

Invasive forest defoliator contributes to the impending downward trend of oak dominance in eastern North America

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Disturbance by non-native insect species can be an important ecological driver shaping long-term changes in vegetation and plant species composition. While impacts of gypsy moth (*Lymantria dispar* L.) outbreaks in North American forests have been extensively studied, the results are quite inconsistent, particularly with respect to the amount of tree mortality associated with defoliation. In this study, we integrate geographical data describing historical gypsy moth defoliation with forest inventory data collected by a national forest inventory programme to quantify regional impacts across several million hectares of forest land in the northeastern US. While observed increases in host tree mortality rates and decreases in growth rates associated with defoliation were expected, the study also indicates that this overstory mortality, coupled with ongoing declines in oak regeneration, will result in a long-term reduction of oak density in defoliated areas. Eventually, these impacts will likely contribute to regional shifts in tree species composition and forest succession pathways. Gypsy moth outbreaks thus appear to exacerbate ongoing declines in young oak age classes in the region.

Keywords: *Lymantria dispar*, gypsy moth, invasive pest, growth and mortality rates

Introduction

Invasions by non-native pathogens and insects can alter the stability and productivity of forest ecosystems around the world (Liebhold *et al.*, 1995a; Holmes *et al.*, 2009; Gandhi and Herms, 2010; Aukema *et al.*, 2011). One such damaging alien pest establishes in the US every other year (Aukema *et al.*, 2010) with the largest concentration of these species in the northeastern states (Liebhold *et al.*, 2013). While the ecological impacts of invasive species in forest ecosystems have been widely studied, the long-term effects of these impacts over large forest regions are not well understood.

A serious challenge to understanding the effects of exotic insects and diseases on eastern US forests is that forest composition has been in flux for several centuries, even in the absence of pest invasions. Humans have greatly altered forest composition in the eastern US beginning with clearance of most of the original forests by European settlers, followed by conversion to agricultural land use, extensive agricultural abandonment and finally regrowth of secondary forests (Ireland, 1999; Bürgi *et al.*, 2000; Thompson *et al.*, 2013). Other factors, such as alteration of presettlement fire regimes and elevated deer populations, have also greatly influenced forest composition (Horsley *et al.*, 2003; Nowacki and Abrams, 2008). Projected climatic change is also anticipated to affect future tree species composition (Iverson and Prasad, 1998; Rustad *et al.*, 2012), but to date, altered disturbance regimes

have had a larger impact on vegetation in the region than climate change (Nowacki and Abrams, 2014).

While most of the non-native insects and diseases that have become established in forests of eastern North America have had minimal, if any impacts, a handful of species have severely altered North American forests in profound ways (Niemela and Mattson, 1996; Aukema *et al.*, 2010). For example, chestnut blight, caused by the fungal pathogen *Cryphonectria parasitica* (Murrill) Barr, rapidly spread through eastern N. America killing virtually all of its hosts, effectively extirpating American chestnut, *Castanea dentata* (Marshall) Borkh, from eastern forests (Woods and Shanks, 1959). Similarly, emerald ash borer 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. An example is provided by gypsy moth (*Lymantria dispar*), which was accidentally introduced near Boston in 1868 or 1869 and has been continuously expanding its range, which currently extends over the entire northeastern US and eastern provinces of Canada (Liebhold *et al.*, 1992; Tobin *et al.*, 2007). Once established in an area, populations exhibit periodic outbreaks in susceptible forests (Johnson *et al.*, 2006). During these outbreaks, large numbers of spring-feeding larvae may totally defoliate host trees. Larvae are

polyphagous and known to feed on many different tree species. According to a study by Liebhold *et al.* (1997b) that ranked US tree species into three gypsy moth host suitability categories based on field and laboratory studies ('susceptible,' 'resistant' and 'immune'), most of the susceptible tree species in the north-eastern US are oaks (*Quercus* spp.). Although oak species grow throughout much of the forest land of the eastern US, the forest areas where oak comprises the plurality of stocking for all live trees are classified in the oak/hickory forest-type group (US Forest Service, 2013).

These outbreaks are often massive with populations rising synchronously over large areas, resulting in millions of hectares of defoliation. The magnitude of these outbreaks may have diminished over the last two decades, apparently as a result of the emergence of an entomopathogenic fungus, *Entomophaga maimaiga* Humber, Shimazu, and Soper first detected in 1989 (Andreadis and Weseloh, 1990; Hajek *et al.*, 1995). However, relatively large outbreaks continue to occur, with over a million hectares defoliated in Pennsylvania and New Jersey from 2007 to 2009 alone (US Forest Service, 2015). These outbreak events continue to represent one of the largest disturbance processes in forests in the eastern US but their consequences are not fully understood.

Several studies of the impacts of gypsy moth outbreaks have been conducted in selected stands, but the results have been

somewhat inconsistent. Some studies indicate relatively small increases in tree mortality (Brown *et al.*, 1979; Gansner *et al.*, 1993) but others reported catastrophic levels of mortality following outbreaks (Kegg, 1973; Campbell and Sloan, 1977). Given these extremes in the consequences of gypsy moth outbreaks on forest conditions in individual stands, there is a need to 'zoom out' and consider impacts at a regional level. Evaluation of impacts caused by invasive species across their entire range has been recognized as critically important (Parker *et al.*, 1999), but only a handful of studies have taken a regional perspective to measuring impacts.

In the case of gypsy moth, the question thus arises: what are the ecological consequences of outbreaks across the invasion range in the eastern US? Consequently, the goals of this study were to (a) characterize the impacts of gypsy moth outbreaks on tree growth and mortality across the entire invaded range of the insect and (b) identify the potential consequences of these impacts on long-term future changes in regional forest composition.

Methods

Data on historical gypsy moth outbreaks came from an archive of annual aerial survey maps documenting gypsy moth defoliation across the north-eastern US over a period of 36 years (1975–2010) (Figure 1A). The

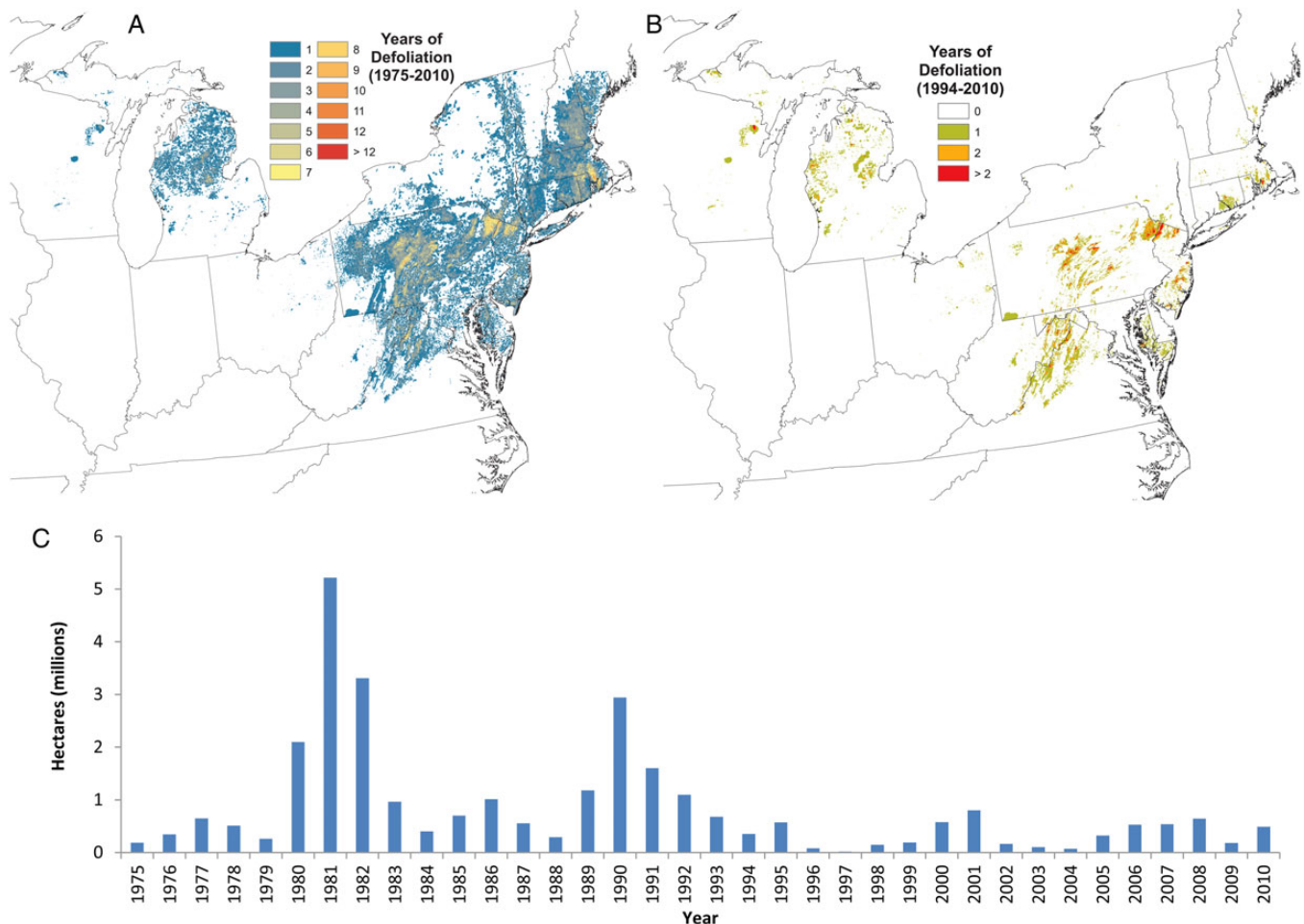


Figure 1 Cumulative gypsy moth defoliation frequency (A) 1975–2010, (B) 1994–2010 and (C) hectares of defoliation by year.

magnitude of these outbreaks may have diminished over the last two decades, apparently as a result of *Entomophaga maimaiga* (Figure 1B). These maps, generated using methodology described in Liebhold *et al.* (1997a), were digitized and represented as sequential 2 × 2 km raster layers in a geographic information system (GIS). Note that Figure 1A, C is presented to illustrate the historical record of gypsy moth defoliation but only data from 1994 to 2010 were used in the analyses presented here (Figure 1B).

The Forest Inventory and Analysis (FIA) programme of the U.S. Department of Agriculture (USDA) Forest Service conducts an inventory of forest attributes nationwide (Bechtold and Patterson, 2005). The current FIA sampling design is based on a tessellation of the US into hexagons of ~2428 ha in size with at least one permanent plot established in each hexagon. Tree and site attributes are measured on plots falling in forest land; at each plot, measurements are taken in four 7.32-m fixed-radius subplots.

Prior to 1999, FIA collected data regionally using a periodic measurement system with sample designs that varied slightly by region. Generally, inventories were conducted in each state every 6–18 years, depending on the state and region (Bechtold and Patterson, 2005). Historical changes in the plot design prohibited the direct estimation of mortality and growth from these older data, but estimates of tree volume at the state-level were published in inventory reports (Supplementary data, Electronic appendices A, B). Additionally, data from the periodic inventory system are only available in a digital format for data collected since about 1980. Therefore, comparisons of recent diameter distributions were made against the oldest available data that were available in a digital form.

Since 1999, an annual inventory system has been implemented across the entire US, which includes the range of gypsy moth. Under this system, some plots are surveyed in each state every year and every plot is remeasured every 5–7 years; this design provides a statistically robust sampling programme for direct estimation of rates of tree mortality and net growth. This study represents the first analysis of annualized FIA data for regional estimation of these rates in relation to gypsy moth defoliation. The 16-state study area includes all states where gypsy moth defoliation occurred between 1994 and 2010: Connecticut, Delaware, Maine, Maryland, Massachusetts, Michigan, New Hampshire, New Jersey, New York, Ohio, Pennsylvania, Rhode Island, Vermont, Virginia, West Virginia and Wisconsin (Figure 1B), which resulted in 36 104 remeasured plots.

To characterize the forest-type groups where defoliation has occurred, the geographical location of each FIA plot was overlaid with historical defoliation data to determine the defoliation frequency at each plot location. Therefore, the forest-type group of each FIA plot is linked with the defoliation history. To assess impacts of defoliation, frequency of defoliation was estimated for the 10-year period prior to plot remeasurement. For example, a plot measured in 2008 was assigned the number of defoliations that occurred in from 1998 to 2007 (10-year window). The GIS overlay resulted in the following sample sizes for the frequency of defoliation classes: 0 (35 050 plots), 1 (858 plots), 2 (162 plots) and 3–4 (34 plots).

Annual net growth rates and annual mortality rates of susceptible and non-susceptible tree species were estimated for the GIS-defined areas classified as having 0, 1, 2 or 3–4 years of defoliation prior to remeasurement. Net growth represents the combined effects of mortality, growth increment and ingrowth (growth of smaller trees into the 12.7-cm diameter class) and removals. Note that growth, mortality and removals are only recorded on trees 12.7 cm and larger in diameter. These net growth and mortality rate estimates were formed for tree species identified as 'susceptible' to gypsy moth (Liebhold *et al.*, 1995b) as well as for species classified as 'resistant' or 'immune'. Hereafter, resistant and immune species are referred to as non-susceptible. Most of the susceptible tree species in the northeastern US are oaks (Liebhold *et al.*, 1997b). Using remeasured plots (initially surveyed 2002–2006 and remeasured 2007–2011), net growth and mortality were computed as proportions of live volume at the time of the initial survey (i.e. annual mortality volume/live volume at time 1). Annual net growth and

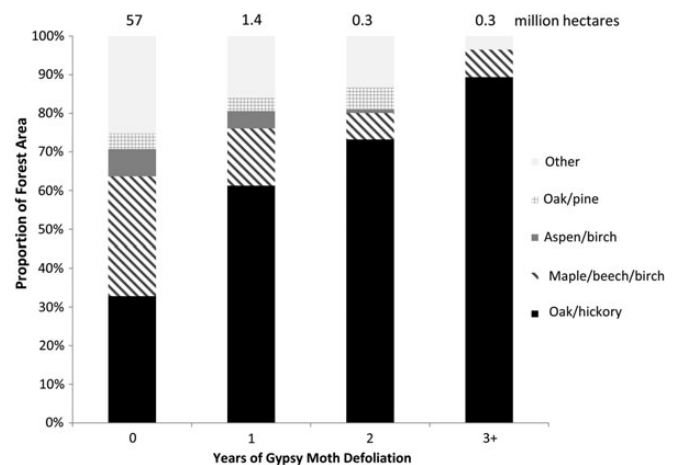


Figure 2 Proportion of forest area by frequency of defoliation and forest type.

annual mortality rates for each group of species were estimated for ranges of number of years of defoliation that occurred in the 10-year window defined earlier.

Gypsy moth has invaded about a quarter of the US forest area that contains host species (Morin *et al.*, 2005), and ~14 per cent of the defoliated area experienced multiple defoliations between 1975 and 2010 (Figure 1A). Most of the defoliation in the 16 years prior to 2010 occurred in Pennsylvania, Michigan, Virginia, West Virginia and southern New England (Figure 1B). More than 60 per cent of the defoliation occurred in the oak/hickory forest-type group, and the frequency of defoliation increased with proportion of forest area in the oak/hickory type group; over 85 per cent of forest land that was defoliated three or more times was in the oak/hickory forest-type group (Figure 2). Because oaks are the most abundant susceptible species in the area historically defoliated (Liebhold *et al.*, 1997b), it is mostly oak species that have been impacted. Therefore, our analyses are focused on forests that are classified as being in the oak/hickory forest-type group. Note that susceptible and non-susceptible species both occur in the oak/hickory forest-type group, but oaks make up the plurality of stocking of live trees in these areas.

Because analyses indicated that most gypsy moth defoliation occurred in the oak/hickory forest-type group, estimates of mortality rates and net growth rates were limited to plots classified into the oak/hickory group. One-way analysis of variance (ANOVA) tested equality of variable means among the defoliation classes and within susceptibility classes. Assumptions of normality and homogeneity of variances were met as tested by the Kolmogorov–Smirnov's and Levene's tests, respectively. Post-hoc Tukey HSD tests of mean net growth and mortality rates among pairs of defoliation classes within susceptibility classes were conducted to assess significant differences ($\alpha = 0.05$). All analyses were performed in SAS Version 9.3.

Results

Recent inventories indicate that annual mortality rates of susceptible species increased with increasing number of gypsy moth defoliations, but this pattern is not seen for non-susceptible tree species (Figure 3). Mortality rates of gypsy moth-susceptible species increased slightly after one defoliation, but increased significantly after two or more defoliation episodes (Figure 3A, Tukey's HSD test, $P < 0.001$). Some effects of mortality can be compensated for by growth of surviving trees. Annual net growth rates of

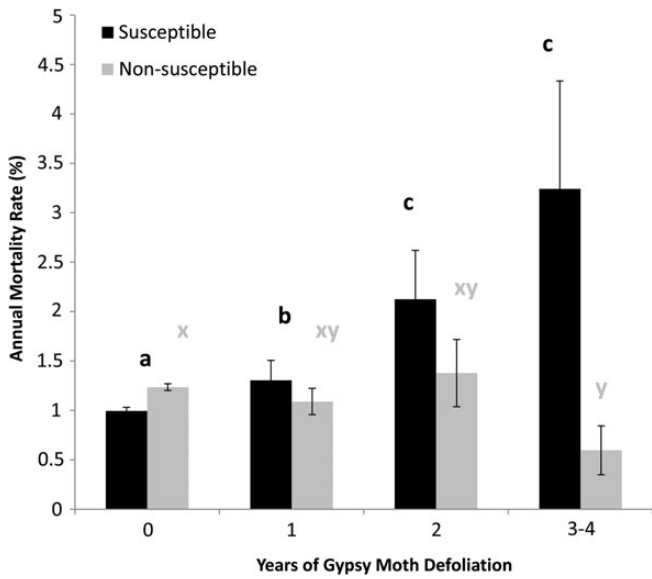


Figure 3 Annual percent mortality in the oak/hickory forest-type group by frequency of defoliation for susceptible and non-susceptible species from remeasured plots (initially surveyed 2002–2006 and remeasured 2007–2011). Error bars indicate 68% sampling errors; different letters designate statistically significant ($P < 0.05$) differences within susceptibility classes, according to pairwise Tukey tests.

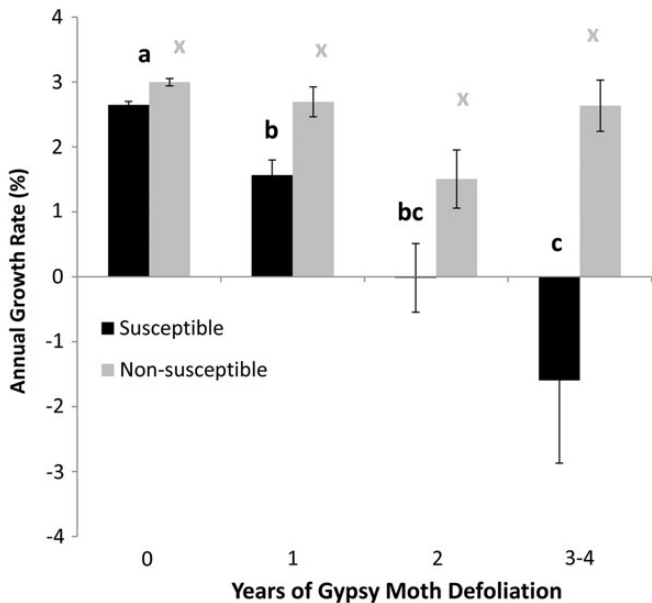


Figure 4 Annual percentage net growth in the oak/hickory forest-type group by frequency of gypsy moth defoliation for susceptible and non-susceptible species from remeasured plots (initially surveyed 2002–2006 and remeasured 2007–2011). Error bars indicate 68% sampling errors; different letters designate statistically significant ($P < 0.05$) differences within susceptibility classes, according to pairwise Tukey tests.

susceptible species have generally decreased with increasing years of defoliation, and after two or more defoliations, net growth becomes negative (Figure 4, Tukey’s HSD test, $P < 0.001$). In other

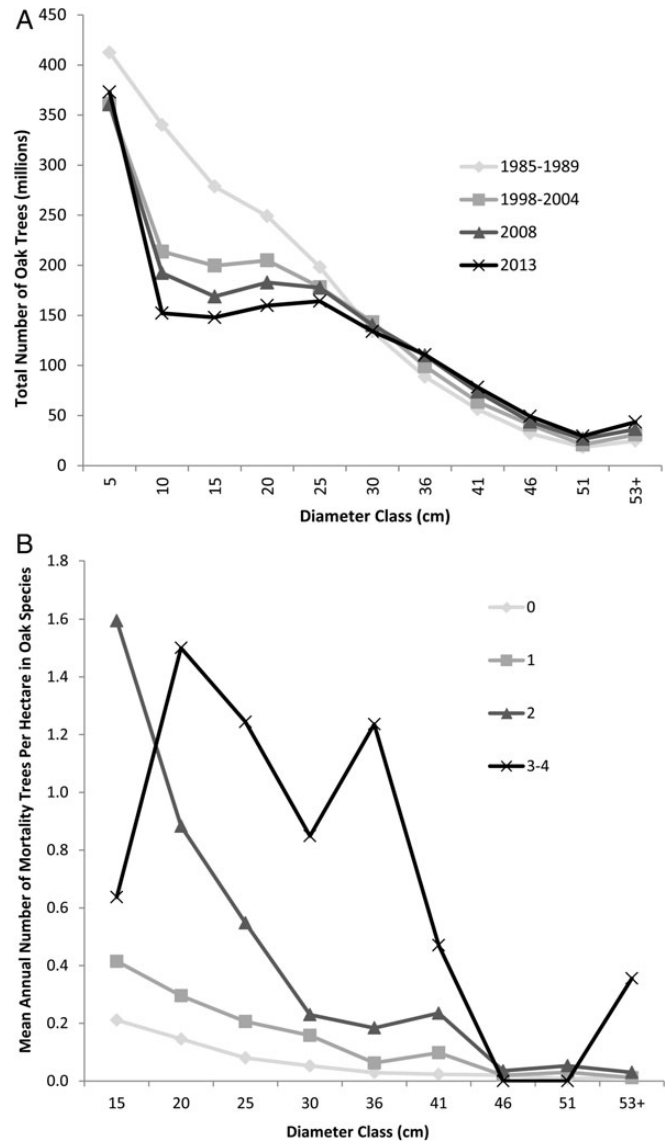


Figure 5 (A) Total number of oak trees by diameter class, Massachusetts 1985, 1998, 2008 and 2013; New Jersey 1987, 1999, 2008 and 2013; Pennsylvania, 1989, 2004, 2008 and 2013; West Virginia, 1989, 2000, 2008 and 2013; and (B) average number of oak trees that died between measurements in the oak/hickory forest-type group by diameter class and frequency of defoliation, Massachusetts, New Jersey, Pennsylvania and West Virginia, 2013 (initially surveyed 2004–2008 and remeasured 2009–2013).

words, the volume added due to growth is not enough to compensate for the volume lost due to tree mortality.

Across the entire oak/hickory forest-type group (not just areas affected by the gypsy moth), numbers of oaks have been decreasing steadily in the 5- through 25-cm diameter classes over the last 25 years (Figure 5A). Based on mortality rate estimates from the most recent inventory, it appears that gypsy moth defoliation is contributing to this decline; incidence of defoliation is associated with increases in mortality of oak trees across nearly all diameter classes, but this increase is most evident in the diameter classes below 30 cm (Figure 5B).

Discussion

The impacts of gypsy moth on growth and/or mortality of host species have previously been studied at selected sites (Kegg, 1971; Campbell and Sloan, 1977; Gansner *et al.*, 1987; Crow and Hicks, 1990). Several of these studies documented very high levels of mortality associated with gypsy moth defoliation particularly with increasing defoliation frequency, duration and intensity (Kegg, 1973; Campbell and Sloan, 1977). Other studies found relatively small increases in tree mortality following outbreaks (Brown *et al.*, 1979; Gansner *et al.*, 1993). Thus, considerable variation in the level of mortality has been observed, and this variation has been related to stand species composition, elevation, drought and other factors (Davidson *et al.*, 1999). It is not surprising that we found increases in mortality and decreases in net growth in tree species that are susceptible to gypsy moth defoliation. However, it is surprising that at a regional scale, mortality rates for susceptible species are high enough in areas where defoliation occurred at least two times that they exceed increment growth and ingrowth to the point where net growth becomes negative (Figure 4). These results indicate that gypsy moth outbreaks may contribute to regional shifts in species composition. Since almost all of these hosts are oak, gypsy moth defoliation appears to contribute to a regional decline in oak abundance within the oak/hickory forest-type group.

Such regional declines in oak abundance must be considered in the context of other trends and drivers of long-term forest change in the region. There is considerable evidence that several factors other than gypsy moth outbreaks are contributing to the regional decline of oak. These include factors that reduce oak regeneration such as fire suppression (Abrams, 1992; Nowacki and Abrams, 2008), management regimes, invasive species (Dey, 2014) and browsing by white-tailed deer (*Odocoileus virginianus* Zimmerman) (Horsley *et al.*, 2003; Rooney and Waller, 2003) as well as factors that reduce overstory oak density like selective logging (Abrams, 2003), and drought (Dwyer *et al.*, 1995; Haavik *et al.*, 2015). Evidence indicates that gypsy moth defoliation also causes at least a temporary decline in oak mast production (Gottschalk, 1990), and oak seedlings are also susceptible to defoliation-induced mortality (McGraw *et al.*, 1990). Thus gypsy moth outbreaks may be impacting the regeneration potential of oak species, and consequently, allowing non-susceptible species to dominate seedling recruitment.

Several studies have identified trends of decreasing replacement of oak-dominated forests after disturbance in the north-eastern US (Marquis *et al.*, 1976; Abrams, 1998, 2003; Nowacki and Abrams, 2008). Supplementary data, Electronic appendix A illustrates how the volume of major oak species in the northern deciduous forests of four northeastern states has been steadily increasing over the last half century. However, volume increases occur mostly in larger diameter trees, and this masks the effect of poor regeneration and decreases in numbers of trees in small diameter classes; these situations limit future dominance and cause concern about the sustainability of oak species. For example, numbers of oaks have been decreasing steadily in the 5- through 25-cm diameter classes over the last 25 years (Figure 5A). It appears that gypsy moth defoliation is contributing to this decline through increases in the number of oak trees that die across nearly all diameter classes associated with defoliation, but this increase is most evident in the diameter classes below 30 cm (Figure 5B).

Conclusions

Results presented here illustrate how invasion by a polyphagous insect species is contributing to declines in regional oak abundance. These impacts are likely to contribute to regional shifts in tree species composition and forest succession pathways over time. Impacts on net growth of gypsy moth-susceptible species are greatest after multiple defoliation events which only occur over a relatively small area (650 000 ha from 1994 to 2010). Thus, the effect of gypsy moth outbreaks on the trend of declining oak dominance is likely to be small compared with effects of deer browsing and fire suppression. Despite all of these influences, total oak volume has continued to increase over the last several decades (Supplementary data, Electronic Appendix A). However, these increases are likely to eventually reverse; decreases in numbers of small diameter trees suggest that large oaks will not all be replaced in the future. Though gypsy moth defoliation adversely affects all oak diameters, regional declines in oak dominance are most pronounced in small diameters, indicating that invasion by the gypsy moth is contributing to this decline. However, the total impact of gypsy moth defoliation requires further study because seedling mortality and reduced acorn crops, in addition to tree mortality studied here, also have major implications for regeneration potential and future species dynamics.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

References

- Abrams, M.D. 1992 Fire and the development of oak forests. *BioScience* **42**, 346–353.
- Abrams, M.D. 1998 The red maple paradox. *BioScience* **48**, 355–364.
- Abrams, M.D. 2003 Where has all the white oak gone? *BioScience* **53**, 927–939.
- Andreadis, T.G. and Weseloh, R.M. 1990 Discover of *Entomophaga maimaiga* in North American gypsy moth, *Lymantria dispar*. *PNAS* **87**, 2461–2465.
- Aukema, J.E., McCullough, D.G., Holle, B.V., Liebhold, A.M., Britton, K. and Frankel, S.J. 2010 Historical accumulation of nonindigenous forest pests in the continental United States. *BioScience* **60**, 886–897.
- Aukema, J.E., Leung, B., Kovacs, K., Chivers, C., Britton, K.O., Englin, J. *et al.* 2011 Economic impacts of non-native forest insects in the continental United States. *PLoS One* **6**, e24587.
- Bechtold, W.A. and Patterson, P.L. (eds). 2005 *The Enhanced Forest Inventory and Analysis Program - National Sampling Design and Estimation Procedures*. USDA Forest Service Gen. Tech. Rep. SRS-80.

- Brown, J.H., Halliwell, D.B. and Gould, W.P. 1979 Gypsy moth defoliation: impact on Rhode Island forests. *J. For.* **77**, 30–32.
- Bürgi, M., Russel, E.W.B. and Motzkin, G. 2000 Effects of postsettlement human activities on forest composition in the north-eastern United States: a comparative approach. *J. Biogeogr.* **27**, 1123–1138.
- Campbell, R.W. and Sloan, R.J. 1977 Forest stand response to defoliation by the gypsy moth. *For. Sci. Monogr.* **19**, 34.
- Crow, G.R. and Hicks, R.R. Jr 1990 Predicting mortality in mixed oak stands following spring insect defoliation. *For. Sci.* **36**, 831–841.
- Davidson, C.B., Gottschalk, K.W. and Johnson, J.E. 1999 Tree mortality following defoliation by the European gypsy moth (*Lymantria dispar* L.) in the United States: a review. *For. Sci.* **45**, 74–84.
- Dey, D.C. 2014 Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. *For. Sci.* **60**, 926–942.
- Dwyer, J.P., Cutter, B.E. and Wetteroff, J.J. 1995 A dendrochronological study of black and scarlet oak decline in the Missouri Ozarks. *Forest Ecol. Manag.* **75**, 69–75.
- Gandhi, K.J. and Herms, D.A. 2010 Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions* **12**, 389–405.
- Gansner, D.A., Herrick, O.W., Mason, G.N. and Gottschalk, K.W. 1987 Coping with the gypsy moth on new frontiers of infestation. *South. J. Appl. For.* **11**, 201–209.
- Gansner, D.A., Arner, S.L., Widmann, R.H. and Alerich, C.L. 1993 Field notes: after two decades of gypsy moth, is there any oak left? *NJAF* **10**, 184–186.
- Gottschalk, K.W. 1990 Gypsy moth effects on mast production. In *Proceedings of the Workshop: Southern Appalachian Mast Management*. University of Tennessee, pp. 42–50.
- Haavik, L.J., Billings, S.A., Guldin, J.M. and Stephen, F.M. 2015 Emergent insects, pathogens and drought shape changing patterns in oak decline in North America and Europe. *Forest Ecol. Manag.* **354**, 190–205.
- Hajek, A.E., Humber, R.A. and Elinton, J.S. 1995 Mysterious origin of *Entomophaga maimaiga* in North America. *Am. Entomol.* **41**, 31–43.
- Herms, D.A. and McCullough, D.G. 2014 Emerald ash borer invasion of North America: history, biology, ecology, impacts, and management. *Annu. Rev. Entomol.* **59**, 13–30.
- Holmes, T.P., Aukema, J.E., Von Holle, B., Liebhold, A. and Sills, E. 2009 Economic impacts of invasive species in forests. *Ann. N.Y. Acad. Sci.* **1162**, 18–38.
- Horsley, S.B., Stout, S.L. and deCalesta, D.S. 2003 White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* **13**, 98–118.
- Ireland, L.C. 1999 *The Northeast's Changing Forests*. Harvard University Press, 432 pp.
- Iverson, L.R. and Prasad, A.M. 1998 Predicting abundance of 80 tree species following climate change in the eastern United States. *Ecol. Monographs* **68**, 465–485.
- Johnson, D.M., Liebhold, A.M. and Bjornstad, O.N. 2006 Geographical variation in the periodicity of gypsy moth outbreaks. *Ecography* **29**, 367–374.
- Kegg, J.D. 1971 The impact of gypsy moth: repeated defoliation of oak in New Jersey. *J. For.* **69**, 852–854.
- Kegg, J.D. 1973 Oak mortality caused by repeated gypsy moth defoliations in New Jersey. *J. Econ. Ento.* **66**, 639–641.
- Liebhold, A.M., Halverson, J. and Elmes, G. 1992 Quantitative Analysis of the invasion of gypsy moth in North America. *J. Biogeography* **19**, 513–520.
- Liebhold, A.M., Macdonald, W.L., Bergdahl, D. and Mastro, V.C. 1995a Invasion by exotic pests: a threat to forest ecosystems. *Forest Sci. Mon.* **30**, 49.
- Liebhold, A.M., Gottschalk, K.W., Muzika, R., Montgomery, M.E., Young, R., O'Day, K. et al. 1995b *Suitability of North American Tree Species to the Gypsy Moth: a Summary of Field and Laboratory Tests*. USDA Forest Service Gen. Tech. Rep. NE-211.
- Liebhold, A.M., Gottschalk, K.W., Luzader, E.R., Mason, D.A., Bush, R. and Twardus, D.B. 1997a *Gypsy moth in the United States, an atlas*. USDA Forest Service Gen. Tech. Rep. NE-233.
- Liebhold, A.M., Gottschalk, K.W., Mason, D.A. and Bush, R.R. 1997b Evaluation of forest susceptibility to the gypsy moth across the conterminous United States. *J. For.* **95**, 20–24.
- Liebhold, A.M., McCullough, D.G., Blackburn, L.M., Frankel, S.J., Von Holle, B. and Aukema, J.E. 2013 A highly aggregated geographical distribution of forest pest invasions in the USA. *Divers. Distrib.* **19**, 1208–1216.
- Marquis, D.A., Eckert, P.L. and Roach, B.A. 1976 *Acorn Weevils, Rodents, and Deer all Contribute to Oak Regeneration Difficulties in Pennsylvania*. USDA Forest Service Research Paper NE-356.
- McGraw, J.B., Gottschalk, K.W., Vavrek, M.C. and Chester, A.L. 1990 Interactive effects of resource availabilities and defoliation on photosynthesis, growth, and mortality of red oak seedlings. *Tree Physiol.* **7**, 247–254.
- Morin, R.S., Liebhold, A.M., Luzader, E.R., Lister, A.J., Gottschalk, K.W. and Twardus, D.B. 2005 *Mapping host-Species Abundance of Three Major Exotic Forest Pests*. USDA Forest Service Research Paper NE-726.
- Niemela, P. and Mattson, W.I. 1996 Invasion of North American forests by European phytophagous insects. *BioScience* **46**, 741–753.
- Nowacki, G.J. and Abrams, M.D. 2008 The demise of fire and 'mesophication' of forests in the eastern United States. *BioScience* **58**, 123–138.
- Nowacki, G.J. and Abrams, M.D. 2014 Is climate an important driver of post-European vegetation change in the eastern United States? *Glob. Change Biol.* **21**, 314–334.
- Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M. et al. 1999 Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invasions* **1**, 3–19.
- Rooney, T.P. and Waller, D.M. 2003 Direct and indirect effects of white-tailed deer in forest ecosystems. *Forest Ecol. Manag.* **181**, 165–176.
- Rustad, L., Campbell, J., Dukes, J.S., Huntington, T., Fallon Lambert, K., Mohan, J. et al. 2012 *Changing climate, changing forests: the impacts of climate change on forests of the northeastern United States and eastern Canada*. USDA Forest Service Gen. Tech. Rep. NRS-99.
- Thompson, J.R., Carpenter, D.N., Cogbill, C.V. and Foster, D.R. 2013 Four centuries of change in northeastern United States forests. *PLoS One* **8**, e72540.
- Tobin, P.C., Liebhold, A.M. and Roberts, E.A. 2007 Comparison of methods for estimating the spread of a non-indigenous species. *J. Biogeogr.* **34**, 305–312.
- U.S. Forest Service. 2013 *Forest Inventory and Analysis national core field guide volume 1: field data collection procedures for phase 2 plots*. <http://www.nrs.fs.fed.us/fia/data-collection/field-guides/ver602/NRSFG6.0.2-Jun2013.pdf> (accessed on 20 May 2015).
- U.S. Forest Service. 2015 *Gypsy Moth Digest*. <http://na.fs.fed.us/fhp/gm> (accessed on 26 March, 2015).
- Woods, F.W. and Shanks, R.E. 1959 Natural replacement of chestnut by other species in the Great Smoky Mountains National Park. *Ecology* **49**, 349–361.