Beech bark disease in North America: Over a century of research revisited

Jonathan A. Cale^{a,*}

Mariann T. Garrison-Johnston^b

Stephen A. Teale^c

John D. Castello^c

Abstract

American beech (*Fagus grandifolia*) in the eastern United States and Canada has experienced more than a century of mortality under a steady expansion of disease agents collectively causing beech bark disease (BBD). In North America, BBD consists of insect (e.g., *Cryptococcus fagisuga* [beech scale] and *Xylococcus betulae*) and phytopathogenic fungal (*Neonectria faginata* and *N. ditissima*) components that can variously interact with host and environment to cause extensive aboveground mortality of beech (i.e., killing front stage). This heavy mortality causes cascading impacts on forest ecosystems, resulting in altered biotic and abiotic conditions in which BBD-induced mortality persists at reduced levels (i.e., aftermath stage). New evidence

suggests that in aftermath conditions, disease agents interact with each other and their environment in ways neither observed nor anticipated from earlier studies of initial disease onset. Previously unrecognized factors such as atmospheric pollution and nutrient imbalances may exacerbate tree susceptibility to this disease. A clearer understanding of BBD-related organisms and their behavior, disease progression and impacts, and interactions between biotic and abiotic factors is needed to support the development of management options aimed at ameliorating economic and ecological consequences of disease-induced forest change. We comprehensively review over a century of literature in order to clarify these aspects in forests newly- and chronically-affected by BBD. Furthermore, we discuss new concerns of a reemergence of heavy mortality in some aftermath forests and present critical knowledge gaps and key considerations to help inform future BBD research and management programs.

Keywords: *Neonectria*; *Cryptococcus fagisuga*; *Fagus grandifolia*; Invasive species; Forest disease

1. Introduction

American beech (*Fagus grandifolia*) is a major component and foundation species in eastern North American forests. Beech populations throughout the region have experienced heavy aboveground mortality from beech bark disease (BBD), a decline disease consisting of both insect (*Cryptococcus fagisuga* [beech scale] Lind. and *Xylococcus betulae* Perg.) and fungal (*Neonectria faginata* [Lohman, Watson & Ayres] Castl. & Rossman and *N. ditissima* [Tul. & C. Tul.] Samuels & Rossman) components. This disease has been spreading from its point of origin

in eastern Canada since around 1890 (Hewitt, 1914). Beech bark disease causes extensive aboveground mortality, with many and varied direct and cascading ecological effects.

Beech bark disease is among the most important forest diseases in eastern North America in terms of temporal and spatial extent as well as negative impact. Although BBD has received sporadic, intense attention, it has not been the target of a sustained research effort presumably due to its slow spread and the low value of beech timber. Beech bark disease has impacted forest economics through secondary effects on desirable timber species (e.g., sugar maple, *Acer saccharum*) by inhibiting regeneration under the heavy beech understory that typically follows mortality in many, but not all, regions (Cale et al., 2013; Hane, 2003; Nyland et al., 2006a). However, the importance of BBD lays predominantly in the loss of nonmarket values, which can be highly varied and substantial following forest disturbance (Holmes et al., 2009). Nonmarket value losses due to BBD include primary productivity, biodiversity, structural sustainability, and mast production, factors influencing forest ecosystem integrity (Busby and Canham, 2011; Cale et al., 2014, 2013; Noble, 2009). Indeed, persistent loss of market and nonmarket values from currently-impacted forests as well as impending losses from at-risk forests makes BBD a significant problem.

Surprisingly little research has been done on the BBD pathosystem since beech scale infestations were first observed on ornamental European beech (*F. sylvatica*) in Halifax, Nova Scotia around 1890 (Hewitt, 1914). However, BBD was not recognized as a problem until Faull (1930) recorded it among forest diseases in Nova Scotia and referred to it as “bark disease of beech.” The first rigorous study of the entomological and fungal etiology, epidemiology, and forest mortality of BBD was conducted by Ehrlich (1934, 1933). Much of what has subsequently been learned of BBD and its impacts resulted from the extensive research of

Houston in the late 20th century, largely summarized in a review (Houston, 1994a). His work spurred further investigation into forest structure changes, infection development, temporal and spatial dynamics of pathogen occurrence, genetic resistance, and biological controls (Cale et al., 2015b; Garnas et al., 2013, 2011a, Kasson and Livingston, 2012, 2009; Koch et al., 2010b).

Over a century after the beech scale was introduced to North America, BBD remains a significant and intractable source of disturbance in eastern forests. Since Houston's (1994a) review, many new insights and questions about BBD biology and ecology have developed. Furthermore, chronic infection and evidence of the reemergence of heavy BBD-induced mortality (i.e., secondary killing fronts) in forests long-affected by BBD (Giencke et al., 2014; McCaskill and Morin, 2013) call for a better understanding of the development, impacts, and potential management of BBD-affected forests into the future. Here, we review over a century of BBD literature, and synthesize current understanding and new questions regarding the BBD pathosystem, ecological impacts, and management strategies in North America.

2. Stand-level progression of beech bark disease

Beech bark disease typically passes through three temporally and biologically recognizable stages at the stand level (Fig. 1) as described by Shigo (1972): advance front, killing front, and aftermath. These stages are readily identified and differentiated in the field using qualitative differences and represent an irreversible transition from BBD-free forest to a chronically diseased state in which the relationships among the host tree and disease organisms are fundamentally different than that in earlier stages of the transition.

2.1 Advance front

Prior to BBD, beech scale and *Neonectria* spp. are absent on American beech, which exhibits low levels of baseline mortality (Fig. 1) caused by senescence, small-scale disturbance, etc. The advance front begins when beech scale arrives and proliferates within a stand (Shigo, 1972). Beech scale populations can slowly and steadily increase for up to ten years before exhibiting rapid growth (Houston et al., 2005) (Fig. 1), reaching densities as high as 270 scales/cm² of bark (Teale et al., 2009). However, the incidence of *Neonectria* spp. is rare during the advance front, and beech mortality is similar to pre-BBD levels (Shigo, 1972) (Fig. 1). *Xylococcus betulae* has been observed in some advance front stands (Miller-Weeks, 1983), where the insect was likely established prior to the arrival of beech scale.

The annual rate of spread of the advance front is temporally and spatially variable. In the Upper Peninsula of Michigan, the annual infestation expansion rate was 6.2 ± 2.2 km / year from 2005 to 2007 but slowed to 2.0 ± 0.8 km / year from 2011 to 2013 (McCullough and Wieferich, 2015). However, in Michigan's Lower Peninsula, infestation expansion was 3.3 ± 0.4 km / year from 2011 to 2013. Beech scale infestations in localized stands may expand as fast as 11.0 km / year (Wieferich et al., 2011), but can accelerate when coalescing with nearby infestations (McCullough and Wieferich, 2015).

2.2 Killing front

The killing front is most prominently characterized by substantially elevated levels of BBD agents and extensive aboveground beech mortality. Beech scale infestations are heavy, widespread, and can rapidly increase in density for five years before declining (Houston et al., 2005; Shigo, 1972) (Fig. 1). High beech scale densities can give trees the appearance of being painted white (Houston, 1994a), and up to 100% of beech within a stand can have some level of

infestation (Ehrlich, 1934). The incidence and severity of *Neonectria* spp. infections during this stage are high (Fig. 1), occurring on up to 90% of beech (Ehrlich, 1934; Shigo, 1972), and can increase for several years before reaching peak levels two years after beech scale infestations begin to decline (Houston et al., 2005). Abundant *Neonectria* spp. infections on beech stems coalesce, girdle the vascular cambium, and kill the crown and stem above the girdle (Ehrlich, 1934; Houston, 1994a). Mortality of mature beech can reach as high as 20% within two years and 50% within ten years of killing front conditions, with the crowns of larger trees dying sooner than those of smaller trees (Ehrlich, 1934; Miller-Weeks, 1983). Ehrlich (1934) observed up to 85% mortality in beech basal area in Nova Scotia. In the Catskill Mountains of New York, BBD-induced mortality was 61 – 81% over seven years, killing 60 – 70 trees per hectare annually (Zabel et al., 1958). Such mortality reduces the abundance of BBD-susceptible trees, resulting in stand-wide declines in beech scale and *Neonectria* spp. populations.

The staggered development of beech scale and *Neonectria* spp. populations during the killing front, along with a more quantitative study (Wiggins et al., 2004) showing positive associations between beech scale and *Neonectria* spp. presence, is consistent with but does not directly support Ehrlich's (1934) hypothesis that beech scale is the sole and necessary predisposing factor to *Neonectria* spp. infection and thus BBD. However, whether *N. ditissima* and *N. faginata* infections are governed by similar factors is unclear, and the general process by which these fungi infect beech lacks conclusive evidence. However, this process has been presumably inferred from that of other systems where *Neonectria ditissima* readily infects bark wounds of other tree species, and thus may exploit bark damage caused by beech scale feeding in a similar manner (Grant and Spaulding, 1939). Whether *N. faginata* follows a similar infection pathway in the killing front is unknown. Furthermore, whether *X. betulae* influences *Neonectria*

spp. presence and overall BBD development in this stage is unknown. The presence of this insect may partially explain spatial variability and intensity of disease-induced mortality in some parts of the affected range, such as that reportedly occurring in Michigan from an undetermined factor, by contributing to the bark damage on beech scale-infested trees (McCullough and Wieferich, 2015).

It is not clear which *Neonectria* species is the dominant BBD pathogen in killing front forests. Study (Houston, 1994b) of killing front stands in Pennsylvania and West Virginia suggests that *N. ditissima* is the dominant pathogen at this stage. However, *N. faginata* was the dominant pathogen in previously unaffected northwestern Maine stands that began experiencing heavy BBD-induced mortality around 2002 (Kasson and Livingston, 2009). The relative abundance of *N. ditissima* in a stand is likely based on the presence of non-beech hosts that serve as reservoirs for this fungus (Houston, 1994b; Kasson and Livingston, 2009).

2.3 Aftermath

Following the heavy mortality of the killing front, forests transition to the aftermath stage characterized by reduced levels of beech scale, *Neonectria* spp., and aboveground beech mortality as well as increased understory beech prevalence (Houston, 1975; Shigo, 1972) (Fig. 1). The aftermath zone currently encompasses most of the current range of BBD, where stands free of beech scale or *Neonectria* spp. are rare or non-existent (Garnas et al., 2013; Morin and Liebhold, 2015). While heavy beech scale infestations are occasionally observed on some trees, densities are typically much lower than those in killing front stands. Beech scale densities of fewer than 40 – 70 scales/cm² have been reported from aftermath stands (Cale et al., 2015a; Teale et al., 2009), and short-term, inter-year variability in scale density is minimal for a given

tree (Cale et al., 2012). Compared to the killing front, the density of *Neonectria* spp. lesions declines in aftermath forests (Cale et al., 2012; Giencke et al., 2014), and mean within-tree densities of both current and previous year lesions of 0.5 – 2.5 cm² canker/dm² bark have been reported in New York State (Cale et al., 2015a, 2012). *Neonectria* spp. and beech scale density may also interact with co-occurring decay fungi (e.g., *Phellinus igniarius* and *Inonotus glomeratus*) (Cale et al., 2015a).

The relative importance of the two *Neonectria* species can change as a stand transitions from killing front to aftermath stages. In one aftermath forest, *N. faginata* completely replaced *N. ditissima* as the dominant pathogen in seven years (Houston, 1994b). However, such replacement may be driven by the amount of *N. faginata* inoculum relative to that of *N. ditissima* (Houston, 1994b), and thus likely does not uniformly occur across the aftermath zone. In parts of Maine and New York, *N. ditissima* continues to cause new infections, and in some cases becomes the dominant pathogen despite decades of *N. faginata* presence (Cale et al., 2015b; Kasson and Livingston, 2009). Further, *N. ditissima* likely persists on beech in aftermath forests due in part to inoculum from non-beech hosts whose basal area is an important predictor of *N. ditissima* levels on beech (Houston, 1994b; Kasson and Livingston, 2009). Infections of both *N. ditissima* and *N. faginata* can co-occur on a single tree (Kasson and Livingston, 2009). These fungi are therefore likely conflated and misidentified leading to inaccurate estimates of *Neonectria* spp. presence in aftermath forests and making it difficult to identify distinct factors associated with each (Cale et al., 2015b).

Factors predisposing healthy beech to *N. faginata* and *N. ditissima* infections seemingly differ between the killing front and aftermath stages (Cale et al., 2015b, 2012; Garnas et al., 2011b). In the aftermath, *N. faginata* infections are positively associated with high beech scale

density, low phosphorus (P) concentrations in bark, and low phloem isorhamnetin, a flavonoid generally involved in tree resistance to biotic agents (Cale et al., 2015b). Cale et al. (2015b) showed low P was the single best predictor of *N. faginata* infection probability and was also proposed to be an important predisposing factor in *N. ditissima* infections. In addition to P, *N. ditissima* infection was proposed to be predisposed by high *X. betulae* density and low bark concentrations of catechin, another defensive flavonoid (Cale et al., 2015b). Further study is needed to substantiate the likelihood of a more complex pathosystem in aftermath conditions compared to killing front forests.

Fewer trees die of BBD in aftermath forests than in the killing front (Fig. 1), although legacy effects of heavy killing-front mortality alter forest structure. Relatively low mortality in aftermath forests is due in part to a low abundance of live overstory beech as well as chronic, relatively light beech scale infestations, and slowly accumulating *Neonectria* infections. Trees surviving the killing front or developing during the aftermath likely endure chronic stress from these infestations and infections, resulting in radial growth reductions of up to 40% compared to non-affected trees (Gavin and Peart, 1993). Roots of dying trees as well as trees killed during the killing front produce dense thickets of clonal, BBD-susceptible sprouts that fully occupy forest understories in many parts of the aftermath zone (Cale et al., 2013; Garnas et al., 2011a; Giencke et al., 2014; Houston, 1975). In some areas, these thickets are largely comprised of seed-origin trees (Giencke et al., 2014; Jones et al., 1989). Beech scale and *Neonectria* spp. infections accumulate on young trees of sprout- and seed-origin due to insect and fungal transmission from overstory to understory beech (Giencke et al., 2014). Such BBD-affected understories are important in allowing beech scale and *Neonectria* spp. to persist and intensify

over time, potentially culminating in heavy mortality of relatively young beech (i.e., a secondary killing front) (Giencke et al., 2014; Houston, 1975).

3. The host tree and beech bark disease organisms

3.1 American beech, host tree

American beech (*Fagus grandifolia* Ehrh.; Fagaceae) is a temperate, shade-tolerant deciduous tree that lives for 300 to 400 years (Tubbs and Houston, 1990). The geographical range of this tree extends from Nova Scotia south to northern Florida, west to eastern Texas, and north to southern Ontario (Tubbs and Houston, 1990). Although it occupies a wide range of ecological conditions, beech commonly occurs on loamy podzol soils with high humus but occurs in high densities on coarse-textured, dry-mesic sites in its northern range, such as the Adirondack Mountains of New York (Morin et al., 2005; Tubbs and Houston, 1990).

American beech is capable of both sexual and vegetative reproduction. Monoecious flowers are produced and wind-pollinated in spring giving rise to an autumnal seed crop of beechnuts (Tubbs and Houston, 1990). Beechnuts are important, high-protein hard mast for wildlife and have heavy peak production at 2 to 8 year intervals, resulting in periodic pulses of beech regeneration. Developing seedlings grow well in the diffuse light of forest understories, and are more sensitive to herbivory than are root sprouts (Beaudet and Messier, 2008). Clonal root sprouts grow more rapidly than seedlings and develop from adventitious buds on wounded roots or roots of dying parent trees with aboveground mortality (Jones and Raynal, 1988, 1986). Heavy mortality from natural or anthropogenic disturbance often induces dense beech root sprout production in forest understories (Morris et al., 2004). Root sprout abundance and density are positively associated with parent size, and 95% to 99% of sprouts are produced within eight to

ten meters of parent trees, respectively (Jones and Raynal, 1987, 1986). This root sprouting ability can drive beech population genetics and structure (Morris et al., 2014, 2004).

Beech trees are affected by a wide variety of pathogens and herbivorous insects. Saprobiic and pathogenic fungi can cause decay whereas endophytic fungi cause latent infections (Chapela, 1989; Tubbs and Houston, 1990). Live trees are also attacked by several insect pests, including hemipterans (*e.g.*, *Fagiphagus imbricator* and *Longistigma caryae*), lepidopterans (*e.g.*, *Heterocampa guttivitta* and *Malacosoma disstria*), and hymenopterans (*e.g.*, *Tremex* sp.) (Tubbs and Houston, 1990). Such threats to beech are relatively minor compared to BBD, which is the single greatest threat to American beech (Houston, 1994a).

3.2 Fungal pathogens, *Neonectria faginata* and *N. ditissima*

The fungal genus *Neonectria* (Ascomycota: Hypocreales, Nectriaceae) includes many necrotrophic pathogens of trees. These fungi produce red, globose perithecia, bearing uniseptate, hyaline ascospores, and have *Cylindrocarpon*-like anamorphs producing micro- and macroconidia in sporodochia (Rossman et al., 1999). Infections are annual and mostly establish in autumn. Asexual and sexual fruiting bodies are produced in the summer and autumn, respectively (Houston and Valentine, 1988; Ostrofsky and Blanchard, 1983; Sinclair and Lyon, 2005). Ascospores are apparently the spore type causing infections of non-infected and already infected trees (Houston, 1994a; Sinclair and Lyon, 2005); however the infectivity of asexual conidia as well as their potential role in disease development has not been investigated.

Neonectria spp. infect and necrotize primarily phloem and cambial tissues in living beech bark, creating annual cankers (lesions) on the bole (Fig. 2A) (Ehrlich, 1934; Houston, 1994a).

Distinctions between *N. ditissima* and *N. faginata* can be made using ascospore or macroconidia

lengths (Cale et al., 2015b; Castlebury et al., 2006; Cotter and Blanchard, 1981; Kasson and Livingston, 2009). However, high ascospore length variability may suggest local co-infection by *N. faginata* and *N. ditissima* (Kasson and Livingston, 2009).

The causal agents of BBD differ between Europe and North America, but may share similar life histories. In Europe, BBD on *F. sylvatica* is caused by *N. ditissima* and *N. coccinea* (Pers.:Fr.) (Castlebury et al., 2006; Chaverri et al., 2011; Hirooka et al., 2013). *Neonectria coccinea* is a known endophyte of *F. sylvatica* that becomes pathogenic when bark moisture declines and oxygen levels increase, such as following wounding (Chapela and Boddy, 1988; Hendry et al., 2002). In North America, BBD is caused by *N. ditissima* (previously *N. galligena*; anamorph *C. heteronema*) and *N. faginata* (previously *N. coccinea* var. *faginata*; anamorph *C. faginatum*) (Castlebury et al., 2006; Chaverri et al., 2011; Hirooka et al., 2013).

Neonectria ditissima was identified as a BBD pathogen in parts of New England by Spaulding et al. (1936). This fungus commonly infects other North American and European hardwoods (Castlebury et al., 2006; Hirooka et al., 2013). Non-beech hosts include *Acer*, *Betula*, and *Quercus* on which this fungus infects branch stubs and wounds and causes perennial cankers (Grant and Spaulding, 1939; Lohman and Watson, 1943; Spaulding et al., 1936). These cankers are likely important inoculum sources for BBD infection (Houston, 1994b; Kasson and Livingston, 2009; Spaulding et al., 1936).

While *N. ditissima* is well documented in North America, the provenance of *N. faginata* on this continent is puzzling because BBD was not reported in the continent before the arrival of beech scale and *N. faginata* is not known to occur in Europe (Castlebury et al., 2006; Chaverri et al., 2011; Hirooka et al., 2013). *Neonectria faginata* is more closely related to *N. coccinea*, which is an endophyte in European beech, than to *N. ditissima* (Chaverri et al., 2011) but has not

been documented as an endophyte in American beech. If *N. faginata* is an endophyte, this may explain the lack of *N. faginata* observations prior to the arrival of beech scale in North America. Alternatively, *N. faginata* may have originated in Europe but has yet to be detected there.

Genetic analyses have been used to investigate the question of whether *N. faginata* may have been introduced to North America from Europe. This fungus exhibits lower genetic variability than *N. ditissima* and thus may be a more recent arrival to North America (Plante et al., 2002). In a comparison of genetic variability among *N. faginata* samples from North America versus *N. coccinea* samples from Europe, Mahoney et al. (1999) similarly concluded that the former likely originated from a founder population, and thus was an introduction from Europe as hypothesized several decades earlier (Spaulding, 1948). However, working with most of the same specimens as Mahoney et al. (1999), Castlebury et al. (2006) determined that many specimens previously described as *N. coccinea* were in fact distinct species. They further determined that the genetic variability of actual *N. coccinea* samples was comparable to that of *N. faginata*, which was only observed in North America. This distinction and observation was recently corroborated using additional specimens (Hirooka et al., 2013). These findings indicate that both *Neonectria* species causing BBD in North America are likely native fungi.

A third fungal pathogen, *Bionectria ochroleuca* (Schw.) Schroers and Samuels (formerly *Nectria ochroleuca*), has also been associated with BBD. This species was observed on dead and dying beech in West Virginia, Pennsylvania, and near Toronto, Canada (Houston et al., 1987; Schroers et al., 1999). Its anamorph, *Clonostachys rosea* (formerly *Gliocladium roseum*) Link: Fr., is an entomopathogenic and mycoparasitic endophyte occurring in temperate and tropical trees (Schroers, 2001; Toledo et al., 2006), and was frequently isolated from chlorotic beech in Pennsylvania and New York experiencing heavy BBD-induced mortality (LaMadeleine,

1973). Inoculations of beech scale-free logs with *B. ochroleuca* suggest that it is less virulent than either *N. faginata* or *N. ditissima* (Houston et al., 1987). This would further suggest that *B. ochroleuca* may be a secondary agent affecting trees already weakened by the other BBD agents. The importance of *B. ochroleuca* in BBD and its potential relationships with the other fungal and insect components of BBD should be further investigated. However, *N. faginata* and *N. ditissima* are apparently the primary BBD pathogens of concern in American beech.

3.2.1 *Neonectria-beech interactions*

Presently, only three studies have investigated the separate roles of *N. faginata* and *N. ditissima* in BBD (Cale et al., 2015b; Houston, 1994b; Kasson and Livingston, 2009). Although Houston (1994b) preliminarily suggests *N. faginata* is the more aggressive pathogen, the relative virulence of these two fungi lacks rigorous scientific investigation. Thus, most of what we know about BBD pathogens is a conflation of potentially different interactions between each *Neonectria* species and its host. Much of the difficulty in understanding the ecology and physiology of BBD can be attributed to the common failure to identify the pathogens to the species level. Nonetheless, several generalities about interactions among “*Neonectria* spp.” and beech can be made.

Cankers of *Neonectria* spp. typically first appear on beech 12 to 37 years old and 2 to 11 cm in diameter, with most first-time infections occurring in trees 20 years old and 6 to 10 cm (Houston and Valentine, 1988). Cankers accumulate annually on a given tree, with the accumulation rate showing inter-annual variation likely due to weather (Cale et al., 2012; Houston and Valentine, 1988), though disease progression may be a more important driver of *Neonectria* spp. fruiting at regional scales (Garnas et al., 2011b). Regardless, the abundance of

cankers increases with tree diameter and age (Ehrlich, 1934; Gavin and Peart, 1993; Houston and Valentine, 1988; Latty et al., 2003).

Following experimentation in Nova Scotia, Ehrlich (1934) described a chronological pattern of BBD progression at the organismal level. This classic BBD development scenario begins with the infestation of susceptible beech by beech scale. Although never clearly demonstrated, beech scale feeding wounds in the bark presumably serve as infection courts for airborne *Neonectria* spp. inoculum (Ehrlich, 1934). Necrotic infections then appear 4 to 5 years after beech scale arrival. Ehrlich (1934) believed scale infestation was the necessary and sole predisposing factor to *Neonectria* spp. infection, with total canker area being proportional to beech scale infestation severity for a given tree (Ehrlich, 1934). As discussed in sections 2.2 and 2.3, while this may be true for killing front stands (Wiggins et al., 2004), alternative or additional predisposing factors likely drive *N. faginata* and *N. ditissima* infections in aftermath stands (Cale et al., 2015b, 2012; Garnas et al., 2011b). Interestingly, there has been one (Spaulding et al., 1936) observation of *N. faginata* infection seemingly in the absence of beech scale.

Beech bark chemistry, namely phenolic compounds, is associated with tree defense against *Neonectria* spp. as well as infection occurrence. *Neonectria* spp. elicit phenolic induction responses in infected phloem, with total phenol concentrations increasing with distance from canker surface toward vascular cambium (Ostrofsky et al., 1984). In some trees, this gradient prevents pathogen ingress into cambial tissue, and potentially allows cambial development of protective necrophylactic periderm (Ostrofsky and Blanchard, 1983; Ostrofsky et al., 1984). Such defensive effects may be attributable to particular compounds as certain bark phenolics are negatively associated with infection probability (Cale et al., 2015b). For example, high concentrations of isorhamnetin and catechin in the bark of non-infected beech is associated

with a low probability of *N. ditissima* and *N. faginata* infection, respectively, the following year (Cale et al., 2015b). However, phenolics likely represent only one aspect of a larger beech-defense system against *Neonectria* spp. infection which may include other secondary metabolites.

Soil factors such as nutrient status and moisture availability have long been recognized as important aspects of BBD development in European beech. Attempting to reconcile disparate observations either supporting or contradicting Erhlich's (1934) model, Lonsdale (1980) showed that in Europe, trees infested with beech scale largely become infected by *Neonectria* spp. and die, yet trees escaping from or resistant to beech scale can still be infected by *Neonectria* spp., and in fact are highly susceptible to infection during abiotic stress (i.e., nutrient or drought stress). Trees under drought conditions also may produce larger *N. coccinea* wounds and, with light beech scale infestations, produce canker densities similar to heavily-infested trees under normal moisture conditions (Lonsdale, 1980; Parker, 1975). Nutrition also appears to influence infection susceptibility in European beech. For example, *Neonectria* spp. cankers were more abundant on European beech on calcareous soils compared to non-calcareous soils despite similar beech scale densities (Lonsdale and Pratt, 1981). Perrin and Garbaye (1984) showed that European beech growing in soils deficient in nitrogen (N) and P are especially prone to *N. ditissima* infection, though in contrast to Lonsdale and Pratt (1981) they suggest that susceptibility is further exacerbated under low soil calcium or magnesium availability.

In North American aftermath forests, the effects of site moisture conditions on infection of American beech by *Neonectria* spp. is unclear. Stands of beech occupying west-facing slopes are presumably subject to lower soil moisture and higher air and soil temperatures, and have fewer *Neonectria*-infected trees than those on east-facing slopes (Munck and Manion, 2006). However, such relationships may vary considerably with season and year (McCann and

MacDonald, 2013; Wiggins et al., 2004). Slope may also directly influence soil conditions, with soils being generally shallower and less-developed on steeper slopes, and perhaps also drier due to lower infiltration rates during precipitation events. Here again evidence is mixed as trees occupying steep slopes experience lower *Neonectria* spp. infection severity than trees on more level ground in some sites (McCann and MacDonald, 2013), while on other sites infection and/or beech scale infestation are greater on steeper slopes (Ehrlich, 1934). *Neonectria* spp. infections can be associated with precipitation as sites with higher late summer/autumn rainfall can support greater fungal carrying capacities (Garnas et al., 2011b). However, canker area can be positively associated with dry conditions, and negatively associated with autumn rainfall of the previous year (Houston and Valentine, 1988). A possible explanation for decreased canker area associated with higher autumn rain is a tree's higher capacity for defensive induction in response to infection due to proper vascular functioning associated with improved site moisture status.

Few studies have evaluated the effects of host physiological factors on BBD development in North America. High bark N levels were suggested to be a cause rather than an effect of disease severity, as measured using a composite beech scale-*Neonectria* spp. index (Latty et al., 2003). Similarly, Cale et al. (2015b) showed that low bark P, potentially from low soil P, was a significant predictor of whether previously non-infected beech became infected by either *N. faginata* or *N. ditissima* the following year. For *N. faginata*, the effect of low bark P in predicting infection in aftermath forests is three times that of beech scale density (Cale et al., 2015b). Investigations of foliar nutrients support these findings, as high foliar N:P ratio is associated with higher probability of infection by *Neonectria* spp. infection (Ouimet et al., 2015). Further, low infection probabilities are associated with high foliar zinc-manganese and magnesium-potassium ratios (Ouimet et al., 2015). Cumulatively, these findings highlight the

importance of nutrient status in BBD development in aftermath forests, and suggest that quantification of bark and/or foliar nutrients may be useful to predictors of *Neonectria* spp. infection of American beech trees.

An interesting perspective on nutrition and BBD arises when we consider that human activities have increased atmospheric N inputs to forests in the northeastern USA by at least 5- to 10-fold since the onset of industrialization (Galloway et al., 1982). Increased N availability in forest ecosystems results in a greater demand for, and thus a lower availability of, P (Rastetter et al., 2013). Thus, nutrient imbalance due to atmospheric N deposition may be a previously unrecognized factor in the American beech-*Neonectria* spp. relationship, which became pathogenic not only with the introduction of beech scale (Ehrlich, 1934), but also with the advent of N pollution (Fakhraei et al., 2014) in the late 1800's. Further investigation of the role of current and historic site and tree nutrition factors in BBD development and severity is warranted throughout the geographical range of American beech.

3.3 Beech scale, *Cryptococcus fagisuga*

Beech scale (Hemiptera: Eriococcidae; previously *Cryptococcus fagi*) is a non-native, invasive scale insect that feeds exclusively on American beech in North America (Ehrlich, 1934). Adults of this soft-bodied scale insect are sessile, covered in white wax, and approximately 0.5 –1.0 mm long and infests living trees ranging from 1.0 cm to at least 35.0 cm in diameter (Fig. 2B) (Brown, 1934; Cale et al., 2015b; Ehrlich, 1934; Munck and Manion, 2006). Using a 2.0 mm long stylet, adult beech scale penetrate the cork layer of tree bark to feed on the contents of individual phloem cells of young trees or, more commonly, the contents of phelloderm cells of older trees (Ehrlich, 1934). These cells die after being fed upon, and, in bark patches where

large numbers of beech scale are feeding in close proximity, clusters of dead cells can lead to the formation of minute bark fissures (Ehrlich, 1934). As males have never been reported, beech scale apparently reproduces parthenogenetically (i.e., in absence of fertilization) (Brown, 1934). Thus, prior to the onset of negative density dependence (Garnas et al., 2011b), scale density from the previous year is an important positive predictor of density in a given year (Cale et al., 2015b).

This insect has differing life cycles in its native and invaded ranges. Beech scale is likely native to the Black Sea region of southeastern Europe, where it produces two broods per year (i.e., bivoltine) on Oriental beech (*F. orientalis*) (Gwiazdowski et al., 2006; Japoshvili et al., 2015). In its native range, scales overwinter as adults (Japoshvili et al., 2015). In North America, beech scale produces one brood per year (i.e., univoltine) (Brown, 1934; Hawboldt, 1944; Japoshvili et al., 2015). In New England, adult females deposit up to 50 pale yellow eggs in the wax coat below their abdomen in June and July. In August and September, eggs hatch and mobile first instars (crawlers) disperse along the tree bole settling in bark cracks and crevices (Brown, 1934; Wainhouse and Gate, 1988). Although some crawlers are carried by wind to nearby trees (Wainhouse, 1980), those maturing on natal trees have greater fitness (Wainhouse and Howell, 1983). Once settled, crawlers secrete wax and molt and the sessile second instars overwinter from October to April, followed by another molt in May. Adult third instars mature in 15 days (Brown, 1934). After death, beech scales and their wax masses may remain affixed to host trees for one to two years (Cale et al., 2012), thereby making accurate measurement of the living portion of infestations difficult (however see Cale et al. 2012). It is unclear what factors influence brood cycle and frequency in beech scale. However differences between Palearctic and Nearctic populations are unlikely to be explained by cumulative degree-days which are similar in parts of the native and invaded ranges (Japoshvili et al., 2015).

As with many other non-native species, beech scale populations are larger in the invaded range compared to the native range. Beech scale infestations on American beech in forests of Massachusetts long-affected by BBD were on average 44.4 times denser than those on Oriental beech in the Caucasus Mountains of Georgia in eastern Europe (Van Driesche and Japoshvili, 2012). However, annual scale cohort survival can be lower in North America compared to Europe (Japoshvili et al., 2015).

3.3.1 Beech scale-beech interactions

The relationship between beech physiology and beech scale populations is poorly understood. Scale infestations can elicit a defensive response from host trees and respond to changes in host chemistry. Higher levels of total phenols are present in infested compared to non-infested bark, but such a difference is seemingly not related to infestation susceptibility (Wargo, 1988). Further, bark from beech scale-infested European beech contain higher concentrations of certain phenolic compounds including several related to plant defense (Dübeler et al., 1997). Phenolic induction in American beech bark can vary with infestation level. For example, two unidentified flavonoids occur only in bark of infested trees (Wargo, 1988). Moreover, 4-hydroxybenzoic acid in beech bark is positively associated with beech scale wax density during the following year (Cale et al., 2015b). However, induction of certain phenolics, such as tannins (condensed and hydrolysable) do not respond to beech scale presence (Wargo, 1988).

Scale insects are well adapted to maximize N utilization from N-poor phloem sap and respond to nutrient availability (Douglas, 2006). Beech bark with greater total or amino N supports higher beech scale populations (Wargo, 1988). Moreover, these populations may be influenced by the concentration of particular amino acids. High concentrations of phenylalanine,

valine, alanine, glutamine, and asparagine in beech bark are associated with established moderate to heavy beech scale infestations (Wargo, 1988). Cale et al. (2015b) showed that infestation density is negatively associated with bark isoleucine levels, but positively associated with leucine concentrations. Leucine is associated with plant defenses (Toril, 2004), while isoleucine acts in cell division and expansion (Yu et al., 2013). This suggests that trees with inhibited tissue development are more susceptible to beech scale infestation, and that leucine induction is involved in tree response to infestation. Studies using scale-*Neonectria* spp. composite indices suggest positive or non-significant relationships between “disease severity” and bark N or soil carbon (C):N ratio, respectively (Griffin et al., 2003; Latty et al., 2003).

In general, physiological resistance of forest trees to biotic disturbances is tied to nutrient availability (Entry et al., 1991; Shaw et al., 1998), with high availability of N being associated with nutrient imbalances and stress (Moore et al., 1994; Wargo, 1980). Hormones signaling downstream production of defensive chemicals, such as phenols, are tied to mineral nutrition (Rubio et al., 2009). In European beech, trees exposed to excess N have lower total phenol levels (Balsberg Pålsson, 1992). However, response of individual phenolics to tree nutrient status is variable. For example, in fine roots of European beech, concentrations of certain phenols decreased while others increased in response to N fertilization (Tomova et al., 2005). Although Cale et al. (2015) did not observe such associations between nutrients and phenolics, more experimental evidence of such relationships in American beech is warranted, particularly in light of historical and ongoing N deposition in the northeastern US (Aber et al., 2003; Fakhraei et al., 2014; Galloway et al., 1982; Holland et al., 2005).

Weather conditions can influence beech scale populations. Scale mortality occurs at temperatures at -34°C and below, and populations may decline under prolonged periods below

this threshold (Barter, 1953; Houston and Valentine, 1988). The number of days with lethal low temperatures over a several year period can be an important predictor of beech scale population growth and its contribution to beech stress (Kasson and Livingston, 2012). Beech scale populations are also affected by autumn rainfall which may wash unattached crawlers from the bole surface (Garnas et al., 2011b; Houston and Valentine, 1988; Kasson and Livingston, 2012). Heavy rainfall may also inhibit infestation development or remove signs of prior infestation, giving a false impression of tree resistance; conversely, beech scale populations can build following drought years (Kasson and Livingston, 2012).

3.4 *Birch margarodid*, *Xylococcus betulae*

Compared to *Neonectria* spp. and beech scale, little is known about the biology and ecology of *Xylococcus betulae* (Hemiptera: Margarodidae; previously *Xylococcus betulae*; birch margarodid), a native North American scale insect (Hubbard and Pergand, 1898). *Xylococcus betulae* are orange-red colored, soft-bodied scale insects that enter bark wounds to feed on phloem sap of living hardwood trees, including paper (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, aspen (*Populus* spp.), and American beech (Hubbard and Pergand, 1898; Shigo, 1962). Adult females are approximately 4 – 5 mm in length, 2 mm in diameter, and have five instars. *Xylococcus betulae* are legless, wax-covered sacs (cysts) except during the first instar and adult stages. Eggs are laid beneath females, and although first instars are mobile it is not known how they are dispersed to new trees (Hubbard and Pergand, 1898). Males closely resemble females but smaller, have six instars (one sessile stage), and are winged as adults (Hubbard and Pergand, 1898). In Michigan, metamorphosis to the adult stage is believed to occur during spring and early summer, and individuals overwinter under host bark as encysted

505 nymphs (Hubbard and Pergand, 1898). *Xylococcus betulae* are easily identified on host trees
506 by the presence of a clear, waxy excretory tube protruding from the bark (Hubbard and Pergand,
507 1898; Shigo, 1962). This tube is produced from anal spinnerets and extends 1.3 – 5.0 cm from
508 the insect's abdomen (Hubbard and Pergand, 1898; Shigo, 1962).

509 The geographical range of *X. betulae* is poorly understood, but the insect occurs on
510 several hardwoods and is widespread in eastern North America. *Xylococcus betulae* has been
511 known since at least 1876 in parts of Michigan and Ontario where it was reported on birch
512 (*Betula* spp.), on which it can cause heavy damage, and aspen (*Populus* spp.), but no mention
513 was made of its occurrence on beech at that time (Hubbard and Pergand, 1898; Shigo, 1962).
514 Additional observations indicate that the geographical range of *X. betulae* includes parts of
515 California, Maine, New Hampshire, New York, North Carolina, Ohio, Pennsylvania, Tennessee,
516 Vermont, Virginia, Washington, West Virginia, and Wisconsin in the US as well as New
517 Brunswick, Nova Scotia, and Prince Edward Island in Canada (Cale et al., 2015a, 2015b;
518 Florence, 1917; Gill, 1993; Kosztarab, 1996; Miller-Weeks, 1983; Petrillo pers. comm. April 19,
519 2016; Shigo, 1962; Towers et al., 1974; Wiggins et al., 2004).

520 *Xylococcus betulae* can cause heavy superficial damage to host trees. On birch, bark
521 layers heave and separate into curls as this insect settles and feeds on cambial and phloem tissues
522 (Hubbard and Pergand, 1898). How *X. betulae* settles in beech is unclear, but it is likely through
523 bark wounds or through corky lenticels as occurs in young birch (Hubbard and Pergand, 1898;
524 Shigo, 1962). Feeding on intact bark creates erumpent wounds (1.3 – 5.0 cm in diameter), which
525 can enlarge and deepen over time as *X. betulae* multiply and force their way deeper in the bark to
526 feed (Hubbard and Pergand, 1898; Shigo, 1962). On beech, *X. betulae* occurs on trees as small
527 as 2.5 cm and at least large as 31.0 cm in diameter (Cale et al., 2015b; Houston, 1975; Munck

and Manion, 2006). Infestations beginning on the undersides of lower crown branches later spread to the bole, and wounds along the bole often occur in longitudinal strips extending from the crown (Shigo, 1962).

3.4.1 *Xylococcus betulae* in beech bark disease development

Xylococcus betulae may be important to BBD ontogeny as it interacts with disease-related agents. Geographical variability in BBD severity may in part be explained by *X. betulae* abundance and its feeding wounds (Shigo, 1962). These wounds are important infection courts for *N. ditissima* (Shigo, 1964; Spaulding et al., 1936), and infection of healthy trees by this pathogen is proposed to be predisposed by the presence of *X. betulae* (Cale et al., 2015b). Such an association is not surprising given that *N. ditissima* readily colonizes bark wounds in other hosts, such as maple (Grant and Spaulding, 1939). *Xylococcus betulae* infestations could positively impact those of beech scale. Large beech scale colonies are commonly observed within the erumpent wounds from *X. betulae* feeding, which presumably provide protected feeding sites for beech scale crawlers and early instars (Houston, 1975; Shigo, 1962). Indeed, evidence suggests that beech scale density is positively associated with *X. betulae* density of the previous year (Cale et al. unpublished data). Taken together, these interactions suggest that *X. betulae* may indirectly facilitate BBD by promoting the development of beech scale infestations and in turn *N. faginata* infection, while simultaneously and directly predisposing beech to *N. ditissima* infection. Thus, *X. betulae* may play a greater role in BBD development than previously recognized. Further, *X. betulae* on beech may originate from source populations on other tree species such as birch, and be followed by *N. ditissima* arrival from infected maples to cause infections on beech.

Whether *X. betulae* populations exhibit temporal variation associated with BBD progression at the stand level is unknown, but it has been suggested that this insect is more abundant in aftermath forests than in unaffected or earlier-stage BBD forests (Houston, 1975). While comparative studies between aftermath and killing front forests are lacking, this insect may cause more total bark damage at the stand level in the aftermath stage than does beech scale in the killing front. Observations of greater prevalence of *X. betulae* wounds relative to those of beech scale initially led Shigo (1964) to classify stands recently affected by BBD as being in the “*Cryptococcus* phase” and long-affected stands as being in the “*Xylococcus* phase” (Shigo, 1964). Moreover, trees resisting disease during the early phase may be susceptible during the later phase due to a shift in damaging agent and wound type (Shigo, 1964). This two-part scheme of disease development was later modified and expanded into the more commonly recognized three-part system (Shigo, 1972).

4. History and spread of beech bark disease agents

Beech scale has been, facilitated by at least one introduction (Hewitt, 1914), expanding from its presumed geographical origin in the Black Sea region of Europe for over 150 years, and has come to be widely established in Europe and North America (Gwiazdowski et al., 2006). In Europe, beech scale was reportedly damaging ornamental European beech on British estates as early as 1851, around which time it was mistaken for a fungus (*Psilonia nivea* Fries) and was not recognized as being associated with *Neonectria* spp. (Ehrlich, 1934). Later, mixed opinions developed on whether beech scale or the subsequent fungal infection caused beech decline (Ehrlich, 1934). Ehrlich (1934) provided a comprehensive review of early European observations. Presently, beech scale has a wide European range, including parts of Great Britain,

574 France, Germany, Slovakia, Romania, and Hungary (Cicak and Mihal, 2002; Houston et al.,
575 1979; Mihal and Cicak, 2007, 2005; Parker, 1983).

576 The spread of BBD in North America began with the introduction of beech scale into
577 Canada from England around 1890 (Hewitt, 1914). In 1911, Hewitt (1914) was sent beech scale
578 specimens collected by the superintendent of the Public Gardens in Halifax, Nova Scotia,
579 Canada, where the insect had been observed on European beech for about twenty years. Hewitt
580 (1914) believed that the Halifax population of beech scale was a likely introduction from
581 England and noted that by 1913 the insect had expanded beyond the public gardens and had
582 become established on American beech throughout Halifax, as also indicated by Braucher (1914).
583 What followed was a steady inland expansion that continues today. Figure 3 illustrates this
584 expansion from 1890 to 2015 using county-level first-detection dates available in Cale and
585 Morin (2017) for Canada and the US. Observations from regional foresters indicate that
586 *Neonectria* spp. were infecting beech in some parts of Nova Scotia as early as 1900, with
587 widespread mortality occurring by 1910 (Camp, 1951).

588 Beech scale rapidly invaded the range of American beech in the Canadian Maritimes (Fig.
589 3). Although survey and governmental reports noted scattered infestations along the south shore
590 and central Nova Scotia in 1924 – 1925, an intensive survey revealed that beech scale was
591 established throughout the province at that time (Hawboldt, 1944). The insect was widespread
592 throughout Prince Edward Island in 1929 and Cape Breton Island, Nova Scotia by 1933
593 (Hawboldt, 1944). In New Brunswick, beech scale establishment began with a reportedly heavy
594 infestation in Dorchester in 1927. By 1942, the insect was absent from only a few northern
595 counties after a westward invasion of the coastal and interior counties during the preceding years
596 (Hawboldt, 1944). Although Hawboldt (1944) inconsistently notes beech mortality in this region

and does not mention *Neonectria* spp., Ehrlich (1934) reported heavy mortality and *Neonectria* spp. presence in Nova Scotia and New Brunswick by 1932.

In Quebec, beech scale and *Neonectria* were first observed in 1965 (Lachance, 1983; Lavallee, 1976). The disease spread westward and numerous affected stands were discovered several years later. Beech scale infestations occurred throughout an estimated 19,000 km² of Quebec's forests by 1975 (Lachance, 1983). However, *Neonectria* spp. were believed to occur on beech in a much smaller portion of this area. Beech scale was present in most of southern and eastern Quebec by 1980 and continued to spread westward while *Neonectria* spp. infections were scattered across areas long-affected by the insect (Lachance, 1983). Presently, beech scale and *Neonectria* spp. occur throughout the geographical range of beech in Quebec with heavy beech mortality occurring in much of the province (Beaudoin et al., 2014). Both *N. ditissima* and *N. faginata* have been detected in BBD-impacted forests (Beaudoin et al., 2014)

Beech scale was also observed for the first time in Ontario in 1981 (Bisessar et al., 1985), though another report (Keizer, 1988) suggests that the insect was first discovered in the province in 1966. Beech bark disease is now widespread across the province with heavy beech mortality occurring throughout much of the affected range (McLaughlin and Greifenhagen, 2012; R. Wilson pers. comm., March 23, 2016). Presently, beech scale occurs throughout the range of beech in Ontario, except several southern counties containing sparse beech populations (R. Wilson pers. comm., March 23, 2016).

In the United States, beech scale was first observed in 1929 on American beech of the Arnold Arboretum in Boston, MA (Ehrlich, 1934). Interest in beech scale peaked in 1931 when surveys for the insect were conducted across Massachusetts, Rhode Island, Connecticut, southern New Hampshire and Maine (Brown, 1934). Although some areas were thoroughly examined,

most received only a cursory survey, focusing on forest stands near roadways. Beech scale was discovered in two areas in northern Maine, several towns in southern Maine and New Hampshire, Gloucester, Massachusetts, and several towns in the Boston metropolitan area (Brown, 1934). *Neonectria* spp. infections were observed in 1933 during an intensive and widespread survey of southern Maine (Brown, 1934).

Beech bark disease continued its southwestern spread across the US over the following decades (Fig. 3). In New York State, beech scale established in the Catskill Mountains by the 1940s and by the 1960s had crossed into the Adirondack mountains presumably from Vermont (Houston, 1994b). Heavy BBD-induced mortality was later reported in the Adirondacks in 1981 (Houston, 1984). However, this mortality likely began as early as 1965 (Sage, 1996). Around this time, Adirondack and Catskill populations of beech scale likely coalesced before expanding westward across the state. Beech scale became established in western New York, and BBD-related mortality was occurring across the eastern portion of the state between 1975 and 1977 (Miller-Weeks, 1983). These organisms were well established across New England by this time. Moreover, Miller-Weeks (1983) reported that *X. betulae* was present throughout New York and New England at this time.

In Pennsylvania, beech scale was first detected in 1958 in the northeastern part of the state, and expanded to a neighboring county by 1964 (Drooz, 1959; Towers et al., 1971). A small number of *Neonectria* spp. infections were discovered in the same region in 1969 (Towers et al., 1971). Although beech scale was widespread throughout northeastern Pennsylvania by 1970, *Neonectria* spp. were not considered abundant in the region at this time (Towers et al., 1971). However, when a marked increase in the number of trees infected with *Neonectria* spp. was observed in 1973, an intensive survey of the surrounding counties revealed that *Neonectria*

spp. were well established in eight additional counties (Towers et al., 1974). Further, this survey discovered beech scale in additional counties.

Although the leading edge of beech scale expansion (with *Neonectria* spp. infections lagging behind) steadily spread westward and southward across the US, a disjunct population was discovered in the Monongahela National Forest (MNF) of West Virginia in 1981 (Mielke et al., 1982). Beech scale was observed on three mountains where the infestation levels suggested insect establishment several years prior to the survey. *Neonectria ditissima* was observed infecting beech on one of these mountains at this time (Mielke et al., 1982). Despite being sought in the survey, *N. faginata* was not observed in these areas (Mielke et al., 1982). However, Houston (1994) states that *N. faginata* was isolated from infected beech in MNF in 1983. Beech scale continued to spread throughout and *N. faginata* became the dominant BBD pathogen in MNF over the next ten years (Houston, 1994b).

Shortly after the discovery of BBD in West Virginia, beech scale was observed in northwestern Virginia in 1983 (Mielke et al., 1985). This infestation presumably originated from that in nearby MNF. No *Neonectria* spp. infections were observed at that time.

On the western edge of the BBD range, beech scale was discovered in northeastern Ohio in 1984 (Mielke et al., 1985). Despite regular insection, the first observation of either pathogen was made nineteen years later in 2003 with a beech growing in the Holden Arboretum was determined to be infected with *N. faginata* (MacKenzie and Iskra, 2005). This infection was apparently not preceded by that of *N. ditissima*, as would be expected from the temporal shift in pathogen occurrence proposed by Houston (1994b).

Beech scale was observed in the Lower Peninsula (LP) of Michigan in 1990 (O'Brien et al., 2001). By 2001, the insect was well established in parts of the Upper Peninsula (UP) and LP.

During this time, *N. ditissima* and *N. faginata* were discovered in the UP and LP, respectively (O'Brien et al., 2001). The insect was established across much of eastern UP, northwestern LP, and a few of islands in the adjoining Great Lakes by 2009 (Wieferich et al., 2011). Presently, beech scale occurs throughout much of northeastern LP and eastern UP, with *Neonectria* spp. infections occurring most abundantly in the eastern UP (McCullough and Wieferich, 2015).

The most recent state-level detection of beech scale occurred in Door County in northeastern Wisconsin in 2009. The insect was observed in ten additional eastern counties in 2010 and 2012 (Wisconsin Department of Natural Resources, 2012, 2010). However, *Neonectria* spp. have presently only been observed in areas with older beech scale infestations in Door County (Petrillo, 2015; Wisconsin Department of Natural Resources, 2012, 2010). Plots have recently been established throughout eastern Wisconsin to monitor the spread of BBD-associated organisms across the state (Petrillo, 2015).

In 1993, disjunct populations of beech scale and *Neonectria* spp. were discovered in North Carolina and in the Great Smoky Mountains of eastern Tennessee (Houston, 1994b; Wiggins et al., 2004). In Tennessee, an intensive surveying and monitoring program established in 1994 recorded large increases in beech scale incidence and infestation levels over the next four years. Incidence and severity of *Neonectria* spp. infections were suggested to have increased with beech scale infestation levels in this area (Wiggins et al., 2004). *Xylococcus betulae* also was reported to occur across the Great Smoky Mountains during the survey period (1994 – 1997) (Wiggins et al., 2004).

Presently, beech scale has been reported from at least 27% of the geographical range of American beech, and in that area, affects about 54% of the total host density (Morin et al., 2007, 2005). *Neonectria* spp. have been observed throughout much of the area where beech scale has

been found (Fig. 3). Further, BBD occupies most of the stands containing the highest proportion of beech basal area, and has spread across the country at an estimated rate of 14.7 to 16.0 km/year (Evans and Finkral, 2010; Morin et al., 2007). Beech bark disease is predicted to continue spreading across the US, occupying most or all of the geographical range of beech within the next 50 years (Morin et al., 2007).

5. Effects of BBD on host trees and forests

5.1 Effects on host trees

Beech bark disease affects radial growth as well as beech crown and bark health. The radial growth rate of beech scale infested-beech is negatively associated with increasing infestation level. For example, trees growing in counties where the insect has been present for over 40 years grow up to four times slower than those in uninfested regions (Morin and Liebhold, 2015). Slower radial growth is also associated with BBD in aftermath stands (Gavin and Peart, 1993; Kasson and Livingston, 2012).

Both beech scale and *Neonectria* spp. severities are negatively associated with host crown health though crown symptoms, including leaf chlorosis and dieback, do not necessarily manifest with initial infestation and infection (Houston, 1994a). Beech scale feeding creates minute bark cracks that may lengthen into fissures on the bole over time, and *Neonectria* spp. infections create annual bark cankers as the fungus kills cambial and phloem tissues. A dark brown slime flux often exudes from developing cankers prior to the appearance of fungal fruiting bodies (Brown, 1934). Two types of cankers are observed on BBD-affected beech: delimited (raised) and undelimited (sunken) (Houston, 1994a). Raised cankers have outward topography resulting from the development of protective necrophylactic periderm separating necrotic from

712 healthy phloem as the host tree attempts to compartmentalize the infection—a tolerance
713 mechanism (Ostrofsky and Blanchard, 1983). Conversely, sunken cankers lack this periderm
714 and thus are depressed into the bark, and presumably indicate the host’s infection intolerance
715 (Ostrofsky and Blanchard, 1983). Factors governing this canker dichotomy have not been
716 investigated. However, for a given tree, the development of one canker type or another may be a
717 function of tree genetics, environmental conditions, genetic-environment interactions, tolerance
718 threshold, and/or pathogen species.

719 As cankers coalesce, large bark patches are killed that may girdle the bole and
720 subsequently kill higher portions of the tree, the likelihood of which increases with tree size
721 because small trees tend to have few cankers (Busby and Canham, 2011; Ehrlich, 1934; Houston,
722 1994a). Cankering also alters radial growth, which declines as trees become increasingly
723 cankered (Gavin and Peart, 1993). Heavily infected trees can experience growth reductions of
724 up to 40% that of non-infected trees (Gavin and Peart, 1993). Growth reductions often indicate
725 extensive defect in the sapwood from callused cankers. These buried cankers reduce timber
726 grade, but not wood volume as most defect is removed in the slab during milling (Burns and
727 Houston, 1987). Beech bark disease therefore has a negligible effect on beech lumber.
728 Furthermore, heavily and moderately cankered trees can be uprooted and are especially prone to
729 bole-break (colloquially termed “beech snap”) in strong winds (Papaik et al 2005). Beech snap
730 may be due in part also to the activity of secondary insects such as the ambrosia beetles that can
731 further weaken trees partially girdled by *Neonectria* spp. cankers (Heyd, 2005).

732 733 5.2 Effects on forests

Beech bark disease has substantial effects on forests at multiple spatial scales. At the landscape level, annual beech mortality rates increase with the duration of beech scale presence in a given region, with marked increases occurring 15 years after scale establishment (Morin and Liebhold, 2015). While there is little variation in mortality rate among size classes at the landscape level (Garnas et al., 2011a), stand-level mortality is less evenly distributed among size classes especially in killing front stands (Houston, 1994a; McCullough and Wieferich, 2015). Though perhaps the most important impact of BBD is the sustained shift toward younger, smaller forests over time, individual stands continue to mature normally as predicted under standard self-thinning relationships as a 10 – 20 year time scale (Garnas et al., 2011a). However, stand dynamics may be more severely altered in BBD forests affected by other biotic disturbances such as hemlock woolly adelgid (*Adelges tsugae*; HWA), where HWA-induced mortality of eastern hemlock (*Tsuga canadensis*) slows beech mortality and stimulates beech growth (Morin and Liebhold, 2015).

Heavy crown mortality of mature beech in killing front forests has legacy effects on the aftermath forest structure and composition. At a landscape level, loss of large diameter overstory beech and an increase in understory beech abundance reduce the mean diameter of beech, though it does not generally change total beech basal area (Garnas et al., 2011a). However, at smaller spatial scales, the impact of BBD on forest structure depends on the duration of beech scale established in the area (Morin and Liebhold, 2015). The response of beech associates to BBD-induced mortality varies by forest strata. For example, while beech thickets inhibit sugar maple regeneration, overstory beech mortality promotes radial growth of established maple (Cale et al., 2013; Digregorio et al., 1999; Hane, 2003). Moreover, simulations suggest that beech canopy windthrow facilitates yellow birch (*Betula alleghaniensis*) and hemlock (*Tsuga canadensis*)

regeneration (Papaik et al., 2005). Further, hemlock growth and dominance increases in stands with BBD-induced mortality of associate beech (Twery and Patterson, 1984). At the landscape level, overstory associates of beech, such as sugar maple, do not exhibit increased survival, reproduction, or seedling survivorship in response to BBD-induced mortality (Garnas et al., 2011a). Overall, BBD-induced effects on associate growth and regeneration may include long-term changes to species composition with cascading impacts on forests (Twery and Patterson, 1984). For example, replacement of beech by sugar maple in the Catskill Mountains has altered forest biogeochemistry by reducing forest floor C-N ratio, increasing nitrified mineralized N, and increasing extractable NO_3^- in the soil and soil solution (Lovett et al., 2010).

While BBD may not affect total beech basal area, it does impact above-ground beech biomass, which tends to decline with BBD duration. Losses of aboveground beech biomass are high in the aftermath, moderate in the killing the front, and low in the advance front (Busby and Canham, 2011). This relationship is likely explained by relative differences in beech mortality among disease stages (Busby and Canham, 2011). In aftermath forests of Maine, beech biomass loss from BBD-induced mortality of mature trees is not offset by biomass from developing saplings, despite an offset of basal area change between these size classes (Busby and Canham, 2011; Garnas et al., 2011a). In an aftermath stand in New York, total tree aboveground biomass declined slightly over 15 years due to which may be explained by changes in species composition as well as disease-induced mortality (Forrester et al., 2003).

Young beech saplings tend to proliferate in understories of BBD-impacted forests (Cale et al., 2013; Garnas et al., 2011a; Giencke et al., 2014; Houston, 1975), and these beech thickets adversely affect local biodiversity in aftermath forests. Regeneration of desirable species such as sugar maple (*Acer saccharum*) is hindered in deep shade cast by beech thickets (Hane, 2003;

Nyland et al., 2006a). Shading and, potentially, deeper beech leaf litter below beech thickets are likely mechanisms explaining reduced groundcover plant richness and diversity in these thickets (Cale et al., 2013). Thickets, however, do not affect the biodiversity of forest fauna such as crane flies, amphibians, and small mammals (Cale et al., 2013).

Wildlife is indirectly affected by BBD as mature, mast-bearing trees are killed. Beechnut production declines over time in BBD-affected forests, with impacted stands producing 40% fewer beechnuts than healthy stands (Noble, 2009; Rosemier and Storer, 2010). Beechnut availability is a likely driver of black bear (*Ursus americana*) and marten (*Martes americana*) reproductive dynamics, with greater reproduction occurring with high beechnut availability (Jakubas et al., 2005). However, small mammal populations appear more resistant to at least short-term changes in beechnut availability and are more influenced by changes in abiotic factors and forest structure (Garneau et al., 2012; Rosemier and Storer, 2010; Storer et al., 2005). Changes in forest structure may affect small mammal populations by altering habitat availability and by increasing coarse woody material abundance on forest floors in areas impacted by BBD (McGee, 2000; Wieferich, 2013).

6. Beech bark disease management

Many strategies to manage or control BBD and its associated agents have been investigated since publication of Ehrlich's (1934) model of disease development, which suggested that a clear approach to thwarting BBD was to control beech scale (Fig. 4). While such approaches may not be appropriate or effective in managing the disease in aftermath forests (Cale et al., 2015b), this simple model has led to management strategies over the past several decades focusing largely on removing beech scale from the BBD equation (Fig. 4). As such, approaches to control the causal

agents, *N. ditissima* and *N. faginata*, have received considerably less attention (Fig. 4). To our knowledge, no strategies for managing *X. betulae* infestations of beech or other trees have been investigated. Regardless, research into potential BBD management options has been diverse including biological control, chemical control, plant breeding, and silviculture (Fig. 4). These strategies have sought to directly manage BBD or indirectly manage disease effects on forests.

6.1 Biological control

A wide variety of potential biological control agents such as parasitic fungi as well as predaceous mites and insects have been studied to manage beech scale and *Neonectria* spp. Entomopathogenic fungi can reduce beech scale populations (LaFlamme et al., 2009). In laboratory trials, both *Beauveria bassiana* and *Lacanicillium muscarium* (previously *Verticillium lecanii*) reduced the abundance of non-crawling nymphal beech scale by about 50% 10 – 11 days post-inoculation (LaFlamme et al., 2009). Although *L. muscarium* causes little mortality of beech scale eggs, it slows their development and its hyphae may rapidly infect the hatching crawlers (LaFlamme et al., 2009). Whether these parasitic fungi, either in combination or individually, can significantly affect beech scale populations under field conditions is unclear.

Arthropod predators of beech scale have also been investigated as candidate biological control agents. Although no predators have been identified in its native range (Japoshvili et al., 2015), the predaceous large red velvet mite *Allothrombium mitchelli* commonly feeds on beech scale in parts of North America (Wiggins et al., 2001). Negative association between beech scale infestation severity and mite incidence suggests that *A. mitchelli* may feed more heavily on scale occurring at low to moderate densities (Wiggins et al., 2001). Beech scale is also preyed upon by species of several other mite genera, including *Anystis*, *Tydeus*, *Abrolophus*, and *Leptus*

(Mayer and Allen, 1983). However, these mites may be generalists, potentially with little long-term effect on beech scale populations (Mayer and Allen, 1983). Additionally, two ladybird beetles (Coccinellidae), *Chilocorus stigma* and *Calvia quatuordecimguttata similis*, and one firefly (Lampyridae), *Ellychina corrusa*, are known to feed on beech scale in the field, but only *C. stigma* has been examined as a potential biological control agent (Brown, 1934; Houston, 1983a; Mayer and Allen, 1983). Although it is a commonly observed predator whose four instars all feed on beech scale and can considerably reduce beech scale densities on individual trees, *C. stigma* densities are insufficient to provide effective control at the stand-level (Mayer and Allen, 1983).

Investigations into biological control agents of *Neonectria* spp. have focused on parasitic fungi (i.e., mycoparasites). In North America, the biotrophic fungus *Nematogonum ferrugineum* (previously *Gonatorrhadiella highlei*) parasitizes both *N. ditissima* and *N. faginata* (Ayers, 1941; Blyth, 1949a, 1949b; Gain and Barnett, 1970; Houston, 1983b). Parasitized *N. faginata* show reduced conidial and perithecial production *in vivo* (Shigo, 1964). Growth of *N. ferrugineum* on this species is likely dependent upon N availability and form (Gain and Barnett, 1970). In field experiments, *N. ferrugineum*-parasitized *Neonectria* spp. colonize beech bark more slowly as well as produce smaller and fewer cankers, and fewer perithecia than non-parasitized fungi (Houston, 1983b). Despite these effects, however, *N. ferrugineum* may have a negligible impact on BBD development (Houston, 1994a). Additionally, the fungus *Fusarium oxysporum* is often isolated from *Neonectria* cankers on beech (Gotwols et al., 1980). Although *F. oxysporum* inhibits *N. faginata* growth in culture (Cotter, 1977), it has no effect on *Neonectria* canker size in the field (Gotwols et al., 1980).

6.2 Chemical control

Research regarding the effectiveness of insecticides and/or fungicides to directly control BBD organisms is limited, and has mostly focused on beech scale as the presumed primary causal organism. An early report (Hewitt, 1914) notes manual scraping together with regular application of paraffin and lye-based blends were effective at controlling this insect on ornamental trees. Modern hemipteran control methods include systemic insecticides such as imidicloprid (Conway and Kring, 2004; Gill et al., 1999), though their effectiveness in controlling beech scale is uncertain. Imidacloprid alone can be ineffective at controlling beech scale on trees receiving stem injections of this insecticide despite annual reapplication (Letkowski, 2009). However, a more preliminary study (Roberts, 2013) showed that annual imidicloprid injections and buprofezin spraying prevented beech scale infestation, though infestations did develop when these compounds were combined with phosphoric acid, which caused bark wounding at injection sites. Fungicides as a means of controlling *Neonectria* spp. in BBD or on American beech has apparently not been investigated. However, some work has been conducted to control *N. ditissima* infections in high value fruit crops such as apples and grapes using copper-based fungicides, or compounds such as captan or dithianone (Walter et al., 2015; Weber, 2014). However, the cost of chemical application across a larger area likely renders these approaches non-feasible for use in forest settings. Intensive chemical-based approaches to BBD control, whether focusing on the scale insects or *Neonectria* fungi, are likely to be costly, and therefore most suitable for protecting high-value ornamental trees.

6.3 Plant breeding

While some European beech exhibit genetically-based resistance to *Neonectria* spp. infection (Perrin, 1985), efforts to breed BBD-resistant American beech have focused solely on beech scale resistance (Koch et al., 2007). Early observations (Shigo, 1972, 1962) suggested at least some portion of northeastern beech populations are beech scale resistant. Using an absence of beech scale as a proxy for BBD resistance, later surveys showed resistant trees comprised approximately one percent of beech in aftermath forests (Houston and Houston, 1994; Houston, 1983c). This component, however, may be an underestimate and may vary with certain environmental factors and among BBD-affected regions (McCann and MacDonald, 2013; Taylor et al., 2013). In some BBD-impacted forests, the genetic diversity and abundance of resistant beech could be much lower than that of susceptible trees, which are often clustered due to the propensity of beech for clonal regeneration following root wounding or major disturbance (Batista et al., 1998; Jones and Raynal, 1988; Morris et al., 2004). Indeed, isozyme studies indicate clusters of resistant trees can have less genetic diversity than susceptible trees (Houston and Houston, 2000, 1994). However, genotype may not correlate with beech scale infestation severity when evaluated with other genetic markers, such as inter-simple sequence repeats (Morris et al., 2002).

Breeding programs for beech scale-resistant American beech have developed to indirectly combat *Neonectria* spp. infection by controlling beech scale. Breeding efforts began with cross pollination-created half- and full-sib families of resistant American beech (Koch and Carey, 2004a, 2004b). Greenhouse-grown seedlings from these families exhibited beech scale resistance in artificial infestation (Houston, 1982) trials indicating resistance heritability (Koch et al., 2010b, 2007; Koch and Carey, 2014). Resistance screenings using artificial infestations can also be performed in the field (Koch and Carey, 2014). Genomic techniques to rapidly identify

beechn scale-resistant genotypes are under development (Koch et al., 2010a, 2010c). However, several beech scale infestation-associated proteins may be a basis for and/or biomarkers of this resistance (Mason et al., 2013). Recent advances in beech propagation methods (i.e., hot-callus stem grafting) has allowed plant breeders to rapidly produce seed-bearing, beech scale-resistant trees with which to establish seed orchards (Carey et al., 2013; Koch et al., 2012). The first beech scale-resistant seed orchard was planted in Michigan in 2011 (Koch and Heyd, 2013), and field trials of candidate beech scale resistant trees for establishment of new planting lines with which to establish additional orchards is ongoing (Koch et al., 2015). Orchards of scale-resistant beech are anticipated to serve as a long-term BBD management strategy by providing resistant seed for forest restoration efforts and resistant plantings to hinder disease advancement (Koch, 2010; Koch et al., 2015; Koch and Heyd, 2013). However, whether such plantings can effectively disrupt BBD development in the aftermath zone must be evaluated given the high abundance of reproductively mature understory beech that are susceptible to BBD (Giencke et al., 2014; Houston, 1975), as well as the proposed importance of predisposing factors other than beech scale, namely *X. betulae* infestation and P limitation (Cale et al., 2015b). Beech scale-resistant plantings may be most effective when used prior to or during early BBD stages where beech scale infestation plays a significant predisposing role for *Neonectria* spp. infection (Cale et al., 2015b; Houston, 1994a).

6.4 Silviculture

Stand-level BBD management strategies have largely sought to predict BBD-induced mortality or mitigate future mortality using silviculture designed to increase the proportion of BBD resistant beech. A mortality risk classification provides forest managers with a means to

estimate future beech loss using pre-disease factors for individual trees (Mize and Lea, 1979).

Important classification factors include: tree diameter, crown damage, branch stubs, sparse crown foliage, and decay fungi presence. Mize and Lea (1979) predict large (>45.7 cm in diameter at breast height) trees with at least one of these factors are most likely to die.

Although these predictions are useful in deciding which trees to harvest in stands with impending disease-induced mortality, a more proactive strategy to prevent further losses is needed for stands where BBD is established. Indeed, long-term selection cuttings that remove infested and infected trees may reduce future mortality by bolstering disease resistance in residual trees (Leak, 2006). In New Hampshire, a stand managed in this way had 275% more basal area in trees without evidence of BBD compared to an adjacent, unmanaged stand of similar age (Leak, 2006). The long-term utility of the cutting method described by Leak (2006) could likely be to inhibit beech scale and *Neonectria* spp. transmission from overstory to understory beech (Giencke et al., 2014). However, high propagule pressures at several spatial scales indicate that targeted removal of highly affected beech may have little long-term chance of reducing BBD incidence (Garnas et al., 2013). Thinning or salvage cutting to reduce beech densities may be similarly ineffective at inhibiting BBD development or spread, because disease incidence and severity may not be associated with host density (Garnas et al., 2013) and beech scale can arrive from long distances by dispersing in air currents carrying it above forest canopies (Wainhouse, 1980). It should be noted, however, that many studies principally apply to aftermath forests, as these comprised the majority of the study areas. Further, several factors such as spatial aggregation by tree size or infection severity as well as temporal variability can be important factors associated with BBD spread (Giencke et al., 2014).

Thinning non-beech species can negligibly or temporarily reduce beech scale and/or *Neonectria* spp. levels (Crosby and Bjorkbom, 1958). Even-aged management likely offers little long-term disease control, as beech scale-resistant seed trees are highly susceptible to decline and death in the absence of surrounding trees (Farrar and Ostrofsky, 2006). Additionally, along with BBD-affected beech, forest managers may wish to consider cutting *N. ditissima*-infected maple (i.e., with target canker) and *X. betulae*-infested birch to limit the spread of these agents to healthy residual overstory beech or potentially later-developing understory beech (Cale et al., 2015b; Kasson and Livingston, 2009). Removal of such maples during the advance front stage (or earlier) may be especially important in reducing mortality in the killing front when *N. ditissima* infection is a critical mortality factor (Houston, 1994b).

Prolific root sprouting following beech harvests and BBD-induced mortality can be managed by chemical and mechanical treatments (Bohn and Nyland, 2003; Houston, 2001; Jones et al., 1989; Nyland et al., 2006b). The herbicides glyphosate and triclopyr are effective methods of controlling beech advance regeneration and inhibit sucker production for two growing seasons post-harvest (Ostrofsky and McCormack, 1986). Indeed, mist-blown glyphosate and triclopyr can reduce beech advance regeneration by 100% and 93%, respectively, and reduced sprout production by 85% and 87%, respectively (Ostrofsky and McCormack, 1986). Hack-and-squirt injections of glyphosate as well as basal spraying of triclopyr are also highly effective at controlling beech understories, although application cost and rate can differ considerably between these methods (Kochenderfer et al., 2004). Root sprouts are easily killed by simple stem girdling (Nyland, 2004), though this method is labor intensive and may not be practical for managing dense beech understories. Such understories are better managed by brush saw treatments (Forrester and Bohn, 2007). Treatments that remove understory beech allow light to

reach the forest floor, likely ameliorating the negative effect of beech thickets on plant diversity (Cale et al., 2013; Forrester and Bohn, 2007; Nyland et al., 2006a).

7. New concerns and future directions

The cyclic, self-perpetuating nature of BBD hypothesized by Houston (1975) is becoming increasingly evident. The prevalence of susceptible beech understories in aftermath forests facilitates the continued presence of beech scale and *Neonectria* spp. fungi as these agents spread from older to younger generations of beech. Indeed, older, BBD-affected trees have recently been shown as an inoculum source for new infestations and infections on understory trees as small as five centimeters in diameter (Giencke et al., 2014). As these understory trees grow, beech scale and *Neonectria* spp. levels intensify (Giencke et al., 2014). This suggests that secondary killing fronts could develop in aftermath forests as smaller stems reach sizes suitable for heavy infestations and infections, and thus are killed prior to host trees reaching the upper forest canopy. However, this mortality may be more locally eruptive than progressive along a leading edge—as occurred during the primary killing front—because BBD agents and understory beech are widely, albeit heterogeneously, distributed throughout the aftermath zone (Garnas et al., 2011a; Houston, 1975). Indeed, secondary killing fronts likely have already begun in this region. In US forests affected by BBD for at least 60 years, BBD-affected beech are exhibiting heavy crown mortality at diameters much smaller than those of parent trees killed during the primary killing front (McCaskill and Morin, 2013). Further, mortality rates of such younger beech have accelerated, relative to non-affected beech, during recent years in other parts of the aftermath zone (Giencke et al., 2014). While it is uncertain how secondary killing fronts will develop in coming decades, managers should prepare for heavy beech mortality as they once did

during the primary killing front. Management objectives should consider the likely long-term ecological impacts of BBD on species composition and forest structure. Management approaches should incorporate recent advances in BBD research, and include strategies that target not only BBD causal agents, but also stand factors such as species composition, BBD resistance, and stand developmental trajectories, as well as site factors such as nutritional status.

Several key points and research directions emerge from our review of the past century of BBD literature as well as from the need to effectively manage this widespread forest disease and its cascading ecological impacts, as follows: (1) *Neonectria ditissima* and *N. faginata* have different biologies, pathologies, and likely different contributions to the impacts of BBD on affected forests (Cale et al., 2015b; Castlebury et al., 2006; Chaverri et al., 2011; Houston, 1994b; Kasson and Livingston, 2009). Therefore, field investigations should identify the *Neonectria* to species in order to interpret study findings without overlooking potentially important differences between the pathogens. (2) The behaviors of and interactions among BBD-related organisms, forest conditions, and beech population demographics likely vary with BBD stage (Cale et al., 2015b; Garnas et al., 2011a; Houston, 1994a; Kasson and Livingston, 2012, 2009; McCaskill and Morin, 2013; Morin et al., 2015; Wiggins et al., 2004). Killing front stands are genetically and structurally diverse, whereas aftermath stands are less structurally diverse and, at least in some parts of the aftermath zone, consist largely of clonal root sprouts that arose from BBD-susceptible root stocks left in the wake of the killing front (Cale et al., 2013; Hane, 2003; Houston, 1975; Nyland, 2008). The roles of tree physiology, beech scale, *X. betulae*, *N. faginata*, and *N. ditissima* in BBD development may differ especially between the killing front and aftermath stages (Cale et al., 2015b), and the failure to interpret results in this context could hinder progress in understanding and effectively managing BBD pathosystems.

Continued research is needed to help build a clear understanding of the distinctions between stages as well as the prediction of conditions occurring as one stage transitions to another. (3) In aftermath forests, BBD has been proposed to result from two sets of fungus-insect interactions that synergize with low tree P and defense-related phenolics: *N. faginata* infection resulting from prior beech scale infestation, and *N. ditissima* infection from prior *X. betulae* infestation (Cale et al., 2015b). Additional research is needed to clarify how prevalent these pathosystems are throughout the aftermath zone and whether they operate in secondary killing front forests. (4) Nutritional and physiological factors (e.g., N, P and phenolics) have been proposed to be are equally or more important than scale insects in predisposing beech to *Neonectria* spp. infection in aftermath forests (Cale et al., 2015b). Interactions between climate, atmospheric deposition, soil chemistry (e.g., widespread soil P limitation in the Northeast), and bark chemistry in initiating and/or exacerbating disease onset and mortality warrants further investigation (Aber et al., 2003; Cale et al., 2015b; Crowley et al., 2012; Gradowski and Thomas, 2008). (5) Although *X. betulae* is an important disease factor, little is known about the ecology of this insect (Cale et al., 2015b; Shigo, 1964, 1962). Future work should seek to understand whether this insect interacts with beech scale and *N. ditissima* in causing beech mortality in killing front stands as well as the potential role of birch trees as reservoirs of *X. betulae* for beech infestations. (6) The history and origin of *N. faginata* remains unclear (Castlebury et al., 2006; Chaverri et al., 2011; Hirooka et al., 2013; Plante et al., 2002). Molecular biological techniques may help to clarify its genetic evolution and potential endophytic habit. (7) Beech thicket occurrence throughout the BBD aftermath zone is inconsistent but an important threat to forest biodiversity and the regeneration of desirable timber species (Cale et al., 2013; Garnas et al., 2011a; Giencke et al., 2014; Hane, 2003; Houston, 1975). A better understanding of the factors and ecology of beech

thicket development is needed to more accurately predict thicket occurrence, intensity, and impact.

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1561 **Figure 1.** The relative incidence of beech scale (*Cryptococcus fagisuga*), *Neonectria* spp., and
1562 American beech (*Fagus grandifolia*) aboveground mortality in forests prior to beech bark disease
1563 (BBD) arrival (Pre-BBD) and during each of the three temporal stages of BBD.

1564

1565 **Figure 2.** A canker of *Neonectria* spp. bearing red perithecia and white sporodochia (A) and the
1566 white wax masses of beech scale (*Cryptococcus fagisuga*) colonies (B) on the bark of American
1567 beech (*Fagus grandifolia*).

1568

1569 **Figure 3.** County-level spread of beech scale (*Cryptococcus fagisuga*) throughout North
1570 America since its 1890 introduction until 2015. County shading indicates the decade beech scale
1571 was first detected, whereas cross hatching indicates the current, reported range of *Neonectria* spp.

1572

1573 **Figure 4.** Treemap showing the relative number of beech bark disease-related publications
1574 focused on methods to either directly (blues) or indirectly (greens) manage beech scale
1575 (*Cryptococcus fagisuga*; left large box) or *Neonectria* spp. (right large box). Small boxes
1576 represent specific management topics within four larger categories: biological control (light blue),
1577 chemical control (blue), plant breeding (light green), and silviculture (green). A list of
1578 publications used to construct this figure is available as Supplemental Table 1.

A

B

Management category

Biological control

Chemical control

Plant breeding

Silviculture