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Confronting challenges to economic analysis of biological invasions in forests[†]

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Abstract

Biological invasions of forests by non-indigenous organisms present a complex, persistent, and largely irreversible threat to forest ecosystems around the globe. Rigorous assessments of the economic impacts of introduced species, at a national scale, are needed to provide credible information to policy makers. It is proposed here that microeconomic models of damage due to specific invading organisms be aggregated across the forest landscape by considering the rate at which acute, short-run economic impacts accumulate over time and space. By estimating the economic costs and damages associated with the most consequential pests within each pest guild and each sector of the forest economy, a better indication of the economic consequences of biological invasions can be obtained and used to inform policy analysis.

Keywords: Invasive species; forests; spatial-dynamic process; economic welfare; microeconomic analysis; non-market value.

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Introduction

Biological invasions by non-native forest insects and diseases pose a substantial, complex, and largely irreversible threat to forests and the provision of forest-based ecosystem services around the globe. For millennia, the world's biota has evolved in independent ecological communities. However, globalisation has established new linkages between geographically dispersed markets, and international trade increasingly provides rapid transit for the introduction of non-indigenous species (Stanaway et al., 2001; Vilá & Pujadas 2001; Levine & D'Antonio, 2003; Work et al., 2005; Caton et al., 2006; McCullough et al., 2006).¹ Although propagules of most non-indigenous species do not become established or are unable to spread throughout their new environment, history has shown that a few species have the potential to become major pests (Williamson, 1996).

Forest ecosystems provide suitable habitats for many invading organisms (Liebhold et al., 1995). Since the European discovery of North America, more than 368 exotic phytophagous insects have become established in forests, woodlots, parks, and orchards (Mattson et al., 1994). Although most non-indigenous forest insects have proved to be innocuous and cause little harm, a few – such as the European gypsy moth (*Lymantria dispar* (L.)), emerald ash borer (*Agrilus planipennis* Fairmaire), and hemlock woolly adelgid (*Adelges tsugae* (Annand)) – have become major pests. The number of non-native tree pathogens that have become established in North America is more difficult to gauge, as many pathogens are innocuous and, in general, no effort is expended to document invasions by micro-organisms unless they have measurable impacts. Nonetheless, a similar pattern emerges for tree pathogens which have become major pests; only a few tree diseases – such as chestnut blight (*Cryphonectria parasitica* (Murrill) M.E. Barr), Dutch elm disease (*Ophiostoma-ulmi* Brasier), and sudden oak death (*Phytophthora ramorum* Werres, De Cock, & Man in 't Veld) – have had substantial consequences.

Biological invasions of forests induce a challenging class of economic problems for two principal reasons. First, economic losses resulting from the establishment and spread of non-native forest pests are difficult to quantify due to the fact that economic damages resulting from biological invasions are externalities, or side effects, of other economic processes (Perrings et al., 2005). As such, transitory disruptions in the flow of economic values derived from forests are subsidiary to primary market forces, and the resulting economic impacts are not easily observed in market prices. Indeed, many of the losses in economic values induced by non-indigenous forest pests are due to

losses of non-market economic values (Leuschner et al., 1996; Holmes et al., 2009), and creative methods are required to isolate and quantify the magnitude of economic impacts. Second, the flow of economic values in the forest economy is linked to the forest ecosystem by a suite of spatial-dynamic processes. Biological invasions of forests are driven by spatial spread characterised by diffusion or dispersal processes which develop over time (Hastings et al., 2005). Although economists are generally familiar with models of temporal dynamics, less attention has been given to spatial-dynamic processes. Further, economic dynamics are linked to, but not identical with, biological dynamics. Consequently, the integration of spatial and temporal bioeconomic dynamics will require the development of new, innovative economic methods (Smith et al., 2009).

Research addressing spatial-dynamic processes inherent to biological invasions of forests is needed before one can develop strategies to indicate where control efforts should be applied to protect values at risk, as well as to permit forecasts of the potential magnitude of economic damages. Because invasive species are often insidious, having a gradual and cumulative effect, and often go unnoticed before impacts become entrenched, the ability to model the dynamics of the joint biological-economic system would enhance decision making by providing better forecasts of potential future outcomes.

In this paper, we provide an overview of the economics of forest invasive species, call for new methods to assess large-scale dynamics of economic damages from forest invasive species, and outline an economic framework designed to measure the economic impacts of biological invasions of forests with explicit recognition of spatial-dynamic processes.

Overview of the economics of biological invasions in forests

Non-indigenous forest invaders cause damages to a suite of forest ecosystem goods and services. While impacts on timber values and timber markets are substantial, and are often the only values considered in decision-making, losses to non-market economic values are important and need to be accounted for. Microeconomic theory provides a foundation for the analysis of the market and non-market economic impacts of biological invasions that is directly relevant to policy makers.

Changes in economic welfare

Within the field of neoclassical economics, welfare

¹ Potential international trade flow adjustments in response to biological invasions of forests are discussed by Prestemon et al. (2006).

economics describes the economic well-being of producers and consumers in responses to changes in prices, quantities, or environmental quality (Varian, 1984). Microeconomic analysis provides the foundation for welfare analysis, and encompasses the behaviour of producers and consumers at the individual level and in terms of aggregates such as markets. A fundamental principle of microeconomic theory is that people attempt to do the best they can, as they see it, within the constraints on their access to resources. When producers or consumers are confronted with natural disturbances, such as forest damages from wildfire or pests, they generally take actions to mitigate their losses. The tendency for people to search for creative ways to avoid or reduce losses creates nuances in economic analysis that need to be recognised when evaluating the economic impacts of non-indigenous forest pests (Holmes et al., 2009).

Microeconomic theory is primarily concerned with understanding tradeoffs among economic variables and how decision makers respond to changes in economic and environmental conditions. In general, economists argue that people make consequential decisions in terms of their anticipated gains and losses relative to a given reference point (this is known as marginal analysis). From a microeconomic perspective, economic values for natural resources are determined by the tradeoffs made by individuals, such as how much one would be willing to pay (a cost or “loss”) to improve the quality of a natural resource relative to a base level (a “gain”). Although previous studies have sought to estimate the economic value of a natural resources in its current condition without reference to alternative states (Costanza et al., 1997), this approach has been criticised for failing to consider economic tradeoffs as the basis for economic valuation (Bockstael et al., 2000).

To illustrate the microeconomic perspective, consider the following juxtaposition between the financial value of standing timber and the suggested economic behaviour for mitigating losses from an invasive forest pathogen. During the early stages of the chestnut blight outbreak in the eastern United States, governmental agencies in Pennsylvania, West Virginia, and North Carolina reported that the financial value of standing chestnut (*Castanea dendata* (Marshall) Borkh.) timber at risk of mortality in those states was US\$82.5 million (in 1912 dollars) (Anagnostakis 1987). In current (2007) dollars, this amount represents roughly US\$1.7 billion in standing timber value. Although this is clearly a substantial sum, it does not represent the loss in economic welfare to timber producers in those states resulting from the chestnut blight. Faced with a threat to the value of their standing stocks of timber, landowners would presumably take action to reduce their losses. This is precisely the advice that was offered by the assistant director of the New York Botanical Gardens during the outbreak: “Utilisation is the big issue. See

that you are advised of the progress of the disease, appropriating money for this if necessary, and market your timber as it approaches. Be businesslike and accept the inevitable in time to make the best of it” (New York Times, 1912). Businesslike behaviour, such as pre-emptive logging of chestnut stocks (a “loss” in terms of harvesting costs), mitigated economic impacts by liquidating some of the standing timber value before trees were killed (a “gain” in value relative to doing nothing). Further, landowners in the affected areas who were not able to harvest live trees were advised by state foresters to salvage what value they could from trees killed by the blight (Anagnostakis, 1987).

Nationwide assessments of economic impacts

In North America, two studies have been conducted that provided estimates of the nationwide economic impacts of invasive species (Pimentel et al., 2000; Coluatti et al., 2006). Each study evaluated the economic effects of biological invasions on a broad suite of terrestrial and aquatic ecosystems, including agriculture, fisheries and forestry. Despite the fact that neither study approached the problem from a microeconomic perspective, and therefore did not address changes in economic welfare, the studies have been useful in drawing attention to the economic significance of this problem.

Pimentel et al. (2000) estimated that economic damages arising from non-indigenous forest pests in the United States are of the order of US\$4.2 billion annually. This estimate is solely based on estimated losses to wood products markets and rests on two assumptions: (i) forest pests reduce overall timber productivity by 9% per year; and (ii) non-indigenous forest insects and diseases account for 30% of the damage caused by all forest pests. Multiplying the estimated volume lost by an estimate of the unit price yields an estimate of damages. Although this procedure provides a simple means of computing economic impacts, it is noted that neither the economic behaviour of consumers/producers nor the spatial-dynamic behaviour of individual pests is considered in their calculation.

Colautti et al., (2006) conducted an assessment of the costs associated with a suite of non-indigenous pests affecting agriculture, fisheries and forests in Canada. Their assessment of biological invasions of forests differed from Pimentel et al. (2000) in that they estimated the economic impacts associated with specific forest pests. However, their economic models were similar to Pimentel et al. (2000) - value losses were computed by multiplying estimates of the proportional loss of resource yield by the total value of products. Proportional losses, ranging between zero and one, for all non-indigenous pests (agriculture, fisheries, and forestry) were estimated and ranked from lowest to highest. The median, quartile, and

half-quartile losses were treated as the maximum, mid-range, and minimum levels of productivity loss. These general loss proportions were then multiplied, in the forestry sector, by the total value of timber in domestic markets as well as exports, the total value of maple syrup and associated products, and the total value of Christmas trees. Using these procedures, it was estimated that the annual loss in value to the forest products industry in Canada was C\$15.9 billion (ranging from C\$12.7 – C\$33.1 billion).

Although the computation of economic impacts obtained by multiplying estimated yield loss and per unit values simplifies analysis, this method provides, at best, an estimate of the revenue lost by wood products producers who are impacted by a biological invasion.² The model, however, does not address the economic impacts experienced by wood products producers who are not impacted by a biological invasion, nor does it address the impacts on wood products consumers. A complete picture of the impacts of forest pests on forest products markets requires a market model in which all participants are accounted for. Such a framework was provided by Holmes (1991) who demonstrated how a catastrophic outbreak of a forest pest induces temporal dynamics in the price of timber.³ Because owners of pest-killed (pest-threatened) timber salvage (pre-emptively harvest) some portion of the dead (threatened) timber stock, market prices fall in response to the pulse of timber onto the market. Thus, in the short run, owners of timber stands not impacted by the pest still face an economic shock in terms of lower timber prices. Lower timber prices are also faced by timber buyers who may benefit from the pulse of salvaged (pre-emptively harvested) timber. A timber market model was also used by the United States Department of Agriculture (USDA) Forest Service (Holmes & Lee, 1991) to evaluate changes in the economic welfare of timber producers and wood-products consumers under various biological invasion scenarios in which pests spread as a travelling wave across the forest landscape.⁴

Non-market economic losses

A potentially enormous source of bias in aggregate estimates of the economic losses due to non-

indigenous forest pests is the failure to account for non-market values. These values encompass a suite of ecosystem services such as water filtration, flood mitigation, wildlife habitat, carbon sequestration, and landscape aesthetics that are not directly traded in markets. Many non-market valuation studies seeking to quantify virtually all categories of forest goods and services have been conducted over the past several decades. However, only a limited number of these have focused attention specifically on the economic impacts of forest insects and diseases (Kramer et al., 2003). The results to date suggest that the residential impacts of forest pests are large and might dominate other categories of market and non-market impacts in developed countries (Leuschner et al., 1996; Reinhardt et al., 2003; Turner et al., 2004; Nowak et al., 2006).

The non-market impacts of invasive species have been studied in an economic welfare-theoretical context using both direct questions about willingness to pay (stated preference methods) and evidence from behaviour in related markets (revealed preference methods). A commonly used approach is the contingent valuation method (CVM) (Boyle, 2003). This method relies on surveys in which respondents are asked the amount of money that they would be willing to pay for a change in environmental conditions in a constructed (hypothetical) market. Because of the hypothetical nature of the experiment, contingent valuation remains a controversial method (Hausman, 1993). Nonetheless, contingent valuation has been used to understand the full cost of invasive species - including aesthetics and other unpriced ecosystem services - in residential areas as well as public lands. For example, several contingent valuation surveys have elicited willingness to pay for better control of gypsy moth in residential landscapes in the United States (Jakus, 1992; Miller & Lindsay, 1993; MacDonald et al., 1997).

The contribution of forest landscape attributes to private property values can be studied using an economic welfare-theoretical method known as the hedonic property value method (Taylor, 2003). This method has been used to estimate the value that trees contribute to the sale values of homes from three perspectives: (i) garden or yard trees contribute to property values; (ii) forest preserves near residential neighbourhoods

² The use of average impacts can obscure important trends. For example, in an expanding (contracting) invasion, an average value will underestimate (overestimate) future impacts. Further, computed yield losses do not account for the substitution of alternative products in the market.

³ Holmes (1991) introduced a partial equilibrium model of the impact of pest-induced timber mortality on timber markets. The partial equilibrium model does not require the analyst to determine how price changes in the primary product market are transmitted to higher stages in the production chain, such as final product markets (which would require the estimation of a general equilibrium model). The partial equilibrium model of forest disturbance has been used to analyse the timber market impacts from other disturbances, such as hurricanes (Prestemon & Holmes, 2000).

⁴ Net changes in producer and consumer welfare over the period 1990 to 2040 due to invasive insect defoliators potentially arriving from Siberia and the Soviet Far East were estimated to range from US\$35-US\$58 billion using a 4% discount rate.

convey value; and (iii) trees in the general forest matrix surrounding residential areas convey value. These studies indicate that trees contribute, roughly, from 2% - 5% to the private property value of private residences (Morales, 1980; Anderson & Cordell, 1988; Garrod & Willis, 1992; Dombrow et al., 2000; Tyrvaïnen & Mietinnen, 2000). Consequently, we would expect that non-indigenous forest pests that cause a visible loss in forest health (Sheppard & Picard, 2006), or that ultimately cause tree mortality, would induce a loss of property values in residential areas.

Although evidence of the impact of non-indigenous forest pests on residential property values is limited, a recent study indicated that private property value losses due to infestations of the hemlock wooly adelgid in residential areas are large and that spillovers from properties with damaged trees to neighbouring properties are evident (Holmes et al., 2006; Huggett et al., 2008). Values reported in those studies indicate that (temporary) losses to residential property values can be as much as tens of thousands of US dollars per hectare of dead and dying eastern hemlock (*Tsuga canadensis* (L.) Carrière.).

In addition to the economic losses borne by private property owners in residential areas, forest pests can cause substantial non-market economic losses on public forest lands (Walsh et al., 1990; Haeefe et al., 1991). Household willingness to pay to avoid non-market economic losses, as measured by contingent valuation studies, is additive across the relevant population of consumers because forest protection is a public good (Holmes et al., 2008). Even conservative estimates of aggregate willingness to pay can be large, and should not be ignored. For example, Moore (2008) used a CVM study of households in North Carolina, USA to evaluate willingness to pay by residents of that state for a 3-year programme to control the hemlock wooly adelgid in the Great Smoky Mountain National Park and neighbouring United States Forest Service lands. He found that household willingness to pay is about US\$50/y. Summing this value across all households in North Carolina, the aggregate value of a 3-year protection programme exceeds US\$100 million/y. The values reported by Moore (2008) are consistent with other CVM studies of forest protection programmes reviewed by Kramer et al. (2003) who concluded that the total non-market economic value derived from protecting the health of public forests is largely due to the knowledge that healthy forest ecosystems exist (existence value) and will be maintained for future generations (bequest value).

A new economic damage framework for estimating large-scale impacts

General considerations

By focusing attention on biological invasions specifically affecting forests, rather than all invasions of terrestrial and aquatic ecosystems, robust bioeconomic methods may be developed that are able to capture the nuances of economic behaviour as well as the spatial-dynamic behaviour of economic damages. Here we offer several perspectives on how the economic basis of nationwide assessments might be improved.

Although large-scale biological invasions of forests can severely alter ecosystem structure and function, the long-term effects of species invasions are not well understood. In some instances, the effects of invaders change over time as various ecological and evolutionary processes come into play, and it has been proposed that it might be useful to think of invasions as having acute and chronic phases (Strayer et al., 2006). The transitory, acute impacts of biological invasions are likely to be more amenable to economic analysis (such as the costs of removing dead trees) than the slow, long-term impacts (such as the gradual alteration of ecosystem services). As suggested more than five decades ago, the separation of time scales into slow and fast variables provides a method for studying economic processes over time, and fast processes can be studied while holding slow processes constant (Samuelson, 1947; Simon & Ando, 1961). Therefore, we suggest that the time domain over which fast economic impacts are measured be carefully circumscribed, and that the time period used for analysis should be representative of damages caused by specific pests over relatively short time periods (perhaps a decade) during which reliable data are available.

A comprehensive assessment of the impacts to the forest economy in the United States resulting from the spread of non-indigenous organisms is needed (Holmes et al., 2009). It may be pragmatic to conduct such an assessment by tracking economic impacts by pest guild (foliage feeders, sap feeders, wood borers, and pathogens), as guilds are related to the pathways by which non-native organisms arrive and spread. Shogren (2000) proposed that pest impacts be modelled as probability density functions that can be shifted by management actions. However, from a practical perspective, it may be too costly to measure

the economic impacts of every non-indigenous forest organism and the data linking management actions and probabilistic outcomes may not be available. Further, Horan et al. (2002) questioned whether probabilities can be meaningfully estimated for biological invasions which have no historical precedent. Alternatively, attention could be focused on measuring the impacts of organisms that cause the greatest economic losses within each guild. Although there is great uncertainty regarding which organisms will ultimately cause future economic disruptions, a cautious approach to decision-making would be to minimise pest damage plus control cost under a worst-case scenario (Moffitt & Osteen, 2006). The development of worst-case scenarios for each pest guild may proceed by focusing on pests that have historically demonstrated severe economic impacts and for which information on spread rates are available.

Further, analysis could proceed by identifying separable economic sectors in the forest economy: (i) the government sector (where data may be available regarding local, state, and federal expenditures); (ii) the market sector (which may include the nursery sub-sector as well as the timber sub-sector); and (iii) the household sector (where data on expenditures by residential forest owners and changes in residential property values are becoming increasingly available).⁵ Governmental and residential expenditures represent transfers of wealth between sectors (such as from homeowners to tree-removal firms). Impacts on residential property values and market-enterprises typically represent wealth that is lost from the economy. Maintaining separate accounts for costs and losses clearly identifies which impacts represent transfers of economic value and which impacts represent the loss of value to the economy.

It is important to recognise that the methods used to compute economic impacts within economic sectors will often dictate that impacts not be added across sectors and sub-sectors. This restriction avoids double counting and inconsistency. For example, within the government sector, federal expenditures may subsidise local expenditures. Or, within the household sector, household expenditures may directly affect changes in residential property values, and therefore, the economic impacts in these sectors should not be summed. Further, the conceptual framework used for analysis may differ across sectors and sub-sectors. Values computed using different economic frameworks (such as government expenditures versus property value loss) should not be summed because the conceptual basis is not consistent across these measures.

Population growth, dispersal, and spatial geometry

For the land-based sectors of the forest economy, it may be possible to model the spread of economic damage over time and space. Each stage of a successful biological invasion involves: (i) population growth; (ii) dispersal of organisms; and (iii) spatial geometry. The classic approach to modelling a biological invasion uses a partial differential equation model which combines logistic population growth with Brownian random dispersal (Skellam, 1951). In one (homogeneous) spatial dimension, the partial differential equation describing population growth and spread is:

$$\frac{\partial N(x,t)}{\partial t} = r N \left(1 - \frac{N}{K}\right) + D \frac{\partial^2 N(x,t)}{\partial x^2} \quad [1]$$

where $N(x,t)$ is the population density of the population as a function of spatial location x at time t , r is the intrinsic (per capita) growth rate, K is the carrying capacity, and D is a measure of the mean squared displacement of individuals per unit time (measured in units of distance²/time). This model produces a traveling wave of invaders that moves across a homogenous landscape at a velocity that approaches $v = 2\sqrt{rD}$ as the invasion unfolds. In the two-dimensional case, the asymptotic wave speed for the one-dimensional case applies, and circular waves spread outward across a homogeneous plain (Holmes et al., 1994). This model provides the prediction of a linear relationship between the square root of the area invaded and time.

The assumption in the classic invasion model that invasion occurs in a homogeneous landscape ignores spatial geometry and landscape pattern. Viewing landscapes as spatially heterogeneous areas, in which the spatial distribution of habitats and populations affect the invasion process, is a key perspective in emerging models of biological invasions (With 2002; Hastings et al., 2005; Dewhurst & Lutscher, 2009). Allowing the quality of habitat patches to vary along a one dimensional landscape, by varying both r and D periodically in space, a travelling wave is obtained (as in the case of a homogeneous landscape). However, the asymptotic velocity of the wave is determined by the arithmetic mean of r (r_a) and the harmonic mean for D (D_h) across the different patches (Shigesada et al., 1986)⁶:

$$v = 2\sqrt{r_a D_h} \quad [2]$$

⁵ The absence of feedback between economic sectors is a reasonable assumption if the time scale of analysis focuses on the short term.

⁶ The harmonic mean is used when an average of rates is desired, such as an average travel speed.

Unfavourable habitats can thus deter the speed of invasion spread. Because harmonic means are much lower than arithmetic means when variation is high, the impact of diffusion variability across patches can have a large impact on invasion speed (Holmes et al., 1994). In addition, recent empirical evidence suggests that landscape geometry can affect both the initiation and spread of forest pest travelling waves (Johnson et al., 2004).

Empirical evidence confirms the prediction of the diffusion Equation [1] that the square root of an invaded area is linearly related to invasion time (i.e. the range expands at a constant rate) for introduced species such as the muskrat (*Ondatra zibethica* L.) in Europe (Skellam, 1951; Andow et al., 1990). However, the spread rates of other invasions appear to increase at an exponential rate over time (Hastings et al., 2005). The dispersal for many organisms is leptokurtic, or fat-tailed, rather than normally distributed (Kot et al., 1996). Long-distance dispersal of invasive organisms can result from dispersal by birds or other wildlife as well as human-mediated transport. Jump-dispersal events, in combination with short-distance dispersal by Brownian diffusion, can create new colonised patches of invaders, which provide new foci for spread, and leads to a faster rate of spread than diffusion from a single focus location (Shigesada et al., 1995).

Dispersals of invading organisms that follow leptokurtic distributions have been studied using integrodifference equation models (Kot et al., 1996). In contrast to partial differential equation models which assume that growth and dispersal occur simultaneously, integrodifference equation models separate these processes into stages which, in turn, affects invasion speed (Neubert & Caswell, 2000). The model includes terms for population growth and dispersal (here along a one-dimensional landscape):

$$N_{t+1}(x) = \int_{-\infty}^{\infty} k(x,y) f[N_t(y)] dy \quad [3]$$

where $N_{t+1}(x)$ is the population density at destination point x , $f[N_t(y)]$ is the population growth function at point y , and $k(x,y)$ is the dispersal kernel that accounts for the movement of organisms across points in space. Thus, Equation [3] determines the population of invaders at any point (x) along the linear transect by accounting for the growth and dispersal of organisms at all origins (y) and their dispersal to x .

An analytical treatment of stratified diffusion, in which organisms spread locally by Brownian diffusion and create remote colonies by a jump process, demonstrates that combined processes can greatly increase invasion rates (Shigesada et al., 1995). Let the size distribution of scattered colonies at time t

be denoted by $s(r,t)$, where $s(r,t)dr$ represents the number of colonies with radii length between r and $r + dr$. The size distribution function is governed by the von Forester equation (Trucco, 1965; Shigesada et al., 1995) which describes the change in $s(r,t)$ as new colonies are created over time and as the radii of colonies expand:

$$\frac{\partial s(r,t)}{\partial t} + v \frac{\partial s(r,t)}{r} = 0 \quad [4]$$

Equation [4] is subject to conditions describing the formation of new colonies: (1) the radius of new colonies is zero at time $t = 0$, and the number of new colonies formed is determined by the rate at which long-distance dispersal is successful. The total area invaded, $A(t)$, is given by the integral:

$$A(t) = \int_0^{\infty} 2\pi r^2 s(r,t) dr \quad [5]$$

If data at a suitable scale are available, the left-hand-side of Equation [5] can be measured directly. Shigesada et al. (1995) define the effective range radii as $\sqrt{A(t)/\pi}$, which increases exponentially over time. They go on to fit this model to historical observations on the spread of cheat grass (*Bromus tectorum* L.) in the western United States, which is thought to be spread by neighbourhood diffusion as well as by animals and transportation facilities.

Despite the elegance and predictive power of theoretical models of biological invasions, the relationship between the arrival of a non-indigenous organism and the time (and extent) of economic damage is not identical. In general, economic damage lags behind the general spread of an invasive organism, and depends upon the population dynamics of invasive species within infected areas. For example, it is anticipated that, in many cases, economic damage in forests results from reductions in tree growth or tree mortality, which are lagged functions of the arrival of an invasive organism. Further, a critical threshold may need to be crossed before economic impacts are observed. The desired approach to conduct economic analysis would directly model the spread of economic damage over space and time.

With this purpose in mind, define the area of economic damage (AED) as the sum of those areas on the landscape that sustain economic damage from a biological invasion. The AED occurs at the spatial intersection of forest resources with specific economic values (such as residential forests) and the presence of damage caused by a non-indigenous organism

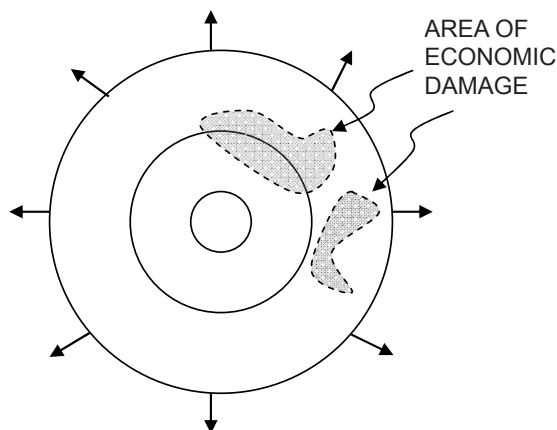


FIGURE 1: Travelling waves and the area of economic damage (AED). The circles represent the range of an organism over successive periods. The shaded polygons represent the areas where economic damage occurs.

(Figure 1). Understanding the spatial geometry of the AED, and how the economic value of these landscapes are influenced by spatial-dynamic processes, is a key aspect in the bioeconomic modelling of biological invasions.

Bioeconomic damage models of spatial-dynamic invasion processes

Bioeconomic damage models of spatial-dynamic invasions are needed that link economic losses at specific geographic locations with spatial models depicting the pattern of range expansion of a non-indigenous organism (Sharov & Liebhold, 1998). This can be accomplished applying models of the spread of a biological invasion to the spread of the AED, recognising that the AED results from spatial invasion dynamics, outbreak dynamics of non-indigenous forest pests, and the actions taken by producers and consumers in the economy to mitigate damages.

The first step in modelling bioeconomic losses is to conduct a site specific microeconomic analysis of producer and/or consumer behaviour at a location, or set of locations, directly impacted by a biological invasion. The behavioural economic model, which represents a sample drawn from the population of locations impacted by an invasive organism, provides information on the economic damage per unit of invaded area.⁷ Spatial units used for analysis (trees,

hectares, etc.) will depend upon the scale of analysis and the data available.

The second step in bioeconomic damage modelling of an invasion process is to identify the number of spatial units per unit of time that are damaged in the way described by the behavioural economic model. The spatial configuration of economic damages across the invaded landscape is a function of the spread of the invasive organism and the location of microeconomic units. The identification of the spatial microeconomic units across the landscape that are impacted by a biological invasion can be accomplished using Geographic Information Systems (GIS). Stochastic simulation using a raster-based GIS surface could then be employed to predict infestation and economic damage (Kovacs et al., 2009).

In general, we would like to know the total area sustaining economic damage in situations where damages are incurred either contemporaneously or as a lagged function of the arrival time of a non-indigenous species, and where economic damages may occur in discrete patches, or colonies. Information on the total AED - due to a specific invader at discrete points in time - can then be used to estimate the rate of spread of economic damages using the scattered colony model described by the stratified diffusion model (Shigesada et al., 1995). The effective range radius (*sensu* Shigesada et al., 1995) of the AED can be estimated simply as:

$$\frac{\sqrt{AED_t}}{\sqrt{\pi}} \quad [6]$$

where AED_t is the total area of economic damage across all economic damage colonies at time t . The rate of radial expansion (v_t) can then be computed as a function of time:

$$v_t = \frac{\left(\sqrt{AED_{t+n}} / \pi + \sqrt{AED_t} / \pi \right)}{n} \quad [7]$$

where n is the number of time periods (Liebhold & Tobin, 2008). If time series data are available, v_t can be regressed on time to estimate empirical range versus time curves. Various functional forms, such as linear versus exponential spread, can be tested and used to evaluate the nature of the range-versus-time curves.

⁷ *Methods of benefit transfer, in which estimates of non-market value obtained in one or more studies are applied to new "policy" sites, may be useful in this step.*

Once a curve is fitted, the slope of the curve can be used to predict the average value of v_t in every time period, which, in turn, may be used to compute the level of economic damage during past, current, and future time periods:

$$D_t = v_t^2 \pi d_t \quad [8]$$

where D_t is the aggregate economic damage across the AED at time t , and d_t is the economic damage per unit at time t . Aggregate economic damage ($D(n)$) across n time periods, discounted to the present, is then simply:

$$D(n) = \sum_{t=1}^n D_t e^{-\kappa t} \quad [9]$$

where κ is the economic discount rate.

Although the spatial-dynamic model underpinning this approach to economic damage assessment assumes that all colonies of economic damage are circular in shape, the spatial geometry of actual AEDs will often be fragmented. Thus, the bioeconomic damage model represented by Equations [6] – [9] is proposed as a reasonable first approximation to estimate total economic losses to non-timber values from the spread of a non-indigenous organism.

Summary and Conclusions

Biological invasions of forests by non-indigenous organisms present a complex, persistent, and largely irreversible threat to forest ecosystems around the globe. Introductions and spread of non-indigenous pests result from economic processes such as international and domestic trade. Although most non-indigenous organisms have a minor impact, a few organisms have major ecological and economic impacts. Rigorous assessments of the economic impacts of introduced species in forest ecosystems, at a national scale, are necessary to provide credible information to policy makers.

In this paper, we propose that economic assessments of the aggregate damages induced by biological invasions need to link microeconomic analyses of site-specific economic losses with ecological models of invasion spread. This is accomplished by recognising that the economic impacts of biological invasions proceed via spatial-dynamic processes, and that the economic landscape is not homogeneous, but is comprised of discrete patches of economic value.

With this purpose in mind, the area of economic

damage was defined as the areas on the landscape that sustain economic damage from a biological invasion. Methods were then described to model the dynamics of the spread of economic damage based on an ecological model of stratified diffusion in which invasions spread both by local and long-distance processes. By rigorously estimating the economic damages associated with the worst pests in each guild of biological organisms which have historically arrived in new territory, and conducting economic analysis for each economic sector that is impacted by the establishment and spread of non-indigenous species, estimates of the economic impacts of biological invasions can be obtained and used to inform policy analysis.

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