Original Research Communications

Nutrition transition in 2 lowland Bolivian subsistence populations

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ABSTRACT

Background: Traditional diets are often credited for the robust cardiometabolic health of subsistence populations. Yet, rural subsistence populations are undergoing nutrition transitions that have been linked to the increase in chronic noncommunicable diseases. Few studies have presented detailed dietary estimates in transitioning populations.

Objectives: We aimed to *1*) characterize and compare dietary profiles of 2 neighboring subsistence populations in Bolivia who vary in market integration and *2*) identify dietary factors contributing to low cardiovascular disease risk.

Design: We used a mixed longitudinal design to estimate nutrient intake via 24-h recall and dietary questionnaires among 1299 Tsimane (aged 30–91 y) and 229 Moseten (aged 30–84 y) men and women. We constructed population-level estimates of energy intake, dietary diversity, and nutrient shortfalls and analyzed dietary changes over time and space using multilevel models. Last, we compared Tsimane and Moseten dietary profiles with those of Americans (NHANES).

Results: The Tsimane diet was characterized by high energy (2422–2736 kcal/d), carbohydrate (376–423 g/d), and protein (119–139 g/d) intakes; low fat intake (40–46 g/d); and low dietary diversity relative to the average US diet. Most calories (64%) were derived from complex carbohydrates. Total energy and carbohydrate intake increased significantly during the 5-y study, particularly in villages near market towns. Tsimane consumption of food additives (lard, oil, sugar, salt) increased significantly [sugar (15.8 g person^{-1} d^{-1}) and oil (4.9 mL person^{-1} d^{-1})] between 2010 and 2015. The more-acculturated Moseten consumed substantially more sugar (by 343%) and oil (by 535%) than the Tsimane.

Conclusions: A high-energy diet rich in complex carbohydrates is associated with low cardiovascular disease risk when coupled with a physically active lifestyle. A transition away from a high-fiber and low-fat, low-salt, and low-processed-sugar diet is a salient health risk for transitioning populations. Evidence of a nutrition transition in Bolivia parallels trends of increasing body fat and body mass index, which suggests that a low prevalence of cardiovascular disease may not persist. *Am J Clin Nutr* 2018;108:1–13.

Keywords: nutrition transition, cardiovascular disease, dietary recall, subsistence populations; traditional diet

INTRODUCTION

A nutrition transition describes dietary and nutritional changes driven by economic, social, and demographic shifts (1, 2). The most common contemporary nutrition transition is from a diet of relatively diverse low-fat, low-salt, high-fiber foods acquired via physically intensive labor to a low-diversity, low-fiber diet of refined and processed foods high in calories, fat, salt, cholesterol, and sugar. In early transitional stages these changes can improve food security and health, but they have also been linked to the increase in chronic noninfectious diseases [e.g., obesity, atherosclerosis, type 2 diabetes (T2D)] (3–5). A detailed examination of the nutritional profiles of transitioning populations can illuminate risk factors and provide further evidence of links between diet and preventable diseases.

The Tsimane are forager-horticulturalists of the Bolivian Amazon who are experiencing increased access to market foods in tandem with greater development and cultural integration with broader Bolivian society. Previous studies have shown that the Tsimane have the lowest levels of coronary artery disease ever recorded (6), a minimal prevalence of hypertension and T2D (<1.5%), and low total and LDL cholesterol (<2% have concentrations >240 mg/dL and >130 mg/dL, respectively), despite a relatively high average BMI (kg/m^2; 24.1) (7, 8) (**Supplemental Table 1**). To date, however, there has been no systematic analysis of Tsimane diets in relation to cardioprotective factors or nutritional transitions.

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Supplemental Tables 1–10, Supplemental Figures 1–5, and Supplemental Methods are available from the "Supplementary data" link in the online posting of the article and from the same link in the online table of contents at https://academic.oup.com/ajcn/.

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Abbreviations used: FVS, food variety score; H, Shannon-Wiener index; IDDS, individual dietary diversity score; LOSS, lard, oil, salt, sugar; TEE, total energy expenditure; TEE_{50}, half of the expected daily total energy expenditure; T2D, type 2 diabetes.

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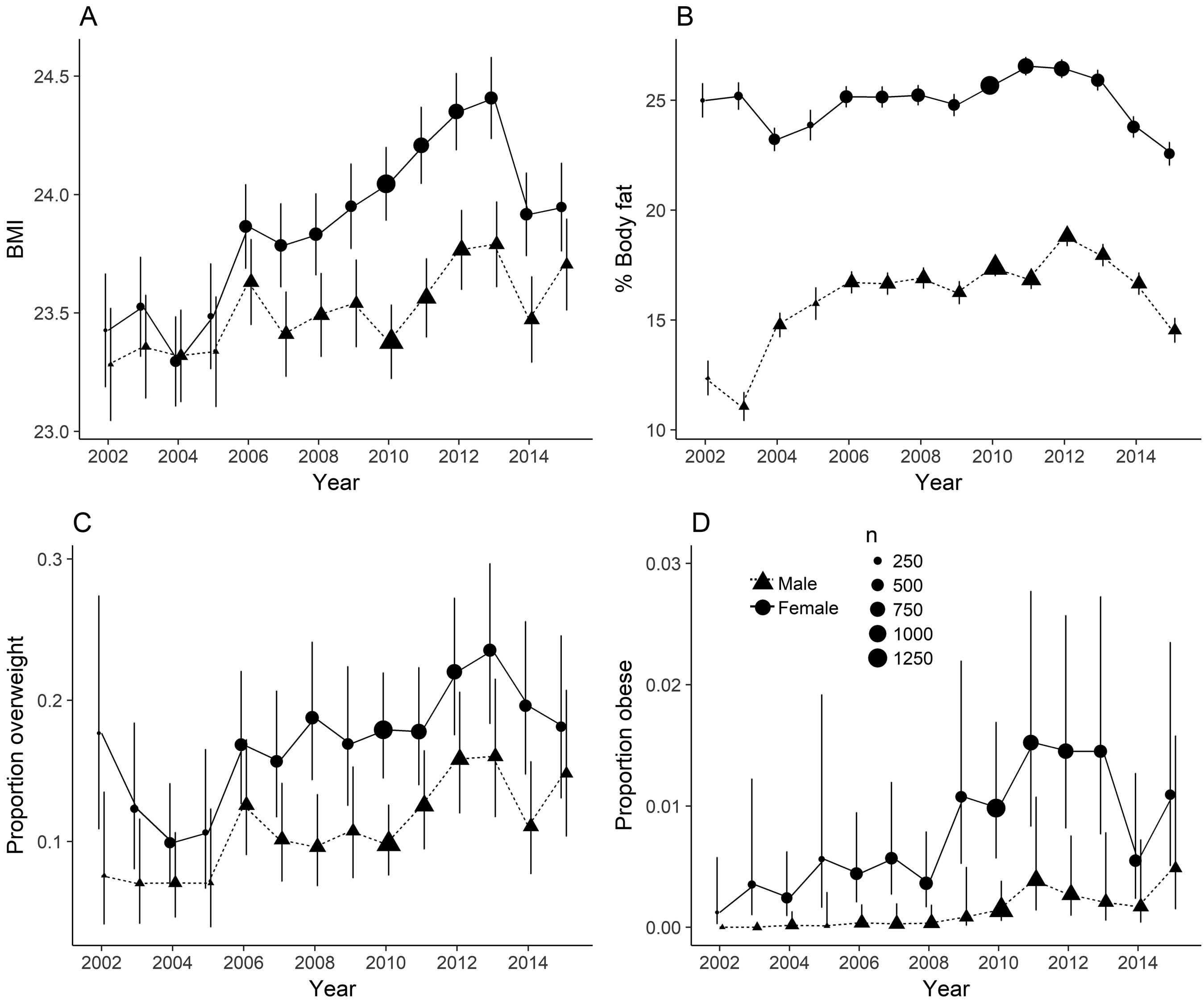

FIGURE 1 Tsimane population-level temporal trends in BMI (A), percentage body fat (B), proportion of the population who is overweight (kg/m^2; 30 > BMI > = 25) (C), and proportion who are obese (BMI ≥ 30) (D). Values represent predicted values from linear mixed effects (A, B) or generalized linear mixed effects (C, D) models of the dependent variable as a function of age, age-squared, sex, season, and year (categorical), including individual and community as random effects. Points and error bars represent means (95% CIs). Decreases beginning in 2014 could represent the effect of a major flooding event in the region.

We expect that the Tsimane diet will share similarities with, but also diverge from, hunter-gatherer diets (9) and other diets associated with lower cardiovascular disease incidence [e.g., Okinawan diet (10), Mediterranean diet (11), Dietary Approaches to Stop Hypertension (DASH) (12)]. For example, we expect low amounts of (saturated) fat intake but high caloric (and especially unrefined carbohydrate) intake. Macronutrient content could reflect the wide range observed across cardioprotective diets (13, 14). Dietary diversity should be greater than diets in fully market-integrated populations but lower than among foragers (15). Furthermore, in our 16 y of conducting research with the Tsimane, we have observed village variance in access to market foods and increases in average body fat and BMI (**Figure 1**). We therefore predict that intakes of total calories, refined sugar, salt, and fat have increased over time, particularly in villages located closer to market towns.

Finally, it has been suggested that periods of food scarcity were common throughout human evolutionary history (16), a pattern with possible health implications (17). Yet, the extent to which shortfalls characterize the diets of hunter-gatherers or horticulturalist-foragers like the Tsimane and Moseten is unclear.

To better understand the diet of this heart-healthy population, we present 5 y of dietary recall data ($n = 2496$) and food-additive intake interviews ($n = 1419$) for the Tsimane collected over 78 villages with variable market accessibility. Furthermore, we estimated dietary intake from the US NHANES (18) and for the Moseten, a genetically and ethno-linguistically related Bolivian population who live in close proximity to Tsimane but who began acculturation into broader Bolivian society decades earlier.

Collectively, these data allow us to directly compare the diets of Tsimane (early stages of nutrition transition) with populations at midstages (Moseten) and late stages (United States) of transition and to address the following questions:

1) Do Tsimane diets conform to expectations for a population with minimal atherosclerosis and T2D?
2) How do Tsimane and Moseten diets compare with US daily recommended intakes?
3) How is the Tsimane diet changing over time and with increasing access to market goods?

METHODS

Study populations

Tsimane and Moseten are neighboring indigenous forager-horticulturalist populations residing in the Beni and La Paz Departments of lowland Bolivia, respectively (**Supplemental Figure 1**). The economy of both populations involves a combination of hunting, fishing, gathering of wild foods, and swidden (slash-and-burn) horticulture (primarily plantain, rice, manioc, and corn), as well as intermittent wage labor. Despite sharing a language and close genetic ancestry, Tsimane and Moseten differ in their level of acculturation and market integration due to historical differences in their interactions with outsiders (19, 20). Tsimane remained largely separated from external social influences until the 1950s, when evangelical and Catholic missionaries set up in the area, and the 1970s, when roads connected Beni Department to La Paz, bringing highland migrants into the rural lowlands. In contrast, the first permanent mission was built in Moseten territory in 1804, putting the Moseten on a path toward greater integration with broader Bolivian society than Tsimane (20). Thus, compared with Tsimane, who remain relatively isolated and without modern amenities, Moseten speak fluent Spanish and have greater access to roads, vehicles, electricity, public health infrastructure, education, and market goods. For more details on the study populations, see "Study populations" section of **Supplemental Methods** and references 19 and 20.

Data collection

Data were collected as part of the Tsimane Health and Life History Project, a panel study of health, aging, and behavior that began in 2002 (19). A mobile team of medical personnel and bilingual (Spanish-Tsimane) research assistants conducted clinical health assessments and collected demographic, socioeconomic, dietary, and anthropometric data among a majority of Tsimane villages annually (21). Since 2015, data collection has been extended to Moseten villages to permit cross-population comparisons.

Participants were recruited from 78 Tsimane and 4 Moseten villages and were aged ≥30 y (**Supplemental Table 2**, **Supplemental Figure 2**). In each village, we attempted to sample all residents of appropriate age, and we typically achieved 88–95% participation among those present in the community. Some Tsimane, but not Moseten, were sampled longitudinally over the study period (maximum = 9, median = 2; dietary recall interviews).

Dietary recall

From February 2010 to September 2015 (Tsimane) and from June 2015 to July 2016 (Moseten), we conducted 24-h dietary recall interviews in study villages. We obtained 2496 dietary recall records (men, $n = 1219$; women, $n = 1279$) composed of 19,640 food-consumption events for the Tsimane and 229 records (men, $n = 120$; women, $n = 109$) composed of 2265 events for the Moseten. Each adult participant was interviewed about all food items or beverages consumed the previous day and, for each item, the time it was consumed, mode of preparation (e.g., cooked in oil, in a stew with other ingredients, salted, raw), and the estimated amount. For further details, see Supplemental Methods.

To facilitate direct dietary comparison with a Western (US) population, we present data from the 2013–2014 NHANES dietary database [Online Supporting Material; CDC and National Center for Health Statistics, 2014 (16)]. Dietary recall results were also compared with previous dietary estimates based on systematic spot observation of "eating hits" conducted from 2002 to 2005 (22) to assess potential recall bias in self-reports. We observed close agreement between methodologies (differences in daily caloric intake: 8–13%; differences in macronutrient intake: 10–32%) (**Supplemental Table 3**).

Lard, oil, salt, and sugar

One problem with 24-h dietary recall is the potential for omission of food additives. Thus, we quantified the consumption of 4 major food additives in the Tsimane and Moseten diets—lard, cooking oil, salt, and sugar (LOSS)—using a separate instrument that queries about the quantity of each additive acquired through purchase, gifting, or exchange in the past month and the quantity consumed within the household in the past month.

We conducted 1419 LOSS interviews with Tsimane ($n = 688$ men, $n = 731$ women) and 231 interviews with Moseten ($n = 124$ men, $n = 107$ women). Questions were asked at the household level, and all values were divided by household size to generate per-capita estimates. Comparison of results from the 2 complementary LOSS survey questions showed high consistency (**Supplemental Table 4**), and thus we only present analyses of LOSS from quantities obtained.

Dietary diversity scores

We explored several indexes for quantifying dietary diversity, including food variety score (FVS) (23), individual dietary diversity score (IDDS) (24), and the Shannon-Wiener index (H). These diversity indexes represent the number of unique food items consumed, the number of WHO food categories consumed, and a composite measure of the number of food groups and their relative amounts consumed, respectively (see "Dietary diversity scores" in **Supplemental Methods**).

Shortfalls in nutrient intake

To assess the extent of daily shortfalls in nutrient intake, we generated empirical cumulative frequency distributions of daily intakes and examined the shapes of those curves. This approach is appealing because it permits assessment of food security without relying on arbitrary cutoffs and can be applied to any aspect of dietary intake (energy, macronutrients, micronutrients, diversity indexes, etc.). We also examined the proportion of each population meeting half of the expected daily total energy expenditure (TEE_{50}) for a given sex using direct estimates of TEE from a previous study that yielded values of 3065 ± 422 and 2186 ± 366 kcal/d (mean ± SD) for men and women, respectively (9). TEE_{50} is thus equal to 1533 kcal for men and 1093 kcal for women (we assumed Moseten TEE was the same).

Statistical analysis

Primary outcome variables were energy, macronutrient, and LOSS intakes. Secondary outcomes were BMI, body fat percentage, and dietary diversity. All analyses were exploratory.

We developed a statistical model of Tsimane dietary intake to assess changes over time, influence of market accessibility [residential distance to San Borja (kilometers)], and their interaction, controlling for sex, body mass (kilograms), education (years of schooling), wealth (summed modern and traditional assets, in Bolivianos), and season (wet compared with dry), with individual- and community-level clustering given the repeated-measures study design. We specified a multilevel linear model using the following form:

$$\begin{aligned} D_{ijk} = {} & B_0 + B_1 \left(\text{age}_{ijk}\right) + B_2 \left(\text{sex}_{ijk}\right) + B_3 \left(\text{weight}_{ijk}\right) \\ & + B_4 \left(\text{distance to town}_{ijk}\right) + B_5 \left(\text{time}_{ijk}\right) \\ & + B_6 \left(\text{time}_{ijk}\right) \left(\text{distance to town}_{ijk}\right) \\ & + B_7 \left(\text{education}_{ijk}\right) + B_8 \left(\text{wealth}_{ijk}\right) + B_9 \left(\text{season}_{ijk}\right) \\ & + \gamma_j + \delta_k + \varepsilon_{ijk} \end{aligned} \tag{1}$$

Where i represents a 24-h recall of individual j in village k. D_{ijk} represents our dietary variables: total energy (kilocalories), protein, fat, and carbohydrates. The model included 2 random intercept terms, γ_j and δ_k, which account for repeated samples on an individual and within a community. Models of LOSS were analyzed with generalized linear mixed models with Tweedie error distributions and log link functions to account for a point mass at zero followed by a right-skewed continuous distribution of outcomes. Due to missing data on wealth (∼50% of observations), models were conducted with and without wealth (Supplemental Table 9). All statistical analyses were conducted in R version 3.4.3 (25).

RESULTS

What do Tsimane and Moseten eat?

The Tsimane diet consisted primarily of 26 types of cultigens (61.9% of average daily calories/person), 43 species of fish (15.6%), 32 species of wild game (6.1%), meat from domesticated animals (7.5%), 15 varieties of wild fruit and vegetables (0.7%), and 17 types of market foods (8.1%) (**Supplemental Table 5**). Main horticultural staples included plantains (60.2% of cultigen calories), rice (18.8%), manioc root (14.0%), and corn (5.2%). Leading game species included collared peccary (24.6% of game calories), paca (12.9%), coatimundi (10.5%), gray brocket deer (9.3%), Brazilian tapir (5.3%), and howler monkey (4.7%). Primary fish included *Prochilodus nigricans* (38.3% of total fish calories), *Hoplias malabaricus* (11.2%), *Curimatella meyeri* (7.9%), and *Pseudoplatystoma fasciatum* (6.3%). Main market foods included pasta (55.4% of market-derived calories), wheat flour (16.9%), bread (12.2%), and sugar (11.6%).

The Moseten diet differed from the Tsimane diet by greater reliance on market and domesticated foods and less reliance on wild fish and game (**Supplemental Table 6**). It consisted of 30 cultigens (46.5% of total daily calories), 12 domesticated meat items (23.8%), 26 market-derived items (19.5%), 11 fish species (5.0%), 7 wild game species (3.7%), and 7 wild fruit (1.0%). Notable population-level differences included greater Moseten intakes of bread, chicken, beef, potatoes, and a variety of soups.

Total energy and nutrient intake across populations

Table 1 shows average daily intakes of macro- and micronutrients consumed by sex for Tsimane and Moseten adults, together with values from the 2013–2014 US NHANES survey.

Total energy intake

Tsimane, but not Moseten, caloric intake exceeded that of Americans when controlling for age, sex, and individual [hierarchical linear model: $\beta(\text{SE})_{\text{Tsimane-US}} = 514(28)$ kcal ($P < 0.001$); $\beta(\text{SE})_{\text{Moseten-US}} = -139(71)$ kcal ($P = 0.05$); **Figure 2**]. Lower caloric intake among Moseten relative to Americans was primarily due to differences between men (Figure 2).

Macronutrients

Tsimane and Moseten protein intakes were elevated relative to NHANES, whereas fat consumption was ∼50% lower (Figure 2, Table 1). Tsimane carbohydrate intake was also significantly higher than that in NHANES (Figure 2). Older adults exhibited lower consumption across populations, particularly in the US and Tsimane populations. Compared with Moseten and US populations, the Tsimane diet contained a high proportion of carbohydrates (63–65% of total caloric intake) and low amounts of fat (15%) (**Figure 3**). Daily intakes of saturated, monosaturated, and polyunsaturated fats were 39–44%, 46–53%, and 42–44%, respectively, of US amounts (Table 1). Protein intake was higher among Tsimane (20–21%) and Moseten (20–23%) than Americans (16%). Sex differences in proportional macronutrient intake were minor in all populations.

Micronutrients

The Tsimane estimated intake of magnesium, potassium, and selenium far exceeded US and Moseten amounts. Tsimane daily fiber intake was also 1.5–2 times higher than US or Moseten intakes. Yet, intakes of dietary sodium, calcium, and vitamins E, D, and K among Tsimane and Moseten were much lower than among Americans (Table 1).

TABLE 1
Daily per-capita macro- and micronutrient intakes for Tsimane, Moseten, and US adults (NHANES) based on 24-h dietary recalls[1]

	Tsimane (2010–2015)		Moseten (2015–2016)		US NHANES (2013–2014)		Daily recommended intake[2]	
Nutrient	Men	Women	Men	Women	Men	Women	Men	Women
Energy, kcal	2736 ± 35	2422 ± 31	1990 ± 99	1916 ± 123	2409 ± 35	1794 ± 23	2600[3]	2000[3]
Carbohydrate, g	423 ± 7	376 ± 6	284 ± 15	258 ± 18	280 ± 4	216 ± 3	130	130
Protein, g	139 ± 2	119 ± 2	114 ± 8	114 ± 9	95 ± 1	69 ± 1	56	46
Total fat, g	46 ± 1	40 ± 1	40 ± 3	44 ± 4	93 ± 2	71 ± 1	20–35% of kcal	20–35% of kcal
Total sugar, g	112 ± 2	111 ± 2	55 ± 4[4]	56 ± 4[4]	120 ± 3	95 ± 2	—	—
Cholesterol, mg	475 ± 9[5]	425 ± 8[4]	391 ± 24[4]	427 ± 31[4]	339 ± 8	238 ± 5	—	—
Fiber, g	29 ± 0.6[4]	26 ± 0.5[4]	15 ± 0.9[5]	15 ± 1.4[5]	19 ± 0.4	16 ± 0.3	38	25
Minerals								
Calcium, mg	241[6] ± 7	239 ± 5	308 ± 18	291 ± 19	1029 ± 18	845 ± 12	1000	1000
Iron, mg	30 ± 0.5	25 ± 0.4	20 ± 1.1	14.6[6] ± 1.4	16 ± 0.2	13 ± 0.2	8	18
Magnesium, mg	557 ± 9[4]	494 ± 8[4]	329 ± 20[4]	307 ± 24[4]	343 ± 5	273 ± 4	420	320
Phosphorus, mg	1685 ± 25	1433 ± 22	1108 ± 67[4]	902[6] ± 83[4]	1564 ± 21	1182 ± 16	700	700
Potassium, mg	6226 ± 102[4]	5608 ± 86[4]	3694 ± 228[4]	3318 ± 235[4]	3016 ± 38	2356 ± 39	4700	4700
Sodium, mg	512[6] ± 110[4]	446[6] ± 87[4]	491[6] ± 67[4]	326[6] ± 77[4]	3982 ± 68	2942 ± 31	1500	1500
Zinc, mg	14.8 ± 0.3[4]	12.6 ± 0.2[4]	15.9 ± 1.5[4]	11.6[6] ± 1[4]	12.7 ± 0.1	9.2 ± 0.1	11	8
Copper, mg	1.5 ± <0.1[5]	1.4 ± <0.1[5]	1.1 ± 0.1[5]	0.8[6] ± 0.1[5]	1.4 ± <0.1	1.1 ± <0.1	0.9	0.9
Manganese, mg	1.7 ± <0.1[5]	1.4 ± <0.1[5]	1.6[6] ± 0.2[7]	1.5[6] ± 0.2[8]	—	—	2.3	1.8
Selenium, μg	175 ± 3.2[5]	152 ± 3.1[5]	82[6] ± 9[7]	78[6] ± 14[8]	134 ± 2	97 ± 1	55	55
Vitamins								
Vitamin C, mg	126 ± 2.9	114 ± 2.4	78[6] ± 16[4]	78[6] ± 14[4]	82 ± 2	76 ± 2	90	75
Thiamin, mg	1.4[6] ± <0.1	1.2[6] ± <0.1	0.7[6] ± 0.1[4]	0.6[6] ± 0.1[4]	1.8 ± <0.1	1.4 ± <0.1	1.2	1.1
Riboflavin, mg	2.1 ± <0.1[5]	1.9 ± <0.1[5]	1.4[6] ± 0.2[4]	1.2[6] ± 0.4[4]	2.5 ± <0.1	1.9 ± <0.1	1.3	1.1
Niacin, mg	30.6 ± 0.5	26.9 ± 0.4	24.7 ± 1.7[4]	19.6[6] ± 2.3[4]	30.6 ± 0.6	21.2 ± 0.3	16	14
Pantothenic acid, mg	5.4 ± 0.1[8]	4.8 ± 0.1[8]	2.2[6] ± 0.3[9]	2.5[6] ± 0.4[9]	—	—	5	5
Vitamin B-6, mg	3.2 ± <0.1[4]	3 ± <0.1[4]	2.3 ± 0.2[5]	2.3 ± 0.2[5]	2.6 ± 0.1	1.7 ± <0.1	1.3	1.3
Folate, μg	312[6] ± 17[4]	281[6] ± 11[4]	177 ± 11[5]	152[6] ± 22[5]	444 ± 7	351 ± 7	400	400
Vitamin B-12, mg	10.5 ± 0.2[4]	7.2[6] ± 0.2[4]	4.6[6] ± 0.5[5]	5.8 ± 0.5[5]	5.6 ± 0.1	3.9 ± 0.1	2.4	2.4
Vitamin A, RAEs (μg)	353[6] ± 64	341[6] ± 77	333[6] ± 131[4]	352[6] ± 67[4]	676 ± 12	599 ± 18	900	700
Vitamin E, mg	2.8[6] ± 0.1[8]	2.3[6] ± 0.1[8]	0.8[6] ± 0.2[9]	0.8[6] ± 0.2[9]	10.2 ± 0.3	8.5 ± 0.2	15	15
Vitamin D, μg	0[6] ± <0.1[7]	0[6] ± <0.1[7]	0.1[6] ± <0.1[9]	0[6] ± <0.1[7]	5.4 ± 0.3	4 ± 0.1	15	15
Vitamin K, μg	8.5 ± 0.2[8]	7.9 ± 0.1[8]	5.3 ± 2.2[9]	5.9[6] ± 0.7[9]	120 ± 5	131 ± 7	120	90
Lipids								
Saturated fat, g	11.3 ± 0.2[4]	9.9 ± 0.2[4]	10.4[6] ± 0.9[5]	9.1[6] ± 1.3[4]	29.9 ± 0.5	22.5 ± 0.3	<10% of kcal	<10% of kcal
Monounsaturated fat, g	15 ± 0.3[4]	12.9 ± 0.3[4]	14.1 ± 1[5]	10.7[6] ± 1.4[4]	32.5 ± 0.5	24.5 ± 0.4	—	—
Polyunsaturated fat, g	9 ± 0.2[4]	7.5 ± 0.2[4]	4.5[6] ± 0.6[5]	4.7[6] ± 1.1[4]	21.4 ± 0.5	17.1 ± 0.3	—	—
trans Fatty acids, g	0[6] ± <0.1[10]	0[6] ± <0.1[10]	0.2[6] ± 0.1[10]	0[6] ± <0.1[10]	—	—	—	—

[1]Values are means ± SEs unless otherwise indicated. RAE, retinol activity equivalent.
[2]Daily recommended intakes are values for men and women aged 31–50 y for Recommended Dietary Allowances or Adequate Intakes (26, 27).
[3]Estimated calorie needs for men and women aged 31–35 y who are "moderately active."
[4,5]Mean percentage of kilocalories consumed for which a given nutrient was unknown due to missing data on the nutritional content of foods (no superscript footnote indicates no missing data): [4]>0–10%, [5]>10–20%.
[6]Value represents median instead of mean if the percentage difference between these summary statistics was >20%, indicating a skewed distribution with outliers.
[7–10]Mean percentage of kilocalories consumed for which a given nutrient was unknown due to missing data on the nutritional content of foods (no superscript footnote indicates no missing data): [7]>30–40%,[8]>20–30%, [9]>40–50%, [10]80–90%.

Dietary diversity

Despite 152 distinct types of food reported in the Tsimane dietary recalls, only 9 items accounted for 75% of total daily calories and 23 items for 90%. Like the Tsimane, 9 items comprised 75% of total daily calories in the Moseten diet, and 26 items comprised 90%. Yet, all 3 measures of dietary diversity (FVS, IDDS, H) indicated that the Moseten diet was substantially more diverse than the Tsimane diet (**Figure 4**). Moseten consumed an average of ∼2.6 more unique food items/d ($FVS_{Moseten} = 7.2$ compared with $FVS_{Tsimane} = 4.6$), items from ∼1.8 more WHO food groups ($IDDS_{Moseten} = 4.0$ compared with $IDDS_{Tsimane} = 2.2$), and had a Shannon's H value ∼0.3 greater ($H_{Moseten} = 0.92$ compared with $H_{Tsimane} = 0.60$) than did Tsimane. Population-level differences in Shannon's H indicated that Moseten diets were more evenly balanced across major food groups than Tsimane diets, as well as included a greater number of individual food items. Compared with Moseten who consumed more calories from dairy, legumes, and other fruit and

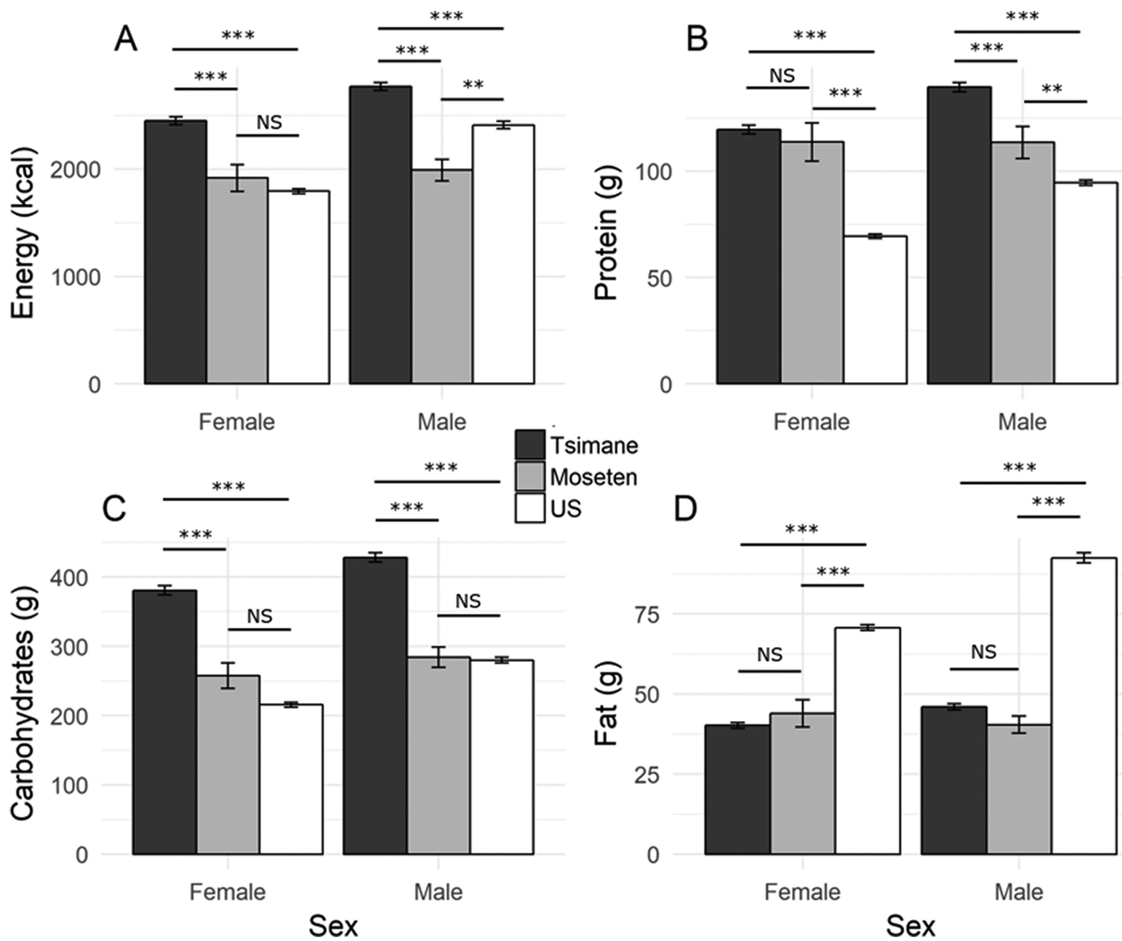

FIGURE 2 Daily energy (A) and macronutrient (B–D) intakes by sex in Tsimane, Moseten, and US populations. Bars represent means ± SEs. Note that US values were calculated from NHANES data and account for the complex survey design used to represent the underlying population. Tsimane values were calculated using linear mixed-effects models to account for repeat observations across individuals. Statistical comparisons are from a linear mixed-effects model of all populations testing for an interaction between sex and population, controlling for age and individual. *P* values were derived from post hoc tests using a Satterthwaite approximation for degrees of freedom and Tukey's adjustment. Complex survey design was not incorporated into this analysis across populations. Tsimane, $n = 2496$; Moseten, $n = 229$, US, $n = 4095$. ***$P < 0.001$, **$P < 0.01$. NS, $P > 0.05$

vegetables, Tsimane consumed more starchy staples and meat and fish (**Supplemental Figure 3**).

LOSS consumption

Reported daily per-capita acquisition of sugar and oil were >2 and 5 times higher, respectively, for Moseten (mean ± SD; sugar: 65.3 ± 69 g; oil: 45.7 ± 43 mL/d) than Tsimane (sugar: 19.0 ± 34 g; oil: 8.5 ± 17 mL/d), whereas Moseten and Tsimane consumed similar amounts of salt (28.5 ± 60 compared with 33.2 ± 68 g/d) and minimal lard (0.6 ± 6 compared with 7.8 ± 24 g/d). A greater proportion of Tsimane households reported obtaining no sugar, oil, or salt in the past month (percentage reporting zero sugar, oil, salt, and lard: 36%, 55%, 42%, and 73%, respectively) compared to Moseten (sugar, oil, salt, and lard: 0%, 0%, 1%, and 98%, respectively). Those reporting consumption of one LOSS component were likely to also consume other LOSS additives (**Supplemental Table 7**).

Population-level frequency of caloric shortfalls

Only 5% of Tsimane and 18% of Moseten consumed <1000 kcal/d. Daily estimates of food intake showed a greater degree of caloric shortfall among Moseten than among Tsimane (**Figure 5**). That is, a greater proportion of Moseten reported consuming less than all values of energy <2000 kcal/d. For illustrative purposes, Figure 5 shows that Moseten men were more than twice as likely to consume less than half of their expected daily TEE (TEE_{50}) than Tsimane men and that Moseten women are >3 times as likely to consume less than TEE_{50} than Tsimane women. Although men consumed more calories than women in general, a greater proportion of men failed to meet their TEE_{50} in both populations. Models assessing seasonal differences in energy intake suggest that shortfalls are more common in the wet season, when horticulture is less productive (**Figure 6**). Similar analyses focused on daily macronutrient intakes suggest that the 2 populations had similar frequency distributions of shortfalls, with the exception of greater overall protein consumption among Tsimane (**Supplemental Figure 4**).

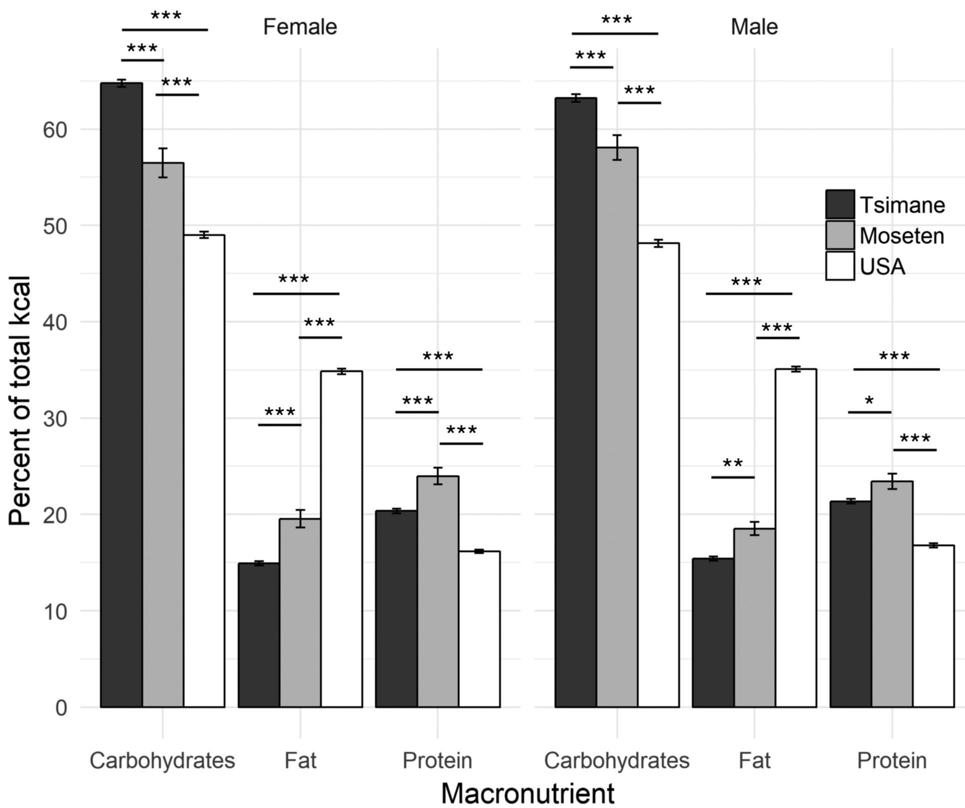

FIGURE 3 Percentage of dietary intake by macronutrient and sex across populations. Bars and error bars represent means ± SEs of the percentage of total daily caloric intake, respectively. Statistical comparisons are from a linear mixed-effects model of all populations testing for an interaction between sex and population, controlling for age and individual. *P* values were derived from post hoc tests using a Satterthwaite approximation for degrees of freedom and Tukey's adjustment. Complex survey design is not incorporated into this analysis across populations. Tsimane, $n = 2496$; Moseten, $n = 229$, US, $n = 4095$. $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

Spatiotemporal trends in the Tsimane diet

BMI, percentage body fat, and proportion of overweight and obese have increased among Tsimane over time (Figure 1), with the exception of 1 y in which there was catastrophic flooding that destroyed major crops (28). Over the ∼5.5-y course of the study, intakes of total energy and carbohydrates, but not protein or fat, increased significantly (Figure 6, **Supplemental Table 8**). Intakes were higher among those living at a greater distance from town in all models. However, a negative interaction between distance from town and time in models of energy and carbohydrates indicates that intakes increased more over time in villages located closer to market towns (**Supplemental Figure 5**). Wealth was not a strong predictor of energy or macronutrient intake in any model (**Supplemental Table 9**). Other covariates showed that men consumed 11% more calories than women, heavier individuals tended to eat more (positive slopes for all variables, but significant relation only for protein), and level of schooling was not associated with intakes of total energy or macro- or micronutrients (Supplemental Tables 8 and 9).

LOSS acquisition was poorly explained by most of the independent variables in our analysis (**Supplemental Table 10**). Two notable exceptions, however, were age (older individuals acquired more LOSS) and the consistent trend with time, showing that amounts of sugar, salt, and oil obtained by Tsimane increased significantly over the course of the study period (**Figure 7**). Sugar and oil increased the most, changing by 15.8 g/d and 4.9 ml/d, respectively, from 2010 to 2015. It is striking that such dramatic changes are visible over the course of only ∼5.5 y. Nonetheless, levels of sugar and oil acquisition by the end of the study for Tsimane were lower than levels acquired by Moseten.

DISCUSSION

Detailed analysis of the Tsimane diet shows the following: *1*) high overall energy intake; *2*) high-carbohydrate, high-protein, low-fat consumption; *3*) low dietary diversity but high intake of micronutrients of potential relevance to cardiovascular health; and *4*) minimal caloric or macronutrient shortfalls. Dietary intake was partially explained by time, geographic location, and their interaction. Furthermore, we observed increasing trends in the consumption of lard, sugar, salt, and oil over time. Although the more-acculturated Moseten consumed many of the same agricultural foods, key differences in diet macronutrient composition and intake of food additives, in addition to spatiotemporal trends in the Tsimane diet itself, belie imminent changes in Tsimane nutrition. Collectively, these features describe a potentially atherosclerotic diet (high-carbohydrate, low-diversity) that is representative of many Amerindian groups (29), but which appears to promote positive health outcomes, at least when coupled with other aspects of the Tsimane lifestyle and environment.

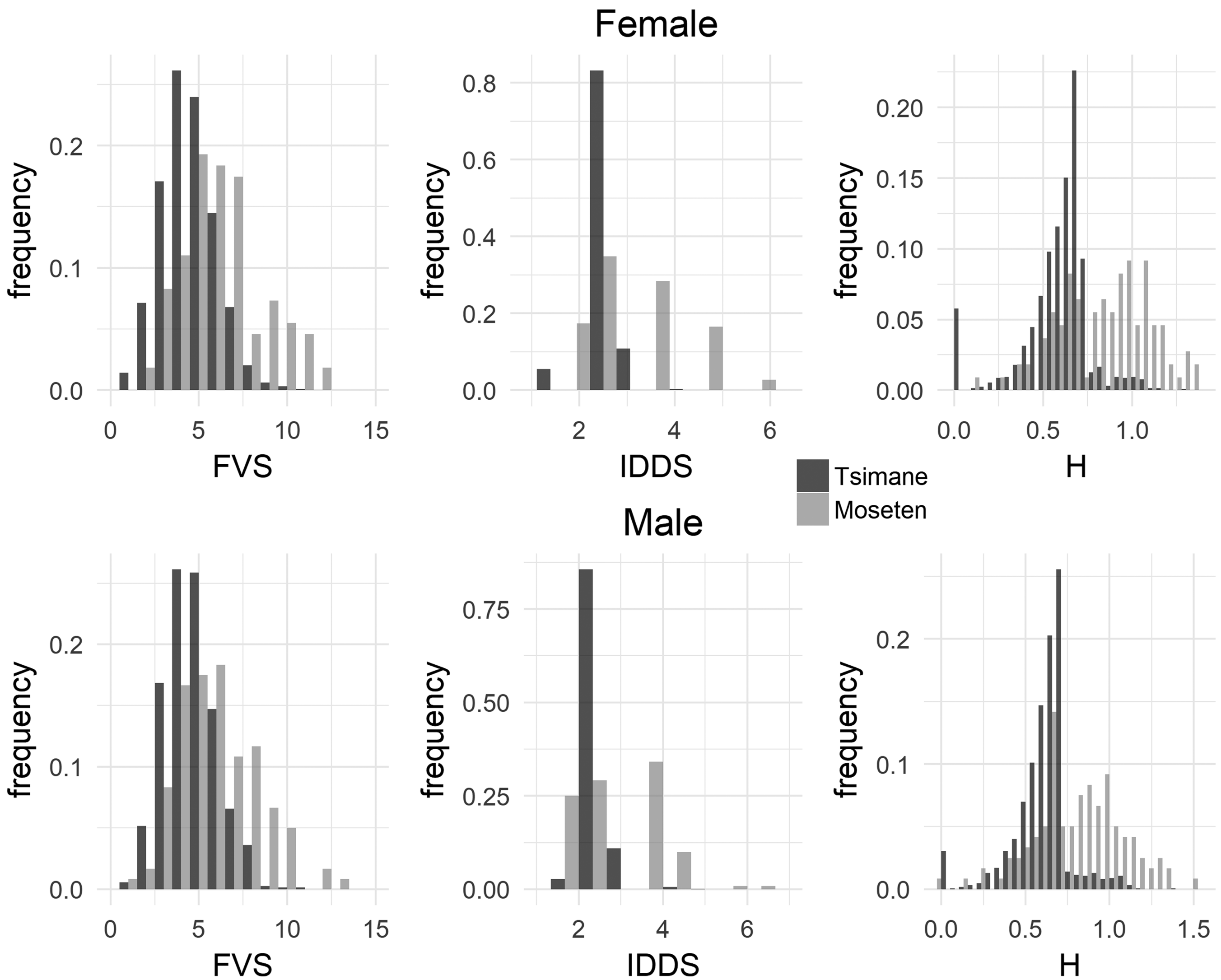

FIGURE 4 Distribution of dietary diversity scores for Tsimane and Moseten populations. Tsimane, $n = 2496$; Moseten, $n = 229$. Tsimane dietary diversity was significantly lower ($P < 0.001$) than Moseten dietary diversity for all diversity scores (linear mixed-effects model controlling for age, sex, and individual). FVS, food variety score; H, Shannon-Wiener index; IDDS, individual dietary diversity score.

Overall energy intake

Tsimane total energy intakes exceeded those of US adults (men = 2736 kcal/d, women = 2422 kcal/d) (Figure 2). High caloric intakes may be related to (and potentially ameliorated by) high resting metabolic rate and daily energy expenditure (9), reflecting high levels of physical activity, immune activation, or both (30). Despite greater access to market goods, Moseten energy intakes were significantly lower (653 kcal/d) than Tsimane, which may reflect reduced energy expenditure related to greater access to motorized transport, reduced pathogen loads, and less time spent foraging.

Tsimane diet is characterized by high carbohydrate intake and low fat consumption

Evidence linking high carbohydrate intake to a greater prevalence of T2D and coronary heart disease has been mixed (21, 31, 32). Our results show that low cholesterol and triglyceride concentrations and minimal prevalence of T2D and heart disease can persist despite high carbohydrate intake. Notably, however, the Tsimane primarily consumed carbohydrates with a high fiber content (estimated minimum intake of 26–29 g/d; Table 1) and a low glycemic index [e.g., manioc, plantain, and corn have a glycemic index of 46, 40, and 53, respectively (33)]. Tsimane rarely reported drinking soda or other sugary beverages, whereas Moseten intakes were consistently higher. Given that specific carbohydrates vary in relation to disease risk (34–37), and cardioprotective diets vary widely in macronutrient composition, our results emphasize the relative importance of quality over macronutrient quantity (38).

Compared with Americans, Tsimane consumed relatively little saturated or *trans*-fats, and monounsaturated and polyunsaturated fat intakes were also low (Figures 1 and 2, Table 1). Although some randomized controlled trials showed that low-fat diets are

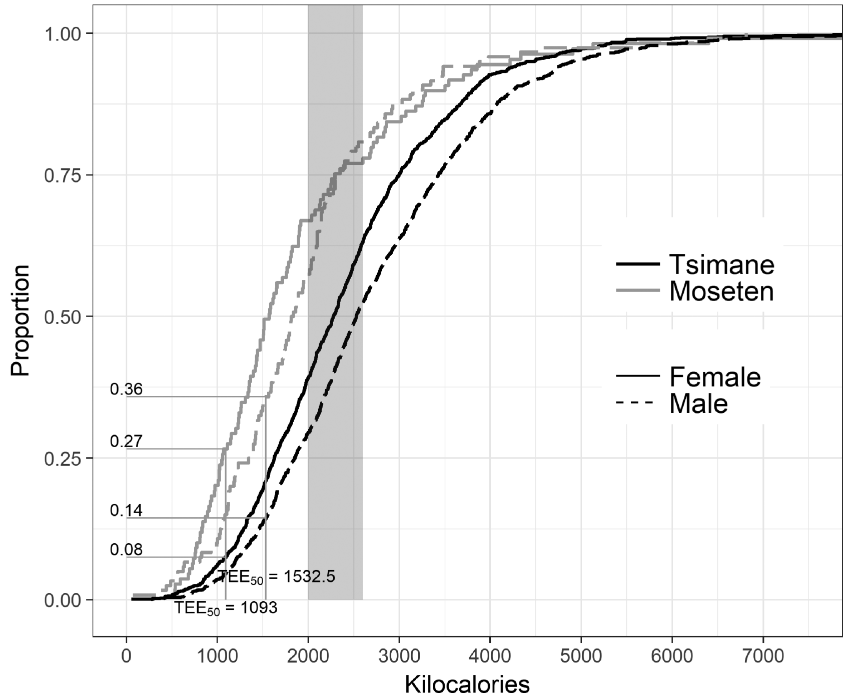

FIGURE 5 Empirical cumulative frequency distributions of caloric intake by population and sex. Values indicate the proportion of person-days in which the population- and sex-specific sample consumed less than or equal to a given caloric intake. Labeled gray lines show points at which the TEE_{50} was met for each sex. The gray-shaded region shows the range of daily reference intakes for male and female US adults. Tsimane, $n = 2496$; Moseten, $n = 229$. TEE_{50}, half the expected total daily energy expenditure.

less effective in promoting weight loss than low-carbohydrate diets (39–41), low carbohydrate intake may result in increased HDL- and LDL-cholesterol concentrations (42). Our observations of moderate BMI and low cholesterol in tandem with high carbohydrate and low fat consumption in Tsimane align with this latter finding.

Tsimane dietary diversity is low compared with other populations, including Moseten

The average FVS of Tsimane was 4.6, compared with 7.2 for Moseten and 29.6, 24.7, 7.9, and 16.7 for populations in Indonesia, Kenya, Ethiopia, and Malawi, respectively (43). Tsimane also had a lower average WHO dietary diversity score (2.2) compared with Moseten (4.0), Indonesians (7.0), Kenyans (7.3), Ethiopians (3.2), Malawians (6.1), and Bangladeshis (3.8) (43). Dietary diversity is broadly indicative of dietary quality, particularly appropriate micronutrient intake (44, 45), and nutritional status and food security (46–49). Despite low dietary diversity, Tsimane micronutrient intakes generally exceeded NIH recommendations (e.g., 28.4 mg Fe/d; Table 1). Meat, wild fruit, and other foraged foods supply abundant micronutrients in Tsimane diets, including minerals with cardioprotective effects such as potassium (50), magnesium (51), and selenium (52) (although dietary calcium amounts were low). Consequently, low dietary diversity metrics may not sufficiently reflect dietary adequacy in this or other subsistence populations (49).

Neither Tsimane nor Moseten exhibit high levels of energy or macronutrient shortfalls

Moseten (compared with Tsimane) and men (compared with women) experienced greater relative frequency of caloric and macronutrient shortfalls, but the observed values were low (Figure 5). Few respondents reported consuming <200 kcal/d (Tsimane: 0.04%; Moseten: 0.8%). Greater shortfalls were evident for lipids and proteins (Supplemental Figure 4), but the prevalence was still low (e.g., 33% and 35% consumed <25 g fat/d and 4.8% and 3.1% consumed <25 g protein/d for Tsimane and Moseten, respectively). The diets of horticultural Bolivians do not exhibit boom-bust dynamics, as is sometimes assumed for hunter-gatherers and agriculturalists (53–55), and positive health characteristics in these populations cannot be ascribed to periodic caloric restriction.

Ongoing nutrition transition in Bolivia

The ongoing nutrition transition among the Tsimane and Moseten is a natural experiment that helps illuminate the relation between diet and the increase in chronic noncommunicable diseases. Tsimane energy and carbohydrate consumption, as well as LOSS access, have increased over time (Figures 6 and 7). Most dramatically, per-capita consumption of refined sugar and oil increased by 15.8 g/d and 4.9 mL/d over the 5.5-y study period. This shift was mainly due to a decrease in the proportion of individuals reporting zero acquisition, which dropped from 53.6% to 20.3% for sugar and 73.8% to 40.9% for oil between the first and last years of the study. The increase in LOSS acquisition suggests

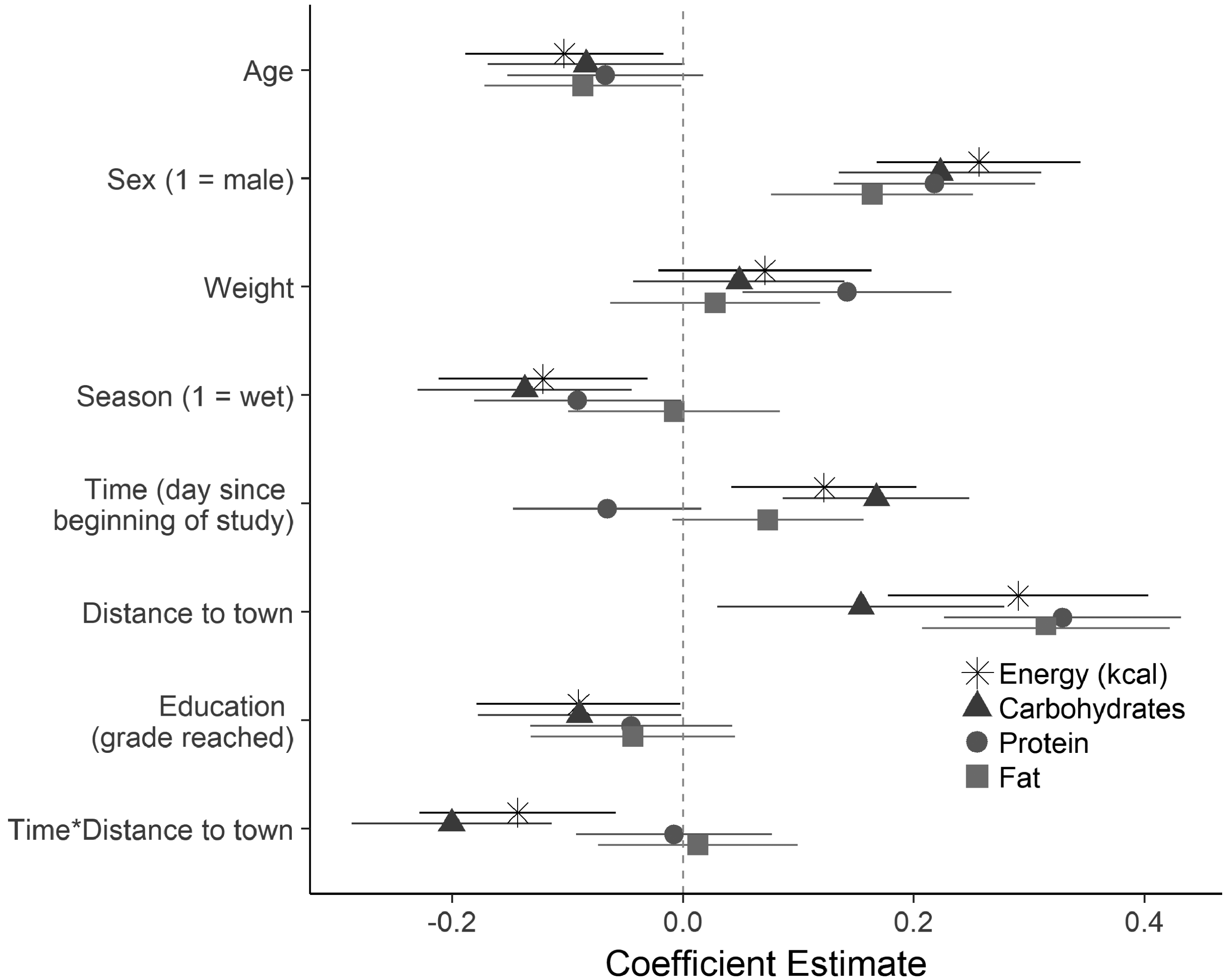

FIGURE 6 Coefficient plots of linear mixed models of energy and macronutrient consumption. Response variables and predictors are standardized for comparability between models. Points and bars represent estimates (95% CIs). $n = 2344$.

that the Tsimane are entering a critical transitionary period in which the diet remains dependent on subsistence products but is supplemented with high-calorie inputs commonly associated with nutrition transitions and elevated disease risk (56, 57).

We also found that Tsimane energy and macronutrient intakes were greater in remote villages, but that villages closer to town showed greater increases in consumption over time (Figure 6, Supplemental Table 8). The relatively lower energy intakes in villages closer to town may reflect comparatively poorer access to hunted and fished foods due to higher population densities or decreased food availability due to sporadic incomes, which may also explain greater frequency of caloric shortfalls in the Moseten. In contrast to a previous study conducted a decade earlier (58), LOSS acquisition was uncorrelated with distance to town. Physical distance may be losing salience as a determinant of market access (Figure 7) due to the recent availability of affordable motorized boats and greater access to roads.

The Moseten had energy and macronutrient intakes intermediate between Tsimane and Americans and consumed more sugar, salt, and oil than did Tsimane. The Moseten also had higher dietary diversity, which parallels previous findings of higher dietary diversity among wealthier and more acculturated Tsimane households (reference 58, but also see reference 59).

Taken together, these findings indicate the potential for mixed future health outcomes for the Tsimane. On one hand, increased access to diverse market foods while maintaining a primarily traditional diet high in complex carbohydrates, wild game, and fish bodes well for maintaining a low risk profile for cardiovascular disease or T2D. On the other hand, rapid increases in the consumption of market foods, particularly sugar and cooking oil, coupled with the replacement of wild game with cheap dried beef, are emblematic of the negative health consequences of nutrition transitions (60). Indeed, >10 y of data show that Tsimane BMI and body fat, as well as lipid concentrations (6), are increasing (Figure 1). These early warning signs suggest that food additives alone may be sufficient to herald the onset of numerous chronic diseases, especially if physical activity levels decline, as evidenced among Suruí Indians of Brazil (61) and Toba/Wichi of Argentina (62). Indeed, Rosinger et al. (63) report greater household expenditures on market

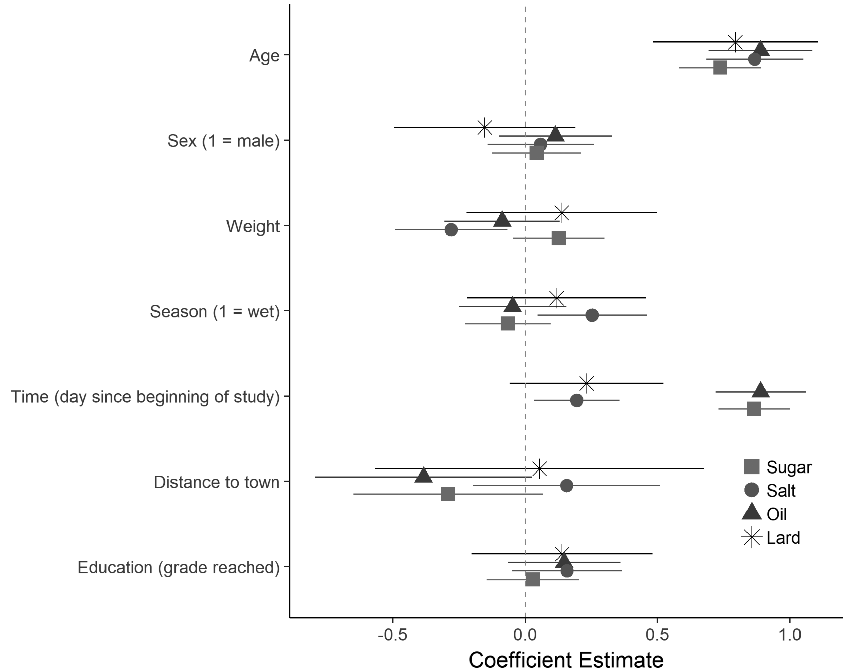

FIGURE 7 Coefficient plots of Tweedie generalized linear mixed models of per-capita amounts obtained in the last month of sugar (kilograms), oil (liters), salt (kilograms), and lard (kilograms). Points and bars represent estimates (95% CIs). The interaction between time and distance to town was dropped from all models because effect sizes were miniscule and the term was not significant. Lard, $n = 1248$; oil, $n = 1251$; salt, $n = 1248$; sugar, $n = 1247$.

foods correlated with modestly increased BMI, body fat, and probability of being overweight or obese.

In conclusion, nutrition transitions are a global phenomenon linked to the increase in many noncommunicable chronic diseases (2). Although there has been an increase in interest in understanding the dynamics of nutrition transitions in different contexts (56, 64), few studies have presented detailed dietary investigations of subsistence populations despite mounting evidence that dietary changes in these societies can lead to rapid increases in "diseases of civilization" (57, 65).

Our study results among 2 subsistence populations collected over 5 y in rural Bolivia show that population-level calorie and carbohydrate intakes, as well as sugar and oil consumption, in the Tsimane are increasing at a rapid pace, mirroring trends of increasing body fat and BMI. If these patterns continue, recent findings of minimal coronary artery disease (6) and T2D are likely to change in the near future.

The authors' responsibilities were as follows—TSK, JS, BCT, MG, and HK: designed the research; JS, BCT, MM, MG, and HK: conducted research; TSK and MM: analyzed the data or performed statistical analyses; TSK, JS, BCT, MM, and MG: wrote the manuscript; TSK: had primary responsibility for final content; and all authors: read and approved the final manuscript. The authors declared no conflicts of interest.

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