

# A first empirical analysis of population stability in North America using radiocarbon records

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## Abstract

Questions regarding population stability among animals and plants are fundamental to population ecology, yet this has not been a topic studied by archeologists focusing on prehistoric human populations. This is an important knowledge gap. The fluctuation of human populations over decades to centuries – population instability – may constrain the expansion of human economies. A first step toward describing basic patterns of population stability would be to identify sizes of fluctuations through time, since smaller fluctuations are more stable than larger fluctuations. We conduct a biogeographic analysis of the long-term stability of human societies in North America using a continental scale radiocarbon dataset. Our analysis compares the stability of summed calibrated radiocarbon date probability distributions (SPDs) with subsistence strategies and modeled climate stability between 6000 and 300 BP. This coarse-grained analysis reveals general trends regarding the stability of human systems in North America that future studies may build upon. Our results demonstrate that agricultural sequences have more stable SPDs than hunter-gatherer sequences in general, but agricultural sequences also experience rare, extreme increases and decreases in SPDs not seen among hunter-gatherers. We propose that the adoption of agriculture has the unintended consequence of increasing population density and stability over most time scales, but also increases the vulnerability of populations to large, rare changes. Conversely, hunter-gatherer systems remain flexible and less vulnerable to large population changes. Climate stability may have an indirect effect on long-term population stability, and climate shocks may be buffered by other aspects of subsistence strategies prior to affecting human demography.

## Keywords

coarse-grained analysis, North America, population ecology, radiocarbon, resilience

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## Introduction

The stability of animal populations over time – the change in populations from year to year, decade to decade, or century to century – is fundamental to understanding both the risk of extinction to local populations, and the health and functioning of ecological communities (e.g. Blaustein et al., 1994; Murdoch, 1966; Murdoch and Oaten, 1975; Rall et al., 2010). In theory, the stability of human populations over time could also affect the risk of both local population extinctions among small-scale societies, especially mobile foragers with low population densities (Hamilton et al., 2009), and the economic performance of larger scale societies. For instance, large irrigation systems rely on a dependable supply of cooperative labor to clean and maintain canals (Hunt et al., 2005). If populations fluctuate wildly from decade to decade, such a system would be difficult to maintain because a steady supply of labor would be highly uncertain. Agricultural production may then decline over the long term as individuals abandon large canals in favor of self-reliant strategies to buffer against the risk of labor shortfalls. Yet, few studies have ever attempted to explain the stability of human populations or societies in general

over archeological time scales (an exception to this is Haury et al., 1955). In this article, we make a first attempt to study the long-term stability of human systems by pushing the bounds of paleodemography using the dates-as-data approach.

Dates-as-data refers to a broad approach to using large samples of radiocarbon dates to study changes in human populations over time (Berry, 1982; Rick, 1987). Most dates-as-data research over the last 20 years studies the effects of sampling biases, possible biases introduced by taphonomy and preservation, and biases introduced by cultural processes to reconstruct trends in human population

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over thousands of years or to correlate episodes of population growth and/or collapse with particular episodes of climate and subsistence change (Bevan et al., 2017; Downey et al., 2016; Freeman et al., 2018b; Jørgensen, 2018; Kelly et al., 2013; Kuzmin and Keates, 2005; Louderback et al., 2010; Peros et al., 2010; Rick, 1987; Riede, 2009; Shennan et al., 2013; Smith et al., 2008, 2015; Spangler, 2000; Surovell and Brantingham, 2007; Surovell et al., 2009; Timpson et al., 2014; Zahid et al., 2016). This article is part of a growing literature that builds upon previous studies by using radiocarbon records to study basic population ecology processes in human societies from a comparative perspective (e.g. Freeman et al., 2018b; Peros et al., 2010; Shennan et al., 2013; Zahid et al., 2016) and, in particular, the neglected concept of population stability.

We treat radiocarbon records as reflecting energy expenditure that correlates positively with population size and more complex social organization (Freeman et al., 2018b), and we propose that the more radiocarbon records fluctuate, the less stable human systems, and their underlying populations, were over time. We specifically hypothesize that locations in which societies eventually adopted agriculture display more stability than those where societies remained hunter-gatherers, but also that these agriculturalists experienced large fluctuations (larger maximum and minimum changes in size) seldom experienced by hunter-gatherers. To evaluate this hypothesis, we study the relationships among climate, population stability, and the presence of agriculture in prehistoric North America over the last 6000 years. The North American continent provides an excellent opportunity to study such relationships because much of the continent was populated by both hunter-gatherer and agricultural societies over the last 6000 years. We conduct a coarse-grained analysis, which investigates large-scale patterns rather than the particulars of any given location (Flack et al., 2013; Ortman et al., 2018). In other words, this strategy necessarily sacrifices a focus on individual trees to observe the whole forest. This does not deny the importance of local variability; coarse graining simply provides one perspective for answering difficult questions about complex population processes.

In the remainder of this article, we first lay out our hypothesis for the potential effects of subsistence on the stability of human systems over the last 6000 years. We then go through our methodology in detail, including the process we used to select sampling units, gather and clean radiocarbon data, calculate stability measurements – including radiocarbon summed probability distribution (SPD), temperature, and precipitation stability – and assign agriculture values. We then present the results of our analysis, and, finally, we interpret these results in the context of our hypothesis, compare our conclusions to previous studies, and suggest future research.

## Background

Few researchers have investigated the long-term stability of human societies over decades to centuries; thus, a dearth of anthropological literature exists on the topic. This is partially because it has been difficult to construct datasets useful for estimating changes in human populations over long time scales (hundreds to thousands of years). The goal of this section is to provide a hypothesis to guide our investigation of human population stability. Drawing on a

dynamic systems model of foraging and farming, we propose that human societies face a long-term performance–vulnerability tradeoff in their demographic systems generated by the adoption of agriculture. The basic idea is that agriculture increases the potential carrying capacity of environments, which leads to larger population densities and more stable populations (higher performance) most of the time but also increases the vulnerability of agricultural populations to rare, large fluctuations, whether positive or negative, greater than those experienced by hunter-gatherers.

Given the lack of literature on the long-term stability of human populations, the literature on animal populations provides a starting point for creating expectations about the stability of human populations. Research on the population ecology of non-human animals demonstrates two basic results. First, the fluctuation of animal populations forms a highly right-skewed distribution, often well fit by a power law-like distribution (e.g. Allen et al., 2001; Halley, 1996; Keitt and Stanley, 1998; Marquet et al., 2005). This means that most increases and decreases in population are small, but occasionally, populations experience large increases or declines. Thus, as a starting point, we expect that human population fluctuations also display similar right skewing, with many small population changes and a few large fluctuations. We expect this because humans, like many mammals, respond to a complex set of internal social dynamics that regulate populations and social systems, as well as external dynamics like climate that perturb populations across scales.

Second, the stability of animal populations results from a complex interaction of climate forcing on the resources for a particular species, internal population processes, life history characteristics, and social processes (e.g. Hidalgo et al., 2011; Jenouvrier et al., 2011; Murdoch, 1966). Thus, holding human life history constant, we expect complex relationships among climate, technological organization, and the stability of human populations. Because the study of human population stability is nascent, we do not attempt to formally model the interaction of all these processes. Rather, we develop a narrative hypothesis for the stability of human populations using a dynamic systems model developed by Freeman et al. (2015) that contrasts forager populations with populations that farm.

Freeman et al. (2015) illustrate the consequences of adopting maize for maximum population density, food supply, and vulnerability of a social-ecological system to environmental change in an idealized forest ecosystem. In this ecosystem, humans may either harvest seeds from the trees of the forest or invest in maize agriculture by clearing the forest. The main dynamics of the model relevant here are as follows. The adoption of maize has the consequence of making the food production system more resilient to environmental change, and maize drastically increases the potential carrying capacity of the system. If one increases the population density parameter of the model, farmer-foragers can maintain an optimal harvest of maize and wild seeds, but the entire system becomes vulnerable to climate variation that may initiate a transformation of the system into a degraded state. This transformation is akin to a poverty trap (Freeman et al., 2015). For example, when a drought hits the system, maize and tree seed productivity are depressed. Individuals respond by clearing more forest to grow more maize to stabilize their intake of food in the short run. The newly denuded forest produces fewer seeds,

which leads to a greater need to grow more maize (Freeman et al., 2015). This positive feedback loop causes the system to flip into the poverty trap.

Two qualitative insights for population stability follow from the results of the model described above. First, we should expect agriculture to increase how well individuals produce food, increasing both the productivity and stability of a food supply most of the time. This occurs because agriculture increases the potential supply of food production per unit area per unit time. This expectation fits well with conventional anthropological wisdom that farming provides an opportunity for increasing the productivity of an environment and decreasing the risk of production shortfall – leading to higher carrying capacity (e.g. Freeman, 2016; Glassow, 1978; Roosevelt, 1984). This carrying capacity increase is reflected by population densities recorded in the ethnographic record. The maximum population density among ethnographically documented hunter-gatherers is between 3.39 and 5 people per square kilometer (Binford, 2001; Kelly, 2013; Roscoe, 2009), while small-scale, subsistence agriculturalists can live at population densities of 200–300 people per square kilometer (Netting, 1993). Although ethnographically recorded population densities fit this expectation, no one has ever compared the stability of populations among archeological sequences where agriculture is adopted versus those where the inhabitants remain hunter-gatherers. We begin to fill this empirical knowledge gap.

Second, though adopting agriculture has the consequence (intended or not) of raising the productivity of food production in the model and, thus, should increase population density and stability in the medium term, agriculture also transforms ecosystems and makes the ecosystem more vulnerable to climate variation that was once easily absorbed. In fact, this is a key lesson of dynamic systems models of human–resource interactions in general (e.g. Anderies, 2006; Barnes et al., 2017; Freeman and Anderies, 2012; Freeman et al., 2015; Lima, 2014), and is consistent with the idea of a ‘rigidity trap’ from resilience theory. A rigidity trap occurs when a system is ‘stuck’ because individuals must spend all their time and effort maintaining what they have, which reduces the opportunity to adapt and innovate (Bocinsky et al., 2016; Hegmon et al., 2008; Holling et al., 2002; Marston, 2015). Thus, although we expect agriculture to stabilize the production of food and, consequently, increase the size of agriculturalist populations relative to those that remain hunter-gatherers, we should also expect agricultural sequences to display much larger maximum and minimum changes in population than hunter-gatherer sequences. This is because agriculture increases the carrying capacity of an environment and, thus, the potential size of the population, much more than foraging innovations, and, on average, agricultural societies should be more vulnerable to falling into ‘rigidity traps’ that are more likely to generate very large collapses.

Several anecdotal lines of evidence are consistent with our second expectation that agriculturalists experience more intense and rare large growth spurts and declines than hunter-gatherer sequences. For example, the adoption of agriculture caused several major biological changes in human societies, specifically health decline, physiological stress increase, nutrition decline, and birth rate increase, among others (Lambert, 2009; Larsen, 1995; Roosevelt, 1984). Notably, following the adoption of agriculture,

populations experienced sudden population growth and aggregation into denser communities (Bocquet-Appel and Bar-Yosef, 2008; Gignoux et al., 2011; Lambert, 2009; Larsen, 1995; Li et al., 2009; Phillips et al., 2018; Shennan et al., 2013), which may suggest an increase in carrying capacity and a fitness-health tradeoff wherein populations are larger but less healthy (Lambert, 2009).

Further, researchers using the dates-as-data approach observe what they call population booms and busts following the adoption of agriculture (Bernabeu Aubán et al., 2016; Shennan et al., 2013; Timpson et al., 2014). For example, with the adoption of agriculture, archeologists observe one or more large population growth and decline cycles in Europe (Gronenborn et al., 2014; Shennan et al., 2013; Timpson et al., 2014; Warden et al., 2017). Some researchers argue that this boom-bust cycle is a result of climatic effects (Gronenborn et al., 2014; Warden et al., 2017), especially when populations are high (Gronenborn et al., 2014), while others argue for internal social-ecological processes, such as demographic transitions or land cover changes and the degradation of agricultural habitat (Shennan et al., 2013; Timpson et al., 2014). Again, while these studies suggest that agriculture may be related to particularly large increase or decrease episodes in population, no one has ever systematically compared the long-term stability of populations, let alone the full distribution of growth and decline values in archeological regions where agriculture was eventually adopted with those that remained hunter-gatherers.

In sum, research into the long-term stability of human populations is rare, especially on archeological time scales. However, insights from animal-based population ecology and a dynamic systems model that contrasts foragers and farmers within the same ecosystem provide a narrative hypothesis useful as a starting point to guide our analysis. We propose that, like all other known animal populations, human populations experience many small changes and a few large changes in population and the size of the economy. In addition, we expect that prehistoric agriculturalists experienced greater stability than hunter-gatherers because, ideally, agriculture has the consequence of improving the productivity and stability of a supply of food, which leads to larger and more stable population densities. Adopting agriculture also increases the potential carrying capacity of an environment, which may lead to population booms, and the increasing reliance on agriculture can transform ecosystems to such an extent that human populations become vulnerable to a rigidity trap and experience very large collapses. Thus, we expect that when rare but large increases and decreases occur, these are more intense among agriculturalists than among hunter-gatherers. We test this hypothesis below.

## Data and methods

Paleodemographic studies have estimated changes in human populations by using tree rings (Berry, 1982; Berry and Benson, 2010; Schwindt et al., 2016), human mortality profiles from burials (Bocquet-Appel and Bar-Yosef, 2008; Kohler et al., 2008), human fecal stanols (White et al., 2019), site catchment analysis (Li, 2013; Roper, 1979), changes in house size or number (Brown, 1987; Gronenborn et al., 2014; Kolb et al., 1985; Schwindt et al., 2016), and radiocarbon time-series – dates-as-data (Bevan et al., 2017; Chaput et al., 2015; Crema et al.,



2016; Downey et al., 2016; Jørgensen, 2018; Kelly et al., 2013; Kuzmin and Keates, 2005; Louderback et al., 2010; Peros et al., 2010; Rick, 1987; Riede, 2009; Shennan et al., 2013; Smith et al., 2008; Spangler, 2000; Timpson et al., 2014). Chamberlain (2006) provides an overview of paleodemography in archeology. The dates-as-data approach is the most widely applicable of these approaches as radiocarbon data are more widespread and accessible than, for example, burials (restricted by burial practices, preservation, and legislation) and tree-ring cutting dates (currently spatially restricted). The basic concept is that each dated archeological artifact presumably represents past human activity, which allows the archeologist to assess relative occupation history in a given region (Berry, 1982; Rick, 1987). While these data are not without their imperfections (see Supplemental Information I, available online, section 'Radiocarbon Interpretations and Taphonomy' for an overview of calibration bias, taphonomic bias, sampling bias, and edge effects), radiocarbon databases provide the opportunity to conduct comparative analyses essential to answer basic population ecology questions about prehistoric North America.

Here, we analyze 5700 years of calibrated radiocarbon ages from North America to estimate changes in population (4050 BC–AD 1650 or 6000–300 cal. BP). Over the past decade, there has been an increase in the analysis of radiocarbon date frequencies to estimate changes in relative human population densities (Kelly et al., 2013; Louderback et al., 2010; Rick, 1987; Shennan et al., 2013) and to analyze relative population growth, decline, and movement (Bevan et al., 2017; Crema et al., 2016; Downey et al., 2016; Gayo et al., 2015; Jørgensen, 2018; Kuzmin and Keates, 2005; Peros et al., 2010; Rick, 1987; Riede, 2009; Smith et al., 2008, 2015; Spangler, 2000; Timpson et al., 2014; Zahid et al., 2016). Freeman et al. (2018b) argue that radiocarbon ages can be usefully thought of as an estimate of energy consumption, which scales sub-linearly with population size. Energy consumption also has a relationship with economic complexity: as economic complexity increases, additional energy is necessary to coordinate populations and to fund critical infrastructure, though economic complexity explains much less of the variance in energy output than population size (Freeman et al., 2018a).

The relationship between radiocarbon and social organization (or complexity) has been noted previously. For example, Santoro et al. (2017) demonstrated that increased community management (social complexity) led to increased radiocarbon ages, while Crombé and Robinson (2014) found that increased sedentism and site size may lead to a decreased number of radiocarbon ages. Similarly, Lechterbeck et al. (2014) found that, in central Europe, the density of radiocarbon dates increases with increased land clearing, since hunter-gatherers would burn the landscape to promote hazelnut tree growth (and hazelnut production), while later agriculturalists would conduct slash-and-burn agriculture. This land use change may, however, reflect increased population size that necessitated increased land clearing. Given that social organization explains much less variation in energy consumption in human societies than population size, these different (contradictory) results make some sense. The effects of changes in social organization and complexity will be harder to detect and more situational because these variables explain much less of the variance in energy consumption than

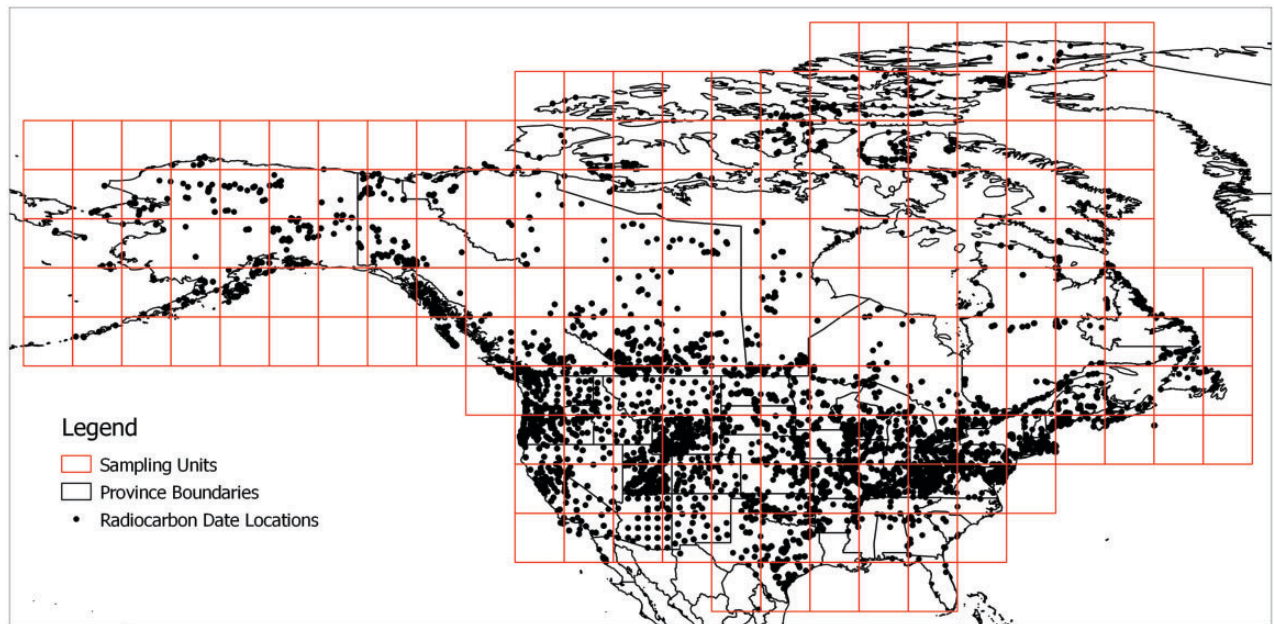
population size. In sum, here we treat radiocarbon date frequencies as an estimate of system size, with population as the dominant dimension of that size (Freeman et al., 2018a). We use SPDs as proxies for the relative size of different human systems over time in well-specified geographic areas.

### Radiocarbon data

To study the stability of human systems between 6000 and 300 cal. yr BP, we gathered radiocarbon ages from the Canadian Archaeological Radiocarbon Database (CARD, 2017) and from the recent NSF-funded project *Populating a Radiocarbon Database of North America* (PI: Robert L. Kelly). We used the following methods to clean the data. We removed all non-archeological dates (bulk sediments, charcoal not associated with human deposits from geological test trenches, etc). We removed all dates with standard deviations (SDs) of more than 300 years and more than 25% of the  $^{14}\text{C}$  date. Despite only studying calibrated ages 6000–300 BP, we retained all uncalibrated radiocarbon dates 8000–0  $^{14}\text{C}$  BP to minimize edge effects (see Supplemental Information I, available online, section 'Edge Effects' for details). We removed all radiocarbon ages missing latitude and longitude. We verified that each radiocarbon age came from a listed radiocarbon lab according to a list provided by *Radiocarbon: An International Journal of Cosmogenic Isotope Research* (Radiocarbon Laboratories, 2019). We ensured each age was only represented once in the dataset by checking and removing the duplicates. If the locational information was different but the  $^{14}\text{C}$  date and SD were the same, and the two duplicates were in the same box, we removed one arbitrarily to count one date within the box. In some cases, either the duplicate lab numbers were not in the same sampling unit or they had the same  $^{14}\text{C}$  date and/or SD. In these cases, we removed all duplicates. After these steps were taken, we had a dataset of 39,636 radiocarbon ages with unique lab numbers within the accepted parameters (Figure 1, data available at DOI: 10.5281/zenodo.3371649).

### Stability measurement methodology

Once we processed the data, we analyze population stability within the United States and Canada by creating 5° grid squares overlaying the continental landmass (Figure 1). This method divided the radiocarbon dataset into sampling units. We used a sampling grid rather than culture areas to minimize sampling bias that may be inadvertently introduced by externally defined cultural areas that change in shape and size over time. We chose 5° boxes as this best balanced the need for sample units with sufficient numbers of radiocarbon ages (>200) and reasonably sized sampling units to capture variation in subsistence technology and climate that may affect stability. In general, larger sample units smooth out climate variation but lead to larger samples of radiocarbon ages. Smaller sample units allow us to better measure climate differences but lead to smaller samples of radiocarbon ages that may limit a stability analysis. We selected only boxes with 200 or more radiocarbon ages to ensure each sampling unit had enough dates to produce an SPD with a reasonable spread. In short, this is one step taken to minimize the potential effects of sample size on the stability of an SPD. Using 5° boxes with 200 or more



**Figure 1.** Continental scale with 196 orange 5° boxes and their specific radiocarbon age locations in black. Country and state boundaries are delineated in black.

radiocarbon ages, we had 39 sampling units with 34,352 radiocarbon ages among them (see Supplemental Information I, available online, section ‘Sampling Bias’).

Within each sampling unit, we used the R programming package, ‘rcarbon’ (Bevan and Crema, 2018) and its function, binPrep, to control the aggregation of radiocarbon ages from the same site within 100 uncalibrated years of one another, which helps limit the sampling bias (Timpson et al., 2014). We examined whether the number of radiocarbon ages within each sample unit affected the results and found no bias created by differences in the number of either radiocarbon ages or bins on our results (see Supplemental Information I, available online, section ‘Sample Size’). We then calibrated the radiocarbon ages using the Intcal13 database (Reimer et al., 2013), then generated an SPD (Williams, 2012). We standardized our SPDs by normalizing them to unity.

For each sampling unit, we summed the annual probabilities into 50-, 100-, and 200-year intervals to study the stability of the radiocarbon record over multiple time scales. We chose these three time scales to facilitate the study of variability in the record. Smaller bin sizes are more likely to be affected by the calibration curve, while larger bin sizes may obscure the variability needed to study stability.

For each of the three time scales, we calculated the first difference values between each bin using the following equation:

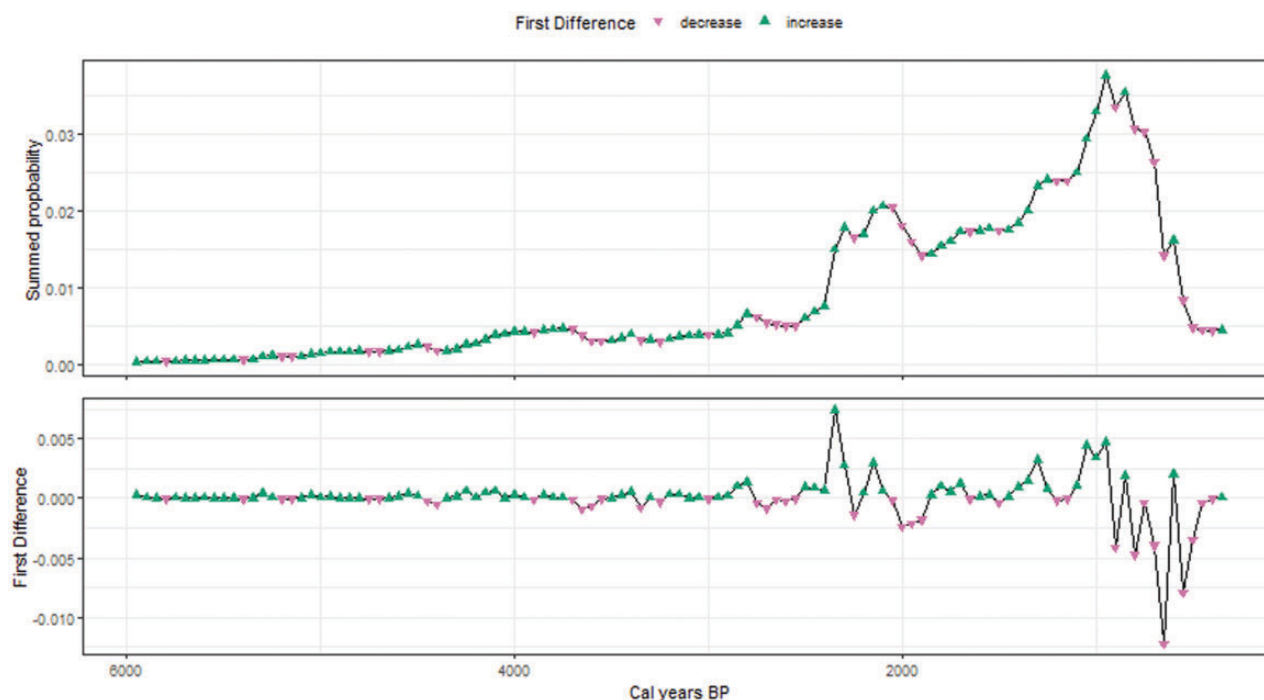
$$SPD_{diff} = SPD_t - SPD_{t-1} \quad (1)$$

$SPD_{diff}$  is the difference between the SPD value from the current time step ( $t$ ) and the SPD value at the previous time step ( $t - 1$ ; Figure 2). This first difference method effectively produces the discrete derivative to identify change over time. It also detrends the SPDs (removes distortions such as a change in the mean over time) and preserves the change in amplitude values around the mean trend of the

SPD. We used the first difference here because all the systems show exponential-like increases in radiocarbon ages over time, suggesting a density-independent growth of the different systems over the last 6000 years. We checked our results with an equation for calculating growth rates that assumes underlying density-dependent dynamics in the growth of system (See Supplemental Information I, available online, section ‘Alternative stability metric’). We conducted this analysis to assess the robustness of our results. This supporting analysis replicates our core results below.

Each positive first difference value demonstrates an SPD increase, while each negative first difference value represents a decrease. To calculate SPD stability per sampling unit, we took the absolute value of the amplitudes and calculated both average and median values. Taking the inverse of each box’s mean or median absolute amplitude value provides a measurement of SPD stability and an estimate of relative population stability within each box. We also separate SPD increases and decreases in the first difference values and use these to represent increases and decreases in relative population and economy size within each sampling unit, with the expectation that the calibration curve should affect agriculture and hunter-gatherer systems in the same way (See Supplemental Information I, available online, section ‘Calibration Effects’). Therefore, any difference between these subsistence strategies’ SPD changes should be a result of relative population change, not an artifact of the calibration curve (but see Bamforth and Grund, 2012).

We considered the entire distribution of amplitude values via density plots to understand the range of variation between the two subsistence strategies. We plotted these amplitude values together, taking the absolute value to exclusively view each first difference value, as well as separately, which allowed us to compare the size of SPD increases and decreases between the two subsistence strategies. We calculated the median and mean amplitude value



**Figure 2.** Calculating the first difference values using sampling unit #18. The first difference values are calculated from subtracting the previous time step ( $t - 1$ ) from the present time step ( $t$ ). The triangles are colored pink if the SPD value of time step  $t$  is less than time step  $t - 1$ , representing a decrease in the SPD. Green triangles represent first difference values that are positive, so the SPD value at time step  $t$  is higher than at time step  $t - 1$ . The graph shows this process for sampling unit #18, located in northern Arizona and southern Utah at the 50-year bin size. Top: SPD values graphed against time for SU #18 with first difference values coded accordingly. Note the exponential trend of increasing SPD values through time. Bottom: First difference values graphed against time. All green triangles are positive first difference values and, therefore, above zero, while all pink triangles are negative first difference values and below zero. The average difference (or absolute value of first difference values) is 0.000911, while the average decrease is  $-0.001321$  and the increase is 0.000705.

for the two subsistence strategies to compare their values independently of the sampling units (code available at DOI: 10.5281/zenodo.3371649).

#### Climate stability methodology

We used PaleoView's climate model to produce our temperature and precipitation stability measurements (Fordham et al., 2017). PaleoView's climate data come from the TRaCE21ka experiment (Liu et al., 2009, 2014; Otto-Bliesner et al., 2014), a Community Climate System Model, version 3 (CCSM3), and a global coupled atmosphere-ocean-sea ice-land general circulation model (AOGCM) with  $3.75^\circ$  latitude-longitude resolution on land and sea and  $3^\circ$  resolution over the ocean. PaleoView re-grids the climate data to provide a  $2.5^\circ \times 2.5^\circ$  resolution on a global scale from 20,050 BC–AD 1989. PaleoView is currently the only source that provides comparable paleoclimate estimates on a continental scale. PaleoView's scale is especially ideal for our coarse-grained analysis. Our goal was to calculate average stability values for each sampling unit, taking into account all variation within the sampling unit, rather than to focus on localized extreme variation, including variation due to altitudinal changes. Essentially, if the localized changes were extreme enough, our method should capture the extremity with a decreased stability value. We chose a  $5^\circ$  grid to balance climate variability with radiocarbon sample size: larger units would have increased our radiocarbon sample but possibly smoothed

out meaningful climate variation, while smaller sampling units would have decreased radiocarbon sample size and could have limited our population stability analysis. Overall, the PaleoView model was an excellent model for our coarse-grained analysis.

To provide one stability measurement for each sampling unit, we followed a multi-step process to convert raw PaleoView data to temperature or climate stability measurements. First, we set the model to produce 10-year averages for temperature and precipitation values from 6000–300 BP for  $5^\circ$  latitude and longitude boxes covering the globe. This resulted in a time-series of temperature and precipitation values at 10-year intervals between 6000 and 300 cal. BP. We then imported these data into R to do the following analyses. We calculated the mean and SD of the temperature and precipitation time-series at three time scales (50-, 100-, and 200-year), so that we had 114 mean and SD values at the 50-year scale (this is because  $(6000 - 300)/50 = 114$ ), 57 at the 100-year scale ( $(6000 - 300)/100 = 57$ ), and 28 at the 200-year scale ( $(6000 - 300)/200 = 28$ ). We calculated stability by taking the inverse of the coefficient of variation ( $1/CV$ ). This metric allowed us to consider not just how mean temperature and precipitation affects human populations, but also how the stability (inverse CV) of these two metrics affects human populations. We then extracted these stability measurements for analysis. Each sampling unit had a temperature and precipitation stability measurement at the 50-, 100-, and 200-year time scale using this methodology (code and extracted data available at DOI: 10.5281/zenodo.3371649).



### Subsistence strategy methodology

Finally, we assigned a binary agriculture variable based on presence or absence of agriculture prehistorically within the sampling areas, with a focus on where within the sampling unit the radiocarbon samples were coming from for the reasons discussed below (Figure 3; see Supplemental Information I, available online, section ‘Assignment of Agriculture ID Variable’). These values were assigned based on documented and dated evidence of the presence of domesticates (e.g. maize, squash, amaranth, and other non-gourd domesticates) in the review literature of archaeological records of North America (Jennings, 1968; Kopper, 1986; Pauketat, 2012; Snow, 1989; Thomas, 1999). Some of the sampling units occur in ‘border land’ areas characterized by a late adoption of agriculture (ca. 800 BP or later) with hunter-gatherers still occupying large portions of the sampling unit. We conducted additional research on these areas to determine the extent of agriculture in the area with an emphasis on the effect of agriculture on the daily life of those living there, including hunter-gatherers, as well as comparing when the majority of our radiocarbon sample for these areas came from (see Supplemental Information I, available online, section ‘Assignment of Agriculture ID Variable’ for border land statements, Supplemental Information I, available online, section ‘Chance of a false positive difference in the mean stability of hunter-gatherer vs. agricultural sequences’ for a false positive check). This coarse-grained approach of assigning a binary agriculture variable allows us to identify general trends in places that adopted agriculture at some point during their occupation (henceforth called ‘mixed agriculturalist’) versus those locations that barely or never adopted agriculture (henceforth called ‘hunter-gatherer’ or ‘forager’). Future work finely parsing these areas will likely depend on the accumulation of more radiocarbon dates to avoid problems associated with very small samples.

We compared the two subsistence strategies across all three time scales in several ways. First, we generated density plots of all amplitude values to observe the differences in detrended SPD first difference means, medians, SDs, and skewness between the two subsistence strategies. We also analyzed the relationship between long-term population stability and climate stability (via temperature and precipitation stability) at the three time scales, controlling for differences based on subsistence strategy.

We hypothesized that human societies face a greater long-term performance–vulnerability tradeoff in their demographic systems by the adoption of agriculture than by societies that remained hunter-gatherers. In other words, while we expected both forager and mixed agriculturalist sequences to display right-skewed distributions of radiocarbon first differences, we also expected mixed agriculturalist sequences to have lower mean population stability than hunter-gatherer sequences. This is because we expected agriculturalists to experience large rare booms and busts but a higher median stability than hunter-gatherer because agriculture improves the stability of a food supply most of the time.

## Results

We found that mixed agriculturalist sample units displayed lower mean SPD stability than hunter-gatherer sample units

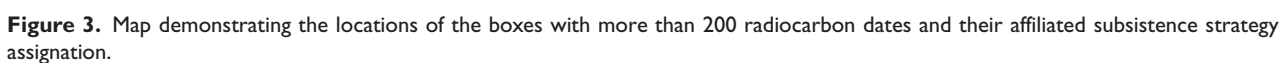
throughout the 5700-year sequences. However, hunter-gatherer sample units have lower median SPD stability than agricultural sample units. This pattern held at all three time scales (50-, 100-, and 200-year). Further, precipitation and temperature stability had no clear relationships with SPD stability among either subsistence strategy. These results support our hypothesis that agriculture initiates a performance–vulnerability tradeoff in human–resource systems.

### Subsistence strategy and SPD stability

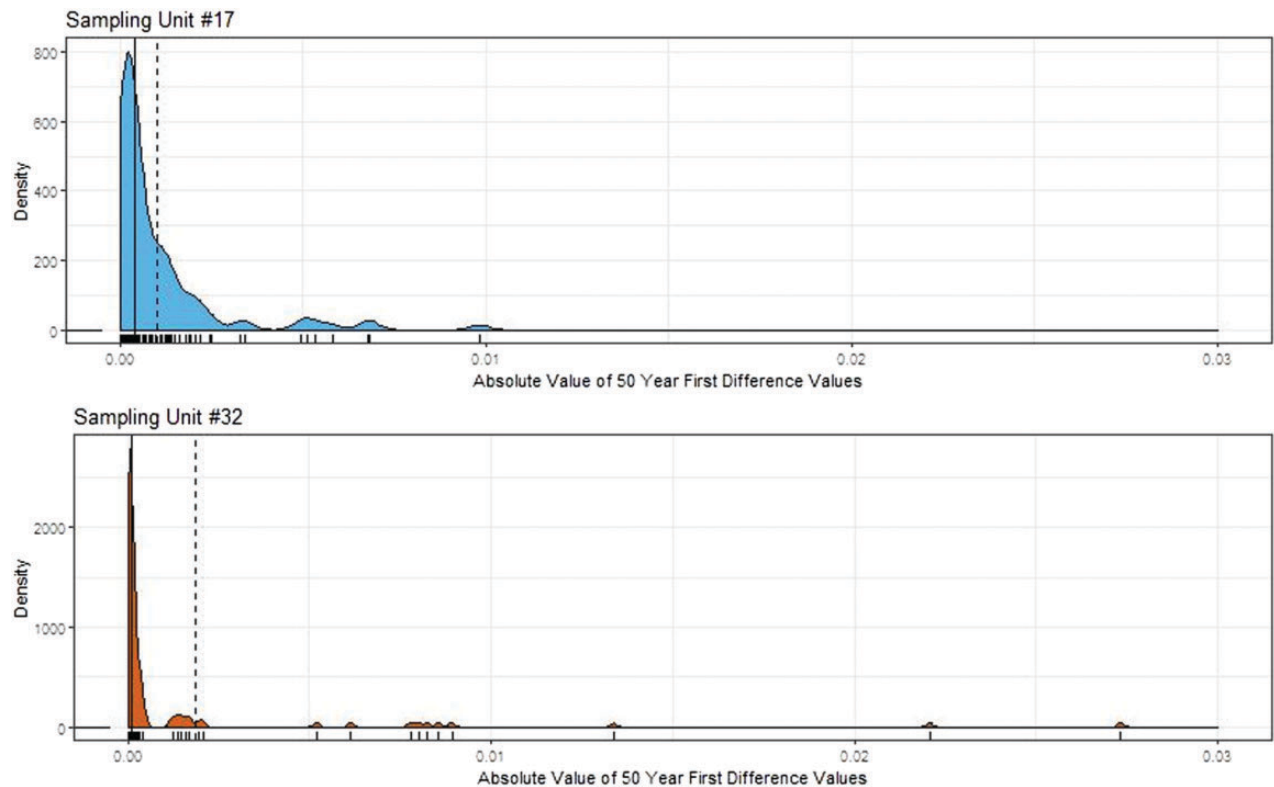
Agricultural sequences displayed a lower mean stability than sequences that remained hunter-gatherers. This indicates that, on average, mixed agriculturalist systems were less stable than hunter-gatherer systems. While mixed agricultural sequences displayed less stability on average than hunter-gatherer sequences, hunter-gatherer sequences actually had lower median SPD stability estimates than the mixed agricultural sequences. For instance, Figure 4 compares the distribution of SPD fluctuations from mixed agriculturalist sampling unit #32 (SU #32) located in southeast South Dakota, northeast Nebraska, and western Iowa with hunter-gatherer sampling unit #17 (SU #17) located in southwest Nevada and southeast California. Both distributions display right skewing. Most of the time, SPD changes are very small, and sequences experience infrequent large changes (either positive or negative). In this case, the SU #32 density plot is more right-skewed and has more outliers. The greater degree of skewing and longer tail in SU #32 leads to a greater mean value of amplitude of change than SU #17. However, SU #17 has a larger median amplitude of SPD fluctuation. This is consistent with our proposal that hunter-gatherer sequences are less stable than mixed agricultural sequences most of the time, but mixed agricultural sequences display rare, extreme changes not observed in hunter-gatherer sequences, which inflate the means of these sequences.

Table 1 and Figure 5 illustrate this pattern in general. Note that in Table 1, hunter-gatherer sequences have larger median amplitudes of change, but mixed agricultural sequences have larger mean amplitudes and SDs. Mixed agriculturalists also have more positive first difference values suggesting that they experience more long-term growth and fewer population declines than hunter-gatherer sequences. This pattern holds across all three time scales (Table 1).

Figure 5 displays the distributions of SPD fluctuations among all hunter-gatherer and mixed agriculturalist sequences at 50-, 100-, and 200-year time scales (see Supplemental Information I, available online, section ‘Additional Plots and Tables’, for graphs and skewness tables for just SPD increases and decreases; see Supplemental Information I, available online, section ‘Boxplots of mean and median stability values’, for boxplots comparing mean and median SPD stability of each sampling unit between the subsistence strategies). Figure 5 shows that mixed agricultural sequences have a longer tail that stretches out to the right farther than hunter-gatherer sequences. The long tail of the mixed agricultural sequences pulls the mean to the right. At the same time, the distribution of SPD fluctuations is more steeply peaked at very small values among mixed agricultural sequences than among hunter-gatherer sequences. This pulls the median value of agricultural sequences more to the







**Figure 4.** Density plots of two sampling units, #17 (located in southwest Nevada and southeast California) on top and #32 (located in southeast South Dakota, northeast Nebraska, and western Iowa) on bottom. #17 was occupied by hunter-gatherers between 6000 and 300 cal. BP, while people living in #32 adopted agriculture at some point. The solid line represents the median, and the dashed line, the mean. #32 is more skewed by outlier population changes than #17, pulling the mean to the right.

**Table 1.** Statistical properties for absolute value of first difference SPD trends for each of the subsistence strategies at all three time scales.

Time scale	<i>n</i>	% Increase	Median	Mean	SD	Skewness
Hunter-gatherer results						
50-year bins	2260	57.8	0.0004	0.0010	0.0016	3.82
100-year bins	1120	57.6	0.0016	0.0030	0.0040	3.12
200-year bins	540	61.5	0.0044	0.0072	0.0081	2.14
Mixed agriculturalist results						
50-year bins	2147	59.4	0.0003	0.0012	0.0027	5.46
100-year bins	1064	60.7	0.0012	0.0037	0.0076	4.78
200-year bins	513	63.7	0.0035	0.0105	0.0190	3.58

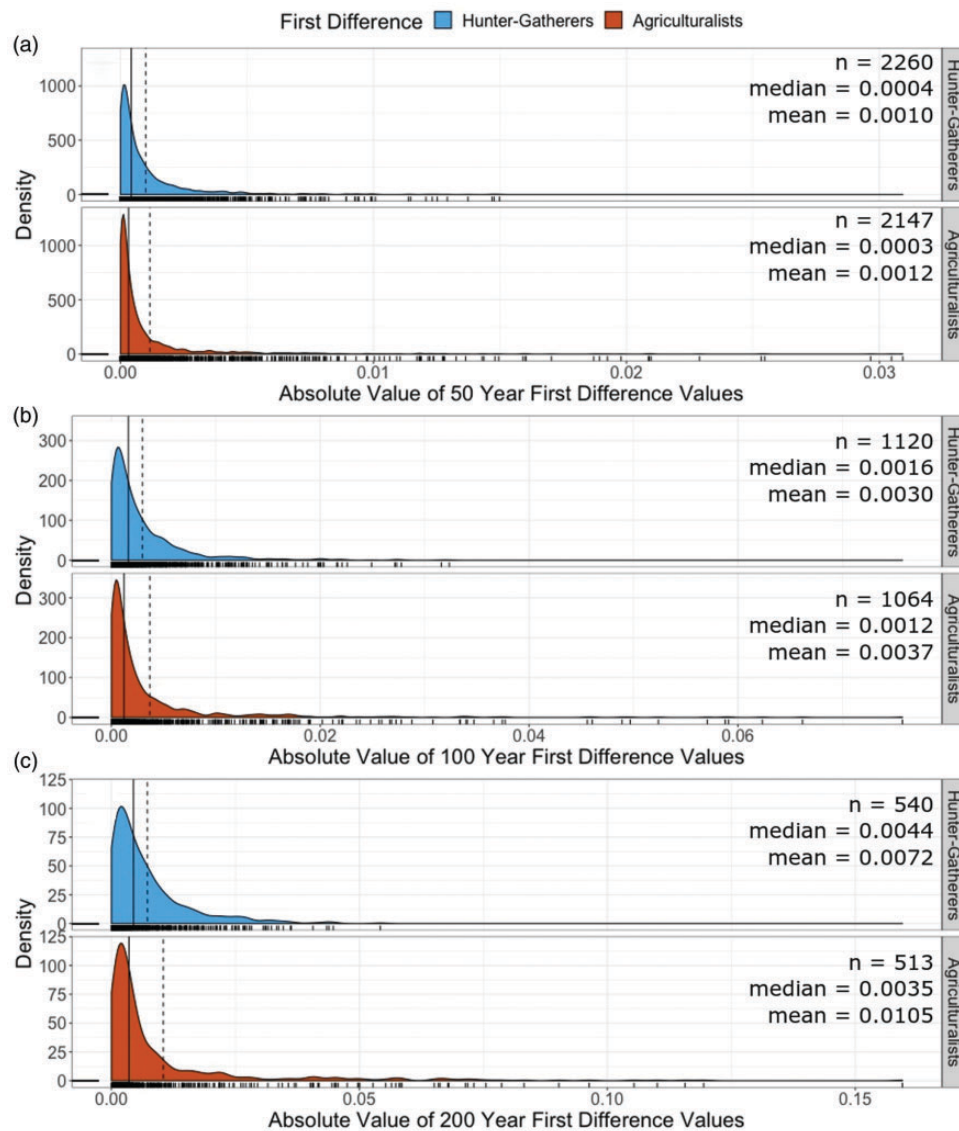
SPD: summed probability distribution; SD: standard deviation.

left of the distribution than among hunter-gatherer sequences. In short, most of the time, mixed agricultural sequences display more stability than hunter-gatherer sequences, but the mixed agricultural sequences experience very large, albeit rare, changes in SPD values that are rarely observed in the hunter-gatherer sequences.

#### *Climate stability and SPD stability*

Figure 6 illustrates the relationship between mean SPD stability among hunter-gatherer and mixed agriculturalist sequences and both temperature and precipitation stability. In general, there are weak relationships between measures of climate stability and the stability of SPD records over time. Mixed agriculturalists and hunter-

gatherers occupy the same range of temperature and precipitation stability (Figure 6b, d and f). Both subsistence strategies display very weak relationships with temperature and precipitation stability. In sum, relationships between climate stability and SPD stability are weak. Most importantly, the differences in mean SPD stability between hunter-gatherer and mixed agricultural sequences remain consistent even when controlling for climate stability (the blue dots are, on average, above the red triangles in Figure 6). Results are similar for median values of SPD stability; mixed agricultural sequences have lower median SPD stability values than hunter-gatherer sequences, regardless of climate stability (see Supplemental Information I, available online, section ‘Additional Plots and Tables’).



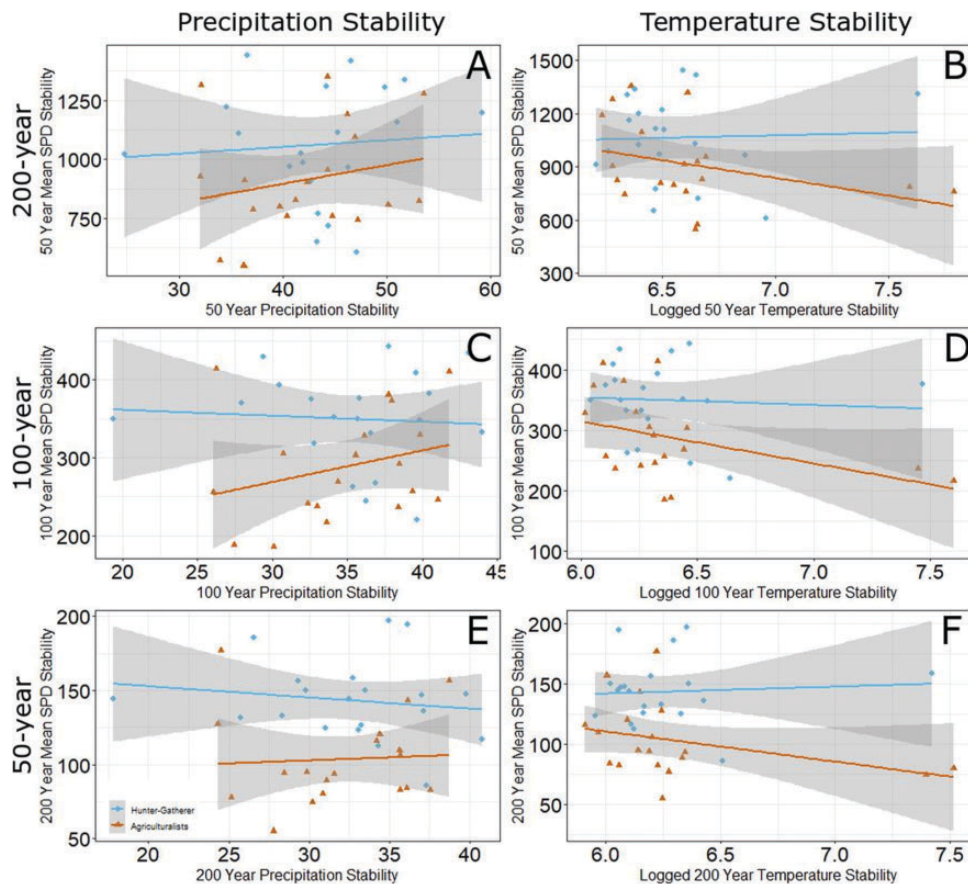
**Figure 5.** Density plots displaying absolute value of first difference values at the (a) 50-year, (b) 100-year, and (c) 200-year time scales. Sampling units that remained hunter-gatherers for the entire 6000-year sequence have amplitudes in light blue, while orange represents sampling units that adopted agriculture at some point during the 6000 years. Solid vertical lines mark the median value, while the dashed lines mark the mean. At all three time scales, hunter-gatherers (blue) have a higher median and lower mean than mixed agriculturalists (orange).

## Discussion

In this article, we have attempted to study the basic process of population stability among human societies. Population stability is widely studied among non-human animals because population stability can have important implications for the functioning of ecological communities and the risk of extinction for the animals in these communities. The stability of human populations may also have significant consequences for humans, both for the long-term functioning of our economies and the risk of population collapse in certain regions. Thus, investigating the ecological dynamics that underlie the stability of human populations is an important topic of research. As a first attempt to study human population stability, we have pushed the bounds of the dates-as-data approach. We used radiocarbon data to represent changes in the size of past human systems. To guide our analysis, we used a narrative hypothesis. This hypothesis simply proposed that the adoption of agriculture

had (unintended) consequences for the stability of human systems. Agriculture led to more stability most of the time, but also to rare, large increases and decreases not experienced by hunter-gatherer systems – a performance–vulnerability tradeoff.

Our results reveal patterns consistent with the idea that the adoption of agriculture generates a performance–vulnerability tradeoff among human populations. (1) Most of the time, mixed agricultural areas display more stability (smaller first differences) than hunter-gatherer regions. This suggests that human populations that adopt (or are geographically close to those who adopted) agriculture experience more stable populations and economies most of the time (higher performance). (2) However, mixed agriculturalist radiocarbon sequences experience large, outlier changes in their SPDs. Such extreme outliers are rare among regions that remained hunter-gatherers, and this is consistent with the idea that mixed agriculturalists



**Figure 6.** The left column (a, c, e) displays the relationship at all three time scales between precipitation stability and respective mean SPD stability, while the right column (b, d, f) shows the relationship between temperature stability and mean SPD stability.

transform landscapes in such a way that they are more vulnerable to a rigidity trap.

A rigidity trap occurs when individuals within socio-environmental systems are so locked into their current strategies that innovation cannot occur fast enough to keep up with environmental change. Societies in such a situation continue investing in their current strategies even when these strategies are no longer profitable or even appropriate, given the environmental conditions. The end of a rigidity trap is marked by a collapse. The extreme agriculturalist radiocarbon SPD decreases may reflect post-rigidity trap collapse. These collapses likely occur through a combination of depressed economic activity, emigration, and/or mortality.

We found very weak relationships between SPD stability and either temperature or precipitation stability. This suggests, at least in this first attempt, that subsistence has a much stronger impact on the stability of human systems than the stability of temperature and precipitation. While we found little relationship between coarse-grained SPD stability and either precipitation or temperature stability, fine-grained studies may find different results. Of course, individual climate events may interact with vulnerabilities generated by social and demographic conditions and could contribute to outlier collapse events. This is an area of future research for coarse-grained studies, but this does shift the focus from broad-scale stability trends to individual collapse events.

Shennan et al. (2013) suggest that, contemporaneous with the adoption of agriculture, populations in Europe

experienced sudden population booms followed by population busts. Our results suggest that the relationship between agriculture and outlier population change events perhaps generalizes beyond Europe. Agricultural sequences in North America have smaller population changes and are, therefore, more stable than hunter-gatherer sequences, but agricultural sequences also demonstrate infrequent and extreme population increases and decreases on a scale never seen in hunter-gatherer sequences. This may occur immediately following the adoption of agriculture, or millennia after the adoption of agriculture. When exactly agricultural populations experience the rare extreme population or SPD increases and especially decreases may vary locally, but they likely will experience these at some point. Notably, the greatest population changes in this study nearly all occurred after 1300 cal. BP, suggesting that the pattern is indeed driven by the effects of agricultural economies.

Internal and external factors likely work interdependently within the agricultural systems to generate such large collapses (busts). Humans occupy a space with a resource base initially able to absorb external shocks (such as climate shifts). As their population increases, however, they put increasing strain on their resource base, which increases their vulnerability to external shocks such as infectious disease, invasion, or drought. When an adequately large external shock hits a sufficiently vulnerable human system, the system can no longer absorb these shocks. This is because positive feedback between human behavior and the state of an ecosystem leads to collapse or major reorganization of society and of the economy (Anderies,



2006; Barnes et al., 2017; Freeman and Anderies, 2012; Freeman et al., 2015; Lima, 2014). In this way, a large population with a strained resource base may be less capable of dealing with external shocks than one less intensively exploiting their ecosystem.

Much research has gone into understanding the changes within a system once human societies adopted agriculture, but little research has directly compared large-scale variation between the population dynamics of both agriculturalists and hunter-gatherers (but see Zahid et al., 2016, for a comparison of growth rates between subsistence strategies). We suggest that the relationship between these subsistence strategies, population stability, and climate stability is complex and interdependent.

## Conclusion

We hypothesized that in locations where populations adopted agriculture, those populations unknowingly initiated a performance–vulnerability tradeoff. To evaluate this hypothesis, we analyzed the relationship between climate, long-term population stability, and subsistence strategy in North America between 6000 and 300 cal. BP using the dates-as-data approach. Consistent with a performance–vulnerability tradeoff, we found that mixed agriculturalists are more stable than hunter-gatherers in general, but experience extreme, unprecedented population changes not experienced by hunter-gatherer societies.

This study is the first attempt to investigate the long-term stability of human systems on a large scale, which pushes the boundaries of radiocarbon dates-as-data analysis. As such, this research contributes to the growing body of literature that uses the dates-as-data approach to study basic population ecology processes among human societies. Investigating population ecology processes via archeological data can inform researchers about the ways in which humans are similar to and different from other species, and improve our understanding of the consequences of key changes in human ecology over the millennia. However, more work is needed.

## Future directions

Future directions for this research may focus on change over time in population stability after the adoption of agriculture: for example, a study focusing on the severity of population increases and decreases relative to how long populations have practiced agriculture. Agriculturalists may experience increasing population stability following the adoption of agriculture but, at the same time, become increasingly susceptible to large, rare busts through time as the agricultural system accumulates landscape capital vulnerable to unexpected climate changes. Similarly, social factors may drive population stability more than subsistence strategy. Socially stratified and sedentary coastal hunter-gatherer-fishers may, for example, have population sizes and stability levels more similar to those of agriculturalists than to mobile hunter-gatherers in xeric regions. Further, very pronounced resource intensification in hunter-gatherer systems may lead to a similar type of performance–vulnerability tradeoff, meaning that such tradeoffs may not be simply a consequence of the presence of agriculture. Larger comparative samples will allow us to begin to answer such questions.

We also suggest continuing to place population stability within a resilience theory framework. An analysis comparing the synchrony of external shocks and population busts may focus on systemic changes contemporaneous with the population bust (see Gronenborn et al., 2014, for an example among the LBK culture in western central Europe). Subsistence intensification contemporaneous with a population bust may result in a reduced ability to deal with external shocks in the future. Quantification of external shocks relative to internal rigidity may help us to understand the size characteristics of population collapse (see Hegmon et al., 2008, for a comparison of society rigidity to social transformation and collapse).

Future studies may also use a similar coarse-grained analysis on a larger (i.e. global) or smaller, finer grained scale. Changing the scale will allow different analyses of the relationship between past human populations and external factors, including biodiversity and vegetation regimes, pathogen stress, and small-scale social stress. The relationship between climate change and population stability may be more visible at a finer scale than it was in our study. Similarly, modifying the coarse-grained methodology to reflect ecological and geographic zones may reveal more about local patterns of movement and the effect of migration and fission/fusion on population stability (see Freeman et al., 2017, for a look at biogeography and social connectedness on the Texas Coastal Plain).

Pairing paleodemographic methodologies may reveal more about past populations than using one method alone (Crombé and Robinson, 2014; Williams, 2012). Radiocarbon by itself reveals information about radiocarbon ages associated with archeological remains on the landscape. Site count analysis (Williams, 2012), dendrochronology (Bocinsky et al., 2016), and ceramic typologies (Ortman et al., 2016) can be linked to radiocarbon to reveal more about social change. Site count analysis may, for instance, reveal increased population density where the number of sites decreased but radiocarbon SPD size increases. Dendrochronology of structures reveals economic expansion that, coupled with radiocarbon, may reveal periods of social expansion (Robinson et al., 2019). Similarly, ceramic typologies reveal information about individuality and inter-societal trade.

Finally, more nuanced estimates of commitment to agriculture may improve our understanding of the stages of agricultural investment relative to population stability. Assigning an ordinal variable that ranks levels of investment in agriculture on different portions of a time series would refine the relationship between the stability of societies and agriculture. This research focuses on the eventuality of agriculture adoption, rather than the moment and intensity of agriculture adoption, which may obscure the change in patterns as agriculture was adopted.

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## Supplemental material

Supplemental material for this article is available online. Data and code may be found at: DOI: 10.5281/zenodo.3371649.

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