



Climate and oceanic condition changes influence subsistence economic adaptation through intensification on the Central Andean coasts

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ABSTRACT

Understanding the causes of subsistence economic adaptation remains a critical topic in archaeology. Here we explore one potential causal phenomenon, climate change, to understand how shifting ecological conditions incentivized adaptation through subsistence economic intensification along the Central Andean coasts. To do so we couple 775 archaeological individuals that have dietary stable isotope data (collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, hydroxyapatite $\delta^{13}\text{C}$) with spatio-temporal core-based proxies of oceanic sea surface temperature and El Niño Southern Oscillation frequency estimates. Using an ensemble machine learning model, we evaluate hypotheses that changes in ocean conditions resulting in decreased marine productivity correspond with isotopic signals of increasing terrestrial resource reliance over the past ~7000 years. Results support the hypotheses, and prior work, showing isotopic signatures of diet across the coastal Central Andes reflect greater incorporation of resources indicative of intensification during times when marine productivity was likely depressed. As near-shore marine productivity declined, people adapted in manners that may have both increased their resiliency to climate change and improved their overall subsistence returns, but at higher investment costs. The overall findings support theoretical intensification expectations, suggesting adaptation through intensification represents one of the key factors in understanding broader behavioral transformation in the face of climate change.

1. Introduction

Subsistence economic adaptation is associated with major social and ecological changes across human history (Matson, 1983; Smith, 2001; Fitzhugh, 2003; Jones et al., 2013; Yeshurun et al., 2014; Weitzel and Coddling, 2016). While the ultimate drivers of adaptation, particularly through intensification, are debated and likely multi-causal (Zeder, 2012; Morgan, 2015) the most frequently invoked causes are human responses to environmental change (e.g., Dillehay and Kolata, 2004), population growth and pressure (e.g., Boserup, 1965; Flannery, 1969; Coddling et al., 2021) and the interactions between them (e.g., Morgan, 2015; Bevan et al., 2017; Roscoe et al., 2021), though social and sociopolitical factors have been cited as well (Ames, 2003; Zeder, 2012). Recent work in the Central Andes has demonstrated that climate change had a large impact on past diets, suggesting shifting climatic conditions altering local environments may explain a large portion of dietary change over the past 7000 years (Wilson et al., 2022). In this region, a

strong body of work has also highlighted links between coastal subsistence, intensification, and climatic or environmental change (Parsons, 1970; Moseley, 1975; West, 1981; Sandweiss et al., 2001, 2004, 2009; Dillehay and Kolata, 2004; Andrus et al., 2008; Reitz et al., 2008; Gerdau-Radonić et al., 2015; Tully et al., 2019; Goodbred et al., 2020). However much of this research is, necessarily, restricted in space or time, providing unique insights into individual and local experiences though not often capturing the overall history of human-environment interaction. To build upon such prior studies, and provide a broad spatio-temporal examination of the relationship between long-term climate change and subsistence intensification, here we expand upon our recent work (Wilson et al., 2022) to explore the impact of shifting oceanic conditions on coastal Central Andean diet. Using reconstructions of sea conditions along coastal Peru and northern Chile over the past 7000 years (Moy et al., 2002; Nürnberg et al., 2015; Salvatelli et al., 2019; Sandweiss et al., 2020) and key light stable isotopes (collagen $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and hydroxyapatite $\delta^{13}\text{C}$) we evaluate if climatic

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change, captured in oceanic conditions, altering marine productivity contributed to dietary adaptation in line with expectations from intensification theory. While social effects and population growth are also likely contributors to adaptation in the area (e.g., [Hastorf and Johannessen, 1993](#); [Roscoe et al., 2021](#); [Wilson and McCool, 2023](#)), here we focus explicitly on parameterizable environmental components to evaluate if and how climate change contributed to the process.

1.1. Background

1.1.1. Regional setting

The Central Andean coasts are semi-arid to arid deserts that become increasingly dry in more southern latitudes and are broken up by river and stream systems that flow from the highlands into the Pacific Ocean. These highly circumscribed coastal valleys ([Carneiro, 1970](#)) supported the development of early complex societies and monumental architecture, with a rich history of use beginning in the late Pleistocene and extending to the present ([Moseley, 1975](#); [Quilter and Stocker, 1983](#); [Quilter, 1991](#); [Rivera, 1991](#); [Billman, 2002](#); [Haas et al., 2004, 2006](#); [Pozorski and Pozorski, 2018](#); [Prieto et al., 2020](#)). The combination of the coastal Andean rain shadow and upwelling of cold, nutrient-rich water off the coast limits terrestrial productivity while providing one of the most productive fisheries in the world. Evidence for terminal Pleistocene (e.g., [Sandweiss et al., 1998](#); [Jackson et al., 2012](#)) and early Holocene (e.g., [Reitz et al., 2008](#); [Dillehay et al., 2017](#)) fisher-foragers along the coast suggests that people made use of the productive marine environments from the beginning of settlement in the Central Andes. By the late Pre-ceramic period there is significant evidence for increasing sociopolitical complexity within societies heavily reliant on marine resources, coupled with evidence of increases in exchange and/or inland resource exploitation, particularly along the north coast (e.g., [Quilter and Stocker, 1983](#); [Stanish, 2001](#); [Haas et al., 2006](#)). While various locations have been nominated as home to the earliest polities, and debates continue regarding the levels of complexity experienced, it is fairly well accepted that between ~4000 and 2500 BP complex political organizations of people with access to significant amounts of labor increasingly appeared on these coastal landscapes (see [Haas et al., 2006](#); [Shady, 2006](#); [Pozorski and Pozorski, 2018](#)).

These polities were likely emerging in conjunction with increasing populations ([Roscoe et al., 2021](#)) and people appear to have varied in their reliance on marine versus terrestrial resources (e.g., [Tykot et al., 2006](#); [Grobman et al., 2012](#); [Carmichael et al., 2014](#); [King et al., 2018](#)). This variation in marine versus terrestrial use continued over time, even as domesticated resources were introduced and rose in importance. While the earliest use of maize (*Zea mays*) extends to ~5000–4500 calBP ([Tung et al., 2020](#)), in general it is first during these periods of initial increasing sociopolitical complexity (~3800–2500 BP) that maize is established as a consistent dietary component, and it seems to become a relatively prevalent subsistence and economic resource by ~1350 BP ([Pearsall, 2008](#); [Haas et al., 2013](#); [Gerdau-Radonić et al., 2015](#)). Generally, even though maize established during the early periods, coastal peoples continued to make significant use of marine resources ([Rostworowski, 1977](#); [Haas et al., 2006](#); [Prieto et al., 2020](#)). Contrary to earlier in time, by around ~1350 BP, political power had dominantly shifted to the highlands (e.g., Wari, Tiwanaku, and, later, Inca), generating trans-Andean economies incorporating maize and many other terrestrial resources as key products for both subsistence and social signaling ([D'Altroy et al., 1985](#); [Hastorf and Johannessen, 1993](#); [Covey, 2000](#); [D'Altroy and Hastorf, 2001](#); [Kellner and Schoeninger, 2008](#); [DeFrance, 2021](#)). Even in these later periods, however, as exchange may have made accessing terrestrial resources easier, and social and ritual practices may have favored terrestrial resource production and use, at least some coastal individuals show evidence of continued heavy reliance on marine resources (e.g., [Sandweiss, 1992](#)).

Generally then, albeit with spatio-temporal variation, the changes in subsistence practices seen over time included increased use of

domesticates often concurrent with landscape modifications to help insulate against severe weather and/or opportunistic extensification of agriculture to make use of newly viable plots (e.g., [Dillehay and Kolata, 2004](#); [Sandweiss et al., 2009](#); [Beresford-Jones et al., 2011](#); [Pezo-Lanfranco et al., 2015](#); [Goodbred et al., 2020](#); [Vining et al., 2022b](#)). Interpretations of the causes of these subsistence changes have ranged from adaptive responses to environmental change, changing sociopolitical pressures and social significance of maize, shifting demographics, or their combinations. Specific to environmental change, people along the coasts had to respond to dynamic oceanic conditions as they were subject to relatively unpredictable inter-annual variations in sea surface temperature (SST) and El Niño Southern Oscillation (ENSO) events that alter marine productivity and precipitation regimes bringing stochastic floods, droughts and megadroughts, earthquakes, and/or landslides ([Reitz et al., 2008](#); [Sandweiss and Richardson, 2008](#); [Tully et al., 2019](#); [Sandweiss et al., 2020](#)).

These inter-annual variations in SST and ENSO events can also bring about drastic biotic change in marine and terrestrial ecosystems ([Pennington et al., 2006](#)). During non-ENSO conditions, the Central Andean coastal ocean environments host abundant plankton which, in turn, support highly productive fisheries which themselves help support seabird and pinniped populations ([Bakun and Weeks, 2008](#)). Conversely, ENSO events limit cold water up-welling which starves the near-shore and ocean surface areas of the Central Andean coasts of nutrients ([Chavez et al., 1999](#)). This process can cause large-scale declines in plankton populations resulting in up-trophic effects significantly decreasing the growth and reproductive success of higher trophic level species ([Barber and Chavez, 1983](#); [Niquen and Bouchon, 2004](#)). Further, ENSO events reduce the size of the up-welling region ([Nixon and Thomas, 2001](#)), thereby reducing both the overall productivity of the coastal ecosystems ([Pennington et al., 2006](#)) and their spatial distributions. Changes in SST, which can be coincident with or independent from ENSO events, are also associated with large-scale biotic change. Warming SST can result in shifts from anchovy to sardine population dominance while pushing out-migration of larger fish species that prefer cold water ([Chavez et al., 2003](#); [Alheit and Niquen, 2004](#)). However, ENSO events appear in multiple 'flavors.' In addition to the warm phases described above, La Niña, a cool phase, inverts the typical ENSO pattern by bringing colder water temperatures and increased up-welling benefitting marine productivity ([Chavez et al., 1999](#)). Thus, depending on the active oceanic condition, Central Andean coastal fisheries can range from highly productive to relatively depressed.

At the same time that ENSO events depress marine productivity they bring significantly increased coastal precipitation (see [Jaksic, 2001](#)). Increasing precipitation along these arid Pacific coasts promotes plant growth and productivity ([Tovar et al., 2018](#); [Broughton et al., 2022](#)). [Coelho et al. \(2002\)](#) suggest that in the northern portions of Peru in particular, ENSO events and increased SST correspond to positive precipitation anomalies which [Vining et al. \(2022a\)](#) have shown can drastically increase gross primary productivity. Such expansions of terrestrial productivity and agricultural potential appear to correlate with North Coast settlement patterns evidencing expansion of agriculture into areas made viable by ENSO driven precipitation ([Vining et al., 2022b](#)). Archaeological evidence suggests there has been significant variation over time in ENSO frequency and severity ([Sandweiss et al., 2020](#)), implying people faced varied conditions both during individual lifespans and over generations. These conditions incentivized adaptations and innovations, with a strong body of work investigating human adaptive responses in the context of risk reduction techniques (e.g., [Dillehay and Kolata, 2004](#); [Vining et al., 2022b](#)). Here we further these investigations of adaptation by adding to risk reduction analyses using a broad subsistence economic intensification perspective.

1.1.2. Intensification

As excellent overviews have highlighted, subsistence economic intensification (intensification or SEI hereafter) has come to possess

many meanings in archaeology, generally being considered any action or innovation that increases productivity (Zeder, 2012; Morgan, 2015). Formally, from a Boserupian perspective (Boserup, 1965), intensification may be conceived of as the adoption or invention of a subsistence economic technique or technology that requires greater investment in time and/or effort than the previous strategy but that results in greater overall returns. Such innovations or actions may enable populations to then expand past the prior carrying capacity of the subsistence economic landscape they inhabit. This approach to intensification has often been viewed through optimal foraging theory frameworks as a plausible explanation for domestication and the emergence of agriculture or other major subsistence shifts (i.e., Matson, 1983; Winterhalder and Goland, 1993; Bettinger, 2006; Kennett and Winterhalder, 2006; Morgan, 2015; Weitzel and Coddling, 2016), in line with the longstanding broad spectrum revolution hypothesis (Flannery, 1969). When related directly to diet, intensification is most commonly associated with the diet breadth model (MacArthur and Pianka, 1966; Charnov, 1976; Stephens and Krebs, 1986) as follows: as encounter rates with high ranked resources decrease, individuals seeking to maximize their rate of subsistence economic return will incorporate increasingly lower ranked resources, and subsequently will intensify their strategy when use of these lower ranked resources requires innovation or implementation of different, more time or energy costly, techniques or technology (Hawkes and O'Connell, 1992; Kennett and Winterhalder, 2006; Coddling and Bird, 2015; Weitzel and Coddling, 2016).

Along the Central Andean coasts, rich fisheries and near-shore environments presented people with access to high return marine resources (i.e., marine mammals, fish, bivalves, seabirds). As Reitz et al. (2008) document in their overview of early peoples on the Central Andean coasts, these marine resources are much more prevalent in archaeological records than are terrestrial resources, with the terrestrial resources typically represented by lizards, small birds, small rodents, and few plants. From a diet breadth model perspective, such terrestrial resources are likely to provide lower return rates than the marine resources, suggesting people should only make increased use of the lower-ranked marine and terrestrial resources in their diet when their ability to obtain high-ranking marine resources declines. Though decreasing encounter rates can be driven by population increase (Boserup, 1965; Weitzel and Coddling, 2016) they also can occur through environmental degradation. While population increase does appear to occur early on the Central Andean Coasts (~4000 calBP), populations seem to stabilize shortly thereafter (Riris, 2018; Roscoe et al., 2021; Wilson et al., 2022) even as subsistence changes occurred. Further, Reitz et al. (2008) have argued that evidence for human driven marine resource depression is lacking along the coasts. As noted above, warming SST and heightened frequency of ENSO events can have drastic effects on the productivity of the Central Andean coasts. Combined with intensification theory, these patterns lead to two general predictions, tied further to dietary markers below. **P1:** increasing SST or ENSO frequency leading to reductions in marine resource availability should incentivize a tradeoff toward greater use of terrestrial resources for dietary purposes relative to marine inclusion. Such adaptive change could include investment in, or innovation with, domesticates. Conversely, **P2:** given the impact of La Niña, decreasing SST values that increase marine availability should favor the opposite tradeoff, incentivizing people to shift away from lower return terrestrial resources in diets and towards heavier marine resource use.

1.2. Stable isotope geochemistry

1.2.1. Bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$

Carbon occurs naturally in two stable forms, or isotopes. ^{12}C is the most common comprising approximately 98.9% of global carbon; whereas ^{13}C , with an extra neutron adding mass, makes up approximately 1.1% of earth's carbon. When atmospheric carbon (CO_2), dissolved CO_2 , or marine bicarbonates (HCO^-) are incorporated into plant

tissues during photosynthesis, metabolic processes alter or fractionate the ratio of ^{13}C - ^{12}C depleting it relative to the substrate from which it was taken. This ratio ($^{13}\text{C}/^{12}\text{C}$) is expressed in delta notation ($\delta^{13}\text{C}$) (Coplen, 2011) as parts per mil (‰) difference from PDB (Pee Dee Belemnite), an internationally recognized standard (Craig, 1957).

The degree of discrimination against $^{13}\text{CO}_2$ covaries with a plant's photosynthetic pathway (Farquhar et al., 1989) and is passed up the food web leaving a diagnostic signature in the tissue of consumers. This isotope signature does not covary with the skeletal element analyzed or with gender, independent of differences in feeding ecology. C_3 plants discriminate heavily against metabolism of $^{13}\text{CO}_2$ (Cerling et al., 1998) expressing a modern mean carbon isotope value of $\sim -26.5\text{‰}$, depleted in ^{13}C relative to atmosphere (-8‰). Trees, temperate season grasses, geophytes, legumes and most forbs use this pathway. In contrast, the C_4 photosynthetic pathway discriminates less against ^{13}C . This pathway was selected for in the late Miocene as an adaption to reduced atmospheric CO_2 concentrations and increased seasonality (Cerling et al., 1997). C_4 plants are thus characterized by enriched $\delta^{13}\text{C}$ values (~ -10 to -13‰) (Ehleringer et al., 1997; Coltrain and Janetski, 2013) and include a subset of forbs and sedges, most tropical grasses and the New World domesticate maize (*Zea mays*).

Plants in archaeological assemblages grown before fossil fuel depletion of atmospheric CO_2 are enriched 1.5–2‰ relative to modern mean values cited above (Marino and McElroy, 1991; Tieszen and Fagre, 1993; Yakir, 2011; Etu-Sihvola et al., 2022). Fractionation between primary producers and consumers approximates 5‰ and enrichment at higher trophic levels is $\sim 1\text{‰}$ (Katzenberg, 1993; Burton and Koch, 1999). Thus individuals primarily reliant on C_3 plant taxa express $\delta^{13}\text{C}$ values of ca. -23 to -20‰ (Petersen-Gordina et al., 2022), whereas those heavily reliant on a C_4 domesticate such as maize average $\delta^{13}\text{C}$ values in the -7 to -8‰ range (Tykot, 2004; Coltrain and Janetski, 2013:Table 5).

Kinetic processes governing bicarbonate (HCO^-) formation in seawater fractionate marine bicarbonates $\sim 7\text{‰}$ relative to atmospheric CO_2 , placing seawater $\delta^{13}\text{C}$ values near 0‰ (Tauber, 1981; Chisholm et al., 1982). Submerged marine plants use a C_3 photosynthetic pathway with its associated heavy discrimination against ^{13}C , yielding mean $\delta^{13}\text{C}$ values typically 7‰ more positive than terrestrial C_3 plants, giving them a distinctive marine label and placing bone collagen from individuals with diets high in marine foods in the -13 to -12‰ range (Coltrain et al., 2004; Coltrain, 2011; Guiry et al., 2015; Laffoon et al., 2016; Alfonso-Durruty et al., 2019). Modern Suess effect surface ocean depletion of ^{13}C is $\sim -0.2\text{‰}$ per decade since the extensive burning of fossil fuels (Bacastow et al., 1996; Gruber et al., 1999; Sonnerup et al., 1999; Eide et al., 2017).

Nitrogen isotope ratios ($\delta^{15}\text{N}$) are measured against atmospheric air, assigned a value of 0‰ (AIR [Junk and Svec, 1958]), and monitor the trophic level of sampled diets. This follows from the understanding that generally $^{15}\text{N}/^{14}\text{N}$ increases ~ 3 – 5‰ with each increase in trophic level, though enrichment can vary outside this general range particularly depending on the trophic level of the consumer (e.g., Hussey et al., 2014; Perkins et al., 2014), thus enriching the isotope signature of consumer nitrogen available for protein synthesis (Ambrose and DeNiro, 1986; Schoeller, 1999). The mechanisms that result in enrichment are not fully understood but are evidenced by the excretion of isotopically depleted urea and retention of enriched $\delta^{15}\text{N}$ metabolites. Most terrestrial plant taxa obtain nitrogen from soil ammonium (NH_4^+) or nitrate (NO_3^-) and those in temperate ecosystems express mean $\delta^{15}\text{N}$ values of 3–6‰ with a 0–9‰ range, situationally contingent upon temperature and aridity (Pate, 1994; Amundson et al., 2003; Bocherens and Drucker, 2003). However prolonged xeric conditions can elevate shallow-rooted plant $\delta^{15}\text{N}$ values due to surface volatilization of ammonium, resulting in further enriched food web $\delta^{15}\text{N}$ (Thornton et al., 2011; Tung et al., 2020; Torres-Rouff et al., 2022). Prehistoric agricultural practices that include the application of seabird guano and/or domesticate animal dung also result in enriched food web $\delta^{15}\text{N}$ values (Szpak et al., 2012, 2014a).

Conversely, plants such as legumes, mosses and lichens growing in association with nitrogen fixing symbionts express mean $\delta^{15}\text{N}$ values of $\sim 1\text{‰}$, with a typical -2 to 2‰ range (Evans and Ehleringer, 1994; Pate, 1994). The effects of nitrogen fixation is evident in depleted $\delta^{15}\text{N}$ values characteristic of high Arctic caribou (*Rangifer tarandus*) and musk oxen (*Ovibus moschatus*) heavily reliant on lichens (Coltrain et al., 2004; Coltrain, 2011).

Phytoplankton are primary producers in marine ecosystems and exhibit nitrogen isotope ratios in the $4\text{--}8\text{‰}$ range with a mean of $\sim 6\text{‰}$ (Fry, 1988; Needoba et al., 2003; Granger et al., 2004). These ecosystems are typically characterized by more trophic levels than terrestrial settings resulting in $\delta^{15}\text{N}$ values as positive as $+23\text{‰}$ in apex predators such as the South American sea lion (*Otaria flavescens*) (Szpak et al., 2012:Table 4; Coltrain et al., 2016:Table 1; Alfonso-Durruty et al., 2019: Table 3).

Human and faunal $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are commonly measured on bone collagen amino acid sequences. Collagen is a triple helix of 19 amino acids (Gauza-Włodarczyk et al., 2017:Table 1) bound by hydrogen bonds, forming the matrix for adhering crystalline hydroxyapatite. The relative abundance of carbon-13 to carbon-12 and nitrogen-15 to nitrogen-14 in these 19 amino acids is primarily diagnostic of dietary protein obtained from either plant or animal intake.

1.2.2. Bone hydroxyapatite $\delta^{13}\text{C}$

Bone hydroxyapatite (apatite) is a calcium phosphate mineral containing carbonate ions (CO_3) substituted in the phosphate position or adsorbed into the crystal hydration layer. During isotope analysis the adsorbed (or labile) carbonate ions subject to exchange are removed, preserving *in vivo* $\delta^{13}\text{C}_{\text{apt}}$ signals. Bone apatite $\delta^{13}\text{C}$ reflects the weighted average $\delta^{13}\text{C}$ value of carbon intake metabolized for energy. Virtually all ingested carbon used in the production of energy leaves the body in the form of CO_2 produced by mitochondrial respiration. Respired CO_2 is in equilibrium with blood bicarbonates (HCO_3^-) from which the carbonates (CaCO_3) in bone apatite or tooth enamel precipitate (Krueger and Sullivan, 1984; Tieszen and Fagre, 1993). Thus, while bone collagen $\delta^{13}\text{C}$ values are heavily biased by the isotope signature of ingested plant and/or animal protein, apatite $\delta^{13}\text{C}$ derives from intake of carbohydrates and/or lipids, macronutrients metabolized for energy, which can lead to more apparent C3 vs C4 differentiation in apatite (Harrison and

Katzenberg, 2003). Fractionation between terrestrial diet and bone apatite $\delta^{13}\text{C}$ averages $\sim 9.5\text{--}10\text{‰}$, $\sim 5\text{‰}$ more positive than the diet-bone collagen offset.

1.2.3. Bone turnover rates

It is generally recognized that adult bone isotope ratios represent the weighted average of long-term diet. As adult bone remodels, merely $2\text{--}4\%$ of osteons undergo resorption at any given time (Antoine et al., 1992; Hedges et al., 2007) and more than 30 years is required to replace the carbon in adult bone collagen with an equivalent amount of carbon (Libby et al., 1964; Stenhouse and Baxter, 1977, 1979). An approximate ten year turnover rate is estimated for the carbon in bone hydroxyapatite (Hedges et al., 2007).

1.3. Predictions

To evaluate the role of climate change in subsistence adaptation via intensification along the coasts, we predict changing oceanic SST and ENSO frequency conditions incentivized subsistence change. Both increasing SST and ENSO frequency are expected to decrease near-shore marine productivity, thereby encouraging people to tradeoff greater marine reliance for increased investment in terrestrial resources, likely maize agriculture on the coasts. We test these expectations using a large database ($n = 775$) of stable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values from archaeological individuals that provides a spatio-temporal proxy of reliance on marine versus terrestrial resource intake. Fig. 1 provides visual context for the below predictions, showing both the general isotopic values of major subsistence resource categories in the Central Andes and the isotopic values of resources in broadly anticipated return rate rank order following the background sections above and Bartelink (2006: Chapter 5).

Specifically, we predict:

P1. $\delta^{13}\text{C}$ values will: a) increase as SST($^{\circ}\text{C}$) increases, b) increase as SST temperature difference ($^{\circ}\text{C}$) increases, and c) increase as ENSO frequency increases.

P2. $\delta^{15}\text{N}$ values will: a) decrease as SST ($^{\circ}\text{C}$) increases, b) decrease as SST temperature difference ($^{\circ}\text{C}$) increases, and C) decrease as ENSO frequency increases.

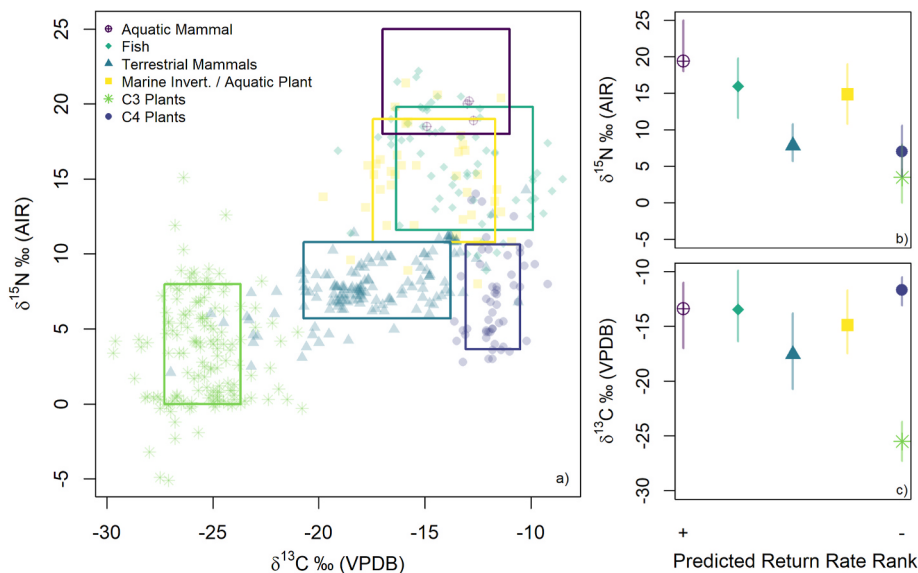


Fig. 1. a) Central Andean resource $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope values by resource category. Points represent 453 individually measured resources and boxes represent the 90th percentile range of the resource category. Data plotted here comes from multiple published records (DeNiro and Hastorf, 1985; Tieszen and Chapman, 1992; Turner et al., 2010; Thornton et al., 2011; Szpak et al., 2012, 2013, 2014b; Williams and Murphy, 2013; Dufour et al., 2014; Gerdau-Radonić et al., 2015; Marsteller, 2015; Díaz et al., 2016; Marsteller et al., 2017; Pezo-Lanfranco et al., 2021). b) Mean and 90th percentile range in $\delta^{15}\text{N}$ per resource category in descending order (left to right) of broadly predicted return rate rank (following Bartelink, 2006: Chapter 5). Rank order follows observations that aquatic and mammalian return rates typically rank with body size while plants requiring extensive investment in field preparation, irrigation, processing, etc. typically rank similar to or below small terrestrial mammals and smaller fish, particularly where small fish may experience economies of scale. For $\delta^{15}\text{N}$, shifting from higher to lower return rate resources may cause significant decreases in $\delta^{15}\text{N}$. c) Mean and 90th percentile range in $\delta^{13}\text{C}$ per resource category in descending order of broadly predicted return rate rank. Shifting from higher to

lower return rate resources may cause relatively smaller shifts in $\delta^{13}\text{C}$ than $\delta^{15}\text{N}$ due to the overlap in values between resource categories. *Note: box for aquatic mammals does not represent the 90th percentile of samples but the general range of such resources due to a limited sample size ($n = 4$).

2. Methods & materials

2.1. Archaeological samples

For reconstructions of broad dietary patterns, we select 775 individuals from a set of 795 we compiled from the Central Andean coasts with bone collagen and hydroxyapatite stable isotope data. The compilation combines individuals from the recently published Central Andean bone collagen dataset in Wilson et al. (2022) with individuals from the same region with $\delta^{13}\text{C}$ measured on bone hydroxyapatite. Following Wilson et al. (2022), and adapting from the natural zones of the Andes (Murra, 1972; Pulgar Vidal, 1981), individuals are considered coastal if they were recovered less than 15 km inland from the coastline and at less than 350 m above sea level (masl). While the coastal zone is broadly defined as 0–500masl, here we combine a distance and elevation measure that is slightly more restrictive to emphasize capturing coastal individuals while omitting those from farther inland but from low elevations (for example, some individuals in the Andes may be 40 km inland but at an elevation of ~300masl due to settlement on valley bottoms). All individuals from under 500masl not considered coastal by our criterion were evaluated for coastal/non-coastal categorization based upon the reporting author's interpretation, resulting in the incorporation of one additional site, Cerro Oreja (Lambert et al., 2012), that it is slightly further inland (~15.03 km from coast). For this work, individuals under the age of five are excluded from analyses to avoid potential nursing or weaning biases. Further, individuals with problematic C:N ratios (see Wilson et al., 2022) are removed. This leaves 775 unique individuals with collagen $\delta^{13}\text{C}$ ($n = 633$), $\delta^{15}\text{N}$ ($n = 631$), and hydroxyapatite $\delta^{13}\text{C}$ ($n = 562$). Individuals range in time from ~7000 to ~400 years before present, spanning the Preceramic to Colonial periods, with significant temporal variation in isotopic values over time (Fig. 2). Few individuals ($n = 9$) are radiocarbon dated; all others are assigned a temporal window based upon the reporting author's assignment. As we use bulk bone collagen and hydroxyapatite values, the isotope measures capture long-term, average diets (Hedges et al., 2007) and not seasonal or life stage variation. All individual data is available in Appendix A.

2.2. Paleoclimate

To capture paleoclimate based upon oceanic conditions, we use three proxies: SST ($^{\circ}\text{C}$), SST difference from mean ($^{\circ}\text{C}$), and ENSO frequency per century. For past SST, we use published SST reconstructions from four ocean cores (M77/2_757, M77/2_024–5, M77/2_003–2, and M135_254–3) located at ~4, 11, 15, and 17° south (Fig. 3). These cores are selected for their comparability as each was taken a similar distance from the modern shoreline and employ alkenone derived SST estimates which, in the region, capture the warmer summer SST periods more so than ENSO temperatures or winter periods (Nürnberg et al., 2015; Salvatelli et al., 2019). For more in-depth discussions of how the U_{37}^k index of organic compounds (alkenones) in algae is used to derive past SST see Herbert (2003) and Prahl and Wakeham (1987). For each SST observation in each core, we also calculate the temperature deviation from the core's overall mean, where the mean SST is the average SST from 7000 calBP to the youngest termination of the core. This provides a comparable measure across cores monitoring if points in time were warmer or cooler relative to the long-term average at their location. To estimate ENSO frequency, we use the estimated number of ENSO events per century data from Moy et al. (2002), derived from a sediment core at Laguna Pallcacocha in southern Ecuador (Figs. 3 and 4). While this record has been questioned (Schneider et al., 2018), it has been supported by recent meso-scale work (Kiefer and Karamperidou, 2019) and has proven useful in understanding ENSO driven ecological changes within the eastern Pacific (Hart et al., 2015; Broughton et al., 2022). Thus, though imperfect, this core provides a useful estimate of ENSO frequency variation on a comparable temporal scale to the isotopically measured individuals. Although ENSO likely varies along a north to south gradient (see Sandweiss et al., 2020), directly comparable, spatially explicit, quantified estimates of frequency are difficult to locate. Therefore, we use only the Laguna Pallcacocha ENSO frequency estimates here. Both SST and ENSO show variation throughout the study period (Fig. 4).

We relate paleoclimate data to individuals within the database following methods employed by Wilson et al. (2022). In brief, uncertainty exists as to what years represent the most likely dates of each

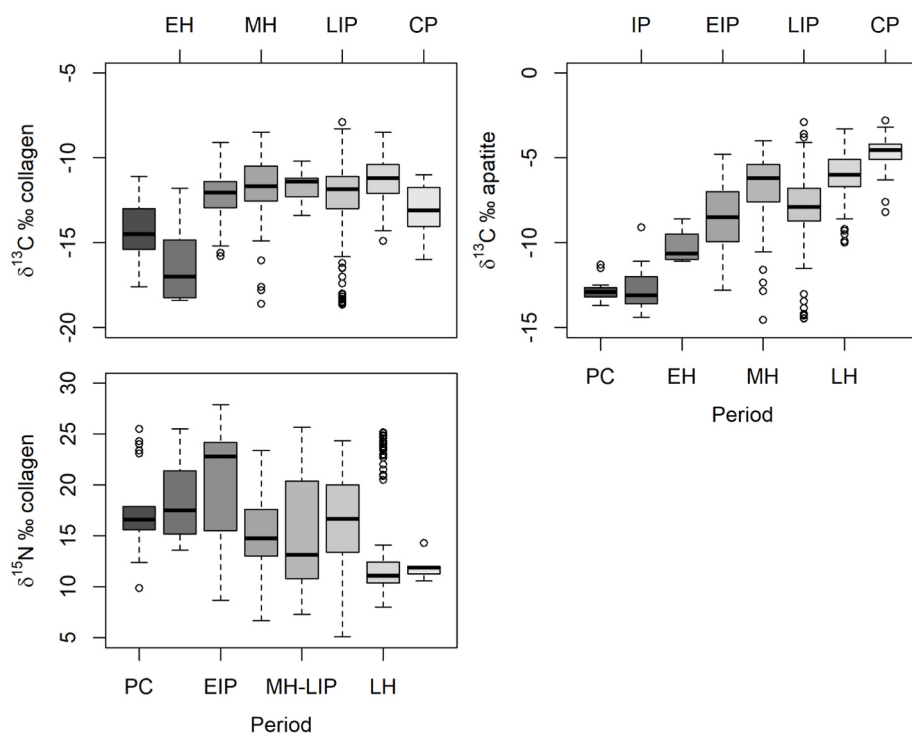


Fig. 2. Boxplots of variation in a) bone collagen $\delta^{13}\text{C}$, b) hydroxyapatite $\delta^{13}\text{C}$, and c) collagen $\delta^{15}\text{N}$ by time period. Time periods follow Moseley (2001): PC = Preceramic (~>3750 BP), IP = Initial Period (~3749–2850 BP), EH = Early Horizon (~2849–2450 BP), EIP = Early Intermediate Period (~2449–1350 BP), MH = Middle Horizon (~1349–950 BP), MH-LIP = Middle Horizon/Late Intermediate Period (~1349–480 BP), LIP = Late Intermediate Period (~949–480 BP), LH = Late Horizon (~479–418 BP), CP = Colonial Period (~<417 BP).

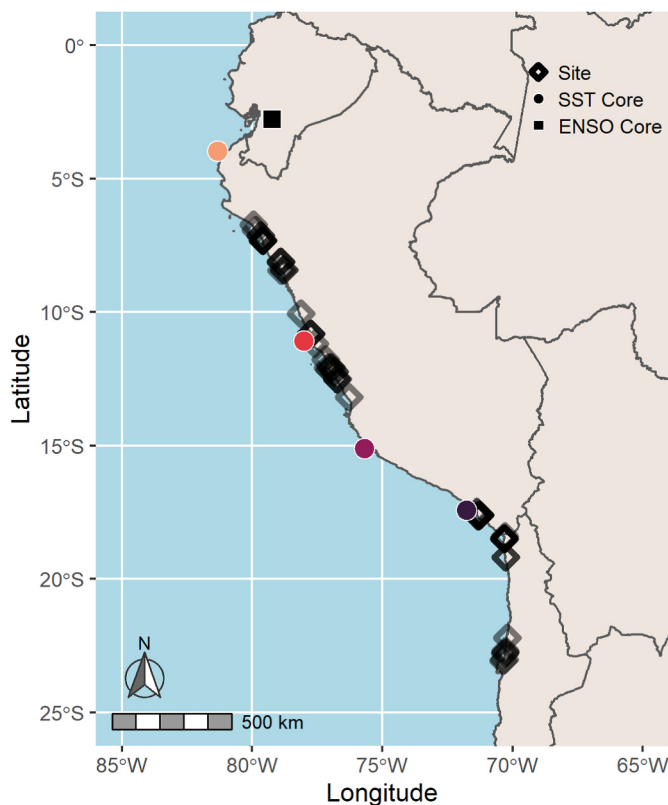


Fig. 3. Map of archaeological site locations, published SST cores (Nürnberg et al., 2015; Salvateci et al., 2019), and the published ENSO frequency per century record (Moy et al., 2002). SST cores, moving from north to south and lighter to darker colors, are M77/2_757, M77/2_024–5, M77/2_003–2, and M135_254–3 respectively.

individuals' life course, regardless of whether they are radiocarbon dated or not, leading to uncertainty regarding which years' ENSO and SST observations are most appropriate for each individual. Therefore, we implement a Monte Carlo style sampling procedure to capture the uncertainty in time and propagate that uncertainty through the statistical modeling (below). For each of the individuals in the dataset we identify the nearest oceanic SST core (Nürnberg et al., 2015; Salvateci et al., 2019). We then subset that core to match the maximum temporal window of the individual, retaining only the SST and SST difference from mean (dfm) observations which fall in this window. We then randomly sample, with replacement, this subset SST data 1000 times using a uniform probability, recording each sample's SST value and SST dfm. We implement the same procedure for ENSO frequency, using the Laguna Pallcacocha data (Moy et al., 2002). This gives 1000 SST, SST dfm, and ENSO frequency estimates per individual, each equally plausible as the most appropriate observation, capturing both the broad trends in the paleoclimate data during each individuals' temporal window as well as the uncertainty in these trends. For the nine radiocarbon dated individuals, we weight the sampling procedure for selecting a year by the probability density of their calibrated, two-sigma radiocarbon range. These procedures, and all statistical analyses, are performed in the R statistical environment (R Core Team, 2023), with complete code for replicating the work available as Appendix B.

2.3. Statistical analyses

To better understand if the relationship between subsistence and oceanic climate change varies over time, we categorize each individual as either early ($n = 207$) or late ($n = 588$) for use as a factor variable in the statistical models. Here early individuals are those from the

Preceramic, Initial Period, Early Horizon, and Early Intermediate Period (>1350 BP) whereas late individuals are those from the Middle Horizon, Late Intermediate Period, Late Horizon, and Colonial Period (<1350 BP). Ideally, there would be enough individuals to analyze the relationships using each period as a factor, however there are not yet enough samples from each period for such an analysis. Thus, our categorization unavoidably may mask nuance in finer-grained social interactive effects with climate change. For example, we will not capture different responses to climate change during the heavily Inka influenced Late Horizon versus the more balkanized Late Intermediate Period (if the responses did differ), though categorization as early or late does allow us to observe if there are broad shifts in the relationship with climate change during periods less or more heavily involved in maize production and less or more socio-politically connected (Moseley, 2001; Pearsall, 2008; Silverman and Isbell, 2008). Categorization as early or late may also encounter equifinality (e.g., the same isotopic pattern appearing in response to climate change in early versus late periods could plausibly derive from different causes), a potential limitation we are unable to directly address without being able to use more categories – though theoretically derived predictions help us partially mitigate this concern. Further, we are currently limited by the data in our ability to evaluate possibilities such as exacerbating interactive effects (e.g., climate change incentivizing greater terrestrial reliance that is then ramped up even further due to changing sociopolitical importance of terrestrial products) or if the influence of climate change is weakened in more or less complex periods. These represent potentially productive future avenues of research, particularly highlighting the need for more data from early periods.

To assess the predictive strength of SST, SST dfm, and ENSO frequency on isotope values we use random forest (RF) regression (Breiman, 2001; Liaw and Wiener, 2002) via the **ranger** package (Wright and Ziegler, 2017) in the R statistical environment. RF regression is a machine learning method employing an ensemble decision tree approach to obtain the mean prediction of a dependent variable when there may be interactions between predictor variables, relationships may be non-linear, predictor variables may be correlated, and where model fits may fail to meet the required assumptions for linear modeling. While RF regression can handle correlated variables, variables with correlation strengths >0.70 may still be problematic (Dormann et al., 2013). We evaluate variable correlations using a correlation matrix via the **corrplot** package in R (Wei and Simko, 2021) and find all variable correlations are under the 0.70 threshold (Appendix B). Although ENSO and SST change are mechanistically correlated phenomena they are not strongly correlated in our data, likely as ENSO is measured as frequency per century whereas SST measures are point estimates and the alkenone SST reconstructions are known to not strongly capture ENSO temperature periods (Nürnberg et al., 2015; Salvateci et al., 2019). This does allow us to separately capture the response to SST change and ENSO frequency variation.

To propagate the temporal uncertainty of our data into the statistical models, we run 3000 RFs (1000 per stable isotope), where each of the RF models uses a single observation of SST, SST dfm, and ENSO frequency per individual. In effect, this treats every observation from our sampling procedures as though it is the most appropriate value and models the relationships as such. For each of the 3000 RF models we save the model R^2 , mean square error (MSE), model residuals, spatial autocorrelation values, and the predicted partial responses, allowing us to capture overall how well the models predict observed isotopic variation while also estimating confidence intervals on model outputs. RF R^2 results detail how much of the variation in each isotope is explained by variability in the oceanic condition measures but do not directly evaluate our predictions. Therefore, we evaluate the response of each isotope measure to change in the predictor variables through the partial response of the isotope to each predictor variable while all others are held constant using the **pdp** package in R (Greenwell, 2017). As we have 1000 partial responses per predictor variable per isotope, we evaluate

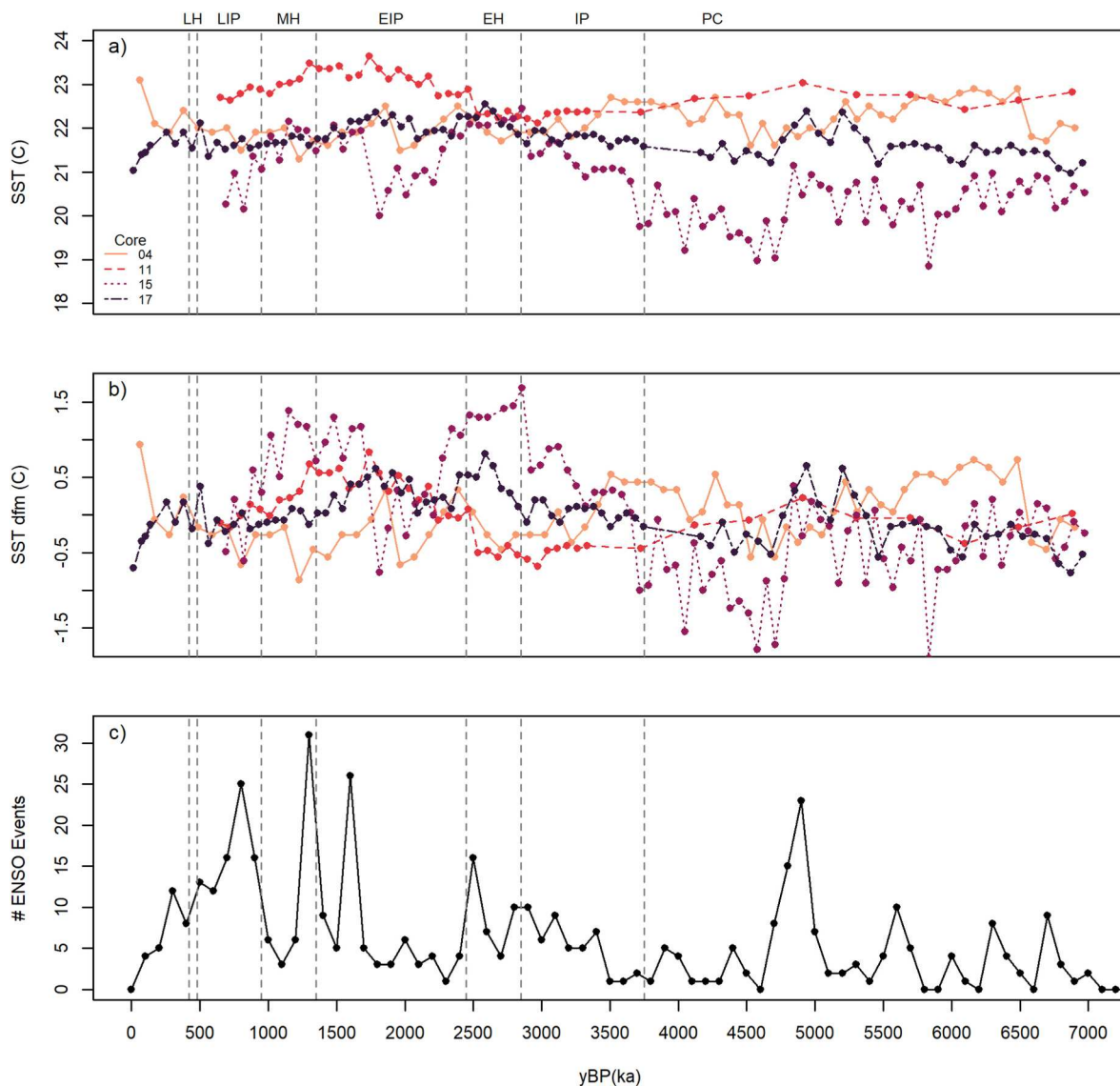


Fig. 4. a) SST (°C) (Nürnberg et al., 2015; Salvatelli et al., 2019), b) SST (°C) difference from mean (dfm), and c) ENSO frequency per century (Moy et al., 2002) variation over the past ~7000 years.

partial response with both the central tendency and 95% confidence intervals. The RF models are validated using root mean square error of results (rmse) and the distribution of model residuals and are checked for spatial autocorrelation in residuals by evaluating the expected versus observed Moran's I values on an inverse distance matrix via the **ape** package in R (Paradis and Schliep, 2019).

3. Results

Visualization of the long-term patterns in stable isotope values by period (Fig. 2), suggests there are broad changes in subsistence in terms of both protein and carbohydrate/lipid sources over time. Generally, the patterns reflect increasing $\delta^{13}\text{C}$, particularly in the hydroxyapatite measure, with a concurrent decrease in $\delta^{15}\text{N}$ moving from early to late in the temporal sequence. RF regression models using SST, SST dfm, and ENSO frequency produce significant results (Fig. 5); the mean R^2 value for $\delta^{15}\text{N}$ is 0.53 with a root mean square error (rmse) of 3.41, the mean R^2 for $\delta^{13}\text{C}$ on collagen are weaker, but significant, at 0.22 with rmse of 1.63, and the mean R^2 for $\delta^{13}\text{C}$ from hydroxyapatite is 0.56 with rmse of 1.62. All models have residuals normally distributed around zero. In aggregate, residuals from the models for both $\delta^{13}\text{C}$ measures do not

show significant ($p > 0.05$) spatial autocorrelation, suggesting the models perform well in accounting for space. Aggregate residuals from the $\delta^{15}\text{N}$ models do show significant ($p = 0.03$) spatial autocorrelation however, to keep the models comparable, and as the coordinates themselves approximate oceanic conditions, we do not include co-ordinates in the $\delta^{15}\text{N}$ models but acknowledge there is some residual spatial autocorrelation.

Most partial responses (Fig. 6) support our predictions. $\delta^{13}\text{C}$ hydroxyapatite increases with increases in SST, SST dfm, and ENSO frequency, supporting **P1**. Also supporting **P1**, $\delta^{13}\text{C}$ collagen increases with increasing SST and ENSO frequency, though it has no obvious relationship with SST dfm. **P2** is partially supported. $\delta^{15}\text{N}$ shows a strong, negative relationship with SST, in line with predictions. However, it has a positive relationship with SST dfm, contrary to predictions, and a neutral relationship with ENSO frequency. The relationships between oceanic conditions and stable isotope measures of diets are largely consistent between early and late individuals (Fig. 6) with the only notably different relationship between early and late individuals within SST and $\delta^{13}\text{C}$ hydroxyapatite, where early individuals show limited response to change in SST whereas late individuals have a strong, positive relationship.

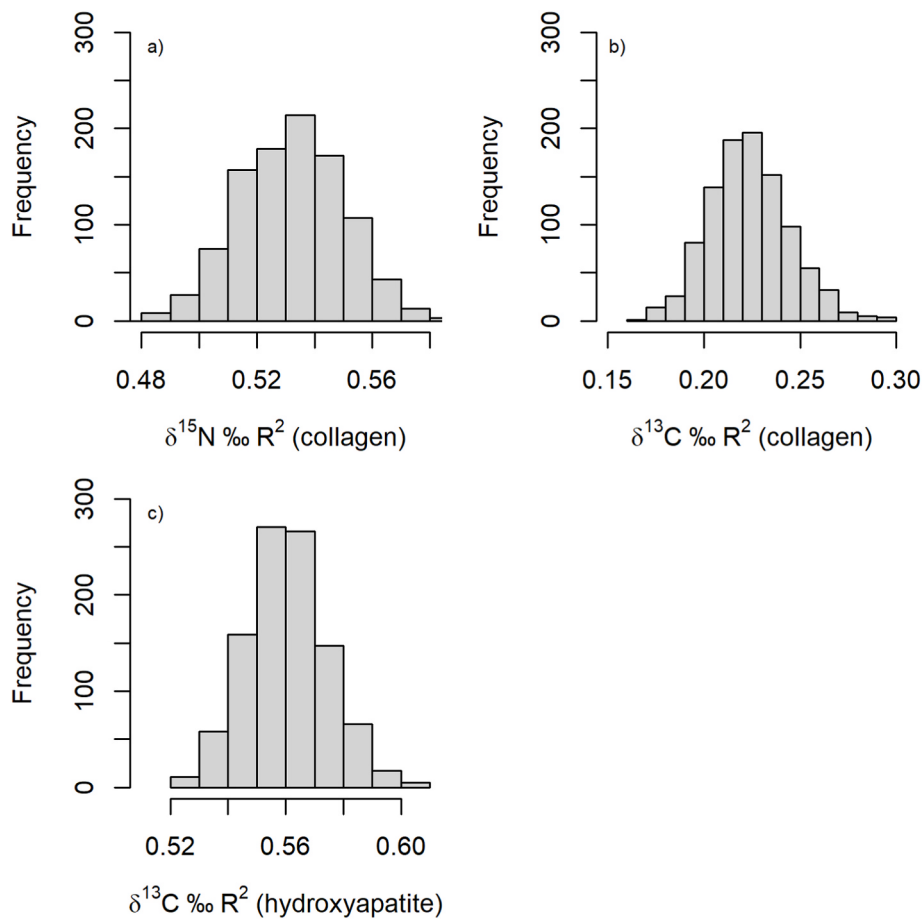


Fig. 5. Histograms of model R^2 values per isotope. Results suggest that SST, SST difference from mean, and ENSO frequency explain a slight majority of the variation in a) $\delta^{15}\text{N}$ as well as c) $\delta^{13}\text{C}$ measured on bone hydroxyapatite. The same variables explain about a quarter of the variation in b) $\delta^{13}\text{C}$ measured on bone collagen.

There are several prominent features in these relationships (Fig. 6). First, decreases in $\delta^{15}\text{N}$ and increases in $\delta^{13}\text{C}$ appear to occur as SST warms above $\sim 21.5\text{--}22^\circ\text{C}$. $\delta^{13}\text{C}$ relationships with SST dfm suggest decreasing $\delta^{13}\text{C}$ as local SST drops below the long-term mean and increasing $\delta^{13}\text{C}$ as SST rises above this mean. The $\delta^{15}\text{N}$ response to SST dfm shows an increase as SST comes to the long-term mean, with a decrease when SST is below the long-term mean. $\delta^{13}\text{C}$ relationships with ENSO frequency are suggestive of a bivariate response; below a frequency of two to three ENSO events per century, $\delta^{13}\text{C}$ remains low, but ENSO frequencies above three results in significantly higher $\delta^{13}\text{C}$ values, though these do not increase with even higher ENSO frequencies.

4. Discussion

Overall, our models using local oceanic condition reconstructions explain over 50% of the variation in space and time for $\delta^{15}\text{N}$ and hydroxyapatite $\delta^{13}\text{C}$ and ca. 25% of the variation in collagen $\delta^{13}\text{C}$, suggesting that human responses to climatic change played a significant, though not exclusive, role in the observed isotopic shifts. While these models do not explain all variation, nor might they be expected to given the concurrent potential influences of changing sociopolitical landscapes and population sizes (e.g., Hastorf and Johannessen, 1993; Roscoe et al., 2021), they provide evidence for how adaptation to changing climates within the Central Andes played a part in subsistence change.

The relationships between climate variables and stable isotope values support P1 and partially support P2, lending broad support to prior suggestions that behavioral responses to climate change contribute to agricultural expansion in the Central Andes (e.g., Sandweiss et al.,

2009; Vining et al., 2022b). Supporting P1, rising SST, particularly when temperatures increased above $\sim 21.5\text{--}22^\circ\text{C}$, results in increasing $\delta^{13}\text{C}$ values, suggesting declining marine productivity (Alheit and Niquen, 2004) leads to greater reliance on terrestrial resources, likely maize (Figs. 1 and 6). This relationship is particularly strong in the later periods where higher SSTs leading to enrichment in collagen $\delta^{13}\text{C}$ moves the per mil values out of the projected ranges for heavy reliance on marine resources (Coltrain et al., 2004; Coltrain, 2011; Guiry et al., 2015; Laffoon et al., 2016; Alfonso-Durruty et al., 2019). At the same SSTs where collagen $\delta^{13}\text{C}$ values increase, $\delta^{15}\text{N}$ values decrease, indicative of greater reliance on lower trophic level foods. These shifts are suggestive of increased reliance on protein sources from terrestrial resources and/or lower trophic level marine resources, likely in response to declining marine productivity. Furthermore, hydroxyapatite $\delta^{13}\text{C}$ (which may better capture C_3/C_4 differentiation) evidences a similar pattern, suggestive of a later period shift from isotopically depleted marine lipids to enriched C_4 carbohydrates providing the dietary macronutrients supplying energy – likely reflecting increased reliance on C_4 resources, such as maize.

The patterns in SST dfm also generally support P1 (Figs. 1 and 6). Hydroxyapatite $\delta^{13}\text{C}$ is enriched as individuals experience warmer than long-term average SST at their location and is depleted as they experience cooler than average temperatures. This is in line with expectations that warmer temperatures decrease marine productivity and vice versa (Barber and Chavez, 1983; Chavez et al., 1999; Niquen and Bouchon, 2004). Cooling is expected to increase the encounter rate with higher ranked marine resources and reduce reliance on lower trophic level organisms, terrestrial or marine, that require greater investment in collection, processing, or other expenses whereas warming reverses the

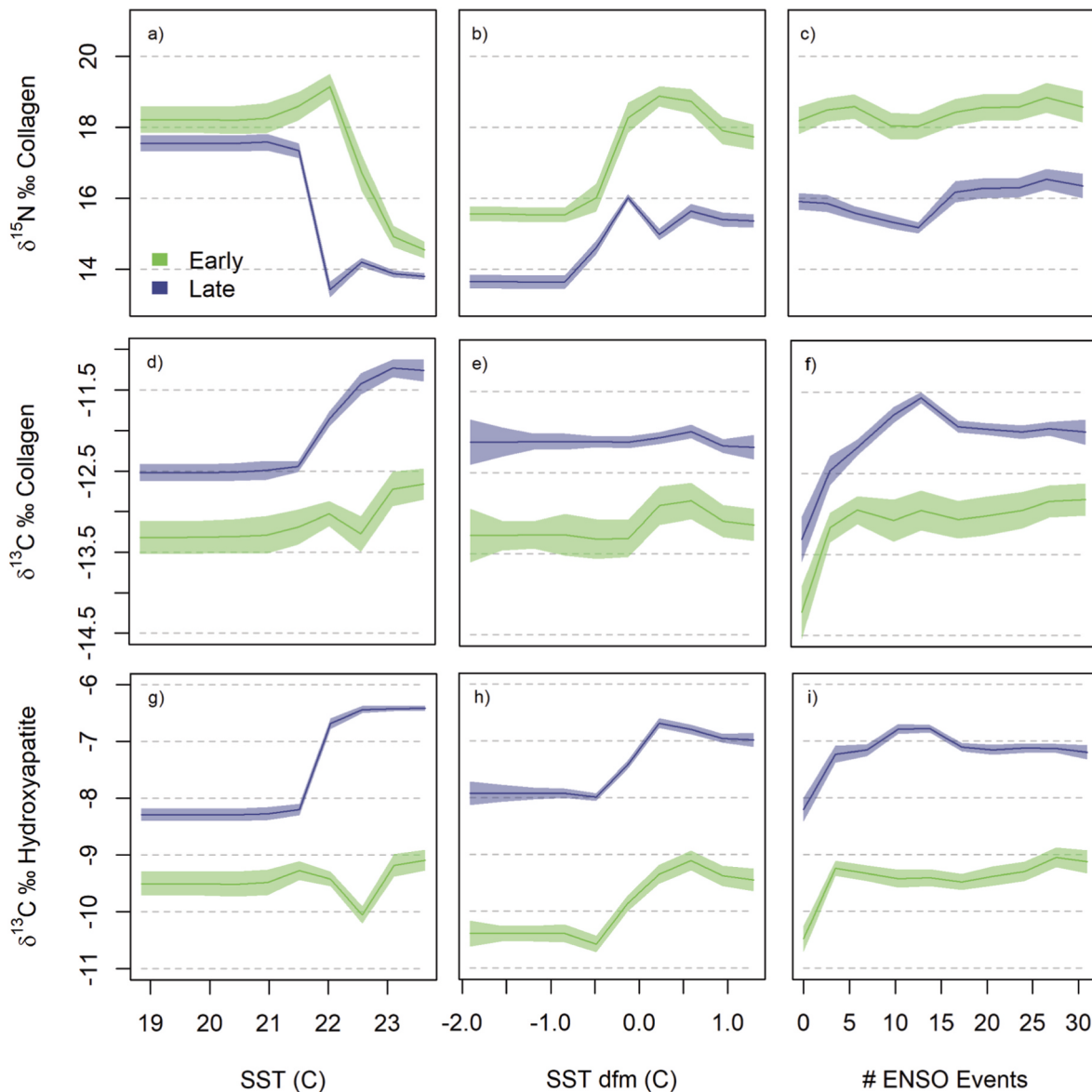


Fig. 6. Partial response of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ (measured on bone collagen and hydroxyapatite) to a/d/g) change in SST ($^{\circ}\text{C}$), b/e/h) SST difference from the core's long-term mean ($^{\circ}\text{C}$), and c/f/i) ENSO frequency per century while the other variables are held constant. The solid, darker, lines depict the mean response across each of the 1000 RF models per isotope with shading providing the 95% confidence intervals.

pattern. Although the response to SST dfm is more muted than the response to absolute change in SST this is to be expected. Response to SST appears to be nearly a state change occurring when local SST either drops below ~ 21.5 or rises above $\sim 22^{\circ}\text{C}$. Relative local warming, while expected to reduce marine productivity, may not produce wholesale biotic change and aquatic migration unless it pushes SST past a critical threshold. Collagen $\delta^{13}\text{C}$ does show a weaker SST dfm than hydroxyapatite, reflecting both the narrow carbon isotopic offset between marine (ca. -17‰ , Coltrain et al., 2016:Table 3) and terrestrial C_4 (ca. -12‰) protein and the reality that, since marine resources are typically higher in protein ($\sim 20\text{g}/100\text{g}$, Hambraeus, 2009:Table 1) than aboriginal maize ($\sim 10\text{g}/100\text{g}$, Glover and Mertz, 1987:Tables 7–5), a decline in marine intake may be obscured by the greater contribution of marine protein to bone collagen per 100g of intake.

The response of $\delta^{13}\text{C}$ values to ENSO frequency also support **P1**. $\delta^{13}\text{C}$ increases in collagen and hydroxyapatite in response to rising ENSO frequency, suggestive of a state change when ENSO frequency exceeds three events per century; or, on average, one ENSO event per generation occurs (Fig. 6f,i). Although ENSO events do appear to improve terrestrial

productivity through increased local precipitation and upstream water runoff (Jaksic, 2001; Coelho et al., 2002; Vining et al., 2022a), these results are not meant to imply ENSO brought enough precipitation to boost terrestrial productivity, or oceanic variance to decrease marine productivity, over the entirety of a generation; the effects of ENSO are typically felt on an immediate or annual rather than decadal or multi-decadal scale. Instead they may be further evidence for people deliberately planning for the occurrence of ENSO phenomena (e.g., Dillehay and Kolata, 2004; Sandweiss et al., 2009; Vining et al., 2022b) and thus being in a position to take advantage of expanded terrestrial resource niches when marine productivity declined. In particular, the isotopic data suggest that such strategies were widely adopted, early and late in time, if individuals anticipated experiencing about one ENSO event per generation (Figs. 1 and 6).

P2 predictions are not as strongly supported as **P1**, with results containing some counterintuitive patterns. As noted above, the $\delta^{15}\text{N}$ response to SST change matches predictions, with increasingly warm conditions producing decreased $\delta^{15}\text{N}$ values across time. This again suggests warming SST reduced marine productivity, incentivizing

expanded incorporation of terrestrial resources (Figs. 1 and 6). However, $\delta^{15}\text{N}$ values show almost no relationship with ENSO frequency. This is a little surprising as it appears that carbohydrate sources changed with ENSO frequency increases, as did protein $\delta^{13}\text{C}$ sources (Fig. 6f,i). One possible explanation is that the use of seabird guano and/or animal dung fertilizers may have enriched soil and maize $\delta^{15}\text{N}$, which research has shown can drastically increase $\delta^{15}\text{N}$ (Szpak et al., 2012; Santana-Sagredo et al., 2021), obscuring the decline in high trophic level marine intake. The $\delta^{15}\text{N}$ pattern is also likely biased by the higher per gram protein content of marine resources relative to that of maize, as noted above. Thus, intake of 100g of fish muscle tissue yields virtually twice the protein as an equivalent amount of maize. $\delta^{15}\text{N}$ response to ENSO frequency change could also be impacted by long-term averaging of stable isotopes in bone collagen. ENSO events tend to last one to two years. A single or even several ENSO events over the course of an adult's lifetime may produce depleted $\delta^{15}\text{N}$ during the event but marine protein intake from all years of life outside of ENSO years may obscure the momentary depletions.

Our last result, the $\delta^{15}\text{N}$ rise in response to increase in SST dfm, is unexpected and counter to our predictions. As local SST increases over the long-term mean $\delta^{15}\text{N}$ values appear to experience a trophic level increase. This could indicate that as local SSTs deviated positively from the long-term average people adapted by taking higher trophic level protein sources, though this would contradict theoretical expectations and would appear contradictory to marine biotic responses where increasing temperatures are expected to have negative cascade effects from plankton to higher trophic level faunal abundances (Barber and Chavez, 1983; Niquen and Bouchon, 2004). Further, the same pattern is not reflected in the $\delta^{13}\text{C}$ collagen response. Alternatively then, local deviations from long-term SST averages may have incentivized human adaptation through fertilization or altered foddering practices, processes which can significantly increase $\delta^{15}\text{N}$ values as noted above (Finucane et al., 2006; Szpak et al., 2012, 2014a). The $\delta^{15}\text{N}$ response to SST dfm is robust for both early and late periods and can provisionally be attributed to intensified agricultural fertilization practices, which in this case would have little to no effect on $\delta^{13}\text{C}$ values but enrich dietary $\delta^{15}\text{N}$. While a SST dfm of +0.0–0.5 °C produces trophic level enrichment in $\delta^{15}\text{N}$ greater than that reported in Szpak et al. (2012; Fig. 6) for maize kernels grown in experimental plots fertilized with camelid dung (+1.8‰) it is less than that reported for maize fertilized with seabird guano (+14.9‰). Thus, some combination of fertilization with guano and/or dung in response to declining marine productivity could plausibly produce the observed $\delta^{15}\text{N}$ response to local SST dfm. The apparent problem with a fertilization hypothesis is that absolute increases in SST above ca. 22 °C result in a decline in $\delta^{15}\text{N}$ during early and late periods, producing what appears to be a state change that matches predictions, leaving this counterintuitive result a productive direction for future work.

Finally, the current analytical models explain ~50% of the observed variation in isotopic values. As the oceanic condition proxies are spatiotemporally limited we suspect that finer-temporal scale (sub-century) tracking of changing SST and ENSO frequency with better spatial resolution (a reconstruction per valley for example) and improved temporal control on individuals would increase the overall variation in dietary isotope values explained by climate change. Such data would also be capable of unveiling locations where people were less constrained by climate conditions and more heavily influenced by social factors, or vice versa. However, it is highly likely that some of the unexplained variation is reflective of non or indirect climate change effects not yet quantified in the statistical models. Population density increases are widely expected to influence subsistence intensification directly (e.g., Morgan, 2015; Coddling et al., 2021) and interact with other physiographic circumstances to alter circumscription (Carneiro, 1970), which may have indirect effects. Marine resource abundance fluctuation combined with increasing population densities may place extra pressure on marine resource bases, significantly incentivizing greater terrestrial

resource use during and outside of climatically triggered marine abundance declines while circumscription limiting the ability for people to leave a local area and find another suitable location may exacerbate local resource base pressures. Exchange/trade, social significance of resources, and imperial impacts are more variables we are unable to parameterize here but that may alter the returns/payoffs for terrestrial produce relative to marine resources. It is strongly suggested that maize became involved in signaling (e.g., Staller, 2006), redistribution within political units (e.g., Stanish, 1997), served as a barter or exchange good (Covey, 2000), and that some communities were forced to grow it (e.g., Hastorf, 1990), particularly later in time. Each of these cultural changes would likely incentivize greater adoption of terrestrial resources than may be expected through climate change alone, could account for unexplained variation in the models, and would be likely to enhance the effects observed in the results. Furthermore, these environmental and social processes may interact, feeding back on one another or creating multiplicative effects.

To begin to evaluate such interconnected possibilities, future research is necessary for quantifying social (trade/exchange, imperial influence, cultural significance of particular resources) and demographic (overall population size and density) change for analysis in comparison with climate reconstructions. Such work will likely provide unique insights into how socio-cultural adaptations interacted with the socio-economic decisions discussed here in the face of climate variation (Zeder, 2012). Further, improving temporal control on both past climate reconstructions and individuals through robust ^{14}C dating schema will be crucial to better link both broad-spectrum and individual climate change events to human responses (e.g., Moseley and Keefer, 2008; Goldstein and Magilligan, 2011; Moseley et al., 2017). In particular, directly dating individuals will enable time-lagged analyses of behavioral change with past climate events to more directly assess causality and evaluate which factors (climate, population, cultural change, etc.) were most influential given it is likely all are involved.

5. Conclusion

Overall, the results of our investigations into how isotopic composition varies with long-term climatic change, proxied by changing oceanic conditions, strongly suggest that people along the Central Andean coasts adapted to climate change through subsistence intensification in line with predictions from optimal foraging theory. As near-shore and accessible marine ecosystems experienced decreases in relative productivity through reduced faunal abundances resultant from warming SST and/or increasing ENSO frequency, people increasingly relied on lower trophic level resources indicative of greater investment and effort in their subsistence economies. These results support prior observations, particularly from the North Coast of Peru, while demonstrating this pattern of adaptation spans the Central Andean coastal spatio-temporal range. People in the Central Andes appear to have responded to climate change not only through risk reduction, as prior works have shown, but also through economic maximization, and it is possible that in this case these two objectives were not mutually exclusive. Though these results are not the entire story of adaptive change, as many additional aspects of human life are involved and may be productively incorporated in the future, they provide additional evidence for how climate change incentivizes subsistence intensification across the human experience.

Author contributions

Kurt M. Wilson: Conceptualization, Methodology, Formal Analysis, Investigation, Data Curation, Writing – Original Draft, Writing – Review and Editing, Visualization, Funding Acquisition. **Weston C. McCool:** Investigation, Resources, Writing – Review and Editing. **Joan Brenner Coltrain:** Conceptualization, Methodology, Investigation, Resources, Writing – Original Draft, Writing – Review and Editing.

Data availability

All data required to replicate this analysis is provided in [Appendices A and B](#).

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quaint.2023.07.002>.

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