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Title: Mountain-pine beetle outbreaks and shifting social preferences for ecosystem services

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Abstract:

Conventional wisdom appears to implicate climate change as the root cause of the unprecedented mountain pine beetle (MPB) outbreak currently underway in the western United States. While climate change is undoubtedly a factor, historic changes in public forest management have resulted in greater numbers of large-diameter host trees in MPB habitat. We present a model that integrates standard economic and ecological principles in an attempt to clarify the roles of climate change and public forest management in the current MPB outbreak. Using data on timber sales, climate change and MPB populations, model simulations illustrate how an increased emphasis on non-timber ecosystem services induced a regime shift from climate-independent to climate-dependent disturbance processes, amplifying the current MPB outbreak.

Keywords: Mountain pine beetle, ecosystem services, public forest management, bioeconomics

Introduction

In western North America, the native mountain pine beetle (MPB, *Dendroctonus ponderosae* Hopkins) plays an important role by removing older and less vigorous trees from the forest.¹ Endemic MPB populations periodically surge creating a natural cycle and periods of considerable forest mortality. Forest insect survey records indicate four to five significant outbreaks in western North America over the last century with the most recent outbreak taking place in the late 1970s and early 1980s [3]. However, recent aerial surveys conducted by the U.S.D.A. Forest Service (USDA FS) show that while the areal extent of the current outbreak is comparable to previous outbreaks, the number of trees killed is nearly three times those previously recorded (see Figure 1). The economic impacts of the current outbreak have been substantial resulting in billions of dollars in manufacturing losses and thousands unemployed [4-6]. However, the current outbreak has less obvious impacts as well. Recent research shows that the current outbreak is occurring in new habitats with unknown ecological consequences [7] and altering the quality and quantity of forest fuels producing unexpected variations in wildfire type and severity [8]. The current outbreak may also be contributing to global warming as vast tracts of forest have been converted from a carbon sink to a carbon source [9].

In order for endemic MPB populations to transition to a large-scale outbreak, two requirements must be satisfied. The first is a sustained period of favorable weather over several years. Winter temperature influences MPB populations through survival while summer temperature and drought indirectly impact populations through MPB attack success which is required for reproduction [10]. Conventional wisdom appears to implicate climate change and a recent sequence of abnormally warm years as the root cause of the increase in outbreak severity

¹ See Samman and Logan [1] and Safranyik and Carroll [2] for an extensive treatment of MPB biology.

[10-14](see Figure 1). The implied argument is that the recent outbreak is abnormally severe because climate change allowed MPBs to successfully attack healthy trees, something that occurred less frequently in previous outbreaks.

However, a second more fundamental requirement of outbreak is a sufficient stock of susceptible host trees. Large stocks of susceptible host trees combined with a homogenous forest structure increase the risk and severity of landscape-level MPB outbreaks [2]. The vast majority of MPB habitat in the U.S. is public land administered by the USDA FS. As a result, historic forest management has played an important role in the current outbreak by regulating the abundance of susceptible host trees. Following the previous outbreak, social preferences for public forest benefits shifted to non-timber ecosystem services favoring forest management with less timber harvesting and a forest with more susceptible host trees [15]. This provides an alternative economic explanation for the current outbreak in which changing social preferences triggered an ecological shift from timber harvesting to MPB outbreaks as a major disturbance process in western forests. While climate change is undoubtedly a factor in the current outbreak, it is becoming increasingly important to quantify the relative contribution of public forest management in an attempt to mitigate unintended climatic amplifications of MPB outbreaks.

A novel approach is employed to separate the contribution of changing social preferences for ecosystem services from the effects of climate change in the current MPB outbreak. Using a bioeconomic model of forest management on USDA FS lands and MPB thermal responses to climate change, we track the shift in social preferences over forest ecosystem services and quantify the resulting impacts of this shift on forest and MPB dynamics. The framework extends [16] to integrate standard economic and ecological models with a thermal response model that links climate to MPB attack success. The economic component determines optimal forest

management given an ecological component that describes forest and MPB dynamics. The thermal response model introduces exogenous, climate-driven changes to a key ecological parameter, which in turn increases MPB attack success. The result is a bioeconomic model of forest management that incorporates both changes in social preferences for ecosystem services and climate change. We then demonstrate that the shift in social preferences for ecosystem services triggered changes in public forest management that exacerbated the current MPB outbreak by increasing susceptible hosts, as well as amplifying the effect of climate change on MPB populations.

Background

Stretching from New Mexico to California and north into British Columbia, the majority of MPB habitat in the U.S. is public land administered by the Forest Service.² Management on these forests has evolved over time due to changes in society's preferences for timber and non-timber ecosystem services provided from public lands. Following a major WWII expansion, USDA FS timber sales in the geographic range of the MPB leveled off after 1960 [17](see Figure 1). Federal legislation such as the Multiple Use Sustained Yield Act of 1960, the Wilderness Act of 1964, and the National Forest Management Act of 1976 required forest outputs other than timber be given due consideration in the management of national forests. In 1990, USDA FS timber sales dropped precipitously in much of the western U.S. This drop has been attributed to the mild recession in the early 1990s, softwood timber trade disputes between the U.S. and Canada starting in the mid-1980s, and federal timber sale restrictions in response to a number of

² In the United States, 74% of lodgepole pine forests – the primary host for MPB – are administered by the Forest Service [17].

high-profile environmental issues [18-20].³ While USDA FS timber harvests are sensitive to changes in price in the short-run [21], they are largely insensitive to changes in price in the long-run [22]. The implication is that macroeconomic conditions and trade disputes may be capable of explaining the initial decline in harvests, but would be unable to explain the sustained reduction in timber sale offerings over the last two decades. In addition, Wear and Murray [19] use an econometric model of the U.S. softwood lumber and timber markets to show that the decrease in public timber sale offerings cannot be explained by decreases in regional or national timber demand. Instead, Wear and Murray find that federal timber sale restrictions led to a shrinking market share for timber producers in the western U.S. Due to the restrictions and increasing public outcry for non-timber benefits from public forests, the USDA FS began favoring ecosystem management over timber management explaining the continued reduction in federal timber sales [15, 23].

These efforts to increase the provision of non-timber ecosystem services reflect a shift in social preferences for forest ecosystem services and have profound effects on forest and MPB dynamics. The decrease in timber harvesting left more susceptible trees standing in the forest [17], which directly increased MPB populations even in the absence of climate change. Historic forest management also indirectly increased MPB populations as climate change makes additional trees more vulnerable to MPB attack [11]. The shift in social preferences triggered an ecological regime shift from relatively climate-independent disturbance processes (timber harvesting) to climate-dependent disturbance processes (MPB outbreaks). The bioeconomic model presented in the following sections highlights how the relationship between the social and ecological shifts plays out in a context of regional climatic change.

³ One particularly influential issue was the proposed listing of the northern spotted owl under the Endangered Species Act in 1989. As a result, a federal court prohibited harvesting on a large share of the national forest timber sale program in the region in 1989 [20].

Ecological model of managed forest

The ecological component of the model presents a dynamic predator-prey relationship between MPB and the forest with time set in annual increments to match the MPB lifecycle [1]. Following Heavilin and Powell [24], the forest is homogeneous but divided into three size classes: seed base (X), young trees (Y), and adult trees (A). Young trees have a diameter at breast height (dbh) less than 8 inches. Although young trees have less defensive mechanisms and could provide enough nutrients for the larvae to develop, they seldom provide enough clearance in the inner bark for larval development. Adult trees are characterized by a dbh 8 inches and larger. While adults have the strongest defenses against MPB attack, they are also large enough to house egg galleries and act as an ample nutrient source. Each size class is measured in trees or seeds per acre. The laws of motion for the beginning-of-period density in each size class are given by:

$$X_{t+1} = (1 - \delta_X)X_t + b_Y Y_t + b_A A_t \quad (1)$$

$$Y_{t+1} = (1 - \delta_Y)Y_t + \delta_X X_t \quad (2)$$

$$A_{t+1} = \underbrace{(1 - d - \pi_t)A_t + \delta_Y Y_t}_{A_t^H} - h_t. \quad (3)$$

Each year, a proportion (δ_X and δ_Y) of the seed base and young trees mature to the successive size class. Contributions to the seed base are made by the young and adult size classes at rates b_Y and b_A . Only adult trees are considered viable for commercial harvest h_t and susceptible to natural mortality (at rate d) or MPB-induced mortality (at rate π_t). In addition, growth and mortality are assumed to occur prior to timber harvesting, differentiating the harvestable stock A_t^H from A_t . To be consistent with available USDA FS data, the severity of MPB damage is measured by the number of trees killed per acre by MPB: $\pi_t A_t$.

Successful MPB attacks have two major consequences. First, females lay as many as 100 eggs in a single gallery. Larvae emerge from hatched eggs and spend the majority of their lifecycle inside the tree. The larvae construct feeding galleries in the phloem or inner bark of the tree. These galleries eventually girdle the tree by cutting off nutrient exchange between the roots and the tree [1]. Second, MPB also carry blue stain fungi which interrupt water translocation, lower wood moisture content, and weaken defense mechanisms. Effects of the fungi coupled with damage to the inner bark and phloem eventually lead to tree death.

The probability a pine tree will die from MPB is determined by the interaction between the number of MPB attacking the tree and the level of tree resistance [25]. The probability of successful attack at the tree level translates into a known rate of MPB-induced mortality at the forest level. Following Heavilin and Powell [24], we define the rate of MPB-induced mortality as

$$\pi_t = \frac{B_t^2}{B_t^2 + a_t^2}, \quad (4)$$

where B_t is the number of MPB per acre and a_t reflects the resistance of susceptible trees to MPB attack in year t . This parameter decreases as trees become drought-stressed or as the emergence distribution of MPB – driven by temperature cues – become more synchronized in time, making the population of attacking beetles more effective in attacking new hosts. Equation (4) is characteristic of the type III functional response in predator-prey interactions [26] and captures threshold dynamics characteristic of MPB [25]. Equation (4) has also been shown to successfully replicate data on MPB attack dynamics at a landscape level [24].

The relationship between MPB populations and the forest stock involves a one-year lag as adult MPBs typically emerge from the tree a year after initial infestation [1]. MPB density at time t is therefore a function of the density of successfully attacked trees at time $t-1$ and

fecundity, φ :

$$B_t = \varphi(\pi_{t-1}A_{t-1})^\nu, \quad (5)$$

where ν is a curvature parameter, modeling a proportional decrease in successful reproduction when large beetle populations begin to over-utilize available host resources. MPB fecundity refers to the number of newly emerged beetles per successfully attacked tree. Together, equations (4) and (5) capture the recursive nature of the MPB population.

Incorporating Climate Change: Thermal Response

The sensitivity of the MPB lifecycle to variations in temperature has been well documented. For example, warmer summer temperatures aid in synchronizing adult beetle emergence, increasing the success rate of subsequent attacks [27] and reducing a_t in equation (4). Likewise, warmer winter temperatures increase larval survival [2] reflected as a larger value for φ in equation (5). Since proportional changes in a_t and φ have little impact on model results, we model the effect of temperature on MPB dynamics by allowing for a change in the overall effectiveness beetles have in any given year φ/a_t [24].

Since MPB development takes place in the phloem or inner bark of the tree, a thermal response model is used to connect measured phloem temperatures to the number of newly infested trees created by a single MPB-infested tree [27]. The model is driven by hourly phloem temperatures for the year between the old and new attacks and calculates a distribution of MPB emergence/day, $P(t)$. The degree to which this distribution exceeds a critical threshold predicts the ratio of new-to-old infestations, r_t . Values of r_t grow or shrink depending on beetle lifecycle events, which are controlled by the phloem temperature. If the emergence distribution is narrow and steep (characteristic of higher average temperatures), the beetles are synchronized and

relatively effective in killing new hosts; broader emergence curves (lower mean temperatures) result in smaller values of r_t .

The thermal response model's r_t predictions can be correlated with the tree resistance parameter, a_t , in the bioeconomic model. The thermal response model predicts

$$\pi_t A_t = r_t \pi_{t-1} A_{t-1} \quad (6)$$

while the bioeconomic model predicts

$$\pi_t A_t = \frac{\varphi^2 (\pi_{t-1} A_{t-1})^{2\nu}}{a_t^2 + \varphi^2 (\pi_{t-1} A_{t-1})^{2\nu}} A_t. \quad (7)$$

The predictions are reconciled at a level of MPB infestation consistent with $\pi_t = 50\%$, which occurs when $a_t^2 = \varphi^2 (\pi_{t-1} A_{t-1})^{2\nu}$, or

$$\pi_{t-1} A_{t-1} = \left(\frac{a_t}{\varphi} \right)^{\frac{1}{\nu}}. \quad (8)$$

We match the two predictions for new MPB hosts at a population level generating 50% stand susceptibility (in year t or $t-1$, depending on the model):

$$r_t \left(\frac{a_t}{\varphi} \right)^{\frac{1}{\nu}} = r_t \pi_{t-1} A_{t-1} = \pi_t A_t = 0.5 A_t. \quad (9)$$

Thus

$$a_t = \varphi \left(\frac{0.5 A_t}{r_t} \right)^{\nu} \quad (10)$$

which links the results of the thermal response model with the ecological component of the bioeconomic model. For a given adult tree stock, higher temperatures trigger larger values of r_t thereby lowering host tree resistance.

Forest management in MPB habitat

Society in the model is made up of many identical households, which receive instantaneous utility from a composite good unrelated to the forest, Q_t , and ecosystem services derived from public forests. Ecosystem services are comprised of timber products h_t and non-timber services such as amenity values, wildlife habitat, and biodiversity. Non-timber ecosystem services depend on the quality of the forest resource, proxied by the stock of living adult trees A_t^H . For tractability, period t utility of the representative household is given by:

$$U(Q_t, h_t, A_t^H; \alpha_t) = \ln(Q_t) + (1 - \alpha_t)\ln(h_t) + \alpha_t\ln(A_t^H), \quad (11)$$

where α_t is the relative weight households place on non-timber ecosystem services in relation to timber ecosystem services. As social attitudes towards ecosystem services change over time so does this key parameter.

Each year the representative household inelastically supplies $L = L_t^Q + L_t^A$ units of labor, which are allocated between the production of the composite commodity (L_t^Q) and the production of timber products (L_t^A). Production of Q_t is directly proportional to labor inputs: $Q_t = L_t^Q$.

Harvesting adult timber requires labor and depends on the harvestable stock according to harvest function:

$$h_t = \rho L_t^A A_t^H \quad (12)$$

where ρ is a scale parameter measuring the efficiency of harvesting activities.⁴ The inclusion of stocks in the harvest function is a simple way of accounting for complex spatial considerations inherent in timber harvesting. For instance, fewer trees in the forest will result in longer distances to transport logging equipment into the forest and drag felled trees back to roads. We also ignore the possibility of harvesting standing dead trees (salvage harvesting) as this harvest

⁴ Thinning activities by the USDA FS are assumed to produce commercially viable material and treated identical to harvesting.

decision is not central to the paper. The decision to harvest a dead tree does not involve the trade-off between timber and non-timber ecosystem services.

Optimal forest management seeks an appropriate balance between timber and non-timber ecosystem services. This balance hinges on society's relative preference for ecosystem services: $0 \leq \alpha_t \leq 1$. Consider the following extremes. When $\alpha_t = 0$ society values USDA FS land entirely for the timber services it produces. Optimal forest management responds to these preferences with large timber harvests. Alternatively when $\alpha_t = 1$ society values public forestland entirely for non-timber services. Optimal forest management then responds by leaving a large number of live adult trees standing in the forest. The level of α_t determines the relative intensity of timber harvesting.

Recognizing the tradeoff between timber and non-timber ecosystem services and the preferences of households (society), the local forest manager selects a time path of harvests to solve the following problem:

$$\max_{\{h_t\}_{t=1}^{\infty}} \sum_{t=1}^{\infty} \beta^{t-1} U(Q_t, h_t, A_t^H; \alpha_t) \quad (13)$$

where $0 \leq \beta \leq 1$ is the discount factor. The problem in (13) is solved subject to the ecological equations of motion (1) – (5), initial conditions for stocks, and the constraints:

$$Q_t + \frac{h_t}{\rho A_t^H} = L, \quad (14)$$

$$h_t \geq 0 \quad (14')$$

while incorporating the negative stock externality that causes each local forest manager to treat MPB risk as exogenous.⁵ The non-negativity constraint in (14') allows managers to harvest a

⁵ The negative stock externality arises due to the local nature of harvesting decisions made by the USDA FS and eliminates the incentive to engage in preventative harvesting (i.e. thinning) intended to lower MPB-induced mortality [16]. The externality is similar to that discussed in the fisheries literature [28].

portion of the stock (interior solution) or harvest the entire stock at a given time (corner solution) which is more consistent with the traditional forest-rotation literature.

The solution to (13) is found through a series of substitutions that incorporate all applicable dynamics, changing the choice variable from harvest to stock of adult trees [29]. Assuming an interior solution and normalizing labor supply to one, the first-order condition requires harvesting to proceed until:

$$\begin{aligned} \frac{1 - \alpha_t}{h_t} - \frac{1}{Q_t \rho A_t^H} = \beta \left\{ \left(\frac{1 - \alpha_{t+1}}{h_{t+1}} - \frac{A_{t+1}^H - h_{t+1}}{Q_{t+1} \rho (A_{t+1}^H)^2} + \frac{\alpha_{t+1}}{A_{t+1}^H} \right) (1 - d - \pi_{t+1}) \right\} \\ + \beta^3 \left\{ \delta_X \delta_Y b_A \left(\frac{1 - \alpha_{t+3}}{h_{t+3}} - \frac{A_{t+3}^H - h_{t+3}}{Q_{t+3} \rho (A_{t+3}^H)^2} + \frac{\alpha_{t+3}}{A_{t+3}^H} \right) \right\}. \end{aligned} \quad (15)$$

While complex, the first-order condition is straightforward and can be rewritten in a more intuitive fashion as

$$NB_t = \beta \{ NB_{t+1} (1 - d - \pi_{t+1}) \} + \beta^3 \{ \delta_X \delta_Y b_A NB_{t+3} \} \quad (16)$$

where NB_t is the marginal net benefit of an adult tree at time t .

Equations (15) and (16) reveal both direct and indirect impacts of harvesting. The left side is the present marginal net benefit of timber harvesting while the right side represents the future marginal costs. Harvesting produces a direct net benefit in period t . However, harvesting a tree in period t means it is not available to provide utility for timber and non-timber benefits in period $t+1$ and will increase the cost of harvesting other trees in future periods through the stock effect. The opportunity cost in $t+1$ of harvesting in period t (the first term on the right side) is lower because the tree may be killed by MPB (at time-varying rate π_t) or natural causes (at rate d) before next period's harvesting decision. In addition, harvesting in period t eliminates the tree's contribution to the seed base represented by the second term on the right side.

Endemic steady state

In order to simulate our model we must first select an appropriate initial condition. Taking USDA FS data as a cue, we assume 1990 marked a discrete point of change in social preferences for ecosystem services from public forests and select this as our initial condition.⁶ Initial forest stocks are selected to be consistent with the model's steady state and 1990 USDA FS harvest levels. This allows us to isolate the effects of the shift in social preferences on the resulting MPB and forest dynamics. An alternative strategy would be to use 1990 U.S. forest stock data as the initial condition. However, this would tend to perpetuate previous disturbances to the forest including past MPB outbreaks, making it unclear what portion of the dynamic response could be attributed to the change in social preferences as opposed to other disturbances.

Economic and ecological parameters are selected to obtain a realistic endemic steady state. The scale parameter ρ measures the efficiency of adult harvesting. On public lands, inefficiencies can arise from changes in the skills of the logging labor employed or the presence of administrative requirements that hinder the efficiency of the harvesting effort. This parameter is scaled to 0.0369 to provide an initial condition where society equally values timber and non-timber ecosystem services: $\alpha_{1990} = 0.5$. We set the discount rate equal to 4% (implying a discount factor of $\beta = 0.96$) in accordance with USDA FS practice [30]. The parameters dictating seed production (b_V, b_A), germination (δ_X), maturation (δ_Y), and natural mortality (d) in Table 1 produce comparable and defensible values for typical USDA FS land in the western

⁶ Of course this is an abstraction. It is more likely that social preferences changed gradually over time but that forest management did not respond until 1990. The implication is that forest management reflects social preferences with some delay due to political and judicial issues. While this is an important topic for future research, this delay does not play a role in our results as what drives the model dynamics is the forest management. Instead of making arbitrary assumptions about the nature and length of this delay, we assume forest management responds immediately to social preferences.

U.S. [31]. These forest-specific parameters also allow the forest to re-establish within 80 to 140 years following a stand-replacing disturbance [32].

MPB-specific parameters a_t , φ , and ν depend on site conditions, tree species, climate, and geography among other things. Proportional changes in a_t and φ have little impact on the model. The key value is the ratio of beetle fecundity to tree resistance φ/a_t . To estimate an endemic steady state we are concerned with measuring tree resistance in 1990: a_{1990} . Using aerial survey data, Heavilin and Powell [24] estimate the ratio of beetle fecundity to tree resistance at approximately 0.071 in 1990. Previous studies provide multiple measures of the fecundity of an infested tree by counting the number of emerging beetles [e.g., 33]. These studies generally place φ between 4,000 and 5,000 beetles per infested tree. This suggests a_{1990} is approximately 63,800 beetles per acre, assuming $\varphi = 4,500$ beetles per infested tree. Finally Berryman et al. [25] report a decreasing relationship between MPB offspring and the number of MPB attacks per square meter of tree surface area. This indicates decreasing reproductive returns from increases in adult-tree mortality and implies a degree of curvature in (5). In the absence of any additional quantitative results to guide us, we set $\nu = 0.5$.

Economic and ecological parameters as well as an initial condition consistent with the model's endemic steady state and 1990 harvest levels are presented in Table 1. This endemic steady state is characterized by a realistic 4,120 MPB and 200 adult trees per acre. A little less than one tree per acre is initially killed by MPB, which is comparable to historical values shown in Figure 1.

Measuring implied social preferences for non-timber ecosystem services

The optimal harvest condition in equation (15) serves as a bridge between household (social) preferences and optimal forest management. Given observed annual USDA FS harvest data, the equations of motion are used to determine the (unobserved) stocks and the first-order condition is “flipped” to solve for the implied relative preference for non-timber ecosystem services, α_t . Starting from our endemic steady state we can then simulate the model to determine how changes in social preferences affect forest and MPB dynamics.

Necessary data to measure implied social preferences include annual harvest of live (green) trees from National Forests in the geographic range of MPB (USDA FS regions 1 through 6). While annual USDA FS harvest data are publically available from Cut and Sold Reports at a regional level, these Reports do not distinguish between live and salvage harvests. Periodic Timber Sale Accomplishment Reports (PTSAR) do distinguish between annual live and salvage timber sales on USDA FS land and were used as a proxy for h_t from 1990 to 2008.⁷ These board foot volume measures of total harvests must be converted to trees per acre. Using historic data from the USDA FS Land Areas Reports (LAR) from 1997 through 2008, we calculate that regions 1 through 6 consistently make up 75% of total USDA FS acreage. This acreage measure is used to calculate average board feet per acre of green timber sold within the geographic range of MPB. The board feet measure is then converted to trees per acre assuming a constant average board foot volume per tree. Board foot per tree will vary depending on species, forest density, and site conditions. Lotan and Critchfield [32] find yields range from 11 board feet per tree for a 50-year old stand to over 80 board feet per tree for a 140-year old stand for

⁷ Using timber sales as a proxy for timber harvest has limitations. While PTSAR indicate the annual volume of timber for the year of the sale, these contracts may cover up to three years so the timber may not have been harvested in the year of the sale. While sales data may not exactly match annual variation in harvest levels, it should capture the underlying shift in preferences toward non-timber ecosystem services of public forestlands that occurred around 1990.

lodgepole pine on medium quality sites in Montana and Idaho. For simplicity, we assume an average stand age of 80 years corresponding to approximately 25 board feet per tree. This provides a measure of the number of pine trees harvested per acre on USDA FS land in MPB habitat from 1990 through 2008.

Using our endemic initial condition and annual USDA FS sales data for h_t , model projections show that the decrease in adult timber harvesting after 1990 coincides with an increase in preferences for non-timber ecosystem services (Figure 2). This corresponds to Wear and Murray's findings [19]. The bioeconomic model takes this result one step further by showing that the increase in preferences for non-timber ecosystem services also increases the number of susceptible trees in the forest, necessarily increasing the MPB stock and the amount of MPB-induced mortality from 1990 through 2008.

However, this history of forest management alone is not capable of replicating the MPB-induced mortality witnessed between 1990 and 2008 (Figure 3). In addition to the changes in forest management, this period has also seen an increase in mean annual temperature throughout the western United States (Figure 1). Temperature increases raise MPB attack success by synchronizing adult beetle emergence and increasing survival. In addition to underestimating MPB-induced mortality, ignoring the influence of climate also fails to capture the full effect of the shift in social preferences. Since increasing temperatures cause trees to be more susceptible to MPB attack, society's desire to leave more trees in the forest also amplifies the effects of climate change on MPB populations. For these reasons, it is essential to accurately measure the effect of climate change in our bioeconomic model.

Measuring the effects of climate change

To parameterize the thermal response model, hourly phloem temperatures are needed for the year between the old and new attacks. A continuous south-side phloem temperature record exists for the Stanley Valley of central Idaho from July 19, 1992 through August 18, 2003. During these ten seasons the local MPB population, which was oscillating toward local extinction until 1995, experienced an outbreak impacting 1400 square kilometers of lodgepole pine; outbreak growth rates peaked in 2000 and subsequently declined due to the absence of susceptible hosts in the valley. The phloem temperature record is used to project temperatures for the years 1990-2050 assuming a 0.0443 C°/year increasing trend in annual mean temperatures.

Using nonlinear rate curves and fitted variances for all eight developmental phases through which a beetle must pass between attack initiation and emergence of brood to attack new hosts the following year, a distribution of MPB emergence/day, $P(t)$, is calculated. The degree to which this distribution exceeds a critical threshold predicts the ratio of new-to-old infestations, r_t :

$$r_t = \int_{152}^{245} \max(8.10P(\tau) - 0.181, 0) d\tau. \quad (17)$$

where 152 and 245 are the Julian Day (JD) measures for June 1 and August 30 in the year of beetle emergence.⁸ The values 8.10 and 0.181 are maximum likelihood estimates for reduced form biological parameters using phloem temperatures measured on the south (warm) side of hosts in the Stanley Valley.⁹

⁸ These dates relate to seasonal cutoffs in emergence that arise due to temperature requirements at various stages of the beetle lifecycle [27]. If beetles emerge earlier than June 1 the larvae are susceptible to the summer heat and the pupae will be present at a time (fall) when they will be frozen. If beetles emerge later than August 30, eggs are likely to be frozen.

⁹ For more information see Powell and Bentz [27].

Before an outbreak saturates we may assume that the number of susceptibles is approximately the initial host density; in the Stanley Valley a reasonable estimate is $A_t = 400$ trees/acre. Using $\varphi = 4,500$ MPB/tree and $\nu = 0.5$ in equation (10) gives the final relationship between the thermal response model and tree resistance

$$a_t = \frac{63640}{\sqrt{r_t}}. \quad (18)$$

The thermal response model was simulated for each year using the temperature projections and tree resistance trajectories outlined above.

To avoid projecting temperature anomalies in the Stanley Valley to the rest of the western U.S., we use the results of the thermal response model to calculate trends in tree resistance. A logarithmic regression was used to estimate constant exponential rates of decrease in a_t from these data, generating rates ranging from 0.29% to 1.1% per year depending on the base year. Combined with historic harvest levels, we find that a decrease in a_t of 0.65% per year is capable of replicating the historic levels of MPB-induced mortality witnessed between 1990 and 2008. The results, presented in Figure 3, are a benchmark of forest and MPB-mortality that incorporate both historic changes in forest management and the effects of climate change.

Results

In the benchmark model, increases in MPB-induced mortality arise from changes in social preferences for ecosystem services and from changes in climate. The shift towards non-timber ecosystem services creates a direct effect on MPB-induced mortality by leaving more susceptible trees in the forest. The recent warming trend within MPB habitat also increased the rate of MPB-induced mortality. These two individual effects combine to produce an indirect

amplification effect. That is, additional trees left in the forest due to changing social preferences are now more vulnerable to MPB attack as a result of climate change.

To isolate the role of changing social preferences in the current MPB outbreak we consider a counterfactual scenario where social preferences for non-timber ecosystem services remain constant. In this scenario of invariant social preferences, the indirect amplification effect is omitted but the direct effect of changes in climate remains. By comparing these results to the benchmark model we are able to isolate the direct and indirect roles of changing social preferences.

USDA FS harvest data and the first-order condition in (15) can be used to estimate relative social preferences between 1990 and 2008. However, ending the sample period in 2008 fails to capture the peak of the current outbreak. To capture the peak, social preferences are assumed to remain at 2008 levels through 2020, at which time the outbreak will have largely run its course. This allows optimal harvest levels to be calculated from 2009 to 2020. Combining these estimated harvested levels with the observed harvest levels from 1990 to 2008 allows us to simulate MPB and forest dynamics over the entire outbreak.

The period 1990 to 2008 is characterized by a drastic decrease in harvest levels along with a brief increase in harvest levels at the end of the period (Figure 4A). Projecting the model into the future, optimal management calls for a gradual decrease in harvest levels from 2009 to 2020 as the stock of trees is reduced by MPB. In this benchmark model, the increasing importance of non-timber ecosystem services and the general decline in harvests combine with a changing climate to induce cycles in the MPB stock due to “echo effects” inherent in the ecological model (Figure 4B). Such cycles are a natural MPB phenomenon causing an outbreak that peaks in 2011 at approximately 12.4 trees per acre killed (Figure 4C).

In the counterfactual scenario where the shift in social preferences never takes place, forest managers optimally respond to climate driven increases in MPB-induced mortality by gradually reducing harvest levels from 1990 to 2020 (as opposed to the drastic decline in harvests when social preferences shift). The counterfactual scenario sees more trees harvested, fewer trees available for MPB to attack, and a less severe increase in adult tree mortality due to climate change. The result is a less severe MPB outbreak that peaks in 2015 at 7.7 trees per acre killed.

Conclusions

This paper focuses on understanding and quantifying the ecological impacts of recent changes in U.S. public forest management. We find that the decrease in timber harvesting after 1990 can be attributed to a shift in public preferences away from timber harvesting and toward valuing the forest for non-timber ecosystem services such as amenity value, wildlife habitat and biodiversity. This shift toward non-timber ecosystem services leaves more susceptible trees in the forest which, in the absence of climate change, leads to an increase in MPB-induced mortality that temporally corresponds to the ongoing outbreak in the western United States. However, the increase in susceptible trees also exacerbates the effects of climate change, amplifying MPB outbreaks further. Simulations indicate that the shift in social preferences for ecosystem services is responsible for a more immediate outbreak and a 60% increase in MPB-induced mortality. These results imply that the current unprecedented MPB outbreak is, at least in part, an artifact of the fundamental change in public forest management that took place nearly two decades ago.

This result highlights how changes in public forest management have altered the disturbance regime in western forests. Following WWII, timber harvesting became the dominant size-dependent disturbance regime while the shift toward non-timber ecosystem services beginning in 1990 eliminated harvesting as a dominant disturbance. In its absence, MPB-induced mortality appears to be claiming that role, implying larger MPB outbreaks even if climatic factors were held constant. However, as a growing body of evidence indicates, the MPB's role as a natural disturbance agent may be fundamentally altered by climate change, leading to even more severe outbreaks in the future. The shift in social attitudes for ecosystem services therefore not only helped create the current outbreak by leaving more trees in the forest but also exacerbated the effects of climate change by shifting from a relatively climate-independent disturbance regime (timber harvesting) to a climate-dependent disturbance regime (MPB outbreaks).

It may be decades before the full impact of the shift in social preferences and the subsequent change in disturbance regimes is revealed given that forests exhibit such a long ecological memory [34]. In the meantime, society needs to weigh the risk of more severe future MPB outbreaks with the desire for less actively managed public forests. If the benefits from increases in non-timber ecosystem services outweigh the corresponding losses from amplified MPB outbreaks, elevated forest mortality may represent part of a painful but necessary transition to a new, less intensively managed forest. If not, there may be a role for more active forest management on public forests. Answering this question is beyond the scope of this paper and we leave it to future work.

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Table 1. Model parameters and initial steady state

Parameter	Definition	Value
δ_X	Rate of germination of seeds in seed base	0.001
δ_Y	Rate of maturation of young trees	0.0019
b_Y	Rate of viable seed production in young trees	0.0018
b_A	Rate of viable seed production in adult trees	0.0018
a_{1990}	Number of MPB/acre required for a 50% chance of MPB-induced mortality in adult trees in 1990	63,800
φ	Average MPB offspring per infested tree	4,500
d	Rate of natural adult tree mortality	0.02
ν	Rate of decrease in beetle reproduction with increases in beetle-induced mortality in adult trees	0.5
ρ	Harvest efficiency parameter	0.0369
β	Discount factor	0.96
Steady state corresponding to 1990 USDA FS harvest data and $\alpha_{1990} = 0.5$		
π	0.4%	B 4,121 beetles/acre
X	6,903 trees/acre	Y 3,633 trees/acre
A	202 trees/acre	Q 0.731

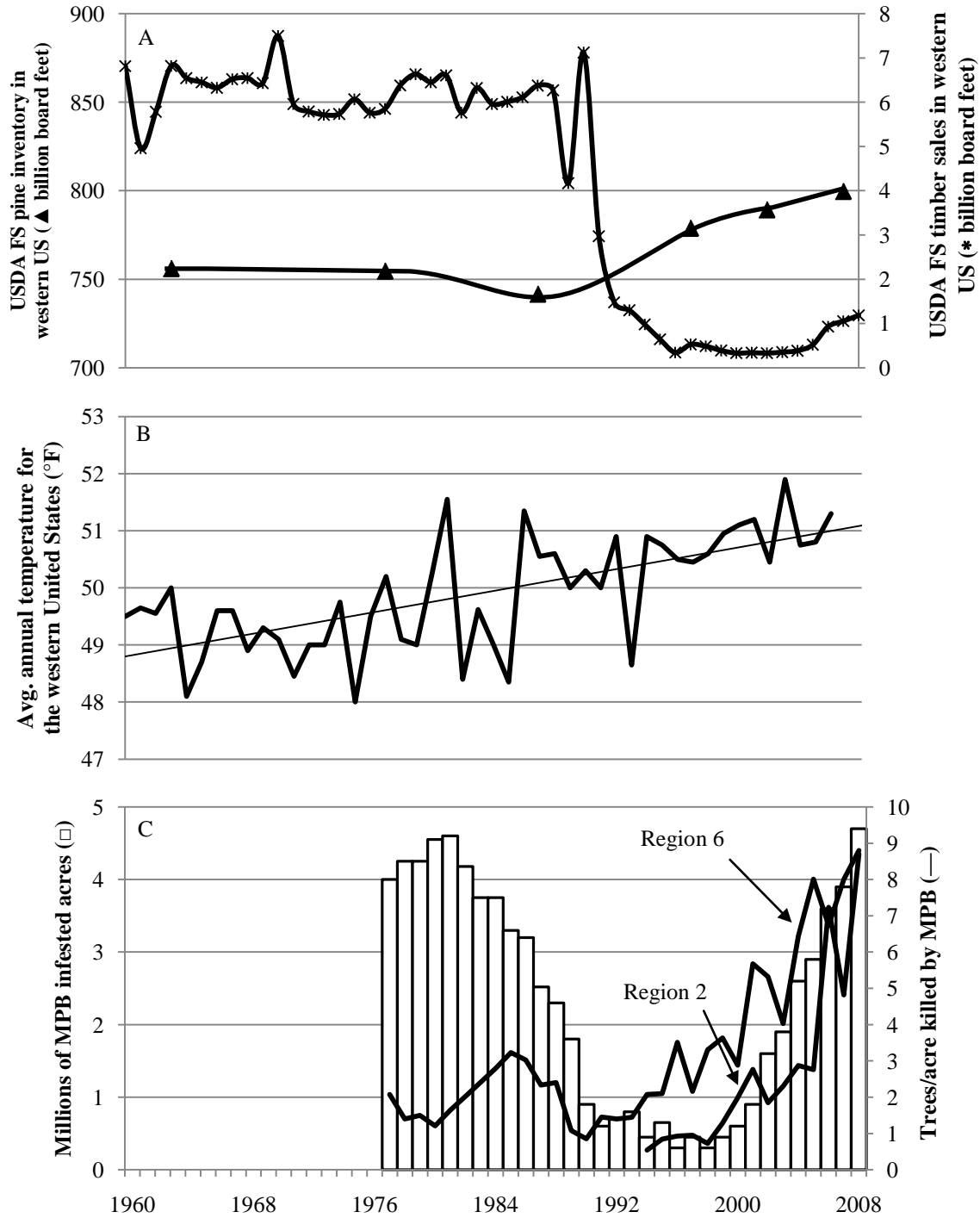


Figure 1. Public forestland management and climate change as primary drivers of MPB outbreaks. (A) Billion board feet of green timber sold (right vertical axis) and pine inventory in USDA FS regions 1-6 (left vertical axis) from 1960 to 2008. (B) Average annual temperature for 11 contiguous western states (bold line) and linear trend. (C) Acres infested by MPB in western US (left vertical axis) and trees/acre killed by MPB in USDA FS region 2 (SD, NE, CO, eastern and central WY) from 1994 to 2008 and in region 6 (OR and WA) from 1977 to 2008 (right vertical axis).

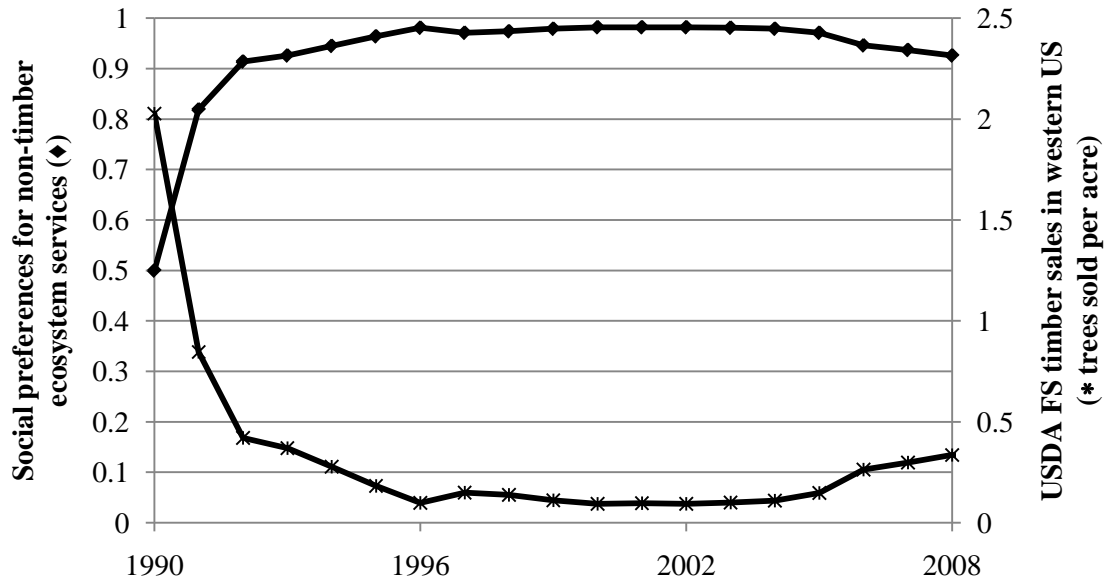


Figure 2. Shift in social preferences implied by USDA FS harvest data. Social preferences for non-timber ecosystems services α_t are measured from first-order condition (15) with USDA FS timber sale data substituted for h_t .

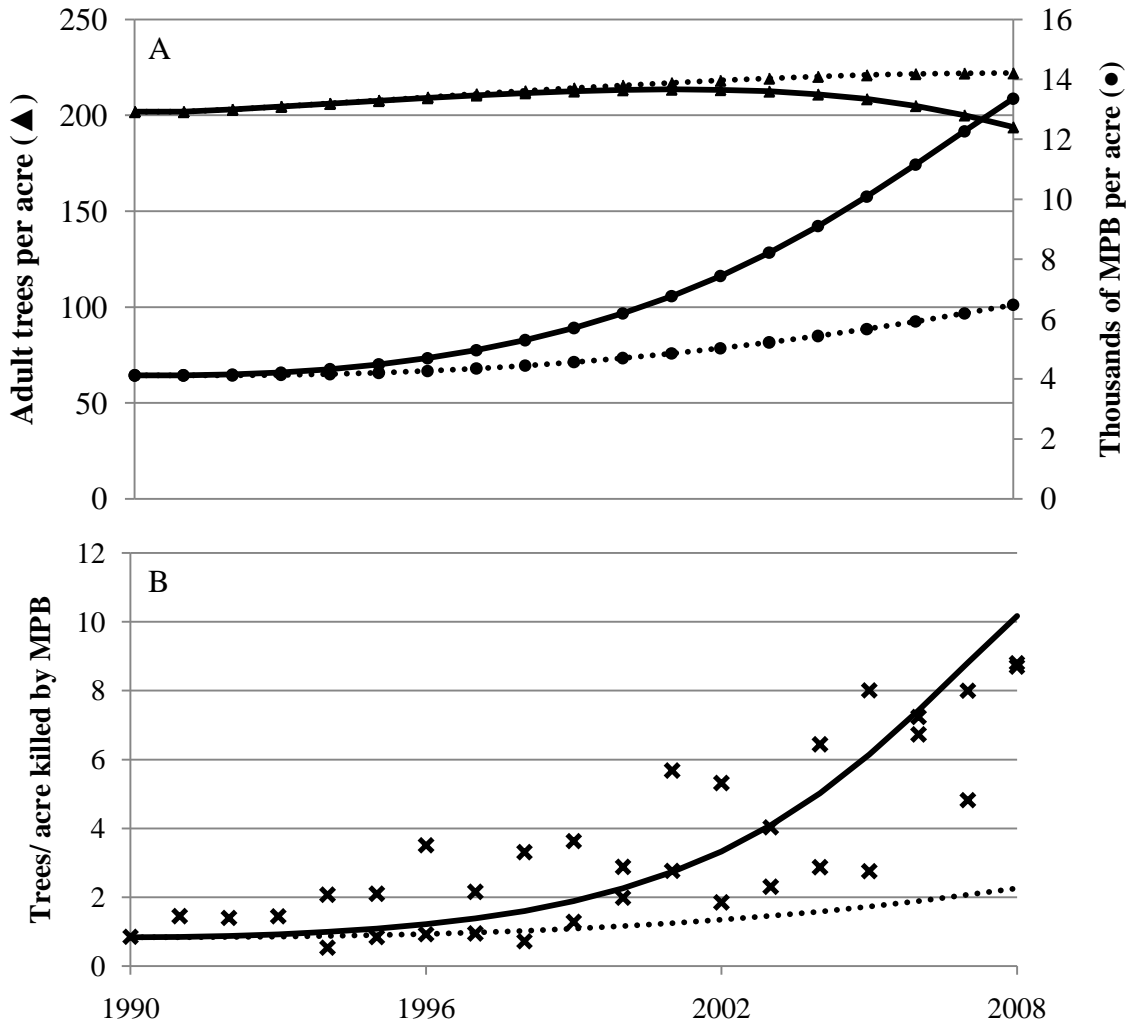


Figure 3. Simulation results from 1990 to 2008 using annual USDA FS timber sales data as proxy for harvests. Model results ignoring the effects of climate change (dotted lines) yield MPB-induced mortality below historic levels in USDA FS regions 2 and 6 (x). The benchmark model (solid lines) includes the effects of climate change to ensure results consistent with observed levels of MPB-induced mortality.

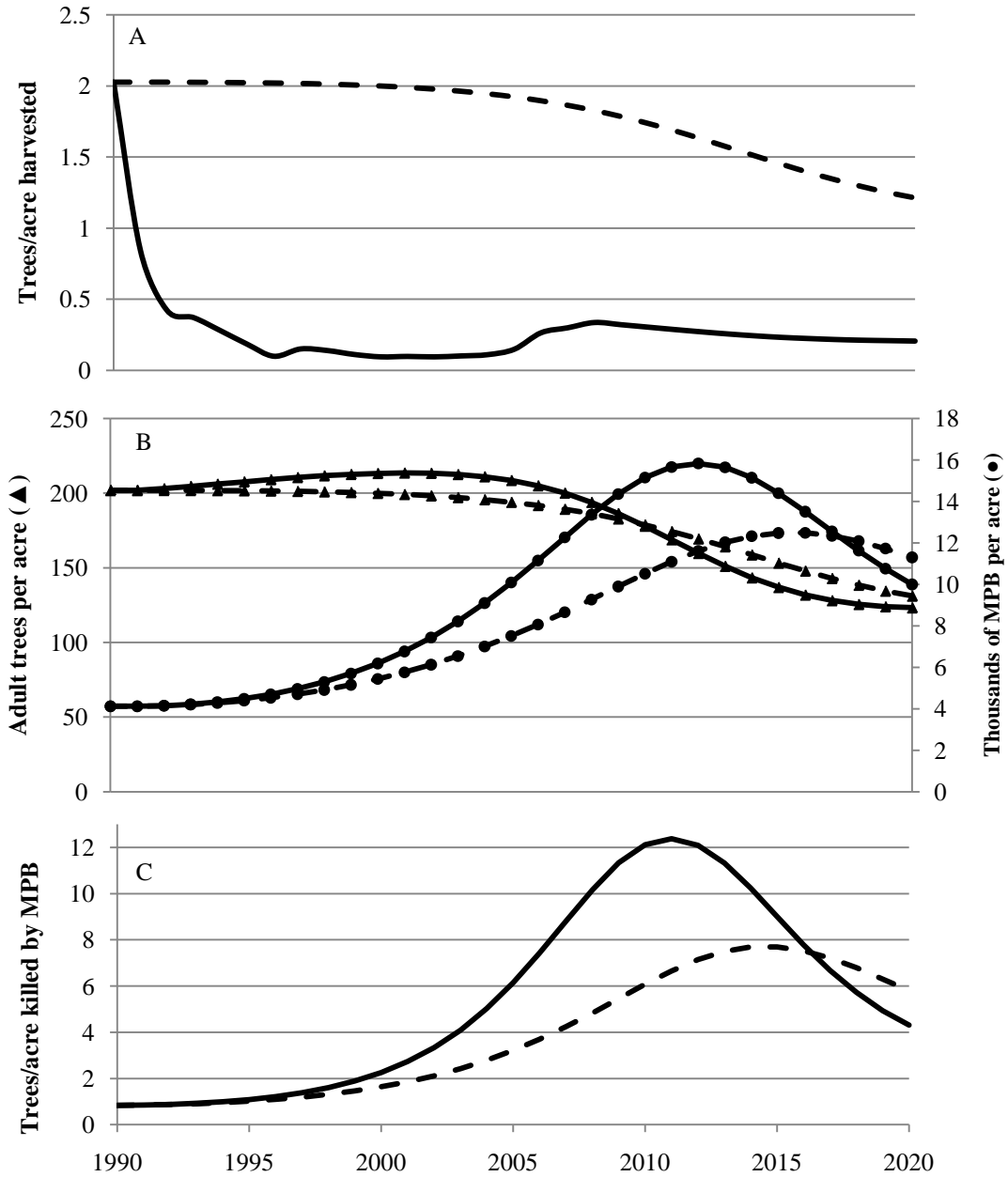


Figure 4. Simulation results from 1990 to 2020 with climate change and optimal forest management. Solid lines reflect benchmark model where the harvest decision reflects a shift in society's preferences towards non-timber ecosystem services. Dashed lines reflect the counterfactual scenario where society's preferences for ecosystem services remain unchanged.