# The Adaptive Nature of Culture

## A Cross-Cultural Analysis of the Returns of Local Environmental Knowledge in Three Indigenous Societies

## by Victoria Reyes-García, Maximilien Guèze, Isabel Díaz-Reviriego, Romain Duda, Álvaro Fernández-Llamazares, Sandrine Gallois, Lucentezza Napitupulu, Martí Orta-Martínez, and Aili Pyhälä

Researchers have argued that the behavioral adaptations that explain the success of our species are partially cultural, that is, 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, 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 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.

Researchers debate the role played by culture in shaping human adaptive strategy. Cultural evolution theory suggests that

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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; Richerson and Boyd 2005; Tomasello 1999). 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 (Henrich and McElreath 2003; Richerson and Boyd 2005). 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 as 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; Gallopin 2006; Nelson, Adger, and Brown 2007; Pelling and High 2005; Smit and Wandel 2006). The term "adaptation" has its origins in evolutionary biology, where it broadly refers to the development of genetic or behavioral outcomes that enable

organisms or systems to cope with environmental changes in order to survive and reproduce (Kitano 2002; Winterhalder 1980). Within anthropology, "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" (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 coevolving systems of inheritance (i.e., genes and culture) shape human behavior (Laland, Odling-Smee, and Myles 2010; Richerson and Boyd 2005).

Despite the presumptive importance of culture for 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 (Derex et al. 2013; Efferson et al. 2008; Horner et al. 2006). Only a few scholars have addressed the topic with observational studies (Atran et al. 2002), yet even these have often been 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 by 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 knowledge.[1] 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, and 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 (Berkes, Colding, and Folke 2000; Turner, Ignace, and Ignace 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 with individual adaptive success. Our test of whether individual local environmental knowledge provides returns on hunting and health is guided by two main hypotheses.

$H_1$.    *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.

$H_2$.    *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 such knowledge.

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

$H_3$.    *Adults with more local environmental knowledge will benefit from larger returns in hunting and health than adults 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

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1. We use the term "local environmental knowledge" to refer to knowledge systems, which include knowledge, practices, and beliefs. Specifically, we draw on Berkes, Colding, and Folke (2000) 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" (1252).

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 of 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 behaviors—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 adults with lower local environmental knowledge.*

*Rationale.* If H₁–H₃ hold true, then one could argue that local environmental knowledge provides myriad 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 indexes 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 et al. 2008*b*) and child health (McDade et al. 2007). However, the extent to which the patterns found in one society hold true for other societies remains unknown. Here, we use a cross-cultural comparative approach to enhance the external validity of our findings (Ember and Ember 2000; Mace and Pagel 1994), 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 (HRAFs; 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 HRAFs in that they use the same research protocols to collect primary data across different societies and 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 at both the individual and the 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 (Flowers et al. 1982; Gross et al. 1979), 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 et al. (2005) on cooperation.

Following this line of inquiry, 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, and 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 commonplace. For instance, in industrial societies the link between individual knowledge and health is hard to estimate owing to the role played by 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 drastically 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 (for reviews, see Ember and Ember 2000; Chrisomalis 2006). 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 as well as strong material and symbolic relations with farmers but are subjected to the monetization and commoditization of their economy (Kitanishi 2006). Most Baka combine hunting and 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 pressure 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, and bezoar stones. Nowadays, however, wage labor—including wages from work in government projects—provides 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). 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 seminomadic, they are now mostly settled in permanent villages with school facilities. Tsimane' rely on slash-and-burn farming supple-mented by hunting, fishing, gathering, and wage labor in logging camps, cattle ranches, and 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 6 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-testing the protocols as well as to collecting 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 worked.[2]

### 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 with 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, and the beliefs and rituals associated with hunting practices. We also conducted free listings on game and medicinal plants, information that was later used in the design of knowledge tests (Reyes-García et al. 2016b). The ethnographic information relating to the lived practice of local environmental knowledge in each society informed the design of quantitative methods and helped put our results into a broader context.

## Quantitative Methods

During the second stage of fieldwork, in addition to participant observation, we also used systematic data collection tools. 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 that were different from the study villages but that had the same cultural background.[3]

## Sampling Strategy

Within each of the three studied societies, we selected two villages located at varying distances from 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 more than 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 plant knowledge using three different methods: an identification task, a self-reported skills questionnaire, and peer ratings (for a complete description, see Reyes-García et al. 2016*a*; table 1).

*Identification task.* We designed a test in which informants were asked to provide the vernacular name for a stimuli corresponding to 10 game species. 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. Items 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.

*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 prey (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. 2016*a*). We first grouped households into kinship affinity groups, from which we formed groups of six evaluators containing three men and three women and people of 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 on the basis of 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 intrasubject 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 values (mean = 0, variance = 1) 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.

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3. The protocols used for data collection can be accessed at http://icta.uab.cat/etnoecologia/lek.

Table 1. Descriptive statistics of the variables used in the different models

| | Definition | Total | Tsimane' | Baka | Punan |
|---|---|---|---|---|---|
| **Explanatory variables:** | | | | | |
| *Variables used to construct hunting knowledge:* | | | | | |
| Game identification | Game stimuli recognized | 5.34 | 4.43 | 6.71 | 4.51 |
| | | (2.11) | (1.79) | (1.65) | (1.87) |
| Hunting skills | Score on a test of hunting practices | 3.72 | 2.84 | 4.94 | 2.94 |
| | | (2.57) | (2.31) | (2.32) | (2.50) |
| Peer rating (hunting) | Rating provided by six evaluators on | 1.16 | 1.20 | 1.07 | 1.14 |
| | subject's hunting knowledge | (1.27) | (1.28) | (1.32) | (1.25) |
| *Variables used to construct medicinal plant knowledge:* | | | | | |
| Medicinal plant identification | Plants recognized as medicinal | 5.74 | 4.95 | 5.75 | 6.38 |
| | | (2.15) | (2.16) | (1.86) | (2.09) |
| Medicinal plant skills | Composite index that accounts for the | 6.59 | 6.58 | 7.82 | 4.89 |
| | medicinal uses known and the last | (3.46) | (3.44) | (3.31) | (2.74) |
| | time those were applied | | | | |
| Peer rating (medicinal) | Rating provided by six evaluators on | 1.29 | 1.46 | 1.69 | .68 |
| | subject's medicinal knowledge | (1.08) | (1.14) | (1.04) | (.63) |
| **Outcome variables for the different models:** | | | | | |
| Hunting returns | Kilograms of game per hour spent in | .98 | .76 | .74 | 1.50 |
| | hunting activities | (2.08) | (1.65) | (1.07) | (2.90) |
| Sickness | Percentage of observed days sick | 5.1 | 2.69 | 7.31 | 4.71 |
| | | (10.1) | (5.78) | (12.67) | (9.21) |
| BMI (men) | Men's BMI | 22.29 | 23.55 | 21.53 | 21.64 |
| | | (2.04) | (1.87) | (1.64) | (1.93) |
| BMI (women) | Nonpregnant women's BMI | 22.10 | 23.28 | 21.79 | 20.8 |
| | | (2.60) | (2.59) | (2.68) | (2.27) |
| MAC (men) | Men's midarm circumference | 27.13 | 27.9 | 25.7 | 27.49 |
| | | (2.18) | (2.15) | (1.88) | (1.81) |
| MAC (women) | Nonpregnant women's midarm | 25.88 | 27.1 | 24.7 | 26.07 |
| | circumference | (2.57) | (2.69) | (2.02) | (2.67) |
| Sum of four skinfolds (men) | Men's sum of skinfold thickness (mm) | 30.61 | 37.3 | 24.89 | 28.5 |
| | | (9.45) | (10.48) | (4.70) | (6.82) |
| Sum of four skinfolds (women) | Nonpregnant women's sum of skinfold | 48.68 | 53.9 | 37.3 | 59.19 |
| | thickness (mm) | (19.37) | (15.67) | (15.65) | (21.62) |
| **Sociodemographic controls:** | | | | | |
| Male | Sex of the person, 1 = male | .51 | .49 | .49 | .52 |
| Age | Estimated age of the person (years) | 36.32 | 37.22 | 35.54 | 37.34 |
| | | (15.85) | (18.57) | (14.30) | (14.76) |
| Household size | Number of people living in household | 6.17 | 6.82 | 6.25 | 5.15 |
| | | (2.76) | (2.41) | (2.89) | (2.40) |
| **Variables used to control for outcome variation:** | | | | | |
| Hunt effort | Share of times the person reported hunting | .16 | .13 | .19 | .14 |
| | | (.18) | (.17) | (.18) | (.19) |
| Traditional weapon use | Share of times the person hunted with a | .32 | .015 | .53 | .35 |
| | traditional weapon | (.39) | (.06) | (.34) | (.46) |
| Medicines use | Share of times the person did not use | 31.93 | 18.53 | 20.56 | 64.78 |
| | medicines when sick | (40.8) | (33.6) | (34.87) | (38.8) |
| **Variables used to construct "exposure to national society" measure:** | | | | | |
| Schooling | Maximum level of formal education attained | 1.41 | 1.64 | 1.08 | 1.33 |
| | | (1.87) | (1.77) | (1.23) | (2.37) |
| Parents read | Father or mother of the person read = 1 | .12 | .14 | .058 | .17 |
| | | (.32) | (.35) | (.23) | (.38) |
| National language | % who do not speak | 23.7 | 28.2 | 31.9 | 6.4 |
| | % who speak 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 |
| **Variables used to construct "integration into market economy" measure:** | | | | | |
| Travel town | Visits to market town in the past 12 months | 2.97 | 5.24 | 1.41 | 1.95 |
| | | (5.22) | (5.53) | (2.36) | (4.31) |
| Wealth | Household wealth, in PPP US$ | 1,739 | 3,140 | 116 | 2,652 |
| | | (2,271) | (22,634) | (59) | (2,599) |

Table 1 (*Continued*)

| | Definition | Total | Tsimane' | Baka | Punan |
|---|---|---|---|---|---|
| Sales | Individual cash income from sales, | 21.45 | 66.89 | 2.47 | 2.67 |
| | in PPP US$ | (116.57) | (211.8) | (3.98) | (20.75) |
| Wage | Individual cash income from wage, | 12.27 | 18.18 | 4.29 | 12.96 |
| | in PPP US$ | (33.39) | (43.45) | (7.92) | (37.80) |
| N | | 393 | 123 | 160 | 110 |

Note. Standard errors are in parenthesis. BMI = body mass index (kg/m²); PPP = purchasing power parity.

*Outcome Variables*

Our outcome variables include hunting returns ($H_1$, $H_3$, and $H_4$), share of days sick ($H_2$, $H_3$, and $H_4$), level of exposure to the national society and integration into the market economy ($H_4$), and nutritional status ($H_5$). 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.* 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 2 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/h). As it was not always possible to obtain the weight of the prey, 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 the 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 2 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 intrasubject correlation of the different measures (Trimble 2003) and then used principal component factor analysis to create a new composite measure that captured 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 (Godoy et al. 2005; Lu 2007): (i) the 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 came from individual interviews collected once a quarter, with a recall of 2 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 dollars. Again, we used principal component analysis to create a composite measure. Results from the intrasubject 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 obtain 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, from which we were able to calculate each individual's body mass index (BMI; kg/m²). We also

Table 2. Items from free listings selected for knowledge tests

| | Game | | | Medicinal plants | | |
|---|---|---|---|---|---|---|
| | Local name | Scientific name | Saliency | Local name | Scientific name | Saliency |
| Baka | 25 respondents, 79 items | | | 24 respondents, 186 items | | |
| | pàmE | *Potamocherus porcus* | .710 | gùgà | *Alstonia boonei* | .442 |
| | sèkò | *Pan troglodytes* | .303 | bòyo | *Entandrophragma cylindricum* | .305 |
| | gbè | *Cricetomys gambianus* | .300 | ngolù | *Terminalia superba* | .231 |
| | mbOngO | *Tragelaphus eurycerus* | .163 | bOsO | *Combreto dendronmacrocarpum* | .031 |
| | bèmbà | *Cephalophus sylvicultor* | .244 | kàngà | *Entandrophragma candollei* | .031 |
| | mboka | *Nandinia binotata* | .095 | ngOyO | *Trichoscypha abut* | .030 |
| | gEkE | *Hyemoschus aquaticus* | .056 | adjadjo | *Pausinystalia yohimbe* | .008 |
| | mbOngO | *Bycanistes subcylindricus* | .053 | bòlòngo | *Fagara* sp. | .005 |
| | yoka | *Dendrohyrax dorsalis* | .040 | bámbu | *Gambeya lacourtiana* | . . .ª |
| | kalu | *Colobus guereza* | .022 | bOtO | *Mammea africana* | . . .ª |
| Punan Tubu | 8 respondents, 84 items | | | 3 respondents, 24 items | | |
| | Bavui | *Sus barbatus* | .969 | Kevouan | *Cinnamomum* sp. | .531 |
| | Telau | *Muntiacus* sp. | .708 | Tata | *Ziziphus* sp. | .333 |
| | Kuyat | *Macaca fascicularis* | .518 | Kecaliu | *Eurycoma longifolia* | .316 |
| | Ketan | *Arctictis binturong* | .410 | Kelalai | Not identified | .222 |
| | Angan | *Paguma larvata* | .303 | Mecout | Not identified | .211 |
| | Munin | *Paradoxurus hermaphroditus* | .305 | Nyamanulabelang | *Selaginella plana* | .140 |
| | Pecaku | *Buceros vigil* | .223 | Bangi | *Piper betle* | .070 |
| | Bowang | *Helarctos malayanus* | .207 | Upa lengot | *Lansium domesticum* | .035 |
| | Owei | *Argusianus argus* | .171 | Tefela | *Durio graveolens* | . . .ª |
| | Megah | *Ratufa affinis* | .129 | Arau | *Elmerilla tsiampacca* | . . .ª |
| Tsimane' | 21 respondents, 114 items | | | 16 respondents, 91 items | | |
| | Naca' | *Cuniculus paca* | .809 | Uambason | *Aspidosper maaff. rigidum* | .281 |
| | Ñej' | *Mazama americana* | .777 | Macha | *Amburana caerensis* | .091 |
| | Shi' | *Tapirus terrestris* | .685 | Buisi ñetas | Not identified | .044 |
| | Mumujñi | *Tayasu pecari* | .518 | Tson'sonty | *Ampelocera edentula* | .041 |
| | Odo' | *Ateles chamek* | .514 | Que'tsejtsej | *Davilla nitida* | .038 |
| | Väsh | *Dasypus novemcinctus* | .440 | Mature | *Acmella oleracea* | .038 |
| | Shätij | *Dasyprocta punctata* | .396 | Yavitus | Not identified | .006 |
| | O'oyoj | *Tamandua tetradactyla* | .352 | Poño'yacdyes | Not identified | .003 |
| | Chu' | *Nasua nasua* | .306 | Arara | *Urerala ciniata* | . . .ª |
| | Oyoj | *Cebus apella* | .086 | Banana | *Musa* sp. | . . .ª |

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

measured midarm circumference (cm) and the thickness of skinfolds (biceps, triceps, subscapular, and suprailiac; mm).

### Control Variables

Some of our control variables (e.g., sex, age, and household size) were selected on the basis of previous research suggesting that individual characteristics may affect the intracultural 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 that 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 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 estimated the individual returns of local environmental knowledge using the general following expression:

$$O_{ihv} = \alpha + \gamma \text{LEK}_{ihv} + \beta P_{ihv} + \zeta F_{ihv} + \lambda M_{ihv} + \Omega S + \varepsilon_{ihv}, \quad (1)$$

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 sociodemographic 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 indexes of exposure to the national society and integration into the market economy (only for H$_4$), $S$ is a vector that includes dummy variables for the society, and $\varepsilon_{ihv}$ 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 H$_1$, we used hunting returns as outcome ($O$) and hunting knowledge as the main explanatory variable (LEK); we controlled only for sociodemographic variables ($P$) and variables related to the outcome ($F$). As our dependent variable is zero inflated and positively skewed, to reduce estimation biases associated with such a 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 | depvar > 0 using a standard ordinary least squares 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 H$_2$ but with medicinal plant knowledge and related variables. Since the variable sickness also includes many zeros (from people who were never observed sick), we also used a two-part model. To test H$_3$, we used our composite measure of local environmental knowledge rather than hunting or medicinal plant knowledge. To test H$_4$, we added to models testing H$_1$ and H$_2$ the proxy measures for exposure to the national society and integration into the market economy. Finally, to test H$_5$ we used the same models as for H$_1$ and H$_2$ but with indicators of nutritional status as the outcome. To test H$_5$, 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. Irrespective of whether we used site or village dummies, all regressions included 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 (ver. 13). As an indicator of statistical significance, we report $P$ values below .10.

## Results

### Measuring Local Environmental Knowledge

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

### Hunting Knowledge and Hunting Returns

The individuals in our sample across all three societies have on average a hunting return of about 1 kg (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; average = 1.59 kg/h; 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 H$_1$ suggests that, indeed, there is a positive and statistically significant association between hunting knowledge and hunting returns. When modeling the probability that a 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 ($P < .05$). In the second part of the model, which actually models the distribution of positive hunting returns (hunting returns > 0), we also observed a positive association. Here, for every unit increase in hunting knowledge, a 0.84 kg/h increase in hunting returns 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 used the measure of local environmental knowledge to test H$_3$. Results from models 3 and 4 also confirm our hypothesis: local environmental knowledge bears a positive and statistically significant association with hunting returns. In these models, the coefficients of the association are higher for the first and lower for the second part of the model compared with hunting knowledge.

Finally, we tested H$_4$ by including our composite measures of exposure to the national society and integration into the market economy (models 5 and 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 with hunting returns. Models 5 and 6 are the ones with the smaller value of the Akaike and Bayesian information criterion, suggesting that they provide a

Table 3. Association between hunting knowledge/local environmental knowledge and hunting returns

| | Hunting returns (kg/h) | | | | | |
| | H₁ | | H₃ | | H₄ | |
| | Model 1 (sites) | Model 2 (villages) | Model 3 (sites) | Model 4 (villages) | Model 5 (sites) | Model 6 (villages) |
|---|---|---|---|---|---|---|
| First part: logistic regression: | | | | | | |
| Hunting knowledge | .868** | .882** | . . .ᵃ | . . .ᵃ | .883** | .919* |
| | (.347) | (.392) | | | (.397) | (.495) |
| LEK | . . .ᵃ | . . .ᵃ | .918** | .992** | . . .ᵃ | . . .ᵃ |
| | | | (.379) | (.398) | | |
| Male | −.037 | .087 | .450 | .577 | −.035 | .064 |
| | (.509) | (.484) | (.426) | (.563) | (.515) | (.695) |
| Age | −.012 | −.012 | −.022* | −.023 | −.006 | −.005 |
| | (.011) | (.012) | (.012) | (.015) | (.012) | (.016) |
| Household size | −.058 | −.039 | −.054 | −.032 | −.057 | −.037 |
| | (.057) | (.061) | (.052) | (.062) | (.053) | (.058) |
| Hunting effort | 13.95* | 14.099* | 13.546*** | 13.676* | 13.80*** | 13.87* |
| | (7.935) | (8.113) | (3.702) | (7.324) | (3.937) | (8.003) |
| Traditional weapon | 2.106*** | 2.335*** | 2.218*** | 2.455*** | 2.170*** | 2.465*** |
| | (.551) | (.495) | (.662) | (.456) | (.652) | (.529) |
| Exposure to national society | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | .287 | .372 |
| | | | | | (.237) | (.310) |
| Integration into market economy | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | −.073 | −.089 |
| | | | | | (.213) | (.253) |
| Wage labor | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | −.007 | −.008* |
| | | | | | (.005) | (.004) |
| Tsimane'ᵇ | 2.978*** | . . .ᵃ | 2.943*** | . . .ᵃ | 3.284*** | . . .ᵃ |
| | (.739) | | (.678) | | (.743) | |
| Bakaᵇ | 1.952*** | . . .ᵃ | 1.957*** | . . .ᵃ | 2.217*** | . . .ᵃ |
| | (.690) | | (.688) | | (.788) | |
| V₁: Tsimane' village 1ᶜ | . . .ᵃ | 2.196*** | . . .ᵃ | 2.185*** | . . .ᵃ | 2.437*** |
| | | (.315) | | (.278) | | (.386) |
| V₂: Tsimane' village 2ᶜ | . . .ᵃ | 2.464*** | . . .ᵃ | 2.401*** | . . .ᵃ | 2.803*** |
| | | (.353) | | (.335) | | (.542) |
| V₃: Baka village 1ᶜ | . . .ᵃ | 1.501*** | . . .ᵃ | 1.577*** | . . .ᵃ | 1.738*** |
| | | (.241) | | (.154) | | (.472) |
| V₄: Baka village 2ᶜ | . . .ᵃ | .714** | . . .ᵃ | .582** | . . .ᵃ | .883** |
| | | (.306) | | (.266) | | (.421) |
| V₅: Punan village 1ᶜ | . . .ᵃ | −1.538*** | . . .ᵃ | −1.512*** | . . .ᵃ | −1.743*** |
| | | (.487) | | (.534) | | (.549) |
| Intercept | −3.109** | −2.591** | −3.009*** | −2.467** | −3.499*** | −2.992** |
| | (1.320) | (1.146) | (.859) | (1.106) | (.998) | (1.476) |
| Second part: OLS regression: | | | | | | |
| Hunting knowledge | .840** | .654* | . . .ᵃ | . . .ᵃ | .825** | .597 |
| | (.330) | (.352) | | | (.398) | (.410) |
| LEK | . . .ᵃ | . . .ᵃ | .491 | .397 | . . .ᵃ | . . .ᵃ |
| Male | −.714 | −.624 | −.173 | −.211 | −.840 | −.789* |
| | (.508) | (.498) | (.475) | (.462) | (.713) | |
| Age | −.013** | −.010 | −.015* | −.011 | −.013 | −.007 |
| | (.007) | (.010) | (.008) | (.010) | (.010) | (.010) |
| Household size | .064*** | .051 | .065 | .052* | .053 | .041 |
| | (.025) | (.032) | (.046) | (.030) | (.045) | (.034) |
| Hunting effort | −.087 | .112 | .267 | .364 | −.183 | .066 |
| | (1.150) | (1.255) | (1.497) | (1.113) | (1.492) | (1.316) |
| Traditional weapon | −.825 | −1.004 | −.867 | −1.063 | −.797 | −1.038 |
| | (1.004) | (1.045) | (1.310) | (1.102) | (1.296) | (1.171) |
| Exposure to national society | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | .035 | .071 |
| | | | | | (.201) | (.177) |
| Integration into market economy | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | .314 | .336* |
| | | | | | (.267) | (.184) |
| Wage labor | . . .ᵃ | . . .ᵃ | . . .ᵃ | . . .ᵃ | .0002 | .002 |
| | | | | | (.004) | (.004) |

Table 3 (*Continued*)

| | Hunting returns (kg/h) | | | | | |
| | H$_1$ | | H$_3$ | | H$_4$ | |
| | Model 1 (sites) | Model 2 (villages) | Model 3 (sites) | Model 4 (villages) | Model 5 (sites) | Model 6 (villages) |
|---|---|---|---|---|---|---|
| Tsimane'[b] | −3.675*** (1.423) | . . .[a] | −3.826*** (1.394) | . . .[a] | −4.001*** (1.401) | . . .[a] |
| Baka[b] | −3.993*** (.954) | . . .[a] | −3.898*** (.786) | . . .[a] | −3.770*** (.873) | . . .[a] |
| V$_1$: Tsimane' village 1[c] | . . .[a] | −2.887*** (.816) | . . .[a] | −2.969*** (.879) | . . .[a] | −3.419*** (.876) |
| V$_2$: Tsimane' village 2[c] | . . .[a] | −2.766*** (.824) | . . .[a] | −2.755*** (.854) | . . .[a] | −2.977*** (.912) |
| V$_3$: Baka village 1[c] | . . .[a] | −3.003*** (.336) | . . .[a] | −2.815*** (.241) | . . .[a] | −2.676*** (.482) |
| V$_4$: Baka village 2[c] | . . .[a] | −2.857*** (.464) | . . .[a] | −2.727*** (.378) | . . .[a] | −2.556*** (.586) |
| V$_5$: Punan village 1[c] | . . .[a] | 1.769*** (.142) | . . .[a] | 1.957*** (.099) | . . .[a] | 1.813*** (.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 |
| AIC | 1,174.4941 | 1,162.9981 | 1,192.9595 | 1,163.0236 | 1,178.5353 | 1,137.5780 |
| BIC | 1,214.2322 | 1,202.7361 | 1,264.4881 | 1,202.7617 | 1,273.5375 | 1,177.1623 |

Note. Standard errors are in parenthesis. Shown are the results of a two-part model, where the first part assesses the probability of depvar being larger than 0 (depvar > 0) using a logit binary choice model and the second part models the distribution of depvar|depvar > 0 using a standard ordinary least squares (OLS) model (regression). For definition of variables, see table 1. AIC = Akaike information criterion; BIC = Bayesian information criterion; LEK = proxy for local knowledge.

[a] Variable intentionally omitted from analysis.

[b] Coefficients for the Tsimane' and the Baka are compared with coefficients for the Punan (omitted).

[c] Coefficients for the village variables are compared with coefficients for V$_6$ (Punan village 2; omitted).

* $P < .10$

** $P < .05$

*** $P < .01$.

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 (table A1, available online)

### Medicinal Plant Knowledge and Health

Adults in our sample reported being sick on 5.1% of the days they were observed (SD = 10.1; table 1). The share of days reportedly sick varied between groups: Baka were reportedly sick on 7.31% of the observed days, Punan on 4.7%, and Tsimane' on 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 with better health. When modeling the probability that a person reports being sick at least once (versus never), we found 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 observed 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 H$_3$, or the relation between our composite measure of local environmental knowledge and health (models 3 and 4), we found 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 with a 0.02 decrease in the share of days reportedly sick ($P < .1$).

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 (H$_4$: models 5 and 6), we found that the coefficient of the association is similar to that of models 1 and 2. As in the case of hunting returns, neither the index that captures exposure to the national society nor the index that captures integration

Table 4. Association between medicinal plant knowledge/local environmental knowledge and health

| | Share of days reportedly sick | | | | | |
|---|---|---|---|---|---|---|
| | H₁ | | H₃ | | H₄ | |
| | Model 1 (sites) | Model 2 (villages) | Model 3 (sites) | Model 4 (villages) | Model 5 (sites) | Model 6 (villages) |
| First part: logistic regression: | | | | | | |
| Medicinal knowledge | .052 | .030 | . . .[a] | . . .[a] | .030 | .016 |
| | (.136) | (.134) | | | (.129) | (.132) |
| LEK | . . .[a] | . . .[a] | .086 | .068 | . . .[a] | . . .[a] |
| | | | (.164) | (.176) | | |
| Male | −.686*** | −.660*** | −.739** | −.703** | −.521* | −.476* |
| | (.262) | (.246) | (.324) | (.321) | (.302) | (.278) |
| Age | .020*** | .019** | .0200*** | .019*** | .020*** | .0200*** |
| | (.007) | (.008) | (.007) | (.007) | (.005) | (.005) |
| Household size | −.024 | −.006 | −.025 | −.007 | −.012 | .003 |
| | (.048) | (.050) | (.048) | (.050) | (.043) | (.045) |
| Medicine use | −.091 | −.064 | −.087 | −.061 | −.183 | −.150 |
| | (.217) | (.247) | (.218) | (.250) | (.225) | (.249) |
| Exposure to national society | . . .[a] | . . .[a] | . . .[a] | . . .[a] | −.033 (.105) | .004 (.110) |
| Integration into market economy | . . .[a] | . . .[a] | . . .[a] | . . .[a] | −.412** (.203) | −.405* (.211) |
| Wage labor | . . .[a] | . . .[a] | . . .[a] | . . .[a] | −.002 | −.005** |
| | | | | | (.002) | (.002) |
| Tsimane'[b] | −.732 | . . .[a] | −.729 | . . .[a] | −.566 | . . .[a] |
| | (.520) | | (.521) | | (.472) | |
| Baka[b] | .642 | . . .[a] | .623 | . . .[a] | .297 | . . .[a] |
| | (.524) | | (.523) | | (.521) | |
| V₁: Tsimane' village 1[c] | . . .[a] | −1.560*** | . . .[a] | −1.560*** | | −1.301*** |
| | | (.092) | | (.094) | | (.153) |
| V₂: Tsimane' village 2[c] | . . .[a] | −1.203*** | . . .[a] | −1.209*** | . . .[a] | −1.174*** |
| | | (.071) | | (.078) | | (.149) |
| V₃: Baka village 1[c] | . . .[a] | −.020 | . . .[a] | −.043 | . . .[a] | −.383*** |
| | | (.070) | | (.062) | | (.134) |
| V₄: Baka village 2[c] | . . .[a] | −.069 | . . .[a] | −.093 | . . .[a] | −.401*** |
| | | (.077) | | (.097) | | (.114) |
| V₅: Punan village 1[c] | . . .[a] | −1.348*** | . . .[a] | −1.351*** | . . .[a] | −1.383*** |
| | | (.073) | | (.070) | | (.091) |
| Intercept | −.712 | −.154 | −.680 | −.113 | −.744 | −.155 |
| | (.890) | (.484) | (.876) | (.453) | (.753) | (.281) |
| Second part: OLS regression: | | | | | | |
| Medicinal knowledge | −.009 | −.008 | . . .[a] | . . .[a] | −.011 | −.012 |
| | (.006) | (.006) | | | (.008) | (.008) |
| LEK | . . .[a] | . . .[a] | −.018** | −.017* | . . .[a] | . . .[a] |
| | | | (.008) | (.009) | | |
| Male | .022** | .024** | .034** | .034** | .021* | .022 |
| | (.011) | (.011) | (.015) | (.015) | (.011) | (.014) |
| Age | .001** | .001** | .001** | .001** | .001 | .001 |
| | (.001) | (.001) | (.001) | (.001) | (.001) | (.001) |
| Household size | .001 | .001 | .001 | .001 | .0002 | .0004 |
| | (.002) | (.002) | (.002) | (.002) | (.002) | (.002) |
| Medicine use | −.036 | −.034 | −.037 | −.034 | −.027 | −.026 |
| | (.023) | (.023) | (.023) | (.023) | (.025) | (.024) |
| Exposure to national society | . . .[a] | . . .[a] | . . .[a] | . . .[a] | −.016 (.010) | −.017 (.011) |
| Integration into market economy | . . .[a] | . . .[a] | . . .[a] | . . .[a] | .0300 (.022) | .032 (.027) |
| Wage labor | . . .[a] | . . .[a] | . . .[a] | . . .[a] | .0003 | .0003 |
| | | | | | (.0002) | (.0002) |
| Tsimane'[b] | −.036** | . . .[a] | −.036** | . . .[a] | −.044* | . . .[a] |
| | (.018) | | (.018) | | (.025) | |
| Baka[b] | −.006 | . . .[a] | −.0004 | . . .[a] | .005 | . . .[a] |
| | (.019) | | (.020) | | (.017) | |

Table 4 (*Continued*)

| | Share of days reportedly sick | | | | | |
| | $H_1$ | | $H_3$ | | $H_4$ | |
| | Model 1 (sites) | Model 2 (villages) | Model 3 (sites) | Model 4 (villages) | Model 5 (sites) | Model 6 (villages) |
|---|---|---|---|---|---|---|
| $V_1$: Tsimane' village 1[c] | . . .[a] | −.042*** (.011) | . . .[a] | −.042*** (.011) | . . .[a] | −.059*** (.018) |
| $V_2$: Tsimane' village 2[c] | . . .[a] | −.047*** (.014) | . . .[a] | −.046*** (.014) | . . .[a] | −.046*** (.022) |
| $V_3$: Baka village 1[c] | . . .[a] | −.012 (.012) | . . .[a] | −.007 (.014) | . . .[a] | −.004 (.021) |
| $V_4$: Baka village 2[c] | . . .[a] | −.017 (.014) | . . .[a] | −.012 (.014) | . . .[a] | −.001 (.021) |
| $V_5$: Punan village 1[c] | . . .[a] | −.026*** (.006) | . . .[a] | −.025*** (.005) | . . .[a] | −.030*** (.006) |
| Intercept | .093** (.046) | .098** (.041) | .084* (.047) | .089** (.042) | .113** (.065) | .120** (.059) |
| N | 389 | 389 | 389 | 389 | 383 | 383 |
| AIC | 290.43 | 279.55 | 290.20 | 279.30 | 265.59 | 254.94 |
| BIC | 330.07 | 319.18 | 329.84 | 318.93 | 305.07 | 294.42 |

Note. See table 3 note.
[a] Variable intentionally omitted from analysis.
[b] Coefficients for the Tsimane' and the Baka are compared with coefficients for the Punan (omitted).
[c] Coefficients for the village variables are compared with coefficients for $V_6$ (Punan village 2; omitted).
* $P < .10$
** $P < .05$
*** $P < .01$.

into the market economy are associated with 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, midarm circumference, and sum of four skinfolds) as the outcomes. We tested the association between these indexes 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 indexes of nutritional status examined. The only association worth mentioning was found between hunting knowledge and BMI (model 1) and midarm circumference (model 2). This association was found only for the male part of the sample. For women, none of the

three knowledge measures bore 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 ($H_1$–$H_3$) and, by extension to nutritional status, a proxy for individual adaptive success ($H_5$). 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 extent, health, but it 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 part we interpret them in the context of the original idea driving this study: the role played by 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 ($H_1$), an association that remains robust

Table 5. Association between hunting, medicinal plant, and local environmental knowledge and nutritional status

| | BMI | Midarm circumference | Sum of four skinfolds |
|---|---|---|---|
| | Model 1A | Model 2A | Model 3A |
| Men ($n = 165$): | | | |
| Hunting knowledge | .963*** | .906*** | 1.234 |
| | (.163) | (.168) | (1.124) |
| Medicinal plant knowledge | −.037 | −.214 | 1.731 |
| | (.299) | (.441) | (1.386) |
| Local environmental knowledge | .585 | .384 | 3.09 |
| | (.319) | (.473) | (1.94) |
| | Model 1B | Model 2B | Model 3B |
| Nonpregnant women ($n = 164$): | | | |
| Hunting knowledge | −.147 | −.237 | −3.365 |
| | (.402) | (.454) | (2.384) |
| Medicinal plant knowledge | .122 | .248 | .998 |
| | (.220) | (.236) | (1.566) |
| Local environmental knowledge | .123 | .269 | .366 |
| | (.414) | (.509) | (2.77) |

Note. Each cell (coefficient and standard error) corresponds to the result of a different regression model using as the dependent variable the variable indicated in the column head and as the main explanatory variable the knowledge variable indicated in the row head. We used the same controls as in tables 3 and 4. BMI = body mass index (kg/m$^2$).
*** $P < .01$.

across all specifications tested. These results dovetail with results from an empirical study among indigenous peoples in Nicaragua, in which Koster (2010) found that hunting ability accurately reflects variation in hunting returns. Analogous tests between medicinal plant knowledge and self-reported health (H$_2$) provide weaker evidence. The negative association found between medicinal plant knowledge and number of days a person reports being 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 H$_2$ (versus H$_1$) 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 being sick is twofold 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 hypothesized, the composite measure of local environmental knowledge does not necessarily provide larger returns than specific measures (H$_3$): local environmental knowledge provides lower returns on hunting than hunt-

ing knowledge but higher returns on health than medicinal plant knowledge. The finding suggests that, despite claims about 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 intracultural distribution of local knowledge is patterned according to individual and social characteristics (Camou-Guerrero et al. 2008; Salpeteur et al. 2015). 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 H$_4$ 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 as-

sociated with hunting returns between groups. For example, as the Baka sell bushmeat, higher hunting returns are directly related to higher income (R. Duda, S. Gallois, and V. Reyes-García, unpublished data). In contrast, as the Tsimane' and the Punan do not sell bushmeat, cash income might relate differently to their hunting returns.

In our last hypothesis ($H_5$), 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 $H_1$–$H_3$, results from testing $H_5$ do not provide enough evidence to 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 $H_1$–$H_3$ 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 indexes of short-term nutritional status are affected by many factors that were not included in our study. Such factors vary from diet composition to levels of physical exercise or the socioeconomic 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 sharing of bushmeat is considered "compulsory," according to social norms. Similarly, sharing information on medicinal plant properties, their location in the forest, and even the preparation of the medicinal plant is routinely done in the three studied societies, at least for common, nonspecialized medicinal plant knowledge (see also Reyes-García et al. 2003). Thus, through the sharing of resources and knowledge, individuals who obtain higher returns on their knowledge might transfer material and nonmaterial 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 with better health but not with 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 of the study of sharing and reciprocity among small-scale societies (Kaplan and Hill 1985; Mauss 1954; Shalins 1972) 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 played by sharing and cooperation in multilevel 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 (Fehr, Fischbacher, and Gächter 2002; Gintis 2000; 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 that result in individuals maximizing the fitness of the group over their own fitness can be found in studies of the sustainable governance of common-pool resources, highlighting how groups develop norms, rules, and institutions to avoid resource overexploitation and degradation (Ostrom 1990; Penn 2003).

Two additional issues merit discussion before concluding. First, for the men in the sample, hunting knowledge is positively associated with two indexes 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*a*). 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 just be reflecting the social gradient of health. Second, our research used only 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 on 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 favoring 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 a group level. Such research can be done only through cross-cultural collaborative projects.

## Acknowledgments

# Comments

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Victoria Reyes-García and collaborators should be commended for their attempt to assess the adaptive process of individuals and not of a social group. They stress that a culturally evolved and environment-specific knowledge should provide individual returns to their individual users. Unfortunately, their effort is from the outset disqualified by wrongly formulated and counterintuitive hypotheses.

Globally speaking, the authors seem to overlook a widely admitted particularity of human society that consists of prioritizing cultural choices that are not necessarily meant to achieve ideal biological fitness. Among foraging societies, satisfying symbolic demands regularly occurs even at the expense of any optimal biological success (Dounias and Colfer 2008; Foley 1985; Garine 1991).

With respect to $H_1$ (adult hunters with more local knowledge of game species should have higher hunting returns), in the context of drastic change that significantly affects the three considered communities (note: why are results provided for only a single Punan Tubu site when the research protocol introduces two comparative sites per ethnic group?), a neophyte hunter who has access to recent technology—for instance, the trivialized use of twisted wire cable for trapping or easier access to increasingly sophisticated firearms (Dounias 2016)—can easily obtain higher yields than an expert in local hunting practices. In that respect, a much more appropriate proxy would be the sustainability of capture modalities rather than the quantity of procured meat.

$H_2$ (adults with more local knowledge about medicinal plants should have lower reports of sickness) accumulates problems. First, a deliberate focus on plants ignores the fact that foraging societies diversely combine immaterial and material elements from vegetal, animal, and mineral origins for medicinal purposes. Considering solely plant-based medicines as a proxy of medicinal skills is misleading. Second, the authors establish an explicit relation between the most valued plants and their secretion of active chemical compounds. Countless ethnopharmacological studies call for caution in establishing such causality (Colfer, Sheil, and Kishi 2006). Third, the authors claim that the majority of medicinal material is equally accessible to the majority of the members of the societies. They totally brush aside the fact that medicinal knowledge is compartmentalized within each society, depending on gender, age, social status, and selective rights regarding the use of medicinal resources, and that traditional healing knowledge is generally retained by very few specialists. Fourth, the pathogenic environment, or pathocenosis (Froment 2008; Grmek 1969; Swedlund and Armelagos 1990), to which a cultural group is exposed varies with time. In situations of pronounced shifts in lifestyles (exactly what the three compared hunter-gatherer groups are experiencing), the pathocenosis can be so heavily transformed that the local pharmacopoeia becomes inefficient to tackle new diseases (Dounias and Colfer 2008; Dounias and Froment 2011; Dounias et al. 2004; Voeks and Sercombe 2000). Fifth, the prediction that a cured individual would implicitly report being sick less frequently is unfounded. A person may report being sick on day 1, recover the same day after taking an appropriate treatment, and feel sick again on day 2. Rate of sick-reported days: 100%; efficiency of treatment: also 100%. The number of days reported as sick can be a proxy only for a preventive therapeutic system. In essence, most local traditional healing systems proceed curatively. Sixth, people may report on disability rather than sickness, with the difference

depending on local perception of sickness and on a formal lexical distinction of both statuses. For instance, will a seriously drunk adult be declared sick? The Baka are heavy drinkers; the Punan only occasionally drink alcohol. The respective appreciation of a sick status related to excessive consumption of alcohol might differ accordingly, and the relative efficiency of treating sickness will inevitably be biased. Seventh, self-medication is a dramatic issue in small-scale societies. In situations where accessibility to good-quality allopathic medicine is prohibitive, the national society and market often lead to addictive consumptions of bad-quality manufactured pills that are detrimental to health, independently of any traditional healing expertise.

$H_4$ (returns to LEK should be lower if the individual is exposed to the national society or integrated into the market economy) cannot appropriately be discussed in societies that are already and heavily exposed to such outside drivers of change. For instance, Dounias et al. (2010) pointed out that the Punan who live near the city and who are most exposed to ostracism and marginalization do not spare efforts to preserve their cultural and material heritage. The best blowpipe makers, the most powerful traditional healers and midwives, and some material artifacts of past Punan culture (like the jars that serve in matrimonial exchange; Césard 2009) are more frequently found near urban sites than in remote settlements. Far from being a systematic cause of acculturation, life in the city may sometimes have a positive incidence on the preservation of traditional knowledge (Levang, Sitorus, and Dounias 2007). It is anything but a surprise that the individual level of exposure to the national society or market poorly reflects the relation between medicinal plant knowledge and health.

$H_5$ (adults with higher LEK should have better nutritional status) severely ignores the incidence of cultural choices and practices. Among the Punan Tubu, Dounias (2007) and Dounias et al. (2007) have shown that elder women, who possess the highest level of environmental knowledge, have also the worst nutritional status indexes. In accordance with Punan tradition, elders who depend on active adults to obtain food have an obligation of self-censorship and must leave the lion's share to the youngest members of the household, especially in times of food shortage. Reyes-García and collaborators evoke cultural choices as an a posteriori explanatory bias instead of considering them as a prerequisite that should have guided the formulation of more appropriate hypotheses.

Since the backbone protocol of their comparative study results in measuring wrongly formulated hypotheses, the positive associations that Reyes-García and collaborators eventually obtain are artifacts of a typical *cum hoc ergo propter hoc* faulty reasoning that occurs when a positive correlation justifies an improbable causality (Damer 1995): after obtaining positive associations for $H_1$ and $H_3$ and a negative one for $H_5$, the authors are led to conclude the presence of a "paradox" in testing the returns of local environmental knowledge. Sharing, which is a fundamental cultural trait among the three compared egalitarian societies, is eventually called to the rescue as

an alternative explanation to the alleged paradox, and it conclusively asserts the supremacy of social rules at the group level over any individual arbitrariness.

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## Economic Cooperation Does Not Presuppose Group Selection

Reyes-García and colleagues bring careful empirical attention to cross-cultural and intracultural variation in hunting ability and medicinal plant use. They suggest that group selection potentially explains why the most successful hunters and healers do not parlay their greater abilities and knowledge into better health, as measured via standard anthropometrics. Although theories and simulations of cultural evolution suggest that group selection may indeed characterize human groups (Boyd and Richerson 2010), cooperative economic behaviors such as sharing hunted meat in rural villages may be parsimoniously explained via conventional models from behavioral ecology without invoking group selection (Jaeggi and Gurven 2013).

Consider a forager who returns from the forest with meat. Sharing portions with others is costly because she could instead consume all of the meat and benefit nutritionally. However, the theoretical models employed by behavioral ecologists demonstrate that there can be individual-level benefits to sharing that outweigh the costs. If the recipients are consanguineal kin, for example, then by sharing the forager can help her relatives to transmit copies of her own altruistic alleles, a mechanism known as kin selection (Griffin and West 2002). Alternatively, if the forager cedes a portion to a partner who is likely to reciprocate at a future date when her need for food is more acute, then sharing can emerge via reciprocal altruism (Nolin 2010). Meanwhile, costly signaling theory notes that successful foragers who share may also be signaling attributes that others notice and seek in their mates and allies, leading to beneficial outcomes that outweigh the initial cost of sharing (Smith, Bird, and Bird 2003). As noted by the authors, human behavioral ecologists have presented abundant empirical research on food sharing that supports these models. Compelling evidence for group selection would reject these models while demonstrating that the sharing of food primarily benefits the group, not altruists and their consanguineal kin. My hunch is that altruism in the authors' study communities is instead directed toward kin, reciprocating partners, and possibly desirable mates and allies.

Among the key results of this study, we learn that successful hunters are those who can identify the morphology or

vocalizations of prey species, who report that they hunt frequently and harvest large game, and who are cited by their peers as being successful. The authors describe these variables as components of ethnobiological "knowledge," but the latter two variables could be regarded as alternative, informant-based measures of hunting success, the outcome variable. In other words, positive correlations seem to be largely inevitable if informants accurately describe their activities and the behavior of their peers. As for the former variable, it is perhaps unsurprising that successful hunters are better able to identify phenotypic traits of prey species. Does that ability specifically require cultural learning, however, or could such abilities be acquired primarily via independent hunting and butchering experience? That is, whereas linguistic conventions such as the naming of species are intrinsically "cultural," it is not clear whether the participants' performance on the identification tasks is a hallmark of the social learning and cumulative cultural knowledge that characterize our species.

As an alternative to most identification tasks, behavioral ecologists seek data on the knowledge that specifically helps foragers acquire food. When they hear a bird's song, for instance, do hunters know which of the surrounding tree species is likely to be harboring their quarry? Are foragers heterogeneously aware of the places and times when they are likely to encounter different prey species? Do they vary in their knowledge of how to stalk an encountered animal without triggering its antipredator responses? Behavioral ecologists hypothesize that this latter type of information underlies variation in foraging prowess, but unfortunately these aspects of ethnobiological knowledge have been difficult to measure ethnographically. Instead, we learn from this study that purportedly successful hunters exhibit superior nutritional status. The correlation is noteworthy, but can we infer causality from such associations? Perhaps they are successful hunters because they are better fed, not vice versa.

I mention these considerations primarily to underscore the challenges that anthropologists face when investigating the adaptive value of ethnobiological knowledge. Analogous criticisms could be forcefully directed toward my recent research on fishing success and knowledge among indigenous Nicaraguans (Koster, Bruno, and Burns 2016). That study showed a similar correlation between individuals' fishing ability and their performance on photo identification tasks. However, it is not clear whether knowledge either facilitates or results from fishing success, nor is it clear whether identification tasks are valid proxies for the domain-specific knowledge that foragers need to be successful. These studies accentuate the need for behavioral ecologists to pioneer new methodological approaches that demonstrate the relationship between ecological knowledge and foraging yields, ideally via longitudinal research that elucidates the temporal dynamics of learning and foraging proficiency across the life span.

In the meantime, Reyes-García and her colleagues provide commendable cross-cultural data on adaptive strategies in subsistence-oriented societies. Their commitment to standardized data collection across societies and study sites is a research design that should be emulated in future anthropological studies. Their rich data can potentially generate insights beyond the analytical results that they report in this paper. For example, the authors mention that opportunities to sell bushmeat may obscure relationships between hunting returns and market integration among the Baka. Such hypotheses can be tested via interaction terms that allow the effects of predictor variables to vary across societies or study sites within societies (e.g., Koster, Grote, and Winterhalder 2013). I eagerly await future papers from the authors that further disentangle the contextual aspects of local ecologies and economies that can explain individual-level adaptations at their respective study sites.

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Reyes-García and colleagues undertake an ambitious task of exploring the interconnections between knowledge acquisition/transmission, resource use, and health in an evolutionary context and seek to identify patterns across diverse study populations in tropical Africa, Southeast Asia, and Latin America. As someone who has co-led cross-cultural and longitudinal research projects among the Waorani, Shuar, Cofán, and Kichwa, I certainly appreciate the effort it takes to collect primary data "informed by a comparative perspective from the outset," as the authors put it. It requires, among other things, training the fieldworkers in a manner that fosters reliability and standardization and conducting fieldwork at many sites concurrently—something much more difficult to do when the sites are thousands of miles apart in Cameroon, Borneo, and Bolivia.

The authors use local environmental knowledge—a cumulative body of practices and beliefs transmitted culturally and intergenerationally about the relationships of organisms with each other and their environment—as 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." Local environmental knowledge is operationalized as both hunting and medicinal plant knowledge and is hypothesized to result in more kilocalories from hunted game, better nutritional status, and lower reported sickness for those individuals with less integration into the market and national society. Reyes-García and colleagues grapple with a slew of important issues of concern to anthropologists, such as the erosion of cultural and ecological knowledge and declining viability of subsistence economies. Just addressing these issues would be a substantial task; in addition, this paper adds another layer of investigation by engaging ideas from evolutionary anthropology.

Reyes-García and colleagues assert that there is a lack of "empirical research on the mechanisms through which culture might shape human adaptive strategy" and, furthermore, that what observational studies do exist are limited to "only one society and one cultural trait." In response, I would strongly suggest that they peruse William Durham's (1991) masterful work *Coevolution: Genes, Culture, and Human Diversity*, which marshals evidence of cultural practices from marriage to dairying to head-hunting from locations ranging from Amazonia to the Tibetan Plateau to West Africa. Durham not only sets the standard for a rich and nuanced presentation of case studies, he illuminates them as examples of various theoretical models of the relationship between genes and culture. In particular, the "enhancement" model that Durham presents appears to be highly appropriate for the approach taken in this paper. Reyes-García and colleagues spend little time elaborating the theoretical framework that illuminates how they conceive of cultural evolution. For example, do the authors conceptualize culture as part of a phenotype or as a distinct channel of informational inheritance? Do they adopt a single fitness principle or, as is more likely, a model of dual inheritance? Durham's (1991) analysis explicitly addresses the gene/culture relationship and does so, in part, by positioning himself in relation to other seminal works on this relationship. A similar clarification of theoretical positioning would lend weight to the authors' assertions and scholarly impact.

Additionally, an investigation of cultural adaptation should specify the ideational unit of cultural transmission. Such a unit is most useful when it meets various criteria, such as actually or potentially guiding behavior; accommodating "variable kinds, quantities, and ways of organizing information"; and demarcating "bodies of information that are . . . differentially transmitted as coherent, functional units" (Durham 1991:188). Arguably, this study would be more appropriately focused not on local environmental knowledge as general hunting knowledge or medicinal plant knowledge but on something more specific—a particular hunting taboo or medicinal plant practice—that constitutes conceptual phenomena handed down through social transmission and represents shared understanding. A category such as hunting knowledge, and possibly even medicinal plant knowledge, can be composed of information that can be acquired through personal experience or trial and error—and thus forming spontaneously each generation—rather than demonstrating ideational descent.

My research has examined integration into the market and indigenous health in Ecuador's Amazon as well as the entanglements of the oil complex in the daily, lived experiences of populations who live in sites of extraction and processing. In both cases, my collaborators and I have had the privilege of conducting research among the Waorani, considered one of the least assimilated indigenous peoples in western Amazonia. They remain a (primarily) small-scale, subsistence-based society who (primarily) reside in and defend the most biodiverse forest on the planet. At the risk of perpetuating the anthropological tendency to use "my" study group as a touchstone, I will briefly highlight insights from my work in eastern Ecuador that might be relevant here. Historically an "isolated" group living in dispersed and mutually hostile extended kin groups, the Waorani were found to possess a limited repository of "traditional" medicinal plant knowledge due to a dearth of endemic disease (Davis and Yost 1983; Larrick et al. 1979). Most other groups did not live under such conditions. The far-reaching ramifications of colonialism in the Americas meant that disease patterns—and the medicinal knowledge generated to combat or ameliorate them—could not be understood without a diachronic perspective informed by analysis of the material, political, and economic changes that accompanied Amazonian colonization. Despite these widespread and enduring changes to the interconnected social practices and ecologies that constitute nature/culture in Amazonia, the Waorani have not experienced complete detachment from traditional norms and customs nor a linear decline in health and well-being. The linkages between social and environmental practices—central to the work of Reyes-García and colleagues—are dynamic to a degree that describing a singular Waorani culture or a clear causal relationship between Waorani culture and something as broad as hunting knowledge or plant use would elide a great many of the cultural and environmental practices that constitute daily life in a Waorani village.

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Reyes-García and colleagues have presented a compelling argument concerning the adaptive nature of culture and its relevance to human health. Their discussion concerning the role played by sharing behavior in achieving greater health equity—especially in terms of access to nutrition—across the population is an intriguing one. By sampling from three different indigenous groups located in different regions of the globe, they were able to achieve a true comparative analysis of how an individual's local knowledge (specifically pertaining to the local environment) in different cultures impacts community health and nutrition.

Ethnobotany, or the study of the relationship between plants and people, has also been referred to as the "science of survival" (Prance 2007). Local knowledge concerning environmental resources, especially plants used in food acquisition (as hunting or fishing implements or as foraged ingredients) and for medicine, is widely held to be important to both individual and community fitness and survival. Importantly, local knowledge is crucial to establishing community resilience in the face of natural and man-made disruptions to the ecosystem, such as climate change.

By taking a very carefully designed quantitative approach, the authors were able to examine the general concepts of how

local environmental knowledge relates to individual and group fitness in a highly rigorous manner. This study stands as an example of the importance of carefully recorded individual use reports for quantitative analysis. Their findings that local environmental knowledge is positively associated with hunting success and that medicinal plant knowledge is positively associated with self-reported health status is not unexpected. However, the lack of a clear link between local environmental knowledge and nutritional status did come as a surprise. It would be expected that those maintaining a higher level of local knowledge concerning additional resources, such as wild edible plants, would have a greater food security and thus greater access to nutrition. The authors' argument that food-sharing behavior is responsible for the data gap between individual knowledge and nutritional status is compelling, and one well supported by their qualitative data from the ethnographic study. For example, the compulsory sharing of food resources (specifically wild game) helps to ensure broader access to nutrition for the entire community. In this scenario, communities with a number of individual experts in local environmental knowledge would benefit most.

Overall, the research team and authors are to be commended on conducting such a thorough, comprehensive study in three different cultures. Their observations and data analyses are very useful for developing a better understanding of how local environmental knowledge impacts both individuals and communities at large. Such insight is critical to the future theoretical development of the field of ethnobotany.

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# Reply

We would like to thank the commentators for having taken the time to read and critically reflect on our work as well as *Current Anthropology* for the possibility to provide a reply. We have no doubt such exchanges are at the basis of scholarly advancements. Given the diversity of opinions and comments our piece has given rise to, we have organized our reply following the structure of the paper.

We set up our work to test whether culturally transmitted and individually appropriated knowledge provides immediate measurable returns to the individuals holding the knowledge and proposed to do so by focusing on two concrete domains of local environmental knowledge (i.e., hunting and medicinal plant knowledge) that could arguably relate to measurable outcomes (i.e., hunting yields, health and nutritional status). At the theoretical level, our work draws inspiration from cultural evolutionary theory and, although we do not quote the work of Durham (as noted by Lu), we extensively cite other authors who have contributed to the establishment of cultural evolutionary theory (e.g., Richerson, Boyd, Efferson, Gintis, Henrich, Laland, and Tomasello). Cultural evolutionary theory emphasizes that two systems of information transmission, genes and culture, are the intertwined components of a common evolutionary process. A large amount of work in the field has been directed at understanding the mechanisms behind the transmission of cultural traits, behaviors, norms, beliefs, attitudes, and institutions (Boyd and Richerson 1985; Henrich and Broesch 2011; Richerson and Boyd 2005), and our work fits in this tradition. Social learning has been proposed as a main mechanism enabling cultural transmission, and many mathematical models have been designed to test theoretical predictions about how different strategies result, over time, in differences in the prevalence of traits in a population. Previous researchers have also used secondary data or primary data collected in a single setting to test related hypotheses. A main contribution of the work presented here is the use of cross-cultural primary data purposely collected to test hypotheses derived from cultural evolutionary theory.

In reaction to Dounias's concern about "the supremacy of social rules at the group level over any individual arbitrariness" and Koster's remark that "economic cooperation does not presuppose group selection," we would like to point out that in our paper group selection is presented as a potential "interpretation" of our results, not as its main finding. However, we remain firm in the idea that the "interpretation fits well both with anthropological theory and with insights from the study of group adaptations in evolutionary biology." The last two decades have seen a proliferation of research frameworks that emphasize the importance of understanding how multilevel processes relate to adaptation (e.g., McElreath and Koster 2014; Richerson et al. 2016; Waring et al. 2015). A main idea of these works is that cultural adaptation cannot be fully explained focusing on a single unit of analysis (e.g., individuals) and that attention needs to be paid to the interactions across social units at different levels (e.g., individuals within a group). In that vein, researchers have proposed that cultural group selection is a powerful adaptive mechanism that helps to explain the spread of complex social dynamics such as cooperation. Traits promoting cooperative behavior can be selected at the group level if they generate large benefits for the group, even if they are costly to the individual (Henrich 2004; Richerson et al. 2016). Our finding that local environmental knowledge does not relate to better nutritional status, despite being associated with more direct proxies of the potential returns of such knowledge (i.e., hunting returns and health) can be interpreted under the same logic. If there were no multilevel interactions and individuals acted only to optimize their survival strategies, one would expect that individual levels of local environmental knowledge would correlate with individual fitness. However, under a multilevel framework one could expect that if sharing local environmental knowledge—and the benefits generated by it—increases group adaptation, then groups in which sharing occurs would be selected. Within a group, sharing plays a leveraging role so that different members of a group—and not only the person holding more knowledge—benefit from it. In sum, in response to

critiques about the use of the argument of group selection, we think that our article is clear about the fact that our data do not provide a test for the validity of the argument but rather presents it as a valid potential interpretation. There might be alternative explanations, including Koster's suggestion that "altruism in the authors' study communities is . . . directed toward kin, reciprocating partners, and possibly desirable mates and allies." Assessing which one has more explanatory power will require further research.

We are pleased to see the unanimous enthusiasm for the cross-cultural comparative component and the commitment to empirical data collection of our work. This indeed has been a major challenge as well as a source of satisfaction in our team's work. We notice, however, that the complex methodological design behind our work had important trade-offs in terms of what data could be collected without threatening comparability. For example, Lu proposes that the study would be more appropriately focused on a particular hunting taboo or medicinal plant practice "that constitutes conceptual phenomena handed down through social transmission and represents shared understanding." While we agree with the comment, we argue that focusing on a single element (i.e., a particular hunting taboo) would have challenged substantially the cross-cultural comparison and would have required far more in-depth ethnographic understanding. Finally, Koster raises an interesting point about comparability between knowledge tests, arguing that some of these tests seem to be better proxies of social learning than others. While this could certainly be a possibility, we have actually found that the measures of knowledge used are correlated with one another (Reyes-García et al. 2016a), suggesting that overall they are robust measures of socially transmitted knowledge.

The commentators made three main critiques to the way in which we present and interpret our empirical results. First, Dounias and Koster notice that we assume causality in the relations tested when indeed our empirical analysis shows only associations. This is a fair critique, and we agree with it. The wording used, often assuming causality, is partly driven by our theoretical framing (assessing returns of knowledge), but we acknowledge that the data collection and statistical techniques used allow us to talk only about associations. We could not agree more with Koster in his remark that the field needs "new methodological approaches" to address the direction of causality "between ecological knowledge and foraging yields." Second, Lu argues that we do not interpret our data in a larger context. While acknowledging the importance of linking our results to the broad social and environmental contexts in which the three societies are embedded, we think there was no place for such endeavor in this comparative piece. Our research group, however, has produced a number of papers and theses (with more coming) focusing on each of the three specific sites as well as more detailed analysis of the surrounding contexts. We invite readers to explore them to obtain a deeper understanding of the particular processes

happening at each study site (http://icta.uab.cat/Etnoecologia/lek). Finally, Dounias argues that we do not take into account knowledge diversity in our study, a comment that seems to us a misreading of our methodological approach. As do others (Gold and Clapp 2011), we focus on lay, not specialized, knowledge. We collected data among all adults in the selected communities (participation rate, >90%) using a protocol designed to capture individual levels of lay knowledge. Moreover, knowledge variation is our main explanatory variable. We acknowledge that in this piece we do not explore in particular how knowledge is distributed, but we refer the interested reader to other works from this project in which we explore different aspects of intracultural knowledge diversity (e.g., Díaz-Reviriego et al., forthcoming; Fernández-Llamazares et al. 2015; Gallois et al. 2015; Reyes-García et al. 2016a).

In our final comment, we would like to challenge Dounias's assessment about our "wrongly formulated and counterintuitive hypotheses." Hypotheses are assumptions that are taken to be true only for the purpose of the argument and that need to be falsified, which we aimed to do with real-world data and statistical analyses. Under the theoretical framework used here, and as also noted by Quave, our finding that local environmental knowledge is positively associated with hunting success and self-reported health status "is not unexpected." Moreover, most of the critiques presented by Dounias do not really challenge the hypotheses themselves but rather the predictions we derive from them. When using the scientific method, there is nothing wrong with having incorrect predictions as a point of departure, as it is understood that they often derive from not having considered some facts in the study design. We agree with some of the concerns raised about our predictions (e.g., using sustainability of capture modalities as a variable) and disagree with others (e.g., urban settings as repositories of local environmental knowledge). But more importantly, we argue that any alternative prediction should be tested. Hence, we would like to stress that a major asset of this study—and one that differentiates it from much previous research in anthropology—is that both the protocol for data collection and the data itself are open to the public and available to anyone who may want to test predictions or hypotheses that go beyond the ones we make. For example, our data set includes information on hunting techniques that would allow testing whether a hunting technique is actually a major variable to explain harvest; it also includes information on village distance to the center town and individual measures of market integration and cultural change that would allow for testing the importance of these variables on knowledge distribution. Indeed, we would be delighted to provide our data to anyone interested in analyzing it.

—Victoria Reyes-García, Maximilien Guèze, Isabel Díaz-Reviriego, Romain Duda, Álvaro Fernández-Llamazares, Sandrine Gallois, Lucentezza Napitupulu, Martí Orta-Martínez, and Aili Pyhälä

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