Forest Ecology and Management 341 (2015) 67–74

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Invasions by two non-native insects alter regional forest species composition and successional trajectories

Randall S. Morin [a,*], Andrew M. Liebhold [b]

[a] USDA Forest Service, Northern Research Station, 11 Campus Blvd., Suite 200, Newtown Square, PA 19073, United States
[b] USDA Forest Service, Northern Research Station, 180 Canfield St, Morgantown, WV 26505, United States

ARTICLE INFO

Article history:
Received 17 July 2014
Received in revised form 17 December 2014
Accepted 18 December 2014
Available online 28 January 2015

Keywords:
Adelges tsugae
Eastern hemlock
Tsuga canadensis
Beech bark disease
Fagus grandifolia
Growth and mortality rates

ABSTRACT

While invasions of individual non-native phytophagous insect species are known to affect growth and mortality of host trees, little is known about how multiple invasions combine to alter forest dynamics over large regions. In this study we integrate geographical data describing historical invasion spread of the hemlock woolly adelgid, *Adelges tsugae*, and beech scale, *Cryptococcus fagisuga*, with regional forest inventory data collected by the US Forest Service's Forest Inventory and Analysis program to quantify the individual and combined impacts of these pest species. This analysis indicates that regional impacts of these insects on their hosts occur surprisingly slow but act to change regional forest succession pathways. Because beech and hemlock commonly co-occur in eastern North American forests, invasions by the two pest species are altering the current and future composition of large forest regions through their impacts on these two late-successional species. Such results demonstrate how forest insect invasions can profoundly modify forest dynamic processes, resulting in long-term changes in forest ecosystems.

Published by Elsevier B.V.

1. Introduction

Invasions by non-native insects and pathogens are major causes of disturbance, affecting the stability, productivity, and economic value of forest ecosystems worldwide (Liebhold et al., 1995; Holmes et al., 2009; Aukema et al., 2011). Most invading forest insects and diseases are not particularly abundant and consequently have negligible effects, but a few have altered forest ecosystems in profound ways (Niemela and Mattson, 1996; Aukema et al., 2010). Over the last century, a large number of invasive species have become established in forests of eastern North America (Liebhold et al., 2013) and some of these organisms, such as chestnut blight, emerald ash borer, and beech bark disease have caused extensive tree mortality.

Forest insect and pathogen invasions can affect forest communities in a multitude of ways, acting both directly and indirectly (Lovett et al., 2006; Loo, 2009). Such effects include changes in tree species composition (Fajvan and Wood, 1996; Jedlicka et al., 2004), tree age structure (Garnas et al., 2011), nutrient cycling (Townsend et al., 2004; Lovett et al., 2006), carbon sequestration (Peltzer et al., 2010), and the abundance of organisms such as aquatic invertebrates (Smock and MacGregor, 1988), large mammals (Kendall and Arno, 1990) and birds (Showalter and Whitmore, 2002; Tomback and Achuff, 2010).

While there is an extensive body of literature on the ecological impacts of invasive species in forest ecosystems, most studies have been limited to sampling from individual stands. The critical importance of evaluating impacts of invaders across their entire range has been recognized (Parker et al., 1999), but only a handful of studies have taken a regional perspective to measuring impacts. Here we use the concept of regional evaluation to quantify individual and combined impacts across the entire range of two invading species. Given trends of continued accumulation of non-native insects and diseases in forest ecosystems worldwide, there is a serious need to assess the impacts of these species at the regional level. The implementation of quarantine measures to exclude future invasions can only be justified based on economic assessments of area-wide impacts of past invasions (Holmes et al., 2009; Aukema et al., 2011), thus highlighting the need for regional estimation of pest impacts over their entire range.

Of particular importance is the need to understand how invading species alter regional trends in forest species composition and thereby alter long-term forest dynamics. Given the extraordinarily large number of damaging forest insect and pathogens species that are accumulating worldwide, an immediate question is what is the cumulative impact of these species on forest dynamics? Many of these invading organisms are capable of causing extensive

* Corresponding author. Tel.: +1 610 557 4054; fax: +1 610 557 4250.
E-mail address: rsmorin@fs.fed.us (R.S. Morin).

http://dx.doi.org/10.1016/j.foreco.2014.12.018
0378-1127/Published by Elsevier B.V.

mortality but little is known about how they may interact to alter long-term trends in forest dynamics and consequently modify long-term forest ecosystem processes.

To address this problem, we explore the individual and combined effects of two major pest species invading the northeastern US: the hemlock woolly adelgid (HWA), *Adelges tsugae*; and beech scale (BS), *Cryptococcus fagisuga*, which is the causal agent of beech bark disease (BBD). Their hosts, eastern hemlock (*Tsuga canadensis* (L.) Carr.), Carolina hemlock (*Tsuga caroliniana* Englem.), and American beech (*Fagus grandifolia* Ehrh.) were known to have dominated large portions of presettlement northern forests (Bürgi et al., 2000; Thompson et al., 2013).

Current forests in the northeastern US differ vastly from those that existed prior to the time of European settlement (Irland, 1999; Bürgi et al., 2000; Thompson et al., 2013). Humans have greatly altered forest composition via harvesting and conversion to agricultural land use, followed by extensive agricultural abandonment. Other factors, such as alteration of presettlement fire regimes and elevated deer populations have also greatly influenced current forest composition (Nowacki and Abrams, 2008; Horsley et al., 2003). Forests in the northeastern US are in flux and it is in this context of a changing forest that the regional impacts of forest insect and disease invasions should be considered. Specifically, dominance by shade-tolerant hemlock and beech is increasing as a result of successional processes (Flinn and Vellend, 2005; Thompson et al., 2013) but it is not clear how this trend is altered by insect and disease invasions.

Therefore, in the analysis presented here we focus on how HWA and BS invasions combine to alter regional succession trajectories. While this analysis is specific to the eastern United States, it provides insight into understanding the more general problem of how alien forest pests affect forested ecosystems, a phenomenon that is affecting forests worldwide.

1.1. Species backgrounds

Beech and hemlock dominate a large fraction of the late-successional forests of the eastern United States (Fig. 1A), and they both fill distinctive roles in forest ecosystems. Mast produced by American beech is a critical source of food for various forest wildlife species. Eastern hemlock is particularly common in riparian areas where it plays a unique role in modifying microclimates, soil chemistry, and stream temperatures. Both species are long-lived, shade tolerant and compose a substantial proportion of the species composition in late-successional forests in the maple/beech/birch type (online Supplement 1).

BBD is an insect-fungus complex involving the non-native BS which feeds on bark fluids from stems of American beech, providing an opportunity for the native canker fungi *Neonectria coccinea* var. *faginata* and *Neonectria ditissima* to invade the inner living bark and cambium leading to dieback and mortality (Mize and Lea, 1979; Houston, 1994). While some trees survive infections for several decades, one effect of the accumulation of cankers is reduced growth (Gavin and Peart, 1993; Gove and Houston, 1996).

The BS was accidentally introduced with live plants imported to Halifax, Nova Scotia from Europe, in the 1890s (Houston, 1994). The scale insect has since slowly spread (~15 km/yr) into the New England states, New York, Pennsylvania, and West Virginia and several discontinuous "jumps" have transported it into North Carolina, Tennessee, and Michigan (Fig. 1B) (Morin et al., 2007; Wieferich et al., 2013). In 2004 the range of BBD comprised about 30% of the range of beech in the USA, but that area included about 50% of the total beech basal area (Morin et al., 2005).

Three phases of BBD are generally recognized: (1) the "advancing front", which corresponds to areas recently invaded by scale populations; (2) the "killing front", which represents areas where fungal invasion has occurred (typically 3–5 years after the scale insects appear, but sometimes as long as 20 years) and tree mortality begins; and (3) the "aftermath forest", which are areas where the disease is endemic (Shigo, 1972; Houston, 1994).

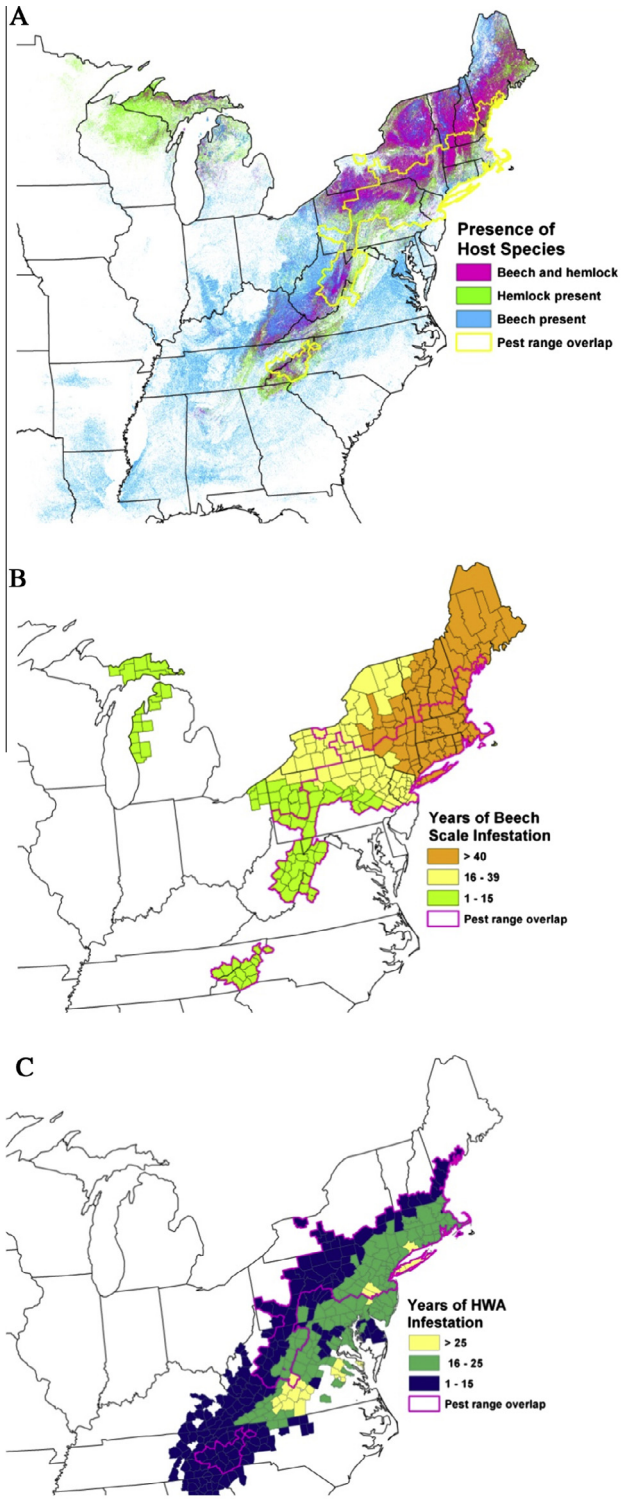

Fig. 1. Maps of species distributions in the eastern United States. (A) Distribution of American beech, *Fagus grandifolia*, and hemlock, *Tsuga* spp. derived from interpolated maps of species volume density from FIA plots (Wilson et al., 2012); (B) historical spread of the beech scale (2006); and (C) historical spread of hemlock woolly adelgid (2006).

The hemlock woolly adelgid, native to East Asia, may have been introduced to the eastern US as early as 1911; however, the first