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Abstract

Quantifying economic damages caused by invasive species is crucial for cost-benefit analyses of control measures. Most studies focus on short-term damage estimates, but evaluating exclusion or prevention measures requires estimates of total anticipated damages from the time of establishment onward. The magnitude of such damages critically depends on the timing of damages relative to a species' arrival because costs are discounted back to the time of establishment. Using theoretical simulations, we illustrate how (*ceteris paribus*) total long-term damages, and hence the benefits of prevention efforts, are greater for species that a) have short lags between introduction and spread or between arrival at a location and initiation of damages, b) cause larger, short-lived damages (as opposed to smaller, persistent damages), and c) spread faster or earlier. We empirically estimate total long-term discounted impacts for three forest pests currently invading North America – gypsy moth (*Lymantria dispar*), hemlock woolly adelgid (*Adelges tsugae*), and emerald ash borer (*Agrilus planipennis*) – and discuss how damage persistence, lags between introduction and spread, and spread rates affect damages. Many temporal characteristics can be predicted for new invaders and should be considered in species risk analyses and economic evaluations of quarantine and eradication programs.

Highlights:

- Exclusion and eradication benefits depend on total long-term invasion damages.
- We model the effects of invasion temporal characteristics on long-term damages.

- We empirically estimate total damages for three important forest pests.
- Invasion lags, damage persistence, and spread rates critically affect total damages.
- Risk and exclusion assessments and should consider temporal aspects of invader impacts.

Keywords: biological invasion; economic impact; damages; gypsy moth (*Lymantria dispar*); hemlock woolly adelgid (*Adelges tsugae*); emerald ash borer (*Agrilus planipennis*)

Introduction

Increasing international trade and travel have had an unintended consequence: the accidental transport of species out of their native ranges into novel environments (1, 2). Although the vast majority of nonnative species are rarely even noticed, a few species have had remarkable impacts that have transformed ecosystem properties, often with severe effects on societal uses of those ecosystems (3, 4, 5). This phenomenon has repeated itself in virtually every corner of the world as nonnative plants, animals, and microorganisms have invaded marine, aquatic, and terrestrial ecosystems.

Quantifying economic impacts is crucial to better understanding invasions and evaluating solutions. Ultimately, measures taken to mitigate invasion impacts are justifiable only if the costs of management are smaller than the impacts avoided (6). Efforts have thus been made to quantify the impacts of individual species (e.g., 7, 8, 9) as well as guilds of species (e.g., 10, 3), and studies have considered costs associated with a range of damage types that include both market and nonmarket values.

Space and time are recognized as critical to the impacts of invasions because species spread over time and affect increasingly large areas, with damages often accruing over long time horizons. Previous work has highlighted some of the temporal factors affecting the expected damages from an invasion (e.g., 11), with particular attention to how the rate of invasion spread can influence damages, and hence the economic benefit of eradicating an incipient population (12, 13, 14, 15). For example, the benefit of eradication is generally greater for species that spread quickly because less time separates the establishment of the species and the timing of its impacts, so total damages, which could be avoided through eradication, are less attenuated when discounted back to the time of nascent population formation. Similarly, the present value of expected damages

and the benefits of eradication or prevention are also affected by the geometry and total area of the invasion region and by the existence of constant versus variable rates of spread (15, 16, 17).

Additional spatial dynamic aspects of invasions also may profoundly influence impact costs, such as the distribution of resources relative to the location of establishment and spread of an invader. For species that arrive farther from at-risk resources, delays before resources are affected will be longer and will diminish the value of impacts discounted back to the initiation of the invasion (17, 18, 19). The spatial distribution of resources also can affect the pattern and rate of species spread (e.g., 19). Thus, economic impacts will vary through time and across space as species expand their ranges across regions that vary in their economic value and their susceptibility to the species.

Because these space-time patterns can be complex and require knowledge of long-term spread patterns as well as local damages, many studies have simplified the estimation of invader impacts by considering specific intervals of time. For example, Aukema et al. (3) estimated the impacts of individual invading forest insect species during “typical” 10-year periods. Others focus on average per unit area damages (e.g., 10).

Such approaches have limitations. Most importantly, short-term and local estimates generally are not informative for evaluating the benefits of preventing pests from becoming established by preventing their arrival (e.g., via quarantine treatments) or eradicating newly established populations. Evaluating the benefits of such measures requires quantifying the total anticipated impacts of a species as it spreads through its new range, beginning from the time of its establishment.

In this work we build on existing research to explore a more comprehensive set of factors that influence the timing of damages, and hence the long-term impacts of an invasive species and the

benefit of its exclusion through eradication or prevention. In addition to spread rates, invasion range sizes, and geographical distributions of resources, we evaluate the influence of invasion and damage lags and the persistence of impacts in an invaded region.

Newly established populations may remain at relatively low densities without spreading for many years. Although such “invasion lags” (21) are common in nature, the processes responsible for them often are not well understood. In some systems, selection for greater fitness occurs during the period after establishment, and the lag in population growth may result from slow genetic changes in the population (22). Lags also may result from low population growth at low densities associated with Allee effects (23). Such lags delay the onset of damages following invader arrival.

Also affecting the temporal distribution of impacts, some invaders may cause impacts in perpetuity following establishment at a specific location, while the impacts of other species may be transient (24). For example, the invasion wave of the chestnut blight fungal pathogen, *Cryphonectria parasitica*, which spread through North America from 1910 to 1950, was associated with nearly 100% mortality of American chestnut, *Castanea dentata* (25). Once the pathogen was established in a stand, chestnuts were eliminated within 10 to 20 years. Although the ecological impacts and “existence value” losses from American chestnut death can persist, the greatest economic impacts of the blight (e.g., loss of timber market value) spanned only a brief period following invasion at any one location. In contrast, other invading pests, such as the gypsy moth, *Lymantria dispar*, can cause persistent damages. Once gypsy moths establish in an area, recurrent outbreaks continue indefinitely (26). Furthermore, the persistence of damages depends on both a species’ interaction with its environment and the human response to its arrival, such as through adaptation or control (27).

Here we explore how various temporal distributions of invasion impacts translate into discounted impacts that would be averted through successful prevention. We first explore these temporal impacts using theoretical simulations that examine the effects of damage persistence, spread and damage lags, patterns of spread, and discount rate on total invasion impacts. We then empirically estimate damages over time and total long-term impacts for three forest insect species that currently are invading North America: the gypsy moth (*Lymantria dispar*), the hemlock woolly adelgid (*Adelges tsugae*), and the emerald ash borer (*Agrilus planipennis*). Because these species vary in their damage persistence, their lag between introduction and spread, and their rates of spread, they provide useful examples for illustrating some of the temporal aspects explored in the theoretical models. They are the most damaging forest pests in the United States within their respective feeding guilds, and we focus our analyses on the largest single type of damage caused by each species: residential property value loss for hemlock woolly adelgid and gypsy moth, and community expenditures for emerald ash borer (3). We evaluate the impact of invasion lags on total damage estimates by comparing the expected net present value of damages for each pest from its time of introduction versus from the time when damages first began to accrue.

Methods

Theoretical models

Using a simple theoretical model, we illustrate the effects of spread velocity, lags, damage persistence, and discount rate on the temporal pattern and total value of invasion impacts. We consider an invasion spread process that includes a lag between species introduction and the initiation of spread. Invasion spread then continues until the species has spread through its entire new range. We employ a conceptual model of spread that represents the invasion as a circular population that grows at either a constant or an increasing radial rate of spread. These two spread

patterns capture the implicit dynamics of a wide range of spread processes (28). A constant radial rate of spread can result from a reaction-diffusion spread process, and an increasing radial rate of spread can result from various processes, including stratified diffusion or other forms of long-distance dispersal that lead to the founding of new colonies that accelerate spread (Fig. 1a,b). Various functional forms can be used to represent an increasing radial rate of spread. For simplicity, we assume a linearly increasing rate.

The invasion radius at t years following introduction for an invasion with potential range size A is calculated as follows:

$$radius(t) = \begin{cases} 0 & t \leq lag1 \\ v_0(t - lag1) + v_1(t - lag1)^2 & lag1 < t \leq T_{max} \\ \sqrt{A/\pi} & t \geq T_{max} \end{cases} \quad (1)$$

where $lag1$ is the lag period before spread begins and T_{max} is the time it takes for the invasion to spread through its entire potential range from the time of introduction. The invasion area I at time t can be calculated as $I(t) = \pi * radius(t)^2$.

We assume constant marginal (per area) damages, allow a delay, $lag2$, between the arrival of an invasion at a location and the commencement of damages at that location, and assume damages persist for P years after they begin at a location. To facilitate comparison of damages from invasions with different persistence, we measure damages D as the total undiscounted damages at a location ($\$/km^2$), such that damages per time period at a location ($\$/km^2/year$) equal D/P .

This model allows that damages may accrue in only a portion of the invaded area at a given time, dependent on delays, persistence, and the timing of invasion arrival at different locations. For example, a location that is not invaded until time t_a , will begin accruing damages at time $t_a +$

$lag2$ and will accrue damages in each year until time $t_a + lag2 + P$, at which time damages drop to zero at that location. At other locations, damages may occur earlier or later.

Total damages at time t can be calculated as follows:

$$Damages_t = \sum_{s=t-lag2-P-1}^{t-lag2} D/P * NewAreaInvaded(s) \quad (2)$$

where $NewAreaInvaded(t)$ is the new area invaded at time t .

The total present value of expected damages (i.e., the sum of discounted damages over time from the start of the invasion) is as follows:

$$PV_Damages_{total} = \sum_{t=1}^{\infty} \sum_{s=t+lag2}^{t+lag2+P-1} \frac{(D/P)*NewAreaInvaded(t)}{(1+r)^s} \quad (3)$$

where $1/(1+r)^s$ is the discount factor and r is the discount rate.

We refer to the constant radial spread model as model A ($v_l = 0$) and consider two different parameterizations of the increasing radial spread rate model to facilitate comparison. The first, which we refer to as model B, employs the same constant radial spread rate parameter (v_0) as model A. This spread pattern represents an invasion with the same local rate of spread as under model A, but subject to long-distance dispersal that leads to an increasing rate of spread over time and a faster overall rate of spread (28). In contrast, for Model C, we parameterize spread such that the total time for the invasion to spread through the landscape (T_{max}) is the same as for the constant radial spread model A; thus early spread is slower than for model A, but the average rate of spread is the same. All parameter specifications are shown in Table S1 of the Supplementary Material.

Empirical examples

For each species (gypsy moth, hemlock woolly adelgid, and emerald ash borer), we estimate damages from their time of introduction through 2070 or later, using methods adapted from Aukema et al. (3). Whereas Aukema et al. (3) focused their estimates on impacts during a select 10-year period, we evaluate the impacts of each species over the entire span of its spread, from initial establishment to total saturation of all suitable geographical areas in the eastern United States, accounting for both historical and future spread. For each species, we use a combination of historical data on past spread and predictive models to simulate future invasion spread. We compare several choices of discount rate and also compare how cost estimates differ dependent on whether net present value is calculated from the time of introduction or from the time when damages begin to accrue, which typically corresponds to the time of discovery. This allows us to examine the effect of lags on the estimated total present value of damages for each species. Detailed methods for damage estimation are provided in the Supplementary Material.

Results

Theoretical model

Interactions among spread patterns, damage persistence, and discounting affect temporal damage patterns. Figure 1 illustrates invasion spread and damages for the three spread model specifications and for persistent and nonpersistent damages. The spread patterns for constant radial growth (model A) and increasing radial spread rates (models B and C) are illustrated in Figs. 1a,b. Models A and B have the same initial radial growth rate, but the rate increases over time in model B. The spread rate is initially lower in model C but increases over time until it fills

the potential invasion range in the same amount of time as for model A. For all three models, the total *area* invaded increases at an increasing rate over time (Fig. 1b).

With these spread patterns, damages accrue more quickly for spread model B and later for model C (Figs. 1 c–f). For nonpersistent damages, the nondiscounted damages are proportional to the new area invaded in each time period: they increase over time and then drop to zero when the invasion has spread through its entire potential range (Fig. 1c). In contrast, persistent damages depend on the total area invaded: they increase over time and then are sustained over the duration of persistence (Fig. 1e). When accounting for discounting, however, future damages are attenuated (Figs. 1d,f). The effects of discounting are greatest for spread pattern C, because more damages occur further in the future (because of slower initial spread). Similarly, persistent damages are affected more strongly by discounting because more damages occur further in the future (Fig. 1f).

The total present value of damages, calculated as the sum of discounted damages across time (Eqn 3), is very sensitive to the discount rate and invasion characteristics (Fig. 2). The present values of total damages decrease with increasing discount rate, and are most similar across different spread processes when the discount rate is very low such that the timing of costs matters less (Fig. 2a).

The total present values of damages also decrease with increasing lags, which delay damages such that they are more affected by discounting (Fig. 2b,c). Similarly, total damages decrease with increasing persistence of damages because longer persistence corresponds to more damages further in the future, when they are more strongly affected by discounting (Fig. 2d)¹. The total

¹ Again, our specification assumes that the same total nondiscounted damages at a location are spread out over a longer time period when persistence is greater. If instead we assumed fixed per area damages per year, longer

present value of damages also increases with baseline velocity because more damages accrue sooner.

The final panel (Fig. 2f) shows how total present value damages depend on the maximum range radius of the invader. Total damages increase with maximum range radius for spread models A and B, but they increase and then decrease with increasing range radius for model C. For model A, total damages increase at a decreasing rate with range size because damages that occur farther from the initial invasion site (i.e., when the invasion is larger) accrue later and are thus more discounted. With spread model B, the rate of spread continues to increase over time, countering some of the effects of discounting, such that the total present value of damages continues to increase with increasing maximum range size. In contrast, model C assumes that an invasion takes the same amount of time to spread through the landscape as in model A, despite increasing rates of spread over time. Consequently, with model C the rate of invasion spread begins lower and increases more slowly for invasions unfolding in larger landscapes. Hence, invasion damages are more delayed (and hence more heavily affected by discounting) when unfolding in larger landscapes.

Also of interest is how lags, persistence, spread rate, and invasion size interact with the choice of discount rate to affect the total present value of damages. For all invasions, we expect the total present value of damages to decrease with an increasing discount rate (e.g., Fig. 2a). However, discounting affects values further in the future more than near-term damages. Thus, the temporal pattern of damages, as affected by persistence, lags, etc., influences the effect of discounting. Indeed, higher discount rates induce a greater percentage reduction in the present value of

persistence would lead to higher total damages, but the net present value of damages would increase at a decreasing rate with the length of persistence because of the discounting of additional years of damage.

invasions that have long persistence, long lags, slow spread, or large potential ranges because a larger proportion of damages occurs further in the future (Figure S1 in Supplementary Material).

Empirical results

The timing and pattern of spread vary greatly among gypsy moth, hemlock woolly adelgid, and emerald ash borer. Combined historical and predicted spread patterns for these species are presented in the top row of Fig. 3 (and Figs. S2–4 in Supplementary Material). Gypsy moth invasion is slowly unfolding across multiple centuries, following its initial introduction in 1869 (Fig. 3a) (29), and damages began following a relatively short lag of about 11 years. In contrast, hemlock woolly adelgid experienced a long lag (about 60 years) between its likely original introduction in 1911 and the first observation of damages, in 1971 (30). Spread is estimated to saturate climatically suitable portions of the United States where hosts are present by about 2050, within a century of when damages first began (Fig. 3b). Emerald ash borer invasion is unfolding far more quickly (Fig. 3c). Thought to have established in the early 1990s (31), this species experienced just over a decade's lag before damages were first noticed, and the species has spread rapidly since then. Our model predicts that emerald ash borer invasion will mostly saturate the eastern United States by about 2050, within just over half a century from the time of its introduction.

We model gypsy moth damages as residential damages from periodic defoliation events associated with population outbreaks. Because outbreaks can continue to occur in perpetuity following gypsy moth establishment in an area, nondiscounted annual damages increase over time, generally tracking the total area invaded (Fig. 3d). Hemlock woolly adelgid damages are modeled as a one-time loss in residential property value at the time of hemlock death. Similarly,

emerald ash borer damages are measured as the one-time cost of ash tree removal and replacement when ash trees die—damages that tend to track the new area invaded over time, rather than the total area invaded (Figs. 3e,f). Our damage predictions suggest that peak annual damages for hemlock woolly adelgid occurred a little over a decade ago, and peak annual damages for emerald ash borer are likely to be reached in the coming decade.

The annual discounted damages from each forest pest are greatly attenuated, particularly when discounted back to the time of introduction (Figs. 3g–i). The effects of discounting are particularly evident for gypsy moth: while nondiscounted annual damages are expected to continue to grow over the next several centuries, estimated discounted damages drop to near zero over this time horizon. For each species, discounting damages back to the time of introduction results in substantially lower annual damages than when discounted back only to the year when damages first began to accrue. This impact difference is particularly large for hemlock woolly adelgid, for which the lag between introduction and the beginning of damages was six decades.

Estimating total present value damages for these species requires summing the annual discounted damages over the span of the invasion. These results are presented in Table 1 for a range of discount rates; net present damages are estimated at the time of introduction and at the time when damages first began. Although annual damages drop to zero by 2070 for hemlock woolly adelgid and emerald ash borer, damages persist much longer for gypsy moth. For gypsy moth, we evaluate annual damages through 2200, when discounted annual damages drop to zero when discounted to the time of gypsy moth introduction at a 3% discount rate.

Discussion

Here, we explore how characteristics of invasions that affect the temporal pattern of damages influence an invasive species' anticipated impacts at the time when exclusion (via either prevention of arrival or eradication) may be contemplated. Using a theoretical model, we show that (all else equal) the impacts of invading species are greatest for species that a) have short lag times between introduction and spread, b) have short lags between arrival at a location and the initiation of damages, c) cause larger, short-lived damages (as opposed to smaller, persistent damages), and d) spread faster or earlier. These characteristics all lead to damages that accrue sooner, when they are more costly, increasing the benefits of prevention. We also confirm the intuition that prevention has higher benefits for invaders that have larger potential range sizes, because more damages can accrue.

Differences in the temporal distribution of damages can be traced back to inherent interspecific differences in both life history and ecology. Temporal lags between initial arrival of a species and the time when spread and/or damages commence have been observed in many species (22). In any specific case, the cause of a lag may be unknown, but lags can arise from both genetic and demographic mechanisms. Lags before the commencement of damage may also arise when time is required for invading species to spread into habitats that are damage prone. This is the case with the hemlock woolly adelgid. More than 60 years transpired between the time of introduction and the time when substantial hemlock woolly adelgid damage began (Fig. 3e) (30).

Consequently, the total present value of hemlock woolly adelgid damages from its time of introduction (when subsequent damages could have been averted through prevention measures) was greatly diminished and amounted to less than \$4 million (2011 USD).

The speed of invasion spread also profoundly affects the net present value of damages and consequently influences the benefit that comes from expenditures on exclusion (e.g., 12, 13, 14,

15). Spread can be decomposed into the coupling of population growth with dispersal. Thus, any differences in life history traits that affect population growth and dispersal can influence spread rates. The effect of spread rate can be seen by contrasting the gypsy moth and emerald ash borer. Gypsy moth females are flightless, and consequently the spread of this insect has been extremely protracted. In contrast, emerald ash borer females are good fliers, and larvae are readily transported in commodities such as firewood. The extremely high total present value of damages associated with emerald ash borer can be partially attributed to its relatively fast rate of spread: emerald ash borer will likely occupy 95% of its range in the eastern United States by 2040, about 50 years after its introduction. In contrast, 50 years after introduction, the gypsy moth still occupied less than 10% of its potential range in the eastern United States (32).

Differences in the ecological relationships between an invading species and its habitat also can lead to very different temporal distributions of impacts following establishment. Whereas some invading species may continue to cause damage indefinitely following establishment, the impacts of other species may be short-lived (24). Our example species illustrate considerable variation in the temporal distribution of impacts. Because they ultimately kill their host trees, emerald ash borer impacts on tree removal and replacement may last only a few decades following establishment in an area and then largely disappear. In contrast, the gypsy moth exhibits recurrent outbreaks that generally do not kill most host trees but result in periodic impacts indefinitely into the future (26). Although the persistence of damages depends strongly on the ecological interactions between a species and its environment, it also can be affected by the human response to the species' arrival, such as through adaptation or control, as well as the types of damages considered (27).

A crucial component in the management of biological invasions is risk analysis. Risk analyses are typically focused on individual species, and these analyses evaluate both the probability of a species' arriving and establishing and the probability and size of damages (33, 34). Such analyses are used to guide the implementation of quarantine policies targeting exclusion of individual species or groups of species. Given the variation among species in the extent to which temporal characteristics constrain the size of damages when discounted back to the time of arrival, we suggest that the likely temporal distribution of damages is a trait, in addition to other species characteristics, that should be considered in risk analyses. This trait may reasonably be predicted by life history characteristics that affect spread and the timing of damages once a species is established. In addition, the temporal pattern of damages may differ across potential introduction locations dependent on the distribution of at-risk resources (19), which also could be included in risk analyses. It is important to consider the timing of a species' damages because the decision of how much resources to expend on exclusion of species must consider not only the magnitude of undiscounted impacts but also the value of these impacts discounted back to the time of pest exclusion. For this reason, a better understanding of how species and environmental characteristics affect temporal invasion patterns would contribute to improved risk analysis, as well as evaluation or targeting of expenditures on exclusion.

The temporal distribution of damages is also relevant for evaluating the net value of expenditures on eradication. Whereas exclusion is aimed at averting initial arrival, eradication is targeted at eliminating newly established populations (35, 36). Since eradication programs are typically initiated once a species is discovered causing damages in a localized area, these efforts are likely to occur some time after the arrival of colonizing populations. Given that expenditures on eradication occur well after the timing of exclusion, their value in averting damages (if

eradication is successful) will always be greater than the value of averted damages caused by prevention (e.g., Table 1). Of course the magnitude of expenditures on prevention may be less than those required for eradication, so the relative net benefits of prevention and eradication will vary considerably among species. However, for many prevention activities (e.g., inspections, treatments), the question is generally how much money or effort to invest in prevention, rather than simply whether to engage in such activities. Indeed, the timing of future damages is critical in determining the benefits from additional investments in prevention, and hence the marginal trade-offs between prevention and other biosecurity activities, such as early detection and eradication.

Bioeconomic studies have considered optimal prevention investments for reducing impacts from invasive species (e.g., 12, 37, 38, 39, 40, 41). These models generally account for post-arrival control decisions when determining optimal prevention levels, since these influence post-arrival impacts. They find that optimal prevention depends on a wide variety of factors, including the interactions among the costs and effectiveness of controls pre- and post-invasion, the growth rate of invaders and their potential range, the expected damages from invasions, and the discount rate. Our analyses highlight some important aspects of invasion and damage spread that are not considered in this previous work. In addition to spread patterns and discount rates, our analyses highlight lags and damage persistence as key temporal aspects of invasion dynamics that can affect optimal management both pre- and post-arrival. A better understanding of these traits and their determinants will improve allocation of limited resources for prevention, with more prevention resources likely targeted to species with short lags and more imminent damages than to species with long lags and damages that are spread out over longer time periods, all else equal.

Economic discounting, even at relatively low rates, can make justification of large prevention expenditures difficult for species whose damages are protracted over long time periods (12), and the choice of a discount rate obviously can have profound influences on policymaking. A similar issue has arisen for evaluating policies that affect other environmental problems, such as climate change, where damages occur long after the point in time when actions could have prevented them (42, 43). One of the suggestions for dealing with intergenerational separation of prevention and impacts in economic analyses is the use of declining discount rates (44), which reduces discounting of damages that occur far into the future. For invasive species, declining discount rates would enhance consideration of future damages when weighing the costs of prevention or other control interventions.

In our theoretical examples, we employed very simple models to capture the basic patterns of spread and damages under general conditions. In reality, spread and damage processes are more complicated and context dependent. Important details include not only the specific factors affecting a species' spread and damages but also the heterogeneity and spatial configuration of the invaded landscape and its vulnerable resources. In our illustrative model, we also do not explicitly consider the effects of control (e.g., eradication or barrier zone efforts) on the patterns of spread. As such, the present values identified for our theoretical models may represent an upper bound on their costs and damages, since control efforts would be applied only if they were expected to reduce total costs and damages relative to uncontrolled spread. In contrast, our empirical present value estimates may represent a lower bound, as our spread models are based on observed rates of spread which include the effects of control.

Our empirical estimates of damages for gypsy moth, hemlock woolly adelgid, and emerald ash borer provide useful examples for exploring the effects of differing temporal patterns on total

invasion damages, but they are coarse approximations that depend on various assumptions and judgments. First, in our empirical examples, we focus only on a limited set of welfare impacts: for gypsy moth and hemlock woolly adelgid, we quantify associated loss in residential housing values, and for emerald ash borer, we consider only residential tree removal and replacement costs. However, many other types of costs and damages are associated with each species, including lost recreation values, lost aesthetic values, lost ecosystem service values, other difficult-to-quantify ecological impacts, and control costs and maintenance expenditures by communities and governments. In addition, for emerald ash borer, we estimated expenditure costs, and therefore our estimates partially capture a wealth transfer and likely overestimate welfare loss from tree removal per se. We also estimated damages and predicted spread across very long time horizons, necessitating numerous assumptions and encompassing many uncertainties that we did not quantify here. For these reasons (and others described in the Supplementary Material), our empirical results represent “back of the envelope” values meant to inform discussions and enhance our understanding of the importance and complexity of temporal aspects of invasion impacts, rather than precise or comprehensive damages caused by these species.

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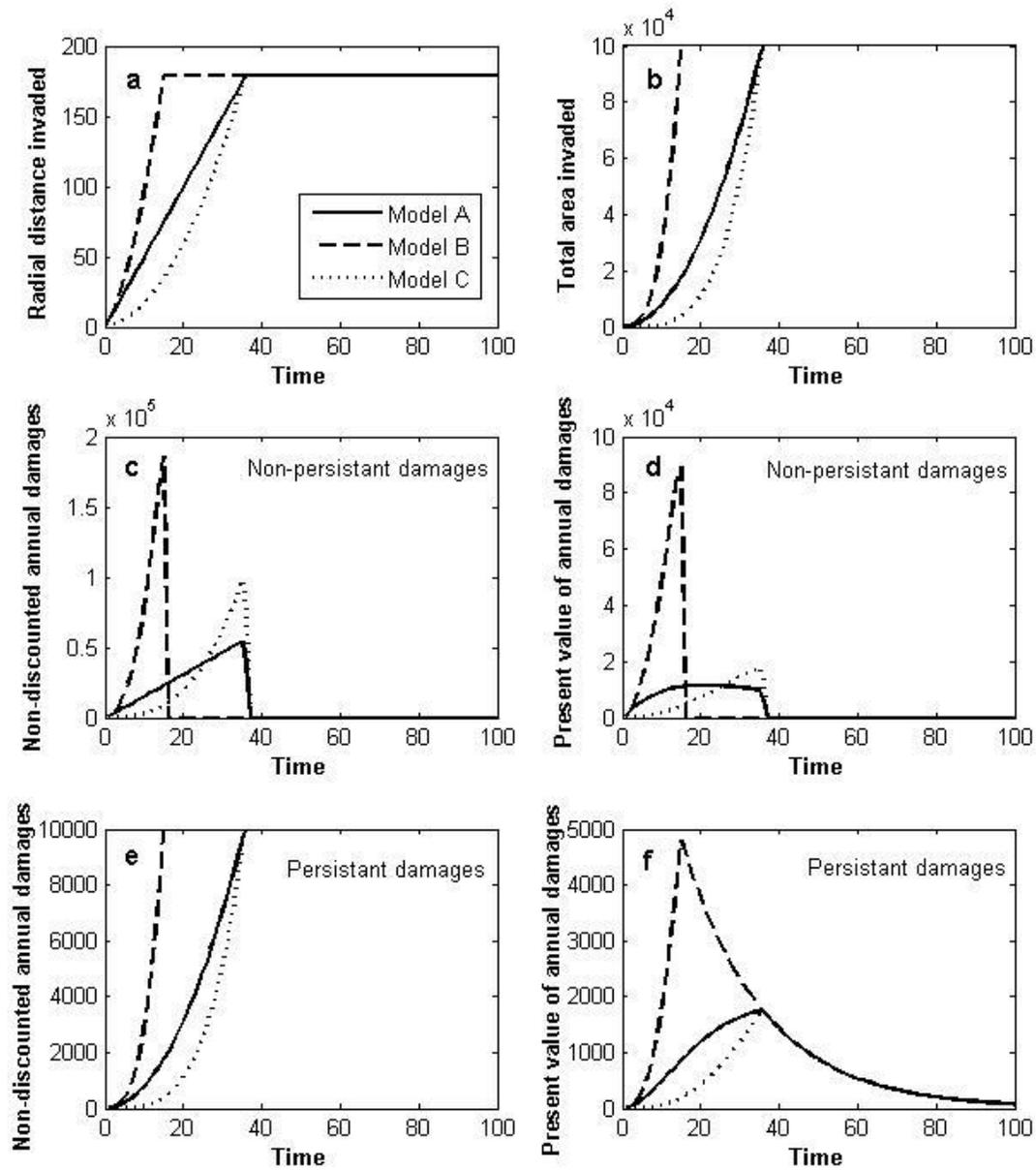


Fig. 1. Panels show the (a) radial extent, (b) invaded area, (c,e) nondiscounted annual damages, and (d,f) present value of annual damages for the first 100 years of invasion for spread models A, B, and C (lines) with the baseline parameterizations. The second row (c,d) shows damages when persistence P is 1 year, and the third row (e,f) shows damages when persistence P is 100 years.

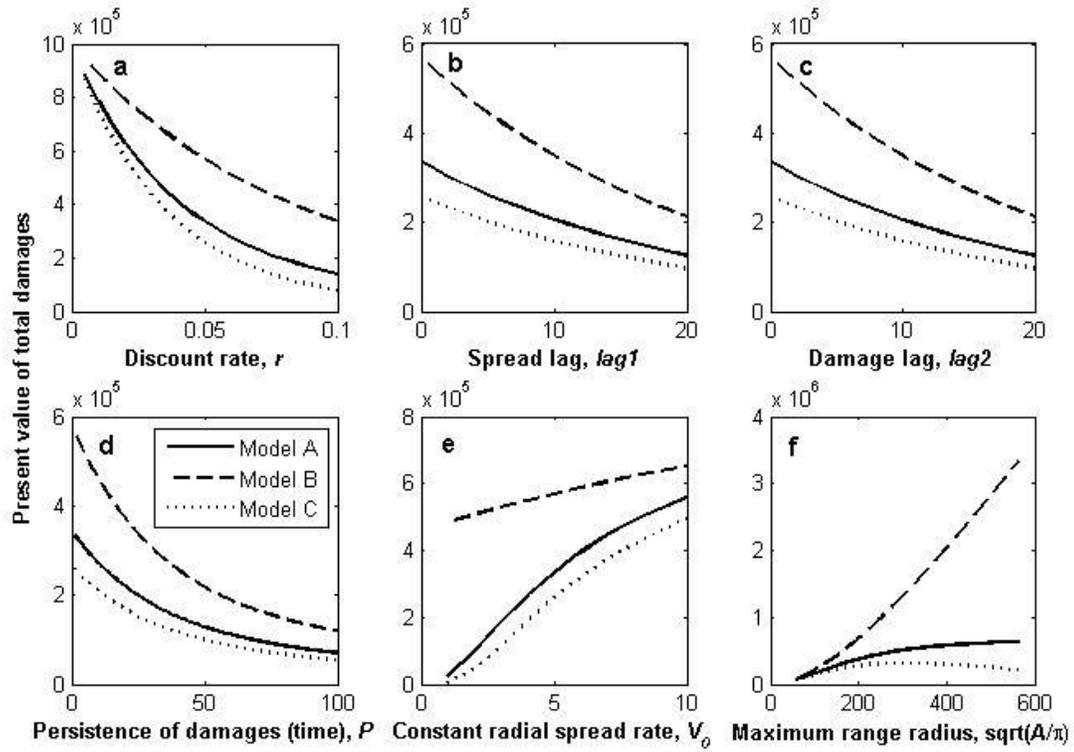


Fig. 2. Present value of total damages as a function of discount rate (r), spread lag ($lag1$), damage lag ($lag2$), persistence of damages (P), constant radial spread velocity (v_0), and total range radius, assuming baseline parameters.

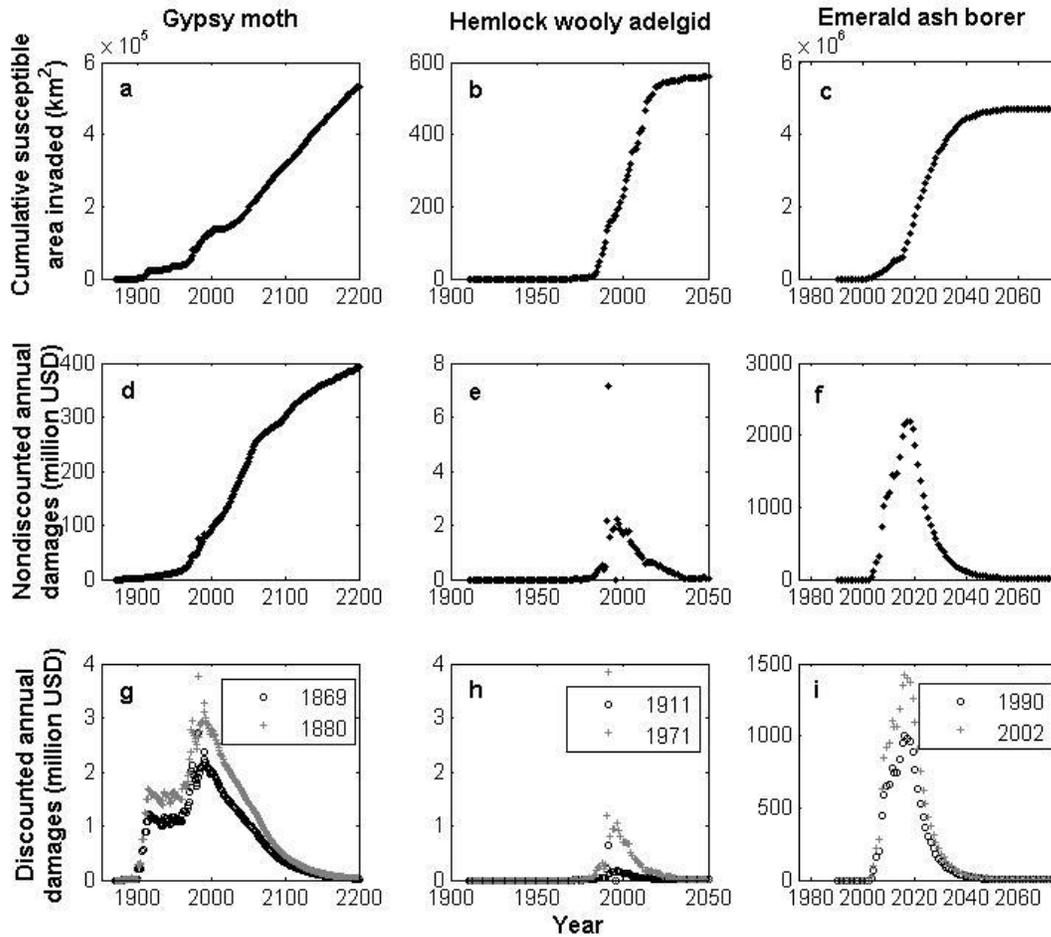


Fig. 3. Estimated invaded area, nondiscounted annual damages, and discounted annual damages for gypsy moth (first column), hemlock woolly adelgid (middle column), and emerald ash borer (right column). The bottom row panels show annual damages discounted back to the year of introduction and the year when damages first began to accrue (open circles and gray dots, respectively). Susceptible area for hemlock woolly adelgid is defined here as residential hemlock area. A 3% discount rate is used.

Table 1. Estimated total present value (millions 2011 USD) of residential damages from gypsy moth and hemlock woolly adelgid and of ash tree removal and replacement costs from emerald ash borer invasion. Present values are calculated from the time of both introduction and initiation of damages (1869 and 1880 for gypsy moth, 1911 and 1971 for hemlock woolly adelgid, and 1990 and 2002 for emerald ash borer). Three discount rates are presented: 1%, 3%, and 5%.

	At establishment <i>r</i> = 3%	At initiation of damages <i>r</i> = 3%	At establishment <i>r</i> = 1%	At establishment <i>r</i> = 5%
Gypsy moth	252	348	6,415	32
Hemlock woolly adelgid	3.5	21	20	0.7
Emerald ash borer	15,400	21,900	26,400	9,200

Table S1. Parameters used in theoretical analyses.

Parameters	Definition	Units	Baseline value	Range examined
v_0	Constant radial spread rate	km/yr	<u>Models A, B</u> : 5 <u>Model C</u> : 0.5	Models A, B: 1–20 Model C: ¼ of Model A, B values
v_1	Linear increase in spread rate	km/yr ²	<u>Model A</u> : 0 <u>Model B</u> : 0.5 <u>Model C</u> : varies to keep T_{max} same as for Model A	—
$lag1$	Lag between introduction and start of spread	years	0	0–20
$lag2$	Lag between arrival at location and start of damages at same location	years	0	0–20
P	Length of damage persistence at location	years	5	1–100
A	Potential range size of invasion (total area that can become invaded)	km ²	100,000	10,000–1,000,000
r	Discount rate	year ⁻¹	0.05	0.01–0.1
D	Total nondiscounted damages at location	\$/km ² Note: annual damages = D/P (\$/km ² /yr)	10	—

Quantification of gypsy moth spread and damages. We used historical invasion records to characterize past invasion spread from the time of its initial introduction in Medford, Massachusetts, in 1868 through 2012. Past spread of gypsy moth from 1868 to 1912 is summarized in Liebhold et al. (1) and Liebhold and Tobin (2) from a variety of historical

records. Spread from 1912 to the present is recorded in county-level quarantine records published by the US Department of Agriculture (US Code of Federal Regulations, Title 7, Chapter III, Section 301.45). Future spread of the gypsy moth was projected based on an assumption of constant radial spread, using a rate of 5 km/yr (the average spread rate estimated for 1999–2012 along the expanding population front in the United States; <http://old-da.ento.vt.edu>). Year of establishment was predicted for each county in 39 eastern states (Fig. S2). We excluded spread into counties whose climates are unsuitable for gypsy moth development (3).

Following Aukema et al. (4), we assumed that residential damages from gypsy moth invasion depend on the number of one- and two-unit houses that experience defoliation from gypsy moth outbreaks in each year and estimated damages as the household's willingness to pay to avoid gypsy moth damage, including the loss of value from nuisance, defoliation, and tree mortality. Aukema et al. (4) assumed a willingness to pay of \$503 per urban household and \$433 per rural. We used the lower value estimate of 433 USD 2011 per house per year of defoliation as our baseline estimate.

Statewide records of the area annually defoliated by the gypsy moth are available for 1924–2010. From this we calculated the percentage of susceptible invaded habitat that was defoliated in each state and year. Susceptible land area is assumed to consist of forested lands with basal area comprising >20% tree species preferred by the gypsy moth; these estimates were derived from national forest inventory data (5). We also calculated the average percentage of susceptible invaded area defoliated across all years (1924–2010) and states, and we used this value as an estimate of the percentage of invaded susceptible area defoliated annually in years and states with no data (i.e., pre-1924 and post-2010). In this way we assumed that future outbreak dynamics would be comparable to past dynamics when projecting future defoliation. Analyses of historical dynamics indicate some temporal variation but overall a relatively constant pattern of gypsy moth outbreak periodicity over the past 85 years (6). The fungal pathogen, *Entomophaga maimaiga*, appeared in North American populations in 1999 and previously had not been known to be present. Though this pathogen causes considerable mortality of gypsy moth, there is no conclusive evidence that this disease has altered gypsy moth outbreak dynamics, since recurrent large regional outbreaks have continued subsequent to its emergence (6, 7).

We estimated the number of potentially affected households in each infested county as the number of one- or two-unit housing structures in the county times the fraction of susceptible area in the county. We calculated the number of affected households in each county in each year as the number of potentially affected households times the average percentage susceptible area defoliated. We multiplied this by the willingness to pay to avoid gypsy moth damage to estimate the expected annual damages to residential properties from gypsy moth invasion.

Estimates of the numbers of one- and two-unit housing structures are not available across the full timeframe of historical and future gypsy moth invasion. Thus we estimate these numbers using available housing structure and human population data. US Census estimates of the number of one-unit housing structures are available by state for each decadal year from 1940 to 2000 (<https://www.census.gov/hhes/www/housing/census/historic/units.html>). In addition, the number of one- and two-unit structures is available at the county level for 2011 (http://factfinder2.census.gov/faces/tableservices/jsf/pages/productview.xhtml?pid=ACS_11_5YR_DP04&prodType=table). We estimated state-level numbers of housing structures for years without data based on state population data. Specifically, we modeled the ratio of one-unit housing structures to human population numbers as a function of year and its standardized quadratic using GLM estimation in Stata. We used a logit link and state fixed-effects to jointly estimate state-specific coefficients and then used the results to predict the house : population ratio for years without housing data. From this, we backed out the number of one-unit housing structures per state based on state population estimates, which were available annually for 1880–2012 (<https://www.census.gov/popest/data/historical/index.html>). Only country-level population predictions are available for 2013–2060 (<https://www.census.gov/population/projections/data/national/2012.html>), so we estimate state-level populations using these data and each state’s proportion of the country’s population in 2012. Furthermore, we estimated county-level housing structure numbers from state estimates by assuming that housing structures were allocated across counties in proportion to their observed 2011 distributions, and that the ratio of one-unit to two-unit housing structures also was constant over time at 2011 values. Given the lack of population data and considerable uncertainty about the ratio of housing structures to population in the future, we assumed constant housing numbers beginning in 2060. Although housing numbers are likely to continue to increase, this assumption

also recognizes that the number of houses with susceptible vegetation may decline over time because of loss of habitat.

Quantification of hemlock woolly adelgid spread and damages. We used historical range data (8) to characterize past invasion spread (1911–2012) and used historical spread rates to predict future spread (2013–2064), assuming a constant radial rate of spread. Specifically, we predicted future spread based on an annual spread rate of 12.5 km/yr, estimated from historical hemlock woolly adelgid spread in the eastern United States by Evans and Gregoire (9). Expansion of range through time was simulated by computing buffers from the current extent in a geographical information system (Fig. S3). A county was considered infested once any part of the land area is infested.

The range of hemlock woolly adelgid is well known to be limited by cold winter temperatures that kill overwintering populations (10). Based on work by Trotter and Shields (11) and Paradis et al. (12), we selected the boundary between climate zones 5a and 4b (13) to define the boundary of unsuitable climate. Any county with all land area falling in zone 4b or colder was assumed to be incapable of supporting damaging hemlock woolly adelgid populations and was excluded from the analysis.

Following initial infestation of a county, we measured spread within a county (i.e. susceptible area invaded) as the area of residential hemlock with severe defoliation. We estimated within-county spread generally following Holmes et al (14) and using the same data on the area of severe defoliation from eight counties in New Jersey at five time points from 1992 to 2001. We used these data to predict the effective range radius of the severely defoliated area within each county as a function of time since hemlock woolly adelgid was first detected in the county. We found that the effective range radius was well predicted by a linear function of time since invasion, supporting a constant radial rate of spread within counties. We assumed this linear rate of spread from the time of initial county infestation until all hemlock residential area in the county, as identified by Holmes et al. (14), is occupied.

Following Holmes et al. (14), we estimated the number of households affected by a severe defoliation in each year as the newly invaded “area of economic damage” (i.e., newly invaded hemlock residential area) in each county divided by the average lot size within the wildland-

urban interface in each county. Average lot size was estimated using housing density and total intermix wildland-urban interface area estimates from Radeloff et al.'s (15) WUI3 Shapefile (1990–2000 by census block) (<http://silvis.forest.wisc.edu/maps/wui3/download>). Housing density in 1990 was used to calculate damages before 1996; housing density in 2000 was used for damages 1996 and later.

Following Holmes et al. (14), we estimated the lost welfare from defoliation (measured as a reduction in residential housing values) as the product of the number of newly affected households in each year and county, the median county-level housing price, and the percentage housing value loss due to severe hemlock defoliation, assumed to be 1%. Therefore, although amenity value losses may be persistent, they are captured here as an instantaneous, one-time welfare loss.

Quantification of emerald ash borer spread and damages. As with the previous species, data on emerald ash borer spread include both historical data on past spread and simulated data on future spread at the county level. Historical records of first detection were available for 380 counties spanning 2002–2012 (USDA APHIS PPQ database). The spread of emerald ash borer is characterized by the founding of satellite populations some distance away from the expanding population front; these colonies expand and eventually coalesce. Given this behavior, the prediction of future spread via the application of a constant spread rate into contiguous counties would be unrealistic. Instead we fit a stochastic spread model that accounted for population “jumps,” particularly into populated areas. The probability that an uninfested county will be colonized in a given year was modeled using a logistic model (intercept 0.9467) as a function of the square root of the centroid-to-centroid distance to nearest infested county (coefficient – 0.4232) and the human population size of the county (coefficient $6.799e-7$). The logistic model was fit to historical emerald ash borer spread data from 2002 to 2012 using Firth’s penalized likelihood approach for sparse data (16). The performances of several model forms were compared by fitting the models to 2002–2008 data and comparing predicted and observed newly invaded areas for 2009–2012. Using the final model, 100 replicate simulations were conducted from 2013 to 2100 (Fig. S4) and used for estimating 100 corresponding replicate economic impact analyses.

We estimated the expected community-level expenditures from emerald ash borer invasion by roughly following the approach of Kovacs et al. (17). Specifically, we estimated the numbers of ash trees within communities in our study region using county-level data on canopy cover in developed areas from <http://www.nrs.fs.fed.us/data/urban> (18). We then estimated the fraction of developed canopy cover located within US communities as the ratio of total canopy cover within US communities to the total canopy cover on developed land for each state, from Kovacs et al. (17, Table 1). We used the regionwide average for states without data. As done by Kovacs et al. (17) we then estimated the number of ash trees per hectare of canopy for each county by applying values derived from urban tree inventories conducted at 16 cities throughout the eastern United States and reported in Kovacs et al. (17, Table 2). Because our study area included a large portion of the southeastern US for which Kovacs et al. (17) had few data, we added data collected from urban areas across Tennessee (19). For each county, numbers of urban ash trees per hectare were estimated by interpolating (average of 5 nearest points weighted by 1/distance) from values provided in both Kovacs et al. (17) and Nowak et al. (19). We assumed that 20% of ash trees were affected in each of the five years following first detection of emerald ash borer in a county, again following Kovacs et al. (17). Rather than assuming dynamically optimal control decisions regarding decisions to remove, remove and replace, or treat ash trees (per Kovacs et al., 17), we assumed that ash trees are removed and replaced as they are affected. We estimated the costs as the weighted average of costs across tree size classes and landowner types, according to their proportional representation based on Kovacs et al. (17, Tables 3 and 4).

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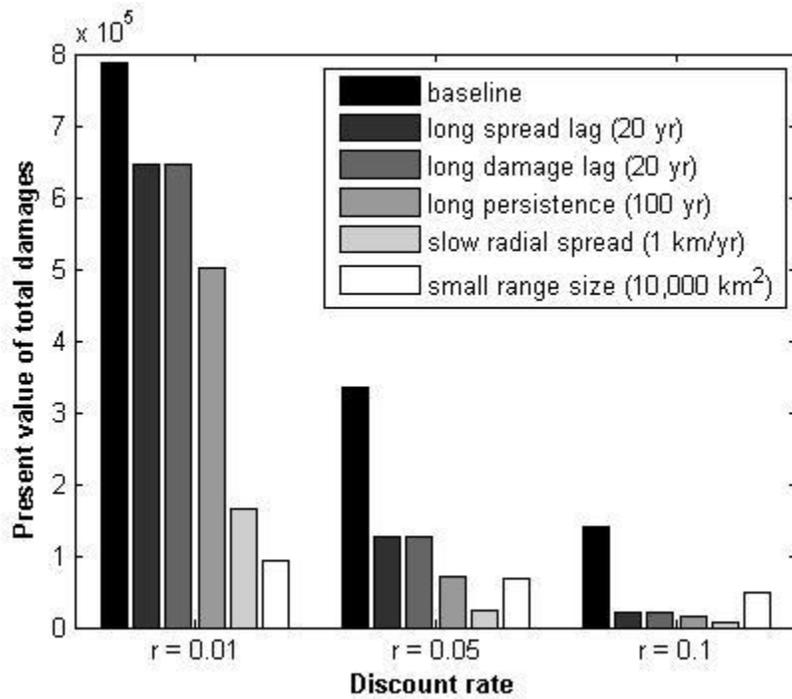


Fig. S1. The effect of discount rate on the net present value of damages for invasions with different spread lags, damage lags, damage persistence, radial spread rates, and range size. All results are for spread model A.

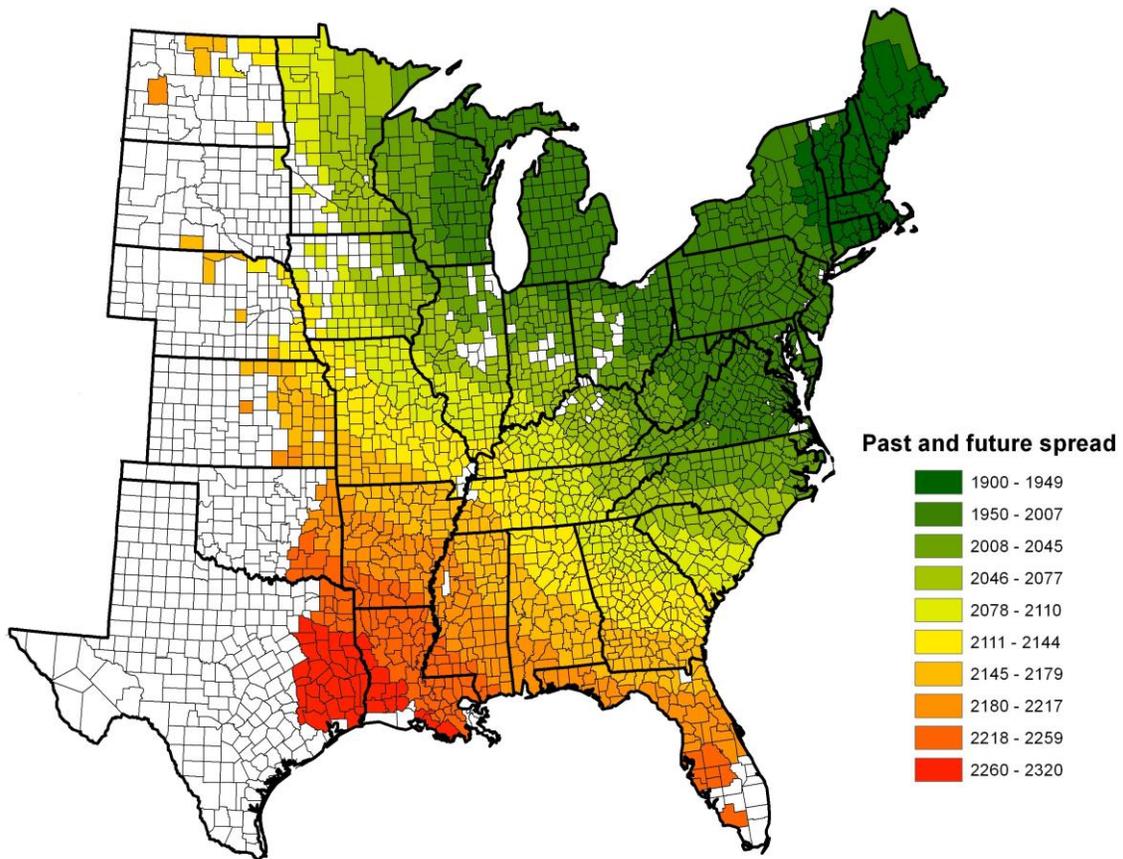


Fig. S2. Past and predicted future spread of the gypsy moth. Year of first establishment is shown by county in 39 eastern US states. Counties lacking suitable forest for gypsy moth outbreaks (5) or climatically unsuitable for gypsy moth establishment (3) are shaded white and not used in damage estimates.

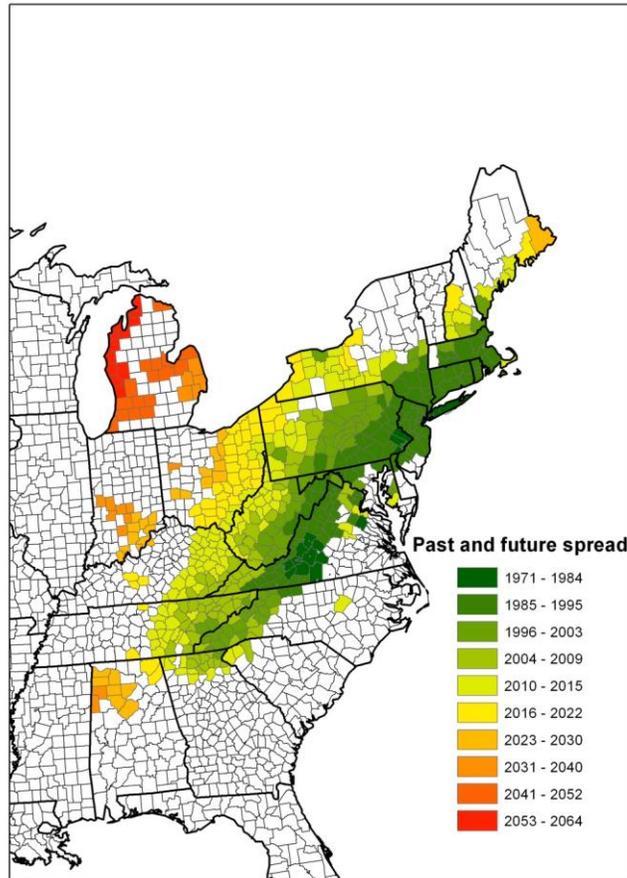


Fig. S3. Past and predicted future spread of the hemlock woolly adelgid. Year of first establishment is shown by county. Counties lacking host hemlock basal area (15) or climatically unsuitable (11) are shaded white and not included in damage estimates.

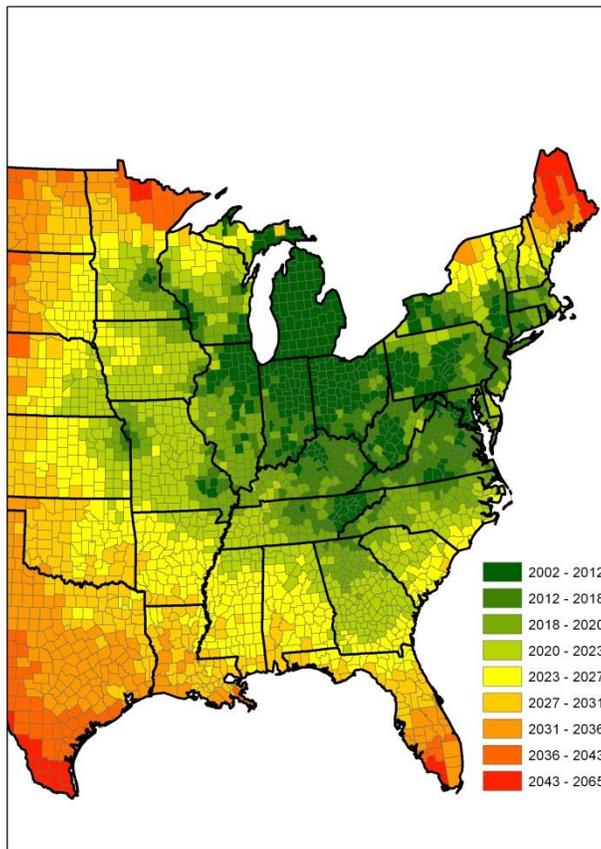


Fig. S4. Past and predicted future spread of the emerald ash borer. Year of first establishment is shown by county in 39 eastern US states. For counties where emerald ash borer was discovered prior to 2013, values shown are actual years of emerald ash borer discovery. For counties where emerald ash borer was not known to be present in 2012, values shown are the average year of establishment predicted from 100 stochastic simulations.