

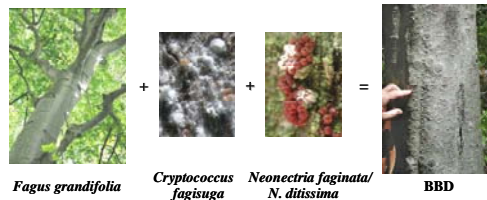
Dispersion in agents of forest disease: spatial pattern among beech bark disease-associated organisms in North America

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INTRODUCTION

Beech bark disease (BBD) in North America is a cankering disease complex of American beech (*Fagus grandifolia*), present in Northeastern forests for up to 100 years and actively spreading throughout the range of beech. BBD is generally accepted to arise from the association between the introduced beech scale (*Cryptococcus fagisuga*) and one of two or more ascomycete fungi of the genus *Neonectria* (Fig. 1).

Fig. 1 – Organisms comprising the BBD complex in North America



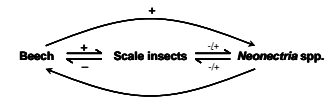
Extensive sampling during 2005-07 has revealed measurable variation in disease incidence and severity at the individual tree, stand and landscape scale. Understanding how this variation is partitioned among trees and stands at varying spatial scales can help us make inferences regarding various aspects of the biology and ecology of beech bark disease-associated organisms and the epidemiology of BBD.

ORGANIZING HYPOTHESES

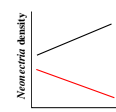
- H1:** Scale and/or fungal populations are aggregated in space at some spatial scales, suggesting dispersal limitation and the potential importance of local or regional contagion, and/or underlying spatial pattern in host resistance or suitability.
- H2:** The association between scale insects and *Neonectria* varies from antagonism to mutualism, and the nature of their interaction is strongly dependent on spatial scale.

DISEASE-AGENT INTERACTIONS

Fig. 7 – Alternative theoretical models describing the nature of the interaction between scale insects and *Neonectria* at varying spatial scales



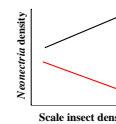
Tree



Rationale

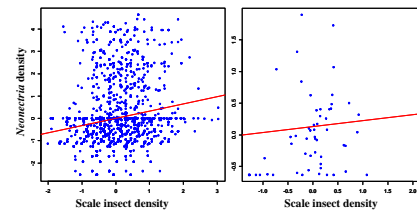
Neonectria requires the presence of scale insects to gain access to beech phloem, but the two players also compete for resources and space. Beech canker responses to fungal infection may create microhabitat refugia for scale insects but could also reduce bark tissue quality, favoring or disfavoring insect persistence.

Stand / forest



BBD-induced changes in the size, age or genetic structure of stands toward dominance by less susceptible life stages or genotypes, reductions in stem density, or the induction of acquired resistance could lead to negative feedback among BBD agents at the stand scale. Alternatively, positive effects on stem regeneration or shifts in tree susceptibility could benefit one or both organisms leading to broad scale synergy.

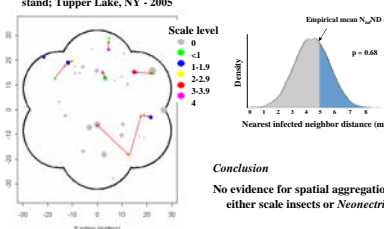
Fig. 8 – A positive correlation between scale insect and *Neonectria* density was found at the scale of individual trees (a) ($r = 0.11$; $p < 0.001$) but not stands within the Northeastern forest ($r = 0.06$, $p = 0.68$). Population density was measured on a 4 point scale and standardized by mean stand infection values.



SPATIAL PATTERN OF BBD INFECTION

TREES WITHIN FOREST STANDS

Fig. 2 – Scale insect dispersion and severity on beech within a mapped stand; Tupper Lake, NY - 2005



Methods

- Spatially mapped all trees (>10 cm dbh) in 7 beech stands. Estimated disease agent density on each using a 4-point scale.
- Randomized location of disease agent populations within each stand. Calculated mean nearest neighbor infected ($N_{nn}ND$) for each trial.
- Iterated 5000 times. Compared empirical mean with resulting histogram representing random dispersion.

Conclusion

No evidence for spatial aggregation of disease agents in 6 of 7 mapped sites for either scale insects or *Neonectria* spp.

STANDS WITHIN A FOREST

Fig. 3 – Stand-level (0.1 ha. plots) estimates of scale insect and *Neonectria* density (blue and red half-circles respectively), Bartlett Experimental Forest, Bartlett, New Hampshire

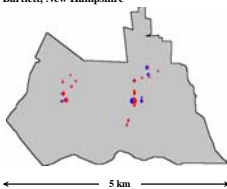
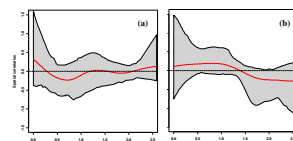


Fig. 4 – Spline correlograms (Bjørnstad and Falck 2001) depicting spatial covariance as a function of distance between sites for (a) scale insect and (b) *Neonectria* populations in Bartlett Forest, NH.



Conclusion

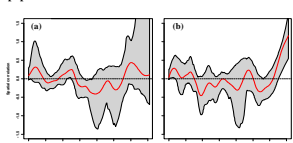
No evidence for significant spatial autocorrelation at the scale of stands within a forest.

STANDS/FORESTS WITHIN THE LANDSCAPE

Fig. 5 – Scale insect severity in the Northeastern United States. Colored rectangles represent sites sampled in 2005 or 2006.



Fig. 6 – Spline correlograms depicting spatial covariance as a function of distance between sites for (a) scale insect and (b) *Neonectria* populations in the Northeastern United States.



Conclusion

No evidence for significant spatial autocorrelation at the scale of stands/forests within the landscape.

SUMMARY AND FUTURE DIRECTIONS

Reject H1. We find little evidence for the spatial aggregation among disease agent populations at the stand, forest or landscape scale.

- Populations are unlikely to be dispersal-limited within current range of BBD. The effect of local contagion appears to be minimal.
- Variation in host resistance/susceptibility either lacks spatial structure, or does not strongly influence disease agent dispersion.

We find correlative support for H2: BBD organisms are positively associated at the scale of individual trees but not forest stands.

H_a: Spatial patterns in disease agent populations are driven primarily by disease history (e.g. duration of infection by scale and/or *Neonectria*), which influences the nature and scale of feedbacks between BBD organisms.

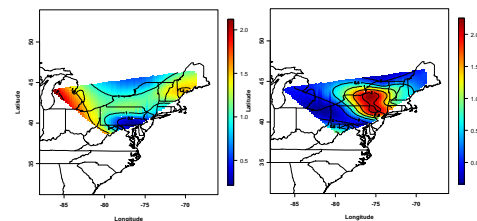


Fig. 9 – Landscape patterns of scale insect (a) and *Neonectria* (b) densities show roughly complimentary distributions of infection severity, suggesting that populations may be antagonistic at large spatiotemporal scales.