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Labour's pain: strenuous subsistence work, mechanical wear-and-tear and musculoskeletal pain in a non-industrialized population

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Musculoskeletal pain is the most debilitating human health condition. Neurophysiological pain mechanisms are highly conserved and promote somatic maintenance and learning to avoid future harm. However, some chronic pain might be more common owing to mismatches between modern lifestyles and traits that originally evolved under distinct premodern conditions. To inform assumptions about factors affecting chronic pain vulnerability prior to industrialization, we assess pain prevalence, perceived causes, and predictors among Tsimane forager-horticulturalists. Habitual subsistence work is the primary reported cause of pain throughout life for both sexes, and pain is more common with age, especially in the back, and for those with more musculoskeletal problems. Sex differences in pain are relatively weak, and we find no association between women's reproductive history and pain, contrary to the hypothesis that reproduction causes women's greater pain susceptibility. Age-standardized current pain prevalence is 1.7–8.2 times higher for Tsimane than other select populations, and Tsimane chronic pain prevalence is within the range of variation observed elsewhere. Chronic low back pain is not a 'mismatch disease' limited to post-industrialized populations. Hominin musculoskeletal changes supporting bipedalism probably imposed health costs, which, after millions of years of evolution, remain an epidemiological burden that may be exacerbated by modern conditions.

1. Introduction

Musculoskeletal pain (e.g. of the lower back, knee, or shoulder) is one of the most debilitating and costliest human health conditions globally, and its burden is underestimated [1,2]. Low back pain in particular, owing in part to ancestral hominin locomotor changes favouring bipedality [3,4], causes more disability today than any other health condition [5]. Despite its salience in humans, neurophysiological pain mechanisms are highly conserved in mammals [6] and certain pain behaviours are shared across species. The dorsal horn of the spinal cord contains the first synapse in pain pathways, and descending control of spinal nociception originates from many brain regions and circuits affecting acute and chronic pain experience. The characteristic aversive pain experience produces a coordinated set of cognitive and behavioural responses (e.g. focused attention, vigilance, and flight) which jointly act to prioritize self-preservation [7,8]. Pain thus serves functions of somatic maintenance and defence: it minimizes tissue damage by limiting movement that could cause further damage, facilitates healing by motivating escape from harmful situations, and motivates learning to avoid future harm [9–11]. Human pain vulnerability and expression may have unique attributes when viewed in comparative cross-species perspective [12]. For example, human pain expression is hypothesized to elicit social support during periods of need including acute illness and injury [12–14].

Unlike acute pain, chronic pain (often defined as pain lasting three months or more, or six months or more and outlasting the above-mentioned functions; [15]) is posited to lack adaptive value. Some chronic pain might be more common owing to mismatches between modern lifestyles and traits that originally evolved under distinct premodern conditions [4,6,16]. Relative to ancestral hominin conditions, modern lifestyles and environments have altered individual experiences and learning, which both serve as key inputs into neurophysiological responses underlying pain sensitivity and thresholds. Compared to rural subsistence settings, in high-income urban settings the relatively high levels of physical inactivity and atypical mechanical loading patterns (e.g. from prolonged sitting in chairs at school or work; sleeping on soft mattresses; and walking on shoes with cushioned heels) are hypothesized to increase risk of pain. Other relatively novel human behaviours (e.g. consumption of prescription-strength analgesic and anti-inflammatory drugs) and common 'mismatch diseases' such as obesity are associated with chronic pain risk in a complex bi-directional fashion [17]. Under these mismatch scenarios, some chronic pain can manifest from malfunctioning peripheral and central sensitization [15], and other pathways including endocrine and immune system changes.

Moreover, global secular trends towards earlier menarche, and demographic transition to lower fertility and higher life expectancy have greatly increased the frequency of menstruation, which is hypothesized to contribute to higher chronic pelvic pain prevalence among women [18]. Sex differences in reproductive effort are hypothesized to cause women's greater susceptibility to pain more generally [19]. It has been posited that male and female mammals face divergent selection pressures influencing pain modulatory circuitry, owing to the presumably greater exposure to traumatic pain in males and visceral pain in females. Both direct and indirect mechanisms linking women's reproductive effort to pain have been posited, but there is a paucity of pain data in high fertility populations lacking formal institutions (which can promote structural inequalities in wealth, schooling, employment opportunities or healthcare access) that confound the association between fertility and pain.

One way to identify environmental, lifestyle, and biological factors contributing to pain aetiology is to focus on small-scale rural subsistence-level populations, which typically experience social, ecological and epidemiological conditions more similar to those found over most of human history. These conditions include physically active lifestyles [20,21], which have been inconsistently associated with pain vulnerability: meta-analyses of controlled trials suggest protective effects of regular exercise [22], but population-based studies indicate high pain prevalence among physically active adults routinely engaging in strenuous labour for sustenance [23]. Other conditions include, relative to the post-industrialized populations where most pain research occurs, fewer opportunities for prolonged rest following pain onset and limited occupational alternatives. These factors are exacerbated by limited formal schooling and limited access to modern pain medication and healthcare. Female musculoskeletal health is further compromised by high reproductive effort, characterized by no reliable access to modern contraception, short interbirth intervals (IBIs), prolonged on-demand breastfeeding, and an early age at first birth that precedes age of peak bone mineral accrual at approximately 25–35 years [24]. Another major difference is that subsistence-level populations are regularly exposed to diverse infectious diseases [25] but a dearth of non-communicable chronic diseases like atherosclerosis, dementia, and metabolic syndrome, which are now globally widespread, co-morbid with each other, and are leading contributors to human disease burden and mortality [26,27]. Despite the fact that these conditions characterized much of human history, few systematic studies of pain have been conducted in small-scale subsistence populations. Comparative studies in non-industrialized contexts are needed to determine the extent to which human pain is a byproduct of relatively novel environments and lifestyles unique to (post)-industrialized populations.

In this paper, we first document self-reported pain prevalence and its causes across the lifespan (greater than 10 years old) among Tsimane forager-horticulturalists of the Bolivian Amazon. We consider multiple definitions of pain (current and chronic) since the experience of pain is subjective and not consistently defined. We then determine whether pain increases with age and female sex, and whether back pain is more prevalent than pain at other anatomical locations. Next we determine whether pain increases with disease burden, as indicated by physician-assigned clinical diagnoses and vital signs. We assess whether certain illness categories (e.g. of the musculoskeletal rather than gastrointestinal system) are more likely than others to co-vary with pain. We consider both infectious and non-infectious illness categories, individually and additively. Then, among women only, we determine whether pain is positively associated with reproductive history, indicated by age at first birth, mean IBI, parity, and recent birth. We also determine whether reported pain is lower with formal schooling, because schooling can foster economic opportunities that reliably reduce exposure to recurrent painful stimuli from strenuous subsistence work. Lastly, we examine whether Tsimane show higher age-standardized current and chronic pain prevalence than other rural and urban populations for which similar data exist, and whether Tsimane sex differences in pain are lower compared to other populations. Higher pain prevalence and smaller sex differences in pain vulnerability may be expected among Tsimane compared to other populations if habitual strenuous subsistence work is a primary pain determinant, and if both sexes regularly experience work-related hazards. On the other hand, relatively large sex differences in pain may be expected because high fertility entails reproductive costs uniquely incurred by women that, together with high strenuous work effort, may later contribute to elevated female morbidity or disability.

2. Methods

(a) Study population

Tsimane are semi-sedentary forager-horticulturalists inhabiting more than 90 villages in lowland Bolivia. Fertility is high (total fertility rate = 9 births per woman; [24]), and infants and toddlers are frequently carried by mothers and to a lesser extent older siblings in slings or in the arms. Tsimane hunt with a diverse toolkit that includes a rifle or shotgun, bow and arrow, machete, slingshot and trap, and sometimes assistance from tracking dogs. Men hunt about once every week or two; the average hunt lasts 8.4 h, covers 17.9 km [28], and often involves carrying carcasses and tools long distances. Fishing typically occurs in rivers, streams or lagoons and involves use of hook-and-line, bow and arrow, machete, plant poison and/or netting. Entire families sometimes go on multi-day fishing and hunting trips that can last from two days to several months. Much of the protein and fat consumed by Tsimane come from hunting and fishing, whereas the majority of total calories come from cultigens grown in small swiddens (mostly rice, plantain, manioc and corn; [29]). To create space for cultigens, Tsimane first use machetes and hoes to clear smaller vegetation, and then they use metal axes (and more recently chainsaws when available) to cut larger trees before planting and burning. Both sexes plant cultigens, clear smaller vegetation and harvest, but the felling of larger trees is typically done only by men. Both sexes carry harvested cultigens from horticultural fields to their homes, often using homemade woven bags (*saraij*) whose straps may be positioned on the head, shoulders, or back during transport (electronic supplementary material, figure S1A). These bags are also used by men to transport hunted game and/or hunting tools (electronic supplementary material, figure S1B).

Many villages have elementary schools taught by bilingual (Spanish-Tsimane) teachers, although until 2000 no village had a middle or high school. School attendance is generally low or inconsistent, and overall adult literacy rate is low (less than 20%). Wage labour opportunities are sporadic and male-biased, and include commercial logging and serving as a ranch hand or translator for non-governmental organizations.

Illnesses of the musculoskeletal system and connective tissue are the most common types of illnesses diagnosed by Tsimane Health and Life History Project (THLHP) physicians [30]. Computed tomography scans show a high prevalence of Tsimane thoracic vertebral fracture compared to Los Angelenos [31]. Bone mineral density estimates from both the axial and appendicular skeleton, particularly from sites rich in trabecular bone including the thoracic vertebrae, calcaneus and distal radius, suggest that osteoporosis is not uncommon, especially for post-menopausal women [24,32]. Early, rapid reproduction and high parity appear to contribute to women's skeletal fragility later in life [24,31]. In a separate sample not analysed in the present study, 76% of adults aged 30+ years ($n = 1569$) that were seen from 2007–2020 on at least two different occasions by a THLHP physician during biannual village visits as part of routine epidemiological surveillance experienced movement restriction during flexion or extension in at least one of nine joints examined, most commonly in the dorsolumbar and shoulder regions (unpublished analyses; mean ± s.d. total visits per person = 4.0 ± 1.7, min = 2, max = 10).

(b) Participants

The sample includes individuals aged greater than 10 years during enrollment (mean ± s.d. age = 34.1 ± 14.0 years, range: 10.9–75.1, 48% female, $n = 388$; see the electronic supplementary material, table S1) who met the additional inclusion criteria of self-identifying as Tsimane and residing in one of the pre-established study villages. Sixteen villages were sampled, and all households within villages were eligible to participate. No Tsimane were excluded based on any health condition and there is no reason to believe that participants are not representative of the population. Very few individuals (less than 5%) refused to participate in the study; primary reasons for not participating included work commitments or temporary absence from the community (e.g. visiting a relative in a different community, or visiting town).

(c) Pain questionnaire

As part of the THLHP's focus on health, ageing and functional ability, M.G. and a Tsimane research assistant queried participants about their own histories of serious accidents (e.g. snakebites, jaguar and other animal attacks), life-threatening illnesses and musculoskeletal pain. Tsimane research assistants provided input in the development of the questionnaire, including identifying common accidents and anatomical locations perceived to be frequently affected by pain. Each question was translated into Tsimane from Spanish, and then independently back-translated into Spanish from Tsimane with the help of multiple bilingual research assistants. All interviews were conducted at participants' homes in the Tsimane language from May 2002 to December 2004. Individuals were systematically asked whether they currently experienced any pain at each of five broad, easily identifiable anatomical locations: the arm (*uñya'*), back (*murujru*), foot (*yuj*), hand (*un*) and leg (*jäñäc*). Words for pain in the Tsimane language (*are'yi* or *cäti*) may connote symptoms of tenderness, swelling and/or stiffness, but here we do not distinguish between individual pain symptoms. These Tsimane words for pain are used by Tsimane to refer to pain in much the same way that, say, native Spanish speakers use synonymous words (e.g. 'dolor' or 'me duele'). For each of the five broad anatomical locations, if any current pain was reported, participants indicated more precisely where the pain was experienced. For example, if leg pain was reported, they might then indicate their knee. They also indicated the pain duration; the perceived cause of the pain origin; whether the pain was experienced during work (which was affirmed in 98% of all person-observations ($n = 1134$ for 336 individuals)); and how the pain was experienced (e.g. 'as a shooting pain from the lower back to the foot', or 'as a muscle ache').

For each of the five broad anatomical locations, sub-questions regarding more precise pain locations and perceived pain causes were open-ended and did not include structured follow-up questions. Participants thus offered varying levels of detail (e.g. some indicated leg pain caused by 'a fall', whereas others indicated leg pain caused by 'a fall while carrying plantains in the rain'). It is thus not always possible to determine from self-reports whether pain-inducing events occurred during work or not. To facilitate data analysis, J.S. (and only J.S.) binned each open-ended response for self-reported pain cause into one of seven macro-categories: (i) subsistence work (hereafter 'work'); (ii) fall/other accident, which may or may not have occurred during work (depending upon the level of detail provided by participants); (iii) social (i.e. either domestic violence, a fall while drunk at a community party, witchcraft, or injuries from playing soccer); (iv) reproduction (e.g. childbirth, or excessive carrying of an infant or toddler); (v) illness; (vi) weather (e.g. 'when it rains'); and (vii) old age (non-specific). Part of the motivation to create these macro-categories was to distinguish causes of pain stemming from food production from other causes. The probability of misattribution was low given the nature of open-ended responses (e.g. 'my back pain results from carrying heavy loads of plantains, or from clearing my horticultural field with my machete'). Sub-categories were created within some macro-categories (e.g. the 'work' macro-category includes sub-categories horticulture, excessive load carrying (hereafter 'overloading'), hunting or foraging and walking long distances (hereafter 'transport')). Because participants offered varying levels of detail in their open-ended responses, our derived macro-categories are not necessarily mutually exclusive (e.g. at least 21% of falls occurred during work), and neither are sub-categories within macro-categories (e.g. at least 27% of 'overloading' occurs during horticultural work, including carrying plantains or rice). We suspect that had we provided relevant prompts that also allowed for multiple simultaneous responses, some pain attributions like 'old age' would be more commonly reported, since there may be cumulative effects of habitual strenuous work (in fact, $n = 3$ 'work' attributions have reported pain durations of 10 years). Thus, the relative contribution of certain categories to perceived pain aetiology is not always precisely estimated, and some estimates represent lower bounds. Nevertheless, these categories offer some ethnographic insight and partly help distinguish perceived causes of pain stemming from food production from other causes.

We consider multiple definitions of chronic pain (i.e. lasting either three months or more, or six months or more at a given anatomical location), both to refine our understanding of the burden of Tsimane pain, and to facilitate population-level comparisons of pain prevalence against published studies using varying chronic pain definitions. There is no gold standard for chronic pain measurement and chronic pain is not consistently defined in the literature. As with reports of current pain, Tsimane report that chronic pain is experienced during work for nearly all person-observations (i.e. 99% of the 275 person-observations for 116 individuals). Therefore, our pain definition for both current and chronic pain is not only based on reported pain or pain duration, but also on whether the pain interferes with work (what others have referred to as 'high-impact' pain; [33]).

(d) Medical exam and socio-demographics

Since 2002 THLHP physicians and Tsimane research assistants have conducted censuses and systematic clinical evaluations with no exclusion criteria in Tsimane villages.

As part of the clinical evaluation, the physician diagnoses up to four conditions using the International Classification of Diseases-10th revision (ICD-10). ICD-10 diagnoses are grouped into the following seven illness macro-categories: circulatory, gastrointestinal, genitourinary, musculoskeletal, other infection, respiratory and skin/subcutaneous tissue. Each illness category is coded as either present or absent, and all categories are summed to obtain a measure of total disease burden. During clinical evaluation, the physician recorded vital signs, including pulse rate, respiratory rate, and blood pressure. Pulse rate was determined manually, by placing the index and middle fingers on the wrist at the base of the thumb (radial artery), counting the number of beats in 30 s, and then multiplying this number by two. Respiratory rate was determined by counting the number of breaths in 30 s and similarly multiplying this number by two. Systolic and diastolic blood pressure were measured on the right arm with a Welch Allyn Tycos Aneroid 5090 sphygmomanometer and Littman stethoscope. Project physicians do not systematically query participants about pain during the medical exam. Information obtained from the pain questionnaire by the anthropologists was not transmitted to the physician, nor did the physician share any patient information with the anthropologists.

Reproductive histories were elicited in the Tsimane language by M.G. and a Tsimane research assistant. Birth years were assigned based on a combination of methods including using known ages from written records, relative age lists, dated events, photo comparisons of people with known ages and cross-validation of information from independent interviews of kin. The outcome of each pregnancy reported during reproductive histories was recorded as either ending in a live birth or terminating pre-term. Whether miscarriages (including stillbirths) are included or omitted from parity counts does not affect results, and results reported here reflect only live births. IBI refers to the number of months between live births for women with equal to or greater than two live births.

As part of the census, participants were also queried about their level of schooling (number of years).

(e) Data analysis

We model four pain outcomes: (i) presence of current pain; (ii) pain duration; and presence of chronic pain lasting either (iii) three months or more, or (iv) six months or more. Each person-observation corresponds to a specific anatomical location, and locations are nested within individuals. A minority of participants (9.5%) were interviewed twice (mean ± s.d. months between interviews = 12.7 ± 3.6, min = 4.2, max = 14.8) and their pain reports were internally consistent in terms of pain presence and duration. All regression models include a random intercept for individual identity (ID). Models also include a random intercept for community ID to account for potential community-level differences in lifestyle or environment that could affect pain experience (community ID explains less variance in each outcome than individual ID). We use generalized linear mixed effects models (glmmTMB package) for modelling both binary (i, iii, iv) and continuous (ii) pain outcomes. We specify a binomial distribution for modelling probability of current and chronic pain, and a generalized Poisson distribution with a single zero-inflation parameter for modelling pain duration. For the latter we used the DHARMa package to examine model diagnostics and we compared model fit indices across several specifications (e.g. using a negative binomial distribution, and including a zero-inflated age parameter). p-values are Bonferroni-adjusted to account for the fact that we model multiple pain outcomes, although outcomes are not independent and thus adjustments should be considered conservative. In an exploratory fashion, we tested for all possible two-way interactions between fixed effects, but no interaction term yielded a significant parameter estimate for any pain outcome, nor did any interaction term improve model fit.

For population-level comparisons of current and chronic pain prevalence, estimates are age-standardized using the direct method. The standard adult population is defined by Waterhouse (https://www.paho.org/hq/dmdocuments/2010/HSA2006_tn.pdf). For current pain prevalence, comparator samples participated in the multi-site World Health Organization International League Against Rheumatism Community Oriented Program for the Control of Rheumatic Disease (WHO-ILAR COPCORD; http://copcord.org/index.asp). This initiative was originally designed to document prevalence and correlates of musculoskeletal pain and disability in low- or middle-income settings (urban and rural) using standardized community-based surveys (response rate range for selected comparator samples: 75–99%). Primary healthcare workers queried participants aged 15+ years about whether in the past week they experienced any pain, tenderness, swelling or stiffness. Data on pain duration and chronic pain were not systematically included in the COPCORD surveys. Although COPCORD surveys included questions about current pain at specific anatomical locations, those locations were generally not comparable to locations included in the Tsimane pain questionnaire. We therefore only compared the aggregate measure of any current pain experienced across populations. For prevalence of chronic pain, comparator samples are from either mixed urban-rural ($n = 5$) or urban ($n = 1$) settings in high-income countries. We selected a combination of representative national and community-based samples (response rate range: 40–82%). Only published studies reporting age-specific estimates throughout adulthood were selected (minimum age for current and chronic pain prevalence = 15 and 16 years, respectively, for comparator samples). For chronic pain, we did not find any comparable studies reporting age-specific prevalence from low- or middle-income countries, including in reviews and meta-analyses such as [34] or the references therein. Neither current nor chronic pain data from non-Tsimane populations were collected in an identical fashion as among the Tsimane, and so the data may be similar but not perfectly comparable.

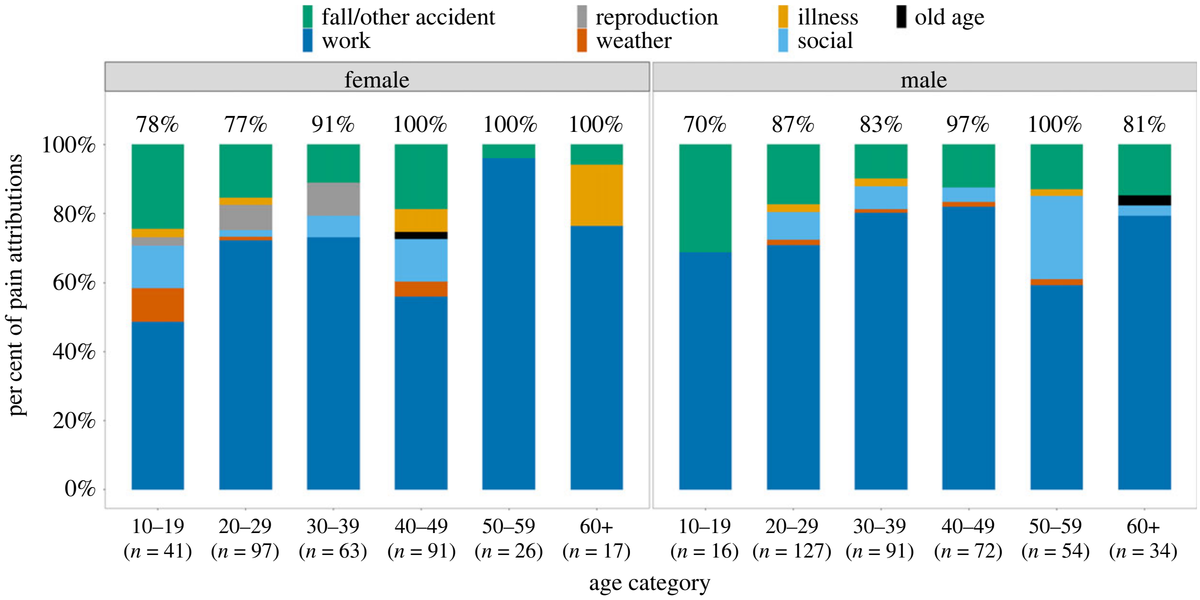

Figure 1. Self-reported causes of pain (current and chronic) by sex and age ($n = 729$ pain attributions for 285 individuals). Note some categories may not be mutually exclusive (e.g. fall and work), and thus the relative contribution of work is a lower-bound estimate. Percentages on top of each bar show the prevalence of pain for a given sex and age category. Sample sizes shown on the *x*-axis refer to pain attributions.

3. Results

(a) Descriptives: Tsimane pain prevalence and duration

Current pain in at least one anatomical location is reported by 87% of participants. The distribution of pain duration is right-skewed (median duration including zeros = 7 days; inter-quartile range (IQR) = 88 ($n = 290$ individuals); median duration excluding zeros = 30 days; IQR = 115 (235 individuals); max duration = 3650 days). Chronic pain in at least one anatomical location lasting three months or more, and six months or more is reported by 35% and 25% of participants, respectively.

(b) Self-reports indicate that most pain results from habitual subsistence work

Physically intensive habitual subsistence work accounts for at least 71% of all pain attributions ($n = 729$ attributions for 285 individuals; figure 1). Work is the dominant non-chronic and chronic pain attribution across nearly all age and sex categories (electronic supplementary material, figure S2). Compared to other pain attributions, work attributions are more variable in pain duration (coefficient of variation = 276%) and show the highest maximum duration (max = 3650 days; electronic supplementary material, table S2). Within the work macro-category, the most common pain attributions are from, in descending order of frequency: horticulture (29%), excessive load carrying (25%, which includes carrying cultigens), other food production (hunting, foraging and fishing; summed = 20%), and transport (17%; electronic supplementary material, figure S3). These four work sub-categories are also the most common attributions for chronic pain. Compared to other work attributions, those from hunting or foraging show higher maximum and mean durations (max = 1825 days, mean = 185; electronic supplementary material, table s3).

(c) Pain increases with age, and is more prevalent in the back relative to other anatomical locations

Older individuals are more likely to report current pain (electronic supplementary material, table S4; figure 2), longer pain duration (electronic supplementary material, table S5; figure S4), and chronic pain (lasting three months or more, or six months or more; electronic supplementary material, tables S6–S7; figure S5). For both current and chronic pain, back pain is more prevalent and of longer duration compared to other anatomical locations.

Women report more pain than men across all four pain outcomes, but sex differences are not statistically significant (Bonferroni-adjusted $p \leq 0.0125$; all p-values ≥ 0.1). In subsequent models containing additional covariates (see below), the magnitude of the sex difference decreases for current pain and pain duration, while for chronic pain it slightly increases.

(d) Pain increases with disease burden, particularly for musculoskeletal conditions

Individuals with greater disease burden, indicated by the sum of clinical diagnosis categories assigned by the physician, are more likely to report current pain (electronic supplementary material, table S8), longer pain duration (electronic supplementary material, table S9), and chronic pain (electronic supplementary material, tables S10–S11). Regarding specific illness categories, diagnosis with a musculoskeletal condition is associated with a higher probability of current pain and longer pain duration, whereas diagnosis with a gastrointestinal condition is associated with a higher probability of chronic pain lasting three months or more (electronic supplementary material, figure S6; table S12). Within the musculoskeletal illness category, the most common physician-assigned diagnoses are nonspecific low back pain (assessed independently by the physician, without input from the anthropologists collecting pain data), myalgia, arthritis, polyosteoarthritis and sciatica. Within the gastrointestinal illness category, the most common physician-assigned diagnoses are gastritis and duodenitis. After adjusting for the number of statistical tests, only diagnosis with a musculoskeletal condition is significantly associated with current pain, and the sum of diagnosis categories significantly predicts current pain, pain duration and chronic pain lasting three months or more. Other broad illness categories (e.g. respiratory or genitourinary illnesses) are

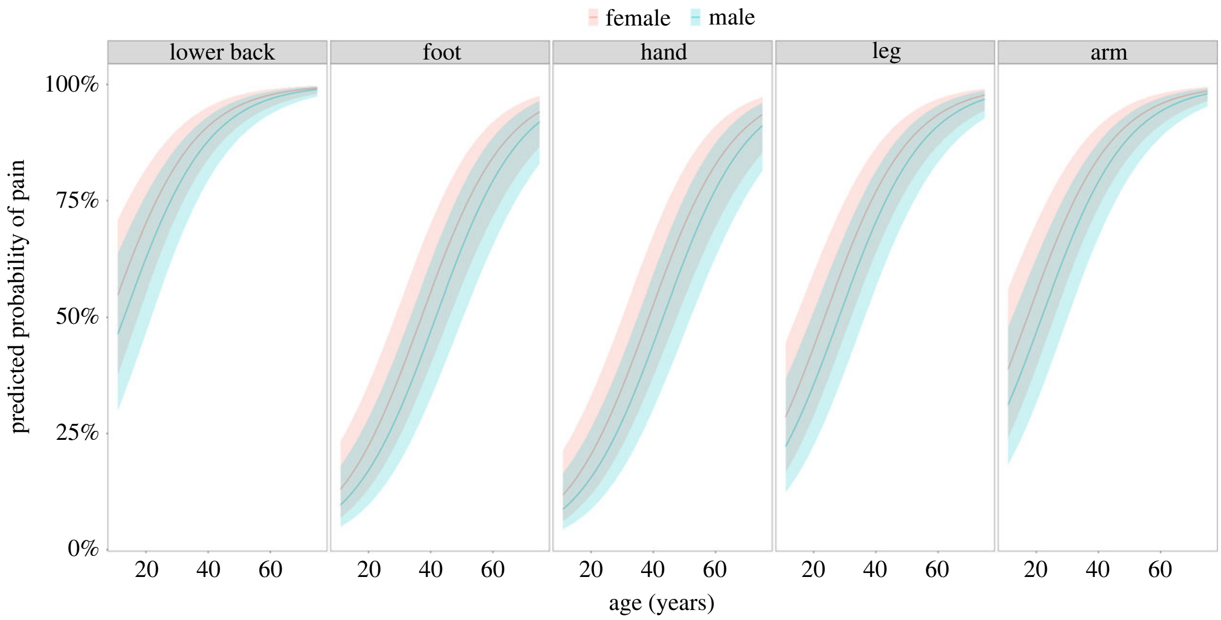

Figure 2. Predicted probability of current pain by age, sex and anatomical location ($n = 2110$ person-observations for 388 individuals across 16 villages). Probabilities are estimated from the model in the electronic supplementary material, table S4.

not significantly associated with any pain outcome in best-fit models. No pain outcome is associated with vital signs (i.e. heart rate, breathing rate, systolic or diastolic blood pressure and pulse pressure (systolic-diastolic)).

(e) For women, pain is not associated with reproductive history

Neither age at first birth, mean IBI, parity nor giving birth in the past year is associated with any pain outcome (electronic supplementary material, figure S7; electronic supplementary material, table S13). We are unable to analyse these associations separately for post-menopausal versus reproductive-aged women with sufficient power because we sampled relatively few older women ($n = 19$ women aged 50+ years). We are also unable to explore associations between pain and age of menarche because we lack reliable menarche data.

(f) Pain declines with schooling, but most participants lack schooling

Schooling is associated with a lower probability of reporting current pain (electronic supplementary material, table S14) and shorter pain duration (electronic supplementary material, table S15), but not chronic pain (electronic supplementary material, tables S16–S17) after adjusting for age, sex, anatomical location and the sum of clinical diagnosis categories. Unlike participants with the modal (i.e. zero) years of schooling, participants with more schooling more commonly attribute work-related pain aetiology to commercial logging (electronic supplementary material, figure S8), which involves use of chainsaws, trucks and other labour-saving mechanized technology, and entails less walking than horticulture, hunting or foraging. Furthermore, participants with more schooling commonly attribute accident-related pain aetiology to falling while inebriated, rather than accidents incurred during work (electronic supplementary material, figure S9). Schooling is also associated with a lower probability of being diagnosed with a musculoskeletal condition, but is not negatively associated with other clinical diagnoses.

(g) Tsimane report more current pain than other populations, and intermediate rates of chronic pain

Age-standardized prevalence of current pain is 2.5–8.2 times higher for Tsimane men, and 1.7–6.5 times higher for Tsimane women compared to other populations (figure 3). The sex difference in current pain prevalence is second lowest among Tsimane (female-to-male ratio = 1.03); the lowest sex difference (female-to-male ratio = 0.99) is observed among a rural Indonesian sample consisting mostly of farmers.

For chronic pain, Tsimane men's age-standardized prevalence is either within the range of variation observed in other populations, or higher (figure 4). Tsimane women's prevalence is also within the range of variation for other populations, with some exceptions (i.e. Sweden and Canada) where prevalence is higher than among Tsimane. The sex difference in chronic pain prevalence is lowest among Tsimane only when chronic pain is defined as lasting six months or more (female-to-male ratio = 1.09).

4. Discussion

Tsimane pain is highly prevalent and widespread throughout the axial and appendicular skeleton. Similar to patterns observed in post-industrialized populations, back pain among Tsimane is especially pronounced, particularly at the thoraco-lumbar region. Strenuous habitual subsistence work is reported as the primary cause of both current and chronic pain across the lifespan for both sexes. Horticultural labour is strongly implicated in pain aetiology, as is hunting, foraging, long-distance walking integral to all subsistence production, and experiencing accidents occurring during work. Common accidents include falling from trees and when crossing slippery footbridges while carrying heavy loads (e.g. hunted game, tree logs for shelter construction, or bags of rice weighing up to approx. 45 kg). Bites, stings, and attacks from snakes, stingrays,

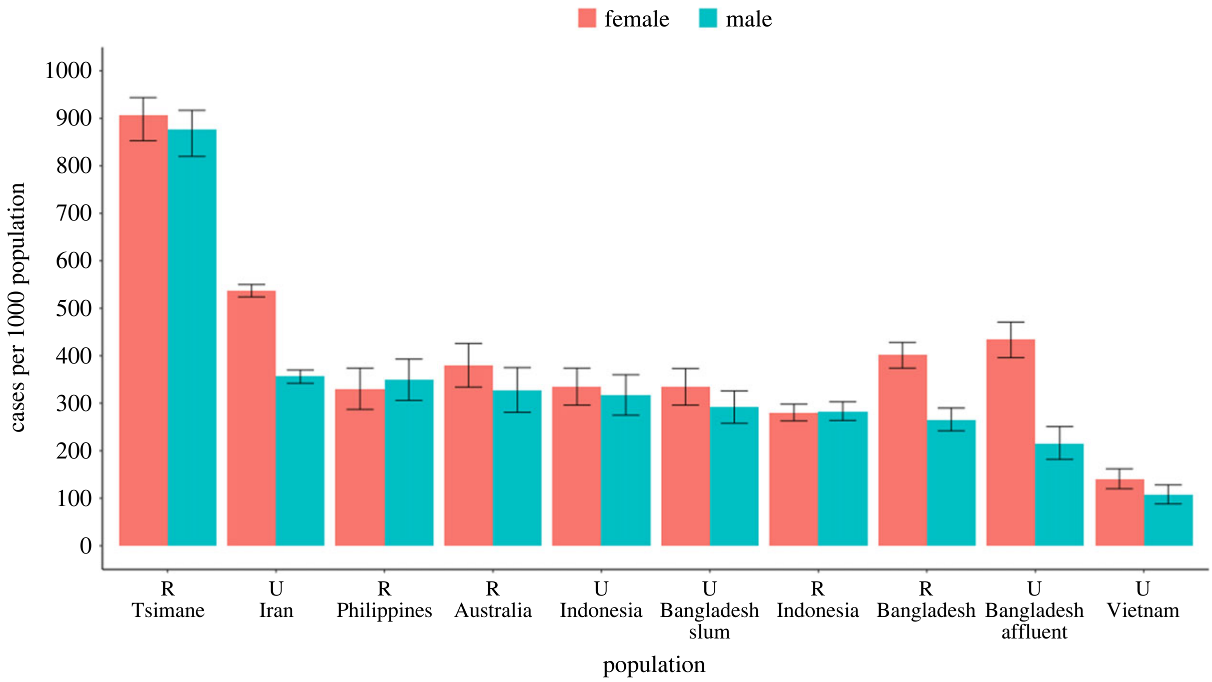

Figure 3. Age-standardized current pain prevalence (using direct method) by population and sex. Populations are shown in descending order of male prevalence; 95% confidence intervals (CIs) are exact binomial. R, rural; U, urban. References: Iran [35]; Philippines [36]; Australia [37]; Indonesia [38]; Bangladesh [39]; Vietnam [40]. Across populations, estimates are derived using the same minimum age of 15 years.

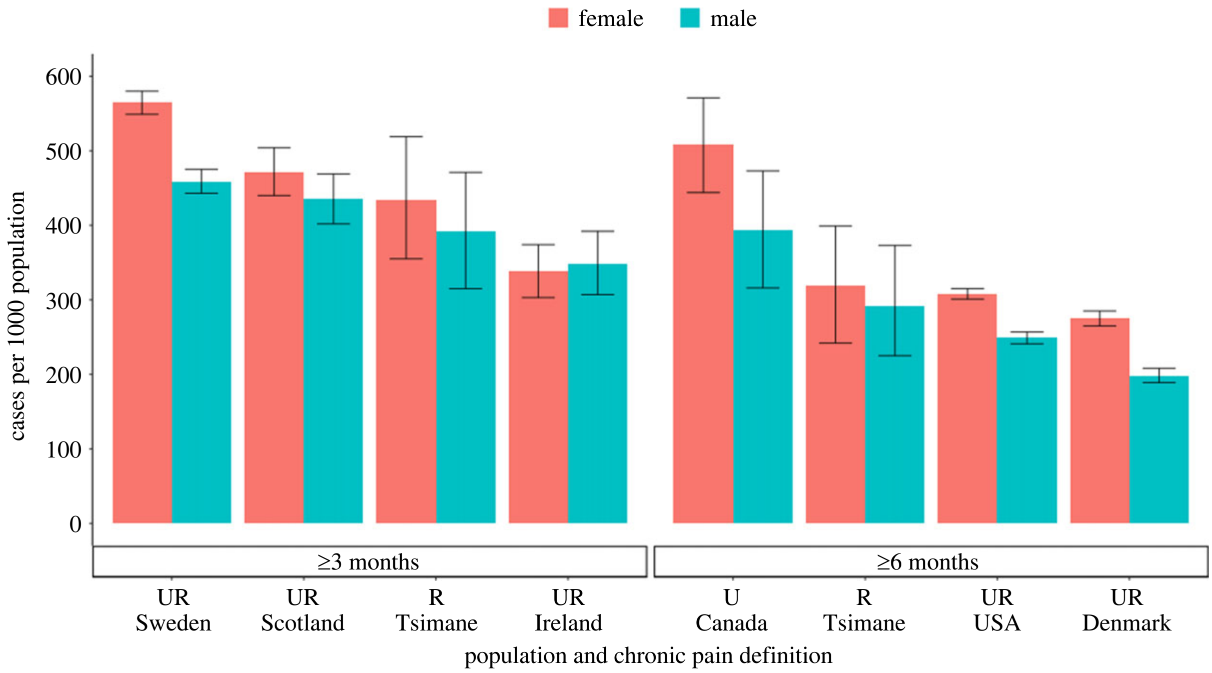

Figure 4. Age-standardized chronic pain prevalence (using direct method) by population, sex and chronic pain definition. Populations are shown in descending order of male prevalence; 95% CIs are exact binomial. UR, mixed urban/rural; R, rural; U, urban. References: Sweden [41]; Scotland [42]; Ireland [43]; Canada [44]; USA [45]; Denmark [46]. Note across populations estimates are not derived using the same mínimum age (range: 16 (Denmark, Tsimane) – 25 (Scotland); for Canada, USA, Sweden and Ireland = 18).

potential prey and a large variety of insects are also burdensome, and infections from those assaults are not uncommon.

Current and chronic pain increase with age. Declining physical condition owing to senescence [47,48] combined with greater cumulative mechanical stress from strenuous habitual work and greater cumulative exposure to environmental assaults (e.g. animal attacks) are probably principal causes of the age-related increase in pain. The fact that most reported pains are experienced during work, even among younger Tsimane, suggests that damaged musculoskeletal tissues fail to completely heal prior to resumption of daily physically demanding activities, which may cause additional tissue damage and pain vulnerability. While sleep can facilitate recovery, Tsimane do not sleep more than individuals in post-industrialized societies [49] and many tissue injuries require at least several weeks to completely heal.

Tsimane women report more pain than men across all pain outcomes, but sex differences in pain are not robust after inclusion of additional covariates. In comparative cross-cultural perspective, Tsimane sex differences in age-standardized pain prevalence are relatively weak (cf. [50]). These results are not surprising in light of the fact that Tsimane men and women both routinely participate in strenuous subsistence work (e.g. clearing brush with machetes, transporting heavy cultigens, and chopping firewood). Both men and women walk long distances [30], and experience work-related hazards that are not limited to falls (e.g. capsized dugout canoes; sunburn; puncture wounds from thorns while walking barefoot). During THLHP medical exams, both sexes also regularly report musculoskeletal problems indicative of osteoarthritis (OA). They both commonly experience diverse gastrointestinal infections [51], and we find that physician-assigned musculoskeletal and gastrointestinal diagnoses are associated with pain (electronic supplementary material, figure S6). While women report childbirth and breastfeeding as a cause of pain (figure 1; electronic supplementary material, figure S2), these reports are confined to early adult life (i.e. prior to age 40) and only represent less than 5% of women's self-reported pain causes. We also find no association between female reproductive history and pain in this high fertility context. Taken together, these results refute the hypothesis that reproductive effort is a prime driver of women's greater susceptibility to pain [18,19]. This hypothesis is partly derived from a vague notion, developed from empirical research in nonhuman animal models, that pain circuitry 'piggybacked' onto previously existing reproductive circuitry in the midbrain and brain stem. Our results also suggest that mechanical or other stress on soft tissues from pregnancy, parturition, and prolonged on-demand breastfeeding does not increase pain vulnerability for women compared to men. Various direct reproductive costs uniquely incurred by women thus do not obviously manifest as excess pain, even if such costs may later contribute to elevated morbidity or disability among women compared to men [52]. We nevertheless acknowledge that our pain questionnaire omitted certain anatomical locations (e.g. the hip and pelvis) which could have contributed to greater sex differences in Tsimane pain. It is also likely that women's frequent carrying of young children contributes to back and perhaps other pain (cf. [31]); in women's self-reports of pain this form of childcare may have been expressed using the more general Tsimane word for 'work' (*carijtaqui*). Some of the greatest compressive vertebral loads occur when weights are carried in front of the body [53,54], which is how Tsimane women routinely carry infants and toddlers.

Given our community-based sampling and participants' limited pain prevention and treatment options, our results may generalize across diverse human populations and time periods. We surmise that some chronic pains were not uncommon prior to dietary reliance on intensive agriculture, and in this sense, chronic nonspecific low back pain is not a 'mismatch disease' limited to post-industrialized populations. Consistent with this idea, degenerative spinal OA is fairly common in early hominin vertebral remains [16,55] and OA is a leading cause of pain in modern humans [56]. Of course, we cannot make direct inferences about early hominin pain vulnerability, and early hominins vary greatly in their morphology, locomotion, and lifespan [4,57]. However, the fact that spinal pathologies in particular appear to be fairly uncommon in quadrupeds including chimpanzees and gorillas [55,58] suggests that transition to orthograde posture and associated changes in compressive loading patterns made bipedal hominins more susceptible to pain from recurrent mechanical stress. Hominin musculoskeletal changes supporting bipedalism probably imposed at least some health costs, which, after millions of years of evolution, remain a significant epidemiological burden that can be exacerbated by modern conditions. In response to recurrent mechanical stress and potential for tissue damage, natural selection is expected to have shaped mechanisms to respond adaptively by altering pain thresholds and salience. Adaptive responses to recurring painful stimuli can, in theory, be characterized by increased pain sensitivity (consistent with the 'smoke detector principle') or decreased pain sensitivity (e.g. during callus formation from recurring skin abrasions) [59]. A key evolutionary question is to what extent modern conditions generate adaptive alterations or deleterious side effects, which can be vulnerable to runaway positive feedback, whereby lower pain thresholds increase chronic pain risk.

In comparative cross-cultural perspective, Volinn [60] hypothesized that musculoskeletal pain (specifically of the lower back) was more prevalent in lower- versus higher-income countries because, in the former, strenuous physical labour is more prevalent and unavoidable given limited occupational alternatives. Consistent with this hypothesis, age-standardized current pain prevalence is 1.7–8.2 times higher for Tsimane than other populations (figure 3), and Tsimane back pain is more prevalent than pain at other anatomical locations. Back and other pain is also prevalent in adults from certain rural low-income African populations whose livelihoods rely on strenuous physical labour [23]. Work-related repetitive mechanical stress or trauma can accelerate senescence of musculoskeletal tissues including load-bearing joints, as suggested by the relatively high rates of often painful OA in the distal interphalangeal joints of textile mill workers [61], in the knees of those with physically demanding occupations entailing frequent knee bending [62], in the hips of farmers regularly lifting heavy weights for prolonged periods [63], and in joints that are rarely affected by OA (e.g. elbows, wrists and metacarpal phalangeal joints) among jackhammer operators [64]. Excessive and repetitive overloading is also posited to be a primary cause of tendinopathy (see [65] and references therein). In open-ended pain questionnaire responses, Tsimane frequently report pain at the shoulder and knee, which are heavily and frequently loaded during horticultural and other subsistence tasks, and which are common sites of tendinopathies for humans more generally.

Yet contrary to Volinn's hypothesis, he showed in a review of population-based surveys that lower back pain point prevalence was approximately 2–4 times higher in high-income countries (range: 14–42%) than low-income countries. Within low-income countries, pain prevalence was higher in urban versus rural samples (urban range: 23–43%; rural range: 0–18%). Despite variation in methodology across studies (e.g. precise wording of questions used to elicit pain responses; sampled age ranges), Volinn concluded that '…either hard physical labour is not necessarily related to low back pain prevalence or that there are other factors in low-income rural populations that intervene and attenuate the relationship' [60, p. 1752]. One potential factor is young age structure, although, if taken at face value, our age-standardized population-level comparisons (figures 3 and 4) render this possibility unlikely. Another potential factor is that limited access to modern pain treatment options in low-income settings renders individuals less attentive to, and thus less likely to report pain, but again our findings render this possibility unlikely.

We note that our population-level comparisons are not so straightforward for several reasons, including lack of standardization across studies in pain data collection methods, and potential group-level variability in norms affecting pain reporting. Reporting bias is also a concern for self-report data, but we have no reason to suspect systematic over- or under-reporting of pain in the Tsimane sample. These considerations aside, a parsimonious explanation for the population-level variation is that routine physical activity including exercise can, up to some point, protect against pain [22], but at excessive levels it causes pain, and that rapid changes in lifestyles and environments accompanying industrialization and urbanization exacerbate evolved susceptibilities to pain-inducing musculoskeletal problems (cf. [66,67]). Candidates for such changes include greater physical inactivity, energetic surplus and obesity, lifespan extension, and inadequate mechanical loading from soft mattresses and shoes with cushioned heels.

5. Conclusion

Pain is reliably associated with overuse, underuse and misuse of the musculoskeletal system across human populations. Recurrent mechanical stress and traumatic accidents that are inextricably linked to habitual strenuous subsistence work constrain the extent to which even highly conserved adaptive pain mechanisms minimize tissue damage and promote healing. Regular exposure to infectious and non-infectious diseases reinforces these constraints, since defences require time and energetic resources. For physically active populations like the Tsimane in the early stages of urbanization, changes in the nature of human capital investments towards greater schooling, and away from reliance on activity-intensive subsistence skill development, provides economic opportunities using labour-saving technology, thereby reducing certain mechanical stress exposures. As urbanization and market integration continue, concomitant reductions in activity levels can potentially be excessive and interact with other lifestyle or environmental features to increase pain vulnerability. How these features interact to influence pain sensitivity remains an open question, and future research in transitioning rural subsistence populations is likely to reveal novel insights.

Ethics. Institutional IRB approval was granted by the University of California-Santa Barbara (no. 3-16-0766), as was informed consent at three levels: (i) Tsimane government that oversees research projects, (ii) village leadership, and (iii) study participants.

Data accessibility. All relevant computer code for variable definitions and statistical analysis is downloadable from the following GitHub repository: https://github.com/ybuoro/labor-pain-tsimane. Individual-level data are stored in the Tsimane Health and Life History Project (THLHP) Data Repository, and are available through restricted access for ethical reasons. THLHP's highest priority is the safeguarding of human subjects and minimization of risk to study participants. The THLHP adheres to the CARE Principles for Indigenous Data Governance, which assure that the Tsimane: (i) have sovereignty over how data are shared; (ii) are the primary gatekeepers determining ethical use; (iii) are actively engaged in the data generation; and (iv) derive benefit from data generated and shared use whenever possible. The THLHP is also committed to the FAIR Principles to facilitate data use. Requests for individual-level data should take the form of an application that minimally details the exact uses of the data and the research questions to be addressed, procedures that will be employed for data security and individual privacy, potential benefits to the study communities and procedures for assessing and minimizing stigmatizing interpretations of the research results (see the following webpage for links to the data sharing policy and data request forms: https://tsimane.anth.ucsb.edu/data.html). Requests for individual-level data will require institutional IRB approval (even if exempt) and will be reviewed by an Advisory Council composed of tribal leaders, tribal community members, Bolivian scientists, and the THLHP leadership. The study authors and the Tsimane leadership are committed to open science and are available to assist interested investigators in preparing data access requests.

The data are provided in electronic supplementary material [68].

Authors' contributions. J.S.: conceptualization, data curation, formal analysis, investigation, methodology, resources, software, supervision, validation, visualization, writing—original draft, writing—review and editing; Y.B.: data curation, formal analysis, methodology, visualization; B.B.: data curation, methodology, software; B.C.T.: writing—review and editing; H.K.: funding acquisition, project administration, supervision; M.G.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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