The Influence of Previous Mountain Pine Beetle *(Dendroctonus ponderosae)* Activity on the 1988 Yellowstone Fires

Heather J. Lynch,[1]* Roy A. Renkin,[2] Robert L. Crabtree,[3] and Paul R. Moorcroft[1]

[1]*Department of Organismic and Evolutionary Biology, Harvard University Herbaria, Harvard University, 22 Divinity Avenue, Cambridge, Massachusetts 02138, USA;* [2]*Yellowstone Center for Resources, Yellowstone National Park, Wyoming 82190, USA;* [3]*Yellowstone Ecological Research Center, 2048 Analysis Drive, Suite B, Bozeman Montana, 59715, USA*

ABSTRACT

We examined the historical record of mountain pine beetle *(Dendroctonus ponderosae* Hopkins) activity within Yellowstone National Park, Wyoming, for the 25-years period leading up to the 1988 Yellowstone fires (1963–86) to determine how prior beetle activity and the resulting tree mortality affected the spatial pattern of the 1988 Yellowstone fires. To obtain accurate estimates of our model parameters, we used a Markov chain Monte Carlo method to account for the high degree of spatial autocorrelation inherent to forest fires. Our final model included three statistically significant variables: drought, aspect, and sustained mountain pine beetle activity in the period 1972–75. Of the two major mountain pine beetle outbreaks that preceded the 1988 fires, the earlier outbreak (1972–75) was significantly correlated with the burn pattern, whereas the more recent one (1980–83) was not. Although regional drought and high winds were responsible for the large scale of this event, the analysis indicates that mountain pine beetle activity in the mid-1970s increased the odds of burning in 1988 by 11% over unaffected areas. Although relatively small in magnitude, this effect, combined with the effects of aspect and spatial variation in drought, had a dramatic impact on the spatial pattern of burned and unburned areas in 1988.

Key words: Yellowstone National Park; l988 Yellowstone fires; fire ecology; mountain pine beetle; insect-fire interactions; Markov chain Monte Carlo.

INTRODUCTION

Both insect outbreaks and forest fires constitute important disturbance processes in North American forests, particularly in the Rocky Mountain West. Research in this area suggests that both insects and fire play a crucial role in the continuation and healthy functioning of the ecosystem (Despain

1990; McCullough and others 1998; Furniss and Renkin 2003). A number of recent studies have examined the phenomenon of disturbance interactions, in which the ''memory'' inherent to the slow regeneration of forests mediates spatiotemporal interactions between disturbance events separated by years or even decades (Amman 1991; Amman and Ryan 1991; Veblen and others 1994; McCullough and others 1998; Fleming and others 2002; Bebi and others 2003; Kulakowski and others 2003; Bigler and others 2005). At their study site in

northwestern Colorado, Kulakowski and others (2003) found that a low-severity fire in 1950 burned more area than would be expected in stands that had been less affected by a 1940s spruce beetle outbreak. They hypothesized that a proliferation of moist understory vegetation that followed beetle-induced mortality in these stands may have prevented the low-severity fire from breaching these beetle-affected areas. They further recognized the need for exploring beetle-stand replacing fire interactions under extreme drought, suggesting fires may behave differently under varying fire weather/beetle intensity conditions.

On the other hand, the idea that forest pests and pathogens may leave forests more vulnerable to fire originated in 1909 (Hopkins 1909) and has recently become of interest to public policy makers concerned about large-scale events that may threaten life or private property. This issue is directly addressed in the recent 2004 Healthy Forests Initiative, which cites that ''decades of hazardous buildup of dense brush and undergrowth, coupled with drought conditions, insect infestation and disease make forests and rangelands. . . vulnerable to often intense and environmentally destructive fires. . . . The combination of continuing drought and an increase of drought stressed and insect damaged trees and brush has resulted in a greater potential for large wildfires in the West.''

Considering the importance of this question to the management of our western forests, these disturbance interactions need considerably more study. In this analysis, we used an extensive and largely unexploited data set documenting the incidence of insect outbreaks in Yellowstone National Park (YNP) to answer the following research question: Did the previous decades of mountain pine beetle activity in YNP have a measurable influence on the spatial pattern of the 1988 Yellowstone fires?

METHODS

Analytical Approach

The forestry and fire community has long embraced the notion that insect outbreaks can affect both the occurrence and the intensity of an extreme fire event. In this analysis, we considered only the final pattern of burned areas in Yellowstone following the 1988 fires in order to understand why some areas burned and some did not, *conditional on* the preexisting conditions amenable to an extreme fire. In addition to the spatial extent and intensity of mountain pine beetle activity from

1963 to 1986, we included information on a number of variables that may have played a role in promoting fire. These variables fall into several broad categories (Table 1): climate/environmental factors, geographic factors, and previous fire history. By including all of these factors, we ascribed as much variability as possible to non–insect-related variables, and the resulting analysis of the role of mountain pine beetle in promoting fire is conservative.

Data

The 1988 Yellowstone fires (Figure 1C) are one of the most well-documented large-scale disturbances in American history (Franke 2000; Turner and others 2003; Wallace 2004). A complete GIS database is available, with a daily record of fire extent and fire type (crown versus ground versus non-forested fire) for the entire duration of the fires (Despain and others 1989; Rothermel and others 1994).

To examine the influence of previous mountain pine beetle activity on the 1988 Yellowstone fires, we compiled all available aerial detection surveys of forest insect activity within the park during the years 1963–86. Hardcopy maps (1:125,000 scale), initially provided by the US Forest Service Northern Region Forest Health Protection Group and archived in YNP, were digitized using a high-resolution scanner and integrated into a complete GIS database by a process of manual (on-screen) vectorization of the polygon data. This geographic database was georeferenced using existing (on-image) map grid points and given attributes (insect agent, intensity of tree mortality) according to the information provided in the original maps. Repeated outbreaks, widespread activity, and the broad distribution of host species (primarily lodgepole pine *[Pinus contorta* Dougl. Var. *latifolia]* and whitebark pine *[Pinus albicaulis* Engelm.]) of the mountain pine beetle corresponded to the broad spatial extent of the 1988 Yellowstone fires. Therefore, this insect was chosen as the agent for this particular analysis. As shown in Figure 2, mountain pine beetle activity during this time was cyclic with a periodicity of approximately eight years. In this analysis, we compared two periods, 1972–75 and 1980–83, of widespread beetle activity to evaluate its impact on fire risk at two different time lags. Figure 1D represents the spatial pattern of areas affected by mountain pine beetles in these two outbreaks.

To account for other potentially important risk factors, we compiled spatial datasets of geographic,

Table 1. Data Sets Used in the Analysis of the Yellowstone Fires

	Data Layer	Abbreviation	Original Data Type	Source
Climate data[a]	Max. daily temp (°F)	tmax	Text	NCDC[b]
	Avg. daily wind speed (mph in 10ths)	wind	Text	NCDC
	Total precip. (100ths of an inch)	prcp	Text	NCDC
	Palmer Drought Severity Index	pdsi	Text	NCDC
Geographic data	Elevation (m)	elev	30-m raster	NPS[C]
	Slope (°)	slope	30-m raster	NPS
	Aspect	[d]	50-m raster	derived from elev
	Pre-1988 cover type	[e]	50-m raster	NPS
Historical	Previous fire history	previous. burn	Polygon shapefile	NPS
	Mountain pine beetle 1972–75	mpb72to75	Polygon shapefile	aerial survey
	Mountain pine beetle 1980–83	mpb80to83	Polygon shapefile	aerial survey

[a]*An inverse-distance weighting was used to extrapolate climate variables from the three nearest weather stations available through the National Climate Data Center (Yellowstone Lake, West Yellowstone, and Yellowstone Park, Mammoth Wyoming). This accounts for broad-scale patterns of climate variability. Factors affecting microclimatic conditions (slope, aspect, elevation) were included as separate variables.*
[b]*NCDC = National Climatic Data Center*
[c]*NPS = National Park Service*
[d]*Aspect was initially divided in eight categories: north (N), northeast (NE), east (E), southeast (SE), south (S), southwest (SW), west (W), and northwest (NW). Areas of zero slope were designated as flat; flat areas were used as the basis of comparison for the other aspect factors.*
[e]*Pre-1988 cover types were grouped into the following categories: aspen (As), Douglas-fir (early [DFO] mid = [DF1] or late-successional [DF2]), Engelmann spruce/subalpine fir (late-successional [ESSF2]), Krumholtz (Kr), lodgepole pine (early [LPPO], mid = [LPP1], or late-successional [LPP2]), pygmy lodgepole pine (PyLPP), whitebark pine (early [WBPO], mid = [WBPl], or late-successional [WBP2], and nonforested.*

topographic, and climatological factors that may have also played a role in determining which areas burned in 1988 and which did not (Table 1). These data layers were resampled or digitized as appropriate on a common 100 m resolution raster grid. This data set was then exported to the statistical software package R (R Development Core Team 2005) and resampled every 500 m, so that each data point represented a 100×100 m pixel from the original data set, spaced 500 m apart (centroid to centroid). The resampling was necessary to reduce the size of the data set for computational speed. The final data set was a 219×209 grid (45,771 pixels) from which pixels with no data (inside the YNP bounding box but outside the park boundary), pixels representing water-cover types, and pixels identified as nonforest were removed. There were 28,748 forested pixels in the final data set.

The aerial survey data are, by their nature, the least spatially accurate data set included in this analysis. Based on aerial survey–satellite comparison (H J Lynch personal observation) and survey sampling protocols (US Forest Service Aerial Detection Survey Accuracy Assessment unpublished), polygons representing insect activity are typically within 250 m of their actual location. Relative to the scale of the insect activity in each of the two periods (see Figure 1D), the accuracy of these data is more than sufficient for this analysis. The resampling also helped to buffer the analysis from minor inaccuracies at the interface between affected and unaffected areas.

Data Analysis

In this analysis, the independent variable of interest was the binary (0,1) variable indicating whether or not a particular area burned in the 1988 Yellowstone fires. As such, we logit transformed the binary response variable in order to perform the following regression analysis:

$$\log\left(\frac{y_i}{1 - y_i}\right) = \beta_0 + \sum_k \beta_k x_{ik} \qquad (1)$$

where y_i represents the burn status of the pixel ($y_i = 1$ if the pixel burned), β_0 represents the intercept, and β_k represents the regression coefficient for covariates k and x_{ik} is the value of covariate k for pixel i.

Ordinary logistic regression implicitly requires that individual data points are independent (Fox 1997); this basic requirement is immediately violated in any analysis involving a spatial context. This is particularly true in the analysis of contagious forest disturbances, in which the underlying contagious nature of fire spread dictates that neighboring regions are not independent. Accurate determination of the regression coefficients requires that the nonindependent nature of the dependent variable be accounted for. One way to account for nonindependence among neighboring y_i is to add the sum of neighboring values as a separate independent variable to the logistic regression model — a technique known as "maximum pseudolikelihood estimation" (PSE) (Besag
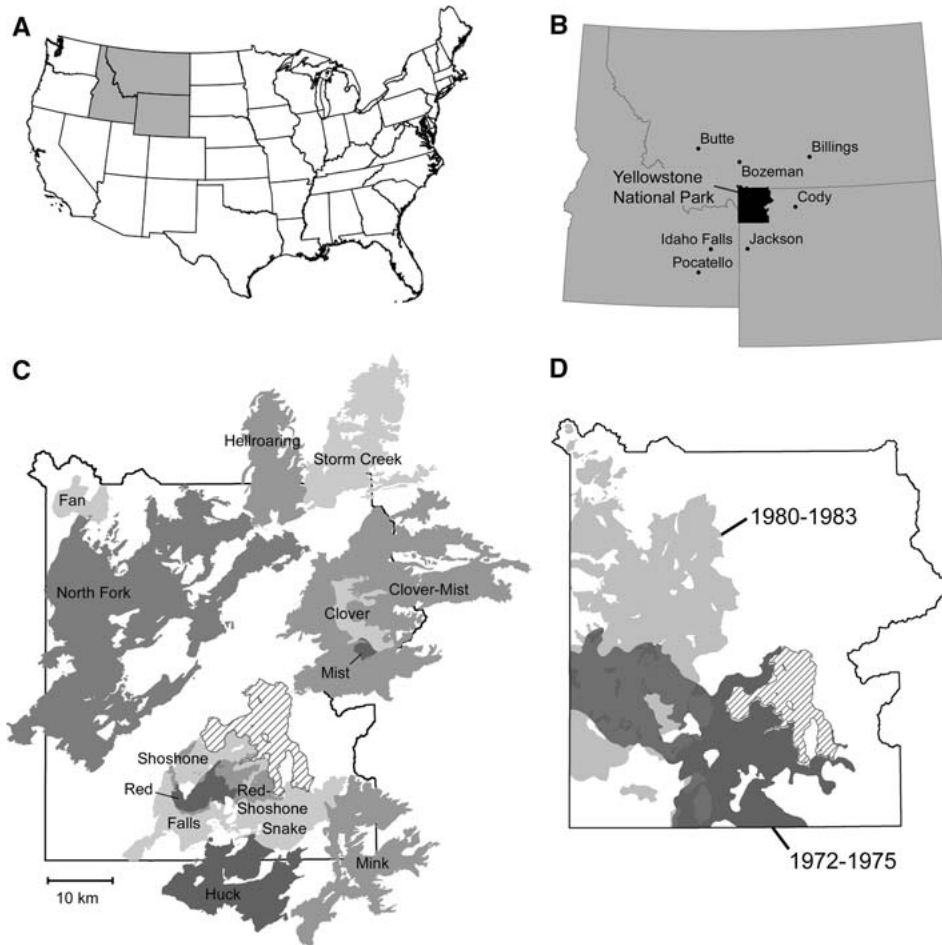
Figure 1. **A** Continental United States. Idaho, Wyoming, and Montana are shaded in gray. **B** ldaho, Wyoming, and Montana. Yellowstone National Park is shown in black. **C** Major fire complexes that comprised the 1988 Yellowstone fires. Yellowstone Lake is hatched in gray. **D** Mountain pine beetle activity in 1972–75 (*dark gray*) and 1980–83 (*light gray*). This figure represents only those areas that were affected by mountain pine beetle activity, of any intensity, in each of the four peak outbreak years.

1975). However, the underlying nonindependence of the neighboring values remains, and, unlike a true maximum likelihood estimator (which is both consistent and asymptotically efficient), the maximum pseudolikelihood estimatior is inefficient, especially in cases where spatial interaction is strong (Besag 1975; Wu 1994).

Recent advances in statistics have provided landscape ecologists with an alternative approach. This technique uses Markov chain Monte Carlo (MCMC), which captures the latent spatial autocorrelation more accurately. In addition, MCMC has been shown to represent the estimate errors more accurately. A brief outline of this method will be presented here. Further details may be found in Huffer and Wu (1998) and Wu and Huffer (1997).

The likelihood function for the regression analysis introduced in Eq. (1) may be expressed as:

$$l(\beta, \gamma) = \frac{\exp{(\alpha' T(y))}}{c(\alpha)} \quad (2)$$

where α represents the vector of regression coefficients in the model (the prime symbol represents the transpose in this equation), and $T(y)$ represents the vector of sufficient statistics; that is:

$$T'(y) = \left[\sum_{i=1}^{N} y_i, \ \sum_{i=1}^{N} x_{1i} \, y_i, \right.$$
$$\left. \sum_{i=1}^{N} x_{2i} y_i, ..., \ \sum_{i=1, \, i \neq j}^{N} \gamma y_i y_j^* \right] \quad (3)$$

The asterisk(*) in Eq. (3) indicates that only nearest neighbors should be summed over, and $c(\alpha)$ (Eq. [2]) represents the intractable normalizing
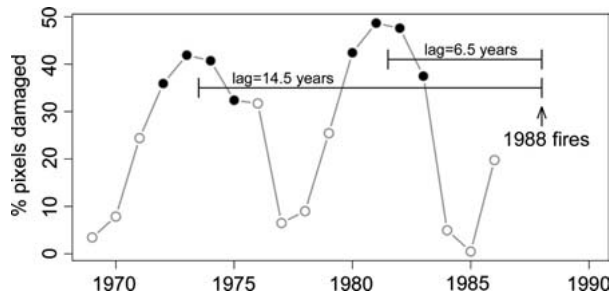
Figure 2. Percent of Yellowstone National Park (YNP) affected by mountain pine beetle activity over the period 1969–86. There was negligible activity from 1963 to 1968, and these data were not included in the plot. Years considered in this analysis are represented by solid circles.

function for the likelihood resulting from the mutual interdependence of the pixel locations in the data set. Note that the γ parameter in Eq. (3) represents the strength of contagious interaction; thus it is another regression parameter to be estimated in the same manner as the other covariates in the model. Although many reasonable definitions of ''nearest neighbor'' have been used in the context of spatial autocorrelation (several are discussed by Huffer and Wu [l997]), we used the scheme in which the four nearest ''rook'' neighbors are considered (Besag 1974). In this way, our analysis remains consistent with earlier work by Huffer and Wu (1998), and Wu and Huffer (1997) while capturing the dominant mode of fire spread (that is, spread over a shared boundary as opposed to less frequent long-distance spread by means of fire ''spotting'').

The basic principle of MCMC in this context is as follows: A Gibbs sampler using initial guesses for the regression coefficients is used to generate a collection of different possible realizations of the data. After a sufficient number of realizations in the Markov chain have been generated, the distribution of these realizations will approach the distribution function of the true likelihood in Eq. (2), which can be maximized numerically to obtain estimates of the regression coefficients $\alpha = \{$the intercept β_0, the covariate regression coefficients β, and the nearest-neighbor coefficient $\gamma\}$. Parameter estimate variances were estimated using the inverse Fisher information matrix, as discussed by Huffer and Wu (1998) and Wu and Huffer (1997).

Model Selection

Because of its computational complexity, MCMC methods are not suitable for model selection (for example, by means of forward step-wise regression), and an appropriate set of models was chosen based on the pseudolikelihood estimation technique. There were 11 variables considered for the final model (Table 1), within which were eight factors for aspect and 12 categories for pre-1988 cover type. In the first step, all 11 variables were put into the model, and a combination of forward and backward stepwise regression (using the R function ''step'') was used to select the best model according to Akaike's information criterion. To further simplify the model, variables that were not significant at the 1% confidence level (slope, cover.typeLPPl, and cover.typeESSF2) were eliminated; the four significant aspect variables (which spanned the continuous range, or northwest-north-northeast-east) were combined into a single variable, which we called ''northeast''. Of the two mountain pine beetle infestations considered, only the 1972–75 outbreak (mpb72to75) was strongly correlated with the 1988 fires, whereas the 1980–83 outbreak (mpb80to83) was not. Therefore, in our final model, we did not include information about the more recent outbreak. Multicollinearity among the independent variables would tend to increase the true variance in our estimated model coefficients and could lead, in theory, to variables being selected for the final model that were not in fact significant. In this analysis, multicollinearity was not a significant problem, and the largest variance inflation factor in the final model was only 1.74 (Fox and Monette 1992).

Because the MCMC method takes into account neighboring burn states to determine the probability of burning, pixels that were not included in the model (such as the boundary of the park, nonforested areas, and water bodies) required (fixed) predefined burn states. Our approach was to assign the park border and interior nonforested areas a burn state according to a binary random variable with probability of burning equal to the actual probability of burning over those pixels ($P_{burn} = 0.415$). The model therefore gets no spatial information from these pixels. Water bodies were set to burn = 0, because under no circumstances would those areas have burned. In reality, the final burn pattern in 1988 was informed to some extent by the actual burn pattern along the boundary and in non-forested areas, and our approach is therefore conservative. Our final statistical model:

$$\text{logit(burn)} \sim \text{pdsi} + \text{northeast} + \text{mpb72to75} \quad (4)$$

contained only three variables: pdsi (Palmer Drought Severity Index), northeast (representing all aspects within 90° of 22.5° NE), and mpb72to75 (which represents all areas repeatedly affected by

Table 2. Best-fit Model Estimates (SE)

	β_0	pdsi	northeast	mpb72to75	γ	Figure 3
Logistic (site-speeific only)	−6.23 (0.18)	−1.13 (0.03)	0.22 (0.02)	1.35 (0.04)		A
MCMC (autocorrelation only)	−4.45 (0.04)				2.25 (0.02)	B
PSE (site-specific + autocorrelation)	−7.15 (0.61)	−0.32 (0.11)	0.26 (0.08)	0.46 (0.12)	2.67 (0.04)	
MCMC(site-specific + autocorrelation)	−5.02 (0.08)	−0.08 (0.01)	−0.09 (0.02)	−0.11 (0.01)	−2.27 (0.02)	C,D

The top line represents the best-fit estimates using standard logistic regression with no autocorrelation variable; the second line represents the results of Markov chain Monte Carlo (MCMC) maximization for the γ-only model; the bottom two lines represent the pseudolikelihood estimates (PSE) and MCMC estimates respectively, for the full model, which includes both site-specific variation in the covariates and autocorrelation.
*Estimated errors for the MCMC-derived estimates are calculated from the Fisher information matrix, as detailed in Huffer and Wu (1998).*
Monte Carlo variability is not reported but is typically a factor of 10 smaller than the reported estimated error.

insect activity of any intensity in each of the four outbreak years) (Table 1).

RESULTS

The results of the analysis are summarized in Table 2 and Figure 3. Figures 4A and B show the burn probabilities as modeled either when no autocorrelation was accounted for, or when only autocorrelation was included (that is, when the model consists of only an intercept and an autocorrelation parameter (Table 2)). As shown in Figure 4A, the simple autologistic model, which ignores spatial autocorrelation in fire spread, does not capture the spatial scale of the 1988 fires; it shows both very small-scale variation in the log-odds of burning (due to the aspect variable) and very large-scale variation (due primarily to drought). This model is also strongly biased and overestimates the overall amount of burning. Figure 4B shows that a model including only nearest-neighbor interactions is able to capture the overall scale at which burning occurs. However, because it lacks spatial information (other than the location of water bodies, which biases the neighboring pixels in the direction of not burning), this model cannot identify which areas are more likely to have burned than others.

Our final (site-specific+autocorrelation) model (Figure 4C and D) captures both the spatial scale of the 1988 fires and its placement across the park. All three covariates in our final model are statistically significant. When random values are used for the nonforested and boundary areas, the model correctly classifies 61.0% of all pixels. The fraction of misclassified burned pixels (6,373 of 15,749) is approximately equal to the fraction of misclassified unburned pixels (4,849 of 12,999); the model therefore produces more or less unbiased predictions of fire risk. Figure 4C illustrates the fit of our model in this case, which captures both the large scale pattern as well as many of the finer scale details of the final burn pattern. This highlights the
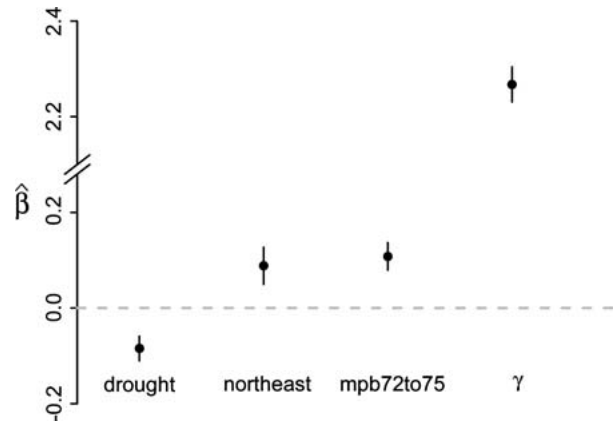
Figure 3. Summary of the results of this analysis. The x-axis represents the various covariates included in the final model. Error bars represent 95% confidence limits for the value of $\hat{\beta}$.

interaction between site-specific fire risk and the strong autocorrelation inherent to fire spread; both components are necessary to generate a reasonably accurate statistical model of the event. However, when the same model is used with the actual pattern of burned patches within the nonforested and boundary areas, the model correctly identifies 87.3% of all pixels. The fit of the model in this case is shown in Figure 4D. The right panels of Figure 4A–D indicate the differences between the model prediction and the actual burn pattern.

Visual inspection of Figure 4 leads us to suspect that the model errors are not spatially random. However, formal tests of autocorrelation among the residuals of a model that itself contains an autocorrelation component are not yet available (Cliff and Ord 1981; Lichstein and others 2002). Here we take advantage of the fact that the number of sites is much larger than the number of constraints imposed by the model, and we calculate Moran's I in the usual manner, using $x_{ij} = 0$ and 1 for correctly and incorrectly identified pixels, respectively (I = 0.86, 0.81, 0.80, 0.69 for Figure 4A–D, respec-
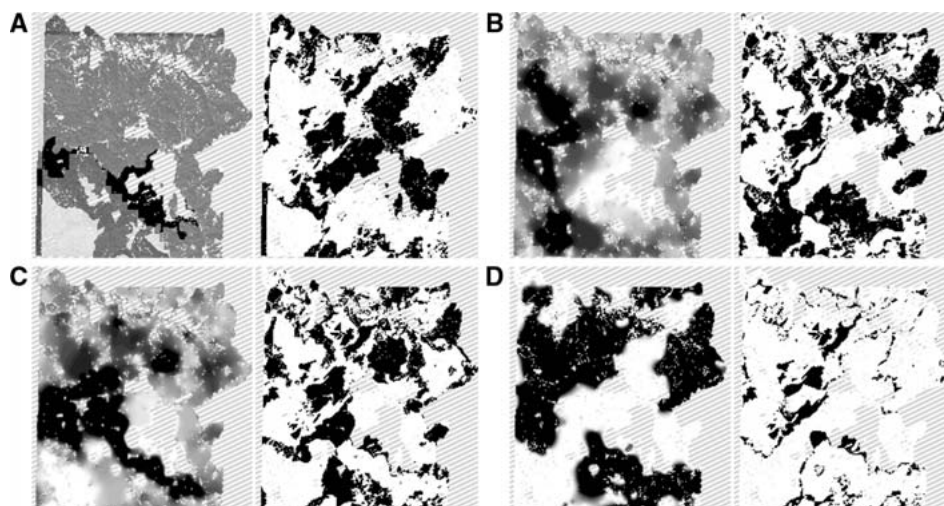
Figure 4. A *Left*: Probability of burning (*black = burned*) from the simple logistic model (see Table 2). *Right*: Misclassified pixels (black). **B–C** *Left* Simulated probability of burning (*black = burned*) from the model incorporating only spatial autocorrelation (**B**) and the full model (**C**) (see Table 2) using a binary random variable for nonforested and boundary pixels. These maps represent the probability of burning (*dark gray = increasing probability of burning*) over 400,000 Markov chain Monte Carlo (MCMC) iterations (sampled every 10 maps) following an initialization period of 50,000 iterations and starting with all forest pixels initially unburned. These maps represented an average over 10 different simulations representing 10 different randomly drawn boundaries. The gray scale ranges from zero probability of burning (*white*) to unity probability of burning (*black*). *Right*: Misclassified pixels (*black*). **D** *Left*: The full model (same as C) is used to simulate the probability of burning using the known burn values in nonforested and boundary areas. The same protocol was used as described for maps B and C except that only one set of values was used for the non-forested and boundary values (the known values) *Right*: Misclassified pixels (*black*).

tively) (Upton 1985). (As noted by Cliff and Ord [1981], in the case of binary data, Moran's I reduces almost exactly to the simpler but generally less powerful join-count statistic). A permutation test based on 999 random permutations of pixels within the error map confirms that the model errors are not spatially random ($P < 0.001$ in all cases) (Cliff and Ord 1981). This is not surprising, given the strong autocorrelation inherent in forest fires and the subsequent spatial aggregation of the burned areas. When the actual pattern of burned patches within the nonforested and boundary areas is used, the model errors occur almost entirely along the boundaries where burned patches abut unburned areas, reflecting the difficulty in predicting exactly where a large fire complex will end.

The variables ''northeast'' and ''mpb72to75'' are both 0/1 factors, therefore, the relative strengths of each factor can be compared using the magnitudes of their coefficients. The range of the variable ''pdsi'' was 2.01, so its overall impact on the odds of burning in 1988 was approximately 65% greater than that of the other two factors. We can use Eq. (1) to calculate the change in the odds of burning in 1988 associated with each of these variables. For example, for areas repeatedly affected by mountain pine beetles during the

1972–75 outbreak ($\hat{\beta} = 0.108$), the odds of burning during the summer of 1988 increased by 11%.

We infer from this that mountain pine beetle activity some 13–16 years prior to the 1988 event served to increase fire risk and may have ultimately influenced the spatial pattern of the burned areas. The effect of repeated beetle activity in this period is comparable in magnitude to other factors in our model that affect fire risk, such as drought and aspect.

DISCUSSION

As noted by other authors (Knight and Wallace 1989), the pre-1988 Yellowstone landscape was a patchy mosaic representing the accumulated history of biological and geological processes. The 1988 Yellowstone fires proceeded across the landscape under the constraints of this heterogeneity, and the final pattern of burned areas represents a complex mixture of site-specific flammability and the contagious nature of fire itself. Using the MCMC technique described above, we are able to untangle these two components to understand what site-specific characteristics, such as previous insect activity, predispose some patches to burn while other patches are left untouched.

Before turning to the main question of how mountain pine beetle activity influences fire risk, it is important to consider the biological relevance of the other two variables that remained significant in the final model—drought and aspect. It is not surprising that fine-scale spatial variation in drought was significant in our model; the role of drought in promoting the extreme fire conditions present in 1988 has already been demonstrated (Christensen and others 1989; Renkin and Despain 1992; Schoennagel and others 2004).

The second factor, aspect, is also known to affect fire spread, although our results suggest a different mechanism than has been proposed by other authors (Heyerdahl and others 2001). South-facing slopes receive more incident sunlight in the northern hemisphere, and the difference in solar radiation received by north- and south-facing slopes is greatest at the 45° latitudes of YNP (Holland and Steyn 1975). Increased solar radiation on south-facing slopes leads to earlier snowmelt in the spring as well as warmer and drier conditions in the summer, thus increasing fire risk (Heyerdahl and others 2001). On the other hand, because more moisture is retained by northern slopes they tend to support higher fuel loads than south-facing slopes. Fires typically spread more quickly upslope; and because the spread of the 1988 fire generally proceeded in a southwest-to-northeast direction, the northeast aspects were typically on the leeward side of the mountains from the advancing fire front. The fires would thus have spread most slowly on the northeast-facing slopes, generally backing downslope. We hypothesize that this slow burning on the northeast-facing slopes, coupled with their increased fuel loads, may have led to relatively more, but slower, fire spread in these areas.

It is important to note that because cover-type was included in the original set of covariates, the effect of aspect is in addition to potential differences in cover-type. Models that included cover type but excluded aspect did not fit the data as well, so we infer that the effect described above—increased risk of fire in areas of northeastern aspect—results from something other than simple differences in the composition or age of the stands in these areas.

The goal of this analysis was to quantify the underlying geographic and historical factors affecting the spatial pattern of forest fires across a landscape, including the temporal history of mountain pine beetle activity. We found that even when a wide range of potential variables were included in our model, mountain pine beetle activity remained a statistically significant factor that correlated well with the final pattern of burned areas after the 1988 Yellowstone fires. Repeated mountain pine beetle activity (as opposed to sporadic or short-duration activity) 13–16 years prior to the fire correlated significantly with the log-odds of burning and was found to increase the odds of burning by approximately 11%. Whereas beetle activity during the first outbreak (13–16 years before the fire) was correlated with an increase in fire risk, activity during the second outbreak (5–8 years before the fire) showed no correlation with the log-odds of burning in 1988 once spatial interaction effects had been accounted for.

Identification of the biological mechanisms leading to this delayed increase in fire risk will require further study, although the time scale of the process is consistent with the time required for significant release of understory vegetation. Vertical heterogeneity, arising from the combination of rapid release of understory trees and the presence of surviving mature individuals may provide ladder fuels sufficient to increase fire risk. It is almost certain that, to varying degrees, both fire-promoting and fire-inhibiting changes are occurring simultaneously in the stand over the decades following substantial insect activity. Our results imply that the secondary effects of beetle activity on stand structure make a greater contribution to the increase in fire risk over the long term than the primary effects of beetle-induced tree mortality (and the subsequent accumulation of dead fuel). In this, we concur with Bigler and others (2005), who also concluded that the more important effect of beetle activity on fire risk is through a change in stand structure and composition, as opposed to an increase in fuels.

These results accord with a number of other studies examining interactions between the mountain pine beetle and forest fires. Kulakowski and others (2003) found that areas affected by a 1940s spruce beetle outbreak were burned less often by a 1950 fire than would be expected. Because there was a difference of only 3 years between the peak of the beetle infestation (1947) and the fire, our interpretation would be that not enough time had elapsed for a sufficient turnover in stand structure to cause an increase in fire risk. In fact, their negative correlation is consistent with the slight (though not statistically significant) negative correlation between the more recent 1980–83 outbreak and the 1988 fires. Moreover, Bigler and others (2005) reported that in 2002 the same areas affected by the 1940s spruce beetle outbreak did, in fact, burn more often than would be expected. This finding is consistent with the overall picture of a delayed increase in fire risk

mediated by a change in stand structure that is associated with beetle-induced defoliation and tree mortality. As noted by Bigler et al. (2005), it is important to emphasize the role of pre-fire stand structure in influencing the spatial pattern of forest fires even under extreme fire conditions such as those experienced during the 1988 Yellowstone fires.

This analysis focused specifically on how the mountain pine beetle may influence landscape-level heterogeneity and affect fire risk. However, there are several other forest pests of concern in the Yellowstone region, including other bark beetles such as Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), spruce beetle (*Dendroctonus rufipennis* Kirby), and western balsam bark beetle (*Dryocoetes confuses* Swaine), as well as defoliating species such as the western spruce budworm (*Choristoneura occidentalis* Freeman). Previous studies have shown that defoliating insects, such as the western spruce budworm, may promote (Fleming and others 2002) or inhibit forest fires (H. L. Lynch and P. R. Moorcroft, unpublished), and it seems likely that the influence that insects exert on fire risk differs according to feeding guild. Further research is needed to improve our understanding of variations in insect–fire interactions that stem from differences in feeding guilds, as well as to identify the mechanisms underlying the complex temporal component of fire risk due to insect activity.

CONCLUSIONS

In this analysis, we found a measurable influence of mountain pine beetle activity in increasing the odds of burning in the 1988 Yellowstone fires, by approximately 11% for sustained activity in the period 1972–1975. More recent insect activity (specifically 1980–1983) was not significantly correlated with increased risk of burning, and mechanisms underlying this delayed increase in fire risk will require further research. The results of this study are an important component to understanding the nature of the 1988 Yellowstone fires, and the interactions between insect activity and forest fire risk more generally. As more detailed and sophisticated spatial data becomes available, it will become increasingly important to develop techniques appropriate to the new information, both in the field of ecology and also in spatial statistics. The highly autocorrelated nature of forest fires make Markov chain Monte Carlo techniques particularly important, and in this analysis we have demonstrated their utility to a question of pressing concern.

REFERENCES

Amman G, Ryan K. 1991. Insect infestation of fire-injured trees in the Greater Yellowstone Area. Technical Report. Research Note INT–398 USDA Forest Service.

Amman GD. 1991. Bark beetle–fire associations in the Greater Yellowstone Area. In: Nodvin SC, Waldrop TA, Eds. Fire and the environment: ecological and cultural perspectives. Proceedings of an international symposium. 1990 March 20–24; Knoxville, TN, USA Asheville (NC): USDA Forest Service Southeastern Forest Experimental Station. p 313–20.

Bebi P, Kulakowski D, Veblen T. 2003. Interactions between fire and spruce beetles in a subalpine Rocky Mountain forest landscape. Ecology 84:362–71.

Besag J. 1974. Spatial interaction and the statistical analysis of lattice systems. J R Stat Soc 36:192–236.

Besag J. 1975. Statistical analysis of non-lattice data. Statistician 24:179–95.

Bigler C, Kulakowski D. 2005. Multiple disturbance interactions and drought influence fire severity in Rocky Mountain sub-alpine forests. Ecology 86:3018–29.

Christensen NL, Agee JK, Brussard PF, Hughes J, Knight DH, Minshall GW, Peek JM, and others. 1989. Interpreting the Yellowstone fires of 1988. BioScience 39(10):678–85.

Cliff A, Ord J. 1981. Spatial processes. London: Pion.

Despain D. 1990. Yellowstone vegetation: consequences of environment and history in a natural setting. Boulder: Roberts Rinehart.

Despain D, Rodman A, Schullery P, shovic H. 1989. Burned area survey of Yellowstone National Park: the fires of 1988. Yellowstone Center for Resources. Yellowstone: National Park.

Fleming R, Candau J, McAlpine R. 2002. Landscape-scale analysis of interactions between insect defoliation and forest fire in central Canada. Clim Change 55:251–72.

Fox J. 1997. Applied regression analysis, linear models, and related models. Thousand Oaks (CA): Sage.

Fox J, Monette G. 1992. Generalized collinearity diagnostics. Am Stat Assoc 87:178–83.

Franke MA. 2000. Yellowstone in the afterglow: lessons from the fires. Technical Report. YCR-NR-2000–03. Mammoth Hot Springs (WY): National Park Service.

Furniss MM, Renkin R. 2003. Forest entomology in Yellowstone National Park, 1923–1957: time of discovery and learning to let live. Am Entomol 49:198–209.

Heyerdahl E, Brubaker L, Agee J. 2001. Spatial controls of historical fire regimes: multiscale example from the interior West, USA. Ecology 82:660–78.

Holland P, Steyn D. 1975. Vegetational responses to latitudinal variations in slope angle and aspect. J Biogeogr 2:179–83.

Hopkins A. 1909. Practical information on the Scolytid beetles of North American forests. I. Barkbeetles of the genus *Dendroctonus*. Technical report. Bulletin 83. USDA Bureau of Entomology.

Huffer FW, Wu H. 1998. Markov chain Monte Carlo for autologistic regression models with application to the distribution of plants species. Biometrics 54(2):509–24.

Knight DH, Wallace LL. 1989. The Yellowstone fires: issues in landscape ecology. BioScience 39:700–6.

Kulakowski D, Veblen T, Bebi P. 2003. Effects of fire and spruce beetle outbreak legacies on the disturbance regime of a subalpine forest in Colorado. J Biogeogr 35:1445–56.

Lichstein JW, Simmons TR, Shriner SA, Franzreb KE. 2002. Spatial autocorrelation and autoregressive models in ecology. Ecol Monogr 72:445–63.

McCullough D, Werner R, Neumann D. 1998. Fire and insects in northern and boreal forest ecosystems of North America. Annu Rev Entomol 43:107–27.

R Development Core Team. 2005. R: a language and environment for statistical computing Vienna: R Foundation for Statistical Computing. Available online at: http://www.R-project.org.

Renkin RA, Despain DG. 1992. Fuel moisture, forest type, and lightning-caused fire in Yellowstone National park. Can J For Res 22(1):37–45.

Rothermel R, Hartford R, Chase C. 1994. Fire growth maps for the 1988 Greater Yellowstone Area fires. Technical Report INT–304: USDA Forest Service General.

Schoennagel T, Veblen T, Romme W. 2004. The interaction of fires, fuels, and climate across Rocky Mountain forests. BioScience 54(7):661–76.

Turner M, Romme W, Tinker D. 2003. Surprises and lessons from the 1988 Yellowstone fires. Front Ecol Environ 1(7):351–8.

Upton GJG. 1985. Spatial data analysis by example. New York: Wiley.

Veblen T, Hadley K, Nel E, Kitzberger T, Reid M, Villalba R. 1994. Disturbance regime and disturbance interactions in a Rocky Mountain subalpine forest. Ecol 82:125–35.

Wallace L, Ed. 2004. After the fires: the ecology of change in Yellowstone National Park. New Haven, (CT): Yale University Press.

Wu H. 1994. Regression models for spatial binary data with application to the distribution of plant species [thesis]. Florida State University.

Wu H, Huffer FW. 1997. Modelling the distribution of plant species using the autologistic regression model. Environ Ecol Stat 4:49–64.