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Shifts in indigenous culture relate to forest tree diversity: A case study from the Tsimane', Bolivian Amazon

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ABSTRACT

Understanding how indigenous peoples' management practices relate to biological diversity requires addressing contemporary changes in indigenous peoples' way of life. This study explores the association between cultural change among a Bolivian Amazonian indigenous group, the Tsimane', and tree diversity in forests surrounding their villages. We interviewed 86 informants in six villages about their level of attachment to traditional Tsimane' values, our proxy for cultural change. We estimated tree diversity (Fisher's Alpha index) by inventorying trees in 48 0.1-ha plots in old-growth forests distributed in the territory of the same villages. We used multivariate models to assess the relation between cultural change and alpha tree diversity. Cultural change was associated with alpha tree diversity and the relation showed an inverted U-shape, thus suggesting that tree alpha diversity peaked in villages undergoing intermediate cultural change. Although the results do not allow for testing the direction of the relation, we propose that cultural change relates to tree diversity through the changes in practices and behaviors that affect the traditional ecological knowledge of Tsimane' communities; further research is needed to determine the causality. Our results also find support in the intermediate disturbance hypothesis, and suggest that indigenous management can be seen as an intermediate form of anthropogenic disturbance affecting forest communities in a subtle, non-destructive way.

1. Introduction

The effects of indigenous peoples' forest management on tropical biodiversity have generated much debate in the conservation literature (Chazdon et al., 2009). In the Amazon, there is growing evidence that the landscapes and biodiversity we currently observe result, not only from natural phenomena, but also by centuries of indigenous management (Denevan, 1966; Heckenberger et al., 2003; Lombardo et al., 2011). While some researchers report only natural influences on the composition of neotropical forests (Espinosa et al., 2011; White and Hood, 2004), others argue that current forest vegetation also reflects the effects of past human disturbances (Chazdon, 2003; Macía, 2008).

Contemporary indigenous peoples have extensively managed a range of useful species such as palms (Macía et al., 2011), sometimes leading to varying stages in the continuum of wild-managed-domesticated plants and implying that many areas are virtually human-modified. In addition, indigenous peoples have managed landscapes to keep large amounts of forest cover, thus enhancing biodiversity (Garí, 2001; Zent and Zent, 2002). For example, it has been argued that slash-and-burn agriculture, as practiced by small-scale societies, can lead to an increase in landscape biodiversity through the creation of a mosaic of habitats (Peters, 2000; Wiersum, 2004), whereas large-scale shifting cultivation systems and intensive agriculture practiced by non-indigenous peoples result in deforestation and biodiversity loss

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(Donald, 2004; Toledo et al., 2003). A potential consequence of this type of management is the current overlap of indigenous territories with areas of high biodiversity (Porter-Bolland et al., 2012; Sunderlin et al., 2005; Toledo, 2001) and the sharp contrast with the harmful effects of non-indigenous management on the same type of environment (Armenteras et al., 2006; Fearnside, 2005; Lu et al., 2010).

Despite general agreement on this overall picture, contemporary changes affecting Amazonian indigenous groups have led some authors to question how indigenous people's lifestyles changes associated with the incorporation of modes and mores of the Western society might affect biodiversity (Gross et al., 1979; Henrich, 1997; Reyes-García et al., 2010). Although answering this question seems critical in face of the spread of bottom-up approaches for biocultural diversity conservation (e.g. community-based conservation models, see Porter-Bolland et al., 2012), we have no evidence of studies addressing the phenomena using real field data.

Here, we analyze the association between cultural change of native Amazonians and tree diversity and structure in old-growth forests surrounding their villages. We proxy cultural change by looking at the changes that take place in the indigenous culture when indigenous people come into continuous first-hand contact with people from other cultures (Berry, 2008; Redfield et al., 1936). In the case of Amazonian indigenous groups, cultural change is linked to the process of integration into market economy, yet it is distinct because it does not refer only to changes on material measures or economic indicators (Godoy et al., 2005). While integration into market economy certainly affects forest management (Reyes-García et al., 2010, Ruiz-Perez et al., 2004), it is probable that cultural change also relates to biodiversity (Geist and Lambin, 2002; Kingsbury, 2001). Our proxy of biodiversity is based on trees because they are the most important structural organisms of forests and provide a reliable estimation of overall biodiversity (Macía, 2008). We also explore the pathways through which cultural change and tree diversity and structure may be associated. Biodiversity is expected to decrease as the impact of indigenous people on the environment grows (Reyes-García et al., 2007; Sunderlin et al., 2005). Therefore, since our data do not allow testing a causal relation, we hypothesized that cultural change would be negatively associated with tree diversity in the forests managed by villages.

2. Methods

2.1. Study area

We conducted our research in the Tsimane' territory, in the Amazonian province of Beni, Bolivia (Fig. 1). The study area extends in a densely forested region between the foothills of the Andes and the savannas of Moxos (14°–15°S, 66°–67°W) within altitudinal ranges of 150–300 m. Annual mean temperature is 25.8 °C and annual mean precipitation is 1743 mm (Guèze et al., 2013). Climate shows a marked dry season of four months with less than 100 mm of rainfall and sporadic strong cold winds from the south. Most soils are quaternary alluvial sediments of fluvial origin (Navarro and Maldonado, 2002). Different broad forest types occur due to the history of flooding, ranging from inundated to seasonally-flooded *bajío* forests to *terra firme* forests, which cover most areas (Guèze et al., 2013). In all forest types, many emergent tree species, such as *Hura crepitans* and *Terminalia amazonia*, are deciduous. In the present study we focus on *terra firme*, where Moraceae, Arecaceae (palms), Euphorbiaceae, and Fabaceae are the foremost families observed (Guèze, 2011).

2.2. The Tsimane' and their lands

The Tsimane' number ca. 12,000 (Reyes-García et al., 2014a). Traditionally they were semi-nomadic hunters-gatherers, although they have long practiced itinerant agriculture and often sell or barter the leaves of a thatch palm, locally known as jatata (*Geonoma deversa*).

Tsimane' villages experiment different levels of interaction with at least five types of outsiders. First, cattle ranching in the open lands (pampas) of the Tsimane' territory has been practiced for centuries, but has intensified in the last decades (Jones, 1991). Second, Christian missionaries have been present permanently in some villages since the 1950s (Martínez-Rodriguez, 2009). Third, Andean colonists often illegally encroach on Tsimane' lands for agriculture, cattle ranching or land speculation (Reyes-García et al., 2014a). Fourth, selective extraction of mahogany (*Swietenia macrophylla*) took place in the past in the area (Gullison et al., 1996), and nowadays logging companies often hire Tsimane' to extract other construction timber. Fifth, itinerant traders, who barter commercial goods by agricultural and non-timber forest products (NTFPs), nowadays reach most of the Tsimane' villages: villages close to market towns are visited by traders on an almost daily basis, whereas remote villages receive their visit on a monthly basis.

Overall, in most remote villages people remain highly autarkic and still practice traditional activities (e.g., subsistence slash-and-burn agriculture, hunting, and fishing with bow and arrow) and hold traditional beliefs. Reyes-García et al. (2005) have shown that knowledge on plant uses was positively associated with the distance to market towns. On the contrary, in villages closer to market towns, people typically work for logging companies, illegal loggers or cattle ranchers, and sell cash crops (Vadez et al., 2008). In these villages, family structure and cultural and sharing codes are modified and people generally no longer hold traditional beliefs and taboos and tend to adopt outsiders' beliefs and behaviors. For example, Luz et al. (in review) found that schooling, more common in villages closer to market towns, is negatively associated to hunting efficiency. This dual pattern, though, is changing rapidly with new possibilities of accessing remote villages and the development of NTFP markets (Pérez-Llorente et al., 2013).

2.3. Data collection

2.3.1. Village sampling

We selected six Tsimane' villages on the basis of homogeneity in old-growth forest cover and population size, but with potential variation in the level of cultural change and market integration. To do so, we first analyzed recent Landsat satellite images to identify villages that displayed a continuous forest cover in their surroundings, without large extents of natural pampas or pastures. Although forest cover is homogeneous, the Tsimane' territory is situated at the transition between three biogeographical regions (Navarro and Maldonado, 2002), and we acknowledge that measured tree diversity might vary according to the overall regional species richness (Leigh et al., 2004; ter Steege et al., 2000). To maximize variation in cultural change and market integration, we used data from a previous survey among most Tsimane' villages (Reyes-García et al., 2012). For each village with continuous forest cover, we calculated the average number of years of schooling of male household heads and the average share of rice sold (out of total rice harvested) as proxies of cultural change and market integration (Godoy et al., 1998). We ranked the villages according to the value of those indices and then selected a total of six villages: two displaying a high level of schooling and market integration, two an intermediate level, and two low levels.

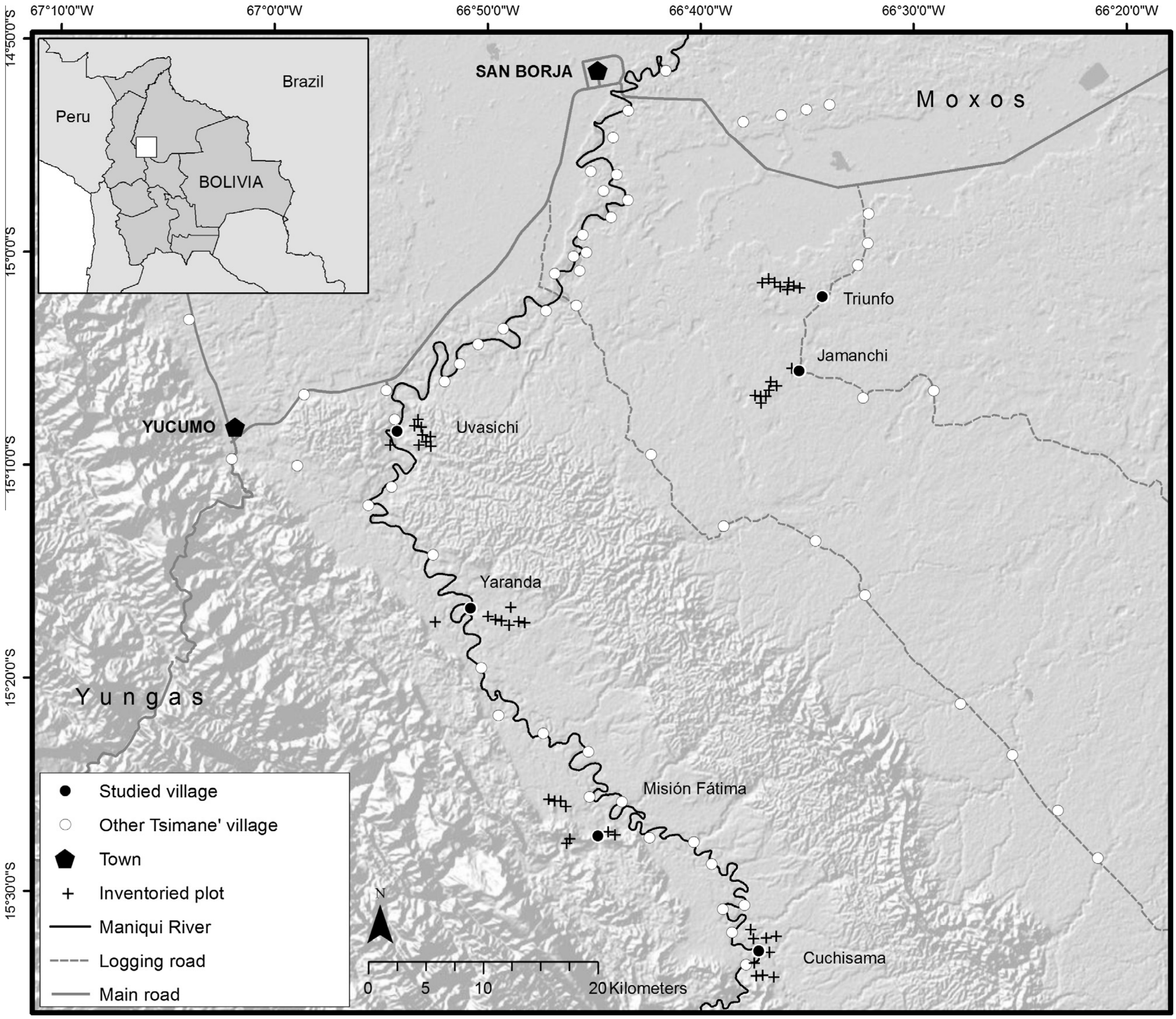

Fig. 1. Map of the study area, showing six Tsimane' villages where data on cultural change were collected, and the location of 48 0.1-ha plots in old-growth forest.

2.3.2. Ecological data

Between March–December 2009, we established 48 0.1-ha plots (50 × 20 m) in *terra firme* forests within the territory of the six Tsimane' villages (i.e., eight plots per village). We used 0.1-ha plots because this method provides good results for the inventory of tree diversity (Phillips et al., 2003), and it allows including understory trees and saplings individuals that are also used by indigenous people. We used a preferential sampling to place the plots in old-growth forests that showed no apparent sign of recent disturbance from human activity (e.g. from selective logging). We placed the plots evenly on flat terrain or gentle slopes, at a minimum distance of 500 m between each plot and from the closest agricultural field or fallow, and avoiding large canopy gaps. We inventoried all tree stems with a diameter at breast height (dbh) $\geqslant$2.5 cm and we collected voucher specimens for all individuals that we could not fully identify. Duplicates of the vouchers are deposited in LPB and MA and unicates are kept in LPB, acronyms according to Thiers (2013).

To obtain edaphic information, we collected one composite superficial (0–15 cm) soil sample in each plot. After being air-dried and 2-mm sieved, soil samples were analyzed for the following variables: pH in KCl, organic carbon, total nitrogen, available phosphorus, exchangeable cations (Ca, Mg, Na, K), and texture (sand, silt, and clay). Further details on soil analyses can be found in Guèze et al. (2013).

To capture the influence of disturbance in areas close to plots, we use three estimates: (1) distance from the plot to the closest logging area, (2) distance from the plot to the closest village, and (3) landscape heterogeneity, measured as the extent of early-growth and degraded forest cover. To calculate the proportion of early-growth and degraded forest cover, we first defined 6-km circular buffers (including all the inventoried plots) from the center of each of the six villages. We then overlaid these buffers with the best land cover classification obtained by Paneque-Gálvez et al. (2013) to extract the percentages of early-growth and degraded forest. Calculations were performed in ArcGIS 10.

2.3.3. Cultural data

To collect data on cultural change, we surveyed the six Tsimane' villages during field campaigns in 2008–2009. Upon arrival to a village we obtained a list of all the households from the headman or a teacher. Free prior, informed, written consent was obtained from the Gran Consejo Tsimane' (the Tsimane' political authority), and informed oral consent was obtained from all participants. We interviewed 10 male household heads chosen at random from this list, or 25% of the household heads if the village had more than 40 households. We focused on male household heads because men use old-growth forests farther from the villages than women, as cultural barriers hinder women from walking deep into the forest (Huanca, 2008).

Individual interviews had two sections. First, we asked respondents their schooling level, their ability to speak Spanish -the national language-, and the number of times they had visited the closest market town over the last year, as a measure of market integration. Second, to obtain an independent individual measure of cultural change we asked respondents to report their self-perceived attachment to Tsimane' traditional values. We specifically asked respondents to rank their attachment to nine Tsimane' habits, traditions, rituals, and beliefs (Table A.1), encompassing important features of the Tsimane' culture (Huanca, 2008). To help people conceptualize their attachment or detachment, we used a drawing consisting of two poles: a "traditional" scene representing a Tsimane' wearing traditional clothes in a traditional house and a "modern" scene representing Tsimane' in a town, using bicycles. A five-step ladder joined the two poles and – for each of the nine questions – respondents were asked to position their finger on the rung depending on whether they felt closer to one image or the other. Since each rung of the ladder had an implicit number from zero to four, we could code the answer of the respondent after the respondent had pointed to the rung. The direction of the ladder was randomized before the interview. Since each rung of the ladder had an implicit number from zero to four, we could code the answer of the respondent after the respondent had pointed to the rung. The direction of the ladder was randomized before the interview.

2.4. Data analysis

We calculated tree Fisher's Alpha diversity index of each plot. This index provides a reliable estimation of the whole alpha diversity in plots (i.e., relating to species richness) and is independent of total sample size (Condit et al., 1998; Magurran, 2004).

We calculated the Cronbach's alpha to test the internal consistency between answers for the nine "ladder" questions. We then assumed that all the questions measured parts of the same construct (see Results section), and summed the values of the nine questions to obtain an individual score of attachment to Tsimane' traditional values. The score ranged from 0 (highest attachment) to 36 (lowest attachment), and we named it "acculturation". Then, for each village, we calculated the average value of acculturation as a proxy for cultural change.

Variables used as controls included (1) plot edaphic variables, (2) plot disturbance, i.e. distances to human activities, and (3) village-level variables, i.e. schooling, integration into the market economy, and the overall village disturbance (degraded forest cover). We calculated schooling and integration into the market as the village mean of informants' values.

We analyzed the relation between Fisher's Alpha and acculturation using multivariate regression models. The measure of tree diversity in one village was based on the average of eight plots. Since analyzing the relation at the village level with a statistically significant number of villages would have required a high number of plots, and we lacked the resources for such intensive inventories, we did analyses at the plot level, repeating village information for each plot.

We ran two sets of regressions to test for the robustness of the relation between acculturation and tree diversity. Due to our reduced sample (48 plots), in each regression we only included up to three control variables. We ran the regressions with the logarithm of acculturation to correct for a non-normal distribution. In the first set (main models) we regressed Fisher's Alpha against acculturation, including (1) only edaphic controls, i.e. the amounts of total *N* and available *P*, two of the limiting edaphic factors for plant growth that have shown an association with alpha diversity in the Amazon (Laurance et al., 2010); (2) only plot disturbance controls, i.e. distances to village and to logging areas; (3) only village controls, i.e. degraded forest cover, travel to the market and village size; and (4) the most significant controls – with the lowest *p*-value in models 1, 2, and 3- for edaphic (total *N*), disturbance (distance to village) and village-level (degraded forest cover). In the second set of analyses, we regressed (1) Fisher's Alpha against log acculturation, including other edaphic controls (C/*N* ratio, sum of cations, sand amount, pH); (2) Fisher's Alpha against log schooling, another proxy of cultural change; and (3) other measures of forest tree diversity and structure (Shannon index, basal area, and tree density) against acculturation. Additionally, we tested if tree diversity was related to within-village acculturation variability using Pearson's correlation between Fisher's Alpha and the standard deviation of acculturation; we also regressed Fisher's Alpha against the SD of acculturation.

A scatterplot of Fisher's Alpha against acculturation showed an inverse U-shape; therefore all regressions were run with a quadratic term of the explanatory variable to capture a nonlinear relation. We used ordinary least squares (OLS) regressions with robust standard errors, clustered by village. Fisher's Alpha values were calculated using R 2.12.0 and regressions were performed using Stata 13.1.

3. Results

Mean Fisher's Alpha index in the 48 plots was 24.69, displaying high variation within and across villages (Table 1). The maximum tree diversity was observed for a plot in Uvasichi ($\alpha = 44.30$), although one plot in the same village had one of the lowest values ($\alpha = 15.98$). Overall, the lowest tree diversity was found in plots around the village of Triunfo ($\alpha = 17.58 \pm 1.21$).

A total of 86 informants in the six villages were interviewed with an average of 14.3 interviews per village. Result from Cronbach's alpha coefficient suggested an internal consistency of the cultural change measure, although the alpha value was below the standard 0.80 ($\alpha = 0.68$). On a range from 0 to 36, the mean village acculturation score was 9.69 (±5.13), yet we could observe differences in the range of individual acculturation scores within each village. For example, the acculturation score ranged from 3 to 25 (the highest value in our sample) in the village of Misión Fátima, but only from 0 to 11 in the village of Cuchisama. To give a more intuitive explanation of the values of acculturation, the village with the highest acculturation (11.4), Triunfo, is about 40 km away from the closest market town, but only 12 km from a major national road (Fig. 1), and one out of three respondents was fluent in Spanish. In turn, the village with the lowest acculturation (6.7), Cuchisama, is about 125 km away from the closet market town after a three-day canoe trip and has no fluent Spanish speakers.

The scatter plot between Fisher's Alpha index and acculturation resembled an inverted U (Fig. 2). Tree diversity increased with acculturation, reaching a maximum in the village of Uvasichi (acculturation value of 10.4), and then decreased for higher levels of acculturation.

The Fisher's Alpha index in plots in the village commons was significantly associated with the average level of acculturation in a village and its squared term (Table 2). Furthermore, this association remained significant independently of the controls used in the model (columns [1] to [3]). The coefficients in column [4] implied that an increase in the average level of acculturation in a village was associated with an increase of the alpha diversity of plots around that village, reaching an inflexion point for an average value of acculturation of 8.84. Only the village of Cuchisama had a value of acculturation below 8.84. Beyond this inflexion point,

Table 1
Definition and descriptive statistics of the variables used in the regression analysis.

	Variable	Description	*N*	Mean	SD
Outcome variables					
Plots ecological variables	Fisher's Alpha index	Fisher's logseries index	48	24.69	7.88
	Shannon	Shannon diversity index	48	3.31	0.33
	Basal area	Overall basal area of all tree species per plot ($m^2\ ha^{-1}$)	48	47.65	13.89
	Tree density	Number of trees (diameter ⩾ 2.5 cm)	48	175.6	33.8
Explanatory variables					
Villages cultural variables	Acculturation	Village average acculturation (i.e., cultural change) score, measured with an index that ranges from 0 (minimum acculturation) to 36 (maximum acculturation). Index calculated based on the answers of 86 informants.	6	9.69	5.13
	Schooling	Village average of the highest school grade reached by the surveyed individuals (ranges from 0 to 13). Average of the answers of 86 people	6	2.51	2.91
Control variables					
Plot edaphic variables	*C/N*	Ratio between total organic carbon and total nitrogen content of the plot	48	9.17	2.73
	N	Total nitrogen content (%)	48	0.14	0.06
	P	Available phosphorus content ($mg\ kg^{-1}$)	48	5.84	3.86
	Sand	Sand proportion (%) in a three-fraction texture (sand, silt, and clay)	48	35.02	19.51
	Sum of cations	Sum of exchangeable calcium, magnesium, sodium and potassium ($cmolc\ kg^{-1}$)	48	6.96	4.03
	pH	Soil pH	48	4.38	0.60
Plot disturbance	Distance to logging	Linear distance from the plot to the closest currently used or recently abandoned logging camp (km)	48	1.49	0.89
	Distance to village	Linear distance from the plot to the closest Tsimane' village (km)	48	2.71	1.06
Village-level variables	Village size	Number of households in the village	6	47.83	21.63
	Travel to market	Village average number of times informants traveled to the closest market town in the 12 months before the interview. Average of the answers of 86 people	6	9.53	11.70
	Early-growth and degraded forest cover	Percentage of early-growth and degraded forest (including early-growth secondary forest, small agricultural plots with fruit trees and remnant scattered trees, and selectively logged forest areas) in a 6-km radius around the village	6	14.99	9.43

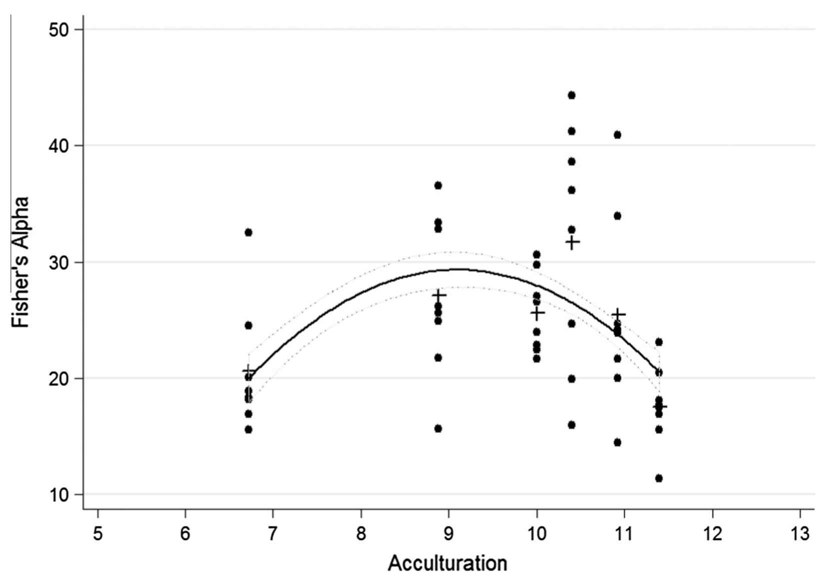

Fig. 2. Scatter plot of Fisher's Alpha index in 48 0.1-plots of the territory of six Tsimane' villages (Bolivian Amazon), against the village average acculturation score. $r = 0.45$. Dotted lines represent 95% confidence interval; plus (+) represent village average Fisher's Alpha.

an increase in acculturation was associated with a decrease in tree diversity in the plots. We could find no correlation between Fisher's Alpha and the SD of acculturation ($r = 0.1779$, $p = 0.2271$); moreover, the regression between Fisher's Alpha and a quadratic term of the SD of acculturation proved insignificant (results not shown).

Additional analysis (Table 3) provided three main results. First, the relation between tree diversity and acculturation was robust to changes in edaphic controls. In the two models with different edaphic controls (columns [1] and [2]), Fisher's Alpha remained significantly associated with acculturation. Second, Fisher's Alpha was not significantly associated with cultural change, as proxied by the average level of schooling in a village (column [3]). Third, acculturation was associated with another diversity index (Shannon index, column [4]) but not with forest structure variables (basal area and total tree density, columns [5] and [6]).

4. Discussion

4.1. Cultural change, management practices and tree diversity

Our results suggest that the degree by which the Tsimane' feel attached to traditional values relates to tree alpha diversity in the

Table 2
Multivariate OLS regression results between Fisher's Alpha in 0.1-ha plots (outcome), acculturation (explanatory), and control variables in Tsimane' villages, Bolivian Amazon ($N = 48$). Four models with different control variables are shown.

Outcome: Fisher's Alpha	[1] Edaphic controls	[2] Plot disturbance controls	[3] Village controls	[4] Most significant controls
Explanatory				
Log (acculturation)	334.7[*] (132.6)	541.1[*] (205.1)	327.6[***] (0.00)	361.4[*] (126.5)
Log (acculturation) (squared)	−76.2[*] (30.5)	−124.6[*] (48.2)	−75.8[***] (0.00)	−83.9[*] (29.9)
Plot edaphic				
N	−34.1 (24.5)	[a]	[a]	−34.9 (16.0)
P	−0.1 (0.4)	[a]	[a]	[a]
Plot disturbance				
Distance to village	[a]	0.0002 (0.001)	[a]	0.0006 (0.001)
Distance to logging	[a]	−0.001 (0.001)	[a]	[a]
Village-level				
Early-growth and degraded forest cover	[a]	[a]	0.50[***] (0.00)	0.17 (0.18)
Travel to market	[a]	[a]	−1.17[***] (0.00)	[a]
Village size	[a]	[a]	−0.09[***] (0.00)	[a]
Constant	−334.9 (142.2)	−556.5 (217.8)	−318.6[***] (0.00)	−360.2 (132.1)
Adjusted R^2	0.15	0.14	0.26	0.16

Notes: Robust standard errors with clustering by villages in parenthesis.
[*] Significance level: 5%.
[**] Significance level: 1%.
[***] Significance level: 0.1%.
[a] Variables intentionally left out.

Table 3
Robustness analysis: multivariate OLS regression between tree diversity and structure measured as different indices (dependent variables) and environmental and cultural variables ($N = 48$).

Outcome:	[1] Fisher's Alpha	[2] Fisher's Alpha	[3] Fisher's Alpha	[4] Shannon index	[5] Basal area	[6] Total tree density
Explanatory						
Log (acculturation)	382.1[**] (88.0)	450.1[*] (157.4)	[a]	13.3[*] (4.49)	−285.2 (463.5)	−595.2 (495.3)
Log (acculturation) (squared)	−86.7[**] (21.1)	−102.3[*] (37.1)	[a]	−3.0[*] (1.0)	64.3 (108.3)	111.7 (123.1)
Log (schooling)	[a]	[a]	−0.1 (2.1)	[a]	[a]	[a]
Log (schooling) (squared)	[a]	[a]	2.8 (2.8)	[a]	[a]	[a]
Control						
C/*N*	0.01 (0.52)	[a]	[a]	[a]	[a]	[a]
Sum of cations	−0.6 (0.3)	[a]	[a]	[a]	[a]	[a]
Sand	[a]	0.08 (0.08)	[a]	[a]	^	[a]
pH	[a]	−0.5 (1.2)	[a]	[a]	[a]	[a]
N	[a]	[a]	−51.3[*] (16.4)	−1.6 (0.8)	63.7 (60.6)	−229.8[*] (83.0)
Distance to village	[a]	[a]	0.0005 (0.001)	0.00006 (0.00003)	−0.002 (0.002)	0.003 (0.006)
Degraded forest cover	[a]	[a]	0.1 (0.2)	0.006 (0.003)	0.14 (0.19)	2.06[*] (0.71)
Constant	−389.2[*] (90.6)	−467.5[*] (165.8)	26.8[***] (5.9)	−11.3 (4.9)	355.9 (498.0)	940.2 (513.2)
Adjusted R^2	0.19	0.14	0.15	0.22	0.04	0.30

Notes: Robust standard errors with clustering by village in parenthesis.
[*] Significance level: 5%.
[**] Significance level: 1%.
[***] Significance level: 0.1%.
[a] Variables intentionally left out.

forest surrounding the village where they live, independently of other socio-economic factors such as population density or frequency of travel to market towns. This finding opens up the question of the pathways explaining how cultural change might be related to tree diversity. We propose that this association is mediated by traditional ecological knowledge (TEK). TEK has been defined as "a cumulative body of knowledge, practice and belief, evolving by adaptive processes and handed down through generations by cultural transmission, about the relationship of living beings (including humans) with one another and with their environment" (Berkes et al., 2000, p. 1252). Cultural change may be associated with the three components of this system (knowledge, practices, and believes), which in turns might relate to forest diversity. While some studies have reported an association between cultural change, TEK and indigenous practices (Reyes-García et al., 2007, 2014b; Shen et al., 2012), they do not address how such associations might actually relate to biodiversity.

Within the Tsimane' context, we can see, at least, two plausible mechanisms that help explain the link between cultural change and tree diversity. First, cultural change might lead to modifications of the beliefs that were an integral part of the Tsimane' TEK system. For example, as in other groups (Berkes et al., 2000), taboos and rituals were strong social mechanisms governing Tsimane' traditional management practices and behaviors. As Tsimane' engage more frequently in activities with outsiders, such as loggers or cattle ranchers, they are more exposed to different ideas and values, that might ultimately modify behavior. Such is the case of sacred groves. Tsimane' sacred groves are important for tree diversity as they contain emergent tree species such as *Ceiba pentandra* or *Terminalia oblonga*, often considered taboo. Such areas were typically protected from any type of management, or even human presence, because they shelter forest spirits who can harm humans (Huanca, 2008). Due to contact with outsiders who do not fear forest spirits, some Tsimane' have lost fear of forest spirits, resulting in the modification of management practices. Changes in the beliefs may affect not only tree diversity in sacred groves but also other areas of the forest. For example, like the outsiders, the Tsimane' no longer see the trees as living beings, which leads to changes in their behavior, such as the intensification of commercial logging practices.

The second mechanism that helps explain the link between cultural change and tree diversity relates to wild edibles. As many indigenous peoples of tropical forests, the Tsimane' extensively manage fruit trees across the forest, facilitating the growth of some species, transporting seeds and seedlings, and often cutting trees to harvest the fruits. As for the beliefs, culturally exposed people may loose the knowledge of which species to manage or how to manage the species, having an impact on tree diversity in the forest.

Since the Tsimane' – and their traditions- are closely inter-related with their environment, the association between cultural change and tree diversity could be interpreted in both causal ways. Hence, while we have discussed above the effects that cultural change may have on tree diversity, we should not exclude the possibility of tree diversity affecting cultural change as well.

4.2. Can cultural change relate to disturbance?

The relation between tree alpha diversity and cultural change was U-shaped, which challenges our assumption that the two variables would be linearly related. This association, however, finds support in the intermediate disturbance hypothesis (Connell, 1978). While anthropogenic disturbances have many forms and intensities and can either modify natural disturbance regime or replace natural disturbances (White and Jentsch, 2001), Balée (2006) proposed that, within the gradient from no management to a Western-type management, indigenous practices, through burning, settlement, or tree cultivation, generate an intermediate level of disturbance. Our results suggest that indigenous cultural change, by means of TEK and practices, relates to the level of disturbance. Balée's hypothesis among cultural systems seems to fit a lower scale of analysis, i.e. *within* the Tsimane' cultural system. The intermediate disturbance hypothesis is set in terms of functional groups (Molino and Sabatier, 2001), which implies that in intermediately acculturated villages, the co-occurrence of several guilds of species would increase overall species richness. In less acculturated villages, anthropogenic disturbance would be too weak to result in this co-occurrence, whereas in more acculturated villages, species richness decreases with cultural change, suggesting that the management becomes closer to a Western-type management, possibly through the adoption of practices such as cash-crop production and commercial logging by the Tsimane' (Vadez et al., 2008).

However, since we placed our plots in old-growth forests avoiding large canopy gaps, interpreting implications in terms of disturbance needs to be handled with care. Our regression models show that including degraded forest cover (e.g. forests in early successional stages) does not affect the relation between alpha diversity and cultural change. Therefore, indigenous practices do not seem to affect landscape heterogeneity (also see Perez-Llorente et al., 2013), and seem to be rather non-destructive, smooth modifications of the forest. Moreover, our data show that although tree diversity is significantly associated with cultural change, forest structure is not. This suggests that the changes in alpha diversity associated with cultural change are important enough to be detected in terms of species richness, but subtle enough not to be detected in terms of forest structure (Wiersum, 2004). Peres et al. (2006) have highlighted the importance of cryptic disturbances, i.e. non-structural disturbances. As other indigenous groups, the Tsimane' modify species richness through a *tolerant* management (Anderson, 1990) that does not affect structure but rather seed dispersal, e.g. enrichment planting or the management of non-timber forest products (Byg et al., 2007; Lawrence et al., 2005), and hunting (Peres et al., 2010). It is possible that forest composition is associated with these types of below-canopy disturbances, in turn associated with cultural change, but further analyses are needed to identify the species affected.

We discuss two main caveats of this work before concluding. First, our samplings were dissimilar for ecological and cultural variables, reflecting the challenge to relate individual cultural change measures to the biodiversity of a commonly managed forest. Ideally, commonly managed areas would require the collection of social data at the village –rather than individual– level (Shen et al., 2012). However, obtaining a reliable measure of tree diversity in one village requires a great sampling effort. Therefore, we based our regression analyses at the plot level, although we acknowledge a lack of statistical power and a simplification of the measure for cultural change. Second, land use history and past cultural change patterns across villages might have affected tree diversity in a way we cannot capture through a simple glimpse of the current situation, although the cultural change gradient we study here intended to solve this issue. Further research should fill these methodological gaps by studying fully comparable ecological and cultural samples, and by studying the relation between cultural change and biodiversity at different scales, either smaller (e.g. village-level) or larger (increasing the ecological sampling effort).

4.3. Conclusion

The present study improves our understanding of how biodiversity is shaped both by ecological and human factors (Byg et al., 2007) and how social changes among indigenous people relate to changes on ecological processes (Lu, 2007). A major implication of our work is that the study of changes in forest diversity considering only the overall forest structure (e.g. through satellite images) misses subtle compositional changes and leads to misunderstanding the pathways of these changes. Field plot inventories thus have an intrinsic value that allows estimating fine-scale forest diversity changes.

This study also provides important insights for the debate on indigenous management and biocultural diversity conservation (Hames, 2007; Smith and Wishnie, 2000) as it highlights the importance of taking into account both human and ecological factors when delimiting priority areas for conservation, as it is mostly the case in European systems (Neumann, 2014). Contrary to what we expected, we found that cultural change is not necessarily associated to a loss o biodiversity. The finding implies that biological conservation in the Amazon could be ensured in the territories of communities that are moderately engaged in national societies. Since such communities are common place in most tropical areas, and since community-based management seems to have a great potential for biocultural diversity conservation (Porter-Bolland et al., 2012), our results support further development of this type of incentives, especially in integrated communities that often fail to obtain land rights over densely forested areas. As the conservation schedule in the Amazon becomes tighter, keeping forests managed by indigenous peoples seems to be, to some extent, a viable strategy to support biodiversity conservation.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.03.026.

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