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Title: Biomass losses resulting from insect and diseases invasions in USA forests

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Abstract: Worldwide, forests are increasingly affected by non-native insects and diseases, some of which cause substantial tree mortality. Forests in the USA have been invaded by a particularly large number (>450) of tree-feeding pest species. While information exists about ecological impacts of certain pests, region-wide assessments of the composite ecosystem impacts of all species are limited. Here we analyze 92,978 forest plots distributed across the conterminous USA to estimate biomass loss associated with elevated mortality rates caused by the 15 most damaging non-native forest pests. We find that these species, combined, caused an additional (above background levels) tree mortality rate of 5.53 TgC per year. Compensation, in the form of increased growth and recruitment of non-host species, was not detectable when measured across entire invaded ranges but does occur several decades following pest invasions. In addition, 41.1% of the total live forest biomass in the conterminous USA is at risk to future loss from these 15 pests. These results indicate that forest pest invasions, driven primarily by globalization, are casting a huge risk to forests in the USA and have significant impacts on carbon dynamics.

Significant Statement: Forests provide a wide variety of vital ecosystem services but are increasingly affected by anthropogenic disturbances. Among these, invasions by non-native pests can adversely affect ecosystem services. However, comprehensive estimates of the impacts of non-native pest on forest biomass loss are limited. Using over 92,000 field plots, we quantified pest-induced biomass loss across the conterminous USA for the first time. We show that invasive pests are causing significant shifts in carbon dynamics in US forests. In addition, two fifths of the total live biomass in USA forests is at risk of invasion by currently established pest species. Our findings are of potential significance in justifying the selection of future policy options and to future carbon dynamics modeling research.

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INTRODUCTION

Forests provide a wide variety of vital ecosystem services, including acting as a large sink of atmospheric carbon. It has been estimated that forests contribute approximately 76% of North America's net terrestrial carbon sequestration (1). Worldwide, a variety of disturbances such as deforestation and fire are known to impact the ability of forests to sequester and accumulate carbon (2). The problem of biological invasions, primarily driven by globalization, represents another way that humans are altering ecosystem functioning worldwide (3). Non-native pests (insects and diseases) can have multifaceted short-term and long-term impacts on forest ecosystems varying from decreased forest productivity to the modification of biogeochemical cycling (4) and geomorphic processes (5), all of which can be detrimental to various ecosystem services forests provide (6, 7). Despite the existence of large-scale pest-specific impact assessments (8-10), empirical measures of the aggregate impacts of all non-native pest species on mortality and carbon budgets in forests are limited.

North American forests have experienced a large number of invasions by non-native insects and tree pathogens; over 450 forest insect and pathogen species are known to be established in the conterminous USA (11-13). The majority of non-native pests that have become established have had minimal impacts on forests (11). Unfortunately, about 83 of these species have caused noticeable forest damage (13), resulting in substantial effects on tree health and productivity, and sometimes causing extensive tree mortality. Such mortality might be expected to impact carbon dynamics by reducing forests carbon sequestration capacity and by converting live materials to dead carbon sources.

In this study, we review the impacts of 83 known damaging non-native forest insect and disease species currently established in the continental US, and we estimate the rate at which live tree biomass is being converted to dead materials (carbon source) by the 15 species that are known to have the greatest impacts on tree mortality. We used data from 92,978 field plots sampled by the U.S. Department of Agriculture (USDA) Forest Service Forest Inventory and Analysis (FIA) program to quantify host tree mortality and biomass losses arising from tree mortality associated with invasions of these pests. Our major objectives are: (a) to estimate the increased mortality and associated live biomass losses caused by non-native forest pest invasions, (b) to quantify the temporal dynamics of non-native pest induced mortality, and (c) to quantify the host tree live biomass at risk of impacts from all major non-native forest pests. The results presented here provide crucial information that can inform policy and management decision-making and future carbon dynamics modeling research.

RESULTS

Among the 83 non-native pests recognized to cause reportable damage in the conterminous USA, 16 species (19%) are wood- and phloem-boring insects, 28 (34%) are foliage-feeding insects, 25 (30%) are sap-feeding insects and 14 (17%) are tree pathogens (see **Dataset S1** for the entire list). Species reviewed were from Asia (35%), Eurasia (29%), Europe (29%), or Australia (7%). We identified 15 species (nine pathogens, four sap-feeders, one wood- / phloem-borer, and one foliage-feeder) that cause substantial tree mortality based on information in the literature (**Dataset S1**). The geographical distributions of these 15 pests and their corresponding hosts can be found in **SI Appendix, Fig. S1**. Eleven of the 15 damaging pests have primarily invaded the eastern USA. Nearly all of the 15 damaging pests are host specialists (at the genus or species level), with the exception of the gypsy moth, *Lymantria dispar*, which is a generalist.

Pest related tree mortality and growth rates

Among the 15 pests that are recorded in the literature causing substantial tree mortality, we found that nine of these species caused host tree mortality rates significantly elevated ($P < 0.001$) above background levels during the study period (**Fig. 1**). Ten of the non-native pests caused host mortality significantly higher than the annual average background mortality rate (1.2%) across all tree species. The most damaging pests, in terms of high total annual biomass loss elevated above background levels, were emerald ash borer (EAB; *Agrilus planipennis*), Dutch elm disease (DED; *Ophiostoma novo ulmi*), beech bark disease (BBD; *Cryptococcus fagisuga*), and hemlock woolly adelgid (HWA; *Adelges tsugae*) (**Table 1**). Each of these four pests caused the annual conversion of > 0.7 TgC of live biomass to dead materials in excess of their host background mortality. The most damaging three pest species, in terms of high annual mortality rate in the invaded range expressed as a percentage of total host biomass loss, are laurel wilt disease (*Raffaelea lauricola,* 11.4%), chestnut blight (*Cryphonectria parasitica*, 6.3%), and butternut canker (*Sirococcus clavigignenti-juglandacearum*, 5.0%). Dogwood anthracnose (*Discula destructiva*), EAB, DED, and red pine scale (*Matsucoccus matsumurae*) all caused more than twice the national annual average mortality rate. The mortality rates for some pests can be deceptive because in some cases a pest may already have killed most of the individuals of its host species prior to the survey period.

During the same time period, no consistent compensatory growth pattern was observed in non-host tree species located on plots that were invaded by each of the 15 pests (**SI Appendix, Fig. S1**). Comparison of gross growth rates for host and non-host species on invaded plots showed that non-host trees had higher growth rates than host trees for eight pest species but lower rates on plots invaded by seven species. Assessment of growth rates for non-host species inside vs. outside the invaded range of each pest also did not reveal evidence of consistent non-host tree growth compensation for host tree mortality; gross growth rates of non-host trees were higher on plots inside the invaded ranges of four pests, but for eight pests non-host growth was higher outside of their ranges.

<u>Pest related tree mortality trends</u>

Analyses of temporal trends in impacts from three selected damaging pests (EAB, HWA, and BBD) showed that, in general, annual host mortality increases with time since invasion (**Fig. 2**). For EAB, host mortality rate appears to increase approximately exponentially with time. Although annual host mortality rate is not significantly elevated in the first three years following first EAB detection, it quickly increased to twice the background mortality five years post detection, and reached > 15% (of live biomass) for areas with > 12 years since first detection. Mortality rates associated with HWA invasion are lower compared to EAB but exhibit a similar trajectory. On average, annual hemlock mortality rate nearly tripled in areas with > 10 years since initial detection compared to areas where HWA is absent (1.9% vs. 0.5%, respectively), and was seven times higher in areas with > 35 years since initial HWA detection. Host mortality associated with BBD invasion exhibited temporal trends different from those associated with EAB and HWA. Annual beech mortality rate was the highest during the first 10 years after invasion and subsequently remained at around 2% of live biomass. While no compensatory growth was observed in non-host trees when averaged across the entire invaded range of each pest (**SI Appendix, Fig. S2**), there was consistently increased growth in non-host trees in regions that had been invaded by pests for 2-5 decades (**SI Appendix, Fig. S3**), indicating compensatory growth as a delayed reaction to pest invasions.

Analysis of tree mortality associated with historical gypsy moth defoliation indicates that local pest-induced mortality is higher than indicated by comparison of invaded with uninvaded counties (**Fig. 3**). There was no apparent increase of tree mortality in areas invaded by gypsy moth compared to background mortality at the county level (**Fig. 1**). However, we observed a strong relationship between numbers of years of gypsy moth defoliation and host mortality observed at a 2x2-km spatial resolution (**Fig. 3**). Gypsy moth outbreaks cause forest defoliation over only a fraction of the invaded area. Mortality was significantly elevated in areas with 2 or more years of defoliation (1994 – 2010) but this comprised a relatively small fraction of the invaded area and impacts are strongly diluted out over the entire invaded range.

<u>Pest related overall mortality impacts</u>

Combined pest induced live biomass loss (i.e., overall host mortality minus background mortality in the invaded area) for all pests was about 5.53 TgC per year (**Table 1**). This estimated annual biomass losses caused by these pests comprises a relatively small fraction (0.04%) of the total live biomass in the conterminous USA (12,643 TgC of dry biomass, note this number is slightly lower than the most recent SOCCR2 (14) estimate, 14,182 TgC, which covered the entire USA). However, these dead materials caused by the invasive pests represent a substantial change in carbon dynamics. Our estimate of 5.53 TgC per year in trees killed by pest invasions across the conterminous US is equivalent to 3.5% of live biomass loss to forest removals (157 TgC per year based on 1.25% annual removal rate, **SI Appendix, Fig. S2**) across the same area. The amount biomass loss due to non-native pest induced mortality, which was primarily concentrated in the eastern USA, is similar in magnitude to trees killed by fire (5.4-

14.2 TgC per year) and by all native bark beetles across the western USA (1.8-24.4 TgC per year) (15).

Moreover, there are substantial amounts of host biomass in both invaded and uninvaded ranges that are at risk of damage from the 15 most damaging pests. Among these 15 pests, 12 have not yet fully invaded the ranges of their hosts (**Table 1**). Five pests have invaded > 90% of their host biomass, three invaded 50-60% of host biomass, while the rest have only invaded less than 35% of their corresponding host biomass. For gypsy moth alone, there are 898 TgC live host biomass in the invaded range and 2,175 TgC in uninvaded areas. For the other 14 pests (which have more narrow host ranges than the gypsy moth), there are 1,128 TgC total live host biomass in their invaded ranges and 1,543 TgC in uninvaded areas (**Table 1**). Discounting the potential range overlap between gypsy moth and sudden oak death (*Phytophthora ramorum*) in the future (primarily on *Quercus* spp.), the total amount of host biomass at risk of damage from these 15 pests is about 5,197 TgC (2,027 TgC in currently invaded ranges and 3,170 TgC in uninvaded ranges), or 41.1% of the total live forest biomass (12,643 TgC) in the conterminous USA.

DISCUSSION

Our study quantifies substantial increases in regional rates of tree mortality caused by insect and disease invasions in the conterminous USA, and associated conversion of live carbon to dead material. We also demonstrate that large amounts of host biomass are at risk of future damages caused by these pests. Results presented here provide key information, not only for the understanding the impact of non-native pests on carbon budgets, but they also provide crucial information on non-native pest impacts that could inform the selection of future biosecurity measures targeting exclusion of additional pests in the future and necessary funding levels for treatment and control measures for established pests.

Methods used here to quantify impacts of forest pest invasions have some limitations and may fail to measure all impacts on biomass loss. As mentioned above, mortality rates may increase over a period of several decades following initial pest invasion (**Fig. 2**) so it is likely that impacts will increase across invaded areas in the future. For species that had already invaded all of their potential ranges (e.g., chestnut blight, DED), pest induced biomass loss could be substantially underestimated as most of their hosts have already died a long time ago. For example, American chestnut (*Castanea dentata*) used to dominate many eastern N. American forests, comprising over one third of the pollen assemblage in some stands (16) and up to 600 metric tons/ha of biomass prior to the invasion and spread of chestnut blight (17), but this tree species currently consists of a minor component of forest understories. In addition, mortality rates vary among species and regions, and can be influenced by environmental conditions such as climate (18, 19). Such geographical variation in mortality rates might introduce errors in our attribution of elevated mortality to pest invasions based upon comparison of mortality rates inside vs. outside of invaded ranges. For example, the host mortality rate for gypsy moth in the invaded region (1.2%) was indistinguishable from the rate estimated in the uninvaded region (1.4%) (**Fig.1**). However, fine-scale analysis indicated that gypsy moth greatly elevated host mortality rate to 2.4% after two years of gypsy moth defoliation and >3.1% in areas with more defoliation (**Fig. 3**). Though such defoliation episodes can cause substantial mortality of hosts in localized areas, this damage is diluted out when averaging mortality across the entire invaded range. Our analysis also only accounts for tree mortality and does not capture crown or root dieback or reductions in tree growth which may be substantial (20, 21). We also did not attempt to estimate release of carbon to the forest floor as a result of defoliation events (4, 22). Indeed, Clark et al. (23) demonstrated that gypsy moth defoliation caused marked changes in local carbon flux. Moreover, pest caused mortality rates can be underestimated due to salvage removal, i.e., harvesting of host trees prior to the next inventory, which has been observed in regional studies (24). However, we did not observe substantial differences in the rate of host biomass harvested within and outside currently invaded ranges for most of the pests in our range-wide analyses (**SI Appendix, Fig. S2**). Finally, the inventory data analyzed here did not include samples from urban areas; our estimates of total biomass losses are under-estimated because they do not include losses from urban tree mortality.

Our estimate of the annual loss of 5.53 TgC live biomass caused by invasions of forest insects and diseases is substantial. However, it is important to emphasize that the loss of live biomass is an intra-ecosystem carbon flux, and not an ecosystem scale net CO2 emission. Following transfer of carbon from live biomass to dead organic matter, carbon will be at least partially released to the atmosphere through gradual decomposition by heterotrophic micro-organisms (25, 26). Decomposition rates vary depending on forest types and climate conditions and some carbon from tree mortality will move into and remain in the soil (14, 27). Also, it can be anticipated that over time, some of the tree mortality triggered by pest invasions will be compensated for by additional growth in unaffected trees and the recruitment of new regeneration. In general, we did not observe substantial compensation by non-host species associated with pest invasions, even though we anticipate that compensation must ultimately occur in response to pest-induced mortality. Compensation may be a prolonged process due to the relatively slow rates of tree growth and recruitment. Indeed, we did find a consistent pattern of increased compensatory growth from non-host trees with the age of pest infestation, though this was a prolonged process delayed by as much as 2-5 decades (**SI Appendix, Fig. S3**). This agrees with previous studies concluding that compensatory tree growth in non-host species may take several decades to recover to pre-infestation biomass levels (6, 9).

While total biomass losses reported here are only a relatively a small percentage of total biomass, it is important to emphasize that the trajectory of future impacts of these pests can be anticipated to increase as most of the damaging pests analyzed here have not invaded the full ranges of their hosts (**Table 1**). Based on the ongoing range expansion of the three selected pest species (**Fig. 2**) and among the 15 major pests, it is evident that many have not yet fully invaded the ranges of their hosts (**SI Appendix, Fig. S1**). Second, for areas that have already been invaded by any of these pests (except chestnut blight), there are still large amounts of host biomass that remains and potentially at risk by these pests in the future. As shown in **Figs. 2 & 3**, additional mortality can be anticipated to be caused by these pests in their invaded areas. Third, given the current rate of approximately 2.5 nonindigenous forest insects establishing per year (11), additional non-native pest species are likely to establish in the future (28-30). There is also the potential for climate change to interact with insect and disease invasions in ways that result in increased spread and additional tree stress (31), causing higher mortality (32). We also note that results presented here indicate that impacts of forest insect invasions on biomass loss are substantial, though we made no attempt to quantify their economic value. In the future, non-native pests could be found to cause additional losses to other ecosystem services that have not yet been quantified on a regional level.

Our results indicate that forest pest invasions, driven primarily by globalization, are causing an annual loss of 5.53 TgC live biomass, representing a substantial shift in carbon dynamics. In addition, 41.1% of the total live biomass in conterminous USA forests is at risk by invasion from currently established pest species. Given the continued range expansion of existing pests and the anticipated establishment of new non-native pests in the future, proactive policies aimed at mitigating future invasions are likely to yield secondary benefits of reducing greenhouse gas emissions.

MATERIALS AND METHODS

Forest inventory data We used forest inventory data from the USDA Forest Inventory and Analysis (FIA) program to study the impacts of pests on tree mortality . FIA data are archived in the publicly available FIA Database (FIADB) and updated on a continual basis (https://apps.fs.usda.gov/fia/datamart/CSV/datamart_csv.html). A copy of the data used in this study was in the Purdue University Data Archive (PURR; DOI: 10.4231/82EJ-B095). The FIA sampling design is based on a tessellation of the US into hexagons approximately 2,428 ha in size with at least one permanent plot established in each hexagon. Tree and site attributes (e.g., species, diameter, etc.) are measured on plots falling in forest land; at each plot, measurements are taken in four 7.32-m fixed-radius subplots. About 10-20% of plots are surveyed in each state annually and each plot is re-measured every 5 to 10 years, which provides a statistically robust sampling program for direct estimation of tree mortality rates. Tree inventory data used in this study were extracted in April 2017, which included all inventory data on 92,978 field plots for 2015 and prior years (see Bechtold and Patterson (33) for detailed inventory methodology). These plots were initially surveyed during 2004-2008 and were re-measured during 2009-2015, depending on FIA survey schedules. For each species, we extracted total growing-stock volume, annual mortality volume, and dry biomass at the county level using standard FIA queries and estimation methodology following Bechtold and Patterson (33). Structured Query Language

(SQL) code for extracting data from the FIADB is archived in PURR (DOI: 10.4231/82EJ-B095) and instructions on how to run the SQL code can be found in **SI Appendix** (supplementary text). All forests, regardless of management history (e.g., natural vs. managed), were included in our analyses as pests are likely to attack all forest areas.

Non-native pest data Our non-native pest data are from the Forest Service Alien Forest Pest Explorer (AFPE) database. The AFPE database contains current distribution data for 69 non-native forest insects and 14 pathogen species at the county level based on field-reporting made by Federal and State forest health specialists (see Liebhold et al. (13) for a more detailed description of the database). In this study, we first reviewed the impacts on tree mortality for all 83 species (**Dataset S1**). We then focused on quantifying the biomass impacts by 15 pests that our review indicated as causing extensive tree mortality. Note that *Anoplophora glabripennis* (Asian long-horned beetle), which can cause substantial mortality, was not included in our analysis due its limited geographical distribution (**SI Appendix, Fig. S1**) and ongoing eradication efforts. Pest distribution data were extracted in April 2017, which included all known pest ranges in December 2015. County-level distributions of the presence of each pest species can be downloaded via PURR (DOI: 10.4231/82EJ-B095).

Mortality, growth, and removal rate calculations Using FIA data, we estimated average annual mortality for host tree species of each of the 15 damaging non-native pests by comparing the status (live or dead) of each tree between successive plot visits (approximately 5-7 years in the eastern US and 10 years in the western US). Host tree species for each pest are based on Liebhold et al. (13) and are available to download via PURR (DOI: 10.4231/82EJ-B095). Using re-measured plots (re-measurement ending in 2015), annual rates were computed as proportions of live biomass at the time of the initial survey (i.e., annual mortality, growth, or removals biomass / live biomass at time 1). We utilized calculations as described for the estimation of ratios in Bechtold and Patterson (33) where the numerator was the estimated mortality, growth, or removals biomass total and the denominator was the estimated standing live biomass (at time 1).

In general, counties are the individual populations of interest (i.e., the basic building blocks for estimation). Counties are often divided into subpopulations that are processed independently, such as when part of a county has an intensified sampling grid that differs from the rest of the county (e.g., intensified grid on National Forest System land). Since populations and subpopulations are mutually exclusive, the estimated totals are additive. Similarly, variance estimates are also additive because different populations and subpopulations are independent. Population totals are calculated by summing attributes to the plot level and then averaging at the stratum level to yield the stratum mean and estimated variance (see page 54 -57 of Bechtold and Patterson (33) for detailed equations used in our calculation). Standard deviations were computed by dividing the estimates into the square root of the variance. General instructions for generating estimates from this paper are included in **SI Appendix** (supplementary text). Additional examples for generating population estimates using the FIADB can be found in Pugh et al. (34).

Annual mortality, growth, and removal rates (biomass per year) for each host species or group of host species were estimated for the invaded and un-invaded areas of each species. FIA does not ascribe mortality to any specific cause so we used mortality rates in uninvaded areas for each host species or group of host species as “background” rates against which mortality rates in the invaded area were compared in order to detect and estimate elevated mortality caused by each pest invasion. To minimize the potential impacts of spatial heterogeneity on computing mortality rates of invaded and uninvaded areas, we only used uninvaded counties in the eastern USA if the pest has mainly invaded in the east, uninvaded counties in the western USA if the pest has mainly invaded in the west, or country-wide if the pest has a wide distribution (**SI Appendix, Fig. S1** for pest distribution). We then multiplied the total host biomass mortality in the invaded range by the difference in mortality rate between invaded and uninvaded areas for each pest to estimate total pest induced biomass losses. We used Welch's *t*-test to test for differences in growth, mortality, and removal rates within vs. outside the invasion ranges and host vs. non-hosts. Given the large number of *t*-tests we performed, we used a more conservative measure ($P < 0.001$) to evaluate the statistical significance of the observed differences.

Temporal dynamics To provide an understanding of the temporal dynamics of pest induced mortality, we further analyzed host mortality rates for three pests for which additional spatiotemporal data were available on their historical invasion spread (range expansion). We only used mortality rates from one time interval but we compared those "current" mortality rates between different subsets of data. These three pests were beech bark disease, hemlock woolly adelgid, and emerald ash borer. For each species, we grouped areas (counties) according to the year since initial invasion. Host species mortality rates within each temporal bin were then summarized for each pest. County level data on historical spread are provided in **Fig. 2**.

In addition, we analyzed the mortality rate for gypsy moth, for which historical distribution of defoliation was available. Note that defoliation does not necessary result in tree mortality, but creates a stress that can mediate mortality events (35). Defoliation map data consisted of aerial surveys compiled by the US Forest Service Forest Health Monitoring program (9). These data were used to classify land areas with 0, 1, 2 and >2 years of defoliation from 1994-2010 as sequential 2 x 2-km raster layers, and we computed rates of host mortality in each of the four land area classes.

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Figure Captions

Figure. 1. Mean annual mortality rate (±SD) of host and non-host tree species in invaded and non-invaded regions for each of the 15 most damaging pests in conterminous USA forests. Mortality is expressed as a percentage of initial biomass. Dashed red line indicates the annual average mortality rate (1.17%) across USA forests. Mortality in the uninvaded area consisted of estimated host mortality occurring outside the current invasion range of a given non-native pests in the eastern, western, or the entire conterminous USA according to the pest distribution in **SI Appendix, Fig. S1**. *Entire host range is invaded by exotic pests.

Figure. 2. Spatiotemporal progression of the invasion process and associated mortality rates (±SD) for beach bark disease (BBD), hemlock woolly adelgid (HWA), and emerald ash borer (EAB) estimated in areas with various ranges of initial invasion. Mortality is expressed as a percentage of initial biomass. Mortality rates were all significantly higher in invaded than uninvaded areas ($P < 0.001$), except for HWA plots that are most recently invaded.

Figure. 3. Number of years of gypsy moth defoliation (1994 - 2010) and levels of average host mortality rates occurring in areas with varying numbers of years of defoliation.