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Exceptionally low mortality despite widespread COVID-19 infection among Indigenous Tsimane and Moseten of Bolivia

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ABSTRACT

We report on the prevalence of and mortality from SARS-CoV-2 among the Tsimane and Moseten, two Indigenous subsistence groups in Bolivian Amazonia, and show that they evidence the lowest infection fatality rate ever reported. These populations have minimal access to medical care, a history of high parasite and pathogen exposures, and upregulated immune responses compared to industrialized populations. Between July and December of 2020, and again March - May of 2021, 85.4% of the Tsimane population aged 17+ were interviewed, and 42.0% provided blood samples. Among the Moseten aged 17+, 38.3% were interviewed and 38.6% provided blood samples. Blood samples were analyzed for SARS-CoV-2 antibodies with a mix of point-of-care IgG/IgM and ELISA with seroneutralization. The pandemic experience of these groups during the initial 2020 wave contrasts sharply with that observed in more industrialized contexts: while 71% and 63% of the Tsimane and Moseten populations were infected with SARS-CoV-2, mortality was minimal, with infection fatality ratios of 0.009% and 0.095%, respectively. The mortality rate for the Tsimane is 1/23rd the expectation based on rates

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observed elsewhere in the world. Disease severity—as measured by length of illness, ELISA antibody titers, and virus neutralizing test titers—did not increase markedly with age. We propose that low fatality, despite high transmissibility and non-negligible severity, may be due to a more vigorous and effective immune response to infection, with implications for future global pandemics.

In North America and Eurasia, SARS-CoV-2 severity and mortality is consistently observed to increase sharply with age, and is associated with co-morbidities indicative of chronic metabolic dysregulation, including diabetes, obesity, and hypertension (Nguyen et al., 2022; Reyes-Sánchez et al., 2022). Historically, Indigenous groups have suffered higher vulnerability to infectious diseases due to several factors, including immunological naivety to infectious agents, high rates of transmission within tight-knit communities, and low access to medical care, medicine, and vaccines (Curtice and Choo, 2020; Díaz de León-Martínez et al., 2020; Kraft et al., 2023; McLeod et al., 2020). At the start of the SARS-CoV-2 pandemic, there was much concern about how the infection might affect vulnerable small-scale populations with minimal health infrastructure (Cupertino et al., 2020). In the U.S. and elsewhere, poverty and minority status have been associated with vulnerability to severe COVID-19 (Fiske et al., 2022; Mishra et al., 2021; Naylor-Wardle et al., 2021). Indigenous communities with substantial prevalence of chronic co-morbidities, such as the Diné and others, suffered substantial loss of life from the disease (Angel de Soto and Hakim, 2020; CDC, 2022; Crimmins, 2020; Kakol et al., 2020; Arrazola et al., 2020).

To date, there have been relatively few detailed systematic studies of SARS-CoV-2 epidemiology in Indigenous populations (see Pickering et al., 2023), and none in Bolivian Indigenous communities (da Silva et al., 2022; Mendes et al., 2022; Sansone et al., 2022; Serrano-Coll et al., 2021). In lowland Bolivia, the Tsimane and Moseten are Indigenous populations that maintain high levels of physical fitness into old age, consume diets based largely on subsistence horticulture and foraging, and experience high burdens of parasitism and infectious disease (Blackwell et al., 2016; Gurven et al., 2017). They also have remarkably low levels of cardiovascular disease–i.e. low coronary artery calcification, peripheral vascular disease, and hypertension–and other metabolic co-morbidities (Gurven et al., 2012; Kaplan et al., 2017; Blackwell et al., 2015). However, respiratory infections, including pulmonary tuberculosis, are recurrent sources of morbidity and mortality (Gurven et al., 2007). Medical facilities are limited, especially among the Tsimane, except for a clinic on the outskirts of San Borja, the San Borja hospital, a few dispersed health outposts, and the Tsimane Health and Life History Project (THLHP) (Kaplan et al., 2020). Preceding and during the initial wave of SARS-CoV-2 in 2020, there were reasons to expect that the Tsimane and Moseten might be particularly vulnerable to the impacts of COVID-19 (Kaplan et al., 2020). Of particular concern was the welfare of elders, who serve important roles as transmitters of cultural practices and traditions (Phillips, 2020).

Here we present profiles of SARS-CoV-2 infection, morbidity, and mortality among the Tsimane and Moseten during the initial 2020 wave of SARS-COV-2, when only ancestral and B.1 lineage strains circulated and immunizations were unavailable (Pastana et al., 2022). Additionally, we compare epidemiological results with those of the general French population during the same period (Carrat et al., 2021), employing identical laboratory methods. Unlike France, the U.S., and other industrialized contexts, our analyses indicate that Tsimane and Moseten display remarkably high prevalence of anti-SARS-CoV-2 antibodies. Metabolic indicators such as fasting blood sugar and body mass index are also unrelated to variation in disease severity within these groups. Most strikingly, the observed mortality rates for older adults in these populations are far below estimates from industrialized settings. Even accounting for their relatively young age structure and lack of predisposing co-morbidities, observed mortality rates among these groups were an order of magnitude lower than those expected from industrialized samples. We discuss several hypotheses to explain why, despite very high overall rates of infection and symptomatic presentation, older Tsimane and Moseten remained relatively well protected from severe disease and mortality. Understanding the factors that protected these populations from COVID-19 mortality despite a high prevalence of infection may provide important insights for lowering mortality from future pandemics.

1. Methods

1.1. Background

The Tsimane cultivate, fish, hunt and gather most of their own food (Kraft et al., 2018). Over 17,000 Tsimane live in over 100 villages. Half of the population is under age 15, and 4% are older than 60 years. Villages consist of small residential clusters and are connected by ties of kinship and social visitation. Most villages lack public sanitation, clean water, and electricity (Dinkel et al., 2020). This physically active population has excellent cardiovascular health (Kaplan et al., 2017)–with a low prevalence of obesity (4.1%), hypertension (12.3%), and diabetes (0.3%) (Kaplan et al., 2023)–but experiences a high pathogen burden that includes diverse micro and macro parasites (Blackwell et al., 2016). Cigarette smoking and drug use are negligible. Since the 1970s, roads and increased availability of motorized transport have facilitated more frequent travel to towns, particularly San Borja (population ~45,000).

The Moseten (population ~3000) are genetically, culturally, and linguistically similar to the Tsimane but began acculturation into broader Bolivian society decades earlier (Lea et al., 2023). Compared to Tsimane, the majority of Moseten have greater proximity to the market, Spanish fluency, schooling, and access to medical and public services (e.g. health posts in villages, running water, electricity) (Kraft et al., 2018). Visits between villages and nearby towns, especially Palos Blancos, are frequent. Despite having a more commercially-derived diet than the Tsimane, the Moseten still maintain a predominantly agrarian lifestyle. Obesity (15%), hypertension (16.6%), and type 2 diabetes (1.6%) are more prevalent (Kaplan et al., 2023), but still low (Gatz et al., 2022; Rowan et al., 2021). Because most Moseten still engage in high levels of physically intensive subsistence work, and exhibit significant infectious burdens, their environment and lifestyle can be considered intermediate between the Tsimane and industrialized populations, but more similar to the Tsimane.

1.2. Biomedical surveillance during the COVID-19 outbreak of 2020

The Tsimane Health and Life History Project (THLHP) has worked with the Tsimane and Moseten since 2002 to study health and aging while providing primary care and emergency medical services (Gurven et al., 2017; Kaplan et al., 2020). Our multinational team–including tribal members, local authorities, and health professionals–collaborated as planners, educators, and primary responders as the pandemic approached and diffused across Tsimane and Moseten territories starting mid-2020 (Kaplan et al., 2020). Interviews regarding individuals' COVID-19 experience were conducted with all available individuals aged 17+ during visits to Tsimane and Moseten communities between July and December of 2020. Follow-up interviews were conducted for a small number of missing individuals between March and May of 2021 (Kraft et al., 2023). Interviews queried self-reports of illness severity; symptoms (including loss of taste or smell, fever, cough, sore throat, difficulty breathing, diarrhea, weakness/fatigue, dizziness, and nausea);

date of symptoms onset; numbers of days ill, unable to work normally, and in bed due to illness; and use of medicinal plants. Physiological measures, like pulse oximetry, respiratory rates or blood biomarkers, were not systematically assessed, and so are not considered here. The THLHP medical team was able to visit and collect blood samples for antibody analysis in a representative sample of 19 Tsimane and 8 Moseten villages during the same period. Based on village census records, among residents of the Tsimane villages aged 17+, 85.4% were interviewed and 42.0% provided blood samples; among residents of the Moseten villages aged 17+, 38.3% and 38.6% were interviewed and provided blood samples, respectively. Sampling targeted all willing adults present in the village during our visit, and was not conditional on COVID status, or symptom history or severity. In models examining whether interviewed participants in our serological sample differed in symptom severity from those who were not included, we found no statistically significant evidence that Tsimane or Moseten who reported more infection severity (e.g. days ill, not working, or in bed; respiratory problems; anosmia or ageusia) were more likely to provide a blood sample.

1.3. Serology testing

An initial assessment of SARS-CoV-2 serological status was performed using FaStep COVID-19 IgG/IgM rapid antibody tests (Assure Tech Ltd., Hangzhou China). From October 10, 2020 to December 18, 2020, dried blood spots (DBS) were collected for a more definitive determination of the SARS-CoV-2 serological status of all samples collected during the first wave (July to December of 2020, one to four months after infection).

We employed a commercial Anti-SARS-CoV-2 Quantivac ELISA IgG (Euroimmun) and an in-house Virus Neutralization Tests (VNT), using the same approach described previously for the French population (Carrat et al., 2021; Gallian et al., 2020, 2023a). DBS were eluted with phosphate-buffered saline (PBS) and analyzed with the commercial ELISA according to manufacturer's recommendations. Specimens with binding antibody units per mL (BAU/mL < 25.6, $25.6 \leq$ BAU/mL < 35.2, BAU/mL ≥ 35.2) were considered negative, equivocal and positive, respectively.

Samples with BAU/mL ≥ 18 were then tested by an in-house Virus Neutralization Tests (VNT). The test consisted of mixing 55 μL of a serially diluted (from 1/20 to 1/160) patient sample in Dulbecco's Modified Eagle Medium (DMEM) with 1% of penicillin/streptomycin, Non-Essential Amino Acids and Glutamine, with 55 μL of a fixed quantity of the SARS-CoV-2 D614G BavPat1 strain (B.1 lineage; courtesy of Prof. Drosten, Berlin) corresponding to 0.5 TCID50/μL of sample dilution. This mixture was then incubated for 1 h at 37 °C. One hundred μL of the mixture was then transferred onto a confluent Vero E6 TMPRSS2+ cells monolayer and incubated at 37 °C under 5% of CO2. On day 5 post-infection, dilutions showing a cytopathic effect (CPE) were considered negative (no neutralization) and those without CPE were considered positive (complete neutralization of the SARS-CoV2 inoculum). The neutralization titer was quantified as the highest serum dilution with a positive result. Specimens with a VNT titer $\geq$40 were considered as positive.

To consider the possibility that antibody or VNT concentrations may have declined if we sampled people long after their illness, we evaluated whether closer timing between reported COVID infection and blood sampling was related to IgG or VNT titer concentrations. We found no significant relationship between the time elapsed between reported dates of infection and of blood sampling for either IgG ($b = 0.414$, $p = 0.255$) or VNT ($b = 0.090$, $p = 0.402$) titers.

Four assays were performed to determine the Common Cold Coronaviruses (CCC) and SARS-CoV-2 pre-pandemic serological status of a subset of individuals ($N = 43$) available from medical visits by the THLHP prior to 2019. The commercial Anti SARS-CoV-2 Quantivac ELISA IgG (Euroimmun) and an in-house Virus Neutralization Tests (VNT) were carried out as described above. The commercial chemiluminescent immunoassay Access II SARS-CoV-2 IgG Antibody (Beckman Coulter) allowed the semi-quantitative determination of IgG antibodies to SARS-CoV-2 receptor binding domain (RBD). The amount of anti-SARS-CoV-2 RBD IgG antibodies in the sample was determined from a stored multipoint calibration curve. All tests were conducted according to the manufacturer's recommendations. A cut-off of 30 IU/mL was used for positivity as recommended by the manufacturer. Finally, an in-house qSAT assay based on the Luminex xMAP platform was performed using the following antigens: the S1 and RBD Spike domains from the 229E, HKU1, NL63 CCCs, the S1 for OC43 CCC, and the trimeric extracellular domain (ECD) (aa 16-1213) of Spike protein in its prefusion form (S), the RBD and the CTD domain nucleoprotein (NCP) from the SARS-CoV-2.

All antigens, with exception of the NCP, were obtained from Sino-Biologicals and were produced in HEK293 cells expression system. The NCP was obtained from the European Viral Archive goes Global (EVAg) repository (www.european-virus-archive.com; ref: 100P-03957). Each antigen (60 pmol/10^6 beads) was coupled to a distinct region of MAG-PLEX® magnetic microspheres (Luminex Corporation) using the xMAP® Antibody Coupling Kit (Luminex Corporation) following manufacturer's recommendations. The coupled beads were resuspended and counted on a Countess™ II Automated Cell Counter (Thermo) to a final concentration of 2x10^6 bead/ml. Samples diluted in Wash Solution (Thermo) at 1/400 were incubated with 1000 coupled beads per well for 1 h at room temperature in a plate shaker protected from light. After two washes, the beads were incubated with R-Phycoerythrin AffiniPure F (ab')$_2$ Fragment Goat Anti-Human IgG (H + L) (Jackson ImmunoResearch) for 1 h at room temperature in a plate shaker protected from light. After washing, antigen-antibody reactions were read on an INTELLIFLEX® system using the xPONENT® software (Luminex Corporation) and the results were expressed as median fluorescence intensity (MFI). Cut-off values for each CCC antigen were obtained from a non-exposed cohort by calculating the mean MFI plus two Standard Deviation (SD). Cut-off values for each SARS-CoV-2 antigen (S, RBD and NCP) are described elsewhere (Inchauste et al., 2024).

Positive and negative status for the CCCs and SARS-CoV-2 (cross-reaction) were then established for each pre-pandemic sample. For each CCC, samples were considered as positive if a qSAT positive result was obtained from both S1 and RBD antigens (except for OC43 where only S1 antigen was available). To evaluate the potential SARS-CoV-2 cross-reaction, positive samples were considered if at least 2 tests (Anti SARS-CoV-2 Quantivac ELISA IgG, Access II SARS-CoV-2 IgG Antibody test, qSAT assay (S, RBD and NCP) and VNT) were positive.

1.4. Health biomarker data collection prior to COVID-19

Measures of metabolic and immune health were available from clinical visits by the THLHP to study communities prior to 2020. These included height and weight; systolic and diastolic blood pressure; fasting blood glucose; white blood cell count; eosinophil count; and IgE (see Kaplan et al., 2017) for laboratory procedures).

1.5. Assessment of mortality

The THLHP collects information on all deaths that occur each year and assesses the cause of each death through a combination of THLHP medical records, hospital records, and verbal autopsies with family members. We ensured that we did not miss any COVID-19-related deaths using two methods. First, in addition to the surveillance by the THLHP, we coordinated and surveyed several local sources: the San Borja municipal hospital staff with whom we confer for Tsimane patients, a health clinic for Tsimane located near San Borja, and health clinics adjacent to Tsimane and Moseten villages. No additional COVID-19 deaths were uncovered from these efforts. Second, we compared all-cause mortality rates from 2018 to 2022 (see Supplementary Table S6). Similar average mortality rates over time are consistent

with no under-reporting of deaths in general, although there is an apparent increase in deaths under age 18 during 2020-21, probably due to the collapse of medical facilities at that time.

1.6. Data analysis

The results from the ELISA test were preferred in the determination of COVID-19 status (positive/negative). All serological results were compared and analyzed with the 67,275 individuals from the French population using the same approach (Carrat et al., 2021). COVID-19 prevalence was modeled as a function of age, sex, population (Tsimane or Moseten), and biomarker variables using logistic regression (i.e. the glm function) in R. Measures of disease severity and duration (days ill, not working normally, or in bed) were modeled as a function of age, sex, population, and symptoms using linear regression (i.e. the lm function) in R. SARS-CoV-2 IgG Antibodies (BAU/mL) and VNT titers were modeled as a function of age, sex, population, severity, symptoms, and biomarker variables using linear regression. This analysis included loss of taste or smell and difficulty breathing as the symptoms most specifically associated with COVID-19 infection.

For the expected mortality calculation, we compared the observed number of Tsimane and Moseten deaths with mortality data from France and the U.S. We based the probability of dying given infection on the composite Infection Fatality Ratios (IFRs) and their 95% uncertainty intervals reported in Sorensen et al. (2022), prior to vaccines and widespread evolution of variants. Direct comparisons between Tsimane/Moseten and French/US mortality statistics are complicated by substantial population-level differences in SARS-CoV-2 risk factors (e.g., age and chronic disease co-morbidities). To discern whether these differences explain population disparities in IFRs, we compared mortality expectations under several scenarios: (1) assuming actual Tsimane and Moseten age structure and comorbidities; (2) assuming age structure and comorbidity prevalences of France and the U.S.; and (3) assuming actual Tsimane and Moseten age structure but comorbidities of France, the U.S. and the world. We used an at-risk epidemiological coverage of 16,000 and 3,400 individuals, for Tsimane and Moseten, respectively. We incorporate the effects of comorbidities by multiplying IFRs by the age-specific hazard ratios for COVID-19 mortality given in Williamson et al. (2020) (for hypertension HR = 1.09; for diabetes HR = 1.95; for obesity HR = 1.40), using comorbidity prevalences for France (Neufcourt et al., 2020; Fontbonne et al., 2023; statista, 2015), the U.S. (Hales et al., 2020; CDC, 2017), and the world (Boutari and Mantzoros, 2022; Mills et al., 2016; Diabetes Federation, 2021).

2. Results

2.1. COVID-19 prevalence among the Tsimane and Moseten during the initial wave of infections

Interviews regarding individuals' experience during the initial wave of COVID-19 indicate that SARS-CoV-2 infections emerged within the Tsimane territories in the first weeks of June 2020, and culminated in a peak in August with around 250-300 cases daily (Fig. 1). Infection rates inferred from IgG antibody analysis were high, with approximately 71.4% and 63.0% of the adults sampled in the Tsimane (N = 685) and Moseten (N = 562) populations testing positive, respectively. Prevalence in both populations was substantially higher than that observed among the French (4.0%) by the end of the same six-month period, consistent with a much more rapid spread. Infection prevalence did not significantly vary by age or sex in either the Tsimane or Moseten (Fig. 2 and Table S1).

2.2. Evaluation of severity of symptoms

The frequency of self-reported symptoms among Tsimane, Moseten and the French population testing positive for SARS-CoV-2 IgG antibodies are given in Fig. 3. Among the Tsimane and Moseten, the rate of self-reported asymptomatic cases among those who were antibody positive was equivalent to that observed among the French (20.5% of positive cases). Among the Tsimane and Moseten, one or more symptoms were reported by 79.5% of individuals, with the most common being headache (73.5%), weakness or fatigue (66.4%), fever (61.2%), cough (61.1%) and loss of taste or smell (54.5%). While severe respiratory distress appears to have been relatively rare, the Tsimane and Moseten reported difficulty breathing in 42.1% of positive cases. Except for diarrhea, both the Tsimane and Moseten reported a higher frequency of every symptom compared to the French population.

Duration of illness and disability also provided a window into severity (Fig. 4). Among individuals with SARS-CoV-2 antibodies, 50% reported being ill for more than 1 week (18% between 1 and 2 weeks, and 33% more than 2 weeks). Most people said that they tried to work even when sick, and relatively few were bedridden for more than a few days. Among those SARS-CoV-2 positive, the number of days ill was significantly higher among the Tsimane compared to the Moseten (Table 1). The number of days in bed and working less were significantly associated with age, but the effects are rather small (Table 1 and Supplementary Fig. S1). Longer durations of illness and disability were associated with loss of taste or smell and difficulty breathing (Table 1). Days ill, in bed, and working less among SARS-CoV-2 positive were not predicted by most pre-infection health measures (BMI, diastolic blood pressure, fasting blood glucose, white blood cell count, eosinophil count, or IgE; Table S2). Previously measured systolic blood pressure showed a

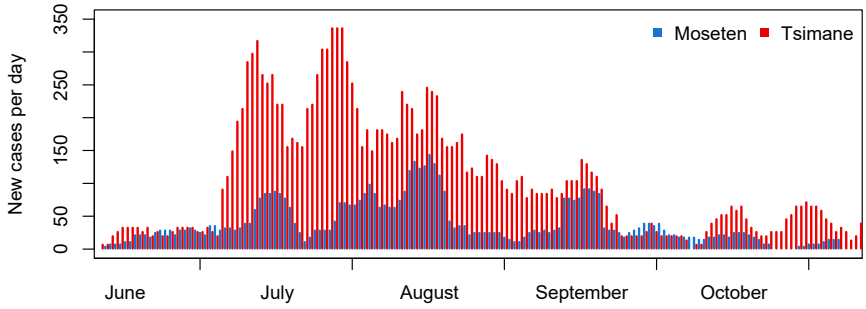

Fig. 1. Time course of SARS-CoV-2 infection in 2020. Timing was based on the first day of illness reported by Tsimane and Moseten with positive COVID-19 antibody tests.

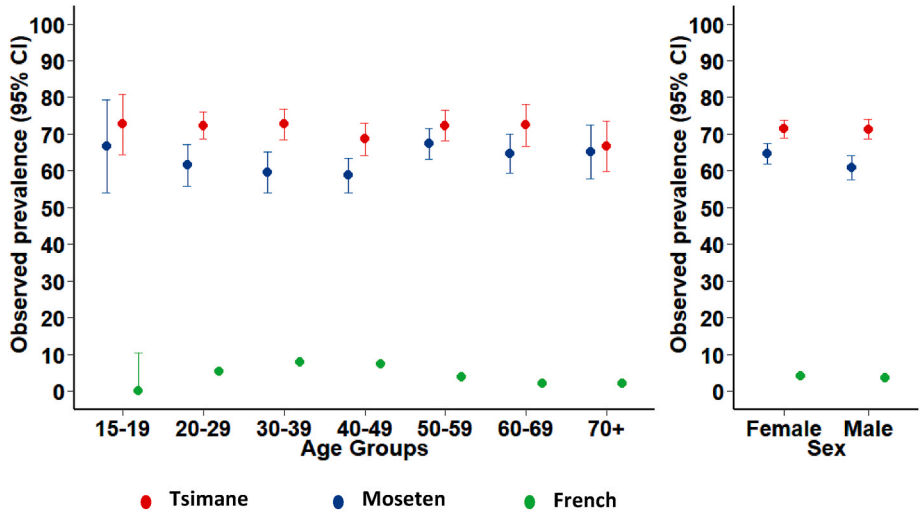

Fig. 2. Observed prevalence of anti-SARS-CoV-2 IgG antibodies, stratified by population (Tsimane, n = 685; Moseten, n = 562; French, n = 67,275), age and sex, with 95% confidence intervals.

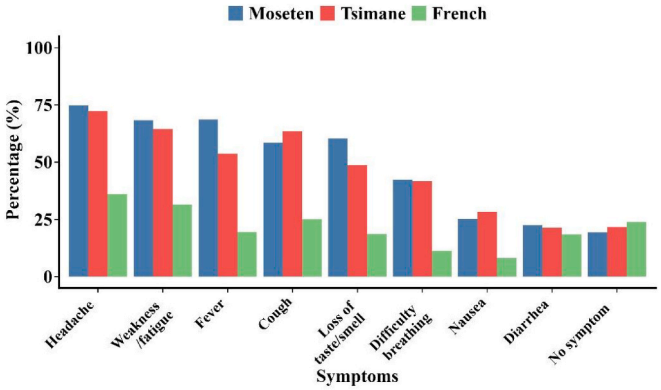

Fig. 3. Frequency of symptoms reported by individuals with positive antibody tests.

weak positive relationship with days spent in bed (Table S2).

2.3. Immune responsiveness and factors associated with anti-SARS-CoV-2 IgG antibody levels

Anti-SARS-CoV-2 IgG antibody levels (BAU/mL) differed greatly among the three populations. Among those testing positive, antibody levels were highest among the Moseten, followed by the Tsimane, and then by the French (Fig. 5a and Table 2a). Both Indigenous populations exhibited much higher antibody levels than the French population for the same period. Both French males and females exhibited mean antibody levels 30-40% lower than the Tsimane female baseline. Among Moseten males and females and among Tsimane males, antibody levels were significantly higher at later ages. The age trend among Tsimane females and French males and females is estimated to be positive but not statistically significant. Fig. 4a shows that the relationship between age and antibody levels in Tsimane women is non-monotonic: lowest in middle age, and highest among those 60+. Most measures of cardiometabolic and immune health collected prior to the pandemic—BMI, systolic and diastolic blood pressure, fasting blood sugar, eosinophil count, and IgE— were not associated with IgG antibodies (Table S3). IgG antibodies were positively predicted by previously measured white blood cell count (Table S3). We also examined whether antibody levels were associated with self-reported indicators of infection severity. IgG antibodies were positively associated with more days spent ill or in bed, fewer days working, difficulty breathing, and loss of taste or smell (Table S4).

2.4. Factors associated with virus neutralization test (VNT) titers

The prevalences of SARS-CoV-2 neutralizing antibodies among SARS-CoV-2 positive Moseten and Tsimane were 53.9% and 53.6%,

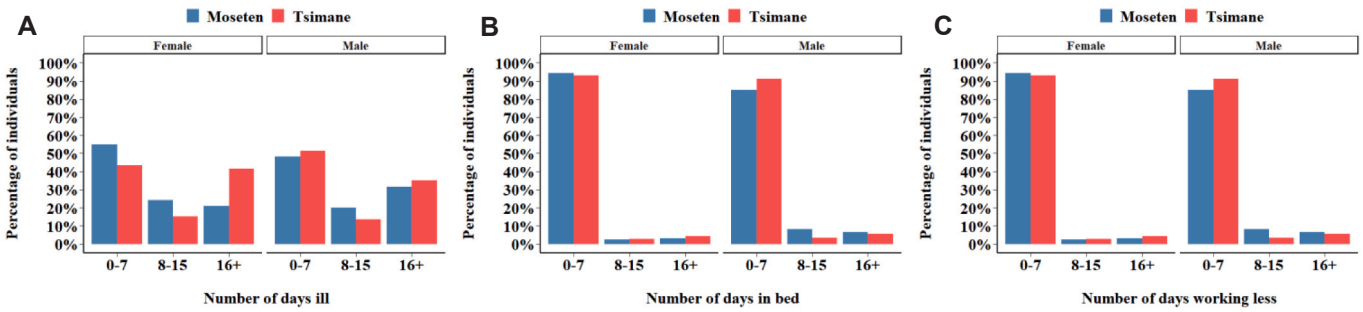

Fig. 4. Distribution of behavioral severity measures–days ill, in bed, and working less–among Tsimane and Moseten testing positive for SARS-CoV-2.

Table 1
Behavioral severity measures by age, sex and population. Linear regressions predicting number of days ill, days in bed, and days working less among Tsimane and Moseten testing positive for SARS-CoV-2.

	Days ill (N = 700; adjusted R^2 = 0.157)			Days in bed (N = 701; adjusted R^2 = 0.102)			Days working less (N = 698; adjusted R^2 = 0.094)		
Parameter	B	SE	p	B	SE	p	B	SE	p
(Intercept)	13.516	1.712	<0.0001	1.063	0.558	0.0570	3.180	1.041	0.0023
Tsimane Females (baseline)	-	-	-	-	-	-	-	-	-
Tsimane Males	−3.139	2.215	0.1569	0.366	0.720	0.6109	−0.081	1.347	0.9521
Moseten Females	−12.577	2.260	<0.0001	−0.867	0.733	0.2368	−2.010	1.372	0.1434
Moseten Males	−9.364	2.556	0.0003	1.300	0.830	0.1177	1.317	1.554	0.3972
Age (centered on 45)	0.074	0.053	0.1629	0.062	0.017	0.0003	0.084	0.032	0.0093
Loss of taste or smell	12.653	2.124	<0.0001	2.153	0.686	0.0018	5.338	1.282	<0.0001
Difficulty breathing	6.693	2.131	0.0018	2.676	0.688	0.0001	3.919	1.287	0.0024

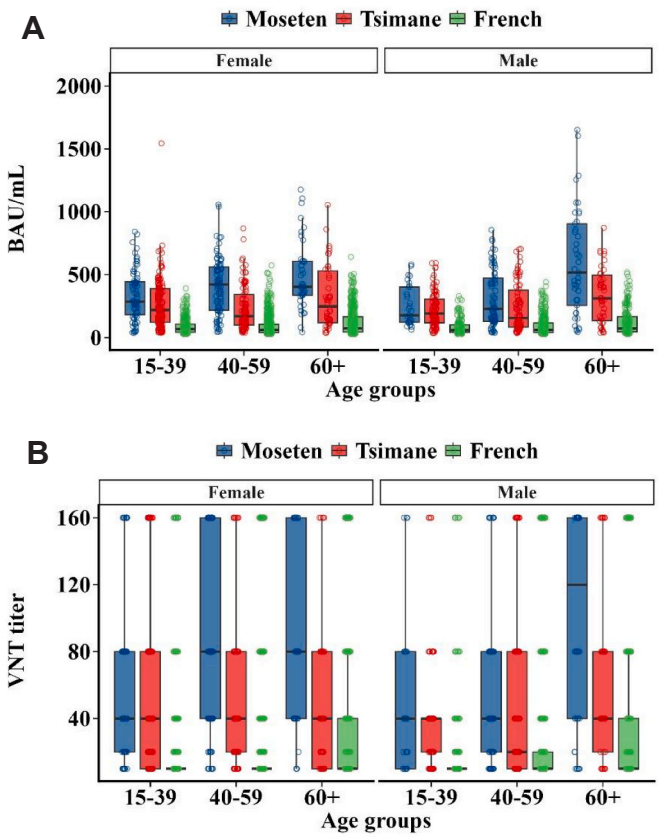

Fig. 5. Antibody responses among Tsimane, Moseten and French. (a) Mean anti-SARS-CoV-2 IgG antibodies levels and (b) mean VNT titer as a function of age, with 95% confidence intervals.

respectively. The French population, in contrast, showed a dramatically lower prevalence of 1.1% for the same time period. VNT titers and SARS-CoV-2 IgG antibodies measurements were closely correlated (Supplementary Fig. S2). Similar to SARS-CoV-2 IgG antibodies levels, VNT titers were significantly higher among Moseten than Tsimane, and were higher with age in all groups but Tsimane females (Fig. 5b–Table 2b). VNT titers were not significantly associated with previously measured BMI, fasting blood sugar, diastolic blood pressure, white blood cell count, eosinophil count, or IgE (Table S4). There was a weak positive relationship between prior systolic blood pressure and VNT titers (Table S5). We also examined whether VNT titers were associated with self-reported indicators of infection severity. In models that adjusted for IgG antibodies, VNT titers were only significantly associated with fewer days working (Table S4).

2.5. Evaluation of pre-existing immunity against coronaviruses among tsimane and Moseten

Serological testing of a pre-pandemic subset (N = 43) revealed high apparent prevalence for all Common Cold Coronaviruses (83.7% for NL63, 100% for OC43, 88.4% for HKU1, and 44.2% for 229E). No humoral cross-reactivity with SARS-CoV-2 antigens was detected across the four assays employed, suggesting that prior exposure to endemic coronaviruses did not generate detectable cross-reactive antibodies against SARS-CoV-2 in pre-pandemic samples.

2.6. Mortality from COVID-19

We report a total of three deaths due to COVID-19 during the first wave of infection (June-December 2020): one Tsimane and two Moseten. The Tsimane case was a 79-year-old man who experienced cough, fever and shortness of breath during the two weeks prior to his death. Before the onset of his illness, his relatives had presented with COVID-19 symptoms. There was no COVID-19 test to confirm his diagnosis. The first case among the Moseten was a 67-year-old man who had cough, fever and shortness of breath one week before his death. He was hospitalized with the diagnosis of COVID-19 in Cochabamba. The second was a 71-year-old ethnically Mojeño-Trinitario man living within the Moseten region.

Fig. 6 reports the observed and age-standardized IFRs for Tsimane, Moseten, France, United States, and the world. The observed IFRs for the Tsimane and Moseten were 0.009% and 0.095%, respectively. Even after standardizing by the global age-structure to account for the younger age of the two populations, the rates are only 0.042% and 0.123%, for the Tsimane and Moseten, respectively. In contrast, the observed IFRs for France and the U.S. are quite high (0.595% and 0.791%, respectively). However, the IFRs for France and the U.S. with global age-standardization (0.266% and 0.453%) are considerably lower than the global ratios (0.73%) (Sorensen, 2022), most likely due to more effective hospital interventions and relative wealth. The lack of adequate hospital facilities and the low income of the Tsimane and Moseten makes their extremely low IFRs even more notable.

To examine whether the low Tsimane and Moseten IFRs are due to their young age-structure and low chronic disease comorbidity, Table 3 compares the observed number of deaths in the two populations with those expected assuming Tsimane/Moseten, French, U.S., or global age

Table 2
Linear regressions predicting ELISA antibody and viral neutralizing test (VNT) titers.

	A. ELISA Antibody Titer (BAU/mL) (N = 3,506, Adjusted R^2 = 0.354)			B. Viral Neutralizing Titer (N = 3,263, Adjusted R^2 = 0.165)		
Parameter	**B**	**SE**	**p**	**B**	**SE**	**p**
(Intercept)	266.904	9.317	<0.0001	52.341	3.575	<0.0001
Tsimane Females (baseline)	-	-	-	-	-	-
Tsimane Males	−14.947	14.031	0.2868	1.78	5.384	0.741
Moseten Females	138.817	14.065	<0.0001	32.779	5.411	<0.0001
Moseten Males	85.157	16.575	<0.0001	27.98	6.361	<0.0001
French Females	−175.492	10.057	<0.0001	−21.531	3.887	<0.0001
French Males	−175.079	10.915	<0.0001	−20.901	4.24	<0.0001
Age (centered on 45)	0.609	0.548	0.2663	0.094	0.21	0.6533
Age x Tsimane Females (baseline)	-	-	-	-	-	-
Age x Tsimane Males	1.887	0.841	0.0249	0.615	0.323	0.0567
Age x Moseten Females	3.455	0.847	<0.0001	1.196	0.325	0.0002
Age x Moseten Males	10.91	1.03	<0.0001	4.048	0.397	<0.0001
Age x French Females	0.45	0.601	0.4541	0.852	0.233	0.0003
Age x French Males	0.638	0.67	0.3413	0.953	0.26	0.0003

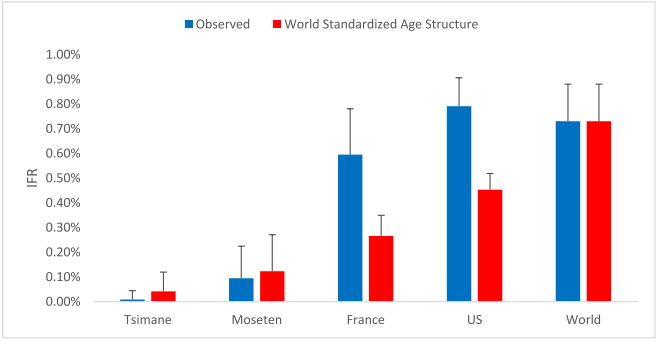

Fig. 6. Infection fatality ratios (IFRs) by population with 95% uncertainty intervals.

structures and their respective prevalences of hypertension, diabetes and obesity, utilizing global age-specific IFRs (Sorensen, 2022). The second column of the table shows the expected number of deaths for Tsimane and Moseten if these populations had the age-structure and comorbidity prevalences of the comparator population (i.e. France, the U.S., or worldwide). The third column provides the expectation based on the age-structure of the comparator population, but utilizing the observed co-morbidities of the Tsimane and Moseten. The decrease in expectation from the second to third columns provides an estimate of the impact of the lower prevalence of co-morbidities among the Tsimane and Moseten. The fourth column provides expected deaths, based on the co-morbidities in the comparator population, but utilizing the observed age-structure of the Tsimane and Moseten. The difference between the second and fourth columns shows that age-structure is the most important factor in determining the expected number of deaths, accounting for a reduction in 63-87% of expected deaths. The fifth column provides the expected number of deaths based on global age-specific death rates, but with the observed age-structure and co-morbidity prevalence found among the Tsimane and Moseten. Comparing the fourth and fifth columns shows the reduction in expected deaths due to

Table 3
Observed and expected mortality (with 95% uncertainty intervals) by age structure and comorbidity.

Population	Observed Number of Deaths			
Tsimane	1			
Moseten	2			
	Expected Number of Deaths based on French Age Structure and Co-morbidity Prevalences (95% uncertainty intervals)			
	French Age Structure & Co-morbidities	French Age Structure & Tsimane/ Moseten Co-morbidities	Tsimane/ Moseten Age Structure & French Co-morbidities	Tsimane/ Moseten Age Structure & Co-morbidities
Tsimane	230 (161, 351)	182 (128, 277)	29 (20, 45)	23 (16, 36)
Moseten	43 (30, 66)	40 (28, 61)	11 (8, 17)	10 (7, 16)
	Expected Number of Deaths based on U.S. Age Structure and Co-morbidity Prevalences			
	U.S. Age Structure & Co-morbidities	U.S. Age Structure & Tsimane/ Moseten Co-morbidities	Tsimane/ Moseten Age Structure & U. S. Co-morbidities	Tsimane/ Moseten Age Structure & Co-morbidities
Tsimane	237 (166, 363)	138 (96, 211)	38 (26, 58)	23 (16, 36)
Moseten	44 (31, 68)	30 (21, 46)	15 (10, 23)	10 (7, 16)
	Expected Number of Deaths based on Global Age Structure and Co-morbidity Prevalences			
	World Age Structure & Co-morbidities	World Age Structure & Observed Co-morbidities	Tsimane/ Moseten Age Structure & World Co-morbidities	Tsimane/ Moseten Age Structure & Co-morbidities
Tsimane	173 (121, 266)	125 (87, 192)	31 (22, 48)	23 (16, 36)
Moseten	32 (23, 50)	27 (19, 42)	12 (8, 19)	10 (7, 16)

comorbidity alone, accounting for 9-39% reduction in expected deaths. Taken together, shifting from a French age structure and comorbidity profile to that of the Tsimane and Moseten decreases the expected number of deaths by 90% and 79% for the Tsimane and Moseten,

respectively, simply due to their young age structure and relatively low comorbidity prevalence (Table 3, column 2 vs column 5). *Remarkably, however, among the Tsimane, the observed number of deaths is still 1/23*rd *of the expected number (4.3%), even after accounting for the actual age structure and co-morbidity prevalences.* The two deaths reported among Moseten are about 1/5th the equivalent expectation (22%).

3. Discussion

COVID-19 swept rapidly across the entire Tsimane and Moseten territories, as predicted by an earlier SEIR (Susceptible-Exposed-Infected-Recovered) network model (Kraft et al., 2023), and despite attempts at voluntary collective isolation (Kaplan et al., 2020). The IgG seroprevalence in these populations (71% and 63%) is higher than levels reported in serology studies in Colombian (58%) and Brazilian Amazonia (44%) (Serrano-Coll et al., 2021; Buss et al., 2021). Days of reported sickness, work loss, and bedridden suggest that most (~80%) cases of SARS-CoV-2 infection were symptomatic. People reported similar symptoms to those identified elsewhere–particularly loss of taste and smell, headache, fever, and cough. Despite high rates of infection and symptomatic illness, the need for hospitalization was minimal. The THLHP had purchased oxygen concentrators to be used in case of emergencies; these were utilized among the Moseten, but were at no point deemed necessary for infected Tsimane.

Most remarkably, we confirm that mortality due to COVID-19 among the Tsimane and the Moseten was extremely low. Even accounting for the relatively young age structure and low prevalence of several chronic morbidities in these groups, IFRs among the Tsimane were approximately 1/23 of those observed elsewhere in Europe, Asia and the Americas (Sorensen, 2022). A recent review and meta-analysis of IFRs in other low-income countries shows IFRs similar or higher than those in high-income countries (Levin et al., 2022). Yet relatively low COVID-19 mortality has also been reported in areas of sub-Saharan Africa (Okonji et al., 2021). Three of the reasons proposed for low reported fatality rates in those regions can be partially discounted here: low testing rates, poor documentation of deaths, and prior humoral immunity to related coronaviruses. Our wide seroprevalence coverage and use of independent surveillance systems for documenting deaths provide confidence that we were not missing undocumented cases or deaths. Our pre-pandemic serology indicates no detectable humoral cross-reactivity, although the limited subset (N = 43) and the absence of T-cell assays leave open the possibility of pre-existing cellular cross-immunity, which we address in detail below.

The young age structure of the Tsimane and Moseten and the low prevalence of co-morbid risk factors account for a significant proportion of the reduced IFR in these two populations. However, the reported deaths are only 4% of the expected number among the Tsimane, and 22% of the expected number among the Moseten, even after taking age structure and comorbidities into account. Fatalities were limited to older adults ages 67-79 years. Self-reports of days sick, and days not spent working or in bed were significantly higher among adults aged 60+. ELISA antibodies and seroneutralization titers were also higher with age in these populations, especially among the Moseten. Nevertheless, the age-related increases in morbidity and mortality were quite small, especially among the Tsimane.

Why, despite high overall rates of symptomatic infection, were elderly Tsimane and Moseten relatively protected from severe COVID-19 illness and mortality? We speculate that a low prevalence of non-infectious chronic disease comorbidities, a low prevalence of metabolic dysfunction at older ages, and high physical activity almost surely played a role in reducing COVID-19 severity and mortality. Minimal obesity, hypertension and diabetes appear to be protective against COVID-19 severity, but such chronic diseases typically account for less than a quarter of COVID-19 deaths in countries where these conditions are highly prevalent (Nguyen et al., 2022; de Almeida-Pititto et al., 2020; Mahamat-Saleh et al., 2021). Meta-analyses suggest that regular physical activity is protective against COVID-19 hospitalization, severity and mortality (Ezzatvar et al., 2022), but effect sizes—even at the high levels of physical activity observed among Tsimane—are too small (RR = ~0.65) to account for the much lower-than-expected mortality rates we observe here.

A low prevalence of vitamin D deficiency may be another contributing factor. It has been proposed that vitamin D supplementation might have a protective effect against COVID-19 severity and mortality by limiting inflammation and affecting other innate immune responses (D'Ecclesiis et al., 2022). It also inhibits renin, a proteolytic enzyme that is part of the renin-angiotensin system that includes the ACE2 binding site for SARS-CoV-2 entry into cells (Malek, 2020). Among Tsimane and Moseten, high skin exposure to sunlight could convert 7-dehydrocholesterol to previtamin D3, and then to vitamin D3, though there is little exogenous vitamin D in the diets of these populations (Kraft et al., 2018). We have no evidence to bear on this hypothesis, but assume vitamin D deficiency would be minimal in populations living largely outdoors in the tropics. On its own, however, this would be insufficient to account for the exceptionally low mortality we observed.

We propose that a more vigorous and effective immune response in the early stages of disease may be the most important contributing factor. The high titers of neutralizing antibodies compared to other populations may be an indicator of the more vigorous and effective response to SARS-CoV-2 infection. Antibody levels to SARS-CoV-2 among the Tsimane and Moseten were more than double the levels observed in the French population (Fig. 5). The proportion of Tsimane and Moseten with neutralizing antibodies (~53%) was far higher than in other populations in the same time period (2.0% in Germany Aziz et al., 2021); less than 5% and 1.1% in French blood donors and general population, respectively (Carrat et al., 2021; Gallian et al., 2023b). In fact, Tsimane and Moseten seroneutralization titers were much higher than those of non-hospitalized French from another study, falling somewhere between those of hospitalized and ICU patients (Legros et al., 2021).

The antibody response itself cannot be responsible for the low mortality, given that the risk of severe symptoms is determined earlier in the time course of disease progression than the production of neutralizing antibodies. However, we speculate that it may indicate a more vigorous or effective immune response in the early stages of disease progression. Blood biomarkers among the Tsimane and Moseten, such as C-reactive protein, white blood cell counts (especially eosinophils), and interferon gamma, suggest a more active peripheral immunity. For example, 24% and 12% of Tsimane and Moseten, respectively, showed elevated white blood cell counts. In addition, Tsimane show very elevated levels of natural killer cells, especially at older ages (Blackwell et al., 2016), which may play an important role in the innate immune response to COVID-19. However, it is possible that the very high levels of Type I IFN antibodies among the Tsimane and Moseten (with more than 75% of individuals having levels greater than 10 pg/mL) may also have been protective against severe disease and death. Literature has reported the impact of autoantibodies (auto-Abs) against Type I IFNs on life-threatening COVID-19 (Manry et al., 2022). In those studies, the prevalence of auto-Abs increased with age in parallel with immuno-senescence, resulting in increased SARS-CoV-2 IFRs.

COVID generally presents in two phases. The first is a flu-like phase, which can be resolved in 7-10 days when the immune system has managed to control and eliminate the viral infection. If the infection is not resolved, a second phase, which presents with a deeper infection of the lungs, can develop leading notably to the fulminant cytokine storm and result in death. Most Tsimane and Moseten experienced the first phase and were symptomatic. However, the vast majority of Tsimane and Moseten never seem to have entered the second phase. The more intense reaction to the infection translated into higher levels of antibodies, but also likely played a role in the early innate response to infection.

Pre-existing cross-reactive T-cell memory may also have contributed

to the protective phenotype, a dimension our archived sera could not address. For example, cross-reactive memory $CD4^+$ T cells recognizing SARS-CoV-2 are detectable in 20–60% of pre-pandemic donors across diverse cohorts, targeting conserved epitopes on spike, nucleoprotein, and non-structural proteins (Mateus et al., 2020; Grifoni et al., 2020). T cells from unexposed individuals preferentially target the highly conserved replication–transcription complex (the co-factor NSP7, the RNA-dependent RNA polymerase NSP12, and the helicase NSP13) expressed early in the viral life cycle (Le Bert et al., 2020; Swadling et al., 2022). Non-spike cross-reactive memory T cells, particularly against nucleoprotein and ORF1-encoded proteins, are associated with protection from infection in exposed household contacts (Kundu et al., 2022) and with rapid viral clearance in exposed individuals who never developed detectable antibodies (Swadling et al., 2022). Because HCoV-reactive $CD4^+$ T cells decline with age in European populations, potentially contributing to age-related COVID-19 severity (Loyal et al., 2021), the sustained lifelong pathogen exposure of the Tsimane and Moseten (reflected in near-universal CCC seroprevalence up to 100% for OC43) may help preserve this cross-reactive repertoire into older ages, offering a coherent mechanism for the muted age gradient in morbidity and mortality we observed. Additionally, some non-spike epitopes (e.g., within NSP7) are conserved among animal betacoronaviruses but weakly homologous to human CCCs (Le Bert et al., 2020), raising the possibility that exposure to zoonotic coronaviruses through subsistence contact with Amazonian wildlife could contribute to this repertoire. Direct testing will require prospective peripheral blood mononuclear cell (PBMC) collection and T-cell–based assays in both populations, and represents an important future research direction.

We hypothesize that the high pathogen burden experienced by the Tsimane and, to a somewhat lesser extent, the Moseten may play an important role in maintaining an effective and vigorous immune readiness, even into old age. The lack of clean water and sanitation, high exposure to mosquito and other insect bites, and repeated bacterial and parasitic infection may all contribute to the maintenance of this immune readiness. It is also possible that widespread geohelminth infection among the Tsimane and Moseten may have been protective, given their effects on immune-regulation and anti-inflammatory activity that could reduce the likelihood of a cytokine storm (Whitehead et al., 2022; Schneider-Crease et al., 2021). Indeed, in a region of Ethiopia with endemic parasitism, parasitic coinfection was associated with lower COVID-19 severity (Wolday et al., 2021). The Tsimane and Moseten have about a 70% prevalence of infection with helminths (Blackwell et al., 2016), and a previous study among the Tsimane found reduced cytokine response to viral antigen stimulation in patients with parasites (Schneider-Crease et al., 2021).

Another possible contributing factor is that tropical Amerindian populations may have protective genetic variants due to a long, continuous history of experiencing a diverse pathogen burden, combined with geographic isolation and genetic drift. Genomic differences in immune-related and parasite-host recognition genes have been highlighted as affecting Amerindian susceptibility to several respiratory and viral diseases, including tuberculosis, herpes virus type 8 (HHV-8), and human T-lymphotropic virus (HTLV). One study among Amerindians of the Brazilian Amazon identified 15 polymorphisms in 5 genes, including those affecting chemokine receptors, interleukin expression and intracellular signaling (Pastana et al., 2022). Among Tsimane, evidence exists for selective sweeps in 21 gene regions, and polygenic selection in five immune traits, including those related to inflammation and coronaviruses (Lea et al., 2023).

These possibilities are not mutually exclusive, and more definitive study will be required to evaluate them. Several protective mechanisms may work in concert to help explain the minimal mortality. Low obesity, hypertension, and diabetes likely play an important role. Differential immune responses due to high helminthic infection, enhanced peripheral immunity (both innate and acquired), genetic resistance, and abundant sunlight represent possible elements of a multi-factorial explanation. Given that the Moseten lifestyle, in terms of both metabolic and infectious risks, lies partway between the Tsimane lifestyle and those of populations living in industrial and post-industrial settings, it is not surprising that their mortality risk from SARS-COV-2 infection also lies partway between the Tsimane and populations in the U.S. and Europe.

4. Conclusion

The Tsimane and Moseten have a mix of characteristics relevant to COVID-19 infection and mortality that are relatively rare in urban areas of the world: they live rural, self-sufficient livelihoods with low market integration and communal living; they are immunologically challenged from diverse infections, but show minimal evidence of many of the chronic comorbidities observed to increase COVID-19 severity and fatality (Nguyen et al., 2022; Reyes-Sánchez et al., 2022). As a result of these factors, the Tsimane and Moseten appear to have shown a more vigorous and protective immune response to SARS-CoV-2 infection.

Indigenous groups living in peri-urban or urban areas do not seem to be protected in the same way, though clear trends are difficult to confirm (Pickering et al., 2023). Other Indigenous Amazonian populations showed high infection rate, but lower infection fatality rate than non-Indigenous peers (Soto-Cabezas et al., 2022; Santos et al., 2021), whereas Indigenous groups in Mexico and in North America have suffered substantial morbidity and mortality (Angel de Soto and Hakim, 2020; Crimmins, 2020; Kakol et al., 2020). Death rates of Indigenous groups in other contexts, especially those in less rural settings, were believed to have been higher than official rates (Pontes et al., 2021), sometimes in association with crowded housing and comorbidities (Kopp et al., 2024). Incidence and mortality rates from COVID-19 were lower among Australian First Nations in 2020 and 2021 than among non-Indigenous Australians, due to travel restrictions, lockdowns and effective public health messaging (Stanley et al., 2021), but mortality rates were higher later once COVID-19 spread (Australian Bureau of Statistics, 2023). Indigenous deaths were reported throughout Amazonia (Sierra Praeli, 2021), but without respect to the social and environmental contexts that might otherwise help explain differential susceptibility and resilience. In any case, deaths are sometimes under-reported among Indigenous groups, contributing to under-estimates of mortality, including in Brazil (Fellows et al., 2021). Indigenous groups inhabiting remote rural areas with minimal health infrastructure continue to be the least well studied in terms of their epidemiological experience with COVID-19, yet if the resilience of Tsimane and Moseten is any indication, there may be important lessons to learn from these contexts.

Given that global pandemics from new pathogens will continue to occur, a better understanding of the factors affecting susceptibility and resilience is of great importance. The decreased effectiveness of the immune response with aging appears to be the hallmark of COVID-19 disease severity and risk of death. The extremely low rates of mortality among the elderly is a salient feature of the Tsimane-Moseten experience. An understanding of how background pathogen exposure and hygienic environments play a role in decreased immune effectiveness with age, and how those factors interact with chronic non-communicable diseases, is clearly in order. Such an understanding may provide tools for prevention of excessive mortality from future pandemics.

Ethics statement

Human subjects approval for this research was granted by the institutional review boards at the University of California, Santa Barbara (#28-21-0788), University of New Mexico (#07–157; #15-133; #17-230), and the Universidad Mayor de San Simon, Cochabamba, Bolivia. Informed consent was established at three levels for each population: individual, community, and the Tsimane and Moseten governing

councils.

Data statement

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. The 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 and Moseten 1) have sovereignty over how data are shared, 2) are the primary gatekeepers determining ethical use, 3) are actively engaged in the data generation and 4) 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 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, community members, Bolivian scientists, and the THLHP leadership. A similar structure exists for the Moseten data. The study authors and the Tsimane leadership are committed to open science and are available to assist interested investigators in preparing data access requests.

CRediT authorship contribution statement

Lucia Inchauste: Formal analysis, Investigation, Methodology, Writing – review & editing. **Xavier de Lamballerie:** Conceptualization, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **Stepháne Priet:** Formal analysis, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. **Maguin Gutierrez Cayuba:** Investigation, Project administration. **Juan Copajira Adrian:** Investigation, Methodology. **Daniel Eid Rodriguez:** Investigation, Project administration, Writing – review & editing. **Raul Quispe Gutierrez:** Investigation, Methodology, Writing – review & editing. **Sarah Alami:** Investigation. **Jacob E. Aronoff:** Investigation, Writing – review & editing. **Kenneth Beutow:** Methodology. **Daniel K. Cummings:** Data curation, Investigation. **Bret A. Beheim:** Data curation, Investigation. **Caleb E. Finch:** Methodology, Writing – review & editing. **Margaret Gatz:** Investigation, Writing – review & editing. **Suhail Ghafoor:** Data curation, Resources. **Thomas S. Kraft:** Data curation, Investigation, Writing – review & editing. **Amanda J. Lea:** Investigation, Writing – review & editing. **Wendy J. Mack:** Methodology. **David E. Michalik:** Methodology, Writing – review & editing. **M. Katherine Sayre:** Data curation, Investigation. **Edmond Seabright:** Data curation. **Jonathan Stieglitz:** Investigation, Writing – review & editing. **Gregory S. Thomas:** Investigation. **Randall C. Thompson:** Investigation. **Benjamin C. Trumble:** Investigation, Methodology, Writing – review & editing. **Hillard S. Kaplan:** Investigation, Methodology, Resources, Supervision, Writing – review & editing. **Michael D. Gurven:** Conceptualization, Formal analysis, Investigation, Methodology, Resources, Writing – original draft, Writing – review & editing. **Paul L. Hooper:** Data curation, Formal analysis, Investigation, Methodology, Writing – original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.socscimed.2026.119493.

Data availability

Data will be made available on request.

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