

POPULATION DYNAMICS OF THE FELTED BEECH SCALE AND ASSOCIATED *NEONECTRIA* SPECIES, CAUSAL AGENTS OF BEECH BARK DISEASE

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ABSTRACT

Biotic threats to tree growth, survival, or reproduction often arise from interactions among a suite of species, primarily insects and fungi, that function together to varying degrees to defeat host defenses, secure resources, and infect new hosts. Where two or more organisms interact, there is strong potential for positive or negative feedbacks that can have large effects on host population and disease dynamics. The strength and direction of such feedbacks are likely to vary spatially and temporally, and may depend in part on factors such as climate, host availability/quality, and forest history. We use a spatially replicated population time series for the two primary causal agents of beech bark disease (BBD) to test hypotheses concerning the potential for coupled dynamics between disease agents, and consider the relative importance of factors such as tree density and size, climate, forest and disease history in determining population dynamics, including the strength and form of density dependence.

BBD arises from the interaction between the felted beech scale (*Cryptococcus fagisuga* Lind.) and either of two ascomycete fungi of the genus *Neonectria* (*N. faginata* and *N. ditissima*). Analyzing population densities on individual trees from 29 sites from Maine to West Virginia sampled

annually from 1979 to 1992, we found strong evidence for negative density dependence for scale insects and fungi across all sites. Surprisingly, scale insect densities in year t and $t-1$ had very little effect on the population growth rate of *Neonectria*, despite the fact that *Neonectria* depends on insect feeding for initial access to phloem resources. Likewise, *Neonectria* density did not influence scale insect population growth to any great extent.

Density dependence for both insects and fungi was variable across sites, and model selection showed that climate variables such as winter temperatures and spring precipitation may influence population dynamics for each. However, the strongest and most general predictor was the duration of infection with BBD, suggesting that BBD may interact with the forest and host trees in ways that feedback to alter disease agent population dynamics over large spatio-temporal scales. This pattern is not adequately explained by other candidate variables that also vary with latitude. The exact nature of such feedbacks is unclear but may include changes in host susceptibility over time (via selection for resistance or patterns of susceptibility linked to forest structure) and likely involve human responses to BBD in the form of forest management.