# Demographic conditions necessary to colonize new spaces: the case for early human dispersal in the Americas

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#### Abstract

During the last decade or so, several authors have discussed human dispersal using mathematical simulations in the Americas (Anderson and Gillam 2000; Aoki 1993; Steele 2002; Steele et al. 1995, 1998; Surovell 2000, 2003), as well as other parts of the world (Gkiasta et al. 2003; Hughes et al. 2007; Mithen and Reed 2002; Pope and Terrell 2008; Ray 2003; Young 2002; Young and Bettinger 1992, 1995). In this journal, Steele et al. (1998) presented a demographic model based on the notion of dispersal affected by environmental variability through time and space. We modified the mathematical formula to make the process stochastic. This allows the exploration of different demographic conditions under which humans could successfully colonize the Americas. The simulations demonstrate two human dispersal scenarios: 1) a single dispersal process with two major tempos or 2) two different dispersal processes, one from Beringia to the Isthmus of Panama and the other for South America.

#### Keywords

Human dispersal; demographic modeling; Early Paleoindian; computer simulation.

### The basics of Steele et al.'s simulation model and our modifications

Steele et al.'s (1998) simulation model is one of the first to discuss the entry of humans into the Americas from a global perspective. They looked for demographic conditions where humans could colonize high-latitude environments during the Late Pleistocene and how such conditions could have contributed to the arrival of humans in Beringia. If it was a fast dispersal process, this implied high rates of population growth, the appearance of cultural and technological innovations and 'a rapid increase of artifact



densities across the whole colonized surface of the Americas' in a very short time span (Steele et al. 1998: 287).

In order to explore these alternatives, Steele et al. (1998) used Fisher's (1937) classic formula. Fisher's equation is one of the most commonly used in population dynamics (Kolmogorov et al. 1937), referred to as the F-KPP equation from here on, and is given as:

$$\frac{dn}{dt} = f(n, K) + D\nabla^2 n \tag{1}$$

where n(r, t) corresponds to the local population density, in this case, humans per unit area, at time t and position r = (x, y). The diffusion parameter D is a constant, whereas the environmental carrying capacity K, which deals with the potential of an environment to support a human population on a sustained basis (Dewar 1984), is a function of position. Finally, f(n,K) describes the rate of dependent population increase and is usually represented in ecology by the logistic function (for more details, see Lanata et al. 2007, 2008; Steele et al. 1995, 1998).

In order to consider environmental variability, Steele et al. (1998) used paleovegetation reconstructions of North America for 13,000, 12,000, 11,000 and 10,000 rcy BP. These reconstructions recognized eight major ecosystems (Steele et al. 1998: 290–4). They also utilized Kelly's (1995) data regarding hunter-gatherer population density in each ecosystem. The Steele et al. (1998) simulations resembled a 'standard demic expansion derived from animal ecology' (1998: 302; see also Hamilton and Buchanan 2007). Similarities between Steele et al.'s simulations and Faught et al.'s (1994) fluted projectile point distribution data in the United States were noted, and they contend that they can be explained as a late glacial colonization with annual population growth rates of 3 per cent and an uneven hunter-gatherer spatial distribution related to environmental properties.

The results obtained by Steele et al. (1998) show a dispersion that evolves as a radial wave front, analogous to the dispersion in an isotropic medium. However, diffusion depends on the characteristics not only of the habitat where the individuals are, but also of the neighboring places toward which they intend to move. Within this framework, we modified the F-KPP equation by adding anisotropic behaviour, as seen in (2) below (Lanata et al. 2007, 2008; Martino et al. 2007), and which implies that the diffusion coefficient is no longer constant but dependent on position. Thus, the resulting equation is:

$$\frac{dn}{dt} = \alpha \ n \left( 1 - \frac{n}{K} \right) + \nabla \cdot \left( D \ \nabla n \right) \tag{2}$$

The first term,  $\alpha n \left(1 - \frac{n}{K}\right)$ , defines population growth where  $\alpha$  is the population's intrinsic maximum growth rate, and K(x,y) is the environment's carrying capacity limit (number of individuals the environment supports per surface unit). The second term,  $\nabla \cdot (D\nabla_n)$ , is linked to the population's diffusion, D(x,y) or diffusion rate. One of the advantages of this formalism is that it allowed us to introduce environmental corridors (EC), which could not be considered using the isotropic equation. The F-KPP equation is basically deterministic because it models the variation of densities at the population level. One of its disadvantages is that it does not allow the analysis of a variety of processes at the

individual level, e.g. birth, reproduction and death, that affect population density within a given space or ecosystem. For that reason, the deterministic models produce macro-level and/or general solutions. Another important point about these deterministic models is that an individual's average life expectancy and reproductive rate are calculated supposing that the variation in population density is representative of the average values that a population reaches. To observe the individual's behaviour in a given population, it is necessary to modify the F-KPP equation so that behavioural variation in time and space by each individual in a population is independent and/or random.

To model a more random population's expansion, we modified the F-KPP equation. Space was divided into a grid composed of  $L \times M$  square cells of length h. These cells are identified with the index (l, m) with 1 < l < L and l < m < M. We assume that in each cell, the population consists of an individual,  $N_{(l,mj)}$ . Each individual can migrate towards any one of its eight neighbouring cells with the probability of transition defined by Martino et al. (2007). With this modification, each individual has the freedom to move to any surrounding space, not necessarily to one that is empty, as happens normally in the case of the F-KPP equation (2). In this way, instead of producing a population expansion in the form of a 'wave of advance', like the deterministic solution, a multidirectional expansion is produced and no empty space is privileged.

Another change we introduced is related to the demographic factors that generate the population density. We included the birth-growth-death process of each individual. It is dependent on three stochastic variables assigned to each individual. At birth, a random number is obtained from a Gaussian distribution with an average value of  $25\pm 5$  years, with a range of 0 to 50 years. This number defines the average life expectancy of the individual; when it is reached, the individual dies. A second variable defines whether the individual is a male or a female with reproductive probabilities of  $p_{rep}$  and  $p_{norep}$ . In the case of females, a third variable is included that indicates an active reproductive life or not. In general, for mammals these probabilities are assigned as 0.9 for females with the possibility of reproducing and 0.1 for sterile females. Therefore, following Steele et al. (1998), the population density has a limit of K. However, we also consider 1) the individual's gender and age, 2) a female's active reproductive period between 12 and 30 years of age and 3) a female's reproductive probability, with a two-year minimum interval between pregnancies, according to a Monte Carlo method.

We used Adams's (1998) paleovegetation maps between 18,000 and 9,000 rcy BP, with intervals of 1,000 years. These paleovegetation reconstructions include seventeen different ecosystems, and, unlike Steele et al. (1998), include all the Americas, not just North America. These maps were digitized and each map pixel is equivalent to 125.5km<sup>2</sup>. The decision to begin the simulations using the paleovegetation maps from 18,000 rcy BP was twofold: on the one hand, it represented the Last Glacial Maximum (LGM) and, on the other hand, we could model human dispersal starting from Beringia.

In summary, our new equation (Martino et al. 2007) allows the use of different population growth rates ( $\alpha$ ) related to individual variability, while still accounting for environmental carrying capacity (K) and the diffusion constant (D). We used the same values of K and D as Steele et al. (1998), and, for new environments incorporated into our simulation that were not originally included in theirs, we used modern analogues that were ranked. We also introduced a variant to our formula that has to do with the use of

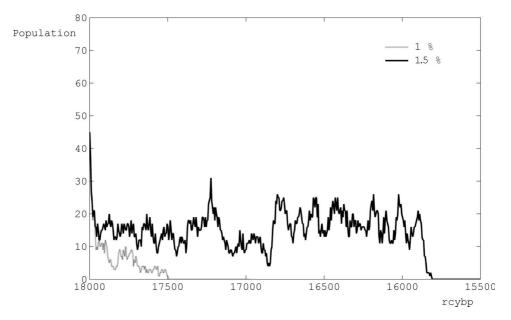
environmental corridors (EC). Elsewhere, we have proposed (Lanata and Garcia 2002; Lanata et al. 2007, 2008) that the human dispersal process can take advantage of EC, accelerating dispersal and making it unnecessary for hunter-gatherers to colonize an ecosystem fully before moving to a new one. There is some support for their use around the world (e.g. Field et al. 2007) and their use has advantages for different population-level evolutionary aspects that are recognized in ecological studies. For North America, human expansion using rivers has been proposed by Anderson and Gillam (2000), Sauer (1944) and Steele et al. (1998) among others. The discussion of a possible entry through a Pacific Ocean Coastal Corridor (POCC) has also been proposed (Dixon 1993, 1999; Goebel et al. 2008), as well as the classic route through the Ice Free Corridor (IFC) (Goebel et al. 2008; Steele et al. 1998). In our simulation, we considered that EC accelerate dispersion, so mean values of K and D were used for the spaces that represent EC in the paleovegetation reconstructions.

Similar to Steele et al. (1998), we used Kelly's (1995) ethnographic data to consider the sustainable population density for each ecosystem, and updated it with Binford's data (2001). The values of K and D remain fixed data types in the simulations, whereas population growth ( $\alpha$ ) can be modified in order to explore different dispersal scenarios by varying ( $\alpha$ ) rates. In our simulations, population growth rates ( $\alpha$ ) are expressed as constant average annual values. We are developing new simulations with simultaneous differential population growth values ( $\alpha$ ) for different environments, but here our interest is to compare our results with those of Steele et al. using the criterion of population growth ( $\alpha$ ) 'which was treated as a global constant' (1998: 295).

Steele et al. (1998: 296) began their simulation at the south end of the Laurentide-Cordilleran IFC with an estimated hunter-gatherer population of 100 individuals and at 13,000 rcy BP. Recent DNA studies by Hey (2005) estimate an initial population size of fewer than eighty individuals living in Beringia (but see Kitchen et al. 2008) in order to disperse successfully into the landscape south of the Laurentide-Cordilleran ice sheets. Therefore, our simulations begin with eighty people at 18,000 rcy BP in Alaska, at the north end of the Laurentide-Cordilleran ice sheets. We used rcy BP, rather than calibrated dates, to be consistent with and directly comparable to Steele et al.'s (1998) work and recent efforts by Jonathan Adams (2008, pers. comm.).

#### **Comparing models**

We ran simulations using 1 and 1.5 per cent annual population growth ( $\alpha$ ) starting at 18,000 rcy BP (Fig. 1). Using these rates, considered normal within ethnographic huntergatherer populations (Binford 2001; Kelly 1995), population fluctuated and became extinguished rapidly, not surpassing the geographic barrier of the Laurentide-Cordilleran ice sheets. However, when  $\alpha = 2$  per cent, the complete colonization of the Americas was possible, but required more than 12,000 years to arrive at northern South America (Fig. 2), and more than 20,000 years to reach Tierra del Fuego. Although the POCC showed hunter-gatherer groups inhabiting it, though not visible in Fig. 2 due to the scale, the population remains to the north of the ice sheet about 4,000 to 5,000 years until the moment at which the IFC opens.



*Figure 1* Demographic population growth curves for  $\alpha = 1$  per cent and 1.5 per cent.

Steele et al. assert that an annual population growth rate of 3 per cent 'seems to us to be the most secure and uncontroversial' (1998: 299) to achieve human dispersal in North America successfully. In a new simulation where  $\alpha = 3$  per cent (Fig. 3), hunter-gatherers north of the Laurentide-Cordilleran ice sheet expanded through the POCC earlier, reaching the end of the ice sheet after c. 2,000–2,500 years, even when the IFC was not yet open. With the  $\alpha = 3$  per cent, it took about 8,900 years for humans to arrive at Tierra del Fuego, with some spaces remaining uninhabited; when the  $\alpha = 4$  per cent (Fig. 4), the time span necessary for humans to reach Tierra del Fuego was reduced to about 5,600 years. The temporal range necessary when  $\alpha = 5$  per cent, being 5,100 years (Fig. 5), was not very different from that when  $\alpha = 4$  per cent. We are aware that  $\alpha$  rates of 4 and 5 per cent are extremely high in modern hunter-gatherer populations, but as a heuristic device it is interesting to see how different the time spans are for human dispersal through the Americas with only an  $\alpha$  increase of 1 per cent in each case. With the  $\alpha = 6$  per cent, the simulated humans would have arrived at Tierra del Fuego in about 4,600 years. The accompanying video (available via the online edition of this article) illustrates the differential dynamic of the dispersal when  $\alpha = 3$  and 6% in the simulations.

By changing  $\alpha$ , it is possible to see different dispersal scenarios. First, a threshold for dispersal was reached when the annual population growth was <2 per cent. With this rate, the hunter-gatherers became extinct north of the Laurentide-Cordilleran ice sheet before being able to cross it, even though it was possible to do so through the POCC. As was expected, as  $\alpha$  increases, the time span necessary to cover the distance between Alaska - Beringia and Tierra del Fuego decreases. And in all the cases, there are always empty regions. The small time span difference between higher growth rates (Fig. 6) is also remarkable.

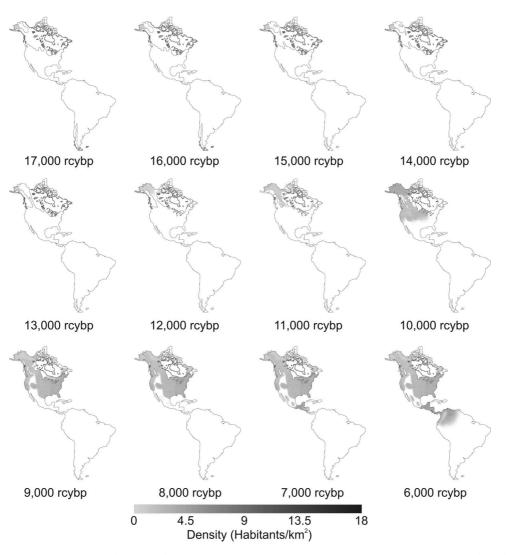
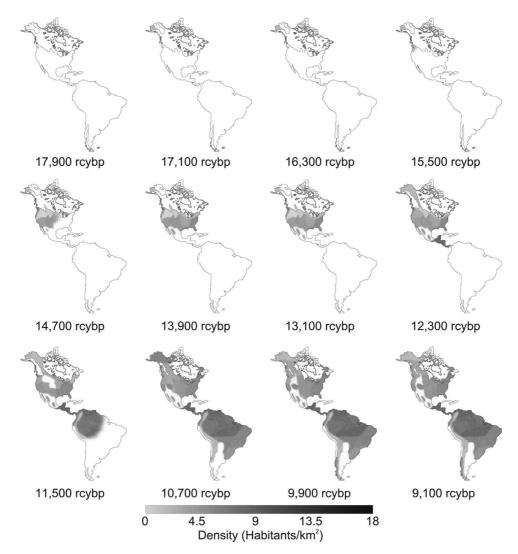


Figure 2 Americas human dispersal simulation with a population annual growth of  $\alpha = 2$  per cent.

These time span differences can be due to the way in which paleoenvironments with greater K are occupied. In our reformulation of the F-KPP equation, it is not necessary that population density reach the maximum allowed by an ecosystem's K for humans to move towards another environment. As mentioned, each individual has the freedom to move to any of the neighboring cells that surround it. In the different simulations (Figs 2 to 5) it can be observed that, as expected, environments with higher K allow populations to continue growing, whereas those with lower K reach their maximum density faster. When we compare the population curves (Fig. 7), Central America and Amazonia, the regions with the highest K value environments, are always those where populations continue growing.



*Figure 3* Americas human dispersal simulation with a population annual growth of  $\alpha = 3$  per cent.

## Some remarks

The different simulations resulted in diverse human dispersal scenarios in the Americas, assuming that populations tended to colonize environments using different tempos and modes. Our simulations seemed to agree with some models, as mentioned above, and to disagree with others. One example where they disagree is in relation to human entry into North America south of the Laurentide-Cordilleran ice sheet. Unlike other models, e.g. Anderson and Gillam (2000), Martin (1973), Mosimann and Martin (1975) and Steele et al. (1998), ours demonstrates a population threshold above which hunter-gatherers living in Beringia could have begun to expand south of the ice sheet successfully, after remaining in Beringia for a period  $\geq$ 4,000 years. If this population had not grown at an

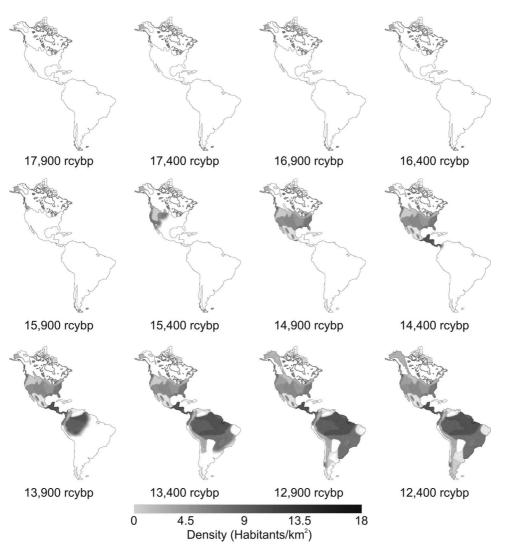
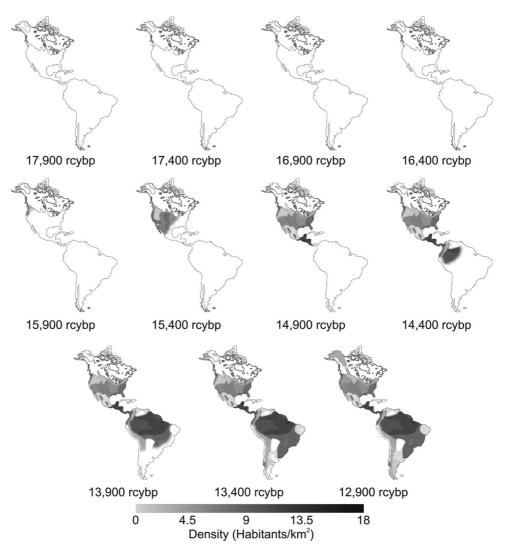
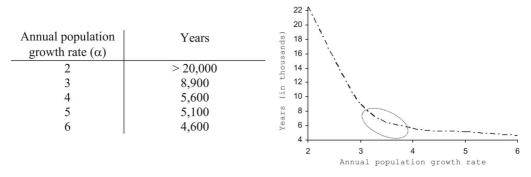


Figure 4 Americas human dispersal simulation with a population annual growth of  $\alpha = 4$  per cent.

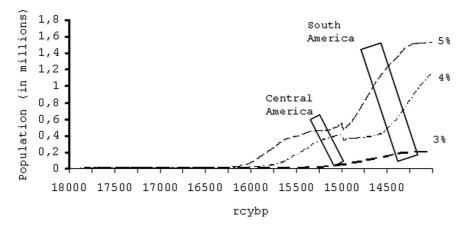
annual rate of at least of 2 per cent, and under the prevailing LGM environmental conditions, these groups would not have survived, regardless of whether the IFC was open. However, if these hunter-gatherers had had a growth rate of 3 per cent, they could have begun to disperse along the POCC. This is significant in that it suggests the minimum demographic conditions under which dispersal into the Americas could have been successful (for an update of Beringian paleoecology, refer to Hoffecker and Elias 2007). DNA studies (Bonatto and Salzano 1997; Hey 2005; Kitchen et al. 2008; Schurr 2004) have suggested some population isolation in Beringia before humans could cross the ice-sheet barrier using the POCC and/or the IFC. In this sense, we propose some minimum demographic conditions for the 'out of Beringia' model (Salzano 2002). It also reaffirms the role of the spatial bottleneck that the Beringia + IFC + POCC +



*Figure 5* Americas human dispersal simulation with a population annual growth of  $\alpha = 5$  per cent.



*Figure 6* Years necessary to cover the distance from Alaska to Tierra del Fuego with different annual population growth rates ( $\alpha$ ); the critical value is somewhere between  $\alpha = 3$  per cent and 4 per cent.



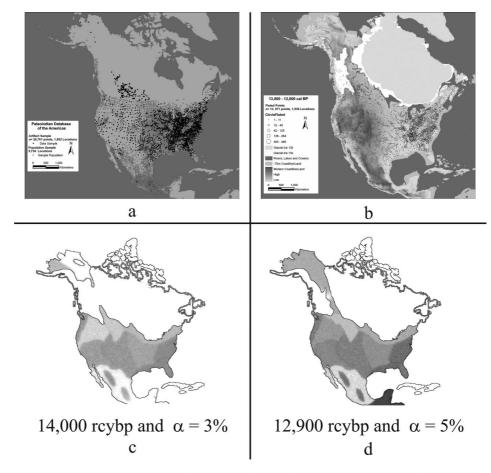
*Figure 7* Demographic population growth curves for  $\alpha = 3$  per cent, 4 per cent and 5 per cent.

Laurentide-Cordilleran ice-sheet systems could have played with regard to the different genetic aspects of the populations that dispersed successfully into the Americas.

Even though our simulations are made with greater paleoenvironmental diversity than Steele et al. (1998) (seventeen ecosystems versus eight), which would suggest faster population fragmentation, human population distributions begin to differentiate when  $\alpha = 3$  per cent, becoming more distinctive with higher  $\alpha$  values. An  $\alpha = 3$  per cent agrees with Steele et al.'s (1998) simulations  $\alpha$  (see also Anderson and Gillam 2000; Surovell 2000).

As was previously noted, Steele et al.'s (1998) simulations resembled Faught et al.'s (1994) distribution of North American Paleoindian fluted projectile points. They also resembled our simulations when  $\alpha \ge 3$  per cent (compare Fig. 8, Anderson and Faught (1998) and Steele et al.'s (1998) figures 11 and 12), but at an earlier point in time (for comments on continental projectile points sample bias, see Shott 2002). Several working hypotheses might explain this time discrepancy: a) Pre-Clovis hunter-gatherers did not select high *K* environments, as seems to be the case with Clovis-like hunter-gatherers (Steele et al. 1998) or b) Pre-Clovis hunter-gatherers were demographically growing annually between 2 and 3 per cent. Another possible hypothesis, proposed by a recent cladistic analysis of North American early paleoindian projectile point assemblages' (Buchanan and Collard 2007: 387). This fast technological expansion could be related to Pre-Clovis hunter-gatherer populations coming through the IFC and/or the POCC, similar to the scenario mentioned by Anderson and Gillam (2000), and consistent with Waters and Stafford's (2007) redefinition of the Clovis time span.

Even when populations in ecosystems with higher K grow demographically, the simulations contain empty spaces. Increased population density in some environments seems to be independent of demographic pressure in occupied spaces. In our simulation, as in Steele et al.'s (1998; see also Hamilton and Buchanan 2007), North American hunter-gatherers selected those spaces with greater carrying capacity (K), such as Central and South America. This could mean that Central America and the Amazon could have been demographically more important than other parts of the Americas because of their paleoenvironmental quality and diversity.



*Figure 8* Distribution comparison of a) PIDBA full projectile points database, b) PIDBA fluted projectile points database, c) expected human population at 14,000 rcy BP with  $\alpha = 3$  per cent, and d) expected human population at 12,900 rcy BP with  $\alpha = 5$  per cent (Figs 8a and 8b from Anderson et al. 2005, available at http://pidba.tennessee.edu/).

In Central America, the region formed by southern Nicaragua, Costa Rica and Panama could have acted as a geographic spatial bottleneck similar in nature to the area north of the Laurentide-Cordilleran ice sheet. This is not to say that the Central American spatial bottleneck could isolate populations, as Beringia probably did. Consequently, this could have created a situation where populations left high *K* environments for low *K* environments with less available space due to a natural threshold being reached in the number of individuals that this region could sustain. However, after crossing this significant reduction of available space, a whole new continent was available to disperse into.

In this case, human dispersal into the Americas was 1) a single process, 2) one process with two different tempos or 3) two different dispersal processes. Although we cannot discuss this in detail here due to space limitations, it is important to consider dispersion into the Americas within the framework of the 'Out of Africa multiple dispersions' model (Lahr and Foley 1994), to understand human dispersal within a general evolutionary framework. In this sense, *Homo sapiens*'s dispersal in the Americas has certain particularities, as also has the Circum-Pacific region (Pope and Terrell 2008).

Eurasian hunter-gatherers expanding to the north east were the foundational populations of Native Americans. During the Late Pleistocene, close to/earlier than the LGM, these hunter-gatherers were colonizing northern Eurasian cold environments (see Steele et al. 1998). They reached Beringia, c. 50° to 70°N, and at the end of the Pleistocene had the chance to disperse into the Americas. After colonizing Beringia's cold environment (Hoffecker and Elias 2007), these hunter-gatherers continued dispersing into new spaces, where the conditions were warmer after the LGM and more space was available. Instead of exploiting lower and patchy K ecoregions, higher K environments being accessible, they may have dispersed into southern, lower latitudes, producing a rapid demic dispersal (*sensu* Hamilton and Buchanan 2007).

However, at 30°N, the available geographic space started to reduce in width and, after crossing today's Sonoran Desert, the first highest K environments were available to hunter-gatherers, producing a demographic increase – a population hot-spot. The reduction in geographic space continues to c. 9°N, where the Isthmus of Panama is no wider than 200km (Karner et al. 2002), and then begins to increase once again along the Andes in north-west South America. Here human populations would have encountered a new continent and had access to different EC: the Pacific and Atlantic Oceans, two corridors along the Andes piedmont and the corridors that separate the semi-desert, desert and savannah ecosystems between the Andes somewhere near the Equator, the Amazon, probably the biggest, high K paleoregion in the Americas, was reached. As our simulations show, populations could have undergone a very large demographic increase, producing a second population hot-spot.

The Andes were patchier than the Amazon, with lower K environments but with the longest, thinnest, north-south oriented EC. These EC could have supported faster human dispersal. The South American Southern Cone shows lower demographic growth in our simulations as a consequence of its semi-desert and desert environments, but with a few spots of higher human density, probably located in coastal and riverine microenvironments. Curiously, Monte Verde (Dillehay 1989) could have been located in one of them. (see Figs 3 to 5 and 8).

In conclusion, the dynamic of human dispersal in the Americas is a complex process and could be characterized as in Figures 9 and 10. In light of this scheme it might be better to

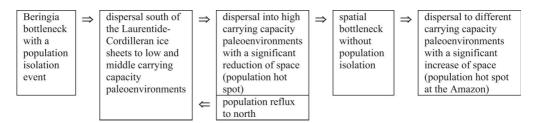
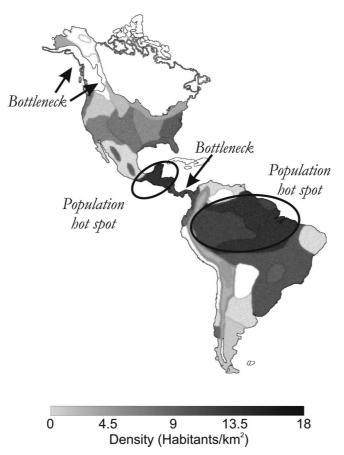


Figure 9 Scheme of the dynamic of human dispersal in the Americas.



*Figure 10* Spatial scheme of the dynamic of the human dispersal in the Americas, showing population distribution at *c*. 13,000 rcy BP, in a simulation with  $\alpha = 5$  per cent, as an example.

consider human dispersal in the Americas as probably being due to two of the three processes mentioned above: 1) a single dispersal process with two major tempos or 2) two different dispersal processes, one from Beringia to the Isthmus of Panama and the other from there to Tierra del Fuego.

### Conclusion

We have evaluated whether Steele et al.'s (1998) assumptions and general formula were still valid for the Americas, and provided a continental-scale dispersal model, beginning at the LGM, independent of genetic, technological and archaeological data, and assuming that all environments could be colonized during the dispersal (note the differences between our simulations independent of the archaeological database and Anderson and Gillam's (2000) four colonization and movement models as an example).

Beyond this, we see similarities between our results and the results of other models. The most significant similarity is that most of the models (Alroy 2001; Anderson and Gillam

2000; Buchanan and Collard 2007; Fix 2002; Hamilton and Buchanan 2007; Kelly and Todd 1988; Martin 1973; Mosimann and Martin 1975; Sauer 1944; Steele et al. 1998; Surovell 2000, 2003) show that human dispersal in the Americas must have had a high population growth rate (however, see Beaton 1991; Hassan 1981; Haynes 1966; Withley and Dorn 1993). As Steele et al. indicated, 'confusion has arisen when it has implicitly been assumed that growth rates are density-independent, and that observed ethnographic dates must therefore represent realistic maxima for past colonizing populations' (1998: 299). We agree with Steele et al. (1998) when they state that ethnographic hunter-gatherer population growth rates reflect today's cultural and environmental conditions.

Our simulations present only scenarios where full human dispersal in the Americas was viable. Even though this seems to be consistent with a one entrance-into-the-Americas model, we do not deny the possibility of more than one entry. According to our simulations, a more-than-one-early-entry into the Americas scenario could be plausible if Late Pleistocene hunter-gatherer populations that would have crossed the Laurentide-Cordilleran ice sheet – first through POCC and later using the IFC – were growing annually at an  $\alpha \leq 2$  per cent rate, but not fully colonizing new spaces and environments. They could have also only or simultaneously been using EC (we are developing simulations where only EC are used during early dispersal; preliminary results show that, depending on which EC is selected, between 2,000 and 2,500 years are necessary to cover the 14,000km from Alaska to Tierra del Fuego) and mobility strategies like those proposed by Anderson and Gillam (2000) and Kelly and Todd (1988). Even though the general tendency of dispersal is toward the south, and humans could reach Tierra del Fuego over the long term, these scattered local populations could become extinct at any moment, notwithstanding previously inhabited spaces. Archaeological evidence of a dispersal process with low equilibrium fitness, where scattered humans were expanding through the continent(s) with local populations becoming extinct and not reaching the minimum viable population density necessary to produce a completely-filled-environment human dispersal, could be useful for Pre-Clovis supporters. As demonstrated for the Old World, small, isolated hunter-gatherer groups generate different cultural innovations, but 'levels of mean population fitness and attractiveness for imitation would have remained low' (Shennan 2001: 13). In this scenario, a great diversity of cultural innovations throughout the Americas is possible, and this could explain the diversity of Pre-Clovis lithic assemblages and the prevalence of a vertical cultural transmission process. As population would have increased, cultural innovations could have spread faster, generating a more homogeneous distribution of traits. This could be the case with Clovis-Folsom technology (see Fig. 8; Buchanan and Collard 2007; Goebel et al. 2008; Steele et al. 1998). And, if Clovis-Folsom hunter-gatherer densities were as high as our simulations' annual rate of 3 per cent or higher, horizontal cultural transmission processes could explain the rapid expansion of Clovis-Folsom technology (see Buchanan and Collard 2007 and a different application in Jordan and Shennan 2003).

Early human dispersal in the Americas seems to have been a relatively rapid process, perhaps with the characteristics of a species invasion (*sensu* Colautti and MacIsaac 2004; Martin 1973), rather than the slower peopling that is normally assumed. We think it could also have been faster than the first dispersals of *Homo sapiens* out of Africa. According to the simulations, it is possible to hypothesize a relatively high average population growth

during the Late Pleistocene. A minimum viable population that could have effectively dispersed and colonized the Americas would have been possible only with an average population growth rate of more than 2 per cent. This is especially important in Beringia, where a lower rate could have driven the hunter-gatherer population to extinction. An opposite scenario could be to think of a pre-LGM slow human dispersal with a lower population growth rate. In this case,  $\alpha = 2$  per cent seems to be required for long-term colonization of the Americas, but it would take tens of thousands of years to reach Tierra del Fuego. Our modelling suggests different tempos and modes for dispersal in the Americas; and, if we focus on their uniqueness and distinctiveness, these American simulations could contribute to a more comprehensive understanding of the global-scale human dispersal process. As scientists interested in global *Homo sapiens*'s dispersal, our challenge is to produce models that can orient research on human dispersal in the Americas towards a new cooperative theoretical and methodological framework.

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#### References

Adams, J. 1998. Global Land Environments since the Last Interglacial: Last Glacial Maximum (18,000<sup>14</sup>C Years Ago). Available at: http://www.esd.ornl.gov/projects/qen/nerc.html.

Alroy, J. 2001. A multispecies overkill simulation of the End-Pleistocene megafaunal mass extinction. *Science*, 292: 1893-6.

Anderson, D. and Faught, M. 1998. The distribution of fluted Paleoindian projectile points: Uptade 1998. *Archaeology of Eastern North America*, 26: 163–87.

Anderson, D. and Gillam, J. 2000. Paleoindian colonization of the Americas: implications from an examination of physiography, demography, and artifact distribution. *American Antiquity*, 65: 43–66.

Anderson, D., Yerka, S. and Faught, M. 2005. Paleoindian database of the Americas: 2005 status report. *Current Research in the Pleistocene*, 22: 91–2.

Aoki, K. 1993. Modelling the dispersal of the first Americans through an inhospitable ice-free corridor. *Anthropological Science*, 101: 79–89.

Beaton, J. 1991. Colonizing continents: some problems from Australia and the Americas. In *The First Americans: Search and Research* (eds T. Dillehay and D. Meltzer). Boca Raton, FL: CRC Press, pp. 209–30.

Binford, L. 2001. Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Sets. Berkeley, CA: University of California Press.

Bonatto, S. and Salzano, F. 1997. A single and early migration for the peopling of the Americas supported by mitochondrial DNA sequence data. *Proceedings of the National Academy of Science*, 94: 1866–71.

Buchanan, B. and Collard, M. 2007. Investigating the peopling of North America through cladistic analyses of Early Paleoindian projectile points. *Journal of Anthropological Archaeology*, 26: 366–93.

Colautti, R. and MacIsaac, H. 2004. A neutral terminology to define 'invasive' species. *Diversity and Distributions*, 10: 135–41.

Dewar, R. 1984. Environmental productivity, population regulation and carrying capacity. *American Anthropologist*, 86: 1565–76.

Dillehay, T. 1989. Monte Verde, a Late Pleistocene Settlement in Chile, Vol. 1, Palaeoenvironment and Site Context. Washington, DC: Smithsonian Institution Press.

Dixon, E. 1993. *Quest for the Origins of the First Americans*. Albuquerque, NM: University of New Mexico.

Dixon, E. 1999. Bones, Boats, and Bison: Archeology and the First Colonization of Western North America. Salt Lake City, UT: University of Utah Press.

Faught, M., Anderson, D. and Gisiger, A. 1994. North American Paleoindian database: an update. *Current Research in the Pleistocene*, 11: 32–5.

Field, J., Petraglia, M. and Lahr, M. 2007. The southern dispersal hypothesis and the South Asian archaeological record: examination of dispersal routes through GIS analysis. *Journal of Anthropological Archaeology*, 26: 88–108.

Fisher, R. 1937. The wave of advantageous genes. Annals of Eugenics, 7: 355-69.

Fix, A. 2002. Colonization models and initial genetic diversity in the Americas. *Human Biology*, 74: 1–10.

Gkiasta, M., Russell, T., Shennan, S. and Steele, J. 2003. The Neolithic transition in Europe: the radiocarbon record revisited. *Antiquity*, 77: 45–62.

Goebel, T., Waters, M. and O'Rourke, D. 2008. The Late Pleistocene dispersal of modern humans in the Americas. *Science*, 319: 1497–502.

Hamilton, M. and Buchanan, B. 2007. Spatial gradients in Clovis-age radiocarbon dates across North America suggest rapid colonization from the north. *Proceedings of the National Academy of Science*, 104: 15625–30.

Hassan, F. 1981. Demographic Archaeology. New York: Academic Press.

Haynes Jr., C. 1966. Elephant-hunting in North America. Scientific American, 214: 104-12.

Hey, J. 2005. On the number of New World founders: a population genetic portrait of the peopling of the Americas. *PLoS Biology*, 3(6): e193.

Hoffecker, J. and Elias, S. 2007. *Human Ecology of Beringia*. New York: Columbia University Press.

Hughes, J., Haywood, A., Mithen, S., Sellwood, B. and Valdes, P. 2007. Investigating early hominin dispersal patterns: developing a framework for climate data integration. *Journal of Human Evolution*, 53: 465–74.

Jordan, P. and Shennan, S. 2003. Cultural transmission, language, and basketry traditions amongst the California Indians. *Journal of Anthropological Archaeology*, 22: 42–74.

Karner, D., Levine, J., Medeiros, B. and Muller, R. 2002. Constructing a stacked benthic  $\delta^{18}$ O record. *Paleoceanography*, 17(3): 2–17.

Kelly, R. 1995. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways*. Washington, DC: Smithsonian Institution Press.

Kelly, R. and Todd, L. 1988. Coming into the country: Early Paleoindian hunting and mobility. *American Antiquity*, 53: 231–44.

Kitchen, A., Miyamoto, M. and Mulligan, C. 2008. A three-stage colonization model for the peopling of the Americas. *PLoS ONE*, 3(2): e1596.

Kolmogorov, A., Petrovsky, I. and Piskunov, N. 1937. Étude de l'équation de la diffusion avec croissance de la quantité de matière et son application á un problème biologique. *Bulletin de la Université d'État à Moscou, Série Internationale*, 1(A): 1–25.

Lahr, M. and Foley, R. 1994. Multiple dispersal and modern human origins. *Evolutionary* Anthropology, 3: 48–60.

Lanata, J. and Garcia, A. 2002. Metapopulation and colonization of space. Paper presented at the Human Global Dispersals British Academy International Networks Workshop. Southampton.

Lanata, J., Martino, L. and Osella, A. 2007. Simulando la dispersión humana en Sudamérica. In *Metodologías Científicas Aplicadas al Estudio de los Bienes Culturales* (eds A. Pifferetti and R. Bolmaro). Rosario: UNR, pp. 413–20.

Lanata, J., Martino, L., Osella, A. and Garcia-Herbst, A. 2008. Ambiente y demografía durante la dispersión humana inicial en Sudamérica. In *Ecología Histórica: Interacciones Sociedad-Ambiente a Distintas Escalas Espacio* (eds C. López and G. Ospina). Pereira: Universidad Tecnológica de Pereira, pp. 24–9.

Martin, P. 1973. The discovery of America. Science, 179: 969-74.

Martino, L., Osella, A., Dorso, C. and Lanata, J. 2007. Fisher equation for anisotropic diffusion: simulating South American human dispersals. *Physical Review E*, 76(3): 1–10.

Mithen, S. and Reed, M. 2002. Stepping out: a computer simulation of hominid dispersal from Africa. *Journal of Human Evolution*, 43: 433–62.

Mosimann, J. and Martin, P. 1975. Simulating overkill by Paleoindians. *American Scientist*, 63: 304–13.

PIDBA (Paleoindian DataBase of the Americas). Available at: http://pidba.utk.edu/main.htm (accessed 30 April 2008).

Pope, K. and Terrell, J. 2008. Environmental setting of human migrations in the circum-Pacific region. *Journal of Biogeography*, 35: 1–21.

Ray, N. 2003. Modélisation de la démographie des populations humaines préhistoriques à l'aide de données environnementales et génétiques. Doctoral dissertation, Département d'Anthropologie et d'Écologie. Université de Genéve, de Villars-Burquin.

Salzano, F. 2002. Molecular variability in Amerindians: widespread but uneven information. *Anais da Academia Brasileira de Ciências*, 74(2): 223–63.

Sauer, C. 1944. A geographic sketch of Early Man in America. Geographical Review, 34: 529-73.

Schurr, T. 2004. The peopling of the New World: perspectives from molecular anthropology. *Annual Review of Anthropology*, 33: 551–83.

Shennan, S. 2001. Demography and cultural innovation: a model and its implications for the emergence of modern human culture. *Cambridge Archaeological Journal*, 11: 5–16.

Shott, M. 2002. Sample bias in the distribution and abundance of Midwestern fluted bifaces. *Midcontinental Journal of Archaeology*, 27: 89–123.

Steele, J. 2002. Evolution, ecology, and human adaptability. In *Tendencias en Arqueología Evolutiva* (eds G. Martínez and J. Lanata). Olavarría: UNC, pp. 207–20.

Steele, J., Sluckin, T., Denholm, D. and Gamble, C. 1995. Simulating the hunter-gatherer colonization of the Americas. *Analecta Praehistorica Leidensia*, 28: 223–7.

Steele, J., Adams, J. and Sluckin, T. 1998. Modelling Paleoindian dispersals. *World Archaeology*, 30: 286–305.

Surovell, T. 2000. Early Paleoindian women, children, mobility and fertility. *American Antiquity*, 65: 493–508.

Surovell, T. 2003. Simulating coastal migration in New World colonization. *Current Anthropology*, 44: 580–91.

Waters, M. and Stafford Jr., T. 2007. Redefining the age of Clovis: implications for the peopling of the Americas. *Science*, 315: 1122–26.

Withley, D. and Dorn, R. 1993. New perspectives on the Clovis vs. pre-Clovis controversy. *American Antiquity*, 58: 626–47.

Young, D. 2002. A new space-time computer simulation method for human migration. *American Anthropologist*, 104: 138–58.

Young, D. and Bettinger, R. 1992. The Numic spread. American Antiquity, 57: 85-99.

Young, D. and Bettinger, R. 1995. Simulating the global human expansion in the Late Pleistocene. *Journal of Archaeological Science*, 22: 89–92.

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