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Analysis

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

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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.

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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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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.