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Recent studies investigating the relationship between crop genetic diversity and human cultural diversity patterns showed that seed exchanges are embedded in farmers' social organization. However, our understanding of the social processes involved remains limited. We investigated how farmers' membership in three major social groups interacts in shaping sorghum seed exchange networks in a cultural contact zone on Mount Kenya. Farmers are members of residence groups at the local scale and of dialect groups clustered within larger ethnolinguistic units at a wider scale. The Chuka and Tharaka, who are allied in the same ethnolinguistic unit, coexist with the Mbeere dialect group in the study area. We assessed farmers' homophily, propensity to exchange seeds with members of the same group, using exponential random graph models. We showed that homophily is significant within both residence and ethnolinguistic groups. At these two levels, homophily is driven by the kinship system, particularly by the combination of patrilocal residence and ethnolinguistic endogamy, because most seeds are exchanged among relatives. Indeed, residential homophily in seed exchanges results from local interactions between women and their in-law family, whereas at a higher level, ethnolinguistic homophily is driven by marriage endogamy. Seed exchanges and marriage ties are interrelated, and both are limited between the Mbeere and the other groups, although frequent between the Chuka and Tharaka. The impact of these social homophily processes on crop diversity is discussed.

crop diversity dynamics | local seed systems | social organization | social networks analysis | exponential random graph models

Smallholder farming systems occupy a large share of arable land, and they are places of foremost importance for the study of crop evolution under the influence of both ecological and anthropic factors (1). In these systems, farmers continue to have a major impact on the genetic diversity of crop populations through their seed selection and exchange practices. Analyzing the collective impact of farmers on crop diversity is a major challenge for the characterization and conservation of their genetic resources.

Although several studies have underlined the impact of farmers' seed selection and exchange practices on the dynamics of crop diversity to relate spatial patterns of crop genetic diversity and farmers' cultural diversity (2, 3), our knowledge of which social mechanisms are involved is still limited (4). In a previous study, we analyzed the relationship between sorghum genetic diversity patterns and the organization of rural societies at the local scale and found that different ethnolinguistic groups living in the same locality grow different landraces (5). At the country scale, Deu and colleagues (6) observed that sorghum genetic patterns coincide with major ethnolinguistic groups, and similar patterns have been observed at the broader scale of African linguistic families (7, 8).

In small-scale farming systems, farmer-to-farmer seed exchanges are a major pathway for gene flows, and are key determinants of crop diversity patterns (9). These studies referred to the hypothesis that homophily [i.e., preferential interaction among members of the same social group (10)] is a key factor in shaping seed exchange networks. This hypothesis postulates that seed exchanges imply trust (11), and are consequently constrained by social barriers (4).

Indeed, in most small-scale farming societies, individuals are not independent because they belong to social groups (which can be permanent or dynamic) with rules and norms that determine how they interact (12, 13). The few studies describing seed exchange networks underlined their dependence on farmers' social organization. The importance of residential and/or kinship ties on seed exchanges has been shown in Ethiopia (14), North Cameroon (15), Mexico (16), Peru (17), and Gabon (3). These studies underlined the need to understand how the different types of social relationships interact and lead to homophily in seed exchange networks.

In social network analysis, exponential random graph models (ERGMs) are increasingly used to assess the influence of homophily on the structure of networks by modeling the probability of tie formation as a function of the social membership of the individuals (18, 19). ERGMs define the probability of observing the network as a function of attributes of the nodes and edges, and the structural characteristics of the network (20). Measuring homophily in seed exchange networks requires controlling for the effect of other mechanisms that may bias its estimation (18). First, the probability of tie formation depends on the composition of the population under study. For instance, the proportion of within-group ties increases with the size of the group (number of individuals) and activity (number of ties). Second, geographic proximity may lead to overestimation of homophily because relatives frequently settle in the same neighborhood (21). Last, tie formation is also induced by social mechanisms independent of the individual and edge characteristics, with the main ones being the propensity of individuals with many ties to establish new ties (activity) and to establish ties with exchange partners' partners (transitive closure) (22).

Significance

This study helps untangle the multiscale processes involved in the relationships between crop genetic and human cultural diversity patterns. It quantifies the effect of homophily on seed exchange networks and details the major role played by kinship systems. By bridging anthropology and crop genetics through an in-depth social network analysis, this study provides a better understanding of the social processes involved in crop diversity dynamics. These findings urgently call for a specification of social and cultural factors in crop metapopulation models, which has been neglected so far.

As stated by Lansing at al (23), in the case of human gene and language coevolution, all broad-scale genetic and linguistic patterns arise from local scale processes. The aim of our study was thus to understand the local homophily processes involved in the large-scale patterns of crop genetic diversity. Drawing on a case study on Mount Kenya, we analyzed the effect of three major types of social relationships on the organization of farmer-to-farmer exchange networks. The results of this study improve our understanding of the processes involved in crop diversity dynamics from the local scale to the continental scale.

The Mount Kenya human population presents significant cultural and linguistic diversity (Fig. 1), because different ethnolinguistic groups coexist within a limited area (24, 25). At the local scale, farmers are members of residence groups (*ntora* in the Kimeru language), which are the smallest social units beyond the family compound. Residence groups are composed of households that share a common feeling of unity despite their spatial scattering (25). Social interactions are favored among members of the same residence group, and hence favor seed exchanges.

At a wider scale, farmers are members of dialect groups, which are important social, cultural, and linguistic units as well as categories of self-identification. Three dialect groups coexist in our study area, the Chuka, the Tharaka, and the Mbeere. The Chuka and Tharaka groups are allied due to their common ancestry (*gichiaro*), and this social proximity is reflected in their cultural and linguistic similarity; they thus represent two dialect groups of a same ethnolinguistic unit, whereas the Mbeere belong to a distinct ethnolinguistic unit (26). These different languages are nonetheless reciprocally intelligible because they all belong to the larger Kikuyu-Kamba language family. This ethnolinguistic organization has a potential impact on seed circulation in the study area.

We investigated sorghum [*Sorghum bicolor* ssp. *bicolor* (L.) Moench] seed exchange networks, which is a major cereal in the midlands and lowlands of the Mount Kenya region and is widespread in Africa because it is adapted to semiarid areas (27). Several landraces or varieties, introduced by extension services, are usually mixed and grown with other cereals in small plots [*Pennisetum glaucum* (L.) R. Br, *Zea mays* L.], and with legume crops [*Vigna unguiculata* (L.) Walp, *Vigna radiata* (L.) R. Wilcz, *Phaseolus vulgaris* L.] (5). Grain crop management is women's responsibility (25, 28). Sorghum seeds are mostly self-produced or purchased at the local market, but farmer-to-farmer seed exchanges are a major diffusion pathway for landraces, most of which are rarely sold on the local market.

We used ERGMs to test whether homophily among members of residence, dialect, and ethnolinguistic groups has shaped sorghum seed exchange networks. Focusing on a limited geographic area in a uniform agroecological environment enabled us to control for potential biases that could be caused by geographic distance or environmental heterogeneity.

Results and Discussion

Of the 197 informants interviewed in the three dialect groups, 156 reported an exchange tie with another informant. The closed exchange network among these 156 informants is composed of 235 undirected edges, representing seed exchange ties between pairs of informants. The density of this undirected network is low

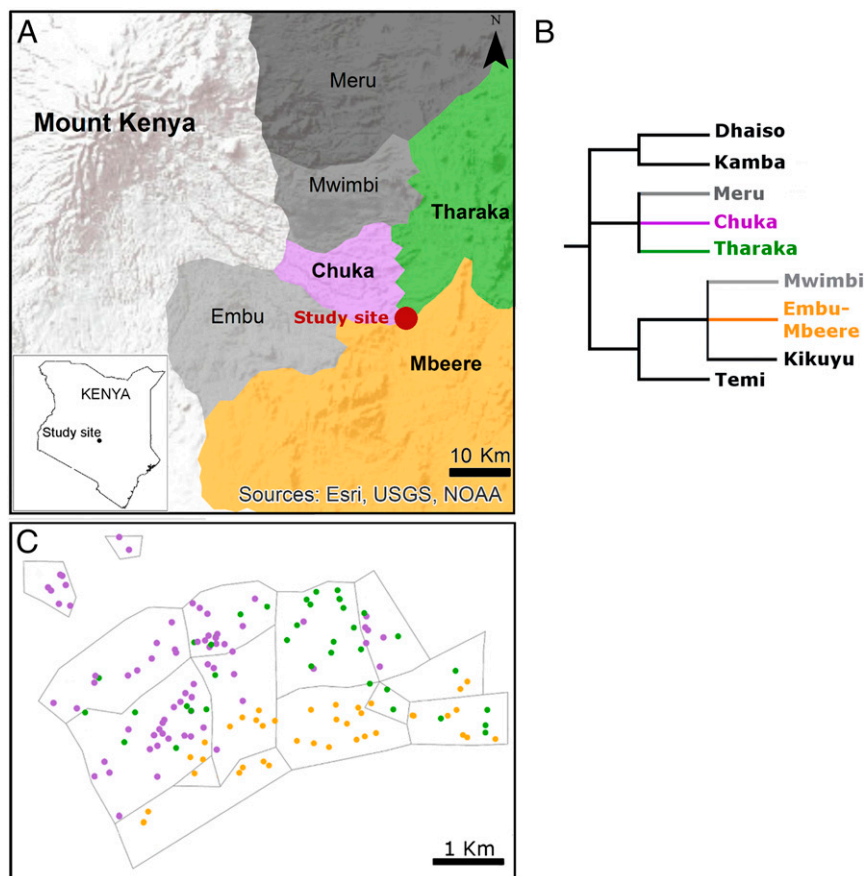**Fig. 1.** Location of the study site. (*A*) Map of the Mount Kenya region. The three dialect groups are shown in different colors: Mbeere in orange, Chuka in purple, and Tharaka in green. (*B*) Classification of Central Kenya Bantu languages following Hammarström et al. (48). (*C*) Locations of the households surveyed (colors correspond to households' dialectal membership, and the residence groups are delimited by gray lines).

Table 1. Results of ERGMs

Terms	M1 (residential)	M2 (residential + dialectal)	M3 (residential + ethnolinguistic)
Edges	−3.11 (0.36)***	−4.71 (0.53)***	−3.71 (0.41)***
Residential homophily (uniform)	0.81 (0.15)***	0.81 (0.15)***	0.80 (0.15)***
Dialectal homophily (Mbeere)		1.84 (0.43)***	
Dialectal homophily (Chuka)		−0.68 (0.42)	
Dialectal homophily (Tharaka)		0.75(0.42)	
Ethnolinguistic homophily (uniform)			0.84 (0.20)***
Exogenous covariables			
Geographic distance (K_m)	−1.07 (0.10)***	−0.99 (0.10)***	−0.98 (0.10)***
Dialect group activity (Chuka)		1.04 (0.35)**	
Dialect group activity (Tharaka)		0.61 (0.25)*	
Ethnolinguistic group activity (Chuka-Tharaka)			−0.12 (0.12)
Endogenous covariables			
Actor activity	4.87 (1.84)**	4.77 (1.82)**	5.02 (1.92)**
Transitive closure	0.75 (0.11)***	0.72 (0.11)***	0.73 (0.11)***
Multiple connectivity	−0.02 (0.04)	−0.01 (0.04)	−0.02 (0.04)
Akaike information criterion	1,850	1,830	1,833

Parameter estimates are expressed in log-odds with their standard deviation (SD) in parentheses. *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

(0.019), because the mean number of ties established by farmers is low (three per farmer, SD = 1.95).

In this closed network, 50% of seed exchange ties occur within residence groups, 59% within dialect groups, and 87% within ethnolinguistic groups. The results of the ERGMs thus confirmed that residential homophily and ethnolinguistic homophily have shaped seed exchange networks; the goodness of fit of the best models is described in Table 1. Geographic proximity among farmers has favored seed exchanges, as indicated by its negative and significant parameter estimate (the greater the geographic distance, the lower is the probability of a tie). Endogenous social factors have also had an impact on the probability of tie formation. The effect of actor activity was positive and significant, indicating that farmers with more ties are more likely to establish new ties. The effect of transitive closure was also significant, indicating that two farmers are more likely to exchange if they have common exchange partners. These widespread mechanisms are observed in most social networks (21, 22).

Effect of Residential and Ethnolinguistic Homophily on Seed Exchange Networks. Fig. 2A shows node clusters according to residence groups, pointing to a higher exchange frequency within residence groups, which was confirmed by the ERGM results [Table 1, model 1 (M1)]. The parameter estimate for the effect of residential homophily was positive and significant (0.81; $P < 0.001$);

members of the same residence groups are thus more likely to exchange among themselves than with members of a different group. This effect of residential homophily was still significant in the models that included the effect of dialectal or ethnolinguistic homophily (M2 and M3, respectively), and its parameter estimate was not affected by the inclusion of either term.

The network graph (Fig. 2B) shows that the Mbeere are mostly located at the periphery and have few ties with the core of the network, which mainly comprises Chuka and Tharaka farmers linked by numerous ties. The results of the ERGM (M2) confirmed that in the Mbeere group, the probability of within-group seed exchange ties is higher than expected under a random hypothesis, with a positive and significant homophily effect for the Mbeere group (1.84; $P < 0.001$), which is not the case for the Chuka and Tharaka. Furthermore, the Mbeere group generally establishes fewer exchange ties than the Chuka and the Tharaka, as indicated by the positive and significant parameter estimates for activity effect in the Chuka (1.04; $P < 0.01$) and Tharaka (0.61; $P < 0.05$) groups. Overall, the results of the model estimating the ethnolinguistic homophily effect (M3) confirmed a higher propensity for seed exchanges within than between ethnolinguistic groups. The parameter estimates for the ethnolinguistic homophily effect were significant (0.84; $P < 0.001$). In addition, residential homophily and ethnolinguistic homophily appear to be independent social processes, because the parameter estimate
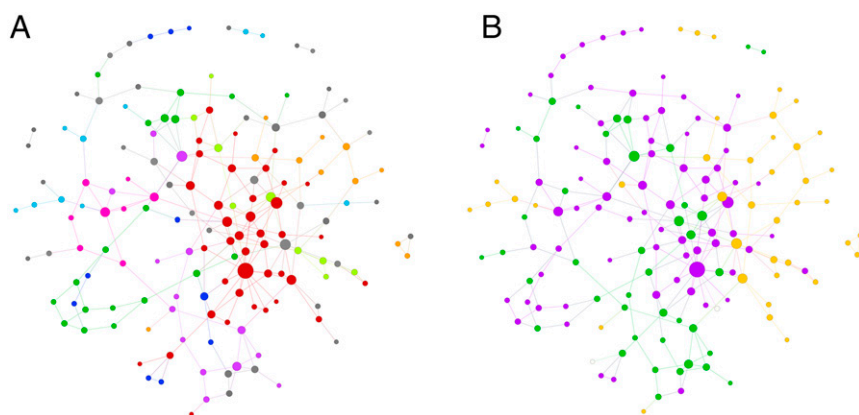

Fig. 2. Closed seed exchange network among the 156 informants (Fruchterman–Reingold representation) according to residence groups (A; colors correspond to the different residence groups) and according to dialect groups (B; Mbeere in orange, Chuka in purple, and Tharaka in green).

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for residential homophily was not affected by the addition of the term controlling for the effect of ethnolinguistic homophily.

Kinship Systems Shape Seed Exchange Networks. Although residential homophily and ethnolinguistic homophily appear to be independent processes in the ERGMs, both can be explained by Mount Kenya kinship systems (29), particularly by patrilineal filiation, patrilocal residence, and marriage rules that interact differently at these two levels. The high proportion of seed exchange ties among relatives (72%) should be interpreted accordingly.

First, residential homophily may be linked to the fact that women intensively exchange seeds with their in-laws within the residence group (Fig. 3). Because a residence group comprises only two to three clans (consanguine groups), most marriages (86%) are between members of different residence groups (exogamy). Following the patrilocal residence rule, the woman leaves her native residence group and the couple settles in the native residence group of the groom's father. In their new residence, women mostly interact and exchange seeds with their in-laws (45% of seed exchange ties in our study area). Exchanges are particularly frequent with their mother-in-law (15%) and with the wives of their brothers-in-law (9%). Such interactions between women and their in-laws are widespread in patrilocal societies (30).

Second, the alliance among members of the three dialect groups explains the effect of ethnolinguistic homophily. Ethnolinguistic endogamy is very high in the study area (86% of the unions; Table 2). Unions are rare between the Mbeere dialect group, on the one hand, and the Chuka and Tharaka dialect groups, on the other hand, whereas they are relatively frequent between the Chuka and Tharaka dialect groups due to their ancestral *gichiaro* alliance (Table 2). This observation is congruent with previous ethnographic studies (31, 32). Because seed exchanges mostly take place among relatives, ethnolinguistic endogamy strongly restricts seed exchanges between the Mbeere and the other groups, whereas the frequent unions between Chuka and Tharaka
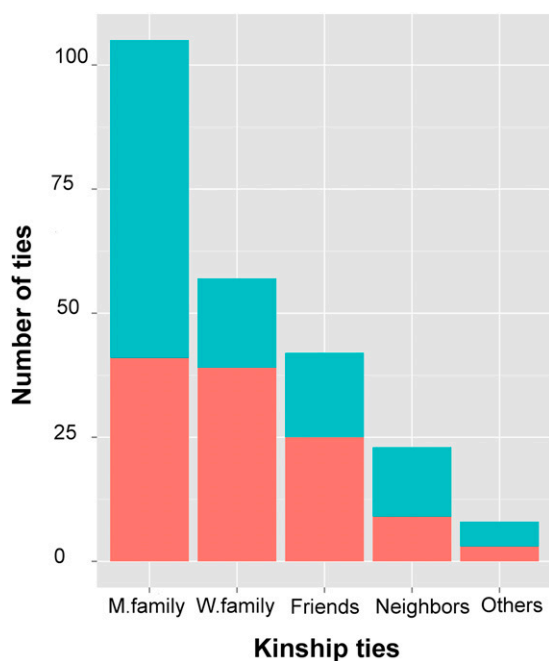

Fig. 3. Relationship between seed exchanges and kinship ties. Proportion of seed exchange ties according to the different relationship categories [man's (M) family, woman's (W) family, friends, neighbors, and others] and the residence group of the donor and receiver (same group, green; different group, red).

Table 2. Endogamy patterns at the dialect group level: Number of marriage ties among the three dialect groups

Dialect group	Chuka	Tharaka	Mbeere
Chuka	21 (20)	18 (26)	2 (15)
Tharaka		29 (34)	3 (20)
Mbeere			21 (12)

Expected numbers under the hypothesis of random mating are given in parentheses (χ^2 test: 88.203, df = 4, $P < 0.001$).

are associated with frequent seed exchanges between the two. This absence of dialectal endogamy explains the absence of dialectal homophily in the study site. This particular situation reveals how marriage endogamy drives ethnolinguistic homophily in seed exchanges.

Thus, residential homophily results from local interactions (women exchanging with their in-law patrilocal family), whereas, at a higher level, ethnolinguistic homophily is driven by marriage endogamy, defining the social space of exchange. Remarkably, the ERGMs dissociated the two aspects.

Social Exchange Networks Shape Crop Diversity. In the Mount Kenya region, the proportion of homophilous ties in seed exchanges increases from residence to ethnolinguistic groups. Therefore, these ties are embedded in farmers' social organization, including the kinship systems. First, seed exchanges between women and their in-laws, in the context of patrilocal residence, favor residential homophily. Patrilocal residence is the most widespread modality of social organization (33). It is involved in human genetic diversity patterns by limiting male migration (34). It is also associated with affinal transmission of knowledge between married women and their in-laws, thus favoring the maintenance of cultural differences (30). Second, ethnolinguistic endogamy strongly limits seed diffusion among ethnolinguistic groups. Such ethnolinguistic endogamy is a widespread modality in rural as well as urban societies (35, 36). It has been shown to induce human genetic differentiation by limiting gene flows among ethnolinguistic groups (37, 38), as well as to maintain cultural differentiation by limiting the dissemination of knowledge and practices between geographically close groups (39, 40). In the same way, patrilocal residence and ethnolinguistic endogamy, driving homophilous seed exchanges, explain the relationship between ethnolinguistic diversity and crop diversity patterns that has notably been observed on country and continental scales for sorghum (6, 7), pearl millet (41), cassava, and taro (3, 42). Thus, considering seed exchanges as major gene flow drivers, the effect of farmers' social exchange networks on crop diversity dynamics can be interpreted in terms of evolutionary forces.

Previous studies in the Mount Kenya region enable us to discuss the effect of partitioned seed networks on crop diversity dynamics at the local level. Sorghum landraces were unevenly distributed among residence groups (43) as well as among ethnolinguistic groups (5), suggesting that the diffusion of seeds and related information is confined by social barriers. These barriers were highlighted in our social network analysis. We can therefore expect that sorghum genetic differentiation exists among residence and ethnolinguistic groups.

We observed an uneven distribution of sorghum genetic diversity among dialect groups (5). Interestingly, these local patterns of sorghum genetic diversity partly mirrored the partitioning of seed exchanges. Indeed, Mbeere farmers, whose ethnolinguistic affiliation is distinct from the ethnolinguistic affiliation of the Chuka and Tharaka, mainly exchange seeds within their dialect group. However, sorghum genetic differentiation was also observed between the Chuka and Tharaka despite the fairly frequent seed exchanges between them. This differentiation indicates that

local processes other than ethnolinguistic homophily are also determinant in limiting gene flows, not only at the residential level (residential homophily) but also on a household scale. In fact, on-farm seed saving limits gene flows among households, and this mechanism, combined with homophily, also appears to be instrumental in shaping sorghum genetic patterns. Analysis of seed exchange networks should therefore take into account the seed-saving component for a better understanding of crop diversity dynamics.

Conclusion

Our study assessed the effects of residential and ethnolinguistic homophily on seed circulation using an analytical, rather than a descriptive, perspective (i.e., by using ERGMs to control for potential confusion factors, such as geographic proximity or differences in group size and activity). It shows that kinship systems that shape farmers' social interaction networks also shape their seed exchange networks. In smallholder farming systems in the Mount Kenya region, seed exchanges are favored within the residence groups and are strongly confined within ethnolinguistic groups. These homophily processes, involved in shaping seed exchange networks, are related to the kinship system, because most seed exchanges occur among relatives. Patrilocality and ethnolinguistic endogamy, which are widespread social norms, contribute to channeling seed diffusion, and are thus involved in crop genetic diversity dynamics.

Our work reveals how important social processes are in shaping crop diversity. It paves the way for improving crop metapopulation models for diversity studies through a more realistic quantification of seed-mediated gene flows, taking into account farmers' relationships and the topology of their social networks.

Materials and Methods

Ethics Statement. This study was a collaborative effort with the Genetic Resources Research Institute of Kenya (KALRO), which has the national mandate for the collection and conservation of all plant genetic resources and documentation of all accompanying information. Based on this mandate, and given that KALRO was partner of our study, no specific permission was required to undertake the study. Although KALRO does not have a body designated as an ethical review board, it has equivalent committees and administrative organs that review proposed research activities before granting approval. Local government administrative, as well as agricultural extension, officers were informed of the study and kept updated about the activities. During the survey, the mandate given to KALRO, as well as the importance of the study both nationally and globally, was explained to the farmers and concurrence was sought before undertaking the study activities. According to KALRO's procedures, prior informed consent was obtained verbally and not recorded. Farmers were informed that the process would only involve anonymous information.

Data Collection. We conducted a survey of 197 households in the three ethnolinguistic groups, with an expected sampling effort of more than 75%. We characterized their informal sorghum seed exchange networks using a name generator procedure. Farmers, mostly female heads of household (86%), were asked to cite all the people with whom they had exchanged (given or received) seeds in their life. We recorded the residence and dialect group of donors and recipients as specified by the informants themselves, as well as their relationship (friends, neighbors, relatives, or unknown). When exchanges occurred between relatives, their kinship relationship was recorded using an unambiguous formalized typology (44). Kinship ties were recoded using the male head of household as a reference, and classified depending on whether they were established with the woman's or the man's family. We also characterized the norms that shape the kinship system, recording the native residence and dialect group of both husband and wife in 94 households. The endogamy rate was computed as the proportion of marriages that took place within groups in the different residence, dialect, and ethnolinguistic groups.

Data Analysis. After removing 41 isolates, we analyzed the closed seed exchange network among the remaining 156 farmers to characterize the influence of residential, dialectal, and ethnolinguistic homophily. This 156-farmer closed network was representative of the global open network involving the

197 farmers of the whole sample (*SI Materials and Methods*). The connectivity matrices of incoming and outgoing seed exchanges were aggregated, and the seed exchange tie Y_{ij} between farmers i and j was coded 1, irrespective of the number and orientation of exchange events involved, or 0 if no exchange was reported. Exchange ties were represented as a 156×156 connectivity matrix **Y**. The corresponding network was hence undirected, and edges were represented by the following relationship: "farmers i and j exchanged seeds."

Descriptive approaches to seed exchanges are limited in several ways, mainly because they do not make it possible to distinguish and quantify the effect of the different mechanisms that produce the observed network. For this reason, ERGMs are an increasingly used method of network analysis (19). ERGMs specify the probability of observing the network y as a function of various mechanisms, resulting from attributes of nodes and edges and endogenous characteristics of the network (20):

$$P(\mathbf{Y} = y) = \frac{\exp\left(\sum_{k=1}^{K} \theta_k Z_k(y)\right)}{c}. \quad [1]$$

The K covariables Z_k correspond to particular network configurations or patterns, each of which results from a given social process (e.g., the number of homophilous ties represents the homophily process), and the θ_k parameters to be estimated weight the relative importance of the different Z_k covariables. Probabilities are constrained to sum to 1 by the denominator c.

For the sake of convenience, ERGMs are usually specified as the conditional log-odds of individual ties. Coefficients can thus be interpreted as the coefficients of a standard log linear model, with positive parameters indicating effects that increase the probability of a tie and negative parameters corresponding to effects that decrease the probability of a tie. ERGMs predict the conditional probability of a tie, given the network configuration, with the log-odds of a tie under a given combination of effects being determined by adding the parameter estimates for all these effects (22).

In this study, we tested whether residential, dialectal, and ethnolinguistic homophily are determinants of the formation of seed exchange ties, while controlling for the composition of the population as well as for the effect of other major endogenous mechanisms involved in shaping social networks. Residential (M1), residential and dialectal (M2), and residential and ethnolinguistic (M3) homophily effects were fitted separately in the three models retained. Each model also included covariables controlling for each group's propensity to establish ties (group activity) and for individuals' propensity to exchange proportionally to their geographic proximity (geographic distance). Four major endogenous effects were also included in the three models: edge corresponds to the baseline propensity to establish ties and is equivalent to the intercept in logistic regression, actor activity controls for heterogeneity in individuals' overall propensity to establish ties, transitive closure controls for their propensity to establish ties with exchange partners' partners, and multiple connectivity is essential to get an accurate estimation of the transitive closure effect (22). The models retained were those models that converged and showed the best goodness of fit. ERGMs were run using the statnet and ergm R packages (45, 46), and all computations were run with R 3.1.0 software (47). More details are provided in *SI Materials and Methods*.

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