

Diffusion and Brownian Motion Analogies in the Migration of Atoms, Animals, Men and Ideas

Gero Vogl

Fakultät für Physik der Universität Wien, Strudlhofgasse 4,
A-1090 Wien

Abstract

The macroscopic laws of diffusion were laid down for the case of liquids by Adolf Fick 150 years ago who realised the analogy of diffusion and heat conduction. 100 years ago Einstein and Smoluchowski put up the equation named after these scientists teaching us how to trace down the motion of a single diffusing particle and thus to understand long time unexplained Brownian motion as a fluctuation phenomenon. In the last fifty years these laws and their combination were boldly but successfully applied to the diffusion, migration, dispersion of single atoms, men, animals and ideas.

We start by showing how the Einstein-Smoluchowski equation makes possible to induce diffusivity from microscopic information on details of the diffusion jump in solids. We then report on Brownian motion and diffusion of our fore-fathers in the Neolithicum following Cavalli-Sforza's ideas and show how this diffusion must have been a mixture of demic diffusion, i.e. the diffusion of people, and the diffusion of technological ideas. Next we risk a glimpse to the immigration of early Americans. We point out the discrepancy a physicist faces in the conclusions of the Archaeologists. We finally discuss the ultra-fast dispersion of the horse-chestnut leaf miner throughout Europe following recent work of ecologists.

1. Introduction

Many a cultural scientist, be it a sociologist, a linguist or a historian, is more than sceptical of any mathematical theory, even any attempt to imply "laws" to processes in the field of the so-called "cultural sciences" [1,2].

On the other hand the last century saw the acceptance of laws from physics in different fields of biology and in particular ecology. In 1951 J.G.Skellam, a biometrist, wrote [3]: "*It is apparent that many ecological problems have a physical analogue and that the solution of these problems will require treatment with which we are already very familiar.*"

We will investigate what can be done in the special field of diffusion, migration, dispersion of men, animals and ideas and compare with diffusion in physics. Since annoying findings in botany stand at the beginning of studies into diffusion we judge that

starting with a view into historic development of this field which all the time oscillated between biology and physics may be an appealing approach to the matter.

In 1827 the renowned British botanist Robert Brown when studying in the microscope plant pollen immersed in water found that they are in vivid motion [4]. First he suspected – following the general tendency of his time - that these pollen were similar to sperms of animals, but when repeating the experiment with “*specimens of several plants, some of which had been dried and preserved in an herbarium for upwards of twenty years, and others nor less than a century*” Brown found the same motion. He now concluded that “vitality” remained beyond the death. But in thorough control experiments Brown discovered the same motion in particles of about one micrometer diameter bruised from silicified wood and eventually from window-glass and further-on “*in every mineral which I could reduce to a powder, sufficiently fine to be temporarily suspended in water*”. Brown deduced - in *contrast* - to all his predecessors that there was a physical force behind the phenomenon, but could not infer more. He had indeed discovered what we term now “Brownian motion”.

In the second half of the nineteenth century numerous researchers attempted to find the physical law behind Brownian motion. Felix Exner from Vienna was probably closest to an explanation. He, however, tried to determine the *velocities* of the suspended particles and to deduce from there the velocities of the molecules assuming equipartition of energy. Exner received velocities about thousand times smaller than expected from statistical physics [5]. At least part of the reason for the discrepancy might have been the impossibility to measure the velocities.

On April 30, 1905 Albert Einstein eventually – after a couple of futile attempts – delivered successfully to the University of Zürich his doctoral thesis on the determination of molecular dimensions and Avogadro’s number from the change of viscosity through dissolving sugar in water [6]. A few days later, on May 11, 1905, *Annalen der Physik* in Leipzig received a paper by Einstein titled “*Über die von der molekulartheoretischen Theorie der Wärme geforderte Bewegung von in ruhenden Flüssigkeiten suspendierten Teilchen*” [7]. This paper on the irregular motion of small particles pushed on by molecules or atoms in liquids was in search of a different approach to determine molecular dimensions and Avogadro’s number than that Einstein had followed in his thesis. Obviously Einstein – different from Exner and many others – had no knowledge of the broad literature on Brownian motion, but discovered only eventually that the phenomenon that he had considered already was known to exist and had been extensively studied. Einstein uses a new audacious argument by stating that molecules and suspended particles at equal concentration will produce the same osmotic pressure. He states “*...man sieht nicht ein, warum einer Anzahl suspendierter Körper nicht derselbe osmotische Druck entsprechen sollte wie der nämlichen Anzahl gelöster Moleküle.*” Einstein derives a relation between diffusivity of suspended particles in a liquid of given viscosity and temperature and the dimension of the particles which is sometimes named the Einstein-Stokes law.

In the same paper Einstein then derives the diffusion equation (Fick's second law) from statistical considerations. He concludes that the probability $f(x,t)$ to find a particle at a given time t in a distance x from its origin follows a Gaussian distribution which is the solution of the diffusion equation

$$f(x,t) = \frac{n}{\sqrt{4\pi Dt}} \exp\left(-\frac{x^2}{4Dt}\right). \quad (1)$$

Here n is the number density of particles and D the diffusivity.

Einstein sarcastically says that one could have expected this result from the theory of errors (*"Die Häufigkeitsverteilung ist also dieselbe wie der zufällige Fehler, was zu erwarten war"*). The width of the Gaussian distribution yields directly

$$\langle x^2 \rangle = 2 D t, \quad (2)$$

the mean (symbolised by $\langle \rangle$) square deviation of a particle in irregular or random motion (Einstein calls the motion *"ungeordnet"*) during time t . This calculation is for the one-dimensional case. Einstein adds that for diffusion in three dimensions $\langle x^2 \rangle = 6 D t$ and consequently it should be $\langle x^2 \rangle = 4 D t$ for the two-dimensional problem.

We should not omit that a year later Marian von Smoluchowski [8] received the same result except for a numerical factor, without having to resort to Einstein's *"Überlegungen indirekter Art..., welche nicht immer ganz überzeugend erscheinen"* (Smoluchowski's criticism). Smoluchowski criticizes e.g. *"die Übertragung der Gesetze des osmotischen Druckes auf jene Teilchen"*, done by the ingenious Einstein with great success, as Smoluchowski does not hesitate to praise (*"von Einstein befolgte, sehr sinnreiche Methoden"*). We therefore usually call equ. (2) the Einstein-Smoluchowski equation for Brownian motion.

To repeat: Einstein predicts $\langle x^2 \rangle$ of the particle. What really is measurable is the distance covered by each individual particle during time t . Its mean value is a little larger than x_{rms} , the root of $\langle x^2 \rangle$, whereas the particle's *velocity* – Exner's aim - is hardly measurable. To measure x_{rms} was what a number of scientists attempted. Particularly successful was Jean-Baptiste Perrin who by a group of students had x_{rms} measured for particles of well-defined size after a well-defined time – usually one minute – in liquids of various viscosities and at various temperatures. Perrin's greatest achievement probably was to produce these mono-disperse particles. He did that by mass separation of resin particles in a centrifuge. Perrin confirmed all predictions of Einstein on Brownian motion and proved the reality of the atom as he stressed proudly in his Nobel prize lecture in 1926 [9]. So for investigations into diffusion the circle between biology and physics was closed. We are going to reopen it in this short review, but now start with diffusion in physics, will then return to biology and extend our considerations to diffusion of men and ideas and finally again animals.

2. Diffusion in solids

The Einstein-Smoluchowski equation for three-dimensional motion $\langle x^2 \rangle = 6 D t$ or the root of the mean square (x_{rms}) which provides a measure of how far a particle has come during time t , is the basis for deducing the diffusivity D from measured mean atomic displacements x_{rms} . We and others have developed “atomistic” methods for determining the elementary diffusion jump in solids. By neutron and x-ray scattering or γ -ray absorption with extremely high energy and size resolution, the elementary jump vector and the jump frequency of *the molecules or atoms* are determined [10], and also NMR accomplishes extremely high frequency resolution [11]. This information is considerably more subtle and detailed than a macroscopic parameter as Fick’s or Einstein’s “diffusion constant” D , but of course also more delicate, therefore has continuously to be checked for reliability.

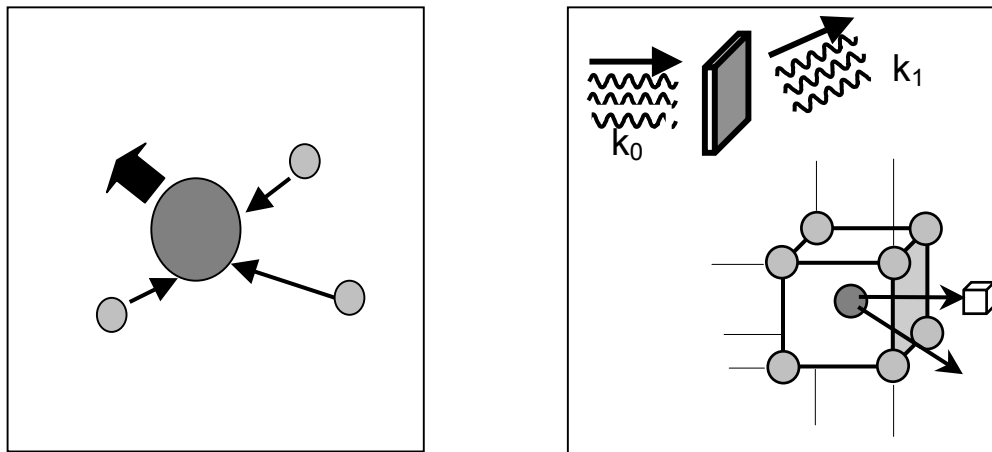


Fig 1: Left: principle of Perrin’s method with size resolution in the range of micrometers (diameter of large particle) and time range of seconds. Perrin followed the motion of the large shaded particle, whereas he could not see the small particles. The method makes use of Einstein’s ideas in order to *indirectly conclude on atomistic details* of the motion of the molecule or atom (whose diameters are in the nanometer range).

Right: modern scattering or resonance method with resolution in the sub-nanometer and nanosecond range. The motion of the molecules or atoms (nanometer range) and the time of the motion (nanosecond range) are directly determined [10].

Note: the difference in the diameters of the large particle and of the small particles by a factor of 1000 can of course not be pictured in this schematic figures.

We may use the Einstein-Smoluchowski equation for deducing from the atomistic detailed result the diffusivities determined by macroscopic tracer diffusion method . Fig. 2 gives a comparison of diffusivities in the intermetallic alloy Fe-Al with three different compositions as determined from tracer data (lines) and from an atomistic method, here in particular Mössbauer spectroscopy on ^{57}Fe . The Mössbauer data have *provided the elementary diffusion jump* which is a jump to a nearest neighbour site. The diffusivities have been calculated by help of Einstein-Smoluchowski and as can be seen the agreement in the diffusivities is excellent.

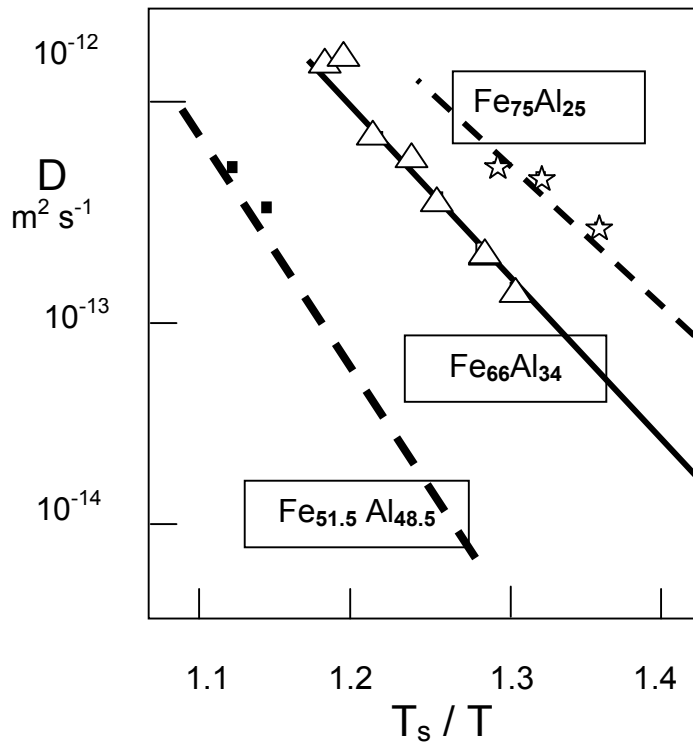


Fig. 2: The diffusivities in intermetallic ordered or partially ordered alloys of iron-aluminium with three different concentrations. The lines correspond to tracer data from Larikov [12] for $\text{Fe}_{51.5}\text{Al}_{48.5}$ and $\text{Fe}_{75}\text{Al}_{25}$ and from Eggersmann et al. [13] for $\text{Fe}_{66}\text{Al}_{34}$. The Mössbauer data are from Sepiol et al. [14] for the same concentrations, namely triangles for $\text{Fe}_{66}\text{Al}_{34}$ (in the case of Eggersmann's data even for the same charge) and asterixes for $\text{Fe}_{75}\text{Al}_{25}$. Only instead of Larikov's $\text{Fe}_{51.5}\text{Al}_{48.5}$ Vogl and Sepiol had slightly different composition ($\text{Fe}_{50.5}\text{Al}_{49.5}$ full squares). The temperatures are normalized to the solidus temperature T_s .

In order to demonstrate the wide applicability of the atomistic methods, here we refer to a new and still somewhat preliminary result of the method. We have recently used nuclear resonance scattering of synchrotron radiation, i.e. the time domain version of the Mössbauer effect, under grazing incidence for determining diffusion in the uppermost layers close to the surface [15]. Fig. 3 shows the diffusivity in the first 25 nanometers below the surface as calculated from the Einstein-Smoluchowski equation.

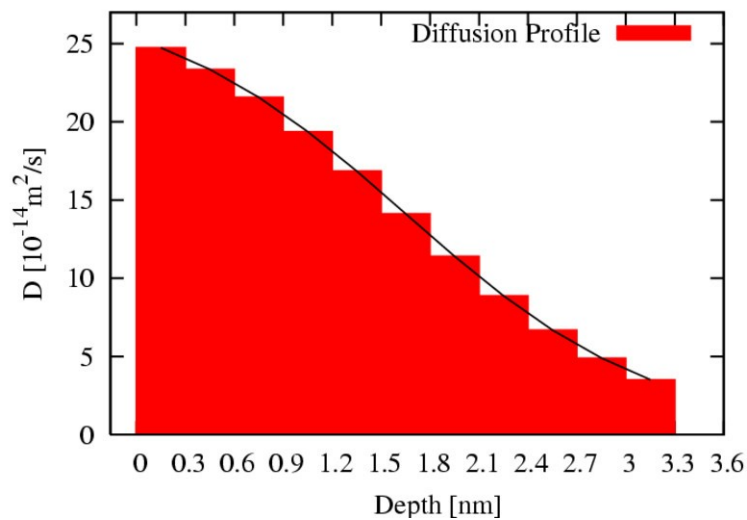


Fig. 3: Fe_3Si at 850 K. Scattering of synchrotron radiation in grazing incidence with energy resolution in the neV range and dimensional resolution in the sub-nanometer range permitted to deduce the diffusivity decay in layers close to the surface. In a depth of several nanometers the bulk diffusivity prevails whereas near the surface diffusion is more than an order of magnitude faster.

3. Diffusion and growth. The Migration of Animals, Men and Ideas.

The solution of the diffusion equation is a Gaussian with $\langle x^2 \rangle = 4 D t$ for the two-dimensional problem. Already in 1951, J.G. Skellam [3] stressed “*Unlike most of the particles considered by physicists, however, living organisms reproduce, and interact. As a result the equations of mathematical ecology are often of a new and unusual kind.*”

It are at least the laws of reactive diffusion which have to be considered if population growth occurs. The equation for reactive diffusion reads for the two-dimensional problem (diffusion on surface of earth, therefore polar coordinates appropriate with r the radius from the origin [16])

$$\frac{\partial n}{\partial t} = \frac{D}{r} \frac{\partial}{\partial r} \left(r \frac{\partial n}{\partial r} \right) + \alpha n. \quad (3)$$

Here Einstein’s probability distribution $f(x,t)$ has been replaced by the number density $n(r,t)$ of individuals, abbreviated here just n , and α is the growth rate.

The solution of this reaction equation looks similar to a Gaussian ,

$$n(r,t) = \frac{n_0}{4\pi Dt} \exp\left(-\frac{r^2}{4Dt} + \alpha t\right), \quad (4)$$

it is a “pseudo-Gaussian” with n_0 the number of individuals at the start in time and space and the additional growth term αt in the exponent. That is why we speak of exponential growth.

To our knowledge the first to consider a case of this exponential growth in a problem of the life sciences was J.G.Skellam [3]. He calculated the dispersion of a population of muskrats, originally only five animals, from a site near Prague over Central Europe from 1905 till 1920. The mean expansion radius follows a linear dependence on time, different from Einstein-Smoluchowski, where x_{rms} is proportional to the root of time. Reason for this difference is the growth: with increasing population the dispersion is of course faster.

More interesting because relevant for longer time is the so-called logistic growth. Here account is taken for saturation of number density occurring in a populated region after some time (the “limits of growth”) leading to a constant population. For a dispersion in preferentially one direction according to Fisher [17]

$$\frac{\partial n}{\partial t} = D \frac{\partial^2 n}{\partial x^2} + \alpha n \left(1 - \frac{n}{k}\right). \quad (5)$$

Here k is the saturation density.

At the expansion front a sort of Gaussian behaviour prevails leading to a front “*wave of advance*” of the number density with constant velocity. Fisher in 1937 [17] who thought of the dispersion of an advantageous genetic mutation in a one-dimensional habitat has estimated the velocity v of the wave front

$$v = 2\sqrt{\alpha D} . \quad (6)$$

D can be calculated from Einstein-Smoluchowski and α can be estimated, therefore the wave front velocity predicted.

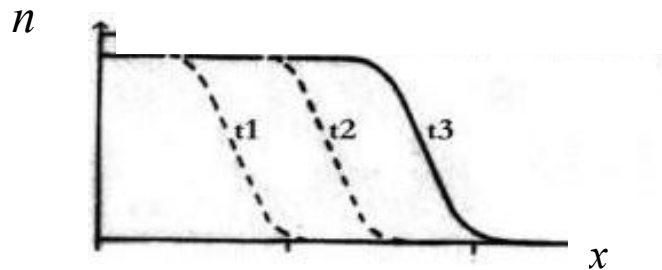


Fig. 4: Wave of advance of the number density n of individuals along one direction x at three different times t_1 , t_2 and t_3 . The front is advancing in time.

The first to apply the Fisher equation to a human society was the geneticist Luigi Luca Cavalli-Sforza. Together with the archaeologist A.J. Ammerman [18] he studied the progress of the Neolithicum, i.e. the civilization which first used agriculture overcoming the earlier lifestyle of gathering and hunting, from the Near East into Europe. Archaeologic findings prove that it lasted 4.000 years until farming was the economic basis all over Europe. In the Near East farming starts at about 8.000 BC, in Ireland and Scandinavia hunting and gathering prevailed until 4.000 BC the propagation rate corresponding to 1 km/year (Fig. 5).

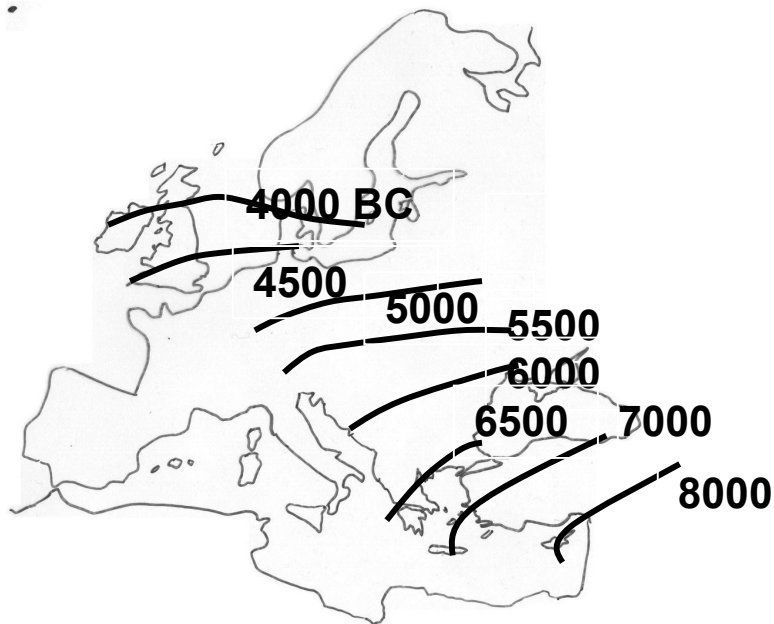


Fig. 5: Advance of agriculture from the Near East and Anatolia over a distance of 4.000 km via Greece and the Balkans to Central and finally Western and Northern Europe [after 18], dates BC according to present state of knowledge, courtesy of E. Lenneis.

Assuming a progress of agriculture as the superior economy in form of a more or less one-dimensional wave of advance one can calculate the velocity if one dares to guess growth rate α and diffusivity D . As a first attempt we may assume a maximum value for the growth rate equal to modern booming agricultural societies, i.e. 3 percent per year. We may further calculate D from Einstein-Smoluchowski by assuming for x_{rms} within one generation the distance over that husband and wife have found together in order to produce children. This guess is of course a guess into a society many thousands years gone, and we may only hope that the habits of farmers have not changed too much over that time – an assumption perhaps not so absurd taking into account the conservative attitude of farmers. This distance is today about 10 km (Cavalli-Sforza's dates from his homeland in Northern Italy), so that for D we get $1 \text{ km}^2/\text{year}$ and therefore for the velocity of the wave of advance an upper value of $0.3 \text{ km}/\text{year}$. This is only about one third of the rate of progress of agriculture in Europe during the Neolithicum. The conclusion: it was not just a "demic diffusion" that took place but the technique of agriculture diffused faster carried by the transfer of the idea. It was – at least partly – the diffusion of ideas. In my opinion as a "diffusion physicist" this implies: we Europeans

are not just descendants of the immigrants from the Near East. We have rather many ancestors among Europe's Palaeolithic hunters and gatherers – the “Old-Europeans”.

This conclusion is corroborated by more and more genetic studies [19] which indicate that our genes are a mixture of Old-European and Near Eastern genes. The problem with these studies is that the “archaeogeneticists” are not sure what the genes of the Old-Europeans were like, they resort to the genes of the Basques who appear to be a singularity in Europe, particularly by their non-Indo European language, but maybe also by their genes. Chikhi et al [19] deduce a significant decrease in admixture across the range from the Near East to Western Europe. They eventually estimate on the above assumption that the Basques are still hundred percent “Palaeolithic” (which they are certainly not as Chikhi et al. note) that on the average 50 percent of the European genes are stemming from the Near East, nearly all in Greece, only about 15 to 30 percent in Germany or France. Realizing the ambiguity of these assumptions we as physicists clinging to simple mathematical models may keep that our calculation of the discrepancy of the velocity of the wave of advance by a factor of three is at least as good an indicator for a high fraction of technology transfer, i.e. diffusion of ideas, cultural diffusion, besides gene transfer, i.e. diffusion of people, demic diffusion, immigration into Palaeolithic Europe.

Extremely attractive because still a subject of vivid controversies: the archaeologically well-documented immigration of early Americans, the “Paleoindians”, during the last maximum glaciation from Siberia via the dry and ice free Bering Street to Alaska about 13.000 or 12.000 years ago (10.000 B.C.) and further down into North America either via an ice-free corridor or along the North American West-coast. The abundance of Clovis type spear heads from 12.000 years before present demonstrates man's presence in today's USA. Finally the dispersion in only about 2.000 years via 12.000 km to Patagonia at the southernmost cone of South America [20] where from this time on human tools are found.

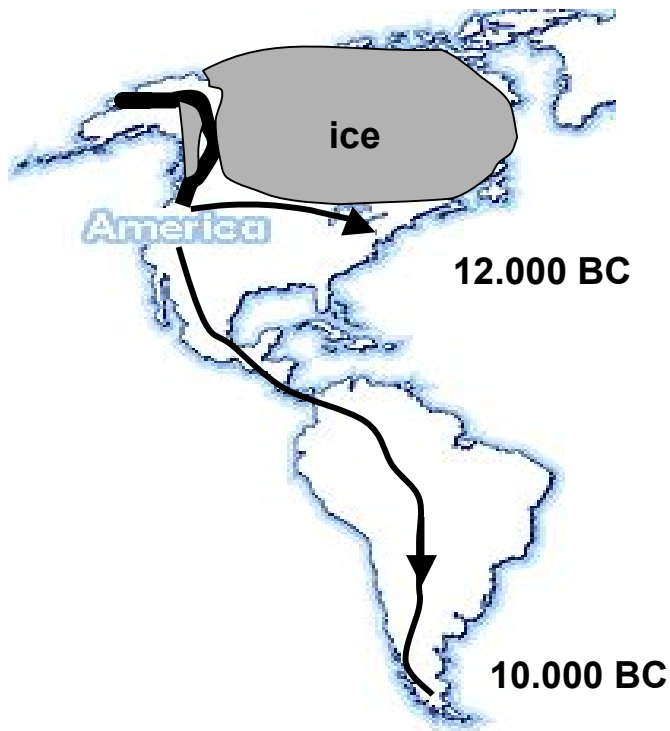


Fig. 6: Possible dispersion of Paleoindian immigrants from Siberia via Alaska and North America to the southern South America.

For estimating D of the immigrants we need x_{rms} . The random migration distance of an early American hunter-gatherer must be guessed from the behaviour of the last surviving hunter-gatherers. We follow Cavalli-Sforza [18], taking x_{rms} from the behavior of the last surviving hunter-gatherers, the pygmies of Central Africa, about 50 km during one generation (25 years), but it might have been as large as say 200 kilometres in a sparse population far from carrying capacity when mate search needed migration over large distances. We then receive $D = 25 \text{ km}^2/\text{year}$ as a minimum and $400 \text{ km}^2/\text{year}$ as a maximum guess. For α we take 0.01 (one percent) per year, certainly an upper limit, if we realize that sucklings have to be carried and during this time no further child can survive. We receive for the velocity of the wave of advance 1 km/year as minimum and about 4 km/year as maximum, certainly even the upper limit too low for overcoming by random walk 12.000 km in 2.000 years.

Again looking carefully at the laws of diffusion teaches us to search for other motives for the fast dispersion of Paleoindians. Two interpretations of this obvious discrepancy are conceivable: an earlier immigration wave from Siberia which eventually reached Patagonia or some type of “directed motion”. Steele et al. consider that early colonists might have moved non-randomly, e.g. along rivers or along the Andean “road of the Volcanoes” where finding landmarks is facilitated in order to minimize dangers. They suggest that attention should be directed into information-seeking and decision-making processes in a colonizing population.

4. The dispersion of the horse-chestnut leaf miner across Europe

In the late eighties of the 20th century the horse-chestnut leaf miner (*Cameraria ohridella*) appeared in Central Europe expanding from the southern Balkans (Fig. 7).



Fig. 7: Dispersion of horse-chestnut leaf miner from the region of Lake Ohrid (former south-western Yugoslavia) into Europe.

The dispersion of that tiny moth has been quite well documented in Germany by observing the brown patches on chestnut leaves which are the cradles of the leaf miners’ larvae. The leaf miner’s “route of success” started in Germany’s south-east at the Austrian border and proceeded as documented by Freise and Heitland [21] as to be seen from Fig. 8.

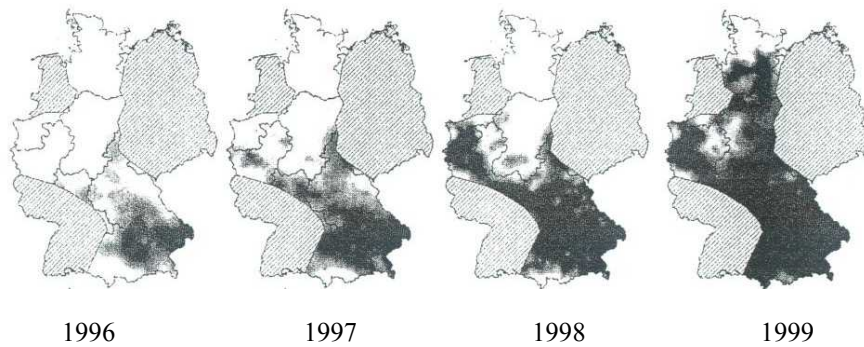


Fig. 8: Observed dispersion of leaf miner via Germany [21]. Well documented are the white regions into which the leaf miner invades, whereas the shaded regions are ill-documented and therefore not considered for further study. In 1996 only regions in Bavaria were infested (black regions), but in 1999 nearly all Germany except some border areas was befallen.

Marius Gilbert has modelled the progress of the infestation. Most interesting in the invasion and expansion of the leaf miner is the combination of normal diffusion and man-made transport.

The dispersion of the insect by diffusion proceeds with an extremely modest diffusion coefficient since the insect keeps floating in the air but does not fly actively. The insect is carried by the wind but x_{rms} of this transport is estimated to be less than one kilometre in one generation. In central Europe there are three generations per year, thus this overall displacement would never lead to the invasion which within 20 years has coloured the leaves of the horse-chestnut trees all over Europe in early summer with brown patches.

It is another transport process which has produced the rapid dispersion of the leaf miner. Gilbert has demonstrated that the centres of expansion of the moth are identical with the urban agglomerations in Germany. He has argued that accidental and unintended transport of infested leaves by cars and railway trains – which proceeds preferentially between cities – transports the moth over large distances from town to town. From there on it then expands quite “naturally” via diffusion. Fig. 9 shows results of such modelling and demonstrates that the model and the procedure have at least to be taken seriously as a possibility.

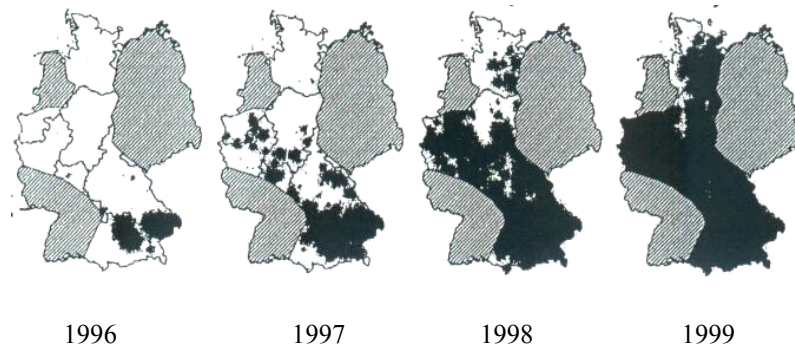


Fig. 9: Simulated dispersion of leaf miner via Germany. From [21].

The convincing success came when Gilbert applied the procedure to data from France where he was able to show that exactly with the same type of arguing and modelling the dominant expansion of the leaf miner was explained. Only in the Massif Central (south west of France) data material was insufficient for a convincing proof [22].

5. Conclusions

Physical laws are progressively accepted by “soft” natural sciences, and more reluctantly by cultural sciences. Diffusion and dispersion as its correlate in archaeology, zoology and ecology may be the fore-runner and spear-head for the transfer of physical models. We have tried to show how the laws of diffusion may be applied to archaeology and ecology. In some cases descriptions appear to be matching, in other cases we find discrepancies which indicate the directions into which more research should be invested. These are e.g. the unusual fast-moving waves of advance of the Neolithicum in Europe or of the Paleoindians in America. For the dispersion of the horse-chestnut leaf miner even man-driven processes beyond diffusional dispersion have to be invoked.

Acknowledgement

I am grateful to Luigi Luca Cavalli-Sforza, Marius Gilbert, Daniel Kmiec, Eva Lenneis, Christa Lethmayer, Bogdan Sepiol, Manfred Smolik, James Steele and Lorenz Stadler for many discussions.

References

- [1] H.Ch. Ehalt (Ed.), *Zwischen Natur und Kultur. Zur Kritik biologistischer Ansätze*, Böhlau, Wien, Köln, Graz, 1985.
- [2] R. Girtler, Die Eigenständigkeit der "Geisteswissenschaften" gegenüber den Naturwissenschaften, in [1], pp. 223-245.
- [3] J.G. Skellam, *Biometrika* 38 (1951) 196-218.
- [4] R. Brown, *Phil. Mag.* 4 (1828) 161-173.
- [5] F.M. Exner, *Annalen der Physik (Leipzig)* 2 (1900) 843-847.
- [6] A. Einstein, Eine neue Bestimmung der Moleküldimensionen, Inaugural-Dissertation, Universität Zürich, K.J.Wyss, Bern (1905); printed with some changes in *Annalen der Physik (Leipzig)* 19 (1906) 289-306.
- [7] A. Einstein, *Annalen der Physik (Leipzig)* 17 (1905) 549-560.
- [8] M.v.Smoluchowski, *Annalen der Physik (Leipzig)* 21 (1906) 756-780.
- [9] J.P. Perrin, *Discontinuous Structure of Matter, Nobel Lectures 1922-1941*, Elsevier, Amsterdam.
- [10] G. Vogl, B. Sepiol, The Elementary Diffusion Step in Metals Studied by the Interference of Gamma-rays, X-rays and Neutrons, in: *Diffusion in Condensed Matter - Methods, Materials, Models*, P. Heitjans, J. Kärger (Eds.), Springer, Berlin, 2005, pp. 65-92.
- [11] P. Heitjans, A. Schirmer, S. Indris, NMR and β -NMR Studies of Diffusion in Interface-Dominated and Disordered Solids, *ibidem*, pp. 369-416.
- [12] N.L. Larikov, V.V. Geichenko, V.M. Falchenko, *Diffusion in Ordered Alloys*, Oxonian Press, New Delhi, 1981.
- [13] M. Eggersmann, H. Mehrer, *Phil. Mag. A* 80 (2000) 1219-1244.
- [14] G. Sepiol, B.Sepiol, *Acta metall. Mater.* 42 (1994) 3175-3181; R. Feldwisch, B. Sepiol, G. Vogl, *Acta metall. Mater.* 43 (1995) 2033-2039.
- [15] D. Kmiec, B. Sepiol, M. Sladeczek, G. Vogl, J. Korecki, T. Slezak, R. Ruffer, K. Vanormelingen, A. Vantomme, *Defect and Diffusion Forum*, 237-240 (2005)1222-1224.
- [16] A. Okubo, *Diffusion and Ecological Problems: Mathematical Models*, Springer, Berlin, Heidelberg, New York, 1980.
- [17] R.A. Fisher, *Ann. Eugen.* 7 (1937) 355-369.
- [18] A.J. Ammerman, L.L Cavalli-Sforza, *The Neolithic Transition and the Genetics of Populations in Europe*, Princeton University Press, Princeton, 1984.
- [19] L. Chikhi, R.A. Nichols, G. Barbujani, M.A. Beaumont, *Proc. Nat.Ac.Sci. USA* 99 (2002) 11008-11013; I. Dupanloup, G. Bertorelle, L. Chikhi, G. Barbujani, *Mol. Biology and Evolution* 21 (2004) 1361-1372.
- [20] J. Steele, J. Adams, T. Sluckin, *World Archaeology* 30 (1998) 286-305.
- [21] M.Gilbert, J.C. Grégoire, J.F. Freise, W. Heitland, *J.Animal Ecology* 73 (2004) 459-468.
- [22] M.Gilbert, private communication (2005).