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Muscio, Hernán Juan
Cardillo, Marcelo

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Evolutionary radiation of mid-Holocene lanceolate points from the highlands of the South Central Andes

Hernán Juan Muscio¹ and Marcelo Cardillo²

¹ *Universidad de Buenos Aires, Consejo Nacional de Investigaciones Científicas y Técnicas*

² *Universidad de Buenos Aires, Instituto Multidisciplinario de Historia y Ciencias Humanas*

Through phylogenetic reconstruction this work analyzes the diversification of lanceolate points of the South Central Andes which began in the early Holocene and spanned the entire mid-Holocene. Based on a regional-scale data, we discuss the links between the increasing mid-Holocene risk conditions, the patterns of diversification of point lineages, demographic change and animal resources consumption. We distinguish a first instance of greater diversity of points, a higher rate of innovation and less class longevity. These trends progressively stabilized, giving rise to a pattern of less innovation, decreasing taxa diversity and greater class longevity as well as an age-related extinction pattern. We show that as projectile points diversified, hunting efficiency increased along the mid-Holocene by the increased representation of high-return fauna in the regional zooarchaeological record. We suggest that this diversification of lanceolate points was an adaptive evolutionary radiation which began with the increase in the rate of innovation for coping with the increasing risk of the beginning of mid-Holocene in the South Central Andes. From this we conclude that technological innovation was a prerequisite for the human specialization in camelid hunting and for the development of a highly economically efficient foraging strategy in the south Andean highlands

Corresponding author's e-mail: hmuscio@gmail.com

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Introduction:

The evolutionary diversification of the lanceolate points of the South Central Andes

Within the cultural-historical approach, Andean archaeologists built chronologies of particular sites and broader areas by using distinctive classes of artifacts as chronometers and cultural markers. The Ayampitin tradition of lanceolate bifacial lithic points illustrates these time-sensitive artifacts (González 1952, 1960). With a duration of roughly 4000 years, between 9000-5000 years cal BP, the spatial distribution of these points includes different Andean regions of the Northwest, Cuyo and Central Hills of Argentina, the north and center of Chile as well as the southern altiplano of Bolivia (Klink and Aldenderfer 2005; Capriles and Albarracín-Jordán 2013; Huguin and Yacobaccio 2012; Jackson et al. 2011; Martínez 2003; Núñez et al. 2005; Ratto 2003; Restifo 2013).

Ayampitin-like bifacial points are well represented in the archaeological record of the highlands of the South Central Andes (Puna of Argentina and North Chile). In the area, a wide range of lanceolate points appeared within a process of morphological diversification that started during the early Holocene (ca 9000 years BP) and spanned the entire the mid-Holocene (see Aschero and Hocsman, 2011; Huguin 2013, 2014; López and Restifo, 2014; Martínez 2007). This proliferation of morphological designs of lithic points gave rise to several new classes of points that followed the extinction of most of the late Pleistocene points, like the fishtail and the unstemmed triangular points. It was suggested that the diversification of the lithic points throughout the mid-Holocene was the result of the adoption of different weapon systems and new hunting tactics (Aschero y Martínez 2001, Martínez 2003, 2005), into the context of the increasing specialization of humans on camelids hunting (Yacobaccio 2001, 2012).

The southern Andean highlands began to be colonized by humans during the Pleistocene-Holocene transition. With colder and more humid conditions (Markgraf 1985), the highlands during the finiglacial were attractive spaces for humans because they offered high quality hunting resources. Wild camelids, guanaco (*Lama guanicoe*), vicugna (*Vicugna vicugna*); and (*Hipocamelus antisensis*), a deer, are the highest ranked animals in the Andes. They are present in the archaeological record of the early human settlement in the area (López 2013, Yacobaccio et al. 2012). The archaeological record of this initial phase of human dispersal to the highlands shows a diversified use of animals that included rodents, deer, and camelids at the Pleistocene-Holocene transition (Muscio 1999). This diverse use of animal resources was made through a high mobility strategy and wide home ranges (Yacobaccio et al. 2012). The mid-Holocene (ca. 8200-4200 cal years BP), was a period of increasing temperatures that gave rise to a

fragmented landscape and warmer, drier and fluctuating conditions (Yacobaccio 2012; Gayo et al. 2012; Morales et al. 2022). This implied a riskier environment for hunting and gathering adaptations that prompted the development of risk management strategies as human responses (Pintar 1995; Pintar and Rodriguez 2022). Towards the end of the mid-Holocene, the regional evidence shows a specialized use of wild camelids and reduced residential mobility (Yacobaccio et al. 2012) This economic specialization has been related to the diversification process of projectile points as well as to changes in the hunting strategies (Martinez 2003, 2005; López and Restifo 2014; Cardillo and Muscio 2021). Also, it was proposed that lithic technology was sensitive to the higher risk conditions of the mid-Holocene, through a strategy that favored the use of reliable projectile point designs (Bleed 1986; Pintar 1995).

Based on the analysis of the anthropogenic signal inferred from diverse radiocarbon time series, it has been proposed that population growth could lead to an increase in technological innovation in the study area (Muscio and Cardillo 2019). The summed probability distribution of the calibrated ages corrected with different models of taphonomic bias (Muscio and López 2016) shows a regional pattern consisting of a phase of low and fluctuating demography of relatively long term duration since the Pleistocene-Holocene Transition to mid-Holocene, followed by a phase of demographic expansion well evident at 5000 cal BP (Muscio and López 2016).

The phylogenetic reconstruction made on the lanceolate points from the highlands of Argentina and Chile documented a robust branching pattern of evolution and growing rates of taxonomic diversification during the mid-Holocene (Muscio and Cardillo 2019, see also supplementary material for detailed explanation of methods and the phylogenetic matrix of prior analyses). In addition, it was proposed the existence of allometric constraints on the metric variation of the lanceolate points (Cardillo 2009), and the existence of directionality in the reduction of the size and other dimensional variables (Cardillo 2009; Cardillo and Muscio 2020). In this work, our goal is to test the evolutionary hypothesis that the diversification of the lanceolate lithic points of the highlands of the South Central Andes was an adaptive radiation that affected human adaptation by increasing foraging efficiency. Based on regional-scale data, we seek to illuminate the links between the increasing mid-Holocene risk conditions, the patterns of diversification of projectile point lineages, demographic change and animal resources consumption.

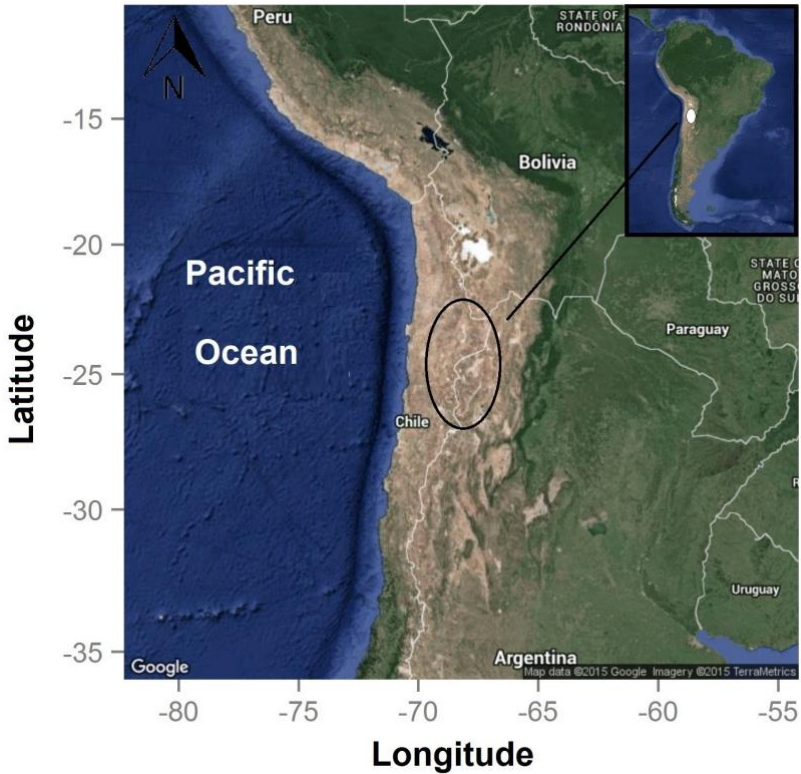


Figure 1. Study area. The highlands of the South Central Andes (Northwestern Argentina and Northern Chile).

Artifacts and evolutionary Radiations

A body of theoretical and empirical research has shed light on the mechanisms and processes of cultural evolution and on the appropriate methodologies to study them (Mace and Holden 2005; Mesoudi, 2011; Tehrani and Collard 2002; Lipo et al. 2007). Evolutionary archeology, for instance, developed several suitable methodologies for reconstructing histories of descent with modification in artifacts (O'Brien and Lyman 2000, 2003; Garcia Rivero 2013). These phylogenetic methods are critical in order to document and explain the patterns and processes behind the proliferation of artifact classes. In a broad sense, the study of cultural

evolutionary radiations requires focusing on the dynamics of innovation and extinction of cultural lineages. Here we consider technological innovations as cultural traits fixed at the population level. On the contrary, cultural extinction is a process by which cultural variants cease to be transmitted and replicated at the population scale.

In a general theoretical way, artifacts have more or less specialized functional roles in technological systems (Nelson 1991; Bousman 1993). The functional roles of the artifacts define how they interact with the environment, which includes other artifacts as well as users and potential replicators (Neff 2001). As long as artifact variants overlap their functional roles, the competitive exclusion principle predicts the selective extinction of the lower performing variants by adaptive biased transmission (Richerson and Boyd, 2005) producing cultural selection (Mesoudi 2011; Borrero, 1993; Dunnell, 1978). In these terms, all the factors with the potential to produce opportunities for lineage divergence become important for understanding when artifacts clades might be expected to radiate. For instance, risk might increase the demand for more specialized technologies as reliable weapons (Bleed 1986; see also Basalla 1988) or increasing manufacturing costs might increase the demand for tools with longer use-life (Shott 1989). Hence, the presence of one or more of these factors can trigger the evolution of artifacts' functional differences and the coexistence of related artifact lineages at the population level.

In macroevolutionary terms, an evolutionary radiation is a rapid increase in the diversity of a clade (Neige 2015; Simões et al. 2015). Documenting and explaining the patterns and processes behind evolutionary radiations constitute one of the major topics in organismic evolution (Venditti and Pagel 2008). As we shall show, the study of evolutionary radiations is important in cultural evolution too. While it has been recognized many different types of evolutionary radiations (Erwin 1992; Kozac et al. 2006; Simões et al. 2015; Boivin et al. 2018), classically the patterns of accelerated lineage diversifications are explained by invoking adaptive processes. In biological terms an adaptive radiation occurs by the divergent evolution of numerous lineages from a common ancestor where descendants' lineages are adapted to a great variety of distinct ecological niches (Futuyma 1998; Hernandez-Hernandez 2019). Whereas Simpson (1959) emphasized the importance of key morphological innovation in adaptation and taxonomic diversification, ecological opportunity is a prerequisite for adaptive radiation in biology (Erwin 1992; Eldredge 2001; Losos, 2010).

We can use this theoretical framework for the study of cultural diversification. Increased cultural diversity, diversification, is a dynamic phenomenon that results from the interaction of two processes: innovation and extinction. Following (Nee 2001, 2006) for the diversification of biotas, the simplest diversification model is

one where apparition (innovation) or extinction is left constant. For example, if cultural innovations evolve without the extinction of their previous forms, ancestral and derived forms will coexist, although with distinct probability of extinction. In this way, those artifact lineages that evolved early in the diversification process will be more likely to disappear than the more recent evolved lineages (Ezard et al. 2012). The adaptive radiation model implies an increase in the rate of adaptive innovation, with a momentum of maximum diversity, followed by the decrease in the rate of innovation (Venditti and Pagel 2008). Consequently, documenting the patterns of diversification, innovation, and extinction is central to discuss evolutionary radiations from null models. Even to distinguish the so-called pseudo-radiations, which are cases where the increasing diversity of a monophyletic group is caused by a drop in extinction rate rather than by a rise in innovation (Simões et al. 2015).

Methods

In evolutionary theory, phylogeny refers to the genealogical history of a group in which the relationships between ancestors and descendants are hypothesized (Kitching et al. 1998, Morrone 2000). On this basis, cladistics is a method used to create a nested series of taxa based on homologous characters shared by two or more taxa and their immediate common ancestor (Kitching et al. 1998; Morrone 2000; Felsenstein 2004). Considering that culture is a system of inheritance, cladistics is successfully applied in evolutionary archeology (O'Brien et al. 2001; O'Brien and Shennan 2010) and cultural phylogenies are documented by using classes as the units of analysis. A class is an ideational unit defined intentionally in terms of its character estates. The definition of a class specifies the necessary and sufficient conditions that every single empirical specimen must display to be considered a member of that class (Dunnell 1971).

In this work we conducted the phylogenetic analyses on a cultural data set composed of thirteen classes of lithic points that were defined in the specialized bibliography (Martínez 2003, 2005, 2007; Aschero et al. 2011; Restifo 2013a; López and Restifo 2014). These classes have a well-established chronological assignment based on the radiocarbon dates of different archaeological contexts of the South Andean Highlands. This chronological information allowed us to derive the life history of each class (figure 1 in supplementary data). It is important to highlight that the dataset only includes those classes composed of specimens not affected by the maintenance-reactivation process (Shott 2011).

For the phylogenetic reconstruction we designed a data matrix suitable for use with the TNT software (Goloboff et al. 2008). The total evidence approach of the TNT's algorithm allows the use of metric, morphological, and discrete characters

in a single matrix. This approach reduces the global uncertainty of the cladistic signal (Goloboff et al. 2006; Catalano et al. 2015).

Based on this, we built four matrices with quantitative, morphometric, and qualitative metric characters (see figure 2 and detailed description on supplementary data). Then, the different matrices were combined into a single one of thirteen classes and eleven characters (see the phylogenetic matrix in the supplementary data).

Based on the resulting phylogenetic tree and using the radiocarbon calibrated dates of each class included in the data set (Cardillo and Muscio 2020); we made a number of estimates that provide relevant information on the pace and the patterns of evolution of the lanceolate points. More precisely, we calculated the frequency of new classes (s) and the frequency of extinctions (e) in 200-year bins. In addition, we estimated the first apparition date FAD, and the last apparition date, LAD, of each class. Based on this, we calculated the longevity of each class as the difference between its FAD, and its LAD (Cardillo and Muscio 2020). Seeking to calibrate the phylogeny with the radiocarbon chronology of the lithic points, we built a chronophylogram (Bapst 2013). For this, we carried out an intensive search of 5000 stochastic resamples of the time ranges of each class. Subsequently, we estimated a consensus tree among all the trees with a confidence level of 0.95 (95%) (Cardillo and Muscio 2020).

Additionally we built the cumulative innovation time series, the cumulative extinction time series, and the taxonomic diversity time series. The diversity of classes, $D(t)$ at any one time is: $D(t) = s(t) - e(t - 1)$; the net difference between cumulative origination and extinction (Hamilton et al. 2019).

On the other hand, in order to assess the existence of a significant change in the diversity of classes over time, we performed the non-parametric Pettitt statistic, which tests for shifts in the central tendency of a time series under the H_0 -hypothesis of no change (Pettitt 1979). Finally, for documenting the existence of directionality in the evolution of the projectile points, we mapped the distribution of the length and the width of each class in the design space of the phylogeny that results from the combination of these two variables of the size. The statistics were performed in R (R Core Team 2022). The chronophylogram was done with the phytools package 0.7.20 (Revell, 2012) and Paleotree 3.3.25 (Bapst, 2012). Temporal series and trend statistics was estimated with forecast 8.17.0 (Hyndman et al., and trend 1.1.4 (Pohlert, 2020) packages.

Finally, foraging return rate scales prey body size (Broughthon et al. 2011). Hence, in order to assess the dynamics of foraging efficiency through zooarchaeological information, becomes critical to monitor the frequency of inclusion in the diet of the largest prey, the highest-ranked resources (Broughthon et al. 2011). On this basis, we analyzed the temporal frequency of the highest-

ranked fauna in the zooarchaeological assemblages of nineteen sites from the highlands dating from the late Pleistocene and mid-Holocene, compiled by Yacobaccio (2012). Accordingly, we calculated for each sample the proportion of high-ranking mammals (Cervidae and Camelidae) measured with the Artiodactyla index (AI) on the Number of Identified Specimens (Nisp, Lyman 2008) (see table in supplementary data).

Results

In previous works, we presented the results of the phylogenetic reconstruction made from our data matrix. (see phylogenetic matrix in supplementary file). The tree-searching algorithms of TNT was able to find a single tree as the most parsimonious tree, with CI = 0.586, and RI = 0.674, and with 85 % of all the branches with bootstrap support between 52 and 87%, (supplementary file figure S3) (Muscio and Cardillo 2019, Cardillo and Muscio 2020). The obtained time-calibrated, chronophylogram, of the tree is shown in Figure 2. Below we present the different patterns of projectile point diversification and the time series of high-ranking fauna.

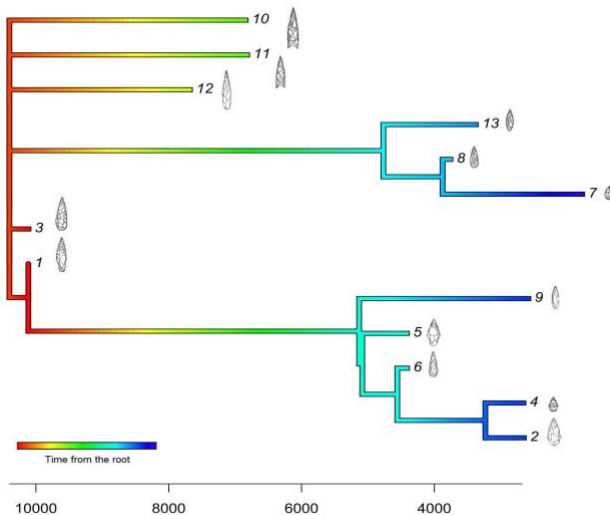


Figure 2. Chronophylogram of the lanceolate points of the South Central Andes. The chromatic scale represents the distance from the root, (from Cardillo and Muscio 2020).

Taxonomic diversity time series:

The taxonomic diversity time series graphically depicts the pattern of class distribution (Figure 3) characteristic of an evolutionary radiation. In this case the radiation amplitude (Ra), the total diversity of the evolutionary radiation is 13. The taxonomic time series has a modal diversity growth curve with a maximum around 5700 cal BP. This peak concentrates the 62 percent of the Ra with 8 classes of lanceolate points coexisting for almost 1000 years, after which taxonomic diversity falls rapidly (Figure 3). This process of cultural innovation occurred in a time interval (ΔTi) that ranges from the first FAD to the last FAD, that is, the time between the first and the last innovation in the data set. This is, $\Delta Te = 10473 - 5792$ years = 4681 years. On this basis, the innovation rate is $I = \Delta Ra / \Delta Ti$. Expressed in millennials, $I = 2.77$, (21%) classes every 1000 years.

On the other hand, the process of class loss occurred in the time interval (ΔTe) that ranges between the first and the last extinction, or the first documented LAD and the last LAD in the dataset. This is, $\Delta Te = 9334 - 3182 = 6152$ years. Then, the pace of cultural loss or the extinction rate is $E = \Delta Ra / \Delta TE$. Expressed in millennials, E is 2.11, (16%) classes every 1000 years. As the difference between rates shows, during the process of evolutionary diversification of lineages, innovation was 5 percent higher than extinction.

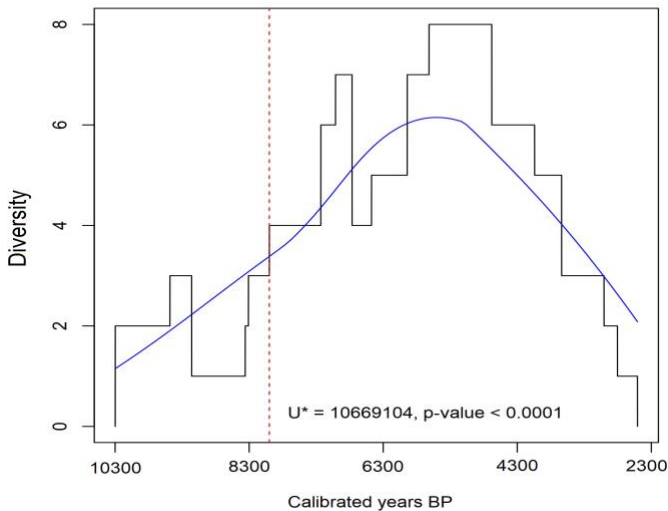


Figure 3. Empirical diversity through time plot and smoothed diversity curve; dotted line: diversity threshold from Pettitt test and Pettitt statistics

The Pettitt test performed on the taxonomic diversity time series shows a significant increase in the diversity of classes, above the mean of the series, towards 8100 years cal BP ($U=10669104$, $p\text{-value}<0.0001$). As we saw earlier, the temporal inhomogeneity of the rate of taxonomic diversity, with a momentum of maximum diversity or burst, is a signature of an evolutionary radiation (Venditti and Pagel 2008).

Radiation in the Lanceolate Phylomorphospace

In previous works, we showed the existence of statistically significant directionality in the evolution of the size of the lanceolate points from the South Central Andes (Muscio and Cardillo 2019; Cardillo and Muscio 2020). This becomes evident in the graph of the chronologically resolved phylogeny in the two-dimensional space formed by the length and the width of the projectile points. Here a displacement of the clade towards the smaller regions of the morphospace is observed (Figure 4). In this phylomorphospace, the lithic points classes are unevenly distributed, probably showing the effects of allometric constraints (Cardillo 2009; Buchanan et al. 2020). A relevant issue to highlight is that the new morphologies do not overlap with the existing ones. Conversely, they move towards previously empty regions of the design space where the greatest diversification occurs (Figure 4). This evolutionary pattern makes sense considering that adaptive radiations are often based on innovations that open up new possibilities for adaptive design (Simpson 1944).

The evolution of the smaller lithic points depicted in phylomorphospace occurred towards the end of the mid Holocene, post 5000 cal BP. These innovations in the size and morphology of the lithic points appear to have compromised the whole propulsion systems and required other technological innovations that allowed the use of lighter lithic heads in weapon systems with greater flight capacity (see discussion).

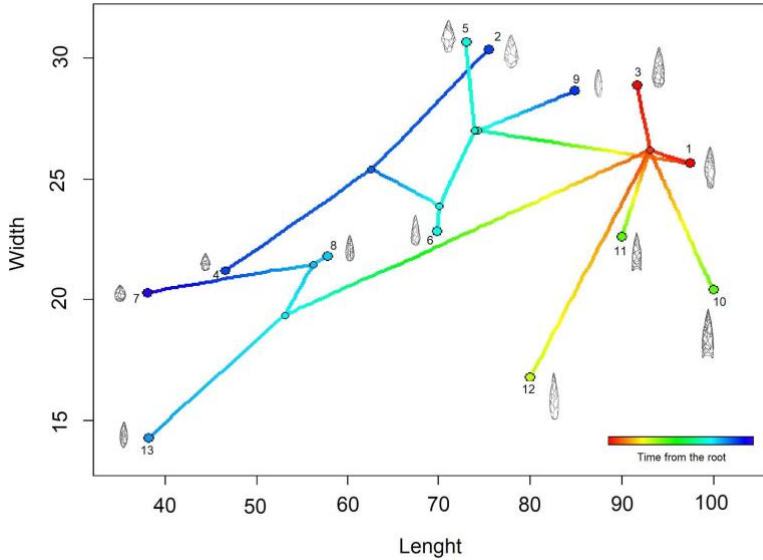


Figure 4. Phylomorphospace diagram showing the displacement of the lanceolate clade in the Cartesian space defined by the length and the width. The chromatic scale refers to the distance from the root.

Innovation and extinction time series

Cumulative innovation and cumulative extinction also show variable rates. The pace of innovation is such that point classes tripled every 1000 years until 5900-5700 years cal BP, beyond which no new classes appeared (Figure 5). Extinction clearly shows an inhomogeneous trajectory disengaged of innovation. For instance, during the period when innovation rate was maxima, only 38% of the total classes disappeared. The rate of extinction seems to accelerate towards 5000 cal BP as 62% of the classes become extinct in a span of about 2800 years (Figure 5.).

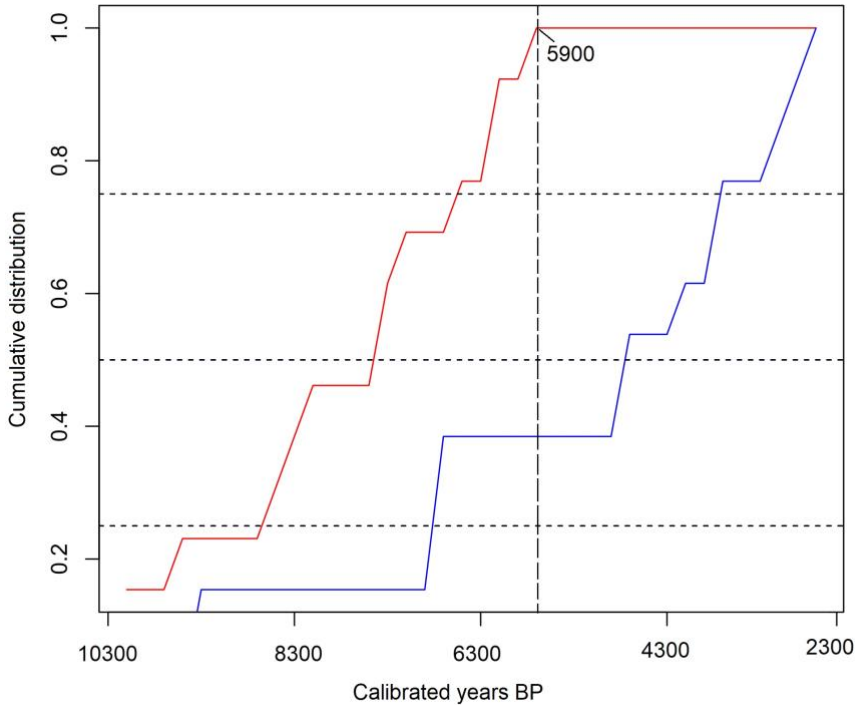


Figure 5. Cumulative innovation rate (red) and cumulative extinction rate (blue), estimated at 200-year intervals. Also the bold line indicates the latest innovation date (5900) for this dataset.

Longevity of classes and pattern of extinction

An interesting finding is the age-related extinction pattern in the evolutionary diversification process of the lanceolate points. The regression between the FAD and the LAD is high and positive ($t = 6.4$, $p < 0.0001$, $R\text{-squared} = 0.79$, slope = 1.128). In this way, as age increases, the extinction date is delayed at a rate of 1.3 (Figure 6). This makes predictable the date of extinction of each class once its date of appearance is known. Also, the pattern is coherent with the growth of class longevity over time, where the persistence time of some classes was twice the average (Figure 7) (see discussion). As linear regression shows, the longevity of the lanceolate point classes increased about 310 years every thousand years, with an average longevity of 2500 years (see also Cardillo and Muscio, 2020).

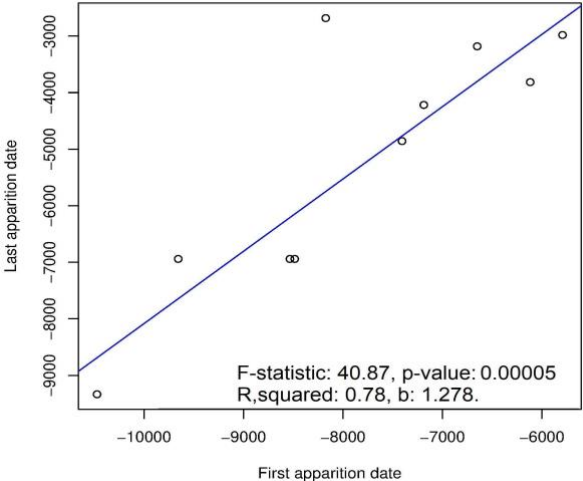


Figure 6. Linear regression between first and last apparition date for each class.

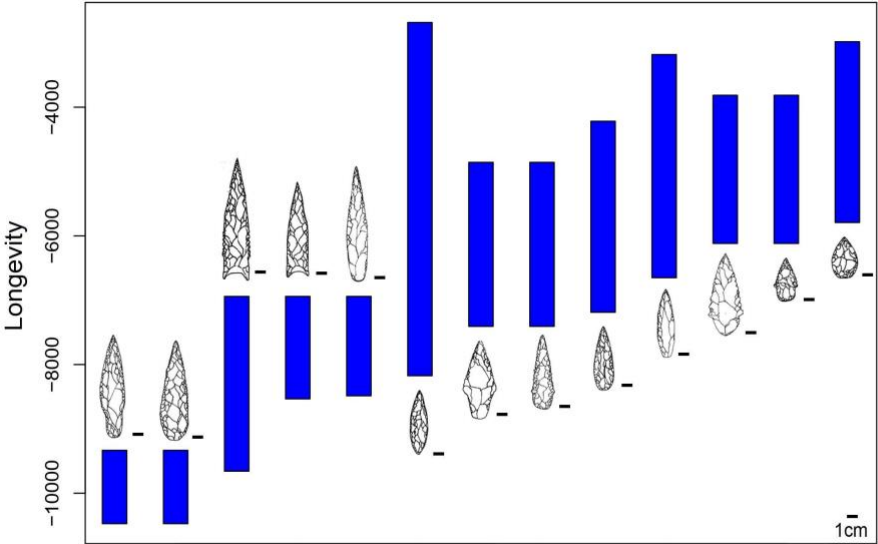


Figure 7. Longevity of classes, and classes ordered according to their first apparition date.

Demography and the evolutionary radiation of the lanceolate points

By restricting the analysis to the time series of the early and mid-Holocene, the Pettitt test shows the existence of a critical point of change in the temporal trend around 6100 cal BP, where a gradual increase in the anthropic signal is evident (Figure 8). This allows us to propose that the point of greatest taxonomic diversity occurred during the middle of the mid-Holocene towards 5700 cal BP. after the inflection point towards a greater demography.

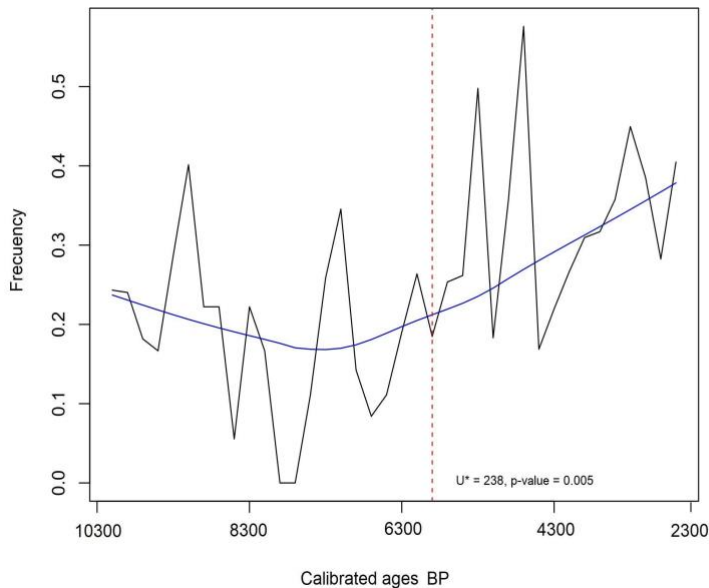


Figure 8. Temporal series of the relative frequency of calibrated ages and mean smoothed trend through time. Dotted line: threshold in mean frequency detected by means of Pettitt test, and Pettitt test statistics.

Time series of High ranked Fauna

As we mentioned before, based on the Artiodactyl Index of the zooarchaeological assemblages of nineteen sites, we built the time series of the representation of high-ranking animal resources. The temporal distribution of the AI shows a gradual increase in the high-ranking faunas, mainly camelids, throughout the Holocene. This increase in the proportion of camelids occurred at the expense of small mammals such as *Lagidium viscacia* and other rodents, such as Chinchillids and birds. Based on linear regression analysis we estimate a rate of increase of

artiodactyla in the assemblages of 8% per millennium (F-statistic: 25.49 , p-value: 0.00006, R-squared=0.50). Also, there is an statistically significant change in the artiodactyla index time series from 7000 years BP (Pettitt Test, $U^* = 147$, p-value = 0.0066). In sum this analysis shows that during the early Holocene the consumption of high-quality fauna was low and markedly uneven. Around 5000 BP, the incidence of high-ranked preys begins to grow above 50 percent. This change in the faunal composition of the archaeological record of the hunter-gatherers from the highlands of the Puna is interpreted as the evolution of specialization in the consumption of camelids (Yacobaccio 2012; López 2013).

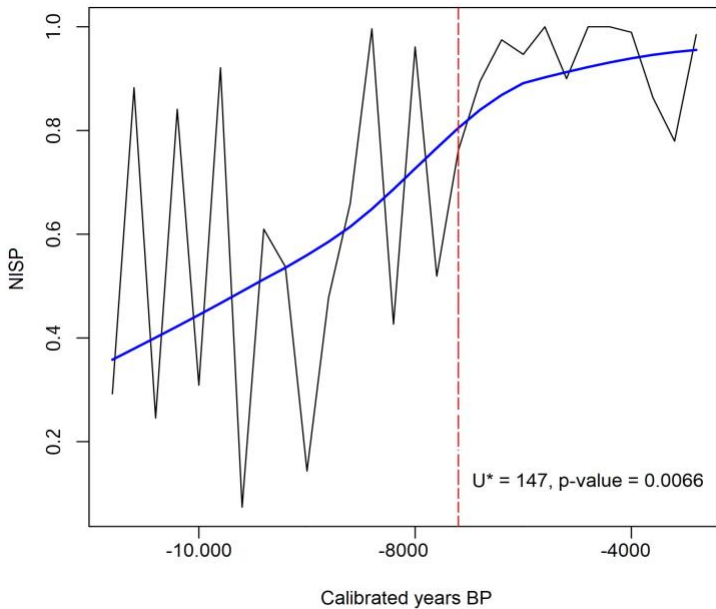


Figure 9. Temporal series of high-ranking faunas through time. Dotted line: threshold in mean frequency detected by means of Pettitt test, and Pettitt test statistics

Discussion

The human peopling of the South Andean Highlands was a process that began during the transition from Pleistocene to Holocene, about 12,000 years ago. For about 9000 years after their initial dispersal, humans maintained a hunter-gatherer way of life adapted to the extreme conditions of the high altitude puna

environments, where camelid hunting was the predominant human subsistence strategy. During the early Holocene the diversity of projectile points was low and the designs were mainly of triangular morphology. These projectile points and other material expressions were identified as the high south central Andean Archaic hunter-gatherer tradition (Osorio et al. 2017). By the end of the early Holocene, during an advanced phase of the peopling process, these triangular points became extinct, substituted by other classes of projectile points such as the lanceolate classes. As the taxonomic diversity time series of the lanceolate points shows the evolutionary diversification of these artifacts exemplifies a cultural evolutionary radiation that took place among hunter gatherers of the highlands of the South Central Andes. The information presented here shows a rapid increase in the diversity of the lanceolate projectile points that began around 9500 cal BP and extended to 5000 cal BP. Then, a rapid decline in taxonomic diversity that lasted up to 2500 BP, is observed. The temporal distribution of classes documents a pattern of evolutionary radiation with a modal diversity growth with a maximum value of taxa diversity around 5700 cal BP. More generally, we distinguish a first instance with a greater diversity of points, a higher rate of innovation and less longevity that around 6000 cal BP turns to an inverse pattern. The new scenario is one of less innovation, greater class longevity; and an age-related extinction pattern. A path to diversity loss may result when innovation rates decrease and do not compensate for increasing extinction Gjesfjeld et al. (2020).

As we mentioned, adaptive cultural selection occurs by the retention of technological variants that perform better their function (Lyman et al. 2009). As selected variants accumulate by cultural transmission this also produces lineage divergence. In this way, identifying the environmental factors with the potential to produce opportunities for lineage divergence become an important issue for understanding when artifacts clades might be expected to adaptively radiate. We suggest that the several changes in the environmental structure that occurred throughout the Holocene fostered technological diversification among the hunter-gatherer populations that occupied the southern Andean highlands and who gradually specialized in the exploitation of camelids. With the beginning of the mid Holocene (ca. 8200-4200 cal years BP) paleoclimatic evidence shows the onset of a process of increasing temperatures which gave rise to a warmer and drier, mainly between 6800 and 4200 cal BP. Regionally, this period was one of sustained increases of aridity. It has been stated that the most extreme period of drought occurred at 5700 cal years BP (Núñez and Grosjean 1994; Morales et al. 2022). This increase in aridity produced a high fragmentation of the landscape, a more fluctuated climatic regime, and a very heterogeneous distribution of animal resources. In this landscape, the populations of wild camelids were concentrated

in habitats that conserved water supply, in high altitude oases called vegas or bofedales.

We propose that this more fluctuating and patched environment of the mid-Holocene constituted a context that stimulated technological innovation, to cope with risk and to increase hunting efficiency. More diverse weaponry should have increased the chances of successful hunting in a greater diversity of hunting strategies and contexts. As we said before, the peak of maximum diversity of point classes is around 5700 cal BP. This is precisely the time of greatest aridity and risk in the highlands of the southern Andes (Morales et al. 2022).

Based on the zooarchaeological record we showed a regional scale pattern of gradual increase in foraging efficiency since the end of the Pleistocene and along the mid-Holocene. Throughout this time period the representation of camelids slowly increased at the expense of lower ranked resources like small mammals and birds. Indeed, during the early Holocene the incidence of high-quality fauna was very low and markedly uneven across the different sites, suggesting the predominance of expensive adaptations (Muscio 1999). We must wait for 5000 cal BP for high-ranked prey to rise above 50 percent and to the end of the mid-Holocene to fully appreciate a hunting economy specialized in the resources with the highest return rate. We estimated a rate of increase of economic efficiency of 8% per millennium, which is the rate of increase of artiodactyls in the assemblages. Importantly, this shows that the diversification of projectile points preceded the economic specialization in camelid hunting and the process of increased foraging efficiency. Hunting specialization required capture tactics tuned to camelid-specific habitats and behaviors (Aschero and Martinez 2001; Martinez 2003, 2007). As we have seen, from the beginning of the mid-Holocene there is evidence of the practice of new hunting strategies, such as hunting by enclosing, the use of hiding structures and delivering systems for hunting at greater distance (Aschero and Martinez 2001). So we can conclude that technological innovation was a prerequisite for the human specialization in camelid hunting and for the development of a highly economically efficient foraging strategy in the south Andean highlands.

Regarding the role of population growth in the pattern of diversification of projectile points, the increase of the anthropic signal around 6100 year cal BP might suggest that technological diversity increased related to demographic growth. However, as we pointed out previously, technological innovation rate begins to increase towards 8100 cal BP., two thousand years before the start of the demographic expansion. This means that the rate of innovation appears to be decoupled from the anthropogenic signal but coincident with the early to mid-Holocene, as the risk hypothesis predicts. From here we can propose some derivations. Human Behavioral Ecology theory asserts that foraging efficiency

translates into fitness (Borgerhoff Mulder and Schacht 2012). Because we documented a broad time scale pattern of increasing hunting efficiency, population growth might have been a consequence, at least partially, of the adaptive technological innovation made by hunter gatherers throughout the mid-Holocene in the south Andean highlands.

On the other hand, we documented a pattern of increasing class longevity over time. In terms of the notion of design space (Stankiewicz 2000), longer longevity could result from the gradual evolution of point designs to optimal or quasi-optimal regions of the technological design space, understood as the possible combination of metric and morphometric variables of artifacts (Stankiewicz 2000; Scheinsohn 2010). This is predictable from a process of technological innovation where the richness of projectile point classes gradually decreases as more-effective classes selectively evolve (Lyman et al. 2009). In this case selection limits variation through time as the points and the rest of the weapon system become more finely tuned to the selective environment and the space for optimal designs becomes saturated.

A similar pattern of rapid increase and abrupt decline in diversity has been documented in other contexts and in different technologies (Lyman et al. 2009; Hamilton et al. 2019; Gjesfjeld et al. 2020). Likewise, the diversification of the lanceolate points shows that innovation and extinction implied slightly different rates, as the time series document. Although both rates are relatively similar, innovation was higher at the beginning of the evolutionary radiation, while extinction accelerated towards its ending (Figure 5).

Besides, as we showed before, important differences can be appreciated in the longevity of the point classes. Analyzing the evolution of automobile models, Gjesfjeld et al. (2020) showed a trend to a reduced longevity, although with the differential persistence of some models with longer life times. This is also the case of the lanceolate points of the South Central Andes, where some classes have very long lifetimes regarding the average longevity of the data set.

On the other hand, Hamilton and colleagues (2019) when analyzing the longevity of projectile points from the United States also showed a pattern of decreasing longevity that accompanied an increasing diversity. In contrast, the information presented here for the lanceolate points suggests a reverse trend. Therefore, we suggest that the relationship between the patterns of evolutionary diversification and the longevity of the evolving taxa is context dependent. In our case study increased longevity would have resulted from a saturated design space.

The phylogenetic morphospace defined by the length and the width, supports previous results that suggested that projectile points diversity was constrained by allometric vectors (Cardillo 2009). This may have resulted from design restrictions that limited size change and affected projectile points performance. Indeed, some

regions of the design space may show more restrictions than others due to the trade-offs between the performance requirements and structural constraints of the technical systems in which the lithic points were used. For example, changes in point size are directly correlated with flying performance and penetration ability in throwing weapons (Hughes 1998).

The evolution of the lanceolate points discussed here, shows a gradual reduction in the length and the increase in the relative width, particularly in the points of later mid-Holocene. The decrease in the size of the points seems to have opened a path to a new unoccupied region of the design space of the lanceolate points allowing the emergence of a greater diversity of morphological classes. The reduction in the size of the points and their correlation to shape changes is a trend that has been repeatedly documented in projectile point sequences from the early and mid-Holocene across the Americas (Hughes 1998; Ratto 2003, 2006, 2013). In this regard, Hughes (1998) pointed out that shape changes might result from the need to maximize cutting surfaces as the points reduce in size. Recently, Buchannan et al. (2020) made progress in the study of the different trade-offs potentially involved in the dimensional change of the American Paleoindian projectile points. They pointed out that the dimensional variability of the points is strongly constrained by performance properties, such as penetration and impact resistance. As we showed earlier, there is a displacement through the allometric vector in the lanceolate design space that suggests the action of cultural selection producing the morphospace expansion and diversification around allometric vectors. This implied the coexistence of a wide diversity of morphologies and sizes, which is consistent with the regional scale evidence of more diverse hunting strategies and technical systems during the mid-Holocene. For example, Ratto (2003) pointed out that some large lanceolate points were not suitable to be launched with spear thrower, and were therefore more plausibly used as thrusting weapons (Ratto 2003, 2006; see also Restifo 2013). Likewise, as Hughes (1998) suggested, the coexistence of technical systems with and without fletching makes greater variability in points designs to be expected, since the performance requirements are different for both variants of shafts.

An important issue to highlight is that while in other andean regions bifacial lanceolate points do not show much taxonomic richness, in the South Central Andes the size of the radiation is relatively large. For example, in the Central Hill of Argentina, only two morphometric classes of Ayampitin lanceolate points are recognized (Rivero and Heider 2016, 2017). The same low diversity of lanceolate bifacial points is documented in other regions of the Andes, such as Asana (Aldenderfer 1989). This suggests a geographic component in the opportunities of these artifacts to diverge along South America and the action of a geographic driver of diversification in the Puna of Argentina and Chile. To clarify this and other issues

it is necessary to extend the spatial and temporal scale of the phylogenetic reconstruction in order to include other classes of points that have not been addressed in this work. Also, the expansion of the geographical scale for phylogenetic reconstruction will allow documenting the existence of other evolutionary projectile point radiations, as well as the historical and functional relationships between the different traits of the points of large areas.

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