



Climate change–induced population pressure drives high rates of lethal violence in the Prehispanic central Andes

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Understanding the influence of climate change and population pressure on human conflict remains a critically important topic in the social sciences. Long-term records that evaluate these dynamics across multiple centuries and outside the range of modern climatic variation are especially capable of elucidating the relative effect of—and the interaction between—climate and demography. This is crucial given that climate change may structure population growth and carrying capacity, while both climate and population influence per capita resource availability. This study couples paleoclimatic and demographic data with osteological evaluations of lethal trauma from 149 directly accelerator mass spectrometry ¹⁴C-dated individuals from the Nasca highland region of Peru. Multiple local and supraregional precipitation proxies are combined with a summed probability distribution of 149 ¹⁴C dates to estimate population dynamics during a 700-y study window. Counter to previous findings, our analysis reveals a precipitous increase in violent deaths associated with a period of productive and stable climate, but volatile population dynamics. We conclude that favorable local climate conditions fostered population growth that put pressure on the marginal and highly circumscribed resource base, resulting in violent resource competition that manifested in over 450 y of internecine warfare. These findings help support a general theory of intergroup violence, indicating that relative resource scarcity—whether driven by reduced resource abundance or increased competition—can lead to violence in subsistence societies when the outcome is lower per capita resource availability.

climate change | population pressure | warfare | lethal violence | Andes

The influence of climate change and population pressure on violence and social instability remains a critically important topic in archaeology and the broader social sciences. Yet, the majority of studies on this topic focus on the last century, when climatic conditions were relatively stable (1–5). Modeled projections of anthropogenic change suggest that climate regimes will become increasingly volatile with prolonged droughts in the coming decades (6, 7), making studies of past human responses to climate across a greater range of variation all the more vital. To predict likely responses, studies that systematically quantify the relative effect of competing variables among prehistoric populations are necessary, but remain limited. Importantly, both climatic and demographic factors have been shown to influence the frequency and severity of human violence (8–13). The interaction between climate and demography further amplifies these dynamics, as climate change may structure population growth rates and carrying capacity (14–16), and both climatic change and population fluctuations influence per capita resource availability (17, 18). As such, understanding the manners in which climate and demographically driven competition interact to increase or decrease warfare remains a difficult and essential task.

Archaeology can provide insight into the effects of climate and demographic change on human conflict over large time scales and during periods of greater climate extremes relative to the 20th century (4, 19, 20). Here, we investigate these effects during a 700-y temporal window (750 to 1450 Common Era [CE]) in the Nasca region, located in the central Andean highlands (Fig. 1), where groups experienced decades-long drought, unpredictable precipitation, unstable population dynamics, and chronic warfare (21–25). This study couples paleoclimatic and demographic data with osteological evaluations of lethal trauma from 149 directly accelerator mass spectrometry (AMS) ^δ¹⁴C-dated individuals from the Nasca highlands of Peru. Multiple local (26) and supraregional (23, 27) precipitation proxies are combined with a summed probability distribution of the AMS ^δ¹⁴C dates for estimating population dynamics during the 700-y study window. Our goal is to 1) provide a high-resolution characterization of the long-term regional trends in lethal violence and 2) assess how population estimates and paleoclimate data correlate with variation in lethal violence.

Significance

Warfare and homicide are pervasive features of the human experience, yet scholars struggle to understand the conditions that promote violence. Climate and conflict research has revealed many linkages between climate change and human violence; however, studies often produce contrary findings, and the driving mechanisms remain difficult to identify. We suggest a solution is to identify conditions producing resource scarcity, which are necessarily a combination of climate and population dynamics. We examine patterns of lethal violence in the Prehispanic Andes and find that favorable climate conditions fostered rapid population growth within a circumscribed landscape, resulting in chronic warfare. Our work suggests that an increasingly unstable climate may promote future violence, where favorable climate regimes incentivize population growth and attendant resource strain.

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The authors declare no competing interest.

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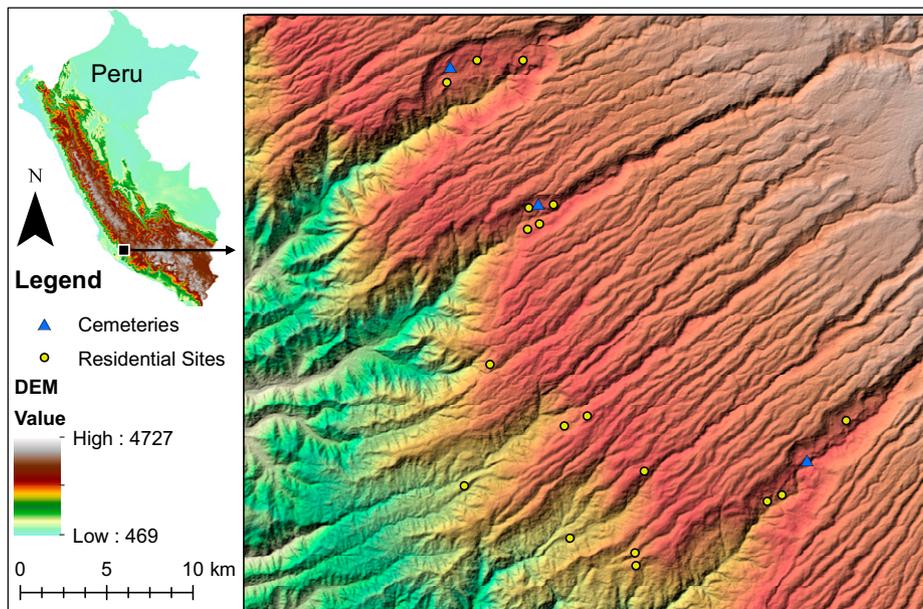


Fig. 1. The Nasca highland region.

Predictions

Theory from population and evolutionary ecology suggests that violence among sedentary, delayed-return societies (e.g., agriculturalists) will yield high payoffs where local resources are scarce and/or unevenly distributed and the costs of theft are high (18, 28, 29). Thus, environments with abundant, homogeneous resources should promote violence aversion and a higher threshold of tolerated theft (29–32), while environments with scarce, clustered resources should promote resource competition, strong theft-prevention measures, and violence-prone economic strategies (28–30, 33, 34). As both climate and demography structure per capita resource availability, we expect that rates of lethal aggression should be higher when climate reduces resource availability, such as through drought, and where population density increases interpersonal competition. We make several alternative, but related, predictions to evaluate if climate, demography, or their interaction is the most influential driver of variation in lethal violence. Rates of violence will be highest when individuals experience: persistent periods of drought (Prediction 1 [P1]) or high local competition due to increased population densities (P2). Alternatively, these conditions may be dependent on one another, such that interpersonal violence increases only when population-induced competition is driven by productive climate conditions, such as high rainfall (P3), or drought conditions hit populations already living at high densities (P4). These four predictions are related in their expectation that a key driving mechanism of violence is resource scarcity, though they differ in whether the causal mechanism is predominantly climate, population density, or the interaction of the two.

We test these predictions using generalized linear models (GLMs) and piecewise structural equation models (pSEMs) to evaluate correlations between a time-averaged measure of perimortem trauma, local pollen precipitation proxies from the Cerro Llamoca peatland core, a supraregional $\delta^{18}\text{O}$ precipitation proxy from the Quelccaya ice cap, temporally lagged supraregional $\delta^{18}\text{O}$ values, and a local population growth estimate (description in *Materials and Methods* and data trends in Fig. 2).

Regional Background

The Nasca highland region in the central Andes is a highly bounded area roughly 2,500 m above the modern city of Nasca, Peru (Fig. 1). Straddling the coastal and sierra ecologies, its deep and narrow river valleys are the definition of ecological circumscription (35), with fast-flowing rivers and well-defined, but limited, patches of open terrain, on which to build the terraces and canals that are necessary for agricultural production. The neighboring high grasslands, or “Puna,” is suitable for herding, but cannot be intensively cultivated due to inadequate precipitation for dry farming and runoff for irrigation. Prior to the Late Intermediate Period (LIP; 950 to 1450 CE), the region was largely unoccupied. Starting in the LIP, the region received a large influx of agropastoral groups that constructed fortified hilltop settlements known locally as “pukara” (hillforts) throughout the region’s narrow river valleys. The region’s agricultural patches and residential sites are densely clustered, with nearest intraregional neighbors averaging only several kilometers distant. Surrounding populations outside of the Nasca highlands are, however, dozens of kilometers away in any direction, creating a buffer zone between the Nasca highlands and neighboring population centers.

W.C.M. recorded 19 LIP residential sites and associated cemeteries located throughout the region’s river valleys (25, 36). Each of the settlements was permanently occupied, as evidenced by dense housing clusters and middens. Either within or immediately adjacent to the hillforts are cemeteries consisting of several dozen to several hundred artificially constructed tombs known as “chullpa.” Each tomb contains the remains of up to several dozen individuals, along with associated mortuary goods. Each interred individual was at one time a desiccated bundle wrapped in a cotton shroud and placed in tight clusters on the ground surface. Excavations at these tombs by W.C.M. in 2019 produced the human skeletal materials used in this paper.

Results

As shown in Table 1 and Fig. 3, the bivariate model of local climate (% Poaceae) shows significant ($P < 0.05$) positive covariance with lethal violence, whereby violence increases during

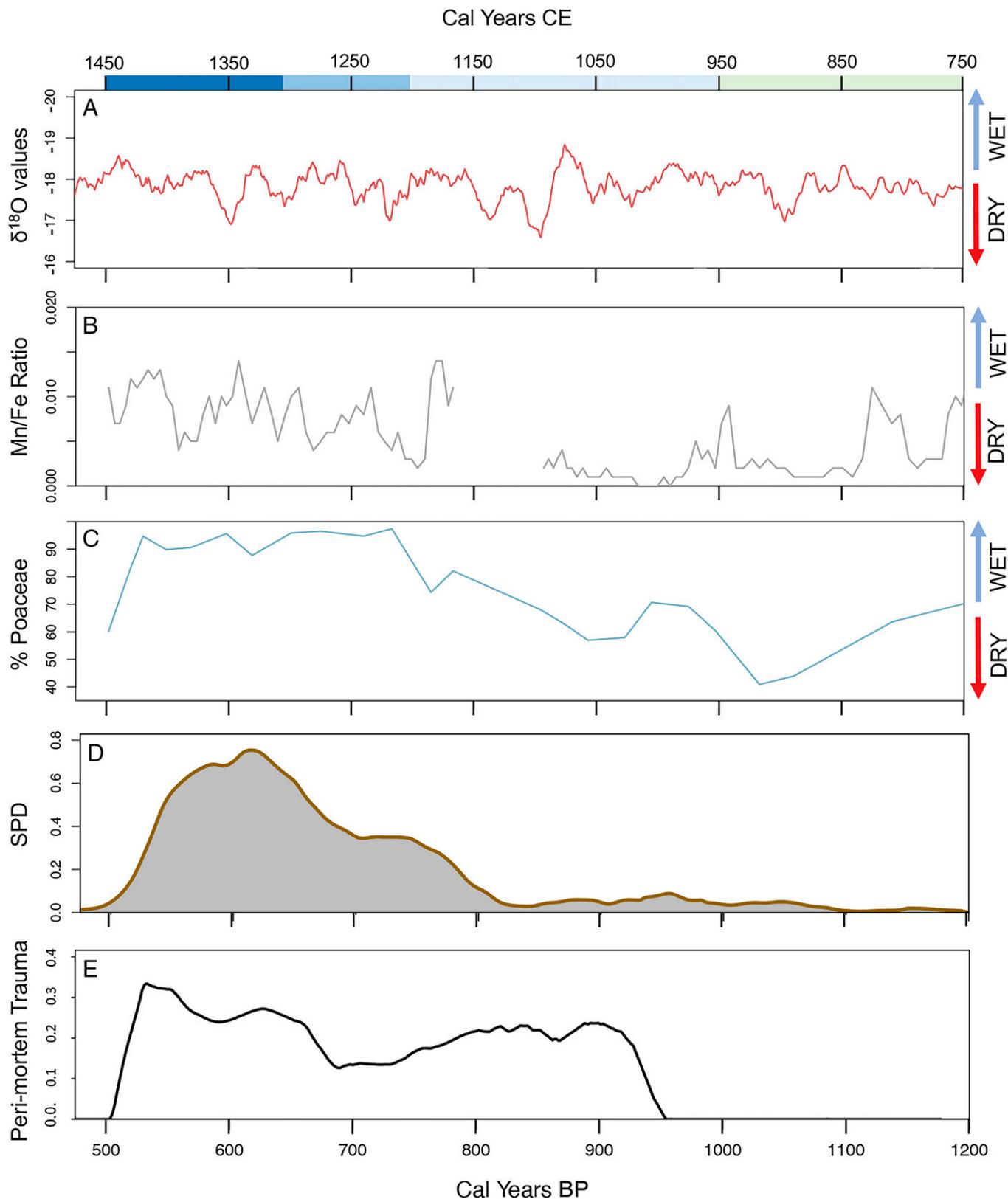


Fig. 2. Smoothed climate trends, population estimate, and time-averaged peri-mortem trauma (*Materials and Methods*) over the study period. (A) Supraregional climate proxy Quelccaya ice cap $\delta^{18}\text{O}$ values. (B and C) The local climate proxies are Cerro Llamoca Mn/Fe ratios (B) and Cerro Llamoca Poaceae percentages (C). (D and E) The population estimate is the SPD (D), and E is the time-averaged peri-mortem trauma. Colored bars indicate chronological phases: green, Middle Horizon; light blue, early LIP; medium blue, middle LIP; dark blue, late LIP. Cal, calendar.

periods of higher precipitation, which does not support P1 for local climate. Bivariate models reveal no significant relationships between lethal violence and supraregional climate,

including the 25-, 50-, and 100-y lags, also not supporting P1 for supraregional climate. Because the bivariate models comparing supraregional climate to violence or significant positive

Table 1. Summary of model results

Model type	Prediction	Predictor	Response	Est./ β	SE	<i>P</i>	r2l
Bivariate	P1	% Poaceae	Peri-mortem	0.0337	0.0151	0.0359	0.16
Bivariate	P1	δ 18O	Peri-mortem	0.0501	0.0416	0.2290	0.00
Bivariate	P1	25-y lag	Peri-mortem	0.0487	0.0403	0.2270	0.00
Bivariate	P1	50-y lag	Peri-mortem	0.0348	0.0408	0.3940	0.00
Bivariate	P1	100-y lag	Peri-mortem	-0.0378	0.0417	0.3650	0.00
Bivariate	P2	SPD	Peri-mortem	2.9774	0.6088	<0.001	0.25
Bivariate	P3	% Poaceae	SPD	0.0806	0.0177	0.0001	0.51
Bivariate	P3	25-y Lag	SPD	0.0077	0.0469	0.8690	0.04
SEM	P3	SPD	Peri-mortem	2.4200	1.2487	0.0650	
		% Poaceae	Peri-mortem	0.4566	1.1035	0.6829	
		% Poaceae	SPD	4.5526	0.9995	0.0001	
SEM	P3	SPD	Peri-mortem	2.7766	0.9048	0.0053	
		% Poaceae	SPD	4.5526	0.9995	0.0001	
Multivariate	P4	SPD * % Poaceae	Peri-mortem	-0.1588	0.1569	0.3227	0.29

Values in pSEM models are centered at their mean and scaled by their SD to facilitate relative comparisons. Est., estimate.

covariance with population density (summed probability distribution [SPD]) reveal relatively flat slopes and *P* values greater than 0.05 (Table 1 and Fig. 3), we do not perform further multivariate or structural equation modeling with these variables.

The proportion of individuals suffering from lethal trauma has an SPD, with higher rates of violence occurring during population peaks, supporting P2. There is, however, some structure in the residuals likely due to residual temporal autocorrelation (TAC).

The pSEMs comparing local precipitation (% Poaceae) and population density (SPD) with lethal violence find a significant direct effect of population density and a significant indirect effect of climate that is entirely mediated through population density, supporting P3, with productive climate conditions correlated with population pressure and resultant lethal violence (Fig. 4).

A multivariate model was generated to test if droughts only induce violence when population densities are high by including an interaction term between the SPD and % Poaceae predictor variables and results in nonsignificant terms (Table 1), thus failing to support P4. To summarize, model results best support P3, provide support for P2, and provide no support for P1 and P4.

Discussion

Comparisons of lethal violence to paleoclimate and demographic conditions over a 700-y period in the Nasca highlands reveal a significant relationship between productive climate conditions and demographically induced resource competition and warfare. The positive correlation between local precipitation and violence in the Nasca highlands differs from many prior studies that show a link between drought and conflict (e.g., refs. 20 and 37–39). Yet, our findings make sense when examining the dynamics between climate, demography, and violence. Specifically, our results show a cascade effect from climate to demography and lethal conflict, whereby improving climatic conditions foster in situ growth and/or in-migration that result in resource stress and violent competition. This process was especially intense in the circumscribed Nasca highlands, where the forced removal from a resource patch or production area would have resulted in severe resource strain. Overall, results suggest a demographic threshold, above which competition over scarce, circumscribed resources promotes lethal violence. These results align with previous work in population ecology, which shows that density-dependent reductions in resource availability lead to increasing competition

(40, 41). Whether population growth was the result of improving conditions fostering increased in situ fertility or exogenous migration is currently unknown; however, genetic and archaeological research in the Palpa region immediately adjacent to the Nasca highlands finds evidence for populations migrating into the local area from the sierra regions to the east during the LIP (22), opening the possibility that a similar process may have occurred in the Nasca highlands.

Despite the significant model fits, there remains unexplained variation, most notably in the escalation in peri-mortem trauma in the mid-LIP when population was low and the persistently high rates of violence in the late LIP while population density was declining. Below, we explore several possible explanations to account for this residual variation.

The initial rise in lethal conflict during the middle LIP when the population was growing slowly was likely the result of two factors. First, increased violence may be due to the emergence of an ideal despotic distribution (41–43) resulting from competition over the limited and circumscribed arable land during regional colonization phases. The region was first occupied by large populations starting in the LIP that distributed themselves among fortified hilltop villages (36). Along with variability in local environmental quality, early migrants likely territorialized high-ranking patches and pushed incoming groups to increasingly marginal areas. If established and incoming groups were equally formidable (i.e., similar coalition strengths), the result may have been territorial contests ending in lethal aggression. Indeed, rates of lethal violence first climbed during an interval of reduced precipitation that would have increased the payoffs for acquiring high-ranking patches better suited for farming. Second, lethal violence emerges circa 1000 CE, coinciding with the collapse of the Wari empire, which spread out of the Ayacucho basin to control much of the central Andes during the Middle Horizon (500 to 1000 CE) (44). While existing evidence suggests that the Wari abandoned the Nasca region prior to their collapse (45, 46), we cannot yet rule out the effects of imperial disintegration on rates of Nasca highland violence or the prospect that local population increase was partially the result of out-migrations from the Wari core in the Ayacucho basin, which itself may be related to local drought conditions. Cross-regional analysis is needed to evaluate the effect of Wari collapse on the variable timing and severity of LIP violence.

The late LIP violence may pertain to mistrust, subsistence constraints, frequency-dependent behavior, and/or territorial

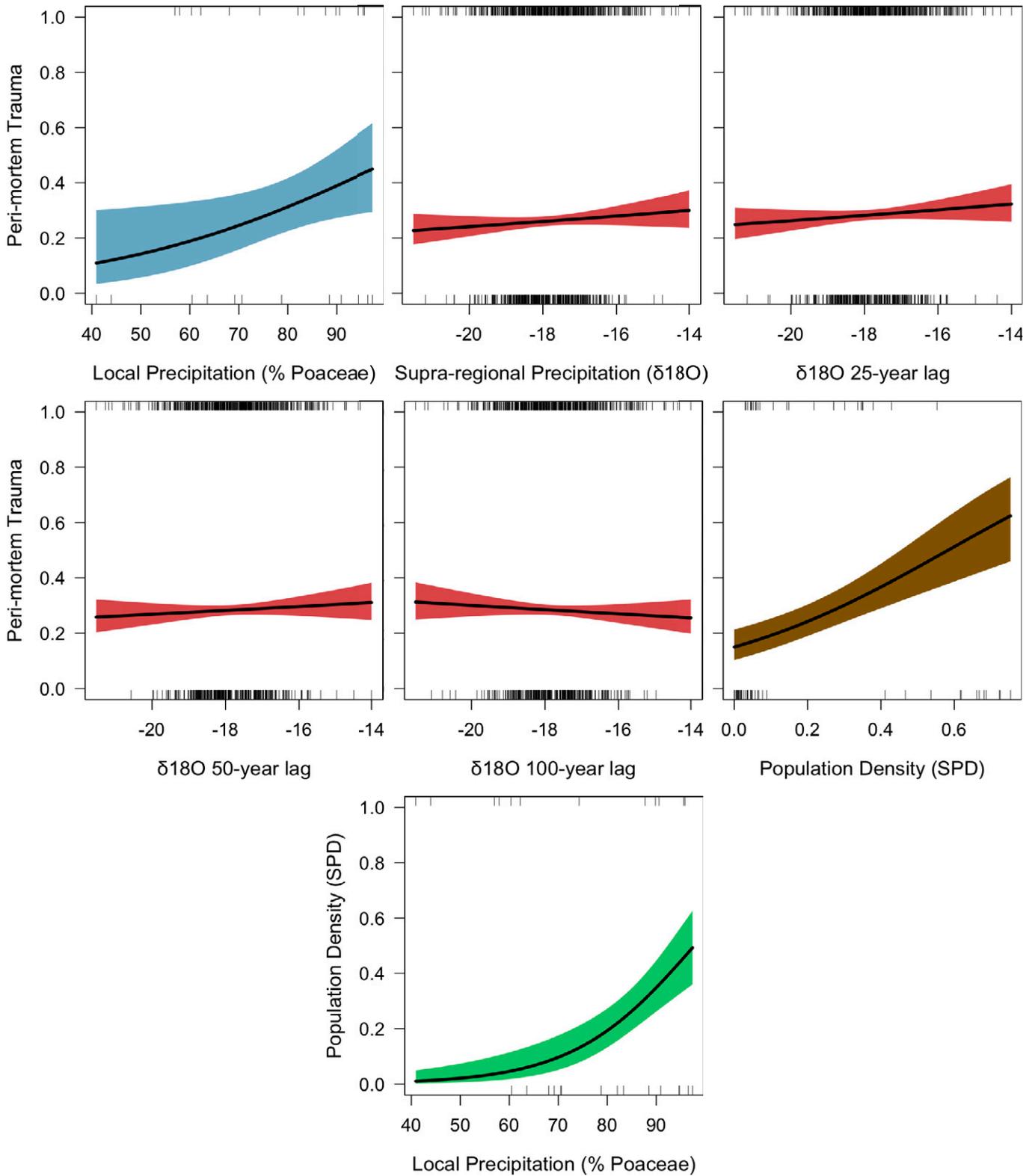


Fig. 3. Plots of bivariate GLMs comparing time-averaged peri-mortem trauma to our predictor variables: % Poaceae (local precipitation proxy) in blue; $\delta^{18}\text{O}$ ratio (supraregional precipitation proxy) along with the 25-y, 50-y, and 100-y lags of the supraregional $\delta^{18}\text{O}$ ratios in red; and the SPD (population estimate) in gold. The bottom plot compares % Poaceae to the SPD in green. Black ticks denote observations.

defense. Mistrust ensues between populations at war, particularly those experiencing resource scarcity (47). Populations living in low-productivity environments (like the Nasca highlands) tend to require large territories and high mobility to obtain sufficient resources, resulting in intergroup uncertainty

regarding territorial boundaries (48). Individuals operating in low-resource-abundance environments, where mistrust is high, may have less information about their neighbor's willingness to punish poachers or trespassers, both of which may lead to frequent violent conflict (28). High mobility and boundary

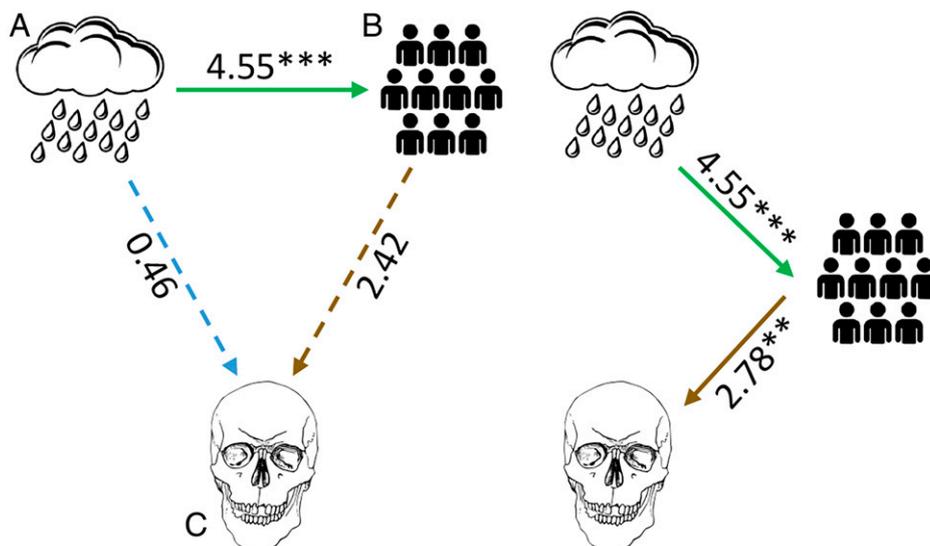


Fig. 4. Summary of piecewise structured equation models evaluating the relative coupled impact of (% Poaceae) (A) on both human population densities (SPD) (B) and time-averaged peri-mortem trauma (C) and of human population densities (B) on time-averaged peri-mortem trauma (C). *Left* shows results that include a direct effect of climate on violence. *Right* shows results where the effect of climate is entirely mediated by population density. Standardized coefficients (β) outside the triangle correspond to the model and denote P value significance using asterisks. Dashed lines denote nonsignificant relationships. Colors correspond to the bivariate model fits.

uncertainty may also result in ecological constraints on violence-avoidance tactics, as large, formidable groups must disperse into smaller, more vulnerable parties to obtain sufficient resources (49–51). Further, frequency-dependent strategies may come into play, particularly if initial violent adaptive strategies for resource competition later transition into reputational contests that can yield status benefits, even when resources are not procured. Lastly, it is possible that the escalation in lethal violence toward the end of the LIP is a response to Inka invasion, which occurred sometime toward the middle of the 15th century. To summarize, mistrust, misinformation, the inefficacy of defensive strategies, frequency-dependent behaviors, and Inka invasion may have perpetuated warfare in the Nasca highlands, even after population pressure declined.

Conclusion

This study assesses the impact of climatic and demographic change on rates of lethal violence in the central Andean region of the Nasca highlands over a 700-y period. Of the various hypotheses proposed to explain the coupled impact of climate and demography on violence, our results support the prediction that improving local climate conditions fostered in situ population growth and/or in-migration that put pressure on the marginal and highly circumscribed resource base. The resulting resource competition promoted intense violence that manifested in over 450 y of inter-necine warfare. These results suggest that local climate is a significant factor in escalating violence, as others have suggested (1–5, 20), but it is mediated by population density. This mediated relationship suggests that, counterintuitively, ameliorating climate conditions may produce societal instability by promoting rapid population expansion and increased resource strain, particularly in circumscribed areas. Importantly, this complements the growing literature on how drought can induce scarcity-driven violence (13, 20, 52) by showing that the opposite environmental conditions can also lead to violence when improving productivity increases local populations and, therefore, local competition. These findings help support a general theory of intergroup violence, indicating that relative resource scarcity—whether driven by reduced resource abundance or increased competition—can lead to violence in

subsistence societies when the outcome is lower per capita resource availability.

Further investigations on how climate change and demographic pressure influence the frequency and severity of human violence are crucial both within the archaeological past and for forecasting future violence. While studies that forecast violence often focus on drought (20, 53, 54), our work suggests that increasingly unstable climates may promote future violence in regions where favorable climate regimes drive rapid population growth and attendant resource strain. We contend that future research on this topic will benefit from the inclusion of both climate and demographic variables to more fully articulate the relationships between climate change, population pressure, resource availability, and human conflict.

Materials and Methods

Osteology. In 2019, W.C.M. excavated a sample of 325 crania from Nasca highlands tombs. Of this sample, 270 crania were sufficiently intact for peri-mortem trauma analysis, and a subsample of 149 crania were directly dated (dataset in *SI Appendix*).^{*} Peri-mortem fractures are diagnosed by observing radiating fracture lines, homogeneity of color between the cranial surface and fracture edges, and bone hinging at fracture margins (55, 56). For more details on the osteological methods, see McCool et al. (25). To decrease the likelihood of sampling bias, tombs were chosen randomly from those with a viable skeletal assemblage and excavated to sterile from a variety of spatial contexts throughout the study region. Tombs exhibit multicentury use-lives and contain a complete demographic mixture of age and sex profiles.

AMS Dating. To evaluate diachronic trends in violence, AMS radiocarbon dates were obtained for 149 crania that were excavated from tombs throughout the study region. Bone collagen for $\delta^{14}\text{C}$ measurement was extracted and purified by using the modified Longin method with ultrafiltration (57) at Penn State University, the University of California Santa Barbara, and the University of California Irvine, where AMS $\delta^{14}\text{C}$ measurement was conducted. Following Ambrose (58), only dates with C:N atomic ratios of 2.9 to 3.6 were included in the analysis. Results were calibrated by using the rcarbon package in the R programming environment (59) with the SHCal20 calibration curve (60).

^{*}Additional details on our osteological dataset can be found in several unpublished sources that are available from the corresponding author upon request.

Climate. The Quelccaya icecap record located in the Cordillera Vilcanota in the high Andean sierra provides a high-resolution paleoclimate record that is sensitive to the position of the Intertropical Convergence Zone and precipitation coming from the Amazon basin (23, 27). Annual ice layers extending back 1,800 y are present in this ice sheet and provide an annual climate record for the sierra (Fig. 2A). Ice-accumulation rates and ratios of $\delta^{18}\text{O}$ provide proxies for average precipitation in the sierra areas, as well as variability in temperature and rainfall. These proxies show drying conditions during the LIP with peak drought in the sierra \sim 1200 to 1250 CE and persisting until 1400 CE. In short, in the sierra regions, the LIP was a time of extreme climatic volatility and drought, particularly during the 13th century CE. To investigate lagged effects of supraregional climate on rates of violence, we generate 25-, 50-, and 100-y lags for the Quelccaya $\delta^{18}\text{O}$ icecap record. We test lagged effects to investigate whether drought in the sierra (as captured by the Quelccaya icecap record) lead to out-migrations into lower-elevation regions, such as the Nasca highlands, that put pressure on the local resource base and fostered violent competition.

Using multiproxy records from lithic ratios in terrestrial sediment cores and pollen records from the Cerro Llamoca peatland in the Palpa highlands (\sim 50 km from the Nasca highlands) (26), it is possible to reconstruct the local Nasca highland climate. Lithic data relies on manganese (Mn) and iron (Fe) content, normalized to titanium (Ti), which is considered to be immobile in peat (26). Mn/Fe ratios are considered a proxy for moisture, with increasing Fe to Mn ratios reflecting increasing moisture (Fig. 2B). Poaceae pollen proxies moisture, with increasing percentages indicating wetter conditions (Fig. 2C). These data show that starting circa 700 CE and persisting until 1250 CE, the Nasca highlands experienced a period of pronounced aridity and moisture variability, marked by low Poaceae percentages and increasing Fe relative to Mn. This resulted in reduced environmental productivity and increased economic uncertainty (22, 26). Between 1250 and 1450 CE, conditions improved dramatically, with consistent humidity and precipitation (26, 61). As the Cerro Llamoca peatland core contains multiple paleoclimate proxies, it is vital that we select a representative proxy for use as the primary predictor variable in our models. We select the percentage of Poaceae for several reasons: First, the original authors of the study (26) rely on Poaceae as a representative marker of local climatic changes. Second, the general trends shown in the Poaceae record of aridity from 700 to 1250 CE and wetter conditions from 1250 CE onward align with findings in multiple coastal moisture proxies (24, 62–64). Third, the Mn/Fe ratios record contains missing (not available) values for the years 787 to 854 B.P. Fourth, Mn/Fe ratios are potentially affected by pH and water saturation. Lastly, the Poaceae record and Mn/Fe record are strongly collinear ($r = 0.55$), such that including both as predictor variables decreases model fit. Cerro Llamoca peatland data were obtained from the National Oceanographic and Atmospheric Administration website.

Demography. To estimate population growth, we use the 149 AMS $\delta^{14}\text{C}$ dates using the dates-as-data approach (65–68). The dates-as-data approach rests on the premise that larger populations should produce and deposit greater amounts of datable materials relative to smaller populations. This method has been increasingly refined and updated since its initial application (67) and has been successfully used to track population histories through time and across space (66, 68, 69). To navigate issues relating to this approach (70–72), we only use dates sampled from human skeletal material, the number of which is not affected by activity intensity. To estimate population changes throughout the LIP between the regions

in our sample, we use the rcarbon package (59) in the R environment to generate an SPD on calibrated radiocarbon dates of human remains (Fig. 2D).

Quantitative Methods. The response variable (peri-mortem trauma) was time-averaged by using the binomial measures of peri-mortem trauma and the 149 AMS $\delta^{14}\text{C}$ distributions for each of the 700 y in the study window (Fig. 2E). All the overlapping $\delta^{14}\text{C}$ distributions for each time step (calendar year) had the average taken for the binomial peri-mortem trauma values to generate a running time average of lethal violence for every calendar year in the study window. For example, if the $\delta^{14}\text{C}$ distributions for 25 individuals overlap the year 1200 CE, the peri-mortem trauma value (zero or one) for each of the 25 individuals are averaged to create a time-averaged peri-mortem trauma measure for that year (SI Appendix). This method permits the estimation of change in rates of lethal violence for each year in the study window and provides far greater statistical power for our models. Time-averaging, however, does artificially inflate sample size with the risk that the resulting annual resolution will produce TAC. When TAC is observed in autocorrelation function plots, we select an interval at which to resample the data to constrain the autocorrelation to within acceptable parameters (SI Appendix). The interval of resampled years was determined separately for each variable based on the number of observations and the trade-off between maximizing sample size and minimizing TAC.

To test our predictions, we fit GLMs with a binomial distribution and log link appropriate to proportional data (time-averaged peri-mortem trauma). These models rely on quasi-likelihood estimation to account for overdispersion. The climate and population predictor variables are in separate bivariate models and, where appropriate, are combined in multivariate models. To determine whether our predictor variables have mediating effects, we employ pSEM using the piecewiseSEM package (73) in R. pSEMs combine multiple variables into a causal network, permitting simultaneous tests of multiple hypotheses. The pSEM technique explicitly assumes causal linkages between exogenous (predictor) and endogenous (response) variables and can quantify both direct and indirect effects. All analyses are conducted in the R programming environment and language (74) (more details about our analysis are available in SI Appendix).

Data Availability. Additional details on our osteological dataset can be found in several unpublished sources that are available from the corresponding author upon request. All study data are included in the article and/or SI Appendix.

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- M. Burke, M. Hsiang, E. Miguel, Climate and conflict. *Annu. Rev. Econ.* **7**, 577–617 (2015).
- P. H. Gleick, Water, drought, climate change, and conflict in Syria. *Weather Clim. Soc.* **6**, 331–340 (2014).
- S. M. Hsiang, M. Burke, E. Miguel, Quantifying the influence of climate on human conflict. *Science* **341**, 1235367 (2013).
- A. Karnieli, A. Shtein, N. Panov, N. Weisbrod, A. Tal, Was drought really the trigger behind the Syrian Civil War in 2011? *Water* **11**, 1564 (2019).
- O. M. Theisen, N. P. Gleditsch, H. Buhaug, Is climate change a driver of armed conflict? *Clim. Change* **117**, 613–625 (2013).
- M. Collins *et al.*, "Long-term climate change: Projections, commitments and irreversibility" in *Climate Change 2013—The Physical Science Basis: Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge University Press, Cambridge, UK, 2013), pp. 1029–1136.
- P. R. Shukla *et al.*, Eds., *Climate Change and Land: An IPCC Special Report on Climate Change, Desertification, Land Degradation, Sustainable Land Management, Food Security, and Greenhouse Gas Fluxes in Terrestrial Ecosystems* (Intergovernmental Panel on Climate Change, Geneva, Switzerland, 2019).
- D. Kennett, A. Anderson, M. J. Prebble, E. Conte, J. Southon, Prehistoric human impacts on Rapa, French Polynesia. *Antiquity* **80**, 340–354 (2006).
- T. Nakagawa *et al.*, Population pressure and prehistoric violence in the Yayoi period of Japan. *J. Archaeol. Sci.* **132**, 105420 (2021).
- P. D. Nolan, Toward an ecological-evolutionary theory of the incidence of warfare in preindustrial societies. *Social. Theory* **21**, 18–30 (2003).
- R. C. Oka *et al.*, Population is the main driver of war group size and conflict casualties. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E11101–E11110 (2017).
- D. D. Zhang, J. Zhang, H. F. Lee, Y. He, Climate change and war frequency in Eastern China over the last millennium. *Hum. Ecol.* **35**, 403–414 (2007).
- D. D. Zhang *et al.*, The causality analysis of climate change and large-scale human crisis. *Proc. Natl. Acad. Sci. U.S.A.* **108**, 17296–17301 (2011).
- R. L. Kelly, T. A. Surovell, B. N. Shuman, G. M. Smith, A continuous climatic impact on Holocene human population in the Rocky Mountains. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 443–447 (2013).
- T. R. McLaughlin, M. Gómez-Puche, J. Cascalheira, N. Bicho, J. Fernández-López de Pablo, Late Glacial and Early Holocene human demographic responses to climatic and environmental change in Atlantic Iberia. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **376**, 20190724 (2021).

16. A. N. Williams *et al.*, A continental narrative: Human settlement patterns and Australian climate change over the last 35,000 years. *Quat. Sci. Rev.* **123**, 91–112 (2015).
17. A. R. Templeton, D. R. Kirsch, M. C. Towner, Contributions of evolutionary anthropology to understanding climate-induced human migration. *Am. J. Hum. Biol.* **33**, e23635 (2021).
18. D. D. Zhang, P. Brecke, H. F. Lee, Y.-Q. He, J. Zhang, Global climate change, war, and population decline in recent human history. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 19214–19219 (2007).
19. M. Collard, W. C. Carleton, D. A. Campbell, Rainfall, temperature, and Classic Maya conflict: A comparison of hypotheses using Bayesian time-series analysis. *PLoS One* **16**, e0253043 (2021).
20. D. J. Kennett *et al.*, Development and disintegration of Maya political systems in response to climate change. *Science* **338**, 788–791 (2012).
21. E. Arkush, T. A. Tung, Patterns of war in the Andes from the Archaic to the Late Horizon: Insights from settlement patterns and cranial trauma. *J. Archaeol. Res.* **21**, 307–369 (2013).
22. L. Fehren-Schmitz *et al.*, Climate change underlies global demographic, genetic, and cultural transitions in pre-Columbian southern Peru. *Proc. Natl. Acad. Sci. U.S.A.* **111**, 9443–9448 (2014).
23. D. J. Kennett, N. Marwan, Climatic volatility, agricultural uncertainty, and the formation, consolidation and breakdown of preindustrial agrarian states. *Philos. Trans. Royal Soc., Math. Phys. Eng. Sci.* **373**, 20140458 (2015).
24. B. Mächtle, B. Eitel, Fragile landscapes, fragile civilizations—How climate determined societies in the pre-Columbian south Peruvian Andes. *Catena* **103**, 62–73 (2013).
25. W. C. McCool, T. A. Tung, J. B. Coltrain, A. J. Accinelli Obando, D. J. Kennett, The character of conflict: A bioarchaeological study of violence in the Nasca highlands of Peru during the Late Intermediate Period (950–1450 C.E.). *Am. J. Phys. Anthropol.* **174**, 614–630 (2021).
26. K. Schitteck *et al.*, Holocene environmental changes in the highlands of the southern Peruvian Andes (14 S) and their impact on pre-Columbian cultures. *Clim. Past* **11**, 27–44 (2015).
27. L. G. Thompson *et al.*, Annually resolved ice core records of tropical climate variability over the past ~1800 years. *Science* **340**, 945–950 (2013).
28. M. W. Allen, R. L. Bettinger, B. F. Coddling, T. L. Jones, A. W. Schmitz, Resource scarcity drives lethal aggression among prehistoric hunter-gatherers in central California. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 12120–12125 (2016).
29. M. Daly, *Killing the Competition: Economic Inequality and Homicide* (Routledge, London, 2017).
30. N. G. Blurton Jones, Tolerated theft, suggestions about the ecology and evolution of sharing, hoarding and scrounging. *Soc. Sci. Inf. (Paris)* **26**, 31–54 (1987).
31. E. Ermer, L. Cosmides, J. Tooby, Relative status regulates risky decision-making about resources in men: Evidence for the co-evolution of motivation and cognition. *Evol. Hum. Behav.* **29**, 106–118 (2008).
32. X. T. Wang, D. J. Kruger, A. Wilke, Life history variables and risk-taking propensity. *Evol. Hum. Behav.* **30**, 77–84 (2009).
33. R. Dyson-Hudson, E. A. Smith, Human territoriality: An ecological reassessment. *Am. Anthropol.* **80**, 21–41 (1978).
34. L. A. Kuznar, Evolutionary applications of risk sensitivity models to socially stratified species: Comparison of sigmoid, concave, and linear functions. *Evol. Hum. Behav.* **23**, 265–280 (2002).
35. R. L. Carneiro, A theory of the origin of the state: Traditional theories of state origins are considered and rejected in favor of a new ecological hypothesis. *Science* **169**, 733–738 (1970).
36. W. C. McCool, Coping with conflict: Defensive strategies and chronic warfare in the Prehispanic Nazca region. *Lat. Am. Antiq.* **28**, 373–393 (2017).
37. E. Arkush, War, chronology, and causality in the Titicaca Basin. *Lat. Am. Antiq.* **19**, 339–373 (2008).
38. C. R. Ember, T. A. Adem, I. Skoggaard, E. C. Jones, Livestock raiding and rainfall variability in Northwestern Kenya. *Civ. Wars* **14**, 159–181 (2012).
39. S. A. LeBlanc, *Prehistoric Warfare in the American Southwest* (University of Utah Press, Salt Lake City, 1999).
40. B. F. Coddling, T. L. Jones, Environmental productivity predicts migration, demographic, and linguistic patterns in prehistoric California. *Proc. Natl. Acad. Sci. U.S.A.* **110**, 14569–14573 (2013).
41. D. J. Kennett, B. Winterhalder, "Demographic expansion, despotism and the colonisation of East and South Polynesia" in *Islands of Inquiry: Colonisation, Seafaring and the Archaeology of Maritime Landscapes*, G. Clark, F. Leach, S. O'Connor, Eds. (Terra Australis, ANU Press, Canberra, Australia, 2008), vol. 29, pp. 87–96.
42. B. F. Coddling, D. W. Bird, Behavioral ecology and the future of archaeological science. *J. Archaeol. Sci.* **56**, 9–20 (2015).
43. S. D. Fretwell, H. L. Lucas, On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheor.* **19**, 16–36 (1969).
44. K. J. Schreiber, *Wari Imperialism in Middle Horizon Peru* (University of Michigan Museum, Ann Arbor, MI, 1992).
45. C. A. Conlee, Transformations of society and power in Ancient Nasca. *Peruvian Archaeology* **2**, 1–35 (2015).
46. M. J. Edwards, K. Schreiber, Pataraya: The archaeology of a Wari outpost in Nasca. *Lat. Am. Antiq.* **25**, 215–233 (2014).
47. C. R. Ember, M. Ember, Resource unpredictability, mistrust, and war: A cross-cultural study. *J. Conflict Resolut.* **36**, 242–262 (1992).
48. A. K. Parker, C. H. Parker, B. F. Coddling, When to defend? Optimal territoriality across the Nomic homeland. *Quat. Int.* **518**, 3–10 (2019).
49. L. Glowacki, R. W. Wrangham, The role of rewards in motivating participation in simple warfare. *Hum. Nat.* **24**, 444–460 (2013).
50. P. B. Roscoe, War and society in Sepik New Guinea. *J. R. Anthropol. Inst.* **2**, 645–666 (1996).
51. P. B. Roscoe, Settlement fortification in village and 'tribal' society: Evidence from contact-era New Guinea. *J. Anthropol. Archaeol.* **27**, 507–519 (2008).
52. J. S. Field, P. V. Lape, Paleoclimates and the emergence of fortifications in the tropical Pacific islands. *J. Anthropol. Archaeol.* **29**, 113–124 (2010).
53. J. F. Maystadt, O. Ecker, Extreme weather and civil war: Does drought fuel conflict in Somalia through livestock price shocks? *Am. J. Agric. Econ.* **96**, 1157–1182 (2014).
54. N. von Uexkull, M. Croicu, H. Fjelde, H. Buhaug, Civil conflict sensitivity to growing-season drought. *Proc. Natl. Acad. Sci. U.S.A.* **113**, 12391–12396 (2016).
55. D. Ortner, "Differential diagnosis of skeletal injuries" in *Skeletal Trauma: Identification of Injuries Resulting from Human Rights Abuse and Armed Conflict*, E. H. Kimmerle, J. P. Baraybar, Eds. (CRC Press, Boca Raton, FL, 2008), pp. 21–86.
56. N. J. Sauer, "The timing of injuries and manner of death: distinguishing among antemortem, perimortem and postmortem trauma" in *Forensic Osteology: Advances in the Identification of Human Remains*, K. J. Reichs, Ed. (Charles C. Thomas, Springfield, IL, ed. 2, 1998), pp. 321–332.
57. D. J. Kennett *et al.*, Archaeogenomic evidence reveals prehistoric matrilineal dynasty. *Nat. Commun.* **8**, 14115 (2017).
58. S. H. Ambrose, Preparation and characterization of bone and tooth collagen for isotopic analysis. *J. Archaeol. Sci.* **17**, 431–451 (1990).
59. A. Bevan, E. R. Crema, rcarbon v1.4.1: Calibration and Analysis of Radiocarbon Dates (2020).
60. A. G. Hogg *et al.*, SHCal20 Southern Hemisphere Calibration, 0–55,000 years cal BP. *Radiocarbon* **62**, 759–778 (2020).
61. V. Soňa, *Impacts of Climate Variability on Pre-Hispanic Settlement Behavior in South Peru: The Northern Rio Grande de Nasca Drainage between 1500 BCE and 1532 CE (Forschungen zur Archäologie Außeuroppäischer Kulturen, Reichert, Wiesbaden, Germany, 2015)*, Vol. 13.
62. G. H. Haug, K. A. Hughen, D. M. Sigman, L. C. Peterson, U. Röhl, Southward migration of the intertropical convergence zone through the Holocene. *Science* **293**, 1304–1308 (2001).
63. B. Rein *et al.*, El Niño variability off Peru during the last 20,000 years. *Paleoceanography* **20**, PA4003 (2005).
64. B. Rein, How do the 1982/83 and 1997/98 El Niños rank in a geological record from Peru? *Quat. Int.* **161**, 56–66 (2007).
65. J. M. Broughton, E. M. Weitzel, Population reconstructions for humans and megafauna suggest mixed causes for North American Pleistocene extinctions. *Nat. Commun.* **9**, 5441 (2018).
66. E. R. Crema, J. Habu, K. Kobayashi, M. Madella, Summed probability distribution of 14C dates suggests regional divergences in the population dynamics of the Jomon Period in Eastern Japan. *PLoS One* **11**, e0154809 (2016).
67. J. W. Rick, Dates as data: An examination of the Peruvian Pre-ceramic Radiocarbon Record. *Am. Antiq.* **52**, 55–73 (1987).
68. S. Shennan *et al.*, Regional population collapse followed initial agriculture booms in mid-Holocene Europe. *Nat. Commun.* **4**, 2486 (2013).
69. A. Bevan *et al.*, Holocene fluctuations in human population demonstrate repeated links to food production and climate. *Proc. Natl. Acad. Sci. U.S.A.* **114**, E10524–E10531 (2017).
70. D. A. Contreras, J. Meadows, Summed radiocarbon calibrations as a population proxy: A critical evaluation using a realistic simulation approach. *J. Archaeol. Sci.* **52**, 591–608 (2014).
71. B. J. Cullen, Crude demographic proxy reveals nothing about Paleoindian population. *Proc. Natl. Acad. Sci. U.S.A.* **105**, E111–E111, author reply E112–E114 (2008).
72. D. J. Kennett, T. W. Stafford, Jr., J. Southon, Standards of evidence and Paleoindian demographics. *Proc. Natl. Acad. Sci. U.S.A.* **105**, E107–E107, author reply E112–E114 (2008).
73. J. Lefcheck, J. Byrnes, J. Grace, Package "piecewiseSEM" R package (version 2.1.2, 2020).
74. R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria, 2020).