USING MODELS TO IDENTIFY FORESTS AT RISK OF MAJOR STRUCTURE AND COMPOSITIONAL CHANGE DUE TO BEECH BARK DISEASE

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Abstract
Relatively few models have been developed to predict changes in forest structure as a result of BBD. A lack of understanding of the critical factors that control the severity of the disease in forests, and at what spatial scale these factors act, continues to limit our ability to predict changes in forest structure and composition following the establishment of BBD. However, historical data sets combined with new measurements across a spectrum of northeastern forest stands may allow us to model the characteristics of uninfected forests that put them at risk of a significant state change of descending into the undesirable condition that has been characterized as ‘beech hell’. We propose to test for hypothesized drivers of this state change by combining measurements of forest structure and dynamics with historical patterns of abundance in the scale insects and fungus that cause BBD. Forest management could benefit from models that identify (1) stands that are at risk of undesirable state change, and (2) key factors that drive the transition. Models may suggest strategies for directing the transition toward more desirable outcomes in aftermath forests. In particular, we hope that empirically based models can be developed to predict the location and attributes of forests that will retain beech production in the presence of BBD.

Introduction
Beech bark disease (BBD) is a result of co-infection of beech trees (Fagus grandifolia Ehrh.) by an ascomycete fungus (Nectria coccinea var. faginata) and the beech scale insect (Cryptococcus fagisuga Lindinger) (Ehrlich 1934). Because initiation of the disease requires some fissures in the bark, many trees do not become afflicted until they have attained a size where establishment and reproduction by the insect is possible. Also, disease progression is very slow relative to some other forest pathogens such as Dutch Elm Disease or Chestnut blight; infected trees may die within several years or may require a decade or more to die. These two details have consequences for the demographics of infected beech populations because they allow persistence of beech even within forests where virtually every tree becomes infected, and virtually every infected tree eventually succumbs to the disease.

In New England and New York State, over 100 years after the introduction of the beech scale - Nectria fungus complex to North America, BBD is still a significant factor affecting forest stand structure and composition. McGee (2000) reported that the disease-killed trees accounted for approximately 22% of coarse woody debris in Adirondack northern hardwood forests. A study in central New York reported that beech trees made up 52% of the gaps in the northern hardwood forest while they represented only 26% of the canopy trees (Krasny and Whitmore, 1992). In an examination of changes in forest structure over a15-year time period (1985-2000) at one northern hardwood forest site, Forrester et al. (2003) found that while beech was still a dominant component of the forest canopy, there was a shift toward greater importance of sugar maple. In New Hampshire forests, growth of severely infected trees was shown to have been reduced by 40% relative to healthy beech trees (Gavin and Peart, 1993). Biogeochemical implications of these changes in forest structure have been suggested, but have yet to be shown consistently.

Contrary to early hypotheses that BBD would lead to widespread replacement of beech by sugar maple and yellow birch, beech has persisted, although with a dramatically altered size distribution that includes large numbers of saplings and small trees, and none of the large trees that were once common. In fact, forest managers commonly report that infected beech stands actually preclude regeneration of economically valuable timber species and that this condition seems to be self-perpetuating (because infected trees tend to produce copious root suckers before dying, which out-compete the seedlings of birch or maple; e.g., Hane, 2003). Also, loss of mature trees, and the dramatically reduced beech nut crops, have negatively affected many wildlife species. Foresters lack any practical tools for remediating stands that have descended into “beech hell”.


Models that will provide tools to identify stands that are at risk of this undesirable state change, and identify key factors of forest dynamics and epidemiology that drive the transition are required. Outcomes of such models may suggest strategies for preventing the transition before it occurs. Models must be based on empirical data and be developed to predict the location and attributes of forests that will retain beech nut production in the presence of BBD.

**Using Models to Predict Future Disease Impacts**

The limited number of models that have been developed to predict the future of northern forest structure due to BBD is likely due to a combination of factors including: 1) Initial lack of interest in beech as a merchantable species and, 2) the fact that beech basal area does not appear to be declining, though the size structure of beech in forests is altered (Forrester et al., 2003). Researchers and managers who have maintained an interest in BBD have now generated enough data to show that the disease, though not eliminating beech from the forest, has serious implications for forest structure and composition, changes in coarse woody debris, and wildlife species dependent upon beech nuts and large trees. All of these threats may affect the economy and ecology of northern forest communities.

Twery and Patterson (1984) developed a matrix using transition probabilities that were based on within stand comparisons between data they collected in Massachusetts and New Hampshire in 1981 and 1982, and historically collected data from those sites in the 1960’s (MA) and the 1930’s and 1950’s (NH) respectively. The goal was to examine potential long-term successional trends in stands of various composition that had been influenced by BBD. The major successional implications from that relatively qualitative model were that 1) stands where hemlock was dominant would tend toward a loss of beech from the canopy and hemlock dominance, (perhaps with an increased red maple or yellow birch component) due to the high beech mortality evident in those plots, 2) beech-dominated stands would remain beech-dominated since some mortality of larger trees will be replaced by advanced regeneration of young beech, and 3) stands co-dominated by beech and sugar maple would also tend to retain their composition. The authors concluded that BBD was a “partial disturbance which acts slowly over a long time period causing a reduction in growth” (Twery and Patterson, 1984). The authors suggested the need to understand how the relative proportions of resistant and susceptible beech might change over time as a function of intraspecific competition. They suggested that over time the proportion of resistant beech in a stand might increase in the absence of growth inhibition by the disease.

Le Guerrier et al. (2003) developed a SORTIE model to examine potential long-term scenarios for the structure of forests containing beech and hemlock (Tsuga canadensis). Therefore, all stands included hemlock, and resistance to BBD was not included in any scenario. The recruitment submodel in SORTIE was not altered since studies had shown that adult vigor does little to change sprout production and survival if the adult tree is alive (Jones and Raynal, 1987). Their models, based on hypothetical stand structure and parameterized with information from the published literature suggest that, over a 300 year time scale, larger beech will again be present in stands where there was high mortality due to the disease complex. Additionally, like Twery and Patterson (1984), they report that hemlock trees benefit from beech mortality in their model scenarios.

Twery and Patterson (1984) and the more recent LeGuerrier et al. (2003) model corroborate each other fairly well and confirm patterns that have been observed from published field studies particularly with respect to the short-term changes in stands and the response of plots with a high hemlock component (Runkle, 1990). They, however, do not explicitly incorporate interspecific competition in the understory, or dynamics that might result from differences in reproductive strategies or success of susceptible versus resistant individuals (mast/seed production, physiology of root sprouts versus seedlings). In addition, a recent study by Hane (This Proceedings) found that, contrary to Jones and Raynal (1987), there was a significant positive relationship between disease severity and the number of root sprouts produced by adult beech. This suggests that future demographic models for forest structure and composition need to include this relationship. Finally, research has yet to clearly identify abiotic or topographic variables that strongly correlate to the level of disease in a given stand. Griffin et al. (2003) found that disease severity was correlated with beech density at spatial scales of 60 - 1000 ha but not at the stand (1 ha.) scale. Twery
and Patterson (1984) found no singular relationship between aspect, solar radiation index, soil type and habitat type and disease severity among plots. Using a multiple regression approach, the best relationship included hemlock basal area, proportion of beech, the proportion of total density in beech, and slope position. The influence of hemlock may be direct (competition for soil moisture) or indirect (influence on air temperature and relative humidity in the canopy).

There is a critical need to continue modeling approaches with the use of current empirical data from experiments and long-term data sets from stands that have been historically measured. Results of these future models may have value in managing forests within the regions that are already infected, and could be useful in projecting the potential impacts in forests that have yet to be infected. Because northeastern forests are currently in all the stages (as described by Shigo, 1972) of the disease progression, we have the opportunity to develop hypotheses using dynamic models parameterized from aftermath forests that have been severely altered by the disease and those that have experienced less beech mortality and/or subsequent community structure changes, and test the hypotheses in stands that are at an earlier stage of the disease (such as stands in Michigan or Maryland). It is clear that future modeling efforts must incorporate data collected in forests from across the range of the disease because the spatial scale at which factors that affect disease severity are still relatively unknown.

**Future Modeling Efforts**

Beech bark disease can apparently trigger a state change from diverse, productive forests to nearly monotypic, self-perpetuating, stands of scrub beech, colloquially known as “beech hell” (Figure 1). However, some stands long afflicted with BBD seem to have stabilized in a condition that is far less affected, with retention of most size classes of multiple tree species, and continue to support much of the native biodiversity. This suggests that forests may be resilient to BBD until some disturbance threshold is reached (Figure 2), beyond which there is rapid, lasting degradation of forest structure and function. We can test these hypotheses, and develop predictive models of BBD impacts, through measurements of stand composition and dynamic trajectories in multiple hardwood stands scattered throughout the northeast. Data that can be used in the model are (1) from forest stands that already have historical baselines of annual measurements of BBD and (2) long-term plots from the USDA Forest Service’s Forest Inventory and Analysis (FIA) surveys, and other large data sets, collected from hardwood forests in the eastern United States with varied histories of BBD.
Using stand structure data from two cycles (approximately 10+ years apart) of sampling in FIA/ FHM plots within regions with a long history of BBD (New England states), a shorter history of BBD (Mid-Atlantic states), and little or no history of BBD (Midwestern states) will allow the testing of model predictions and identify the conditions under which forests do and do not become low diversity stands dominated by beech saplings. Data on changes in beech age and size structure from intensive study sites can be integrated into models to strengthen the validity of models that evaluate the consequences of different scenarios of BBD using FIA data. The model above will allow one to test changes in transition probabilities that can yield an abrupt state change in forests, as hypothesized in Figure 2, and if so, which specific demographic attributes are most critical, and where response thresholds could be expected. Data from other sites not used to generate the model will be used to test hypotheses developed with historical data, particularly with respect to coarse-scale spatial variables (vegetation type, soil, elevation, etc). These models will provide a tool for forest managers to identify sites that are at risk in the near future, and may suggest strategies for minimizing risks of degradation on a longer time frame. Model outcomes can be compared to those developed using hypothetical scenarios (Le Guerrier et al., 2003).

The goal of these predictive models should be to forecast future forest structure based on (1) the historical abundance of scale insects and fungi that produce BBD and (2) easily measurable stand characteristics that may reasonably influence BBD or those that have been identified by the literature as possible correlates with disease severity (i.e. previous density and dispersion of mature beech, previous size distribution of co-dominant tree species, soil type, and climate). Once developed and validated, these models will provide a tool for forest managers to identify sites that are at risk in the near future, and may suggest strategies for minimizing risks of degradation on a longer time frame.

The hypothesis that BBD can induce a state change in forest dynamics predicts that the dominance of beech saplings in 2004-2006 is a threshold function of BBD severity 10-20 years previously (as in Fig. 2). Resampling historical sites will allow us to estimate the current abundance of scale insects and fungi for comparison with old data. This will permit a test of the hypothesis that there are geographic hotspots in the abundance of scale insects and Nectria that are temporally stable, vs. the alternative that high intensity of BBD in one decade leads to reduced abundance of scale insects and Nectria in the next decade (perhaps because of depletion of suitable host trees). If the latter, this would be a form of delayed negative feedback that could produce predictable multi-decadal oscillations in forest structure. We will also be able to evaluate several other hypotheses to explain spatio-temporal patterns in the abundance of scale insects and Nectria. If abundance is strongly influenced by climatic patterns, there should be high spatial correlations (e.g., abundances in NH and VT should tend to go up and down in approximate synchrony). If instead, abundance of scale insects and Nectria is strongly influenced by local abundance of mature, susceptible, host trees, there should be little spatial correlation (stands with low and high abundances should be interspersed), and average abundances should be positively correlated with the density of large infected beech trees (many of which will now be dead, but still evident as deadfalls or logs). We may also be able to test for effects on BBD severity of soil types, site index, and the frequency of putatively resistant beech genotypes.

**Products of this Modeling Approach**

1. Improved ability to identify stands in the northeast and beyond that are at risk of severe BBD impacts. Such stands would be candidates for preventive silvicultural treatment before transition and may warrant special attention for monitoring and protection along advancing fronts.

2. Characterization of long term trajectories in stands with a range of infection severity. If severely afflicted stands appear destined to grow out of it, patience may be prudent, but if they enhance the infection of other stands, sanitation may be warranted. We will be able to compare our model predictions with those of others (i.e. LeGuerrier et al.,2003).

3. Improved ability to identify stands that may retain significant beech production. This would aid wildlife managers and conservation efforts.

4. Identification of manageable forest attributes that promote beech nut production and minimize transitions to an undesirable state. This may suggest strategies that can be applied to forest landscapes to improve forest health.
Refinement, and knowledge transfer, of standardized cost-effective monitoring programs for BBD in the northeast and beyond. The protocol developed by Houston for quantifying BBD severity may have general utility for forest health assessments. Surprisingly, there is presently no standardized program for monitoring the spread and intensity of BBD in U.S. forests.

Literature Cited


Contains invited papers, short contributions, abstracts, and working group summaries from the Beech Bark Disease Symposium in Saranac Lake, NY, June 16-18, 2004.

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