

# MODELING EMERALD ASH BORER DISPERSAL USING PERCOLATION THEORY: ESTIMATING THE RATE OF RANGE EXPANSION IN A FRAGMENTED LANDSCAPE

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## ABSTRACT

The dispersal of organisms is rarely random, although diffusion processes can be useful models for movement in approximately homogeneous environments. However, the environments through which all organisms disperse are far from uniform at all scales. The emerald ash borer (EAB), *Agrilus planipennis*, is obligate on ash (*Fraxinus* spp.) in a widespread but slightly aggregated and spatially correlated pattern at landscape scales. Figure 1 shows the distribution of ash in Southeast Michigan and North Ohio. Modeling random dispersal through a landscape with pattern at a range of scales cannot be done with diffusion processes alone: a mechanism is required to model the spatial structure of the habitat itself.

Whereas *diffusion* processes ascribe the random, “drunkard’s” walk or ‘Polya process’ to the quantity moving, in *percolation* processes, the random movement is determined by the structure of the medium—for example, water “percolating” through ground coffee in a percolator or filter.

The structure of square lattices, such as the 1-km<sup>2</sup> cell map of ash density in Figure 1, are defined by the probability,  $p$ , that adjacent cells are connected. This probability is a good measure of the degree of fragmentation of the landscape: at low  $p$ , the landscape is made up of a large number of disconnected clusters, while at high  $p$ , the landscape is nearly uniform, with a small number of small voids. A characteristic of square lattices is that, at the critical value of  $p = p_c \approx 0.6$ , a large number of clusters coalesce into a single “super-cluster” that spans the lattice. The appearance of the spanning cluster occurs very rapidly near  $p = 0.6$  in a “phase transition” (Figure 2) that permits percolation across the lattice.

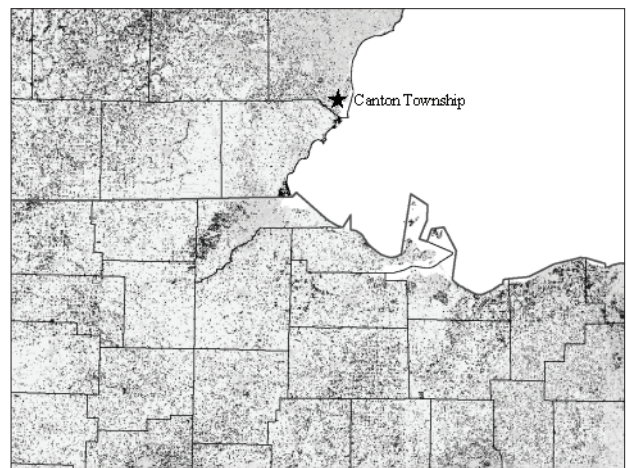


Figure 1. Percolation on a 320 x 400 quadratic lattice representing ash distribution in 1-square-kilometer cells.

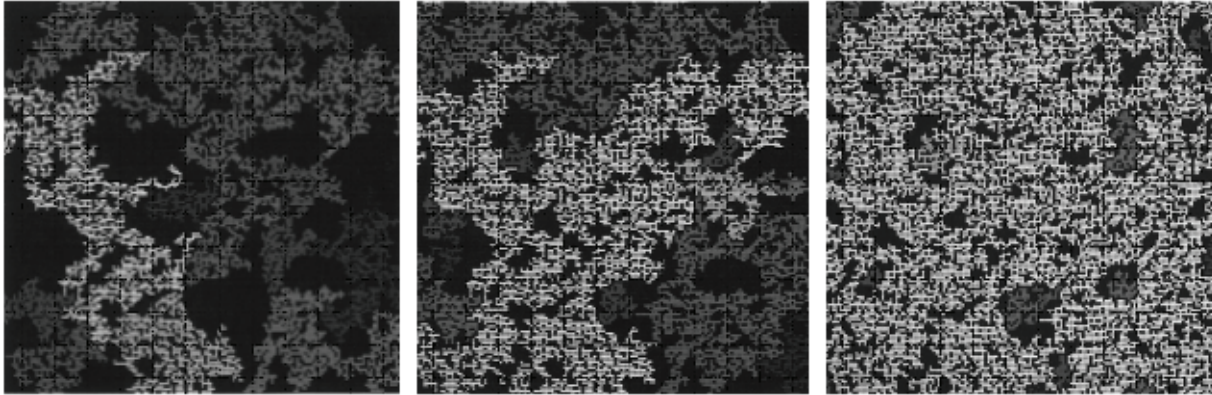


Figure 2. Increasing the occupation probability  $p$  from 0.58 (left) to 0.62 (right), many clusters combine in a “phase transition” at  $p = p_c \approx 0.6$  (center) to span the lattice. The parameter  $p$  is a useful variable to quantify landscape fragmentation.

For organisms capable of moving between clusters, a population can span lattices with  $p$  well below the critical value of 0.6. Thus, the speed with which organisms can cross landscapes will depend on their ability to cross the gaps in the landscape as well as the degree of fragmentation of the landscape. Their ability to cross the gaps is determined by the shape of the relationship between dispersal distance ( $D$ ) and numbers dispersing ( $N$ ). A general function relating  $N$  and  $D$  is  $N = \exp(a + b \cdot D^c)$ , where  $a$  specifies the source population,  $b$  defines the distance scale, and  $c$  defines the curvature. When  $c = 2$ , dispersal is pure diffusion by the Polya or drunkard’s walk, and as  $c \rightarrow 0$ , the dispersal curves become increasingly steep, with very long tails representing a small number traveling extreme distances. The diffusion function was fitted to flight endurance data of gravid female EAB obtained from flight mills (Figure 3), and an estimate of  $c = 1.7$  was obtained.

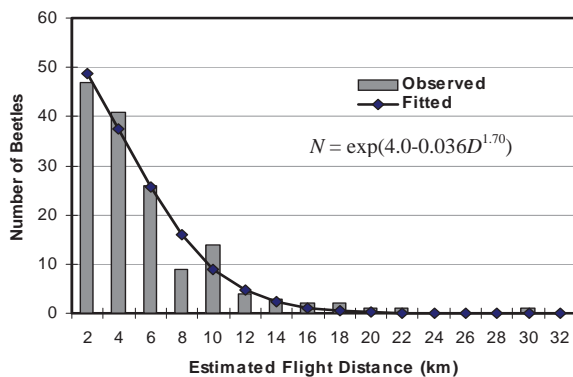


Figure 3. Observed and fitted flight range of gravid female emerald ash borer on flight mills.

reproduction rate of  $r = 10$  and an offspring sex ratio of 50%. Flight mill data show that mated females are most likely to fly long distances and thereby found new populations; thus, the net production of migrants  $r_m = 5$ . To reduce the intense computational requirements of the simulation, only the flights of females were modelled. Ash trees were assumed dead four generations following invasion. Simulations were run until EAB had spanned the map either north-south or east-west. The time in generations taken to span the map and the proportion of ash-populated cells invaded were then recorded.

To model EAB dispersal through the fragmented ash landscape of southeast Michigan and north Ohio, we have combined transport between cells defined by the diffusion function with percolation processes in a cellular automaton model that “flies” EAB between  $1 \text{ km}^2$  cells with ash basal area represented in Figure 1. Population growth was proportional to the ash basal area in each cell. Simulations were run for 90 combinations of  $c$  and  $p$  with the population origin at Canton Township, Michigan, for one gravid female having a net

In general, the longer it took to span the map, the more cells were occupied (Figure 4). In particular, the lower the habitat fragmentation (high  $p$ ) at high  $c$ , the more rapidly spanning occurred, while at high  $p$  and low  $c$ , the longer it took to span the map. Unfortunately, the most rapid spanning occurred at  $c = 1.7$ , the empirical estimate for EAB (Figures 3 and 4a). Most ash cells are invaded at low  $c$  and low  $p$  (high fragmentation), suggesting that increasing fragmentation by clear-cutting ash is unlikely to slow the spread and may result in higher proportion of unoccupied cells being invaded per generation. This does not mean that manipulation of the distribution of ash at the landscape scale cannot help slow the spread, but the strategy will require new approaches.

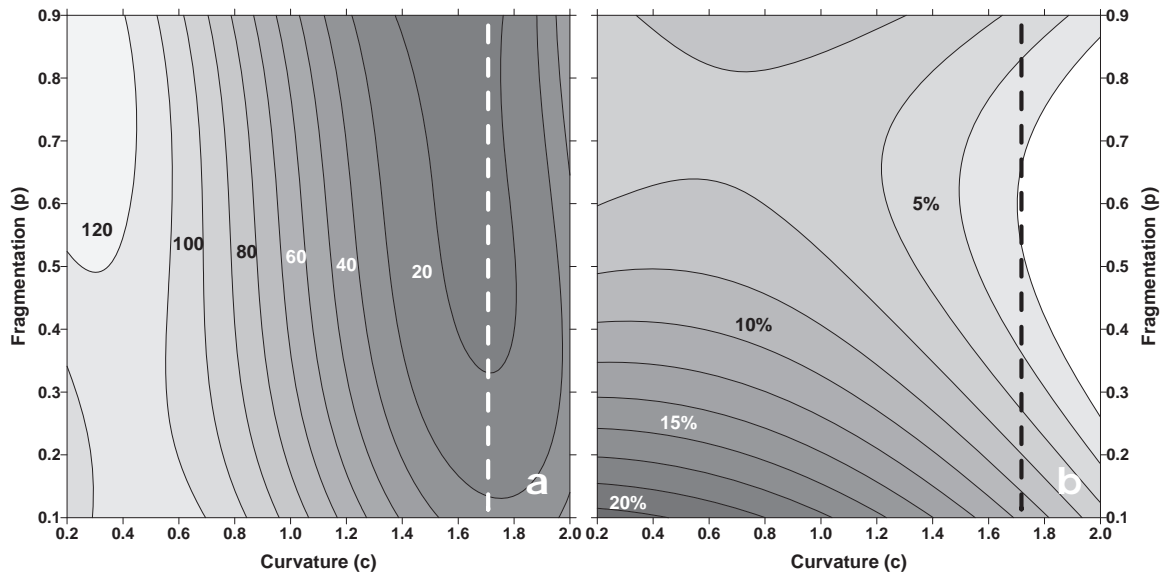


Figure 4. The rate of map spanning. a) The number of EAB generations required to span the ash map in Figure 1 depends strongly on  $c$ , with most rapid population expansion occurring at  $c = 1.7$ ; b) the percentage of cells invaded at spanning is highest at low  $p$  and low  $c$ .

It must be noted that spread in this model is strictly due to the beetles' flight; it does not take into account automobile phoresy or transport by other human agencies. Also, the results presented should not be interpreted quantitatively, although the qualitative results are useful and agree broadly with experience. To develop a quantitatively predictive model, EAB's reproductive rate and relationship between EAB density and ash morbidity must be better quantified and modeled.