Biol Invasions
DOI 10.1007/s10530-016-1296-x

ORIGINAL PAPER

Regional assessment of emerald ash borer, *Agrilus planipennis*, impacts in forests of the Eastern United States

Randall S. Morin · Andrew M. Liebhold · Scott A. Pugh · Susan J. Crocker

Received: 26 February 2016 / Accepted: 12 October 2016
© Springer International Publishing Switzerland (outside the USA) 2016

Abstract Native to Asia, the emerald ash borer (*Agrilus planipennis* Fairmaire) has caused extensive mortality of ash tree species (*Fraxinus* spp.) in the eastern United States. As of 2013, the pest was documented in 18 % of counties within the natural range of ash in the eastern United States. Regional forest inventory data from the U.S. Forest Service Forest Inventory and Analysis program were used to quantify trends in ash mortality rate and volume per hectare relative to the year of initial emerald ash borer detection. Results indicate that the annual ash mortality rate increases by as much as 2.7 % per year after initial detection of the pest in a county. Corresponding decreases in ash volume (as much as 1.8 m^3 per hectare per year) continue for several more years until most live ash is killed. These results, while not necessarily representative of the effects on ash in urban ecosystems, document the severe impact this invading herbivore is having on forests as it expands its range in North America.

Keywords *Agrilus planipennis* · *Fraxinus* spp. · Emerald ash borer · Invasive pest · Mortality rates · Forest inventory

Electronic supplementary material The online version of this article (doi:10.1007/s10530-016-1296-x) contains supplementary material, which is available to authorized users.

R. S. Morin (✉)
USDA Forest Service, Northern Research Station, 11 Campus Blvd., Suite 200, Newtown Square, PA 19073, USA
e-mail: rsmorin@fs.fed.us

A. M. Liebhold
USDA Forest Service, Northern Research Station, 180 Canfield St., Morgantown, WV 26505, USA

S. A. Pugh
USDA Forest Service, Northern Research Station, 410 MacInnes Dr., Houghton, MI 49931, USA

S. J. Crocker
USDA Forest Service, Northern Research Station, 1992 Folwell Ave., St. Paul, MN 55108, USA

Introduction

Invasions by non-native insects and pathogens can alter the productivity and stability of forest ecosystems around the world (Liebhold et al. 1995; Gandhi and Herms 2010a; Holmes et al. 2009; Aukema et al. 2011). On average, one such damaging alien pest establishes in the United States every other year (Aukema et al. 2010) with exceptionally high numbers of these species in the northeastern USA (Liebhold et al. 2013).

While most of the non-native insects and pathogens that have become established in forests of eastern North America have had minimal, if any impacts, a handful of species have severely altered forests in profound ways (Niemela and Mattson 1996; Aukema

Published online: 18 October 2016

et al. 2010). For example, chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica* (Murrill) Barr, rapidly spread through eastern North America killing virtually all of its hosts, effectively extirpating American chestnut, *Castanea dentate* (Marshall) Borkh, from eastern forests (Woods and Shanks 1959). Similarly, emerald ash borer (EAB-*Agrilus planipennis* Fairmaire) is currently expanding its range in much of this same region and is poised to eliminate the vast majority of its hosts in the genus *Fraxinus* (Herms and McCullough 2014).

By contrast, there are other non-native species that have become established but do not eliminate their hosts. Instead, they exhibit recurrent and sometimes cyclical outbreaks. For example, the gypsy moth (*Lymantria dispar* Linnaeus) was accidentally introduced near Boston in 1868 or 1869 and has been continuously expanding its range, which currently extends over the entire northeastern U.S. and eastern provinces of Canada (Liebhold et al. 1992; Tobin et al. 2007). Once gypsy moth becomes established in an area, populations exhibit periodic outbreaks in susceptible forests (Johnson et al. 2006) resulting in varying levels of host tree mortality (Davidson et al. 1999), but host species continue to persist even many decades after invasion (Morin and Liebhold 2016).

Native to Asia, EAB was initially detected in Michigan and Ontario in 2002 although it probably originally established in the early 1990s (Bray et al. 2011; Siegert et al. 2014). As of 2013, EAB had been discovered in 18 % of counties in the 37 state region that comprise the natural range of ash species (*Fraxinus* spp.) in the eastern United States (Fig. 1a). Some of the areas with the highest ash densities had yet to be invaded by EAB based on 2013 detection reports; these include portions of northern Minnesota, northern Wisconsin, northeastern Pennsylvania, and southern New York (Fig. 1a). The substantial impacts of EAB on ash species in individual stands has been well documented (Smith 2006; Gandhi et al. 2008; Smitley et al. 2008; Knight et al. 2013; Burr and McCullough 2014; Klooster et al. 2014). One regional study of the Great Lakes States quantified a major decline in ash abundance within 50 km of its introduction point near Detroit, Michigan (Pugh et al. 2011). As it continues to spread, EAB has the potential to functionally extirpate ash with extensive economic and ecological impacts (Gandhi and Herms 2010b; Herms and McCullough 2014; Klooster et al. 2014).

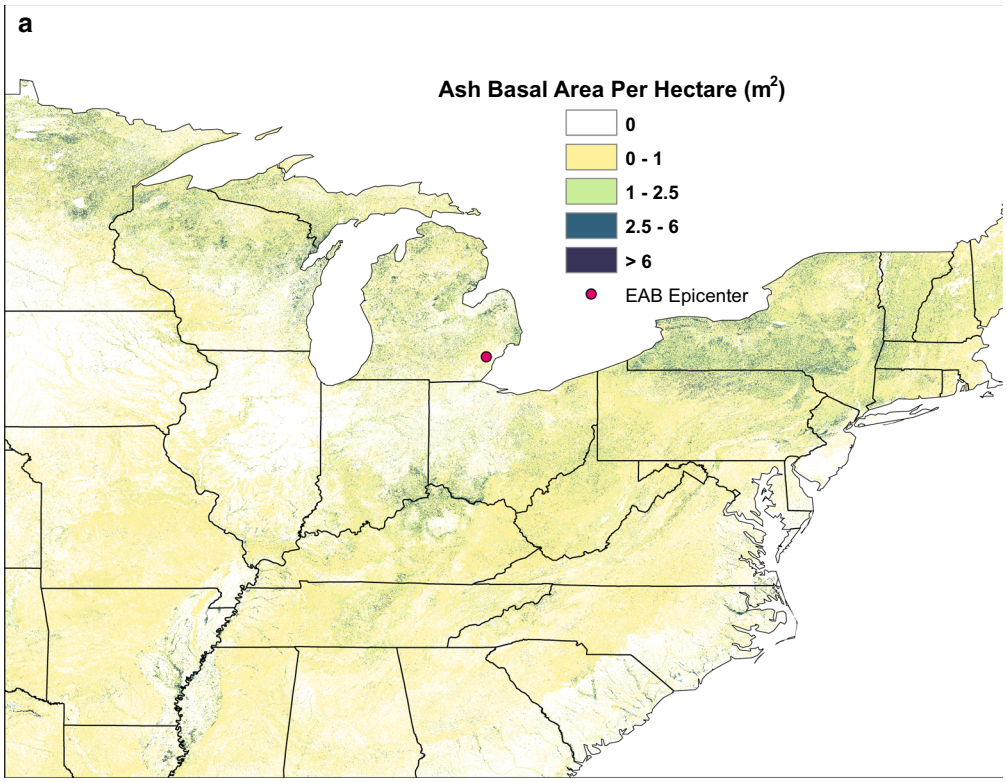
Fig. 1 **a** Distribution of ash basal area per hectare in the eastern United States with EAB epicenter and **b** year of initial EAB detection by county, 2013 (as of Dec. 31, 2013) ▶

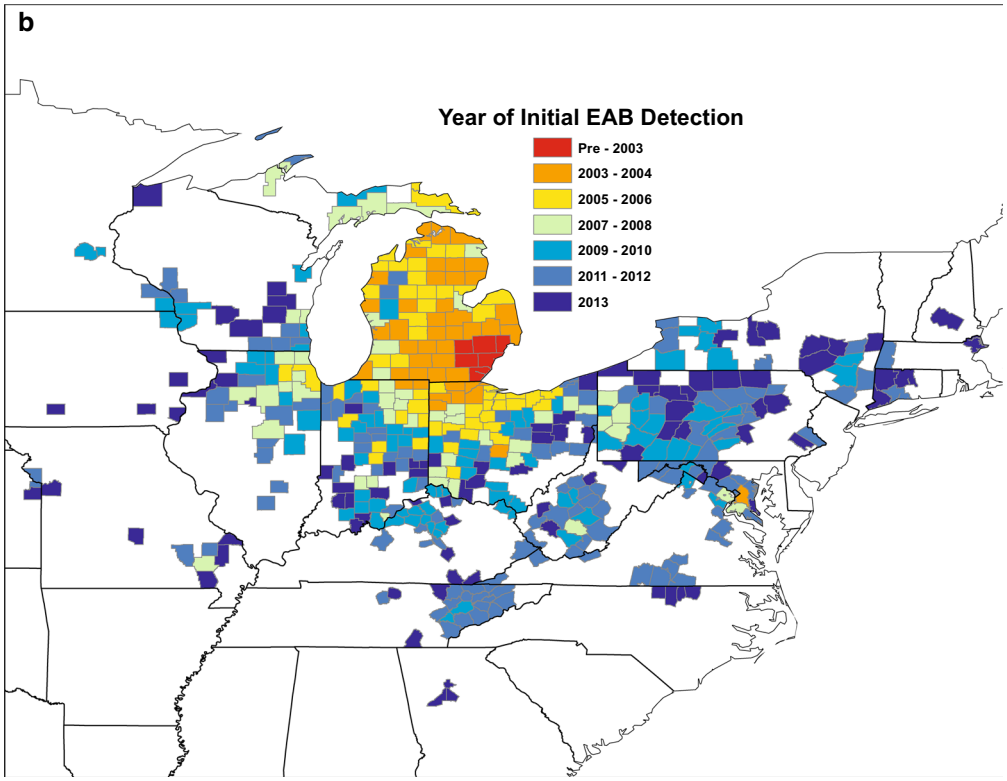
An essential part of the management for any invasive pest is measuring the extent of its impacts over time (Parker et al. 1999). Here, we analyze remeasured regional forest inventory data from the U.S. Forest Service Forest Inventory and Analysis (FIA) program to quantify regional trends in live ash volume and ash mortality, relative to the historical invasion of EAB. As this analysis uses data from across the entire range of the EAB invasion in the United States, it provides unique information related to the regional wave of tree mortality associated with EAB that can be used to predict impacts as this species continues to expand its range.

Methods

The Forest Inventory and Analysis (FIA) program of the U.S. Department of Agriculture (USDA) Forest Service conducts an ongoing inventory of forest attributes nationwide (Bechtold and Patterson 2005). The current FIA sampling design is based on a tessellation of the United States into hexagons approximately 2458 hectares in size with at least one permanent plot established in each hexagon. The population of interest (forest land area) is stratified and plots are assigned to strata to increase the precision of estimates. Tree and site attributes are measured for forested plots established in each hexagon. Plots consist of four 7.2-m fixed-radius subplots on which standing trees and various other environmental characteristics are inventoried (Bechtold and Patterson 2005).

The study area used in this analysis includes counties in the 22 states in the eastern United States where EAB had been detected as of 2013: Connecticut, Georgia, Illinois, Indiana, Iowa, Kansas, Kentucky, Maryland, Massachusetts, Michigan, Minnesota, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Tennessee, Virginia, West Virginia, and Wisconsin (Fig. 1b). Annual estimates of forest conditions from 2009 through 2014 were calculated using individual years of inventory data for counties grouped by the year of first EAB detection. Although we utilized EAB detection data only up through 2013, we chose to include forest inventory data


a
Ash Basal Area Per Hectare (m2)
0
0 - 1
1 - 2.5
2.5 - 6
> 6
EAB Epicenter


b
Year of Initial EAB Detection
Pre - 2003
2003 - 2004
2005 - 2006
2007 - 2008
2009 - 2010
2011 - 2012
2013

through 2014 in order to ascertain trends including the most recent data that were available. Due to sample size all ash species were combined in our analyses. Two metrics were calculated to assess the impact of EAB on regional dynamics of all ash species in the study area: live ash volume per hectare and annual ash mortality rate. This rate was computed from remeasured forest inventory data and expressed as the percentage of initial ash volume that died between measurements. The uninvaded area provides "background" mortality rates for ash species which can be compared against the rates in invaded areas order to attribute broad impacts of EAB at a regional geographic scale. The number of plots used to generate the estimates and the associated sampling errors are included as supplementary material (Online Resources 1, 2).

Counties were grouped according to their year of first EAB detection; since the exact year of establishment was unknown, year of first detection was used as a proxy for the timing of establishment. Note that we use the term invasion interchangeably with detection but acknowledge the difference. Linear regression models were fit to test for temporal trends in mortality rate and volume per hectare as functions of number of years since first detection. Although the individual regressions are based on only six points, it is important to note that in most cases each estimate is based on hundreds of plots (Supplementary Tables 1 and 2). Plots of residuals versus predicted values were examined to ensure that the assumptions of linearity and homoscedasticity were met, and normal probability plots of residuals were inspected to test for normally distributed errors. In addition, we evaluated leverage and found that no individual points unduly influenced the regression equations. Note that the mean annual change according to the annual estimates and the slopes according to the regression models are presented in the results tables. Additionally, annual estimates of mortality rate for invaded counties were pooled and an exponential regression model was fit to mortality as a function of years since invasion. This model is presented to illustrate the time lag between EAB detection and impacts on mortality.

Results

The annual mortality rate for ash species across all uninvaded counties (i.e., "background mortality") in the 22-state study area remained close to 1 % of volume across all inventory years (Table 1; Fig. 2), but increases generally become evident 6–7 years after first EAB detection (Fig. 3). The annual mortality rate generally rises with increasing years since invasion (Figs. 2, 3). For example, the annual mortality rate increase ranges from 0.8 % per year in the counties invaded in 2007 and 2008 to 2.7 % per year in the counties invaded in 2003 and 2004. Despite the stable trend in annual mortality rate in the uninvaded areas, the increasing annual mortality rates in the EAB-invaded area cause an overall increase of 0.2 % per year for the full 22-state study area. The exceptions to these trends are the 2002 invasion category and the counties invaded in 2009 or more recently. The annual mortality rate in the counties invaded in 2002 decreased by 1.4 % per year from a high of 23 % in 2009, and the annual mortality rates in the counties invaded in 2009 or more recently have not risen substantially above background mortality as of 2014 (Table 1; Fig. 2).

Trends of decreasing ash volume per hectare are evident in EAB-invaded areas (Table 2). From 2005 to 2010, ash volume increased by about 0.3 m^3 per hectare per year across all uninvaded counties in the 22-state study area, but drastic decreases occurred 5–10 years after first EAB detection (Fig. 4). The rate of and direction of change in ash volume per hectare varied with years since invasion (Fig. 4). For example, decreases in ash volume per hectare ranged from 1.8 m^3 per year in counties invaded in 2005 and 2006 to 1.4 m^3 per year in counties invaded in 2003 and 2004, and ash volume per hectare is still increasing in the counties invaded in 2009 and 2010. Although ash volume per hectare continues to increase at 0.1 m^3 per year across the full 22-state area, the impacts of increasing mortality in the EAB-invaded areas caused the increase in ash volume to slow relative to the uninvaded counties where ash volume per hectare increased by 0.3 m^3 per year. The exceptions to these trends are the 2002 invasion category, the counties invaded in 2007 and 2008, and the counties invaded in 2011 and more recently. The volume per hectare in the counties invaded in 2002 remained low during the entire period with no clear trend. In counties invaded after 2007, there has not yet been a substantial decrease in volume (Table 2; Fig. 4).

Table 1 Annual ash mortality rate by EAB detection history and parameters of linear regressions

EAB detection year	Annual ash mortality rate (%)						Mean change	Parameters of linear regression		
	2009	2010	2011	2012	2013	2014		Coefficient	*p**	R-square
Undetected	0.9	1.2	1.1	1.0	1.2	1.4	0.1	0.0700	0.0696	0.6024
Pre-2003	23.1	23.6	21.4	21.3	21.4	16.1	-1.4	−1.1860	**0.0371**	0.7026
2003–2004	3.9	6.0	6.4	6.5	14.3	17.4	2.7	2.6410	**0.0112**	0.8322
2005–2006	2.4	2.4	3.6	7.0	8.3	10.8	1.7	1.8100	**0.0015**	0.9371
2007–2008	1.2	0.8	0.3	3.8	7.0	5.3	0.8	1.2230	**0.0393**	0.6948
2009–2010	1.4	1.0	2.1	2.3	2.4	1.5	0.0	0.1460	0.3402	0.2264
2011–2012	0.9	0.9	1.0	1.9	1.0	2.0	0.2	0.1960	0.1244	0.4848
2013	2.2	0.9	1.0	1.3	1.5	1.0	-0.2	−0.1140	0.3648	0.2069
Total (22-state area)	1.3	1.4	1.5	1.9	2.3	2.3	0.2	0.2250	**0.0034**	0.9064

Sampling errors and number of plots are presented in Supplementary Table 1

* Bold indicates significance at the $\alpha = 0.05$ level

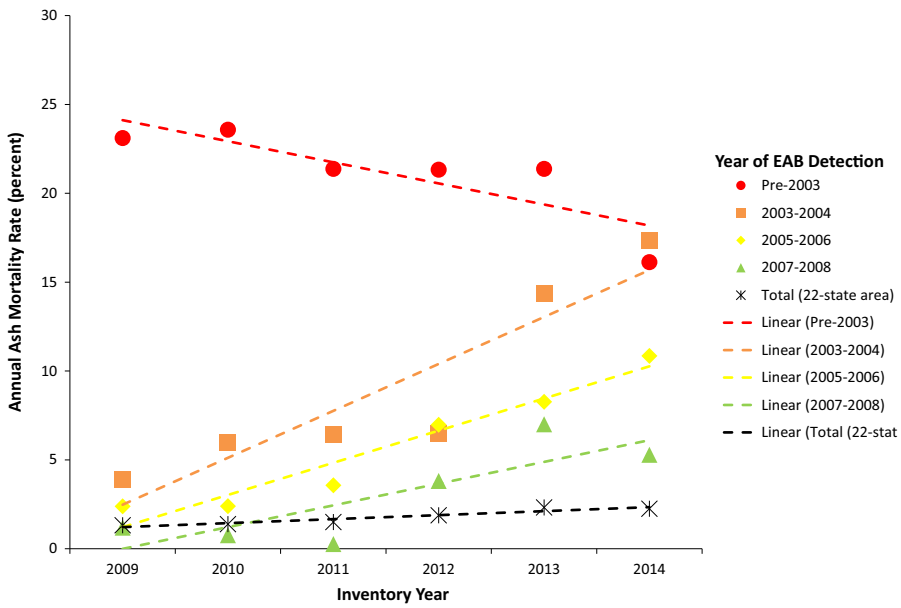


Fig. 2 Ash mortality rate by EAB detection status and inventory year with linear regression lines

Discussion

The impact of EAB invasion on ash mortality has been clearly demonstrated in localized areas (Smith 2006; Gandhi et al. 2008; Smitley et al. 2008; Knight et al. 2013; Burr and McCullough 2014; Klooster et al. 2014) as well as in a much smaller regional analysis (Pugh et al. 2011). Some studies provide evidence that impacts (Smith 2006) and susceptibility (Anulewicz et al. 2008) vary among ash species but all ash species are susceptible (Herms and McCullough 2014). Our study aims to quantify the overall increase in mortality of all ash species across the range of EAB.

As EAB continues to spread across the range of ash in the United States, regional inventory data can be used to quantify trends in ash mortality and subsequent decreases in ash density across time. Our analyses highlight upward trends in annual mortality rates and the corresponding decreasing trend in ash volume with increasing years since EAB invasion. The one invasion category that behaved consistently different through time was the group of counties invaded in

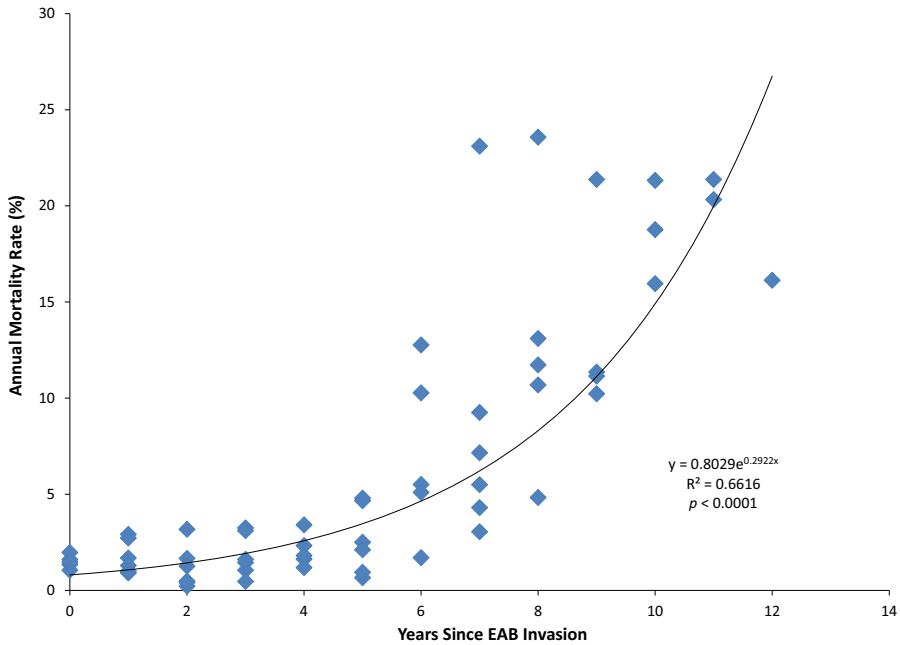


Fig. 3 Annual ash mortality as a function of years since EAB detection with exponential regression line

Table 2 Ash volume per hectare (m^3) by EAB detection history and parameters of linear regressions

EAB invasion status	Annual volume per hectare (m^3)						Mean change	Parameters of linear regression		
	2009	2010	2011	2012	2013	2014		Coefficient	*p**	R-square
Undetected	3.9	4.5	4.6	4.8	5.0	5.4	0.3	0.2616	**0.0018**	0.9322
Pre-2003	0.6	0.0	0.1	0.4	1.6	0.2	−0.1	0.0873	0.5911	0.0784
2003–2004	8.4	7.8	7.2	6.9	4.7	1.6	−1.4	−1.2449	**0.0105**	0.8375
2005–2006	12.6	10.6	8.5	7.3	5.1	3.6	−1.8	−1.7875	**<0.0001**	0.9953
2007–2008	6.2	8.3	5.2	5.3	4.7	3.6	−0.5	−0.6751	0.0645	0.6158
2009–2010	7.9	9.0	8.7	8.9	9.4	9.6	0.3	0.2667	**0.0256**	0.7506
2011–2012	6.3	5.8	5.2	6.3	6.8	7.1	0.2	0.2269	0.1901	0.3831
2013	7.2	7.6	9.4	8.3	8.7	9.0	0.4	0.3273	0.1129	0.5062
Total (22-state area)	4.9	5.4	5.4	5.5	5.6	5.6	0.1	0.1188	**0.0396**	0.6935

Sampling errors and number of plots are presented in Supplementary Table 2

* Bold indicates significance at the $\alpha = 0.05$ level

2002. Siegert et al. (2014) reported that EAB had invaded the area surrounding Detroit, Michigan, a decade or more before it was initially discovered in 2002. Therefore, the largest wave of mortality had likely already occurred prior to the collection of the data utilized in this study. This would explain both the low ash density (Fig. 1a; Table 2) and declining mortality rates (Table 1) in counties where EAB was initially discovered in 2002. Declining mortality rates are likely due to a dearth of host material to colonize, but also because natural enemies (such as *Atanycolus* spp.) begin to exert a regulatory effect on populations (Duan et al. 2015). Mortality and changes in ash volume were analyzed in detail for this area by Pugh et al. (2011).

The lag period between initial detection and the onset of ash volume decrease can be attributed both to demographics of invading populations and the nature of the scale of historical invasion data; a county is considered invaded once EAB is found reproducing in

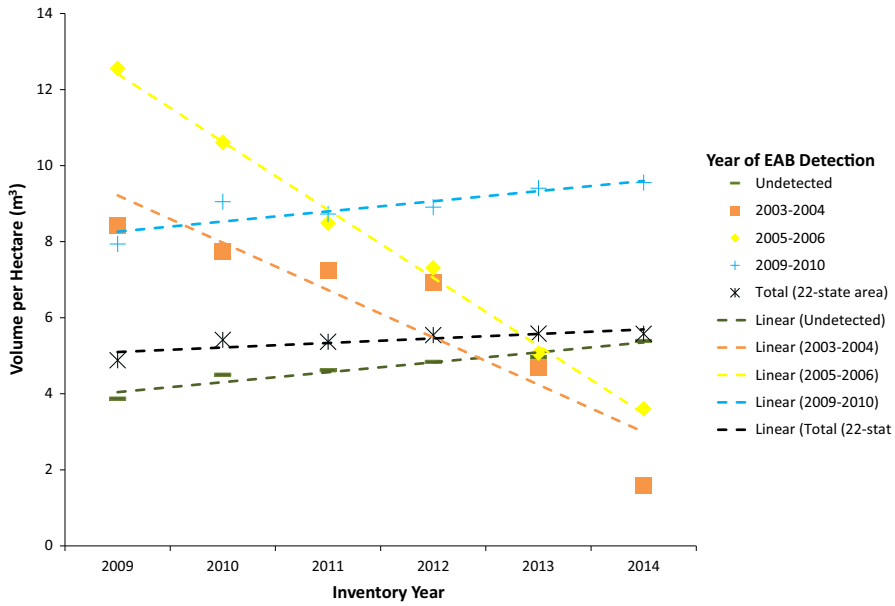


Fig. 4 Ash volume per hectare by EAB invasion status and inventory year with linear regression lines

any location but it may take several years for the insect to invade the entire county. Once populations are established in an area, it may take several more years for their populations to build to a level sufficient to kill a significant fraction of hosts (Flower et al. 2013). Such lags are a common phenomenon in the dynamics of invading populations and may arise from a multitude of reasons (Crooks 2005). Because highly sensitive methods for detecting low-density EAB populations are lacking, in most cases, EAB may be present in an area for years prior to detection (Herms and McCullough 2014). Thus, the lag between initial establishment and the accumulation of substantial tree mortality may actually be much greater than the 7–10 years detected here. Other factors that may impact this lag include ash density and EAB spread phenomena such as variation in insect flight, the 1- or 2-year life cycle, and transport by humans. Additionally, awareness of EAB has increased markedly since the early 2000s which may contribute to earlier detections.

The magnitude of damages inflicted by EAB on a regional scale greatly exceeds that of most outbreaking forest insects. For example, over the course of only 5 years, there was an 81 % decrease in ash volume in counties where EAB was first discovered in 2003 and 2004, even though ash volume was actually increasing in uninvaded areas (Table 2). By contrast, although increases in host species mortality due to invasive forest insect outbreaks have been documented regionally, the degree of mortality reported was substantially lower for gypsy moth (Morin and Liebhold 2016) and hemlock woolly adelgid (Morin and Liebhold 2015). The extreme magnitude of these impacts most likely reflects the low level of resistance present in most North American ash species to attack by this insect (Herms and McCullough 2014). This massive pulse of tree mortality no doubt has effects on other parts of forest communities but only a few of these have been measured (Gandhi and Herms 2010b; Flower et al. 2013; Koenig et al. 2013).

A critical question about the impacts of EAB that remains unresolved is what fraction of ash trees will survive once the invasion is complete. Data shown here (Table 1) indicate that in the areas where EAB has been the longest (first detected in 2002), mortality rates declined between 2009 and 2014. While this suggests that the initial EAB epidemic associated with the invasion wave may be subsiding in these areas, there is little ash left in these areas (Table 2) and it is not clear whether most of the remaining ash will die (Knight et al. 2012).

Conclusion

Remeasurement of regional forest inventory data can provide powerful information to characterize the

impacts of an invasive pest by quantifying mortality rates and volume trends across large areas. An increase in ash mortality and corresponding decrease in ash volume generally begins 6–7 years after EAB is first detected in a county and continues for several more years until the live ash resource is reduced to very low levels in the region. As EAB continues to spread, it has the potential to functionally extirpate a large fraction of the ash component with potentially devastating economic and ecological impacts. Further monitoring and analysis will be needed to quantify the timing and magnitude of EAB impacts as this species expands its range across the eastern United States and Canada.

Acknowledgments We would like to thank Greg Liknes and Louis Iverson for their constructive reviews of an earlier version of this manuscript. We also thank Douglas Bopp, USDA APHIS PPQ, for providing historical EAB detection records.

References

Anulewicz AC, McCullough DG, Cappaert DL, Poland TM (2008) Host range of the emerald ash borer (Agrilus planipennis Fairmaire) (Coleoptera: Buprestidae) in North America: results of multiple-choice field experiments. Environ Entomol 37:230–241

Aukema JE, McCullough DG, Holle BV, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of non-indigenous forest pests in the continental United States. Bioscience 60:886–897

Aukema JE, Leung B, Kovacs K, Chivers C, Britton KO, Englin J et al (2011) Economic impacts of non-native forest insects in the continental United States. PLoS ONE 6:e24587

Bechtold WA, Patterson PL (eds) (2005) The enhanced forest inventory and analysis program—national sampling design and estimation procedures. USDA For. Serv. Gen. Tech. Rep. SRS-80

Bray AM, Bauer LS, Poland TM, Haack RA, Cognato AI, Smith JJ (2011) Genetic analysis of emerald ash borer (*Agrilus planipennis* Fairmaire) populations in Asia and North America. Biol Invasions 13:2869–2887

Burr SJ, McCullough DG (2014) Condition of green ash (Fraxinus pennsylvanica) overstory and regeneration at three stages of the emerald ash borer invasion wave. Can J For Res 44:768–776

Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion. Ecoscience 12:316–329

Davidson CB, Gottschalk KW, Johnson JE (1999) Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. For Sci 45:74–84

Duan JJ, Bauer LS, Abell KJ, Ulyshen MD, Van Driesche RG (2015) Population dynamics of an invasive forest insect and associated natural enemies in the aftermath of invasion: implications for biological control. J Appl Ecol 52:1246–1252

Flower CE, Knight KS, Gonzalez-Meler MA (2013) Impacts of the emerald ash borer (*Agrilus planipennis*) induced ash (*Fraxinus* spp.) mortality on forest carbon cycling and successional dynamics in the eastern United States. Biol Invasions 15:931–944

Gandhi KJ, Herms DA (2010a) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. Biol Invasions 12:389–405

Gandhi KJ, Herms DA (2010b) North American arthropods at risk due to widespread *Fraxinus* mortality caused by the alien emerald ash borer. Biol Invasions 12:1839–1846

Gandhi KJK, Smith A, Long RA, Taylor RAJ, Herms DA (2008) Three-year progression of emerald ash borer induced decline and mortality in the forests of southeastern Michigan. In: Mastro V, Lance D, Reardon R, Parra G (eds) Proceedings of the emerald ash borer and asian longhorned beetle research and technology development meeting, 23–24 October 2007, USDA Forest Health Technology Enterprise Team, FHTET-2008-07, Pittsburgh, PA

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. Annu Rev Entomol 59:13–30

Holmes TP, Aukema JE, Von Holle B, Liebhold A, Sills E (2009) Economic impacts of invasive species in forests. Ann NY Acad Sci 1162:18–38

Johnson DM, Liebhold AM, Bjornstad ON (2006) Geographical variation in the periodicity of gypsy moth outbreaks. Ecography 29:367–374

Klooster WS, Herms DA, Knight KS, Herms CP, McCullough DG, Smith A, Gandhi KJK, Cardina J (2014) Ash (*Fraxinus* spp.) mortality, regeneration, and seed bank dynamics in mixed hardwood forests following invasion by emerald ash borer (*Agrilus planipennis*). Biol Invasions 16:859–873

Knight KS, Herms D, Plumb R et al (2012) Dynamics of surviving ash (*Fraxinus* spp.) populations in areas long infested by emerald ash borer (*Agrilus planipennis*). In: Sniezko R, Yanchuk A, Kliejunas J, Palmieri K, Alexander J, Frankel S (eds) Proceedings of the 4th international workshop on the genetics of host-parasite interactions in forestry: disease and insect resistance in forest trees, U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. Gen. Tech. Rep. PSW-GTR-240, Albany, CA, pp 143–152

Knight KS, Brown JP, Long RP (2013) Factors affecting the survivial of ash (*Fraxinus* spp.) trees infested by emerald ash borer (*Agrilus planipennis*). Biol Invasions 15:371–383

Koenig WD, Liebhold AM, Bonter DN, Hochachka WM, Dickinson JL (2013) Effects of the emerald ash borer invasion on four species of birds. Biol Invasions 15:2095–2103

Liebhold AM, Halverson J, Elmes G (1992) Quantitative analysis of the invasion of gypsy moth in North America. J Biogeogr 19:513–520

Liebhold AM, Macdonald WL, Bergdahl D, Mastro VC (1995) Invasion by exotic pests: a threat to forest ecosystems. For Sci Mono 30:49

Liebhold AM, McCullough DG, Blackburn LM, Frankel SJ, Von Holle B, Aukema JE (2013) A highly aggregated geographical distribution of forest pest invasions in the USA. Divers Distrib 19:1208–1216

Morin RS, Liebhold AM (2015) Invasions by two non-native insects alter regional forest species composition and successional trajectories. For Ecol Manag 341:67–74

Morin RS, Liebhold AM (2016) Invasive forest defoliator contributes to the impending downward regional trend of oak dominance in eastern North America. Forestry. doi:10.1093/forestry/cpv053

Niemela P, Mattson WI (1996) Invasion of North American forests by European phytophagous insects. Bioscience 46:741–753

Parker IM, Simberloff D, Lonsdale WM et al (1999) Impact: toward a framework for understanding the ecological effects of invaders. Biol Invasions 1:3–19

Pugh SA, Liebhold AM, Morin RS (2011) Changes in ash tree demography associated with emerald ash borer invasion, indicated by regional forest inventory data from the Great Lakes States. Can J For Res 41:2165–2175

Siegert NW, McCullough DG, Liebhold AM, Telewski FW (2014) Dendrochronological reconstruction of the epicenter and early spread of emerald ash borer in North America. Divers Distrib 20:847–858

Smith A (2006) Effects of community structure on forest susceptibility and response to the emerald ash borer invasion of the Huron River watershed in southeast Michigan. Thesis, The Ohio State University

Smitley D, Davis T, Rebek E (2008) Progression of ash canopy thinning and dieback outward from the initial infestation of emerald ash borer (*Coleoptera*: *Buprestidae*) in southeastern Michigan. J Econ Entomol 101:1643–1650

Tobin PC, Liebhold AM, Roberts EA (2007) Comparison of methods for estimating the spread of a non-indigenous species. J Biogeogr 34:305–312

Woods FW, Shanks RE (1959) Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. Ecology 49:349–361