Dynamical scaling of the DNA unzipping transition

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We report studies of the equilibrium and the dynamics of a general set of lattice models which capture the essence of the force-induced or mechanical DNA unzipping transition. Besides yielding the whole equilibrium phase diagram in the force vs temperature plane, which reveals the presence of an interesting re-entrant unzipping transition for low T, these models enable us to characterize the dynamics of the process starting from a non-equilibrium initial condition. The thermal melting of the DNA strands displays a model dependent time evolution. On the contrary, our results suggest that the dynamical mechanism for the unzipping by force is very robust and the scaling behaviour does not depend on the details of the description we adopt.

The replication of DNA is a correlated process involving many proteins and other molecules [1] working at different points in space and time. An understanding of the nature and origin of this correlation is expected to shed light on this complex mechanism. It has recently been shown [2–6] that the force induced unzipping of DNA is a genuine phase transition different from the thermal melting transition of DNA. It was then hypothesized [2] that the initiation of replication at the origins along the DNA, e.g, by dnaA for E.Coli [1,7] or by the "origin recognition complex" (ORC) in eukaryotes [8] is like this unzipping near the critical threshold (with dnaA or ORC acting as the force-inducing agent) and the resulting correlation during unzipping leads the co-operativity required for replication.

In contrast to real biological situations, techniques like laser tweezers [9], atomic force microscopes (AFM) [10–12] etc have been used to study DNA by pulling at one end. This has led to strand separation by force. In particular, AFM experiments reported hysteresis in the unzipping process, indicating the presence of a first order transition. These mechanical unzipping experiments have opened up new ways of thinking about DNA, just as similar stretching experiments of DNA showed the possibility of several structures other than the most prevalent B-DNA [13]. The activities of polymerases, topoisomerase etc on single stranded DNA have now been analyzed in terms of the force they exert or the force applied against them [14–16]. What needs to be investigated, to mimic the biological situation, is the coupling between the opening of the strands and the subsequent events during replication. Such a study involves the dynamics of the unzipping process [3].

The purpose of this paper is to define a set of simpler models, in the spirit of Poland and Sheraga [17], for which the unzipping transition can be studied exactly. On the basis of this, the dynamics can be understood. The proposed lattice models (bubble models: b-models) incorporate the mutual-avoidance (hard-core repulsion) of the strands (and also self-avoidance). A further simplification is obtained by suppressing the bubbles along the chains, thereby defining a "fork model" or "Y-model". The phase diagram of the equilibrium system displays in both cases a re-entrant region at low T: for a finite range of forces the molecule gets unzipped by *decreasing* the temperature. The dynamics of both the b- and the Y-models in the various phases and on the phase boundary are then studied, by starting from a zig-zag non-equilibrium bound state as the initial condition. We find that in all regimes above or below the critical line in the phase diagram, the time evolutions of the order parameters follow dynamical scaling laws.

The models and their equilibrium phase diagram: We model the two strands of DNA by two directed self and mutually avoiding walks. In two dimensions, on the square lattice (see Fig.1), this means that the two walks are forced to follow the positive direction of the diagonal axis $(1, 1)$ (i.e. the coordinate along the direction $(1, 1)$, to be called the z direction, always increases). The force is then acting along the direction perpendicular to direction z, i.e., $(-1, 1)$: this transverse direction is called the x-direction. By measuring the x separation in unit of the elementary square diagonal, we say that two complementary monomers are in contact when $x = 1$: a (positive) binding energy ϵ is gained for each contact. Due to the geometrical properties of the lattice, all these contacts contributing to the energy involve monomers labelled by the same z-coordinate, as one would require for base pairing in DNA (see Fig. 1).
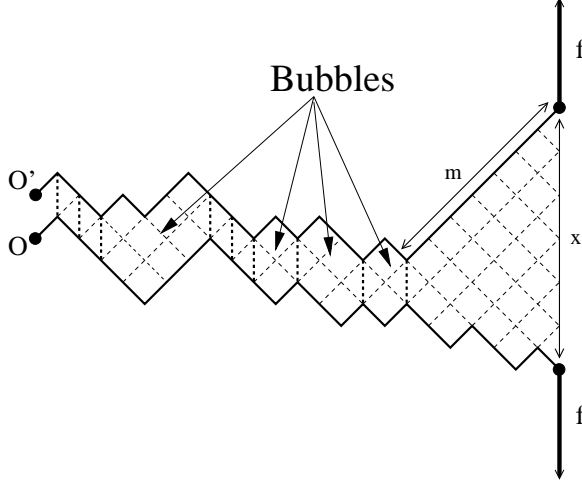
FIG. 1. A typical configuration of the two DNA-strands as modelled on a square lattice. Dashed lines indicate monomers which are in contact. The quantities m and x are graphically represented.

By fixing $\epsilon = +1$ throughout the calculations, all the thermodynamic properties of the system depend on the temperature $T = \beta^{-1}$ and on the force f. We have set $k_B = 1$. The partition function of the two n-step chains, one starting at $(0,1)$ and the other at $(1,0)$ is

$$\mathcal{Z}_n(\beta, f) = \sum_{x \geq 1} d_n(x) \exp\left(\beta f x\right) \sim e^{-n\beta \mathcal{F}}, \quad (1)$$

where $d_n(x)$ represents the fixed distance partition function, i.e., the sum over all interacting pairs of directed chains whose last monomers are at distance x [18] and $\mathcal{F}$ is the free energy density. The quantity $d_n(x)$ whose β dependence has been omitted, obeys simple recursion relations. In $d = 2$, on the square lattice, the recursion relation is

$$d_{n+1}(x) = [2d_n(x) + d_n(x+1) + d_n(x-1)]$$
$$\times \left[1 + \left(e^\beta - 1\right)\delta_{x,1}\right], \quad (2)$$

valid for $x \geq 1$ with the conditions $d_0(x) = \delta_{x,1}$ and $d_n(0) = 0$ for all n. Note that this kind of equation appears also in other models of DNA [17,19] and in studies of random walks adsorption [20]. The model can be asymptotically solved by locating the singularity closest to the origin of its related generating function [21]

$$\mathcal{G}(\beta, f) = \sum_{n=0}^{\infty} z^n \mathcal{Z}_n(\beta, f). \quad (3)$$

A phase transition is indicated by any singular change in the location of the closest singularity.

With some simple calculations a critical line, $f_c(T)$, separating the zipped from the unzipped phase can be obtained

$$f_c(T) = T \cosh^{-1}\left[\frac{1}{2}\frac{1}{\sqrt{1 - e^{-\beta}} - 1 + e^{-\beta}} - 1\right], \quad (4)$$
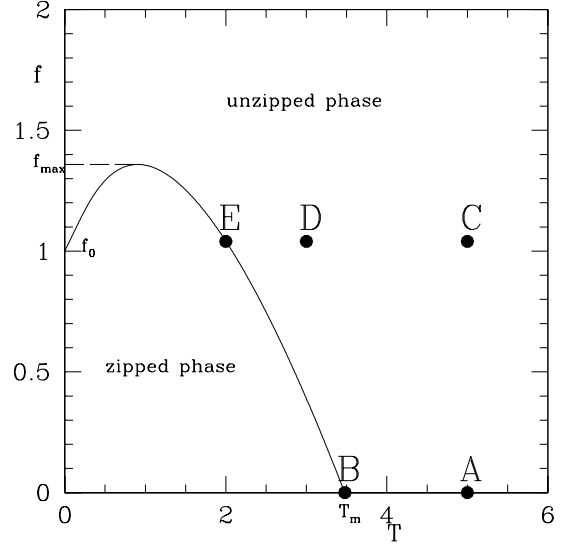
and it has been plotted in Fig. 2.

FIG. 2. The plot of the force vs. temperature phase diagram for the model on the directed lattice.

At $f = 0$ the critical melting temperature is $T_m = \frac{1}{\log 4/3}$, the critical force at $T = 0$ is $f_0 = 1$ whereas for $f > f_{\max} = 1.358806...$ the system is always in the unzipped state. Similar results can be obtained for the physically relevant three dimensional case and for higher dimensions [6]. The average fraction of contacts Θ is zero (not zero), when $f > f_c(T)$ $(f < f_c(T))$ while the average end-to-end distance $\langle x \rangle = -N\frac{\partial \mathcal{F}}{\partial f}$, where N is the number of base pairs in each chain, and the average number of "liberated" monomers (i.e. from the last contact to the end), m (See Fig. 1) have the opposite behavior. The transition line is first order at any point with $f_c(T) \neq 0$ in $d = 2, 3, 4, 5$ and everywhere for $d > 5$.

We notice that there is a re-entrance in the $f - T$ phase diagram. For $f_{\max} > f > f_0$ the usual denaturation transition is present but if the temperature is further lowered the two strands separate again through a "cold unzipping" [22,23].

A further simplification to this model can be obtained by suppressing the bubbles along the chain, i.e. by considering only conformations having the first $N - m$ monomers bounded, whereas the remaining m are separated in a Y-like conformation.

This Y-model will be extremely useful to study the unzipping dynamics and it presents a phase diagram similar to the one previously obtained but, for example, with $T_m = \frac{1}{\log 2}$, $f_0 = 1$ and $f_{\max} = 1.282143...$ [24] in d=2.

Dynamics. We now consider the dynamics of the models previously introduced, the b-model of directed walks and the simplified Y-model. In both cases, we start from a non-equilibrium "zero-temperature" initial condition

with the two chains zipped in a zig-zag configuration, and let the system evolve at a temperature T and under a force f, with T and f chosen so that the equilibrium state is either on or above the critical line. The simpler 2-dimensional case will be presented first and the generalization to higher dimensions will be discussed later.

The five regimes considered are marked A-E in Fig. 2. Numerically, a Monte-Carlo dynamics is used to monitor the time evolution of the order parameters m and x previously introduced (see also Fig. 1). For the dynamics, we selected only local physical moves, so that the model should be the lattice counterpart of the Rouse model in the continuum. In all cases we find that, far from saturation, the order parameters evolve as power laws as functions of time t: in particular we can define two exponents θ_1 and θ_2 as

$$m(t) \sim t^{\theta_1}, \quad \text{and} \quad x(t) - x(0) \sim t^{\theta_2}, \qquad (5)$$

Notice that m and x in Eq. (5) refer to the ensemble average values, but average signs have been omitted for simplicity of notation. We in fact find the following dynamical scaling laws to hold:

$$\frac{m(t)}{N^{d_1}} = G_m\left(\frac{t}{N^{z_1}}\right), \frac{x(t)-x(0)}{N^{d_2}} = G_x\left(\frac{t}{N^{z_2}}\right), \qquad (6)$$

where N is the length of the chains and $G_{m,x}$ are two scaling functions. Eq. 6 also defines the exponents $d_{1,2}$ and $z_{1,2}$ for the two variables. Note that $\theta_1 = \frac{d_1}{z_1}$, $\theta_2 = \frac{d_2}{z_2}$ and that $d_{1,2}$ can be obtained through equilibrium considerations as one requires $m(t) \overset{t\to\infty}{\sim} N^{d_1}$ and $x(t) \overset{t\to\infty}{\sim} N^{d_2}$. The crossover to the equilibrium behavior is described by the "dynamic" exponents $z_{1,2}$. The possibility of the two quantities having different relaxations is kept open by two different exponents.

The values of the exponents in Eqs. (5) and (6) obtained from simulations, for both the Y-model and the b-model, are shown in Table I. They were obtained by collapsing Monte-Carlo data according to eq. (6) and by using a recently proposed search algorithm [26] (see Fig. 3)
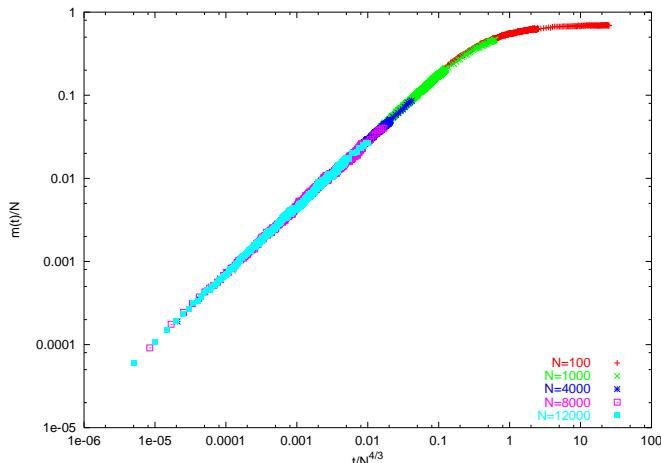
FIG. 3. Plot of $\frac{m(t)}{N}$ vs $\frac{t}{N^{\frac{4}{3}}}$ for various values of N: the collapse of all curves indicates that $d_1 = 1$, $z_1 = \frac{4}{3}$ and $\theta_1 = \frac{3}{4}$.

It is possible to explain the exponents for the Y-model found numerically. There are two relevant mechanisms which can drive the separation of the strands: the unbinding of bases at the bifurcation point and the stretching of the strands at the extremes. The combination of these two processes controls the overall behavior in different regimes.

Regime A: $f = 0$, $T > T_m$: Above the critical temperature the dominance of the entropy implies that at every time step one base pair breaks, yielding a linear behavior with $\theta_1 = 1$ and $d_1 = 1$. Also $x(t)$ tends to increase, up to its equilibrium value $N^{\frac{1}{2}}$: this is reflected in the equilibrium probability distribution $P_{eq}(x)$ which displays an upward derivative at $x = 1$. This suggests (see [25]) that the dynamics of this quantity should be in the same universality class of the one-dimensional Kardar-Parisi-Zhang equation [25], and so $\theta_2 = \frac{1}{3}$, $d_2 = \frac{1}{2}$, and $z_2 = \frac{3}{2}$.

Regime B: $f = 0$, $T = T_m$: In this regime $\theta_1 = \frac{1}{2} = z_1^{-1}$ because at criticality the probabilities to increase and to decrease m are expected to be equal, so that m performs, roughly speaking, a random walk in time with reflecting boundaries at $m = 0, N$. Also for the end-to-end distance, steps toward larger or smaller values of x are equally probable, and this means that the equation obeyed by x should stay in the same universality class as the one-dimensional Edward-Wilkinson equation, and therefore $\theta_2 = \frac{1}{4}$ and $z_2 = 2$.

Regime C: $f > 0$, $T > T_m$: The strands microscopically tend to stretch along the direction of the pulling force. However, once we have pulled the two chains up to an end-to-end distance x, to increase x further by one unit we first need to move all the stretched part, which would take a time typically of order x. In other words, one has $x(t + t_0) \sim x(t) + \frac{t_0}{x}$ and we expect the dynamical exponent θ_2 to be $\frac{1}{2}$ (of course $\theta_1 = 1$ as before and $d_1 = d_2 = 1$).

Regime D: $T < T_m$, $f > f_c(T)$: Here the only microscopic mechanism for opening the fork is through the applied force: the strands must stretch completely in the vicinity of the bifurcation point and only at this point will the fork liberate one more monomer, because otherwise the opening is energetically very unlikely. Thus we expect that $x \sim m$ and, using arguments as done for regime C, $\theta_1 = \theta_2 = \frac{1}{2}$, $d_1 = d_2 = 1$. In ref. [3] it was found, in the mean field approach and in a model resembling our Y-model, that the time necessary to unzip the two strands completely is of the order of N^2. This is in agreement with our analysis, but works only in this regime.

Regime E: $T < T_m$, $f = f_c(T)$: At criticality, one expects that the cost for unzipping and zipping is the same (the equilibrium probability distribution of having

m monomers unzipped or an end-to-end distance equal to x is flat), therefore $x(t + t_0) = x(t) \pm \frac{t_0}{x}$ with equal probability. Therefore, the end-to-end distance makes a random walk in the rescaled time $\frac{t}{x}$ so that $x \sim (\frac{t}{x})^{\frac{1}{2}}$ and $\theta_2(= \theta_1) = \frac{1}{3}$ and $d_1 = d_2 = 1$ since at coexistence there is a finite fraction of liberated monomers.

Another way of obtaining $\theta_1 = \frac{1}{3}$ is to demand that a kink liberated at the fork needs to diffuse out of the end before the next one is released. In other words, the rate of change of m is determined by the diffusion of a kink over a distance m. The latter time-scale being of order m^{-2}, we expect $dm/dt \sim m^{-2}$ which gives $m \sim t^{\frac{1}{3}}$.

This simple model deserves some observations. Remarkably, it displays two different time scales in its dynamics, mirrored in the difference of the exponents $z_{1,2}$ in regimes A and C. The first time scale ($t \sim N^{z_1}$) quantifies the time necessary for the unbinding (or unzipping) of the bases while the second ($t \sim N^{z_2}$) gives the time needed to open (and to stretch whenever $f \neq 0$) the two chains up to their equilibrium end-to-end distance. At $T < T_m$ the two processes are virtually the same, because the unbinding (or unzipping) is dragged by the stretching. However, above T_m, the processes decouple and the unbinding gets faster, being controlled by the temperature, and therefore $z_1 < z_2$.

Furthermore, in the numerical calculations we found large sample-to-sample fluctuations, thereby requiring a huge number of runs to get good averages of $m(t)$ and $x(t)$. This is due to the long time correlation that exists in the system, which keeps samples with different initial histories far apart for any t.

Turning to the b-model with bubbles, amazingly the dynamical exponents in regimes B, E and D with $T \leq T_m$ are the same as found in the Y-model. This establishes that at $T < T_m$ not only for statics, as we saw in the previous section, but also for the dynamics, bubbles are not relevant in the scaling properties (for $T = T_m$ the equality is due to another reason [27]). At $T \geq T_m$, on the other hand, the opening of bubbles heavily affects the base unpairing process, unlike the Y-model case where bubbles are forbidden. The length of the unzipped part in the present case now can change by $\pm l(t)$, where $l(t)$ is the typical length of bubbles, and the motion of the fork point can by no means be approximated by a simple random walk (and so θ_1 changes as shown in Table I). The quantity $x(t)$ instead has a dynamics in the b-model similar to the fork case and indeed θ_2 is the same for both the models in all regimes. We show in Fig.3 the collapse leading to $\theta_1 = \frac{3}{4}$ in regime A.

An important question is that of the dependence of these results on dimensionality. As for the Y-model, the arguments we gave suggest that there be no d-dependence. For the b-model, instead, this should be true only in regimes D and E for $T < T_m$, where the Y-model gives the exact result; at $T \geq T_m$, on the other hand, bubbles play a dominant role and so we expect a dependence on d. We confirmed this picture with some

calculations on a simpler model which should be in the same universality class of the one under study: that of a single random walk, pinned at the origin by an attractive interaction and subject to a stretching external force. In this system m is defined as the number of monomers from the last visit to the origin to the end of the walk. For $T > T_m$, in regimes A and C, our calculations show that the exponent θ_1 increases as dimension increases, apparently with no upper critical dimension. Just at criticality at zero force, instead, we find that the exponent θ_1 is very close to $\frac{1}{2}$ in any d. The emerging picture of robust results for $T < T_m$ and model-dependent dynamics for $T \geq T_m$ would be preserved even if, in the original models, the directedness constraint is relaxed (as is the case for the statics [23]).

The arguments presented so far could be generalized to add other ingredients of dynamics also. An example is the nonlocal effects in dynamics, as is the case $e.g.$ in the Zimm model. In ref. [3], the author suggests that, in the regime we call D, in the mean field approximation, non-locality could speed up the opening so that $\theta_{1,2}$ would be $\frac{1}{1+u}$ instead of $\frac{1}{2}$ (u is the exponent characterizing the length dependence of the mobility as defined, e.g., for the Zimm model, see [3] for the notation and [29] for a review). In regime E, we can combine our arguments with the same reasoning to get $\theta_1 = \theta_2 = \frac{1}{2+u}$. As we expect, the Rouse model results are obtained with $u = 1$.

Lastly, the above analysis can also be extended to binary disorder in the contact potential, which is of course a realistic feature to be included in the model, $i.e.$ the energy of the contact of the i-th base may be $\epsilon_i = \epsilon + \Delta_i$, Δ_i being a random variable with binary distribution and zero mean. The Y-model offers a good starting point for the study of the effects of heterogeneity, because the critical line of the quenched model can be proved to be the same as that of the pure model with energy ϵ. If we call $\mathcal{F}(m)$ the free energy density of a configuration with m (out of N) unzipped monomers, we expect on general grounds that $P(m,t)$, the probability of having m monomers unzipped at time t, will obey a master equation with transition rates $W_{\pm,m}$ depending on the realization of disorder, $i.e.$ we expect that $W_{\pm,m} \propto \min\left\{e^{\mp\beta N \frac{d\mathcal{F}(m)}{dm}}, 1\right\}$, with $N\beta\frac{d\mathcal{F}(m)}{dm} = +\frac{\Delta_{N-m}}{T} + \frac{\epsilon}{T} - \log(1 + \cosh(\frac{f}{T}))$ [28], which can be seen to consist of a zero-mean random "noise" ($\frac{\Delta_{N-m}}{T}$) plus a "bias". We thus believe that the dynamics of the Y-model can be mapped onto Temkin's model of a random walker in a random environment [30] (provided that at $T < T_m$ we rescale time as described above in regimes D and E), so that, following Ref. [31], there will be a region around the critical line, at $T < T_m$, in which $m, x \ll t^{\frac{1}{2}}$ (and just on the critical line at $f \neq 0$ one is tempted to expect $m, x \sim \left(\log\left(\frac{t}{x}\right)\right)^2$). The quantities m, x are now quenched averages over realizations of disorder. The scenario we propose is sketched in Fig.4. The curve bounding the region where, at $T < T_m$, disorder

should be important for the dynamics has been found by applying the criterion of Ref. [31] to the system with the above transition rates. This curve coincides with the critical line of the static model with annealed disordered. Preliminary runs at very low T suggest that as $T \to 0$, for a given realization of disorder and with any force between ϵ_1 and ϵ_2 (the two binding energies), the unzipping will take place as far as the first more attractive base pair is found. Besides, the probability that the monomer of index m_0 will ever be unzipped decays exponentially: $P(m_0) \propto 2^{-m_0}$. This is consistent with the mapping suggested above. A detailed study of the effect of disorder will be done elsewhere.

Conclusion. We obtained the phase diagram of a lattice model for the unzipping transition of a double stranded DNA by a force. This model incorporates both the mutual and self-avoiding nature of the two strands and the equilibrium problem can be solved exactly. A still simpler model has been defined by suppressing the bubbles that are important for thermal denaturation. This simpler version is also exactly solvable and is shown to retain the basic features of the b-model. Thanks to the exact knowledge of the phase boundary, we have been able to investigate the dynamics of unzipping from a non-equilibrium bound state both on and away from the phase boundary. The dynamics shows scaling behaviors in different regimes of the phase diagram. These scalings in most cases could be understood from the plausible mechanisms of unzipping and denaturation as discussed in the previous sections. We end with two notable features. In the case of the b-model with bubbles, the unzipping at high temperatures remains a puzzling issue, especially the dynamic exponent $z_1 = \frac{4}{3}$ with or without force. We believe that this has to do with the statistics of bubbles, though no satisfactory answer could be found. This remains an open problem. Lastly, on a positive note, the unzipping dynamics on the phase boundary in the presence of a force is found to be distinctly different from the thermal denaturation at zero force. Whether a real biological system takes advantage of these differences to distinguish the unzipped region of DNA from a fluctuation-induced bubble formation remains to be probed.
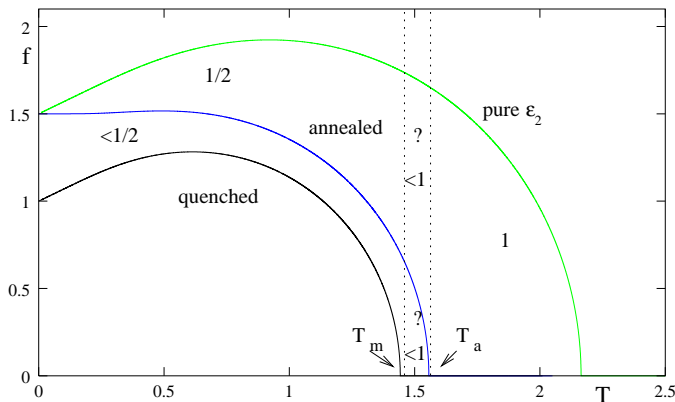

FIG. 4. Plots of the phase diagram for homo-DNA (top) made up of the more attractive base ($\epsilon_2 > \epsilon_1$), and for the annealed (middle) and quenched (bottom) disordered models. The numbers refer to the values of the exponent θ_1 in the various regions of the phase diagram, which we believe to hold on the basis of the mapping onto Temkin's model. Note that above the annealed critical line at $T < T_m$ and everywhere at $T > T_a$ the pure system results are recovered. Interestingly, the annealed line does not show the re-entrant behavior found in Section II and in the quenched system. "?" indicates the regime where we do not have numerical evidence in support of our results. We took $\epsilon_2 = 1.5$ and $\epsilon_1 = 0.5$ in the calculations.

Regime	d_1	z_1	θ_1	d_2	z_2	θ_2
A:Y	1	1	1	1/2	3/2	1/3
A:b	1	4/3	3/4	1/2	3/2	1/3
B:Y	1	2	1/2	1/2	2	1/4
B:b	1	2	1/2	1/2	2	1/4
C:Y	1	1	1	1	2	1/2
seb C:b	1	4/3	3/4	1	2	1/2
D:Y	1	2	1/2	1	2	1/2
D:b	1	2	1/2	1	2	1/2
E:Y	1	3	1/3	1	3	1/3
E:b	1	3	1/3	1	3	1/3

TABLE I. "Dynamic" and equilibrium exponents for the Y-model (Y) and the b-model with bubbles (b) as defined in eq.(6). The regimes A,B,C,D and E are those shown in Fig.1.

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[18] Notice that along the x-direction the configurations are those of two interacting random walks which never intersect each other. This differs from the model considered by Poland and Scheraga [17] with $f = 0$, where the two walks can intersect. This difference seems at first subtle but it is indeed crucial: in our model a finite temperature transition exists in the other one not.

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[24] The critical line of this model is given by $f_c(T) = T \cosh^{-1}\left[\exp\frac{1}{T} - 1\right]$ and can be easily obtained by modifying the recursion relation of $d_n(x)$ in the case $x = 1$.

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[27] The exponent θ_1 in regime B in the b-model can be explained if we postulate that a waiting time τ is needed for the merging of a bubble into the liberated part (and also for the opposite process since at criticality the two processes equilibrate). The waiting time may reasonably be proportional to $l(t)^2$, the time needed for the distance between the ends of the just opened bubble (which should obey the Edward-Wilkinson equation, [25]) to get to an "equilibrium" value $\propto l(t)^{\frac{1}{2}}$, and this gives $m \sim l(t)\left(\frac{t}{l(t)^2}\right)^{\frac{1}{2}} = t^{\frac{1}{2}}$.

[28] At $f = 0$, $N\beta\frac{d\mathcal{F}(m)}{dm}$ displays also a subleading (for large m) entropic contribution which in $d = 2$ is $-\frac{1}{2m}$. This should not affect the mapping proposed in the text except perhaps just at the critical temperature T_m.

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