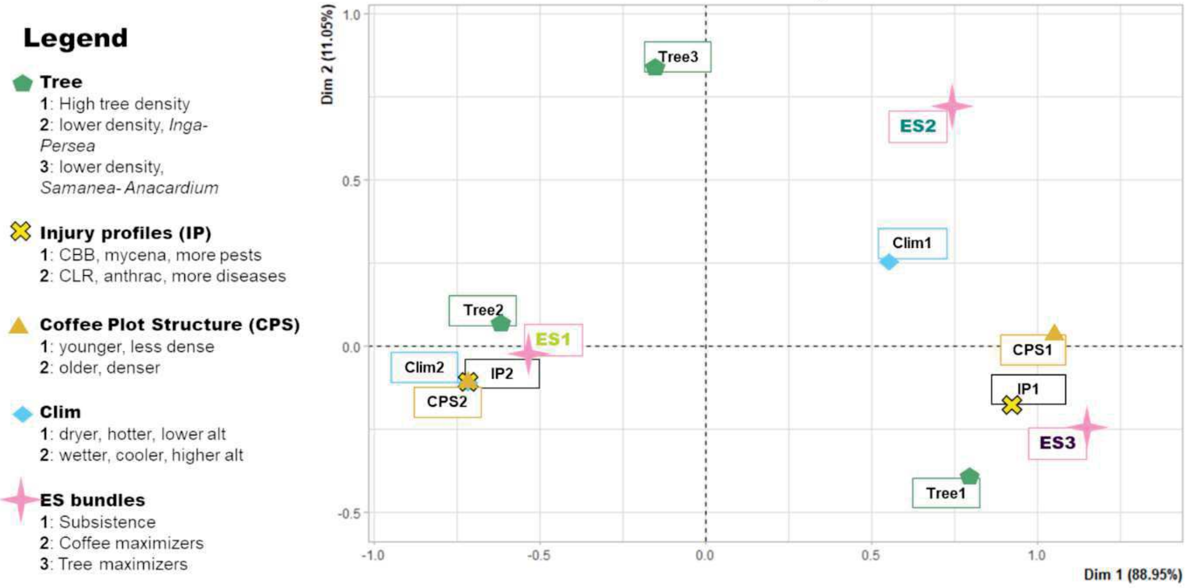


Figure 4. Correspondence Analysis plot showing associations between clusters from typologies based upon agroforestry system characteristics (Tree: tree composition; Clim: Bioclimatic and elevation data; CPS: coffee plot structure; IP: pest and disease injury profiles, in red) **and upon ecosystem service indicators** (ES, in blue). Abbreviations used are as follows: CBB: Coffee Berry Borer (*Hypothenemus hampei*), mycena: *Mycena citricolor*, CLR: Coffee Leaf Rust (*Hemileia vastatrix*), anthrac: Anthracnose (*Colletotrichum sp*). Tree2, Tree3 are labelled according to their dominant legume tree.

4. Discussion

We found considerable agrobiodiversity in the CAFS surveyed in our study. We focused on trees and crops present within the areas of agroforestry systems in which coffee was grown, and may therefore underestimate the total diversity of these compartments. Furthermore, we did not look at herbaceous and shrubby species beyond food crops, though they were also present (pers. obs.) and may have had other uses. As such, total plant biodiversity in these systems is almost certainly greater than what is reported here. Nevertheless, Species richness in Haitian CAFS (7.9 on average, range 4-13, excluding coffee), is comparable to values reported from Ethiopian coffee forests (9 on average, range of 6-15,) and diversified homegardens (16 on average, range of 8-22), though their Shannon diversity indices (H'= 0.97 on average) are lower (H'=2.75 and H'= 2.61 for Ethiopian coffee forests and homegardens, respectively, Seid and Kebebew 2022).

4.1. Haitian coffee farms are generally diversified, aging, and subject to common pests and diseases

Comparison of Haiti to Ethiopia is interesting in light of the former's high level of coffee varietal diversity within farms, and the latter's status as the crop's area of origin and diversification. Five varietal groups were identified in Haiti. Admixed individuals were also widespread, indicative of genetic mixing and seedling recruitment from soil seedbanks (see also Millet et al. 2024). This level of diversity is rather atypical of Arabica coffee farms. While there are relatively few reports on the varietal composition of coffee farms in Arabica-growing regions (Pruvot-Woehl et al. 2020; Koutouleas et al. 2022), many appear to have little to no varietal diversity (Notaro et al. 2022; Läderach et al. 2011; Harvey et al. 2021, but see Ward, Gonthier, and Nicholls 2017; Ehrenbergerová et al. 2018). The rich and dynamic diversity of coffee observed in Haitian farms in therefore more similar to Ethiopian systems, which combine local landraces and improved coffee diversity, and their levels of gene diversity (H_e) are in fact similar (Zewdie et al. 2022), despite Haiti's coffee trees all descending from the main traditional lines (Millet et al. (in press))

Among the varietal groups identified, the most common by far was the historically significant Typica (present in 92.9% of farms) which has been grown in Haiti since 1726 (Ukers 1922). CR95/Catimor-like plants, widely adopted in the last decades throughout Latin America following the arrival of Rust on the continent (Avelino et al. 2015; Harvey et al. 2021; Queneherve, Boccara, and Descroix 2015; McCook 2006), were present in 53.6% of surveyed farms. Monovarietal farms were exclusively Typica.

Mean stand age was 34 years, and most farms contained old, architecturally complex coffee trees (with some farms having up to 4.6 vertical axes per tree on average). This is indicative of a lack of frequent pruning to rejuvenate vegetative tissue, which negatively impacts potential yield (Somarriba and Quesada 2022). On average, ~65% of Coffee trees within stands were productive, ~19% were immature, and ~13% were senescent.

On average, over 91% of coffee trees per farm showed signs of disease, and over 62% showed signs of pest activity. Rust was the most common disease, with a mean incidence 0.76. This is in the upper range of what has been reported for Central America (Allinne, Savary, and Avelino

2016). CBB was the most common pest (mean incidence 0.42). Our results are consistent with previous reports of Rust, CBB and stand aging being major causes of coffee production decline in Haiti (Amaya et al. 1999; Vital 2014).

4.2. Tree strata are typical for tropical agroforestry systems, but help conserve local genetic resources

Shade tree strata in Haitian CAFS were generally diversified, with an average of 5.7 species (and a range of 2-11) per farm transect. Tree species richness observed on the surveyed farms was comparable to that of organic coffee farms in Guatemala and Nicaragua, greater than conventional farms in these countries, and greater than both conventional and organic farms in Costa-Rica (Haggar et al. 2015). At least 55% of the taxa identified were native (though most have a broad neotropical distribution), and a further 16% have been present since the Pre-Columbian period. The proportion of native species is likely underestimated, as some taxa (e.g. genus *Ficus* or "Lauriers" of family Lauraceae) may represent several species. Anecdotally, we observed other species outside of the established quadrats, both native (*Clusia sp, Ceiba pentandra*) and introduced (*Theobroma cacao, Cocos nucifera, Morinda citrifolia*). The present species list greatly overlaps that of a previous farm survey in another region of Haiti (Jean-Denis et al. 2014), in which other native species were also recorded (e.g. *Pachira emarginata, Mammea americana* or *Schaefferia frutescens*). Agroforestry systems, including CAFS, are therefore important reservoirs of native tree species, and likely contribute to conserving their genetic diversity, particularly for species of conservation concern (e.g. *Cedrela odorata*, IUCN category "Vulnerable", Mark and Rivers 2017). However, non-native species are more common overall, both within and across farms.

In fact, many of the common species found in Haitian CAFS are widespread in pantropical diversified agroforestry systems and homegardens. Fruit trees, particularly mango (*Mangifera indica*) and avocado (*Persea americana*), but also breadfruit genus (*Artocarpus*), *Citrus*, guava (*Psidium guajava*), cashew (*Anacardium occidentale*), soursop genus (*Annona*), and timber trees such as mahogany (*Swietenia*) are mainstains of such systems in tropical Africa (Sebuliba et al. 2022; Seid and Kebebew 2022; Whitney et al. 2018), Asia (Chandrashekara 2009; Mohri et al. 2013), the Pacific islands (Thaman, Elevitch, and Kennedy 2006), the Americas (Villa and García 2017; Miller, Penn Jr., and Van Leeuwen 2006), and the Caribbean (e.g. Cuba, Agnoletti, Pelegrín, and Alvarez 2022; Wezel and Bender 2003). Agroforestry systems can thus be very diverse, yet also very similar across regions. This has occurred through a process historians have dubbed Neo-Columbian exchange (McCook 2011) whereby American plants were exported to the Paleotropics, while African, Asian and Oceanian species were introduced in the Neotropics. In particular, very useful trees like mangoes were broadly disseminated across CAFS, which explains why we found non-native tree species to have a greater number of reported uses on average. Still, some species typical of Haitian CAFS are more restricted, such as "Haitian oak" *Catalpa longissima*, a common Caribbean endemic that has been introduced to much fewer areas (Plants of the World Online, accessed 2024).

4.3. Associated crops are an important source of diversification in Haitian CAFS

Seven associated non-perennial crop taxa were identified over all surveyed agroforestry systems, with CAFS having 1-4 associated crop species. The most common were yams

(*Dioscorea sp*), which is one of the major crops in Haiti and of which several species, native (*D. trifida*) or introduced, are cultivated (Shannon 2001). Bananas and plantains (*Musa*) as well as “Malanga” (or taro, members of Aroideae subfamily, primarily *Colocasia esculenta*) were also widespread (over a third of farms). It is important to note that the overall agroforestry system crop diversity may have been underestimated due to the focus on crops associated with coffee plots. Furthermore, CAFS were often part of a broader farming system that may also include more open areas that are solely focused on annual crops such as beans (*Phaseolus vulgaris*) and maize (*Zea mays*). This integration of agroforestry and open cropland is a common feature of Haitian agriculture (Jean-Denis et al. 2014) and likely affects farmers’ decision to incorporate crops into CAFS (Sinclair 1999).

4.4. CAFS mostly fall along a regeneration spectrum tied to Catimor variety adoption

The typologies related to Coffee genetic and varietal diversity (Gen), Tree and Associated crop (Crop) diversity, Coffee plot structure (CPS), and Injury Profiles (IP) highlighted a wide variety of CAFS structure, composition and management (fig. 5). The Gen typology separated CAFS along varietal diversity and composition, and the Tree and Crop along plant number and composition. Haitian CAFS were typically diversified traditional polyculture “coffee gardens”, with some more akin to commercial polycultures (*sensu* Toledo and Moguel, 2012). The CPS typology highlighted the wide range of Coffee tree management practices. Mean Coffee plot density was ~1471 trees.ha^{-1} for CPS1, of which 68.6% were productive, and ~7005 trees.ha^{-1} for CPS2, of which 65.3% were productive. This puts some Haitian farms above average densities reported elsewhere for Arabica, and others below. Plot densities are therefore in a suboptimal range (Allinne, Savary, and Avelino 2016; Teodoro, Klein, and Tscharntke 2008; DaMatta 2004). Most coffee plots were composed of multiple overlapping generations of coffee trees, from seedlings and saplings originating from the seedbank to very old, architecturally-complex trees (fig. S4). The IP typology opposed two injury profiles that differ in their dominant pathogens, as well as in the extent of both pest and pathogen damage. The Clim typologies were strongly associated with farms’ department of origin, reflecting geographic differences in environmental conditions. There was also a big North-South division in agronomic strategies and choices (Tree, CPS, IP typologies) which may explain their associations with Clim. However, given that topoclimatic conditions are known drivers of coffee injury profiles (Allinne, Savary, and Avelino 2016), and that plant diversity in agroforestry systems often varies alongside them (Birhane et al. 2020; Muche et al. 2022), these associations may be more direct.

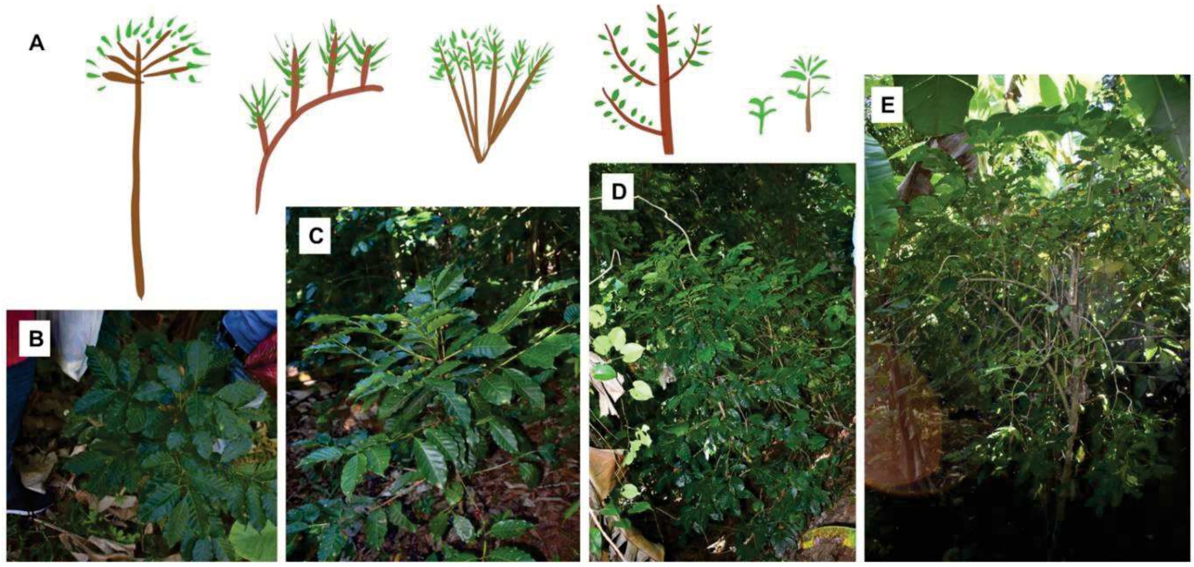


Figure S4. Diversity of ages and tree architectures represented in Haitian coffee plots. A. Schematic representation of several architectural forms found in coffee plots. Left to right: very tall tree with denuded base; complex tree with large vertical secondary axes; coppice or coppice-like growth; "standard" tree with one or two vertical primary axes; seedling and sapling. B-E: photographs of coffee trees sampled for genotyping on the same farm, N03, showing the diversity of ages and structures growing concurrently in coffee plots.

Our analyses also revealed associations between typologies. Coffee plots with CR95-like Catimors (Gen2) were generally part of the "Renewed farms" and were generally younger and less dense (CPS1). This may be due to their relatively recent introduction on Haitian farms by development projects as part of technical packages that included coffee replanting (Queneherve, Boccara, and Descroix 2015). They were also associated with the IP1 injury profile, with higher ALS and less rust. This is due to Catimors having greater rust resistance, but higher ALS susceptibility (Ribeyre and Avelino 2012). This injury profile was also associated with more densely-forested Tree1 cluster, consistent with previous studies showing that more closed canopies favor *Mycena citricolor*' development (Avelino et al. 2007) as well as CBB infestation (Bagny Beilhe et al. 2020) through its effect on microclimate. While the Gen and Tree typologies were not significantly associated, most Catimor-containing farms belonged to the Tree1 cluster (denser), which may exacerbate the incidence of ALS.

The IP2 injury profile, with higher rust, anthracnose, and leaf miner, and lower %disease-free plants, was associated with Gen1 and especially Gen 3 clusters, which have contrasting diversity levels but mostly consist of rust-susceptible varieties, primarily the traditional Typica. These coffee plots are also older and denser (CPS2, with a mean crop age of 52.5 years), and constitute the "Aging farms", which have not been regenerated. Many varietal introductions (Bourbon, Caturra…) took place in the 1970s (Ester 1978), before the rust epidemic reached Haiti, explaining why Aging farms may have diversity, but not CR95-like Catimors. The IP2 profile is also associated with low-density Tree2 cluster. This echoes previous findings linking canopy openness with greater rust incidence (Gagliardi et al. 2021).

4.5. The ES typologies focus on specific components of system diversity, only some of which are constrained by trade-off

We also performed a clustering analysis on ecosystem service indicator variables, in which CAFS were classified in 3 differentiated clusters representing distinct service bundles. The ES1 farms had lower coffee performance (production and health—as % leaf loss), and less predominant tree strata (lower AGB and tree utility scores), but higher Household Dietary Diversity Score HDDS. As the most numerous, and the only type found in Grande-Anse, these farms are seemingly representative of common CAFS management practices and difficulties encountered. These are seemingly subsistence systems, focused on producing a diversity of food items. The ES2 farms appeared to be Coffee-related service maximizers with greater-than-average production and Tree strata that are more geared towards supporting the Coffee crop, with lower Species Richness but greater importance of Legumes. These farms also had lower HDDS, but did not differ from the others in Crop density. Therefore, farmers that maximize Coffee services do not neglect associated crops, but do not focus on maximizing their diversity within the Coffee-cropping system either. Finally, ES3 farms were tree-related service maximizers, with a greater number of species and thus uses. Interestingly, Coffee plants in these farms had lower-than-average leaf loss and therefore better health, possibly through various ecological processes supported by biodiversity; including pest and disease regulation (Venzon 2021; Altieri 1999; Ratnadass et al. 2012).

This typology partially results from trade-offs between ecosystem services. For instance, greater Coffee production is associated with greater proportion of Legumes in the Tree strata, and thus lower tree diversity (as only two Fabaceae were recorded, *Inga vera* and *Samanea saman*). Farmers who focused on maximizing their coffee harvests may favor service trees that enrich soils in N to support coffee growth. By contrast, farmers who seek to maximize the utility of their non-coffee trees may be sacrificing some coffee productivity. Beyond the Coffee-Legume association, there were comparatively fewer synergies between services. Indeed, many positively correlated variables reflected overlap in the CAFS component they represent (for instance, between Tree and Crop richness on one hand, and overall system richness—Tree+Crop—on the other).

Some service variables had few or no correlations to others. Density of associated crops was only correlated to Crop diversity variables, and was not even associated to Coffee or Tree density. This suggests that there is not much competition for space or environmental resources between associated Crops and other CAFS components. This may explain why Coffee (ES2) and Tree (ES3)-related service maximizers do not have significantly lower crop diversities than Subsistence systems ES1): farmers need not sacrifice associated crop production to maintain or increase their coffee harvest, or the various services provided by shade Trees.

Likewise, AGB, which is both an indicator of Carbon sequestration and timber provision, was not correlated to other ecosystem service variables. Farmers may therefore be able to increase the on-farm biomass without compromise. However, it is important to note that the present study does not include data related to tree canopy openness or extent of shade in the system. While shade is determined by Tree density, it is also dependent on the architecture, spatial arrangement, and (lack of) trimming of trees. These characteristics all influence the possibility of coexistence between trees and annual crops. For instance, Timyan (1996) observed that crops such as banana and sweet potato (*Ipomea batatas*) are often grown under the shade of "Haitian oak" (*Catalpa longissima*) thanks to its sparse crown and frequent trimming, which additionally improves its value as lumber and provides fuelwood. Shade extent also determines tree impacts on coffee yield components through competition for nutrients and light, and modification of coffee growth and phenology (Charbonnier et al. 2017; Bote et al. 2018). It also plays an important but complex and context-dependent role in dispersal, incidence and regulation of pests and diseases (Gagliardi et al. 2021; Durand-Bessart et al. 2020; Avelino et al. 2023). In yield-maximizing, relatively more intensive Latin-American coffee-growing systems, farmers are often advised that shade do not exceed 35% (Cerda, Allinne, et al. 2017; Koutouleas et al. 2022). However, systems in which tree-based provisioning services are also important to farmers often exceed this threshold, such as in Nicaragua where farms were found to be 73% shaded on average (Durand-Bessart et al. 2020)

The proportion of native Tree species was also independent from other ES, suggesting that the contribution of CAFS to biodiversity conservation can be improved through greater incorporation of native, multi-use species. For instance, other Legumes trees (such as native *Erythrina spp*) could potentially be incorporated as service trees alongside *Inga*. However, despite the existence of a few valuable information sources (Timyan 1996; Bossa et al. 2005), there is still a need to better characterize native tree functional traits and their relationship to service delivery (Willmott et al. 2023; Isaac et al. 2024).

Across the ES clusters (fig. 3,5), ES3 (tree service-maximizing farms) had higher overall delivery scores. This is explained by the fact that many of the ecosystem service indicators considered in this study are tied to the tree strata (such as aboveground biomass or number of tree uses). Trees are also the CAFS component most likely to be the most important overall, as they provide many more services such as habitat for wildlife and epiphytic flora (De Leijster et al. 2021; Jezeer et al. 2017). ES1 and ES2 clusters had lower scores. In the case of ES2, this seems tied to a choice to focus on Coffee, and therefore service trees (legumes) to the detriment of more diverse, useful tree strata. ES1 appears less constrained by such choices, and their lower ES delivery scores may be associated (as cause, effect, or both) with socioeconomic and environmental hardships experienced by rural Haitian communities. In particular, many farms in Grande-Anse were impacted by natural disasters such as Hurricane Matthew in 2016 (ACAPS 2016, pers. obs), which may have contributed to lower Coffee production and health, loss of Trees, and overall lower ability to deliver ecosystem services. The 2023 magnitude 7.2 earthquake (ACAPS 2021), which predominantly affected Grande-Anse, may have put additional pressure on these CAFS, including possibly accelerating the cutting of trees for cash. Still, the higher HDDS scores in these farms suggest that they contribute to farmers' and their families' immediate nutritional needs. These ES1 farms could be improved through trajectories towards greater coffee production (ES2) or strengthening the tree strata (ES3).

4.6. The ES typology linked to the regeneration spectrum and geographic location

We tested for associations between the descriptive variable CAFS Typologies and the ES indicator Typology, and for significant differences between service indicator values within typologies, in order to determine how the composition of systems impacted their ecosystem service delivery. We found significant associations between the ES1 cluster and the “Aging farms” side of the regeneration spectrum, which likely explains ES1 farms’ lower Coffee harvests, greater leaf loss, and lower AGB (as for Tree2). The CAFS in the ES2 and ES3 clusters are “Renewed farms”. These are predominantly in the Nord, explaining the absence of ES2 and ES3 clusters in Grande-Anse. This geographic divide may therefore be due to farmers in the North having access to more support to regenerate their farms, namely through Catimor adoption. Northern farms are close to Cap-Haitien, the second largest Haitian city and a seat of both NGO and private sector activity, including in agriculture. In fact, most Northern ES1 cluster farms were also aging, monovarietal Typica farms located in the most remote and hard-to-access areas (pers. obs.). Grande-Anse farms are comparatively more isolated from major areas of commerce, particularly as gang violence in recent years has made road traffic between the area and Port-au-Prince (the capital) much more difficult.

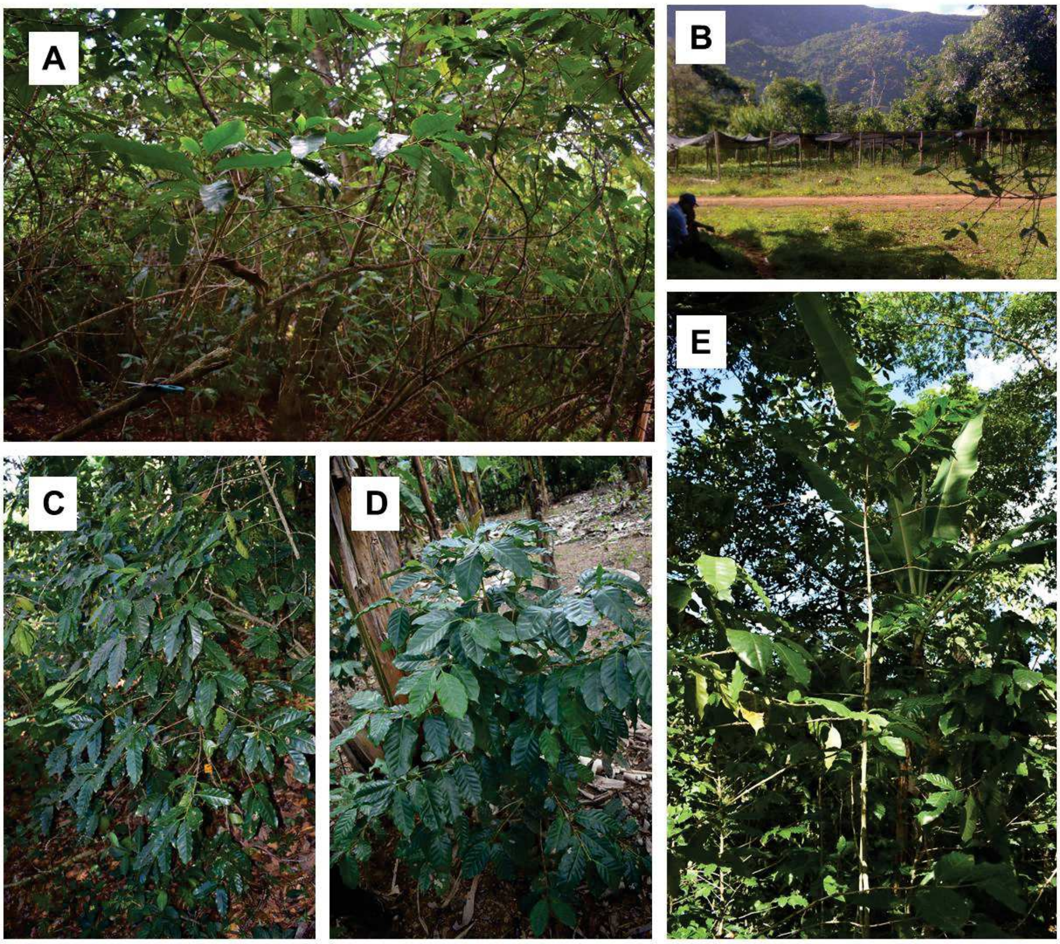


Figure 5. Photographs of Haitian Coffee agroforestry systems from contrasting typologies. **A.** Farm from the Subsistence ES1 cluster with old, dense, architecturally complex, low-

diversity coffee plots (Gen1, CPS2). **B.** Nursery belonging to the owner of a Coffee-maximizing ES2 cluster, illustrating the focus on Coffee, including propagation for regeneration. **C.** Rust-susceptible traditional Typica. **D.** Rust-resistant, ALS-susceptible, compact CR95-like Catimor in a farm from the Coffee maximizing ES2 cluster (Gen2, CPS1). **E.** Farm from the Tree-maximizing ES3 cluster (ES3, Tree1, Gen2, CPS1). Photo credit: Claude Patrick Millet

Interestingly, and despite the Gen typology being a major feature of the CAFS regeneration spectrum, it was not associated with the ES typology. There were no significant differences in coffee production nor % leaf loss between Gen clusters. This is likely due to the fact that the relationship between yield and overall plant health and coffee varietal composition is mediated by agronomic factors such as variety-specific nutritional requirements. Overall, management-related factors (e.g. stand age) and biotic stresses (injury profiles) appear as stronger determinants of coffee plant performance in Haitian CAFS than genetics. Furthermore, and somewhat counter-intuitively, there was no correlation between Coffee production and % leaf loss. The likely explanation is that our production indicator, as a farmer-reported variable, is not a measure of potential or accessible yield (Nutter, Teng, and Royer 1993), but of the amount of coffee harvested by farmers from CAFS. Farmers may be limited by labor availability, insufficient market access or demand and personal circumstances, and may therefore not be harvesting their coffee to the fullest extent. This may also promote the incidence of CBB, with unpicked cherries serving as refuge for the pest (Aristizábal et al. 2023). Furthermore, studies modelling primary and secondary yield losses in coffee have shown a temporal decoupling between foliar pest and disease injuries and yield, due to staggered effects of the former on the latter (Cerda, Avelino, et al. 2017). Overall, our study provides insights into possible improvement of ecosystem service delivery by acting upon CAFS structure and management.

4.7. ES delivery by CAFS goes beyond identified bundles

The present study focused on several ecosystem services for which we had access to quantitative indicators, but others merit future attention. For instance, while our indicator of Coffee production is useful to describe the current state of affairs, there remains a need to quantify the accessible yields and actual yield losses in these systems in order to compare their efficiency and production potential, especially in relation of genetic and varietal identity (World Coffee Research 2019). Furthermore, many others are also delivered by CAFS. While we looked at conservation of native trees, these systems provide habitats for a variety of organisms such as insects, birds and reptiles (including many endemic species), and herbaceous understory and epiphytic plants (pers. obs. consistent with reports from Colombia by De Leijster et al., 2021). While they typically hold fewer species than natural forests, CAFS still constitute valuable biodiversity reservoirs (Haggar et al. 2019; Bhagwat et al. 2008; Kessler et al. 2012), a role which is likely greater in the context of Haiti with >99% primary forest loss (Hedges et al. 2018). Indeed, studies have shown that agroforestry systems can provide important habitats for native and migratory birds (Exantus, Beaune, and Cézilly 2021), as well as insects (Beaujour and Cézilly 2022), even when embedded in urban landscapes. In fact, greater insect order richness was measured in these peri- and intra-urban agroforestry landscapes than in comparable remnant forest fragments (Beaujour and Cézilly 2022). These systems could be mobilized as way of improving native fauna and flora conservation, though the perceptions and opinions of farmers must be surveyed and considered for this to be successful (Kross et al. 2018). As a major type of tree cover on the island, CAFS are also important for erosion control (Blanco Sepúlveda and Aguilar Carrillo 2015). In addition, these systems provide a variety of cultural services. Haitian Coffee agroforests are traditional systems that arose after the nation acquired its independence, partly as a repudiation of colonial plantation systems (Lundahl 1984; Moral 1955), and are still host to the historically significant heritage Typica variety. Finally, they arguably contribute aesthetically to the Haitian landscape, and many of the trees they hold, such as *Ficus spp* and *Cedrela odorata*, hold great importance in local belief systems (A. Tarter 2015).

4.8. Identifying ES bundles may elucidate trajectories towards greater system sustainability

The ES bundles described in the present study correspond to different strategies of CAFS biodiversity planning and management. These strategies can be tweaked, updated or altogether modified to bring systems towards a state of ecosystem service delivery ever more aligned with farmers' needs and goals. Our study contributes to the still-limited knowledge of service delivery by agroforestry systems in general, and of Haitian CAFS in particular. The limits and constraints on CAFS optimization are unclear. This is in part due to the diversity, complexity, and context-specificity of trajectories that could lead to improving CAFS' ability to respond satisfactorily and sustainably to economic and ecological needs (Poncet et al. 2024; Cunningham et al. 2013). This is compounded by the uncertainties faced by farmers in light of the unstable, precarious social-political-economic conditions that prevail in Haiti. Farmers strive for more profitable systems, which cash crops such as coffee could theoretically provide under appropriate conditions, but they also strongly value farm resilience, agricultural portfolio diversification, and food sovereignty (Steckley and Weis 2017; 2016). Much more research on the relative importance of these values is needed for the improvement or optimization of CAFS.

Previous studies have shown that CAFS need not conform to a single structure to provide multiple ecosystem services, but that there exist combinations of agroforestry structure and management practices that can provide these outcomes (Cerda et al. 2020). While management of these systems is quite different from Haitian CAFS, with annual to biannual pruning, and application of fungicides and (in most cases) fertilizer, we have shown that pathways for improvement can be similarly varied. Our study, as others discussed above, highlight the need for service delivery evaluation methodologies that are holistic and consider the complex interactions both within and between the various components of agroforestry systems, and the trade-offs in service delivery that may result from them (Rapidel et al. 2015; Notaro et al. 2022).

4.9. Conclusion

In the present study, we have shown that Haitian CAFS vary in the diversity and structure of their components, and have established typologies to classify them. We have also described the major ecosystem services these systems deliver, and have identified both the presence and absence of trade-offs between them. Finally, we have shown that the delivery of specific service bundles across a farm regeneration spectrum is tied to their diversity and structure. We believe that studies such as this one can be tools to accompany farmers in the conception of better cropping systems which can respond to their needs and expectations, particularly in the context of a changing climate that threatens coffee production. This may be done through adoption of more appropriate coffee varieties and suitable agronomic practices, but also through other components of the system. Indeed, in the absence of favorable market conditions for coffee, farmers may opt to optimize tree or other crop-associated services. Regardless of chosen paths, the crucial importance to Haiti of agroforestry systems and a diversified standing tree cover must never be overlooked or underprioritized.

We have shown that, within the considered range, certain systems have higher levels of ecosystem service delivery, while others are able to achieve better coffee performance. These farms serve as promising examples which, combined with the understanding of interactions between different services, can help identify realistic roadmaps for improving service delivery. In so doing, it is our hope that this study will contribute to the emergence of better systems for both people and biodiversity.

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Author contributions (CRediT)

CPM: Conceptualization, Data Curation, Formal Analysis, Investigation, Methodology, Writing – Original Draft Preparation, Review & Editing; **WJ**: Project Administration, Funding Acquisition, Supervision; **JSG:** Project Administration, **LASA:** Project Administration, **JFA:** Investigation, **GD:** Investigation, **RBJL:** Investigation, **BR:** Investigation, **VP**: Funding Acquisition, Supervision, Writing – Review & Editing; **CA**: Conceptualization, Data Curation, Funding Acquisition, Methodology, Supervision, Writing – Review & Editing

Data availability statement

The data that support the findings of this study are available in the DataSuds repository (IRD, France) at xxxxxxxxxxxxxxx (pending, DOI to be generated)

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Conflict of Interest statement

The authors declare no competing interest.

Supporting Information

The following supporting information were directly included within the chapter text for better legibility

Figure S1. Commonness and usefulness of trees in Haitian Coffee agroforestry systems of different origins. Native or Pre-Colombian trees were compared with those introduced during or after the Colonial era to highlight changes in species composition. A. Percentage and B. Number of farms in which the categories are present, C. Mean number per farm of trees of each category. D. Mean number of recorded uses for trees in each category.

Figure S2. Variation in agrobiodiversity among Haitian coffee-based agroforestry systems. Surveyed farms in the Nord (top) and Grande-Anse (bottom) departments colored according to the typology cluster to which they were assigned by hierarchical clustering performed on A. coffee genetic and varietal diversity variables (Gen), B. Shade tree composition (Tree) and C. Associated crop composition (Crop).

Figure S3. Tree and crop composition and abundance data. A. Mean density (per 1000m^2 quadrat) of trees in farms belonging to the three clusters of the Tree data-based typology. B. Mean density (per 1000m^2 quadrat) of coffee agroforestry system-associated crops in farms belonging to the three clusters of the crop data-based typology

Figure S4. Diversity of ages and tree architectures represented in Haitian coffee plots. A. Schematic representation of several architectural forms found in coffee plots. Left to right: very tall tree with denuded base; complex tree with large vertical secondary axes; coppice or coppice-like growth; “standard” tree with one or two vertical primary axes; seedling and sapling. B-E: photographs of coffee trees sampled for genotyping on the same farm, N03, showing the diversity of ages and structures growing concurrently in coffee plots.

The following supporting information are shown below:

Table S1. Pairwise association matrix between clusters of typologies established from coffee genetic and varietal diversity, Tree composition, Associated crop composition, Bioclimatic variables and elevation data, Coffee Plot Structure characteristics, and pest and disease injury profiles

Table S2. Pairwise Pearson’s product-moment correlation matrix between ecosystem service delivery indicators measured in up to 39 Haitian coffee agroforestry systems in Nord and Grande-Anse departments.

Table S3. Variation in ecosystem service delivery indicators (rows) across clusters of typologies established from coffee genetic and varietal diversity, Tree composition, Associated crop composition, Bioclimatic variables and elevation data, Coffee Plot Structure characteristics, and pest and disease Injury Profiles

Table S4. Associations between Clusters of Ecosystem service delivery variables (ES, rows) and clusters of typologies based on coffee genetic and varietal diversity, Tree composition, Associated crop composition, Bioclimatic variables and elevation data, Coffee Plot Structure characteristics, and pest and disease injury profiles

Table S1. Pairwise association matrix between clusters of typologies established from coffee genetic and varietal diversity ("Gen"), Tree composition ("Tree"), Associated crop composition ("Crop"), Bioclimatic variables and elevation data ("Clim"), Coffee Plot Structure characteristics ("CPS") and pest and disease injury profiles ("IP"). Abbreviations used are as follows: catimor: CR95-like catimor coffee variety, alt: altitude, CBB: Coffee Berry Borer (*Hypothenemus hampei*), mycena: *Mycena citricolor*, CLR: Coffee Leaf Rust (*Hemileia vastatrix*), anthrac: Anthracnose (*Colletotrichum sp*). Tree2, Tree3 are labelled according to their dominant legume tree, Crop1 and 2 to their dominant crop species. Cluster overlaps are expressed in proportions, and significance levels are given for Fisher's exact tests: *<0.05, **<0.01, ***<0.001, NS= not significant.

Classes		**Gen**				**Tree**				**Crop**				**Clim**			**CPS**		
		1	2	3	*p*	1	2	3	*p*	1	2	3	*p*	1	2	*p*	1	2	*p*
Gen	**1**: lower diversity																		
	2: higher diversity, catimor present																		
	3: higher diversity, catimor absent																		
Tree	**1**: High tree density	**0.07**	**0.25**	**0.04**	**NS**														
	2: lower density, *Inga-Persea*	**0.14**	**0.07**	**0.18**															
	3: lower density, *Samanea-Anacardium*	**0.11**	**0.11**	**0.04**															
Crop	**1**: lower density, banana-dominated	**0.12**	**0.12**	**0.15**	**NS**	**0.08**	**0.3**	**0**	**										
	2:lower density, yam-dominated	**0.04**	**0.08**	**0.08**		**0.05**	**0.08**	**0.05**											
	3:higher density	**0.15**	**0.23**	**0.04**		**0.19**	**0.08**	**0.16**											
Clim	**1**: dryer, hotter, lower alt	**0.21**	**0.36**	**0.04**	*	**0.28**	**0.08**	**0.18**	***	**0.14**	**0.11**	**0.27**	**NS**						
	2: wetter, cooler, higher alt	**0.11**	**0.07**	**0.21**		**0.05**	**0.36**	**0.05**		**0.24**	**0.08**	**0.16**							
CPS	**1**: younger, less dense	**0.05**	**0.42**	**0**	***	**0.37**	**0.04**	**0.07**	**	**0.15**	**0.04**	**0.27**	**NS**	**0.44**	**0.04**	***			
	2: older, denser	**0.16**	**0.05**	**0.32**		**0.11**	**0.37**	**0.04**		**0.23**	**0.08**	**0.23**		**0.07**	**0.44**				
IP	**1**: CBB, mycena, more pests	**0.05**	**0.32**	**0**	*	**0.31**	**0.03**	**0.06**	***	**0.13**	**0.03**	**0.23**	**NS**	**0.34**	**0.06**	***	**0.42**	**0**	***
	2: CLR, anthrac, more diseases	**0.23**	**0.14**	**0.27**		**0.09**	**0.47**	**0.03**		**0.32**	**0.1**	**0.19**		**0.09**	**0.5**		**0.04**	**0.54**	

Table S2. Pairwise Pearson's product-moment correlation matrix between ecosystem service delivery indicators measured in up to 39 Haitian coffee agroforestry systems in Nord and Grande-Anse departments. Abbreviations used are as follows: spRich: Species richness. H': Shannon diversity index, HDDS: Household dietary diversity score, AGB: Above-ground biomass, ⌀legumes/⌀total: ratio of the sum of diameter at breast height of all legume trees on the farm to that of all trees.

p: *<0.05, **<0.01, ***<0.001, ·= not significant (<0.1), NS= not significant (>0.1). When significant, correlation coefficients are in parentheses.

Peason's product-moment correlation matrix	**Coffee-related**			**Tree-related**				**Crop-related**			**System-wide diversity**			**AGB** (Mg. ha^{-1})
	Diversity (H_e)	**Productivity** (kg. ha-1)	**% Leaf Loss**	**SpRich$_{tree}$**	**H'$_{tree}$**	**% Native species**	**Tree utility score**	**SpRich$_{crop}$**	**H'$_{crop}$**	**Crop density**	**HDDS**	**SpRich$_{system}$**	**H'$_{system}$**	
Productivity (kg. ha^{-1})	NS													
% Leaf Loss	NS	NS												
SpRich$_{tree}$	NS	.	* (-0.43)											
H'$_{tree}$	NS	*(-0.42)	NS	*** (0.86)										
% Native species	NS	NS	NS	NS	NS									
Tree utility score	NS	NS	*** (-0.64)	*** (0.65)	NS	NS								
SpRich$_{crop}$	.	* (-0.36)	NS	NS	NS	NS	NS							
H'$_{crop}$	.	* (-0.36)	NS	NS	NS	NS	NS	*** (0.94)						
Crop density	.	NS	NS	NS	NS	NS	NS	* (0.36)	* (0.38)					
HDDS	** (-0.51)	.	NS	NS	** (0.45)	NS	NS	*** (0.53)	**(0.50)	NS				
SpRich$_{system}$	NS	** (-0.49)	NS	*** (0.91)	*** (0.85)	NS	** (0.51)	* (0.36)	*(0.36)	NS	* (0.39)			
H'$_{system}$	NS	** (-0.49)	NS	* (0.40)	**(0.43)	NS	NS	*** (0.68)	***(0.77)	NS	**(0.51)	*** (0.65)		
AGB (Mg.ha^{-1})	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	
$\varnothing_{legumes}/\varnothing_{total}$	**(0.56)	*** (0.59)	*(-0.35)	NS	NS	NS	NS	*** (-0.55)	*** (-0.57)	NS	*** (-0.55)	* (-0.38)	*** (-0.59)	NS

Table S3. Variation in ecosystem service delivery indicators (rows) across clusters of typologies established from coffee genetic and varietal diversity ("Gen"), Tree composition ("Tree"), Associated crop composition ("Crop"), Bioclimatic variables and elevation data ("Clim"), Coffee Plot Structure

characteristics ("CPS") and pest and disease Injury Profiles ("IP"). Presented as means (M) and standard deviation (SD), along with the significance level of the parametric (ANOVA "aov") or nonparametric (Kruskal-Wallis, "kw") test (as appropriate). Letters above the p values correspond to significant differences among clusters as identified by post-hoc tests (Tukey for aov, Dunn-Bonferroni for kw). Abbreviations used are as follows: In columns: div: diversity, CR: CR95-like catimor coffee variety, alt: altitude, CBB: Coffee Berry Borer (*Hypothenemus hampei*), mycena: *Mycena citricolor*, CLR: Coffee Leaf Rust (*Hemileia vastatrix*), anthrac: Anthracnose (*Colletotrichum sp*). Tree2, Tree3 are labelled according to their dominant legume tree, Crop1 and 2 to their dominant crop species. In rows: spRich: Species richness. H': Shannon diversity index, HDDS: Household dietary diversity score, AGB: Above-ground biomass, ⌀legumes/⌀total: ratio of the sum of diameter at breast height of all legume trees on the farm to that of all trees.

Classes			**Gen**			**Tree**			**Crop**			**Clim**		**CPS**		**IP**	
			1: lower div	**2: higher div, CR**	**3: higher div, no CR**	**1: High density**	**2: lower density, *Inga***	**3: lower density, *Samanea***	**1: lower density, banana**	**2:lower density, yam**	**3:higher density**	**1: dryer, hotter, lower alt**	**2: wetter, cooler, higher alt**	**1: younge, less dense**	**2: older, denser**	**1: CBB, mycena, +pests**	**2: CLR, CBD, +diseases**
Coffee	**Productivity (kg. ha-1)**	**M**	84.31	314.16	237.71	169.60	265.94	344.00	**100.29**	**601.42**	**221.60**	**338.75**	**105.21**	247.19	102.63	197.03	99.13
		SD	65.78	342.47	295.02	214.82	549.07	386.45	**76.39**	**720.37**	**304.46**	**490.99**	**113.15**	310.91	109.11	238.39	106.01
									a	**b**	**a**						
		p	NS (kw)			NS (kw)			***(kw)**			*** (kw)**		.(kw)		.(kw)	
	% Leaf Loss	**M**	64.61	53.55	67.32	**50.00**	**64.35**	**63.39**	63.39	63.39	63.39	**63.39**	**63.39**	**63.39**	**63.39**	**63.39**	**63.39**
		SD	17.03	13.49	8.62	**16.08**	**9.26**	**2.88**	12.67	11.92	15.82	**14.68**	**9.10**	**11.25**	**7.59**	**11.16**	**9.46**
						a	**b**	**ab**									
		p	NS (aov)			*** (aov)**			NS (aov)			**** (kw)**		***** (aov)**		***** (aov)**	
Tree diversity	**spRich$_{tree}$**	**M**	5.56	5.83	4.71	**7.38**	**5.00**	**4.56**	6.14	5.43	5.38	6.00	5.33	**6.77**	**5.29**	**7.38**	**5.32**
		SD	1.67	2.72	1.50	**2.10**	**1.41**	**2.46**	2.38	2.23	2.06	2.59	1.75	**2.71**	**1.38**	**2.43**	**1.45**
						a	**b**	**b**									
		p	NS (kw)			**** (aov)**			NS (aov)			NS (aov)		**. (kw)**		*** (kw)**	
	H'$_{tree}$	M	1.62	1.47	1.50	1.67	1.57	1.41	1.66	1.61	1.46	1.52	1.62	1.54	1.62	1.66	1.62

		SD	0.31	0.49	0.25	0.36	0.28	0.49	0.29	0.37	0.40	0.41	0.30	0.44	0.25	0.41	0.27
		p	NS (aov)			NS (aov)			NS (aov)			NS (aov)		NS (aov)		NS (aov)	
	% Native species	**M**	0.50	0.42	0.55	0.47	0.68	0.22	0.58	0.49	0.45	0.41	0.61	0.42	0.60	0.43	0.63
		SD	0.25	0.24	0.27	0.13	0.16	0.18	0.15	0.26	0.29	0.22	0.21	0.22	0.21	0.18	0.19
						a	**b**	**c**									
		p	NS (aov)			***** (aov)**			NS (aov)			**** (aov)**		*** (aov)**		**** (aov)**	
	Tree utility score	**M**	30.00	60.25	27.14	91.62	29.06	21.78	53.14	33.71	50.69	62.76	31.28	86.54	33.43	87.38	31.89
		SD	18.34	45.31	15.67	50.69	12.71	9.81	57.49	18.10	38.96	54.11	13.38	56.84	13.35	55.58	13.30
						a	**b**	**b**									
		p	NS (kw)			***** (kw)**			NS (kw)			NS (kw)		**** (kw)**		***** (kw)**	
Crop diversity	**spRich$_{crop}$**	**M**	**2.75**	**1.45**	**2.71**	1.83	2.41	2.63	2.36	1.86	2.38	**1.95**	**2.61**	**1.75**	**2.71**	**1.75**	**2.58**
		SD	**1.04**	**0.52**	**0.76**	0.94	0.94	0.92	0.93	0.90	1.02	**0.91**	**0.92**	**0.75**	**0.91**	**0.75**	**1.02**
			a	**b**	**a**												
		p	**** (aov)**			NS (aov)			NS (kw)			*** (aov)**		**** (kw)**		*** (kw)**	
	H'$_{crop}$	**M**	**0.77**	**0.28**	**0.77**	0.42	0.65	0.78	0.64	0.34	0.68	0.49	0.72	0.45	0.75	0.41	0.71
		SD	**0.46**	**0.32**	**0.35**	0.43	0.44	0.40	0.43	0.39	0.45	0.42	0.44	0.43	0.41	0.42	0.45
			a	**b**	**a**												
		p	*** (aov)**			NS (aov)			NS (aov)			. (kw)		. (aov)		. (aov)	
System-wide diversity	**HDDS**	**M**	**4.00**	**3.27**	**3.43**	3.25	3.76	3.88	3.64	3.57	3.63	3.42	3.83	3.25	3.86	3.33	3.84
		SD	**0.00**	**0.47**	**0.53**	0.45	0.56	0.83	0.50	0.79	0.72	0.51	0.71	0.45	0.66	0.65	0.60
			a	**b**	**ab**												
		p	**** (kw)**			*** (kw)**			NS (kw)			NS (kw)		*** (kw)**		*** (kw)**	
	spRich$_{system}$	M	8.63	7.00	7.43	9.08	7.41	7.38	8.50	7.29	7.75	7.95	7.94	8.33	8.00	9.00	7.89
		SD	1.85	2.45	1.51	2.35	1.70	3.11	2.10	2.21	2.62	2.59	2.13	2.84	1.71	2.83	1.76
		p	NS (aov)			NS (aov)			NS (aov)			NS (aov)		NS (aov)		NS (aov)	

	H'$_{system}$	**M**	**1.05**	**0.75**	**1.08**	0.96	1.00	0.94	1.09	0.87	0.91	0.93	1.02	0.90	1.07	0.87	1.07
		SD	**0.31**	**0.31**	**0.25**	0.37	0.36	0.40	0.38	0.26	0.37	0.37	0.35	0.44	0.30	0.46	0.31
		p	* (aov)			NS (aov)			NS (aov)			NS (aov)		NS (aov)		NS (aov)	
C & N	**AGB** (Mg.ha^{-1})	**M**	136.08	153.07	107.20	**203.14**	**51.13**	**142.91**	93.30	158.41	131.70	**184.04**	**51.74**	165.68	106.77	**151.17**	**85.06**
		SD	238.43	168.68	123.40	**223.46**	**52.87**	**112.16**	135.26	158.76	183.67	**187.91**	**50.63**	155.70	194.87	**150.70**	**169.86**
						a	**b**	**a**									
		p	NS (kw)			** (kw)			NS (kw)			** (kw)		NS (kw)		* (kw)	
	$\varnothing_{legumes}$/ $\varnothing_{total}$	**M**	**0.08**	**0.43**	**0.25**	0.39	0.23	0.23	0.22	0.37	0.30	0.33	0.23	**0.43**	**0.21**	**0.40**	**0.20**
		SD	**0.07**	**0.24**	**0.17**	0.23	0.21	0.25	0.16	0.28	0.26	0.29	0.14	**0.24**	**0.16**	**0.23**	**0.14**
			a	**b**	**ab**												
		p	** (kw)			NS (aov)			NS (kw)			NS (kw)		** (aov)		** (aov)	

Table S4. Associations between Clusters of Ecosystem service delivery variables (ES, rows) and clusters of typologies based on coffee genetic and varietal diversity ("Gen"), Tree composition ("Tree"), Associated crop composition ("Crop"), Bioclimatic variables and elevation data ("Clim"), Coffee Plot Structure characteristics ("CPS") and pest and disease injury profiles ("IP", columns). Cluster overlaps are expressed in proportions, and significance levels are given for Fisher's exact tests: *<0.05, **<0.01, ***<0.001, NS= not significant.

Classes		**Gen**			**Tree**			**Crop**			**Clim**		**CPS**		**IP**	
		1	2	3	1	2	3	1	2	3	1	2	1	2	1	2
ES	**1: Subsistence systems**	**0.29**	**0.18**	**0.21**	**0.1**	**0.41**	**0.15**	**0.3**	**0.11**	**0.27**	**0.21**	**0.46**	**0.07**	**0.52**	**0.09**	**0.59**
	2: Coffee maximizers	**0**	**0.11**	**0.04**	**0.03**	**0.03**	**0.08**	**0**	**0.05**	**0.08**	**0.13**	**0**	**0.11**	**0**	**0.06**	**0**
	3: Tree service maximizers	**0.04**	**0.14**	**0**	**0.21**	**0**	**0**	**0.08**	**0.03**	**0.08**	**0.21**	**0**	**0.3**	**0**	**0.25**	**0**
	p	**NS**			***			**NS**			***		***		***	

General Discussion

The main goal of this thesis has been to characterize agrobiodiversity in Haitian coffee-based agroforestry systems, both at the species (for coffee) and at the system level. Two of the chapters focus, totally or in part, on describing the genetic, varietal and, unexpectedly, species diversity of coffee (Fig.1). Genetic characterization of Haitian crops of any kind is a recent and still very incomplete undertaking. Much of it has focused on annuals such as beans (Durán *et al.*, 2005; Montero-Rojas *et al.*, 2013), though PITAG has also conducted genotyping of Haitian cacao (*Theobroma cacao*) trees. Recently, a study was published describing the development of Haitian sorghum (*Sorghum bicolor*) lines resistant to a globally-problematic aphid (Muleta *et al.*, 2022) through breeding under smallholder farming conditions, a notable reminder of the value of agrobiodiversity. The third chapter focused on describing ecosystem services delivered by Haitian agroforestry systems, and the underlying agrobiodiversity. Prior studies have considered specific uses and benefits of Haitian agroforests which fall under the ecosystem service umbrella (Glenn R. Smucker & Joel C. Timyan, 1995; Jean-Denis *et al.*, 2014; Tarter, 2015; Andrew Tarter *et al.*, 2018), but, to my knowledge, none have directly focused on characterizing the various components of agroforestry systems and their associations with multiple ecosystem services, nor the existence of potential trade-offs between services. In the following paragraphs, we will discuss lessons learned, remaining knowledge gaps, and future directions for the study of Haitian coffee-based agroforestry systems.

1. Lessons from characterizing coffee diversity and varietal mixtures in Haiti

The relatively long history of coffee in Haiti, the fact that varietal trials and introductions had been reported with little follow-up on their spread, combined with the tree's status as a long-lived perennial made it important to understand the genetic composition of coffee stands. A key finding of our study is the fact that varietal mixtures (often >2 varieties) and inter-varietal hybrids appear to be the norm on Haitian farms. Furthermore, there is incomplete overlap between the genetic identity of coffee plants and the label they are given locally, which means that exchange networks are likely to increase this phenomenon. Nevertheless, the Typica variety is still a mainstay of these systems, and the variety for which local, vernacular identification is the most consistent with genetic identity. Should one wish to collect seeds (or vegetative material for clonal propagation) of Typica plants (or any variety, for that matter), with an eye towards ex-situ germplasm conservation or farm regeneration, care must be taken that the material obtained belongs to the intended varietal group. For Typica, the safest option is likely to obtain material from monovarietal farms, which tend to be the most isolated. Our results also raise the possibility that distribution networks, including nurseries and agriculture development projects, may be providing misidentified or admixed coffee plants, which should be considered when regenerating coffee stands.

Figure 1. Photographs of coffee frees from the five varietal groups identified in Haitian agroforestry systems based on genotyping. Clockwork from left: Typica, Unlabeled group, Bourbon/Caturra-like, CR95(Catimor)-like, and Kent/I-60-like. Photo credit: Claude Patrick Millet

By design, our sampling strategy on coffee farms aimed at capturing the diversity present in the fields by maximizing that of our samples, rather than being representative of the composition of coffee stands and the relative abundance of each group. Therefore, two farms for which our studies revealed a similar level of diversity might very well have contrasted coffee stand compositions. One could imagine a genetically diverse farm in which coffee stands are composed of a homogenous mixture of trees belonging to different varieties, with seedlings from all groups, as well as inter-group hybrids, growing in their shade. However, such a farm could also consist in a large stand of old, "pure" Typica in the periphery of which farmers have planted a few newly-acquired trees of different varieties, some which, possibly unbeknownst to them, are actually of mixed parentage. My personal observations in the field suggest that both situations, and several intermediate scenarios, are likely occurring. All of this points to the fact that more scientific inquiry into Haitian coffee diversity is needed.

2. Haitian coffee diversity: knowledge gaps, perspectives and future directions

When considering Haitian coffee stands' genetic diversity and gene flow, the first question that may arise is: what are the agronomic implications? In particular, the admixed individuals that likely make up a large proportion of coffee stand may represent novel genotypes that could also be associated with novel phenotypes. At the beginning of the sampling process, we enlisted the help and knowledge of each farmer, asking them to help us identify interesting plants (for instance, their favorite, most productive or disease-resistant trees, or the ones they felt did not "behave" as the others). Out of 19 plants (across the 28 farms sampled for genotyping, Table 1) pointed out by farmers as atypical, exceptional or remarkable in the field, 13 were found to be admixed. Seven were singled out for their productivity, and another was simply stated to be the growers' favorite. Interestingly, the latter was a CR95/Bourbon-like hybrid, and the grower also pointed out another plant as its offspring, which was assigned as an admixed CR95-like. Two admixed Typicas were also pointed out for their tendency to produce cherries that stayed yellow, reminiscent of the *Typica amarillo/amarelho* variant discovered in Brazil in 1871 (Haarer, 1923).

Much like modern F1 breeders seek to develop coffee trees that combine pest and disease resistance, cup quality and suitability for agroforestry systems (Breitler *et al.*, 2022; McCook & Montero-Mora, 2024), one could hypothesize that gene flow between coffee stands may results in trees that inherit a combination of their parent's agronomically desirable traits. This may result in coffee trees that correspond to an "ideotype" that is particularly suited to local agroforestry conditions. To test this, phenotyping of the genotyped coffee trees is necessary. It would be necessary to gain a measure of the individual trees' level of disease tolerance of resistance, its attainable yield, and architecture. It would also be important to harvest these trees and perform organoleptic testing on collected beans. Private sector companies in Haiti have the capacity to carry out quality testing (Gael Pressoir, CHIBAS, pers. comm.), but care must be taken that the sovereignty of farmers over their genetic material be respected. More broadly, the diverse varietal mixtures in Haitian farms may provide an opportunity to identify varietal groups that best perform in Haitian agroecosystems, given current management practices, as well as test the effect of varietal mixtures on coffee crop performance.

Table 1. Haitian Arabica field samples identified as atypical or remarkable by farmers, and their varietal assignment.

Sample ID	**department**	**sNMF group**	**What makes this individual atypical? (according to farmer)**
G08_06	GA	Unlabeled	Not susceptible to coffee leaf rust
G13_04	GA	Typica	Quite productive
N01_01	Nord	Unlabeled/admixed	Has lower incidence of coffee berry borer
N01_04	Nord	Typica	3 seeds/fruits
N02_01	Nord	Admixed CR95/Bourbon	Grower's favorite
N02_02	Nord	CR95/admixed	Grown from N02_01
N02_14	Nord	Admixed	Very productive
N04_24	Nord	CR95-like	Very productive
N04_25	Nord	Admixed	Very productive
N04_26	Nord	Unlabeled/admixed	Very productive
N05_01	Nord	Unlabeled	Very productive but not long-lived
N06_04	Nord	Admixed CR95/Typica	Very productive
N08_04	Nord	Typica/admixed	Fruits stay yellow, never turn red
N08_05	Nord	Typica/admixed	Fruits stay yellow, never turn red
N08_13	Nord	Admixed	Very productive
N09_11	Nord	CR95-like	Very productive
N09_18	Nord	CR95/admixed	Very productive
N10_01	Nord	Unlabeled/admixed	Stands out for its productivity

Furthermore, while our results suggest Haitian coffee genetic diversity to be dynamic and subject to change, the actual processes at play have not been identified. In particular, the relative roles of natural and farmer selection are unknown. Because Haitian coffee trees freely reproduce, and individuals can be recruited from the seed bank, we can expect them to be subject to natural selection, with seedlings that succumb to pest and disease being removed from the gene pool (Bousset & Chèvre, 2013). However, given the low genetic diversity of Arabica coffee (Anthony *et al.*, 2001) and the complexity of factors that can impact the health of coffee trees (as discussed in chapter III), the extent of this process is difficult to determine. Research on the impact of natural selection on crop species has, understandably, mostly focused on annual plants for which this process is easier to detect (Zeven, 2000; Newton *et al.*, 2010). Landraces are generally understood as having adapted to their cultivation context, at least partially via natural selection, though an interplay with artificial selection is likely (Zeven, 2000; Pusadee *et al.*, 2014). It would be particularly interesting to consider the role that the "Big Rust", the 2008-2013 coffee leaf rust epidemic discussed in Chapter II, might have played in determining the genetic composition of Haitian coffee stands. Indeed, farms had been heavily impacted (Clémentine Allinne, pers. comm.), which may have constituted a strong filter on the seedlings and saplings, though many rust-susceptible adults evidently also survived this epidemic, as proven by the many aging Typica trees on farms. Simultaneously, farmers may favor certain trees, as evidenced by the fact that some farmers were able to point out "exceptional" trees during sampling, and may preferentially propagate their progeny (e.g. Barnaud *et al.*, 2008; Duputié *et al.*, 2009 for examples involving annual sorghum and cassava, *Manihot esculenta*). Comparing the genetic diversity, composition, and differentiation of the various generations of coffee trees present in the stands may help determine to which extent they are subject to evolutionary processes. Therefore, phenotyping studies would also need to be able to estimate tree age. Even so, it remains to be seen whether the markers used would allow to adequately detect changes in allele frequencies between younger and older trees that may be indicative of selection processes. Additional conversations should also be had with farmers in order to understand the way they manage seedlings, and therefore engage in selection (Elias *et al.*, 2000; Duputié *et al.*, 2009).

Phenotyping studies were planned as part of this thesis, and the genotyped trees were labeled to that end. Because of this, we only genotyped coffee plants that were sturdy enough to have the labels affixed to them with reasonable expectation that they would retain it and survive the following years. Therefore, genotyping of seedlings for the purpose of comparing their gene pool with that of older trees (without expectation to phenotype them) was also planned. Because of the socio-political instability and dangerous security conditions that prevailed, these plans were not carried out. Should the tree labels persist and identification of genotyped trees remain possible, these phenotyping studies should be a priority for any follow-up to the PITAG project, which ended in September 2024. In fact, this thesis has produced phenotyping and seedling collection protocols that may still be of use. If it is no longer possible to identify genotyped trees, phenotyping studies may still target farms with higher proportions of admixed individuals. While sampling is not representative of relative abundance of varietal groups within farms, we assume that the proportion of admixed individuals is less biased, as we were never told of any during samplings and did not include them in our sampling strategy (beyond asking for "atypical" trees, which we hypothesized could benefit from hybrid vigor). Farmers who own large proportions of hybrids could then be asked again about exceptional plants, which could be phenotyped (and, if possible, genotyped). Should interesting phenotypes be identified, they could then be propagated clonally (which will be especially necessary in the case of admixed individuals, to prevent seed segregation following sexual reproduction, McCook & Montero-Mora, 2024).

The genotyping studies performed during this thesis also revealed the presence and cultivation of *Coffea canephora* in Haiti. The species does not seem to be widespread, as only one of the sampled farms grew it, and we could only find one other possible report (Eitzinger *et al.*, 2019), which only used the vernacular name of *Kafe brezil*, also given to our field samples. There appears to be confusion around Kafe Brezil/Robusta's status as a different species than Arabica. This is not restricted to Haiti, but is consistent with the coffee market's tendency to refer to Arabica and Robusta as two varieties of coffee (Montagnon *et al.*, 2012). Farmers must be made aware of this difference, particularly those that seek to access specialty markets, lest they find themselves offering Robusta-Arabica blends which may damage the reputation of Haitian coffee. Nevertheless, it would be interesting to better understand the current distribution of Robusta cultivation in Haiti, taking care to include vernacular terminology in surveys. With many current Arabica-growing areas expected to lose suitability in upcoming decades due to climate change (Eitzinger *et al.*, 2013; Bunn *et al.*, 2015), Robusta, which is more adapted to warmer conditions (International Trade Centre, 2021), may be incorporated in the planned revitalization of the coffee sector in areas where Arabica does not perform well (González-Orozco *et al.*, 2024).

3. Lessons and perspectives from agrosystem and ecosystem service characterization

Through identifying the historical factors that have shaped Haitian coffee genetic diversity, describing diversification of agroforests, and characterizing their ecosystem service delivery, a view of Haitian agricultural systems emerges. It is generally one of bet-hedging systems in which farmers value multifunctionality to increase resilience and access to ecosystem services, but are nevertheless vulnerable to the social, economic and political instability that prevails in the country, as evidenced by the historical and present challenges faced by farmers. I argue, based on our work as well as others (Zimmermann, 1986; Feller *et al.*, 2006; Steckley & Weis, 2016; Poncet *et al.*, 2024), that diversified agroforestry systems are a necessary part of the fabric of rural communities, livelihoods, and environments of Haiti. However, these systems are not perfect, and the fact that many participants in our study still face precarious economic conditions cannot be ignored. Of the 39 farms studied, 34 said their farm's coffee productivity was decreasing, including 5 out of 8 "coffee-maximizing" service bundle farms (*cf* Chapter III).

The farm typologies we have established provide realistic models for systems that can be achieved within the context and limitations of Haitian systems, and may serve as achievable roadmaps to bring the lowest-performing farms closer to the better-performing ones. We have identified a typology of ecosystem service bundles enabled by agrobiodiversity, and suggested that they arise from specific strategies that focus on maximizing the benefits gained from different components of the system, but we did not directly have access to data about farmer priorities, choices, desires, and perceptions on the performance of their systems, nor did our study directly consider management practices beyond looking at the structure of coffee stands. One question in particular that needs to be solved through both coffee tree phenotyping and surveying farmer practices is whether the yield (attainable or actual, *sensu* Nutter *et al.*, 1993) or coffee tree is the limiting factor for farm productivity (as defined in the third chapter: the amount of cherries that is collected from the system), or whether it is limited by factors such as an incomplete harvest. In the latter case, reasons, whether economic, labor availability-, or farmer choice-related, would also need to be investigated.

On a more basic level, the extent to which farmers may consider coffee a priority should be also considered. While some may wish to devote a sizeable part of their land to growing coffee as a cash crop-maximizing strategy, others may prefer to transition their coffee farms to growing other crops, even exports crops such as cacao, perhaps retaining some coffee as a supplementary source of income, or for household consumption.

By characterizing agrobiodiversity (Fig. 2) and associated ecosystem service delivery, and identifying trade-offs and synergies between them, it may become possible to "optimize" agroforestry systems by striking the balance between the expectations of social, economic and ecological benefits placed upon them (Rapidel *et al.*, 2015). This would be achieved by re-thinking and re-organizing the composition, spatial arrangement and management of their agrobiodiversity. For example, some possible steps would include:

- Harmonizing coffee varieties' level of shade tolerance (Koutouleas *et al.*, 2022) with the actual extent of tree shade in the system (possibly within a mosaic of canopy openness and coffee varieties)
- Increasing the proportion of legume trees and implementing adequate management such as frequent pruning (with trimmings left on the ground to return nutrients) to enhance soil fertility (Haggar *et al.*, 2011; Sauvadet *et al.*, 2019)
- Increasing the proportion of associated crops that are better aligned with farmers' priorities and farm bioclimatic conditions (even, if need be, at the expense of coffee production)
- Incorporating animals and their byproducts into the system in order to increase ecosystem services. This could take a number of forms, from using manure to increase soil fertility to implementing apiculture for greater pollination and new sources of income (Hill & Webster, 1995; Alexandre *et al.*, 2021)
- incorporating trees with greater timber value or nutritional benefits, and more.

One important aspect of agrobiodiversity planning for resilience is considering the impact of climate change on coffee production (and agricultural production in general). I know of only one (non-peer-reviewed) study modelling how climate change will affect the extent of land suitable for coffee in Haiti (Eitzinger *et al.*, 2013). Because intraspecific genetic groups may not all have the same vulnerability to climate change (de Aquino *et al.*, 2022; Vi, 2023), integrating genetics and climate change will also help agrobiodiversity planning.

It is important to keep in mind that, as this thesis in one of very few studies of Haitian agrobiodiversity, it likely offers but a partial view of it. We may not have captured the entirety of the genetic diversity of coffee: given for instance that we only found Robusta on one Haitian farm, one might wonder what other locally "rare" genetic groups—or indeed species—could be found if more farms were sampled. We have also certainly captured but a limited portion of the agroforestry tree diversity, as some unrepresented species are reported in the literature (Timyan, 1996; Jean-Denis *et al.*, 2014), and were even observed outside of the transect (*cf* Chapter III). Similarly, there are probably many more crops and other useful herbaceous species present in agroforestry systems, and the genetic, varietal or in some cases like *Dioscorea sp* yams, species diversity of associated crops was not described as that of coffee. While our studies targeted geographic locations in which they were both pertinent and needed, there would be much value in characterizing other areas, particularly Thiotte and Baptiste, where other dynamics may be at play, particularly due to the greater influence of niche market expectations for the Haitian Bleu trademark (Dunnington & Lenaghan, 2004). Also, some larger private sector companies do produce coffee under more intensive cultivation (Clémentine Allinne, pers. com.), and the links (or lack thereof) between these and the more traditional systems may also be of interest. Similarly, as discussed in Chapter III, we have not produced a comprehensive survey of ecosystem services delivered by Haitian coffee agroforests. Cataloguing more of them will improve the ability to propose strategies for improving the economic and ecological benefits of these systems. Finally, other environmental determinants of agroecosystem processes and function, such as soil characteristics (type, erosion…), should be considered (Blanco Sepúlveda & Aguilar Carrillo, 2015; Sauvadet *et al.*, 2021; Chaves *et al.*, 2021).

4. Coffee agroforests provide insights for agricultural planning as a whole

The view of coffee-based agroforests that emerges is also one that supports previous assertions that standard development and technification schemes are unlikely to be successful, at least sustainably so (Steckley & Weis, 2016, 2017; Jayaram, 2018). There has been a plethora of attempts from governmental, private sector, and international cooperation programs to strengthen Haitian agriculture, but they have evidently had no—or very limited—success. They have typically focused on technification and adapting to the needs and demands of the market rather than those of farmers, and have not sufficiently paid attention to the way that farmers manage their farms to increase autonomy, resilience, and access to multiple ecosystem services, which partly explains their unmet goals.

The history of reforestation project failures and successes can provide useful lessons for agricultural revitalization projects. In the 1970s, as concerns about the rate of deforestation in Haiti rose, development agencies began implementing tree-planting programs (Zimmermann, 1986), but they seldom had lasting impacts until anthropologists were enlisted to understand the symbolic ways that Haitian *peyizan* (smallholder farmers in rural areas) viewed trees and tree-planting programs (Murray, 1987; Murray & Bannister, 2004). They discovered that these programs had been implemented with a western conservationist view that was unconvincing to *peyizan*, who saw it as a threat to their land sovereignty and a possible path towards dispossession. They also found that land tenure was complex and mostly-unofficial, and that *peyizan*'s perceptions of their land tenure security impacted the patterns and intensity of tree harvesting. They proposed reforestation programs that positioned trees as investments for the landowner, and on which they had complete ownership, including the right to cut them down as needed or desired, and in doing so managed to increase secondary forest cover in Haiti in a process anthropologist dubbed "wood domestication" (Murray, 1987).

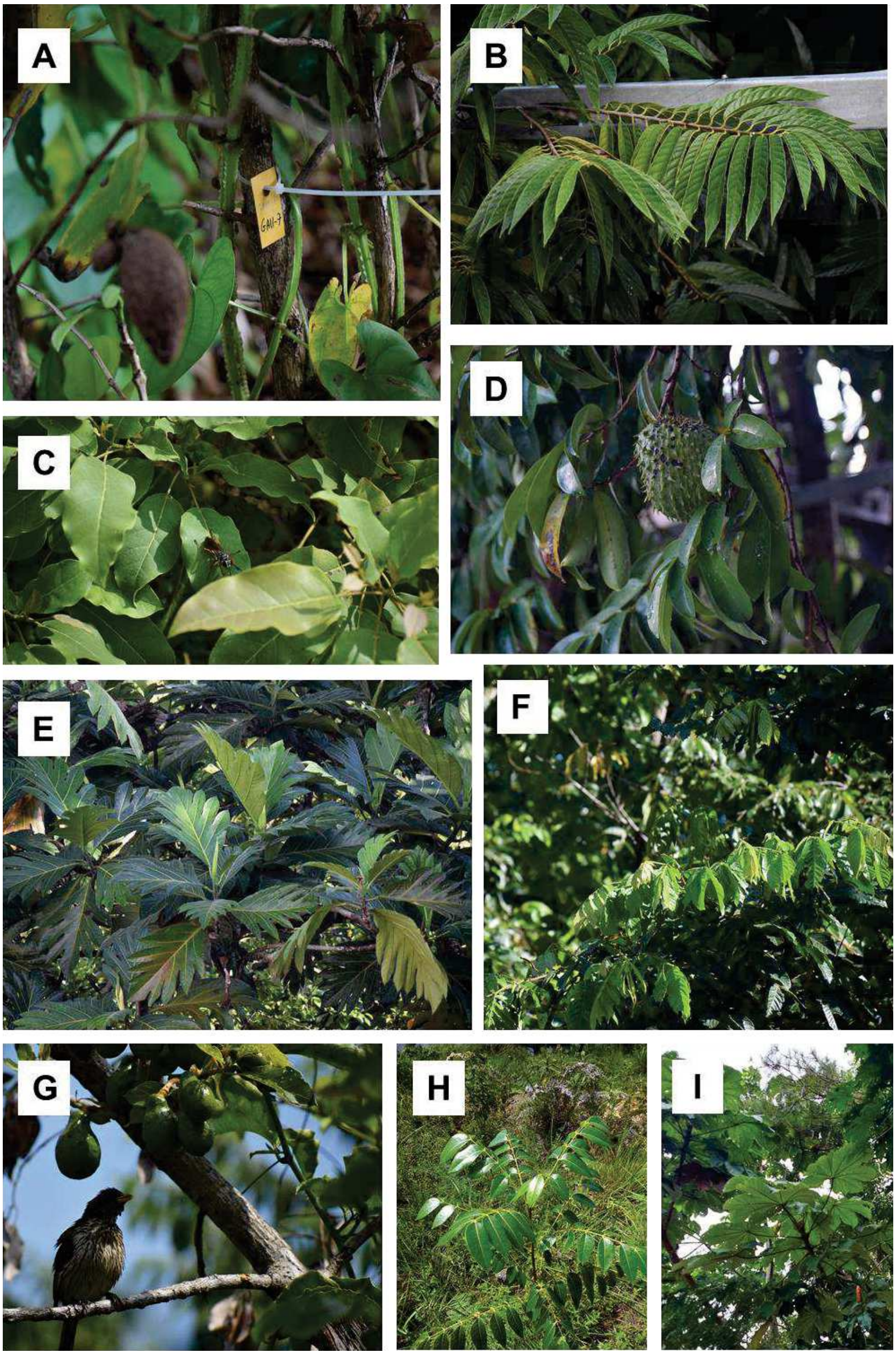


Figure 2. Photographs of the agrobiodiversity represented in Haitian coffee-based agroforestry systems. A. Yams (*Dioscorea sp.*) growing over a sampled coffee tree. B. Ox heart tree or *kachiman* (*Annona reticulata*). C. Haitian oak or *chêne* (actually a Bignoniaceae, *Catalpa longissima*). D. Soursop or *Corossol* (*Annona muricata*). E. Breadfruit tree or *arbre véritable* (*Artocarpus altilis*). F. the service tree *Sucrin (Inga vera*). G. Avocado tree (*Persea americana*) with perching Palmchat (*Dulus dominicus*). H. Mahogany tree or acajou (*Swietenia mahagoni*). I. *Trompette* (*Cecropia sp*., likely *C. schreberiana*). Note: most photographs were taken outside of study sites, but are indicative of surveyed diversity. Photo credit: Claude Patrick Millet

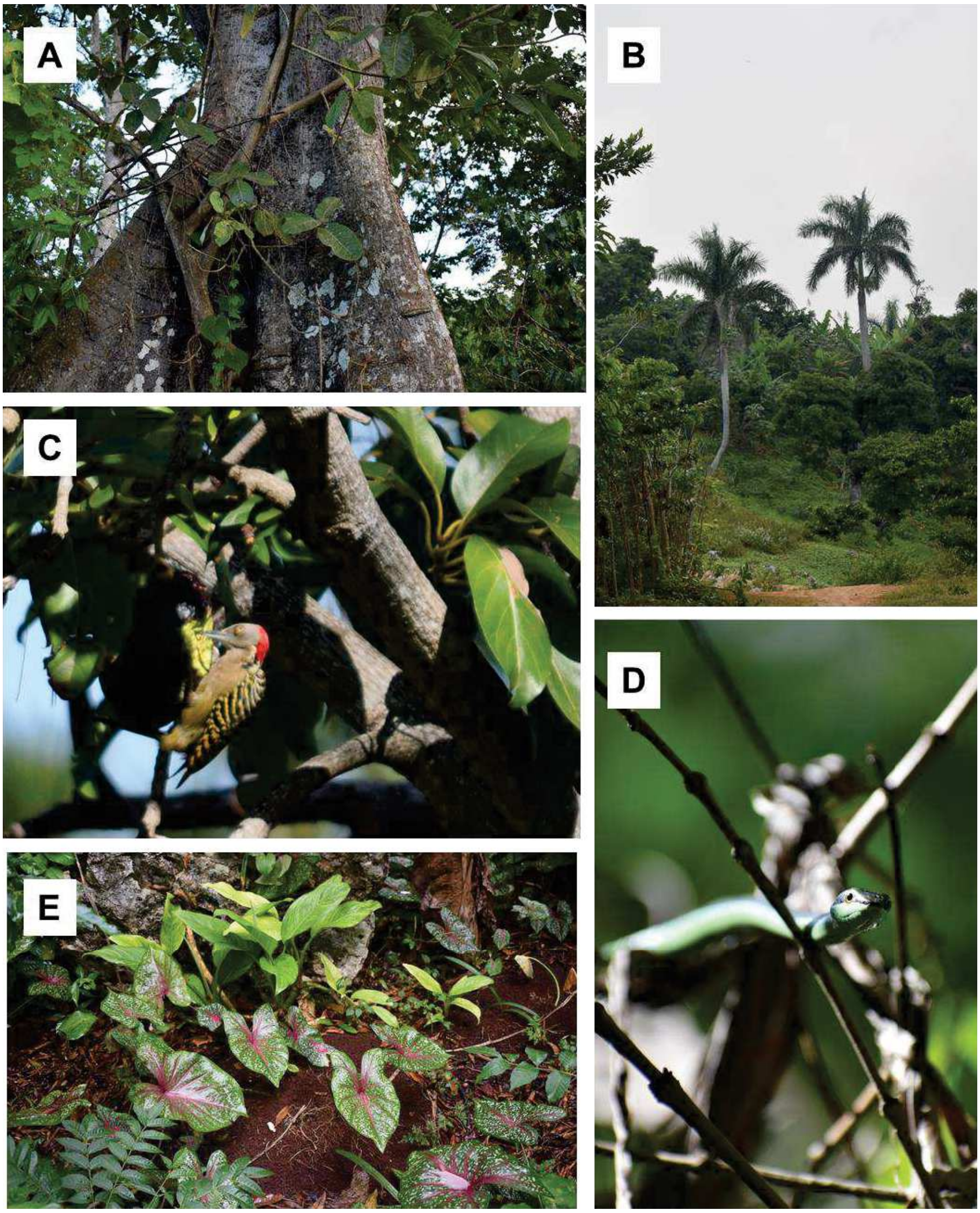


Figure 3. Coffee-based agroforestry systems deliver cultural and biodiversity-conserving ecosystem services. A. Old *Ficus sp.* (likely *F. citrifolia*), a tree that is often attributed mystical properties in Haitian folklore. B. The "Palmiste", *Roystonea borinquena*, a familiar element of local landscape, is the national tree of Haiti, featuring on the flag. C. Shade and fruit trees such as the pictured avocado (*Persea americana*) provide habitat and food for native and migratory birds, including the pictured endemic Hispaniolan woodpecker (*Melanerpes striatus*). D. Agroforestry systems also provide habitat for reptiles such as the pictured endemic blunt-headed Hispaniolan vine snake (*Uromacer catesbyi*). E. The floristic diversity of agroforestry system also includes non-crop herbaceous species such as *Caladium bicolor* (introduced) and *Dieffenbachia sp.* (likely introduced, though some species are native). All pictures except C. were taken during fieldwork. Credit: Claude Patrick Millet

Similarly, efforts to strengthen Haitian agriculture must consider smallholder farmer perceptions, how they value land and food sovereignty and livelihood resilience through diversification, as well as individual preferences, and embed these considerations into program designs (Valencia *et al.*, 2015; Singh *et al.*, 2016; Smith Dumont *et al.*, 2019). Differential patterns of land-use were identified in Haitian farming systems, both spatially, based on proximity to farmers' houses, and temporally, evolving along with family structure to meet its needs (Jean-Denis *et al.*, 2014). This is reminiscent of the patterns observed in the case of wood domestication. However, one should not be under the impression that smallholder farmers are a monolithic, homogenous entity. Indeed, participants in the PITAG program came from a fairly broad range of walks of life, as illustrated by some information collected by the project. For instance, of the 39 surveyed farms owners, 23% (n=9) said that agriculture represented less than half of their household revenue, 54% (n=21) said that it represented more than half, and another 23% (n=9= said that it represented the totality of revenue. Of 20 smallholder farmers who reported having professions outside of the agricultural sector, 3 worked in trades (plumbing and masonry, woodworking, and carpentry), 11 worked as merchants or shopkeepers, 5 were teachers, and one was a retired civil servant. This variety in farmer profiles is likely associated with a variety of priorities and possibilities in farm management.

It is necessary to increase scientific knowledge about farms in order to enable collaborations and information exchanges with farmers that can, possibly, lead to co-construction of better, more resilient systems. Anthropologists and ethnobotanists have proposed collaborative, participative and inclusive methods that can allow such exchanges, such as serious games (Notaro, 2019; Andreotti *et al.*, 2020), or focus groups and other such workshops (de Souza *et al.*, 2012; Purnawan *et al.*, 2022). Such workshops were initially planned as part of this thesis, but could not be undertaken. However, individualized reports were produced for farmers in the hope that increased knowledge of their farm's genetic composition will help them in their management decisions.

Moreover, farmers likely cannot undertake the process of farm improvement or optimization alone. Among the principles of agroecology is the integration of the various actors and stakeholders involved in agricultural production chains, including agronomists, researchers, and political and market decisionmakers (de Groot *et al.*, 2012; Dumont *et al.*, 2021). Networks should be established or strengthened both among farmers, and between farmers and these other actors, to ensure greater viability and sustainability of the attempts at ecological intensification and economic performance improvement. These actors may all be able to participate constructively in the co-conception of improved cropping systems, markets, and food distribution networks.

5. The ecological dimension of coffee-based agroforestry systems must be reinforced

While past experiences have shown that a focus on conservation is unlikely to gain much traction among farmers, the ecological dimension of agroforestry systems is also of great importance, as explained in the general introduction (supported by some results from Chapter

III). Many studies have shown that diversified agroforestry systems can serve as habitat for native fauna and flora, though these are often performed in regions where there remain relatively large tracts of primary forest, such as Central America (Greenler & Ebersole, 2015) and Indonesia (Murniati *et al.*, 2001; Kessler *et al.*, 2009, 2012). These studies therefore often reach the conclusion that agroforestry can mitigate some of the biodiversity loss that may otherwise occur through the process of converting forests to cropland (Perfecto & Vandermeer, 2008; Boinot *et al.*, 2022), though it remains itself a form of habitat degradation.

In the case of Haiti, however, there is almost no primary forest left (Sergile & Woods, 2001; Hedges *et al.*, 2018), and agroforestry systems appear to be the best candidate to replace them in delivering a majority of important ecosystem services, including biodiversity conservation (Exantus *et al.*, 2021). It can seem rather callous to devote significant resources to biodiversity conservation when Haitians face so many existential threats, but the fact remains that Haiti is a biodiversity hotspot facing an extinction crisis, which is an irreversible process. As such, it is necessary to further study, promote and improve the ability of human-modified habitats, namely diversified agroforests, to participate in biodiversity conservation by serving as habitat or corridors for wildlife (Fig. 3). It is also necessary to understand how these systems interact with areas of conservation concerns such as remaining primary forest fragments. It can be expected that they serve a buffering function that may help protect them (Murniati *et al.*, 2001; Perfecto & Vandermeer, 2008; Saj *et al.*, 2017; de Almeida Campos Cordeiro *et al.*, 2018), especially when the alternative is open cropland or barren earth surrounding these fragments (Fig. 4). However, they may also constitute a threat, for instance through their expansion or via introduction of exotic species (Richardson *et al.*, 2013). In fact, some of the surveyed farms were concerningly close to Macaya national park, one of Haiti's main hotspots of endemism, so that the eponymous mountain, which is central to the park, could clearly be seen from them (pers. obs.). With so few data available on Haitian biodiversity in these hotspots, most studies have focused on describing and cataloguing it (Ionta *et al.*, 2012; Majure *et al.*, 2013; Joly *et al.*, 2023), or monitoring its loss via land use changes (Hedges *et al.*, 2018; Pauleus & Aide, 2020). However, understanding how they are embedded in the larger Haitian landscape will provide insights on how to protect them.

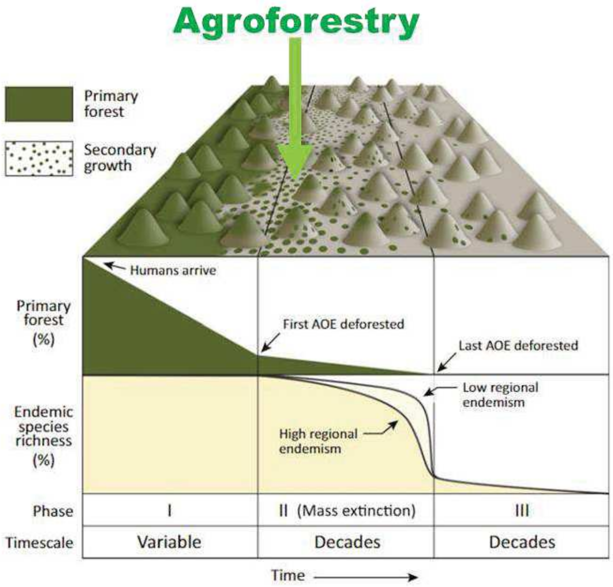


Figure 4. Place of agroforestry within Haiti's trajectory of ecosystem degradation. Agroforestry systems can conceivably serve as outcomes or catalysts of degradation, or as buffers and corridors for primary forest. Base image Taken from Hedges *et al.* (2018). (original caption from the source article: "***Dynamics of species loss linked to deforestation.*** *Model shows hypothetical landscape of mountains (areas of endemism, AOEs) with primary forest and secondary growth in a defined region (island, country, etc.). Phase I: primary forest or any original habitat holds the greatest species richness, and this begins to decline after humans arrive, initially causing regional species extirpations but few extinctions. Timescale: hundreds to thousands of years. Phase II (mass extinction): major species extinctions occur, beginning when primary forest is lost from the first AOE, increasing in rate as other AOEs are lost, and decreasing in rate as primary forest in the last AOE is lost. Regional endemism and patterns of deforestation affect shape of decline in richness. Phase III: only secondary growth or other degraded habitat remains, supporting a small fraction of the original biodiversity*.")

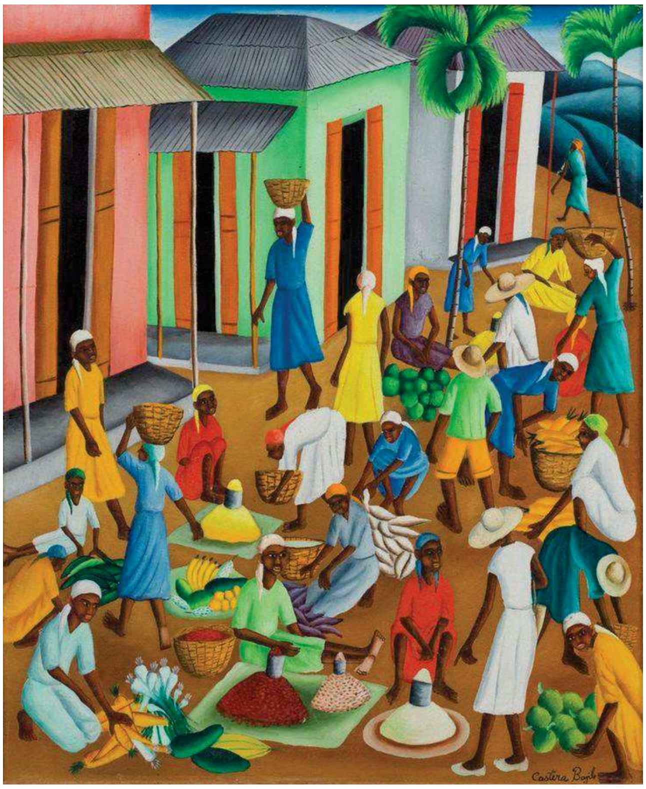


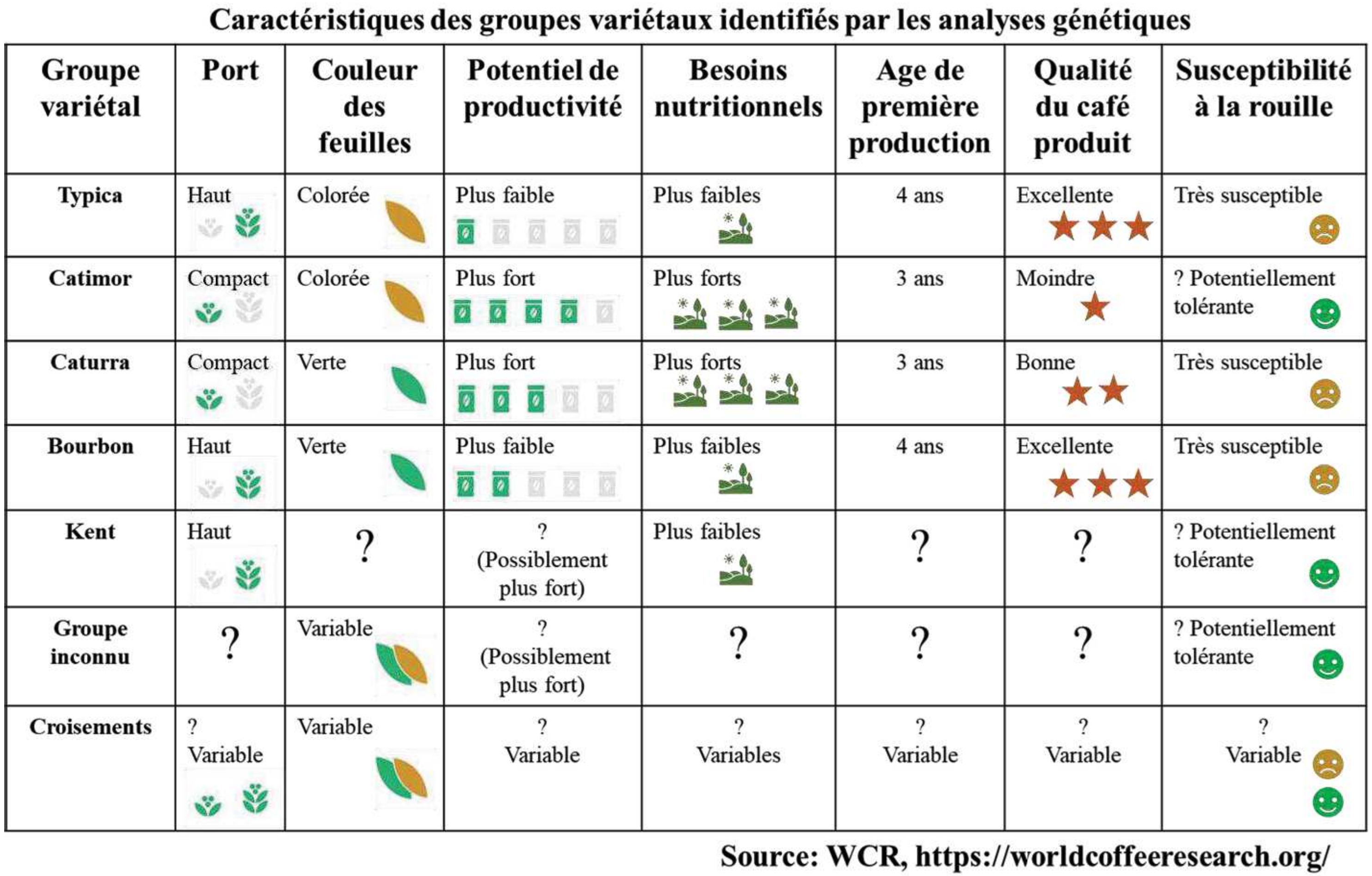
Figure 5. Agrobiodiversity is at the core of rural livelihoods, but is also an eduring source of artistic and cultural inspiration. Painting by Castera Bazile (1923-1966).

6. Conclusion

Shortly after a writing session working on this manuscript, I participated in a stakeholders' meetings for PITAG, in which some of the projects' findings and propositions were presented. When an agronomist floated the idea that farmers might want to move away from coffee towards other crops such as cacao, one smallholder exclaimed that coffee was part of his identity, remembering a time when every tree stand in his hometown sheltered coffee trees. Another noted that while hot chocolate was a perfectly fine beverage, his drink of choice to start the day was always coffee. These exchanges illustrate the cultural and emotional attachment to coffee, and the desire of Haitians to see the crop once again contribute to the country's agricultural vitality. These are all sentiments I myself share. Through this thesis, we aimed to participate in these efforts by producing knowledge on coffee genetic resources, and on coffee-growing systems. We have shown that diversification is manifested at all levels, in complex and dynamic ways, with implications on ecosystem service delivery, and possible pathways for improvement. However, scientific research on this topic in the local Haitian context is still in its infancy. It is my hope that this thesis will provide a starting point for other scientists, agronomists, local universities, and development projects to continue generating the needed knowledge and experimenting with ways to improve the productivity of coffee stands, the livelihood of farmers, and ecological health of the local environment.

Annex I. Coffee variety guide (French)

Included in individualized reports to farmers and reports to PITAG. Produced by Claude Patrick Millet based on data from WCR



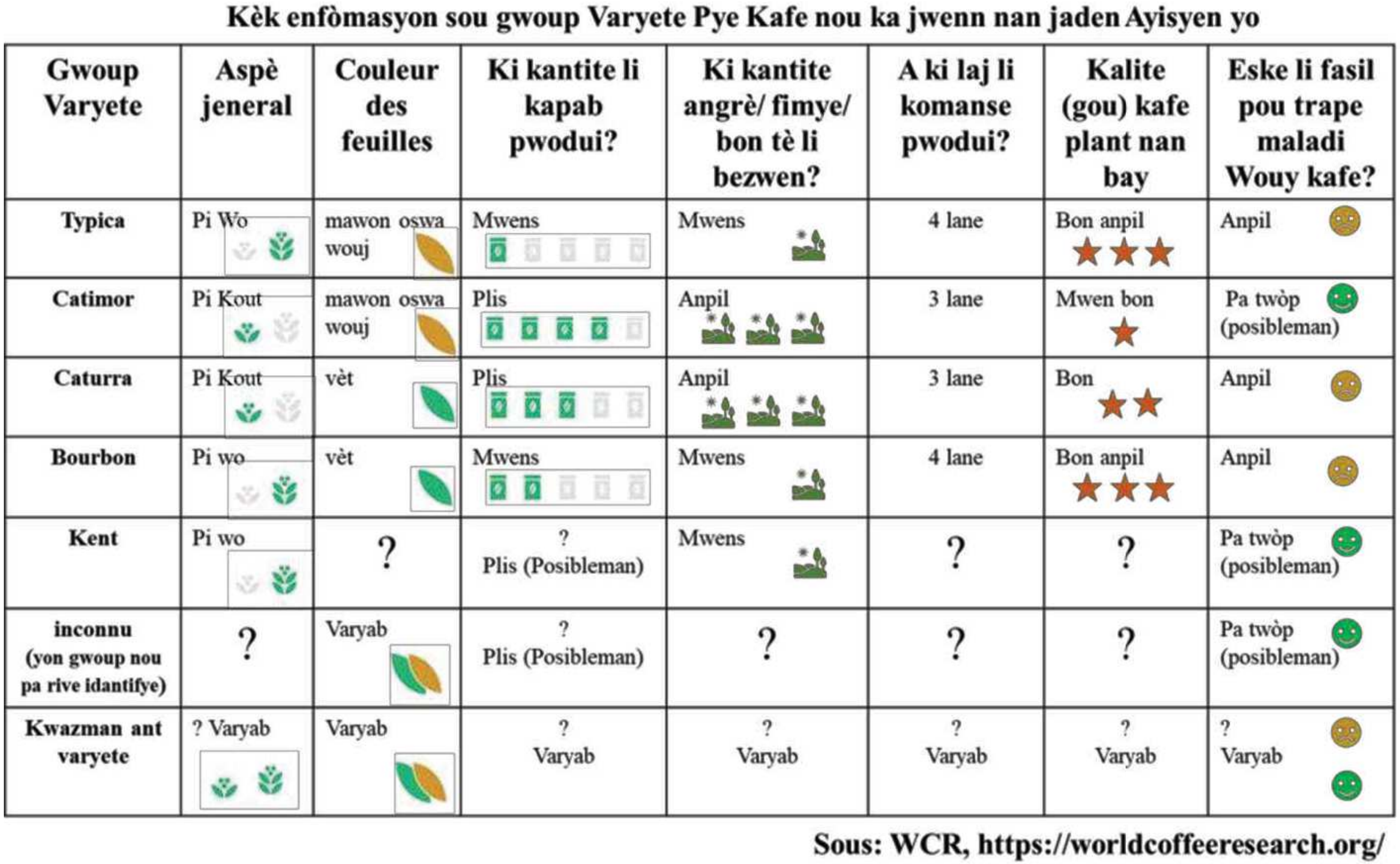
Caractéristiques des groupes variétaux identifiés par les analyses génétiques

Groupe variétal	Port	Couleur des feuilles	Potentiel de productivité	Besoins nutritionnels	Age de première production	Qualité du café produit	Susceptibilité à la rouille
Typica	Haut	Colorée	Plus faible ■□□□□	Plus faibles	4 ans	Excellente ★★★	Très susceptible ☹
Catimor	Compact	Colorée	Plus fort ■■■■□	Plus forts	3 ans	Moindre ★	? Potentiellement tolérante ☺
Caturra	Compact	Verte	Plus fort ■■■□□	Plus forts	3 ans	Bonne ★★	Très susceptible ☹
Bourbon	Haut	Verte	Plus faible ■■□□□	Plus faibles	4 ans	Excellente ★★★	Très susceptible ☹
Kent	Haut	?	? (Possiblement plus fort)	Plus faibles	?	?	? Potentiellement tolérante ☺
Groupe inconnu	?	Variable	? (Possiblement plus fort)	?	?	?	? Potentiellement tolérante ☺
Croisements	? Variable	Variable	? Variable	? Variables	? Variable	? Variable	? Variable ☹ ☺

Source: WCR, https://worldcoffeeresearch.org/

Annex II. Coffee variety guide (*Kreyòl*)

Included in individualized reports to farmers and reports to PITAG. Produced by Claude Patrick Millet based on data from WCR



Kèk enfòmasyon sou gwoup Varyete Pye Kafe nou ka jwenn nan jaden Ayisyen yo

Gwoup Varyete	Aspè jeneral	Couleur des feuilles	Ki kantite li kapab pwodui?	Ki kantite angrè/ fimye/ bon tè li bezwen?	A ki laj li komanse pwodui?	Kalite (gou) kafe plant nan bay	Eske li fasil pou trape maladi Wouy kafe?
Typica	Pi Wo	mawon oswa wouj	Mwens ■□□□□	Mwens	4 lane	Bon anpil ★★★	Anpil ☹
Catimor	Pi Kout	mawon oswa wouj	Plis ■■■■□	Anpil	3 lane	Mwen bon ★	Pa twòp (posibleman) ☺
Caturra	Pi Kout	vèt	Plis ■■■□□	Anpil	3 lane	Bon ★★	Anpil ☹
Bourbon	Pi wo	vèt	Mwens ■■□□□	Mwens	4 lane	Bon anpil ★★★	Anpil ☹
Kent	Pi wo	?	? Plis (Posibleman)	Mwens	?	?	Pa twòp (posibleman) ☺
inconnu (yon gwoup nou pa rive idantifye)	?	Varyab	? Plis (Posibleman)	?	?	?	Pa twòp (posibleman) ☺
Kwazman ant varyete	? Varyab	Varyab	? Varyab	? Varyab	? Varyab	? Varyab	? Varyab ☹ ☺

Sous: WCR, https://worldcoffeeresearch.org/

Annex III. Protocol for ex-situ Typica conservation produced for PITAG

Produced by Claude Patrick Millet and Clémentine Allinne

Protocole de récolte de semences de Typica dans les parcelles Haïtiennes

Pour la mise en collection de caféiers de la variété TYPICA/ "Vieux café Haïtien", il faudra récolter des graines dans les parcelles monovariétales de plants n'ayant pas eu l'occasion de se croiser avec d'autres variétés. Les analyses génétiques réalisées ont permis d'identifier les parcelles suivantes comme étant monovariétales. Il faudrait collecter autant que possible des graines des plantes qui ont été étiquetées pour l'étude génétique.

Departement/ commune	Parcelle/ Jardin	Propriétaire	Tel	Notes
Nord/BAHON	Mompoint	Redacted for privacy	Redacted for privacy	Guerlande Duval et Franddy Mulatre ont visité les deux parcelles de Bahon
Nord/BAHON	Grenier	Redacted for privacy	Redacted for privacy	La propriétaire est décédée, il faudra parler à ses enfants
Grande-Anse/PESTEL	K gous	Redacted for privacy	Redacted for privacy	Rochelin Pierre-Louis a visité les deux parcelles de Pestel.
Grande-Anse/PESTEL	Mabilai	Redacted for privacy	Redacted for privacy	Collecter les plantes à étiquettes **SAUF le plant G14-21** qui est à éviter

Pour l'échantillonnage des caféiers dans les parcelles Typica, deux cas de figure peuvent se présenter.

1) Cas optimal : Si les arbres échantillonnés (étiquetés) sont encore accessibles et sont en production, collecter de préférence les fruits de ces plantes.

- **Ne pas mélanger les fruits de parents différents**.
- Mettre les fruits dans des sacs en plastique à raison d'un sac par plant mère et identifier

les sacs. **Inscrire le code de la plante mère (code de la parcelle + numéro de la plante, ex. N14-01) sur le sac contenant ses fruits.**

2) Cas alternatif : Si les arbres échantillonnés ne peuvent pas être retrouvés ou ne sont pas en production, collecter des fruits d'autres caféiers.

- Choisir de préférences les plants très productifs, plutôt jeunes si possible (4-8 ans), à croissance vigoureuse et à l'aspect sain, qui présentent les caractéristiques qu'on souhaite propager.
- Si possible, privilégier les plantes à rendement stable, à l'intérieur des parcelles plutôt que sur les bords de chemin.
- Dans ce cas, les fruits collectés peuvent être mis dans le même sac (à raison d'un sac par parcelle), sur lequel le nom de la parcelle (origine des fruits) doit être inscrit. **Ne pas mélanger les semences de parcelles différentes.**

Protocole de collecte de matériel génétique pour la propagation

1. Choix des variétés à propager

Les variétés à propager sont choisies en fonction des critères désirés: productivité, qualité des fruits, résistance aux maladies et ravageurs, âge de maturation (précocité de la productivité), altitude optimale, adaptation aux conditions locales, etc.

2. Choix des parcelles de caféiers

Les cerises de caféiers seront collectées dans des parcelles ou groupes de plantes en bonne santé, avec le moins de signes de maladies que possible.

3. Choix des plants mères

Choisir de préférences les plants très productifs, plutôt jeunes si possible (4-8 ans), à croissance vigoureuse et à l'aspect sain, qui présentes les caractéristiques qu'on souhaite propager. Si possible, privilégier les plantes à rendement stable, à l'intérieur des parcelles plutôt que sur les bords de chemin (pour réduire les chances de croisements extérieurs).

4. Préparation préalable

Se munir de paniers ou autres contenants propres, employer un personnel qualifié

5. Collecte des semences

Collecter les meilleurs fruits (cerises mûres, sans défaut, sans piqûre d'insectes, trous de scolytes, etc.), situées à hauteur intermédiaire sur le plant. Eliminer les grains qui ne paraissent pas conformes, présentent des malformations, des maladies et moisissures. Lors de collecte, prendre soin à ne pas endommager les plants mères.

6. Stockage des cerises

Stocker les cerises dans un lieu frais (idéalement 15°C) à l'abri de la lumière, dans un contenant ou un sac fermé hermétiquement.

Traitement humide des semences

Une fois le processus de récolte des semences soigneusement mis en oeuvre, le matériel collecté sera traité pour pouvoir être utilisé pour la propagation. Il sera dépulpé, fermenté, démucilaginé, lavé et séché afin de préserver la qualité des semences.

ATTENTION : les semences d'origine différentes ne doivent pas être mélangées : chaque lot doit être traité séparément, et toujours identifiés à chaque étape du protocole.

1. Récolte

   Collecter des cerises mûres et sans défaut, scolyte, etc.
2. Tri des semences

Trier les semences pour écarter tout fruit vert. Submerger les fruits dans l'eau pour éliminer ceux qui flottent (qui sont troués ou sans graines)

3. Dépulpage

   Séparer les grains de café de la pulpe des cerises

4. Démucilagination

   Le mucilage est la couche glueuse ou gélatineuse qui recouvre les grains. Pour l'enlever, il convient de mettre les grains 12 heures dans une pile de fermentation. Il faut ensuite laver les grains pour éliminer les restes de mucilage

   Si un système de démucilagination (appareil pour dépulper et/ou démucilaginer) est disponible, il peut aussi être utilisé
5. Séchage des graines

   Les graines sont étalées et séchées à l'abri des rayons du soleil, dans un lieu dont la température n'excède pas 40° C pour éviter d'endommager le germe de la graine

   Les grains doivent être séchés entre 3 et 7 jours, en les retirant toutes les 30 minutes

Sélection finale des semences

Avant le stockage des semences, les graines doivent passer par une sélection finale pour ne garder que celles qui sont adéquate. Il faudra donc éliminer toute graine présentant des malformations afin de ne pas impacter la qualité et le développement des plantules. Les graines sélectionnées doivent être uniformes et de bonne taille. Un tamis à grosses mailles peut être utilisé pour éliminer les trop petites graines, ou celles-ci peuvent être enlevées à la main. Il faut aussi éliminer les grains cassés ou endommagés, vides ou trop légers, malformés, moisis ou présentant encore une couche de pulpe ou de mucilage.

Exemples de défauts de graines de café

Grains moisis ou brunis

Grains noirs ou décolorés

Grains endommagés par les insectes/moisis

Exemples de grains malformés

Source: https://coffeebeanroad.com/coffee-bean-defects-vs-taste/

Stockage des semences

Les semences mises en stockage perdent progressivement de leur viabilité, réduisant ainsi le pourcentage de germination. Il faut donc autant que possible privilégier les graines récemment collectées et stockées dans des conditions favorables: température de 20 à 25°C, humidité relative de 65 à 90%, donc dans un lieu frais et humide, dans un espace fermé et à l'abri de la lumière et des animaux.

Si les grains seront conservés plus de 30 jours, ils doivent être conservés à un taux d'humidité de 30% (un hygromètre peut être utilisé pour mesurer ce taux) dans des sacs de plastique capables de conserver cette humidité.

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