

Comment: The Geographical Structure of Populations

Stanley Sawyer

Peter Jagers has given an excellent description of population models of branching process type and of how easy it is to obtain information about population structure in branching process models. Although Jagers has not done so explicitly, one can handle geographical structure as well by including the position of an individual in its "genotype." Then a movement or "migration" is modeled as a death together with the birth of an offspring at a nearby location, and in this way one can model the geographical distribution of a population as well as geographically dependent "life patterns." It is useful to use the term "branching random field" (BRF) for a branching-process description of a population distributed in space.

Perhaps the main reason why branching process models are not more widely used is the assumption that individuals (and their offspring) must develop independently of their sibs (and their offspring). Thus there is no easy way to model interactions between sibs, for example those caused by the finite carrying capacities of environments. When thinking about population models in biology, I like to think about the distribution of rabbits in my suburban neighborhood. Most yards in my area have enough shrubbery to easily support 5–10 rabbits. If the number of rabbits in any yard grew much larger than that, the homeowner (or local predators) would take an interest, and in any event there may not be enough forage. Occasionally there are no rabbits, due perhaps to either an especially cold winter or to a visit by an especially effective predator. The yard will then remain empty until it is recolonized from the outside.

While local extinction and recolonization are naturally modeled in a branching random field, the effect of local carrying capacity is not. Local population bursts of arbitrarily large size can occur in branching models. The purpose of this comment will be to try to compare their effect on the distribution of populations, in comparison with models which have strict local carrying capacities built in.

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The conclusion will be that the branching random field is a good approximation for some purposes and might be preferable in those cases because of the ease of analysis. A second conclusion will be that the instabilities associated with critical branching random fields (i.e., Malthusian parameter $\alpha = 0$) may not be as bad an approximation to nature as one might otherwise suspect.

Migration models in the genetics and ecological literature are often versions of the "stepping stone" model of Kimura and Malécot (see, e.g., Nagylaki 1986, 1989; Sawyer, 1976a). Stepping stone models assume a fixed array of "colonies" and are essentially branching random fields conditioned on the events that each colony always has a fixed predetermined size. One is then interested in the distribution of similarity as a function of distance, or in the distribution of subtypes within the larger population. In the sense of a constraint on total population size, the "stepping stone" analog of the Galton–Watson process without geographical structure is the Wright–Fisher model. For definiteness, we consider a stepping stone model whose colonies are the d -dimensional lattice J^d with nearest-neighbor migration but positive probability of staying put, and assume the simplest type of branching random field for comparison: (a) there is only one type, (b) surviving individuals die and have offspring at constant Poisson rates, (c) individuals are distributed in d -dimensional Euclidean space R^d , (d) the "migration" process is Brownian motion (i.e., individuals follow independent Brownian motion processes between birth events) and (e) the initial state of the branching random field is a Poisson random field with mean density $r > 0$.

Suppose we are interested in the distribution of the surviving offspring of a typical individual whose offspring have survived. Equivalently, assume that the individuals are initially of distinct types, and consider the size and spatial distribution of a typical surviving type at time t . For a stepping stone model, this can be measured by the probability $I(t, 0, x)$ that two individuals chosen randomly at time t , one at 0 and one at x , belong to the same subtype. Then for dimensions $d \leq 2$

$$(1) \quad \lim_{t \rightarrow \infty} I(t, 0, x) = 1 \quad \text{all } x \in J^d, d \leq 2$$

(Sawyer, 1976a), indicating that clumps of larger and larger size form naturally as time progresses. (If $d > 2$, the limit is strictly between zero and one.) It follows from the argument that Jagers quotes that each individual clump or lineage has finite lifetime and must eventually die out. Nevertheless, the lineages that exist at time t can be quite large. As an indication of their size,

$$I(t, 0, x_c(t)) \rightarrow \sqrt{\frac{2}{\pi}} \int_c^\infty e^{-y^2/2} dy$$

(2) for $x_c(t) \sim Ac\sqrt{t}$, $d=1$, $c > 0$,

$$I(t, 0, x_c(t)) \rightarrow 1 - c$$

for $|x_c(t)| \sim t^{c/2}$, $d=2$, $0 < c < 1$,

as $t \rightarrow \infty$ (Sawyer, 1977). The corresponding results for branching random fields depend on the Malthusian parameter α . The results for $\alpha = 0$ are closest to the stepping stone case. Then (1) holds for dimensions $d \leq 2$, indicating that clumps also form in BRF's for $d \leq 2$. The size of the branching process clumps is indicated by the relations

$$I(t, 0, x_c(t)) = c$$

(3) for $x_c(t) \sim \sqrt{2t \log t}$, $d = 1$, $0 < c < 1$,

$$I(t, 0, x_c(t)) = c$$

for $|x(t)| \sim A_c\sqrt{t}$, $d = 2$, $0 < c < 1$,

for large t (Sawyer, 1976b). The similarity of (2) and (3) suggests that the lack of a bound on local carrying capacity has only a small effect on the extent of these clumps. However, the *density* of individuals within the branching-process clumps becomes infinitely large. Let $w_0(t, x) dx$ be the expected number of individuals at x of the same type as an individual at 0. Then $w_0(t, x) \sim C\sqrt{t}$ for fixed x if $d = 1$ ($\alpha = 0$) and $\sim C \log t$ if $d = 2$ (Sawyer, 1976b). If $N(A, t)$ is the number of individuals at time t in an arbitrary bounded set $A \subset R^d$, then $N(A, t) \rightarrow 0$ in probability at $t \rightarrow \infty$ for $d \leq 2$. If $d = 1$, $N(A, t) \rightarrow 0$ a.s. (i.e., A eventually becomes forever empty), but a.s. A is visited at increasingly rare large times if $d = 2$ (Sawyer and Fleischman, 1979). Also, $\sqrt{t}P(N(A, t) > c\sqrt{t}) \rightarrow A_1(c)$ for $d = 1$ ($c > 0$), and $\log tP(N(A, t) > c \log t) \rightarrow A_2(c)$ for $d = 2$ (Fleischman, 1978).

As Jagers suggests, the population structure of branching random fields for $\alpha > 0$ is quite regular, and, with geographical structure, no large irregu-

lar clumps or open spaces appear. Nevertheless, the stepping stone results suggest that the clumping that occurs with $\alpha = 0$ may be an important part of nature, although the arbitrarily high local densities is probably not.

As another point of comparison, assume that individuals mutate to a new subtype at a constant rate $u > 0$, as in Taib's (1987) model. Each new type is new to the population and has the same birth-and-death and migration behavior. Let $I(t, 0, x)$ be the probability that individuals found at time t at positions 0 and x have the same type. Then $I(t, 0, x) \rightarrow I(0, x)$ as $t \rightarrow \infty$ in the stepping stone model, where $0 < I(0, x) < 1$. The asymptotic behavior of $I(0, x)$ for large x gives the likelihood that distant individuals can have the same genotype without providing evidence for selective advantage. However, in the BRF model, $\lim_{t \rightarrow \infty} I(t, 0, x) = 0$ for all x if either $\alpha > 0$ or $\alpha = 0$, $d \leq 2$ (Sawyer, 1976b). The reason for the BRF results is as follows. If $\alpha > 0$, a constant proportion of initial individuals have surviving offspring, and each kinship becomes increasingly uniformly distributed in space. Thus a randomly chosen pair of individuals is likely to have no common ancestors, since time $t = 0$, and as $t \rightarrow \infty$ cannot be the same type. Similarly, random pairs of individuals in a high-density local clump have relatively ancient common ancestors in a critical BRF.

It is comforting to know that Kimura's result that, for neutral mutations, the population-wide substitution rate is the same as the individual mutation rate also holds for these very general branching population models. Taib (1987) and Jagers correctly identify Kimura's result as the equivalence of a backwards and a forwards mutation rate. Nevertheless, it is interesting to note that, in their models with $\alpha > 0$, there is no such thing as a population-wide substitution rate: A randomly chosen pair of individuals from a supercritical branching process will have common ancestors only in the first few generations of the process (Bühler, 1971), and so will tend to share no mutations that were not present when their species began. Most biological models assume that contemporary individuals are more closely related to one another than to the common ancestor of the species, but this may not be correct for a rapidly expanding population.