

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

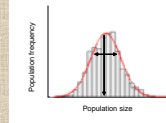
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ABSTRACT: We evaluated three competing population models for their ability to explain population fluctuations seen in *Dendroctonus frontalis*, the southern pine beetle (SPB). A model with multiple equilibria was supported by a distinctly bimodal frequency 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.

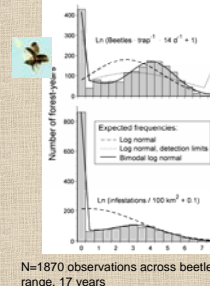
Evaluating the population models

1) Single noisy equilibrium



Predicts a frequency distribution with mean = to average population size, variance reflecting 'noise'

Observed distributions



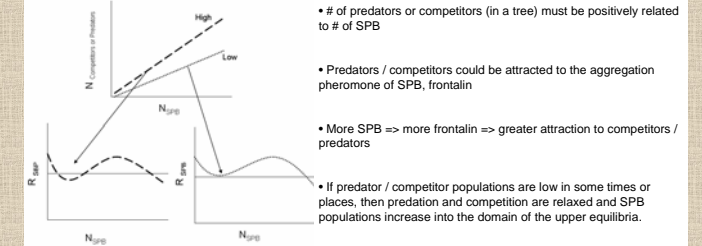
Actual frequency distributions, measured both as # of beetles and # of aggregate beetle populations, is strongly bimodal. No evidence for a single equilibrium.

N=1870 observations across beetle range, 17 years



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 pheromone of SPB, frontalin
- 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 equilibria.



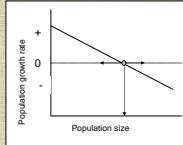
Studied pairs of lightning-struck trees. Trees were same species, located within 1km of each other, similar in size, and recently (7-10 days) struck by lightning.

One tree in each pair was baited with frontalin. Observed activity of predators and competitors



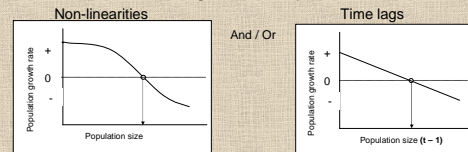
What population models allow for extreme fluctuations?

1) Single noisy equilibrium



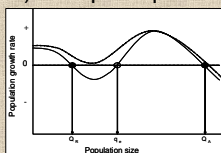
Population regulated around single equilibrium, but with fluctuations caused by exogenous variables.

2) Complex-endogenous dynamics



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

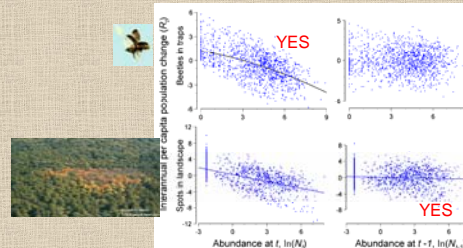
3) Multiple equilibria



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

2) Complex-endogenous dynamics

Non-linear relationships or time lags?



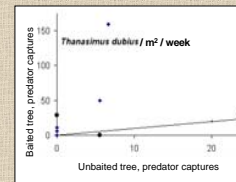
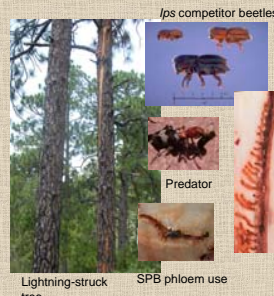
3) Multiple equilibria

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

Relatively little is known about the ecology of SPB when they are rare. Evaluation of a multiple equilibria model required further study of these populations.

Ecology of rare SPB

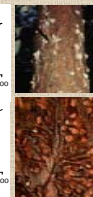
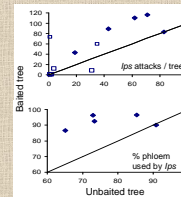
- Inhabit lightning-struck trees
- Rich community of bark beetles, predators, etc.
- Compete with other bark beetle species (*Ips*) for tree phloem
- Share predators



Observations

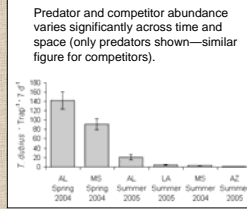
Predators landed more on frontalin-baited trees.

Thanasimus dubius is a shared predator of SPB and *Ips* beetles. When SPB are rare, *T. dubius* populations are maintained on *Ips* beetles.

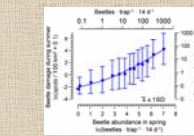


There were higher attack rates from competitors on frontalin-baited trees.

Competitors used more phloem in frontalin-baited trees.



Possible Management Implication: If rare populations of SPB are regulated by competition and predation, forests with higher levels of these beetles may be less prone to SPB outbreaks.



Positive density dependence (non-linear, accelerating function) observed at the landscape level (similar patterns have already been observed at other levels in this system).

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

