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Transport on fractal river networks: Application to migration fronts

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Abstract

A quantitative model of the US colonization in the 19th century is presented. We explore the idea that landscape heterogeneities should have strongly affected this process, as the need for water made the colonizers follow the routes of main rivers and set up their towns near them. So, we study transport processes on fractal networks modeling river basins, a case which may have a great ecological relevance for the study of hydrochory, and in general for species which spread along corridors. The analytical reaction–diffusion model presented here allows to predict the propagation rate of fronts spreading through Peano-like basins, and comparison with the *Optimal Channels Network* model is also reported. Finally, the propagation rates observed are compared with the results from our model, concluding that migration through fractal media, in spite of being a mathematical idealization of the problem, mimics the dynamics of real systems reasonably well.

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1. Introduction

Modeling human-range expansions may contribute to understanding and predicting how populations behave when settling into new territories (Ammermann and Cavalli-Sforza, 1984; Fort and Méndez, 1999). One of the best-known range modern expansions is the colonization across the US in the 19th century. By 1790, the North-American population of European origin was concentrated in the Atlantic region, but along the following decades the internal migrations led to a displacement of the established population westwards. According to the data and atlases revised, the average expansion rate for this transition between 1790 and 1910 was approximately 13.5 ± 0.8 km/yr (Flanders, 1988).

An essential characteristic of the US transition westwards was the fact that settlers did not occupy all of the territory, as homogeneous models (Fort and Méndez, 1999) assume, but followed the course of the greatest rivers

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and lakes (Faragher, 1979; Flanders, 1988) and settled near them to make use of their resources. Therefore, landscape heterogeneities should have played an essential role in the process of migration.

This situation is similar to the case of dispersion of biological species along the margins of rivers and streams (Johansson and Nilsson, 1993; Campbell et al., 2002), showing the ecological interest of our study for transport processes limited spatially by river lines (Speirs and Gurney, 2001), as well as other natural or artificial corridors.

2. Model

In the last few years great efforts have been made in order to describe the intricate geometry of river networks (Rodríguez-Iturbe and Rinaldo, 1997). This field has received great attention especially since the importance of the fractal properties of these networks were revealed (Mandelbroot, 1983; Marani et al., 1991), attracting the interest of researchers from different areas. However, few researches have been performed on the transport properties

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of these structures, in spite of the applications that this field offers, as spread of biological species using rivers as corridors (Johansson and Nilsson, 1993) or longitudinal dispersion of particles through the channels (Rutherford, 1994).

Here we propose the study of transport processes through fractals modeling river networks and, specifically, we focus on the analysis of reaction-diffusion (RD) processes, our main objective being to determine analytically the speed of RD fronts spreading through these networks. However, we must first note that mathematical modelization of real media as a fractal involves some nontrivial assumptions. The most obvious is that ideal fractals imply self-similarity at all scales, unlike fractals in nature where self-similarity is necessarily restricted by lower and upper bounds. Another important point is that one expects transport in fractals (at least in the asymptotic regime) to be independent of the starting point chosen, that is, the property of translational invariance holds, an idea which is also difficult to justify for structures in nature. We shall discuss below whether these limitations may affect the results and the conclusions of our work.

The model proposed to date which seems to describe the evolution and formation of the river basins better and agrees with most of the observations is the Optimal Channels Network (OCN) model, based on some optimization principles which minimize the energy expenditure by the network (Rodríguez-Iturbe et al., 1992; Rinaldo et al., 1993). The evolution rules described by this model lead to fractal structures as that shown in Fig. 1 (left). Nevertheless, these structures are very irregular and so their analytical study is nearly impossible. Then, analytical approaches require to work with a simpler structure; a good choice is the Peano basin (Fig. 1, right), a spacefilling loopless fractal which has already been used before for the modelization of river basins (Marani 1991; Flammini and Colaiori, 1996) and whose similarities and differences with OCN's structures have been studied in Colaiori et al. (1997). In this work we will study the transport properties of the Peano basin and our results will be finally compared with those numerically obtained from the OCN model.

First we present the theoretical framework that we will use for describing these dynamical processes, which is based on the well-known Continuous-Time Random Walk (CTRW) (Hughes, 1995). According to this, in an RD process the evolution of the particle density $\rho(x, t)$ follows the expression

$$\rho(x,t) = \int_0^\infty dt' \varphi(t') \int_{\mathbb{R}} dx' \Phi(x') \rho(x-x',t-t') + \int_0^t dt' \phi(t') f[\rho(x,t-t')]$$
(1)

where the first term accounts for the diffusion of particles and the second one describes production and annihilation processes. The reader can find in Méndez et al. (2004) as to how this equation can be derived straight from the master equation in the CTRW framework.

In Eq. (1), $\varphi(t)$ is defined as the waiting-time distribution, $\varphi(t) = \int_t^{\infty} \varphi(t) dt$ is the probability of a walker to remain at least for a time *t* at a site before jumping, $\varphi(x)$ is the jump distance distribution, and f(x, t) is the function growth for production and annihilation processes; here, we choose $f(\rho) = a\rho(1-\rho)$, a logistic growth function (where *a* is the growth rate parameter), as usual for many biological and ecological applications (Murray, 1993).

Recently (Méndez et al., 2004b), it has been shown that introducing an appropriate rescaling, Eq. (1) can be written as a Hamilton–Jacobi-type equation in the form

$$\frac{1}{\hat{\varphi}(s)} = \hat{\Phi}(p) + \frac{a}{s} \left(\frac{1}{\hat{\varphi}(s)} - 1 \right)$$
(2)

where $\hat{\varphi}(s)$ and $\hat{\Phi}(p)$ are the Laplace and bilateral transforms of $\varphi(t)$ and $\Phi(x)$, i.e.,

$$\varphi(\mathbf{H}) = \int_0^\infty e^{-Ht} \varphi(t) \, dt, \qquad \qquad \hat{\Phi}(p) = \int_{-\infty}^\infty e^{px} \Phi(x) \, dx.$$
(3)



Fig. 1. River basins modeled by the (a) OCN's model and (b) the Peano basin fractal. For the Peano structure, the numbers below the branches point out the order of each branch.

Likewise, using the Lagrangian formalism and the Hamilton equations the expression for the speed of fronts (in case wavefront solutions are allowed by the system) can be found to be

$$v = \min_{s} \frac{s}{p^*(s)},\tag{4}$$

where $p^*(s)$ is the solution of Eq. (2), so that, this Hamilton–Jacobi method allows us to find the wavefront speed for an RD process for any distributions $\varphi(t)$ and $\Phi(x)$ describing the diffusion pattern by individuals.

Now, let us consider a random-walk through a Peano basin (with all the individuals standing at the site A at t = 0) for the *myopic ant case*, that is, a walker at a certain site o of the structure can jump, after a residence-time τ , to each one of its z_o first neighbors with a probability $1/z_o$. Previous studies have already analyzed random-walks on tree-like structures as the Peano basin (Mathan and Havlin, 1990), obtaining some averaged properties. There, the movement of the walkers through the backbone (i.e., the direction AB in Fig. 1) was studied and each secondary branch emerging from a site of the backbone was assumed to introduce a waiting-time distribution of jumps from this site to the adjacent sites in the backbone. Here, as we are concerned with the study of propagation of fronts, we will choose AB as the direction of advance for the fronts and we will also use this idea of waiting-time distributions introduced by the branches.

The branches order in the Peano basin is indicated in Fig. 1 (numbers below the branches). It can be seen that when a walker reaches the backbone site corresponding to a first-order branch, it can jump to another site of the backbone with probability $2 \cdot \frac{1}{4} = \frac{1}{2}$ or get into the secondary branch with probability $\frac{1}{2}$. Then, the waiting time is τ with a probability $\frac{1}{2}$; analogously, the waiting time is 3τ with probability $\frac{1}{4}$ and so on. In general, we have that, for the first-order branches

$$\varphi(t) = \sum_{i=1}^{\infty} p_i \delta(t - (2i - 1)\tau), \tag{5}$$

where $\delta(t)$ is the Dirac delta function, so only times τ , 3τ , 5τ ... are allowed. Now we define $\varphi_N(t)$ as the waiting-time distribution for a branch of order *N*. From the arguments above, we have that for the first-order branches in the Laplace space

$$\hat{\varphi}_1 = \frac{1}{2}\hat{\varphi}_0 \sum_{i=0}^{\infty} \left(\frac{1}{2}\hat{\varphi}_0^2\right)^i = \frac{\hat{\varphi}_0}{2 - \hat{\varphi}_0^2},\tag{6}$$

where $\hat{\varphi}_0(s) = \exp(-\tau s)$ is the distribution when no secondary branches are present (equivalent to a classical random-walk in one dimension).

Analogously, the distribution for the branches with N > 1 can be found analytically following some rules

partially discussed before by Van den Broeck (1989) for one dimensional random-walks:

(a) when the particle goes into a further structure (it is, when it moves away from the backbone), the probability of the walk to take a time (or number of steps) t is a convolution of factors; then, it becomes a product in the Laplace space. Finally, the total probability distribution arises from the sum over all the possible times t (from 0 to ∞).

(b) when the particle reaches a crossing and it must choose between two possible ways, the total probability is the sum of both probabilities.

For instance, for N = 2 we find

$$\hat{\varphi}_2 = \frac{1}{2}\hat{\varphi}_0 \sum_{i=0}^{\infty} \left(\frac{1}{2}\frac{\hat{\varphi}_0^2}{4}\sum_{j=0}^{\infty} \left(\frac{\hat{\varphi}_0^2}{2} + \frac{\hat{\varphi}_0^2}{4}\right)^j\right)^i = \frac{4\hat{\varphi}_0 - 3\hat{\varphi}_0^2}{8 - 7\hat{\varphi}_0^2}, \quad (7)$$

where the sums in i and j follow from the arguments in rule (a). Eq. (7) is in perfect agreement with the values found when random-walk simulations are performed in the Peano, and we also verified by means of simulations the expressions found for higher N from the above rules (not shown).

So, the waiting-time distribution for any different branch can be found as a function $\hat{\varphi}_N = f(\hat{\varphi}_{N-1}, \hat{\varphi}_{N-2}, \dots, \hat{\varphi}_0)$ or, equivalently, $\hat{\varphi}_N = f^*(\hat{\varphi}_0)$.

The jump distance distribution $\hat{\Phi}(p)$ is much easier to find; for an isotropic random-walk across the backbone it is just

$$\Phi(x) = \frac{1}{2} (\delta(x + \Delta x) + \delta(x - \Delta x)) \qquad \Rightarrow \qquad \hat{\Phi}(p)$$

= cosh (p\Delta x), (8)

defining Δx as the distance between first neighbors in the lattice. Now, we can introduce the distributions $\hat{\Phi}(p)$, $\hat{\varphi}_1(s)$, $\hat{\varphi}_2(s)$... into (2–4) and find the resulting wavefront speed v numerically. Likewise, some analytical results can also be found if the asymptotic regime ($\tau \ll t$ and $\Delta x \ll x$) is considered, as usual. Expanding the expressions for $\hat{\Phi}(p)$ and $\hat{\varphi}_i(s)$ up to first order we obtain

$$v = \sqrt{2a\frac{\Delta x^2}{\tau\beta}},\tag{9}$$

with $\beta = \sum i(p_i i)$. This expression is a generalization of the well-known Fisher's speed (Murray, 1993) (the classical case is recovered when no secondary branches are considered, so then $\beta = 1$).

Fig. 2 summarizes the results obtained from the Hamilton–Jacobi formalism (lines) in Eqs. (2–4) and compares it to random-walk simulations on the Peano basin up to order N = 10 (empty points) and OCNs (full points). In our simulations, all the walkers were initially on the left-hand side of the lattice and so the front advanced to the right. A logistic growth $g(x, t) = a\rho(1-\rho)$ was introduced at every site at every time step to simulate the reaction process. For the OCNs, we averaged over ten different 200×200 networks generated.



Fig. 2. Plot of the results for the front speed vs the parameter *a*. The points are obtained from simulations of the stochastic process on the OCNs (full points) and the Peano basin (empty points). The lines correspond to theoretical values from Fisher (solid) and from Eqs. (2–4) for N = 1 (dotted), N = 2 (dashed) and N = 5 (dotted–dashed).

From the plot of the speed v as a function of a (which is independent of the diffusion process), we observe that simulations on the Peano lattice and the OCN network lead to very similar results. Although these structures show some topological differences (Colaiori et al., 1997), we think that these similarities in their dynamics are due to the fact that the speed of fronts in fractals is mainly determined by the fractal parameter d_{\min} (which scales the distance between points within the structure with the more usual Euclidean distance between them) and the existence of loops in the structure, as we have stated in recent works (Méndez et al., 2004a; Campos, 2005).

Both the Peano basin and the OCNs are loopless structures with $d_{\min} = 1$, so this could explain the results obtained.

We also show that as a higher N is considered in our equations, a better agreement is found with simulations (the complexity of the expression $\hat{\varphi}_N$ for high N prevents us from performing the analysis up to very high orders; however, we have verified that the values for v converge very fast and so N = 5, the highest order shown, is a good approximation to the exact result). Only for high values of a do we observe some differences between the theory and simulations; it is probably due to the discretization effects involved in our simulations, a problem that we have addressed recently (Campos et al., 2004). However, from Fig. 2 we can state that our model seems to give an appropriate approximation to the problem of propagation across river networks.

The comparison performed also allows us to address the problems about the modelization of real landscapes by means of fractals. In our model, it is clear that self-similarity at all scales cannot be atained, as we need to introduce "by hand" a lower bound in distances which is given by the jump length of the particles Δx . Moreover, in

our analysis (both analytical and numerical) we never reach the case $N \rightarrow \infty$, equivalent to considering ideal (nonrealistic) fractals. Actually, we have seen that the value of v converges fast as N grows, so we can conclude that the problem of self-similarity at all scales does not represent a drawback in our work.

The problem of translational invariance mentioned before for transport of fractals remains a limitation of our model, where all the points of the structure are treated as equivalent. Bearing in mind the possible applications on the field of biological migrations, a more realistic model should include possibly some explicit dependences in space which could account for the minor details of the real territory considered. Nevertheless, we notice that this generalization would lead to a model much more difficult to treat mathematically and the analytical methods used here would not give a satisfactory solution (in that case).

3. Application to migration fronts

We now illustrate the usefulness of our results by applying them to real migration fronts. For some human (prehistoric) migrations, the wave-of-advance model was proposed (Ammermann and Cavalli-Sforza, 1984; Fort and Méndez, 1999), where population fronts spread into new regions and population density saturates behind the front. So, RD models have proved useful before for the modelization of human migrations.

According to the data and atlases revised, the average expansion rate for the transition of the North-American colonizers between 1790 and 1910 was approximately 13.5 ± 0.8 km/yr (Flanders, 1988).

The parameters in our model were estimated as follows: the time between jumps τ for biological migrations is found to be equivalent to the time between successive generations; for humans, the value $\tau = 25$ yr is usually taken (Fort and Méndez, 1999).

The growth parameter *a* was computed directly from Lotka (1956), who fitted the population vs time plot for the US in the 19th century to a logistic curve, obtaining $a = 0.031 \pm 0.001 \text{ yr}^{-1}$.

Regarding the distribution of jump lengths, we know that the settlers did not always cover the same distance, so the distribution $\Phi(x)$ should include the possibility of different jump lengths, in contrast with (8). It can be done by fitting the observed data to a continuous distribution, but another option is to determine the averaged distance covered by settlers and use this value as Δx in (8). Here we will explore both possibilities.

In our case, the jump distances covered by settlers were estimated by individual records obtained from the 'migrations.org project' database (available at www.migrations.org). We collected 400 individual records from the database and measured the distance covered by colonizers from their birthplace till the place they were 25 years after, i.e., after a time τ (only the distances in the E–W direction were considered, in accordance with the onedimensional

nature of our model). The jump length distribution thus obtained is represented in Fig. 3.

However, it does not take into account that fraction f of people who remained at their birthplace after 25 years without migrating. Ferrie's works (Ferrie, 1996) based on the censuses of the 19th century allowed us to estimate $f = 0.3 \pm 0.05$. Taking all this into account, the best fit for our data corresponded to an exponential decay distribution of the form $\Phi(x) = Ae^{-x/w}$ (where A is a normalization factor and $w = 640 \pm 23 \text{ km}^{-1}$) and the averaged distance found was $\Delta x = 810 \pm 93 \text{ km}$.

By introducing these distributions and parameters into (2-4) one obtains the results for the speed pointed out in Table 1. There we have included the results for different values of N because the settlers, according to historical reports, moved by mainly following the major river valleys, so that, one could think that the small details in the structure of the Peano (that is, tertiary, quaternary and higher-order channels) are not decisive for the dynamics of the migration process, and so a low order in N is desirable here.

In any case, we can observe from Table 1 that the geometrical constraints of the fractal networks involve strong corrections over the speed of the fronts, which was



Fig. 3. Plot of the distribution of distances covered by migrants in the E-W direction during the 19th century, according to the 400 individual records taken.

Table 1

Observed front speed and predictions obtained from theory and simulations on fractal basins for the case of the US colonization.

Observed Speed	$13.5\pm0.8~km/yr$
Fisher's prediction $(N = 0)$	$40.3 \pm 2.9 \text{ km/yr}$
Continuous $\Phi(x)$ ($N = 2$)	$19.4 \pm 3.2 \text{ km/yr}$
Continuous $\Phi(x)$ ($N = 5$)	$18.9 \pm 3.1 \text{ km/yr}$
Averaged $\Delta x \ (N=2)$	$16.5 \pm 2.7 \text{km/yr}$
Averaged $\Delta x \ (N = 5)$	$14.7 \pm 2.4 \text{ km/yr}$
Simulations on Peano	$14.5 \pm 0.1 \text{ km/yr}$
Simulations on OCN's	$14.4\pm0.1\ km/yr$

our main objective here. Indeed, the classical prediction by Fisher clearly overestimates the observed speed of the migration front, while both the results found from simulations (for the Peano and the OCN) and the theoretical predictions agree reasonably with the observations. This leads us to the hypothesis that colonization of the US during the 19th century should have been strongly affected by the landscape constraints, giving as the result that heterogeneities would have reduced the propagation rate substantially. Here, we have assumed for simplicity that these heterogeneities are given only by river streams, but one may also think about the effects of mountains. deserts, valleys... For this situation, maybe our ideas could still be extended in order to consider the whole territory as a fractal landscape where the settlers move. In case topological studies could confirm this hypothesis, it would support the interest and relevance of models based on transport through fractals as that presented here.

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References

- Ammerman, A.J., Cavalli-Sforza, L.L., 1984. The Neolithic Transition and the Genetics of Population in Europe. Princeton University Press, Princeton, NJ.
- Campbell, G.S., Blackwell, P.G., Woodward, F.I., 2002. Can landscapescale characteristics be used to predict plant invasions along rivers? J. Biogeog. 29, 535–543.
- Campos, D., 2005. Diffusion and propagation through fractal media. Ph.D. Thesis, Universitat Autònoma de Barcelona.
- Campos, D., Méndez, V., Ortega, V., 2004. Discrete vs. Continuous reaction-diffusion: Prediction of the wavefront speeds (unpublished).
- Colaiori, F., et al., 1997. Analytical and numerical study of optimal channel networks. Phys. Rev. E 55, 1298–1310.
- Faragher, J.A., 1979. Women and Men on the Overland Trail. Yale University Press, New Haven CT, p. 5.
- Ferrie, J.P., 1996. A new sample of males linked from the public use microdata sample of the 1850 US federal census of population to the 1860 US federal census. Hist. Methods 29,1, 41–156.
- Flammini, A., Colaiori, F., 1996. Exact analysis of the Peano basin. J. Phys. A: Math. Gen. 29, 6701–6708.
- Flanders, S. A., 1988. Atlas of American Migration. Facts of File, New York, pp. 86–90.
- Fort, J., Méndez, V., 1999. Time-delayed theory of the neolithic transition in Europe. Phys. Rev. Lett. 82, 867–870.
- Hughes, B.D., 1995. Random Walks and Random Environments. Random Walks, Vol. 1. Oxford University Press, Oxford, pp. 241–320.
- Johansson, M.E., Nilsson, C., 1993. Hydrochory, population dynamics and distribution of the clonal aquatic plant Ranunculus lingua. J. Ecol. 81, 81–91.
- Lotka, A.J., 1956. Elements of Mathematical Biology. Dover, New York, pp., 64–69.
- Mandelbroot, B.B., 1983. The Fractal Geometry of Nature. Freeman, New York.
- Marani, A., Rigon, R., Rinaldo, A., 1991. A Note on Fractal Channel Networks. Water Resour. Res. 27, 3041–3049.

- Mathan, O., Havlin, S., 1990. Mean first-passage time on loopless aggregates. Phys. Rev. A 40, 6573-6579.
- Méndez, V., Campos, D., Fort, J., 2004a. Dynamical features of reaction-diffusion fronts in fractals. Phys. Rev. E 69, 016613.
- Méndez, V., Campos, D., Fedotov, S., 2004b. Front propagation in reacton-dispersal models with finite jump speed. Phys. Rev. E 70, 036121.
- Murray, J.D., 1993. Mathematical Biology. Springer, Berlin.
- Rinaldo, A., et al., 1993. Self-Organized Fractal River Networks. Phys. Rev. Lett. 70, 822–826.
- Rodríguez-Iturbe, I., et al., 1992. Energy dissipation, runoff production, and the three-dimensional structure of river basins. Water Resour. Res. 28, 1095–1103.
- Rodríguez-Iturbe, I., Rinaldo, A., 1997. Fractal River Basins. Cambridge University Press, Cambridge.
- Rutherford, J.C., 1994. River Mixing. Wiley, Chichester.
- Speirs, D.C., Gurney, W.S.C., 2001. Population persistence in rivers and estuaries. Ecol. 82, 1219–1237.
- Van den Broeck, C., 1989. Waiting times for random walks on regular and fractal lattices. Phys. Rev. Lett. 62, 1421–1424.