Appendix B: Fronts, roughening and universality

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Models for spatial invasion often adopt a reaction-diffusion formalism, treating population densities as continuous variables. A deterministic reaction-diffusion system may yield an analytic approximation for invasion speed, given by the asymptotic velocity of a traveling wave [Andow et al. 1990, Caraco et al. 2002, Murray 2003]. But traveling waves invoke infinitesimal population densities [Durrett and Levin 1994, Pachepsky and Levine 2011], and the linearized front can be "pulled" by reproduction and dispersal of the invader at locations where its population density is near 0 [Lewis and Kareiva 1993, Snyder 2003]. Deterministic reaction-diffusion theory neglects the discreteness of individuals, the fundamental source of endogenous, random fluctuations, and consequently overestimates the velocity of an individual-based, dispersal-limited dynamics [Escudero et al. 2004]. Therefore, deterministic reaction-diffusion equations, and their generalizations, oversimplify the dynamics of rarity [Clark et al. 2003]; they cannot capture consequences of strong dispersal limitation, in particular, the spatially correlated variability along the interface we studied experimentally.

Discrete (individual-based) models reveal effects of nonlinear, stochastic growth processes driving an ecological interface [Wilson 1998, Moro 2001]. Discrete models predict front-propagation behaviors that differ from results of deterministic diffusion models

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[van Saarloos 2003]. When dispersal is limited to a local neighborhood, the interface is "pushed" at a velocity less than that of the corresponding deterministic diffusion model [Moro 2003]. As a stochastic model's interface roughens, the distance over which density fluctuations are correlated grows [Rácz and Gálfi 1988, Majumdar and Comtet 2004]; consequently, the front-runner's lead is an extreme value among dependent random variables.

Given the assumption that a spatially clustered invader displaces a resident competitor, the front is pushed into a meta-stable medium

[Korniss and Caraco 2005, O'Malley et al. 2006a]. If the same invader were to propagate into empty space (i.e., a region where the invader does not encounter biotic resistance), the front would be pushed into an unstable medium. Invasion velocity is, of course, slower in the former case [Allstadt et al. 2009]. Interestingly, the two fronts will roughen similarly; the same interface-length dependent scaling will emerge.

Assuming an ecological interface advances as a pushed front, consider the scaling relationships of a self-affine interface [Barabási and Stanley 1995]. During development, roughness increases with time according to $\langle w^2(L,t) \rangle \sim t^{2\beta}$. The time of crossover to statistical equilibrium increases with interface length according to $t_{\times} \sim L^z$. After saturation, roughness increases with interface length according to $\langle w^2(L,\infty) \rangle \sim L^{2\alpha}$. Figure 1 summarizes these relationships graphically.

Our scaling model is based on combined analytical and computational study of stochastic partial differential equations for surface growth. A lattice-based model should, for proper choice of length scale, induce a continuum equation which approximates an interface defined by discrete heights $h_y(t)$ with a smooth curve [Barabási and Stanley 1995]. The resulting equation for $\partial h_y(t)/\partial t$ can include both growth terms depending on the



Figure 1: Roughening over time, both scaled logarithmically. $\langle w^2 \rangle$ increases as a power law during interface development. Time of crossover and degree of roughening at saturation both scale with interface length.

 $\partial h_y(t)/\partial y$, the local gradient in height, and a noise term. Scaling relationships suggested by analysis of the continuum equation can be verified in simulation [Kardar et al. 1986].

Different models for individual-level demographic processes driving invasion may exhibit the same dependence of roughening on time, and the equilibrium width may exhibit the same dependence on interface length. Such roughened interfaces belong to the same "universality class;" universality offers powerful generalization. O'Malley et al. (2006b) analyzed a model for an advancing front in a habitat where dispersal-limited species compete for growth sites. They found that the model's roughening behavior belongs to the KPZ universality class, for Kardar-Parisi-Zhang [Kardar et al. 1986]. For the broad class of models exhibiting KPZ universality, roughening of a one-dimensional interface (hence the habitat has two dimensions) implies that the dynamic exponent z = 3/2, the growth exponent $\beta = 1/3$, and the roughening exponent $\alpha = 1/2$. The growth exponent of our experimental fronts was close to 1/3, but the roughening exponent was < 1/2. Hence, the clover growth we observed was more "space-filling" than an interface belonging to the KPZ universality class.

Despite successful application of KPZ scaling relationships to a series of real-world questions, the model's assumptions are fragile. The nonlinear stochastic differential equation underlying the derivation of the scaling exponents includes additive Gaussian noise, uncorrelated in space and time. If the noise, instead, has spatial or temporal power-law correlation, or if the noise remains an uncorrelated, but non-Gaussian process, then the exponents change [Sneppen 1992].

References

- [Allstadt et al. 2009] Allstadt A, Caraco T, Korniss G (2009) Preemptive spatial competition under a reproduction-mortality constraint. J Theor Biol 258:537–549.
- [Andow et al. 1990] Andow DA, Kareiva PM, Levin SA, Okubo A (1990) Spread of invading organisms. Land Ecol 4:177–188.
- [Barabási and Stanley 1995] Barabási A-L, Stanley HE (1995) Fractal concepts in surface growth. (Cambridge University Press, Cambridge). 386 pp.
- [Caraco et al. 2002] Caraco T, Glavanakov S, Chen G, Flaherty JE, Ohsumi TK, Szymanski BK (2002) Stage-structured infection transmission and a spatial epidemic: a model for Lyme disease. Am Nat 160:348–359.
- [Clark et al. 2003] Clark JS, Lewis M, McLachlan JS, HilleRisLambers J (2003) Estimating population spread: what can we forecast and how well? Ecology 84:1979–1988.

- [Durrett and Levin 1994] Durrett R, Levin SA (1994) The importance of being discrete (and spatial). Theor Pop Biol 46:363–394.
- [Escudero et al. 2004] Escudero C, Buceta J, de la Rubia FJ, Lindenberg K (2004) Extinction in population dynamics. Phys Rev E 69:021908, 9 pp.
- [Kardar et al. 1986] Kardar M, Parisi G, Zhang Y-C (1986) Dynamic scaling of growing interfaces. Phys Rev Lett 56:889–892.
- [Korniss and Caraco 2005] Korniss G, Caraco T (2005) Spatial dynamics of invasion: the geometry of introduced species. J Theor Biol 233:137–150.
- [Lewis and Kareiva 1993] Lewis MA, Kareiva P (1993) Allee dynamics and the spread of invading organisms. Theor Pop Biol 43:141–158.
- [Majumdar and Comtet 2004] Majumdar SN, Comtet A (2004) Exact maximal height distribution of fluctuation interfaces. Phys Rev Lett 92:225501, 4 pp.
- [Moro 2001] Moro E (2001) Internal fluctuations effects on Fisher waves. Phys Rev Lett 87:238303, 4 pp.
- [Moro 2003] Moro E (2003) Emergence of pulled fronts in fermionic microscopic particle models. Phys Rev E 68:025102, 4 pp.
- [Murray 2003] Murray JD (2003) Mathematical biology, Vol 2. (Springer, New York).
- [O'Malley et al. 2006a] O'Malley L, Basham J, Yasi JA, Korniss G, Allstadt A, Caraco T (2006a) Invasive advance of an advantageous mutation: nucleation theory. Theor Pop Biol 70:464–478.
- [O'Malley et al. 2006b] O'Malley L, Kozma B, Korniss G, Rácz Z, Caraco T (2006b) Fisher waves and front propagation in a two-species invasion model with preemptive competition. Phys Rev E 74:041116, 7 pp.

- [Pachepsky and Levine 2011] Pachepsky E, Levine JM (2011) Density dependence slows invader spread in fragmented landscapes. Am Nat 177:18–28.
- [Rácz and Gálfi 1988] Rácz Z, Gálfi L (1988) Properties of the reaction front in an $A + B \rightarrow C$ type reaction-diffusion process. Phys Rev A 38:3151–3154.
- [Sneppen 1992] Sneppen K (1992) Self-organized pinning and interface growth in a random medium. Phys Rev Lett 69:3539–3542.
- [Snyder 2003] Snyder RE (2003) How demographic stochasticity can slow biological invasions. Ecology 84:1333–1339.
- [van Saarloos 2003] van Saarloos W (2003) Front propagation into unstable states. Physics Rep 386:29–222.
- [Wilson 1998] Wilson W (1998) Resolving discrepancies between deterministic population models and individual-based simulations. Am Nat 151:116–134.