

# Comment: The Geographical Structure of Populations

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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  $d \leq 2$

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