POTENTIAL EFFECTS OF BEECH BARK DISEASE AND DECLINE IN BEECH ABUNDANCE ON BIRDS AND SMALL MAMMALS

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Abstract
Non-native forest pests and diseases present an important threat to North American forests. Some impacts of these diseases on wildlife have been documented. We use these documented examples as well as information about the biology of beech (Fagus spp.) to discuss some of the potential ecological impacts of beech bark disease on North American forests. Beech bark disease continues to have significant impacts on beech resources within the range of American beech (Fagus grandifolia). This paper reviews some of these potential impacts as they relate to wildlife, especially birds and small mammals. The resources provided to wildlife by American beech include vegetation structure, mast, and cavities. As beech bark disease changes the structure of beech populations, these resources will be altered, and subsequent impacts on animal communities are likely. These impacts may result both in population increases and decreases in taxa that rely on beech for various resources, but these effects should be considered to be negative because they are the result of a non-natural disturbance agent.

Introduction
Along with the threats posed by habitat loss and a changing global climate, the introduction of exotic species is one of the most serious threats to ecosystem processes and biodiversity worldwide (Mooney and Hobbs 2000). Much attention has been drawn to exotic organisms and some of their direct impacts on native ecosystems. Although the autecology of exotic species is of interest, there is a potential to greatly expand our knowledge of general ecological relationships by simultaneously studying exotic species and the environments they invade (Crooks 2002). Few studies have sought to examine the potential broader influences of exotics in terms of both direct and indirect effects on population and community ecology in newly invaded areas. In recent years, the study of multi-trophic level community interactions has become common in the field of ecology (e.g., Jones et al. 1998). These types of studies are needed to examine the complex relationships between exotics and the systems they invade. Studies of this kind go beyond the historically preferred examination of pairwise interactions which, while their relative simplicity makes them favorable for short-term investigation, may oversimplify the system.

The invasion of forests by beech bark disease (BBD) presents an opportunity to examine the potential cascading effects of a disease-induced environmental disturbance. This widespread invasion of a highly virulent exotic disease complex allows us to examine a level of environmental manipulation that would not normally be feasible. Any understanding of how exotics behave as they invade a novel habitat and how native organisms respond to invasion is useful in predicting, managing, and potentially preventing similar invasions in the future (Lewin 1987).

Invaders with the largest impacts are those that directly modify ecosystems and have cascading effects through many trophic levels (Crooks 2002). Significant effects on natural communities may also occur if ecosystem engineers are removed from a system (Jones et al. 1994). This may be particularly relevant when considering exotic species that have strong negative effects on dominant tree species that can be considered autogenic engineers, i.e. ecosystem engineers that change the environment via their own physical structures of living and dead tissues.

In this paper we present several documented impacts of forest pests and diseases as well as information about the importance of the beech resource to animal populations. We use this information to discuss the potential impacts of beech bark disease on wildlife populations in North American forests.

Impacts of Exotic Pests and Pathogens on Forest Systems
A frequent direct impact of exotic species on forests is the loss of overstory trees, and these canopy losses can
directly affect animal populations. For example, in northern Minnesota mixed deciduous forests, Dutch elm disease, drought, and windstorms altered species composition of trees and converted closed canopy forests to a more open habitat. Increased density of ground vegetation and increased light levels resulted in increased breeding by bird species that preferred this type of habitat (Canterbury and Blockstein 1997). Additional evidence documenting wildlife impacts exists from Dutch elm disease in Britain. Some bird species declined from 1971-79 on plots affected by Dutch elm disease compared with unaffected plots, while some bird species experienced short term declines and subsequent recovery. In addition, one species (willow warbler, *Phylloscopus trochilus*) appeared to benefit from the loss (Osborne 1983).

The gypsy moth (*Lymantria dispar*) provides similar examples of wildlife impacts related to changes in canopy structure. In Pennsylvania oak stands with gypsy moth, black capped chickadees (*Parus atricapillus*) and wood thrushes (*Hylocichla mustelina*) were less abundant in defoliated stands, while house wrens (*Troglodytes aedon*) were more abundant in defoliated stands. However, although a defoliated forest may look devastated, the overall breeding bird community may not be greatly affected (DeGraaf 1987). In West Virginia oak stands, gypsy moth defoliation is not likely to be a devastating ecological event for shrub and sub-canopy nesting birds. In fact, more nesting habitat for these birds may be created as a result of defoliation (Bell and Whitmore 2000).

Multi-trophic level studies have demonstrated the wide range of impacts an exotic pest may have on forest communities. For example, in oak dominated forests in Massachusetts, increased density of gypsy moth was associated with declines in density of white-footed mice (*Elkinton* et al. 1996). Changes in density of white-footed mice were positively correlated with density of acorn crops. Therefore, reduced mast production reduced the population of this gypsy moth pupal predator (*Elkinton* et al. 1996). Additional evidence suggests that gypsy moth outbreaks result from reduced populations of white-footed mice, while addition of acorns increases mouse density, deer density and black-legged tick density (Jones et al. 1998).

These examples all suggest that the introduction of a non-native forest pest or pathogen can result in changes to native wildlife populations. In the examples outlined above, changes in vegetation structure and mast availability appear to be the drivers of subsequent changes in animal populations. It is likely that beech bark disease will impact animal populations in a similar manner.

### The Importance of Beech Resources

American beech is an important component of many northern hardwood forests in the eastern United States. Detailed studies of the closely related European beech, *Fagus sylvatica*, have demonstrated the importance of beech to herbivorous and wood-infesting insects (e.g., Nilsson and Baranowski 1997), and insectivorous and granivorous birds and mammals (Nielsen 1977; Nilsson 1985).

As a co-dominant tree within the beech-maple forest type, beech influences many physical and biotic properties of the forest, including maintaining canopy closure and understory light and moisture regimes. American beech also provides other important resources used by arthropods, birds, and mammals. These include food (foliage, mast/beechnuts), foraging locations (bark and foliage; Holmes & Schultz 1988), nest site locations (cavities and open nests; Robb & Bookhout 1995), and travel pathways facilitated by coarse woody debris (Greenberg 2002; Graves et al. 1988). The masting aspect of beech biology is particularly important to some species of birds (Perrins 1966; Linnard 1987) and mammals (Wolff 1996; Jenson 1982) that rely heavily on this periodic food source.

Masting of American beech was monitored in Michigan from 1959-68. During that period, there was one high mast year, 2 years where mast failed, 4 low years and 3 intermediate years. Of beech nuts caught in traps, less than 10% of them were sound (Gysel 1971). In studies of masting of European beech in Denmark from 1967 to 1974, 8-61% of the endosperm in the beech nuts was lost to insects and barren seeds. After dispersal, seed predation was found to be low, and between one and 34 g of seed were available per square meter per year. Of the seed production, 90-95% entered the detritus pathway (Nielsen 1977). The importance of mast has been studied in other systems. For example, in Virginia oak forests, deer consumed 70% of acorns placed out during mast fall, and chipmunks and squirrels consumed 61% of...
acorns placed out later in the fall. It was concluded that high deer densities may limit populations of more mast dependent animal species, particularly at low acorn densities (McShea and Schwede 1993). In mast years in European beech forests in Denmark, rodent consumption was estimated at 1.0-10.3% of endosperm production, while in non-mast years, rodent consumption of mast was 30-100%. Bank vole (Clethrionomys glareolus) populations varied more than other small mammals, and outbreaks of bank voles occurred in years following high seed production (Jensen 1982).

Beech mast can also have important effects on birds. In European beech forests in Sweden, densities of nuthatches (Sitta europaea) in the fall were positively correlated with beech mast crop. Territory size decreased with increased beech mast, and birds assessed winter food supply in the fall and adjusted their territory sizes accordingly (Matthysen 1989). Studies of nuthatches in Belgium indicated that fall survival of juvenile nuthatches was higher in mast years, though the same effect was not evident for adults, and winter survival of nuthatches was not related to beech mast (Enoksson and Nilsson, 1983). In the case of great tits (Parus major) in Europe, there are more birds in a given summer than the previous summer if there is a good mast crop during intervening winter. Evidence suggests that eruptive movements of great tits are a result of food shortage rather than high population density (Perrins 1966).

Description of the Disease and its Effects
Like all tree species, American beech is subject to damage by a broad array of insects and pathogens. Beech bark disease, an exotic disease complex consisting of an exotic scale insect, Cryptococcus fagisuga, and several species of Ascomycete fungi in the genus Nectria, has the potential to cause dramatic declines in populations of American beech (Houston 1994). Beech mortality ranges from 50-85% in the killing front (Houston et al. 1979; Houston 1994) and may occur in 3-6 years after the scale insect is detected in an area (McCullough et al. 2001).

The beech scale insect, Cryptococcus fagisuga (Homoptera: Coccidae) was unintentionally introduced to Nova Scotia in 1890 (Houston and O’Brien 1983). Since that time, it has spread throughout the eastern United States, as far south as North Carolina and Tennessee, and as far north and west as the upper and lower peninsulas of Michigan (McCullough et al. 2001). C. fagisuga has a one year asexual life cycle (Wainhouse and Gate 1988). The crawler or nymph stage is responsible for dispersal, which is facilitated by wind. Second stage nymphs secrete a white, woolly substance that protects them from desiccation, predation, and parasitism and is the most obvious sign of infestation by C. fagisuga. There are few natural enemies, although some species of ladybird beetle (Coleoptera: Coccinellidae, Chilocorus spp. and Exochomus spp.) and gall gnats (Diptera: Cecidomyiidae, Lestodiplosis spp.) may be effective in reducing populations of C. fagisuga, especially at high scale densities.

The relatively thin bark of F. grandifolia makes it both vulnerable to injury and a prime target for sap-feeding insects like the beech scale (Burns and Houston 1987). Colonization is common in bark fissures, callous tissue near old wounds, areas under branches, and patches of bark covered by protective coatings of mosses and lichens (Houston et al. 1979). Older (>15 years in European beech), larger (>8” diameter) trees appear to be more susceptible to attack by the beech scale, although younger trees may also be colonized (Wainhouse and Gate 1988). Colonization and feeding activity of the beech scale leaves host trees vulnerable to infection by various species of Nectria fungi (Houston 1994).

In North America, beech trees infested with the beech scale insect are susceptible to infection by three species of Nectria fungi; Nectria coccinea var. faginata, N. galligena, and N. ochroleuca (McCullough et al. 2001). N. galligena typically infects trees in stands recently colonized by beech scale, while the more dominant BBD pathogen N. coccinea var. faginata often replaces N. galligena over time (Houston 1993). N. galligena is a native fungus that causes perennial cankers on hardwoods, but N. coccinea var. faginata is an exotic species that has followed the spread of the beech scale (Houston 1994). N. ochroleuca has been found in association with BBD in Pennsylvania, West Virginia, and Ontario (McCullough et al. 2001).

Fungal infection by Nectria often results in tarry spots that ooze a brownish fluid (Houston and O’Brien 1983). The outer and inner bark is killed by the fungi; an orange color is present on the inner bark where Nectria is invading. If large areas are infected, the tree may be girdled and die; smaller areas of infection cause formation of callus tissue.
The pattern of spread of BBD is usually classified into three stages or fronts (Shigo 1972; Twery and Patterson 1984): the advancing front, the killing front, and the aftermath forest. The advancing front is where the disease appears for the first time with infestation by the beech scale (Houston and O’Brien 1983). Although C. fagisuga is present at the advancing front, infection by Nectria is just beginning in these areas (Shigo 1972). Stands may be heavily infested with scale without Nectria infection for several years, particularly if a forest is isolated from areas where BBD is more prevalent (McCullough et al. 2001). The killing front refers to stands where both beech scale populations and infection by Nectria are high with associated high tree mortality (Shigo 1972).

The final stage, the aftermath forest, is characterized by residual beech trees that are declining or trees that escaped the disease through chance or resistance (Shigo 1972); when mortality of beech is high and all agents of the disease complex are endemic, a forest is considered to be in the aftermath zone. Populations of beech scale tend to be lower in these areas (Shigo 1972), and remaining trees are often small and deformed (Houston 1994). The loss of large trees leads to the release of beech sprouts from the roots of the dying trees. These can form dense thickets that inhibit the growth of sugar maple seedlings and saplings and profoundly alter the ground and subcanopy vegetation layers (Holmes and Sherry 2001; Houston 1975). Resistance of American beech to BBD is rare and is the subject of ongoing studies in Michigan (McCullough, pers. comm.).

**Ecological Impacts of Beech Bark Disease**

The progression of ecological events associated with BBD can be represented along a continuum of change from a forest with beech as a prominent overstory tree species to a forest with beech as a rare or uncommon overstory species (Figure 1). Numerous ecosystem, population, and community level changes are likely to be associated with this progression. Arthropod and vertebrate communities will likely respond to the initial arrival and spread of BBD as a result of changes in vegetation structure, mast production, and availability of cavities (Figure 2).

We envision a sequence of changes unique to different taxa and functional guilds. These changes will result from the loss of American beech as a dominant canopy tree species and general changes in forest structure as the BBD disturbance progresses. A massive die-off of a large proportion of overstory trees, regardless of species, will result in large-scale changes in habitat structure. Additionally, beech has some unique functional roles (e.g., masting) in the forest community not easily replaced by other tree species. Thus, after recovery of the forest from the BBD disturbance, the forest community will likely be structurally and functionally different than the pre-disturbance forest. Moreover, successional trajectories following BBD disturbance will likely differ from successional patterns following other types of disturbance because of continued impacts of the disease. Arthropod, bird, and small mammal communities are all likely to be sensitive to these changes.

When considering responses to beech bark disease, positive and negative effects, in terms of increases and decreases of populations, may be evident. Some wildlife populations may increase (e.g. woodpeckers, salamanders, some fish species) because of increases in dead and dying trees and coarse woody debris, while
some wildlife species may decline (e.g. canopy nesting and foraging birds) because of the loss of a dominant canopy species. The changes that do take place in animal populations will depend upon how the specific resource they utilize is changed by BBD. That resource will likely be related to beech mast and vegetation structure. Whether populations increase or decline, both responses are the result of a non-natural disturbance agent and therefore should perhaps be considered to be negative. Diseased beech forests have reduced foliage and mast, and increased snags, coarse woody debris and invertebrates on the main stem. The potential long term effects of beech bark disease include the loss of a dominant or codominant tree species, the loss of major mast producing species in many areas, elevated coarse woody debris and altered tree community structure. Long term impacts on animal populations will depend upon the resilience of each population to the changes that occur as a result of BBD.

**Conclusion**

Indirect impacts of exotic tree pathogens on wildlife are often difficult to measure and may be confounded by many other factors. However, some hypothesized effects can be anticipated, and can thereby inform and guide research and management. More research is needed to characterize impacts on wildlife populations and to demonstrate the mechanisms underlying these impacts. An improved understanding of these impacts may be useful in policy decisions relating to exotic species introductions, and to the restoration of beech forests.

The current natural range of beech includes the eastern portion of the Upper Peninsula of Michigan, and contains uninfected areas as well as areas in the advancing and killing fronts. The absence of beech from the western part of the Upper Peninsula allows comparisons between sites with and without beech, as well as between sites with and without beech bark disease. We have research underway to examine the relative value of American beech vs. sugar maple seed to small mammals, to investigate if and how small mammal populations/communities are affected by the incipient invasion of BBD, and to determine the effects of beech bark disease on wood infesting insects, ground dwelling arthropods and other insect taxa that can be used in assessments of biodiversity.
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Literature Cited


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