Biomass losses resulting from insect and disease invasions in US forests

Songlin Fei[a,1], Randall S. Morin[b], Christopher M. Oswalt[c], and Andrew M. Liebhold[d]

[a]Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47906; [b]Northern Research Station, Forest Service, US Department of Agriculture, Newtown Square, PA 19073; [c]Southern Research Station, Forest Service, US Department of Agriculture, Knoxville, TN 37919; and [d]Northern Research Station, Forest Service, US Department of Agriculture, Morganton, WV 26505

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Worldwide, forests are increasingly affected by nonnative insects and diseases, some of which cause substantial tree mortality. Forests in the United States have been invaded by a particularly large number (>450) of tree-feeding pest species. While information exists about the 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 United States to estimate biomass loss associated with elevated mortality rates caused by the 15 most damaging nonnative forest pests. We find that these species combined caused an additional (i.e., above background levels) tree mortality rate of 5.53 TgC per year. Compensation, in the form of increased growth and recruitment of nonhost 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 United States is at risk of future loss from these 15 pests. These results indicate that forest pest invasions, driven primarily by globalization, represent a huge risk to US forests and have significant impacts on carbon dynamics.

pest invasion | carbon | forest ecosystem | biomass

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 ∼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, driven primarily by globalization, represents another way in which humans are altering ecosystem functioning worldwide (3). Nonnative pests (insects and diseases) can have multifaceted short-term and long-term impacts on forest ecosystems, ranging from decreased forest productivity to the modification of biogeochemical cycling (4) and geomorphic processes (5), all of which can be detrimental to the various ecosystem services that forests provide (6, 7). Despite the existence of large-scale pest-specific impact assessments (8–10), empirical measures of the aggregate impacts of all nonnative pest species on mortality and carbon budgets in forests are limited.

North American forests have experienced numerous invasions by nonnative insects and tree pathogens; more than 450 forest insect and pathogen species are known to be established in the conterminous United States (11–13). The majority of nonnative pests that have become established have had minimal impacts on forests (11), but unfortunately, 83 of these species are known to 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 nonnative forest insect and disease species currently established in the continental United States and estimate the rate at which live tree biomass is being converted to dead materials (carbon source) by the 15 species known to have the greatest impacts on tree mortality. We used data from 92,978 field plots sampled by the US 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 were to estimate the increased mortality and associated live biomass losses caused by nonnative forest pest invasions, quantify the temporal dynamics of nonnative pest-induced mortality, and quantify the host tree live biomass at risk for impacts from all major nonnative 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 nonnative pests recognized to cause reportable damage in the conterminous United States, 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. (Dataset S1 presents the entire list.) Species reviewed were from Asia (35%), Eurasia (29%), Europe (29%), or Australia (7%). We identified 15 species (9 pathogens, 4 sap-feeders, 1 wood/phloem-borer, and 1 foliage-feeder) that cause substantial tree mortality based on information in the literature (Dataset S1). The geographical distributions of these 15 pests

Significance

Forests provide a wide variety of vital ecosystem services but are increasingly affected by anthropogenic disturbances. Among these, invasions by nonnative pests can adversely affect ecosystem services. Comprehensive estimates of the impacts of nonnative pest on forest biomass loss are limited, however. Using more than 92,000 field plots, we quantified pest-induced biomass loss across the conterminous United States for the first time. We show that invasive pests are causing significant shifts in carbon dynamics in US forests. In addition, >40% of the total live biomass in US forests is at risk for invasion by currently established pest species. Our findings are of potential significance in justifying the selection of future policy options and in future carbon dynamics modeling research.

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[1]To whom correspondence may be addressed. Email: sfei@purdue.edu.

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and their corresponding hosts are shown in *SI Appendix*, Fig. S1. Eleven of these 15 damaging pests have invaded primarily the eastern United States. Nearly all of the 15 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. We found that among the 15 pests recorded in the literature as causing substantial tree mortality, 9 caused host tree mortality rates significantly elevated ($P < 0.001$) above their background levels during the study period (Fig. 1). Ten of the nonnative pests caused significantly higher host mortality 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 4 pests caused an annual conversion of >0.7 TgC of live biomass to dead materials in excess of their host background mortality. The 3 most damaging pest species, in terms of high annual mortality rate in the invaded range, expressed as a percentage of total host biomass loss, were 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*) were associated with a mortality rate exceeding twice the national annual average. 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 before the survey period.

During the same time period, no consistent compensatory growth pattern was observed in nonhost tree species located on plots invaded by each of the 15 pests (*SI Appendix*, Fig. S1). Comparison of gross growth rates for host and nonhost species on invaded plots showed that nonhost trees had higher growth rates than host trees in plots invaded by 8 of the pest species but lower rates on plots invaded by the other 7 species. Assessment of growth rates for nonhost species inside vs. outside the invaded range of each pest also did not reveal evidence of consistent nonhost tree growth compensation for host tree mortality; gross growth rates of nonhost trees were higher in plots inside the invaded ranges of 4 pests but higher in plots outside of the invaded ranges of 8 pests.

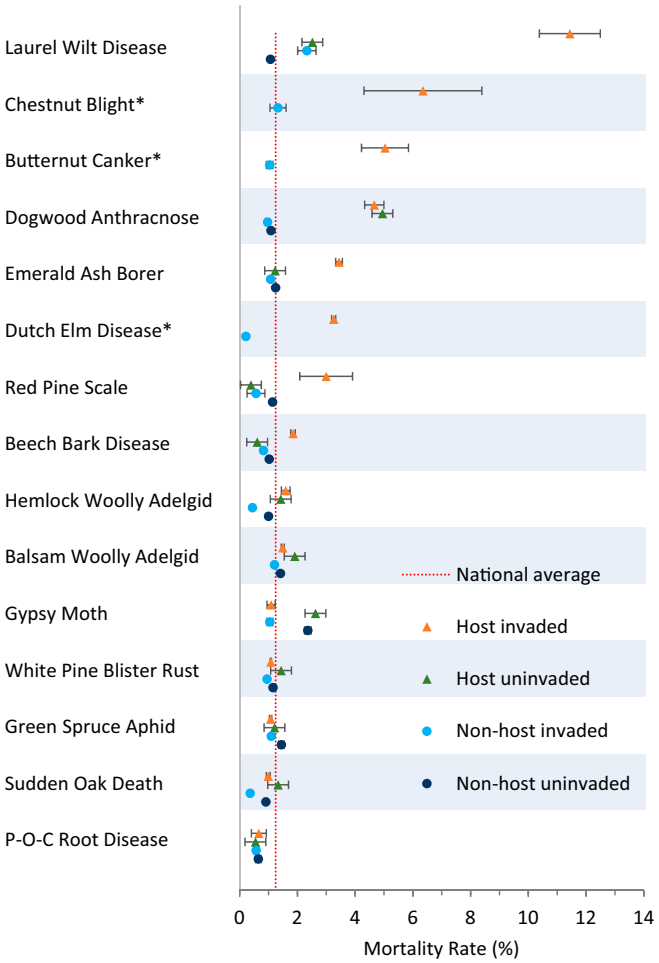

Fig. 1. Mean annual mortality rate (± SD) of host and nonhost tree species in invaded and noninvaded regions for each of the 15 most damaging pests in conterminous US forests. Mortality is expressed as a percentage of initial biomass. The dashed red line indicates the annual average mortality rate (1.17%) across US forests. Mortality in the uninvaded areas consists of estimated host mortality occurring outside the current invasion range of a given nonnative pests in the eastern, western, or the entire conterminous United States according to the pest distribution shown in *SI Appendix*, Fig. S1. *Entire host range is invaded by exotic pests.

Pest-Related Tree Mortality Trends. Analyses of temporal trends in impacts from 3 selected damaging pests (EAB, HWA, and BBD) show 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 was not significantly elevated in the first 3 y following first EAB detection, it quickly increased to twice the background mortality by 5 y after detection and reached >15% (of live biomass) in areas with >12 y since first detection. Mortality rates associated with HWA invasion are lower than those with EAB but exhibit a similar trajectory. On average, annual hemlock mortality rate nearly tripled in areas with >10 y since initial detection compared with areas where HWA is absent (1.9% vs. 0.5%), and was 7 times higher in areas with >35 y since initial HWA detection. Host mortality associated with BBD invasion exhibits different temporal trends than those associated with EAB and HWA. Annual beech mortality rate was the highest during the first 10 y after invasion and subsequently remained at approximately 2% of live biomass. While no compensatory growth was observed in nonhost trees when averaged across the entire invaded range of each pest (*SI Appendix*, Fig. S2), there was consistently increased growth in nonhost trees in regions that had been invaded by pests for 2 to 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 is indicated from a comparison of invaded and uninvaded counties (Fig. 3). There was no apparent increase in tree mortality in areas invaded by gypsy moth compared with 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 2 × 2-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 to 2010), but this represents a relatively small fraction of the invaded area, and impacts are strongly diluted out over the entire invaded range.

Pest-Related Overall Mortality Impacts. Combined pest-induced live biomass loss (i.e., overall host mortality minus background mortality in the invaded area) for all pests was ~5.53 TgC

Table 1. Host biomass and mortality rate in invaded and uninvaded ranges by each nonnative pest

Pest common name	Host biomass, TgC		Mortality rate, %			
	Invaded	Uninvaded	Invaded	Uninvaded	% Invaded	Annual Loss*, TgC
Balsam woolly adelgid	317.17	292.47	1.494	1.905	52.0	—
Beech bark disease	90.22	63.71	1.849	0.606	58.6	1.121
Butternut canker†	1.09	—	5.033	—	100.0	0.042
Chestnut blight†	0.03	—	6.348	—	100.0	0.002
Dogwood anthracnose	0.93	2.31	4.663	4.946	28.8	—
Dutch elm disease†	114.38	—	3.256	—	100.0	2.386
Emerald ash borer	81.87	210.81	3.442	1.228	28.0	1.813
Green spruce aphid	146.77	280.30	1.089	2.624	34.4	—
Gypsy moth	897.77	2,174.13	1.079	1.434	29.2	—
Hemlock woolly adelgid	59.40	58.03	1.596	1.422	50.6	0.103
Laurel wilt disease	0.55	18.14	11.437	2.517	2.9	0.049
Port Orford cedar root disease	2.77	0.27	0.664	0.545	91.1	0.003
Red pine scale	0.28	52.60	2.996	0.390	0.5	0.007
Sudden oak death	76.68	547.60	0.989	1.332	12.3	—
White pine blister rust	236.46	17.02	1.071	1.205	93.3	—

*Annual elevated mortality of host biomass in invaded region above background mortality for each pest species.
†Entire host range is invaded by exotic pests.

per year (Table 1). This estimated annual biomass loss caused by these pests is a relatively small fraction (0.04%) of the total live biomass in the conterminous United States (12,643 TgC of dry biomass). (Note that this number is slightly lower than the most recent SOCCR2 estimate of 14,182 TgC, which covers the entire United States; ref. 14.) However, the 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 United States is equivalent to 3.5% of live biomass lost to forest removals (157 TgC per year based on 1.25% annual removal rate; *SI Appendix*, Fig. S2) across the same area. The amount of biomass loss due to nonnative pest-induced mortality, which was concentrated primarily in the eastern United States, is similar in magnitude to that of trees killed by fire (5.4 to 14.2 TgC per year) and of trees killed by all native bark beetles across the western United States (1.8 to 24.4 TgC per year) (15).

Moreover, there are substantial amounts of host biomass in both invaded and uninvaded ranges that are at risk for 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, 3 have invaded 50% to 60% of their host biomass, and the rest have invaded <35% of their corresponding host biomass. For gypsy moth alone, there are 898 TgC of 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 of 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 in *Quercus* spp.), the total amount of host biomass at risk for damage from these 15 pests is approximately 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 United States.

Discussion

Our study quantifies substantial increases in regional rates of tree mortality caused by insect and disease invasions in the conterminous United States, converting live carbon to dead material. We also demonstrate that large amounts of host biomass are at risk for future damage caused by these pests. Our results presented here provide key information on the impact of nonnative pests on carbon budgets. They also provide crucial information on nonnative pest impacts that could inform the selection of future biosecurity measures targeting exclusion of additional pests in the future, as well as necessary funding levels for treatment and control measures for established pests.

The methods that we used here to quantify the 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 because most of their hosts already died a long time ago. For example, American chestnut (*Castanea dentata*) used to dominate many eastern North American forests, composing more than one-third of the pollen assemblage in some stands (16) and up to 600 t/ha of biomass before the invasion and spread of chestnut blight (17), but now constitutes only 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 have introduced errors in our attribution of elevated mortality to pest invasions based on comparisons 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 a significantly elevated host mortality rate of 2.4% after 2 y of gypsy moth defoliation and >3.1% in areas with more defoliation (Fig. 3). Although 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 accounted for tree mortality and did not capture crown or root dieback or reductions in tree growth, which may be substantial (20, 21). We also did not attempt to estimate the release of carbon to the forest floor as a result of defoliation events (4, 22). Clark et al. (23) demonstrated that gypsy moth defoliation caused marked changes in local carbon flux. Moreover, pest-related mortality rates may be underestimated due to salvage removal (i.e., harvesting of host trees before the next inventory), which has been observed in regional studies (24). However, we did not observe substantial differences in the rates of host biomass harvested within and outside currently invaded ranges for most of the pests in our rangewide analyses

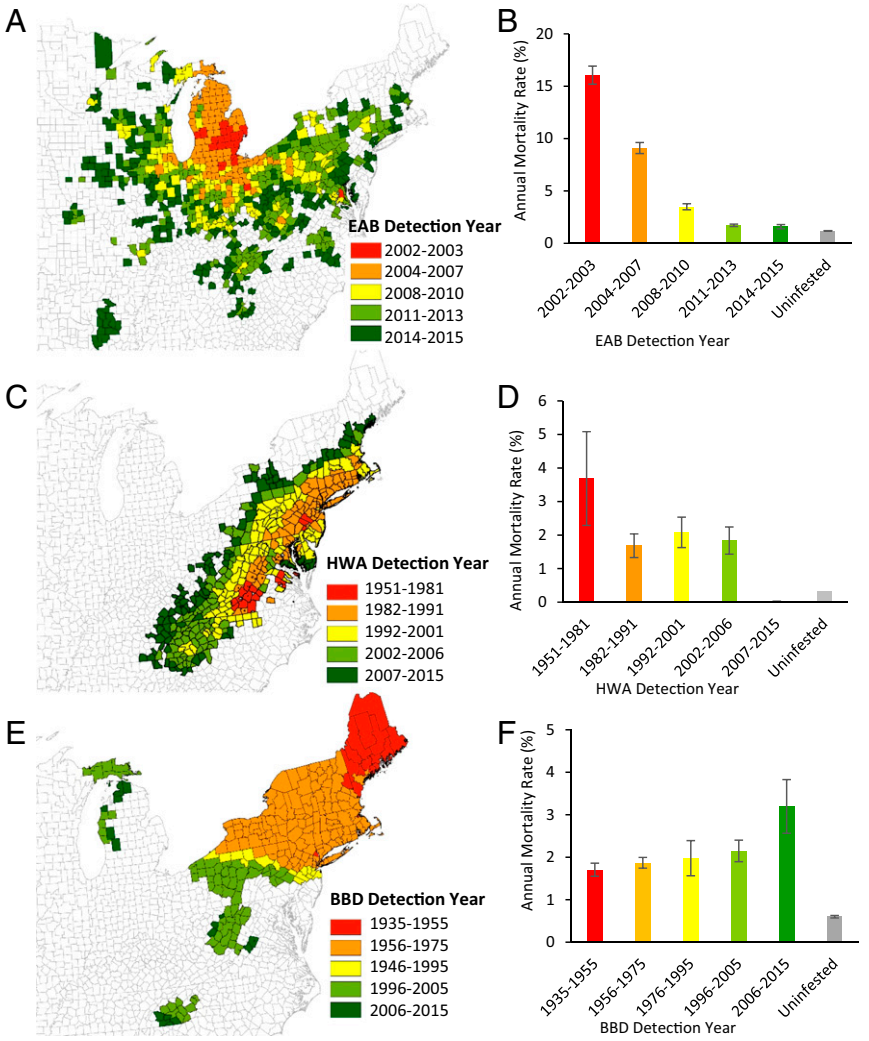

Fig. 2. Spatiotemporal progression of the invasion process (*A*, *C*, and *E*) and associated mean mortality rates (± SD) (*B*, *D*, and *F*) estimated in areas with various ranges of initial invasion for EAB, HWA, and BBD, respectively. Mortality is expressed as a percentage of initial biomass. Mortality rates were all significantly higher in invaded areas compared with uninvaded areas ($P < 0.001$), except in HWA plots that were most recently invaded.

(*SI Appendix*, Fig. S2). Finally, the inventory data analyzed here did not include samples from urban areas; our estimates of total biomass loss are underestimated because they do not include losses from urban tree mortality.

Our estimated annual loss of 5.53 TgC of 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 intraecosystem carbon flux, and not an ecosystem scale net

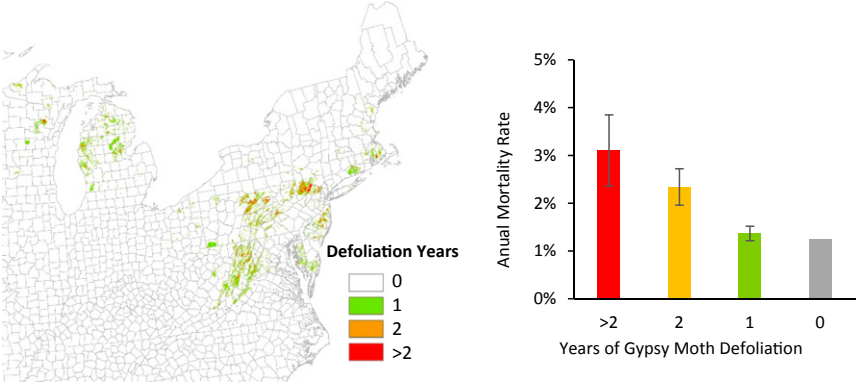

Fig. 3. Number of years of gypsy moth defoliation (1994 to 2010) and levels of average host mortality rates occurring in areas with varying durations of defoliation.

CO_2 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 microorganisms (25, 26). Decomposition rates vary depending on forest type 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 nonhost 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 nonhost trees with the age of pest infestation, although this was a prolonged process, delayed by as much as 2 to 5 decades (*SI Appendix*, Fig. S3). This agrees with previous studies concluding that compensatory tree growth in nonhost species may take several decades to recover to pre-infestation biomass levels (6, 9).

While the total biomass losses reported here are only a relatively a small percentage of the 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 3 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). Moreover, for areas that have already been invaded by any of these pests (except chestnut blight), there remain large amounts of host biomass that are potentially at risk from these pests in the future. As shown in Figs. 2 and 3, additional mortality can be anticipated to be caused by these pests in their invaded areas. Finally, given the current rate of establishment of ~2.5 nonindigenous forest insects per year (11), additional nonnative 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 (19), causing higher mortality (31). We also note that the results presented here indicate that the impacts of forest insect invasions on biomass loss are substantial, although we made no attempt to quantify their economic value. In the future, nonnative 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 of live biomass, representing a substantial shift in carbon dynamics. In addition, 41.1% of the total live biomass in conterminous US forests is at risk of invasion from currently established pest species. Given the continued range expansion of existing pests and the anticipated establishment of new nonnative 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 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 is available in the Purdue University Data Archive (PURR; doi: 10.4231/82EJ-B095). The FIA sampling design is based on a tessellation of the United States into hexagons of ~2,428 ha with at least 1 permanent plot established in each hexagon. Tree and site attributes (e.g., species, diameter) are measured in plots falling in forest land; in each plot, measurements are taken in four 7.32-m fixed-radius subplots. Roughly 10% to 20% of these plots are surveyed in each state annually, and each plot is remeasured every 5 to 10 y, which provides a statistically robust sampling program for directly estimating tree mortality rates. Tree inventory data used in this study, which included all inventory data on 92,978 field plots for 2015 and previous years, were extracted in April 2017. The inventory methodology is described in detail elsewhere (32). These plots were initially surveyed during 2004 to 2008 and were remeasured during 2009 to 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 (32). 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 are provided in *SI Appendix*. All forests, regardless of management history (e.g., natural vs. managed), were included in our analyses, because pests are likely to attack all forest areas.

Nonnative Pest Data. Our nonnative pest data were obtained from the Forest Service Alien Forest Pest Explorer (AFPE) database. The AFPE database contains current distribution data for 69 nonnative forest insects and 14 pathogen species at the county level based on field reporting done by federal and state forest health specialists. The database is described in more detail elsewhere (13). 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 identified as causing extensive tree mortality. Note that *Anoplophora glabripennis* (Asian long-horned beetle), which can cause substantial mortality, was not included in our analysis because of its limited geographical distribution (*SI Appendix*, Fig. S1) and ongoing eradication efforts. Pest distribution data, which included all known pest ranges in December 2015, were extracted in April 2017. County-level distributions of the presence of each pest species can be downloaded from 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 nonnative pests by comparing the status (live or dead) of each tree between successive plot visits (approximately 5 to 7 y in the eastern United States and 10 y in the western United States). Host tree species for each pest are based on the work of Liebhold et al. (13) and are available to download from PURR (doi: 10.4231/82EJ-B095). Using remeasured plots (remeasurements 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 of biomass/live biomass at time 1). We used calculations as described for the estimation of ratios by Bechtold and Patterson (32), in which the numerator was the estimated total mortality, growth, or removal of biomass 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; detailed equations used in our calculations are available elsewhere (32, pp 54–57). SDs 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*. Additional examples for generating population estimates using the FIADB can be found in Pugh et al. (33).

Annual mortality, growth, and removal rates (i.e., biomass per year) for each host species or group of host species were estimated for the invaded and uninvaded 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 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 used uninvaded counties in the eastern United States only if the pest had invaded mainly in the east, uninvaded counties in the western United States only if the pest had invaded mainly in the west, or country-wide if the pest had a wide distribution (*SI Appendix*, Fig. S1). We then multiplied the total host biomass mortality in the invaded range by the difference in mortality rates 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

in hosts vs. nonhosts. Given the large number of *t* tests that we performed, we used a more conservative measure ($P < 0.001$) to evaluate the statistical significance of the observed differences.

Temporal Dynamics. To provide insight into the temporal dynamics of pest-induced mortality, we further analyzed host mortality rates for 3 pests for which additional spatiotemporal data on their historical invasion spread (i.e., range expansion) were available: BBD, HWA, and EAB. We used mortality rates only from a single time interval but compared those "current" mortality rates between different subsets of data. For each species, we grouped areas (i.e., 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 data were available. Note that defoliation does not necessary result in tree mortality, but creates a stress that can mediate mortality events (34). 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 y of defoliation from 1994 to 2010 as sequential 2 × 2-km raster layers, and rates of host mortality in each of the 4 land area classes were computed.

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