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Teaching is associated with the transmission of opaque culture and leadership across 23 egalitarian hunter-gatherer societies

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Despite extensive work on the evolution of cooperation, the roles of teaching and leadership in transmitting opaque cultural norms—foundations of cooperative behaviors—are underexplored. Similarly, while teaching is well-studied in the evolution of instrumental culture, little attention is given to its role in transmitting opaque culture, such as social values and norms. Transmitting opaque culture often requires teaching, and group leaders are well-positioned to facilitate this process. Using comparative ethnographic data, we explore teaching, leadership, and instrumental versus opaque culture by examining whether opaque culture is primarily transmitted via teaching, which age groups tend to learn these norms, and whether leaders are disproportionately involved in teaching. Drawing on ethnographic data from 23 egalitarian foraging societies, we find teaching is more strongly associated with transmitting cultural values and kinship knowledge than subsistence skills and is closely linked to opaque culture and leadership. Leader-directed teaching may drive cooperation, suggesting new research avenues.

The success of human societies is fundamentally linked to our ability to internalize and adhere to complex social norms¹⁻⁴. These norms are often opaque-meaning they are not readily inferred through direct observation or imitation-making their learning particularly challenging. Unlike instrumental culture, which often involves observable and directly learnable skills, opaque cultural elements require deeper cognitive processing, contextual understanding, and explicit instruction for effective transmission. A central aim within the field of cultural evolution is to understand how complex, opaque cultural norms are effectively passed down through generations^{5,6}. As a feature of our evolved life history strategy, teaching is a universal and significant aspect of human social learning⁷⁻¹⁰. Teaching typically begins in infancy^{11,12}, but opaque culture is understood and internalized by middle childhood^{13–15}. As such, the teaching of opaque culture may be primarily targeted towards older children, reflecting their more developed social cognition and abstract reasoning abilities^{16,17}.

Like teaching, leadership is also a human universal¹⁸. Evolutionary scholars define leaders as individuals who disproportionately influence group members' views, cognition, or behaviors to achieve shared

goals¹⁹⁻²¹. Leaders emerge in all social groups, including families, residential communities, extended kin networks, and economic or poliorganizations²²⁻²⁴, and are often characterized tical as hypercooperators^{19,25}. At the community level, leaders often attain their positions of influence through the respect garnered by their success in culturally valued domains, especially in more egalitarian social contexts²⁶. Core services leaders provide to followers include advising, counseling on proper behavior, and teaching-this is true across diverse nonindustrial societies and in postindustrial contexts^{18,27,28}. Leaders can provide such services more effectively and efficiently than non-leaders because of their disproportionate social influence, specialized knowledge, and opportunities for one-to-many transmission²⁹. In many societies, the transmission of social norms and values is closely tied to both teaching and leadership. In a representative cross-cultural sample of largely nonindustrial societies, Barry and colleagues³⁰ found that authority figures, including community leaders and elders, play a crucial role in the early socialization of children, imparting cultural norms through both direct instruction and structured learning environments. Being described as knowledgeable

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or intelligent was found to be the most common quality of leaders in a sample of the ethnographic record of 59 diverse, largely nonindustrial societies¹⁸. In another similar sample, individuals with expertise in observable motor skills (i.e., instrumental culture) were often teachers with specialized knowledge associated with providing particular services like medical care³¹.

A deeper understanding of how complex social norms are transmitted through teaching can yield multiple societal benefits³². Better models of norm transmission can enhance educational outcomes by aligning teaching strategies with cultural expectations³³, improve public health initiatives through culturally tailored campaigns³⁴, and facilitate economic development by driving local business practices and social contracts towards group and individually beneficial outcomes^{35,36}. Here, we investigate the social learning of cooperative behaviors and linkages with teaching and leadership among ethnographically described egalitarian hunter-gatherers. Egalitarian hunter-gatherers can inform evolutionary theoretical models given that (1) egalitarianism is believed to have deep evolutionary roots among the genus Homo, and (2) the diversity of socio-political organization across human societies during the Pleistocene would have likely developed from cooperative norms evolved in egalitarian socioecological contexts. Therefore, cultural packages of opaque cooperative norms were, putatively, the foundation for the emergence of more intensified and diverse social, economic, and political structures during the Upper Pleistocene and into the Holocene^{37,38}.

Theories associating leadership and cultural transmission have primarily focused on imitation²⁶, with relatively limited attention paid to leader-directed teaching as a mechanism for the evolution of opaque culture. Much of the empirical work on cultural transmission has also predominantly focused on imitation as a mechanism for learning, with less attention paid to the role of teaching³⁹⁻⁴². When social learning scholars have examined teaching, most empirical and theoretical work has concentrated mainly on instrumental culture, with less emphasis on the teaching of opaque culture^{12,43,44}. A refined understanding of these features of human sociality can provide new insights into our species' cultural and ecological success. In what follows, we discuss the role of leaders in promoting cooperation-enhancing social norms, emphasize the cooperative nature of teaching⁴⁵, and outline the distinction between instrumental and opaque culture. We then present results from text analyses, penalized regression analyses, and Bayesian multi-level modeling using comparative ethnographic data from a sample of egalitarian hunter-gatherers. Our results collectively suggest new paths for research on teaching, social influence, and opaque cooperative norms, which we frame as the leader-directed teaching hypothesis.

Given their strong emphasis on personal autonomy, egalitarian hunter-gatherer community members are not necessarily obligated to cooperate, and generally, leaders lack coercive capacity, and there is limited social stratification⁴⁶⁻⁵¹. The transmission and maintenance of cooperative norms from generation to generation are collective action problems egalitarian societies must overcome via social and normative behavioral strategies, rather than institutional or coercive control. Among egalitarian hunter-gatherers, leaders are often respected, skilled in culturally valued domains, accomplished, have reputations for sound decision-making, strong oratory skills, and embody cultural ideals for proper behavior^{22,52}. Recurrent descriptions of leaders as knowledgeable, intelligent, experienced, and accomplished indicate high levels of neural capital18,53-55, or the components of embodied capital⁵⁶ associated with cognition and learning. Within groups, an important function of leaders includes using their expert knowledge and intelligence to provide counsel and direction to followers-essential elements of teaching^{18,57,58}. In turn, leaders benefit from influencing followers by enhancing their social status, access to material resources, strengthening alliances, opportunities for marriage and mating, and promoting group cohesion¹⁸-all of which promote their own wellbeing, survival, and success. This suggests that leader-directed teaching may be an important mechanism for transmitting complex social norms. Thus, here, we investigate whether leaders play a disproportionate role in teaching opaque culture and how this teaching influences the perpetuation of cooperation-enhancing norms across generations.

Following cognitive psychologists and evolutionary anthropologists7,10,44,59, we define teaching as a process of social learning occurring when an individual modifies their behavior at some cost to themselves, specifically to impart knowledge, skills, or behaviors to a learner. It is a taxonomy of behaviors that solve adaptive problems created by the pressures for effective social learning7. Although teaching is not a uniquely human behavior^{7,45,60}, the cognitive basis, process, function, and qualitative nature of human teaching represents a significant evolutionary development in the hominin lineage^{61,62}. Unlike other forms of social learning, such as observation, imitation, or collaborative learning^{49,63}, teaching requires deliberate effort to overcome informational asymmetries and facilitate a directional transfer of knowledge. Teaching is thus inherently cooperative, involving not only the investment of time and resources by the teacher (parent, elder, ritual leader, or technical specialist) but also the active engagement of the learner. Both the teacher and learner may thus benefit from this interaction, but each also incurs at least the opportunity costs of their participation^{32,45,64-66}.

As the scope and complexity of essential cultural information broaden, teaching becomes more critical for effective cultural transmission⁶⁷. Teaching begins as early as infancy and is a common practice with young children. Hewlett & Roulette¹², for instance, documented teaching behaviors in infancy among Aka hunter-gatherers in the Congo Basin, where caregivers used ostensive cues like pointing and vocalizations to guide learning. Boyette & Hewlett¹¹ further found that while foundational social norms are reinforced through teasing and feedback starting in early childhood, direct instruction-a more intensive form of teaching⁷-becomes more common as children grow older. During middle childhood, teaching not only increases in frequency but is also targeted toward transmitting skills that are challenging to learn, such as spear hunting, basketry, sharing, and cooperation^{11,68-70}. By ten vears, the development of several cognitive processes, including analogical reasoning, relational processing, and episodic memory, contribute to increased capacities for abstract reasoning¹⁷. At this stage, children are thus able to grasp complex and opaque cultural information, including supernatural beliefs^{13,14} and sharing norms^{15,71}. Considering that, for transmission to be successful, teachers must also be attuned to the pre-existing knowledge and cognitive maturity of the learner⁶⁹, here we investigate whether the teaching of opaque culture disproportionately occurs from middle childhood onwards.

Opaque culture refers to socially transmitted information that encompasses complex beliefs, values, norms, and practices. Unlike instrumental culture, which deals with tangible skills and material practices, opaque culture includes elements such as cultural history, social norms, kinship systems, appropriate language use (i.e., linguistic pragmatics), and the nuance of social etiquette^{1,72,73}, which are all embedded in broader, often non-intuitive cultural frameworks. It also includes symbolic culture, such as religious beliefs and representations, ethnic ideologies, and moral norms and values^{74,75}. Despite the fundamental role of opaque culture in human sociality, the evolutionary literature on social learning and teaching has primarily focused on the transmission of instrumental culture^{12,68,76–80}, with less emphasis on the processes of transmission associated with learning opaque culture.

Yet, opaque culture often requires explicit instruction or deep contextual understanding for effective transmission and is not easily inferred through direct observation or imitation¹⁰. The successful transmission of opaque culture may often involve a process of deuterolearning, where individuals not only learn specific cultural content but also develop the cognitive frameworks necessary to interpret and internalize this information within their cultural context⁸¹. Deuterolearning enables individuals to 'learn how to learn' complex norms, making it possible for them to apply and adapt abstract principles across various social situations. Ethnographic work on the Mbendjele BaYaka in the Congo Basin provides a compelling example⁸², where the concept of ekila serves as a moral framework guiding behavior and cooperation. From an early age, Mbendjele children learn about ekila through implicit pedagogical actions that provoke curiosity, such as observing parents' food taboos, or overhearing remarks about ekila. By middle childhood, however, more explicit teaching, such as explanation, advice, and initiation, is provided to help increasingly curious children understand the complex, non-observable rules of ekila. In turn, ekila acts as a vital structure for social harmony and well-being within the group⁸². Because opaque culture forms the foundation of much of human cooperation, here we investigate the mechanisms and socio-ecology associated with the transmission of such norms.

We aim to quantitatively evaluate relationships between evidence for teaching, potential differences for instrumental versus opaque culture, and associations with community leadership. We thus address three related questions:

- 1. Is teaching more prevalent in the transmission of opaque versus instrumental culture?
- 2. What age groups are primarily targeted for teaching opaque culture?
- 3. Are community leaders or socially influential individuals likely to engage in teaching?

By exploring these questions, here, we show that opaque culture is transmitted primarily through teaching, particularly from older individuals to children in middle childhood, and that community leadership is tied to such instructional processes. In contrast, instrumental culture is often learned through non-teaching social learning, such as observation and imitation, indicating distinct pathways for acquiring different forms of cultural knowledge.

Results

To address our aims, we conducted exploratory analyses using ethnographic data from the hunter-gatherer social learning (HGSL) database⁸³, developed by Garfield et al.⁶³ using the electronic Human Relations Area Files World Cultures Database (eHRAF), a digitized repository of thousands of primary ethnographic texts describing more than 300 societies. These texts have been subject coded by the HRAF at the paragraph level following the outline of cultural materials (OCM) subject classification system, which consists of more than 900 subject codes covering all aspects of social life and human culture. The OCM classification system is hierarchical and nested, consisting of major groups that are composed of conceptually related individual codes. The HGSL data includes a sample of ethnographic paragraphs that discuss social learning, their associated OCM codes, and researcher-coded variables on specific descriptions of social learning, where each paragraph may include multiple unique instances of social learning description (henceforth termed instances). The database structure and coding process is further described in the "Methods" section and in the Supplementary Methods.

Our analyses relied on three sources of evidence at both the instance and paragraph levels. First, we used the OCM major subject and individual codes associated with the sample paragraphs to visually explore relationships between teaching and instrumental versus opaque culture and to statistically model counts of evidence for teaching at the paragraph level using the complete set of major subject codes as predictors. We then used a term-document matrix developed from the corpus of ethnographic paragraphs and text analytic techniques to identify the lexical content of ethnographic paragraphs associated with the OCM codes, indicating transmission of both instrumental and opaque culture. Lastly, we regressed instances of teaching, compared to other non-teaching social learning processes, on researcher-coded variables from the ethnographic paragraphs using a Bayesian multilevel logistic regression model. The model included cultural domain, mode of social learning, and the age and gender of the learner as predictors and accounted for the hierarchical structure of our data. These analytic approaches leverage three distinct (albeit related) sources of evidence: researcher-coded data, eHRAF-provided data, and original text produced by ethnographers, from which results could potentially converge.

The HGSL data includes 149 ethnographic paragraphs describing social learning among 23 egalitarian hunter–gatherers (see Supplementary Note 1). These paragraphs collectively include 277 descriptions of instances of social learning. See Fig. S1 for the geographic distribution of the sample and Garfield et al.⁶³ for additional background information and descriptive results.

Opaque culture is primarily taught

The mosaic plot in Fig. 1 depicts the relationship between evidence for teaching versus non-teaching social learning (based on researchercoded data) and opaque versus instrumental cultural transmission (based on eHRAF OCM individual subject codes), at the instance level (see also Table S2). Although instrumental cultural transmission frequently occurs through both teaching and non-teaching social learning, opaque cultural information is predominantly transmitted through teaching, with relatively fewer instances of non-teaching social learning social learning. This descriptive relationship suggests the transmission of opaque culture is more commonly associated with teaching than other non-teaching social learning processes in the ethnographic record of hunter-gatherers.

Opaque culture positively predicts evidence for teaching

At the paragraph level, we used eHRAF's major subject codes as predictors of evidence for teaching using an elastic net Poisson regression model (with lasso penalty, i.e., many predictors are shrunk to zero). Figure 2 displays non-zero coefficients from this model, indicating positive and negative predictors of teaching. In this model, coefficients correspond to the subject code groups predictive of greater counts of evidence for teaching at the paragraph level. Under the optimized λ_{MIN} model the strongest positive predictor was Community Leadership with History And Culture Change, Kinship, Religious Practices, Religious Beliefs, and Traditional Ecological Knowledge being weak positive predictors-all features of opaque culture. The strongest negative predictors were Settlement Patterns; Art; Woodworking; Food Processing; Leather, Textiles, And Fabrics; and Sickness-all features of instrumental culture (excepting Art, which we return to in the "Discussion"). Under the more conservative λ_{1-SE} estimates, *Community Leadership* is the only meaningful positive predictor.

Lexical structure in the ethnography of instrumental versus opaque cultural transmission

Figure 3 displays non-zero coefficients from text analytic elastic net regression models (with lasso penalty). In these models, coefficient values correspond to the words within the complete 9945 word corpus (2909 unique words) of ethnographic paragraphs predictive of paragraphs being associated with the transmission of instrumental culture (i.e., paragraphs associated with the subject Code *868 Transmission of skills*) or with the transmission of opaque culture (i.e., paragraphs with either subject codes *867 Transmission of cultural norms* or *869 Transmission of beliefs*).

Positive predictors tentatively associate the transmission of instrumental culture with subsistence skills and knowledge (*bow, hunt, food, plant*), manufacturing (*canoe*), and learning via imitation (*imi-tate*). Negative predictors dissociate the transmission of instrumental culture with teaching (speculatively, *tell*), behavior (*act*), leadership or social status (*respect, power, role*), kinship relations (*wife, relative, family, generation, sibling*), and religion and cosmology (*religious, dream*).



Non-teaching social learning

Fig. 1 | Mosaic plot of relationship between evidence for teaching and nonteaching social learning versus evidence for instrumental and opaque culture. Mosaic plot illustrating the relationship between evidence for teaching and nonteaching social learning, based on a binary researcher-coded measure of teaching at the instance level (1 = evidence for teaching, 0 = evidence for non-teaching social learning) with opaque versus instrumental culture (evidence for Opaque culture if that instance stems from a paragraph associated with OCM codes Transmission of cultural norms (867) or Transmission of beliefs (869): evidence for Instrumental

For the transmission of opaque culture, predictors tentatively imply positive associations with social behavior (behavior, act, people), leadership and status (respect), the supernatural and religious domains (sacred, dream), and teaching (tell, instruct, teach). Negative associations with the transmission of opaque culture include learning by imitation (imitate), material technology (canoe), and subsistence (shoot, fish, food, plant, hunt(er)). Note terms associated with interpersonal and family relationships included positive predictors (people, wife, child) and negative predictors (girl, daughter, accompany).

Opaque culture is taught by older individuals to children in middle childhood

At the instance level, we used researcher-coded variables to predict evidence for teaching (compared to non-teaching social learning) using a Bayesian multi-level logistic regression model, which accounted for the hierarchical structure of our data (i.e., instances within paragraphs within documents). See Fig. 4, Supplementary Data 1, and Supplementary Note 3 for model results. Contrast analysis of posterior distributions identified meaningfully different posteriors between levels within *Domain, Age,* and *Mode,* but not *Gender* (see Table S6). Evidence for teaching was more likely to be associated with social learning of cultural values and kinship compared to social learning of subsistence skills ($\Delta \hat{\beta} = 2$, LCI 1.05, UCI 3) and manufacturing skills $(\Delta \beta = 1.8, \text{ LCI } 0.41, \text{ UCI } 3.3)$; middle childhood compared to early

Teaching

culture if that instance stems from a paragraph associated with the OCM code Transmission of skills (868)). Areas of the bars are proportional to the counts of instances in that category. For illustration purposes, we removed 19 instances where both opaque and instrumental culture were associated with the paragraph providing the instance, as these were nearly evenly distributed between the evidence for teaching and non-teaching social learning and, thus, were not informative (n = 258 instances). Raw data are given in Supplementary Note 2.

childhood ($\Delta \hat{\beta}$ = 2.5, LCI 0.889, UCI 4.12); and vertical or oblique modes of transmission compared to horizontal transmission (contrast of vertical and horizontal reported here: $\Delta \hat{\beta} = 3.2$, LCI 1.71, UCI 4.81).

Discussion

Based on comparative analyses of a sample of the ethnographic record of 23 egalitarian hunter-gatherers, we found evidence that the transmission of opaque culture was more frequently described as occurring via teaching, whereas instrumental culture was described as being transmitted via both teaching and other non-teaching forms of social learning (e.g., observation, copying). Older adults were more likely to be teachers and to teach individuals from middle childhood onwards. We also found that the OCM code Community Leadership was the strongest positive predictor of evidence for teaching in a penalized logistic regression model. In what follows, we illustrate these findings using the ethnographic record and interpret them considering cultural evolutionary theory.

Opaque culture was more commonly associated with teaching than instrumental culture. Features of opaque culture often include proscriptions for proper prosocial behavior and are more likely to require teaching specifically because they are opaque and difficult to observe or intuit. Aranda boys in the central Australian desert, for example, undergo an intense initiation process before marriage, designed to teach the intricacies of sharing norms among affinal kin. Penniman⁸⁴ (pp. 31–32) explains:



Fig. 2 | Results from elastic net lasso regression of counts for teaching within paragraphs (n = 145 paragraphs). Coefficients are standard Poisson regression coefficients (i.e., log count ratio per standard deviation of predictor). Model weights were set at the number of instances per paragraph. All variables were standardized before fitting. Coefficients under λ_{MIN} (right) represent the optimized model determined via 10-fold cross-validation. Coefficients under λ_{ISE} (left) are

those under λ within one standard error of λ_{MIN} (i.e., more conservative estimates). Triangles indicate positive coefficients, and circles indicate negative coefficients. Blue points indicate subject codes identified as opaque culture. Red points indicate subject codes identified as instrumental culture. Point color is for interpretation only and was not incorporated into the model fitting.

"The phratry into which a boy is to marry first tries him out in the Alkirakiwuma, throwing him into the air, beating, and generally hazing him...While he remains in a dazed condition, he is instructed in the primary duties of generosity about food, and of respect for those who are older and wiser. The food which he gets by his own endeavors must be divided among his future father-in-law, his own wife-to-be, and children. What remains is to be divided between himself and his mura and ipmunna women, the women by whose marriage his wife is determined."

Figure 2 revealed the subject codes positively associated with teaching exclusively captured opaque cultural domains (i.e., *Community Leadership, History and Culture Change, Kinship, Traditional Ecological Knowledge, Religious Practices*). In contrast, negative predictors primarily captured instrumental culture (e.g., *Settlement Patterns, Woodworking, Sickness, Food Quest*). *Art*, which we defined as opaque culture, but includes instrumental components, was also a negative predictor. Relatedly, text analysis of the transmission of opaque versus instrumental culture indirectly suggests that teaching (e.g., *tell, teach*) is associated with opaque culture. In contrast, other forms of social learning (e.g., *imitate*) are associated with instrumental culture (Fig. 3). Results from the Bayesian model of researcher-coded data (Fig. 4) further show that teaching is more likely for the transmission of cultural values and kinship than for manufacturing and subsistence, relative to non-teaching social learning.

These findings suggest that elements of instrumental culture may be more easily learned through less costly, non-teaching forms of social learning, such as observation and imitation, and horizontally in collaborative play groups. Shostak⁸⁵ (p. 107) describes opportunities for social learning of subsistence, manufacture, domestic work, and childcare among San children in southern Africa:

"Many of their [children's] games are imitations of adult activities: hunting, gathering, singing and trancing, playing house, and playing at parenthood and marriage. (Little children, carried about by older children, often become the "sons and daughters" of these "mothers and fathers.") Occasionally their imitations become reality–foraging roots and berries in the area just beyond the village, or even catching or trapping small animals and birds. Because little formal teaching is done–observation and practice are the basis of all learning–it is in these groups that children acquire many of the skills that will make them productive adults."

We also found that teaching was likely to be developmentally biased towards middle childhood and adolescence. These developmental stages are critical as individuals begin to understand the complexities of sociality. Wiessner⁸⁶ (p. 32321) illustrates, "as individuals mature, they become increasingly aware of the complexities of cooperation with people in the outer layers of the onion of society." In



Text analysis of hunter-gatherer social learning ethnography

opaque culture sacred behavior people stav dream wife unknown respect tell male churinga bidarky lifé occasion adult woman mean dame child term girdle feach instruct vine fruit learn mother uncle baby play huntei art swing girl encourage village dance hunt plant water accompany food skill kare household shoot canoe hold imitate -0.5 00 0.5 10

Words predicting transmission of

Fig. 3 | **Non-zero coefficients (log odds) from text analytic elastic net lasso regression models (***n* **= 145 paragraphs).** Coefficients indicate the words whose frequencies in each paragraph best predict association with **A** transmission of

instrumental culture or **B** transmission of opaque culture (based on eHRAF subject codes). Positive values are represented by blue triangles and negative values are represented by red circles.

addition to learning important subsistence skills, Innokentii⁸⁷ (p. 105) explains the emphasis on teaching of opaque cultural knowledge among Aleut adolescents in the North American Arctic:

"During the long training period, children learned not only the skills necessary to livelihood; they were also taught the proverbs and legends, the mores and values, the ideal and actual behaviors which constitute Aleut culture. Traditional controls were thus instilled in the children and the largely informal social structure was handed down."

Finally, we found that teaching was most likely to have occurred via oblique and vertical modes—that is, from adults. The OCM code *Community Leadership* was the strongest positive predictor of evidence for teaching in a penalized logistic regression model, further suggesting that, although any adult may teach, leaders are often adept teachers. Among the Ona in Tierra del Fuego, Gusinde⁸⁸ (p. 1455) explains that while anyone can teach during Klóketen, a boys' initiation ceremony, elder leaders take on the primary instructional role:

"To be sure, everyone present is entitled to admonish and teach the candidates, but he does this rather casually and fragmentarily. The first and coherent teachings are the duty of the leader or of the man whom he appoints for this. This teacher, as I should like to call him, should basically be a dignified and influential elder, with blameless character and moral superiority, for whose uprightness others show the greatest respect."

Leaders and prestigious individuals are ideal teachers because they will often be repositories of accumulated, domain-specific cultural information and because they tend to have teaching-related skills. For example, among Bolivian Tsimane, community leaders mediate disputes and possess traits such as extroversion, trustworthiness, confidence, and the ability to attract the attention of other group members^{20,89}. Among Ethiopian Chabu, elected community leaders scored higher on peer-rated measures of intelligence and prestige (i.e., respect) and were more likely to be nominated as ideal mentors for learning culturally important skills compared to non-leaders^{27,90}.

We now put forward the leader-directed teaching hypothesis to spark new research towards advancing our understanding of the evolution of cooperation, our capacities for teaching, our leaderfollower psychology, and human uniqueness^{91–95}. Cultural evolutionary theories of human cooperation have often emphasized the role of prestige and prestige-biased learning in influencing group behavior



Fig. 4 | Posterior distributions in log odds of coefficients from categorical-level predictors of the probability that an instance of social learning provided evidence for teaching compared to other, non-teaching social learning processes

(*n* = 277 instances). Points and error bars are posterior means with 95% credible intervals. The shaded areas and distributions respectively represent 50, 80, and 95% of the posterior distributions.

and shaping cultural change^{22,26,54,96,97}. A notable example is the Big Man Mechanism proposed by Henrich and colleagues⁹⁸, which suggests that prestige-based leadership plays a fundamental role in fostering cooperation within societies and that prestigious individuals, who derive status from skills and knowledge in culturally valued domains, can influence others to cooperate by modeling culturally appropriate behavior²⁶. Theories of prestige-bias have been informative and influential in helping build contemporary evolutionary thinking on leadership and cooperation. Prestige-biased imitation, however, is only one side of the coin. Furthermore, systematic crosscultural studies^{54,63} have only documented limited evidence that highstatus, prestigious individuals are functional sources of learning through observation and imitation. Our findings suggest there is ethnographic evidence supporting teacher-directed social learning.

Several authors have implicated teaching in the transmission of more complex culture or in cumulative cultural evolution^{11,49,66,80}. Norms concerning proper social behavior, kinship obligation, reciprocal economic exchanges, cultural histories, and religious values are difficult to both teach and learn, in part due to their opacity. Yet individuals and their groups can benefit if other group members comply with cooperative, complex norms. Within any group, leaders are well-positioned to transmit opaque cultural norms because their role provides them with a platform for broadcasting information to a wide audience. Leaders would be incentivized to actively teach naive individuals opaque cooperation-enhancing norms because promoting prosocial behavior will benefit themselves, but also their kin, and their social partners^{99,100}, as well as better equip their groups to compete against and cooperate with other groups¹⁰¹. Thus, both within and between group cooperation will be enhanced if informed and influential group members actively teach prosocial opaque culture to naive and influenceable individuals. Leaders may also be further compensated for teaching via additional prestige, reciprocal altruism, mating opportunities, direct payments, or other "knock-on" benefits^{102–104}. In sum, leader-directed teaching of opaque cooperative norms would be a mutually beneficial strategy, where the costs incurred by influential teachers are, at least partly, outweighed by the long-term benefits of cultivating cooperation within the group.

Importantly, we do not believe community leaders are especially likely to achieve their widespread social influence because of demonstrated success as teachers. The leader-directed teaching hypothesis predicts, instead, that individuals who have already attained social influence through various means may use their position to teach opaque cultural norms, thereby reinforcing their influence and ensuring the transmission of prosocial norms and behavior. Teaching can enhance a leader's influence, but leadership is typically established through broader contributions to the community.

Among egalitarian societies in particular, respected individuals who have a disproportionate level of influence and who are informed on opaque culture, will be a key mode by which the cognitively challenging and costly instruction of opaque culture can occur; what Garfield et al.⁵⁴ and Hagen et al.¹⁰⁵ refer to as providing a "computational service" (see also ref. 100). However, leaders in egalitarian

societies must balance this role with the risk of ridicule or loss of status if they appear to boast about their knowledge, as prestige-avoiding norms discourage overt displays of expertise^{18,51,106}. To maintain influence and provide prosocial investments to the community, leaders need others to adopt the same opaque norms yet must find ways to share their knowledge without appearing boastful. Teaching provides an ideal solution, allowing leaders to demonstrate their knowledge prosocially, much like how hunters share meat to subtly display their skill without directly seeking praise. As our results demonstrate, the ethnographic record from egalitarian hunter–gatherer societies supports the prevalence of teaching practices closely associated with the transmission of intricate opaque cultural norms and social influence.

Our study faces limitations inherent in ethnography-based analyses, particularly in interpreting and coding ethnographic texts. Among the primary challenges is the potential for conceptual ambiguity in the language ethnographers used and their subjective biases. Our text analysis focused on the lexical dimensions of ethnographic passages, identifying patterns in cultural transmission by examining the usage and frequency of specific terms within the passages. This approach, however, is necessarily constrained by the inherent subjectivity of ethnographers and the specific cultural contexts they documented. To address these limitations, we examined potential sources of meta-ethnographic bias by fitting a Bayesian bias assessment model that considered factors such as the total number of pages of ethnography available for each society, document page count, publication date, and the presence of a woman co-author. Results suggested that none of these factors were associated with evidence for teaching in our data (see Fig. S3 and Supplementary Data 3). However, other unknown factors related to ethnographer variation might still influence our results.

Additionally, the ethnographic record is subject to the absence-ofevidence problem, where observable and public behaviors, such as teaching, might be reported more frequently than more subtle forms of social learning. Finally, since our sample is restricted to relatively egalitarian hunter–gatherer societies, we cannot generalize these patterns to all societies or societies characterized by other forms of social organization or subsistence economics. Our results provide insight into patterns within the ethnographic record, but generalizations should be made with caution. They are particularly useful, however, for evaluating theoretical models and generating hypotheses for further testing.

Here, we operationalized instrumental and opaque culture as a dichotomy. However, we acknowledge that in practice, instrumental and opaque cultural knowledge are rarely transmitted in isolation from each other¹⁰⁷. Specifically, instrumental knowledge may represent a foundation upon which higher-level competencies and strategic adaptations, including opaque knowledge, is layered. Visual arts, such as painting, sculpture, and craftwork, are clear examples. Future theoretical work should examine the cumulative and interactive nature of instrumental and opaque knowledge¹⁰⁸.

In principle, this work could face concerns related to the ecological fallacy, which arises when one infers individual-level processes from aggregate data. However, our analyses are conducted at the paragraph level, and our conclusions are similarly framed at that level rather than generalized to societies. We also include random intercepts for paragraphs and documents, thus capturing the nested structure of the data. Importantly, our findings are descriptive: they spotlight recurrent patterns rather than offer causal claims about individuals or societies. Subsequent investigation collecting finergrained data on individual behaviors could shed light on the causal processes underlying these patterns. Future work should also examine how society-level norms and environmental factors shape leaderdirected teaching. This might involve testing whether cultural traditions, phylogenetic relationships, or other socio-ecological dimensions map onto the paragraph-level patterns reported here. More granular field or observational data would help clarify how such macrolevel influences interact with the more micro-level individual teaching processes we hypothesize.

Additional studies should also explore the mechanisms and decision-making processes through which opaque norms are transmitted and maintained within human groups. We suspect kinship intensity plays a role in shaping moral judgments. In a cross-cultural study based on ethnographic texts from 146 societies Curtin and colleagues⁶ found societies with high kinship intensity–defined as the degree to which social relationships, obligations, and moral judgments within a society are strongly influenced by the closeness and strength of kinship ties¹⁰⁹–tend to rely less on mental states and intentions when making moral judgments, instead focusing more on outcomes. Therefore, focusing on macro-level, cross-societal variation in social structures could be insightful in understanding how norms and values related to morality are reproduced and maintained in different cultural contexts, including beyond egalitarian social contexts¹¹⁰.

The leader-directed teaching hypothesis suggests an integration and exploration of interactions between teaching, leadership, and the evolution of cooperation. The motivations and behaviors of informed, influential individuals and the responses of naive individuals to their teachings provide opportunities for further investigation and stands to enrich our understanding of human social dynamics, cultural evolution, and the emergence and maintenance of cooperation among human societies. It is our hope that future work will apply results from comparative analyses presented here in the field, the lab, and in formal modeling, towards testing and further developing the leader-directed teaching hypothesis.

Methods

This work complies with all relevant ethical regulations and was determined exempt from ethical review by the Institutional Review Board at Washington State University, given that no human subjects' data were collected, and analyses exclusively rely on published archival texts.

The hunter-gatherer social learning database

We draw on the hunter-gatherer social learning (HGSL) database, initially developed by Garfield et al.63 and now publicly available83. The HGSL data set includes all the egalitarian hunter-gatherers available in the eHRAF at the time of its development, which included ethnographic texts on social learning. And here, egalitarianism is used to exclude hunting and gathering societies Kelly¹¹¹ would describe as complex hunter-gatherers, e.g., hunting and gathering societies with substantial and institutionalized social stratification. It also excludes the equestrian foragers, which tended to demonstrate substantial inherited inequality. It does not include, for example, the Manus from Oceania. Although they are classified as hunter-gatherers, they are also characterized by hereditary slavery and do not meet the criteria of egalitarianism. This data set, like much of the evolutionary anthropological social learning literature, focuses on more egalitarian communities because it is assumed children have more agency and capacity for self-directed learning. There was no self-selection of societies or ethnographic documents by us or by Garfield et al.⁶³ in the sample construction process.

The HGSL data includes 149 paragraphs from 80 ethnographic documents describing social learning among hunter–gatherers taken from the electronic Human Relations Area Files World Cultures (eHRAF) database (https://ehrafworldcultures.yale.edu), in compliance with eHRAF terms of service. These 149 paragraphs included 277 unique descriptions of social learning, referred to as instances of social learning. Each instance was coded for the social domain in which learning occurred (e.g., subsistence skills, cultural values and kinship), the mode of learning (e.g., horizontal, vertical), the process of social learning (e.g., teaching, observation, stimulus enhancement, trial and

error), and the gender and age of the learner (see Table 1). For our purposes here, we made the following revisions to the original coding scheme: we collapsed the *Language* and *Miscellaneous skills* domains, we collapsed the oblique mode with the two oblique subtypes; we also collapsed the three teaching processes into *teaching*, all other processes into *non-teaching social learning*; and lastly, and we removed the *Individual learning* data. This provides our binary measure of teaching, which is coded as 1 when an instance provides evidence of teaching and 0 when it provides evidence for another non-teaching social learning process.

The HGSL database also provides paragraph and society-level meta-data. For each paragraph the associated eHRAF document ID is provided, the raw text, as well as every outline of cultural materials (OCM) code associated with the paragraph. The OCM coding scheme is an ethnographic classification system of human behavior, social life and customs, material culture, biology, and human-ecological environments, designed to capture a wide range of topics relevant to the human sciences. The core and unique feature of the HRAF World Cultures database has been to associate each of more than 2.5 million paragraphs, stemming from more than 6000 primary ethnographic documents, describing more than 350 societies, with the relevant OCM codes discussed in the paragraph. The OCM coding scheme is hierarchically organized and includes more than 90 OCM major categories (such as 550 Social Stratification and 740 Health and Welfare) which contain more than 700 individual codes (such as 554 Status, role, & prestige; 744 Public Health & Sanitation). The HGSL database used three OCM codes in an advanced search to extract ethnographic paragraphs on cultural transmission: 867 Transmission of Cultural Norms, 868 Transmission of Skills, and 869 Transmission of Beliefs for a subset of relatively egalitarian hunter-gatherer societies-all the egalitarian hunter-gatherer societies, following definitions from Kelly¹¹¹, available at the time of data collection (see Garfield et al.⁶³ for further details). The HGSL database also includes society-level meta-data, such as geocoordinates for each society and the region and sub-region (provided by HRAF). This database provides quantitative measures developed from a systematic sample of ethnographic paragraphs on hunter-gatherers, suitable for quantitative analyses, with limited selection bias (e.g., due to "cherry-picked" cases, documents, or societies).

Analytic strategy

We use text analysis, exploratory graphical methods, Bayesian regression, and penalized regression towards addressing our aims. All empirical analyses were conducted with R version 4.3.2 (2023-10-31).

Descriptive visualization

We use a mosaic plot to visually explore the relationship between teaching and the transmission of opaque versus instrumental culture. Figure 1 illustrates the relationship between evidence for teaching versus non-teaching social learning and the type of cultural transmission (opaque versus instrumental) across the instances of social learning. Specifically, the plot depicts the counts of instances which provide evidence for teaching or non-teaching social learning and how these instances are associated with either opaque or instrumental culture OCM codes within the respective paragraphs.

For clarity, we excluded 19 instances where both opaque and instrumental culture were associated with the same paragraph, as these cases were nearly evenly distributed between teaching and nonteaching social learning and did not contribute additional information.

Text analysis of hunter-gatherer cultural transmission

We conduct text analysis to explore the lexical content of the ethnography of social learning in reference to transmission of opaque versus instrumental culture. We created a term document matrix of all informative words in our corpus of texts, which captures the frequency of each unique term within each paragraph. We first identified if each paragraph provided evidence for transmission of instrumental culture (i.e., paragraphs associated with the OCM code *868 Transmission of skills*) and/or opaque culture (i.e., paragraphs associated with either *867 Transmission of cultural norms* or *869 Transmission of beliefs*). We then fitted an elastic net logistic regression model (with the lasso penalty, $\alpha = 1$) of both of these outcomes as a function of the frequencies of all 2909 unique words using the glmnet package¹¹². Words that were strong positive predictors epitomized the lexical content of paragraphs which provided evidence for that type of social learning and negatively associated with that type of social learning.

This approach allows the ethnographic record to speak for itself by uncovering patterns in lexical content that may not be apparent through manual coding methods, providing an additional level of validation. It also offers readers a window into the content of the paragraphs without directly reading them. Moreover, by analyzing the raw text independent of researcher-coded variables, we include a source of evidence that has not been directly shaped by our research design choices. This not only strengthens the case for the alignment between lexical content and OCM codes but offers some assurance that patterns in the data emerge from the text in its own right, rather than being overly shaped by prior frameworks.

Penalized regression model with OCM predictors

We leveraged the OCM codes provided by eHRAF as predictor variables to identify the topics and features commonly associated with ethnographic descriptions of teaching among egalitarian hunter–gatherers. We use the OCM categories (specifically the sum of the number of OCM individual codes per category, for each paragraph), as predictors of evidence for social learning via teaching.

Given the relatively large number of OCM categories available as predictor variables (76) for evidence of teaching at the paragraph level and the relatively small sample size of ethnographic paragraphs in our sample (164), we employed the glmnet package¹¹² to fit a penalized lasso regression model with Poisson errors. Penalized regression, such as lasso, is particularly useful when the number of predictors (p) is large relative to the number of cases (n) and is often recommended in such scenarios because it helps address multicollinearity and reduce the potential for overfitting through the introduction of a penalty term^{112,113}. This modeling approach identifies the OCM code categories predictive of greater counts of evidence for teaching at the paragraph level. We used 10-fold cross-validation to determine the optimum value of the penalty term λ , which minimized cross-validation error. Additionally, we employed a second λ , representing the largest value of λ within one standard error of the minimum, to provide more conservative parameter estimates by increasing shrinkage. We report coefficients from both the optimal λ_{MIN} model and the more conservative λ_{1-SE} model. All variables were centered and standardized by one standard deviation prior to fitting. For interpretation purposes, we categorized each OCM code group as either Instrumental or Opaque culture, although this categorization did not influence the model fitting process. OCM codes that are positive predictors reveal the subjects most associated with ethnographic descriptions of teaching, while negative predictors indicate subjects associated with other, nonteaching, processes of social learning.

Bayesian model with researcher-coded predictors

To better understand socio-ecological variation in teaching on a more fine-grained level we used Bayesian multi-level logistic regression to identify predictors of evidence for teaching (coded as 1) compared to other forms of social learning (coded as 0), at the instance level (there are eight instances of non-social learning in the HGSL data which we exclude from all analyses here). Bayesian models employed an index variable approach for categorical predictors¹¹⁴, including random

Table 1 | Variable operational definitions. Reproduced from Garfield et al. (2016)

Variable	Value labels	Definition
Domain	Subsistence skills and knowledge	Knowledge or skills related to food acquisition, includes hunting, gathering, food processing, production and use of subsistence-related tools, knowledge of edible plants and animals
	Religious beliefs and practices	Knowledge or skills related to the spiritual, religious, or supernatural domain, includes folk mythology, ritual training, and initiation dealing with the supernatural
	Language	Speaking skills, vocabulary, grammar, and other features of language acquisition
	Ecology	Knowledge or skills concerning the physical environment, including nonedible plants, ethnobotany, medicinal plants, astronomy (non-spiritual, e.g., navigation, naming constellations), weather patterns, geographical knowledge
	Miscellaneous skills	Knowledge or skills related to general locomotion, basic operation of crafts (e.g., canoes), swimming, basic climbing, dancing, singing, basic tool use (not directly tied to subsistence, or manufacture), alloparenting, toilet training, and some domestic skills (not directly related to subsistence, e.g., sewing)
	Manufacture (non-subsistence)	Knowledge or skills involving production of useful items, including watercrafts, other transportation crafts, craft manufacture such as basketry, textile manufacture, tool manufacture, and building dwellings
	Cultural values and kinship	Knowledge or skills concerning culturally preferred social behavior, including gender roles, morality, social norms (e.g., sharing, generosity), proper behavior between kin, kin terms, age-graded social distinctions, emotional behavior, and culturally preferred conduct
Modes	Horizontal	Learning from individuals of the same generation, age group, or cohort within approximately 5 years of age (e.g., children-children, adult-adult)
	Oblique	Social learning between individuals of distinct generations or age groups (e.g., uncle to nephew, adult to child, adolescents to young children)
	Oblique-prestige bias	Social learning from a culturally identified expert to member(s) of a different generation or age group
	Oblique concerted	Several adults agree upon what should be transmitted to an individual (usually in initiation context)
	Vertical	Children learning from their parents
	Unknown	The context was not specific enough to justify coding, but some information of a domain and a process was mentioned
Process	Collaborative learning	Individuals of approximately equal age, skill, knowledge, and cognitive ability collectively contribute to the learning of a specific skill or knowledge
	Collaborative learning-play	Type of collaborative learning that involves the transmission, acquisition, or practice of cultural knowledge or skills through informal play or miscellaneous games
	Collaborative learning-role playing	Type of collaborative learning that involves individuals of similar age collectively playing social roles (e.g., play house, husband-wife)
	Local enhancement	The learner gains knowledge or skills by interacting with the local environment because other individuals expose the learner to the setting or environment (e.g., parents take children gathering or walk through forest)
	Stimulus enhancement	The learner is given an object to facilitate learning how to use the object
	Observation and imitation	The learner directly observes some skill or behavior and attempts to replicate the observed actions or behaviors
	Teaching	An individual modifies his or her behavior specifically to impart knowledge, skills, or behaviors, to a learner, but there is insufficient information to code as demonstration or storytelling
	Teaching-demonstration	Type of teaching where an individual demonstrates knowledge, skills, or behaviors, to a learner, and may offer feedback and examples during the process
	Teaching-storytelling	Type of teaching where an individual actively imparts specific (within one of the defined domains) knowledge, skills, or behaviors to a learner by verbal communication of stories or metaphors
	Individual learning	Individual exhibits repeated attempts to learn a skill or develop new skills or knowledge on his or her own. Includes trial and error and individual practice
Gender	Male	Social learning instance is specific to male learners
	Female	Social learning instance is specific to female learners
	Gender neutral	Social learning instance is gender-neutral
Age	Infancy	Social learning is specific to infants, less than approximately one year old
	Early childhood	Social learning is specific to early childhood, approximately between age one and seven
	Middle childhood	Social learning is specific to middle childhood, approximately between age eight and 12
	Childhood	Social learning is specific to childhood (but not specific to early or middle childhood)
	Adolescence	Social learning is specific to adolescence, approximately between ages 13 and 17
	General	Social learning is not specific to any age range or developmental stage

effects for paragraph and document to account for multiple instances per paragraph and multiple paragraphs per document. The model was specified to capture the nonlinear associations between the predictors and the outcome. We compared model fit to an intercept-only model, as well as identical models that additionally included a random effect for either continental region or society, using the loo package for model selection (Table S3).

Models were fit using brms, which interfaces with Rstan to fit Bayesian models using Hamiltonian Markov Chain Monte Carlo. Markov chain convergence was assessed using standard diagnostics (number of effective samples, the Gelman-Rubin diagnostic, and visual inspection of trace plots). Following McElreath¹¹⁴, we compute the expected difference (contrasts) between levels within categorical predictors by subtracting the two posterior distributions (e.g., posterior $\alpha_{\text{domain},1}$ – posterior $\alpha_{\text{domain},2}$) and interpret the 95% intervals of contrast distributions which do not include 0 as meaningful differences between levels within categorical predictors (reporting mean differences of two distributions, $\Delta \hat{\beta}$, and their lower and upper 95%

credible intervals, LCI and UCI). The probability of an instance of social learning involving teaching was modeled as a function of four key predictors: learner age [Infancy, Early childhood, Childhood, Middle childhood, Adolescence, General], learner gender [Female, Male, Neutral], mode of instruction [Oblique, Vertical, Horizontal, Unknown], and cultural domain [Cultural values and kinship, Religiosity, Ecology, Misc. skills, Manufacturing, Subsistence]. The model was structured to allow for a direct estimation of the nonlinear effects of these categorical predictors on the log odds of teaching presence without including an intercept. This approach enables us to represent the contributions of each level of each predictor rather than defaulting to a baseline level of teaching presence. Specifically, the response variable is modeled as a Bernoulli distribution, where the probability parameter μ_i is defined as the sum of several indexed intercepts corresponding to the levels of each predictor and random effects associated with the document and text record identifiers, u_i and v_i .

The multi-level Bayesian logistic regression modeling approach is described as:

$$\begin{aligned} \text{teaching}_{i} \sim & \text{Bernoulli}(\mu_{i}) \\ \mu_{i} = \alpha_{domain[j]} + \alpha_{mode[k]} + \alpha_{age[l]} + \alpha_{gender[m]} + u_{i} + v_{i} \\ \alpha_{domain,j} \sim & \text{Normal}(0, 1), \text{ for } j = 1, \dots, 6 \\ \alpha_{mode,k} \sim & \text{Normal}(0, 1), \text{ for } k = 1, \dots, 4 \\ \alpha_{age,l} \sim & \text{Normal}(0, 1), \text{ for } l = 1, \dots, 6 \end{aligned} \tag{1}$$
$$\begin{aligned} \alpha_{gender,m} \sim & \text{Normal}(0, 1), \text{ for } m = 1, \dots, 3 \\ u_{i} \sim & \text{Normal}(0, \sigma_{u}^{2}), \sigma_{u} \sim & \text{Exponential}(1) \\ v_{i} \sim & \text{Normal}(0, \sigma_{v}^{2}), \sigma_{v} \sim & \text{Exponential}(1) \end{aligned}$$

The intercepts $\alpha_{domain,j}$, $\alpha_{mode,k}$, $\alpha_{age,l}$, and $\alpha_{gender,m}$ correspond to the levels of the categorical predictors domain, mode, age, and gender, respectively, where each intercept follows a normal distribution with a mean of 0 and a standard deviation of 1, reflecting a neutral prior belief about the direction and magnitude of these effects and to impose a regularizing effect constraining parameter estimates^{114,115}. For the standard deviations of the random intercepts for document and paragraph, we used exponential priors with a rate of 1, indicating an expectation for moderate variation across documents and paragraphs.

The model was estimated using Hamiltonian Monte Carlo (HMC) sampling, with four chains, each running for 4000 iterations, including a warm-up phase of 2000 iterations. To improve the convergence properties of the sampler and the accuracy of posterior estimates, we set the adapt_delta parameter to 0.99, aiming for a high acceptance rate of proposed samples. We conducted a prior sensitivity analysis, which showed that weaker priors provided better predictive performance; however, the alternative priors did not lead to different interpretations. Results are reported in Supplementary Note 4 and Supplementary Data 2.

We also fit a bias assessment model to investigate potential influences of meta-ethnographic bias, such as document publication date, the presence of a woman author, document page length, and continental region. All variables, excluding the presence of a woman author, were provided by eHRAF. We manually coded if each document included a woman author or co-author, drawing on previously published information when available^{18,116-118}. Results revealed these potential sources of bias were conclusively not associated with evidence of teaching. We, therefore, do not include them in our predictor model. See Supplementary Note 5 for additional details.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The variables coded from eHRAF-sourced ethnographic texts used in this study have been deposited in the Hunter–Gatherer Social Learning data R package available on GitHub and archived on Zenodo available under Creative Commons Attribution 4.0 International.

Code availability

Code available at the Open Science Foundation.

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Author contributions

Z.H.G. initiated the project, designed the analytical framework, conducted the analyses, was primarily responsible for interpreting the results, and produced the first draft of the paper. S.L.L. provided extensive review and feedback on the paper and contributed to developing the core ideas and hypotheses.

Competing interests

The authors declare no competing interests.

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