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Social Organization of Crop Genetic Diversity. The $G \times E \times S$ Interaction Model

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Abstract: A better knowledge of factors organizing crop genetic diversity *in situ* increases the efficiency of diversity analyses and conservation strategies, and requires collaboration between social and biological disciplines. Four areas of anthropology may contribute to our understanding of the impact of social factors on crop diversity: ethnobotany, cultural, cognitive and social anthropology. So far, most collaborative studies have been based on ethnobotanical methods, focusing on farmers' individual motivations and actions, and overlooking the effects of farmer's social organization *per se*. After reviewing common shortcomings in studies on sorghum and maize, this article analyzes how social anthropology, through the analysis of intermarriage, residence and seed inheritance practices, can contribute to studies on crop genetic diversity *in situ*. Crop varieties are thus considered social objects and socially based sampling strategies can be developed. Such an approach is justified because seed exchange is built upon trust and as such seed systems are embedded in a pre-existing social structure and centripetally oriented as a function of farmers' social identity. The strong analogy between farmers' cultural differentiation and crop genetic differentiation, both submitted to the same vertical transmission processes, allows proposing a common methodological framework for social anthropology and crop population genetics, where the classical interaction between genetic and environmental factors, $G \times E$, is replaced by a three-way interaction $G \times E \times S$, where "S" stands for the social differentiation factors.

Keywords: crop genetic resources; cultural transmission; *in situ* conservation; interdisciplinary approach; maize; seed exchange; social differentiation; social network; sorghum

1. Introduction

As conservation programs for protected areas and plant genetic resources (PGR) expanded from single species approaches to ecosystem/agrosystem strategies which include the participation of local actors, anthropologists have become increasingly involved in studies and conservation of biodiversity [1]. At the same time, conservation biologists became increasingly aware of the impossibility of maintaining a significant proportion of PGR *ex situ*. Consequently, *in situ* approaches turned out to be essential for preserving agrobiodiversity as well as the underlying processes [2]. In this context, farmers' traditional knowledge has been recognized as a key component of germplasm diversity [3-6]. Thus, both disciplines have had the opportunity to share a common research field and a close collaboration was expected. However, cultural ecology of PGR has mainly focused on the relationship between farmers' behavior and genetic resources, and particularly on farmers' practices and decisions with an effect on genetic selection [1]. As a matter of fact, the contribution of social anthropology has been very limited. Indeed, the social organization of farmers has most often been overlooked as a factor influencing crop genetic organization, and close cooperation between social anthropology and population genetics has remained exceptional. Such a cooperative approach would entail that experts of each discipline develop their methodology in a way that the causes and consequences of observed phenomena can be assessed by experts of the other discipline.

There are several reasons for a limited collaboration. Academically, biological and social sciences remain distinct by promulgating a conception where the "natural" and biological world is opposed to the social and human one [7]. At their interface, social factors are usually reduced to individual choices in the analyses, which constitutes a barrier for social anthropology to step in. The individual based approach is not accidental. It has been the one promoted by the classical western individualistic economic model, which ignores the fact that individuals are part of social networks. This model has been implicitly extended to *in situ* crop genetic studies in conservation biology, where the social component is too often reduced to a sum of individual decisions, motivations and actions. Farmers' networks of relations, which are linguistically and socially structured, have rarely been considered as a factor structuring also *in situ* crop genetic diversity.

The classical economics model, inherited from the seventeenth century, operates with an atomized, *undersocialized* conception of human action referring to a utilitarian tradition. As mentioned by Granovetter [8], the effects of social structure and social relationships on production, distribution, or consumption are weak or inexistent in this model. Individuals do not noticeably influence supply or demand, which are considered as components of the economic system itself. They are anonymous and can be swapped without any effect on economic transactions, which take place without supposing any pre-existing sound social relationships between protagonists. Rather, competition determines the terms of trade, and individual choices are rational by maximizing profitability. Such a conception is favored

by Lacy *et al.* [9] when they hypothesize that sorghum varieties of Malian farmers are a “choice optimizing outputs” in the face of environmental variation.

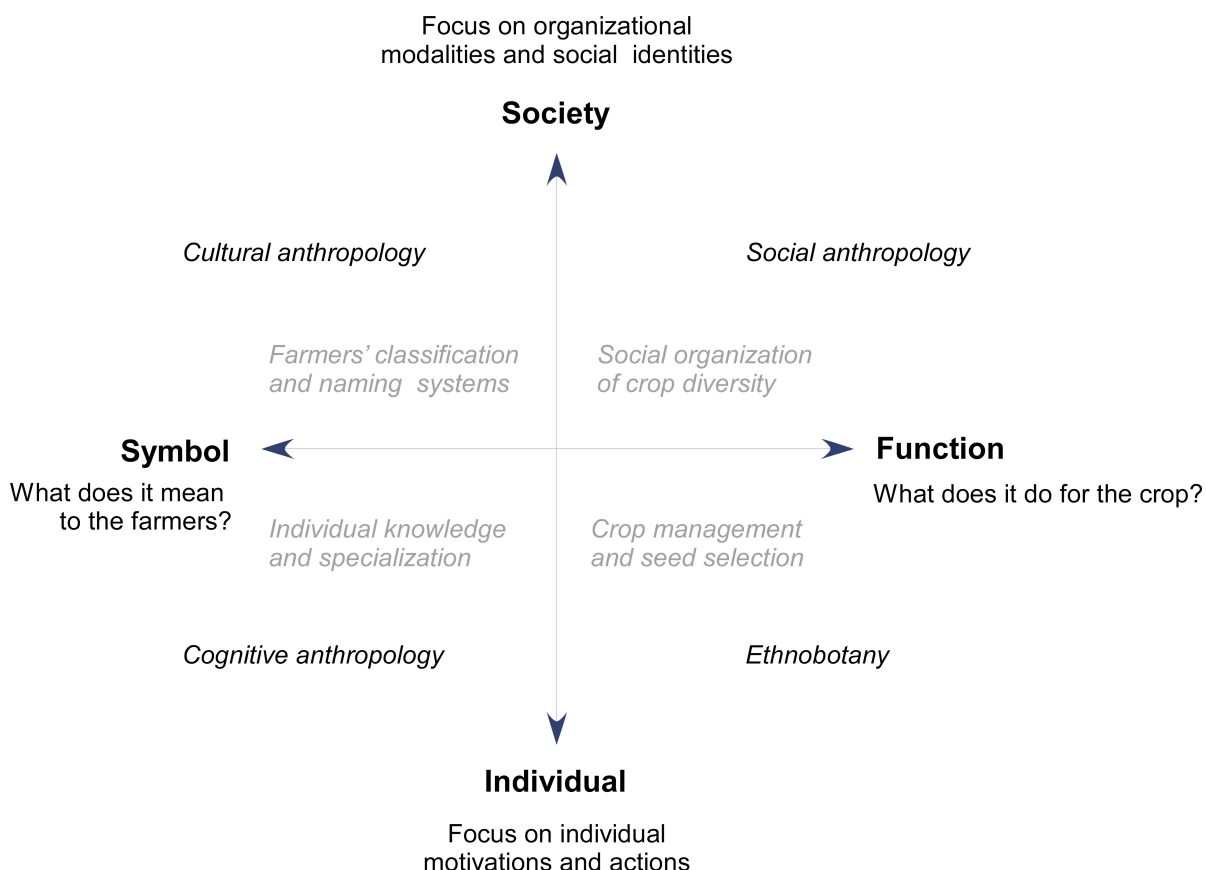
The atomistic view of the individual based approach is familiar in crop population genetics too. Indeed, crop populations are most often considered as an aggregate of individual plants that are interchangeable under the null hypothesis (e.g., permutation test). However, structure is also central in the discipline. Testing homogeneity among populations imposes recognizing factors that could allow their differentiation, through genetic isolation, genetic erosion, and differential selective pressures. A crucial point is that the recognition of populations to be tested, and the factors to be tested, are intrinsically related, and together determine sampling and testing procedures. If a factor is not isolated in the sampling protocol, its effect cannot be measured in terms of population structure.

As for wild plant population studies, sampling strategies adopted for cultivated populations have emphasized “natural” diversification factors, such as geographic distances and barriers, environmental variations with attendant natural selection. Concerning human factors, landrace sampling has placed emphasis on the effects of farmers’ practices, selection, both conscious and unconscious, management, and uses, (e.g., culinary preference, agronomic objectives, adaptation to soil and altitude, traditional knowledge) [10]. Implicitly or explicitly, farmers’ practices themselves have been associated with particular ethnic groups to explain crop genetic diversity [11] and justify *in situ* conservation.

The present article analyzes why an individual based approach is limiting in crop genetic studies and how social anthropology can contribute to correct this situation, with its classical framework for social organization, cultural transmission and differentiation processes. Observing that the transmission of seeds and the associated knowledge are affected by marriage and residence rules through inheritance and exchange, it describes how social factors organize crop genetic diversity *in situ*. Considering domesticated genetic resources as social objects, it proposes an integrative approach that can be used to design sampling strategies for different levels of sociological integration.

Figure 1 presents studies on the social component of crop genetic diversity in a diagram based on a double contrast. While farmers can be studied individually (as actors), or socially (comparative sociology and economy), the effect of the social component can be tackled from a functional perspective (“what does it do to the crop?”) or a symbolical perspective (“what does it mean for the farmer?”). The left side of the diagram includes the traditional fields of cognitive (lower left) and cultural (upper left) anthropology, while the right side encompasses the traditional fields of social anthropology (upper right) and ethnobotany (lower right). In the horizontal axis, the symbolical perspective considers farmers’ world perception, including folk taxonomy (bearing on humans, plants, animals, and environment), whereas the functional perspective places emphasis on what the observer can deduce on farmers’ practices referring to his/her own perception or theoretical background—e.g., functional analyses in ecology [12,13]. The vertical axis presents the contrast between individual based approaches, where emphasis is placed on farmer management and practices, and social based approaches, which emphasize social organization of farmers. In the latter case, the contribution of social anthropology is essential in considering rules that organize marriage, post marital residence, filiation, inheritance, and determine residential or linguistic endogamy. The fact that these rules organize exchanges within and among groups, including seed movements, justifies the specific contribution of social anthropology in the study of crop diversity.

Figure 1. Diagrammatic representation of the main fields of anthropology that study the social factors affecting crop diversity, with examples of specific areas (in grey), according to the focus on functional vs. symbolical analysis, using either individual or social based approaches.



Thus, Figure 1 situates this contribution of social anthropology when combined with crop population studies as compared to classic ethnobotanical approaches. Crop genetic diversity studies mostly belong to the right half although cognitive and cultural aspects have functional consequences on crop management. Most field studies fall in the lower right quarter, as they focus on functional analyses of individual farmers' practices and knowledge, attempting to deduce mechanisms of crop genetic diversification and measuring their relative effects at the field, farm, or village scale. Their protocols combine ethnobotanical methods and genetic analyses. Individuals can be further grouped into *a priori* categories (by gender, age, access to the market, economic status), or a typology resulting from multivariate analysis [14–18].

As far as PGR are concerned, the upper right quadrant has been much less explored. Indeed, few studies have used a social based approach with a sampling strategy addressing the effect of social organization on crop genetic diversity *in situ*, at different levels of social and geographical integration. Zimmerer [19] studied seed movements of potato and ulluco in the Peruvian Andes and showed how social and environmental factors can produce a multilevel geography of seed networks and seed uses. van Etten [20–22] followed a similar approach for maize in Mayan communities of Guatemala, adding an historical perspective to explain the observed geographic pattern of maize genetic diversity. Inspired by Granovetter's approach and emphasizing social embeddedness of transactions,

Badstue [23] considered seed exchanges under an economic perspective, focusing on the dynamics of maize diversity (conservation) and the introduction of improved varieties (innovation). She based her social approach on the concepts of social network, social capital, involving trust in seed transactions, and collective action. Perales *et al.* [24] and Brush and Perales [25] have tested the effects of cultural contrasts on crop management and resulting genetic differentiation. Here we propose to extend this approach and use the tools of social anthropology, involving residential and kinship organization [26], to investigate the effect of social factors on the dynamics of crop genetic diversity.

Can social embeddedness of seed exchanges improve our theoretical and empirical approach of *in situ* crop genetic diversity? Do farmers' social and linguistic identity as well as correlative social differentiation processes shape *in situ* crop genetic diversity by compartmentalizing seed exchange systems and limiting seed-mediated gene flow? Based on a review of maize and sorghum studies, and embracing a social anthropological approach, this article aims at showing that *in situ* crop genetic diversity *cannot* be fully understood without taking into account the social organization and the cultural identity of farmers. Following Granovetter's network methodology, our hypothesis considers that farmers' purposive actions are instead embedded in concrete, ongoing systems of social relations. Farmers are neither anonymous nor interchangeable as they are members of groups where persons have to trust each other when exchanging information and seeds that are so important for their subsistence [23].

Section 2 reviews *in situ* crop genetic studies. It focuses on the two most extensively studied cereal models, namely sorghum and maize, pointing out to the shortcomings of the $G \times E$ approach (G and E representing respectively genetic and environmental sources of variation) at different levels of spatial integration. Section 3 presents the basis of Granovetter's social network methodology and the anthropologist's concepts of cultural diversity. Human cultural identities result from historical processes implying social barriers, which do not necessarily involve isolation by distance. In consequence, crop diversity studies taking into account social identity of farmers may not fit well into the most common metapopulation models and more specific models are needed [27]. The explanatory models used in social anthropology for the organizational modalities of human societies and cultural diversity are presented, and their interest for crop genetic diversity studies is discussed. In the third section, crop varieties are considered as social objects, inherited and exchanged in the same way as other cultural traits (*i.e.*, rules for marriage, postmarital residential group, filiation, *etc.*). Many examples illustrate that traditional knowledge as well as seed exchange systems are embedded into social structure, favoring vertical transmission of both knowledge and PGR through a centripetal system. The overall discussion focuses on the social based approach that allows us to consider crop diversity organization as resulting not only from an interaction between genetic and environmental factors, $G \times E$, but from a three-way interaction $G \times E \times S$, where " S " stands for the social differentiation factors. Implications for *in situ* sampling strategy and participatory plant breeding are worked out.

These $G \times E$ and $G \times E \times S$ expressions are inspired from the usual practice of analysis of variance for variety trials. Basic analyses of population genetics work in the same way, comparing components of variation in crop populations at different levels. Whether considering quantitative traits variation or genetic diversity, the common point is that any particular factor must be specifically represented in the data structure to be correctly analyzed and interpreted. Thus, the $G \times E \times S$ expression highlights

the need to consider farmers' social organization as a specific factor in the collection of data and their analysis.

2. Overview of *in situ* Crop Genetic Diversity Studies

Among studies on *in situ* crop genetic diversity, the two most explored crop models are sorghum in Africa and maize in Mesoamerica. A number of studies have attempted to establish a link between farmers' management (involving folk classification, exchange and selection of seed) and the organization of genetic diversity as observed at different spatial scales (continental, national, regional and local). However, as far as we know, no published study has clearly taken into account the effect of farmers' social organization on crop genetic resources. So far, geographic and social factors have not been analyzed separately, and reference studies have mostly followed a $G \times E$ approach, where the effects of social organization have been blurred.

2.1. Sorghum Studies

Sorghum (*Sorghum bicolor* ssp. *bicolor*) is a major cereal, domesticated in Africa about 8,000 years ago [28], widely cultivated in the semi-arid tropics and the warm temperate regions of Africa, Asia, and America as a staple, fodder, and/or for the preparation of beer and syrup. Sorghum is wind-pollinated and predominantly autogamous. However, outcrossing is not negligible, with rates ranging from 5 to 40%, as estimated from biochemical and molecular markers [29-31].

The infraspecific classification of *Sorghum bicolor*, by Harlan and de Wet [32] and de Wet [33], recognizes three subspecies, subdivided into races. The concept of "race" was defined first by Anderson and Cutler [34] to classify morphological maize diversity as "a group of related individuals with enough characteristics in common to permit their recognition as a group". It constitutes for both sorghum [35] and maize [25] the unit of analysis of *in situ* crop diversity (although it is not a valid level of plant taxonomy). No interfertility barriers have been reported between sorghum infraspecific categories.

Sorghum bicolor ssp. *bicolor* regroups domesticated grain sorghums, including their five basic races (bicolor, guinea, caudatum, durra and kafir), with particular, although overlapping, geographic ranges, and ten hybrid races that combine characteristics of at least two of these basic races [32]. The morphological distinction of grain sorghum races is essentially based on spikelet morphology, correlated to panicle shape, and their unity would be related to the ethno-geography of the peoples who cultivated sorghum, as first proposed by de Wet and Huckabay [36].

Thus sorghum represents a rare case where the importance of social factors on genetic diversity is recognized in the foundation of a scientific classification. As stated by de Wet [33] "racial evolution of grain sorghums is closely associated with ethnological, ecological and geographical isolation. Variation within races is determined by conscious selection for particular uses, and to satisfy the individual fancies of cultivators" [33]. For example, according to Stemler *et al.* [37] and Harlan and Stemler [38], the race caudatum was associated with the speakers of the Chari-Nile languages in Africa and the race kafir was derived from early bicolor of northern Africa and carried south, primarily by Bantu speakers. In this picture, two social factors, differential selection and restricted seed exchanges

between ethnic or linguistic groups appear to have played an essential role in shaping the current morphological differentiation of sorghum races.

2.1.1. Sorghum Diversity at the Continental Scale

The hypothesis of de Wet and Huckabay [36], where the differentiation of African farmer languages is presented as a factor having shaped sorghum diversity across Africa, has never been tested, even though it has been mentioned by many authors [33,37-39]. Indeed, most studies at the continental scale have used the racial classification of Harlan and de Wet [32] as an interpretation grid, “race” being treated as a biological factor. Several studies have tested the consistency of this classification with morphological [40,41], biochemical [42] and molecular markers [43-48]. The racial classification was partly validated by morphological analyses, whereas biochemical and molecular markers have situated most of the genetic variation at the accession level, giving relatively little importance to races or the race $\times$ origin interaction in the organization of genetic diversity. The social identity of farmers was never taken into account in the sampling strategy, but considered as a discussion point supporting *a posteriori* the interpretation of data. For instance, from their RFLP study, Deu *et al.* [45] concluded that “the neighbour-joining analysis suggests two major geographic poles for sorghum evolution (...), [agreeing] with indications of ethnic divisions between northern (Nilotic and Sudanian languages) and southern Equatorial Africa (Bantu languages)”.

2.1.2. Sorghum Diversity at the National Scale

Despite the wide geographic range covered by national studies (Ethiopia, Eritrea, Sudan, Benin, Burkina Faso, Niger, Morocco, India), most of them, based on an essentially G $\times$ E approach, have produced strikingly similar pictures. “Regions” were only defined in geographical terms, and not characterized sociologically. Sampling was sometimes limited and/or done through *ex situ* collections [48,49], so the social identity could not be tested. In those studies using direct field sampling, few fields were selected in each region or locality. For instance, Djè *et al.* [50] and Medraoui *et al.* [51] used a hierarchical sampling design with five “regions” and four provinces, respectively, from north-western Morocco. Djè *et al.* [50] selected four fields within each region and, in each one, 15 inflorescences from randomly harvested individuals. The sampling strategy of Medraoui *et al.* [51] involved an average of 2.4 localities per province and 12 individuals per locality. Kayode *et al.* [52] used 72 “farmers’ varieties” randomly sampled (the number of farmers is not specified).

These studies show divergent patterns of geographical/environmental distribution for morphological and genetic diversity. Morphological diversity is mostly found among regions or distant fields [53-56]. Environmental adaptation is mostly observed through quantitative variation, affecting very few qualitative traits such as panicle compactness and shape [53,57,58]. By contrast, biochemical and genetic diversity is found essentially at the local level, and even at the field level [30,50-52,55,57-60]; its organization shows no environmental component, even when the geographic range of the studies include sharp altitudinal or precipitation gradients [29,48,61].

In most of these studies, the weak contribution of geographic distance to the organization of genetic diversity has been attributed to open and extensive seed exchanges among farmers, a fact which has not been verified in a systematic way. Furthermore, this interpretation is difficult to reconcile with

observations on the structure of morphological diversity at the regional and local levels. How can gene flow be significant at the region or country level, but not at the local scale or even field level, where it is much more likely? The contradiction is particularly visible in the successive studies of Djè *et al.* [30,50,55,56], who explained the wide morphological variation across fields and regions by limited seed exchanges and divergent selection practices among farmers, while their biochemical/molecular results led them to conclude on widespread seed exchanges, and to consider morphological differentiation as the direct effect of farmers' selection.

Widespread seed exchanges at the national level is further contradicted by the only study integrating an explicit ethnic component, carried out in Niger by Deu *et al.* [62]. This survey is also the most extensive national study, bearing on 484 accessions from 79 villages and taking into account environmental, ethnic as well as sorghum racial data. In each village, all local varieties listed by a representative group of farmers were sampled. The superposition of geographical and ethnic patterns causes "strong geographical $\times$ ethno-cultural interactions in the structure of crop genetic diversity" entailing a difficulty to distinguish between these factors. In any case, genetic differentiation was much lower between rainfall zones than between geographical regions $\times$ ethnic groups, indicating that historical patterns prevailed upon environmental conditions. Furthermore, a spatial correlation of genetic diversity was detected within 100 km, even after correcting for the "racial" component of sorghum organization, pointing to restricted seed exchanges among farmers, even within ethnic groups.

The few studies of sorghum genetic diversity carried out at the local level have focused on the fields, landraces, farmers' practices, and individual characteristics of farmers living in a same village (e.g., [14,15]), and have not addressed the effects of social structure on the organization of sorghum genetic diversity.

2.2. Maize Studies

2.2.1. Maize Diversity at the Continental Scale

Maize (*Zea mays* ssp. *mays*) is intimately related to Native American societies, and more particularly to the Mesoamerican cultural area. Archaeological, glottochronological and genetic data consistently point to a very ancient domestication of maize, 7,000 to 10,000 years ago, in Mexico [63-65]. The crop soon started to diffuse both northward and southward, around 4,000–3,000 BP, according to available macrobotanical remains [66,67], or much earlier (8,000 BP), according to microbotanical remains [66]. The earliest macrobotanical remains in southern South America are dated *ca.* 2,000 BP. Genetic studies of modern maize races indicate a progressive expansion of maize, with subsequent isolation by distance and a concomitant loss of diversity; the high correlation between geographical and genetic distances shows a strong geographical component in the organization of genetic diversity at the continental scale [68]. Genetic variation among races is limited to 7–8% of the total [68].

The very ancient history of maize cultivation has resulted in an impressive morphological and phenological diversity. In a first modern effort of classification, based on morphological as well as on genetic, cytological, agronomic characteristics and the geographical distribution, Wellhausen *et al.* [69] recognized 25 Mexican races, classified in four main racial groups, plus seven unclassified morphotypes that would have arisen through hybridization. The racial classification was extended and

systemized to more germplasm in Mexico as well as many other countries, using the methods of numerical taxonomy. This approach has been enriched with biochemical markers (isozymes, kernel components, secondary metabolites) and molecular markers, which were most useful in describing new races (for a total of 59 to 75 for Mexico) and their relations and in identifying racial complexes [70].

There are consistent indications of social factors affecting maize racial diversity. Hernández and Alanís [71] identified a link between a northern Mexican racial complex and the races from the southwestern USA, suggesting that the latter diversified as a result of northward migrations, through consequent geographic isolation and new selective pressures, related to new environments or new culinary and religious uses. Similarly, the isozyme analysis of the southwestern USA maize demonstrates “a correlation between the cultural-linguistic identity of the Indian tribes and the corn that they grow” [72]. Benz [73] observed an association between a dozen races and farmers speaking Otomanguean languages, this geographic coincidence indicating that both human linguistic and maize racial differentiation have resulted from closely related human cultural and crop biological histories. Going further along this line in an attempt to reconstruct the evolution of the crop from 7,000 to 2,500 BP, Bird [74] defined six maize-cultural regions by comparing the geographic distribution of races and racial complexes of maize to those of cultural traits of past civilizations at a continental scale.

2.2.2. Maize Diversity at Regional Scales

As a biological model, maize mostly differs from sorghum in its clearly allogamous breeding system. However, there are many common aspects between the two cereals, and most subregional diversity studies have produced strikingly similar results. Indeed, farmers are reported to exchange a small but not negligible proportion of their seeds, and they sow several landraces in a same field, allowing for frequent cross-pollination. As in sorghum, the weak regional organization of maize neutral genetic diversity, considered by most authors as the result of an open seed system, contrasts with a marked morphological differentiation [5,24,75-79]. Some of the variation in quantitative traits is attributed to environmental adaptation, particularly in relation to altitude, but most morphological differentiation has been attributed to the phenotypic selection exerted by farmers. As in sorghum, seed lots are very limited in size (1–2% of the harvested ears being used for seed), and selection is mostly exerted on characteristics of harvested ears and their kernels, but other traits are genetically associated [5,80,81]. Therefore, the maintenance of landraces should imply a considerable level of consensus both among and within the communities exchanging their seeds. In fact, the ideotypes shaping the outcome of maize selection vary among ethnolinguistic groups [24,79].

Brush and Perales [25] tested the effect of social origin of farmers on maize population across Chiapas landscapes, comparing practices of *mestizos*, Spanish speaking people who identify to the Mexican national culture, and indigenous people, primarily speakers of one of several Mayan languages. They put forward the recurrent differences between the two groups concerning the economic orientation (commercial vs. subsistence), races of maize grown, predominance of local vs. improved varieties, age of seed lots, seed color, as well as the seed exchange systems. Seed exchanges are more within-community oriented for indigenous people than for *mestizos*. Bellon and Brush [80] suggested that maize diversity is also influenced by social organization, notably land fragmentation, and the *ejido* rule favoring non-partible inheritance of land and prohibition against selling and renting

lands. These case studies point out the importance of the social context, as many practices can be interpreted in terms of cultural attributes of the considered social groups affecting crop diversity.

Despite the relative consensus of most research teams, the picture of maize diversity mostly driven by small but significant seed exchange in traditional systems may still look unsatisfactory on several aspects. Thus, a professional breeder might be surprised by the presumed efficiency of mass selection, focused on a few traits, maintaining phenotypically and phenologically well differentiated landraces of an outcrossing crop in an open system (while seed companies have to grow and screen several generations to breed a new cultivar, to be propagated under highly controlled isolation). In addition, as for sorghum, if seed exchange exists at the regional scale, the reason why genetic differentiation is higher at the local scale [77] than at the regional level remains unclear.

Interestingly, a few studies have challenged the model of open maize genetic system. Dyer and Taylor [82] underlined that case studies have often been incomplete and biased because they were designed to explain maize diversity on individual farms, neglecting farmers' practices after introduction, seed demography across farms and its diffusion through seed systems. For example, most introduced seed is replaced after its first year, at about twice the rate for local seed. According to their country-level dataset for Mexico and their demographic model, seed diffusion varies widely, with 1% of lots multiplied 10-fold in 5 years and 60% not diffusing at all. Exchange rates reported for Cuizalapa [75] are usual for western Mexico, but up to 10 times higher than in other localities. Saved seed acquired locally diffuses more than expected, while new introduced seed does not diffuse so much. Dyer and Taylor highlight that maize diversity is maintained at the locality level, not at the farm level, the former being the unintended result of individual farmers' actions.

Van Etten [21] underlined that studies on regional distribution of maize diversity had not taken into account geography and history, while archaeology suggested radically different spatial distributions in pre-Columbian and early colonial times. His revision of the central Guatemalan history led him to the hypothesis that seed dynamics might have followed regional interactions, concentrated in catastrophic events and massive migrations, and trade relations, embedded in a political economy that is narrow in its geographical scope, because it necessarily reflects the ties between communities. By contrast, most daily social interactions were very local in scope, allowing for the development of maize diversity under geographic isolation. Van Etten *et al.* [20] tested part of these hypotheses in 13 localities from four townships of Chimaltenango (Guatemala), using SSR (single sequence repeats) markers and morphological characterization. It is interesting to note that people in these townships speak different dialects of a same language [83]. Cluster analysis of SSR data showed a clear spatial genetic structure, as clusters mostly corresponded to localities and were further associated by township. In two cases, similar germplasm was found in different townships, indicating some regional seed exchange. A high isotropic spatial autocorrelation indicated isolation by small distances within localities (less than 8 km), probably caused by a much higher exchange rate among close neighbors (let us note the similarity with Bellon *et al.* [84] study reporting 92% of seed lot exchanges within 10 km in Mexico). At a wider scale, between townships, geographical distance does no longer constitute the main factor, and seed movements have followed another logic, combining environmental (altitude) and/or historical constraints, as well as relations with traders (centrality of provincial market, consumer acceptance, *etc.*). According to Van Etten *et al.* [20] low regional genetic differentiation, as found by his group in

Guatemala and by the other teams in Mexico, does not imply currently high levels of gene flow, and could be explained by intensive gene flow in the past. This argument is similar to the interpretation of Deu *et al.* [62] about the historical determinants of the distribution of sorghum genetic diversity in Niger.

3. Farmer Social Organization and Cultural Diversity

Our review of the sorghum and maize cases shows that most agrobiodiversity studies have placed emphasis on the environment and reproductive biology as organizing factors, social factors being considered as a particular component of the crops' general environment. Indeed, they were most often restricted to farmer practices, whose impact on the crop can readily be integrated in an individual based approach (falling in the lower right quarter of Figure 1). As such, the cultural identity of farmers, including their social organization (upper right quarter of the figure), and its interaction with crop genetic diversity have remained understudied. Before discussing this interaction, we shall recapitulate Granovetter's views on economic transactions and summarize basic explanatory models used in social anthropology to explain cultural diversity.

3.1. Social Embeddedness and the Orientation of Exchanges

Many studies on social networks show that individual behaviors cannot be analyzed without referring to the concrete network of social relations. A parallel can be drawn with the approach promoted since the 1970's in economics by Granovetter. Following the development of the economic anthropology after Polanyi [85], he has changed the way of thinking about the modern economy by focusing analyses not on individuals, but on *relations*, thus calling into question the premises of the classical theory according to which transactions result from rational choices of individuals considered as independent. Instead, Granovetter shows that, in modern societies, economy is embedded into social relations that are to be considered in the analyses of exchanges. In fact, economy is not a separate domain of sociology.

As mentioned by Laville [86], embeddedness is observed at two levels: the first one, interpersonal, refers to the concrete relations between individuals, and the second one, structural, depends on the characteristics of the network itself, which can be coupled or decoupled [87]. A *coupled network* is one where all individuals are linked to all others by many relations, and a *decoupled network* is one where two or more primary networks are linked together by weak ties. Presence of weak ties between primary networks favors the diffusion of information. Granovetter [88] points out the "strength of weak ties" resulting from their role as a "bridge" between primary networks. Conversely, the absence of bridges between two primary networks means that they are strictly decoupled and that the information available in the first one cannot diffuse to the second. In such a case, the exchange system is necessarily within-group oriented.

Such a methodological approach fits quite well with the anthropological analyses of social differentiation that imply decoupled networks. A good illustration is that of the linguistic differentiation of human communities, supposing that spatial isolation or social barriers are maintained over generations. Besides, other organizational modalities of human communities, described by social anthropology, may also impact the orientation of the exchange systems.

3.2. *The Anthropologist's Concepts of Cultural Diversity*

Social organization refers to the internal differentiation of human society, considering that society is not a homogenous mass or a simple collection of individuals. Many levels of sociological integration can be considered here: family, lineage, village or residential group, tribe, sub-tribe, linguistic groups. These levels correspond to different sets of cultural traits. The membership to a social unit can be inherited (descent groups) or result from recruitment (e.g., professional activities).

The correlative concept of social identity is a means of categorizing oneself and others in an organizational sense. As stated by Longley [89], “the we/them dichotomy is based upon the implicit or explicit contrasts between one’s own group and that of others”, implying the maintenance of boundaries through social processes of exclusion and incorporation [90]. As a social group is more than the sum of its individual members, its characterization cannot be based on that of individual behaviors and choices. Organizational modalities of collective life have been usually described through affiliation, residence, and marriage rules. Functionally combined, these rules support the social identity of human groups.

3.2.1. Organizational Modalities of Human Societies

The anthropological concept of consanguinity refers to members that are true or putative descendants from a common ancestor. Affiliation can be patrilineal (common in African, Circum-Mediterranean, and East Eurasian societies), matrilineal (Insular Pacific and North America) or a combination of both (America) [91]. The anthropological concept of consanguinity cannot be assimilated to the biological concept of consanguinity. It is a cultural attribute defining the membership to the lineage or clan. The impact of the differentiation process through affiliation on human collective life is further strengthened by marriage rules. Indeed, lineage exogamy implies that a member of one lineage cannot marry another member of the same lineage. Thus, lineage affiliation practically divides the human’s world in two fundamental categories: the one where he/she cannot find a mate (same lineage) and the second where he/she can (different lineage). A third organizational modality of collective life is the postmarital residence or transfer of residence of man or woman. The most common form is patrilocal residence, where the woman comes to live at the husband’s location.

The composition of the residential group is determined by the combination of affiliation, marriage and post marital residence rules. Obviously, spatial distribution of differentiated groups is an integral part of the social process. It is common that members from a same lineage are distributed in multiple residential groups and can get marriage within (residential endogamy) or out of their own residential group (residential exogamy). The residential endogamy rate indicates how open (or closed) is the between-groups social relation network, but this rate must be related to the considered social/spatial scale. Indeed, the endogamy rate may increase with the level considered (residential group, tribe, or linguistic group). The maximal endogamy rate indicates the level of sociological integration where the process of exclusion and incorporation maximizes centripetal relations and exchanges through marriage.

The basic assumption underlying cross-cultural research is that “the elements of any culture tend over time to become functionally integrated or reciprocally adjusted to one other” [91]. Functional analyses focus on combined organizational modalities, for instance, correlating marital residence to the

female contribution to subsistence [92], or studying the social evolution from matrilineal cultures that become patrilineal when they acquire cattle [93].

Data sets including cultural traits allow phylogenetic approaches that are similar to those used in biology even though the rhythms and modalities in the transmission of cultural and biological traits are not the same [94,95]. The analogy also concerns linguistic differentiation as an isolation process, linguistic divergence occurring after speech communities have divided “in a similar process to speciation among isolated biological populations” [96,97]. Geographic isolation is a powerful driver of linguistic differentiation, as exemplified by the evolution of Austronesian languages, spoken in islands. On the other hand, it cannot explain that of bantu languages that “are spoken across the continental land mass of sub-Saharan Africa” [96]. Indeed, among the 6,809 languages around the world, 2,058 (30%) are spoken in Africa [98], including Bantu languages. In this latter case, as highlighted by Holden [96], “social factors rather than geographical barriers must have maintained distinct speech communities”. Thus, the island explanatory model is not sufficient to explain cultural and linguistic diversity, just as it is insufficient to explain crop genetic diversity.

3.2.2. Cultural Diversity Explanatory Models

Cultural diversity is closely related to mechanisms of cultural transmission, which refer to the process of social reproduction in which a culture’s technology, knowledge, behavior, language, and beliefs are communicated and acquired [94]. Hewlett *et al.* [99] revised the three basic models developed to explain cultural diversity. The *cultural diffusion model* assumes that cultural traits diffuse between groups (horizontal transmission). Social groups in closer geographic proximity will share more cultural traits because they should interact more regularly. In this case, the social distance should be correlated with geographical distance. In contrast, the *demic diffusion model* emphasizes the vertical transmission of cultural traits (“semes” in Hewlett’s terminology), based on parent-to-child transmission, and strengthened by the trait frequency in the group [94]. According to this model, which appears very similar to genetic transmission, cultural traits diffuse together with group members. Thus, they tend to be reproduced within the group over generations, favoring social differentiation. This conservative model should be crucial in crop genetic studies considering crop varieties as cultural objects. The third one is the *local adaptation model*, or cultural ecology theory of Steward [100], hypothesizing a correlation between environmental conditions, technology and social organization. Accordingly, social differentiation cannot be explained in this model without considering environmental constraints and technical systems.

In a combined analysis of 42 cultural traits, genetic (26 loci), linguistic and geographic distance data from 36 African ethnic groups, Hewlett *et al.* (2002) showed that demic diffusion explains the transmission of 20 cultural traits, especially those related to kinship, family and organizational modalities of collective life, and shifting cultivation. These traits are very conservative by comparison with others and their distribution is “due to expansion of particular people rather than cultural diffusion or local adaptation”. Cultural diffusion explains the distribution of 12 semes related to house construction and postpartum sex taboos. Only four semes are linked to local adaptation, and they appear to be variations of demically transmitted traits [99]. The clear dominance of vertical transmission over the two other models is also expressed in the general convergence between human

genetic distances, linguistic distances, and cultural distances. As stated by Hewlett *et al.* [99], cultural traits and genes coincide “because both are affected by the conservatism of vertical transmission”.

Thus we propose to consider domesticated genetic resources as social objects, whose transmission is governed by a combination of social and biological processes. As a working hypothesis, we state that if seeds circulation is affected by marriage and residence rules, then they are submitted to the same vertical transmission processes that govern social reproduction. The resulting genetic structure of crop genetic resources will depend on the interactions between this social process (defining rules of residence and transmission involving seed exchanges) and the biological processes of local adaptation and spontaneous genetic exchange, mostly through pollen-mediated gene flow. Verticality in genetic transmission will be associated with seed saving, within-group-oriented seed exchanges (influenced by the rate of residential endogamy), clonal reproduction, and plant autogamy, whereas horizontality will be associated with among-groups seed exchanges (residential exogamy, local and national seed markets), plant allogamy and wide pollen dispersal. In this view, social and biological factors must be considered simultaneously and at the same level in the analyses, using a common theoretical and methodological multidisciplinary framework.

4. Mechanisms Leading to Social Organization of Crop Genetic Diversity

Among the drivers of crop genetic differentiation, only mutation can be overlooked as far as the interaction of social and biological factors is concerned. Genetic drift is affected indirectly, through the size of the plant (sub) populations managed at different stages of cultivation, while selection and migration are likely to be directly affected by the organization of agricultural societies. Selection will be affected mostly through crop management and uses, therefore it will depend on the distribution of knowledge, practices and preferences among and within human groups. Migration will be affected by any barrier to seed exchanges related to social differentiation. Human effects on both selection and migration must be considered at all levels of sociological integration.

4.1. Traditional Knowledge, Perception of Crop Diversity and Conservative Selection

Analyses of ethnobotanical knowledge reveal the dominance of vertical transmission. Thus, comparing vertical, horizontal and oblique transmission, Reyes- García *et al.* [101] found no evidence of horizontal transmission of ethnobotanical knowledge in the Tsimane from Amazonia. Lozada *et al.* [102] underlined the role of the family in a rural community of Patagonia, demonstrating the essentially vertical transmission of wild plant knowledge, while Ohmagari *et al.* [103] estimated that 80% of indigenous knowledge of Cree communities (93 items or skills were analyzed) are acquired from parents and grandparents.

Hewlett and Cavalli-Sforza [104] present a remarkable study on foraging techniques among Aka Pygmies, associated with Bokola villagers who live in the same section of the village. This situation provides a favorable context to illustrate the verticality of knowledge transmission and the mechanisms of ethnic isolation. Analyzing the cultural transmission of 50 foraging skills among 72 Aka individuals, Hewlett and Cavalli-Sforza [104] showed that vertical (parent to child) transmission is by far the most important mechanism, accounting for 86.9% of the cases studied. Correlatively, Bokola villagers are poor contributors in this transmission (1.6%). Thus, despite the close geographic

proximity allowing for daily interactions between Aka and Bokola, the latter do not contribute significantly to the Aka knowledge. The verticality of the knowledge transmission favors the cultural differentiation between the two groups, as stated by Cavalli-Sforza and Feldman [94]. The cultural transmission concerning crop diversity should follow the same mechanisms, as agriculture and seed selection are family domains.

Intercultural comparisons on perception of crop genetic diversity are difficult and very few studies have addressed this subject at this level. In their analysis of 16 species among 29 communities in eight countries, Jarvis *et al.* [105] observed great differences among communities from the same country. For a better comparison, we have selected from their data pairs of communities settled in similar environments. Thus, in the Amazon lowlands of Peru, farmers from the Aguaytia valley manage intraspecific cassava variability with 39 named categories while their neighbors of the Pichis-Pachitea valley, distant of 80 km, use twice this number, with 89 categories. Similarly, in the Ethiopian highlands, the Ankober manage five categories for barley, while the Tarmaber manage 12, only 52 km further. In Burkina Faso, the Pobe, as compared to the Tougouri distant of 207 km, manage twice the number of categories for pearl millet (18 vs. 9) as well as for sorghum (27 vs. 15). In Mexico, the Yaxcaba and Ichmul distant of only 47 km, manage similar numbers of categories for beans (7 and 8 respectively), chili (4 and 5) and squash (3), but not for maize (14 and 9). Such figures not only point to the contribution of cognitive and cultural processes in crop diversity distribution or classification, but also to the fact that, conversely, this distribution reflects social differentiation between communities (but see potential effect of economic orientation [25]).

If the biological potential for differentiation is roughly constant within a given crop species, understanding the operation of farmer classification becomes essential to interpret variation among nomenclatural and classification systems used for on-farm management. An intercultural comparison of crop genetic diversity obliges us to adopt a new interdisciplinary approach. Biological variability, indeed, is usually considered as a cause and the number of categories (or farmer-named varieties) as a result. However, if farmer crop selection is based on prerequisite “mental images” with a particular place in the classification system, the cultural process appears to be first and the biological existence of the distinguished morphotypes a result. In other words, farmer categories have to exist in farmers’ minds before they exist in their fields. In any case, there is necessarily a cultural consensus [106] on crop classification to ensure both the transmission of knowledge over generations and the communication between farmers.

Studies on farmers’ traditional agricultural knowledge or on their ability to distinguish and to name varieties have been mainly carried out at the village level within a same linguistic group, emphasizing on individual-level variations ([107], for an overview). James Boster, a pioneer in this domain, has shown how the cognitive aspect is influencing crop selection with reference to the intraspecific classification system: “crops show the effect of the cultivator’s eye as well as hand. [...] perceptual distinctiveness is a necessary condition for cultivar maintenance; cultivars must be distinguishable before they can be selected...” [108]. Thus, the “mental image” of the variety is just as necessary for farmer selection as is the *ideotype* for professional breeding. Moreover, perceptual distinctiveness and classification systems also constitute a key component of the adoption process. Selection and adoption proceed similarly. Identification based on an existing categorization is needed to apply selection and a “new” variety is considered as such and adopted only if it can be distinguished from already known

varieties. In both cases, the cultural intraspecific classification system works as a conceptual frame of reference through identification (to select the same) or distinction (to adopt the new). In Cuzalapa (Mexico), farmers' seed selection practices essentially aim at maintaining the phenotypic integrity of their traditional maize cultivars [81]. In a more precise study, Benz *et al.* [79] have shown how Tzeltal and Tzotzil farmers maintain separate maize populations through perceptual distinctiveness, each ethno-linguistic group being able to recognize its own landraces from those of the other group. In Guyana, Elias *et al.* [17] described how the Makushi care for spontaneous cassava seedlings, select and assign them to their previous categories. Those seedlings that are too distinct from existing varieties do not receive specific new names. Duputié *et al.* [109] reported a similar practice among the Wayãmpi of French Guiana, and showed that off-type phenotypes are counter-selected in subsequent vegetative cycles.

When managing to reproduce its categories at each cultivation cycle, first selecting the seed genitors, the farmer is confronted to the contradiction between the biological continuum of individual variation and the radical discontinuity of her/his cultural classification. This contradiction depends partly on the plant reproduction system. Indeed, in their wide comparison of nomenclature systems across species, cultures, and countries, Jarvis *et al.* [105] show that farmers use more detailed classifications for clonally reproduced crops (33.4 terms) than for inbreeders (12.8 terms), partial outbreeders (10.9 terms) or outbreeders (9.3 terms).

Many anthropologists, following Berlin's work [110-112], have compared folk classification, internal to the studied society, with the western scientific nomenclature as an external reference. Others, like Martin [113], have argued against such analyses, underlining the incongruity of the comparison, which finally consists in detecting in folk classifications the hierarchical, Linnean or varietal, system developed in western cultures. Indeed, the reference to an external system, used in a very different social and cultural context (where scientists themselves should be considered as a social group), neglects the essential link of the folk classification to the group involved, *i.e.*, the fact that the objects only exist as such because they take a place into a culturally defined system of oppositions, which makes sense to the group. Thus, a much more meaningful approach would pay attention to the coherence of the classificatory series inside a society itself by paying equal attention to their use in different domains (which leads us to the upper left quadrant of Figure 1), for example by relating the identity of crop categories to the social classification of the farmers themselves. A common case is when landraces from other groups are recognized and named as such. Thus, Mexican farmer communities distinguish their maize landraces from those of other communities, calling their germplasm as "our maize", and they maintain its morphological distinctiveness [24,79]. In some cases, farmers may consider differences in the reproduction process, even though they do not translate into genetic, morphological or agronomical differences. Keralan Farmers (southern India) perceive, name, evaluate and manage distinctively coconut hybrids that are genetically and morphologically identical. They value better those spontaneous hybrids that they identify in their fields, than those obtained through technically controlled pollinations in experimental stations [114]. Haudricourt [115] provides an even more striking example where he describes a parallel between the social classification of a New Caledonian society into patrilineal clans and the categorization of yam clones. With 72 categories, there are as many clones of yam as there are clans. At the rite of enthronement of the leader of a new

clan, a new clone is taken from the fallows. The sexual reproduction guarantees the originality of this material associated to the new clan.

This brief analysis of the relationship between social differentiation, cultural transmission, and perception of crop diversity, with consequences on the processes of selection and adaptation of biological materials, shows that the cultural process is causal in shaping intraspecific morphological diversity. Accordingly, cultural and linguistic surveys have to precede the definition of the strategy for crop germplasm sampling.

4.2. Seed Exchange Embedded into the Social System and Vertical Transmission

If crop categories are social objects, their transmission follows the rules corresponding to each particular level of sociological integration, so their differentiation not only results from differential perception of the crop categories, but also from the process of their vertical transmission within the group. While the former affects the crop diversity through individual farmers' selection, the latter affects migration, mainly by limiting seed-mediated gene flow among farmer groups. Thus, the perception of group membership *per se* (social identity) becomes central in the analysis of crop genetic diversity.

4.2.1. Basic Levels of Sociological Integration

At the individual farm level, the main parameter limiting seed-mediated gene flow is the seed saving rate. Several studies show that farmers usually produce 75–80% (range between 58% and 99%) of their seeds on their own farm, which of course strongly reduces the proportion of acquired seeds (Table 1). Moreover, these on-farm studies show that seeds are more often acquired from within the community than outside, or from the “informal” as compared to the “formal” (commercial) sector [84,116,117]. Unfortunately, these in-out typologies rarely consider characterizing the social network and thus ignore the possibility that the “informal” sector can be itself formally structured from an anthropological point of view. Indeed, the seed circulation system logically operates according to the prevailing exchange system *within a given social organization* [118], so farmers must be characterized sociologically to understand the structure and functioning of the seed system.

Table 1. Sources of seeds in traditional agriculture.

Country	Crop	Farmer saved seeds	Family and neighbourhood	Total	References
Burkina Faso	Sorghum	70%–99%	NA	70%–99%	[119]
Costa Rica	Maize	79%	19%	98%	[117]
Costa Rica	Beans	58%	21%	79%	[117]
Guatemala	Maize	59%	31%	90%	[22]
Honduras	Maize	75%	13%	88%	[117]
Honduras	Beans	79%	15%	94%	[117]
Mexico	Maize	90%	9%	99%	[120,121]
Mexico	Maize	58%	34%	92%	[75]
Mexico	Maize	79%	NA	79%	[5]
Mexico	Maize	NA	87%	87%	[76]

Table 1. Cont.

Country	Crop	Farmer saved seeds	Family and neighbourhood	Total	References
Mexico	Maize	NA	95%	95%	[79]
Mexico	Maize (Tzeltal)	84%	9%	93%	[24]
Mexico	Maize (Tzotzil)	87%	10%	97%	[24]
Mexico	Maize	76%	11% *	87%	[23]
Mexico	Maize	76%	21%	97%	[84]
Nicaragua	Maize	81%	12%	93%	[117]
Nicaragua	Beans	72%	14%	86%	[117]
Peru	Potatoes/ulluco	91%	6%	97%	[19]
Sierra Leone	Rice	70%	NA	70%	[89]

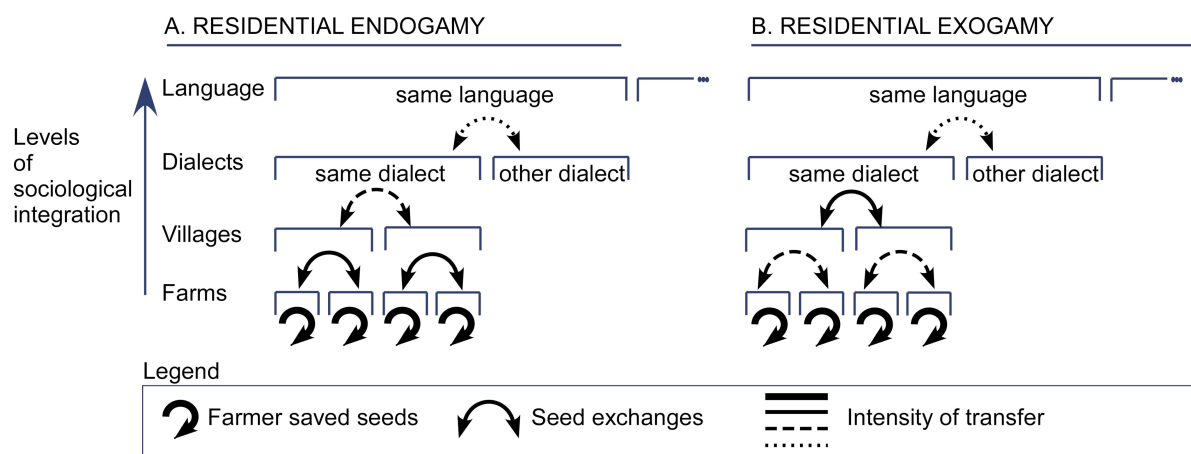
* This percentage refers only to family members that made up 47.5% of seed providers.

Beyond the individual farm level, a few studies have shown the interest of considering the social organization, characterizing the protagonists and the relations they maintain beyond the agricultural domain. The fact that exchanged seeds are mainly obtained through trusted persons, members of the same family, the same village or the same community has been documented for maize in Mesoamerica [121,22]; Andean tubers in Peru [19], sorghum in Ethiopia [122]; and rice in Gambia [116]. Badstue *et al.* [121] characterize more precisely the persons from whom the 10.3% off-farm seeds are obtained in a Mexican community: family members (46.5%), *compadres* (4.7%), neighbors (1.3%), friends (7.2%) and acquaintance (29.6%, a category including sharecropper relations and owners of neighboring fields). Where several ethnic groups live in the same village, the seed exchanges are preferentially (up to 90%) concluded with members of the same ethnic group [117,119]. In the end, seeds are rarely supplied by outsiders. In the cases studied by Badstue [121] only 1% of the seeds come from such sources. Badstue *et al.* [23] describe more precisely why informal seed systems are mostly based on traditional social alliance and family relations. In their case study, farmers clearly distinguish maize seeds for planting and grain for consumption. The quantity of seed involved in farmer-to-farmer transactions is “often quite small”. However, when farmers have to replace lost seed, seed quality can be neither guaranteed nor tested (seed is not “transparent”), and “farmers depend largely on the quality of the information offered by the seed provider” [23]. Thus, trusted transactions must be already embedded into a concrete social network, interpersonal relations being experienced inside as well as outside the agricultural domains, which cannot be studied as a separate sector, but as a component of a whole.

Another interesting example of the embeddedness of seed exchanges in the social organization is provided by the observations of Longley [89] in Sierra Leone, showing how “the geographical patterns of marriage also map the pathways along which seed rice varieties travel”. The Limba tend to marry individuals from the local area, whereas Susu marriage networks are geographically more extensive. As a result, Susu farmers acquire larger proportions of non self-saved rice seed from outside their own village as compared to the Limba. Even so, friends and family are still favored sources as compared to traders. This example introduces the importance of residential endogamy as a social factor affecting the orientation of the seed exchange system and, by the way, the geographic organization of crop genetic diversity. Figure 2 shows that, in the case of a high residential endogamy rate (marriage

concluded within the same village), seeds obtained from the in-law family originate from the same residential group, favoring genetic differentiation among villages. Conversely, a low residential endogamy rate would induce an out-of-village-oriented seed exchange, and the social network structure would be necessarily “decoupled” [87]. In the latter case, crop genetic differentiation can be expected to be lower among villages than within villages. Thus, the seed system must not be analyzed only in terms of geographic distance, but also through organizational modalities of human collective life, basically, filiation, residence, marriage and inheritance rules.

Figure 2. Expected effects of residential endogamy on the orientation of seed exchanges and spatial distribution of crop genetic diversity. Pattern (A): Baka communities (Cameroon). Residential endogamy (husband and wife are from the same village): seeds are obtained from the in-law family which is from the same village; this favors genetic differentiation among villages; Pattern (B): Nzimo communities (Cameroon). Residential exogamy: (husband and wife are from different villages): seed exchanges are oriented outwards, which results in lower genetic differentiation among villages. Patterns A and B produce different structures of crop metapopulations, affecting crop genetic organization at different levels of sociological integration.

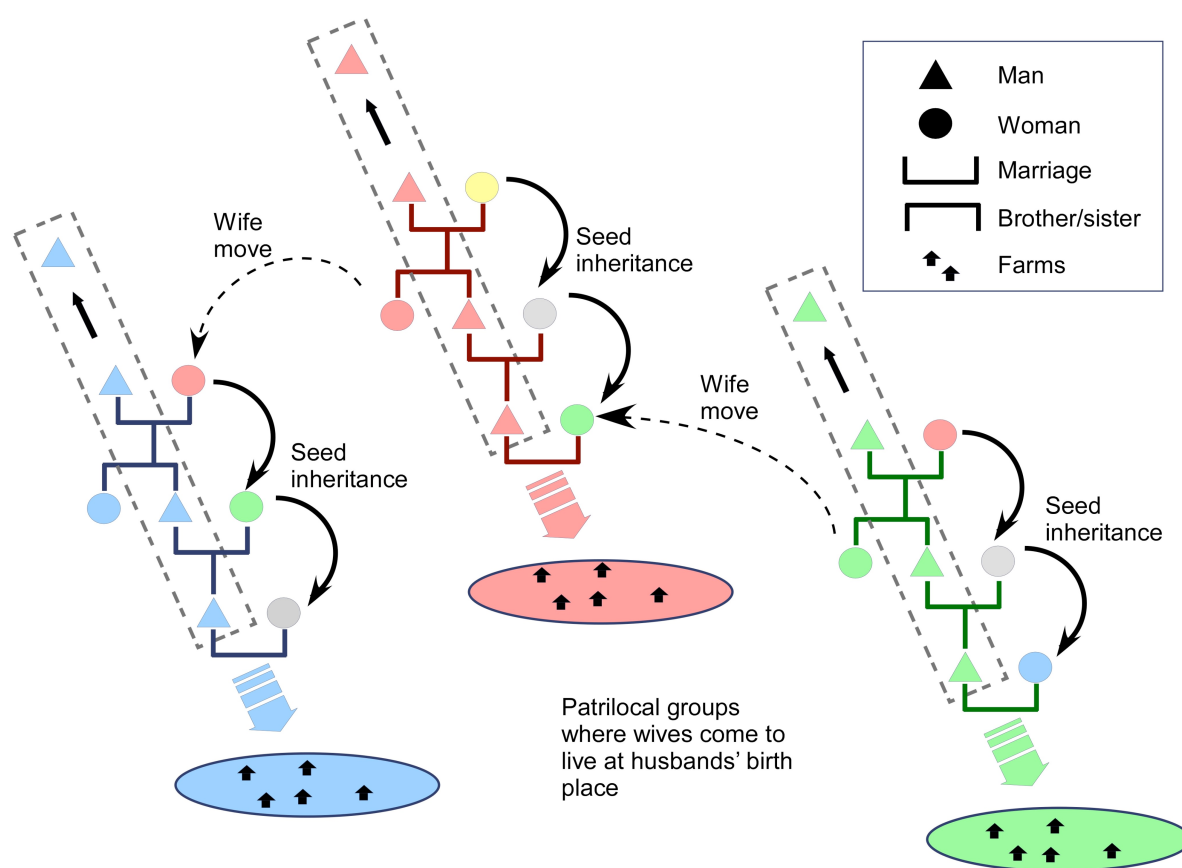


Affiliation rules combined with residential rules and gender role affect the geographic organization of crop genetic diversity. Where crop management is a female domain, matrilineal residence will allow seeds to stay in the village, while patrilineal residence will favor seed diffusion among villages, through women mobility. The latter trend is reinforced when the residential group is constituted by one lineage (localized patrilineage, e.g., Nzimo, Cameroon), implying marriage out of the residential group. Indeed, as patrilineal descent groups are exogamous, marriages have to be concluded with women from other villages. In the other case, if the village is constituted of several lineages or clans, residential endogamy is possible and part of the seed exchanges, through in-law family relations, can be concluded within the village.

The latter analysis shows that seed systems can be both geographically open, which is always true up to some level, and socially closed with marriage and kinship ties or other social relations linking providers and recipients, spatially distant or not. Such variation is necessarily expressed in space [19,20,22].

Figure 3 presents an example of the combined effects of filiation, post-marital residence and seed inheritance on the spatial structure of crop genetic diversity. This example shows their importance for both the definition of crop genetic diversity sampling strategies and the interpretations of studies where social relations have not been characterized prior to sampling.

Figure 3. Vertical transmission of seeds in Muthambi communities on Mount Kenya. Colors represent different clans. Those communities are characterized by patrilineal filiation i.e. men live in the clan they were born and wives leave their own clan to join that of their husband when they get married. Wives establish their first fields with sorghum seeds traditionally obtained from their mother-in-law. It follows that the founding germplasm remains in the same residential group over generations, thus contributing genetic adaptation to the local environment.



4.2.2. Higher Levels of Sociological Integration

The vertical transmission of crop genetic diversity is even more prevalent at higher sociological levels, as the seed system is necessarily more within-oriented with increasing sociological integration level, as shown in Figure 2. Thus, crop genetic diversity and its organization may be interpreted in the light of cultural transmission theories for cultural traits, by considering farmer varieties as cultural objects. The crop genetic sampling strategy must then be based on the cultural identity of farmers, beyond the circle of personal relationships.

The importance of the higher levels of farmer social differentiation (beyond families and residential groups) was first realized empirically by plant breeders, when it appeared to be a limiting factor for

improved seed diffusion. Indeed, social differences among communities and ethnic boundaries can slow down the diffusion process and reduce the general impact of breeding programs [117,123]. Among these social differences, linguistic differentiation is essential. There is no seed exchange without information exchange and communication is possible only if provider and recipient speak the same language. Inter-groups exchange could be common between allied villages speaking the same language, and rare or inexistent between two differentiated linguistic groups. Of course, vehicular language can be used to link two distinct vernacular linguistic groups, but the fact that vernacular languages have differentiated the two groups remains an important marker of farmers' social organization resulting from historical processes and, thereby, an important factor structuring exchanges and crop genetic diversity. As noted by Harlan and Stemler [38], "correspondence between the distribution of the basic races of sorghum and the distribution of the major linguistic groups of indigenous Africans may be not fortuitous. Guinea is a sorghum of the Niger-Congo family, kafir a Bantu sorghum. Durra follows the Afro-Asian family fairly closely, and caudatum seems to be associated with the Chari-Nile family of languages". According to the same authors, more detailed study of minor variations in sorghum may prove this correspondence revealing with respect to human history and ethnic isolation.

The relation between linguistic community and germplasm exchange is bidirectional. Studying rice cultivar names in Gambia, Nuijten and Almekinders [116] observed that their uniformity reflects the intensity of seed exchange. "When there is limited inter-village seed exchange, a variety is likely to end up with different names in different villages. In the case of multiple seed exchanges of the same variety between two villages, (...) that variety may obtain the same name in both villages". Thus, farmer variety names are exchanged as other language elements. Again, we observe how crop germplasm is treated in the same way as other cultural objects.

Very interestingly, this principle can be applied at different scales and levels of sociological integration. We come here to the basic principle of the method of historical linguistics: the similitude of words used reflects the intensity of past contacts and the importance of the common historical heritage, which allows to develop a strong parallel between the vertical transmission of words (inheritance within speech communities) and the vertical transmission of crop germplasm, both phenomena concurring to the organization of human societies and their crop genetic resources. Applying phylogenetic methods to Bantu languages, Holden [96] confirmed the prevalence of social factors over geographical barriers in maintaining distinct speech communities and observed how language evolution was consistently correlated to the archaeological evidence for the spread of farming across Bantu-speaking Africa. Similarly, Philippon and Bahuchet [124] could use the linguistic method for tracing the diffusion of crops originating from America through their transmission in the Bantu languages of Africa. In Polynesia, bread fruit diffusion, as reconstituted with genetic markers, also reflects the human peopling of the archipelago [125]. Perrier *et al.* [126] propose a reconstruction of the movement and cultivation of bananas from New Guinea to West Africa during the Holocene, based on a combination of genetic, linguistic and archaeological data.

The social structuring of diversity is also particularly noticeable in animal populations due to greater mastery of their reproduction. The interdependence relationship established between cattle and man has made it possible to trace back the migratory channels taken by the pastoral societies that introduced them into Africa from the genetic imprint remaining in existing cattle populations [127].

That inference is possible because the diversity of that resource is socially structured. Despite the time that has passed since their introduction, cattle cross-breeding has never blurred the original trace left on a molecular level, precisely because herd management is clearly differentiated among human groups. In this and other cases [128,129], the history of domesticated resources and the history of the human groups ensuring its perpetuation from generation to generation shed light on each other because domesticated resources have been affected by the conservatism of vertical transmission.

5. Conclusion

While vertical transmission, together with many cultural traits, including agricultural practices, plant uses, and knowledge, affects crop genetic diversity, the resulting structure is necessarily expressed in space and time. Indeed, human groups also utilize spatial distribution to signalize their differentiation. Then, environmental adaptation will also play a more prominent role at higher levels, as two groups living in different, distant, environments should exploit different resources. This interaction poses a methodological problem for the study of crop genetic diversity at levels where the impacts of social and environmental factors cannot be distinguished. Indeed, an ideal situation would allow a double comparative approach, by a comparison of different groups in the same environments and comparing the effects of different environments exploited by a same group. This is generally feasible at small to medium scales, as, for example, in the situation described by Zimmerer [19] in the Peruvian Andes. We are also studying sorghum diversity among and within related ethnolinguistic groups distributed along an altitudinal gradient on Mount Kenya. The simultaneous control of social and environmental factor is more difficult at larger spatial scales, because of the correlation between distance and environmental variation. However, the $G \times E \times S$ interaction model can be tested in wide regions with similar ecological conditions, as in Sahel, where ethnolinguistic groups are distributed across precipitation gradients that constitute most of environmental variation (see sorghum studies of Ollitrault *et al.* [29] and Deu *et al.* [62]).

The link between linguistic, cultural, and biological diversity has been described at the interspecific level [130]. In the present paper, we have revised, among the main aspects structuring human societies, those that are most likely to affect the organization of crop genetic diversity, in both social and geographical spaces. First, rules of filiation, inheritance and marriage mostly play vertically in the transmission of seeds. These rules combine with those of residence in determining the spatial distribution of both people and their crop genetic resources, residential endogamy favoring a centripetal orientation of exchange systems. In this respect, seeds and crops must be analyzed as social objects.

All studies of farmers' seed sources show the importance of self-produced seeds and within-community exchanges, which constitutes another strong element of verticality. Several authors have interpreted their results assuming significant seed exchanges among communities. Still, this hypothesis has not been convincingly supported and is subject to debate. A major point in this debate is that seeds are but one component of social networks of exchange. Given their importance for the farmers' success and subsistence, communication and trust are even more important and the main restriction to wide seed exchanges is the risk accompanying foreign seeds.

After seed inheritance and seed saving, a third important element of verticality lies in the necessary consensus on the linguistic sign, *i.e.*, the unambiguous link between a signifier and a signified [131],

within farming communities, which is a prerequisite to the intergenerational transmission of knowledge, including all elements of folk taxonomy. Perception of crop diversity and their conservation through phenotypic selection cannot be conceived out of this cultural framework.

Our review of two widely studied traditional crop models has shown us that sampling strategies have often overlooked the role of society. However, when ethnic factors have been partially taken into account, as in the study of Deu *et al.* [62] or those of Brush and Perales [25] and Benz *et al.* [79], diversity studies have brought significant progress in our understanding of social and biological processes and their interactions. But the sampling strategy is usually validated *a posteriori*. As stated by Sagnard *et al.* [132], the observed crop diversity results from a historical and dynamic evolution, where “the number of processes involved and their interaction allow the same image to be produced from different combinations of factors”. The analysis of a given genetic organization is thus confronted to the limits of final cause reasoning, where the geneticist measures the impact of the factors he/she has selected, without having the possibility of observing their action directly and without excluding that other factors can be at work. Interestingly, this situation is also true for anthropologists studying cultural diversity. Indeed, human group diversity also results from historical processes implying many factors and their interactions, and a hypothetic-deductive approach through comparisons is also needed.

At the functional level, the factors explaining the crop genetic differentiation in biology and those explaining social differentiation of farmers in anthropology are analogous with vertical and horizontal transmission processes. Indeed, gene inheritance is a vertical process, maintaining differentiation between populations, while gene flow is a horizontal one that, in the absence of barriers, leads on the contrary to crop genetic homogenization. On the social side, cultural differentiation processes are similar, because of the existence of vertical and horizontal transmission processes, as defined by Cavalli-Sforza and Feldman [94]. Thus, farmers’ cultural and crop genetic differentiation could be analyzed with the same conceptual frame using the genetic sampling strategy as the focal point of interdisciplinarity.

For an efficient integration of the relevant social factors, we have proposed modifying the classical “ $G \times E$ ” approach by a “ $G \times E \times S$ ” one, where the social component is explicitly taken into account. As stated above, this imposes a sampling strategy respecting the linkages between given social groups and their crop populations, so as to test the social identity of farmers as an organizing factor of crop genetic diversity. In other words, we recommend a joined farmer/crop sampling strategy, the farmer with its social characteristics becoming the factor, and the crop population characteristics, the dependent variables. In this strategy, environmental variation should be as independent of social group distribution as possible, so avoiding confusion in the interpretation of results. Such a design imposes a thorough analysis of the social groups involved, aiming at understanding social structures and historical factors at play at all scales. According to the means and specific objectives of the study, the most significant level of sociological integration/differentiation must be identified.

In these conditions, it should be possible to show that cultural diversity works hand in hand with agrobiological diversity. This hypothesis is confirmed *a contrario* in the recent history of western agriculture. For example, while French farmers massively adopted homogenous cultivars acquired from breeding companies (hybrid maize, triploid beet, wheat pure lines, *etc.*), they became socially more homogenous as actors of a widespread intensive agricultural system [18].

The understanding of the social drivers of crop genetic diversity, as explicated in the $G \times E \times S$ model, is essential in participatory plant breeding, ensuring the efficient selection of consensual phenotypes, and promoting their diffusion through an adequate choice of participants. Here again, the parallel with the network model may be fruitful in the development of strategies allowing to exploit both strong links within solidarity groups, and weak links among them.

While biologists must take into account the social organization of human societies in the analysis of crop genetic differentiation, the anthropologists may benefit from the reverse proposal. We have mentioned the Hannote *et al.* [127] study where the genetic imprint of ancient cattle migrations allows inferring the migratory channels of African pastoral societies thanks to the anthropological fact that societies have maintained their differentiation up to the present. As hypothesized for sorghum in Africa [33,37-39,62], and bread fruit in Polynesia [125], similar approaches may be envisaged with other plants, using crop molecular markers as historical correlates of past human relations.

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