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Local working collections as the foundation for an integrated conservation of *Theobroma cacao* L. in Latin America

Andréanne Lavoie[1,2*†], Evert Thomas[2†] and Alain Olivier[1]

[1]Département de phytologie, Faculté des sciences de l'agriculture et de l'alimentation, Université Laval, Québec, QC, Canada, [2]The Alliance of Bioversity International and CIAT, Latin American Office, Lima, Peru

The intraspecific diversity of cacao has traditionally been preserved in genebanks. However, these establishments face various challenges, notably insufficient funding, accession redundancy, misidentification and lack of wild cacao population samples. In natural environments, it is expected that unknown varieties of cacao may still be found, but wild populations of cacao are increasingly threatened by climate change, deforestation, habitat loss, land use changes and poor knowledge. Farmers also retain diversity, but on-farm conservation is affected by geopolitical, economic, management and cultural issues, that are influenced at multiple scales, from the household to the international market. Taking separately, *ex situ*, *in situ* and on-farm conservation have not achieved adequate conservation fostering the inclusion of all stakeholders and the broad use of cacao diversity. We analyze the use of the traditional conservation strategies (*ex situ*, *in situ* and on-farm) and propose an integrated approach based on local working collections to secure cacao diversity in the long term. We argue that national conservation networks should be implemented in countries of origin to simultaneously maximize alpha (diversity held in any given working collection), beta (the change in diversity between working collections in different regions) and gamma diversity (overall diversity in a country).

KEYWORDS

cacao diversity, on-farm conservation, *ex situ*, *in situ*, cacao's region of origin and domestication, living collection

EDITED BY
David Jack Coates,
Department of Biodiversity, Conservation and Attractions (DBCA), Australia

REVIEWED BY
Fábio De Almeida Vieira,
Federal University of Rio Grande do Norte, Brazil
Roxana Yockteng,
Colombian Corporation for Agricultural Research (AGROSAVIA), Colombia

*CORRESPONDENCE
Andréanne Lavoie
andreanne.lavoie.3@ulaval.ca

†These authors have contributed equally to this work

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Introduction

Cacao originated in Amazonia, more than 9 million years ago (Bergmann, 1969; Young, 2007; Richardson et al., 2015). It possesses multiple centers of diversification which are the result of natural processes of isolation, local adaptation and domestication (Clement et al., 2010; Thomas et al., 2012). While cacao plantations were more predominant in Mesoamerica than in South America at the time of the European conquest (Stone, 1984; Young, 2007), it has a long-standing history of human management in Amazonia (Motamayor et al., 2008; Loor Solorzano et al., 2012; Thomas et al., 2012). Since the human occupation of Amazonia, people started protecting, dispersing and cultivating species that were useful to them and removed those that were not (Levis et al., 2018). The earliest evidence of cacao domestication in South America is from the northern Peruvian and southern Ecuadorian Amazon, dating back some 5,300 years (Olivera Núñez, 2018; Zarrillo et al., 2018; Valdez, 2019).

Communities that first selected cacao focused on the sensory traits that appealed them, particularly those of the pulp surrounding the cacao beans (Henderson and Joyce, 2006; Loor Solorzano et al., 2012). They ate the fruits of their favorite trees and took care of them on site. The seeds of these fruits ended up in dump heaps at camp sites (Anderson, 1969), which provided favorable conditions for the development of mature trees that could produce fruits for consumption on future visits (Miller and Nair, 2006). This practice gradually evolved into active planting in homegardens (Valdez, 2019), as well as exchanges with neighboring and more distant communities (Stone, 1984) which resulted in the dispersal of the preferred phenotypes (Bartley, 2005; Clement et al., 2010).

Ways to describe cacao diversity have evolved over time. Moving away from the traditional classification of Forastero, Criollo and their hybrid form, Trinitario (Cheesman, 1944), a system of genetic clusters proposed by Motamayor et al. (2008) is more commonly used nowadays. Although this classification system provides a more accurate representation of cacao diversity, it is still incomplete, as evidenced by the discovery of new genetic groups (Zhang et al., 2012; Osorio-Guarín et al., 2017; Gopaulchan et al., 2020). Far less does the current classification system account for the native varieties and landraces distinguished within genetic groups that are increasingly attractive to craft bean-to-bar chocolatiers who have experienced a boom in the past 20 years (Giller, 2017; Santander Muñoz et al., 2020; Cadby et al., 2021; Figure 1 presents part of the diversity of cacao Chuncho, a cultivar from *La Convención* province in the Cusco department, Peru). In this paper, we will therefore refer more generally to the diversity of cacao using the terms population, germplasm, accession, variety, landrace, and cultivar (please refer to Box 1 for use of terms).

Cacao diversity has the potential to further enhance the quantity and quality of production (Vaast and Somarriba, 2014), build in resistance to biotic and abiotic stress factors (Zhang and Motilal, 2016) and bolster the resilience of cropping systems and people who depend on them (Jarvis, 2000), especially in times of accelerated climate change (Medina and Laliberté, 2017; Ceccarelli et al., 2021). However, cacao genetic resources are increasingly threatened. On the one hand, local cacao diversity found in farmers' fields is under increasing pressure to be replaced by non-native commercial varieties (Bartley, 2005; Bidot Martínez et al., 2015). On the other hand, wild cacao populations are threatened by the conversion of forest to other land uses, along with other threats (Vieira et al., 2008; Santos et al., 2011). At the same time many areas in the current distribution of *Theobroma cacao* L. have not yet been explored. Therefore, genetic material holding traits of interest related to productivity, fruit quality, resistance to pests and diseases and resilience to changing growth conditions might be lost before we even have a chance to explore their potential.

FIGURE 1
Cacao pods. Credit: Lavoie, A. 2017 Echarate, Peru.

BOX 1: Cacao diversity vocabulary.

Accession: "Usually a sample (e.g., seed lot) but may be a set of genetically related samples." (Linington and Pritchard, 2001).
Cultivar: typically considered as "synonymous with variety; the international equivalent of variety." (Miglani, 2017) However, in the case of cacao, cultivar is typically used for referring to those varieties or groups of varieties that clearly bear the marks of human domestication (Motamayor et al., 2008).
Germplasm: "refers to a set of genotypes (genetic constitution of an organism) that may be conserved or used; synonymous with genetic resources." (Sthapit, 2014).
Landrace: "farmer developed varieties of crop plants that are heterogeneous, adapted to local environmental conditions and have their own local names and distinguishing traits." (Sthapit, 2014).
Population: "a group of organisms, all of the same species, which occupies a particular area. The term may describe the number of individuals of a particular species in an ecosystem, or any group of like individuals." (Allaby, 2019).
Variety: "a subdivision of a species. An agricultural variety is a group of similar plants that by structural features and performance can be identified from other varieties within the same species." (Miglani, 2017).

Nevertheless, a new interest for local elite materials (van der Kooij, 2013), which in Latin America are often fine flavor cacao (FFC; ICCO, 2015; please refer to Box 2 for definition), could encourage the diversification of plantations (Maas et al., 2020). This provides opportunities to enhance the conservation of cacao genetic resources through their use (Berthaud, 1997), but requires that farmers have access to the cultivars and varieties that best meet their needs in a context of changing environmental conditions (Ceccarelli et al., 2022).

The conservation of cacao genetic resources is conventionally conducted through three main strategies: *ex situ*, *in situ*, and

BOX 2: Fine flavor cacao (FFC).

According to the International Cocoa Organization (ICCO) **fine flavor cacao** is defined as "cacao characterized by a complex sensory profile that integrates well-balanced basic attributes and aromatic and flavor notes; the complementary attributes can be clearly perceived and identified in the expression of its aromas and flavors, resulting from the interaction between (i) a particular genetic composition, (ii) the favorable conditions of the growing environment/terroir, (iii) specific plantation management, (iv) the characteristics of harvesting and post-harvest practices, and (v) the stable chemical and physical composition and integrity of the grain" (UNCTAD, 2022).

on-farm conservation. *Ex situ* cacao conservation is achieved through living collections, due to the species´ recalcitrant seeds. *Ex situ* collections can take different forms, from the classical germplasm collection whose principal aim is the long-term conservation of cacao genetic resources, to working collection (clonal gardens or seed orchards) whose main aim is the production of propagation material for the establishment of new or the renovation of existing cacao plantations. Due to the elevated costs of establishing, and especially maintaining *ex situ* collections, only small subsets of the existing cacao diversity can be conserved under this modality. Therefore, to achieve an effective conservation of cacao diversity, *ex situ* conservation needs to be complemented by conservation in natural settings (*in situ*) and in farmers' fields (on-farm; Brush, 1991; Berthaud, 1997; Dulloo et al., 2010; Schroth et al., 2011; Rao and Sthapit, 2013; Bellon et al., 2017; Westengen et al., 2018). *In situ* conservation is often considered to include on-farm conservation in agrobiodiversity conservation, but for the purpose of this paper, we will distinguish both concepts.

On-farm conservation recognizes the predominant roles of farmers in creating crop diversity, as well as maintaining characteristics that are relevant to them (Jarvis, 2000). It is an essential part of traditional agricultural systems (Clawson, 1985; Altieri and Merrick, 1987; Brush, 1991). Among the farmers who conserve agrobiodiversity, some are particularly recognized for their commitment to this task. The concept of custodian farmers was first proposed by Subedi et al. (2003) who suggested that nodal farmers play a central role in the exchange of germplasm in and outside their communities. Custodian farmers maintain, adapt and/or promote crop varieties—and their associated knowledge—(Sthapit et al., 2013), including those that are best-adapted to their environment, most interesting for the market, and most appealing to them. Custodian farmers are typically driven by conservation ideology, are highly motivated and self-directed and demonstrate a consistent commitment to the diversity they preserve (Sthapit et al., 2013). They are recognized as stewards of agrobiodiversity in their community, while this acknowledgement is almost always absent at the national or international levels (Sthapit et al., 2015).

Until recently, cacao conservation, like that of the vast majority of other crops, has mainly focused on *ex situ* strategies (Engels and Ebert, 2021). To some extent *in situ* preservation of wild cacao populations has also been supported, mostly indirectly through the establishment and management of protected areas. In contrast, formal on-farm conservation strategies are rare to non-existent, as are synergistic approaches that interlink the three conservation strategies.

We review the current state of cacao conservation in *ex situ* facilities, in *in situ* areas and on farms in Latin America. From an analysis of their strengths and challenges, we suggest an integrated strategy for the conservation of intraspecific cacao diversity, based on the complementarity of the three conventional strategies. We propose the establishment and strengthening of local working collections in the regions of origin of cacao genetic groups and landraces as a pragmatic way to consolidate the better integration of *ex situ*, *in situ* and on-farm conservation.

Materials and methods

We used a combination of keywords (landrace, cultivar, variet*, germplasm, diversity, resource, population), (cocoa, cacao, *Theobroma*), (*ex situ*, on farm, *in situ*) found in the title or the abstract of papers, to search CabAbstract (conducted on June 15, 2021), Web of Science (conducted on June 2, 2021) and Google Scholar (conducted on June 22, 2021). We found 72 articles in CabAbstract, 99 in Web of Science and 163 in Google Scholar. The keyword conservation was considered redundant with the keywords *ex situ*, *in situ* and on farm, which imply conservation. After eliminating duplicates and irrelevant papers, as well as those specific to Africa and Asia, we selected 70 articles for further review and coded them in NVivo software (Release 1.4.1, QSR International Pty Ltd, 2021) for a qualitative analysis of their content. References to the 70 articles analyzed are provided in Supplementary material.

Results and discussion

Cacao conservation strategies

Ex situ conservation was mentioned in 48 of the selected papers, while on-farm conservation was mentioned in 29 and *in situ* conservation in 16, which is consistent with the understudied nature of *in situ* and on-farm conservation compared to *ex situ* conservation (Laliberté et al., 2018). Publication dates range from 1994 to 2021, with half of them published between 2009 and 2013. 2011 and 2013 were the years with the most papers published ($n=7$). Twenty six papers focused on South America, 16 on Mesoamerica and 10 on the Caribbean; the remaining ones did not have a specific region of interest. Table 1 presents a compilation of the strengths, weaknesses and challenges found in the 42 articles reviewed regarding *ex situ,* on-farm, and *in situ* conservation. The remaining 28 articles were not deemed relevant for our analysis and were not considered further.

TABLE 1 Strengths, weaknesses, and challenges of *ex situ*, on-farm and *in situ* conservation in the 70 articles analyzed.

Strengths	**Weaknesses**	**Challenges**
Ex situ		
• Core representation of diversity (Van Treuren et al., 2009; Motilal et al., 2013); • Safeguard against vulnerability to diseases, pests, and abiotic stresses (Bekele and Bekele, 1996) • A lot of diversity is preserved on a small area (Lindo et al., 2018); • Conservation effective for breeding programs and continued genetic improvement (Bekele and Bekele, 1996; Adu-Gyamfi and Wetten, 2012; Osorio-Guarín et al., 2017; Arevalo-Gardini et al., 2019); • Documenting genetic diversity will secure its use (Osorio-Guarín et al., 2017).	• Mislabeling / Misidentification (Faleiro et al., 2002; Motilal and Butler, 2003; Schnell et al., 2005; Zhang et al., 2006, 2008, 2009; Motamayor et al., 2008; Irish et al., 2010; Motilal et al., 2012, 2013; Boza et al., 2013; Ji et al., 2013; Bidot Martínez et al., 2015; Lindo et al., 2018); • Redundancy (Faleiro et al., 2002; Van Treuren et al., 2009; Zhang et al., 2009; Motilal et al., 2013; Lindo et al., 2018); • Unbalanced composition (Van Treuren et al., 2009; González-Orozco et al., 2020); • Difficult to manage (Zhang et al., 2008; Irish et al., 2010) and expensive in terms of space and labour (Ronning and Schnell, 1994); • Vulnerability to natural disasters (Adu-Gyamfi and Wetten, 2012; Gopaulchan et al., 2020); • Number of accessions is limited (Van Treuren et al., 2009).	• Conserve a broad spectrum of diversity, while trying to do so with a minimum number of accessions (Ronning and Schnell, 1994; Irish et al., 2010; Motilal et al., 2013; Santos et al., 2015; Avendaño-Arrazate et al., 2018); • Identify a specific goal to limit size, duplication, and unbalanced collection (Van Treuren et al., 2009); • Get a full understanding of what is currently conserved in existing *ex situ* collections (Thomas et al., 2012); • Distribute core collections in various places to ensure their long-term safety (Gopaulchan et al., 2020); • Limited financial resources for conservation (Samuel et al., 2013).
On-farm		
• Diversified agroecosystem (Bidot Martínez et al., 2015); • Support the evolution process under the ecological and agricultural system ((Zhang et al., 2011; Ji et al., 2013); • Better living conditions for the farmer from compensation through FFC market (Arevalo-Gardini et al., 2019); • Variability available for participatory selection in low inputs small-scale context (Zhang et al., 2011) and exchange between farmers (Ruiz et al., 2011); • Inclusion of farmer-selected agronomic traits (Leal et al., 2008; Ji et al., 2013; Santos et al., 2015), which can secure conservation (Zhang et al., 2011; Bidot Martínez et al., 2015).	• Subject to geopolitical, economic, management and cultural issues (Motilal and Butler, 2003; Aragon et al., 2012; Périchon and Quique, 2013; Samuel et al., 2013; López et al., 2021); • Actual diversity influenced by previous diversity (less new material because of reproductive propagation, inbreeding or Wahlund effect) (Aragon et al., 2012; Lindo et al., 2018).	• Limited financial resources for conservation (Samuel et al., 2013); • High phenotypic diversity (Quevedo Guerrero et al., 2020) and large variation in desired characteristics due to sexual reproduction (Trognitz et al., 2013) • Selection of high-performance local material (Trognitz et al., 2013) • Gene flow from wild populations can impact on-farm diversity (Zhang et al., 2011).
In situ		
• Conservation of the entire environment in which the diversity has been created (Motilal and Butler, 2003); • Support the evolution process under the ecological system (Zhang et al., 2011; Périchon and Quique, 2013); • Reservoir of adaptations (adaptability, resistance, etc.) (Thomas et al., 2012; Zhang et al., 2012; De Schawe et al., 2013) and unique alleles (Whitkus et al., 1998; Thomas et al., 2012); • Wild germplasm can be directly used in breeding or commercial production (Zhang and Motilal, 2016)	• Susceptible to climate change, deforestation, habitat loss or changes in land uses (Iwaro et al., 2003; Bekele et al., 2006; Silva et al., 2011; Thomas et al., 2012; Samuel et al., 2013; González-Orozco et al., 2020); • Subject to geopolitical, economic and cultural issues (Motilal and Butler, 2003; Samuel et al., 2013); • Less diversity found per area, in comparison with *ex situ* facilities and some on-farm collections (De Schawe et al., 2013); • Too limited information on *in situ* populations characteristics to establish clear conservation strategy (Silva et al., 2011).	• Discovery of new material is pending and ongoing (Zhang et al., 2009, 2012; Cosme et al., 2016); • Priority areas for germplasm collection missions would be areas where high levels of genetic diversity and locally common alleles are observed (Thomas et al., 2012), but should also be planned over a wide geographic range (Bekele and Bekele, 1996; González-Orozco et al., 2020); • Gene flow from on-farm diversity can impact *in situ* populations (De Schawe et al., 2013); • Limited financial resources for conservation (Samuel et al., 2013).

Ex situ conservation

Formal cacao sample collection expeditions began in the 1930s (Iwaro et al., 2003; Zhang et al., 2009). The first official cacao germplasm bank was built in 1930 in Trinidad and Tobago (ICGT, n.d.): the International Cocoa Germplasm at the University of the West Indies. The other main international cacao genebank was founded in 1948 at the *Centro Agronómico Tropical de Investigación y Enseñanza* (CATIE), Costa Rica (Morera, 1991). Since then, most Latin America countries that produce cacao on a commercial basis started setting up national collections (Laliberté, 2015). About 10 years ago, CacaoNet (2012) reported the existence of 42 germplasm collections around the world, 23 of which were located in Latin America containing nearly 24,000 accessions. Considering all the initiatives at the local level which have multiplied in recent years, it is expected that these numbers are much higher today. In Peru alone, only 4 collections were mentioned in the CacaoNet report, while recent work has shown that the country has more than 45 collections (Ceccarelli et al., 2022).

Ex situ collections depend on the supply of genetic material from *in situ* and on-farm environments. Thus, the genetic material stored in *ex situ* collections represents only a fraction of the material existing in the wild and in farmers' fields (Louafi et al., 2013). Certain cacao populations may therefore be under or over-represented in *ex situ* collections. Furthermore, cacao relatives in the *Theobroma* and *Herrania* genera are not sufficiently conserved in these facilities either (Santos et al., 2011; Castañeda-Álvarez et al., 2016; Laliberté et al., 2018).

When maintained in a well-managed facility, *ex situ* conservation of a core collection—i.e., a subset comprised of the smallest number of accessions that maximizes the diversity conserved (van Hintum et al., 2000)—, represents a cost-effective option (Iwaro et al., 2003; Van Treuren et al., 2009; Zhang et al., 2009; Bidot Martínez et al., 2017; Osorio-Guarín et al., 2017; Laliberté et al., 2018). Yet, few institutions have established a core collection based on clear objectives and such efforts remain expensive and difficult to fund in the long term (Marcano et al., 2007). In addition, many facilities face challenges such as a high number of duplicates and misidentification of almost 25% of their accessions (Motilal and Butler, 2003; Van Treuren et al., 2009; Motilal et al., 2012, 2013). Therefore, although *ex situ* is a powerful tool for conservation, the curating work needed may not be sustainable in the long term for many institutions.

Access to *ex situ* germplasm is also increasingly difficult: logistic and regulatory constraints to transfers are tedious (Westengen et al., 2017). For example, while Costa Rican farmers can easily obtain access to germplasm from CATIE (small-scale farmers count for 15% of the users), small-scale farmers outside Costa Rica must pay for a phytosanitary certificate, an export permit, and shipping costs, making the process prohibitive and therefore infrequent (Ebert, 2008). Although one of the main objectives of international *ex situ* conservation facilities was to make genetic material available to any organization or individual requesting access (López Noriega et al., 2013), in practice, achieving this goal remains a challenge (Westengen et al., 2017).

On-farm conservation

On-farm conservation enables the protection of diverse agroecosystems (Bidot Martínez et al., 2015), which support evolutionary processes within ecological and agricultural systems (Zhang et al., 2011; Ji et al., 2013). All the farms in the world combined have a greater potential to store genetic resources than genebanks. (Brown 1999; Veteto and Skarbø 2009). The availability and accessibility of genetic material in small-scale context also promotes participatory selection and experimentation (Zhang et al., 2011), which in return can enhance on-farm conservation. The inclusion of farmers' preferences, such as particular agronomic traits (Ji et al., 2013), can increase the conservation of the genotypes or varieties that possess them (Zhang et al., 2011; Bidot Martínez et al., 2015).

Conservation of native cacao cultivars, landraces and the alike can also provide higher farm incomes through specialty markets, such as premiums offered in the FFC (Arevalo-Gardini et al., 2019), organic or fair trade markets (Nelson et al., 2002; Schneider et al., 2017; Bidwell et al., 2018), payment for ecosystem services (PES; Obeng et al., 2020) or payment for agrobiodiversity conservation services (PACS; Drucker and Ramirez, 2020). On-farm conservation also echoes the risk mitigation function of diversity in changing climatic, socioeconomic, and pest-pressure conditions (Vaast and Somarriba, 2014; Bidot Martínez et al., 2015).

However, the diversity maintained in farms is also influenced by farmer preferences and behavior. Farmers cannot be expected to maintain diversity that does not meet their criteria, whether these are related to productivity, resistance, or taste (Lindo et al., 2018). Farmers can face multiple pressures to abandon or change the diversity used on their farms, from geopolitical, economic and cultural issues (Motilal and Butler, 2003; Samuel et al., 2013). This puts into perspective one of the challenges of on-farm conservation, which is also its competitive advantage, i.e., the individuality of all farmers who contribute to preservation of a collective heritage. Farmers are the creators, curators, and beneficiaries of this agrobiodiversity, but also the first ones affected by its loss. Since we are collectively indebted to them for their work, it is important that farmers who protect diversity be supported and encouraged, not made vulnerable by their commitment.

Finally, none of the papers analyzed the diversity maintained on specific farms. At best, the papers presented aggregated information at a regional scale (e.g., Sereno et al., 2006; Ji et al., 2013; Arevalo-Gardini et al., 2019), without providing any details on the dynamics of on-farm conservation or the role played by custodian farmers, who are known to play a central role in agrobiodiversity conservation (Ruiz Muller and Vernooy, 2012). The main issue raised by these articles is that we need to correctly identify and characterize the material being conserved, in the spirit that you cannot protect what you do not know. Additionally, such a characterization is key to understand and document farmers' decision-making process surrounding on-farm conservation. Integrating the individuality of farmers into analyses is essential to understanding the mechanisms of on-farm conservation.

In situ conservation

In situ conservation aims to protect part of the ecosystems where the wild populations or relatives of a target crop have evolved, and viable natural populations occur. *In situ* populations are often considered as reservoirs of local adaptations (adaptability, resistance, etc.; De Schawe et al., 2013) and unique alleles

(Whitkus et al., 1998). One of the main concerns for the *in situ* conservation of cacao is the loss of wild populations. Wild populations are primarily threatened by deforestation—and conversion of land to other uses—(Chirif, 2019), forest degradation, anthropogenic forest fires and climate change, among others. It has been estimated that the wild populations of cacao could decline by 50% by 2050 (ter Steege et al., 2015). Further, expanding cacao cultivation into areas holding wild cacao populations results in increasing possibilities of genetic pollution of wild cacao by cultivated ones (Zhang et al., 2011; De Schawe et al., 2013). Protection of wild cacao populations in their natural environment not only conserves their genetic diversity, but also that of other members of the genus *Theobroma*.

However, the cost of effective *in situ* conservation is prohibitive. The number of accessions of different varieties that can sustainably be conserved per unit area (compared to an *ex situ* facility with a core collection) is often low (De Schawe et al., 2013). Securing vast areas of land in the long term can be difficult for geopolitical, economic and cultural reasons (Motilal and Butler, 2003). Furthermore, it is often difficult to obtain information on *in situ* populations characteristics, making it harder to create consistent conservation strategies (Silva et al., 2011).

In sum, cacao conservation is still largely focused on *ex situ* conservation; we do not have a comprehensive plan to support on-farm cacao conservation; and we still do not know the scope of on-farm and *in situ* conservation. We argue that achieving a more efficient and cost-effective conservation of the intraspecific diversity of cacao calls for a holistic system approach that integrates all types of conservation. In this respect, lessons can be drawn from conservation strategies developed for other perennial crops such as the particular focus on including a diversity of stakeholders in the global apple conservation strategy (Bramel and Volk, 2019); the need for increasing *in situ* collections in the case of coffee (Bramel et al., 2017); the importance of the role of regional collections for the circulation of banana germplasm (MusaNet, 2016); and consolidating on-farm and *in situ* coconut conservation activities (COGENT, 2017). However, these strategies also show that it is challenging to develop functional linkages between all conservation components and its stakeholders, which we believe in the case of cacao could be achieved through the establishment of working collections at the local level as explained next.

Toward an integrated cacao conservation system

The underlying principles of an integrated cacao conservation system that will optimize cacao diversity conservation are:

- being firmly **anchored in a conservation-through-use approach**, whereby cacao diversity is optimally employed to overcome key cultivation challenges and responds to farmers' prerogatives (e.g., pest and disease resistance, high productivity, site and climate adaptation, etc.), in addition to meeting consumer interests (e.g., flavor profiles, bean vs. pulp uses, etc.), which is pivotal for a cash crop;

- **being inclusive** by involving different stakeholders interacting with cacao genetic resources, where appropriate, from indigenous and local communities and protected area managers over (custodian) farmers and managers of local working collections to *ex situ* facility managers and cacao market and value chain actors;

- **fostering the dynamic nature of cacao genetic resources**, through the maintenance of selective processes exerted by farmers and changing environmental conditions under on-farm and *in situ* conditions.

We believe that a system integrating the three conventional strategies would represent a major improvement to the current conservation, without completely changing the present working mechanisms. To be effective, however, its implementation must be based on a strengthened collaboration between farmers, cacao cooperatives and associations, non-governmental organizations (NGOs), academia, cacao buyers, public, parapublic and private organizations, and the local to national governments. All these actors depend on cacao diversity, thus they must all be involved in its conservation. Figure 2 describes the links that need to be built between all local partners to ensure that all parts of the integrated system work together to promote the conservation of cacao genetic diversity through its use.

We propose working collections to become centerpiece of this system for facilitating the interconnectedness of *ex situ* collections, cacao farmers and custodian farmers, and *in situ* conservation areas. Working collections should be locally anchored and serve direct farmer needs and preferences in terms of agronomic and sensorial traits. They should contain a limited set of cacao genotypes of which farmers can obtain propagative material for direct use in their farms and which can have originated either from *ex situ* genebanks, (custodian) farmers' fields, or directly from *in situ* settings. As such, working collections need to have sufficient production capacity of grafting materials (clonal gardens with enough copies per genotype) and seeds to produce rootstock material (seed orchards) to meet the demand of local farmers. Working collections are different from the classical *ex situ* collections. While the main purpose of *ex situ* collections is to conserve as much diversity as possible of both potential and actual use in the long term (each genotype represented by only few copies), working collections contain only a restricted set of genotypes of direct use by farmers and these genotypes may change over time, in response to emerging agronomic needs and market preferences. This implies that planting materials included in working collections need to count with reliable characterization data, so farmers have a reasonable level of certainty of what to expect from the different types of planting material in terms of agronomic and sensorial traits. In regions where cacao is part of native vegetation, working collections should prioritize local genotypes for fruit production to allow the conservation of cacao genetic material in its territory of origin. As such they would also constitute knowledge hubs for local varieties (CacaoNet, 2012). At the same time this will ensure the genetic integrity of local cacao populations and allow the development of denomination of origin schemes and market differentiation. This is particularly the case for FFC and the specialty market at large. Genotypes to be used as rootstock by contrast can be sourced nationally or even internationally as they are not allowed to enter the reproductive phase and hence are not expected to influence local genepools.

Working collections should be established in all regions where cacao is cultivated but also occurs in natural vegetation and where specific genetic groups of cacao are found, often following the Amazonian river networks (Motamayor et al., 2008; Thomas et al., 2012). Ultimately, the creation of multiple working collections across the different regions in a country where unique cacao landraces, varieties or cultivars occur should form the basis of a true nationwide conservation network. National conservation networks should thus be implemented to simultaneously maximize alpha (diversity held in one working collection), beta (the change in diversity between working collections) and gamma diversity (overall diversity in a country).

The institutions responsible for the establishment, use and maintenance of working collections typically serve the interests of farmer collectives such as farmer cooperatives or associations, NGOs, buyer companies, etc. They therefore have a critical role to fulfil in providing advice, training, and tools to participating farmers and communities.

To ensure that they count with the most appropriate planting material, depending on the growth conditions, local threat exposure and sensorial interests among others, working collections need to develop strong linkages with each other, as well as with other key actors in the conservation chain (Figure 2). Most importantly, working collections need to build trustworthy relations with local cacao farmers and particularly custodian farmers who serve not only as receptors of planting materials but also suppliers of promising genotypes. While most farmers will only have a limited diversity of cacao genotypes on their farms, custodian farmers typically conserve many more (Sthapit et al., 2013). Box 3 briefly presents a custodian cacao farmer in *La Convencion* province in the Cusco department, Peru.

In recognition of their contribution to the preservation of cacao genetic diversity, in essence a public good, compensation schemes can be developed for (custodian) farmers willing to share part of the diversity under their custody with other farmers through working collections. Aside from local compensation schemes, formal recognition of custodian farmers by local, regional, or national governments can be a powerful mechanism to promote on-farm agrobiodiversity conservation, as demonstrated by examples in India, Indonesia, and Nepal (Clancy and Vernooy, 2016). Formal recognition by public authorities can give farmers even more acknowledgement in their local community, but especially at other scales, where they almost always lack formal recognition. It can also grant custodian farmers certain privileges such as getting specific training to strengthen the conservation and characterization of the materials under their custody, forming part of a dedicated network of custodian farmers to facilitate exchange of knowledge and genotypes. There is also a recurring and important concern among custodian farmers who have developed collections on their farm: they often have difficulty passing on the plant genetic heritage they have accumulated owing to the lack of family members or successors willing to continue their mission (Sthapit et al., 2015). Being part of a network might help farmers to connect with peers interested in maintaining their genetic resources.

BOX 3: Cacao Chuncho: from Matsigenka communities to today's custodian farmers.

The Peruvian chocolate industry was founded more than 100 years ago in the cultural overlap region in the lowlands of the Cusco department where the Incas maintained trade relations with the Amazonian Matsigenka who played a key role in the domestication of chuncho cacao cultivar, one of the most sought-after cacaos today. What makes chuncho cacao particularly unique is that multiple varieties are distinguished in the cultivar., each with their own local names and flavor profiles (Rojas et al., 2017; Eskes et al., 2018). The word chuncho means "the savages" in Quechua, the language of the Incas, and was used by them to refer to the Amazonian peoples (Rénique, 2009). After the European conquest numerous haciendas were established in the Cusco lowlands in which a high diversity of chuncho cacao varieties were concentrated. After the Peruvian agrarian reform, some of the people who used to work on the haciendas established their own plantations from seeds collected from the diverse chuncho varieties they used to care for. The father of Francisco Torres was one of these workers and today he has taken up the conservation of possibly one of the most diverse remaining chuncho cacao collections. As such, Francisco represents one of the main custodian farmers of chuncho cacao today.

Another key source of cacao genotypes for working collections are cacao populations in natural forest vegetation. Many watersheds and forests in the Amazon basin have yet to be explored to collect genetic material and it is expected that undocumented populations and genetic groups can still be found. Contrary to common belief, cacao populations in natural forest are not necessarily wild, but may be remnants of domestication efforts by native societies (Motamayor et al., 2002; Sereno et al., 2006). For example, genetic evidence showed that putatively wild cacaos from the Lacandona rainforest from Mexico were actually remnants of Criollo trees cultivated by the Mayas whose populations persisted as the rainforest grew back (Motamayor et al., 2002). Also in South America, evidence is mounting that humans may have shaped the diversity of cacao populations across the Amazon Basin (Thomas, 2017; Levis et al., 2018).

Hence, aside from traits related to plant vigor and pest and disease resistance, cacao populations in natural vegetation can be an important source of planting material that combine high productivity with interesting flavor profiles.

To preserve wild cacao populations, it is vital to protect the landscapes and environments in which they are found. Protected areas and territories under community forest management are among the best strategies to counter these threats. 44.3% of the Amazon basin is currently under the sustainable management of indigenous communities (and 9% are in strict conservation reserves; ter Steege et al., 2015). However, the contribution of protected areas and territories to the *in situ* conservation of cacao populations could be greatly enhanced through their mapping, characterization (e.g., in terms of quality, productivity, pest and disease resistance and adaptation to specific site conditions) and management (e.g., by removing competing plants, pruning,

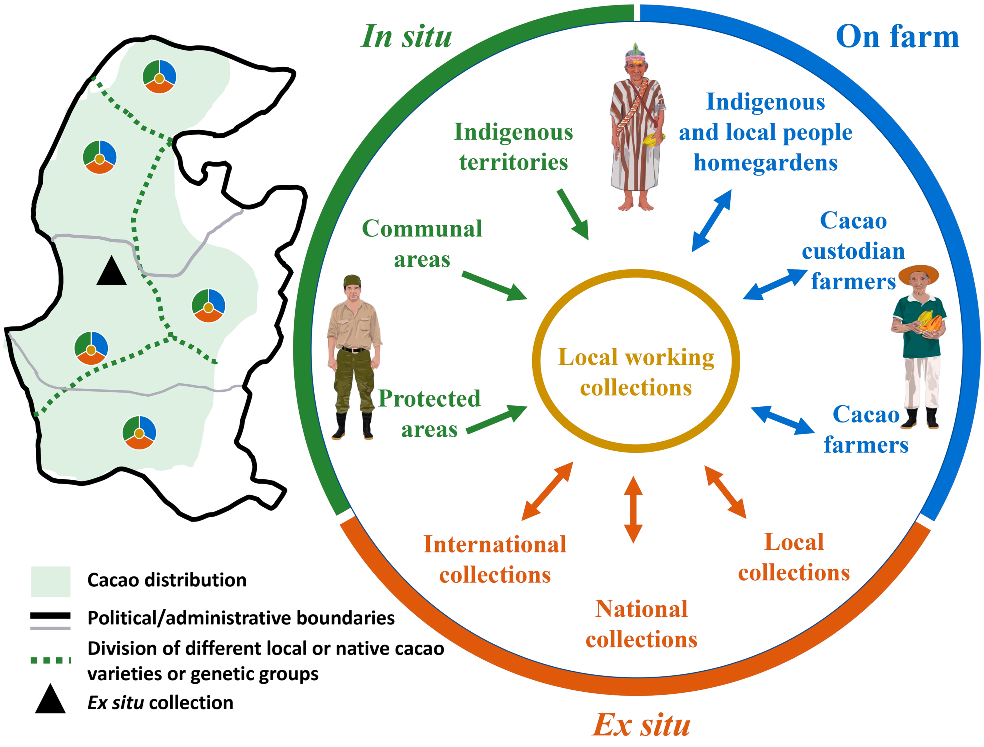

FIGURE 2
Detail of an integrated system of cacao conservation. The map on the left-hand side shows an imaginary cacao region in which several integrated conservation systems and one centralized *ex situ* collection have been set up across the cacao distribution range to preserve the diversity of local cacao varieties. The schematic representation on the right-hand side shows how working collections form the centerpiece of each of the regionally implemented integrated conservation system and link all the actors in the integrated system (blue for the on-farm actors, red for the *ex situ*, green for the *in situ* and yellow for the working collection). The different stakeholders exchange germplasm or vegetative material (arrows), thus strengthening their links and ensuring that local diversity is protected, but also widely used.

facilitating regeneration, etc.). This would require the active involvement of protected area managers and indigenous and local communities (Tauli-Corpuz et al., 2020). Similar compensation schemes and forms of formal recognition as described above for custodian farmers can be developed for protected areas and community forest management, such as formal recognition of communities as guardians of cacao diversity. It is also clear that a better recognition of the rights and full powers of indigenous communities over their territories is likely to lead to better protection of local cacao diversity through better protection against deforestation (Nepstad et al., 2006; Soares-Filho et al., 2010; Nolte et al., 2013; Blackman et al., 2017; Blackman and Veit, 2018; Jusys, 2018; Baragwanath and Bayi, 2020; Walker et al., 2020).

Important to mention here is that any new collections should be carried out with the free, prior, and informed consent (FPIC) of indigenous and local communities or farmers and where relevant the benefits for people through participation in the integrated system should be agreed upon in line with the Nagoya protocol (CBD, 2011) and existing national laws and procedures.

While interesting cacao genotypes can be incorporated directly in working collections from *in situ* sources, *ex situ* collections can often serve as a first filter. As mentioned above, the main function of *ex situ* collections is to safeguard an as wide as possible diversity of cacao genotypes of both current and potential value. Sufficient *ex situ* collections should be established as to cover the whole distribution range of cacao in a country each containing representative samples of predefined sections of the distribution range. Deciding on what to include in a collection is always a tradeoff between what is useful or desirable and what is possible in terms of budget. Cacao populations occurring in unprotected natural settings with a high risk of being destroyed should be the priority for new collections missions that target the conservation of as wide as possible genetic diversity. In protected areas, community forest areas and custodian farmer collections and the alike, only a selection of materials of interest may be sufficient given their *in situ* or on-farm conservation state. The latter illustrates how an integrated system can help sharing the risks and challenges linked to the conservation of cacao diversity among all partners involved. However, this requires that all partners be held mutually accountable, according to their available resources and capacities.

The role of external stakeholders in strengthening the integrated conservation strategy

The integrated system we proposed here will only work if all stakeholders agree to commit to it, support it and take ownership of it. To ensure its implementation, the approach must be locally anchored and reflective of local community priorities and market interests, involve all relevant stakeholders and encourage them to strengthen their links, as well as acknowledge the essential role of all conservation components (*ex situ*, on-farm, *in situ* and working collections) for achieving the effective preservation and use of cacao diversity (Enjalbert et al., 2011). Box 4 presents an example of a working collection implemented in Peru by the *Cooperativa Agraria Norandino*.

BOX 4: Working collection in the department of Piura, Peru.

Some cooperatives in Peru have begun the establishment of working collections to provide propagative material of superior native FFC to their members to renovate or rehabilitate their plantations. An example of this is the *Cooperativa Agraria Norandino*, which implemented working collections of their six best genotypes of Piura white cacao which is part of the Nacional genetic cluster shared with Ecuador. The selection process started in 2007 with the identification of 1,160 cacao plants producing white, pink, or violet seeds all across the Piura department. This number was gradually reduced by selecting the trees with superior sensorial quality and productive potential and culminated in the establishment of a small genebank holding 25 of the most promising genotypes. The different genotypes in the genebank were further evaluated in terms of yield, stability of producing white beans (characteristic for high sensorial quality) and resistance to pests and diseases and the six best ones were next established in a clonal garden containing dozens of copies of each genotype to form the working collection. Initial experiments have confirmed the higher yields obtained from these genotypes at plantation level and the working collection is now actively being used to support farmers with the renewal and rehabilitation of their plantations.

Achieving this is likely to require facilitation, the development of incentive mechanisms and clear rules of engagement. Public authorities have a clear role to play in this, but also multiple external stakeholders (private companies, NGOs, academia, etc.) can and should contribute substantially. Figure 3 illustrates potential roles of external partners to strengthen the integrated conservation system.

The mutual benefits that can be reaped through participating in an integrated conservation system can serve as a strong incentive for internal and external stakeholders to get involved. For example, custodian farmers could gain new material and better incomes for their varieties, farmers could receive training on desired topics, such as plant breeding, pest control, fermentation of cacao beans, etc., research partners could help with the characterization and identification of promising genotypes, breeders would have access to preselected cacao genotypes, and buyers and chocolate companies could on the one hand guide the selection of genotypes with high market potential and on the other hand benefit from a source of distinct cacao genetic material.

Conclusion

The current cacao diversity conservation system with three conventional strategies working independently needs to be improved. Conservation of cacao genetic resources has until now (1)

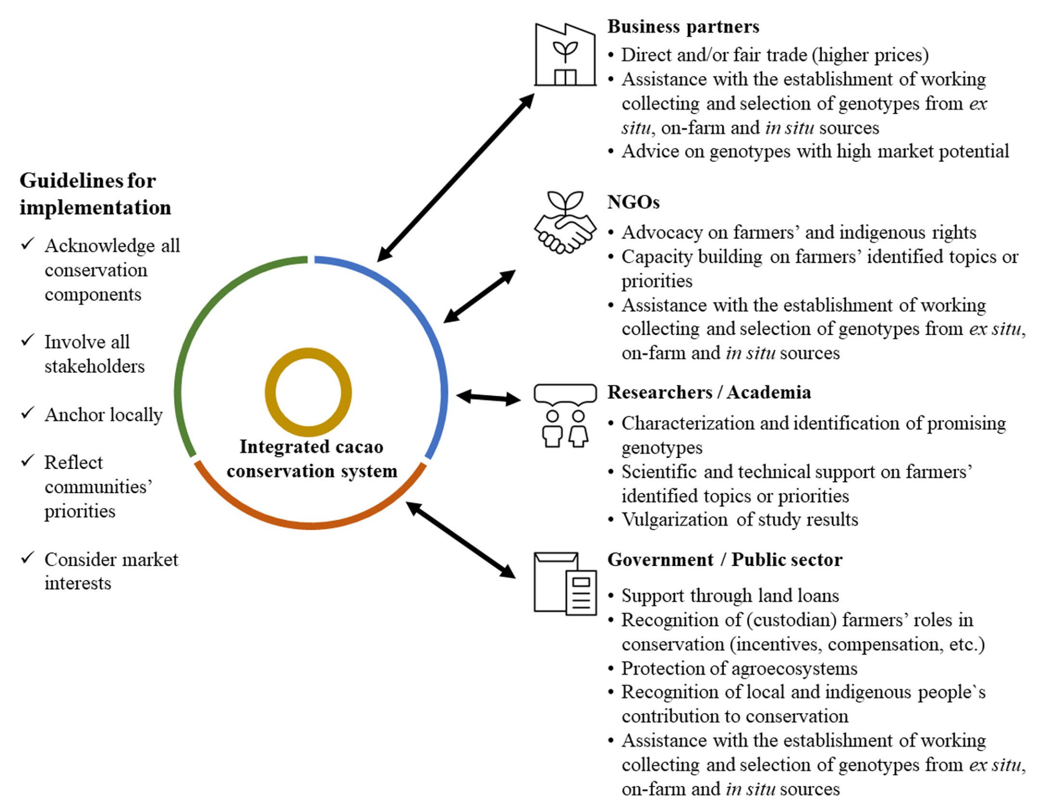

FIGURE 3
Potential roles of conservation actors outside of local community.

mainly focused on ex situ facilities; (2) relied mainly on protected areas for the conservation of wild cacao populations; and 3) largely neglected the importance of on-farm conservation strategies, including the role of cacao custodian farmers.

We call for the integration of the three conservation strategies to potentialize their complementary strengths and argue that working collections established in a representative manner across the distribution range of cacao can be an efficient way to practically implement such integration. To our knowledge, the recently adopted Peruvian plan on the development of the value chain of cacao and chocolate (MIDAGRI et al., 2022) presents the first nation-wide formal attempt to operationalize an integrated conservation system for cacao. We hope this initiative will be followed by other countries in cacao's region of origin and domestication in the years to come.

A fundamental role of working collections is operationalizing a conservation through use approach while maintaining the dynamic nature of cacao diversity. However, the realization of such an integrated system depends on the involvement and commitment of multiple stakeholders. This may require multiple incentives such as formal recognition of indigenous communities and farmers as custodians of wild and cultivated cacao, or buyers of cacao beans guiding the selection of cacao genotypes in working collections with the greatest market potential in return for access to cacao beans with unique flavors.

An integrated conservation system centered around working collections could also serve as a model for other tree crops, as well as for cacao in regions outside of Latin America, in spite of the absence of wild populations there. Farmers in Africa or Asia have developed cacao landraces that also merit preservation and we believe our proposed conservation approach can be adapted to such contexts as well.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethics approval has been obtained for the AL's PhD research from the *Comité plurifacultaire d'éthique de la recherche* of Université Laval under approbation number 2018–055 R-4/17-03-2022.

Author contributions

AL initiated the work, after which AL and ET both contributed equally to the manuscript. AL conducted the literature review. ET provided guidance and supervision and AO provided supervision and feedback on the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1063266/full#supplementary-material

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