Ecological Economics 116 (2015) 146–153

Contents lists available at ScienceDirect

Ecological Economics

journal homepage: www.elsevier.com/locate/ecolecon

Analysis

Benefits of invasion prevention: Effect of time lags, spread rates, and damage persistence

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ARTICLE INFO

Article history:
Received 7 November 2014
Received in revised form 26 March 2015
Accepted 9 April 2015
Available online xxxx

Keywords:
Biological invasion
Economic impact
Damages
Gypsy moth (*Lymantria dispar*)
Hemlock woolly adelgid (*Adelges tsugae*)
Emerald ash borer (*Agrilus planipennis*)

ABSTRACT

Quantifying economic damages caused by invasive species is crucial for cost-benefit analyses of biosecurity 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.

1. Introduction

Increasing international trade and travel have had an unintended consequence: the accidental transport of species out of their native ranges into novel environments (National Research Council, 2002; Perrings et al., 2010). 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 (Aukema et al., 2011; Lodge et al., 2006; Vitousek et al., 1996). 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 understand invasions and evaluate solutions. Ultimately, measures taken to mitigate invasion impacts are justifiable only if the costs of management are smaller than the impacts avoided (Olson, 2006). Efforts have thus been made to quantify the impacts of individual species (e.g., Kaiser, 2006; Connelly et al., 2007; Kovacs et al., 2010) as well as guilds of species (e.g., Pimentel et al., 2010; Aukema et al., 2011), 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., Epanchin-Niell and Hastings, 2010), with particular attention to how the rate of invasion spread can influence damages, and hence the economic benefit of eradicating an incipient population (Olson and Roy, 2005, 2008; Eiswerth and Johnson, 2002; Sharov and Liebhold, 1998). 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 (Sharov and Liebhold, 1998; Smith et al., 1999; Epanchin-Niell and Wilen, 2012).

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 (Epanchin-Niell and Wilen, 2012; Holmes et al., 2010; Epanchin-Niell et al., 2014). The spatial distribution

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http://dx.doi.org/10.1016/j.ecolecon.2015.04.014

of resources also can affect the pattern and rate of species spread (e.g., Hastings et al., 2005). 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 or space. For example, Aukema et al. (2011) estimated the annual impacts of individual invading forest insect species during "typical" 10-year periods. Others focus on average per unit area damages (e.g., Pimentel et al., 2000). These types of values are particularly useful for highlighting the economic importance of invasive species, but they generally have limitations for policy analysis. 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 spread 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" (Crooks and Soulé, 1999) are common in nature, the processes responsible for them often are not well understood. In many cases, such observed lags may be "inherent lags" in which absolute population growth is low early in an invasion simply due to low population numbers at the location (Crooks and Soulé, 1999). In some systems, however, populations can experience "prolonged lags" due to a variety of factors (Crooks and Soulé, 1999). For example, selection for greater fitness may occur during the period after establishment, and a lag in population growth may result from slow genetic changes in the population (Sakai et al, 2001). Lags also may result from low population growth rates at low densities associated with Allee effects (Taylor and Hastings, 2005). Invasion lags can result in delayed spread of an invader following its initial establishment (spread lag) or delayed onset of damages following invader arrival at a location due to initially low population densities (damage lag).

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 (Simberloff and Gibbons, 2004). 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* (Freinkel, 2007). 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 (Johnson et al., 2005). 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 (Perrings et al., 2002).

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 (*L. 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 (spread lag), 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 (Aukema et al., 2011). 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.

2. Methods

2.1. 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 (Shigesada and Kawasaki, 1997). 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 lags, 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.

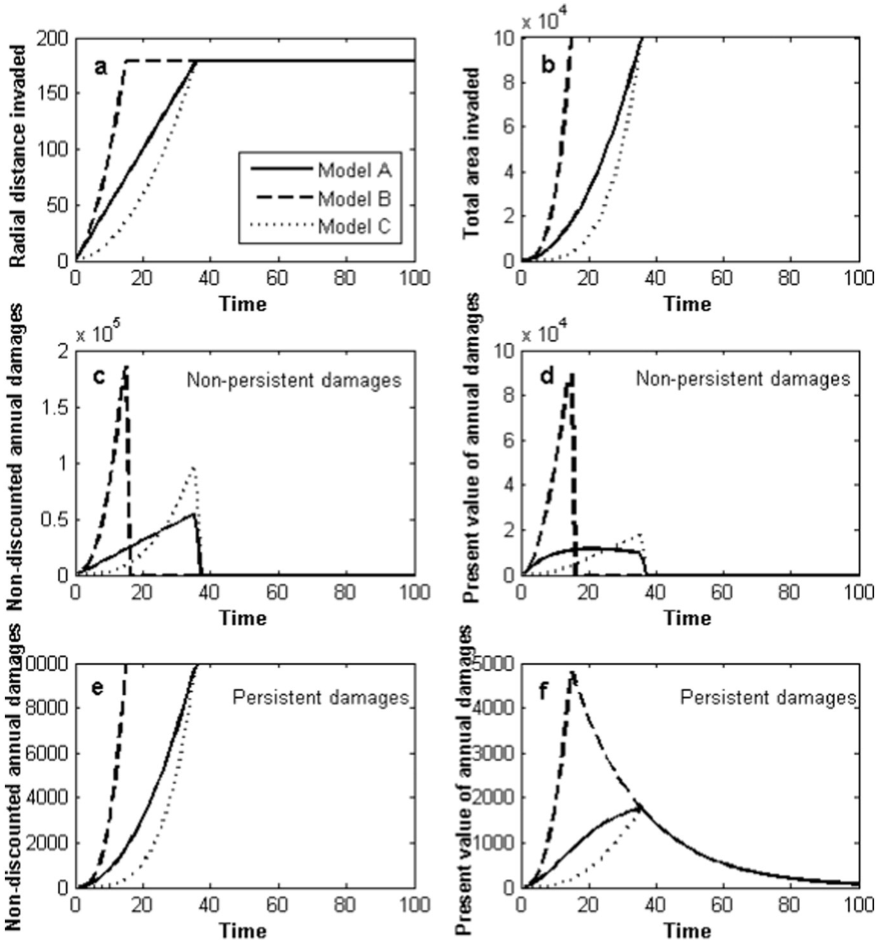

Fig. 1. Panels show the (a) radial extent, (b) invaded area, (c,e) nondiscounted annual damages, and (d,f) present value of annual damages for the first 100 years of invasion for spread models A, B, and C (lines) with the baseline parameterizations. The second row (c,d) shows damages when persistence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

Total damages at time t can be calculated as follows:

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

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:

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

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 ($v_1 = 0$) 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 (Shigesada and Kawasaki, 1997). 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.

2.2. Empirical Examples

Our empirical damage estimates focus on three species that have been identified as the most damaging forest pest in their feeding guild. 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. (2011), Kovacs et al. (2010), and Holmes et al. (2010). Whereas these studies 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 and overviewed below.

The gypsy moth was accidentally introduced to Medford, Massachusetts in 1869, but damage was not noticeable until 1880 (Forbush and Fernald, 1977; Liebhold and Tobin, 2006). Most damage associated with the gypsy moth is caused by tree defoliation. We modeled spread using historical gypsy moth spread records and by projecting future spread based upon a current spread rate of 5 km/year. Following Aukema et al. (2011), 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 we 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.

The hemlock woolly adelgid was most likely originally introduced to North America in a garden in Richmond, Virginia, in 1911 (Havill and Montgomery, 2008). Because this location had very few hosts, the insect was not even noticed until the 1940s, and noticeable damage did not occur until the 1970s. We modeled spread using records of historical spread (Morin et al., 2009) and projected continued spread of 12.5 km/year within climatically suitable areas. We estimated spread and damage within counties following Holmes et al. (2010). We assumed that the area of severe tree defoliation and subsequent mortality within a county depended on the time since the invasion was first detected in the county, and the lost welfare from defoliation (measured as a reduction in residential housing values) was estimated as the product of the number of newly affected households in each year and county, the median county-level housing price, and the percentage property value loss due to severe hemlock defoliation.

The timing of the initial introduction of the emerald ash borer to North America is uncertain but dendrochronological reconstruction indicates that it most likely arrived near Detroit, Michigan, in the early 1990s (Siegert et al., 2014). We used data on historical spread of the insect through 2012 to fit a stochastic model that was then used to make multiple projections of spread through 2065. Roughly following Kovacs et al. (2010), these spread scenarios were combined with information about numbers of urban ash per county to reconstruct historical damage as well as project damage into the future, as measured by the cost of removal and replacement of dying ash trees.

3. Results

3.1. Theoretical Model

Interactions among spread patterns, damage persistence, and discounting affect temporal damage patterns. Fig. 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 Fig. 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 (Fig. 1c–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 (Fig. 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 (Eq (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 present value of damages also increases with baseline velocity because more damages accrue sooner (Fig. 2e).

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, because damages accrue across larger areas and the invasion spread rate at a location does not depend on the total range size in these models. 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, for model C the rate of invasion spread begins lower and increases more slowly for invasions unfolding in larger landscape — a pattern that is not reflective of nature, but rather a construct of our tying T_{max} to that of model A for comparison in other scenarios. Because the pattern and rate of spread depends on range size in model C, it does not make sense to consider the effect of range size on total damages for this model. Instead, results for model C are shown only for comparison with models A and B for a given range size. Indeed, invasion damages under model C are more delayed (and hence more heavily affected by discounting) relative to models A and B 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 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).

3.2. 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) (Liebhold and Tobin, 2006), 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 (Havill and Montgomery, 2008). 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

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[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.

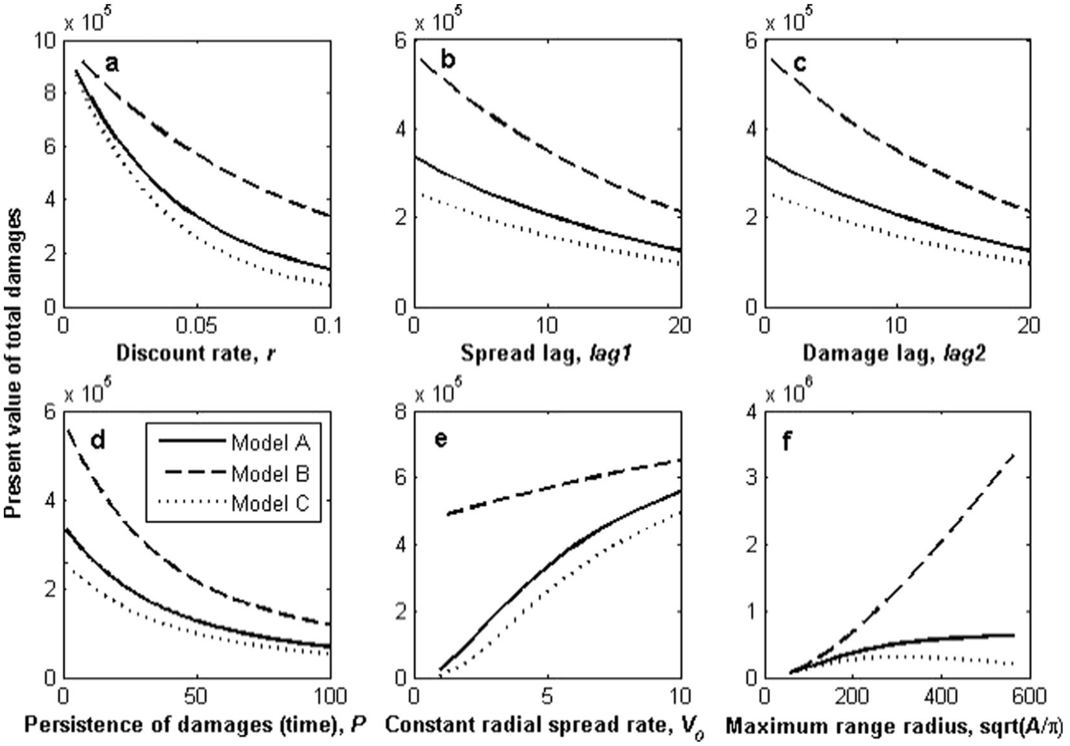

Fig. 2. Present value of total damages as a function of discount rate (r), spread lag ($lag1$), damage lag (lag2), persistence of damages (P), constant radial spread velocity (v_0), and total range radius, assuming baseline parameters.

the early 1990s (Siegert et al., 2014), 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 cumulative 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 newly area invaded over time, rather than the cumulative area invaded (Fig. 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. These peaks roughly follow the period when these species reach their maximum spread into new areas of at-risk resources.

The annual discounted damages from each forest pest are greatly attenuated, particularly when discounted back to the time of introduction (Fig. 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.

4. 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 (Crooks and Soulé, 1999; Sakai et al, 2001). 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) (Havill and Montgomery, 2008). Consequently, the

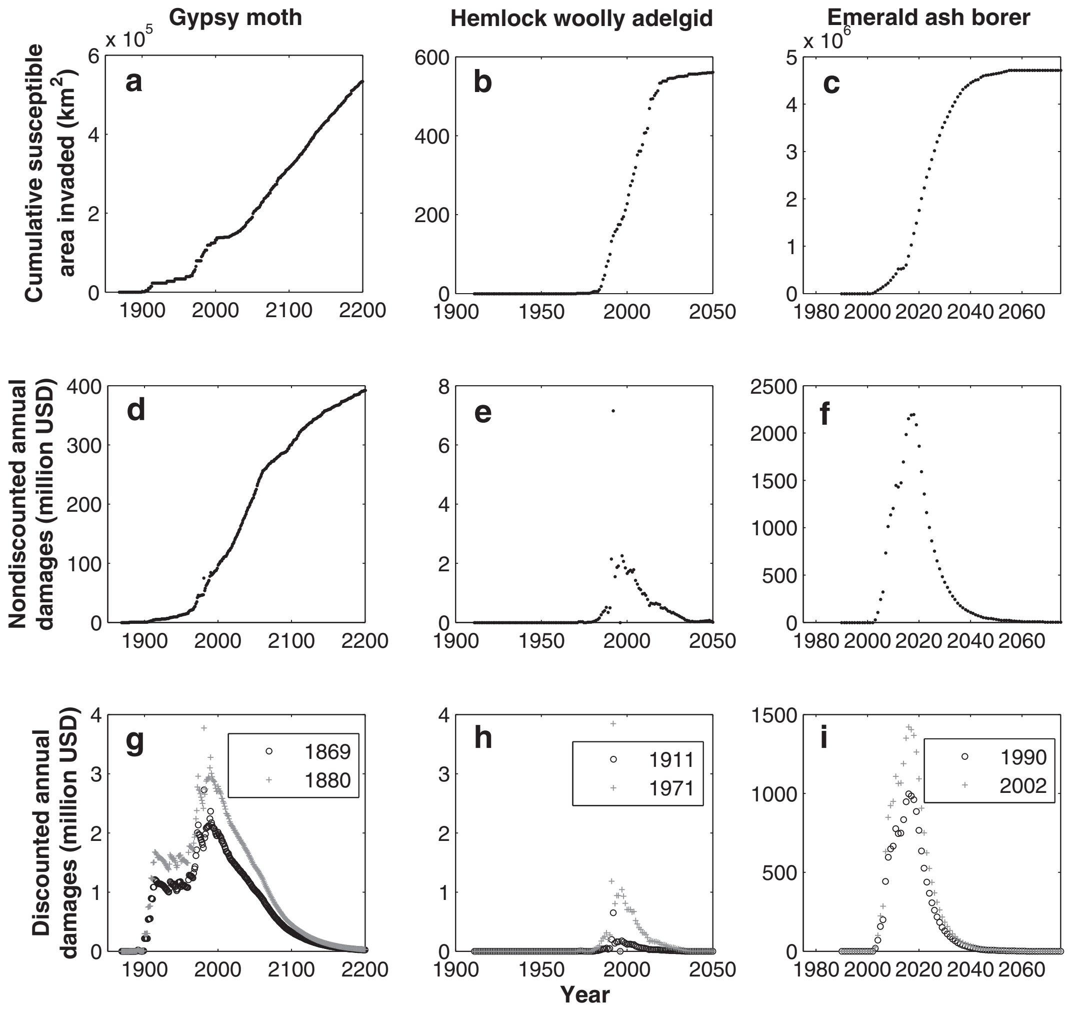

Fig. 3. Estimated susceptible area invaded, nondiscounted annual damages, and discounted annual damages for gypsy moth (first column), hemlock woolly adelgid (middle column), and emerald ash borer (right column). The bottom row panels show annual damages discounted back to the year of introduction and 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.

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., Olson and Roy, 2005, 2008; Eiswerth and Johnson, 2002; Sharov and Liebhold, 1998). 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 (Liebhold et al., 1992).

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,

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 (r) are presented: 1%, 3%, and 5%.

	Estimated total present value			
	At establishment $r = 3\%$	At initiation of damages $r = 3\%$	At establishment $r = 1\%$	At establishment $r = 5\%$
Gypsy moth (residential property value loss)	252	348	6415	32
Hemlock woolly adelgid (residential property value loss)	3.5	21	20	0.7
Emerald ash borer (community expenditures on tree removal and replacement)	15,400	21,900	26,400	9200

the impacts of other species may be short-lived (Simberloff and Gibbons, 2004). 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 (Johnson et al., 2005). 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 (Perrings et al., 2002).

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 (Andersen et al., 2004; Stohlgren and Schnase, 2006; Hulme, 2012; Leung et al, 2012). Such analyses are used to guide the implementation of quarantine policies targeting exclusion or control of individual species or groups of species. Analysis of impacts is an underdeveloped, but critical component of risk assessments, with quantitative damage assessments and discounting remaining rare in such analyses (Hulme, 2012; Leung et al, 2012).

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, our results support that the likely temporal distribution of damages should be considered in risk analyses. Life history characteristics, including factors influencing anthropogenic dispersal, may be used to predict rates of spread (Hastings et al., 2005). Similarly, habitat suitability modeling provides approaches for predicting invasion range (Guisan and Thuiller, 2005; Elith and Leathwick, 2009). The temporal pattern of damages also may differ across potential introduction locations dependent on the distribution of at-risk resources (Epanchin-Niell et al., 2014), and risk mapping approaches (Venette et al, 2010) may facilitate accounting for the differential timing of damages across introduction locations in risk analyses. Unfortunately, while we have shown that invasion lags have substantial economic importance and thus would be an important consideration in risk analysis, this temporal trait is particularly challenging to predict (Crooks and Soulé, 1999; Larkin, 2012) and in substantial need of further research. Indeed, a better understanding of how species and environmental characteristics affect temporal invasion patterns would contribute to improved risk analysis for evaluating or targeting exclusion measures, the values of which depend on the magnitude of impacts discounted back to the time of pest 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 (Hulme, 2006; Liebhold and Tobin, 2008). 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 expected 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 (Hulme, 2012; Leung et al, 2012).

Bioeconomic studies have considered optimal prevention investments for reducing impacts from invasive species (e.g., Olson and Roy, 2005; Carrasco et al., 2010; Kim et al., 2006; Finnoff et al., 2007; Leung et al., 2002; Rout et al., 2011). 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 (Olson and Roy, 2005), 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 (Beckerman and Hepburn, 2007; Broome, 2008). One of the suggestions for dealing with intergenerational separation of prevention and impacts in economic analyses is the use of declining discount rates (Arrow et al., 2013), 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, which is beyond the scope of this paper but an important area for future analysis. As such, however, 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, but we do not account for the cost of quarantine efforts.

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 esthetic 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 example, hemlock woolly adelgid and gypsy moth spread were estimated based on past spread rates and assuming a constant rate of spread, rather than considering the influence of resources on spread rates. Similarly, while we accounted for spatial variability in human population for affecting spread of emerald ash borer, the distribution of resources (ash trees) only affects damages at a location, rather than local spread rate, in our models. 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.

Acknowledgments

We thank R.H. Haight, K. Kovacs, and T. Holmes for advice on analyses and E. Luzader with assistance in preparing GIS data and figures. This work was made possible, in part, by Agreements from the United States Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) and US Forest Service (USFS) Eastern Forest Environmental Threat Assessment Center. It may not necessarily express APHIS' or USFS' views.

Appendix A. Supplementary material

Supplementary material to this article can be found online at http://dx.doi.org/10.1016/j.ecolecon.2015.04.014.

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