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The adaptive nature of culture. A cross-cultural analysis of the returns of local environmental knowledge in three indigenous societies

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Abstract

Researchers have argued that the behavioral adaptations that explain the success of our species are partially cultural, i.e., cumulative and socially transmitted. Thus, understanding the adaptive nature of culture is crucial to understand human evolution. We use a cross-cultural framework and empirical data purposely collected to test whether culturally transmitted and individually appropriated knowledge provides individual returns in terms of hunting yields and health and, by extension, to nutritional status, a proxy for individual adaptive success. Data were collected in three subsistence-oriented societies: the Tsimane' (Amazon), the Baka (Congo Basin), and the Punan (Borneo). Results suggest that variations in individual levels of local environmental knowledge relate to individual hunting returns and to self-reported health, but not to nutritional status. We argue that this paradox can be explained through the prevalence of sharing: individuals achieving higher returns to their knowledge transfer them to the rest of the population, which explains the lack of association between knowledge and nutritional status. The finding is in consonance with previous research highlighting the importance of cultural traits favoring group success, but pushes it forward by elucidating the mechanisms through which individual and group level adaptive forces interact.

Keywords

adaptation; cross-cultural research; hunter-gatherers; hunting; medicinal plants; sharing; traditional knowledge

Introduction

Researchers debate the role of culture in shaping human adaptive strategy. Cultural evolution theory suggests that the behavioral adaptations that explain the expansion of our species are—at least partially—cultural, in the sense that they are cumulative and transmitted by social learning (Henrich and McElreath 2003; Tomasello 1999; Richerson and Boyd 2005). Since all humans share the same basic genetic endowment, only culture can explain the diversity of locally adapted behaviors that have allowed human societies to adapt to the array of environments they have come to inhabit, from mountain ranges to coastlines, and from the Tropics to the Arctic (Richerson and Boyd 2005; Henrich and McElreath 2003). Cultural knowledge embodies information and skills that no single person could have developed in a lifetime, and this cumulative knowledge—evolutionary anthropologists suggest—has allowed for human adaptation to many different environments (Castro and Toro 2004; Richerson and Boyd 2005). Cultural rather than just genetic adaptation should therefore be considered at the basis of humanity's achievements.

Although definitions of *adaptation* vary across disciplines, they all capture the idea of adjustments in order to cope with stress or change, which in turn should lead to better fitness (i.e., an increased probability of reproduction or persistence) (Smit and Wandel 2006; Nelson, Adger, and Brown 2007; Pelling and High 2005; Gallopin 2006). The term adaptation has its origins in evolutionary biology, where it broadly refers to the development of genetic or behavioral outcomes which enable organisms or systems to cope with environmental changes in order to survive and reproduce (Winterhalder 1980; Kitano 2002). Within anthropology, the term adaptation was first used to refer to the persistence of a social system despite new socioeconomic or environmental conditions. For example, Steward (1955) used the term “*cultural adaptation*” to describe the adjustment of societies to the natural environment through subsistence activities; and Denevan (1983) defined it as a “process of (cultural) change in response to a change in the physical environment or a change in internal stimuli, such as demography, economics and organization” (p. 401) thereby broadening the range of stresses to which human systems adapt. Using a different perspective, cultural evolution theory has adapted the biological definition, highlighting that in the case of humans, two co-evolving systems of inheritance (i.e., genes and culture) shape human behavior (Richerson and Boyd 2005; Laland, Odling-Smee, and Myles 2010).

Despite the presumptive importance of culture on human adaptation, we lack empirical research on the mechanisms through which culture might shape human adaptive strategy. Much research on the adaptive nature of culture has been theoretical, based on formal models (Richerson and Boyd 2005; Wakano and Miura 2014) and more recently on experimental work (Horner et al. 2006; Efferson et al. 2008; Derex et al. 2013). Only a few scholars have addressed the topic with observational studies (Atran et al. 2002), yet even these have been often limited to only one society and one cultural trait. Furthermore, most previous work on the adaptive nature of culture has focused on group characteristics, such as cultural traits favoring group success (Henrich 2004; Soltis, Boyd, and Richerson 1995), thus largely neglecting individuals' contributions to the adaptive process.

The work presented here aims to contribute to research on the adaptive nature of culture using a novel approach that complements previous work. Specifically, in this work we use real-world data to test a pathway through which cultural knowledge might enhance human adaptive strategy: the individual returns (in terms of hunting yields and health) to culturally-evolved and environment-specific knowledge¹. The underlying assumption of this work is that individuals should also be considered active agents in their cultural and natural environments as they optimize their survival strategies in diverse demographic, institutional, and ecological environments (Handwerker 1989). In other words, cultural beliefs and practices exist at the group level, but these beliefs can be rejected, strengthened, developed, or modified by individuals (Winterhalder and Smith 2000). By testing the assumption that individual representations of cultural knowledge provide positive individual returns, we provide a new angle and analytical focus to the question of the adaptive nature of culture, thus adding to previous research on the topic.

Some previous work has attempted to explain part of the behavioral diversity in individuals as a consequence of environmentally contingent responses made in adaptive efforts (Winterhalder and Smith 2000). Behavioral strategies are considered to be designed to solve adaptive problems such as producing food, mating, investing in offspring, or managing social interactions. Furthermore, researchers have argued that -in subsistence societies- locally developed knowledge systems about the environment guide several of these adaptive behavioral strategies, such as food procurement (Quave and Pieroni 2015), habitat management (Turner, Ignace, and Ignace 2000; Berkes, Colding, and Folke 2000), and attempts to prevent and cure diseases (McDade et al. 2007). If this is the case, then local environmental knowledge provides an ideal case to test the idea that the way in which individuals appropriate specific cultural traits results in different outcomes that can potentially affect the adaptive process. In such a framework, the empirical work presented here assesses the individual returns of local environmental knowledge on individual hunting yields, health, and nutritional status, traits that are presumably associated to individual adaptive success. Our test of whether individual local environmental knowledge provides returns on hunting and health is guided by two main hypotheses.

H1. Adults with more local knowledge of game species (hereafter hunting knowledge) will have higher hunting returns than adults with less hunting knowledge.

Rationale

Researchers argue that societies have developed a comprehensive knowledge on local ecology to guide strategies of food procurement (Koster 2011). If this is the case, then people with more hunting knowledge should be able to make better decisions with regard to their hunting activities (e.g., when and where to hunt), which in turn should result in higher hunting returns.

¹We use the term local environmental knowledge to refer to knowledge systems, which include knowledge, practices and beliefs. Specifically, we draw on Berkes et al. (2000:1252) work and define local environmental knowledge as a “cumulative body, practices and beliefs handed down through generations by cultural transmission, about the relations of living beings (including humans) with one another and with their environment”.

H2. *Adults with more local knowledge about medicinal plants (hereafter medicinal plant knowledge) will have lower reports of sickness than adults with less medicinal plant knowledge.*

Rationale

Researchers have demonstrated that many plants are used by humans for medicinal purposes owing to the effects of their chemical compounds (Laird 2002; ten Kate and Laird 1999). Given this, in societies with limited access to Western medicine, people who know about the location, properties, and use of medicinal plants should be expected to have better health than those with less of such knowledge.

We then extend our work to pose two more, related, hypotheses.

H3. *Adults with more local environmental knowledge will benefit from larger returns in hunting and health than individuals with lower local environmental knowledge.*

Rationale

It has been argued that local environmental knowledge is a comprehensive system in which the different parts are interrelated (Berkes, Colding, and Folke 2000). If the different parts of the system create synergies, then an inclusive measure of local environmental knowledge (i.e., a measure that simultaneously accounts for hunting and medicinal plant knowledge, hereafter local environmental knowledge) would result in a stronger positive association with the selected outcomes than any of the specific measures alone.

H4. *The returns to local environmental knowledge will be lower for individuals with higher levels of exposure to the national society and integration into the market economy.*

Rationale

As they engage in different economic activities and adopt new behavior, for example allocating less time to the procurement of wild food (Behrens 1992), individuals with higher levels of exposure to the national society and integration into the market economy might detach themselves from traditional norms and customs, including a detachment from local knowledge systems (Gomez-Baggethun et al. 2010). In such situations, we expect an attenuation of the returns of local environmental knowledge systems in the measured outcomes.

In our last hypothesis, we extend our test to a different outcome: nutritional status.

H5. *Adults with higher local environmental knowledge will present better nutritional status than individuals with lower local environmental knowledge.*

Rationale

If H1-H3 hold true, then one could argue that local environmental knowledge provides a myriad of individual returns that, overall, might result in better individual adaptive success. We test this hypothesis by assessing whether any of our three measures of local knowledge (hunting, medicinal plant and local environmental knowledge) are associated with different

indicators of nutritional status. Indicators of nutritional status are recognized as good indices of protein and energy status and reserve (Frisancho 1990; Shetty and James 1994). As the nutritional status of adults from forager societies is low relative to reference values from industrial nations (Foster et al. 2005), in such contexts, higher levels of nutritional status indicate higher levels of caloric and nutrient reserves and –from a physiological point of view- are therefore probably good proxies for individual adaptive success.

The empirical approach: Comparative research in three small-scale societies

Previous research provides some evidence that ethnobotanical knowledge, a type of local environmental knowledge, provides health returns. For example, in previous work we have found a positive association between individual ethnobotanical knowledge and nutritional status (Reyes-García, McDade, et al. 2008) and child health (McDade et al. 2007). However, the extent to which the patterns found in one society hold true for other societies remains still unknown. Here, we use a cross-cultural comparative approach to enhance the external validity of our findings (Mace and Pagel 1994; Ember and Ember 2000) with our aim being to reach conclusions that, rather than hinging on the choice of a particular society, can be more generalized. In doing so, we also add to cross-cultural research in anthropology.

While there is a long-standing tradition of cross-cultural research in anthropology, most of it has focused on culture as the unit of analysis and has been based on ethnographic data collected for the Human Relations Area Files (HRAF) (Ember 2006). Few anthropological studies have addressed the collection of primary data informed by a comparative perspective from the outset. The latter differ from cross-cultural research based on the HRAF in that they use the same research protocols to collect primary data across different societies and in that they shift the unit of analysis to the individual, comparing individuals across societies. The use of comparable research protocols to collect primary data allows researchers to overcome problems associated with the use of secondary data (i.e. comparability of samples, coding reliability). The shift in unit of analysis -from the society to the individual- allows researchers to show commonalities and differences both at the individual and societal level. Some classical examples of anthropological cross-cultural research using primary data collected with the same research protocols include Whiting's studies of childhood (1963), the work of Gross and colleagues on the capacity of natural systems to sustain human populations (Gross et al. 1979; Flowers et al. 1982), the work of Gray and colleagues in resource use and conservation among indigenous peoples and migrant populations in Ecuador (Gray et al. 2008; Lu 2007), and the work of Henrich and colleagues (2005) on cooperation.

Following this line of enquiry, we set up our cross-cultural study in three indigenous, small-scale, subsistence-based societies: the Baka (Congo Basin), the Punan (Borneo), and the Tsimane' (Amazonia). To date, all three societies have relatively little (albeit increasing and uneven) involvement in market economies, school-based education, or modern health care systems. In addition, the three societies resemble one another in that they depend on the consumption of local natural resources through a combination of foraging and farming in an

environment where such societies have historical continuity of resource use. We selected these three societies for three main reasons. First, contemporary foragers offer the opportunity to study human behavioral variability. Indeed, if people who now forage for a living are constrained by features of local ecology, then variation in these constraints, including the trade-offs they impose and the solutions adopted by individuals differing in age, sex and reproductive status, are open to direct ethnographic observation. Second, relatively isolated indigenous societies allow for the rare and diminishing possibility for researchers to estimate relations that become ever harder to spot once external influences become common place. For instance, in industrial societies the link between individual knowledge and health is hard to estimate owing to the role of intervening mechanisms such as governmental health care programs or other public programs. Similarly, once the use of writing (or other external information storage strategies) is adopted, the process of transmission of knowledge changes (Leonti 2011). In small-scale, isolated societies, where writing is mostly absent, such external mechanisms are greatly attenuated. Last, we selected societies in different areas of the world to minimize effects of cultural influence, or what in cross-cultural research is known as Galton's problem (see Ember and Ember (2000) and Chrisomalis (2006) for a review). Below we share some glimpses into the nature of the studied societies and additional references for the interested reader.

The Baka are one of the hunter-gatherer groups indigenous to the tropical rain forests of the Congo Basin. Numbering somewhere between 30,000 and 40,000, the majority of Baka live in what is today southeastern Cameroon. Living in semi-nomadic groups and depending mainly on wild resources for their livelihood, they are closely associated with neighboring sedentary farming villages in a relation of mutual interdependence (Bahuchet 1993). At the turn of the 1960s, following the decline of elephant populations and missionary attempts to sedentarize and educate the Baka, they regrouped themselves along logging roads and started to cultivate their own fields, modifying their spatial and temporal organization (Leclerc 2012). Nowadays, the Baka maintain a high level of mobility between villages and forest camps, and strong material and symbolic relations with farmers, but are subjected to the monetization and commoditization of their economy (Kitanishi 2006). Most Baka combine hunting-gathering with work for farming neighbors, wild products trade, and cultivation of cassava and plantains, their major staple crops.

Our second study society, the Punan, is found in mountainous interior Indonesian Borneo. Although the Punan are no longer nomadic, they still engage in long travels and seasonal stays in the forest for hunting wild boars and gathering wild edibles and other forest products (Kaskija 2012; Levang, Sitorus, and Dounias 2007). Previously, their traditional livelihood was largely based on preparing starch from hill sago, hunting bearded pigs, and bartering with the locally settled farmers (Kaskija 2012). Yet, the Punan started to shift to a more sedentary lifestyle during the mid-1950s, under pressures from government programs (Kaskija 2012). At present, the Punan number ~10,000 people, living in East Kalimantan Indonesia (Levang, Dounias, and Sitorus 2005). An important source of cash income for the Punan is the commercialization of non-timber forest products such as eaglewood (*Aguilaria spp.*), head of hornbill, or bezoar stones. However, nowadays, wage labor -including wage from work in government projects-provides the significant and regular income for many Punan.

Our third case study society is the Tsimane', a small-scale indigenous society of foragers and farmers in the Bolivian Amazon. The Tsimane' number ~ 12,000 people living in ~100 villages of commonly ~20 households per village, concentrated along rivers and logging roads (Reyes-García et al. 2014). Up until the late 1930s, the Tsimane' lived much like they did prior to first contact with the national culture, maintaining a traditional and self-sufficient lifestyle. However, their interactions with the Bolivian society have steadily increased since the 1940s (Reyes-García et al. 2014). Previously semi-nomadic, they are now mostly settled in permanent villages with school facilities. Tsimane' rely on slash-and-burn farming supplemented by hunting, fishing, gathering, and wage labor in logging camps, cattle ranches, and in the homesteads of colonist farmers. Their main cash crops are rice, maize and plantain, although the barter of thatch palm also provides an important source of income for many households (Vadez et al. 2008).

Methods

The empirical work presented here is based on 18 months of fieldwork among the above mentioned societies. Prior to fieldwork, the team spent six months getting familiarized with the research areas and drafting the research tools. Following this, six researchers (two per society) lived for 18 months in one of the selected societies, each in a different village. Each researcher teamed up with local research assistants who helped in data collection and translations. Once in the field, the teams devoted the first five months to pilot-test the protocols, as well as to collect contextual and ethnographic information. The following 12 months were spent collecting quantitative data in the six villages. In between the two periods, the research team met over the course of one month to discuss and make consensual decisions on the structure and content of the data collection protocols. We obtained Free Prior and Informed Consent from each village and individual participating in this study, as well as agreement from the relevant political organization representing each indigenous group where we workedⁱⁱ.

Qualitative methods

Qualitative data collection methods were integrated into the entire stretch of fieldwork, but were particularly predominant during the first months, a period mostly devoted to learning the local languages, getting adapted to the local mores, building up trust with participants, and collecting background ethnographic information. During this time, we conducted semi-structured interviews with key informants on local livelihoods (i.e., techniques, division of labor, seasonality, and assets associated to subsistence activities) and on the content of local environmental knowledge (Davis and Wagner 2003). Semi-structured interviews allowed us to gain a deeper understanding of the meaning, values, and beliefs of each of the studied domains of knowledge. The themes of the interviews covered, for example, the most common illnesses and their remedies, the behavior of different animals, the different hunting techniques used, or beliefs and rituals associated to hunting practices. We also conducted free-listings on game and medicinal plants, information that was later used in the design of

ⁱⁱThis research adheres to the Code of Ethics of the International Society of Ethnobiology and has received the approval of the ethics committee of the Autonomous University of Barcelona (CEEAH-04102010).

knowledge tests (Reyes-García et al. in press). The ethnographic information relating to the lived practice of local environmental knowledge in each society informed the design of quantitative methods and helped to put our results into a broader context.

Quantitative methods

During the second stage of field work, we collected primarily quantitative data. In order to make our research as locally-specific as possible, we adapted our protocols for each site (e.g. referring to local species and practices). However, to allow for the comparability of data across the three societies, the questions were generated in the same way and the protocol's general structure and administration was identical across sites. All the protocols were pilot-tested and refined in villages different from the study villages, but with the same cultural backgroundⁱⁱⁱ.

Sampling strategy

Within each of the three studied societies, we selected two villages at varying distances to the main market town. Within each village, we worked with all adults willing to participate. We defined adults as people 16 years or older, because at about this age people in the selected societies start forming a household. The participation rate was over 90%. As researchers visited each informant several times to collect different sets of data, the sample size varies from one measure to another. We excluded from the analysis presented here adults without information for all the selected variables, leaving us with a sample of 160 Baka, 110 Punan, and 125 Tsimane' adults (with slight variations between models).

Explanatory variables

We collected data on hunting and medicinal plants knowledge using three different methods: an identification task, a self-reported skills questionnaire, and peer ratings (see Reyes-García et al. in press for a complete description) (Table 1).

Identification task—We designed a test in which informants were asked to provide the vernacular name for a stimuli corresponding to 10 species of game. We first categorized game cited in free-listings into terciles according to their saliency (Smith and Borgatti 1998). We then randomly chose five items from each group (15 items), which were reduced to 10 after testing (Table 2). In the identification task for hunting knowledge, we presented informants with stimuli from a known origin (e.g., a skull provided by the prey's hunter) and asked them to provide the vernacular name of the species. The stimuli included pictures, recordings (e.g., a bird's song), and animal parts (e.g., a skull, a feather). Since the stimuli were from a known origin, we generated the hunting scores by contrasting informant responses with information from the known origin. Plants for the identification task for medicinal plants were selected in a similar way, with the exception that we included two plants not listed as medicinal (Table 2). Assistants read out to the informant the name of the 10 selected plants and asked them whether they knew the plant, and –if so– whether it has a medicinal use. We created a knowledge score corresponding to the number of plants with medicinal use reported by the informant.

ⁱⁱⁱThe protocols used for data collection can be accessed at <http://icta.uab.cat/etnoecologia/lek>.

Self-reported skills questionnaire—We asked informants to self-report their ability on practices that, according to our ethnographic information, embody hunting and medicinal plant knowledge. For example, to assess hunting skills, we asked informants to self-report on hunting frequency, weapons used, and success with difficult-to-catch preys (i.e., wild boar for Baka, sun bear for Punan, and tapir for Tsimane'). The hunting skills' score was created by evaluating self-reports of skills. To measure skills regarding medicinal plants, we asked informants to report the last time they had prepared (for themselves or for others) the remedies listed in the medicinal plant identification task. We created a score that accounts for both the total number of medicinal uses reported and the last time each of those was reportedly put in practice.

Peer rating—Our third score was constructed by asking informants to evaluate their peers (Reyes-García et al. in press). We first grouped households into kinship affinity-groups, from which we formed groups of six evaluators containing three men and three women and people from different ages. We then randomly grouped the names of adults in lists containing 20 names and assigned a list to each group of evaluators, who were asked to rate subjects based on their knowledge. For example, we asked the informant to evaluate each subject on the list on the basis of questions such as: "Is [*name*] a good hunter?" Evaluators could rate the person's ability as excellent (4 points), good (3 points), average (2 points), not so specialized (1 point), or not applicable (as they do not practice the skill) (0 points). The knowledge score from peer ratings corresponds to the average of the rating provided by the six evaluators rating the subject.

We used the scores generated with our three methods (identification task, self-reported skills questionnaire, and peer ratings) to construct three composite measures: hunting knowledge, medicinal plant knowledge, and local environmental knowledge. We first assessed the intra-subject consistency of our measures by running a series of Pearson correlations of the different measures in the two selected domains. We further explored the internal consistency of our measures by calculating the Cronbach's alpha coefficient for each domain. As we found internal consistency (see below), we used principal component factor analysis to generate new composite variables by using standardized (mean 0, variance 1) values of the different scores. The measure of hunting knowledge is constructed with the score of the three hunting knowledge tests; the measure of medicinal plant knowledge with the score of the three medicinal plant knowledge tests; and the measure of local environmental knowledge with the score of the six aforementioned tests.

Outcome variables

Our outcome variables include hunting returns (H1, H3 and H4), share of days sick (H2, H3 and H4), level of exposure to the national society and integration into the market economy (H4), and nutritional status (H5). As seasonality most probably affects the outcomes, we collected repeated observations over the course of 12 months and calculated averages for each individual in the sample.

Hunting returns were measured as the amount of meat obtained per hour invested in hunting (including trap preparation). To collect data, we used an anthropological technique known as

scan observations (Reyes-García et al. 2009). Each week, on a given day chosen at random, we visited each household and asked the adult(s) present about all the animals killed by themselves in hunting activities in the previous two days. This method generated an average of 19.2 observations per person (SD 6.9). We also asked about time invested in hunting activities. We calculated hunting returns as the kilograms of meat caught per hour invested (kg/hour). As it was not always possible to obtain the weight of the preys, we used published data to estimate the weight of different animals (mostly Kingdon (1997) and Gautier-Hion, Colyn, and Gautier (1999) for Central Africa, Payne and Francis (2007) for Borneo, and Myers et al. (2006) for Bolivian Amazon). In our estimations, we differentiate between the weight of males and females. We assigned the value of half the weight of the same sex adult to any juvenile specimen reported.

Sickness—We used self-reported information on health. Specifically, during our scan observations, we asked about the occurrence of any illness or symptom during the two days prior to the interview. We then calculated the share of times the person had been reportedly sick from all the times observed. Since we collected several observations per informant over the 12 months of quantitative data collection, our measure captures seasonal variability.

Level of exposure to the national society—We collected data on standard proxies for the multiple dimensions of exposure to the national society (Dressler, Balieiro, and dos Santos 1998; Lara et al. 2005; Sternberg et al. 2001; Zane and Mark 2003). We asked informants to report the maximum grade they had completed in school and to recall whether any of their parents could read. We assessed each informant's fluency in the national language (French for the Baka, Bahasa for the Punan, and Spanish for the Tsimane'), distinguishing between informants who could communicate fluently and well enough in the national language and those who could not. Finally, we assessed the informant's literacy by asking them to read some sentences in the national language. We assessed the intra-subject correlation of the different measures (Trimble 2003) and then used principal component factor analysis to create a new, composite measure that captures the multidimensionality of our construct. The first factor (eigenvalue 1.98), explaining 52% of the variation in the data, was retained as a measure of exposure to the national society.

Level of integration into the market economy—We also collected data on four standard variables that researchers have used to measure an individual's degree of integration into the market economy (Lu Holt 2007; Godoy, Reyes-García, Byron, et al. 2005): i) number of visits to the main market town in the previous year; ii) the value of a set of market items owned by the subject; iii) cash income from the sale of wild meat, agricultural and forest products; and iv) cash income from wage labor. Information to construct the last two variables comes from individual interviews collected once a quarter, with a recall of two weeks, and averaged to obtain a single measure for each individual. For cross-country comparisons, we used purchasing power parity (PPP) exchange rates. Thus, all monetary values express PPP adjusted US\$. Again, we used principal component analysis to create a composite measure. Results from the intra-subject correlation of the different variables suggest that cash income from wage labor was not associated with the rest of the variables, so we constructed the index only with the other three variables retaining the first

factor (eigenvalue 1.48) which explained 44% of the variation in the data. We included income from wage labor as an additional variable in our regression models.

Nutritional status—We collected anthropometric information to get estimates of nutritional status. We followed the protocol of Lohman, Roche, and Martorell (1988) and measured subjects in light clothing without shoes or hats. We recorded stature (standing height) to the nearest millimeter using a portable stadiometer and body weight to the nearest 0.20 kg using a standing scale, both from which we were able to calculate each individual's Body Mass Index (BMI; kilograms/meters²). We also measured mid-arm circumference (cm), and the thickness of skinfolds (biceps, triceps, subscapular, suprailiac; mm).

Control variables

Some of our control variables – e.g. sex, age, and household size - were selected based on previous research suggesting that individual characteristics may affect the intra-cultural distribution of knowledge within a group (Boster, Berlin, and O'Neill 1986; Camou-Guerrero et al. 2008; Salpeteur et al. 2015). For each model, we also included variables which might be related to the particular outcome. Thus, in estimations using hunting returns as outcome, we control for hunting effort (or the share of times the person was observed hunting from all the times we have scan data for the person) and capital inputs (share of times the person used a traditional weapon). When assessing the effect of medicinal plant knowledge on health, we controlled for the the use of medicines (or the share of times the person reported using any type of medicine when sick, versus not using any).

Data analysis

We estimate the individual returns of local environmental knowledge using the general following expression [1]:

$$O_{ihv} = \alpha + \gamma LEK_{ihv} + \beta P_{ihv} + \zeta F_{ihv} + \lambda M_{ihv} + \Omega S + \varepsilon_{ihv} \quad [1]$$

where O is the selected outcome (i.e., hunting returns, sickness, or nutritional status) for subject *i* of household *h* in village *v*. LEK is our proxy for local knowledge (i.e., hunting, medicinal plant, or local environmental knowledge). P_{ihv} is a vector of variables to control for socio-demographic characteristics that might affect the studied relation (sex, age, and household size). F_{ihv} is a vector of additional controls specific to each outcome (i.e., hunting effort and capital input for hunting returns and use of medicines for sickness). M_{ihv} is a vector that includes our two indices of exposure to the national society and integration into the market economy (only for H4). S is a vector that includes dummy variables for the society. And ε_{ihv} is the error term, or the information that remains unexplained by the model.

We adapted this general model to test our different hypotheses. Thus, to test H1, we used hunting returns as outcome (O) and hunting knowledge as main explanatory variable (LEK); we only controlled for socio-demographic variables (P) and variables related to the outcome (F). As our dependent variable is zero-inflated and positively skewed, to reduce estimation

biases associated to such distribution (McElreath and Koster 2014), we used a two part model in which we specified the same dependent and independent variables. In the selected model, the first part models the probability that $depvar > 0$ using a logit binary choice model. The second part models the distribution of $depvar \mid depvar > 0$ using a standard OLS model (regress). As estimates of hunting returns become imprecise with a declining number of sampled number of trips per individual (Hill and Kintigh 2009), we also fit a multilevel mixed-effects linear regression in which we specified frequency weights at the individual level as the total number of observations for any given subject. Regressions were run only with the subsample of people who had returns in –at least- one of the trips.

We used the same equation to test H2, but using medicinal plant knowledge and related variables. Since the variable sickness also include many zeros (from people who was never observed sick), we also used a two part model. To test H3, we used our composite measure of local environmental knowledge, rather than hunting or medicinal plant knowledge. To test H4, we added to models testing H1 and H2 the proxy measures for exposure to the national society and integration into the market economy. Finally, to test H5, we used the same models as to test H1 and H2, but using indicators of nutritional status as the outcome. To test H5, we separated between the sample of men and women, and excluded pregnant women from the sample.

To control for societies fixed-effects, or invariant characteristics of societies that might affect the estimated association, in our core regressions we included a set of dummies for the society of study. In additional analyses we replaced site by village dummies. Irrespectively of whether we used site or village dummies, all regressions include clusters by village, to indicate that the observations may be correlated within villages, but would be independent between them. For the statistical analysis we used STATA for Windows, version 13. As indicator of statistical significance, we report p-values below 0.10.

Results

Measuring local environmental knowledge

Results of a Cronbach's alpha suggest that the three measures used to capture different domains of knowledge are highly inter-correlated. Thus, the alpha coefficient for the three measures of hunting knowledge was of 0.73; the alpha coefficient for the scores of medicinal plants was of 0.74. The alpha coefficient for our overall measure of local environmental knowledge, constructed with the scores of the six knowledge tests, was of 0.74.

Hunting knowledge and hunting returns

The individuals in our sample across all three societies have on average a hunting returns of about one kilogram (0.980 kg) of game per hour spent hunting, with large differences between sexes (average 1.66 kg for males vs. 0.29 kg for females) and groups (the most productive being the Punan, $avg = 1.59 \text{ kg/hr}$) (Table 1). Forty six percent of informants (71% of women and 21% of men) did not report any hunting activity during scans.

The test of H1 suggests that, indeed, there is a positive and statistically significant association between hunting knowledge and hunting returns. When modeling the probability

that the person obtains hunting returns (versus no returns at all), we find that, for every one unit change in hunting knowledge, the log odds of obtaining hunting returns increases by 0.87 (Table 3). Exponentiating the results to facilitate the interpretation, we can say that for a one unit increase in hunting knowledge, the odds of having hunting returns (versus not having them) increase by a factor of 2.38 ($p < 0.05$). In the second part of the model, which actually models the distribution of positive hunting returns (hunting returns > 0), we also observe a positive association. Here, for every unit increase in hunting knowledge, a 0.84 kg/hour increase in hunting return is predicted, holding all other variables constant. The coefficients remain relatively unaltered when including village (rather than society) dummies (Model 2), although the coefficient in the second part of the model is lower.

Models 3 and 4 (Table 3) resemble the previous models except that here we use the measure of local environmental knowledge to test H3. Results from Models 3 and 4 also confirm our hypothesis: local environmental knowledge bears a positive and statistically significant association with hunting returns. In those models, the coefficients of the association are higher for the first and lower for the second part of the model, when compared to hunting knowledge.

Finally, we test H4 by including our composite measures of exposure to the national society and integration into the market economy (Models 5-6). Contrary to our expectations, we did not find a lower coefficient of association between hunting knowledge and hunting returns when including such controls. However, the change in the coefficient is small, and the level of statistical significance resembles those of Models 1 and 2. Neither the index that captures exposure to the national society nor the index that captures integration into the market economy are strongly associated to hunting returns. Models 5 and 6 are the ones with the smaller value of the Aike and Bayesian information criterion (AIC and BIC), suggesting they provide a better fit to the data. All results discussed so far, are equally significant when using a multilevel regression model with frequency weights to account for the fact that some individuals were more heavily sampled than others (Supplementary Material, Table S1)

Medicinal plant knowledge and health

Adults in our sample reported to be sick in 5.1% of the days they were observed ($sd=10.1$) (Table 1). The share of days reportedly sick varies between groups: Baka were reportedly sick in 7.31% of the observed-days, Punan in 4.7%, and Tsimane' in 2.7%. About 60% of the people in our sample never reported a sickness or ailment, again with an unequal distribution between sites: 76% of Tsimane', 63% of Punan, and 46% of Baka, never reported a sickness.

Models 1 and 2 in Table 4 do not provide enough evidence to support the hypothesis that medicinal plant knowledge bears a positive association to better health. When modeling the probability that the person reports being sick at least once (versus never), we find that higher medicinal knowledge bears a positive association with the log odds of reporting sickness, although the association is not statistically significant (Table 4, Models 1 and 2). However, in the second part of the model, which actually models the variable sickness, we observe a negative association. Here, for every unit increase in medicinal knowledge, the share of days reportedly sick decreases by 0.01. The results, however, are not statistically significant.

In our test of H3, or the relation between our composite measure of local environmental knowledge and health (Models 3-4), we find similar results for the first part of the model. The second part of the model also suggests a negative, and this time statistically significant association with sickness, with every unit increase in local environmental knowledge, being associated to a 0.02 decrease in the share of days reportedly sick ($p < 0.1$).

Finally, when testing the relation between medicinal plant knowledge and health when considering levels of exposure to the national society and integration into the market economy (H4: Models 5 and 6), we find that the coefficient of the association is similar to Models 1-2. As in the case of hunting returns, neither the index that captures exposure to the national society nor the index that captures integration into the market economy are associated to sickness. This finding suggests that in the studied societies the relation between medicinal plant knowledge and health is not altered by the individual level of exposure to the national society or integration into the market economy.

Local environmental knowledge and nutritional status

In Table 5 we present results for additional regression models. The models run resemble models in previous tables but use our three indicators of nutritional status (i.e., BMI, mid-arm circumference, and sum of 4 skinfolds) as the outcomes. We tested the association between these indices of nutritional status and our three measures of knowledge: hunting, medicinal plant, and local environmental knowledge, using each of those variables in different regressions. All regressions include controls for age, household size, and average number of days reportedly sick. We ran separate regressions for men and women and excluded from the analysis women who reported being pregnant at the time of taking their anthropometric measurements. Table 5 reports the coefficient, standard error, and statistical significance of the knowledge variable tested.

Overall, we did not find a consistent relation between any of our measures of knowledge and the three indices of nutritional status examined. The only association worth mentioning was found between hunting knowledge and BMI (Model 1) and mid-arm circumference (Model 2). This association is found only for the male part of the sample. For women, none of the three knowledge measures bear any statistically significant association with our selected indicators of nutritional status. The results do not vary greatly when we add our controls for level of exposure to the national society and integration into the market economy.

Discussion

This study is an attempt to use empirical data and a cross-cultural framework to test whether culturally transmitted and individually appropriated knowledge provides individual returns in terms of hunting returns and health (H1-H3) and, by extension to nutritional status, a proxy for individual adaptive success (H5). The test of our hypotheses gives support to the idea that variations in individual levels of local environmental knowledge relate to individual hunting returns and –to a lower extend–health, but does not support the idea that variations in individual levels of local environmental knowledge relate to better nutritional status. In the first part of this section, we discuss results related to our original hypotheses and in the

second we interpret them in the context of the original idea driving this study: the role of individuals in shaping cultural adaptation.

Data interpretation

The most robust finding of this work relates to the positive and statistically significant association between hunting knowledge and hunting returns (H1), an association that remains robust across all specifications tested. These results dovetail with results from an empirical study amongst indigenous peoples in Nicaragua, in which Koster (2010) found that hunting ability accurately reflects variation in hunting returns. An analogous test between medicinal plant knowledge and self-reported health (H2) provide weaker evidence. The negative association found between medicinal plant knowledge and number of days the person reports to be sick would be in line with the work of McDade et al. (2007), who also found a positive association between individual ethnobotanical knowledge and child health. It is possible that the weaker association found when testing H2 (versus H1) relates to our measurement of health through self-reports. Researchers have argued that self-reports of health capture perceptions of physical and emotional states relative to a culturally agreed standard (Murray and Chen 1992). To be sick translates into not meeting the acceptable characteristics of good health, which often differ from one culture to another. This could explain why, for example, the average number of days the Punan reported to be sick is two-fold as compared with the other two groups. More importantly, the fact that self-reports of health are largely mediated by cultural understandings also provides a plausible explanation for the overall importance of village and site dummies, as cultural understanding of health is a fixed and unseen factor largely shared within a group, but with important variations across groups.

Contrary to what we have hypothesized, the composite measure of local environmental knowledge does not necessarily provide larger returns than specific measures (H3): local environmental knowledge provides lower returns on hunting returns than hunting knowledge but higher returns on health than medicinal plant knowledge. The finding suggests that, despite claims on the interrelation of the different domains of local knowledge systems (Berkes, Colding, and Folke 2000), it should not be assumed that such relations necessarily create synergies that might generally result in better outcomes. Many studies have shown that the intra-cultural distribution of local knowledge is patterned according to individual and social characteristics (Salpeteur et al. 2015; Camou-Guerrero et al. 2008). Such patterns change from one domain of knowledge to another and from one society to another. If different domains of knowledge (i.e., hunting and medicinal plants) are patterned differently across these individual and social characteristics (e.g., men know more about hunting, whereas women know more about medicinal plants) and across societies (e.g., in some societies both men and women hold similar medicinal plant knowledge), then it is not surprising that the composite measure of local environmental knowledge does not consistently provide larger returns.

Also in contradiction to our original intuition, the test of H4 suggests that the association between our measures of knowledge and related outcomes does not change as a result of individual levels of exposure to the national society and integration into the market

economy. We can think of at least two possible explanations for this finding. First, it is possible that the level of exposure of the studied societies is relatively low for our measures to capture the effect. Second, it is also possible that the proxies used have different associations with the studied outcomes in each of the studied societies. From field observations we know that cash income may be differently associated to hunting returns between groups. For example, as Baka sell bush meat, higher hunting returns is directly related to higher income (Duda, Gallois, and Reyes-García under review). Contrarily, as the Tsimane' and the Punan do not sell bush meat, cash income might relate differently to their hunting returns.

In our last hypothesis (H5), we aimed to assess whether local environmental knowledge is associated with nutritional status, a proxy for individual adaptive success from a physiological point of view. Despite the associations spotted in our tests of H1-H3, results from testing H5 do not provide enough evidence that allow us to conclude that the individual level of local environmental knowledge of a person is a strong predictor of individual levels of nutritional status. We are thus left with a paradox: if there is an association between individual levels of knowledge and specific outcomes related to such knowledge- as the tests of H1-H3 seem to suggest-, why then is this not reflected in nutritional status?

Explaining the paradox in the returns of local environmental knowledge

A plausible explanation for the paradox found in results testing the returns of local environmental knowledge relates to omitted variable bias. Individual indices of short term nutritional status are affected by many factors which were not included in our study. Such factors vary from diet composition, to levels of physical exercise, or the socio-economic status of the person (Frisancho 1990). Such factors do not play a significant role in the association between knowledge and specific outcomes derived from such knowledge, but they do vary with nutritional status. Failure to include such controls might affect the coefficients of the association studied.

Our ethnographic information, however, suggests an alternative explanation. We had assumed that the outcomes resulting from local environmental knowledge would mainly benefit the individual, but field experience suggests that, in the context of the studied societies, such outcomes are largely socialized, as in the three studied societies there is an important prevalence of sharing. For example, although hunting seems a rather specialized economic activity with 46% of informants not reporting any hunting activity, the sharing of hunted game seems to be ubiquitous. Among the Punan, for example, the share of bush meat is considered as “compulsory”, according to social norms. Similarly, sharing information on medicinal plant properties, their location in the forest, or even the preparation of the medicinal plant is routinely done in the three studied societies, at least for common, non-specialized medicinal plant knowledge (see also Reyes-García et al. (2003)). Thus, through the sharing of resources and knowledge, individuals who obtain higher returns to their knowledge might transfer material and non-material resources to the rest of the group. Such transfers might result in a group-level (not just individual-level), improvement in nutritional status, which might explain why higher medicinal plant knowledge (for instance) is associated to better health, but not to better nutritional status.

This interpretation fits well both with anthropological theory and with insights from the study of group adaptations in evolutionary biology. On the one hand, there is a long tradition in anthropology on the study of sharing and reciprocity among small-scale societies (Mauss 1954; Shalins 1972; Kaplan and Hill 1985), and adaptive benefits for individuals who share (Gurven et al. 2000; Hawkes, O'Connell, and Blurton Jones 2001). On the other hand, the study of group adaptations in evolutionary biology has also highlighted the key role of sharing and cooperation in multi-level adaptations (Gardner and Grafen 2009; Michod 2006; West, Griffin, and Gardner 2007). According to such research, social behavior evolves when selection operates at levels of organization higher than the individual: behaviors that bring benefits to the group are favored by group selection, even if they are costly for the individual (Gintis 2000; Fehr, Fischbacher, and Gächter 2002; Okasha 2006). From this perspective, sharing could also be seen as an adaptive mechanism that increases group fitness by redistributing resources. Many examples of social adaptations favoring traits which result in individuals maximizing the fitness of the group over their own fitness can be found in studies on the sustainable governance of Common-Pool Resources, highlighting how groups develop norms, rules and institutions to avoid resource overexploitation and degradation (Ostrom 1993; Penn 2003).

Two additional issues merit discussion before concluding. First, for the male part of the sample, hunting knowledge is positively associated to two indices of nutritional status. This finding fits well with research on the social gradient of health without contradicting the arguments presented before. Research on the social gradient of health has found an association between social rank, or position in dominance hierarchies, and individual health (Sapolsky 2004; Wilkinson 2000), including a positive and statistically significant association between social rank and indicators of nutritional status in a forager society (Reyes-García et al. 2008). As, among the three studied societies, hunting abilities are culturally very valued and can be considered locally-relevant measures of social rank, the association found between men's hunting knowledge and nutritional status might be just reflecting the social gradient of health. Second, our research has only used one proxy of individual adaptive success, nutritional status, which does not allow us to generalize about the potential association between measures of local knowledge and other proxies of adaptive success (i.e., reproductive success).

Conclusion

This study is an explicit attempt to use empirical data and a cross-cultural framework to test whether culturally transmitted knowledge provides hunting and health returns to the individual. The test of our hypotheses reveals some paradoxical findings: while we find an association between individual levels of knowledge and specific outcomes related to this knowledge, we do not find an association between such knowledge and a general proxy for individual adaptive success (in our work proxied through indicators of nutritional status). We argue that the answer to this paradox lies in the fact that through the sharing of resources and knowledge, individuals who achieve higher returns to their knowledge transfer material and non-material resources to the rest of the group. The finding is in consonance with previous research highlighting the importance of cultural traits favouring group success, but develops it further by elucidating the mechanisms through which individual and group level adaptive

forces interact. Further research aiming to use empirical data to test whether the sharing of returns provided by local environmental knowledge provide group adaptive advantages faces the challenge of obtaining a sample large enough to test the hypothesis at group level. Such research can only be through cross-cultural collaborative projects.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

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Table 1

Descriptive statistics of the variables used in the different models

| | Definition | Total | Tsimane' | Baka | Punan |
|--|--|------------------|------------------|------------------|------------------|
| <i>Explanatory variables</i> | | | | | |
| <i>Variables used to construct hunting knowledge</i> | | | | | |
| Game identification | Game stimuli recognized | 5.34 (2.11) | 4.43 (1.79) | 6.71 (1.65) | 4.51 (1.87) |
| Hunting skills | Score on a test of hunting practices | 3.72 (2.57) | 2.84 (2.31) | 4.94 (2.32) | 2.94 (2.50) |
| Peer rating (hunting) | Rating provided by 6 evaluators on subject's hunting knowledge | 1.16 (1.27) | 1.20 (1.28) | 1.07 (1.32) | 1.14 (1.25) |
| <i>Variables used to construct medicinal plant knowledge</i> | | | | | |
| Medicinal plant identification | Plants recognized as medicinal | 5.74 (2.15) | 4.95 (2.16) | 5.75 (1.86) | 6.38 (2.09) |
| Medicinal plant skills | Composite index that accounts for the medicinal uses known and the last time those were applied. | 6.59 (3.46) | 6.58 (3.44) | 7.82 (3.31) | 4.89 (2.74) |
| Peer rating (medicinal) | Rating provided by 6 evaluators on subject's medicinal knowledge | 1.29 (1.08) | 1.46 (1.14) | 1.69 (1.04) | 0.68 (0.63) |
| <i>Outcome variables for the different models</i> | | | | | |
| Hunting returns | Kg of game per hour spent in hunting activities | 0.98 (2.08) | 0.76 (1.65) | 0.74 (1.07) | 1.50 (2.90) |
| Sickness | Percentage of observed-days sick | 5.1 (10.1) | 2.69 (5.78) | 7.31 (12.67) | 4.71 (9.21) |
| BMI (men) | Men Body mass index (weight in kg/height in m2). | 22.29 (2.04) | 23.55 (1.87) | 21.53 (1.64) | 21.64 (1.93) |
| BMI (women) | Non-pregnant women Body mass index. | 22.10 (2.60) | 23.28 (2.59) | 21.79 (2.68) | 20.88 (2.27) |
| MAC(men) | Men's mid-arm circumference. | 27.13 (2.18) | 27.99 (2.15) | 25.70 (1.88) | 27.49 (1.81) |
| MAC (women) | Non-pregnant women mid-arm circumference | 25.88 (2.57) | 27.17 (2.69) | 24.77 (2.02) | 26.07 (2.67) |
| Sum 4 skinfolds (men) | Men's sum of skinfold thickness (mm). | 30.61 (9.45) | 37.32 (10.48) | 24.89 (4.70) | 28.5 (6.82) |
| Sum 4 skinfolds (women) | Non-pregnant women sum of skinfold thickness (mm). | 48.68 (19.37) | 53.97 (15.67) | 37.32 (15.65) | 59.19 (21.62) |
| <i>Socio-demographic controls</i> | | | | | |
| Male | Sex of the person, 1=male | 0.51 | 0.49 | 0.49 | 0.52 |
| Age | Estimated age of the person, in years | 36.32 (15.85) | 37.22 (18.57) | 35.54 (14.30) | 37.34 (14.76) |
| Household size | Number of people living in the household | 6.17 (2.76) | 6.82 (2.41) | 6.25 (2.89) | 5.15 (2.40) |
| <i>Variables used to control for outcome variation</i> | | | | | |
| Hunt effort | Share of times the person reported hunting | 0.16 (0.18) | 0.13 (0.17) | 0.19 (0.18) | 0.14 (0.19) |

| | Definition | Total | Tsimane' | Baka | Punan |
|--|---|-------------------|------------------|------------------|------------------|
| Traditional weapon use | Share of times the person hunt with a traditional weapon | 0.32 (0.39) | 0.015 (0.06) | 0.53 (0.34) | 0.35 (0.46) |
| Medicines use | Share of times the person did not use medicines when sick | 31.93 (40.8) | 18.53 (33.6) | 20.56 (34.87) | 64.78 (38.8) |
| <i>Variables used to construct the “exposure to the national society” measure</i> | | | | | |
| Schooling | Maximum level of formal education attained | 1.41 (1.87) | 1.64 (1.77) | 1.08 (1.23) | 1.33 (2.37) |
| Parents read | The father or the mother of the person read=1 | 0.12 (0.32) | 0.14 (0.35) | 0.058 (0.23) | 0.17 (0.38) |
| National language | % who does not speak | 23.7 | 28.2 | 31.9 | 6.4 |
| | % who speaks a little | 48.1 | 57.3 | 53.8 | 29.4 |
| | % who are fluent | 28.2 | 14.5 | 14.4 | 64.2 |
| Literate | % unable to read | 73.3 | 75.8 | 86.6 | 51.4 |
| | % read with difficulties | 10.0 | 4.0 | 12.1 | 13.8 |
| | % read well | 16.7 | 20.2 | 1.3 | 34.9 |
| <i>Variables used to construct the “integration into the market economy” measure</i> | | | | | |
| Travel town | Visits to market town in the last 12 months | 2.97 (5.22) | 5.24 (5.53) | 1.41 (2.36) | 1.95 (4.31) |
| Wealth | Household wealth, in PPP US\$ | 1739 (2271) | 3140 (22634) | 116 (59) | 2652 (2599) |
| Sales | Individual cash income from sales, in PPP US\$ | 21.45 (116.57) | 66.89 (211.8) | 2.47 (3.98) | 2.67 (20.75) |
| Wage | Individual cash income from wage, in PPP US\$ | 12.27 (33.39) | 18.18 (43.45) | 4.29 (7.92) | 12.96 (37.80) |
| <i>N</i> | | 393 | 123 | 160 | 110 |

Table 2

Items from free-listings selected for knowledge tests

| Tsimane' | | | | | |
|-------------------------------------|----------------------------------|----------|---|-------------------------------------|----------|
| Game (21 respondents, 114 items) | | | Medicinal plants (16 respondents, 91 items) | | |
| Local name | Scientific name | Saliency | Local name | Scientific name | Saliency |
| Naca' | <i>Cuniculus paca</i> | 0.809 | Uambason | <i>Aspidosper maaff. rigidum</i> | 0.281 |
| Ñej' | <i>Mazama americana</i> | 0.777 | Macha | <i>Amburana caerensis</i> | 0.091 |
| Shi' | <i>Tapirus terrestris</i> | 0.685 | Buisi ñetas | Not identified | 0.044 |
| Mumujñi | <i>Tayasu pecari</i> | 0.518 | Tson'sonty | <i>Ampelocera edentula</i> | 0.041 |
| Odo' | <i>Ateles chamek</i> | 0.514 | Que'tsejtsej | <i>Davilla nitida</i> | 0.038 |
| Vähsh | <i>Dasyopus novemcinctus</i> | 0.44 | Mature | <i>Acmella oleracea</i> | 0.038 |
| Shätij | <i>Dasyprocta punctata</i> | 0.396 | Yavitus | Not identified | 0.006 |
| O'oyoj | <i>Tamandua tetradactyla</i> | 0.352 | Poño'yacdyes | Not identified | 0.003 |
| Chu' | <i>Nasua nasua</i> | 0.306 | Arara | <i>Urerala ciniata</i> | ^ |
| Oyoj | <i>Cebus apella</i> | 0.086 | Banana | <i>Musa sp.</i> | ^ |
| Baka | | | | | |
| Game (25 respondents, 79 items) | | | Medicinal plants (24 respondents, 186 items) | | |
| Local name | Scientific name | Saliency | Local name | Scientific name | Saliency |
| pàmE | <i>Potamocheirus porcus</i> | 0.710 | gùgà | <i>Alstonia boonei</i> | 0.442 |
| sèkò | <i>Pan troglodytes</i> | 0.303 | bòyo | <i>Entandrophragma cylindricum</i> | 0.305 |
| gbè | <i>Cricetomys gambianus</i> | 0.300 | ngolù | <i>Terminalia superba</i> | 0.231 |
| mbOngO | <i>Tragelaphus eurycerus</i> | 0.163 | bOsO | <i>Combretum dendronmacrocarpum</i> | 0.031 |
| bèmbà | <i>Cephalophus sylvicultor</i> | 0.244 | kàngà | <i>Entandrophragma candollei</i> | 0.031 |
| mboka | <i>Nandinia binotata</i> | 0.095 | ngOyO | <i>Trichoscypha abut</i> | 0.030 |
| gEkE | <i>Hyemoschus aquaticus</i> | 0.056 | adjadjo | <i>Pausinystalia yohimbe</i> | 0.008 |
| mbOngO | <i>Bycanistes subcylindricus</i> | 0.053 | bòlòngo | <i>Fagara sp</i> | 0.005 |
| yoka | <i>Dendrohyrax dorsalis</i> | 0.040 | bámбу | <i>Gambeya lacourtiana</i> | ^ |
| kalu | <i>Colobus guereza</i> | 0.022 | bOtO | <i>Mammea africana</i> | ^ |
| Punan Tubu | | | | | |
| Game (8 respondents, 84 items) | | | Medicinal plants (3 respondents, 24 items) | | |
| Local name | Scientific name | Saliency | Local name | Scientific name | Saliency |
| Bavui | <i>Sus barbatus</i> | 0.969 | Kevouan | <i>Cinnamomum sp.</i> | 0.531 |
| Telau | <i>Muntiacus sp.</i> | 0.708 | Tata | <i>Ziziphus sp.</i> | 0.333 |
| Kuyat | <i>Macaca fascicularis</i> | 0.518 | Kecaliu | <i>Eurycoma longifolia</i> | 0.316 |
| Ketan | <i>Arctictis binturong</i> | 0.410 | Kelalai | Not identified | 0.222 |

| Tsimane' | | | | | |
|-------------------------------------|-----------------------------------|----------|--|-----------------------------|----------|
| Game (21 respondents, 114 items) | | | Medicinal plants (16 respondents, 91 items) | | |
| Local name | Scientific name | Saliency | Local name | Scientific name | Saliency |
| Angan | <i>Paguma larvata</i> | 0.303 | Mecout | Not identified | 0.211 |
| Munin | <i>Paradoxurus hermaphroditus</i> | 0.305 | Nyamanulabelang | <i>Selaginella plana</i> | 0.14 |
| Pecaku | <i>Buceros vigil</i> | 0.223 | Bangi | <i>Piper betle</i> | 0.07 |
| Bowang | <i>Helarctos malayanus</i> | 0.207 | Upa lengot | <i>Lansium domesticum</i> | 0.035 |
| Owei | <i>Argusianus argus</i> | 0.171 | Tefela | <i>Durio graveolens</i> | ^ |
| Megah | <i>Ratufa affinis</i> | 0.129 | Arau | <i>Elmerilla tsiampacca</i> | ^ |

^ Plants not listed as medicinal during free-listings, but included in knowledge tests on medicinal plants.

Table 3

Association between hunting knowledge/local environmental knowledge and hunting returns

| | Hunting returns (Kg/hour) | | | | | |
|--|---------------------------|----------------------|-----------------------|----------------------|----------------------|----------------------|
| | <i>H1</i> | | <i>H3</i> | | <i>H4</i> | |
| | Model 1 (Sites) | Model 2 (Villages) | Model 3 (Sites) | Model 4 (Villages) | Model 5 (Sites) | Model 6 (Villages) |
| <i>First part: Logistic regression</i> | | | | | | |
| Hunting knowledge | 0.868 ** (0.347) | 0.882 ** (0.392) | | | 0.883 ** (0.397) | 0.919 * (0.495) |
| LEK | | | 0.918 ** (0.379) | 0.992 ** (0.398) | | |
| Male | -0.037 (0.509) | 0.087 (0.484) | 0.450 (0.426) | 0.577 (0.563) | -0.035 (0.515) | 0.064 (0.695) |
| Age | -0.012 (0.011) | -0.012 (0.012) | -0.022 * (0.012) | -0.023 (0.015) | -0.006 (0.012) | -0.005 (0.016) |
| Household size | -0.058 (0.057) | -0.039 (0.061) | -0.054 (0.052) | -0.032 (0.062) | -0.057 (0.053) | -0.037 (0.058) |
| Hunting effort | 13.95 * (7.935) | 14.099 * (8.113) | 13.546 *** (3.702) | 13.676 * (7.324) | 13.80 *** (3.937) | 13.87 * (8.003) |
| Traditional weapon | 2.106 *** (0.551) | 2.335 *** (0.495) | 2.218 *** (0.662) | 2.455 *** (0.456) | 2.170 *** (0.652) | 2.465 *** (0.529) |
| Exposure to national society | | | | | 0.287 (0.237) | 0.372 (0.310) |
| Integration into market economy | | | | | -0.073 (0.213) | -0.089 (0.253) |
| Wage labor | | | | | -0.007 (0.005) | -0.008 * (0.004) |
| Tsimane' | 2.978 *** (0.739) | | 2.943 *** (0.678) | | 3.284 *** (0.743) | |
| Baka | 1.952 *** (0.690) | | 1.957 *** (0.688) | | 2.217 *** (0.788) | |
| V1: Sta Maria | | 2.196 *** (0.315) | | 2.185 *** (0.278) | | 2.437 *** (0.386) |
| V2:Cuchisama | | 2.464 *** (0.353) | | 2.401 *** (0.335) | | 2.803 *** (0.542) |
| V3:Ngola | | 1.501 *** (0.241) | | 1.577 *** (0.154) | | 1.738 *** (0.472) |
| V4: Bizam | | 0.714 ** (0.306) | | 0.582 ** (0.266) | | 0.883 ** (0.421) |

| Hunting returns (Kg/hour) | | | | | | |
|--|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| | H1 | | H3 | | H4 | |
| V5:Long Ranau | | -1.538 *** (0.487) | | -1.512 *** (0.534) | | -1.743 *** (0.549) |
| Intercept | -3.109 ** (1.320) | -2.591 ** (1.146) | -3.009 *** (0.859) | -2.467 ** (1.106) | -3.499 *** (0.998) | -2.992 ** (1.476) |
| <i>Second part: Ordinary Least Square regression</i> | | | | | | |
| Hunting knowledge | 0.840 ** (0.330) | 0.654 * (0.352) | | | 0.825 ** (0.398) | 0.597 (0.410) |
| LEK | | | 0.491 (0.304) | 0.397 (0.244) | | |
| Male | -0.714 (0.508) | -0.624 (0.498) | -0.173 (0.475) | -0.211 (0.462) | -0.840 (0.713) | -0.789 * (0.431) |
| Age | -0.013 ** (0.007) | -0.010 (0.010) | -0.015 * (0.008) | -0.011 (0.010) | -0.013 (0.010) | -0.007 (0.010) |
| Household size | 0.064 *** (0.025) | 0.051 (0.032) | 0.065 (0.046) | 0.052 * (0.030) | 0.053 (0.045) | 0.041 (0.034) |
| Hunting effort | -0.087 (1.150) | 0.112 (1.255) | 0.267 (1.497) | 0.364 (1.113) | -0.183 (1.492) | 0.066 (1.316) |
| Traditional weapon | -0.825 (1.004) | -1.004 (1.045) | -0.867 (1.310) | -1.063 (1.102) | -0.797 (1.296) | -1.038 (1.171) |
| Exposure to national society | | | | | 0.035 (0.201) | 0.071 (0.177) |
| Integration into market economy | | | | | 0.314 (0.267) | 0.336 * (0.184) |
| Wage labor | | | | | 0.0002 (0.004) | 0.002 (0.004) |
| Tsimane' | -3.675 *** (1.423) | | -3.826 *** (1.394) | | -4.001 *** (1.401) | |
| Baka | -3.993 *** (0.954) | | -3.898 *** (0.786) | | -3.770 *** (0.873) | |
| V1: Sta Maria | | -2.887 *** (0.816) | | -2.969 *** (0.879) | | -3.419 *** (0.876) |
| V2:Cuchisama | | -2.766 *** (0.824) | | -2.755 *** (0.854) | | -2.977 *** (0.912) |
| V3:Ngola | | -3.003 *** (0.336) | | -2.815 *** (0.241) | | -2.676 *** (0.482) |
| V4: Bizam | | -2.857 *** (0.464) | | -2.727 *** (0.378) | | -2.556 *** (0.586) |

| Hunting returns (Kg/hour) | | | | | | |
|---------------------------|---------------------|---------------------|---------------------|---------------------|-----------------------|---------------------|
| | <i>H1</i> | | <i>H3</i> | | <i>H4</i> | |
| V5:Long Ranau | | 1.769*** (0.142) | | 1.957*** (0.099) | | 1.813*** (0.165) |
| Intercept | 5.678*** (1.724) | 4.717*** (1.148) | 5.458*** (1.486) | 4.466*** (1.080) | 5.8037*** (1.6134) | 4.717*** (1.281) |
| N | 393 | 393 | 393 | 393 | 387 | 387 |
| <i>AIC</i> | 1174.4941 | 1162.9981 | 1192.9595 | 1163.0236 | 1178.5353 | 1137.5780 |
| <i>BIC</i> | 1214.2322 | 1202.7361 | 1264.4881 | 1202.7617 | 1273.5375 | 1177.1623 |

Note: Standard errors in parenthesis. Results of a two part model, where the first part assesses the probability of depvar being bigger than 0 (depvar>0) using a logit binary choice model and the second part models the distribution of depvar | depvar>0 using a standard OLS model (regress). For definition of variables see Table 1. * $p < 0.10$, ** $p < 0.05$, *** $p < 0.01$. ^ variable intentionally omitted from analysis.

Table 4

Association between medicinal plant knowledge/local environmental knowledge and health

| | Share of days reportedly sick | | | | | |
|--|-------------------------------|----------------------|----------------------|----------------------|---------------------|----------------------|
| | <i>H1</i> | | <i>H3</i> | | <i>H4</i> | |
| | Model 1 (Sites) | Model 2 (Villages) | Model 3 (Sites) | Model 4 (Villages) | Model 5 (Sites) | Model 6 (Villages) |
| <i>First part: Logistic regression</i> | | | | | | |
| Medicinal knowledge | 0.052 (0.136) | 0.030 (0.134) | | | 0.030 (0.129) | 0.016 (0.132) |
| LEK | | | 0.086 (0.164) | 0.068 (0.176) | | |
| Male | -0.686*** (0.262) | -0.660*** (0.246) | -0.739** (0.324) | -0.703** (0.321) | -0.521* (0.302) | -0.476* (0.278) |
| Age | 0.020*** (0.007) | 0.019** (0.008) | 0.0200*** (0.007) | 0.019*** (0.007) | 0.020*** (0.005) | 0.0200*** (0.005) |
| Household size | -0.024 (0.048) | -0.006 (0.050) | -0.025 (0.048) | -0.007 (0.050) | -0.012 (0.043) | 0.003 (0.045) |
| Medicine use | -0.091 (0.217) | -0.064 (0.247) | -0.087 (0.218) | -0.061 (0.250) | -0.183 (0.225) | -0.150 (0.249) |
| Exposure to national society | | | | | -0.033 (0.105) | 0.004 (0.110) |
| Integration into market economy | | | | | -0.412** (0.203) | -0.405* (0.211) |
| Wage labor | | | | | -0.002 (0.002) | -0.005** (0.002) |
| Tsimane' | -0.732 (0.520) | | -0.729 (0.521) | | -0.566 (0.472) | |
| Baka | 0.642 (0.524) | | 0.623 (0.523) | | 0.297 (0.521) | |
| V1: Sta Maria | | -1.560*** (0.092) | | -1.560*** (0.094) | | -1.301*** (0.153) |
| V2:Cuchisama | | -1.203*** (0.071) | | -1.209*** (0.078) | | -1.174*** (0.149) |
| V3:Ngola | | -0.020 (0.070) | | -0.043 (0.062) | | -0.383*** (0.134) |
| V4: Bizam | | -0.069 (0.077) | | -0.093 (0.097) | | -0.401*** (0.114) |
| V5:Long Ranau | | -1.348*** (0.073) | | -1.351*** (0.070) | | -1.383*** (0.091) |
| Intercept | -0.712 (0.890) | -0.154 (0.484) | -0.680 (0.876) | -0.113 (0.453) | -0.744 (0.753) | -0.155 (0.281) |

| Share of days reportedly sick | | | | | | |
|--|---------------------|----------------------|---------------------|----------------------|--------------------|----------------------|
| | <i>H1</i> | | <i>H3</i> | | <i>H4</i> | |
| <i>Second part: Ordinary Least Square regression</i> | | | | | | |
| Medicinal knowledge | -0.009 (0.006) | -0.008 (0.006) | | | -0.011 (0.008) | -0.012 (0.008) |
| LEK | | | -0.018** (0.008) | -0.017* (0.009) | | |
| Male | 0.022** (0.011) | 0.024** (0.011) | 0.034** (0.015) | 0.034** (0.015) | 0.021* (0.011) | 0.022 (0.014) |
| Age | 0.001** (0.001) | 0.001** (0.001) | 0.001** (0.001) | 0.001** (0.001) | 0.001 (0.001) | 0.001 (0.001) |
| Household size | 0.001 (0.002) | 0.001 (0.002) | 0.001 (0.002) | 0.001 (0.002) | 0.0002 (0.002) | 0.0004 (0.002) |
| Medicine use | -0.036 (0.023) | -0.034 (0.023) | -0.037 (0.023) | -0.034 (0.023) | -0.027 (0.025) | -0.026 (0.024) |
| Exposure to national society | | | | | -0.016 (0.010) | -0.017 (0.011) |
| Integration into market economy | | | | | 0.0300 (0.022) | 0.032 (0.027) |
| Wage labor | | | | | 0.0003 (0.0002) | 0.0003 (0.0002) |
| Tsimane' | -0.036** (0.018) | | -0.036** (0.018) | | -0.044* (0.025) | |
| Baka | -0.006 (0.019) | | -0.0004 (0.020) | | 0.005 (0.017) | |
| V1: Sta Maria | | -0.042*** (0.011) | | -0.042*** (0.011) | | -0.059*** (0.018) |
| V2:Cuchisama | | -0.047*** (0.014) | | -0.046*** (0.014) | | -0.046** (0.022) |
| V3:Ngola | | -0.012 (0.012) | | -0.007 (0.014) | | -0.004 (0.021) |
| V4: Bizam | | -0.017 (0.014) | | -0.012 (0.014) | | -0.001 (0.021) |
| V5:Long Ranau | | -0.026*** (0.006) | | -0.025*** (0.005) | | -0.030*** (0.006) |
| Intercept | 0.093** (0.046) | 0.098** (0.041) | 0.084* (0.047) | 0.089** (0.042) | 0.113* (0.065) | 0.120** (0.059) |
| N | 389 | 389 | 389 | 389 | 383 | 383 |
| <i>AIC</i> | 290.43 | 279.55 | 290.20 | 279.30 | 265.59 | 254.94 |
| <i>BIC</i> | 330.07 | 319.18 | 329.84 | 318.93 | 305.07 | 294.42 |

Note: See Note in Table 3.

Table 5

Association between hunting, medicinal plant, and local environmental knowledge and nutritional status

| | BMI | Mid-arm circumference | Sum 4 skinfolds |
|--------------------------------|------------------|------------------------------|------------------------|
| A.- Men (n=165) | | | |
| | Model 1A | Model 2A | Model 3A |
| Hunting knowledge | 0.963 (0.163)*** | 0.906 (0.168)*** | 1.234 (1.124) |
| Medicinal plant knowledge | -0.037 (0.299) | -0.214 (0.441) | 1.731 (1.386) |
| Local environmental knowledge | 0.585 (0.319) | 0.384 (0.473) | 3.09 (1.94) |
| B.- Non-pregnant women (n=164) | | | |
| | Model 1B | Model 2B | Model 3B |
| Hunting knowledge | -0.147 (0.402) | -0.237 (0.454) | -3.365 (2.384) |
| Medicinal plant knowledge | 0.122 (0.220) | 0.248 (0.236) | 0.998 (1.566) |
| Local environmental knowledge | 0.123 (0.414) | 0.269 (0.509) | 0.366 (2.77) |

Note: Each cell (coefficients and standard error) correspond to the result of a different regression model using as dependent variable the variable indicated in the column head, and as main explanatory variable the knowledge variable indicated in the row head. We used the same controls than in Tables 3-4.