

‘Modelling Paleoindian dispersals.’

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Abstract

It is reasonable to expect that the global dispersal of modern humans was influenced by habitat variation in space and time: but many simulation models average such variation into a single. Homogeneous surface across which the dispersal process is modelled. We present a demographic simulation model in which rates of spatial range expansion can be modified by local habitat values. The broad-scale vegetation cover of North America during the late last glacial is reconstructed and mapped at thousand-year intervals. 13.000--10.000 radiocarbon years BP. Results of the simulation of human dispersal into North America during the late last glacial are presented: output appears to match observed variation in occupancy of habitats during this period (as assessed from discard rates of diagnostic artefacts), if we assume that intrinsic population growth rates were fairly high and that local population densities varied as a function of environmental carrying capacity. Finally, a number of issues are raised relating to present limitations and possible future extensions of the simulation model.

Keywords

Demographic modelling: paleoecology: human dispersals: Fisher..Skellam: Paleoindian: Clovis: fluted point.

1. Introduction.

Expansion of the hominid geographical range into high latitudes came late. It may only be within the last twenty thousand years that humans colonized the tundra to the northeast of the Verkhoyansk Range in eastern Siberia (Hoffecker *et al.* 1993). But once this had occurred, there was little other impediment than glacial ice to the spread of humans into eastern Beringia, and thence southward into the rest of the Americas. What is surprising is the apparent rapidity of this subsequent southward expansion. A number of terminal Pleistocene sites in southern South America appear to be contemporary with, or to predate, the best-dated North American Clovis sites (e.g. Steele, Gamble & Sluckin in press). Demographically, such a rapid spread implies a high intrinsic reproductive rate - and this has been seen by some as inconsistent with observed demographics of extant hunter-gatherer populations (Whitley & Dorn 1993). This puzzling situation has led some workers to suggest that humans were already present in South America before the last glacial maximum - despite the lack of clear traces of such a long-lasting population. Thus we are faced with two startlingly different scenarios. In the prevailing scenario, there were one or more late glacial dispersals, characterized by high rates of dispersal and rapid population growth rates. This scenario implies an archaeological signature of a sudden appearance of a cultural record and a rapid increase in artefact densities across the whole colonised surface of the Americas, with a compressed time range for the dates of earliest occupation at different locations on that surface. Alternatively there is another, less widely-favoured scenario which states that there were one or more much earlier (pre-last glacial maximum) colonization events characterized by low rates of dispersal and population growth. This scenario implies gradual increase in the visibility of a cultural record, and a clearer gradient in dates of earliest occupation at progressively greater distances from the origin of the dispersal.

Overall, the archaeological data appear to support the first scenario over its competitor (for judicious reviews of the evidence and arguments, see Meltzer 1993, 1995). In either scenario, taphonomic and sampling effects will make it hard to identify the earliest occupation remains. Nonetheless, in all of the Americas no candidate for a site with occupation predating the last glacial maximum has yet been verified to conventional standards of proof. The earliest sites with securely-dated Paleoindian associations appear quite abruptly during approximately the 12,500-11,000 BP period, with little clear contrast between the dates of the more southerly sites and those nearer the origin of the dispersals in the north. Following the dates of earliest occupation in most regions surveyed, there is generally a rapid increase in recorded artefact densities. However, there are also conflicting data. In North America, the greatest densities of Early and Middle Paleoindian fluted points appear to be in the south and east, although dispersal is assumed to have originated in the northwest (Faught *et al.* 1994). In South America, the earliest securely-dated sites are contemporary with, if not slightly earlier than, the North American Clovis sites, implying not just gaps in the North American radiocarbon record, but also an initial phase of long-distance exploratory dispersal by some proportion of the colonizing populations. On the face of it, neither of these observations seem consistent with existing 'wave of advance' models of rapid late glacial Paleoindian dispersals. In this paper we propose that the answer lies not in rejecting the prevailing scenario of a late glacial Beringian colonization of the Americas, but in making refinements to existing demographic expansion models to make them more realistic.

2. Spatial Range Expansion: the Standard Model.

For our own first phase of simulation 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 (Williamson 1996, Shigesada & Kawasaki 1997; cf. Young & Bettinger 1995).

The Fisher equation is:

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

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 K are functions of position. The function $f(n) = \alpha n(1 - \frac{n}{k})$ describes the rate of density-dependent population increase, and is the logistic function widely used in theoretical ecology (Murray 1990); the quantity α denotes the intrinsic maximum population growth rate.

In order to work with discrete time (in iterated steps) and discrete space (in a lattice of cells), we approximate time differentials at particular sites by finite differences (Press *et al.* 1986):

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

Typically we use $\Delta_t = 1$ year.

Space differentials are similarly approximated by finite differences:

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

where for a given position \mathbf{r}_0 the sum is taken over nearest neighbour sites \mathbf{r}_{α} 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 $\frac{2}{3}$ for sites α along the lattice axes and $\frac{1}{6}$ along the diagonals. The effective diffusion parameter D_{α}' , appropriate to motion between the sites \mathbf{r}_0 and \mathbf{r}_{α} , 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 and Cavalli-Sforza 1984). In general individuals will move from their birth place a distance λ during their generation time τ . The square of this distance will in general be proportional to the time available; the constant of proportionality is the diffusion constant D :

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

It is an assumption of the standard model that individual dispersal is equally likely in all directions.

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 traveling with velocity:

$$v = 2\sqrt{D\alpha} \quad (5)$$

A more detailed account of our methodology is given elsewhere (Steele, Sluckin, Gamble and Denholm 1995).

We obtain estimates of realistic values of α , K and D from the ethnographic and archaeological literatures. α we take conservatively to be in the range 0.01-0.03/yr, since ethnographic evidence suggests that human populations can expand at rates of up to 4% per year when colonizing new habitat (Birdsell 1957). We note, *contra* Hassan (1981), that this is consistent with the much lower observed rates of increase in contemporary hunter-gatherer populations which are close to carrying capacity - the density-dependent logistic growth function implies that a population at 95% of its carrying capacity K will be growing at a rate of 0.05α (or 0.15 %/yr, assuming $\alpha = 0.03$). K , in turn, we estimate for different habitats from observed hunter-gatherer population densities, on the assumption that ethnographic populations are usually observed at or close to their equilibrium limit. D we estimate from archaeological evidence for raw material transport distances, which we take to be indicators of mean individual lifetime mobility during the colonization phase. We return to the question of realistic values for D in a later Section.

3. Paleovegetation Reconstruction.

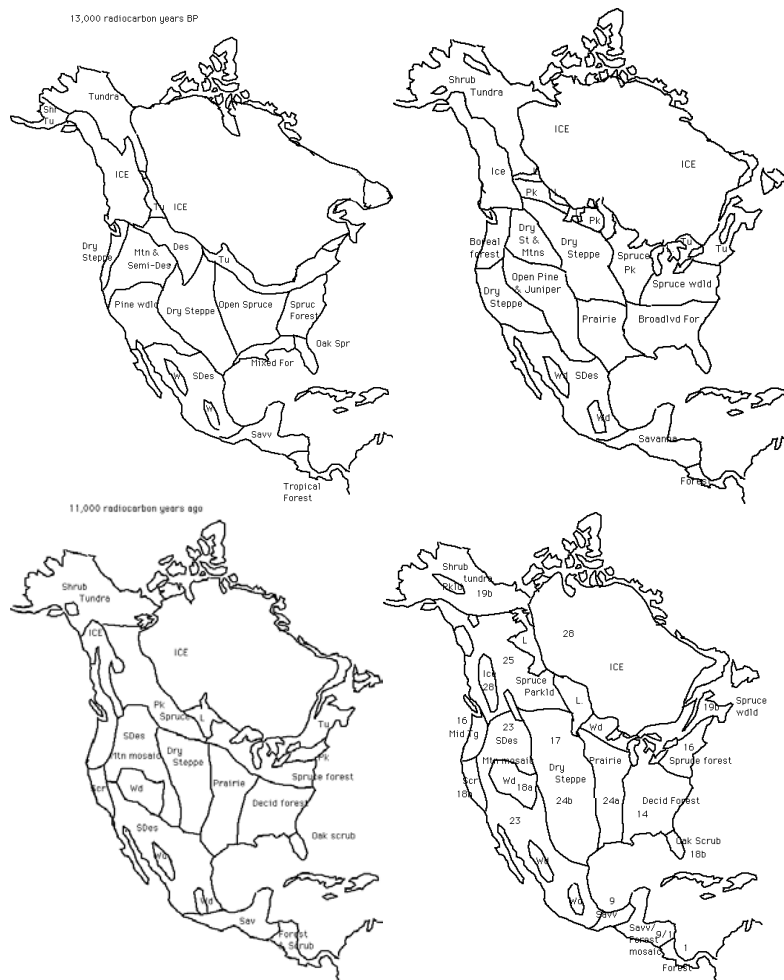
Because observed hunter-gatherer densities vary greatly according to habitat, it is necessary to take account of paleohabitat distribution in order to simulate accurately population densities at different locations on the surface of the Americas during the Paleoindian dispersal phase. Many different sources of evidence can be used to contribute towards reconstructing broadscale vegetation cover of the past. The most direct and useful evidence comes from the fossil remains of plant types characteristic of each vegetation zone, indicating for example prairie or temperate forest. Unfortunately, plant fossils are normally only preserved in lakes, swamps and river deposits, and if the climate in an area was dry then such preservation sites would have been an infrequent component in the landscape. Often, a shortage of plant fossil data means that the vegetation cover can only be reconstructed indirectly using other indicators to 'fill in' the large spatial gaps between sites. Even at those sites where plant fossil evidence has been obtained, natural transport processes or decay could have selectively concentrated certain plant remains to give a misleading impression of what the local vegetation was actually like. Thus it is always desirable to cross check the picture from plant fossil evidence against other indicators of past vegetation coverage.

These additional sources of data include sedimentological indicators such as particular buried soil types or buried sand dunes, which can indicate the general nature of the vegetation cover which once existed there. Animal fossils can also suggest the existence of a vegetation habitat that suited them; for example the presence of the extinct American horses (which closely resembled Eurasian species) may be taken to indicate that open grassy vegetation was an important part of the landscape in the past.

In the present study, all these various sources of evidence have been combined to produce an overall picture. Because many palaeovegetation sites are ambiguously dated (due to problems, for example, of 'age plateaus' in the radiocarbon record), it is only possible to put forward fairly tentative time scenarios for the time course of vegetation change. The general timing of broadscale environmental changes shown in the maps is based on extrapolation from particular well dated sites, assuming that climates at other less well dated sites changed roughly in synchrony with these. Even the background of events at the best dated sites is to some extent ambiguous because the radiocarbon chronology that most of them are based on is often subject to uncertainties of thousands of years.

In general, the greatest uncertainty exists for the older timeframes. For the more recent timeslices, especially after about 11,000 years ago, the large number of dated pollen sites makes vegetation reconstruction much easier. For North America, the task has been greatly aided by graphical display packages such as ShowTime, which illustrates the percentage of each pollen type at sites across North America for progressive time intervals. The maps reproduced here are part of a larger series in preparation depicting the evolution of vegetation cover of the Americas since the last glacial maximum (Adams, 1998).

Due to restrictions on space, neither full range of literature sources nor a full list of sites is given here. Only some general comments are given, together with a few key papers and the names of some of the most important sites. A broader range of relevant literature sources can be obtained by accessing the QEN atlas site of the World Wide Web.



Figures 1-4. Paleovegetation maps of North America at 13,000 B.P., 12,000 B.P., 11,000 B.P. and 10,000 B.P. (^{14}C years). **KEY:** Tu=grassy tundra, Des=extreme desert, Sdes=semi-desert, ShrTu=shrub tundra, Pk=parkland, L=lake, Wd=woodland, Scr=scrub.

Figure 1. 13,000 radiocarbon years ago. In the aftermath of the last glacial maximum, indicators of a significant warming and moistening of climate begin to appear by around 14,000 BP, but only in some areas. In Alaska, a widespread change from herb-dominated to moist shrub-dominated tundra had occurred at around 14,000 BP, suggesting moister and slightly warmer conditions (Andrews & Brubaker 1993). A similar trend towards moister and warmer conditions is seen in the changing tundra flora and insect fauna on the eastern part of the Beringian land bridge (Elias *et al.* 1996). Elsewhere in North America, conditions seem to have remained dry and cold. In the High Plains of the MidWest, desert conditions remained widespread, with continuing dune activity and the absence of mammal fossils from this time (Wells 1992). Further west, across Washington State, pollen diagrams suggest that dry and very cold conditions dominated the Cordilleran region, with a sparse parkland existing on the coastal plain and polar desert inland and at higher altitudes (Thompson *et al.* 1993). In the central Mexican uplands, an increase in woodlands and a reduction in grasslands after 15,000 ^{14}C y.a. suggests a switch to more humid - but still cooler - conditions than had occurred previously (Lozano-Garcia *et al.* 1993). Cooler conditions may have lasted up until about 9,000 y.a. (Lozano-Garcia *et al.* 1993).

However, continuing glacial retreat was exposing new surfaces in North America. At around this time, according to the mapping chronology of Dyke and Prest (1987), a continuous ice-

free corridor opened for the first time between Alaska and the contiguous USA. However, for a considerable part of its length (about 750 km) it would have been less than 50 km wide, and further obstructed in several places by large meltwater lakes. The chronology of the first appearance of the ice free corridor is not completely settled however; Bobrowsky & Rutter (1992) conclude that although the southern and northern ends were open by this time, it is quite possible that the central region was still closed.

Conditions at the southern end of the ice-free corridor (e.g. in the area around 50°-52° N and 110°-115° W, reviewed in detail by Beaudoin *et al.* 1996) still seem to have been very arid. Burns *et al.* (1993) note the absence of radiocarbon dates on faunal remains between about 21,300 and 11,600 ¹⁴C y.a. in the Edmonton area, suggesting that the landscape was incapable of supporting fauna during this interval.

Figure 2. 12,000 radiocarbon years ago. By around 12,000 radiocarbon years ago, boreal forest had spread through the western lowlands of Washington State (north-west USA), indicating the continued effects of warming and moistening of climate as the ice sheets retreated (Thompson *et al.* 1993, & ShowTime database). On the eastern part of the Beringian land bridge, insect communities suggest that present-day temperatures had been reached (Elias *et al.* 1996).

The ice-free corridor through Canada had by this time widened considerably, though it remained wholly or partly obstructed by large meltwater lakes (Dyke & Prest 1987). To the north, birch shrub-tundra had suddenly become widespread throughout deglaciated areas of Alaska and north-west Canada.

The desert area which had occupied much of the the High Plains of the Midwestern USA began to show signs of moister conditions, with dune stabilization and the spread of shortgrass prairie vegetation and its associated grazing mammals (Wells 1992). At the southern and western fringes of the High Plains, pine and spruce woodland seems to have begun to spread in at around this time (Wells 1992).

Temperate tree species began to spread and increase in abundance through the forests and open woodlands of the eastern USA, although the vegetation remained dominated by boreal conifers (Overpeck *et al.* 1992, ShowTime database). A map of vegetation distribution for 12,000 y.a. has been assembled by Overpeck *et al.* (1992) for the eastern USA, using pollen data.

Through much of the southern and central Cordilleran area of the USA, conditions may have been slightly moister than at present (although generally semi-arid), with greater woodland and scrub cover than at present. The same appears to have been the case for the lowland American and Mexican deserts to the south (Thompson *et al.* 1993, Benson *et al.* 1997).

Figure 3. 11,000 Radiocarbon years ago. The picture of climate and vegetation change at around 11,000 radiocarbon years ago is complicated by the fact that in many areas there was a cold and arid event that correlates with the 'Younger Dryas' cold event in Europe. Changes in pollen spectra from the eastern seaboard, the midwest and the nw Pacific coast suggest colder, drier conditions, with a mean annual temperature decline of about 3°-4° C across these areas (Anderson 1997). A relatively dry phase in the Great Basin (comparable in aridity with the present-day)- following on from the previous initial moist phase - also corresponds in age to the Younger Dryas (Benson *et al.* 1997).

However in most regions of North America the Younger Dryas interval was apparently a time of continuing colonization by interglacial-type vegetation, quite unlike the major setback that it represented for European and Eurasian forests. In fact, insect assemblages from the Beringian land bridge suggest that summer temperatures were several degrees warmer than today's around 11,000 ^{14}C y.a. (Elias *et al.* 1996), though this might hypothetically have been just before a cooling event.

Rising sea levels seem to have finally cut off the land bridge of Beringia at around this time (rather later than was previously thought), according to recent studies by Elias *et al.* (1996).

The retreating North American ice sheets had by now exposed an ice-free corridor that was some 500 km or more wide along much of its length (Dyke & Prest 1987). Animal remains start to appear at the southern end of the corridor about this time. Tree species began to colonize deglaciated parts of Canada, with conifer parkland appearing in the Rocky Mountains at about 11,000 years ago (Thompson *et al.* 1993). A number of pollen sites have been obtained from this general area, and the summarized 'ShowTime' pollen abundances appear to suggest that spruce (*Picea*) parkland was also widespread at the southern end of the ice-free corridor. However, this picture may be based on poor radiocarbon dates. In a review of the environmental history of the southern end of the corridor, Beaudoin *et al.* (1996) suggest that most of the vegetation was in fact non-arboreal, with birch shrubs. They note that earlier studies suggested spruce woodland already important in the landscape by this time, but that this is now in doubt because the radiocarbon-dated materials were contaminated by coal and carbonates.

Shrub tundra, and not parkland, also seems to have remained the main vegetation type across most of Alaska and in the northern part of the deglaciated corridor.

In southeastern Alaska, a short-term climate cooling that coincides with the Younger Dryas age occurred between about 10,600 and 9,900 ^{14}C years ago was marked by expansion of tundra elements and deposition of inorganic sediments (Hansen & Engstrom 1996). To the south of the southern entrance to the ice-free corridor, both dune and zoological evidence suggests a temporary return of desert conditions to the High Plains of the American Midwest (Wells 1992), although the timing and relative severity of this event remains highly uncertain. The parkland and conifer woodland that had covered the eastern prairie zone during the full glacial period had by now mainly disappeared, being replaced by treeless grassland, although from the high conifer pollen percentages it seems that a band of conifer parkland may still have existed across the northern part of the prairie zone (ShowTime database).

In the eastern USA, deciduous forest species continued to increase in abundance. In the deglaciated areas of the north-east, however, the predominant vegetation remained tundra and spruce parkland (ShowTime database).

Figure 4. 10,000 radiocarbon years ago. The colder, relatively arid phase associated with the Younger Dryas seems to have ended shortly before this time slice (around 10,200 radiocarbon years ago), in those areas which it had affected. In many areas of North America, forest vegetation continued to spread in, although it had not yet attained its Holocene coverage and remained an open parkland or forest-grassland mosaic in many areas, especially in Canada (ShowTime database).

The ice sheets of North America were by this time greatly reduced in size. Large lake systems had formed around the fringes of the Laurentide ice sheet but the retreat of the western Cordilleran ice sheet had left a broad area of lowland which was gradually becoming colonized by conifer parkland or open forest (ShowTime database). Beaudoin *et al.* (1996) suggest that conifer forest was present in the south-eastern foothills of the Rocky Mountains in Canada by around this time. Note that the parkland was probably much sparser towards the ice sheet margins, with a treeless zone of several hundred km resulting from lags in tree colonization in the areas exposed by the rapidly-retreating ice sheets. For example, pollen ecological studies by Ritchie in southern Canada suggest a lag of 2000 ¹⁴C years at many sites between deglaciation of a site and subsequent colonization by spruce and other boreal trees.

However, in the north-eastern USA/south-eastern Canada, colonization by trees had progressed up to the stage of giving boreal conifer forest in many areas. Deciduous tree species continued to increase in range and abundance through the eastern USA (ShowTime database).

In the western USA, such as the Owens Lake site in the Great Basin, earliest Holocene conditions may have been moister than present (with open juniper scrub vegetation replacing the more open semi-desert) between about 10,000 and 9,000 ¹⁴C y.a., followed by dessication to conditions similar to those of today (Benson *et al.* 1997).

It is necessary to emphasize again that these vegetation map reconstructions and the accompanying text descriptions must be regarded as a preliminary and incomplete view of the environmental changes which took place in the Americas during deglaciation. More information is continually becoming available, and no doubt significant changes to these maps will be needed when a more complete picture becomes possible. Nevertheless, most of the broad vegetation trends and the general timing of events appear well supported at present.

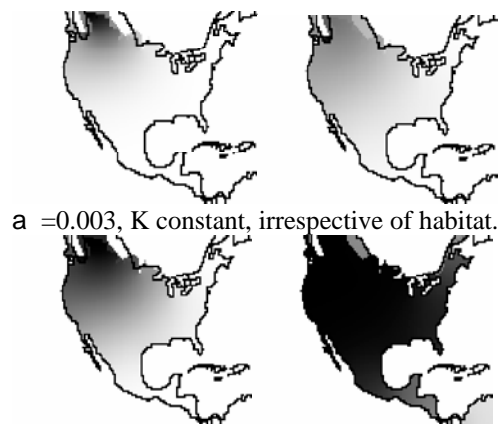
4. Results.

In our simulations, we have studied the effects of habitat on dispersals by varying K , taking median observed hunter-gatherer population densities in different habitats as the source for our carrying capacity values. Table 1 gives the relevant data from Kelly 1995, and the paleovegetation categories which we have assimilated to Kelly's broader habitat types for this study. We might also expect that in reality, D would be inversely correlated with K across habitat types: but relevant ethnographic data is too sparse to enable us to assign habitat-specific values of D in this way.

CLASS	N	MEAN	MEDIAN	RANGE	ADAMS EQUIVALENTS
Arctic	18	9.7	3.0	0.2-65	Tundra, Shrub Tundra
Subarctic/ Cold Forest	37	4.0	1.4	0.2-23.5	Boreal Forest, Spruce Woodland, Mid Taiga, Open Pine and Juniper, Coniferous Forest, Park, Spruce Parkland
Temperate Deserts	16	7.3	4.7	1-19	Semi-Desert, Semi-Desert/ Montane Mosaic
Temperate Forests	14	12.4	7.2	1.3-38	Deciduous Forest, Broadleaved Forest, Scrub, Oak Scrub
Plains	9	3.2	3	1.4-5.8	Dry Steppe, Dry Steppe/ Montane, Prairies
Tropical/ Subtropical Deserts	31	28.5	7.6	0.2-200	Savanna, Savanna/ Forest Mosaic
Seasonal/ Wet Tropical Forests	19	31.7	18.7	3-86	Tropical Forest, Tropical Forest and Scrub.

Table 1. Hunter-Gatherer Population Densities (p.p. 100 km²) In Different Broad Habitat Classes (derived from Kelly 1995:222).

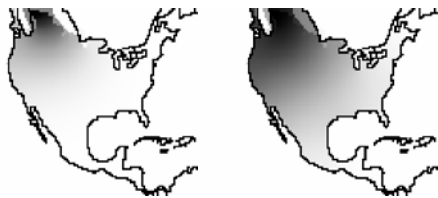
We have assumed that the Early and Middle Paleoindian phase lasted 2,000 years, from approximately 12,000 to approximately 10,000 ¹⁴C years BP. Figures 5-10 give cumulated population density plots (in person-years) for the first 1,000 years and also for the first 2,000 years after dispersal from the southern end of the ice free corridor, for each location on the surface of North America south of the ice sheets. We held D as a global constant in all experiments, with the value $D = 900$ (implying a mean individual mobility of 250-300 kms between birth and reproduction, a figure consistent with observed raw material transport distances from this period - e.g. Tankersley 1992,). Direct empirical data on initial population growth rates is lacking. Powell and Steele (1994) report a mean age of 3.5 years for formation of linear enamel hypoplasias in the teeth of Late Paleoindian skeletons, which may imply late weaning and thus decreased fertility rates: but these skeletons are Early Holocene in date. Between our simulation runs we varied the value of a , which was treated as a global constant. In some simulations we took K to be uniform for all locations on the colonizable surface, while in others we used the inferred habitat-specific values of K (see above, Table 1), using as our basemaps the paleovegetation reconstructions for the 12, 11 and 10 kyr intervals. In the latter case, we used the 12 kyr map for the first 500 years of the simulation, the 11 kyr map for the next 1,000 years, and the 10 kyr map for the final 500 years.



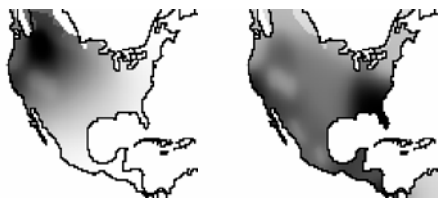
a = 0.01, K constant, irrespective of habitat.



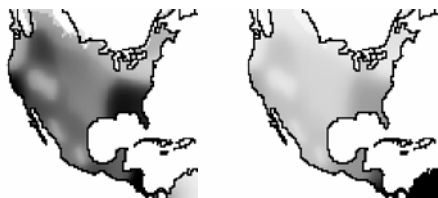
a = 0.03, K constant, irrespective of habitat.



a = 0.003, K varies with habitat.



a = 0.01, K varies with habitat.



a = 0.03, K varies with habitat.

Figures 5-10. Cumulated occupancy of North America by a colonizing population over the first 1,000 years (left hand maps) and over the first 2,000 years (right hand maps), under different assumptions about intrinsic rates of increase (a) and carrying capacity (K). All experiments assumed an initial population of 100 individuals originating at the southern end of the ice-free corridor. Grey scale values are autoscaled within each map to maximize contrast, and do not conform to a single absolute scale of values across the series.

1,000-Year Runs

Experimental Condition	Final Population Size	Cumulated Total Occupancy (Millions of Person/Years)
a =0.003, K constant, irrespective of habitat.	1,941	0.7
a =0.01, K constant, irrespective of habitat.	199,085	53.2
a =0.03, K constant, irrespective of habitat.	401,278	234.9
a =0.003, K varies with habitat.	1,831	0.7
a =0.01, K varies with habitat.	173,033	44.6
a =0.03, K varies with habitat.	554,301	265.8

2,000-Year Runs

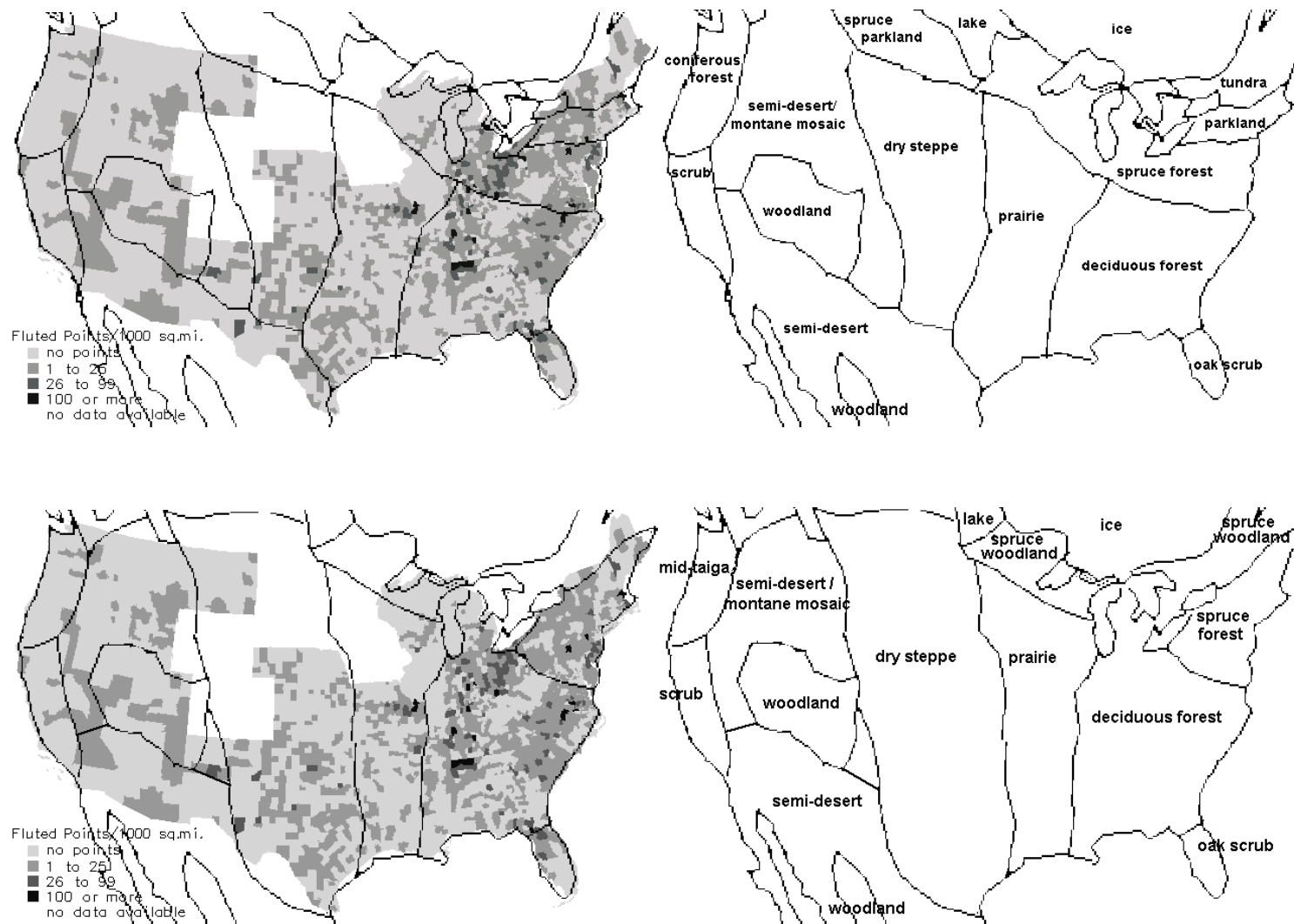
Experimental Condition	Final Population Size	Cumulated Total Occupancy (Millions of Person/Years)
a =0.003, K constant, irrespective of habitat.	33,568	13.7
a =0.01, K constant, irrespective of habitat.	418,910	364.6
a =0.03, K constant, irrespective of habitat.	426,320 (=K for entire grid)	420.5
a =0.003, K varies with habitat.	29,936	12.5
a =0.01, K varies with habitat.	533,478	407.6
a =0.03, K varies with habitat.	635,718 (=K for entire grid)	638.1

Table 2. Final Population Sizes and Cumulated Total Occupancy for the Simulation Runs Represented in Figures 5-10.

As our control data, we use the distribution map of fluted point densities for the contiguous United States compiled by Faught, Anderson and Gisiger (1994), based on a database of 10,198 points (Figures 11-12 below; see Anderson 1990: 168 and 1995: 148 for comments on problems in its compilation). We make the grossly simplifying assumptions that the variation in artefact densities in this map reflects variation in Paleoindian discard rates and not just variation in recent recovery rates (cf Anderson 1990: 171), and that the rate of discard was a simple function of the number of person-years lived at any location. For our limited purposes here — comparing mean densities across biomes at the continental scale — such assumptions are more likely to be reasonable than they would be at finer scales, where variation in discard behaviour and in recovery rates will be most significant.

Figures 5-10 are each shaded to best represent variation across the colonized surface in cumulated person-years: we are interested in matching simulated gradients of cumulated occupancy to observed gradients in discard rates. There is enormous variation in the absolute numbers of occupants in the grid at the end of the different simulations, and in the cumulated number of person-years of occupancy of the colonized cells of the grid: and this variation is summarised in Table 2, which would be relevant for predictions of absolute discard rates. For example, if we assume that the plotted sample of recovered Fluted Points represents 0.1% of the total number originally discarded (thus total discards = c. 10 million), and that only men in the later third of their life used and discarded these artefacts (so that the number of person-years of the discarders among the cumulated experimental population is one sixth of the cumulated total occupancy), and also that only 80% of the simulated colonization surface is included in the Fluted Point dataset, then estimated rates of discard per Fluted Point user range from six points every year, to one point every eight years. But the assumptions made in this example are arbitrary and for illustration only.

It is clear from the Figures that certain conditions must be met for our simulated population histories to match the observed variation in fluted point densities. In those simulations in which K was held as a global constant (with a value equivalent to 0.03 persons per square kilometre), the simulated population history inevitably shows a greater cumulated density of person-years at the assumed northwestern origin of the dispersals. This conflicts with the fluted point data, which suggest greatest density of occupation in the eastern woodland habitats (Figures 11-12). In those simulations in which K was varied in accordance with observed habitat-specific variation in hunter-gatherer population densities in the ethnographic record, the simulated population history best matched the observed fluted point data when a was set at a relatively high value in the range 0.01-0.03 (which is also the range which best matches observed natural rates of increase in human populations far from carrying capacity). This is because with D held constant, only high values of a enable the travelling wave to diffuse across the surface fast enough for the higher carrying capacity of the southern and eastern areas to affect the cumulated population plot within the 2,000-year span of the simulation. Even with $a = 0.01$, the greatest density of cumulated occupancy after the initial 1,000 years is still in the dry steppe/montane region of the Rockies to the south of the ice free corridor, whereas when $a = 0.03$ the predicted densest cumulated occupancy is already found by that time to be in the eastern woodlands. With lower values of a (e.g. $a = 0.003$), v (the velocity of expansion) is low, and the travelling wave does not reach the eastern woodlands soon enough to show an effect of varying K with habitat. Thus in our simulations, where the standard demic expansion model is used and realistic values selected for D , a and K , there is no conflict between a late glacial dispersal scenario and the North American data which shows a greater density of late glacial occupation in the eastern woodlands.



Figures 11-12. Early and Middle Paleindian Fluted Point Densities for the contiguous United States, with overlays of the paleovegetation maps for 11,000 ¹⁴C years B.P. (top) and 10,000 ¹⁴C years B.P. (bottom). Artefact plot after Faught *et al.* (1994).

5. Dispersal and Mobility: Constraints of the Standard Model.

There are, however, other aspects of the North American Paleoindian data which remain in conflict with this standard model of demic expansion. Our experiments assumed that Early Paleoindian population expansions into new habitats were constrained by carrying capacity values analogous to those seen in ethnographic hunter-gatherer societies. This assumes, in turn, that the Early Paleoindian populations were initially already fully adapted to exploit the resources of each new habitat zone: and this is in conflict with a common assumption of the prevailing scenario, which is that Early Paleoindian mobility reflected a big game focus and that only later did populations adapt to more generalist foraging strategies exploiting the full resource base of each habitat zone. Of course, that assumption may be mistaken: we do not really know how quickly a human forager population was capable of adapting to the resource structure of a new habitat zone to the degree seen in the ethnographic record. But another, related observation is that there appears to have been an increase in population density in the later part of this period, as indicated by increases in numbers of sites and in artefact frequencies in higher layers of sites with more than one episode of occupation (Anderson 1990:199). This would also suggest an increase in the carrying capacity of habitats as Paleoindian populations became culturally adapted to their particular resource opportunities.

In fact, it may be that while dispersal velocities were high, the initial colonization of the surface of the Americas remained patchy and tethered to key resources or landmarks while initial populations accumulated knowledge of their new environments. Anderson (1990) has argued that initial dispersals may have followed major river valleys, with aggregation sites located close to dramatic and easily relocatable natural landmarks. Compared with the random movement assumption of the standard demic expansion model, Anderson's account places far greater weight on the ways in which spatial dispersal patterns may have been constrained by the information requirements of a colonizing population during the initial settlement phase.

When we consider the South American data, the limitations of the standard model become even more apparent. If we assume that the terminal Pleistocene sites with clear Paleoindian occupation represent a demic expansion from an origin in North America after the last glacial maximum, then it becomes necessary to assume extremely high rates of exploratory mobility through the more productive open South American habitats (including the open montane habitats of the Andean chain) if we are to account for the presence of very early dates from sites in the southern cone (Gibbs, Glass and Steele 1998). These rates of exploratory dispersal are inconsistent with the standard model of range expansion, in terms of which such velocities would imply mean lifetime dispersal distances of the order of thousands of kilometres, random with respect to direction. Such extremely rapid dispersal velocities are more consistent with more qualitative models of exploratory dispersal such as Beaton's 'transient explorers', highly mobile foragers with narrow diet breadth and generalised, conservative toolkits who repeatedly relocate (in preference to settling and learning to adapt to a more specialized exploitation of the spectrum of resources available in a given habitat).

One feature which is often associated with hypotheses of extremely rapid dispersal is movement along linear habitats, seen as dispersal corridors. With regard to the initial entry into the Americas south of the ice sheets, it has been demonstrated by Aoki that colonization of an inhospitable ice free corridor by a standard demic expansion process is highly unlikely, due to the probability of stochastic extinction of local groups. This does not mean that such a

route of entry is implausible, merely that successful entry via such a route requires it to be treated as a corridor connecting preferred habitat patches. We can envisage a simple decision rule for mobility along such corridors, in which a given resource threshold must be exceeded for the decision to be made to continue exploratory movement outwards, but in which a further, higher resource threshold must be crossed before the decision is made to settle in a home range. It is a property of successful dispersal corridors that resource availability is such that the first of these thresholds should be exceeded, but not the second. The ice-free corridor between the receding Cordilleran and Laurentide ice sheets is not the only linear habitat which may have served as such a corridor to early Paleoindian populations. Other candidates include parts of the western coastal margin, the major river systems, and the open montane habitat of the Andean chain. Perhaps part of the reason for the cluster of early sites at the furthest reaches of the southern cone is simply that colonists followed such a decision rule, treating the Andes as a corridor, until they reached the point beyond which further outward movement was impossible.

Our experiments with the Fisher-Skellam model have demonstrated that realistic dispersal models must, at the very least, recognize both the density-dependent nature of population growth and the determining role of vegetation structure on maximum equilibrium population density (or carrying capacity). Paradoxically, the assumption of the late glacial colonization scenario that is most often called into question in this context — namely, that there is a high natural rate of increase of human hunter-gatherer populations, $a \approx 0.03/\text{yr}$ — seems to us to be the most secure and uncontroversial. The reason for this confusion appears to lie in the low observed rates of increase of ethnographic hunter-gatherer populations close to carrying capacity. As we have shown, these low observed rates are in fact consistent with far higher natural rates of increase, since we may assume that growth rates are density dependent. That is, we assume that as a population approaches carrying capacity so mortality increases relative to fertility, due to pressures on resources and to diseases of crowding. It is well known that human hunter-gatherer populations adapt to these constraints by cultural mechanisms of fertility regulation, such as infanticide, delayed weaning and lactation-induced amenorrhea. Confusion has arisen when it has implicitly been assumed that growth rates are density-independent, and that observed ethnographic rates must therefore represent realistic maxima for a past colonizing population.

It would be far more productive, in our view, to question the assumption of the standard demic expansion model that dispersal can be represented by a single constant representing a mean distance travelled between birth and reproduction, with an equal probability that that distance will be travelled in any given direction. It is well established that travelling wave velocities in demic expansions are more influenced by the shape of the distribution of dispersal distances than by other, demographic parameters (van den Bosch, Hengeveld and Metz 1992). Although the standard model assumes a single value for D , derived from an underlying assumption of a two-dimensionally symmetric and normal distribution of dispersal distances, it is clear that this does not always match the empirical realities of animal movement even in the simplest invertebrate cases. To take the case of the observed distribution of dispersal distances in *Drosophila*, redistribution kernels with better empirical fit than the normal distribution have been shown to generate travelling waves with velocities as much as an order of magnitude greater than those predicted by the standard model (equation 5, above) (Kot 1996). Moreover, in some cases these velocities may be accelerating rather than constant (Kot 1996).

The assumption of symmetry in the distribution of dispersal distances in two dimensions can also be called into question. It is a feature of the logistic model of density-dependent growth that as a population approaches carrying capacity, so there is a linear decline in the net rate of increase. Consequently if we assume a colonizing population of fitness-maximizers seeking to maximize their individual reproductive rate, we will predict that people will disperse preferentially into those areas of adjacent habitat in which human occupancy is furthest from carrying capacity. However, positive density-dependent dispersal may not of itself imply accelerated rates of range expansion. Newman (1980) proposed that when the diffusion coefficient has the density-dependent form $D\left(\frac{n}{K}\right)^b$, the velocity of range expansion $v\sqrt{(2D\alpha)}$ can be predicted from the value of b . If $b = 0$, $u = \sqrt{2}$, giving the standard model's solution (equation [5] above). If $b > 0$, it seems that $u \approx (b + 1)^{-1}$; from which it follows that if $b = 1$, then individual dispersal distances when $n=K$ (and dispersal distance is assumed to be greatest due to crowding) must be at least 3 times the value taken for mean lifetime dispersal distance in the standard model, for range expansion to be *faster and not slower* than in the standard model. By contrast, when $b < 0$ (such that dispersal distances are greatest at low densities, due for instance to mate searching), then u assumes any value. We might then expect that density-dependent dispersal will accelerate range expansion when it is negatively density-dependent and driven by mate searching, and when α is low - such that at a given location, n is slow to approach K .

In raising such questions about the standard model's assumption about individual mobility - which is that, in aggregate, dispersal can be approximated as rotationally symmetric, density-independent, and proportional to the mean squared individual displacement distance per generation time - we are identifying a key philosophical issue of ecological modelling. On the one hand whatever the redistribution kernel used, the random movement assumption remains appropriate if it adequately predicts observed rates of population expansion, even if individuals are known to have used complex and intelligent navigational behaviour relying on environmental cues. This is because models of population-level processes should aim to suppress any such detail which is irrelevant to the simulation of spatial patterns at the population scale (Andow *et al.* 1990). On the other hand, such 'behavioural minimalism' may be inappropriate where the complex navigational decisions of many individuals follow common rules such that their movements are correlated, leading to population-level deviation from the simple random dispersal pattern. Lima and Zollner (1996: 132) have emphasised the importance for understanding animal movement and dispersal of the perceptual range, defined as "the distance from which a particular landscape element can be perceived as such (or detected) by a given animal". An extended perceptual range decreases the risks of mortality of a dispersing animal searching for a suitable habitat patch, and can thus act as a determinant of landscape connectivity. At the initial phase of colonization, learning the distribution of patches at large spatial scales may have been risky if it required repeated abandonment and relocation of potentially widely spaced patches (*ibid.*). It is plausible to assume that one of the main priorities of the early Paleoindian settlers of the Americas was balancing the risks and potential benefits of exploratory dispersal as local groups extended their perceptual range.

As we have seen, such information-based approaches to animal movement and habitat selection are implied by accounts of Early Paleoindian dispersal patterns such as Anderson's, with its emphasis on the importance of rivers as dispersal corridors and on clearly-

recognizable places as aggregation sites in the initial colonization phase. They may also be necessary to explain dispersal through inhospitable habitat corridors, and for explaining the apparent rapidity of Paleoindian dispersal into the southern cone of South America, when the standard model would entail populations of individuals dispersing hundreds or thousands of kilometres in every direction during their lifetimes, while simultaneously maintaining high natural reproductive rates. Beaton's 'transient explorer' strategy is an example of a qualitative model of foraging decision-making which would lead to such rapid, long-distance mobility. Standard dispersal models which assume random movement at the population level may need to be modified to take account of foragers' decisions and their perceptual basis, when these are correlated among individuals - leading to non-random dispersals which deviate from the rotationally symmetric assumption of the 'information-free' approach. One good reason for examining such 'information-based' approaches in more detail is that we do not yet understand their implications for the velocity of range expansion.

We have demonstrated in this paper that the United States fluted point distribution is consistent with a late glacial colonization from the northwest, given realistic assumptions about population growth rates, about mobility, and about equilibrium population densities as they vary between biomes. This has been demonstrated by a series of computer simulations using the standard demic expansion model derived from animal ecology. It is very likely that understanding may be further improved by more sophisticated treatments of the information-seeking and decision-making processes affecting individual dispersal distances in a colonizing population.

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