Insect–Fire Interactions in Yellowstone National Park: The Influence of Historical Mountain Pine Beetle (*Dendroctonus ponderosae*) Activity on the Spatial Pattern of the 1988 Yellowstone Fires

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Abstract

We examined the historical record of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) activity within Yellowstone National Park, Wyoming, for the 25-year period leading up to the 1988 Yellowstone fires (1963–1986) in order to determine how prior mountain pine beetle activity and 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 (MCMC) method to account for the high degree of spatial autocorrelation inherent to forest fires. Our final model included four statistically significant variables: drought, aspect, moderate mountain pine beetle activity in 1975, and heavy mountain pine beetle activity in 1975. Of the two major mountain pine beetle outbreaks to precede the 1988 fires, the older outbreak (1971–1976) was significantly correlated with the burn pattern, whereas the more recent outbreak (1980–1983) was not. Although regional drought and high winds were responsible for the overall scale of the event, we concluded that mountain pine beetle activity in the mid-1970s increased the odds of burning ~13.0–15.0% and, along with aspect and spatial variation in drought, contributed to the spatial pattern of burned and unburned areas.

Introduction

Both insect outbreaks and forest fires constitute important disturbance processes in the Greater Yellowstone Ecosystem (GYE), and research suggests that both insects and fire play a crucial role in the continuation and healthy functioning of the ecosystem (Despain 1990; Parker and Stipe 1993). Several authors have directly addressed the role of fire in promoting or inhibiting certain forest insects in the GYE (Amman 1991; Amman and Ryan 1991; Rasmussen et al. 1996). The converse question (Does insect activity promote or inhibit forest fire in the GYE?) has received surprisingly less attention, with no scientific consensus having yet been reached. With regard to mountain pine beetle (mpb), Parker and Stipe (1993) concluded that "[there] is no question . . . that the increased fuel loading from the beetle-killed trees has made the remaining lodgepole pine forest more susceptible to wildfires," while Despain (1990) argued that "[f]uels suitable for crown fires may be reduced by the beetles to the point of retarding fires."

Table 1. Datasets used in the analysis of the 1988 Yellowstone fires.

	Data layer	Abbreviation	Original data type	Source
Climate data[a]	Min. daily temp (°F)	tmin	text	NCDC[b]
	Max. daily temp (°F)	tmax	text	NCDC
	Ave. daily wind speed (mph in tenths)	wind	text	NCDC
	Total precip. (hundredths of an inch)	prcp	text	NCDC
	Palmer Drought Severity Index	pdsi	text	NCDC
Geographic data	Elevation (meters)	elev	30-m raster	NPS[c]
	Slope (degrees)	slope	30-m raster	NPS
	Aspect	see footnote[d]	50-m raster	derived from elevation
	Pre-1988 fire cover type	see footnote[e]	50-m raster	NPS
	Previous fire history	previous burn	polygon shapefile	NPS
Historical data	Mountain pine beetle activity (1963–1986)	mpbyy(severity)[f]	polygon shapefile	digitized from 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). 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 divided into 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 (DF0), mid- (DF1), or late-successional (DF2)), Engelmann spruce/subalpine fir (late-successional (ESSF2)), Krumholtz (Kr), lodgepole pine (early (LPP0), mid- (LPP1), or late-successional (LPP2)), pygmy lodgepole pine (PyLPP), whitebark pine (early (WBP0), mid- (WBP1), or late-successional (WBP2)), and non-forested.
[f] Severity classes were based on the original datasets and were grouped into the following categories: vl=very light, l=light, m=moderate, h=heavy, and vh=very heavy.

Mountain pine beetle (*Dendroctonus ponderosae*) activity in a stand initiates a long and complex cascade of ecological changes. In the short term (up to a year), needle death may increase canopy fuel loads, but subsequent needle drop and decomposition may actually eliminate much of the flammable fuels in the stand. Over longer timescales, fire risk will depend on both dead and downed coarse woody debris and on new growth, which may arise via the release of understory trees or through recruitment of new individuals. As noted by Despain (1990), most of the dead and downed trunks in the GYE are larger than three inches in diameter, and the bulk of this downed biomass will not burn even under the most intense fire conditions. Additionally, a study in northwestern Colorado (Kulakowski et al. 2003) suggested that the opening of the canopy may lead to a proliferation of moist understory vegetation that may prevent low-severity fires from burning. On the other hand, vertical heterogeneity arising from rapid release of understory trees combined with surviving mature individuals may provide ladder fuels sufficient to increase fire risk. It is almost certain that both fire-promoting and fire-inhibiting changes have occurred simultaneously, to varying degrees, over the decades following substantial insect activity in the GYE. Nevertheless, by analyzing the historical record of insect activity and fires in Yellowstone National Park (YNP), we can hope to identify the net effect of these concurrent, stand-level changes on the future risk of forest fire.

Historical data indicate that very large fires occur naturally in the GYE every 200–300 years (Romme and Despain 1989). It has been suggested that under these extreme circumstances, landscape heterogeneity arising from site-specific canopy and fuel load conditions plays no significant role in determining fire risk (Turner et al. 2003). In this analysis, we used an extensive and largely unexploited dataset of insect outbreaks in YNP to answer the question: Did the previous decades of mpb activity in YNP have a measurable influence on the spatial pattern of the 1988 Yellowstone fires?

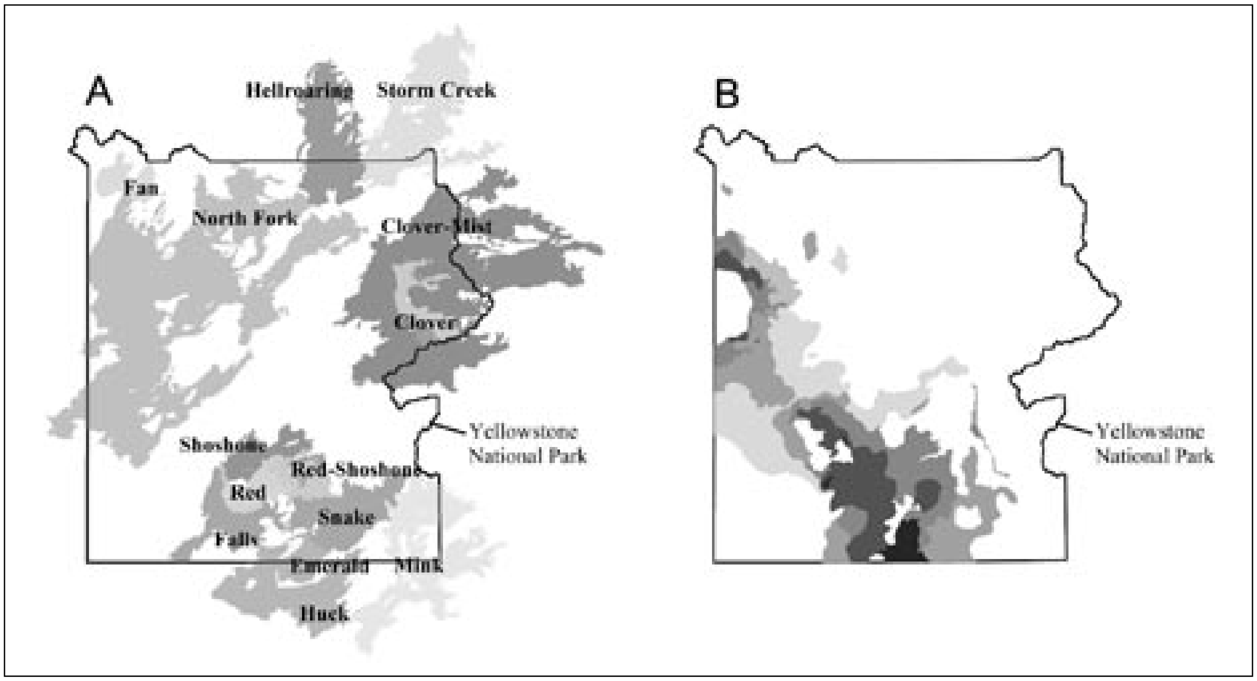

Figure 1A. Major fire complexes that comprised the 1988 Yellowstone fires.

Figure 1B. Tree mortality due to mountain pine beetle activity in 1975 (darker shades of gray represent more intense activity).

Methods

Analytical approach

The forestry and fire communities have long embraced the notion that insect outbreaks may affect both the occurrence and intensity of extreme fire events. 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 upon pre-existing conditions being amenable to an extreme fire. In addition to the spatial extent and intensity of mpb activity from 1963 to 1986, we included information on a number of variables that potentially played a role in promoting fire. These variables fell into several broad categories (see 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 mpb in promoting fire was conservative.

Data

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

To understand the influence of previous mpb activity on the 1988 Yellowstone fires, we compiled all available aerial detection surveys of forest insect activity within the park covering the years 1963–1986. Hardcopy maps (1:125,000 scale), initially provided by the U.S. Forest Service's Northern Region Forest Health Protection Group and archived in Yellowstone National Park, were digitized using a high-resolution scanner and integrated into a complete GIS database by a process of manual (on-screen) digitization. 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.

From 1962 to 1986, two different insect intensity scales were used in the aerial detection surveys: an ordinal scale with five categories ranging from "very light" to "very heavy" (1964, 1970–1976, 1980, 1986) and a cardinal scale indicating the approximate number of trees affected by insect activity (1969, 1977–1985). Two years used both scales (1962 and 1967), and in 1965, no intensities were indicated. Fortunately, in some cases, both scales were used, allowing us to develop an approximate conversion between the two scales of measure in order to treat insect activity intensities uniformly across the entire database. This conversion is included in Table 2.

The aerial surveys and the corresponding database included all pests or pathogens that could have been detected by aerial survey, including mpb, Douglas-fir beetle (*Dendroctonus pseudotsugae* Hopkins), spruce beetle (*Dendroctonus rufipennis* Kirby), western balsam bark beetle (*Dryocoetes confuses* Swaine), and defoliating species such as the western spruce budworm (*Choristoneura occidentalis* Freeman). The insects whose activity was detected and recorded in this database are listed in Table 3. 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 mpb complemented the broad spatial extent of the 1988 Yellowstone fires, making the mpb the choice insect agent for this analysis. Figure 1B represents the spatial extent of tree mortality due to mountain pine beetles in 1975, a year of extensive insect activity and one that was ultimately significant in our analysis.

Table 2. Conversion table for the cardinal and ordinal scales for reporting insect activity intensity.

Cardinal category	Ordinal range (n = # trees affected per hectare)
Very light	n ≤ 0.5
Light	0.5 ≤ n ≤ 5
Moderate	5 ≤ n ≤ 10
Heavy	10 ≤ n ≤ 50
Very heavy	n ≥ 50

To account for other potentially important risk factors, we compiled spatial datasets of geographic, topographic, and climatological factors that may also have played a role in determining which areas burned in 1988 and which did not (Table 1). These data layers were re-sampled or digitized as appropriate on a common 100-m-resolution raster grid. This dataset was then exported to the statistical software package

Table 3. Historical data on the presence or absence of various insect and fungal pathogens as represented in the aerial survey maps discussed in the text.*

	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986
Comandra rust (*Cronartium comandrae*)	X			X								X													
Douglas-fir beetle (*Dendroctonus pseudotsugae*)	X	X	X			X							X						X		X	X	X	X	X
Fir engraver (*Scolytus ventralis*)	X	X	Y	Y																					
Lodgepole needle miner (*Coleotechnites milleri*)	X																								
Mountain pine beetle (*Dendroctonus ponderosae*)	X		X	X		X		X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Pine engraver (*Ips pini*)													X												
Spruce beetle (*Dendroctonus rufipennis*)								X																	
Western balsam bark beetle (*Dryocoetes confuses*)			Y	Y		X		X								X	X	X			X		X	X	X
Western spruce budworm (*Choristoneura occidentalis*)	X	X	X	X		X		X		X	X	X	X	X		X	X	X	X	X		X	X	X	X

*X represents presence; Y represents potential presence.

R (R Development Core Team 2005) and re-sampled every 500 m so that each data point represented a 100 × 100-m pixel from the original dataset, spaced 500 m apart. The re-sampling was necessary to reduce the size of the dataset for computational speed. The final dataset was a 219 × 209-pixel 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 non-forest were removed. There were 28,748 pixels in the final dataset.

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. Accordingly, we transformed the original dependent variable y_i to regress the log-odds of burning in 1988 against its potential covariates as follows (Equation 1):

$$\mathrm{logit}(y_i) = \log\left(\frac{y_i}{1-y_i}\right) = \beta_0 + \sum_i \beta_i x_i$$

in which y_i represents the burn status of the pixel ($y_i = 1$ if the pixel burned), β_0 represents the intercept, and the β_i represents the regression coefficients for the covariates x_i.

Ordinary logistic regression implicitly requires that individual data points are independent; this basic requirement is immediately violated in any analysis involving a spatial context. This is particularly true in the analysis of "contagious" forest disturbances; the underlying contagious nature of fire spread dictates that neighboring regions are not independent. Accurate determination of the regression coefficients requires one to account for the non-independent nature of the independent variable. Several schemes have been developed to account for autocorrelation in logistic regression analysis. Besag's (1972, 1974) coding method divides the pixels into two interlocking sets of points arranged like the red and black tiles on a checkerboard; the two sets depend on each other, but the points within each set are assumed to be independent. The pseudolikelihood approach simply adds the sum of nearest-neighbor values as an additional covariate to the regression model; this technique has been studied by many authors (Besag 1975; Ripley 1988) and can be easily applied using standard regression software. More recently, a spatial filtering approach has been suggested (Griffith 2004) by which the eigenvectors of a modified spatial weights matrix are added as additional regression covariates; these eigenvectors serve as surrogates for unknown latent factors underlying the spatial autocorrelation. Finally, a Markov Chain Monte Carlo (MCMC) approach (Wu 1994; Wu and Huffer 1997; Huffer and Wu 1998) has been developed that can approximate the maximum likelihood function for probability densities known up to a constant of proportionality.

In this analysis, we use the MCMC approach as developed by Huffer and Wu, who used the technique to understand the underlying environmental factors responsible for plant species distributions. As shown in several case studies (Huffer and Wu 1998; Hubbell et al. 2001), the MCMC approach more accurately captures the latent spatial autocorrelation of these types of ecological problems and has been shown to more accurately represent the estimate errors. Although the details of our analytical technique have been reported elsewhere (Lynch et al. in press) and will not be described here, it is sufficient to note that ultimately, our regression analysis involves estimating the maximum likelihood function (Equation 2):

$$\ell(\beta,\gamma) = \frac{e^{\beta'\sum_i x_i y_i + \gamma \sum_i \sum_{j^*} x_i y_i y_j}}{\sum\limits_{\text{all map possibilities}} e^{\beta'\sum_i x_i y_i + \gamma \sum_i \sum_{j^*} x_i y_i y_j}}$$

where y_i, x_i, β, and γ represent the burn state at pixel i, the covariate values at pixel i, the transpose of the covariate regression coefficients, and the nearest-neighbor regression coefficient, respectively. Note that the denominator involves a sum over all possible permutations of burned and unburned pixels; this intractable normalizing constant cannot be evaluated analytically and must be estimated using MCMC methods. Further details on the general technique may be found in the papers by Huffer and Wu (Wu and Huffer 1997; Huffer and Wu 1998). A clear and straightforward overview of this technique as applied in an ecological context may be found in Hubbell et al. (2001).

Model selection

Because of their 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 approach described above. In the first step, all 80 variables were put into the model, and a combination of forward and backward step-wise regression (using the R function "step") was used to select the best model according to Akaike's Information Criterion (a criterion used for selecting among nested models). To further simplify the model, variables that were not significant at the 5% confidence level (slope, mpb85(l), mpb74(m), and mpb73(m)) were eliminated (see Table 1), and the four significant aspect variables (which spanned the continuous range from northwest–north–northeast–east) were combined into one variable, which we called "northeast." Finally, we narrowed our focus to consider only insect activity in 1975, which had the most robust effect on the fire model independent of the particular formulation of the model.

Because the MCMC approach 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, non-forested areas, and water) required (fixed) predefined burn states. Our approach was to assign the park border and interior non-forested 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. Areas of water were set to burn=0, because under no circumstances would those 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 was therefore conservative. We excluded from our final model covariates that were not robust to the random values of the border pixels (ESSF2 and mpb75(vh) (see Table 1). Our final statistical model, represented in Equation 3 (below), contained only four variables: pdsi (Palmer Drought Severity Index), northeast (representing all aspects within 90° of 22.5° northeast), mpb75(m) (moderate mountain pine beetle intensity in 1975), and mpb75(h) (heavy mountain pine beetle intensity in 1975).

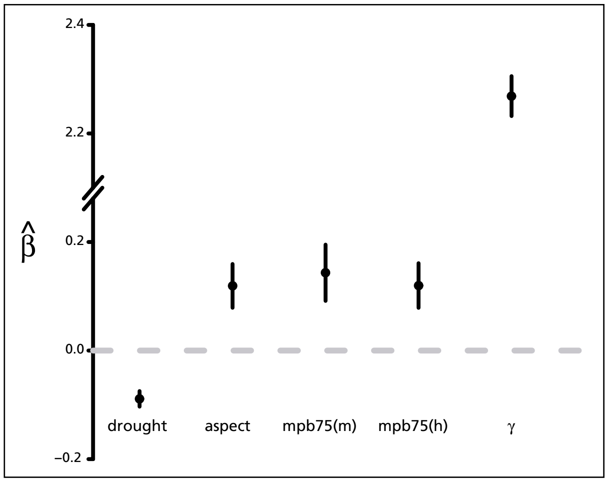

Figure 2. Graphic summary of the results of this analysis. The x-axis represents the various covariates included in the final model. Error bars represent 95% confidence limits for the value of $\hat{\beta}$.

$$\mathrm{logit}(y_i) \sim pdsi + northeast + mpb75(m) + mpb75(h)$$

Results

The results of the analysis are summarized in Figure 2 and Table 4. Figures 3A and B represent the burn probabilities as modeled either when no autocorrelation was accounted for (see Table 4) or when only autocorrelation was included (i.e., when the model consisted of only an intercept and an

Table 4. Best-fit model estimates (and standard errors) discussed in the text.

	ß0	pdsi	northeast	mpb75(m)	mpb75(h)	λ	Fig. 3
Logistic (site-specific only)[1]	–4.96(0.16)	–0.90(0.03)	0.25(0.02)	1.37(0.06)	1.77(0.06)		A
MCMC (autologistic only)[2]	–4.47(0.04)					2.25(0.02)	B
PSE (site-specific+ autocorrelation)[3]	–6.46(0.49)	–0.20(0.09)	0.28(0.08)	0.46(0.16)	0.72(0.21)	2.67(0.04)	
MCMC (site-specific +autocorrelation)[3]	–5.05(0.06)	–0.09(0.01)	0.12(0.02)	0.14(0.03)	0.12(0.02)	2.27(0.02)	C

[1] The top line represents the best-fit estimates using standard logistic regression with no autocorrelation variable.

[2] The second line represents the results of MCMC maximization for the gamma-only model.

[3] The last two lines represent the pseudolikelihood estimates 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 ten smaller than the reported estimated error.

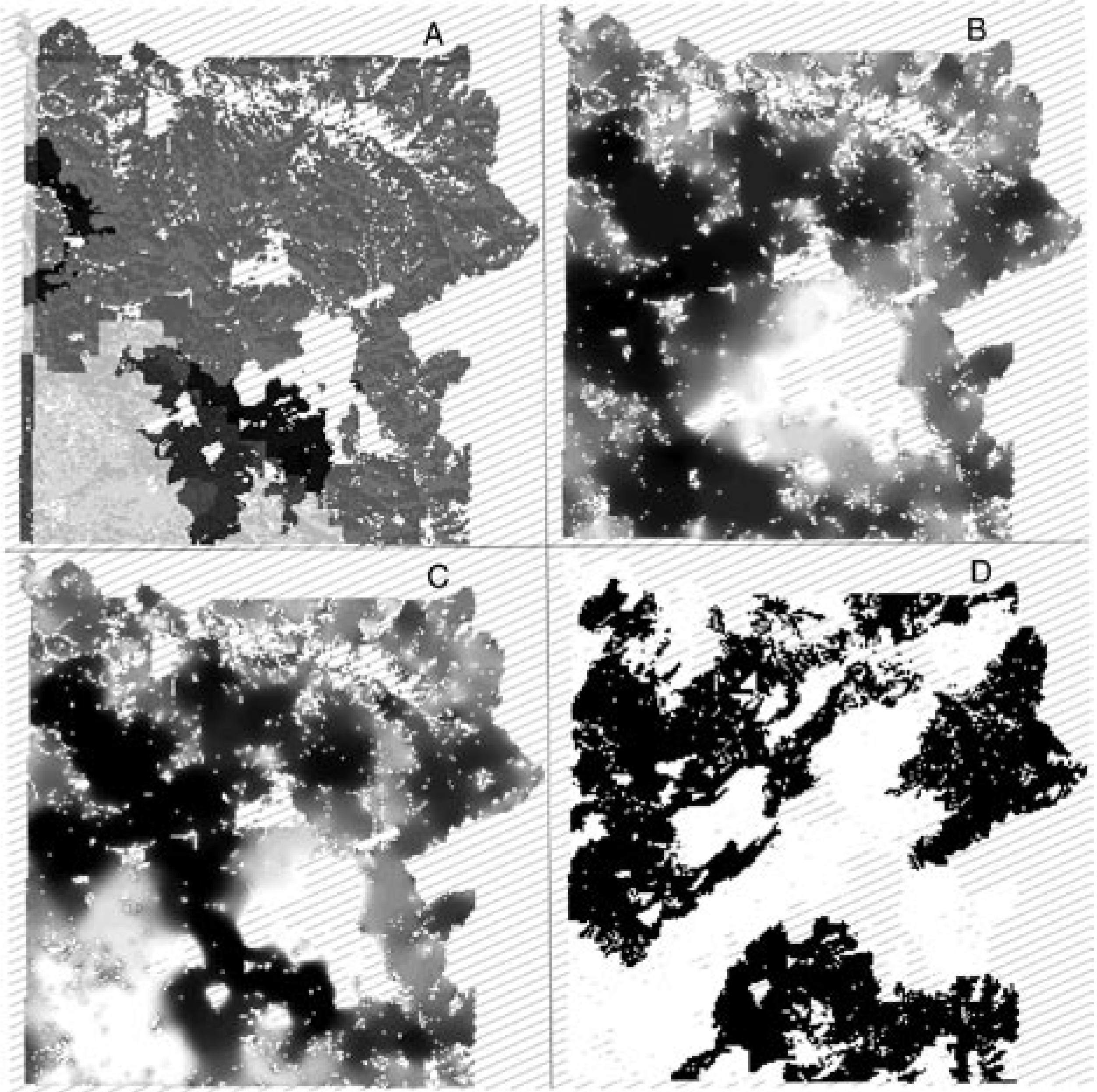

Figure 3. Figures 3A–C illustrate the probability of burning from the best-fit models, and Figure 3D illustrates the actual 1988 burn map (black=burned). Maps A–C correspond to the models incorporating no autocorrelation (A), only autocorrelation (B), and the full model (C) as indicated in Table 2. Map A represents the probability of burning according to the best-fit standard logistic model. Maps B and C represent the probability of burning (with darker shades of gray representing increasing probability of burning) over 20,000 MCMC iterations following an initialization period of 2,000 iterations starting with all forest pixels initially unburned. As discussed in the text, boundary pixels and non-forested areas (pixels left blank in the map) were drawn from a binary random variable. These maps represent an average over ten different simulations representing ten different randomly drawn boundaries. The grayscale ranges from zero probability of burning (white) to unity probability of burning (black).

autocorrelation parameter, see Table 4). As seen in Figure 3A, the simple auto-logistic model, which ignores spatial autocorrelation in fire spread, does not capture the spatial scale of the 1988 fires, and 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. A model including only nearest-neighbor interactions (Figure 3B) accurately captures the overall scale at which burning occurs, but with no spatial information (other than the locations of the water bodies, which biases 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 3C) captures both the spatial scale of the 1988 fires and their placement across the park. All four covariates in our final model are statistically significant, including moderate and heavy mpb activity occurring in 1975. The model correctly classifies 64.7% of all pixels. The number of misclassified burned pixels (5,556 of 15,749) is approximately equal to the number of misclassified unburned pixels (4,605 of 12,999); the model, therefore, produces approximately unbiased predictions of burn risk. Figure 3C illustrates the fit of our model, which captures both the large-scale pattern and many of the finer-scale details of the final burn pattern (Figure 3D). This highlights the 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 for the event.

The vertical error bars in Figure 2 represent the 95% confidence envelope of the value presented, and are associated with the probability that a particular variable is different than zero. This leads us to investigate the statistical probability that both of the insect-related βs are zero; that is, what is the probability that mpb activity played no role in the 1988 Yellowstone fires? The multivariate Wald statistic Z_0^2, which under the null hypothesis of zero insect activity effect is distributed as $\chi^2(df=2)$, is 146.0. Therefore, the probability that both β_{insect} values are actually zero is effectively nil.

The variables “northeast,” “mpb75(m)”, and “mpb75(h)” are all 0/1 factors; therefore, the relative strengths of each can be compared using the magnitudes of their coefficients. The range of the variable “pdsi” was 2.01, making the overall impact of that variable on burn risk similar to that of the other three factors. All four variables are approximately equal with regard to their impact on the log-odds of burning, and we can use Equation 1 to calculate the change in fire risk associated with any of these variables. For example, moderate mpb intensity in 1975 ($\hat{\beta}$ =0.14) is associated with a 15.0% increase in the odds of burning during the summer of 1988. Although it may seem counterintuitive that each of the four variables has such a small effect on the fire risk and yet the full model fits the actual burn pattern so well, the overwhelming spatial autocorrelation inherent to forest fires dominates the actual pattern of fire spread, and the underlying factors identified in our model function primarily to break the isotropy of the landscape in regard to fire spread.

Therefore, mpb activity some 10–12 years previous to the 1988 fire event served to increase fire risk and ultimately may have influenced the spatial patterning of burned areas. The effects of previous moderate- and high-intensity beetle activity are comparable in magnitude to other factors affecting fire risk, such as drought and aspect, in our model.

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 were able to untangle these two components in order to understand which site-specific characteristics, such as previous insect activity, may predispose some patches to burn while other patches are left untouched.

Before considering the main question of mpb activity and fire risk, it is important to consider the biological relevance of the other two variables that remained significant in the final model: average drought and northeastern aspect. It is not surprising that fine-scale spatial variation in drought was significant in our model, because others have demonstrated the role of drought in promoting the extreme fire conditions present in 1988 (Christensen et al. 1989; Renkin and Despain 1992; Schoennagel et al. 2004). The second factor, aspect, is also known to affect fire spread. Southward-facing slopes experience the most incident sunlight, and the subsequent drying is known to increase fire risk. Northern aspects, on the other hand, tend to support higher fuel loads because they retain moisture more effectively than southern aspects. Fires typically spread more quickly upslope, and because 1988 fire spread was generally 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, then, would have spread most slowly on the northeast-facing slopes, generally backing downslope. We hypothesize that this slow burning on northeastern-facing slopes, coupled with increased fuel loads, may have allowed for relatively slower, but more, 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 independent of any differences in cover type, and must result from something other than differences in stand composition or stand age.

The results of this analysis demonstrate that even when considering a wide range of potential variables, mpb activity remains a statistically significant factor when choosing models to explain the final pattern of burned areas for the 1988 Yellowstone fires. Moderate- to high-intensity mpb activity is particularly correlated with the risk of burning, and represents a factor that increased the odds of burning by 12.7–15.0%. Consistent with this conclusion, we note that in the period 1974–1986, areas that eventually burned in 1988 had consistently higher average mpb activity than those that did not burn in 1988. It is interesting to note that in the 25 years prior to 1988 for which we have complete insect activity records, there were two major outbreaks of mpb: one during the period 1971–1976, and the other during 1980–1983. Whereas beetle activity during the first outbreak is correlated with an increase in fire risk, activity during the second outbreak was either uncorrelated or negatively correlated with the log-odds of burning in 1988, once spatial interaction effects had been accounted for. This result—that mpb activity increases fire risk only after a period of 10–12 years—was unexpected, but is consistent with earlier work pointing to a strong time-dependence in the strength of insect–fire interactions (Lynch and Moorcroft in review). The biological mechanisms leading to this delayed increase in fire risk require further study, although the timescale of the process would be consistent with the time required for significant release of understory vegetation.

In this analysis, we considered each category of beetle-induced tree mortality (very light, light, moderate, heavy, and very heavy) as separate and independent binary factors in order to avoid making any assumptions about the relative impact of varying levels of insect activity. For example, high levels of insect activity may cause widespread mortality and changes in stand structure and composition, whereas light damage may cause only scattered mortality with no widespread recruitment from the understory. There is no obvious ordinal relationship in the fire risk associated with these different ecological changes, and it was more appropriate to consider each activity level independently. Our results consistently demonstrated that moderate and heavy mpb activity were most strongly associated with fire risk, whereas very light, light, and very heavy activity were not significantly correlated with a change in the log-odds of burning. More field work will be required in order to understand why areas experiencing such intermediate activity are at the highest risk of future burning.

This analysis focused specifically on the influence of mountain pine beetles in landscape-level heterogeneity in fire risk. There are several other forest pests of concern in the Yellowstone region, including other bark beetles such as Douglas-fir beetle, spruce beetle, and western balsam bark beetle, and defoliating species such as the western spruce budworm. A previous study has shown that defoliating insects may actually inhibit forest fires (Lynch and Moorcroft in preparation), and it seems likely that the influence of insects in affecting fire risk differs according to feeding guild. Preliminary analysis suggests that western spruce budworm activity in the period studied is associated with decreased risk of burning in 1988, although this requires further study.

Conclusion

In this analysis of the 1988 Yellowstone fires, we found a measurable influence of mpb activity in increasing the odds of burning in 1988, by 15.0% and 12.7% for moderate and heavy insect activity in 1975, respectively. More recent insect activity was not significantly correlated with increased risk of burning, and mechanisms underlying this delayed increase in fire risk will require further research. Plot studies of fuel load changes following insect activity are now being planned (M. Simard, pers. comm.) and it is likely that studies such as these will help illuminate the underlying biological changes involved in the delayed increase in fire risk we report here.

Finally, the results of this study highlight the importance of regular, long-term, and spatially explicit mapping of insect and pathogen activity within the park. Yellowstone National Park, under the current wildland fire program, is a unique natural laboratory for understanding the spatial and temporal dynamics of these complex phenomena. Ongoing efforts toward a complete digital database of park terrain, biogeography, and forest disturbance within the park will continue to spur important developments in both basic and applied research.

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