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A synthesis of emerging health issues of eastern white pine (*Pinus strobus*) in eastern North America☆

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ABSTRACT

Eastern white pine (*Pinus strobus* L.) is one of the most important conifer species across eastern North America. However, emerging health issues of eastern white pine have increased dramatically in recent decades, raising serious concerns over the health and future of this species. These emerging issues are due to native pests and pathogens that were mostly innocuous in the past and hence, have been rarely studied. One fungal pathogen of concern, *Caliciopsis pinea* Peck, is associated with severe resinosis, crown thinning, dieback, cankers, and bark cracks/fissures. Reports of *C. pinea* have been on the rise since the mid-1990s, particularly in the northeastern U.S. An insect of concern, eastern white pine bast scale (*Matsucoccus macrocicatrices* Richards), is a sap-sucking pest associated with branch flagging, dieback, and canker formation. Although described as early as 1958, this insect was not reported in the southeastern U.S. until 2006, when it was found on eastern white pine with dieback symptoms. A foliar complex of fungal pathogens has also been on the rise since 2006 in the northeastern U.S. and southern Canada, known collectively as White Pine Needle Damage. This complex results in needle discoloration and necrosis, premature needle drop, and branch dieback. In combination, these emerging health issues are occurring at levels not previously reported and across several regions, indicating an imminent range-wide health concern for eastern white pine. Our goal is to synthesize the ecology, evolutionary and post-settlement history, silvicultural practices, and abiotic and biotic stressors of eastern white pine. By unifying the known ecology and stressors of eastern white pine, we aim to provide a forest health framework to assist resource managers in developing a cohesive conservation, management, and restoration plan for this critical conifer species in North America.

1. Introduction

Eastern white pine (*Pinus strobus* L.) is one of the most ecologically, culturally, and economically important conifer species in eastern North America. Its ecological importance is underscored by its versatility as both an early and late successional species, capable of thriving in environments ranging from low-elevation glacial outwash to high-elevation hardwood forests. Whether in pure stands or more often as a scattered super-canopy tree, eastern white pine provides habitat heterogeneity and resources (e.g., food) for many wildlife species (Abrams et al., 1995). It is also the most widely planted tree species in eastern North America and has become common in urban and suburban areas (Wendel and Smith, 1990). Further, the species dominates the sawtimber market in Maine, Massachusetts, New Hampshire, and Rhode Island, where it has the highest volume of sawtimber (McCaskill and McWilliams, 2012; Morin and Woodall, 2012).

For the past two centuries eastern white pine has been subjected to unprecedented shifts in habitat and disturbance regimes due to anthropogenic actions such as intensive logging, agricultural land abandonment, fire exclusion, changing climate, and invasion by non-native herbivores. Yet the new millennium has ushered in a different suite of new, largely unexplained, and previously innocuous factors affecting the health of eastern white pine (Llewellyn, 2013; Lombard, 2003; Mech et al., 2013; Munck et al., 2012, 2015a). Symptoms are multiple, including the presence of cankers on branches and stems, severe resinosis, branch flagging, loss of needles, branch and/or stem dieback,

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and in some instances mortality. Saplings to mature trees are affected, with seedlings and saplings experiencing more than 90% mortality in the southern Appalachians (Mech et al., 2013; Schulz et al., 2018a *this issue*, personal observations). Many of these symptoms are occurring from Ontario, Canada (Llewellyn, 2013) to northern Georgia, U.S. Mech et al. (2013), which has led to a consensus that novel, associated phenomena are affecting eastern white pine range-wide. Suggested causal agents include *Caliciopsis pinea* Peck, a native canker-forming pathogen; eastern white pine bast scale (*Matsucoccus macrocicatrices* Richards), a native scale insect correlated with dieback and canker formation; and White Pine Needle Damage (WPND), a complex of foliar pathogens associated with reductions in tree crowns and vigor (Lombard, 2003; Mech et al., 2013; Ray, 1936; Wyka et al., 2017a). These native agents have received little attention in the last 60 years (Delatour, 1969; McCormack, 1936; Watson et al., 1960), likely because of their low economic and ecological impacts to tree health. Yet recent increases in activity, incidence, and prevalence of these relatively innocuous, native stress agents in association with symptomatic trees suggests that something has drastically changed in the etiology of eastern white pine, which merits serious investigation.

In this article, we review the evolutionary, biological, and anthropogenic history, as well as past abiotic and biotic stressors of eastern white pine, to help outline and synthesize the health risks this species faces and the likely drivers behind them. While there are multiple stressors of eastern white pine, we focus only on those that are directly managed (Ostry et al., 2010). Finally, we put a timely spotlight on these unique and emerging forest health issues, formally outlining the observable symptoms, and discussing potential agents affecting eastern white pine health range-wide. Our overall intent is to synthesize and unify the scope of eastern white pine ecological research, so that solutions to health issues can be efficiently and effectively developed for long-term conservation and sustainable use in eastern North America.

2. Recent evolution of eastern white pine

Eastern white pine belongs to the North American five-needle pine subgenus, which is commonly referred to as the “white pine” subgenus and includes nine native pine species: *P. albicaulis* Engelm., *P. aristita* Engelm., *P. balfouriana* Balf., *P. flexilis* James, *P. lambertiana* Dougl., *P. longaeva* D.K. Bailey, *P. monticola* Douglas ex D. Don, *P. strobiformis* Engelm., and *P. strobus*. However, eastern white pine is the only five-needle pine native to eastern North America (Gernandt et al., 2005; Price et al., 1998). The divergence between eastern white pine and the five-needle pines of western North America occurred in the middle Eocene due to the unstable tectonic, climatic, and biogeographic events that characterized part of the Tertiary era (Eckert and Hall, 2006; Richardson and Rundel, 1998). There are two recognized varieties of eastern white pine: *P. strobus* var. *strobus* and *P. strobus* var. *chiapensis*. The Chiapensis pine variety currently resides in the moist mountain regions of southern Mexico and likely became a disjunct lineage during the late Pleistocene (Farjon, 2010), although some consider it to be a distinct species (del Castillo et al., 2009). The strobus variety, referred to as eastern white pine herein, can be found from Minnesota and southeastern Manitoba, across southern Canada to Newfoundland, and south to Georgia and South Carolina (Little, 1971, Fig. 1). It can also be found as an invasive species in central Europe (Hadincová et al., 2008; Mandák et al., 2013).

As ice receded after the last glacial maximum, eastern white pine reappeared on the landscape in Virginia’s Shenandoah Valley around 13,000 years ago (Craig, 1969; Jacobson, 1992). Refugial populations on the mid-Atlantic coast and northwest Georgia likely provided viable seed sources (Davis, 1983; Nadeau et al., 2015). Since then, the species experienced rapid northern and westward expansion, arriving in the northeastern U.S. around 10,000 years ago, southeastern Canada 8000–10,000 years ago, eastern Great Lakes region 8000–9000 years ago, and western Great Lakes region around 7000 years ago (Davis, 1983; Jacobson et al., 1987; MacDonald et al., 1998; Zinck and Rajora, 2016). Eastern white pine prefers warm and dry temperate conditions, and around 5000 years ago reached its northern range limit in northeastern Canada (Davis, 1983). The climate then cooled, resulting in the species’ retreating southward to slightly warmer climates (Davis, 1983). A similar climatic response can be seen in the Great Lakes region between 8000 and 4000 years ago: as the climate became cooler and moister, eastern white pine moved into the more arid western Great Lakes region, while population numbers declined in the southern Great Lakes (Davis, 1983; MacDonald et al., 1998). The highest genetic diversity in eastern white pine occurs in the southern Appalachian Mountains, and three distinct lineages developed after migration including (1) west of the Great Lakes, (2) from the Hudson River to the Great Lakes region, and (3) along the eastern seaboard through the Appalachian Mountains (Zinck and Rajora, 2016).

Throughout much of North America, eastern white pine appeared to follow jack pine (*P. banksiana* Lamb.) and red pine (*P. resinosa* Aiton) as they migrated north and west, albeit more slowly. In many regions, jack pine dominated until eastern white pine became established (MacDonald et al., 1998). On mesic soils, eastern white pine could succeed until deciduous hardwoods arrived and outcompeted the species (Davis, 1983). This combination of climate shifts and species’ range shifts led to a peak abundance of eastern white pine, around 4000 years ago in northeastern North America and around 1000 years ago in the western Great Lakes (Jacobson, 1992).

3. Biological and ecological traits of eastern white pine

The vast distribution of eastern white pine is a testament to its versatility to grow from sea level to 1220 m in elevation, on a wide variety of soils, and in 28 different forest cover-types (Wendel and Smith, 1990). It grows especially well on low to moderate quality and well-drained sandy soils where hardwoods struggle to compete for resources. Densities of eastern white pine trees tend to peak in riparian valleys and in dry, nutrient-poor uplands (Abrams, 2001). Hardwoods typically outcompete eastern white pine on mesic, rich sites, while eastern hemlock (*Tsuga canadensis* L. Carrière) usually dominates in cool, moist sites (Abrams, 2001; Stiell et al., 1994).

Saplings and young trees have thin, smooth bark that thickens and develops deep fissures as they mature. The root system consists of three to five large, wide-branching roots for support. Root grafting is common and thriving individuals can exchange nutrients with suppressed individuals when interconnected (Bormann, 1966). When 5–10 years old, trees begin to bear cones and maintain reproductive vigor for more than 200 years (Wilson and McQuilkin, 1963). Pulses of seed production typically occur every three to five years. The growth rate of eastern white pine is high compared to other pines and hardwoods. Seedlings require at least 20% sunlight to survive, but once released from shading they grow rapidly. Annual increment growth typically peaks at 10–20 years of age (Wendel and Smith, 1990), however after 20 years the growth rate of eastern white pine often exceeds that of its competitor species (Barrett, 1933). Additionally, eastern white pine is the tallest and one of the longest-lived trees in eastern North America and can easily remain a fixture in the canopy for hundreds of years across its distribution.

Historical records show that eastern white pine was seldom the most predominant species regionally in pre-settlement forests, which is also the case today (Abrams, 2001). However, it does represent a major component of five forest cover-types: (a) eastern white pine, (b) red pine, (c) white pine-chestnut oak, (d) white pine-hemlock, and (e) white pine-northern red oak-red maple (Wendel and Smith, 1990). The species is an especially vital associate of eastern hemlock and Carolina hemlock (*T. caroliniana* Engelm.) forests in the Appalachian Mountains. The role of eastern white pine as a canopy tree has become even more important with widespread hemlock decline due to the invasive hemlock woolly adelgid (*Adelges tsugae* Annand) (Lovett et al., 2006).

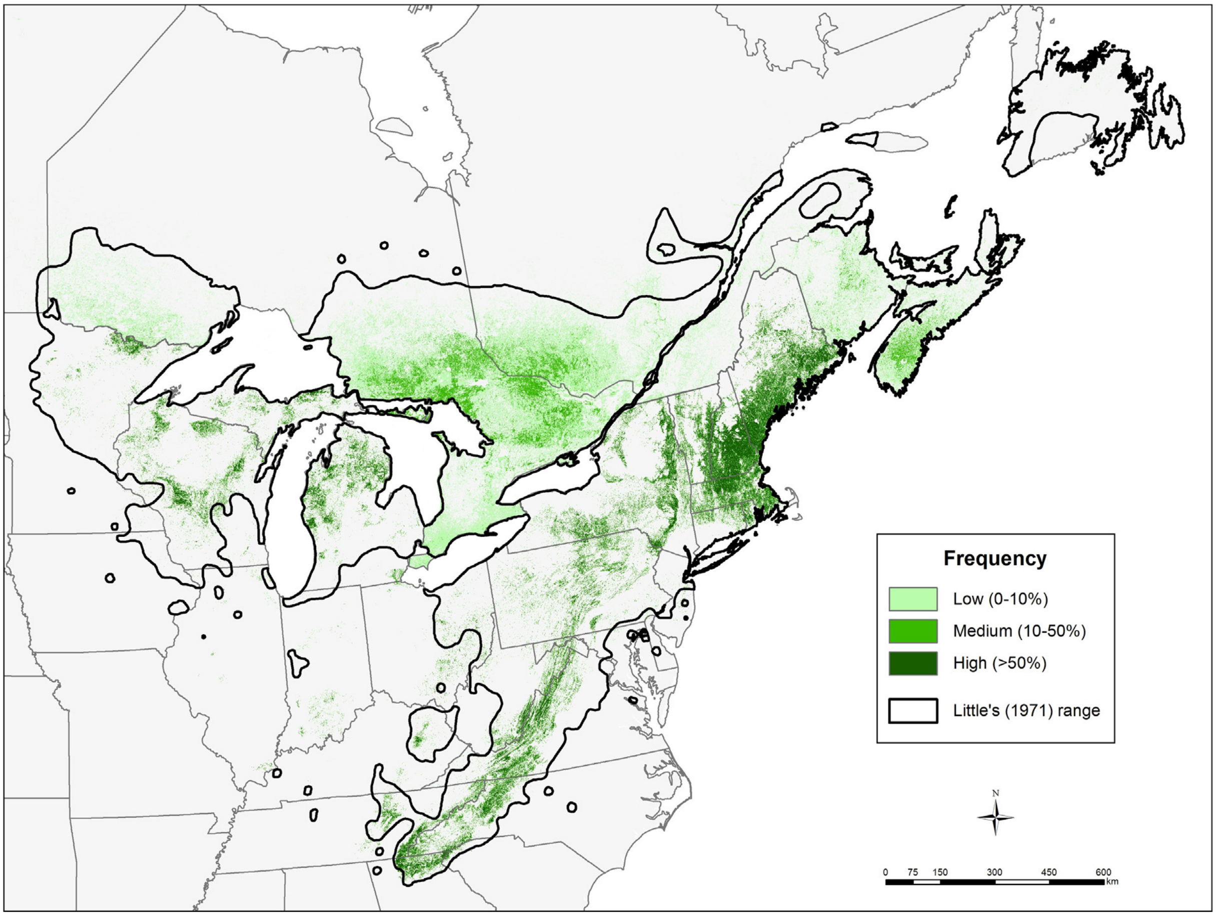

Fig. 1. Native range of eastern white pine (*Pinus strobus* L.) in North America. Frequency refers to the percentage of eastern white pine comprising total tree species composition for individuals ≥12.7 cm dbh, at 250 m resolution. Little's (1971) published range is indicated in bold. Figure produced by Anthony Elledge, USDA-FS Forest Health Protection, using Forest Inventory and Analysis (FIA) data and Canadian Forest Service Inventory data.

Changes in forest structure and function are inevitable with the loss of one or both conifer tree species, as these areas may become dominated by mid-story (e.g., *Rhododendron* spp.) and upper-story hardwood trees (e.g., black birch, *Betula lenta* L.) (Brantley et al., 2013; Small et al., 2005).

Eastern white pine responds well to disturbance, excelling as a pioneer species. With its relatively low shade tolerance when young, but high growth rate compared to other pines and hardwoods, eastern white pine easily establishes in early- to mid-successional communities, quickly colonizing abandoned fields and filling canopy gaps created by fire, windfall, and insect/disease outbreaks (Abrams, 2001; Black and Abrams, 2005; Wendel and Smith, 1990). Despite the lack of serotinous cones or the ability to sprout vegetatively, eastern white pine grows most favorably under a disturbance regime consisting of a 150–300 year fire cycle with intermittent surface-level fires occurring every 20–40 years (Frelich, 1992). Once established and mature, its bark is thick enough to withstand surface-level fires, and its height and longevity allow it to dominate the canopy for centuries (Abrams, 2001; Frelich, 1992). Given its valuable ecophysiological traits (e.g., high growth rate, longevity, and ability to establish on marginal soils), eastern white pine is commonly planted to control erosion, reclaim surface mined sites, and increase productivity on previously cultivated slopes (Hepp et al., 2015).

Although there are no known specialist associates, countless wildlife species rely on eastern white pine. Pure stands provide storm shelter for wildlife when young and dense, and they foster a well-developed herbaceous layer when mature, increasing habitat richness for wildlife (Carey, 1993). As a scattered super-canopy tree in mixed stands, eastern white pine provides a vertical heterogeneity in the canopy that other pines fail to replicate (Rogers and Lindquist, 1992). This multi-layered quality yields additional foraging and nesting opportunities for birds and mammals compared to communities where eastern white pine is absent (Rogers and Lindquist, 1992). For instance, black bears (*Ursus americanus* L.) prefer these trees as refuge and bedding sites when raising their cubs (Elowe and Dodge, 1989), and eagles (*Haliaeetus leucocephalus* L.) and osprey (*Pandion haliaetus* L.) prefer these trees to more common species for nest building (Kingsley and Ramquist, 1993). The seeds, bark, and foliage of eastern white pine are also important resources for birds and wildlife. Its seeds represent a major component of seed caches belonging to white-footed mice (*Peromyscus leucopus* Rafinesque) and red-backed voles (*Clethrionomys gapperi* Vigor) (Abbott and Quink, 1970), its inner bark is a favorite winter food of porcupines (*Erithizon dorsatum* L.) (Hazard, 1982), and its foliage supports insect food for pine warblers (*Setophaga pinus* Wilson) (Green, 1992). More examples of birds and wildlife species that utilize eastern white pine are summarized by Green (1992), Rogers and Lindquist (1992), and Yamasaki (2003).

4. Anthropogenic history and practices involving eastern white pine

Eastern white pine is considered a “cultural keystone species” that greatly shaped the identity of Native American Tribes and European settlers (Uprety et al., 2013). The Kitcisakik Algonquin community of Canada places high value on the ecological restoration of this species on their ancestral land (Asselin, 2015; Uprety et al., 2013), as does the

Menominee community of northern Wisconsin (Wood and Dewhurst, 1998). The Iroquoians of the Saint Lawrence Valley considered it a "Tree of Peace" (Quenneville, 2007). Eastern white pine was a key component of daily living such that the resin, bark, wood, and needles were used for construction, food, and medicine (Krochmal et al., 1969). This tree is also an integral part of Native Americans' traditional stories and myths, and art forms (Asselin, 2015). At the time of European Settlement, eastern white pine trees captured the imagination of many European explorers, naturalists, and writers. Currently, eastern white pine is the state tree of Maine and Michigan, U.S., the provincial tree of Ontario, Canada, and it continues to be an important cultural icon for eastern North American forests (Ontario-MNRF, 2014; USDA-USNA, 2016).

During the 18th and 19th centuries, eastern white pine trees were some of the tallest, straightest, and largest individuals in the forest, producing wood that was relatively lightweight. Trees could reach 45–55 m, and diameters upto 100–130 cm (Abrams, 2001). These characteristics made the species ideal for timber, and thus the white pine logging industry was born. The early logging of eastern white pine focused on old-growth trees and can be divided into two distinct time periods: when logging began around 1700 in northeastern North America and 1830 in the Great Lakes Region (Abrams, 2001; Jacobson, 1979). This gap in time is closely related to settlement patterns and changes in forest composition: as old-growth eastern white pine populations were harvested in eastern areas, the search for additional old-growth trees spread westward towards the Great Lakes. While the logging industry was growing, large swaths of forestland were being cleared for agricultural purposes. This was particularly prevalent in New England, but other regions experienced deforestation at smaller scales (Foster, 1992; Hooker and Compton, 2003). However, by the end of the 19th century there was a shift away from farming and agriculture towards industrialization, and many of these cleared agricultural lands were abandoned (Barton et al., 2012; Foster, 1992; Hooker and Compton, 2003). Reforestation of logged and agricultural lands occurred throughout the 20th century, with eastern white pine often regenerating naturally on these abandoned lands, particularly on open pasture lands (Foster, 1992). The species can quickly colonize these sites due to its ability to mast with wind-dispersed seeds that can readily establish on cleared, marginal soils (Dovčak et al., 2005). In the southern U.S., many clearcuts and abandoned agricultural lands were planted with eastern white pine, which was a highly preferred species by the Civilian Conservation Corps in the 1930s. Continuing into the 1950s, more than 20 million eastern white pine seedlings were planted in North Carolina, in large part by the Civilian Conservation Corps (Vimmerstedt, 1962).

In addition to logging, agricultural clearing, and reforestation, another influential anthropogenic disturbance was fire exclusion, which began in the early 1900s. In the Appalachians, fire exclusion resulted in denser, closed forest canopies, which in turn limited regeneration in oak (*Quercus* spp.) and southern pine (*Pinus* subg. *Pinus* spp.) stands. These changes in fire regimes allowed low to moderate shade tolerant species like eastern white pine, red maple (*Acer rubrum*), and black gum (*Nyssa sylvatica*) to regenerate (Copenheaver et al., 2006; Harrod and White, 1999). However, many of these regenerating species are fire intolerant, thus if fire returns to the landscape it could once again alter species composition.

As a result of these multiple and compounded anthropogenic disturbances, eastern forests changed dramatically over the past 300 years. For instance, prior to settlement Wisconsin forests had more than seven million ha containing eastern white pine (Ostry et al., 2010; Spencer et al., 1992). By 1980, this eastern white pine forest type was reduced to 203,564 ha across Wisconsin, Michigan, and Minnesota combined (Ostry et al., 2010; Spencer et al., 1992). Additionally, in pre-settlement times Maine's Penobscot River watershed contained three times greater volume of pine sawtimber compared to recent inventories (Wilson, 2005). As such, very few pre-settlement eastern white pine stands remain in North America today. However, field abandonment in the northeastern U.S. and fire exclusion in the southeastern U.S. have favored higher concentrations of second-growth eastern white pine to develop.

Currently, eastern white pine continues to be an important species for the forest products industry e.g., the standing value of white pine saw logs in the U.S. is estimated to be at least $18.6 billion (Livingston, 2016). There is more than 600 million m^3 of standing eastern white pine timber ($>$ 12.7 cm dbh) in the U.S. alone. The species is also heavily managed for other purposes, including the Christmas tree industry, historical and cultural significance, and biodiversity and ecological benefits (Ostry et al., 2010; Schroeder, 1992).

Silvicultural techniques are key to maintaining healthy eastern white pine stands. The species produces reliable seed masts, and silvicultural prescriptions are frequently timed with seed events. For example, shelterwood cuts, uniform or irregular, are often encouraged because the species regenerates well afterwards (Lancaster and Leak, 1978). An initial shelterwood cut removes 40–60% of the overstory and occurs during or immediately after a seed year. After seedling establishment, a second cut (overstory removal) occurs to remove the original shelter trees, usually 5–10 years after the first cut. However, this second cut can be delayed to reduce white pine weevil (*Pissodes strobi* Peck) damage (Ostry et al., 2010) or increase the value of crop trees (Leak and Lamson, 1999; Seymour, 2007). Where tree quality is an objective, pruning to a height of 5–8 m can increase the value of butt logs (Seymour, 2007; Smith and Seymour, 1986).

In regards to site selection, hardwood trees will outcompete eastern white pine on sites with better soils. At best, eastern white pine will be part of a mixed species stand, or else herbicide treatments may be needed to increase the pine component on these soils (Lancaster and Leak, 1978). Eastern white pine can be grown in plantations, but white pine weevil damage (Katovich and Mielke, 1993; Major et al., 2009; Ostry et al., 2010) and hardwood competition (Lancaster and Leak, 1978) are limiting factors. Hence, successful silviculture of eastern white pine typically involves natural regeneration on well-drained soils using shelterwood systems.

5. Biotic stressors affecting eastern white pine health

There are at least 277 known insect and fungal agents of eastern white pine, of which 23 are significant (Wendel and Smith, 1990). Frequent insect agents include defoliators such as white pine sawfly (*Neodiprion pinetum* Norton) and introduced pine sawfly (*Diprion similis* Hartig), which feed on old and new foliage; pine leaf adelgid (*Pineus pinifoliae* Fitch), which feeds on current-year shoots; white pine aphid (*Cinara strobi* Fitch), a sap-sucking insect that feeds on twigs and branches; and eastern pineshoot borer (*Eucosma gloriola* Heinrich), which attacks new shoots (Wilson, 1998). Root rots caused by fungal pathogens such as *Heterobasidion irregulare* Garbelotto and Otrosina, *Leptographium* spp., and *Armillaria* spp. are also common in eastern white pine stands. They can kill roots and, if the fungus girdles the tree's root collar, kill the tree. Additionally, whitetail deer (*Odocoileus virginianus* Zimmerman) and snowshoe hare (*Lepus americanus* Erxleben) can severely browse pine seedlings (Kittredge and Ashton, 1995).

Two significant biotic stress agents impacting eastern white pine management throughout the 1900s and 2000s include white pine blister rust (*Cronartium ribicola* J.C. Fisch) and white pine weevil. White pine blister rust, a non-native fungal pathogen, arrived in North America in 1906. As a result of extensive logging, eastern white pine seedlings were imported from Europe for planting in North America in an attempt to increase the population (Spaulding, 1911). However, some of the imported seedlings were infected with blister rust, and the disease spread rapidly through North America. The pathogen has a complex life cycle involving two obligate hosts: five-needle pines and currant species (*Ribes* spp.). Basidiospores disseminate from currant leaves and enter the pine host through stomatal openings in needles. Infections begin as a needle lesion and then grow from the foliage into twigs and woody tissue, killing cambial tissue and causing branch and stem cankers. The tree responds with excessive resin production at cankers, which are typically located at whorls where branches attach to the main stem. These cankers can eventually girdle the tree and result in mortality (Kinloch, 2003; White et al., 2002). Young trees are highly susceptible, and can die quickly. Because the pathogen cannot spread from pine to pine, one of the leading management recommendations is eradication of all currants. In Maine, a currant eradication program was established in 1917, after which it became illegal to plant or grow currants (Ostrofsky et al., 1988). As a result, there was greater than 50% reduction in blister rust incidence in the state over a 70-year treatment period (Ostrofsky et al., 1988). At present blister rust remains common in eastern North America, and in western North America it is causing significant damage and mortality in western white pine species (Brar et al., 2015; Munck et al., 2015b).

White pine weevil is native to North America and is another major pest of eastern white pine, especially in commercial stands. Eastern white pine is the most suitable host, however the weevil can attack more than 20 conifer species including jack pine, Norway spruce, (*Picea abies* L.), Sitka spruce [*P. sitchensis* (Bong.) Carrière], and Engelmann spruce (*P. engelmannii* Parry ex Engelm.) (Hamid, 1995). White pine weevil overwinters in the organic material at the base of the tree. In the spring adults will emerge, climb or fly to the base of terminal buds, feed, and then females lay eggs in these feeding cavities, which hatch 1–2 weeks later (Hamid, 1995). Hatched larvae continue to feed on the terminal shoot and burrow down it, causing further damage. After four molts, adults emerge in late summer by chewing holes in the terminal shoots, and will eventually make their way to the base of a host tree to overwinter (Hamid, 1995). White pine weevil damage greatly reduces the tree's commercial value by causing crooks, multiple leaders, and "bushy" stems (Hamid, 1995; Maine Forest Service, 2016; Wendel and Smith, 1990; Wilson, 1978). However, mortality from weevil damage is infrequent. Further, because the insect prefers open-grown trees with large terminal leaders, appropriate silvicultural management can effectively reduce damage. For example, maintaining high stand densities and delaying overstory removal will produce trees with shaded and smaller, less suitable terminal leaders, in turn reducing weevil attack (Ostry et al., 2010).

Historically, landowners have managed for these established, well-known stressors to eastern white pine and have been able to maintain productive pine stands. Ostry et al. (2010) noted that "with appropriate management and a long-term commitment, many eastern forests can be beneficially reforested to eastern white pine with little impact from blister rust and other damaging agents." Although these established stressors are manageable, additional native stress agents have become increasingly prevalent in the last few decades. They are interacting in novel ways and producing novel symptomology not previously reported. To effectively manage future eastern white pine populations, it is critical to understand these native stress agents, how they interact with other biotic and abiotic factors, and how these relationships might continue to change in the future.

6. Emerging health issues: symptoms and novel stress agents of eastern white pine

In the early 1990s, forest health specialists in the northeastern U.S. began observing development of symptoms in eastern white pine that could not be attributed to white pine weevil or white pine blister rust, yet were resulting in a reduction of healthy, high-quality trees (Fig. 2). In this region, host symptoms on trees (> 10 cm dbh) included the presence of branch and stem cankers (Fig. 3A), many causing severe resinosis (Fig. 3B), along with significant crown thinning (Fig. 3C) and large bark cracks/fissures (Lombard, 2003; Maine Forest Service, 2008; Vermont Department of Forests, Parks, and Recreation, 2001).

Fig. 2. A healthy, asymptomatic eastern white pine tree in the northeastern U.S. Healthy trees typically have full crowns, high live crown ratios, green needles, and few bark damages or deformities. Photo courtesy of Isabel Munck.

Yellowing and browning of needles (Fig. 3D), along with premature needle drop in June, were later reported around 2006 (Broders et al., 2015; Munck et al., 2012; Wyka et al., 2017a). Many of these symptoms were subsequently reported range-wide, but varied by region.

In the southeastern U.S., multiple branch and/or stem cankers were a common occurrence, and the yellow to brown necrotic tissue that enlarged over time was reported to eventually girdle the branch or stem on some saplings and mature trees (Mech et al., 2013; Schulz et al., 2018a, 2018b *this issue*). Additional symptoms included flagged needles in the lower canopy, followed by branch dieback (Fig. 3E), eventually causing highly reduced crowns and possible mortality (Fig. 3F). These southeastern symptoms were reported in 2006–2007 in Virginia and West Virginia, and 2010 in Georgia (Asaro, 2011; Mech et al., 2013; Rose, 2011; Schulz et al., 2018b *this issue*). In the Great Lakes region, specifically Michigan, seedling mortality and canker formation were observed since 2006 (Chhin, 2013; Griesmer and Adams, 2012; Michigan Department of Natural Resources, 2015). In southern Canada, needle discoloration, premature needle drop, and canker occurrence were documented as early as 2013 on mature trees, however pathogens and insects have not been isolated from these cankers to date (Llewellyn, 2013). The overlap in symptomology and the similarity of reports indicated a range-wide phenomenon. Further, these symptoms had been attributed to a suite of stress agents such as *C. pinea*, *M. macrocicatrices*, and a complex of fungal pathogens referred to as White Pine Needle Damage.

Based on concern over these symptoms, there has been an increase in research and health surveys on emerging health issues of eastern white pine over the last several years. Survey results for canker and dieback symptoms indicate that symptoms are widespread, but vary in intensity throughout southern Appalachian and northeastern forests. Universally, all symptoms are more prevalent as stand density increases (McIntire et al., 2018b *this issue*; Munck et al., 2015a; Schulz et al., 2018a *this issue*). Crown thinning also appears to be most severe in intermediate sized pole-timber (12.5–30.0 cm dbh), whereas young

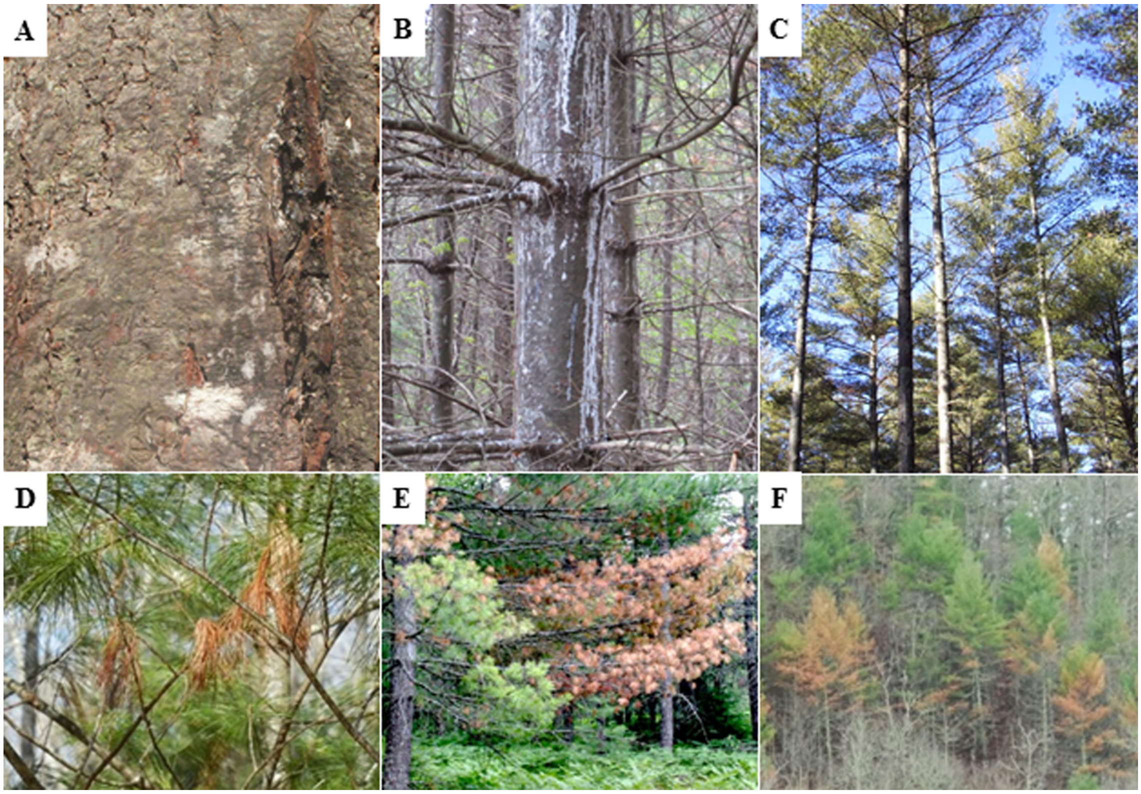

Fig. 3. Novel symptomology observed in association with emergent health issues on eastern white pine trees. Symptoms include (A) stem cankers, (B) excessive resinosis, (C) crown thinning, (D) yellowing and browning of foliage, (E) dieback, and (F) mortality, particularly in smaller size classes. Symptoms can occur in combination or individually. Photos courtesy of Lori Chamberlain, Kara Costanza, Isabel Munck, Joseph O'Brien, Jennifer Weimer, and Thomas Whitney. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

saplings are the most susceptible size class to mortality. These symptoms have not been attributed to any single agent, but rather to the suite of agents listed above, interacting in novel ways not previously reported. The following is an in-depth review of these agents (*C. pinea*, *M. macrocicatrices*, and White Pine Needle Damage), along with a discussion of the relevant factors increasing the risk of health issues for eastern white pine in North America.

6.1. Caliciopsis canker

Caliciopsis canker, a disease thought to be caused by the native fungal pathogen *Caliciopsis pinea* Peck, has become increasingly prevalent since the mid-1990s. The ascomycete fungus, in the Coryneliaceae family, was first reported on an eastern white pine tree near Ithaca, New York in 1880 (Fitzpatrick, 1920; Peck, 1880). It has since been reported on shortleaf (*P. echinata* Mill), mountain (*P. pungens* Lamb), pitch (*P. rigida* Mill), loblolly (*P. taeda* L.), and scrub (*P. virginiana* Mill) pines in eastern North America, as well as on other conifers outside the genus *Pinus* in western North America (Fitzpatrick, 1920; Funk, 1963; Munck et al., 2015a). In Europe, the pathogen has been documented on several pines (*Pinus* spp.) (Capretti, 1978; Delatour, 1969; Fitzpatrick, 1920; Munck et al., 2015a; Ray, 1936). However, *C. pinea* is most frequently reported on eastern white pine, where it is a virulent pathogen known to cause significant damage (Munck et al., 2015a; Ray, 1936). It is commonly found on the stem of saplings and mature trees. Fruiting bodies can be present on the bark throughout the year, with black stromata protrusions that resemble long spines or clusters of eyelashes (Fig. 4). Once mature, the ascospores are disseminated by wind, rain splash, or stemflow (Delatour, 1969; Funk, 1963). While previous studies reported damage and occasional mortality due to Caliciopsis canker, they were infrequent (Fitzpatrick, 1920, 1942; Overholts, 1930; Ray, 1936). Since the 1990s, however, there have been steadily increasing reports of Caliciopsis canker causing damage and occasional mortality to eastern white pine trees (Asaro, 2011; Chhin, 2013; Griesmer and Adams, 2012; Lombard, 2003; Mech et al., 2013; Munck et al., 2015a; Rose, 2011; Sakalidis pers. comm. Oct., 2016).

Fig. 4. *Caliciopsis pinea* ascocarps (fruiting bodies) located on the bark of eastern white pine in central New Hampshire. Photo courtesy of Kara Costanza.

In the northeastern U.S., symptoms caused by *C. pinea* infection include resinosis, crown thinning, cankers, and bark cracks/fissures, predominantly on mature trees (Fig. 5A–C). The heavy resin pitching causes significant downgrades in lumber quality and value, while the cankers can greatly reduce growth and vigor of the tree, sometimes resulting in mortality (Costanza, 2017; Lombard, 2003; Munck et al., 2015a). For example, a recent study indicated that canker incidence increases on trees with thin crowns, reduced sapwood area, and slower

Fig. 5. Symptoms associated with *Caliciopsis pinea* including (A) thin crowns and (B) necrosis of the xylem, which is often associated with external cankers and (C) bark cracks/fissures. Photos courtesy of Kara Costanza.

growth, particularly after extreme weather events such as droughts or floods from hurricanes (Costanza, 2017). Definitions of Caliciopsis cankers vary, but three distinct types emerge: (1) small, sunken, reddish/brownish depressions in the bark; (2) areas of roughened bark below branches; and (3) bark cracks/fissures (Fig. 6A–D) (Lombard, 2003; Munck et al., 2015a; Overholts, 1930; Ray, 1936). These cankers are typically associated with internal damage to the host, such as necrotic xylem tissue and pockets of resin surrounding the necrotic regions (Fig. 6E–F).

Infection occurs when disseminated ascospores encounter a suitable substrate and penetrate the bark. The fungus needs an entry point such as a crack or wound, a natural bark fissure, an insect feeding site, or possibly an old lenticel for successful colonization of the host (Fitzpatrick, 1942; Funk, 1963; Lombard, 2003; Munck et al., 2015a). Fungal hyphae can then grow into the vascular cambium, killing the host tissue and forming necrotic lesions that follow the circumference of the cambium. The host responds by attempting to "pitch out" the pathogen, resulting in excessive resin production seen as streaking on the bark and resin soaking around the necrotic xylem tissue (Haines et al., 2018 *this issue*).

Caliciopsis canker can be difficult to assess in the field due to a wide range of general symptoms. Crown thinning and branch flagging are general symptoms, and can be associated with White Pine Needle Damage, eastern white pine bast scale, drought, and other common stress agents (Broders et al., 2015; Mech et al., 2013; Munck et al., 2015a). Resinosis resembles damage from other disease agents like white pine blister rust, however Caliciopsis canker-associated resin streaks occur between branch whorls, starting from a canker (Lombard, 2003). As trees age and the bark becomes more furrowed, resin symptoms become more challenging to observe. Furthermore, older resin streaks turn black and blend in with the bark, making it difficult to assess past damage (Munck et al., 2015a).

Since first documentation in 1880, only a handful of research studies have investigated Caliciopsis canker (Delatour, 1969; Fitzpatrick, 1920, 1942; Funk, 1963; McCormack, 1936; Overholts, 1930; Peck, 1880; Ray, 1936). Existing publications focus primarily on the fungus, with even fewer studies assessing host response. Yet over the last three decades, there has been a clear increase in reported Caliciopsis canker occurrences and associated eastern white pine damage, as discussed above. While each of these reports differed by region, a few common trends emerged: (1) Caliciopsis canker incidence and severity was greater than previously reported; (2) significant eastern white pine damage was occurring, both in sapling- and pole-size stands, along with some mortality; and (3) other stress agents and symptoms were co-occurring with Caliciopsis canker disease. From these trends, it is evident that additional research is needed, particularly focused on the distribution of Caliciopsis canker, the pathogen's life cycle (e.g., timing of infection and establishment, pathogen lifespan, and conditions favoring spore dispersal and infection), host impact, and the novel relationships occurring between multiple stress agents acting on eastern white pine. Current studies are underway in Maine, New Hampshire, Georgia, and Michigan.

Overstocked stands, as well as stands on poorly drained and excessively drained soils, tend to have higher incidence and severity of Caliciopsis canker symptoms in the northeastern U.S. (Munck et al., 2015a, 2016). Additionally, higher stand density, smaller crowns, and slower growth are associated with greater canker incidence and severity, further indicating that overstocked stands increase the risk of eastern white pine to fungal infection and canker development (Costanza, 2017). Based on the current understanding of Caliciopsis canker, management recommendations include thinning stands to increase sunlight and temperature in the tree canopy and upper bole (Lombard, 2003; Munck et al., 2015a), to reduce competition, increase tree vigor, and also reduce moist conditions favorable for fungal infection. However, the exact relationship between thinning and Caliciopsis canker occurrence is still being investigated, and as new information becomes available, management guidelines may be modified.

6.2. Eastern white pine bast scale

The eastern white pine bast scale, *Matsucoccus macrocicatricies* Richards (Hemiptera: Matsucoccidae), is a sap-sucking insect now widely associated with symptoms of eastern white pine dieback, as well as Caliciopsis cankers. Forest health specialists in Virginia discovered the immature cysts of eastern white pine bast scale embedded in cankers and bark crevices of symptomatic trees in 2007 (Mech et al., 2013). This finding was unexpected because the range of eastern white pine bast scale was previously only known to include Nova Scotia, New Brunswick, Ontario, Québec, New Hampshire, and Massachusetts (Garcia et al., 2016). Further, the scale insect had never before been associated with tree injury, mortality, or fungal canker formation. In the ten years since it was first documented outside of its purported native range in New England and the Canadian Maritime Provinces, eastern white pine bast scale has been found in at least 12 states spanning the range of eastern white pine (Georgia, Maine, Massachusetts, Michigan, New Hampshire, North Carolina, Pennsylvania, South Carolina, Tennessee, Vermont, Virginia, West Virginia).

The genus *Matsucoccus* Cockrell, commonly known as the "pine bast scales," consists of 33 extant species inhabiting temperate, subtropical, and tropical regions across the northern hemisphere, 17 of which are found in North America (Foldi, 2005; Gill, 1993). All pine bast scales exclusively feed and complete their life cycles on pine trees (*Pinus* spp.), and although most species cause negligible feeding damage to their hosts, some are notorious pests. Notable examples include red pine scale (*M. matsumurae* Kuwana) killing red pine in New England (Booth and Gullan, 2006), maritime pine scale (*M. feytaudi* Ducasse) killing

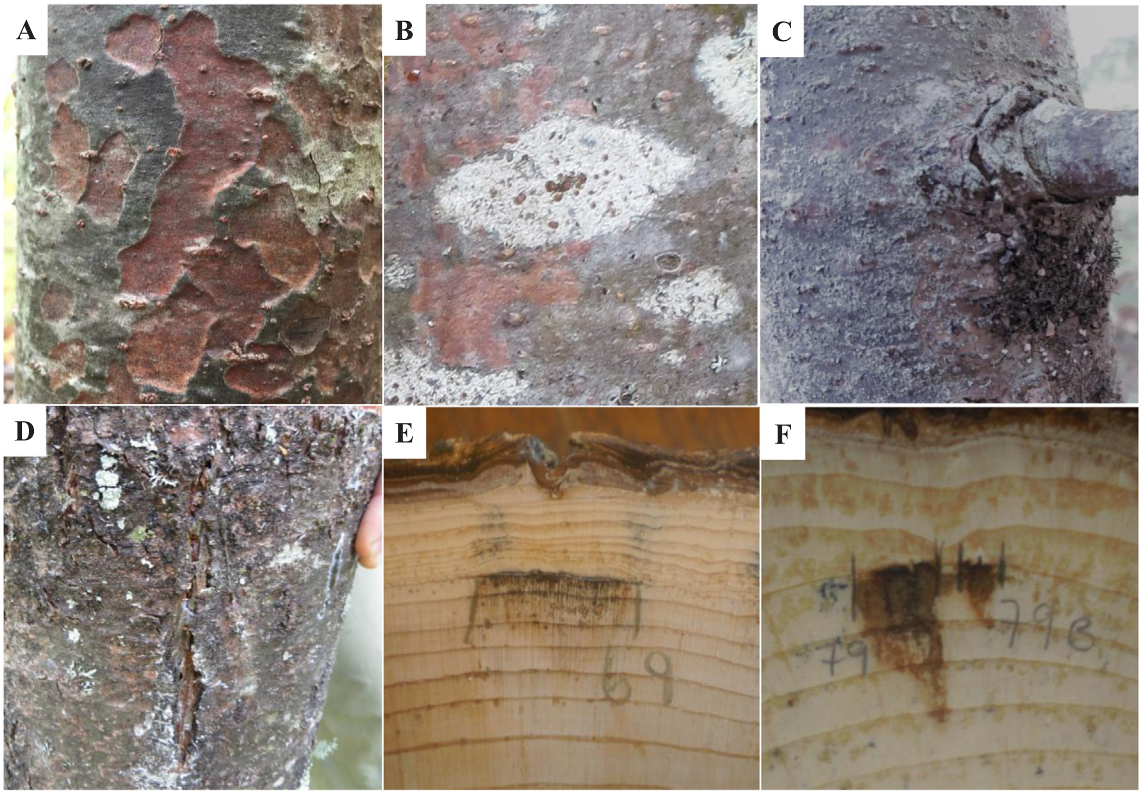

Fig. 6. Common cankers and damage associated with *Caliciopsis pinea* infections. Cankers can include (A–B) small, sunken, red/brown depressions, common on thin barked areas of the stem; (C) roughened bark under branch whorls, in this case with small black stromata visible protruding from the canker; and (D) bark cracks/fissures that are colonized by ascospores. Cankers are external manifestations of successful fungal colonization, and are often associated with (E–F) internal damage such as necrotic xylem tissue and resinosis. Photos courtesy of Kara Costanza (B–F) and Thomas Whitney (A).

maritime pine in Mediterranean countries (Kerdelhue et al., 2014), and Israeli pine scale (*M. josephi* Bodenhiemer and Harpaz) killing Aleppo pine (*P. halepensis* Miller) in Israel (Mendel, 1998).

Eastern white pine bast scale is a specialist of eastern white pine, but its phenology is not fully understood. Before 2007, the only studies on the insect were conducted in Canada during the 1950 s, where they reported a two-year life cycle (Richards, 1960; Watson et al., 1960). This appears to be true of populations at high latitudes, but development in the warmer southeastern U.S. has been observed to finish in a single year (Mech et al., 2013, personal observations). All eastern white pine bast scales spend the majority of their life cycle as 2nd instar cysts, the stage most noticeable to observers (Fig. 7A). They resemble black, oblong pearls often found embedded in tight spaces on eastern white pine bark, such as in branch crotches, under lichen, or along the edge of cankers. This is a sessile feeding stage; cysts extract sap starting in summer through their long stylets (Fig. 7B), which are perpetually inserted into the tree's vascular tissue. Once the cysts have fully grown to ~1.5 mm in spring, the adults emerge (Fig. 7C and F). Winged adult males develop in five instars (Fig. 7C–E) and are quite ephemeral. Females develop in three instars, attract mates with pheromones, and lay hundreds of eggs in bark crevices within a silken mass. Mobile 1st instar "crawlers" hatch from eggs (Fig. 7H–I) in late spring, disperse by wind (most likely), and choose new feeding sites to settle. They then undergo a molt, thus completing the cycle into 2nd instar cysts.

There are no prior reports of eastern white pine bast scale being present south of Massachusetts or being linked to any significant tree damage or fungal pathogens (Mech et al., 2013). However, this species is much more widespread than previously thought and the presence of its cysts is highly associated with symptoms of dieback in eastern white pine. For instance, Mech et al. (2013) surveyed southern Appalachian sites in six states and found eastern white pine bast scale cysts on symptomatic trees, but none on healthy trees. When observing symptomatic eastern white pine in Georgia, scales were found to colonize 92% of cut branches (Mech et al., 2013). Schulz et al. (2018b *this issue*) later conducted an expanded survey, finding a high incidence of eastern white pine bast scale in both New England and southern Appalachian sites. Density of scales was positively correlated with both the number of dead branches on a sapling (a measure of dieback), as well as the size of Caliciopsis cankers (Schulz et al., 2018b *this issue*). This was further supported by a New Hampshire survey on 344 eastern white pine saplings, where they found 3% of saplings had Caliciopsis cankers only, 5% had neither cankers nor eastern white pine bast scales, 24% had only scales, and 68% had both cankers and scales present (Weimer, 2017). Lastly, Whitney et al. (2018 *this issue*) found that the presence and densities of scales on eastern white pine in Georgia was highly correlated with that of Caliciopsis cankers in terms of tree size class and position in the canopy. Together, the colonization patterns of these two organisms mirrored the bottom-up trend in branch dieback that has been observed range-wide (Whitney et al., 2018 *this issue*). These studies show distinct correlations between eastern white pine bast scale and the symptoms of dieback in saplings, but mechanistic research is now underway to assess how insects may be influencing the phenomenon.

We have formulated hypotheses as to how this scale insect may be contributing to recent dieback and mortality in eastern white pine. Given that its presence and density are strongly correlated with cankers, especially those formed by *C. pinea*, we postulate this organismal complex may resemble that of the beech bark scale (*Cryptococcus fagisuga* Lindinger) providing native pathogens (*Neonectria* spp.) an infection court on beech trees (*Fagus* spp.) (Houston and O'Brien, 1983; Shigo, 1972). As mentioned above, feeding wounds caused by eastern white pine bast scale may allow pathogens entry to infect eastern white pine subcortical tissue. There is also a precedent within the *Matsucoccus* genus to support this hypothesis, as the Israeli pine bast scale has been

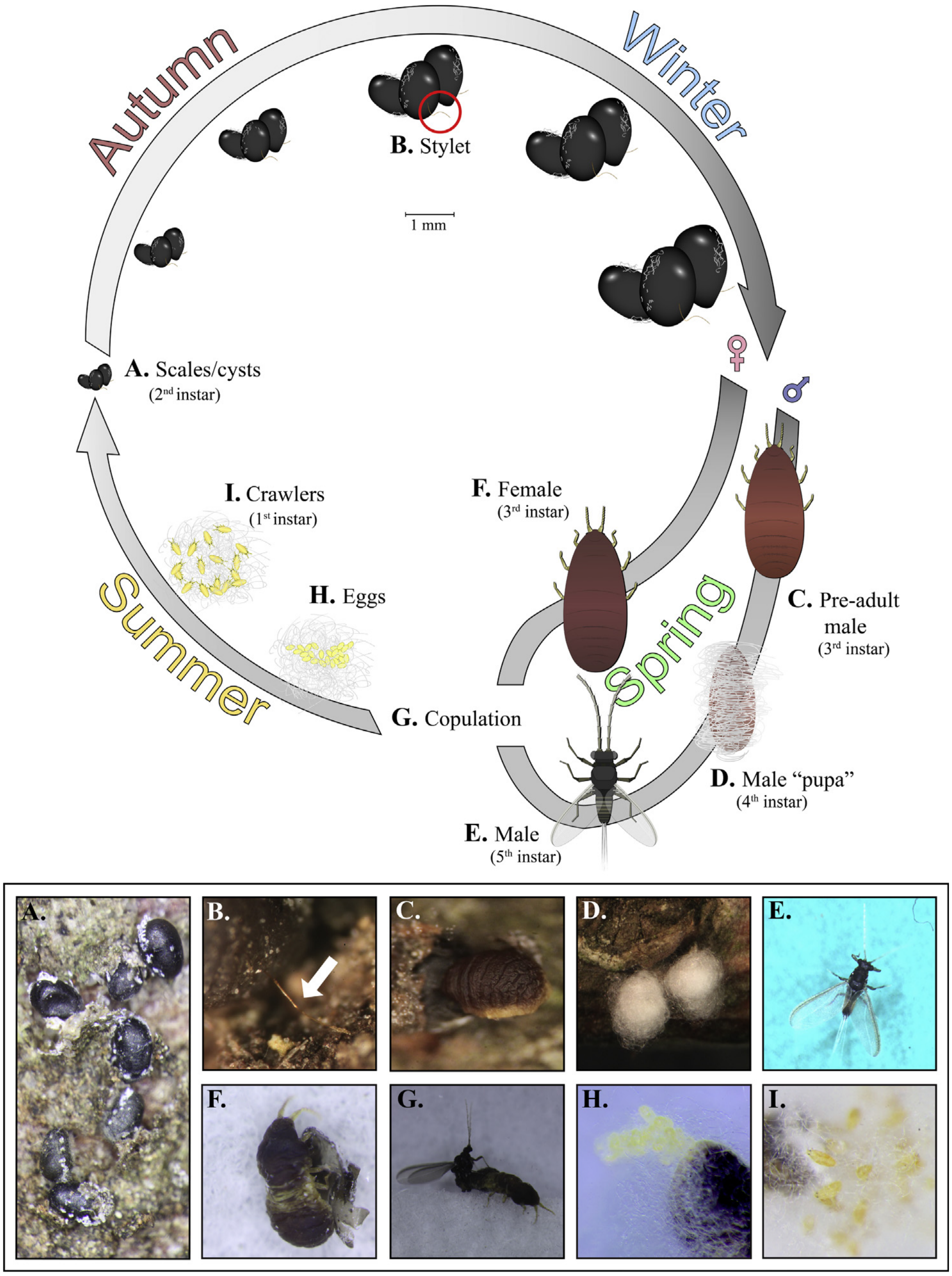

Fig. 7. Life cycle of the eastern white pine bast scale, *Matsucoccus macrocicatrices* Richards. (A) Second instar nymphs, commonly called scales or cysts, are sessile feeders. Scales extract vascular fluids with (B) long, thin, copper-colored stylets (mouthparts), and beginning in July–September, they steadily grow until spring in southern Appalachian sites (one-year cycle) or until the following spring at higher latitudes (two-year cycle). Males emerge first as (C) pre-adults and subsequently undergo a metamorphosis resembling that of a holometabolous insect (complete metamorphosis), enclosing themselves in (D) cocoon-like structures to protect their "pupal" instar. They ultimately develop into (E) an alate (winged) adult male. The end of adult male development coincides with the emergence of (F) adult females, which are nearly indistinguishable from pre-adult males based on morphology alone. (G) Mating occurs and females lay (H) eggs in a silken mass. After 2–3 weeks of incubation, (I) first instar "crawlers" hatch. In the summer, crawlers will disperse mostly by wind and settle on new feeding sites on eastern white pine. They subsequently molt and begin their second instar development. Photos courtesy of Thomas Whitney.

shown to enhance the transmission of fungal inoculum [*Sphaeropsis sapinea* (Fr.) Dyko and B. Sutton] on Aleppo pine (Madar et al., 2005). Ultimately, the interactions between insect feeding and fungal pathogens appear to facilitate, or at least expedite, the formation of Caliciopsis cankers that girdle and can eventually kill eastern white pine.

Also unclear is why eastern white pine bast scale, a native of North America never before associated with tree damage, now appears to be implicated in this dieback complex. One hypothesis posits that eastern white pine bast scale has evolved to live independently from a symbiotic relationship with the fungus *Septobasidium pinicola* Couch. The early literature discusses an obligate mutualism where 1st instar crawlers settle on the edges of *S. pinicola* mats to molt into 2nd instar cysts (Watson et al., 1960). The mat grows to envelop the cysts, providing protection for some individuals while simultaneously penetrating the cuticle and feeding on the insides of other cysts (Couch, 1938; Watson et al., 1960). The parasitism of some individuals may have acted as biological control in the past, but recent surveys find that a vast majority of cysts are free-living outside of *S. pinicola* mats (Mech et al., 2013). This may indicate an "enemy release" from *S. pinicola* has occurred (Keane and Crawley, 2002) if fungal control pressure on scales has dampened in recent decades, or perhaps the obligate nature of this relationship has been overstated in past accounts. An alternative hypothesis for why eastern white pine bast scale became more widespread and damaging proposes that climatic stress has increased susceptibility of their hosts. Eastern white pine is moderately to highly susceptible to water stress (Gustafson and Sturtevant, 2013; Niinemets and Valladares, 2006), and under more frequent drought conditions due to global climatic change (Joyce and Rehfeldt, 2013), areas such as overstocked stands growing on poor soils will be particularly susceptible. Forthcoming research using population genetics will seek to determine whether (1) eastern white pine bast scale has been present in the Great Lakes region and southern Appalachians, but has gone overlooked until now, or whether (2) a range expansion or introduction (s) to these adventive areas occurred recently. Determining the biogeographical history of this scale insect can elucidate if it is behaving like an invasive species, which will help inform future research

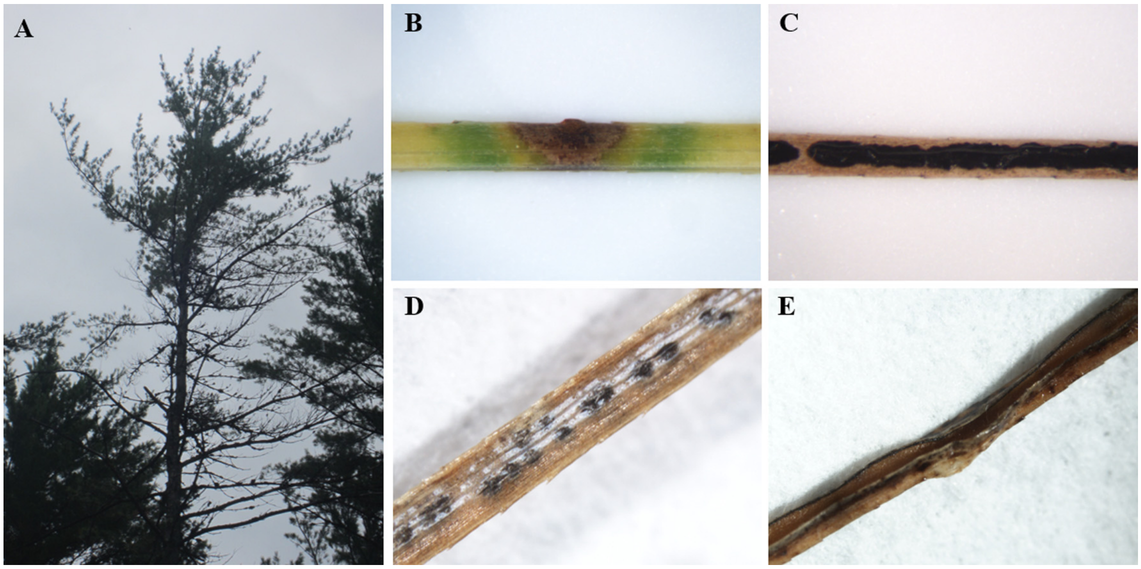

Fig. 8. Signs and symptoms of White Pine Needle Damage. (A) Thinned crowns following summer defoliation, (B) fungal fruiting bodies on needles can most often be attributed to brown spot needle blight (*Lecanosticta acicola*), (C) *Bifusella linearis*, (D) *Septorioides strobi*, and (E) Dook's needle blight (*Lophophacidium dooksii*). Photos courtesy of Cameron McIntire (A-C) and Stephen Wyka (D-E).

directions and subsequent management strategies.

6.3. White Pine Needle Damage

White Pine Needle Damage (WPND) is a disease complex comprised of at least four ascomycete fungi that persist either independently or collectively on the foliage of eastern white pine, from seedlings to mature trees. The known causal agents are brown spot needle blight (*Lecanosticta acicola* Thümen, formerly *Mycosphaerella dearnessii* M.E. Barr) (Quaedvlieg et al., 2012), Dook's needle blight (*Lophophacidium dooksii* Corlett and Shoemaker, formerly *Canavirgella banfieldii* Merr, Wenner, and Dreisbach) (Laflamme et al., 2015), *Bifusella linearis* Peck (Minter and Millar, 1984), and *Septorioides strobi* Wyka and Broders (Wyka and Broders, 2016). Identification of fungi can typically be distinguished through observation of the unique reproductive structures on recently cast needles (Fig. 8A–E). Each of these pathogens is considered to be native within the northeastern range of eastern white pine, however their virulence on the species in the past decade is novel.

The most ubiquitous fungi associated with WPND was originally thought to be *L. acicola*, the causal agent brown spot needle blight (Broders et al., 2015), which has historically been a problem of longleaf pine (*P. palustris*) plantations and Scots pine (*P. sylvestris*) in the U.S. (Huang et al., 1995; Skilling and Nicholls, 1974). The discovery and subsequent analysis of prevalence for the newly described species *S. strobi* has shown that it has established within 60% of 70 eastern white pine stands sampled from 2011 to 2014 throughout Maine, Massachusetts, New Hampshire, and Vermont (Wyka et al., 2017a). In comparison, brown spot needle blight, Dook's needle blight, and *B. linearis* were documented at 53%, 27%, and 40% of these locations, respectively. Further, co-occurring needle pathogens were found at 63% of symptomatic sites, indicating that it is more common for WPND associated fungi to be found together rather than exclusively (Wyka et al., 2017a). Among the stands sampled by Wyka et al. (2017a), only 7% were found to be asymptomatic for all fungi associated with WPND. The first observations of significant needle damage were reported in Maine in 2006, followed by unprecedented outbreaks from 2009–2010 throughout New England (Munck et al., 2012). Presently, WPND persists and continues to spread, establishing itself as a chronic issue in eastern white pine stands throughout the northeastern U.S. and Canada.

While the timing of signs and symptoms for each pathogen differs slightly, it is most common to observe needle chlorosis and necrosis between the months of April and June (Broders et al., 2015; Munck et al., 2012). A distinct yellowing of second and third year foliage is typically followed by defoliation of infected needles in late June and continuing through July. The spores of each fungal species are dispersed by rain splash; therefore, the bottom portions of infected crowns tend to have the highest incidence and severity of defoliation. During the month of June, spores are spread to and infect through the stomata of current year foliage, where the fungus will overwinter and mature. The rain-dispersed nature of WPND fungi often leave the upper portion of infected trees relatively free of symptoms, making this disease complex notoriously difficult to map from aerial surveys via observations of the tops of crowns. In the lower most portions of the crown it is common to observe branch dieback following multiple years of defoliation, resulting in low live crown ratios in diseased individuals. The premature casting of infected older foliage in the early summer causes trees to have markedly thinned crowns, in extreme cases only harboring the current year foliage. In the northeastern U.S. the current year foliage of eastern white pine begins developing in the month of May and continues through August (Wang and Chen, 2012), thus the foliage is only partially elongated when WPND induced defoliation occurs. The premature loss of mature foliage represents several months of the growing season in which potential carbon assimilation is significantly reduced in diseased trees. Dendrochronology analyses have shown a distinct reduction in stem growth within WPND-infected stands coinciding with outbreaks initiating around 2009 (McIntire et al., 2018a *this issue*). Presently, mortality attributed to WPND remains relatively low, most often observed in individuals in intermediate canopy positions and compounded by other stressors such as Caliciopsis canker, poor soil quality, or resource competition within overstocked stands.

Climate is thought to play a central role in the establishment, spread, and year-to-year severity of WPND in the northeast region. Generally, warmer and wetter conditions have been regarded as beneficial to fungal development and reproduction while increasing the probability of northward migration of pathogens from southern latitudes (Broders et al., 2015). Temperatures in the northeastern U.S. have risen at a rate of 0.25 °C per decade since 1970 and are projected to warm by 2.9–5.3 °C through 2070–2099 (Dukes et al., 2009; Hayhoe et al., 2007). Additionally, the northeastern U.S. is projected to experience an increase in annual precipitation on the order of 7–14% through the end of the century (Hayhoe et al., 2007). Wyka et al. (2017a) reported an increasing trend in the northeastern growing season (April–September) mean temperature and cumulative precipitation from 1950 to 2014, with six years from 2003 to 2014 ranked in the top 10% for annual precipitation on record and four years ranked in the top 10% for mean annual temperature. Modeling of seasonal climatic indices found the cumulative precipitation from May–July was the strongest single predictor variable for WPND outbreak severity of the following year, coinciding with fruiting body development and spore dispersal (Wyka et al., 2017a). The abnormally warm and wet springs leading up to the 2010 WPND outbreaks are thought to have played a critical role in the outbreak of these native fungal pathogens in the northeastern U.S.

Removing high-risk trees (e.g., trees with repeated needle yellowing and defoliation in consecutive Junes) and increasing the distance between crowns is thought to mitigate the dispersal of WPND associated fungi, as inoculum abundance has been shown to decrease significantly at distances greater than 3 m from infected host trees (Wyka et al., 2017b). Silvicultural thinning in mature WPND-infected stands has shown to improve overall tree health and reduce defoliation severity in the first two years following treatments (McIntire et al., 2018b *this issue*). However, this research does not address the long-term response of foliar pathogen incidence and severity to variation in residual stocking densities. Presently, following proper stocking guidelines for eastern white pine is being recommended to reduce both pathogen pressure and stress caused by intraspecies competition (Lancaster and Leak, 1978). Eastern white pine regeneration is presumed to be highly susceptible to WPND as the fungi are often present below infected mature trees, thus an easy target for rain dispersed spores. However, no research is currently being conducted on the long-term impacts of WPND on seedling establishment, growth, and survival. Little is known about the presence of WPND outside of the northeastern range of eastern white pine; additional research is thus necessary to define the extent of WPND and associated fungi.

7. Abiotic and interacting factors influencing eastern white pine health

Eastern white pine genetics is a factor that will determine the tree's response to its environment. After glaciation, refugial populations of eastern white pine from the southeastern U.S. provided a source for recolonization of the northeastern U.S. and the Great Lakes region (Nadeau et al., 2015; Zinck and Rajora, 2016). Regional genetic differences due to post-glacial recolonization may result in regional differences in the species' response to stressors. Further, the effects of post-colonial harvesting and reforestation efforts are currently unknown, potentially reducing overall genetic diversity and/or facilitating the intermingling of eastern white pine genotypes. Elucidating these important genetic factors will help determine the risk of eastern white pine to other stressors, and could help explain why similar stressors are found throughout the range but elicit varying symptoms by region.

Climate and weather can also explain regional variation by increasing the susceptibility of eastern white pine to other stressors, both indirectly and directly. For fungal pathogens, a key factor increasing a tree's risk of infection includes moist, humid conditions favoring spore dispersal, germination, and growth into needle stomata, wounds, or other openings. For example, cooler and moister sites in Minnesota had higher incidence of blister rust compared to pines grown at lower elevations with warmer and drier conditions (White et al., 2002). Further, high precipitation in May and June creates conditions that favor fungal infection and dispersal associated with WPND. Climate (e.g., drought) can also affect trees directly by reducing vigor or increasing host susceptibility to other stress agents (Kolb et al., 2016; Manion, 1991). Drought did incite mortality of eastern white pine in southern Maine (Livingston and Kenefic, 2018 *this issue*). Hurricanes can produce strong winds that damage stems and yield heavy rains that flood pine stands, presumably killing root tissue and reducing water uptake (Costanza, 2017). Drought and hurricane-induced floods have been associated with increased Caliciopsis canker incidence (Costanza, 2017). Canker incidence, in turn, is positively associated with the occurrence of eastern white pine bast scale (Schulz et al., 2018b *this issue*).

Anthropogenic influences can also increase the risk of eastern white pine to additional stressors. For example, cutting of prized eastern white pine trees was common once Europeans settled North America, resulting in loss of original seed source. Subsequent reforestation efforts, particularly during the time of the Civilian Conservation Corps, allowed the movement and intermingling of several genotypes. Today, many eastern white pine stands are artifacts of agricultural land clearing (plus subsequent field abandonment) and fire exclusion. Old field abandonment allowed eastern white pine to regenerate on soils that restricted rooting depth due to colonizing shallow sites typically regenerating red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* L.). Alternatively, field abandonment resulted in soil changes (plow pan, fine textured soils overlaying sand, etc.) that restrict rooting depth (Livingston and Kenefic, 2018). Further, these "field pines" are early successional pioneers, establishing at high densities and later experiencing higher competition for resources. They are also at increased risk of white pine weevil attack (Katovich and Mielke, 1993; Ostry et al., 2010). In combination, anthropogenic disturbances have greatly affected eastern white pine populations and created conditions to which the species has not evolved (Barton et al., 2012; Foster, 1992; Hooker and Compton, 2003; Livingston and Kenefic, 2018 *this issue*), resulting in more eastern white pine stands at risk of stressors than in pre-settlement North America.

Site conditions such as soil and stand density also play a key role in the risk of eastern white pine trees to additional stressors. In Maine, Fries (2002) and Livingston and Kenefic (2018 *this issue*) found that trees grown on shallow soils with restricted rooting depth experienced greater mortality following a drought. Higher pine mortality also occurred on sites with higher stand densities (Livingston and Kenefic, 2018 *this issue*). In many instances, these common abiotic threats do not individually result in mortality, however they can increase the vulnerability of trees to damage from additional stressors, such as native insects and fungal pathogens.

The abiotic factors discussed above (climate, anthropogenic, site conditions, stand density) result in potentially increased risk of eastern white pine to other stressors. We recognize three major interacting biotic factors that have become prevalent in the last few decades and that merit serious investigation for the sustainability and health of eastern white pine: (1) Caliciopsis canker – its severity and incidence have increased since the 1990s, and occurrence is positively correlated with overstocked stands, stands growing on excessively drained soils, drought, and in special cases a hurricane and a poorly timed harvest (Costanza, 2017; Munck et al., 2015a, 2016). (2) Eastern white pine bast scale – this insect is now reported in regions of North America where it was never previously documented and is closely correlated with the pathogen *C. pinea*, but canker and crown symptoms may differ across the range. Further, *C. pinea* and other fungi have been found developing at the feeding sites of eastern white pine bast scale, suggesting that scale feeding facilitates the infection process (Mech et al., 2013; Schulz et al., 2018a, 2018b *this issue*; Weimer, 2017). (3) WPND – this disease complex is now widespread in the northeastern U.S. and southeastern Canada where it is correlated with wet springs. Defoliation induced by associated needle pathogens is presently a chronic issue in the region, and has significantly reduced the retention of mature second- and third-year needles within infected crowns.

Overall, eastern white pine stands growing on abandoned fields are at higher risk of fungal infections (e.g., Caliciopsis canker, WPND), as well as eastern white pine bast scale infestations due to adverse site conditions and stand densities. Multiple stressors can also increase the risk of mortality from other agents, such as *Armillaria* root disease or *Ips* sp. attack (Brazee and Wick, 2011; Livingston and Kenefic, 2018 *this issue*). Understanding which abiotic and biotic factors are affecting eastern white pine health and how they will affect the future management of the species will be challenging, but it is critical in developing successful, long-term plans for the sustainability and management of this important tree species.

8. Future outlook and management implications

As the disturbance, dominance, and density of eastern white pine changed significantly over the last few centuries in eastern North America, the species has continued to be one of the most culturally, ecologically, and economically significant conifer species. Current eastern white pine management strategies work well for various site conditions and familiar stressors, such as white pine blister rust and white pine weevil as they have been researched. However, new stressors have emerged that are interacting in novel ways, and the complexity of these interactions will affect future management practices. Further, the intensity and frequency of extreme weather events such as droughts and hurricanes is increasing (Kunkel et al., 2013). In turn, this will increase the incidence and severity of the issues described in this paper, further underscoring the importance of continued monitoring and research on this pine species. Below we summarize current trends in eastern white pine health and provide recommendations for future research and management.

Management strategies for decreasing threats to eastern white pine health will improve as more is learned about the system, but presently there are some simple silvicultural recommendations that may increase the resilience of eastern white pine. For example, emphasizing site selection and reducing competition may reduce the tree's vulnerability to stress agents. Sites should be selected that avoid factors that restrict rooting depth within 30 cm of the surface, such as plow pans and bedrock, to avoid drought-induced mortality (Livingston and Kenefic, 2018 *this issue*). Sites with excessively drained soils should also be avoided (Munck et al., 2016), as well as sites with better soils favoring hardwood competition (Lancaster and Leak, 1978) or *Ribes* spp. (Ostry et al., 2010). Because regenerating eastern white pine under a canopy helps reduce the risk of white pine weevil and white pine blister rust, the recommended silvicultural approach of shelterwood cuts for regenerating eastern white pine (Lancaster and Leak, 1978) on properly selected sites will likely help reduce the risk of future health issues.

Stand densities may also be frequently regulated. At early stages, it is best to maintain dense stands to minimize white pine weevil damage, but then to thin stands as soon as trees reach 6 m in height, according to recommended stocking levels (Katovich and Mielke, 1993; Leak and Lamson, 1999; Seymour, 2007). Intermediate thinning treatments may include removal of poor-vigor trees from lower crown classes (Livingston and Kenefic, 2018 *this issue*). Thinned stands will increase sunlight and temperature in the canopy, which may decrease moisture and reduce optimal fungal growing conditions for *C. pinea* and WPND fungi. Another useful management strategy is to harvest in the winter if stands have Caliciopsis canker or WPND to avoid spreading inoculum.

Our understanding of the factors and complex interactions associated with the emerging health issues on eastern white pine is still in a nascent stage. To this end, we recommend specific areas of research related to the health of eastern white pine as follows: (1) identify various biotic and abiotic factors (e.g., climatic and site conditions) affecting the population and community ecology of fungal and insect agents, particularly focusing on the possibility that eastern white pine bast scale feeding increases a tree's risk of infection by fungal pathogens; (2) assess the effects of pine dieback on changes in forest structure and composition, nutrient cycling, and successional pathways as based on forest-type and latitude; (3) provide control strategies (e.g., biological, chemical, or silvicultural) for Caliciopsis canker, eastern white pine bast scale, and WPND; (4) develop new regeneration guidelines for eastern white pine under the paradigm of these novel biotic stress agents; and (5) sustain and expand monitoring of eastern white pine health to assess temporal and spatial changes across the species' distribution range. These broad areas of research may allow resource managers to develop a cohesive, complete management plan for the long-term persistence and sustainability of eastern white pine stands in North American forests.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2018.02.049.

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