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Research

On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases

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Unlike other animals, humans are heavily dependent on cumulative bodies of culturally learned information. Selective processes operating on this socially learned information can produce complex, functionally integrated, behavioural repertoires—cultural adaptations. To understand such non-genetic adaptations, evolutionary theorists propose that (i) natural selection has favoured the emergence of psychological biases for learning from those individuals most likely to possess adaptive information, and (ii) when these psychological learning biases operate in populations, over generations, they can generate cultural adaptations. Many laboratory experiments now provide evidence for these psychological biases. Here, we bridge from the laboratory to the field by examining if and how these biases emerge in a small-scale society. Data from three cultural domains—fishing, growing yams and using medicinal plants—show that Fijian villagers (ages 10 and up) are biased to learn from others perceived as more successful/knowledgeable, both within and across domains (prestige effects). We also find biases for sex and age, as well as proximity effects. These selective and centralized oblique transmission networks set up the conditions for adaptive cultural evolution.

Keywords: cultural transmission; networks; prestige-biased transmission; dual inheritance theory; Fiji; cultural adaptations

1. EVIDENCE FROM FIJIAN VILLAGES FOR ADAPTIVE LEARNING BIASES

Long before agriculture and the emergence of complex societies, humans with the same basic genetic endowments expanded across the globe into a dizzying range of environments, from the arid deserts of Australia to the frozen tundra of Alaska. Survival in this range of environments, many of which are ill-suited for a tropical primate like us, depends on large bodies of culturally transmitted practices, beliefs, values and know-how. Examples include the (i) complicated manufacturing processes for arrow poisons, bows, traps, blowguns and kayaks; (ii) complex practices to detoxify critical food sources, such as acorns, cycads and cassava [1,2] or to release essential nutrients from plants [3]; (iii) taboo repertoires that protect mothers and their offspring from dangerous marine toxins [4]; and (iv) recipes and taste preferences for antimicrobial spices that reduce pathogen threats posed by meat in warm climates [5,6]. Such cultural products appear functionally well-designed to address local environmental challenges, usually in subtle ways not recognized or explicitly understood by the people reliant on them. Such anthropological observations mean that understanding the nature and success of our species requires explaining the emergence of such *cultural adaptations* [7].

To approach this issue, we draw on work applying evolutionary thinking to understanding culture and cultural change. This enterprise can be partitioned into three inter-related lines of research. The first involves applying evolutionary reasoning, often aided by the construction of formal models, to generate hypotheses about how natural selection might have shaped human psychology to most effectively extract adaptive ideas, practices, beliefs and values from the behaviour of others (e.g. [8,9]). Building on this foundation, the second line takes these hypothesized, and empirically grounded, elements of human psychology and considers how they create and influence population-level processes of cultural evolution, including the emergence of cultural adaptations. That is, this line of research, which is itself disciplined by formal cultural evolutionary models [10], considers how aspects of our psychology, operating through interaction in social groups, can give rise to everything from sophisticated technologies (like arrow poisons)

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One contribution of 26 to a Discussion Meeting Issue 'Culture evolves'.

and adaptive taboos to large-scale cooperation, social norms [11], ethnicity [12] and social stratification [13]. Using culture–gene coevolutionary models, the third line explores how the emergence of such cultural products, including both sophisticated tools and social institutions, feeds back to influence the genetic evolutionary processes that shape our brains and bodies [14–16].

Here, we aim to contribute to understanding the evolution of cultural adaptations by empirically exploring the psychological biases in observational learning, and the consequent transmission networks that they produce. The application of evolutionary theory to understanding to whom learners should pay attention for cultural transmission and how they should integrate information from different models has generated a wide range of hypotheses about human cognition, many of which have found empirical support, especially from recent laboratory experiments (see below). Hypotheses about *model selection biases* propose that learners should preferentially attend to those individuals in their social world ('models') deemed most likely to possess adaptive information that can be acquired by learners [17]. To locate these *preferred models*, learners should give weight to a variety of cues that indicate which individuals are most likely to be worthy of imitation (i.e. possess adaptive information). Sets of proposed cues include (i) skill (competence), knowledge, success and prestige, (ii) health, (iii) age and (iv) self-similarity (e.g. based on sex, ethnicity, personality and physical attributes). These cues allow learners to identify not only those individuals in their social environment who are likely to possess adaptive information, which could be acquired via cultural learning, but also select those most likely to have information suitable to the learner in future roles, or as stepping stones in the acquisition of increasingly complex skills or repertoires. A variety of models (examples cited above) formalize these assumptions about human learning and examine how they generate cumulative cultural products over generations.

This line of theorizing also proposes that learners should weigh the potential gains of learning from their preferred models against the costs of accessing those models [17]. If access costs are too high, learners should adjust their selected models to those with lower access costs. In particular, this consideration emphasizes that some potential models have evolutionary incentives to transmit adaptive information to the learner, such as parents, siblings and other close relatives. Much cultural transmission benefits from the consent or cooperation of the model. Novice learners in particular, who have little to gain from community experts over their own family early in their development, should learn first from their most accessible models, later shifting over to their preferred models (see electronic supplementary material). In its simplest form, this proposal suggests a two-stage learning model in which individuals first acquire information from their parents (or other household members), and then later update this information based on transmission from their preferred models [18]. Recent empirical work in Fiji broadly supports this two-stage model in the domain of food taboos [4].

This theoretical framework in general, and these predictions about model selection biases in particular, organize a large body of findings from laboratory experiments across the social sciences. Work in psychology and economics supports the above predictions by showing that people use cues of success, competence and prestige in learning from others by modifying their preferences, beliefs, practices, opinions and food choices—among other things. Participants do this spontaneously, unconsciously and whether or not they are paid for their performance (reviewed in [19]). There is also evidence that success in one domain crosses over to influence other domains [17]. Recent experimental work has tested these models in sophisticated ways, sometimes measuring the relative importance of success biases over other learning mechanisms (e.g. individual experience). Success-bias consistently emerges as an important component of complex learning strategies [20,21], though access costs are important, as expected [22].

Developmental psychology has recently focused on selective imitation in young children, providing evidence consistent with the above predictions. Young children (typically 3 and 4 year olds) spontaneously track the competence of potential models in labelling objects and knowing the function of artefacts, and then preferentially imitate more competent models, even after a one week delay (reviewed in [23]). Although children show a capacity to identify skill differences indirectly using cues about age, confidence and experience [24,25], they selectively weigh competence over age by taking the word of a previously accurate child over an inaccurate adult [26,27].

These studies contribute substantially to exploring and testing the psychological foundations of cultural learning predicted by our evolutionary approach. However, they are limited in being laboratory studies. It remains to be established how important these psychological biases are in real life, and whether they could generate adaptive cultural evolution in fitness-relevant domains. We begin to bridge this gap between the laboratory and field by assessing whether these same predictions bear out in the cultural transmission networks of a small-scale society.

Here we sharpen some of the model selection hypotheses mentioned above with the goal of testing them using data from three Fijian villages. In presenting these predictions, we sketch the supporting evolutionary logic (see electronic supplementary material):

— *Perceived success or knowledge*: since perceived success or knowledge in a particular domain is a potential indicator of the adaptive value of cultural variants possessed by an individual, a learner's perceptions of others' success or knowledge in a domain should be an important predictor of their model choice. We examined this using five measures of perceived success and knowledge.
— *Cross-domain success* (*prestige*): because more direct cues of success and skill may be noisy, unreliable or unavailable, learners should also weight perceived success or prestige in other locally valued domains. For example, individuals perceived as great fishermen may also be selected as models for learning about yams. Such cross-domain weightings may be adaptive for a number of

reasons. Individuals who are most effective at acquiring skills from one domain may also be effective at acquiring adaptive information in other domains; or, successful individuals may possess general traits or practices, which can be acquired, that promote success in multiple domains (e.g. thrift and temperance). We use perceived success from two highly valued domains to predict model selection in other domains.

— *Age*: it is a potentially valuable cue to possessing fitness-enhancing information for three reasons [17]. First, older individuals have had more years to acquire know-how through both social learning and experience. Second, merely by getting to be old, individuals have passed through a selective filter—not everyone gets to be old. Therefore, learners should preferentially target more senior community members, *ceteris paribus*. However, this effect may be nonlinear as very old individuals may experience cognitive losses. Third, children may focus on somewhat older models as a way of scaffolding themselves up to increasingly complex skills.

— *Sex*: if there are divisions in the skills or specializations of community members based on individual-level factors (e.g. sex), learners should target their attention using cues related to these factors in two ways. First, since learners want to acquire know-how that is suitable to them in their social roles (or future roles), attending to those who are similar to oneself on these factors customizes information acquisition. That is, for sex, we should expect that women should preferentially choose other women as models, *ceteris paribus*. Second, when sexual divisions of skill sets exist, learners can use sex as an indirect cue of their chances of knowing much about a particular domain (e.g. if a boy wants to know about nursing an infant, he should probably not ask a man).

— *Access*: learners must balance the costs of accessing high-quality models against the quality of information available for transmission [17]. Thus, we expect learners to differentially copy from others that live in their same households and villages, as well as preferentially learn from those to whom they are most closely related. Since we are primarily testing adolescents and adults, we expect households and relatives to be less important as many of our participants will have learned nearly all they can from their co-householders and close relatives.

— *Network centrality*: if there is a distribution in the perceived quality of potential models (e.g. variation in perceived success or suitability), the overall patterns of model selections for different kinds of cultural information should reflect this at the network or community level. The more important these cues are, and the more agreement among community members on these cues, the more centralized the transmission networks should be. If most people suggest their parents, other family members or vary idiosyncratically in their model selection, these networks should not be particularly centralized.

2. ETHNOGRAPHIC SKETCH AND METHODS

The data presented here were collected as part of an in-depth, ongoing study of life on Yasawa Island, which lies in the northwestern corner of the Fijian archipelago. Our project mixes ethnographic observation with extensive interviewing and a range of experiments. Economically, Yasawans rely primarily on horticulture, fishing and littoral gathering. Fishing is the most important source of protein, and spear-fishing is the most productive form of fishing for those with sufficient skill. People also fish with lines and nets. Yams and cassava provide the caloric staples, although yams are preferred, traditional and necessary for ceremony life. Men compete informally to grow the largest yams. Political units are composed of interrelated clans called Yavusa, which are governed by a council of elders and a hereditary chief. Social life is organized by a complex web of kinship relations and obligations. At the time of the study there were no cars, TVs, markets or public utilities in these villages. These data come from the villages of Teci, Dalomo and Bukama, with populations ranging from 100 to 250 people in each. Teci and Dalomo, which lie about 10 min apart, jointly form one Yavusa. Bukama is about 2.5 h away (on foot) and forms its own Yavusa.

These data were collected between 2003 and 2008 by trained Fijian interviewers who did not have kinship or other ties with the communities. Interviews about preferred models and perceived success networks were conducted in private settings with only the researchers present. The methods deployed to gather each of our measures are discussed in turn (details in the electronic supplementary material):

Cultural transmission networks. These interviews were conducted in 2008 with everyone in the three villages over the age of 6. Participants' responses were used to construct the cultural transmission networks that serve as our three outcome variables for the regressions below. These naturally bounded networks are created by asking individuals to whom they would go for advice if they had a question in a given domain. We asked 'who would you go to for advice if you had a question about' (i) 'fish or fishing' (hereafter Fishing); (ii) 'planting or growing yams' (Yams); or (iii) 'using a plant as a medicine' (Medicinal Plants). When people stopped listing names they were prompted with 'Is there anyone else?' This continued until the participant communicated that he had finished. People readily listed between zero and five individuals, self-limiting to five or fewer. We emphasize here that these are not direct measures of actual cultural transmission events. Instead, we assume these data approximate who individuals would look to, or rely on, in acquiring information in these domains. Below, we discuss the limitations of using such data as a proxy for the actual pathways of cultural transmission, and consider how this approach complements and converges with other lines of work on cultural transmission.

Perceived success and knowledge measures. In 2006, the team conducted an interview with all villagers over the age of 10 that was designed to measure perceptions of who in the community were considered to be the most successful, skilled or knowledgeable across a variety of domains. After participants' initial responses, they were queried as to whether there was anyone else besides those listed who should be added. This continued until participants communicated that no one needed to be added. All questions followed a similar format, asking participants to name those in their Yavusa first. We used participant responses from these questions: who (i) knows the most about fishing, (ii) are the best line fishers, (iii) are the best spear fishers, (iv) are the best yam growers, (v) knows the most about growing yams, and (vi) knows the most about medicinal plants, to construct perceived success/knowledge measures. These data are unavailable for Bukama.

Note that these success and knowledge interviews were conducted *2 years prior* to the network interview above, which served as our dependent variables. If these instruments were deployed at the same time (despite asking different questions), or within a relatively short delay, it is possible that participants might be responding similarly to both sets of questions because they were linking their two responses in some way. However, given the long delay between interviews, it seems unlikely that participants would recall their responses to the success/knowledge interviews when responding to the cultural transmission network questions.

An important question is how well people's subjective perceptions correspond to actual measurements of success or production. Our aggregate ranking of the best fisherman correlates 0.84 with our actual measures of fishing efficiency, based on weights for over 1700 fish collected over 6 years (see electronic supplementary material). These findings are consistent with work on hunting among foragers, which also indicates that locals' subjective evaluations are very accurate [28]. We lack data to evaluate success in growing yams and using medicinal plants.

Demographic measures. Using a demographic database that has been updated yearly since 2003, we drew information on age, gender and years of formal schooling for all respondents.

Kinship measures. Using a kinship diagram going back approximately three generations from those living in 2003, we calculated a coefficient of relatedness (r) matrix for Teci and Dalomo.

Time allocation measures of association. From 2003 to 2008 our team collected time allocation for a few months each year. Every day during each sampling month, several individuals were randomly selected to be sampled at a random time. At the appointed time, researchers located the individual and recorded what he or she was doing, and who they were with. We used these observations to generate a matrix where a cell in row i, column j, would contain the proportion of times that individual j was present when individual i was sampled. This control variable allows us to show that our findings do not represent merely common association patterns.

Using these measures, we estimated a series of regression models to assess the relative importance of each of our predictor variables for selecting the cultural models (based on our outcome variable). To statistically examine the relationship between our predictor and outcome variables, given the non-independence of network data, we constructed exponential random graph (ERG) models [29]. Our ERG models assume every tie (a selection of one person as a cultural model by another person) between every possible pair of individuals to be a random variable that can take a value of 1 if the tie is present or 0 if it is not. Assuming this, it is possible to construct all of the possible network configurations that have the same number of nodes as the observed network. If the process that generates the connections between individuals in the observed network was completely random, one would expect there to be identical probabilities for every tie existing between every dyad in the network. However, if this process is non-random, for example if individuals are more likely to go to people who are of the same sex for their cultural information, then the probability of ties between same-sex individuals will be higher than ties between individuals of the opposite sex. If one specifies how a set of variables relates to the probability of a tie existing between two individuals, it is possible to compare the observed network with the distribution of possible networks and estimate coefficients that maximize the probability of generating networks that are similar to the observed network. The electronic supplementary material expands on ERG models.

We explore two categories of effects with this approach: (i) *main effects*, which capture the relationship between individual-level attributes (e.g. age, sex and education) with the number of times that an individual is selected as a model by others, and (ii) *dyad effects*, which measure the effects of similarities and differences between dyads, or some character of their joint relationship. If, for example, two individuals match on sex this may influence the likelihood of a connection (directed tie) between them. Alternatively, the coefficient of relatedness matrix (r) can be used to estimate how kinship influences the likelihood of a cultural transmission tie. Because we have all the variables discussed above for both Teci and Dalomo but only a subset of them for all three villages, we present our findings in reference to the *Teci–Dalomo sample* ($n\sim65$ individuals with 4160 directed ties), and the *full sample* (approx. 200 individuals with 39 800 directed ties).

While small, these communities provide a particularly suitable environment for our methodological approach. The small size and remote nature of these communities mean that we have bounded networks, and less concern that people might obtain information in these domains from books, newspapers, the Internet or formal education. We explain below that these cultural transmission networks naturally bounded themselves, with very few people seeking models beyond their Yavusa, and no one in the Teci–Dalomo sample doing so. This avoids otherwise prickly analytical challenges.

3. RESULTS

Before presenting the regression models, we discuss what the network visualizations tell us. Figure 1 shows the networks for all three villages in our three domains. Visual inspection suggests that all three networks are centralized. Network centralizations range from 16 per cent for the full yams network to 41 per cent for the Teci–Dalomo medicinal plants network (see electronic supplementary material). A network in which everyone is selected equally frequently has a centralization of 0 per cent while a network in which everyone picks the same person has a centralization of 100 per cent. This degree of centralization is consistent with the prediction that people substantially share notions about who is a good cultural model (network centrality), but that individuals' model selections are influenced by multiple factors.

Figure 1 also reveals that people see their primary sources of cultural information to be members of their own Yavusa. Yasawans in villages of Teci and Dalomo, which together form a Yavusa, are inclined to select those in their own village, but do also look to the other village within their Yavusa. They do not look to Bukama (the next closest village). Those in Bukama limit their choice almost entirely to their own Yavusa, with just a handful of people from Bukama choosing models in distant communities (not shown). The fact that Bukama forms bounded networks independent of Teci–Dalomo in figure 1 is not owing to our explicit instructions: Yasawans spontaneously limited themselves in this fashion, though substantial rates of inter-village marriage mean that individuals flow readily among all these communities.

To present our findings, we focus on our Teci–Dalomo sample (4160 dyads) and use our set of theoretically relevant variables to create baseline models. These baseline models, one for each domain, use the following variables to predict a person's chances of being selected as a model: (i) perceived success or knowledge within the target domain, (ii) age and age difference, (iii) sex and same sex (1 for same-sex dyads and 0 otherwise), (iv) proximity (same village and same household) and genetic relatedness (r), and (v) education. We also discuss models that add cross-domain success measures as predictors to this baseline and models that add our time-allocation measures of association to the baseline. Finally, using the full sample (39 800 dyads), we consider how dropping our measures of success, knowledge and relatedness affect the other coefficients on the predictor variables. This allows us to assess the robustness of our coefficient estimates using a larger sample.

Figure 2*a*,*b* (inset) presents our regression coefficients as odds ratios. All the variables represented come from our baseline regressions, *unless* they are cross-domain success and knowledge variables—in which case they come from a model that includes the baseline predictors plus our cross-domains success and knowledge measures. For example, if you are looking at the odds ratio for predicting who people seek out for information about yams (in red), the bars for best spear fisher come from a model that has the cross-domain predictors added to the baseline model. However, the odds ratio shown for most yam knowledge and sex are from the baseline model. Mixing coefficients drawn from different models greatly simplifies the presentation, and is justified because none of our baseline estimates of our coefficients change significantly when we add our cross-domain predictors. Unless otherwise stated below, all of our findings are robust across several alternative specifications and in the full sample regressions (see electronic supplementary material).

Within-domain success and knowledge. As expected, individuals' perceptions (measured 2 years earlier) were by far the most powerful predictors of being selected as a model. For the domain of Fishing, believing someone to be among the best spear or line fishers increases their chances of selection by 9.9 and 2.2 times, respectively (95% CI are on figure 2). For yams, believing someone to be among the best yam growers or the most knowledgeable about yams increases their chances of selection by 7.3 and 2.2 times, respectively. For the domain of Medicinal Plants, believing someone to be among the most knowledgeable about such plants increases their chances of selection by 25 times.

It is interesting to note that in the two domains in which we did use measures of both knowledge and success—Fishing and Yams—we find that success is far more important than knowledge. The coefficient for our measures of perceived fishing knowledge is small, and cannot be distinguished from unity. For our measure of yam knowledge, the coefficient is significant, but the coefficient on yam success is more than three times larger. Coupled with our finding on the immense importance of medicinal plant knowledge on model choice, we suspect that when certain cultural domains provide clear direct (observational) evidence of success (e.g. catching big fish and growing big yams), people weight this more heavily in selecting their models. Healing people with plants is a fuzzier business.

Cross-domain success (*prestige*). To explore this, we used our measures of success and knowledge in one *valued* domain to predict selection as a model in another domain. To select our valued domains, we used data collected in 2005–2006 in which a sample of participants listed those arenas of village life that had to be mastered to be considered a respected member of the community. Fishing and yam growing were near the top, though medicinal plant usage was not (see electronic supplementary material). For learning about fishing, being perceived as a successful yam grower makes one 2.2 times more likely to be selected as a model. This effect size is roughly equal to that found for the effect of success in line-fishing on selection as a model for Fishing, but much less than within-domain success of spear-fishing. For Yams, success in spear-fishing increases one's likelihood of selection by 2.4 times, which is not distinguishable from the impact of our measures of possessing the most yam knowledge. For Medicinal Plants, our measures of yam success increase one's chance of selection as a model by 2.5 times (see electronic supplementary material).

Age. We examined both a main effect for age (are older people selected more frequently?) and a dyadic effect using age difference (do learners seek out people older than themselves?). Age was a significant predictor for the Yam and Medicinal Plant models for the Teci–Dalomo sample, and for Fishing and Medicinal Plant models in the full sample (interestingly, the coefficient on age for the yam model in the full sample is larger than that for the other two domains, but it is not estimated with sufficient accuracy). For medicinal plants and yams in the Teci–Dalomo sample, an individual who is 20 years older than another receives between two and two-and-a-half times more selections as a cultural model. In analyses not shown, we also examined the coefficient on age^2 and found no evidence for an elderly decline in the age cue. By contrast, age difference was never a significant predictor in any of our models, including in the full sample.

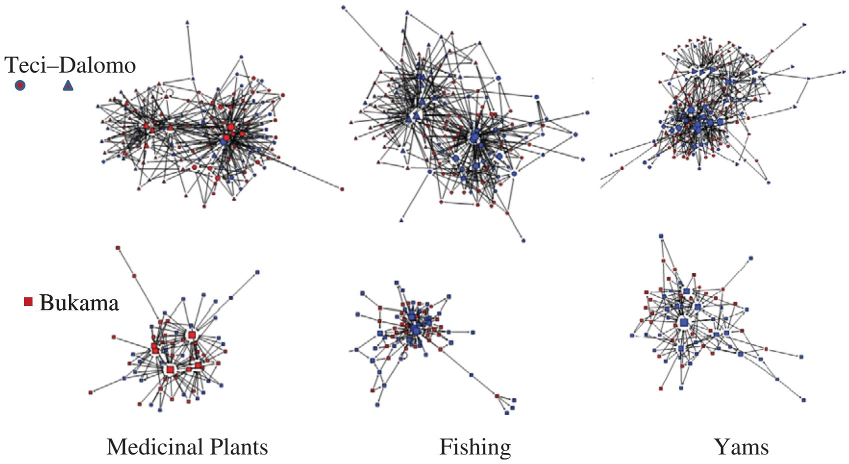

Figure 1. Inferred cultural transmission networks for our three domains. The top row shows the networks for the villages of Teci and Dalomo while the bottom row shows Bukama. Each column represents one of the three domains. Nodes represent individuals. The lines and arrows point towards the selected model. Node sizes are proportional to the number of individuals who selected that person as a model. Node shapes and colours mark individuals' villages and sexes. Blue, males; red, females.

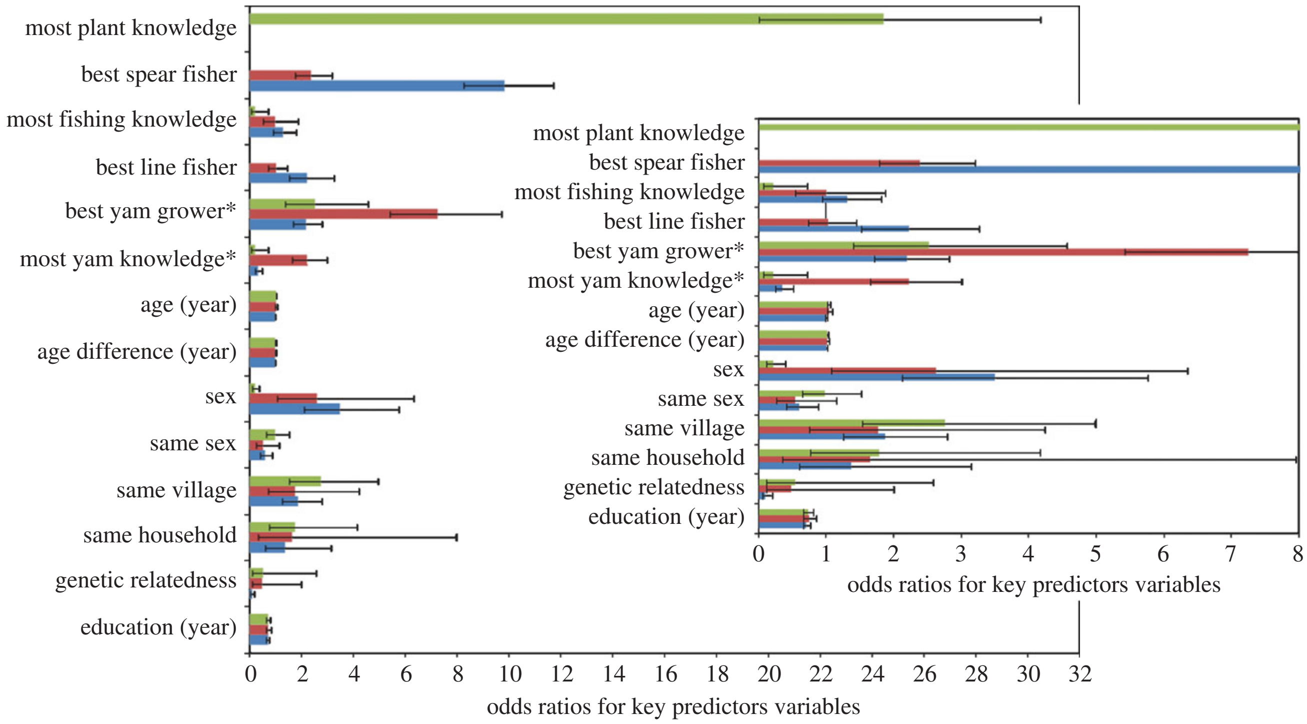

Figure 2. Effect sizes and confidence intervals for our primary predictor variables in odds ratios. The inset plot is the same as the larger plot except that the axis is rescaled so the smaller odds ratios can be seen. The bars give the odds ratios for our estimated coefficients. Odds ratios greater than 1 indicate positive effects while those less than 1 indicate negative effects. The error bars are 95% CI estimated by resampling. The bar colours mark the different cultural domains. Green, Medicinal Plants odds ratio; red, Yams odds ratio; blue, Fishing odds ratio.

We would expect age, as an indirect cue of possessing adaptive know-how, to be most important when information about success is less available or less accurate. If success in spear fishing is most evident to learners, then the pattern observed in the Teci–Dalomo sample (with success controlled for) makes sense. And, it also makes sense that when our success measures are dropped, age emerges as an important predictor of whom to seek out for fishing information. However, why the significance of the age effect disappears for yams in the full sample remains puzzling.

Sex: We analysed sex for a main effect, asking if either males or females are preferentially selected as models, and as a dyadic effect (same sex), asking if males tend to pick males and females tend to pick females. Consistent with ethnography, analyses of sex indicate that both Fishing and Yams are predominantly male domains (everyone is biased to pick males), while Medicinal Plants represent a predominantly female domain (everyone is biased to pick females). Being male, independent of other variables including perceived success, makes one between 2.5 and 3.5 times more likely to be selected as a cultural model for fishing and yam growing. However, in the full sample analysis for yams, with our success and knowledge measures dropped, sex is not significant, though its coefficient remains large.

Same sex. For both yams and fishing, learners were roughly twice as likely to select those of the *opposite* gender when compared with one's own. For medicinal plants, we found no effect in the Teci–Dalomo sample but did find the same opposite-sex effect in the full sample. We discuss and interpret this unanticipated finding below.

Proximity and relatedness (*access costs*). Broadly, being from the same village increases an individual's likelihood of being selected as a model between 1.8 and 2.76 times across all three domains. However, while the coefficient on same village for yams is significant in the full sample analysis and across all our other specifications, it is not significant in our baseline model (see the electronic supplementary material).

Clear results do not emerge from our analyses of our same household variable or from genetic relatedness variable. In our baseline models for yams and medicinal plants neither coefficient is significant. For Fishing, the coefficient on genetic relatedness actually predicts that greater relatedness makes an individual less likely to be selected as a cultural model. However, in additional analyses in the electronic supplementary material, we show that this result depends on having both same household and genetic relatedness in the model at the same time. If same household is dropped, the coefficient for genetic relatedness is non-significant. In the full sample analyses, which lack our success/knowledge variables and our genetic relatedness measures, same household is a significant predictor for medicinal plants and fishing, but not for yams.

Education. More years of formal education reduce selection as a model in all three of these traditional domains, across all specifications and in the full sample. In the baseline model for Fishing, if two individuals varied only in their level of education, the one who completed 10 years of schooling would be 30 times less likely to be sought after for advice than an individual who had had no formal schooling. Effects in the other two domains are of similar magnitude.

Time allocation. The electronic supplementary material provides models that include our measures of time allocation as dyadic predictor variables. Theoretically, it is not clear that such time-allocation measures should be controlled for, as time allocation could be seen as the consequence of selecting preferred models (along with many other variables) rather than as a predictor. However, as a robustness check, we included a model specification in which our time-allocation measures were included as predictors. The above described results all hold when this variable is included. Time allocation itself is significantly associated with selecting cultural models for learning about yams and medicinal plants, but not for fishing. For yams and medicinal plants, the proportion of times that two individuals were observed together during random point samples is related such that a 10 per cent increase in the proportion of times individual j was observed with individual i would result in i being 1.2 (yams) and 1.5 (medicinal plants) times more likely to go to j for advice.

4. DISCUSSION

These results add to and complement prior work on establishing the pathways and mechanisms of cultural transmission in small-scale societies (reviewed in [30]). This prior work suggests important roles for both vertical and oblique transmission, but provides only hints about the nature of that oblique transmission (see electronic supplementary material), including whether it is capable of producing cultural adaptations. The above findings fill an important gap regarding the nature of this oblique transmission, addressing the question of whether people select their oblique models in an adaptive and predictable manner capable of generating cumulative cultural evolution.

Methodologically, our efforts provide an additional tool for addressing the puzzles of cultural transmission. Much prior work—though not all—has typically asked about cultural learning retrospectively, or relied on general ethnographic descriptions. Research on social network methods suggests that retrospective approaches tend to underestimate the so-called 'weak ties' [31], which may be precisely the kind of pathways in which we are interested. Our work, while still interview-based, asks people whom they would go to for cultural information now, given what they currently know. This approach avoids two potential shortcomings of prior methods in which memory biases (recalling past learning) and cultural beliefs about socialization (which biases recall and frame discourse) could influence the results. Of course, as we discuss below, our approach has its own limitations.

This retrospective method may help explain the long emphasis on vertical (parent–offspring) transmission that emerged from this work [4,30]. Consider, for example, what this approach would elicit if our two-stage model of cultural transmission were correct. Young learners would first acquire cultural information from their family, and principally from their parents. Then, perhaps starting in adolescence, learners would update their cultural information by attending to a set of preferred models, selected using the above described cues. Even though in this system the process of updating from selected models is the essential mechanism for generating cultural adaptations, recall-based interviews and casual ethnographic observation will mostly elicit stage 1 (vertical or family-based transmission) for two reasons. First, if the system is at or near the adaptive equilibrium, many learners would not update from their preferred models because their parents would have already transmitted to them the same information possessed by nearly everyone else in the community. Thus, stage 2 would not often occur when the system is at equilibrium [4]. Second, assuming learners do update from their preferred models, they would still have learned much of what they know from their parents. The updating process only refines previously acquired knowledge. If you ask an individual where they learned to make a bow, and they learned it first (80%) from their dad and then updated (20%) from the best hunter, they might be inclined to name their father (say, 80% of the time, or more).

To look for any evidence that younger (mostly adolescent) learners were more likely to choose genetic kin (e.g. parents) as models, we performed an additional set of ERG models where we split the sample into two subsets, one for ages 10–20 and another for ages 20 and older. If younger participants were more likely to choose genetic kin as models, we would expect differences in the significance, magnitude or direction of the coefficients for our genetic relatedness variable. We observed no such differences in any of our three domains. Further, there were no significant relationships between the age of the learner and the models that they nominated in any of the domains. It seems that neither the 10–20 age cohort, nor the group adults over 20 were inclined to seek out parents or other close relatives.

As our approach asks people whom they would seek out now, given their current knowledge, we are targeting more precisely the updating (second stage) component of the two-stage process. We think that this view of our method best explains why perceptions of within-domain success and knowledge are so potent, along with indirect assessments of the likelihood of possessing adaptive information (not already possessed by the learner), including cross-domain perceptions of success, age and sex. Both the within- and cross-domain effects, as well as age, are consistent with prior theoretical predictions. The effects for age, independent of perceived success and knowledge measures, are consistent with evolutionary arguments about why elders receive prestige-based deference across many societies [17]. Below we propose an explanation for why the effect of age disappeared for the Fishing domain. The effects of sex indicate a distinct sexual division of cultural information, with two of our domains being male (fishing and yams) and one being female (Medicinal Plants).

We think this view of our cultural transmission networks helps make sense of some of our more puzzling findings. First, our variable same sex had coefficients that went in the opposite direction to that predicted in two domains, and had no significant impact in the third. Viewing this post hoc and in light of the strong sexual division of information, we now suspect that individuals may have figured that opposite-sex people were more likely to possess useful information *not already possessed by the learner*, once success and knowledge-related measures are controlled for. That is, given one does not know something and one has learned most of what one knows from same-sex individuals, it is more likely that someone of the opposite sex knows it, *controlling* for success and knowledge. People may be more sophisticated cultural learners than our method anticipates.

Also puzzling was that neither same household nor genetic relatedness revealed the expected effects robustly. However, taking into account the 'right now' nature of our measures, this is less surprising. By adulthood, or even adolescence, individuals may have already sapped their household models and close relatives of much cultural information. The predictive effects observed for same village are consistent with this view, in that individuals have probably not yet fully tapped everyone in their village by adulthood. Beyond the village, a lack of sufficient information about potential cultural models, or simply higher access costs, might deter individuals from tapping those outside their village and Yavusa. It is also possible that both same household and genetic relatedness have their influence through our success or knowledge measures.

For the final puzzle, we found no effect for age difference. While age is an indirect cue of possessing adaptive information, age difference should be most important for younger children who need to scaffold themselves up to complex skills. Given that we focused on adolescents and adults (but not children), it is not surprising that we obtained a null result for this variable. Taken together, these patterns suggest that our measures tap the second stage—locate preferred models—in the two-stage transmission model.

Our results also reveal several patterns that were not anticipated by the existing theoretical work, and deserve further study. To begin, in domains where we have measures of both perceived knowledge and success, there are stronger effects for perceived success. In fact, cross-domain success is about as important as within-domain knowledge. This may be owing to the relative perceived accuracy of assessments of these in different domains. Assessing success in some domains can be accomplished by attending to distinct outcomes (e.g. who brings home the largest fish catch). Ethnographic observations suggest that not only are these outcomes most salient to observers, but they are also readily spread among community members. Information about spear-fishing success, in particular, comes in on a daily or weekly basis, while yam growing success arrives yearly. Information about line-fishing success also circulates, especially when big fish are caught, but line fishing does not produce many large fish, or the substantial hauls, of spear-fishing. Meanwhile, successes with medicinal plants are relatively noisy and sporadic (medicines of all kinds frequently fail) such that asking about success directly is unproductive. Another possibility is that knowledge may be seen as less connected to what the learner themself wants to achieve. Modelling work has begun to address such cultural dynamics [32].

A second related pattern that emerged, which we did not predict *a priori* (but should have), involves understanding why the effects of age disappear in the fishing domain. The relative accuracy of individuals' perceived assessments of success may illuminate this phenomenon. Effects from indirect cues like age should be strongest when other clear indicators of success are not available to learners. The clearer the direct indicators of success in a particular domain, the less important indirect cues like age should be.

This same effect may also explain why our time-allocation measures are not predictive for Fishing, but are for the other two domains. Accurately assessing model quality in Fishing may be easier than for Yams and Medicinal Plants, which may require the close contact captured by our time-allocation measures. As noted, our ethnography strongly suggests that people's assessments of success in fishing are likely to be substantially more accurate than in the other two domains. Although more work is needed to quantify the differences between our cultural domains, these findings suggest that future research should attend to the details of how learners acquire information about their models.

A third pattern, which has been suggested elsewhere, is that education is negatively associated with selection as a model in all three of our domains. This is interesting as some readers might view formal education as a general proxy for intelligence, skills or knowledge. However, for the domains under investigation, being in school means not spending time fishing, planting yams or dealing with medicinal plants. While formal education does promote skills that are valued in the developed world, the hours spent in school may result in fewer opportunities for learning other life skills that are not taught in schools [33].

This opens the largely unaddressed question of how cross-domain success (prestige) effects operate. Theorists have suggested that success or prestige achieved in one domain (e.g. Nobel prizes) should carry over to and influence learning in other domains, especially domains perceived as similar to the source domain. Our findings are broadly consistent with this view, as success in fishing predicts being selected as a cultural model for learning about yams, *independently* of success in yam growing, but it does not predict being sought for information about medicinal plants. Success in growing yams predicts being sought for information about both fishing and medicinal plants. Greater education, which does ethnographically carry a general air of prestige, negatively predicts being sought for advice in all three domains. We speculate (wildly) that growing yams and fishing are perceived as similar because they are both male domains, that growing yams and using medicinal plants are perceived as similar because both involve culturally valued plants, and that education is perceived negatively for learning about these domains because it runs opposite to pursuing a traditional Fijian livelihood.

The major limitation in this approach—as in other field studies—involves the connection between our interview-based measures of whom people would seek out for cultural transmission and from whom they actually learn. The methods employed here may not fully capture the dynamics of cultural learning events. For example, learners may observe multiple preferred models and then copy the most commonly observed strategy (conformist transmission). Our method would potentially capture the models that a learner might assess, but it would not capture the learning algorithms used to integrate the information obtained from different models.

An alternative approach we are currently pursuing in Fiji involves studying the correlations in actual cultural traits among individuals and trying to analytically back out the transmission pathways. This avenue avoids having to rely on participant reports of transmission, but it can only be done in cultural domains with at least moderate degrees of inter-individual variation. Empirically, however, we have found many cultural domains, including some of the most important, which show very little inter-individual variation [4]. Under many conditions, this is what we would expect when the two-stage model has reached equilibrium in an important domain. Thus, even this approach has limitations. Ongoing fieldwork in our Fijian communities aims to illuminate more precisely the connection between our networks and the actual distributional patterns of various cultural traits.

Given that all approaches to assessing the pathways of cultural transmission in humans have important—but different—limitations, we believe our findings here are best interpreted in light of converging research lines from psychology, where laboratory-experimental evidence reveals similar patterns of transmission to those inferred from our village networks, and from phylogenetic analyses of actual cultural traits, which reveal patterns of oblique transmission consistent with our findings [34]. It is only through converging lines of evidence using different methodological approaches in diverse populations that we can address this key evolutionary question.

5. CONCLUSION

Understanding the success of our species involves delineating the processes responsible for assembling the adaptive information about tracking, tool manufacture, plant use, environmental dangers and shelter construction that have allowed a tropical primate to inhabit such a diversity of environments. Theorists have proposed three kinds of mechanisms capable of generating these cultural adaptations: (i) individual learning (plus vertical cultural transmission), (ii) selective cultural learning biases, and (iii) natural selection acting on cultural variation [7]. Our findings, combined with prior field studies and recent experimental work, point towards the importance of selective cultural learning biases. This does not mean that neither individual learning nor natural selection are unimportant in particular circumstances. However, it does suggest that if our learning biases are as strong as they appear, cultural evolution driven by such biases can overcome individual learning effects in creating cultural products, and natural selection will often have little impact on cultural variation, as the rates of adaptive cultural evolution created by such biases will often be very fast compared with natural selection. Efforts to model cultural evolution and culture–gene interactions should consider the effects of selective learning biases, as well as vertical cultural transmission, and individual learning.

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