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Simulating hunter-gatherer colonization of the Americas

1 Introduction

Simulation modelling of the Palaeoindian expansion into the Americas was pioneered by Paul Martin, who proposed an 'overkill' model in 1967. Taking demographic parameters from a compilation of data by Joseph Birdsell (1957), he calculated that humans reproducing at a rate of about 3.5% per annum, with directional migration southwards at an average rate of 16 kilometres per year, would have reached Tierra del Fuego 1,000 years after entering the land south of the ice sheets. His model had a dense 'front' of pioneers overexploiting the megafauna in their path, and moving on to leave a faunally depauperate environment occupied by humans at merely one tenth of that initial population density (Martin 1973). With James Mosimann, he developed this 'overkill' model in a later paper in 1975, in which it was demonstrated that hunters with unchecked population growth and moderate or heavy kill rates, or alternatively a focus on preferred mammoth and mastodon prey, could push their prey species into extinction throughout North America in a period of 300-500 years (Mosimann/Martin 1975). Calculations of the velocity of expansion of the front were also made in this paper, and reinforced the finding that rapid growth (2.5 to 3.5% per annum) was a necessary condition of very rapid expansion, although a slow growth model was summarized in which pioneers reached the Gulf of Mexico 1,157 years after entry at Edmonton, with an intrinsic growth rate of only 0.65%.

In our own work, we have been concerned to evaluate the effect of spatial habitat variation, and of the distribution of geographical barriers to dispersal, on the rate and routes of expansion of pioneer Palaeoindian populations. Such effects have generally been omitted in previous models, which have used averaged habitat values applied to the whole continental land area; but their importance has nonetheless been noted. Mosimann and Martin (1975: 306) observed that 'while we acknowledge their importance in an ideal model, we do not attempt to [...] incorporate the inevitable local differences in carrying capacity at the time of invasion.' Whittington and Dyke (1984: 462), who developed the Mosimann and Martin model, also observed that 'a better approximation of reality than uniform population densities would be a model that allows for interactions between megafaunal and human populations whose densities were based on the distribution of various resources. Since this would be a radical departure from Mosimann and Martin's simulation, a reformulation of the model was not undertaken.' Finally, Belovsky (1988: 353) also set the parameters for his own simulation of Palaeoindian expansion so that 'rather than tracing the growth of the human population from vegetation type to vegetation type across the two continents, an average primary productivity was used.'

2 The simulation model

In modelling the effects of barriers and habitat variation on the rate of expansion of pioneer human populations, we have departed radically from the simulation paradigms of these workers. We have discretized both time and space for our simulations, using a two-dimensional lattice in which each cell has cell-specific fixed values for the habitat terms, and an updated cell-specific value for the human population size. The update algorithm is a discretized approximation of a continuous differential equation describing the process of demographic expansion. For our initial phase of work, we have been using a discrete approximation of R.A. Fisher's classic equation for the 'wave of advance' of advantageous genes (Fisher 1937), which has already been generalized to the case of animal range expansion and is widely used for this purpose in biogeography. Fisher's model is also the basis for Ammerman and Cavalli-Sforza's work on the expansion of Neolithic colonists in Europe.

The Fisher equation is:

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

where $n(\mathbf{r},t)$ denotes the local human population density (number per unit area) at time t and position $\mathbf{r} = (x,y)$. The diffusion constant D (in $\text{km}^2\ \text{yr}^{-1}$) and the carrying capacity $\mathbf{K}$ are functions of position. The function

$$f(n) = \alpha n\,(1 - \frac{n}{k})$$

describes the rate of population increase, and is the logistic function widely used in theoretical ecology (Murray 1990); the quantity α denotes the annual population growth rate.

We approximate time differentials at particular sites by finite differences (Press *et al.* 1986):

$$\frac{dn(\mathbf{r},t)}{dt} \approx \frac{n(\mathbf{r},t+\Delta_t) - n(\mathbf{r},t)}{\Delta_t} \qquad (2)$$

Typically we use $\Delta_t = 1$ year.

Space differentials are similarly approximated by finite differences:

$$D\nabla^2(\mathbf{r}_0) = h^{-2}\sum_{\alpha} w_\alpha D_\alpha[n(\mathbf{r}_\alpha)-n(\mathbf{r})], \qquad (3)$$

where for a given position $\mathbf{r}_0$ the sum is taken over nearest neighbour sites $\mathbf{r}_\alpha$ on the lattice, and where the lattice size is h. There are two types of neighbour sites: those along the lattice axes and those along the diagonals. The sum is weighted appropriately with parameters w_α; this parameter is typically 2/3 for sites α along the lattice axes and 1/6 along the diagonals. The effective diffusion parameter D_α', appropriate to motion between the sites $\mathbf{r}_0$ and $\mathbf{r}_\alpha$, is given by

$$D_\alpha' = \sqrt{D(\mathbf{r}_\alpha)D(\mathbf{r}_0)}.$$

In practice in any given simulation, only two values of D are used: $D = D_0$ and $D = 0$, the latter representing the fact that the particular cell is inaccessible.

The crucial input parameters for the model are then the carrying capacity K, the so-called Malthusian parameter α and the diffusion constant D. D represents the degree of mobility of an individual (e.g., Ammerman/Cavalli-Sforza 1984). In general individuals will move from their birth place a distance λ during their lifetime τ. The square of this distance will in general be proportional to the time available; the constant of proportionality is the diffusion constant D:

$$D = \frac{\lambda^2}{4\tau} \qquad (4)$$

The differential equation (1) in the case of constant D and K, and for populations which can only move in one rather than two dimensions, predicts that there will be a population wave of advance, with the frontier travelling with velocity (Ablowitz/Zepetella 1979):

$$\nu = 2.04\,\sqrt{D\alpha} \qquad (5)$$

Our discretized model gives accurate results so long as the natural length scale in this equation

$$\xi = \sqrt{\frac{D}{\alpha}} > h$$

Otherwise the simulated velocity is faster than that predicted analytically. For simulations with $h \sim 50$ km with $0.005\ \mathrm{yr}^{-1} < \alpha < .05\ \mathrm{yr}^{-1}$, and with $D > 10\mathrm{km}^2\ \mathrm{yr}^{-1}$, our discretized lattice yields consistently accurate results (fig. 1).

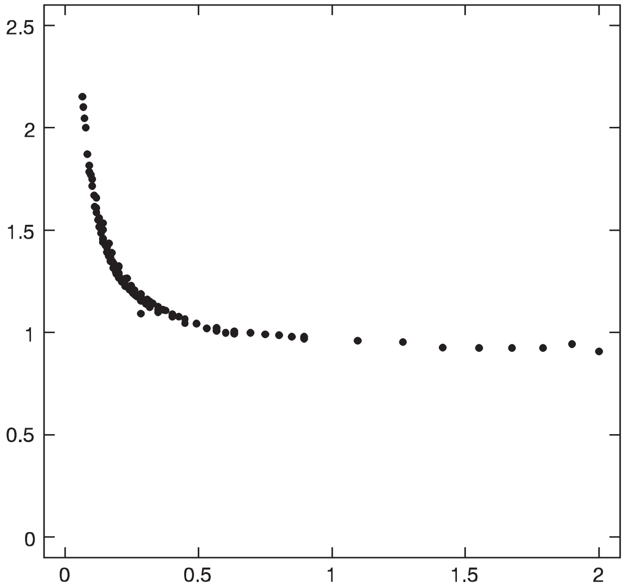

Figure 1. Ratio of simulated to theoretical velocity of expansion of the front, plotted against the 'natural length scale' (the independent variable). The latter is given by dividing $\sqrt{(D/\alpha)}$ by the cell dimension (in these simulations, 50 km).

We note also a methodological point; in principle (even if in practice this will be difficult!) we may have independent estimations of D, α, K and ν. We predict that ν will be independent of K and dependent on D and α according to equatation (5). If these predictions are not borne out — if, for example, the values of D and α required to be consistent with archaeologically sensible values of ν are not themselves plausible — we are bound to use more sophisticated models of population movement, for which the Fisher equation, at least in its naive form, would no longer be helpful.

3 The use of geographic information in the lattice model

For the first set of experiments, we have used a projected representation of the surface of North America and its surrounding oceans, rasterized from an interpolated surface generated in IDRISI from the original vector format point file as a grid of cells coded for their accessibility to a diffusing population. Sea and other impassable areas are '0', colonizable land is '1'. Population can either diffuse into the cell, or not. The projection transformation (Transverse Mercator, meridian 90° W., scale factor = 1) was selected to avoid distortion of area and orientation, and the interpolated vector file was used to generate raster output with a cell size of approximately 50 km by 50 km. To make it easier to understand the real time output to

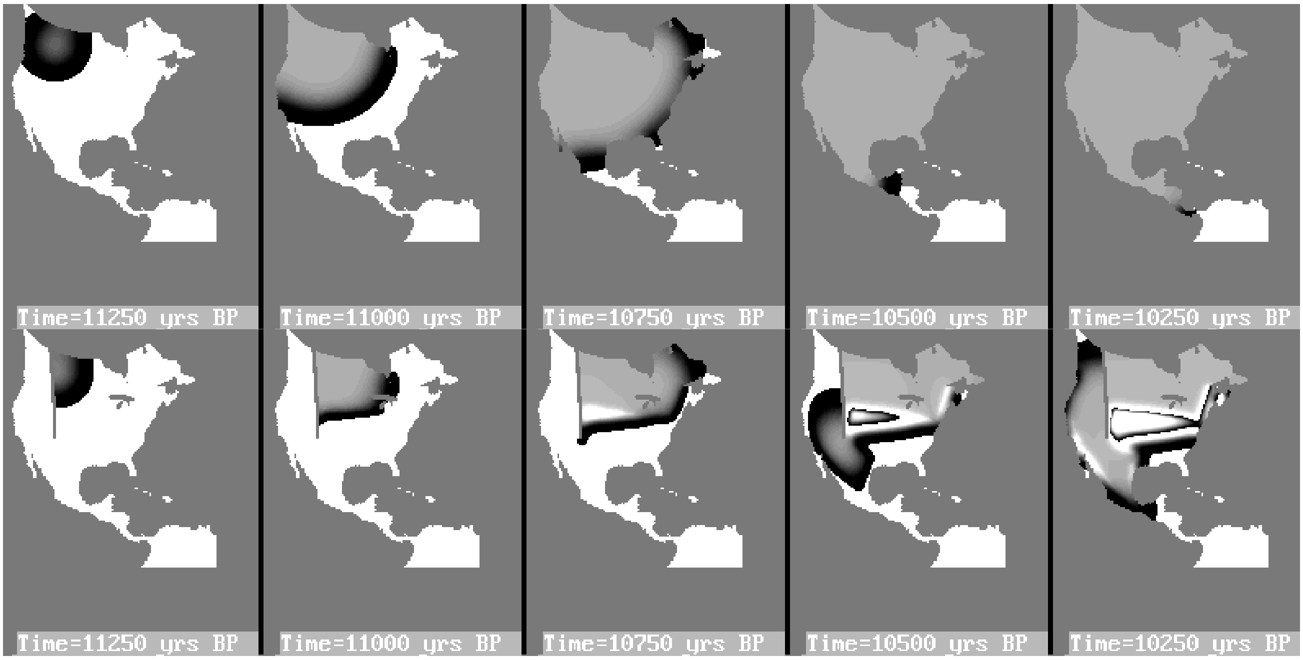

Figure 2. Screen capture shots of the travelling wave at t = 250, 500, 750, 1000 and 1250 years. Seed population at Edmonton. Carrying capacities: 0.04 p.p.km^2 (background), 0.2 p.p.km^2 (coasts and plains). Population growth rate = 0.03 p.a. (background), 0.01 p.a. (coasts and plains). Dispersal rate = 400 km^2 p.a. (background), 100 km^2 (coasts and plains).

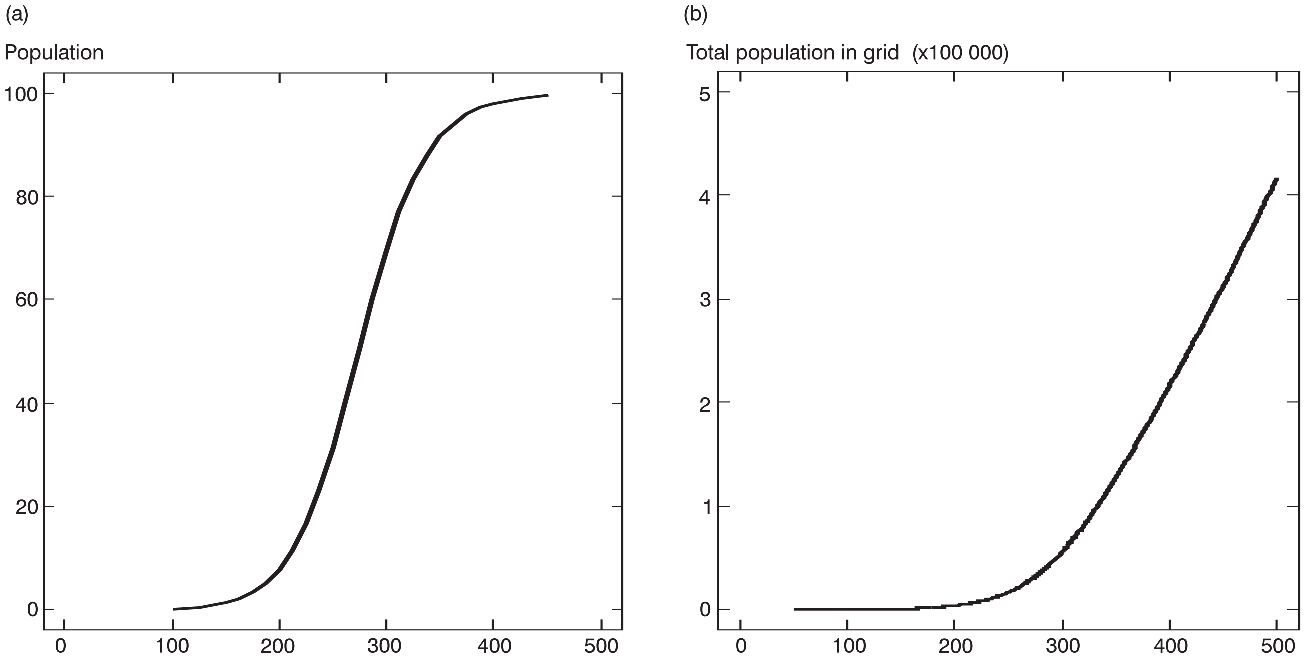

Figure 3. Population growth curves for (a) a sample cell and (b) the whole grid, for a sample set of conditions (α = 0.03, D = 500). K = 100 persons per cell.

screen while the simulation is running, barrier cells are coloured blue — since they are mostly sea — while cells where people can go are coloured green (since they are nearly all areas of land surface with significant primary plant production). Population densities on the colonized portion of the accessible surface are grey-scaled, making it easy to follow the expansion of the front as it is updated and written to screen in real time during the simulation (fig. 2). Figures 3 (a) and (b) show the curves for increasing population in a single cell and in the whole colonizable portion of the grid, against time, for an example set of values for the demographic parameters. It is evident from these that while the population in each of the cells follows a logistic growth curve, the growth curve for the total population is exponential. This is what we would expect from the original model.

The simulations shown in figure 2 also demonstrate the effects of varying the barrier locations and the demographic parameters as cell-specific attributes. The first series represent demographic expansion over a homogeneous plane, while the second series has barriers at the Rockies and the Great Lakes, and two categories of habitat with covariation in the carrying capacity (κ), mobility (D) and growth rate (α) terms. The varying times taken to first colonization of points on the surface if they are located beyond such hypothetical barriers, or in habitats with differing carrying capacities or disease ecologies, will clearly be detectable in archaeological radiocarbon dating of earliest cultural remains at such locations. Thus the simulation model is capable of generating archaeologically testable predictions about the effect on demographic expansion of spatial heterogeneity in barriers and in vegetation zones.

4 Future development of the model and its applications

These initial results are now being extended in a second phase of development of the model, in which ice sheet locations and vegetation mosaics at successive periods in the earliest Holocene of the Americas will be reconstructed by a palaeoecologist and used to predict spatial variation in Palaeoindian carrying capacities, and more extensive sets of simulations will be run to generate alternative predictions about possible effects of such spatial variation on colonization rates and routes.

Young and Bettinger (1995), in a study which independently developed the same demographic diffusion equation to model late Pleistocene human demic expansions, suggest that the high values of α and D needed to generate the observed velocity of Palaeoindian expansion into the New World under the conditions of Fisher's model are nonetheless biologically plausible. They suggest values for α of 0.03 and for D of 1000 $\mathrm{km}^2/\mathrm{yr}$ (which would mean the travelling front would reach Tierra del Fuego in about 1,500 years). We believe that such values for the diffusion constant are, in fact, biologically implausible for almost all hunter-gatherer social systems for which recent ethnographic parallels exist. It is essential to remember that the diffusion term denotes mobility which is random with respect to direction: it is not a term denoting 'directional migration'. The value for D chosen by Young and Bettinger (1995) implies a lifetime mean dispersal distance for all individuals of about 300 km from the place of birth, or of about 600 km for the dispersing sex where diffusion is due to dispersal from the natal group by all members of one dispersing sex. It is difficult to see how such a high level of lifetime mobility, random with respect to direction, could be adaptive in a landscape that was also sustaining such a high net population growth rate. We therefore suspect that the rate of colonization of the Americas was driven by some further dynamic, such as directional migration by 'over-exploiters' up a gradient of herbivore prey densities in a very fragile ecosystem, and we are currently exploring new models which can be implemented in the existing discrete time and space simulation paradigm.

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