A multiple equilibria model for *Dendroctonus frontalis* with predation and competition

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**Abstract:** We evaluated three competing population models for their ability to explain population fluctuations seen in *Dendroctonus frontalis*, the southern pine beetle (SPB). A model with multiple equilibria was supported by a distinctly biomodal frequency distribution and evidence of a region of positive density-dependence (Allee effect). We showed that the generalist predator *Thanasimus dubius* was experimentally attracted to increasing levels of frontalin, a pheromone of SPB, and that predation pressure was higher on lightning-struck trees baited with frontalin. Competition with *Ips* bark beetles was also higher in frontalin-baited trees. Predation, and possibly interspecific competition, could create a locally stable equilibrium in small populations of SPB. Marked spatiotemporal variation in predator abundance among forests seems sufficient to allow SPB populations to occasionally escape the predation regulating their lower equilibrium, and increase into the domain of the upper equilibrium. Although our studies did not provide unequivocal support for any of the three models that we evaluated, they make untenable the simplest model (single equilibrium with exogenous fluctuations), and the currently favored model (complex endogenous dynamics from predator-prey cycles). Furthermore, they make a reasonably compelling case that there is some element of multiple equilibria in the population dynamics. We suggest possible management strategies for a species with multiple equilibria.

**What population models allow for extreme fluctuations?**

### 1) Single noisy equilibrium

Population regulated around single equilibrium, but with fluctuations caused by exogenous variables.

### 2) Complex-endogenous dynamics

- **Non-linearities**: Population size
- **Time lags**: And / Or

Population regulated around single equilibrium, but with fluctuations caused by endogenous feedback that is delayed and / or non-linear.

### 3) Multiple equilibria

Population regulated around two equilibria, with populations occasionally switching between them, causing extreme fluctuations.

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**Evaluating the population models**

1. **Single noisy equilibrium**

   - Predicts a frequency distribution with mean = to average population size, variance reflecting ‘noise’
   - Observed distributions

2. **Complex-endogenous dynamics**

   - Non-linear relationships or time lags?

   - Population regulated around single equilibrium, but with fluctuations caused by exogenous variables.

3. **Multiple equilibria**

   - Predicts two regions of negative density dependence, a region of positive density dependence, and a mechanism for moving between the two regulated equilibria.

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**Could predators or competitors regulate small SPB populations?**

Model for SPB population regulation at low population sizes, and mechanism for escape

- # of predators or competitors (in a tree) must be positively related to # of SPB
- Predators / competitors could be attracted to the aggregation
- More SPB => more frontalin => greater attraction to competitors / predators
- If predator / competitor populations are low in some times or places, then predation and competition are relaxed and SPB populations increase into the domain of the upper equilibrium.

**Observations**

- Predators landed more on frontalin-baited trees.
- Thanasimus dubius is a shared predator of SPB and Ips beetles. When SPB are rare, T. dubius populations are maintained on Ips beetles.

**Synthesis**

- The single noisy equilibria model failed to fit the observed beetle distributions
- The non-linearity and time-lag observed were not sufficient to create population fluctuations like we observe in these beetles
- The evidence suggests that there may be two regulated equilibria
- Maintaining SPB populations beneath an escape threshold, or manipulating the threshold may increase management strategies
- We encourage exploration of developing a population model that includes both multiple equilibria and some elements of complex-endogenous feedback