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Modelling demographic dynamics and cultural evolution: The case of the early and mid-Holocene archaeology in the highlands of South America

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ABSTRACT

Based upon the modelling of the dynamics of populations occupying low-quality environments with varying technological innovation rates, this work constructs some generalizations about expected patterns of cultural evolution which could be documented in the regional archaeological record of populations which occupied heterogeneous and spatially-structured environments. These expectations are discussed on the basis of the archaeological record of the Puna of Argentina and Chile. This record supports the derived hypothesis that from the early Holocene to the end of the mid-Holocene, the rate of adaptive cultural evolution increased as human populations increased in size. Cultural flow was an important mechanism for the technological transfer of adaptive technological innovations between local populations connected through larger social networks which exceeded the Puna region, since the beginnings of the human colonization of the area when the risk of local extinction was high. More broadly, the archeological record of the Puna region supports the theoretical prediction that population pressure was not the cause of the major trends in cultural evolution, but the consequence. Based on this, the interrelation between population size dynamics and cultural evolution is highlighted.

1. Introduction

Modern humans colonized South America during the Pleistocene–Holocene transition. In the Southern Andes of Argentina and Chile, there is agreement that many of the major changes in the archaeological record began during the mid-Holocene. The adoption of new hunting practices accompanied with new technologies for capturing and processing resources, economic intensification, decrease of mobility, emergence of spatial circumscription, increment of social interactions through extended exchange networks, development of social complexity and the beginning of the domestication of camelids, are believed to have started during the mid-Holocene. There are reasons to suspect that these changes were adaptive responses to broad-scale environmental changes, particularly to the increase of temperature and aridity of the so-called hypsithermal event. This warm period covered roughly the interval 8000–5000 BP, with a maximum aridity at 6000 BP in the Puna of Atacama region (Núñez and Grosjean, 1994; Núñez et al., 2005).

Another possible source of causation for this significant increase in the rate of evolutionary change is population pressure (Castro and Tarragó, 1992). However, the archaeological record of northwestern Argentina, and the Puna of Chile, does not show a dramatic population increase during the mid-Holocene, or a punctuated and massive emergence of new technologies. On the contrary, the demographic signal strongly supports the prevalence of small populations occupying a fragmented and heterogeneous landscape, at least until about 5000 BP. Importantly, the absence or discontinuity of human occupations in certain areas of the region between 7500 and 5000 BP suggests that some populations were prone to local extinction during the times of maximal aridity.

From an evolutionary perspective, this paper aims to examine the causes of the increasing rate of cultural evolution during the mid-Holocene in northwestern Argentina and northern Chile, by modeling the impact of social learning, between population connectivity and technological innovation on long-term population dynamics. Thus, the content of this paper is mainly theoretical. Its archaeological application is not restricted to any particular case. The theoretical framework presented here is potentially applicable for building hypotheses about the processes and patterns of cultural and demographic evolution expected in the regional archaeological record of populations who occupied heterogeneous and fluctuating environments. However, in order to show the explanatory potential of this theoretical framework, some of its predictions are discussed briefly on the basis of the archaeological record of the mid-Holocene of the Puna of Argentina.

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2. Material and methods

The first step is to develop a series of algebraic models of cumulative evolution of adaptive innovations, following the work of Boyd and Richerson (1985) and Henrich (2010). In order to obtain insights for detecting archeological patterning, the second step is to integrate these models into a code for the iterative modelling of the expected dynamics of populations occupying low-quality environments (Foley, 1997), with varying technological innovation rates.

3. Modeling cultural innovation as a function of population size

Cultural novelties arise from several processes of inventions, but only when a cultural novelty is selectively retained at the population level does it become an adaptation (O'Brien and Lyman, 2000). Upon this base, henceforth this analysis distinguishes between *inventions*: the creation of something new; and *innovations*, those inventions that became fixed at the scale of the population as a result of biased transmission and selective replication. Briefly, cultural innovations are evolved products of the Darwinian selection of cultural novelties.

Selection needs variation at first. In cultural systems, the combination of inventiveness and cultural transmission errors create such variation. To model invention as partially dependent on population size, consider β as the proportion of innovative individuals of a local population with size n, whereas ϕ is the mean rate of adaptive inventions produced by every single innovative individual, a parameter independent of population size. After this, the expected amount of adaptive technological novelties produced at the population level is:

$$L = \phi n\beta. \tag{1}$$

In Eq. (1) the product $(n\beta)$ is the net number of innovative individuals. Because by definition this parameter is relative to population size, it follows that the rate of invention of adaptive cultural novelties will partially depends on population size. Indeed, inventiveness increases as population size increases, because of the increment of the number of individuals producing lucky errors and successful recombination of pre-existing cultural variation (Henrich, 2004). On this basis, leaving the mean rate of inventions per innovative individuals constant, larger populations will have higher invention rates. Nevertheless, the chance of this novel variation to be retained at the population level depends on the probabilities of the innovative individuals to become role models for other individuals (Boyd and Richerson, 1985).

3.1. Selection of technological variation as a function of population size

Suppose that a technological novelty x has an economic utility value U_x which is superior to the utility of any other alternative variant. Consider that the utilities associated to the alternative technological variants are consistently correlated with the Darwinian fitness of the individuals possessing them. Finally, assume that the individuals of a given population can perceive the potential utility of adopting or rejecting x, and they have all the materials means for adopting it through social learning and replication. Then, under these conditions, x will selectively outcompete all the alternative variants. Given its adaptive superiority, x will spread across the population by the action of mechanisms of adaptive learning and natural selection.

For modeling the selective process, take η as the total number of technological adaptations already available in the cultural pool of a local population in time t. Assume that the set of social learners of the population have a bias to adopt and replicate locally optimal technological novelties, with indifference to the origins of the novelties, which may be local or non-local. Consider that the force of this adaptive bias is bounded by the actual capacity of the social learners to detect the potential utility of the new technologies as well as by their learning abilities to replicate them. Designate α as the force with which the adaptive bias acts, ranging from 0 to 1. Note that α measures the rate of the adaptive social transmission. This parameter is independent of population size. For simplicity, consider that whenever α is greater than zero, the adoption of a novel cultural variation x against a potential alternative variant x' follows the conditions:

$$x \text{ always is adopted if } \begin{cases} u_x > 0;\, u_{x'} = 0 & \text{condition a} \\ u_x - u_{x'} > 0 & \text{condition b} \end{cases}$$

Condition "a" says that as long as the local selective value of a technological novelty is a positive number and given the absence of any other alternative variant for a particular adaptive role (so that $u_{x'} = 0$), the new variant will be adopted as an adaptation filling a vacant technological niche. Therefore, the size of the cultural pool will increase, becoming $\eta + 1$. Condition "b" says that a technological novelty with a superior performance in a local environment will always displace the pre-existing alternative variant from its technological niche, replacing it. Consequently, in this case the technological pool will not change in size but in composition. In both cases, the rate of technological evolution rests in the magnitude of α.

For modeling the selective process, let J be the proportion of social learners of a given population. Consider L_a as the subset of the technological variation that accomplishes condition "a" and which pertains to the more inclusive set L (which as was established in Eq. (1) is the total amount of technological novelties produced at the population level). Similarly, consider that L_b is the subset of L which accomplishes condition "b". After this, the total amount of technological innovations of the population after a period t of invention and selection is:

$$\eta_{t+1} = \eta_t + \alpha J_{t+1}(L_a + L_b)_{t+1}. \tag{2}$$

The term $\alpha J_{t+1}(L_a + L_b)_{t+1}$ gives the amount of technological innovations evolved in the population during one period of time. Note that Eq. (2) says that the selective process driving the cumulative evolution of technological innovations depends partially on population size. The background assumption is that, as in the case of the innovative individuals, the number of social learners in a given population is a function of the size of the population. In the ideal case when $\alpha = 1; J = 1$ (meaning that everyone in the population is a social learner adopting always the best options), and for $L_a = 0$, (by which the whole set of technological novelties emerged in the population has not competitive variants), all the new technologies will be retained at the population level. Also, this situation implies that everyone in the population will become a role model for new social learners. In this scenario the rate of adaptive technological evolution will tend to be maximal. More realistically, the number of social learners would be just a fraction of the population, and with a value of α mainly limited by their imperfect ability to learn and detect the best solutions to complex adaptive problems (Boyd and Richerson, 1985). Similarly, the bulk of the technological inventions will have some alternative variants already present in the cultural pool. Hence, these considerations attenuate the expected rates of cumulative adaptive technological evolution. In the opposite extreme, when $J = 0$ all the technological novelties qualify as mutations with no replicative success (O'Brien and Lyman, 2000). Thus, this transient variation will not contribute to the cumulative technological evolution of the population.

As was shown above, both invention and innovation depend on population size. Therefore the cumulative evolution of technological innovations can be modeled as a Darwinian process of selection in combination with other processes controlling the dynamics of population size.

4. Modelling population dynamics and cultural innovation

In order to model the effects of the cumulative evolution of adaptive cultural innovation on the demographic dynamics of human populations colonizing empty habitats, Verhulst's equation (3) gives an appropriate framework. Also known as the logistic equation, this model is one of the simplest and more extended tools for assessing the dynamics of natural populations in contexts of limited resources. The rate of change of population density N is given by:

$$\frac{\mathrm{d}n}{\mathrm{d}t} = rN\left(1 - \frac{N}{K}\right). \tag{3}$$

The variable r, also called the Malthusian parameter, is the rate of population increase, the proportional growth of N along one unit of time. This figure results from the difference between the birth rate b and the death rate d of the population.

$$r = d - b. \tag{3a}$$

The parameter K is the equilibrium population density at a level of a population pressure given by the ratio N/K. When this ratio is 0, the population grows at its maximum rate and there is no population pressure; when it is 1, density-dependent mechanisms prevent population growth.

For assessing the effects of cultural innovations on population dynamics, assume that r is dependent on the contribution of technology to the Darwinian fitness of the individuals (O'Brien and Lyman, 2000). Additionally, assume that K is not constant, but dependent on the technologies used for obtaining resources. This allows modelling a feedbacking effect between technological evolution and population increase into a recursive equation of population growth (Rogers, 1992). With this goal, the utility of a given technology can be considered as a fraction of K. For instance, a technological variant x will be associated with a utility value $U_x = 0.1$ percent of K. Also, for simplicity, assume that this utility contributes to the fitness of the individuals, by modifying the r of the population. The background hypothesis is that as long as a new technology raises the environmental carrying capacity, it also increases the velocity of population growth by improving the fitness of the individuals.

In addition to these assumptions, let M be the total amount of technological innovations evolved in the population during one period of time t, with a utility value U_t resulting from the sum of the utilities of every single innovation retained along t. Then, when the effects of technological innovation are considered, the values of r and K after one unit of time are given by:

$$K_{t+1} = (1 + U_{t+1})K_t \tag{4}$$

$$r_{t+1} = (1 + U_{t+1})r_t \tag{5}$$

4.1. Adding environmental stochasticity

Environmental stochasticity refers to variation in birth and death rates in response to weather, disease, competition, predation, or other factors external to the population. Even though it may occur in all populations, it is generally important in populations that are already fairly small, occupying fluctuating environments. For considering the effects of environmental stochasticity is usual to define r as random variable with a mean value and a corresponding standard deviation (STD) denoting the magnitude of the fluctuations (Foley, 1997). This procedure was followed in modelling the dynamics of small populations by introducing environmental stochasticity into Eq. (5).

4.2. Adding the effects of cultural flow

Cultural flow is the social transfer of information between local populations. Verhulst's equation describes the growth of a closed population. Consequently, for modelling the dynamics of a system composed by populations which are more or less open to the transference of adaptive innovations, the parameters governing the strength of cultural flow must be incorporated in the dynamics of each single population. The critical variable here is between-populations connectivity. In the case of biological processes were migration and gene flow are of evolutionary importance, connectivity decreases with distance and increases with the dispersive abilities of the organisms (Olivieri and Gouyan, 1997; Wiens, 1997). The same is expected for cultural flow. However, as social transmission among human populations may occur in absence of the movement of people, another important factor affecting connectivity is the amount and the efficiency of the transmission devices. In this way, geographically distant populations may successfully exchange adaptive information if they have efficient transmission technologies and social institutions that increase information flow. For instance, exchange networks increase the connectivity between distant populations and the spatial scale of information flow. Accordingly, when the distance between local populations increases and when the amount and the efficiency of the transmission devices decrease, the frequency of interaction between social learners and potential role models from different populations will diminish. Hence, connectivity resumes the chance of occurrence of cultural transference between local populations, which is mediated not just by the distance separating each population and the physical movement of people, but also by the technology and the social institutions which are functional for connecting people into a social network. After this, consider that f is the distance-based probability of interaction and information transmission of the individuals of two separated populations, whereas s is the probability of the individuals of each population for interact and transmit information based on the availability of technologies and social institutions connecting them. Hence, in probabilistic terms the connectivity between the individuals of the two geographically separated populations is $c = (f + s)/2$, the average between f and s.

Next, consider a system consisting of two populations where X is a source population and Z is a receiver population of cultural innovations produced at the source. Hence, the cultural flow has the direction $X \rightarrow Z$. Considering c as the connectivity index between the two populations, the expected K and r of Z after a cycle of local cultural evolution and lateral cultural transference are given by:

$$Kz_{t+1} = (1 + Uz_{t+1})Kz_t + cU_{Xt+1} \tag{6}$$

$$rz_t = rz_{(t-1)} + Uz_{(t-1)} + cU_{Xt} \tag{7}$$

In equations (6) and (7), the product cU_{Xt} expresses the utilities values of the total amount of adaptive cultural innovations laterally adopted by Z from X and controlled by connectivity, where c equals 1 all the new cultural innovations evolved at X at a time t result adopted by Z. Note that, for simplicity, this model assumes the synchronic occurrence between the evolution of cultural innovations in the source and the process of adoption by the receiver population.

5. Results

Solving Eq. (3), and introducing the parameters discussed above into a numerical code, produces an iterative model of population dynamics affected by technological innovation. The code allows the simulation of population growth under different conditions. This section will discuss the results of two series of simulations. The first was designed for exploring the effects on population growth of varying rates of social transmission. The second series of simulations was oriented to detect the effects of the cultural transference of technological innovations on the viability of small populations.

5.1. Case 1: social transmission of adaptive technologies and the growth of small populations

A simulation was done in order to explore the dynamics of small-sized populations experiencing varying rates of social transmission of local cultural innovations. Hence the focal variable was α. Remember that this parameter measures the capacity of the social learners to detect the potential utility of the new technologies as well as their learning abilities to replicate them. An initial value of $K = 100$ was considered. As before, this parameter is relative to the available technology. For simplicity, a very low upper limit of $3\,K$ for the technology-generated carrying capacity was fixed. This means that technological efficiency could only triplicate the extraction resources before the onset of population pressure. For example, under some conditions, cooperative hunting triplicates prey capture (see Sosis, 2001).

On the other hand, it was assumed an initial population density of 1% of K, growing unconstrained by resource limitation at a rate of 1% per year. This value of r is very low, but seems reasonable for hunter-gatherers living in marginal environments, as those of the highland desert of the Puna of Atacama. Moreover, assuming that useful inventions are rare, the proportion of innovative individuals of the population was fixed at a constant value of $\beta = 0.2$ (the 20% of N), and the rate of technological innovations was assumed to be $\phi = 0.2$, with an averaged adaptive value of each innovation of 0.001 of K.

Under the assumptions of the model, even for modest adaptive values per innovation population always grows quickly towards the K equilibrium threshold. For values of α differing in one order of magnitude, population density reaches the 3 K equilibrium in less than 1000 years, along a process of growth completely indifferent to the initial value of K (Fig. 1). This implies that in the hypothetical scenario where the available technology triplicates environmental carrying capacity, even very small populations will always reach the new population pressure threshold very quickly. Hence, the evolution of a technology that increases the availability of food will not retard population pressure and competition for longer. On the contrary, it will accelerate its onset.

Only when the force of social transmission decays three orders of magnitude, to a very small value of $\alpha = 0.005$, population pressure consistently retards its beginning but, again, for the upper 3 K equilibrium threshold, leaving behind the phase of population pressure started in less than 1000 years. Hence, only when the rate of cultural evolution is very slow and when the rate of intensification by innovation is also very slow, population pressure may be retarded at a scale above the millennium, by the selective accumulation of adaptive innovations that slowly increase economic efficiency. Richerson et al. (2009) have correctly stated that the most important factor governing the time scale of population pressure is the rate of intensification by innovation. This is also true when considering that the rate of population growth also increases with the individual fitness gains per innovation.

Natural selection based on population pressure could be delayed for some millennia only under a very slow rate of adoption of technologies that slightly increases environmental carrying capacity and the fitness of the individuals. This would imply a population of individuals with very poor abilities for recognizing the economic potential of the inventions of others, or with very limited learning capabilities to replicate these inventions. Thus, for archaeologists working into a Holocene time framework, this implies that natural selection based on competition and population pressure should be taken for granted after any human process of successful colonization of an empty space, and it will increase as the rate of adaptive cultural evolution increases.

5.2. Case 2: technological transfer between populations enhances the viability of small populations

A second simulation was done for assessing the effects of technological transfer and cultural flow on the viability of small size populations. A system composed by one source population

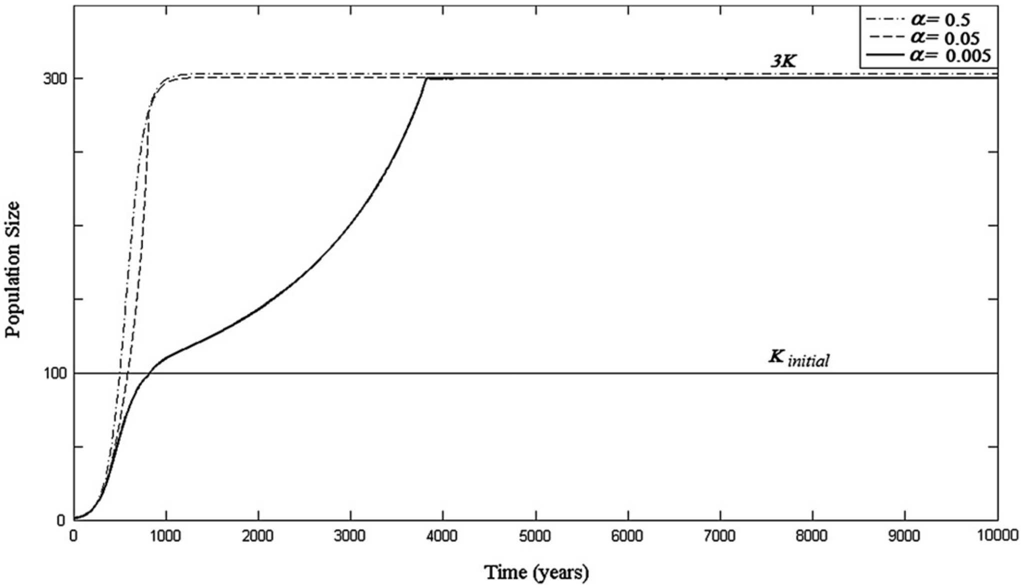

Fig. 1. The dynamics of small size populations experiencing varying rates of social transmission of local cultural innovations (α).

(population 1) and two receiver populations (populations 2 and 3) was modeled. For populations 1, 2 and 3, an initial population size of 1% of K was considered, being $K = 100$ in the three cases. In considering the effects of environmental stochasticity on population growth, the source population was left to grow with an initial r of mean = 1% per year, and a random fluctuation of ±1 STD. Receiver populations 2 and 3 where modeled as sink populations, occupying marginal and more unstable habitats. In sink populations deaths exceed births, therefore they are prone to extinction (Pulliam, 1988). Then, populations 2 and 3 were left to grow with an initial r of mean = −0.1% per year, and with a random environmental-induced fluctuation of ±2 STD. As in case 1, it was assumed that useful inventions are rare. The proportion of innovative individuals along the three populations was fixed at $\beta = 0.2$ (the 20% of N), and the rate of technological innovations per innovative individuals was assumed to be $\phi = 0.2$, with a rate of intensification by innovation of 0.001 of K. A fixed rate of social transmission of $\alpha = 0.005$ was considered for the three populations. In order to explore the effects of cultural connectivity on the viability of sink populations, f was assumed to be zero. This means that populations 2 and 3 are isolated from population 1 by distance. For population 2, s was considered to be zero, whereas for population 3, s was assumed to be 0.5. So, despite its geographical isolation, population 3 is connected to population 1 by the existence of technologies and social institutions which promote cultural transmission, whereas population 2 is geographically and culturally isolated (see section 4.2).

Fig. 2 shows the growth dynamics for each population. Population 1, even fluctuating, grows as expected under the temporal scale imposed by the exponential growth. Population pressure starts at a short temporal scale Fig. 2(a). Population 2, restricted for adopting adaptive innovations from the source population, can delay extinction for some millennia as a consequence of the adaptive effects of locally evolved technological innovations Fig. 2(b). So, adaptive cultural evolution may improve the viability of isolated small populations which are prone to extinction. Under this context a pattern of divergent cultural evolution is expected, along a declining and fluctuating population size pattern. As the rate of invention and the rate of adoption of innovations both partially depend on population size, the rate of cultural evolution is also expected to decline along time. In addition, as population becomes smaller, the frequency of role models will decrease and complex technologies will tend to be lost as a result of random loss or incomplete transmission, a process called the Tasmanian effect (Henrich, 2004). Population 3 depicts another interesting dynamic (Fig. 2c). In this case, after an initial phase of a quasi-steady state of a temporal scale longer than the millennium, the population can exponentially grow because of the transferred adaptive innovations originated at the source population. This case exemplifies the potential of cultural flow and technological transfer to produce a long- term rescue effect of sink populations. In this case, the cultural rescue effect involves a source- sink dynamics, where sink populations avoid extinction for the adoption of technologies and information from the source. As the rate of adoption of technological innovations from the source increases, the viability of the sink population also increases. Therefore, this dynamic depends on the cultural connectivity between populations. Processes like this are expected to occur when small human populations occupy poor quality and highly fluctuating environments. From an archaeological point of view, beside the assessment of a particular local occupational history, the documentation of shared cultural lineages, past social networks, and the use of technologies for connecting small populations become critical.

6. Discussion

The archaeological record of the Puna of Atacama supports many of the expectations presented above. The Puna is a high-altitude desert located over 3000 m above sea level. This biome of low primary productivity and fluctuating rainfalls has a markedly patchy distribution of habitats of different quality for human populations. However, the availability of wild camelids made the Puna region a very attractive space for hunter-gatherers populations seeking for high-ranked prey types.

Modern humans colonized the Puna region during the early Holocene, around 11,000 BP. The humid conditions of the early Holocene allowed the dispersion of hunter–gatherer populations in the region. These first colonizers were primarily camelid hunters who entered into a space without other relevant carnivorous competitors. During this first phase, hunting technology was based

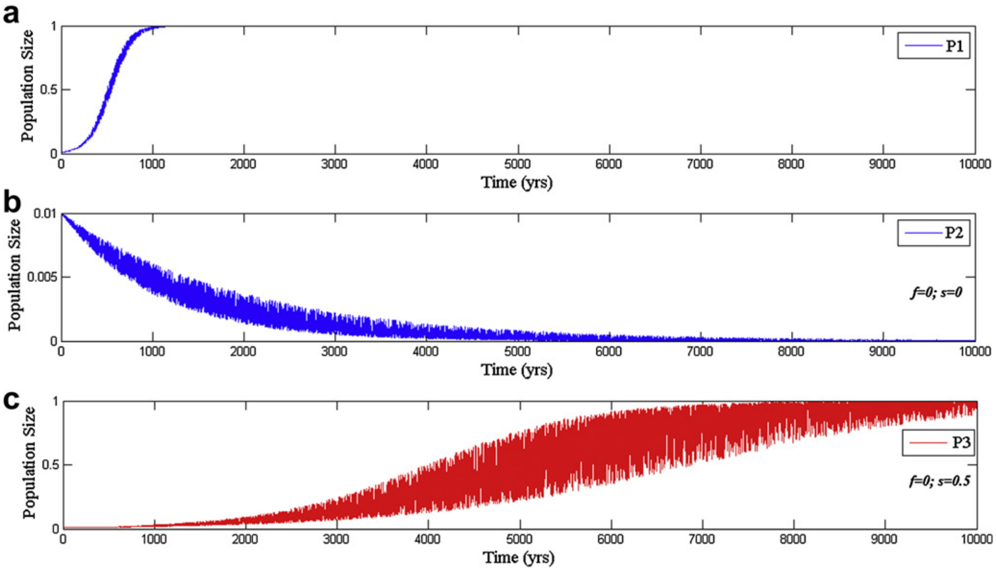

Fig. 2. Population growth and technological transfer between fluctuating populations; a) P1 is a source population; b) P2 is a sink and isolated population; c) P3 is a sink population rescued by cultural flow. Connectivity is measured by the probability of interaction and information transmission of the individuals of separated populations which depends on distance (f), and which also depends on the availability of technologies and social institutions connecting them (s).

on unstemmed triangular shaped projectile points, designed for hunting in open spaces with a tactic involving few individual hunters (Aschero and Martínez, 2001). This evidence strongly suggests that these early hunter populations were colonizing adaptations that expanded the distributional range of more dense populations occupying the highlands and the lowlands of the northern Andes. Under these conditions, the expectation is one of a rapid phase of exponential population growth. This demographic success seems to be confirmed by the rapid expansion of humans into the region, and by the continuous occupation of high quality spaces such as Pastos Grandes (López, 2008), and of Quebrada Seca 3, both in the Puna of Argentina. Also, the evidence of early occupations with broad niches suggests colonizing populations with suboptimal adaptations that occupied low quality habitats which were prone to rapid saturation (Muscio, 1998a, 2009). Furthermore, the archaeological record of the Puna of Argentina strongly suggests that this area was colonized from denser populations which were already successfully established in areas of lower altitude (Muscio, 1998b). A simple biological framework for explaining this early process of dispersion and colonization of the Puna of Argentina can be built under the logic of the mainland-island model (Wiens, 1997). Along the altitudinal gradient this would imply demographic connectivity between source populations, localized at lower altitude, and patchy populations localized in the Puna. Importantly, it would also imply cultural connectivity and cultural flow when cultural transmission is considered. The archeological evidence supports this reasoning.

The exclusive use of triangular shaped projectile points during the whole early Holocene is a strong signal of a low rate of technological innovation. As was established earlier, a low rate of technological evolution is expected among small populations. There is agreement that this is the case (Aschero, 2007; Yacobaccio, 2007). Independent evidence strongly indicates that early Holocene human populations were small, highly mobile and highly interconnected. A high mobility strategy and the implementation of broader exchange networks were adaptations to fluctuating resources. For reproductive reasons alone, mobility would have been exceedingly high. The archaeological record shows the existence of very inclusive exchange networks that connected the Puna with lowland regions since the early Holocene (Núñez and Dillehay, 1978; Rodríguez and Martínez, 2001; Aschero, 2007). These long distance exchange networks must have diminished the extinction rates of the smaller populations living in fluctuating environments by providing migrants and technologies. But, if connectivity decreases, cultural innovation acting on small and fluctuating local populations subject to hard selection does not avoid extinction. This might explain some cases such as the Salar de Atacama, in northern Chile, where the whole area seems to have been abandoned by 8130 until 6150 BP (Núñez and Grosjean, 1994; Núñez et al., 2005), and other cases in the eastern border of the Puna of Argentina which show occupational discontinuities longer than three millennia (Yacobaccio and Morales, 2005).

It is not until the mid-Holocene when new hunting tactics and new designs of projectile points appeared. Interception hunting with darts and spears evolved around 8600 BP. Towards 7000 BP, bifacial lanceolate shaped points appear along a broad diversification of projectile point designs, and with the first evidences of collective hunting. This new hunting tactic required special facilities used as parapets (Aschero and Martínez, 2001). All these technological innovations, which raised environmental carrying capacity, occurred gradually since the beginning of the mid-Holocene. While the onset of the middle Holocene environmental conditions produced a high degree of local variation in the archaeological record (Yacobaccio and Morales, 2005), what is clear is an increased rate of adaptive cultural evolution for this period. This increase in the rate of technological innovation is the expected result of growing populations, even with very modest rates of population increase.

The landscape of the Puna during the hypsithermal was one of increased spatial heterogeneity. The archaeological record of the Puna of Argentina suggests that mobility reduction was the adaptive response to this context (Aschero, 1994). More broadly, mid-Holocene hunter-gathers in the Puna of Argentina and Chile coped with the shift towards aridity, and higher temperatures, between 8000 and 5300 BP, by basically changing their mobility strategies and not abandoning the area (Yacobaccio and Morales, 2005). Hence, the hypothesis of a sustained population growth which increased the rate of adaptive evolution is fully compatible with a more irregular distribution of people across the landscape during the hypsithermal. Further, this adaptive environment must have favored increasing exchange networks, as the archaeological record shows (see Aschero, 2007; Yacobaccio, 2007).

Importantly, even a regional context of low demography and highly localized populations will produce a strong diffusion of innovations if cultural connectivity is high. By the end of the mid-Holocene, there is a significant body of evidence showing the emergence of complex hunter–gatherers integrated in extensive social networks, and with practices of protecting herding, suggesting the onset of a local process of camelid domestication (Yacobaccio, 2004). But an important point to remark is that many, if not all, of the behavioral and technological innovations which were functional to rise environmental carrying capacity during the Holocene in the Puna of Atacama, required specific skills, which are difficult to acquire. For instance, the manufacture of bifacial tools demands sophisticated operational skills (Hocsman, 2007). Therefore, the cultural flow between connected populations, and the vertical transmission within populations would explain the rapid expansion of highly adaptive innovations. The adoption of herding practices in the Puna of Argentina and Chile could have started in this way.

Around 5000 BP, bifacial and unifacial lanceolate shaped tools appear as the dominant tools in the lithic assemblages along the region, with very large and highly concentrated surface accumulations of debris (Fernández Distel, 1978; Muscio 1998b, 2009). Probably, the rapid spread of these bifacial technologies was the result of a higher rate of transmission of highly adaptive innovations between highly interconnected local populations with reduced residential mobility (Muscio, 2009). These technological transferences did not impede the emergence of branching evolutionary patterns among cultural lineages. The lanceolate shaped points of San Antonio de los Cobres, in the Puna of Argentina, show a very strong phylogenetic signal, documenting a cladogenetic process (Cardillo, 2001). Around 5000 BP, the number of occupations and the rate of artifacts deposition increase, while the intensification of the exploitation of camelids also increases. This suggests a phase of increase of population pressure and strong selection for efficiency (Muscio, 2009), resulted from the cumulative evolution of technologies and behaviors that, by increasing economic efficiency, enhanced the reproductive success of the individuals and population growth. Importantly, in this context the northern Puna of Argentina shows a gradual change towards an increasing use of blades for making different classes of lithic artifacts (see Restifo and Hoguin in this volume), which strongly suggests an adaptation of maximizing energy efficiency (López, 2008). This case documents a process of divergent technological evolution between the northern and the southern Puna of Argentina.

7. Conclusions

The models presented in this work assumed a dependence of the rate of adaptive evolution on population size. This assumption does not imply that the temporal scale of population growth and the temporal scale of adaptive cultural evolution would always overlap. The last one partially rests on the rate of invention per innovative individual in the population; producing cultural mutations (see section 3). Upon these inventions, selection acts mainly based on the capacity of the social learners to detect the utility of the new variants and to learn how to replicate them. These two factors are independent of population size. As Henrich (2010) empirically demonstrated, useful inventions are rare and mostly unintentional. Therefore, the expected time-scale of adaptive cultural evolution usually would be largest than the short time-scale of the exponential population growth (Richerson et al., 2009).

On the other hand, as was shown in section 5.2, a collection of populations distributed along a spatially heterogeneous and fluctuating environment and forming a network connected by cultural flow, will produce a pattern where the spatial distribution of adaptive cultural variation, originated at different nodes of the network, will be spatially structured. In this network, large-size populations occupying high quality habitats will show the greatest innovation rates. Also, the extinction rate of small and fluctuating populations will depend on cultural and biological connectivity. In highly fluctuating environments, isolated and small populations will be able to enhance viability, without avoiding extinction, by accumulating locally optimal innovations. Cultural flow by connecting populations which are prone to extinction with larger and viable populations has the potential to produce a cultural rescue effect, by the transference of adaptive cultural innovations from large-size populations to small-size populations.

The archaeological record of the Puna of Argentina and Chile supports the hypothesis that since the early Holocene to the end of the mid-Holocene the rate of adaptive cultural evolution increased as human populations increased in size, simply because large populations have more inventors and are more resistant to losses by chance. This does not entail the assumption that technological innovations systematically followed population pressure. On the contrary, episodes of augmented population pressure must have followed the adoption of adaptive technological innovations. The evidence suggests that one of these episodes of augmented population pressure resulting from the accumulation of adaptive cultural innovations occurred around 5000 BP in the Puna of Argentina. In this case the increase in population pressure was not the cause of cultural evolution but the consequence. As was shown, the record also indicates that cultural flow was an important mechanism for the technological transfer of adaptive technological innovations between local populations connected into a large social network that exceed the Puna region.

These hypotheses require expanding our archaeological knowledge, by estimating the rates of cumulative cultural evolution and the dynamics of population growth in the Puna region. Phylogenetic reconstruction is a means to document descent with modification, as well as rates of evolution inferred from phylogenetic trees. However, a simpler way is the estimation of the number of adaptive innovation, documented in the archaeological record, per time unit and the patterning of this parameter along broader regions. Regarding paleoenvironmental research, it is especially important to determine the scales of spatial heterogeneity, for assessing the potentials of the local habitats for the long-term human occupation within a given region. This is critical for applying a source-sink model of population dynamics or other models based on spatially-structured populations.

There are theoretical and empirical reasons to suspect that the cultural evolution in the Puna of Argentina and Chile cannot be explained solely in terms of intensification. Indeed, the message of this work is that the rate of cultural evolution in this spatially-structured region since the early Holocene to the end of the mid-Holocene was causally correlated mainly with the rate of population growth, as well as with the demographic and cultural connectivity of the populations, but not with the short time-scale of population pressure.

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References

Aschero, C.A., 1994. Reflexiones desde el Arcaico tardío (6000–3000 AP) Rumitacana. Revista de Antropología 1 (1), 13–17.

Aschero, C.A., 2007. Iconos, huancas y complejidad social en la puna sur argentina. In: Nielsen, Axel E., Clara Rivolta, M., Seldes, Verónica, Magdalena Vázquez, María, Mercolli, Pablo H. (Eds.), Producción y circulación prehispánicas de bienes en el sur andino. Brujas, Córdoba, pp. 135–165.

Aschero, C.A., Martínez, J.G., 2001. Técnicas de caza en Antofagasta de la Sierra, Puna Meridional Argentina. Relaciones de la Sociedad Argentina de Antropología 26, 15–41.

Boyd, R., Richerson, P., 1985. Culture and the Evolutionary Process. University of Chicago Press, USA.

Cardillo, M., 2001. Transmisión cultural y persistencia diferencial de rasgos. Un modelo para el estudio de la variación morfológica de las puntas de proyectil lanceoladas de San Antonio de los Cobres, Provincia de Salta, Argentina. In: Martinez, G.A., Lanata, J.L. (Eds.), Perspectivas integradoras entre arqueología y evolución. INCUAPA-Olavarría, pp. 97–120.

Castro, V., Tarragó, M.N., 1992. Los inicios de la producción de alimentos en el cono sur de América. Revista de Arqueología Americana 6, 91–124.

Fernández Distel, A., 1978. Nuevos hallazgos precerámicos en la región de Salinas Grandes, Puna de Jujuy, Argentina. Revista del Instituto de Antropología 6, 15–62.

Foley, P., 1997. Extinction models for local populations. In: Hanski, I., Gilpin, M.E. (Eds.), Metapopulation Biology. Ecology, Genetics, and Evolution. Academic Press, San Diego, pp. 215–246.

Henrich, J., 2004. Demography and cultural evolution: why adaptive cultural processes produced maladaptive losses in Tasmania. American Antiquity 69, 197–221.

Henrich, J., 2010. The evolution of innovation-enhancing institutions. In: Shennan, S., O'Brien, M. (Eds.), Innovation in Cultural Systems: Contributions from Evolutionary Anthropology. The MIT Press, London.

Hocsman, S., 2007. Producción de bifaces y aprendices en el sitio Quebrada Seca 3-Antofagasta de la Sierra, Catamarca (5500–4500 años ap.). In: Nielsen, A.E., Clara Rivolta, M., Seldes, Verónica, Magdalena Vázquez, María, Mercolli, Pablo H. (Eds.), Producción y circulación prehispánicas de bienes en el sur andino. Brujas, Córdoba, pp. 55–82.

López, G., 2008. Arqueología de cazadores y Pastores en tierras altas. Ocupaciones humanas a lo largo del Holoceno en Pastos Grandes, Puna de Salta, Argentina. BAR International Series 1854, Oxford.

Muscio, H.J., 1998a. Colonización humana del NOA y variación en el consumo de recursos: la ecología de los cazadores- recolectores de la puna durante la transición Pleistoceno-Holoceno. http://www.naya.org.ar/articulos/index.htm.

Muscio, H.J., 1998b. Arqueología de San Antonio de los Cobres (S.A.C), poblamiento prehistórico y evolución en el NOA: Primeras interpretaciones del registro arqueológico de superficie. Estudios Sociales del NOA año 2 N 4, 121–164. Tilcara.

Muscio, H.J., 2009. Nicho y estrategia predominante. Dos conceptos útiles en arqueología evolutiva. In 150 Años Después. In: Barboza, M.C., Davis Avila, J., Pícolli, C., Cornaglia Férnandez, J. (Eds.), La vigencia de la teoría evolucionista de Charles Darwin. CEIA, UNR, Rosario, pp. 83–105.

Núñez, L., Dillehay, T., 1978. Movilidad giratoria, armonía social y desarrollo en los Andes Meridionales: Patrones de tráfico e interacción económica. Universidad del Norte, Antofagasta.

Núñez, L., Grosjean, M., 1994. Cambios ambientales pleistoceno-holocénicos: Ocupación humana y uso de recursos en la Puna de Atacama (Norte de Chile). Estudios Atacameños 11, 11–24.

Núñez, L., Grosjean, M., Cartajena, I., 2005. Ocupaciones humanas y Paleoambientes en la Puna de Atacama. Instituto de investigaciones arqueológicas y museo. Universidad Católica del Norte-Taraxacum. San Pedro de Atacama, Chile.

O'Brien, M.J., Lyman, R.L., 2000. Applying Evolutionary Archaeology. Plenum, New York.

Olivieri, I., Gouyan, P., 1997. Evolution of migration rates and other traits: the metapopulation effect. In: Hanski, I., Gilpin, M.E. (Eds.), Metapopulation Biology. Ecology, Genetics, and Evolution. Academic Press, San Diego, pp. 293–324.

Pulliam, H.R., 1988. Sources, sinks and population regulation. The American Naturalist 132, 652–661.

Richerson, P.J., Boyd, R., Bettinger, R.L., 2009. Cultural innovations and demographic change. Human Biology 81, 211–235.

Rodríguez, M.F., Martínez, J.G., 2001. Especies vegetales alóctonas como recursos arqueológicos en el ambito puneño. Asociación paleontológica argentina, publicación especial 8. Buenos Aires, pp. 139–145.

Rogers, A.L., 1992. Resources and population dynamics. In: Smith, E.A., Winterhalder, B. (Eds.), Evolutionary Ecology and Human Behavior. Aldine de Gruyter, New York, pp. 375–402.

Sosis, R., 2001. The emergence and stability of cooperative fishing on Ifaluk Atoll. In: Cronk, L., Chagnon, N., Irons, B. (Eds.), Human Behavior and Adaptation: an Anthropological Perspective. Aldine de Gruyter, New York, pp. 437–472.

Wiens, J.A., 1997. Metapopulation dynamics and landscape ecology. In: Hanski, I., Gilpin, M.E. (Eds.), Metapopulation Biology. Ecology, Genetics, and Evolution. Academic Press, San Diego, pp. 27–42.

Yacobaccio, H.D., 2004. Social dimensions of camelid domestication in the Southern Andes. Anthropozoologica 39, 237–247.

Yacobaccio, H.D., 2007. Población, intercambio y el origen de la complejidad social en cazadores recolectores surandinos. In: Nielsen, Axel E., Clara Rivolta, M., Seldes, Verónica, Magdalena Vázquez, María, Mercolli, Pablo H. (Eds.), Producción y circulación prehispánicas de bienes en el sur andino. Brujas, Córdoba, pp. 277–286.

Yacobaccio, H.D., Morales, M., 2005. Mid-Holocene environment and human occupation of the Puna (Susques, Argentina). Quaternary International 132, 5–14.