All My Sons: A Model of Evolutionary Branching

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Introduction

Of the many ideas introduced by Darwin[1] in his classic work, one concerned the branching of species. In the fourth chapter of "The Origin of Species" Darwin discusses the process of speciation, and describes a mechanism to explain it. He calls this mechanism by the "divergence of character principle" and summarizes it as: "[...] during the modification of the descendants of any one species, and during the incessant struggle of all species to increase in numbers, the more diversified these descendants become, the better will be their chance of succeeding in the battle of life. Thus the small differences distinguishing varieties of the same species, will steadily tend to increase till they come to equal the greater differences between species of the same genus, or even of distinct genera."

[1] Charles Darwin. *On the Origin of Species by Means of Natural Selection.* John Murray, London, 1859

Evolutionary branching, or adaptive speciation, is a feature that is hard to account for in usual mutation-selection systems.: it requires adaptive dynamics, which makes a link between ecological and evolutionary theory. It considers both the usual influence of the environment on the population through fitness and the reverse influence of the population on the environment as the ecological interactions modify fitness.

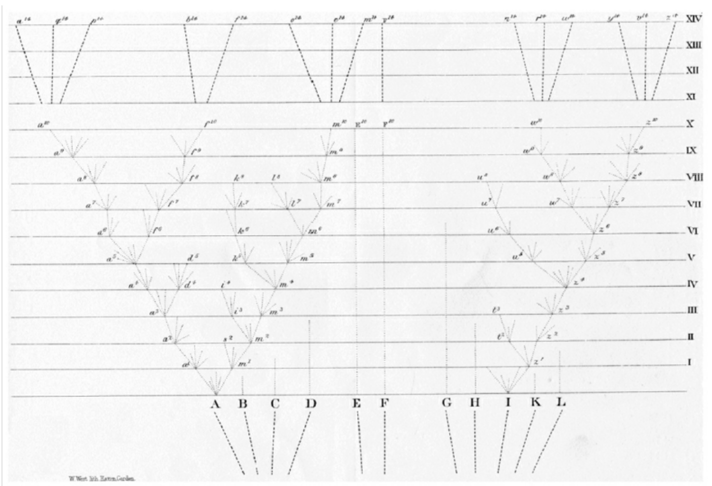

Figure 1: Darwin's diagram of evolutionary branching.

Genleys *et al.*[2] proposed a modified Fisher-type equation, a special case of the general stochastic models[3], in which the morphology of an individual is represented by a one-dimensional variable x, and the function $f(t, x)$ represents the density of individuals which have the morphology x at time t (density in the sense that the number of individuals with morphologies in the range x to $x + dx$ is $f(x, t)dx$). The model then assumes that the population at x will increase at a maximum rate aK, but that increase is opposed by

[2] S. Genieys, N. Bessonov, and V. Volpert. Mathematical model of evolutionary branching. *Mathematical and Computer Modelling*, 49(11-12):2109–2115, June 2009 2009

[3] Nicolas Champagnat and Sylvie Méléard. Invasion and adaptive evolution for individual-based spatially structured populations. *Journal of Mathematical Biology*, 55:147–188, 2007. 10.1007/s00285-007-0072-z

a competition for resources, and that the competition is strongest for individuals with similar morphology. The competition, then, is given by

$$C(f)(t,x) = \int_{\Omega} \Phi(x - x')f(t,x')dx',$$

where the integration is taken over the whole range of morphologies, Ω, but the function Φ has limited range. For example, one may use the rectangular function

$$\Phi(x) = \frac{1}{2b} \sqcap (-b, b|x)$$

where $\sqcap(a, b|x)$ is 1 for $a < x < b$, 0 elsewhere. There is also a tendency for the population to spread in the morphological space from generation to generation. This described by a diffusion-like term, proportional to the gradient of f: a highly specialised population will tend to diversify. The overall equation is then

$$\frac{\partial f}{\partial t} = af(K - C(f)) + d\frac{\partial^2 f}{\partial x^2}$$

where the first term on the right hand side describes ecological interactions whereas the second term describes evolutionary phenomena.

If we explore this equation we should find that diversification appears only when the evolutionary phenomena are slow enough compared to the ecological ones (in fact for the competition kernel described above the homogeneous solution $f = K$ is stable). Set up a numerical solution using a regular mesh in the $0 \leq x \leq L$ direction, with centred finite differences for the derivative and a trapezium rule for the integration. Use periodic boundary conditions. Begin with an explicit forward Euler method for the time derivative. Consider a range of parameters and starting conditions, including $a = 1$, $K = 1$, $b = 0.5$, $d = 0.001$, $L = 2$ starting from a $f = 1 + \text{small random part}$, and $a = 1$, $K = 1$, $b = 0.5$, $d = 0.001$, $L = 1.7$ starting with $f = 0$ except for $f(0.85) = 1$.

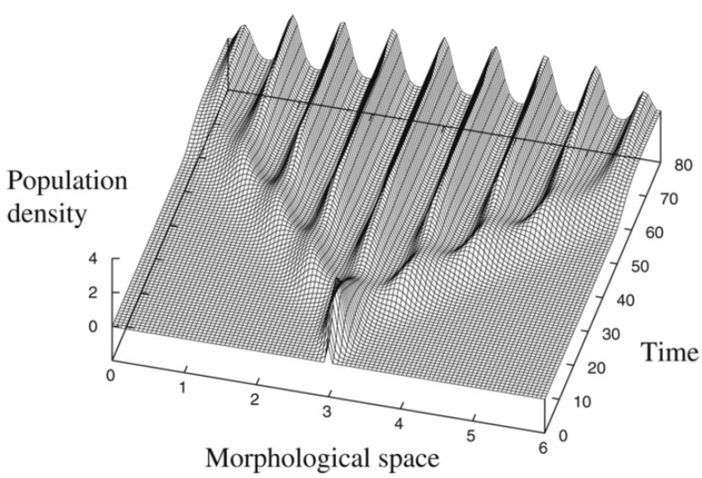

Figure 2: Numerical simulation with similarity to Darwin's diagram of evolutionary branching, with the parameters $a = 1$, $K = 1$, $b = 0.5$, $d = 0.001$, $L = 7$.

You will almost certainly find that the time-steps you need to use are so short that the computation time becomes prohibitive. Modify your numerical scheme to use a centred Euler implicit scheme. You will need to be careful about implementing the integration in your calculation, and you will find that the band-width of the matrix is much wider than that of the tridiagonal matrices discussed in the lectures on time-dependent heat flow, but as the matrix only needs to be inverted once this should not make the computation too lengthy.

Consider different kernel functions Φ, including unsymmetrical ones.

Possible Extensions

The problem can be extended to consider two morphological parameters. If time permits, try to extend your model to this situation.

References

[1] Nicolas Champagnat and Sylvie Méléard. Invasion and adaptive evolution for individual-based spatially structured populations. *Journal of Mathematical Biology*, 55:147–188, 2007. 10.1007/s00285-007-0072-z.

[2] Charles Darwin. *On the Origin of Species by Means of Natural Selection*. John Murray, London, 1859.

[3] S. Genieys, N. Bessonov, and V. Volpert. Mathematical model of evolutionary branching. *Mathematical and Computer Modelling*, 49(11-12):2109–2115, June 2009 2009.

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