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Assessing the Cost of an Invasive Forest Pathogen: A Case Study with Oak Wilt

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Abstract Economic assessment of damage caused by invasive alien species provides useful information to consider when determining whether management programs should be established, modified, or discontinued. We estimate the baseline economic damage from an invasive alien pathogen, *Ceratocystis fagacearum*, a fungus that causes oak wilt, which is a significant disease of oaks (*Quercus* spp.) in the central United States. We focus on Anoka County, Minnesota, a 1,156 km^2 mostly urban county in the Minneapolis-Saint Paul metropolitan region. We develop a landscape-level model of oak wilt spread that accounts for underground and overland pathogen transmission. We predict the economic damage of tree mortality from oak wilt spread in the absence of management during the period 2007–2016. Our metric of economic damage is removal cost, which is one component of the total economic loss from tree mortality. We estimate that Anoka County has 5.92 million oak trees and 885 active oak wilt pockets covering 5.47 km^2 in 2007. The likelihood that landowners remove infected oaks varies by land use and ranges from 86% on developed land to 57% on forest land. Over the next decade, depending on the rates of oak wilt pocket establishment and expansion, 76–266 thousand trees will be infected with discounted removal cost of \$18–60 million. Although our predictions of removal costs are substantial, they are lower bounds on the total economic loss from tree mortality because we do not estimate economic losses from reduced services and increased hazards. Our predictions suggest that there are significant economic benefits, in terms of damage reduction, from preventing new pocket establishment or slowing the radial growth of existing pockets.

Keywords Pest risk analysis · Impact analysis · Pest invasion · Economic impact assessment

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Introduction

Invasive alien pathogens are one of the most significant causes of tree mortality in the United States (Loo 2009). For example, once-widespread American chestnut trees (*Castanea dentata*) were defenseless against the introduced chestnut blight (caused by *Cryphonectria parasitica*), and American elms (*Ulmus americana*) succumbed in large numbers to Dutch elm disease (caused by *Ophiostoma* sp.). Similar fears are engendered by recent discoveries of the Sudden Oak Death pathogen (*Phytophthora ramorum*) in

California (Rizzo and Garbelotto 2003). While individual landowners have several options to mitigate the effects of incoming invaders (e.g., prophylactic fungicide treatment of uninfected elm trees), more effective approaches involve landscape-level management to prevent or slow the introduction, establishment and spread of damaging invaders (Liebhold and others 1995, Lodge and others 2006, Venette and Koch 2009). The public good quality of these landscape-level approaches may justify public investment.

The argument for public investment to manage forest pathogens depends in part on the economic benefits of these investments. Relative to a baseline of no management, the benefits of a management plan are the damages avoided because that management plan is in place. Damages from a pathogen include expenditures to treat or remove infected trees as well as economic losses from reduced ecosystem services and commerce and increased hazards associated with tree infection or mortality. To compute economic benefits, it is important to first have an estimate of the baseline damage for the situation where the pathogen grows without restraint. The second step is to compute the net economic benefits of alternative management plans by estimating the benefits (damages avoided) and management costs of the alternatives. Any plan with positive net benefits would be an improvement over the baseline because the damages avoided would outweigh the management costs.

We undertake the first step and estimate the baseline economic damage from unfettered spread of a forest pathogen population. The calculation of the baseline damage is challenging in a heterogeneous landscape with multiple cover types, land owners, and land uses. First, a landscape-level model of pathogen spread is needed to predict the pattern of tree mortality over time that is likely to be caused by the current infestation. Second, a measure of economic damage associated with trees lost due to the pathogen is needed to compare in the same terms to the cost of management. We address these two challenges to estimating baseline damage from an invasive alien pathogen, *Ceratocystis fagacearum*, the fungus that causes oak wilt. We contribute a new method for predicting mortality from oak wilt spread and a well-reasoned metric for economic damage resulting from that mortality. Our methods are appropriate for heterogeneous landscapes where biological and economic factors vary across space.

Oak wilt is the most significant disease of oaks (*Quercus* spp.) in Minnesota, Iowa, Illinois, Wisconsin and Texas (Ostry and Juzwik 2008). Oak wilt was first identified in Wisconsin in 1942, but evidence suggests the pathogen is not native to the United States (Juzwik and others 2008). The disease is currently found in many eastern and midwestern states. Oak wilt affects many varieties of oak species, but the effects on red oaks species (section Lobatae) are the most serious as red oak mortality is highly probable within a year of infection (Koch and others 2010). Although the geographic extent of oak wilt has remained relatively unchanged in past decades, the number of trees affected by oak wilt continues to grow within the area where oak wilt is currently present. Long-distance dispersal into entirely new areas is possible as with the first detection of oak wilt in New York state in 2008 (Jensen-Tracy and others 2009) and the disease appearance in the Upper Peninsula of Michigan (Juzwik and others 2008). Human transport (e.g., firewood movement) is the most likely pathway for long-distance dispersal.

We focus on Anoka County, Minnesota, a 1,156 km^2 county with 327,000 people (as of 2008) in the Minneapolis-Saint Paul metropolitan region (Fig. 1). Anoka County has a large native population of red and white oaks, which have experienced significant mortality from oak wilt over the last two decades. We chose this study area because of

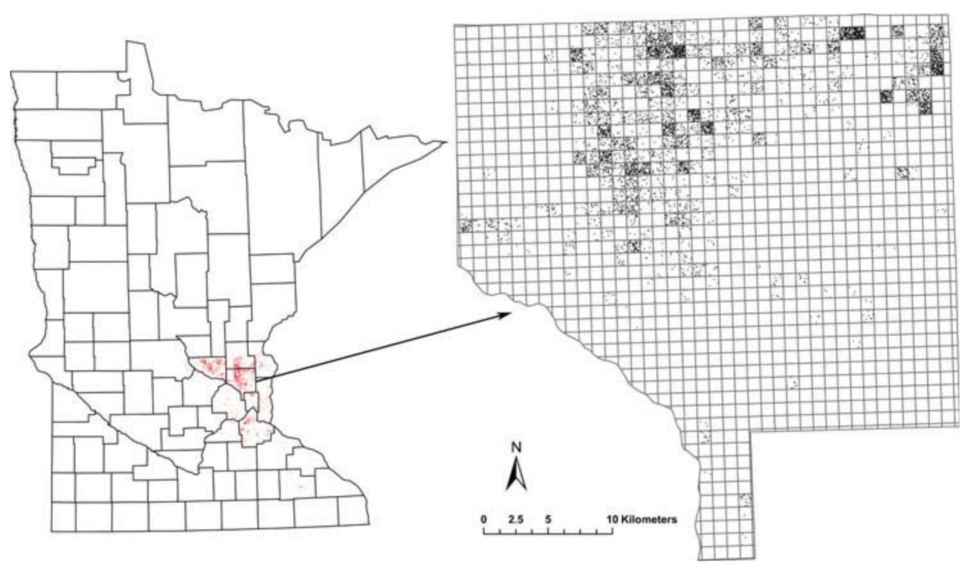

Fig. 1 Density of infected oaks (1 *dot* = 5 trees) in Anoka County, Minnesota, relative to the distribution of oak wilt pockets detected between 2003–2006 within the state

the severity of oak wilt mortality, the existence of estimates of oak wilt spread (Shelstad and others 1991), and the availability of digital maps of oak wilt pockets, land use, and land cover.

Our first objective is to develop a landscape-level model of oak wilt spread that accounts for the two common means of oak wilt transmission: underground and overland spread. Root systems of related (within the same section) and adjacent oak trees are frequently grafted together, and the disease can be transmitted underground through the root grafts between diseased and healthy trees. This transmission mechanism is responsible for the characteristic landscape pattern of oak wilt infection known as an infection center or "pocket," which expands in size over time. New pockets are established when beetles (family Nitidulidae) feed on the fungal mats of *C. fagacearum*, acquire spores, and move to trees that have been freshly wounded. This type of transmission is known as "overland spread" (Gibbs and French 1980).

Our second objective is to estimate some of the economic damage from oak wilt if the disease were to spread without management. For this objective, we use removal cost as a metric. Ordinances in many cities require residents to remove diseased and dangerous trees that are close to structures and frequently visited areas. Even without these ordinances, diseased trees are likely to be removed to avoid liability associated with their falling and causing injury or property damage. However, we recognize that not all trees are removed by property owners, so we use a unique data set to estimate the propensity to remove trees according to land use. Our approach is a form of partial budgeting, a common method to estimate the economic impact of invasive alien species (Soliman and others 2010).

When diseased or dead trees are removed, in addition to paying for tree removal, landowners lose the services that trees provide. While there are methods appropriate for measuring the value of these services, we restrict ourselves to removal costs as just one component of the economic damages from tree mortality. As such, our methodology provides a lower bound estimate of the total economic damages associated with unfettered spread of the pathogen population.

Methods

In this section we discuss the development of a landscape-level model of oak wilt spread and the calculation of tree removal cost associated with mortality caused by the pathogen. Since oak wilt pockets grow slowly and infect neighboring trees, our geographic unit of analysis is a 1 km^2 grid cell. In each cell, we estimate oak density, the current number of oak trees infected, and area proportions in land uses. To forecast the number of oak trees infected over time, we use a model of overland spread to create new pockets and a model of radial spread to expand existing pockets. To estimate removal cost, we estimate the proportion of the infected trees that are removed based on observed oak wilt treatments in different land uses. Thus, we take advantage of cell-specific data to estimate the number of infections and removals over time in each cell. Aggregating these numbers provides a picture of the overall severity of the oak wilt problem in the study area.

Model of Oak Wilt Infection and Tree Removal

We divide our landscape into N grid cells and model the number of infected oak trees $x_i(t)$ in cell i year t over a T-year horizon. Each year, some fraction f_i of newly infected trees $x_i(t) - x_i(t-1)$, is removed in each cell with average per-tree removal cost c. The total cost of oak wilt infections is the present value of these removal costs evaluated using the discount rate δ

$$PV = \sum_{i=1}^{N} cf_i x_i(0) + \sum_{t=1}^{T} \sum_{i=1}^{N} \frac{cf_i[x_i(t) - x_i(t-1)]}{(1+\delta)^t}. \qquad (1)$$

We assume that a fraction of the newly infected trees is removed each year because infected red oaks die quickly and landowners who remove dead trees do so immediately to avoid property damage. We can easily extend the model to increase the times between infection, mortality, and removal if needed.

Our model of number of infected trees in each cell, $x_i(t)$, $t = 1,\ldots,T$, is based on an age-class model of oak wilt pockets that incorporates the two types of pathogen spread: pocket establishment and pocket expansion. For each cell i, we define $n_{ij}(t)$ as the number of pockets age j in year t. Defining $\lambda_i(t)$ as the number of new pockets that establish in cell i in year t, we can write a system of equations for updating the age distribution of pockets:

$$\begin{aligned} n_{i1}(t) &= \lambda_i(t) \\ n_{ij}(t) &= n_{ij-1}(t-1) \quad j = 2,3,\ldots;\ t = 1,\ldots,T; \end{aligned} \qquad (2)$$

where the initial age distribution of pockets, $n_{i1}(0)$, $n_{i2}(0)$,…, is estimated based on an inventory of pockets in each cell.

The age distribution of oak wilt pockets is used to calculate the number of infected oaks in each cell. We assume that oak wilt pockets grow steadily in a circular pattern with a constant radial growth rate, r. Defining a_j as the area of a pocket age j, we calculate pocket area based on radial growth:

$$a_j = \pi(rj)^2 \quad j = 1,2,\ldots \qquad (3)$$

Given an estimate of oak tree density in each cell, d_i, we compute the number of infected trees as the product of oak density and total area of oak wilt pockets:

$$x_i(t) = d_i \sum_j n_{ij}(t) a_j \quad t = 0, \ldots, T. \tag{4}$$

The upper limit on the number of trees infected in a cell is the number of oaks susceptible to infection $\bar{x}_i$.

Empirical Model Components

To apply this model of oak wilt infection and removal, we need estimates of oak density and the initial number and size of oak wilt pockets in each grid cell. We also need estimates of the radial growth rate of existing pockets, the establishment rate of new pockets, the fraction of the newly infected trees that are removed in each cell, and the cost of tree removal. Finally, we need to set the time horizon and discount rate. Our approach involves dividing Anoka County into 1240 grid cells so that we can accommodate the spatial heterogeneity in existing oak wilt pockets, oak density, and oak wilt treatment. Grid cells are 1 km^2 except on the edge of the county where they are smaller. In this section, we describe our data sources, outline the steps taken to estimate cell attributes, and describe our simulation model for projecting oak wilt infections over time.

Number and Area of Existing Oak Wilt Pockets

We estimate the number and area of existing oak wilt pockets in each cell using the ReLeaf database, a statewide inventory of oak wilt pockets maintained by the Minnesota Department of Natural Resources (MN-DNR). The database includes the location and size of each pocket, the year in which the pocket was detected, whether the pocket was treated, and the types of treatments applied. The database includes 4,283 pockets in Anoka County recorded from 1992–2007, and the boundaries of the pockets are represented by polygons in a digital map. We use the number and area of oak wilt pockets discovered between 2003 and 2006 for our starting conditions because many new oak wilt pockets were discovered in 2003 and few oak wilt pockets discovered prior to 2003 are probably active now. Himelick and Fox (1961) showed that on average, infection centers actively spread for 4.3 years, but, then may undergo a quiescent period of on average 2.7 years in which no spread is observed, only to resume spreading later, depending on the number of trees in the infection center.

We use ArcMap (Environmental Systems Resource Institute (ESRI) 2009) to spatially join our grid surface with the digital map of oak wilt pockets in Anoka County. For each grid cell, we first compute the number and area of pockets and average pocket area. Then, we assign the average pocket an appropriate age based its area and the rate of radial growth, *r*. Finally, we assume that all pockets in the cell are the same age so that the initial age distribution of pockets, $n_{i1}(0)$, $n_{i2}(0)$,…, includes zeros except for the age class of the average pocket, which has a value equal to the number of pockets in the cell.

Oak Density

We estimate the density of oak trees in each cell using three sources of information: an oak wilt treatment compliance database from MN-DNR, a land cover database from the Minnesota Land Cover Classification System (MLCCS) (Minnesota Department of Natural Resources 2009), and a forest inventory database from the Forest Inventory and Analysis (FIA) section of the U.S. Forest Service (USDA Forest Service 2011). The oak wilt treatment compliance database includes a digital map of 27 oak wilt pockets in Anoka County that were treated in 2004 and checked in 2007. The attributes of each pocket include area, type of treatment, number of infected oaks that had been removed, and number of healthy oaks that had been removed preemptively or injected with fungicide. The MLCCS includes a digital map of land cover polygons classified into 252 cover types for Anoka County. The FIA database includes estimates of number of trees by species and size class on forest land in Anoka County.

We estimate oak density in the six primary land cover types included in the MLCCS database: forest, woodland, shrubland, herbaceous, cultivated vegetation, and artificial surface. The primary cover types are distinguished by the level-one land cover designation (i.e., the first digit of a 5-digit classification code). First, we use ArcMap to spatially join the primary cover type map with a digital map of the 27 oak wilt pockets that underwent compliance checks. Next, we counted the number of pockets that contain each cover type. Finally, we compute the average oak density of each primary cover type based on the oak densities in the pockets that include the cover type. Attributes of the pockets that were used to generate these estimates are described in Table 1. Because the compliance-check plots are located in non-forest cover types, we use the estimate of oak density obtained from the FIA data base for our estimate of oak density in the forest cover type. Based on forest inventories conducted between 2001 and 2005, 3.1 million oaks (±0.1 million SEM; $n = 91$) grow on 19,270 ha of forestland in Anoka County for an average density of 160.9 trees/ha (Miles 2011). In the FIA database, forest land has a specific definition—area at least one acre (0.405 ha) in size, at least 120 feet (36.6 m) wide, at least 10 percent stocked with trees, and with an understory undisturbed by another non-forest land use—and can be thought of as forest outside of developed areas. We assume that the forest cover type from the MLCCS database, which covers 19,848 ha in Anoka County, is equivalent to forest land as defined in the FIA database.

Table 1 Attributes of infection centers used to estimate likelihood of oak removal and oak densities in non-forest cover types of Anoka County, MN, USA

	Likelihood of oak removal[a]	Oak densities[b]			
Primary land cover type	n[c]	n[d]	Minimum area (ha)	Maximum area (ha)	Mean area (ha)
Artificial surfaces	3,452	25	0.26	6.31	1.67
Cultivated vegetation	524	1	NA	NA	6.31
Forest	1,509	NA	NA	NA	NA
Woodland	345	3	0.28	6.75	2.69
Shrubland	159	1	NA	NA	3.51
Herbaceous	739	6	0.27	6.75	4.11

NA not applicable

[a] Data from MN Department of Natural Resources ReLeaf database of treated infection centers

[b] Data from MN Department of Natural Resources compliance checks of treated oak wilt infection centers

[c] *n* is the number of oak wilt infection centers in Anoka County that include the cover type

[d] *n* is the number of oak wilt infection centers with compliance checks in Anoka County that include the cover type

We estimate oak density of each cell, d_i, by first joining the grid surface with the primary cover type polygons and calculating the area proportions of each cell. Then, we multiply the oak densities of the cover types by the area proportions of the cover types and sum to obtain the cell's oak density. Multiplying oak density by cell size gives the expected number of oaks in the cell, which serves as an estimate of the number of trees susceptible to infection, $\bar{x}_i$. The product of the cell's oak density, the initial number of oak wilt pockets, and area of the average oak wilt pocket gives the initial number of infected oaks, $x_i(0)$ (Eq. 4).

Oak Removal

The fraction of newly infected trees removed may vary across cells because of differences in land use. While residential property owners are often compelled by city ordinances to remove diseased or dead trees, rural residents may allow dead trees to remain standing because the cost of removing them outweighs the cost of leaving them. We estimated the likelihood of removal of newly infected oak trees for each primary land cover type. First, we extracted 4,283 records of oak wilt pockets in Anoka County from the MN-DNR ReLeaf database and noted whether or not each pocket was treated. We used oak wilt treatment as a proxy for oak removal because treatment sometimes involved actions other than tree removal. These treatments represent real dollar investments as a consequence of oak wilt and reflect propensity to pay. Next, we joined the digital map of oak wilt pockets with the map of the primary land cover types from the MLCCS database and counted the number of pockets that contain each cover type (Table 1). Finally, we applied logistic regression to these data to estimate the likelihood of removal of newly infected oak trees for each cover type. We estimated the fraction of newly infected oak trees removed in each cell, f_i, by multiplying the cover type proportions for the cell by the likelihoods of removal for the cover types and then summing.

Other Model Parameters

a. Pocket radial growth rate, r: Shelstad and others (1991) tracked oak wilt infection centers in Minnesota over a ten-year period. They report a mean value for the radial growth rate r of 3.47 m year^{-1} with a range of 2.42–4.43 m year^{-1}. To account for the range of possibilities, we report results for $r = 2.42$, 3.47, and 4.43 m year^{-1}.
b. Pocket establishment rate, λ: Shelstad and others (1991) report a mean establishment rate of 0.015 pockets ha^{-1} year^{-1} in forestland in Anoka County with a range of 0.011–0.025 pockets ha^{-1} year^{-1}. To account for the range of possibilities, we report results for $\lambda = 0.000$, 0.011, 0.015, and 0.025. To convert λ to a pocket establishment rate for a grid cell with forest and non-forest cover types, we calculate the probability that an individual tree will become infected by multiplying the pocket establishment rate (e.g., 0.015 pockets ha^{-1} year^{-1}) by the area of forest land in Anoka County (19,270 ha) and dividing by the number of oaks on forest land (3,091,671 trees). For example, for a pocket establishment rate of 0.015 pockets ha^{-1} year^{-1}, the probability of a tree becoming infected and starting a new pocket is 0.0000935 year^{-1}. For a given pocket establishment rate, we assume that the per tree infection rate is constant across grid cells and time. The number of new pockets in a grid cell ($\lambda_i(t)$ in Eq. 2) is calculated using a series of $q = \bar{x}_i - x_i(t)$. Bernoulli trials with probability p, where q is the

number of healthy trees and p is the annual per tree probability of infection.

c. Per-tree removal cost, c: We assume that infected trees are removed at a cost of \$360 per tree. McPherson and others (2006) report a removal cost of \$11.81 per cm diameter at breast height (d.b.h.) for public trees and \$15.75 per cm for yard trees. We assume an average public tree is 30.5 cm d.b.h. and an average yard tree is 22.9 cm d.b.h.

d. Discount rate, δ: The annual costs of removal were discounted to the present using a 2% real discount rate. Howarth (2009) observes that the future benefits of a public good should be discounted at a rate close to the rate of return for risk-free financial assets, even when the public good has risk characteristics equivalent to those of risky forms of wealth.

e. Time horizon, T: We report results for a 10-year time horizon, from 2007–2016. We chose a decade for our analysis because human caused dispersal of the pathogen may have significantly altered the pattern of infection in longer time periods. Empirical evidence also suggests that a single infection center will naturally stop spreading in 6–13 years, depending on the number of trees in the infection center (Himelick and Fox 1961). Infection centers with three or fewer trees are likely to stop spreading in 5 years or less. Infections centers with more than three trees are likely to stop spreading in 2 to 13 years. Based on data from the MN-DNR compliance checks, 70% of the infection centers had more than three trees. Projecting the oak wilt infestation and costs further than a decade would require assumptions that are difficult to justify.

Simulation Model

We simulate oak wilt infection in each cell over a 10-year horizon (Eqs. 2–4) and compute the total discounted cost of removing infected trees (Eq. 1). In the first year, we compute the average area and radius of existing oak wilt pockets, classify the existing number of pockets into an age distribution, $n_{i1}(0)$, …, $n_{iJ}(0)$, and calculate the number of infected trees $x_i(0)$ (Eq. 4) and removal cost, $cf_i x_i(0)$ (first term in Eq. 1). At the beginning of each subsequent year, we update the age distribution of oak wilt pockets (Eq. 2) and calculate the number of infected trees (Eq. 4). If the number of infected trees is greater than the estimate of the number of trees susceptible to infection $\bar{x}_i$, the number is set to this upper bound. Next, we compute the discounted cost of newly infected trees that are removed based on the difference in number of infected trees from the previous year (second term in Eq. 1). Finally, we add new oak wilt pockets ($\lambda_i(t)$ in Eq. 2).

The simulation model is stochastic because the number of new pockets in each grid cell each year is a binomial random variable. For a given set of model parameters, we estimate the expected number of trees infected and discounted removal cost from the results of 100 independent replications of the simulation. For sensitivity analysis, we repeat the simulations for 12 combinations of pocket establishment rate and radial growth rate.

Results

We estimate that Anoka County has 5.92 million oaks located in 1237 (99%) of the 1240 grid cells. Individual cells contain 3-15858 oaks. Cells with higher oak densities occur primarily in the northern third of the county (Fig. 2).

Oak densities vary with land cover type (Table 2). Cover types associated with human development (i.e., artificial surfaces and cultivated vegetation) cover 52% of Anoka County and natural vegetation types cover 48%. Oak density ranges from 160.9 trees ha^{-1} in the forest cover type to 3.5 trees ha^{-1} in the shrubland type. Oak density in the artificial surface cover type is 46.2 trees ha^{-1} and includes oaks growing on residential and commercial property and along streets. We acknowledge that the data from the MN Department of Natural Resources compliance checks emphasized areas with an artificial surface cover type. Oak density estimates for shrubland and cultivated

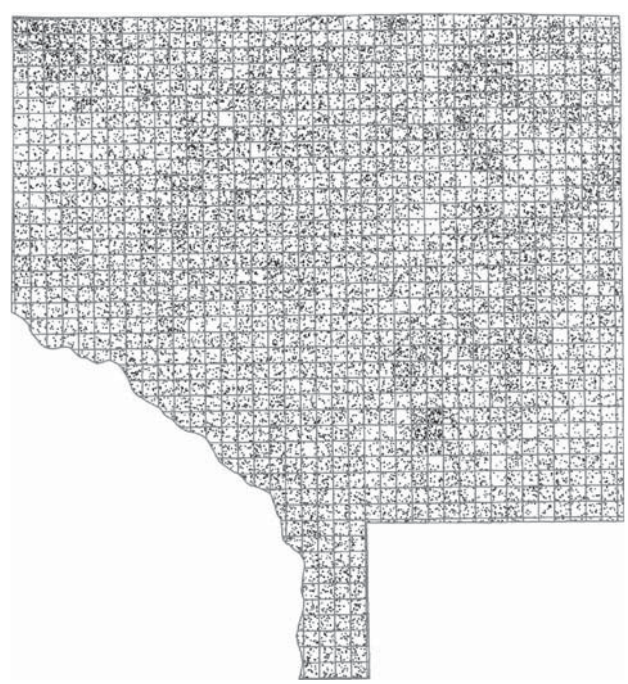

Fig. 2 Dot density plot of the initial number of oaks per grid cell. One *dot* is equal to 200 trees. Dot placement does not represent tree location

Table 2 Attributes of primary land cover types of Anoka County, MN, USA

Primary land cover type	Proportion of county[a]	Oak density (trees/ha) ± SEM	Likelihood of removing infected oak ± SEM[b]
Artificial surfaces	0.34	46.2 ± 7.6[c]	0.86 ± 0.01
Cultivated vegetation	0.18	8.7 ± NA[c]	0.71 ± 0.04
Forest	0.18	160.9 ± 6.2[d]	0.57 ± 0.02
Woodland	0.03	97.5 ± 56.6[c]	0.73 ± 0.04
Shrubland	0.06	3.5 ± NA[c]	0.62 ± 0.06
Herbaceous	0.21	26.1 ± 17.5[c]	0.67 ± 0.03

NA not applicable

[a] Data from MN Land Cover Classification System

[b] Data from MN Department of Natural Resources ReLeaf database of treated infection centers

[c] Data from MN Department of Natural Resources compliance checks of treated oak wilt infection centers

[d] Data from Forest Inventory and Analysis, US Forest Service

vegetation are based on information from one infection center per cover type (Table 1) and cannot be considered statistically valid. Nevertheless, the estimate for cultivated vegetation (e.g., farmland) is consistent with our presumption that oaks would only occur on the periphery of cultivated areas and thus would be less dense than in most other cover types. We had no presumption for oak densities in shrubland, but this cover type only represents 6% of the area of the county. We used all oak density estimates because no other information was available.

From the statewide inventory of oak wilt pockets in years 2003-2006, we estimate that Anoka County has an initial population of 885 oak wilt pockets located in 328 (26%) of the 1240 grid cells and covering 5.47 km^2. Average pocket sizes in the cells are 11–66949 m^2. Assuming a radial growth rate of 3.47 m year^{-1}, the ages of the average pockets are 1–42 years with most pockets being less than 10-years-old. Oak wilt pockets include 33583 infected trees, which are clustered in the north-central and northeastern parts of the county (Fig. 3).

The likelihood of removal of infected oaks varies by land cover type (Table 2) and ranges from 0.86 on developed land (artificial surfaces) to 0.57 on forest land. Proportions of infected oaks likely to be removed are higher in the southwestern part of Anoka County where development is dominant and lowest in the northeastern part where forest and herbaceous cover types dominate (Fig. 4).

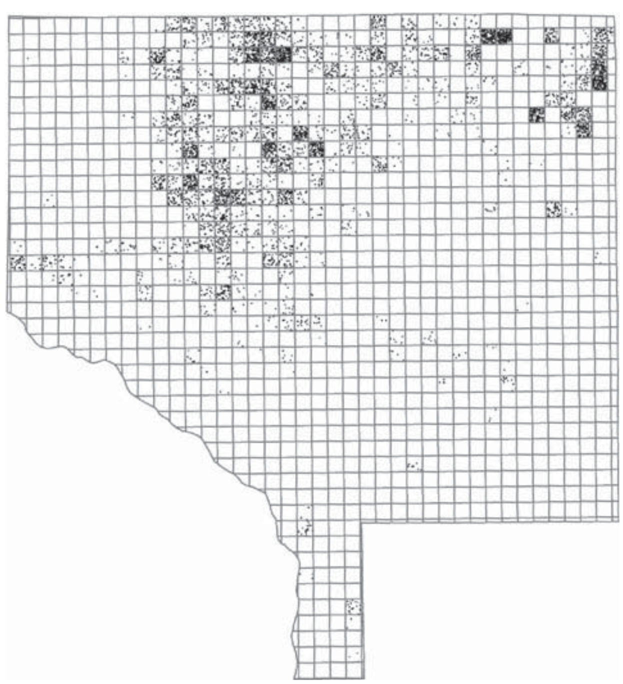

Fig. 3 Dot density plot of the initial number of trees infected with oak wilt per grid cell. One *dot* is equal to 5 trees. Dot placement does not represent tree location

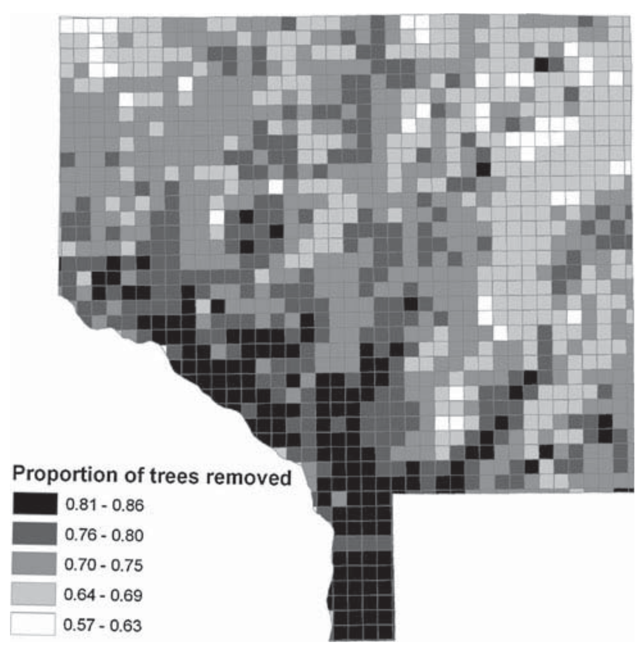

Fig. 4 Proportion of oak-wilt infected trees likely to be removed

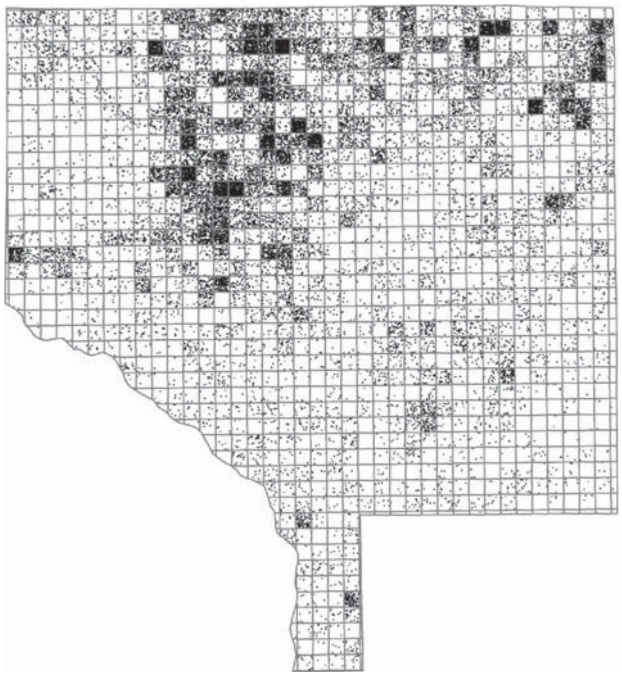

Fig. 5 Dot density plot of the number of trees infected with oak wilt after 10 years per grid cell. One *dot* is equal to 5 trees. Dot placement does not represent tree location. The dot density plot represents one outcome out of 100 independent replications of the stochastic simulation model

In the base case simulation with pocket radial growth of 3.47 m $year^{-1}$ and establishment rate of 0.015 pockets ha^{-1} $year^{-1}$, we project 156.3 thousand trees will be infected with oak wilt in ten years (Table 3A), less than 3% of the estimated 5.92 million at the start of the simulation. The highest densities of infected oaks are in the north-central and northeastern parts of the county where most of the initial oak wilt pockets occur (Fig. 5). Small numbers of infected oaks are projected to occur throughout the county as new pockets become established.

Using the likelihoods of oak removal associated with the various land use types (Table 2), we estimate the discounted cost of removing infected oaks over ten years is \$35.4 million (Table 3B). If all infected trees are removed, mean discounted cost is \$50.9 million (Table 3C), which is 44% greater than our estimate of the cost of partial removal. This result shows the importance of estimating likelihoods of tree removal to obtain accurate estimates of total expenditures for tree removal.

The numbers of infected trees and discounted costs of removal are greatest in the forest and artificial surfaces cover types (Table 4). These land types cover large areas of Anoka County and have relatively high oak densities (Table 2).

Relative to the base case, decreasing (increasing) pocket establishment or radial growth rates decreases (increases) the number of infected trees and discounted removal cost (Table 3). For example, lowering the establishment rate from 0.015 to 0.000 pockets ha^{-1} $year^{-1}$ while maintaining the pocket radial growth rate of 3.47 m $year^{-1}$ reduces the number of infected trees by 32% and discounted cost by 31%. Slowing the radial growth from 3.47 m $year^{-1}$ to the lower end of the observed range (2.42 m $year^{-1}$) while maintaining the pocket establishment rate of the base case (0.015 pockets ha^{-1} $year^{-1}$) reduces the number of infected trees by 34% and discounted cost by 33%. These results suggest that there are significant economic benefits, in terms of damage reduction, from preventing new pocket

Table 3 Estimates[a] of number of trees infected with oak wilt and discounted costs of partial removal[b] and complete removal over a 10-year horizon

Pocket establishment (pockets ha^{-1} $year^{-1}$)	Pocket radial growth (m $year^{-1}$)		
	2.42	3.47	4.43
A. Number of trees infected (thousands)			
0.000	76.9	105.6	133.9
0.011	95.7	142.7	193.5
0.015	102.5	156.3	215.0
0.025	119.5	190.0	269.0
B. Cost of partial removal[b] (\$ millions)			
0.000	18.0	24.4	30.6
0.011	22.1	32.4	43.5
0.015	23.5	35.4	48.2
0.025	27.3	42.7	59.9
C. Cost of complete removal (\$ millions)			
0.000	26.0	35.2	44.3
0.011	31.8	46.7	62.7
0.015	33.9	50.9	69.3
0.025	39.2	61.3	86.0

[a] Estimates are averages computed over 100 simulations of oak wilt pocket establishment and expansion. The standard errors associated with the averages (not shown) are less than 0.1% of the means

[b] Estimates of the cost of partial removal are computed using the likelihoods of removing infected oaks associated with the various land use types (Table 2)

Table 4 Estimates[a] of number of trees infected with oak wilt and discounted costs of partial removal[b] and complete removal by cover type for the base case simulation with pocket radial growth of 3.47 m $year^{-1}$ and establishment rate of 0.015 pockets ha^{-1} $year^{-1}$

Primary land cover type	Number of trees infected (thousands)	Cost of partial removal ($ millions)	Cost of complete removal ($ millions)
Artificial surfaces	39.8	9.5	12.9
Cultivated vegetation	24.3	5.5	7.9
Forest	45.9	10.1	15.0
Woodland	4.3	1.0	1.4
Shrubland	9.2	2.0	3.0
Herbaceous	32.8	7.3	10.7
Total	156.3	35.4	50.9

[a] Estimates are averages computed over 100 simulations of oak wilt pocket establishment and expansion. The standard errors associated with the averages (not shown) are less than 0.1% of the means

[b] Estimates of the cost of partial removal are computed using the likelihoods of removing infected oaks associated with the various land use types (Table 2)

establishment ($11.0 million) or slowing the radial growth of existing pockets ($11.9 million).

Discussion

Strengths and Weaknesses of the Oak Wilt Model

We contribute a new method for predicting the mortality due to the spread of a forest pathogen at a landscape-scale (i.e., a county > 1,000 km^2). By assembling a spatially rich data set from several sources, we are able to estimate the current number of healthy and infected oak trees. Then, we use the literature about oak wilt pocket establishment and expansion to predict oak wilt mortality over a ten-year period. The simulation model is developed based on the pathology of the oak wilt fungus including both means of dispersal—underground and overland spread.

While we used existing knowledge of oak wilt pathology to construct our model, much of that knowledge is based on experiments and observations conducted at spatial scales equivalent to the size of an oak wilt pocket (<0.1 km^2). At this scale, factors such as soil texture, topographic slope, species composition, tree diameter, and inter-oak distance are known to affect the rate of disease spread (Menges and Loucks 1984, Bruhn and others 1991). Explicit incorporation of these factors would require finer resolution information than is available and would become computationally overwhelming for our spatial scale of interest. Although oak wilt may spread more quickly or slowly at a particular site than out model suggests, we believe our sensitivity analysis captures the typical range of oak wilt pocket expansion across Anoka County and provides a reasonable measure of the degree of uncertainty associated with our economic assessment. Because Anoka County has sandy soils, numerous red oaks, and severe oak wilt infections (Juzwik 2009), the economic impact of oak wilt in this county may be more substantial than in other counties where the disease has been reported.

While we benefited from the richness of the data and the available information, we were still limited by knowledge and data gaps. For example, the ratio of red oaks to white oaks may play an important role in sustaining oak wilt epidemics at the scale of a U.S. state (Juzwik 2009), but the quantitative effect of a change in this ratio on rates of pocket formation or expansion have yet to be determined. In general, long distance dispersal processes are not well understood and establishment of new pockets of infection could be a function of the number and spatial configuration of infected trees on the landscape relative to the site of interest. Evidence also points to the risks posed by construction activities, as tree damage makes oaks vulnerable to infection. While these factors may be important, they haven't been quantified in a way that we could use in our model. Landowner perceptions and responses to dead trees are presumed to remain constant over time, but responses may change as landowners gain information about damaging agents or if economic conditions or mortality patterns change. If landowners who initially decided not to remove dead trees revisit their decision and decide to remove trees two or more years after they are killed, substantially more trees would be removed than our current model predicts.

Our model, reflected in Eqs. 1–4, provides a simple, general framework to describe the course of oak wilt infections at a regional scale and could be applied to other areas with appropriate information, including estimates of oak density, number and area of existing oak wilt pockets, and likelihood of removal of infected trees. Our estimates of these parameters are derived from information sources that are unique to Minnesota, especially the ReLeaf database of oak wilt infection centers and the Minnesota Land

Cover Classification System, and our estimates may not apply outside of Anoka County. The certainty of estimates of parameters for the oak wilt model in Anoka County and beyond could be improved by collecting and assembling three types of information: a systematic sample of oak trees in urban cover types, an inventory of the location and size of existing oak wilt pockets, and information about treatment behavior of residents with infected trees. The costs of inventorying and monitoring invasive species and their hosts can be weighed against the benefits of having more certain information about host range, extent of invasion, and behavior of landowners to inform decisions (e.g., Haight and Polasky 2010).

Rationale for Using Removal Costs

Our model of oak wilt spread gives us predictions of oak tree mortality over time. When trees become diseased, residential property owners must cut down dead trees or be subject to liability—dead trees fall over more easily, and the owners of these trees would be responsible for any damage, including loss of life and property, caused by falling trees. In addition, landowners may not like the looks of a dead tree on their property. This potential liability and negative appearance move landowners to remove their dead trees rather than allow them to stay standing. When trees are removed, a property owner loses the value of services such as shade, aesthetics, and wildlife habitat—commonly called "landscape value"—that healthy trees provide. The economic loss from the death of an oak tree is therefore the sum of two components: removal cost and landscape value.

There are challenges associated with estimating both components based on available information. While the cost of tree removal is reflected in market price data, the determinants of these prices are not readily available. Furthermore, even with the compelling reasons to remove dead trees, landowners may be unable to keep up with tree mortality when the problem becomes severe and the propensity to remove trees may be sensitive to the size of the problem and other economic factors.

Estimating landscape value presents even more of a challenge, even with the significant literature surrounding the estimation of non-market environmental values (e.g., Freeman 2003). Conceptually, the appropriate underlying measure is straightforward: it is either an individual's willingness to accept compensation in exchange for incurring a loss or their willingness to pay to avoid a loss. Fundamentally, as with any consumer good, individuals exhibit diminishing marginal utility: the satisfaction that an individual gets out of the first unit of a good is generally higher than the satisfaction received from subsequent units. Diminishing marginal utility translates into downward sloping demand curves: an individual is willing to pay a higher amount for the first unit of a good (the first mature tree on a person's property) than for the second unit. The willingness to pay for the third unit is lower still, and so on. Conversely, individuals' willingness to accept compensation will be much less for the first tree lost than on the last tree left standing. One approach to estimating willingness to accept or willingness to pay for non-market goods based on market data is the hedonic property value method. For residential trees, studies have estimated the effects of individual trees or tree cover on home sale values (Anderson and Cordell 1985, Holmes and others 2010, Sander and others 2010), and these price effects reflect the changes in the present value of the stream of services that trees provide. Another method, the averting expenditure method (Courant and Porter 1981, Abdalla and others 1992), exploits the fact that individuals try to mitigate the effects of losses in environmental quality by purchasing substitutes, thereby revealing information about the value of that lost environmental quality. In the context of trees on residential property, homeowners may react to the loss of their mature trees by planting replacement trees. While replacement trees are not perfect substitutes for lost mature trees, these expenditures do indicate that homeowners place value on residential trees. Collecting data on replacement behavior would be a necessary first step to conducting this type of analysis.

Other approaches used in the literature and in practice are less consistent with underlying economic principles. Estimating tree values based on replacement behavior is entirely different from assuming that all landowners replace lost trees and including these replacement costs as economic damages associated with tree mortality as in, for example, Sydnor and others (2007). Another approach is to use a property appraisal method commonly used for insurance claims and litigation to determine the amount of money needed to compensate landowners for tree losses. The accepted practice is to use replacement cost as an estimate of landscape value (Council of Tree and Landscape Appraisers (CTLA) 1992, Nowak and others 2002). Because large trees can't be replaced, a formula is applied to the cost of a smaller replacement tree to determine the compensatory value of a large tree. A more sophisticated approach makes the choice to replace trees an option in a model of landowner behavior (Kovacs and others 2010). The cost of tree mortality becomes the cost of the best choice among several that landowners have to choose from. This approach relies on a known functional relationship between tree size and tree value.

Because there is a small literature that examines the non-market values associated with residential trees, it is tempting to apply the results of these studies into this new setting. However, besides the challenge of transferring location-specific real estate values from one study to new locations and contexts, a per-tree landscape value can't be multiplied by the number of lost trees to get a total landscape value. Nevertheless, because diseased residential trees are generally removed by property owners and because removal prices are primarily determined by a formula, removal cost can justifiably be multiplied by the number of lost trees to arrive at a total removal cost.

Conclusion

We are extraordinarily conservative in our estimate of economic damage. Not only do we avoid ascribing a per-tree landscape value based on studies conducted in a different time, place, and context, we also allow for incomplete tree removal because not all landowners choose to cut down their dead trees. Further, the estimate of per-tree removal cost is an average which may understate the cost of removing trees in urban landscapes where obstructions such as houses and power lines make tree removal more difficult and costly. Despite our conservative approach, our prediction of economic damage from a single invasive forest pathogen in a single county remains substantial: over a ten-year period, the estimated discounted sum of economic damages ranges from \$18 to \$60 million, depending on assumptions about pocket establishment and expansion.

Our predictions of baseline damage from an unmanaged oak wilt infestation can be used to evaluate the net benefits of management activities that reduce spread via underground and/or overland means. Underground spread via root grafts can be limited by severing roots that connect infected and healthy trees and by injecting healthy white oaks with fungicides. Picnic beetles, the vector involved in overland spread, are ubiquitous and not host-specific, and as a result, limiting their abundance is not a management option. However, the chances of overland spread can be reduced by avoiding tree damage during susceptible periods (e.g., April to June in Minnesota), removing and covering potential spore producing trees, and restricting movement of tree material containing the fungus (e.g., firewood) to new areas. A study by Koch and others (2010) examines the effectiveness of these options. Treatment efficacy and costs could be combined to determine the most cost-effective management strategy to reduce oak wilt spread. In particular, understanding the effectiveness of actions focused on containment and prevention of new infections can help to justify devoting resources to both activities

The issue of allocating management effort between containment and prevention is an important general question in invasive species management (Leung and others 2002). It may very well be less costly to prevent a new establishment than to contain a population once it has become established. However, it would be difficult to justify abandoning the containment effort in favor of all-out prevention across the wide area that is vulnerable to oak wilt. As Finnoff and others (2007) point out, prevention lowers, but does not eliminate, the probability of establishment: establishment can still occur with a prevention program, and a population may not establish even when no prevention program exists. A cost-effective overall strategy will balance the incremental cost of reducing the probability of new infections between the two types of management: containment and prevention.

The net economic benefit of a management plan is the difference between the benefits (damages avoided) and costs of management. Of course, increasing net benefits is just one criterion that a government agency uses to select a management plan. Another consideration is the total cost to the agency of implementing the management plan and the agency's ability to raise funds to cover that cost. Determining cost-effective management plans and designing equitable funding mechanisms are problems left for future work.

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