

Evaluating the Importance of Multiple Drivers in Outbreak Population Dynamics

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INTRODUCTION

- Several bark beetle species exhibit dramatic fluctuations in abundance and are capable of causing massive mortality within pine forests during outbreaks.
- Bark beetle population dynamics are often attributed to variations in natural enemies, climate, or host tree resistance, and multivoltine species are likely differentially impacted by various factors throughout the year.
- Here, we studied the effects of endogenous feedback systems (tree-beetle interactions, predator-prey interactions, and an interaction chain) on the population dynamics of the southern pine beetle, *Dendroctonus frontalis*.
- *D. frontalis* has 4-6 generations a year and outbreaks every 7-12 years. Time-series analyses indicate that ~1/2 of the temporal variance in beetle abundance is attributable to endogenous feedback and the remainder to exogenous effects. Part of the tendency for complex endogenous dynamics is due to delayed density-dependence from predators (i.e. clerids).
- Also, *Tarsonemus* mites, bluestain fungus (*Ophiostoma minus*), mycangial fungi, and *D. frontalis* appear to form a chain of species interactions that affects beetle populations.

Objectives

- 1: Quantify tree-beetle interactions (resin flow on attack rate and intraspecific competition) and mite-fungal interaction chain on the reproductive output of *D. frontalis* in pine.
- 2: Evaluate, with simulation models, the theoretical expectation that positive density-dependence at low populations (allee effects) tend to destabilize population dynamics that already include some form of negative density-dependence.
- 3: Compare the relative affect of multiple drivers on *D. frontalis* populations within and between years; i.e. incorporate variable density-dependent effects (ephemeral predators, mites-fungi-beetles interactions, resin defenses).

METHODS

- Tested for positive density-dependence in *D. frontalis* by experimentally manipulating attack rates on trees with varying levels of pre-formed and induced oleoresin.
- Incorporated positive density-dependence into mathematical equations¹ to determine the relative effect of tree-beetle interactions and negative density-dependence on beetle dynamics.
- Surveyed bluestain & mite abundance and beetle reproductive success in multiple infestations in AL and MS between June 1999 and October 2001.

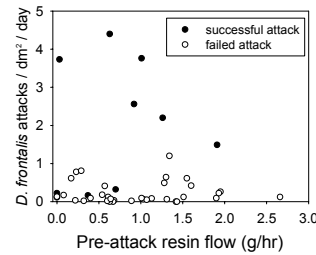


Figure 1

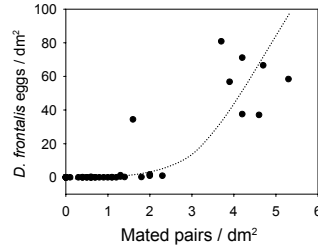


Figure 2

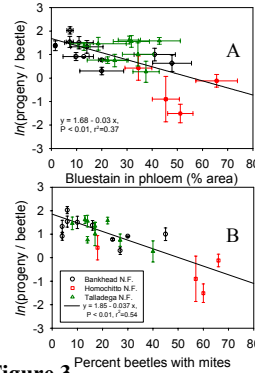


Figure 3

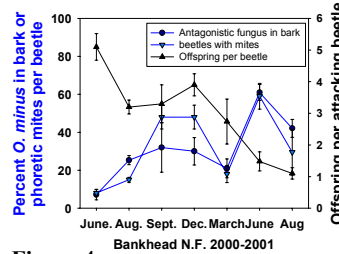


Figure 4

RESULTS: Density-dependent factors

- Beetle attack success was positively correlated with beetle landing rate and final beetle entry density. All trees suffering from >1.20 attacks/dm²/d were successfully colonized (Fig. 1).
- Fecundity was positively related to final entry densities (Fig. 2).
- Population growth declined with increased mite (Fig. 3B) and *O. minus* density (Fig. 3A). *O. minus*-mite complex gradually increased as beetle infestations progressed, affecting the eventual decline of beetle populations within the year (Fig. 4).
- Variation in feedback of the interaction chain (Figs. 3-4) on *D. frontalis* may be a product of *O. minus*-mite performance in relation exogenous factors.
- Negative effect of interaction chain is comparable with other known mortality factors. For example, an increase in bluestain from 8 to 49% per infestation would reduce population growth by 85% (Fig. 3A).

¹ Reeve, J.D. and P. Turchin. 2002. Evidence for predator-prey cycles in a bark beetle. *In*: Population Cycle: The case for trophic interactions (Berryman, A. ed.). Oxford Univ. Press. NY.

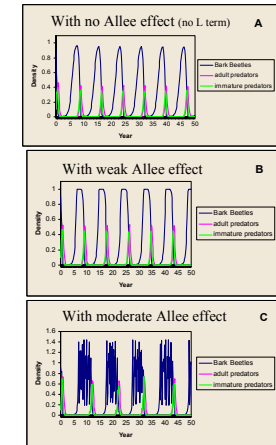
Predator-prey model with Allee effect

Beetles: $N_{t+1} = N_t^{(1-N_t/K)(1-N_t/L)} f(P_t, N_t)$
 Adult Predators: $P_{t+1} = (1-\delta)P_t + \epsilon_t Q_t$
 Immature Pred.: $Q_{t+1} = cN_t(1-f(P_t, N_t)) + (1-\epsilon_t)Q_t$

Density-dependence functions:
 $f(P_t, N_t) = \exp(-sP_t)$: Nicholson-Bailey
 $= \exp(-dP_t/(w+N_t))$: Ratio-Dependence

L=under population parameter (produces allee effect)
 ε=proportion of immature predators that emerge at time t
 δ=proportion of adult predators dying at time t
 c=conversion efficiency of prey
 s=search rate of adult predators
 d=per capita demand for resources by predators
 w=ratio dependence in model
 q=coefficient of curvature (intraspecific competition)

Figure 5



RESULTS: Population Model

- The addition of positive density-dependence to the predator-prey models¹ resulted in extended periods of outbreaks and reduced the frequency of cycles over time (Fig. 5).
- In general, the Allee effect promoted increased *D. frontalis* growth rate during the outbreak phase, uncoupled the predator-prey interactions and destabilized the logistic model (Figs. 5B & C).
- Altering within-year dynamics of predators also resulted in extended periods of outbreaks and reduced cycle frequency (no figure). This was accomplished by incorporating delayed effects within the year and reducing predation pressure during periods when predators are known to be uncommon (i.e. Aug.-Sept, Dec.-Feb.).

CONCLUDING REMARKS

- Within year dynamics of mites and fungi (interaction chain) are important drivers in beetle outbreak dynamics (Figs.3-4), particularly in the summer when predators are uncommon, and need to be incorporated into *D. frontalis* population models.
- Affects of environmental variation (e.g. seasonal climate, site condition) likely result in ecologically significant changes in endogenous factors that affect both within- and between-year beetle population dynamics.
- The transition between endemic and epidemic populations appear to be influenced by multiple feedback hierarchies; *D. frontalis* is limited by host-tree resistance at low densities (Figs. 1-2), by predators during initial outbreak phase and outbreak decline (Fig.5), by mite-*O.minus* complex during high population densities (Figs. 3-4), by regional abundance (infestations) during initiation of infestations each spring (no fig.), and by resource availability (trees) in the absence of all other feedback processes.

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