Evolution of kinship structures driven by marriage tie and competition

Kenji Itao[a] and **Kunihiko Kaneko**[a,b,1]

[a]Department of Basic Science, Graduate School of Arts and Sciences, University of Tokyo, Meguro-ku, Tokyo 153-8902, Japan; and [b]Center for Complex Systems Biology, Universal Biology Institute, University of Tokyo, Tokyo 113-0033, Japan

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The family unit and kinship structures form the basis of social relationships in indigenous societies. Families constitute a cultural group, a so-called clan, within which marriage is prohibited by the incest taboo. The clan attribution governs the mating preference and descent relationships by certain rules. Such rules form various kinship structures, including generalized exchange, an indirect exchange of brides among more than two clans, and restricted exchange, a direct exchange of brides with the flow of children to different clans. These structures are distributed in different areas and show different cultural consequences. However, it is still unknown how they emerge or what conditions determine different structures. Here, we build a model of communities consisting of lineages and family groups and introduce social cooperation among kin and mates and conflict over mating. Each lineage has parameters characterizing the trait and mate preference, which determines the possibility of marriage and the degree of cooperation and conflict among lineages. Lineages can cooperate with those having similar traits to their own or mates', whereas lineages with similar preferences compete for brides. In addition, we introduce community-level selection by eliminating communities with smaller fitness and follow the so-called hierarchical Moran process. We numerically demonstrate that lineages are clustered in the space of traits and preferences, resulting in the emergence of clans with the incest taboo. Generalized exchange emerges when cooperation is strongly needed, whereas restricted exchange emerges when the mating conflict is strict. This may explain the geographical distribution of kinship structures in indigenous societies.

social physics | kinship structure | incest taboo | multilevel selection

In human society, a family and kinship are formed by marriage and descent. In indigenous societies, families sharing a common ancestor are called a lineage. Lineages form a socially related group, called a clan, in which common culture is shared (1–3). Social relationships with others, such as cooperation, rivalry, or marriage, are mostly determined by the clans the parties belong to (1). In particular, people rarely marry within a clan (4–8). This prohibition of the marriage of "siblings as a category" is called the incest taboo, whose origin is thought to be cultural, rather than genetic (2). Furthermore, each clan has some rules on marriage as to which of the other clans it prefers in choosing mating candidates, as well as on the descent as to which clan their children belong to (2). With these rules among clans, they form a certain kinship structure. Indeed, the elucidation of such rules and corresponding kinship structures lies at the core of cultural anthropology studies (1). However, it is still unknown how and why the incest taboo and certain kinship structures emerge.

Lévi-Strauss classified kinship structures according to marriage and descent relationships (1, 2). Examples of structures are shown in Fig. 1, where two different arrows $\Rightarrow, \rightarrow$ represent the flow of women and children, respectively. Here, the flow of children means that the flow of attributions of children, neither the location nor parental authority (9). For example, when children inherit a mother's surname and live in a father's village, children's affiliation, which is determined by both surname and location, differs from both father's and mother's. Fig. 1 shows the classes of kinship structures: the incest structure, without the incest taboo (Fig. 1*A*); dual organization, a direct exchange of brides between two clans (Fig. 1*B*); restricted exchange, a direct exchange of brides with the flow of children to different clans (Fig. 1*C*); and generalized exchange, an indirect exchange of brides among more than two clans (Fig. 1*D*). Suppose men in clan A marry women in clan B. In a generalized exchange, men in clan B marry women in clan C, whereas in restricted exchange, they marry women in clan A. Thus, the flow of women as a whole is $A \Rightarrow B \Rightarrow \cdots \Rightarrow X \Rightarrow A$ in generalized exchange, whereas it is $A \Leftrightarrow B$ in restricted exchange. Descent relationships are observed by tracing the clan attribution of fathers and children. Generalized exchange is observed in India and China and leads to the emergence of status differentiation between social classes. Restricted exchange is mainly observed in Australia and leads to a stable and egalitarian social structure (2). Nonetheless, it is still unknown why different structures are observed.

Mathematically, kinship structures are characterized by defining the marriage cycle (C_m) and descent cycle (C_d) as the length of cycles of the flow of women and children, respectively. $C_m = C_d = 1$ in the incest structure (Fig. 1*A*). Lévi-Strauss defined the system as restricted exchange if $C_m = 2$, regardless of C_d. However, he called the system with $C_m = 2$ and $C_d = 1$ a dual organization (Fig. 1*B*), which he assumed to be the original

Significance

Cultural anthropology has revealed kinship structures with certain rules of marriage and descent as the basis of social relationships in indigenous societies. However, it remains unanswered how they have emerged or what determines different structures. Here, we build a simple model of family groups, in which exchange of brides and resultant cooperation and competition are considered, by applying an agent-based model and multilevel evolution. The incest taboo and several kinship structures, consistent with field studies, spontaneously emerge. Different structures appear, depending on the strengths of cooperation and conflict, which can explain the distribution of kinship structures in indigenous societies. The theoretical studies by simple constitutive models, as presented here, will unveil universal features and formulate a general theory in anthropology.

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The authors declare no competing interest.

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Data deposition: Source codes for these models can be found at https://github.com/KenjiItao/clan.git.

[1]To whom correspondence may be addressed. Email: kaneko@complex.c.u-tokyo.ac.jp.

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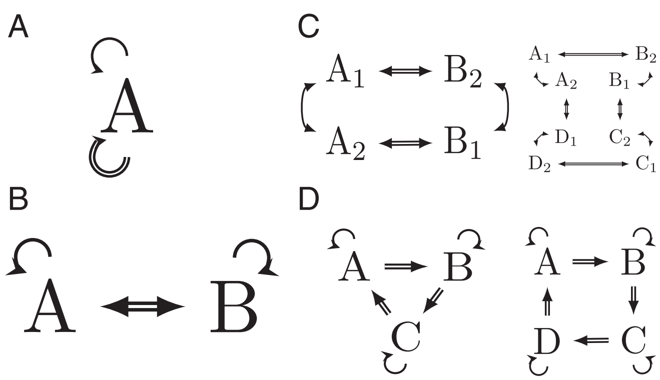

Fig. 1. Examples of kinship structures. Each symbol A, A_1, A_2, B, $\cdots$ is a clan. When clans are identified by a single trait, we denote them by characters as A, B, $\cdots$, whereas when they are represented by two traits, they are denoted both by characters and indices as A_1, B_1, $\cdots$. The double arrow from clan X to Y ($X \Rightarrow Y$) shows the marriage rule indicating that women in clan X marry men in clan Y. The arrow from clan X to Y ($X \rightarrow Y$) shows the descent rule indicating that children belong to clan Y when their fathers belong to clan X. Hereafter, we refer to the length of cycles of $\Rightarrow$ and $\rightarrow$ needed to return to the original point, as marriage cycle C_m and descent cycle C_d. Structures are classified according to those cycles. (*A*) $C_m = C_d = 1$ for incest structure. (*B*) $C_m = 2$, $C_d = 1$ for dual organization. (*C*) $C_m = 2$, $C_d \geq 2$ for restricted exchange. (*D*) $C_m > 2$, $C_d = 1$ for generalized exchange.

pattern of both generalized and other restricted exchanges. Here, we limit the use of restricted exchange to the case with $C_m = 2$ and $C_d \geq 2$ (Fig. 1*C*), to distinguish it from the dual organization. He defined generalized exchange by $C_m \geq 3$ and $C_d = 1$ (Fig. 1*D*). Structures with $C_m > 2$ and $C_d > 1$ are rarely observed* (Table 1). When $C_d = 1$, children inherit from and belong to the same clan as their father/mother, the rule of which is called "unilineal descent." By contrast, when $C_d \geq 2$, a child inherits the character (A, B, $\cdots$) (e.g., land) from his or her father and the index (1, 2, $\cdots$) (e.g., name) from his or her mother, as in Fig. 1*C* (2); this is called "bilateral descent."

The advantage of the incest taboo has been discussed biologically and economically (12, 13). As for kinship structures, how marriage and descent rules are chosen were numerically investigated, under given clan separation (14). Group-theory analysis, known as "kinship algebra," reveals structures that satisfy transformation symmetry under marriage and descent rules (15–17). These studies, however, can explain neither the social origin of the incest taboo (including the distinction between fathers' sisters' daughters and fathers' brothers' daughters) nor the emergence and transition of kinship structures.

Note that an important point was not considered in the earlier theoretical studies: Marriage brings social unity. Indeed, field studies revealed that lineages cooperated and conflicted with each other according to their social relatedness and mate preferences. Socially related lineages mutually cooperate and constitute a clan (2). Each lineage proposes marriage to certain lineage(s) depending on its mating preference (2). After marriage, the lineage of the bridegroom and that of the bride cooperate (2, 18), as well as social kin that share common traits (19, 20). There also exist strong conflicts among rival lineages competing for mates (21–24).

Here, we introduce an agent-based model of indigenous societies adopting the multilevel evolution of lineages and communities. Lineage is a unit of the dynamics, and community is an ensemble of lineages within which the interaction of lineages can take place. Unmarried women are exchanged by marriage over lineages. We assign each lineage a trait t and a mate preference p as an optimal trait of the bridegroom. Marriage takes place according to the mating preference given by t, p. Lineages with similar traits cooperate with each other as well as with mates, whereas those with similar preferences compete for mates. Depending on the cooperation and conflict, the population of a lineage grows. By introducing mutations in t, p values, lineages with higher population growth are selected.

With numerical simulations, lineages were found to form clusters in (t, p) space under a certain condition. For each cluster, marriage occurs only with a certain different cluster, resulting in the incest taboo. Lineages in the same cluster cooperate with each other, as well as with those in the bride's cluster, whereas conflict for brides occurs only within a cluster. Such clusters are regarded as clans. Thus, clan (= cluster of lineages) is an emergent property in this model. Next, by introducing multiple traits (and preferences), such as habitats, names, and occupations, we uncovered the transition from dual organization to generalized and restricted exchanges, depending on the strengths of cooperation and conflict.

The present paper is organized as follows. In the next section, we describe the model with one trait. Then, with evolution simulations, we show the emergence of clans and incest taboo and present the condition for it. Next, we introduce the model with two traits and demonstrate the emergence of kinship structures. In the last section, we discuss the correspondence of our results with ethnographic records.

Model 1: One-Trait Model

Fig. 2 shows a schematic of our model. Lineages grow by interacting with other lineages in the same community (Fig. 2*A*). Each lineage splits into two when its population reaches twice the initial and is eliminated when the population goes to zero. Communities split and are eliminated in the same way in which their populations change by doubling and elimination of lineages within. When a community splits into two, one community, selected at random from the system, is removed to fix the total population of communities, to introduce community-level selection by removing communities with lower fitness. This multilevel selection on lineages and communities follows the so-called hierarchical Moran process, as adopted in the studies of biological and social evolution (25–31).

We assign a pair of a trait and a preference (t_i, p_i) to each lineage i, which is culturally transmitted to the next generation. When a lineage splits into two, daughter lineages inherit (t, p) of the mother with slight variation, because cultural traits are modified when transmitted (32). Specifically, (t, p) are "mutated" each step by adding a small noise component η, following a uniform distribution in $[-\mu, \mu]$. This variation corresponds to a genetic mutation in biology, but the inheritance and variation of traits here are of a cultural basis. Human beings categorize social groups even without genetic relatedness (33).

We introduce cooperation among social kin and that by marriage (blue and orange solid lines in Fig. 2*B*). Here, relationships of lineages are recognized by comparing the trait and preference values with a tolerance parameter σ. Thus, lineages i and j cooperate when $|t_i - t_j|/\sigma$, $|t_i - p_j|/\sigma$, or $|p_i - t_j|/\sigma$ is sufficiently small. The density of cooperators for each lineage i, denoted

Table 1. Classification of kinship structures

$C_d \backslash C_m$	2	3∼
1	Dual	Generalized
2∼	Restricted	(Murungin?)

*Lévi-Strauss assumed that the so-called Murungin structure fulfills these conditions; however, this was later proved to be a mere generalized exchange with alternative pathways (3, 10, 11).

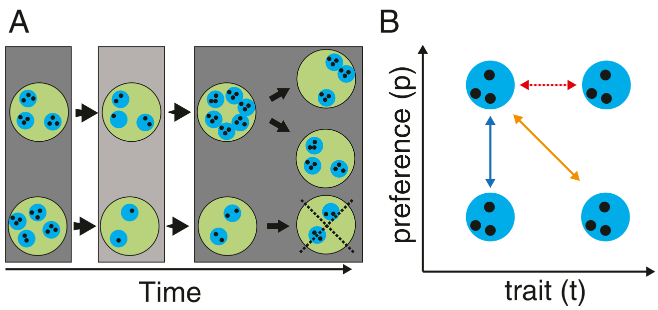

Fig. 2. Schematic of the model. (*A*) Life cycle in the model. Communities (green) consist of lineages (blue), whose population (black) can grow. Generation is separated into children (dark gray) and adults (light gray). As children grow up, some die because of a lack of cooperation or mating conflicts. Adults mate, give birth to children, and die. When the population of a lineage (community) goes beyond a given threshold, the lineage (community) splits. When a community splits, another community is removed from the system at random to keep the number of communities fixed—i.e., we adopt the hierarchical Moran process. (*B*) Lineages cooperate (solid line) and conflict (dashed line), depending on their traits *t* and mate preferences *p*. Kin and mates cooperate, whereas mating rivals conflict. Lineages *i* and *j* are kin (blue) when $|t_i - t_j|/\sigma$ is sufficiently small, mating rivals (red) when $|p_i - p_j|/\sigma$ is sufficiently small, and mates (orange) when $|t_i - p_j|/\sigma$ or $|p_i - t_j|/\sigma$ is sufficiently small. Only the relationships with the upper left lineage are shown.

by $friend_i$, is calculated by summing the degree of cooperation across all lineages. A larger *friend* value implies that the lineage gains more cooperation, resulting in larger growth of its population, where d_c is a parameter that gives the decline of death rate by cooperation (or a disadvantage of noncooperation).[†]

Mating conflict of lineages i and j occurs when $|p_i - p_j|/\sigma$ is sufficiently small (red dashed line in Fig. 2*B*). The strength of conflict depends only on the number of lineages with close preferences and is independent of that of preferred lineages, because the conflict occurs even when there are sufficient bridegrooms and brides (22). The density of rivals, denoted by $rival_i$, is calculated by summing the degree of conflict across all lineages. A larger *rival* value implies a larger suppression of the growth rate, where d_m is a parameter indicating the decline of the population by conflict.

There is a mating chance for each lineage in each step. Each lineage i likely chooses lineage j when $|t_i - p_j|/\sigma$ is sufficiently small. Then, unmarried men in lineage i and unmarried women in lineage j form couples in lineage i. Thus, women move into their husbands' lineage after marriage. Children belong to and inherit (t, p) of their father's lineage.

The initial values of t, p are zero in this model. Thus, at first, every couple can get married, even within a lineage. However, no qualitative changes are observed under other initial conditions, such as the uniform distribution of $(t, p) \in [0, 1]^2$ or the Gaussian distribution. See Materials and Methods for details. Source codes are available online (34) The notations and parameter values adopted in the simulations are summarized in Table 2.

Emergence of Clans with the Incest Taboo. This one-trait model was simulated by changing the parameters shown in Table 2. (t, p) values of lineages in a community after 500 steps of simulation are plotted in Fig. 3 *A–C*, and their time series are shown in Fig. 3 *D–F*. As in Fig. 3 *B* and *C*, they form a few clusters under a certain range of parameter values. Here, we used the X-means method to optimize the number of clusters by adopting the Bayesian information criterion (35).

When clusters are formed as shown in Fig. 3, lineages in a cluster prefer those in one of the other clusters as their mates, which is determined by comparing the trait and preference values of cluster centers. Thus, people get married not within a cluster but across clusters. Marriage exchange among clusters emerges. In Fig. 3*B*, two clusters—namely, A (red) and B (blue)—conduct direct exchange as A ⇔ B, whereas in Fig. 3*C*, three clusters—namely, A (red), B (green), and C (blue)—conduct indirect exchange as A ⇒ B ⇒ C ⇒ A. We define these clusters as clans. Here, lineages in the same clans cooperate because of social relatedness, and those in different clans are united by marriage. Because siblings of the same sex belong to the same clan, a father's brother belongs to the same clan, and, thus, marriage with a father's brother's daughter is prohibited, when the incest taboo is organized. In contrast, because siblings of the opposite sex belong to a different clan by the move of brides to husbands' lineages, a mother's brother belongs to the mate's clan, and, thus, marriage with a mother's brother's daughter is promoted. Such distinction between the cross and parallel cousins is observed in the different social relationships, as reported in ethnographic records (2). The clans here are fluid compositions; this observation is consistent with that of a previous study (36). In this manner, the social kinship with marriage exchange in indigenous societies spontaneously emerges.

The preferential relationships, resulting in the incest taboo, are sustained by multilevel selection. The relationships are cyclic unless there would be some lineages without having or sending brides. Then, we define the length of the marriage cycle (C_m) by counting the number of clans engaged in the cycle. Time series of C_m are shown in Fig. 4 with and without the community-level selection, in addition to lineage-level selection. Thus, the number of communities in the system is one in Fig. 4*A* and 100 in Fig. 4*B*. If there is just one community, the structure of marriage exchange will soon collapse because of random drifts in trait t and preference p. Whereas if there exist many communities competing with each other, collapsed communities will be eliminated, and, as a whole, the structure with $C_m \geq 2$ is sustained, when d_c and d_m are sufficiently large (orange line in Fig. 4*B*).

By imposing this multilevel selection, we simulated the model over 500 steps and 50 times for every condition to obtain C_m. Recall that the existence of the incest taboo is equivalent to $C_m \geq 2$. Fig. 5 shows the phase diagram of the incest taboo. Here, society is defined to achieve the incest taboo when more than 90% of communities satisfy $C_m \geq 2$ (see *SI Appendix*, Fig. S1 for the dependence of C_m on d_c and d_m). As d_c increases, there is more pressure to eliminate isolated lineages without cooperators so that lineages form clusters. In contrast, large d_m creates pressure to eliminate lineages with many mating rivals, so that lineages become diverged. Hence, if both d_c and d_m are sufficiently large, lineages are clustered and diverged, leading to the formation of clans with marriage exchange. Fig. 5 also shows that as μ increases, it becomes more difficult to establish

Table 2. Parameters

Symbol	Explanation	Value
r	Intrinsic growth rate	4
μ	Mutation rate for t_i and p_i	Variable
d_c	Decline of death rate by cooperation	Variable
d_m	Increment of death rate by mating conflict	Variable
σ	Tolerance for similarity	1.0
Pop.	Initial population in a lineage	5
N_l	Initial number of lineages in a village	50
N_c	Number of communities in a system	100

[†]In reality, cooperation is achieved after the marriage. Thus, p_i and the actual t_j of a bridegroom's lineage *j* may slightly differ. Here, we neglect this slight deviation, because the difference is of the order of μ ($\ll \sigma$), according to the result of the simulation, and the representation of cooperation solely by the present (t, p) is easier to formulate.

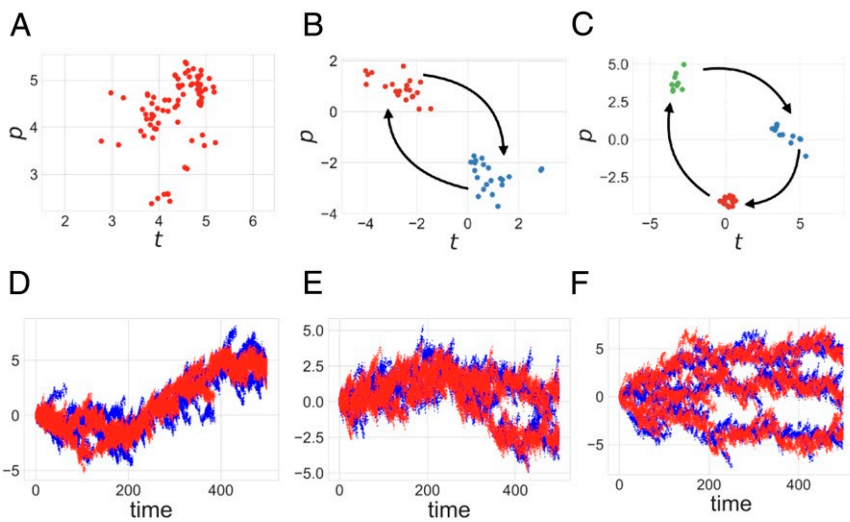

Fig. 3. Example of clan separation. (*A–C*) (t, p) values for lineages in a community after 500 calculation steps. Clusters of lineages are generated, which are clans. The arrow shows the preferential relationship that corresponds to ⇒ in Fig. 1. (*D–F*) Time series of separation of lineages. Temporal evolution of the values of traits and preferences of lineages in a community are represented in blue and red, respectively. Parameters are $d_c = d_m = 0.1$ in *A* and *D*; $d_c = d_m = 0.5$ in *B* and *E*; and $d_c = 0.5$, $d_m = 2.0$ in *C* and *F*; $\mu = 0.1$ for all cases.

the incest taboo. For larger μ, the changes in traits and preferences are larger, so that the structure of marriage exchange is more fragile.

Here, lineages spontaneously form clans and the incest taboo emerges. The structures with various C_m values emerge as in Fig. 3. In this model, however, children always belong to their fathers' clans and, thus, $C_d = 1$. Thus, this model is insufficient for modeling some kinship structures, such as the restricted exchange shown in Fig. 1*C*.

Model 2: Two-Trait Model

Recalling that children can belong to different clans from parents by inheriting traits from both parents, as in Fig. 1*C*, we extended the model to have two culturally independent traits and preferences, $\boldsymbol{t} = (t_1, t_2)$ and $\boldsymbol{p} = (p_1, p_2)$. These traits are inherited maternally or paternally. Because there are only two sexes, there exist only two pathways of inheritance. If several traits are inherited via father/mother, they can be effectively regarded as one trait. Thus, the two-trait model is sufficient for considering kinship structures with multiple traits.

In the previous model, children belong to and inherit t, p from their father's lineage. In reality, however, a child can inherit some traits from father and other traits from mother, as observed in many indigenous societies (2, 37, 38) (e.g., Fig. 1*C*). For example, he or she inherits land from the father and the name of the mother. We assume that children inherit t_1, p_1 from their fathers. Next, each lineage can choose whether they inherit t_2, p_2 from the father or mother. The former (latter) corresponds to a unilineal (bilateral) descent rule. Suppose men in lineage i marry women in lineage j. If lineage i adopts a unilineal descent rule, children possess traits and preferences $\boldsymbol{t^i}$, $\boldsymbol{p^i}$. By contrast, if a bilateral descent rule is adopted, lineage i adopts the trait and preference to $\boldsymbol{t} = (t_1^i, t_2^j)$, $\boldsymbol{p} = (p_1^i, p_2^j)$. For both cases, children's lineages and fathers' lineages' kin cooperate. In the initial generation, either of the rules is assigned at random, and the rule would switch with a probability $\mu_d = 0.01$.

Emergence of Kinship Structures. Lineages are clustered into clans in $(\boldsymbol{t}, \boldsymbol{p})$ space as with one-trait model. For the two-trait model, descent relationships of clans emerge, as well as those of marriage. Fig. 6 shows examples of the final state after 500 steps of simulation. In Fig. 6*A*, there are three clans where only the first trait is clustered into three groups (Fig. 6 *A*, *1*), whereas the second is not (Fig. 6 *A*, *2*). The green clan prefers red, the red prefers blue, and the blue prefers green. The relationship of marriage exchange forms a three-period cycle. Thus, generalized exchange in Fig. 1*D* emerges. In Fig. 6*B*, there are four clans, where each trait is clustered into two, and thus two-by-two clans are formed (Fig. 6 *B*, *1* and *2*). Considering the two-dimensional distance of preference relationships, red and purple clans prefer each other, as do blue and green clans. Here, most lineages adopt bilateral descent rules. A child of a father in a red clan and a mother in a purple clan inherits t_1 from red and t_2 from purple and, thus, belongs to a green clan. Hence, restricted exchange in Fig. 1*C* emerges. Such structures are classified as shown in Fig. 1, by computing the marriage cycle (C_m) and descent cycle (C_d).

Fig. 7 shows the phase diagram of kinship structures. We use the classification in Fig. 1. Incest taboo is not generated (orange in Fig. 7) when d_m is small, as in the previous model. As d_m increases, dual organization (green) appears, and, thus, the incest taboo emerges. Then, more sophisticated structures as generalized exchange (red) and restricted exchange (purple) emerge. When both d_m and d_c are large, population suppression is so strong that it is hard to achieve high cooperation and low competition to overcome the suppression. Hence, all communities are extinct in the upper right region in Fig. 7 (blue). In this model, other structures with $C_m > 2$ and $C_d > 1$, such as the

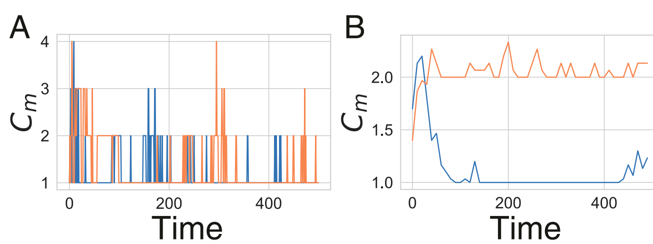

Fig. 4. Time series of C_m. (*A*) Time series of C_m in a single community, i.e., under lineage-level selection without community-level selection. (*B*) Time series of the average C_m over 100 communities both under lineage- and community-level selection. $\mu = 0.01$. Blue and orange lines show the results under parameter values of $d_c = d_m = 0.1$ and $d_c = d_m = 0.5$, respectively.

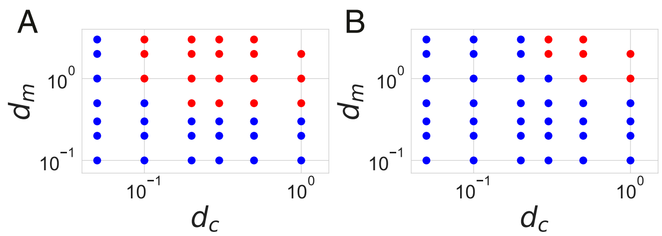

Fig. 5. Phase diagrams on the emergence of the incest taboo against the parameters d_c and d_m. At the parameter values with red points, the frequency of incest taboo is more than 0.9, whereas with blue points, it is less than 0.9. (*A*) $\mu = 0.03$. (*B*) $\mu = 0.1$.

so-called Murungin structure, are scarcely observed. This time, various structures emerge, depending on the relative weight of d_c and d_m. As the relative weight of d_m increases, the emergent structure generally changes from the dual organization to generalized exchange and then to restricted exchange, because a larger d_m/d_c favors reducing mating rivals at the expense of cooperators. Furthermore, this phase diagram is robust against the choice of the initial values. For example, even if generalized or restricted exchange is set initially, it will soon collapse when d_c and d_m are small.

Restricted exchange needs the separation of two traits by each cluster, whereas generalized exchange needs that of only a single trait, as shown in Fig. 6. With larger μ, clan separation is more fragile, as shown in Fig. 5, and thus restricted exchange is replaced by generalized exchange (see *SI Appendix*, Fig. S2 for diagrams with larger and smaller μ values).

Discussion

We have shown that the incest taboo emerges spontaneously by considering the cooperation of kin and mates, as well as the mating conflict of rivals. Furthermore, all of the kinship structures observed in the indigenous society emerge in the model with two traits and preferences. When clans are formed as clusters of lineages with close values of traits and preferences, marriage within the same clan is prohibited. Thus, people in the same clan are recognized as "siblings as a category." Because women change lineages after marriage, a distinction between the cross and parallel cousins is made, such as mother's brother's daughters and father's brother's daughters, which some ethnographic records emphasized, but previous biological or mathematical studies ignored (2). Here, as a result of the dynamics and clustering of lineages, the social categories of siblings and the incest taboo simultaneously emerge.

A small "mutation rate" μ facilitates the emergence of the incest taboo and sophisticated kinship structures. The speed of change in cultural traits is known to be faster (i.e., μ is larger) in societies with mass teaching by teachers than in those with education within families (32). Furthermore, a small μ indicates that people likely marry according to the mate preferences of parents, which requires strong lineage connections. As the societies are centralized and parental influence is decreased, μ increases. Then, sophisticated kinship structures disappear, as shown in our model.

Generalized exchange and dual organization emerge when cooperation is important, whereas restricted exchange emerges when the avoidance of mating conflict is more important. This suggests that dual organization is similar to generalized exchange rather than restricted exchange, in contrast to Lévi-Strauss's classification. If the mating conflict is little, the community with a small number of clans united by marriage is fitted. As mating conflict becomes stronger, it would be better to separate clans within villages to avoid conflicts. Then, restricted exchange emerges. In this case, however, each clan has more than one noncooperative clan, such as B_1 for A_1 in Fig. 6. Thus, restricted exchange emerges only when the avoidance of conflict is more important than cooperation, i.e., d_m/d_c is sufficiently large.

The present study sheds light on why different kinship structures are adopted in different societies. Restricted exchange is mainly observed in hunter-gatherer societies, such as the Aboriginal in Australia and Yanomamo in the Amazon, whereas generalized exchange is observed in Chinese peasants, agricultural societies such as the Kachin in Myanmar, and fishery societies such as the Nivkh in Russia (2, 39–43). Studies on the Aboriginal and Yanomamo reported that conflicts over females often cause fights among lineages in the hunter-gatherer societies (21–23). By contrast, agriculture needs massive cooperation, including that for wars over land or food (21). In fishery societies, massive fishing and competition for access to fishing rights require cooperation (44, 45). To conclude, the tribes under stricter mating conflict conduct restricted exchange, whereas those requiring stronger cooperation conduct generalized exchange, as is consistent with the observation.

Of course, for a better understanding of the emergence of kinship structures, detailed analyses are needed on the degree of cooperation and mating conflict in each indigenous society—for example, by examining the cause of conflicts and deaths therein. Furthermore, it is necessary to clarify the relationship between lifestyles and parameters—d_c, d_m, and μ.

The present model has some limitations. First, we did not consider the direct interaction of communities. However, massive wars between communities, for example, need a strong tie among lineages, and, thus, it can be implicitly included as the increase of d_c. Second, we use the same fixed value of σ for measuring social relatedness and the possibility of marriage. In reality, lineages can propose marriage to more or fewer lineages than others. However, with sufficiently large d_m, those proposed to more lineages would be eliminated by stricter mating conflict, whereas those proposed to fewer lineages would suffer from lack of mates. Thus, even if we introduce the evolution of σ_m for the possibility of marriage, it would remain finite. Hence, for simplicity, we set $\sigma_m = \sigma$. Third, our model cannot explain the emergence of social strata as Lévi-Strauss discussed (2) or relationships between kinship structures and social systems as Todd discussed (46). For such issues, one needs to consider economic activities and/or social factors besides kinship—for example,

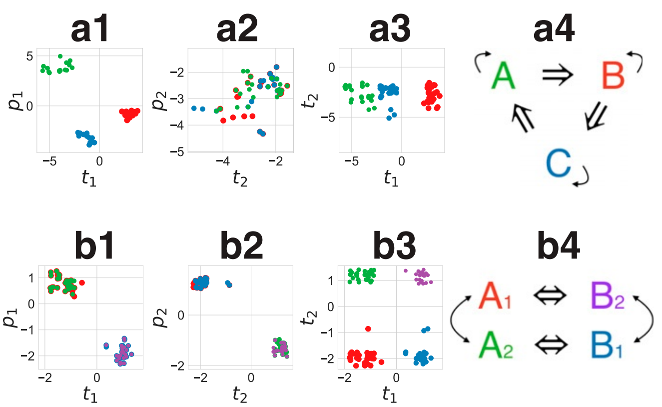

Fig. 6. Examples of emergent structures. ***t***, ***p*** values for lineages in a community after 500 steps of simulation. Images show the $t_1 - p_1$ map, $t_2 - p_2$ map, $t_1 - t_2$ map, and the corresponding structure from left to right. Kinship structures emerge as the marriage and descent relationships of clusters. (*A*) Generalized exchange. Green, red, and blue clusters correspond to clans A, B, and C, respectively, in Fig. 1. (*B*) Restricted exchange. Red, green, blue, and purple clusters correspond to clans A_1, A_2, B_1 and B_2 respectively, in Fig. 1.

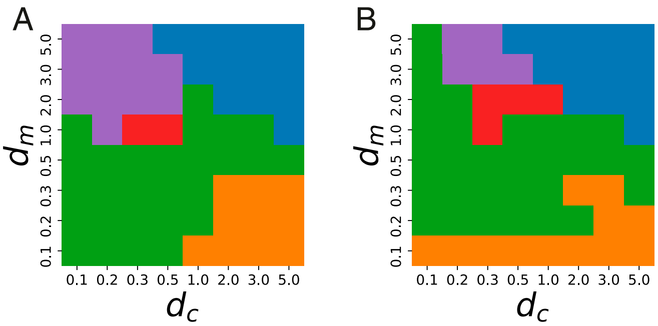

Fig. 7. Phase diagrams of kinship structures against the parameters d_c and d_m. Images show the classes of structures that appear most frequently under several conditions, according to the classification in Fig. 1. Incest structure is plotted in orange, dual organization in green, generalized exchange in red, and restricted exchange in purple, whereas the conditions with which all communities are extinct are plotted in blue. (*A*) $\mu = 0.01$. (*B*) $\mu = 0.1$.

wife-purchasing marriages that appear under the unbalanced population among clans.

To conclude, we have shown that the incest taboo and kinship structures spontaneously emerge by considering social tie and competition by marriage. The incest taboo emerges when the necessity of cooperation, the conflict for mating, and cultural similarity across generations are sufficiently large. The distribution of kinship structures is explained in terms of the strengths of cooperation and conflict. Generalized exchange emerges when the former is higher, whereas restricted exchange emerges when the latter is stronger.

Leach (47) emphasized the general logic underlying the structural pattern of indigenous societies. In addition to field studies, theoretical studies by simple constitutive models, as we present here, will open a door for social anthropology to construct a general theory therein.

Materials and Methods

To simulate the population dynamics considering cooperation and conflict among lineages, the possibility of marriage and the degrees of cooperation and conflict were measured by a Gaussian function of traits and preferences. For example, the degree of cooperation between social kin is given by $\exp(-(t_i - t_j)^2/\sigma^2)$. Furthermore, we introduce the suppression term of the population with *friend* and *rival*. In the present model, the suppression term is represented by $1/(1 + d_c \times (1 - friend))$ and $1/(1 + d_m \times rival)$. In these forms, the suppression of population is relaxed from $1/(1 + d_c)$ to 1 by cooperation as *friend* increases from 0 to 1, whereas it is amplified from 1 to $1/(1 + d_m)$ with the increase of *rival*. Note that the results to be presented are qualitatively independent of these specific forms as long as cooperation enhances and conflict suppresses the population.

We adopted the following algorithm for the population change in lineages. For lineage i of time step n, the number of boys, girls, unmarried men, unmarried women, and couples are denoted by B_i^n, G_i^n, M_i^n, F_i^n, and C_i^n, respectively. The intrinsic growth rate is denoted by r. Next, we represent the set of lineages in a community by Λ and the set of lineages that accept lineage i as a husband by Λ_i. Then, the population change in lineage i is given by

$$\lambda_i^n = r \times C_i^{n-1},\ B_i^n = \mathrm{Poisson}(\lambda_i^n),\ G_i^n = \mathrm{Poisson}(\lambda_i^n), \quad [1]$$

$$t_i^n = t_i^{n-1} + \eta,\ p_i^n = p_i^{n-1} + \eta, \quad [2]$$

$$friend_i^n = \sum_{j \in \Lambda} \frac{\exp\left(-\min\left(|t_i^n - t_j^n|, |p_i^n - t_j^n|, |p_j^n - t_i^n|\right)^2/\sigma^2\right)}{\#\Lambda}, \quad [3]$$

$$rival_i^n = \sum_{j \in \Lambda} \frac{\exp\left(-\left(p_i^n - p_j^n\right)^2/\sigma^2\right)}{\#\Lambda}, \quad [4]$$

$$M_i^n = \frac{1}{1 + d_m \times rival_i^n} \times \frac{1}{1 + d_c \times (1 - friend_i^n)} B_i^n, \quad [5]$$

$$F_i^n = \frac{1}{1 + d_m \times rival_i^n} \times \frac{1}{1 + d_c \times (1 - friend_i^n)} G_i^n, \quad [6]$$

$$C_i^n = \min\left(M_i^n, \sum_{j \in \Lambda_i} F_j^n\right). \quad [7]$$

Couples in each lineage give birth to children following the Poisson distribution, as given by Eq. **1**. Noise component is added to (t, p), following the uniform distribution in $[-\mu, \mu]$ as Eq. **2**. As they grow up, the population is suppressed with regards to *friend* and *rival*, as given by Eqs. **3**–**6**. People get married according to the traits and preferences of their lineages. After marriage, the women move into husbands' lineage, as in Eq. **7**. Here, we assumed monogamy, but the result is qualitatively independent of such a marriage system.

Data Availability. Source codes for these models can be found at https://github.com/KenjiItao/clan.git.

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1. R. Fox, *Kinship and Marriage: An Anthropological Perspective* (Cambridge University Press, Cambridge, UK, 1983), vol. 50.
2. C. Lévi-Strauss, *Les Structures Élémentaires de la Parenté* (Presses Universitaires de France, Paris, France, 1949).
3. K. Maddock, Alliance and entailment in Australian marriage. *Aust. J. Anthropol.* **7**, 19–26 (1969).
4. B. Malinowski, *Sex, Culture, and Myth* (R. Hart-Davis, London, UK, 1963).
5. G. P. Murdock, *Social Structure* (Macmillan, New York, NY, 1949).
6. K. Hopkins, Brother-sister marriage in Roman Egypt. *Comp. Stud. Soc. Hist.* **22**, 303–354 (1980).
7. W. H. Durham, *Coevolution: Genes, Culture, and Human Diversity* (Stanford University Press, Stanford, CA, 1991).
8. K. R. Hill *et al.*, Co-residence patterns in hunter-gatherer societies show unique human social structure. *Science* **331**, 1286–1289 (2011).
9. A. K. Romney, P. J. Epling, A simplified model of Kariera kinship. *Am. Anthropol.* **60**, 59–74 (1958).
10. L. R. Hiatt, Authority and reciprocity in Australian aboriginal marriage arrangements. *Aust. J. Anthropol.* **6**, 468–475 (1967).
11. L. R. Hiatt, *Arguments About Aborigines: Australia and the Evolution of Social Anthropology* (Cambridge University Press, Cambridge, UK, 1996).
12. K. Aoki, Y. Ihara, M. W. Feldman, "Conditions for the spread of culturally transmitted costly punishment of sib mating" in *Explaining Culture Scientifically*, M. J. Brown, Ed. (University of Washington Press, Seattle, WA, 2008), pp. 100–116.
13. N. W. Thornhill, The evolutionary significance of incest rules. *Ethol. Sociobiol.* **11**, 113–129 (1990).
14. J. P. Treuil, "*Emergence of kinship structures: A multi-agent approach*" in Artificial Societies: The Computer Simulation of Social Life. N. Gilbert, R. Conte, eds. (Routledge, Abindgon, UK, 1987), pp. 48–71.
15. A. Weil, "Sur l'etude algébrique de certains types de lois de mariage" in *Les Structure Élémentaires de la Parenté*, C. Lévi-Stauss, Ed. (P.U.F, Paris, France, 1949), pp. 279–285.
16. R. R. Bush, "An algebraic treatment of rules of marriage and descent" in *An Anatomy of Kinship*, H. C. White, Ed. (Prentice-Hall, Englewood Cliffs, NJ, 1963), pp. 159–172.
17. R. R. Bush, *An Algebraic Treatment of Rules of Marriage and Descent* (1963).
18. M. Alvard, Kinship and cooperation: The axe fight revisited. *Hum. Nat.* **20**, 394–416 (2009).
19. R. McElreath, R. Boyd, P. J. Richerson, Shared norms and the evolution of ethnic markers. *Curr. Anthropol.* **44**, 122–130 (2003).
20. R. A. Hammond, R. Axelrod, The evolution of ethnocentrism. *J. Confl. Resolut.* **50**, 926–936 (2006).
21. J. Helbling, The dynamics of war and alliance among the Yanomami. *Sociologus* **1** (suppl.), 103–116 (1999).
22. N. A. Chagnon, Life histories, in blood a tribal revenge, and population warfare. *Science* **239**, 985–992 (1988).
23. G. Blainey, *Triumph of the Nomads: A History of Aboriginal Australia* (Overlook Press, New York, NY, 1976).
24. K. F. Otterbein, The origins of war. *Crit. Rev.* **11**, 251–277 (1997).
25. A. Traulsen, M. A. Nowak, Evolution of cooperation by multilevel selection. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 10952–10955 (2006).
26. C. S. Spencer, E. M. Redmond, Multilevel selection and political evolution in the valley of Oaxaca, 500–100 BC. *J. Anthropol. Archaeol.* **20**, 195–229 (2001).
27. N. Takeuchi, P. Hogeweg, K. Kaneko, The origin of a primordial genome through spontaneous symmetry breaking. *Nat. Commun.* **8**, 250 (2017).
28. D. S. Wilson, Altruism and organism: Disentangling the themes of multilevel selection theory. *Am. Nat.***150**, S122–S134 (1997).

29. D. S. Wilson, E. O. Wilson, The quarterly review of biology. *Lancet* **207**, 918 (2003).
30. T. Peter, Warfare and the evolution of social complexity: A multilevel-selection approach. *Struct. Dyn. J. Anthropol. Relat. Sci.* **4**, 1–37 (2010).
31. P. Turchin, S. Gavrilets, Evolution of complex hierarchical societies. *Soc. Hist. Evol.* **8**, 167–198 (2009).
32. L. L. Cavalli-Sforza, M. W. Feldman, *Cultural Transmission and Evolution: A Quantitative Approach* (Monographs in Population Biology, Princeton University Press, Princeton, NJ, 1981), vol. 16.
33. D. Sperber, L. A. Hirschfeld, The cognitive foundations of cultural stability and diversity. *Trends Cognit. Sci.* **8**, 40–46 (2004).
34. K. Itao, Evolution of Kinship Structures. GitHub. https://github.com/KenjiItao/clan. Deposited 3 December 2019.
35. D. Pelleg, A. W. Moore, "X-means: Extending k-means with efficient estimation of the number of clusters" in *Proceedings of the Seventeenth International Conference on Machine Learning*, P. Langley, ed. (Morgan Kaufmann Publishers Inc., San Francisco, CA, 2000), pp. 727–734.
36. C. T. Palmer, B. E. Fredrickson, C. F. Tilley, Categories and gatherings: Group selection and the mythology of cultural anthropology. *Evol. Hum. Behav.* **18**, 291–308 (1997).
37. G. P. Murdock, Double descent. *Am. Anthropol.* **42**, 555–561 (1940).
38. J. Goody, The classification of double descent systems. *Curr. Anthropol.* **2**, 3–25 (1961).
39. L. E. Sponsel, Yanomami: An arena of conflict and aggression in the Amazon. *Aggress. Behav.* **24**, 97–122 (1998).
40. M. Houseman, D. White, "Taking sides: Marriage networks and Dravidian kinship in Lowlands South America" in *Transformations of Kinship*, M. Godelier, T. Trautmann, F. Tjon Sie Fat, eds. (Smithsonian Institution Press, Washington, D.C., 1998), pp. 214–243.
41. E. R. Leach, *Political Systems of Highland Burma: A Study of Kachin Social Structure* (G. Bell and Sons, Ltd., London, UK, 1964).
42. M. La Raw, "Toward a basis for understanding the minorities in Burma: The Kachin example" in *Southeast Asian Tribes, Minorities, and Nations*, P. Kunstadter, Ed. (Princeton University Press, Princeton, NJ, 1967), vol. 1, pp. 125–146.
43. L. Black, The Nivkh (Gilyak) of Sakhalin and the Lower Amur. *Arctic Anthropol.* **10**, 1–110 (1973).
44. E. Bennett *et al.*, Towards a better understanding of conflict management in tropical fisheries: Evidence from Ghana, Bangladesh and the Caribbean. *Mar. Policy* **25**, 365–376 (2001).
45. J. M. Acheson, Anthropology of fishing. *Annu. Rev. Anthropol.* **10**, 275–316 (2003).
46. E. Todd, *La Diversité du Monde: Structures Familales et Modernité* (Seuil, Paris, France, 1999).
47. E. R. Leach, *Rethinking Anthropology* (LSE Monographs on Social Anthropology, Berg Publishers, Oxford, UK, 1961), vol. 22.