Microsatellite data show recent demographic expansions in sedentary but not in nomadic human populations in Africa and Eurasia.

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Abstract:

The transition from hunting and gathering to plants and animals domestication was one of the most important cultural and technological revolutions in the history of humans. According to archeologists and paleoanthropologists, this transition must have triggered major demographic expansions. However, few genetic studies have found traces of Neolithic expansions in the current repartition of genetic polymorphism, pointing rather toward paleolithic expansions. Here, we used microsatellite autosomal data from 60 African and Eurasian populations to show contrasted demographic patterns between sedentary and nomadic populations. Indeed, despite their variability in location and environment, we found expansion events for all sedentary farmer populations, while we inferred constant population size for all hunter-gatherers and most herder populations, which could result from constraints linked with a nomadic or semi-nomadic life-style. As an exception, we inferred expansion events for herder populations from Central-Asia. This might be linked with the arid environment of this area, which may have limited the amount of farmable areas, resulting in less competition for land between farmers and herders. Alternatively, current Central-Asian herders may descent from populations who have first experienced a transition from hunter-gathering to agropastoralism, thus having potentially led to demographic expansions, and then a second transition to nomadic herding. Finally, probably due to the combination of a higher mutation rate and the possibility to analyze several loci as independent replicates of the coalescent process, the analysis of microsatellite data allowed us to infer more recent expansion events than in previous genetic studies, potentially resulting from the Neolithic transition.

Keywords: lifestyle, demography, population genetics, Neolithic transition, Beast, coalescent.

Introduction:

Reconstructing the demographic History of human populations remains a strongly investigated issue in many disciplines, including paleoanthropology, archeology and population genetics. In particular, the transition from hunting and gathering to plant and animals domestication, which occurred independently in several regions of the World during the Neolithic period (10 000 – 3 000 years before present, YBP), is widely assumed by paleoanthropologist and archeologists to have driven recent human population expansions (Bar-Yosef and Belfer-Cohen, 1991; Bocquet-Appel and Bar-Yosef, 2008; Bocquet-Appel, 2011). This transition, which probably represented one of the most important cultural and technological revolutions in the history of *Homo sapiens*, led to deep changes in many aspects of life (diet, technologies, social organization…) and to the sedentarization of many populations (Bar-Yosef and Belfer-Cohen, 1991; Mazoyer and Roudart, 2006; Bocquet-Appel and Bar-Yosef, 2008). Bocquet-Appel (2011) showed an increase in both the number of enclosures and the proportion of subadults in Eurasian burial sites during the Neolithic, which was interpreted as a proof of a demographic expansion resulting potentially from the Neolithic transition in sedentarized farmer populations. During this transition, other populations remained nomadic. While some kept a hunter-gatherer lifestyle, others developed new means of subsistence like nomadic herding. To date, the impact of nomadic herding on demographic processes has been scarcely investigated.

Population genetic studies have brought some complementary insights into the understanding of human demographic history. Numerical methods based on the coalescent theory (Kingman, 1982) allow inferring demographic parameters from current population genetics data (see Emerson *et al.*, 2001; Excoffier and Heckel, 2006 and Kuhner, 2008 for reviews). In particular, many studies based on sex-specific non-recombining markers, namely the Y chromosome and the hypervariable control region (HVS-I) of the mitochondrial DNA, have detected strong middle and upper Paleolithic expansions in both Africa and Eurasia. With HVS-I data, expansion onsets have been dated from 80 000 to 30 000 YBP in African populations (Harpending *et al.* 1993; Watson *et al.*, 1997) and 63 000 YBP to 17 000 YBP in Eurasia (Harpending *et al.* 1993, Chaix *et al.*, 2008). Estimations obtained from the analysis of the Y-chromosome are generally more recent (from 15 000 to 12 000 YBP for Africa and 40 000 to 11 000 in Eurasia; Pritchard *et al.,* 1999; Chaix *et al.*, 2008), but still predate the Neolithic transition. In addition, some authors used neutral autosomal DNA regions to take advantage from the possibility to combine inferences from several independent loci. This allowed refining the dating of Paleolithic expansions in Africa from 50 000 to 25 000 YBP (Voight *et al.*, 2005; Laval *et al.,* 2010). All these studies pointed to expansions starting in the Paleolithic, without a sign of a subsequent stronger Neolithic expansion. It might be explained by methodological issues. Indeed, ancient events leave stronger signals in current genetic data than more recent events. If the population is not in genetic equilibrium due to past growth events, then the effects of more recent events may not be detectable (Lavery *et al.,* 1996).

Regarding the relationship between life-style and demographic history, a recent study based on complete mitochondrial sequences (Batini *et al.* 2011) showed constant population sizes for hunter-gatherer populations in Africa, while it showed demographic expansion events for farmer populations that started about 60 000 YBP. In another work, using both the mitochondrial HVS-I region and autosomal sequences data, we also found contrasted demographic history between sedentary and nomadic populations predating the Neolithic transition in both Africa and Central-Asia, thus suggesting that stronger Paleolithic expansions may have ultimately favored the emergence of agriculture in some populations (C. Aimé, G. Laval, E. Patin, P. Verdu, L. Ségurel, R. Chaix, L. Quintana-Murci, E. Heyer, F. Austerlitz; unpublished). However, as ancient expansions could have masked a potential signal of more recent expansions, these findings do not preclude the possibility of a second expansion event resulting from the Neolithic transition.

Autosomal microsatellites have been used in many studies to infer demographic patterns at the inter-population level (divergence, admixture, *etc.*) and/or to investigate the current genetic structure of human populations (Rosenberg *et al.*, 2002; Ségurel *et al.,* 2008; Verdu *et al.*, 2009; Martinez-Cruz *et al.*, 2011). However, although they offer both the advantage of a high mutation rate and the possibility to analyze several loci as independent replicates, autosomal microsatellites have been scarcely used to detect past variations in effective size in humans at the population level. Nevertheless, recent simulation studies and empirical studies on non-human species showed that autosomal microsatellites can reveal very recent demographic events (*e.g.* Cornuet *et al.*, 2010; Hu *et al.*, 2011; Fontaine *et al.,* 2012) that more slowly mutating markers such as DNA sequences may fail to detect.

Here, we analyzed several autosomal microsatellite data sets using a coalescent-based approach, in order to investigate the past demographic history of 60 African and

Eurasian populations with contrasted life-styles (*i.e.* sedentary farmers, nomadic hunter-gatherers and nomadic herders). We aimed at determining whether these markers allowed us to detect recent Neolithic expansions events and if these expansions occurred similarly in populations characterized by different lifestyles. First, we focused on Central-Africa, where we studied a set of populations (commonly called Pygmies) that have kept a nomadic life-style based on hunter-gathering, as well as neighboring farmer populations. These two groups of populations are genetically differentiated and their divergence time was inferred at about 60 000 years ago (Patin *et al.*, 2009; Verdu *et al.*, 2009), thus long before the Neolithic sedentarization of farmer populations which occurred about 5 000 YPB in this area (Bocquet-Appel and Bar-Yosef, 2008). Second, we analyzed a sample of populations from four distant geographical regions of Eurasia (Middle-East, Pamir, Russia and East-Asia), where sedentary farmers coexist with nomadic herders, studying one herder and one farmer population from each region. Finally, we performed a more detailed study on farmer and herder populations from Central-Asia. This area is of peculiar interest as it presents a very specific environment, with a more arid climate than in the rest of Eurasia, which could have impacted the development of farming and the demography of humans (Dirksen and Van Geel, 2004). Moreover, although Central Asia is thought to have been a major corridor during the successive Eurasian migration waves (Nei and Roychoudhury, 1993; Cavalli-Sforza *et al.*, 1994), many questions about the history of this area remain open. In particular, whether nomadic herding in Central Asia appeared directly from hunting and gathering or if the ancestors of current nomadic herders have experienced two successive shifts (*i.e.* the first to agropastoralism, and then to nomadic herding) is still unknown.

Material and methods.

Population Sampling and Marker Sets.

For Africa, we used the data set of Verdu *et al.* (2009, 2013), which consists of 12 farmer populations, with a total of 337 individuals, and ten Pygmy hunter-gatherer populations, with a total of 281 individuals (**Table S1**). These individuals were genotyped for 28 unlinked autosomal microsatellite locus located on 18 different chromosomes.

For Eurasia, we selected eight populations from the HGDP-CEPH Human Genome Diversity Cell Line Panel (Cann *et al.*, 2002; Rosenberg *et al.,* 2002). To avoid any bias of geographic structure in the sampling, we first identified four distant areas where farmer and herders coexist (Middle-East, Pamir, Russia and East-Asia), and then selected randomly one traditionally nomadic herder population and one neigbouring sedentary farmer population from each of these regions (Han Chinese and Mongols from East Asia, Pathans and Balochi from Pamir, Palestinians and Bedouins from Middle-East, and Russians and Yakut from Russia). This represented a total of 231 individuals (**Table S1**). For our detailed study of Central Asia, we used data from 30 populations from West Uzbekistan to East Kyrgyzstan: 17 herder populations, for a total of 584 individuals, and 13 farmer populations, for a total of 382 individuals (**Table S1**). Among these populations, 26 had been genotyped in previous studies (Ségurel *et al.* 2008, Martinez-Cruz *et al.* 2011). The four other populations (KIB, TAB, KIM, and TAM) were genotyped for this study, using the same PCR and genotyping procedures as in Ségurel *et al.* (2008). For all Eurasian and Central-Asian populations, we used the 27 autosomal microsatellites markers selected by Ségurel *et al.* (2008) from the HGPD-CEPH panel.

All sampled individuals were healthy donors from whom informed consent was obtained. The study was approved by appropriate Ethic Committees and scientific organizations in all countries where samples have been collected.

Data analysis.

We computed the likelihood distribution of demographic parameters (Kuhner *et al.*, 1995) using the MCMC algorithm implemented in BEAST v1.7.4 (Drummond and Rambaut, 2007). We tested the four demographic models implemented in this software: constant effective population size (N_0) ("Constant model"), exponential variation of N_0 ("Exponential model"), logistic variation of N_0 ("Logistic model") and expansion starting at a given moment in the past from an ancestral population of constant size N_1 ("Expansion model"). This allowed us to infer the current effective population sizes (N_0) and growth rates (g) for all analyzed populations. For the "Expansion model", we also inferred the ancestral population size (N_1). We then inferred the dates of expansion onsets (t) using the following formula: $t = (1/g)\times\ln(N_1/N_0)$, applied to each step of the MCMC algorithm. We used a single step mutational model (SSM), which takes homoplasy into account. The implementation of microsatellite models in BEAST v1.7.4 is described in Wu and Drummond (2011).

We performed three runs of $2.8\text{x}10^8$ steps per population and per demographic model for the African populations, and three runs of $2.7\text{x}10^8$ steps for the Eurasian populations (which corresponded for all populations to three runs of 10^7 steps per locus). We recorded one tree every 1 000 steps, which thus implied a total of 10^5 trees per locus and per run. We removed then the 10% first steps of each run (burn-in period) and combined the runs to obtain acceptable effective sample sizes (ESS of 100 or above, *e.g.* Couvreur *et al.*, 2010; Gignoux *et al.,* 2011). The convergence of these runs was assessed by visual inspection of traces using Tracer v1.5 (Rambaut and Drummond, 2007) to check for concordance between runs, and also by the computation of the Gelman and Rubin's (1992) convergence diagnostic using R v2.14.1 (R Development Core Team, 2011) with the function "gelman.diag" available in the add-on package coda (Plummer *et al.*, 2006).

In order to facilitate a large exploration of the parameter space, for the autosomal sequences, we chose uniform priors between 1 and 10^6 for $2N_e$ and between -0.1 and 0.1 per generation for g. In agreement with previous studies, we assumed a uniform prior between 10^{-4} and 10^{-3} per generation for the mean mutation rate (μ) (*e.g.* Verdu *et al.*, 2009), and the mutation rate of each locus was drawn independently from a Gamma distribution (mean=μ and shape=2). We assumed a generation time of 25 years (*e.g.* Chaix *et al.*, 2008; Patin *et al.*, 2009; Laval *et al.*, 2010). For each population and demographic model, we obtained the mode and the 95% HPD of each parameter, inferred from the posterior distributions obtained using the add-on package Locfit (Loader, 1999) in R v2.14.1. Then, we computed the Deviance Information Criteria (DIC) of each model, as the model with lower DIC is considered as the best-fitting model for the observed data (Spiegelhalter *et al.*, 2002). DIC is computed as $DIC = p_D$ $+$, where p_D represents the effective number of parameters of the model, defined as $- D(\bar{\theta})$. $D(\bar{\theta})$ is the deviance parameter calculated as -2 log (p (y| θ)), where p (y| θ) represents the likelihood function, substituted here with the probability of the data (y) given the posterior mean of the parameter values (θ). is the expectation of the likelihood associated with the means of posterior parameters distributions ($= E^{\theta}$ [D ($\bar{\theta}$)]). To obtain , we performed again all analyses using the posterior mean of each parameter as punctual priors. A difference of five points in DIC was considered as significant (Spiegelhalter *et al.*, 2002; Bolker, 2008).

Results.

Contrasted demographic histories for sedentary and nomadic populations, and the Central-Asian exception.

For Africa, we showed signals of demographic expansions for sedentary farmer populations, while we found no such signal in any nomadic hunter-gatherer populations. Indeed, the "Expansion model" had the lowest DIC value (*i.e.* best fitted the data) for all sedentary farmer populations. Conversely, the constant model best-fitted the data for all nomadic hunter-gatherer populations (**Table 1**). Note that the differences in DIC values between the best-fitting model and the others were higher than five points for all populations except one farmer population (Ewondo). For this population, the Expansion and the constant model could not, therefore, be distinguished (**Table S2**).

For Eurasia, among the eight populations from the HGDP-CEPH panel, we showed a significant signal of demographic expansion for sedentary farmers, while we found no such signal for nomadic herders. Indeed, the expansion model best fitted the data for farmer populations, while it was the constant model for herder populations (**tables 1, S2**). Conversely, when focusing on Central-Asian populations, we found that the Expansion model best fitted the data for both farmer and herder populations (**tables 1, S3**). The modes and 95% HPD of all inferred parameters are presented in **table S3** for each population separately.

Inferred expansions may have started during or after the Neolithic transition.

For sedentary farmer populations from Africa, we inferred expansion signals starting between 3 036 and 6 939 [1 217 – 23,054] YBP, concomitantly with the Neolithic transition in this area, about 5 000 YPB (**Table 2, S3**). For all Eurasians farmers, as well as for Central-Asian nomadic herder populations, we estimated estimation onset times from 5 111 [2 669 – 30 851] YBP for Palestinians to 2 864 [2 669 – 30 851] YBP for Han Chinese (**Table 2, S3**). The modal estimates of the expansion onsets were after the Neolithic transition in all cases but the 95% HPD included the upper Paleolithic period (**Table 2**).

Discussion

In this study, we clearly showed demographic expansions for all sedentary farmer populations from both Africa and Eurasia, while we inferred constant population sizes for all nomadic hunter-gatherer populations in Africa and most nomadic herder populations in Eurasia. As an exception, the nomadic herders from Central-Asia showed an expansion signal similar to that of the farmer populations of this area. For both African and Eurasian populations, the modal estimate of expansion times were consistent with a beginning for these expansions during or after the Neolithic expansion, while the 95% HPD showed that the data were also consistent with late Paleolithic expansions (up to ~30 000 years ago). It is important to note that the method used in this study makes the assumption that populations are isolated and panmictic, which is questionable for human populations. Nevertheless, we analyzed a large set of populations sampled in very distant geographical regions (*i.e.* Central-Africa, Middle-East, Central-Asia, Pamir, Russia and East-Asia). The main conclusions of this study rely on consistent patterns between most of these areas, and it seems unlikely that processes such as admixture could have biased the estimates similarly everywhere.

Since we used many independent nuclear loci, we can also be confident to have avoided any confounding effect of selection.

*Contrasted demographic histories for sedentary and nomadic populations***.**

For Africa, our findings are consistent with previous population genetic studies, who found demographic expansion events in farmers but not in hunter-gatherers using autosomal DNA sequences (Patin *et al*., 2009; Laval et *al.,* 2010) or complete mitochondrial DNA sequences (Batini *et al*., 2011). These results are also consistent with our previous work, which showed with HVS-1 data strong signals of expansion in both African and Eurasian sedentary farmer populations, weaker expansion events in Eurasian herders and no expansion in African hunter-gatherers (C. Aimé, G. Laval, E. Patin, P. Verdu, L. Ségurel, R. Chaix, L. Quintana-Murci, E. Heyer, F. Austerlitz; unpublished). Up to our knowledge, no other studies have demonstrated different demographic patterns between farmers and herders, the two major post-Neolithic human groups.

Despite their variability in life-style and environments, we inferred similar patterns of expansion for all studied sedentary farmer populations for both Africa and Eurasia. Moreover, except for Central-Asia, we found constant population size for both nomadic hunter-gatherers and nomadic herders. These findings are consistent with paleo-anthropological and archeological records, which suggest that human population growth occurring after the Neolithic transition resulted from the processes of sedentarisation in farmer populations (Bar-Yosef and Belfer-Cohen, 1991; Bocquet-Appel and Bar-Yosef, 2008). Conversely, both herders and hunter-gatherers may have remained at constant size due to constraints of a nomadic way of life. For instance, birth intervals are generally longer (at least four years) in nomadic populations than in sedentary populations (*e.g.* Short, 1982). In addition, competition between farmers and nomadic populations for land may have led to a reduction and fragmentation of available habitat and ressources for nomads, thus also limiting their possibilities of expansion (Diamond, 2002).

It is interesting to note that we detected expansion signals for both sedentary farmers and nomadic herders in Central Asia. This could be linked with the arid continental climate in this area, which have strongly impacted the cultural development and limited the spread of farmer civilizations up to 3 000 YBP (Dirksen and Van Geel, 2004), resulting probably in less competition for land between farmers and herders, allowing herders population size to increase in this favorable area for herding. Alternatively, as suggested by Renfrew (1996) from linguistic data, current Central-Asian herders may descent from sedentary agropastoralist populations (Jeitun culture). In this case, these populations may have experienced two successive transitions, the first occurring from hunter-gathering to agropastoralism and having potentially led to demographic expansions, and the second occurring from agropastoralism to nomadic herding.

Autosomal microsatellites allow inferring more recent expansions as compared to other markers.

Using autosomal microsatellite data, our estimated expansions onset times were more recent than those of previous genetic studies. Indeed, although confidence intervals were quite large, the modal estimates of the expansion onsets in this study were during or after the Neolithic transition for all farmer populations for Africa and Eurasia, as well as herder populations from Central Asia. Conversely, most of the previous studies focusing on the past demographic history of African and Eurasian populations have inferred upper or middle Paleolithic expansions. This finding appears to be robust to the uncertainty of generation time in humans. Indeed, using a generation time of 29 years (Tremblay and Vezina, 2000) instead of 25 years (*e.g.* Chaix *et al.*, 2008; Patin *et al.,* 2009; Laval *et al.,* 2010) lead to estimations that are 1.2 times more ancient, thus still after the Neolithic transition (data not shown).

For Africa, using mitochondrial or autosomal sequences data, many authors have inferred expansion times ranging from 80 000 to 25 000 YBP (*e.g.* Harpending *et al.* 1993; Watson *et al.*, 1997; Voight *et al.*, 2005; Laval *et al.,* 2010; Batini *et al.*, 2011). Using Y-chromosome microsatellites, Pritchard *et al.* (1999) estimated more recent but still Paleolithic expansion times, between 15 000 and 12 000 YBP. Finally, analyzing separately different mitochondrial haplogroups, Atkinson *et al.* (2009) found several successive paleolithic expansion waves, occurring at different times depending upon the population, respectively between 213 000 YBP and 156 000 YBP; 86,000 YBP and 61 000 YBP; 20 000 and 12 000 YBP; and 12 000 and 8 000 YBP. However, up to our knowledge, no previous genetic study has inferred Neolithic expansions in Africa. For Eurasia, Chaix *et al.* (2008) showed estimations of expansion times ranging from 63 000 and 17 000 YBP using HVS-I data, and between 40 000 and 11 000 YBP using Y-chromosome microsatellites (see also Pritchard *et al.*, 1999). Accordingly, Harpending *et al.* (1993) inferred an expansion event starting around 40 000 YBP in Europe using HVS-I data. Finally, one study (Fu *et al.,* 2012) showed expansion events in early Europeans farmers, starting at least 12 000 YBP according to their unbiased sample of complete mitochondrial DNA sequences. Altogether, these results suggest that different type of markers can be informative at different time-scale. Autosomal microsatellites appear thus as a very useful tool to infer recent demographic events.

Moreover, a previous study on Paleolithic expansions in Eurasia showed an East-to-West gradient of expansions onset (Chaix *et al.,* 2008). Conversely, in this study, we found a more recent expansion event in East-Asia than in the rest of Eurasia. It suggests that we may have detected another set of expansion events, resulting potentially from the Neolithic transition. These events do not appear thus to have followed the same East-to-West process as the Paleolithic expansions. Similarly, while our previous on HV1 sequences (C. Aimé, G. Laval, E. Patin, P. Verdu, L. Ségurel, R. Chaix, L. Quintana-Murci, E. Heyer, F. Austerlitz; unpublished) show evidences of moderate expansion for most herder populations in Eurasia since the Paleolithic (much weaker than the farmer population expansions), we found no expansion signal for the herder populations here, except in Central Asia. This difference between the inferences from these two kinds of markers may stem form a lower power of microsatellite markers to detect expansions. They may also reflect the fact that these herder populations underwent a Paleolithic expansion, but no or limited expansion in the Neolithic, maybe as a result of the competition with farmers (see above).

The fact that microsatellites may allow detecting more recent events than other type of markers with coalescent-based methods have been already showed in simulation-based analyses (*e.g.* Cornuet *et al.*, 2010) and empirical data analyses on non-human organisms (Hu et al, 2011; Fontaine *et al.,* 2012). This specificity of microsatellites could be linked with several peculiar properties of microsatellite markers, in particular their high mutation rate. However, although Y-chromosome microsatellite-based studies (*e.g.* Pritchard *et al.,* 1999; Chaix *et al.*, 2008) generally inferred more recent events than those using nuclear or HVS-I sequence data, all of these studies point toward Paleolithic expansion events, more ancient than those that we found here with autosomal microsatellites. High levels of mutation rates can therefore not be the only explanation of the higher sensibility to recent events that we observed for autosomal microsatellites. We suggest that this pattern could result from the combination of a high mutation rate and the possibility to analyze several loci as independent replicates of the coalescent process, which is offered by free recombining autosomal microsatellites, but not Y-chromosome microsatellites, which are transmitted as a single block. Indeed, mutations can accumulate on the different Y chromosome haplotypes, and even if homoplasy may reduce punctually the differences between haplotypes, these differences are expected to increase with time over long periods. Conversely the autosomal microsatellites evolve independently and therefore this process of accumulation cannot occur, the high mutation rate allowing the detection of recent events, the signal of more ancient events being erased by homoplasy. Altogether, the high mutability and the independence between loci may thus yield that autosomal microsatellites are more prone to detect recent demographic events.

Conclusion and further work

Using microsatellite autosomal data for a large set of populations from several distant geographic areas, we showed contrasted demographic histories correlating with life-style. Benefiting from the high mutation rate of microsatellites and the simultaneous analysis of several independent loci, we detected also more recent expansion events than in previous studies. These expansions may result from the sedentarization of farmer populations during the Neolithic transition. Finally, comparing our results with previous studies, we have showed that different types of markers can be informative at different time scale. It will be therefore interesting to extend those analyses to other types of genetic markers such as SNP data. Simulation studies may also help to better understand the specific responses of each type of genetic markers to past demographical events.

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Conflict of interest.

The authors declare no conflict of interest.

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