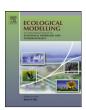
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A Hierarchical Bayesian model of wildfire in a Mediterranean biodiversity hotspot: Implications of weather variability and global circulation

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ABSTRACT

In this study we combined an extensive database of observed wildfires with high-resolution meteorological data to build a novel spatially and temporally varying survival model to analyze fire regimes in the Mediterranean ecosystem in the Cape Floristic Region (CFR) of South Africa during the period 1980-2000. The model revealed an important influence of seasonally anomalous weather on fire probability, with increased probability of fire in seasons that are warmer and drier than average. In addition to these local-scale influences, the Antarctic Ocean Oscillation (AAO) was identified as an important large-scale influence or teleconnection to global circulation patterns. Fire probability increased in seasons during positive AAO phases, when the subtropical jet moves northward and low level moisture transport decreases. These results confirm that fire occurrence in the CFR is strongly affected by climatic variability at both local and global scales, and thus likely to respond sensitively to future climate change. Comparison of the modelled fire probability between two periods (1951–1975 and 1976–2000) revealed a 4-year decrease in an average fire return time. If, as currently forecasted, climate change in the region continues to produce higher temperatures, more frequent heat waves, and/or lower rainfall, our model thus indicates that fire frequency is likely to increase substantially. The regional implications of shorter fire return times include shifting community structure and composition, favoring species that tolerate more frequent fires.

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1. Introduction

Over half of the world's terrestrial ecosystems are dependent on fire to maintain ecological structure and function (Shlisky, 2007). Fire regimes in these regions have a profound ecological role (Bond, 1995) that can be strongly influenced by weather and climate (McKenzie et al., 2004). Thus in addition to the direct physiological impacts of changes in temperature, precipitation, and CO₂ concentration due to climate change, changes in the fire regime will have potentially major effects on these fire-driven ecosystems (Bond et al., 2003). Since the 1980s there has been speculation about the impact of climate change on wildfire regimes (Balling et al., 1992; Clark, 1988; Layser, 1980), and some studies have produced evidence of changes in fire regimes associated with recent climate change (Gillett et al., 2004; Westerling et al., 2006). How-

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ever, most of this work has been limited to North America, Europe, and Australia, and much uncertainty remains regarding the sensitivity of wildfire to weather trends and variability in many other fire-prone regions of the world. In this study we present a novel model for fire return times that allows integration of decades of regional-scale weather data at high spatial and temporal resolution, while retaining the temporal dependence structure of a fire survival model. We apply this model to some of the richest fire occurrence data and high-resolution climate data in the world, that for the Mediterranean-climate shrub lands of the Cape Floristic Region (CFR) of South Africa, a global biodiversity hotspot. Specifically we model the influence of local weather, variability in weather, and global circulation patterns on fire return times across the region (Fig. 1).

The CFR experiences a Mediterranean climate (Köppen, 1931) with hot, dry summers and cool, wet winters in the western half, that transitions to more even precipitation seasonality in the east, with mean annual rainfall ranging from 60 mm to 3345 mm (Schulze, 1997). The region is an internationally recognized hotspot of floral biodiversity and is home to approximately 9000 plant species, 69% of which are endemic (Goldblatt and Manning, 2002).

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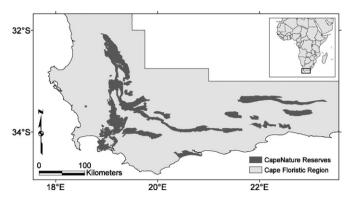


Fig. 1. Map illustrating the location of the Cape Floristic Region of South Africa in relation to the African continent and the locations of the protected areas (\sim 11,000 km²) included in this analysis (dark shaded areas). These areas are predominantly mountain *fynbos*, a sclerophyllous Mediterranean shrub-land ecosystem. This area was divided into a 0.02° (\sim 4 km²) grid to facilitate analysis.

In contrast to other regions of the world with high levels of biodiversity, the CFR species tend to be locally abundant but have small ranges and limited dispersal capabilities (Cowling and Lombard, 2002; Latimer et al., 2005; Schurr et al., 2007). These factors may make the region's flora vulnerable to decreased precipitation and shifts in the seasonality of precipitation predicted under future climate change (IPCC-WGII, 2001, Section 10.2.3.4). In fact, bioclimatic models of species distributional shifts under the projected climate of 2050 predict a 51–65% reduction in the area of the *fynbos*, the Mediterranean-climate shrub lands that currently dominate the region (Midgley et al., 2002).

Most previous work investigating climate change impacts on plant species has focused on the direct impact of changes in temperature and precipitation and overlooked potential ecological changes due to shifts in the fire regime. Since various plant species have different strategies for responding to fire (some rely on seeds that require fire for germination, while others re-sprout from the rootstock), fire return time and seasonality are important determinants of the community makeup. For example, in some areas of the CFR the dominant species (such as *Protea neriifolia* or *P. repens*) can persist only within a narrow range (\sim 10–35 years) of fire return times (van Wilgen, 1992, p. 63). In the higher rainfall areas, fire also plays a key role in preventing the incursion of forest species (Bond et al., 2003). Fire in the CFR is also a significant hazard for people living in the region, as in other Mediterranean-climate regions. For example, in the austral summer of 2000, unusually extensive fires burned over 18,000 ha in the Western Cape Province, including 20% of the natural vegetation on the Cape Peninsula (encompassing metropolitan Cape Town and Table Mountain National Park). These fires damaged crops, destroyed over 270 residences on the Cape Peninsula alone, and resulted in an estimated US\$500 million in insurance claims. The month prior to the fires was one of the driest on record and the preceding five days were extremely windy and near record high temperatures (~41 °C) (Calvin and Wettlaufer, 2000).

As in many areas of the world, a changing fire regime in the CFR could have major ecological (range shifts and changing community composition) and societal (risk to agriculture and residential areas) impacts. However, projections of future change are difficult in the absence of a thorough understanding of how the fire regime has responded to meteorological fluctuations in the recent past. There is some evidence that the fire return interval has decreased over the past few decades in some areas of the CFR to below historical means of 11–30 years (Brown et al., 1991; van Wilgen et al., 1991). However there has been no region-wide modelling of the historical fires to understand the sensitivity of fire return time to local weather characteristics and global circulation patterns. These ques-

tions are especially important in the context of climate change, as the sensitivity of the system to changes in climate at different scales could spur other ecological shifts. In this paper we present a high-resolution spatio-temporal model, as well as simulation results based on the model, relating observed fire to weather records from the CFR in an effort to understand how sensitive the fire regime is to anomalous weather, and how responsive to it is to oscillations in global circulation.

2. Materials and methods

2.1. Data

This analysis integrates historical fire data, interpolated weather, and climate indices from several sources. The fire data were compiled from field reports collected in protected areas (about 11,000 km²) across the Western Cape Province by the Cape-Nature management organization and consist of geo-referenced burned area polygons and supplementary information including the date and cause of fire, if known (de Klerk, 2008, see Fig. 1). These protected areas are mostly expanses of contiguous mountainous landscapes with largely intact native vegetation and are rarely influenced by human activities, except at lowland boundaries. The vast majority of area burned (90%) was from unplanned wildfires. For a more thorough description of the fire database, see Forsyth and van Wilgen (2007). Fire monitoring and recording has been relatively consistent since the late 1970s, with more patchy records going back further, and includes over 1500 fire records ranging in size from less than a hectare to 580 km². To ensure that variation in the data did not reflect a historical trend in sampling effort, we used fire occurrence data from the period 1980-2000 only, but used weather data from 1950 to 2000, as explained below. To facilitate modelling, these data were converted to a 0.02° grid $(\sim 2 \text{ km} \times 2 \text{ km})$ covering the monitored protected areas. We scored fires as present in a grid cell during a season if at least 25% (\sim 1 km²) of the cell burned in that season. In total, 2105 (81%) of the 2611 cells burned at least once and 10% burned 3 or more times.

The Climate Systems Analysis Group at the University of Cape Town provided weather data that had been interpolated from a dense network of meteorological stations using a downscaled regional climate model (Hewitson and Crane, 2006). These data consist of daily maximum and minimum temperature (with a resolution of 0.05°, about 25 km²) and precipitation (0.1°, about 100 km²) covering the period from 1950 to 2000. Seasonal indices of temperature and precipitation were developed from this daily data, for the seasons defined as winter (JJA), spring (SON), summer (DJF), and autumn (MAM). The seasonal data were standardized by subtracting the seasonal means in each grid cell (e.g. for grid cell number 10 in winter of 1980, the seasonal winter temperature is the average temperature for winter 1980 minus the mean of all winter temperatures in that grid cell from 1980 through 2000). The seasonal climate variables in the model are thus "anomalies" or deviations from the long-term local seasonal average. This standardization means we can interpret the relationship of fire to these seasonal variables as an association with inter-annual variation in seasonal weather. The effect of intra-annual variability among seasons was then captured in the model as seasonal fixed effects via indicator variables for each season (see details below). This framework allows separation of the overall mean response of fire probability to inter-seasonal fluctuations in temperature and precipitation and the response due to variation within seasons around those means. Using these data, we also calculated the precipitation concentration coefficient, following Schulze (1997) and Markham (1970). This is an index that quantifies precipitation seasonality, with high values meaning that rainfall is concentrated in a short period within the year, and low values meaning rainfall occurs evenly over the whole year. In the CFR the concentration is high in the west (where most rain falls in the winter) and gradually decreases to the east. In addition, we included the Antarctic Ocean Oscillation (AAO, also known as the Southern Annular Mode) to explore the potential relationship between fire and large-scale circulation patterns (Marshall, 2003). The AAO is known to influence precipitation and moisture transport in the CFR by shifting the subtropical jet shifts northwards and increasing moisture flux into the region, resulting in increased precipitation and humidity (e.g. Mason, 1995; Reason and Jagadheesha, 2005; Reason et al., 2002).

2.2. Model overview

Most regional-scale modelling approaches relating fire and weather at the landscape scale rely on summarizing total burned area data into coarse regions which are analyzed separately (e.g. McKenzie et al., 2004; Swetnam and Betancourt, 1990), or by combining data from the entire region of interest (e.g. Duffy et al., 2005). This facilitates construction of regression models, but offers little explanation of the patterns of fire within a region and does not account for the complex mosaic of different stand ages (and therefore fuel load) which can be especially important in systems with relatively short fire return intervals such as savannahs or Mediterranean-climate shrub lands. Biomass in the fynbos increases each year after fire for about 25 years, after which live biomass decreases as the adult shrubs begin to senesce (van Wilgen, 1992, p. 40). Thus a coarse-resolution modelling approach would be unable to account for the different fire histories of local areas, or for the increasing probability of fire over time in those areas due to fuel accumulation after fires.

Our model is related to statistical survival analysis, because it estimates the probability that no fire occurs in each grid cell at each seasonal time step (i.e. grid cell survival), given the observed data and given that no fire occurred in the previous season (see Section 2.3). There are two major innovations in the model, each of which allows us to extract more information from the data than standard fire regression analyses. First, by defining distinct probabilities of fire (i.e. "failure to survive") in each time step at each location, the model is qualitatively similar to a Kaplan-Meier semiparametric survival analysis (Venables and Ripley, 2002), but unlike this class of model, our approach builds an explicit regression relationship between survival probabilities in each location at each time step and the associated high-resolution explanatory variables. Second, our modelling framework also handles the heavily censored nature of fire data in a novel way. The first fire interval for most grid cells (those in which there was no fire in the first time step) is only partially observed (i.e. left-censored). In order to estimate the cumulative probability of survival for each grid cell in the first time step, we had to account for fires that happened prior to the beginning of our dataset (i.e. pre-1980). This was accomplished by effectively predicting survival probabilities back in time using the parameters fitted from the 1980 to 2000 period. These probabilities for the seasons that make up the censored time period together define a multinomial probability for each grid cell that represents the distribution of previous fire times, so that these unobserved fire occurrences were estimated along with the other parameters in the models. This allowed us to incorporate into our parameter estimates the censored information contained in the fire records for the cells that did not burn and for other cells with long periods without fire.

2.3. Model details

Our model specification reflects the fact that we study fire incidence within given time intervals and the fact that covariates which influence the probability of a fire vary over time. So, we build our model conditionally, in the spirit of survival analysis (e.g. Klein and Moeschberger, 2003). We model the probability of a fire in a given time interval given no fire up to that interval. More precisely, let Z_i be the time since last fire in cell i and let $p_{it} = P(Z_i > t | Z_i > t - 1)$, so that the cumulative probability that a grid cell burns increases over time. So, $1 - p_{it}$ is the probability of a fire in the interval $\{Z_i \in \Re | t - 1 < Z_i \le t\}$ given no fire up to time t. Note that $p_{it} = S_i(t)/S_i(t-1)$ where $S_i(t) = P(Z_i > t)$, the so-called survivor function. We use a standard generalized linear model form, with the probit transform, to relate the probabilities, p_{it} to the environmental factors that are the explanatory variables for each grid cell at each time step, i.e. probit(p_{it}) = $X_{it}^T \beta$. It is possible to extend β to β_t , enabling time-varying coefficients or to β_i , enabling spatially varying coefficients (Banerjee et al., 2004). Note that, under this specification, the chance that time since last fire is in the interval $\{t-1 \le Z_i \le t\}$ can be calculated recursively. That is, the unconditional probability, $P(Z_i > t) = S_i(t) = p_{it}p_{i,t-1} \cdots p_{il}$ and $P(Z_i \in \{t-1 < Z_i \le t\}) = S_i(t) - S_i(t-1) = (1-p_{it})p_{i,t-1} \cdots p_{il}$. Expressed in different terms, every observed fire time is interval-censored and is modelled as a multinomial trial with interval probabilities as

Finally, we recognize that we have further censoring of the data. At any cell i, we do not know the time since the first fire (if there has been a fire at that location); we only know that it was before we started collecting data. Similarly, we do not get to see the time of the last fire at site i; we only know that it occurred after we stopped collecting data (i.e. post-2000). We treat the first situation as a missing data problem. If we knew the time of the previous fire before data collection began, we would know the time since last fire for the first fire in i, hence we could write down the likelihood as above. On the other hand, if we know the values of the model parameters, we can write down the conditional distribution for the missing fire time. With a defined conditional distribution, we can introduce a Gibbs sampler in our Markov Chain Monte Carlo (MCMC) algorithm to sample the unobserved fire times from the posterior distributions of the unknown parameters (Gelfand and Smith, 1990). A key comment here is that this requires the historical (1950–1980) X_{it} s (i.e. climate data) which, fortunately, we have. For the second situation, the unknown time of the next future fire for each grid cell, we know that the time is at least the time up to the end of the study period, so we can again use the expressions above to specify the associated probability (in this case, this is the probability that no fire has occurred before the end of the time period for which we have data). Finally, with multiple fires at i during our observation period, we reset the survival probability to 1 for the first season following after each fire.

2.4. Model fitting details

Each data point Z_i (i.e. time since last fire in cell i) has an associated set of covariate vectors $\{X_{ij}, j=-112, \ldots, 0, 1, \ldots, T\}$, where 112 is the number of seasons prior to the beginning of the fire record (1951–1979) and T=80 seasons of fire data 1980–2000. We observe Z_i in an interval between two fires, say I_t , or else after the last observed fire. We can denote the times of the fires in a cell as t_i . For each cell i, there is one initial time of fire t_{i0} that is unknown, since this fire occurred before the beginning of the data set. Subsequent fires in the same cell have been observed, so the times t_i of those fires are known. As described above, these fire times are observed as conditionally independent multinomial trials with possible values $t_{i0}+1$, $t_{i0}+2$, ..., T, >T (call this last interval I_{T+1} for convenience) with probabilities $q_{ij}=(1-p_{ij})\prod_{(t_{i0}+1<1< j)}p_{il}$, $j=t_{i0}+1$, ..., T with (for notational convenience), $q_{i,T+1}=(t_{i0}+1<1< T)p_{il}$. So, formally, the likelihood is,

Table 1Seasonal parameters estimated in the full model—the coefficient for winter represents the overall intercept and the other seasons were estimated using winter as the baseline.

Season	Mean	95% credible interval
Winter	3.22	3.16, 3.29
Spring	2.63	2.50, 2.76
Summer	2.16	2.03, 2.29
Fall	2.47	2.35, 2.6

$$L(q;Z) = L(\beta;Z) = \prod_i f(Z_i|q_i) = \prod_i \prod_j q_{ij}^{V_{ij}}$$

where $V_{ij} = 1$ if $Z_i \in I_j$, and $V_{ij} = 0$ otherwise. Practically, we only have the q_{ij} for which $V_{ij} = 1$. With a prior on β we have a fully specified Bayesian model. In fact, for the unknown t_{i0} , we adopt a discrete uniform prior on $\{-112, -111, \ldots, -1, 0\}$ and then do Gibbs updates for the t_{i0} given β , followed by updates for β given all of the t_{i0} s.

Because of the time-varying X_{ij} s, the q_{ij} s are complicated functions of β . However, p_{il} only depends upon X_{il} , i.e. under a probit model, $p_{il} = \Phi(X_{il}^T\beta)$, where Φ is the standard or unit normal cumulative probability distribution. It is often easier to introduce latent Gaussian variables in probit models (Albert and Chib, 1993). In the present setting consider independent $W_{il} \sim N(X_{il}^T\beta, 1)$ so that $P(W_{il} > 0|\beta) = p_{il}$, i.e. we interpret $W_{ij} < 0 \Leftrightarrow Z_i \in I_1$. Then, we can augment the model to:

$$\prod_{i} f(Z_{i}|\{W_{ij}\}) \prod_{i} \prod_{j} f(W_{ij}|\beta) f(\beta)$$

Now, in addition to updating β and the t_{i0} s, we have to update the W_{ij} s. However, given Z_i , we know the constraints on the W_{ij} and so we sample them as normal variables, truncated accordingly, as is standard in a probit model (Albert and Chib, 1993).

2.5. Model selection

We considered two candidate models, the full model described above and the full model without the AAO index. Model selection was accomplished by comparing the deviance information criterion (DIC), which penalizes for poor model fit and model complexity and selected the model with the lower DIC (Gelman et al., 2004). The model was coded and run in the R statistical environment (R Development Core Team, 2008). All models were run with two chains for 10,000 iterations after a burn in of 2000 iterations, resulting in 20,000 samples from the posterior probability distribution. Convergence was assessed after visual inspection of the chains and with Gelman and Rubin's diagnostic (Gelman and Rubin, 1992).

3. Results

The model revealed the important influence of weather on the probability of a grid cell's *surviving* without fire in each time step across the CFR. We modelled the influence of environmental factors on the probability of fire *survival*, given survival in the previous season, and thus the signs of the coefficients are opposite of what might be expected in a typical regression framework. For example, the seasonal effects, which represent the contribution of the mean seasonal weather to survival probability across all grid cells, reflect the relative probability of absence of fire in each season, so that, for example, summer has the lowest coefficient value and thus the highest probability of fire (Table 1).

The influence of climatic factors are interpreted using the posterior regression coefficients. Since this is a probit regression with standardized covariates, the coefficients represent the amount

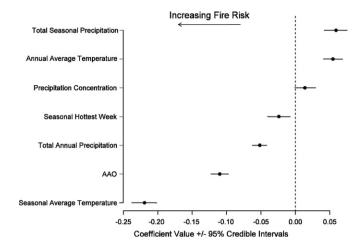


Fig. 2. Plot of the regression coefficients and their 95% credible intervals, sorted by value. Negative values indicate correlation with decreased chance of survival (increased chance of fire). Precipitation concentration is an index defining the extent to which rainfall is restricted to a few months, AAO is the Antarctic Ocean Oscillation index, seasonal average temperature is the average temperature during summer (DJF), fall (MAM), winter (JJA), or spring (SON) seasons.

of change of seasonal fire probability in standard deviations on the probit curve (which is the inverse of the cumulative normal probability distribution) due to a standard deviation change in the covariate. Seasonal average temperature had by far the largest influence of all climatic factors on fire probability, with a comparatively large negative coefficient (-0.219, 95% CI: -0.238, -0.201) indicating substantially higher fire probability in anomalously high-temperature seasons. Average temperature of the hottest week similarly had a significant, although small, negative coefficient (-0.024, 95% CI: -0.040, -0.008). Average annual temperature, by contrast, had a relatively small positive coefficient (0.055, 95% CI: 0.041, 0.069). Since seasonal and annual temperature are related, to assess the net effect of temperature on fire survival probability, it is necessary to account for both the effect of the previous season and the current season. Here, in any particular season, fire probability is dominated by the mean temperature of the season, offset to a lesser degree by mean annual temperature. The highest probability of fire thus occurs in a year of high-temperature contrasts, where temperature overall may not be high, but which includes anomalously hot periods.

An analogous contrast was observed in the effects of precipitation, although the absolute size of the coefficients was smaller. Higher precipitation in the preceding year was negatively associated (-0.052, 95% CI: -0.063, -0.042) with the probability of survival without fire, while higher precipitation in a particular season had a positive influence (0.059, 95% CI: 0.042, 0.075) on the probability of survival (Fig. 2). As with temperature, the greater contrast associated with a dry season in a wet year enhanced the probability of fire occurrence.

The AAO had the coefficient with the second largest magnitude (significantly negative at -0.110, 95% CI: -0.123, -0.097), indicating substantially decreased probability of survival without fire during positive AAO phases. The model including AAO was strongly preferred over the model including only local weather variables (DIC = 33,733 versus 33,974). Precipitation concentration, which is an indicator for the East–West difference in rainfall seasonality was slightly positive (0.014, 95% CI: -0.001, 0.029) indicating a slight tendency for increased fire risk in the eastern regions, after controlling for other variables.

Using the estimated parameters, it is possible to predict mean fire probability (defined as 1 minus the cumulative survival probability) through time and across space. Mean region-wide fire

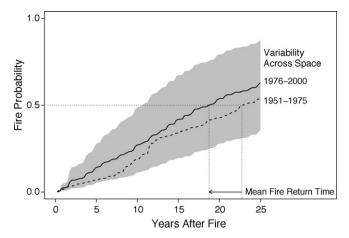


Fig. 3. Modelled cumulative fire probabilities from two time periods, 1951–1975 and 1976–2000. The dark line is the mean cumulative probability of fire due to the observed weather (estimated using the fitted coefficients) averaged across all cells from 1976 to 2000. The gray region represents the boundaries of the 2.5 and 97.5 quantiles (95% of the data) of the cumulative fire probability and represents the spatial variability in fire probability across the region from 1976 to 2000. The dotted line is the cumulative probability of fire from 1951 to 1975, which is calculated from the coefficients estimated using the 1980–2000 fire data and weather (see text for details). The arrow identifies the shift in mean fire return time from the earlier to the later time period.

probability curves are displayed in Fig. 3, starting with a value of 0 in the first season (i.e. assuming a fire occurred in the previous season), and increasing over a 25-year time period in seasonal increments that depend on the environmental conditions in each successive season. This facilitates a comparison between posterior predictions of fire probabilities for the two periods 1951–1975 and 1976-2000, based on the fitted model. The curves show more rapid increase in predicted fire probability, and thus shorted mean fire return time (defined as the time the fire probability increases above 50%) for the more recent decades (1976-2000). The model predicts a mean fire return time of 18.75 years for 1976–2000, versus 22.75 years for 1951–1975. The broad uncertainty envelope shown in Fig. 3 reflects spatial variation in predicted mean return time, as shown in Fig. 4. This variation is related to extensive spatial climatic variability across the region—for example, annual rainfall varies from 60 mm to 3345 mm, and rainfall seasonality that ranges from nearly aseasonal to highly concentrated in 2 months.

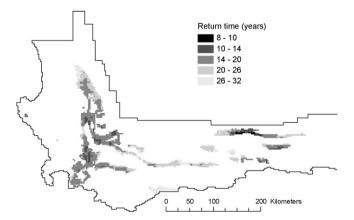


Fig. 4. Predicted mean fire return times for the modelled portion of the Cape Floristic Region. For each $2 \text{ km} \times 2 \text{ km}$ grid cell, the grayscale shade represents the mean return time, as indicated in the legend. The mean for each grid cell is the number of years after a previous fire at which cumulative fire probability is predicted to exceed 0.5, averaged over predictions using all posterior samples of the model parameters.

4. Discussion

The probability that a patch of CFR fynbos vegetation will survive a season without fire is most strongly influenced by seasonal temperature (primarily seasonal average but also hottest week), and secondarily by precipitation. The negative coefficient for total annual precipitation may reflect an increase in biomass and especially fine fuels after an anomalously wet previous year, as has been observed in other systems (Esque et al., 2003; Grau and Veblen, 2000) as well as in the CFR (Seydack et al., 2007).

Fire in the CFR is also strongly influenced by global circulation patterns, as indexed by the AAO. This relationship has not been previously reported. During the negative phase of the AAO, the subtropical jet shifts northwards and low level moisture transport to South Africa increases, leading to wetter winter and spring conditions in the Western Cape, and generally higher humidity in summer (Reason and Rouault, 2005). Thus the negative coefficient reflects a lower fire survival probability (i.e. greater fire probability) when the AAO is in a positive phase. The AAO has had an increasing trend since the late 1960s, possibly due in part to changes in stratospheric ozone concentrations and greenhouse gases (Thompson and Solomon, 2002). As an additional mechanism relating largescale atmospheric and ocean circulation, sea surface temperatures in the South Atlantic are known to affect precipitation and moisture transport across the Western Cape (Blamey and Reason, 2007; Reason and Jagadheesha, 2005; Reason et al., 2002). Large-scale circulation patterns have been found to be correlated with fire events in Tasmania, (Nicholls and Lucas, 2007), Alaska (Duffy et al., 2005), the continental United States (Gan, 2006), and Argentina (Kitzberger, 2002). This finding also raises the possibility of using the AAO, which may be predictable several months in advance, to inform prediction of fire activity in forthcoming seasons in the CFR.

This novel modelling framework offers significant advantages over traditional regression methods and other commonly used methods for analyzing spatial fire data. Because we are modelling the probability of survival (absence of fire) for each time step, it is possible to examine the estimated survival probability curve for any observed time period and any particular location (with a full estimate of the associated uncertainty). This facilitates quantitative comparisons between sites and across years. Our approach could be duplicated in regions that have additional or different environmental drivers by incorporating these into the matrix of X_{it} s. For example, variables such as humidity and wind speed are also likely correlated with fire probabilities (but these data were unavailable for our region). One advantage of the statistical modelling framework presented here is the flexibility to investigate the effects of various drivers without needing to fully specify the mechanistic link. Of course, as a statistical regression-based model, it describes phenomenological relationships between environmental factors and fire, not mechanistic relationships based on the physics of ignition and flame propagation that are incorporated into fire behavior models. In contrast to mechanistic models with fixed parameters, our Bayesian approach results in full posterior distributions for all unknown model parameters (Clark, 2007). This allows us to estimate the unknown parameter values (fire probabilities and their relationship to weather variables) from the observed data, rather than specifying them a priori. The goal of our approach is distinct from and complementary to such physical models: we aim to quantify and describe patterns in fire regimes and correlations with potentially driving factors over large scales in space and time, rather than to simulate the dynamics of individual fires. Our model was constructed to analyze regional fire patterns over a period of 20 years in a system with an average return interval of about 20 years. The spatially explicit approach allowed us, in effect, to substitute space for time and allow estimation of the influences of weather variables despite the relatively short record.

There have been some changes in fire management strategies and other socioeconomic shifts including the end of apartheid and rapid urbanization over this time. Nevertheless, our methods are fairly robust to these factors because we are looking for broad scale patterns in fire probabilities from season to season across the entire region, rather than trying to explain the cause of any specific fire. Thus our approach is robust to potential errors in the data (such as an occasional missing fire or uncertainty in the interpolated temperature) or various socioeconomic drivers that may influence the fire regime.

This analysis confirms that fire probability in the *fynbos* regions of the CFR is sensitive to local- and global-scale fluctuations in climate. The regional implications of a changing fire frequency include shifting community composition towards more fire tolerant species and the possible elimination of plant species that are obligate seeders. As mentioned earlier, many areas of the CFR are dominated by plants (such as P. neriifolia or P. repens) that require time to reach reproductive maturity and so can persist only within a narrow range (\sim 10–35 years) of fire return times (van Wilgen, 1992, p. 63). For example, a shift in community composition has been observed in response to prescribed short interval fires in the Jonkershoek valley of the CFR. van Wilgen (1981) compared vegetation from areas with three fire histories (average return time 6 years, 21 years and >37 years) and found that the short 6-year return interval reduced biomass from 35 t ha⁻¹ to 6 t ha⁻¹ and eliminated long-lived, reseeding-dependent shrubs.

The short-term hydrological effects of fire may also be important in *fynbos*. In the Swartboskloof research area, streamflow volume increased 16% in the first 2 years after fire (van Wilgen, 1992, p. 219). The loss of biomass after fire leads to decreased interception and evapotranspiration, which ultimately increases runoff. Because vegetation biomass increases relatively quickly after fire, these increases are likely to be short lived; however, given increasing water demand in the region and growing urban population in Cape Town, even slight changes in supply may have meaningful policy implications in some parts of the region (Hewitson, 2006; Smith and Hansen, 2003).

These results also suggest that the fire regime in the CFR is likely to respond to future climate change. Our comparison of mid- and late-twentieth-century conditions graphically illustrates how fire probabilities are inferred to have shifted in response to historical changes in precipitation, temperature, and global circulation, decreasing 4 years between mid- and late-twentieth century (Fig. 3). If, as projected for the region (cf. Hewitson, 2006), climate change in the CFR continues to lead to higher seasonal temperatures, more frequent heat waves, and lower seasonal rainfall, our model projects that fire frequency is likely to continue to increase. However, an important unknown is how biomass accumulation rates may change in a warmer, drier future. Therefore projections of fire frequency into the future should take dynamic biomass accumulation rates into account. Most research on the ecological impacts of climate change has focused on the direct impacts of changes in temperature and precipitation. However, in firedependent ecosystems, the indirect effects of changes in fire regime may be even more important. This research has important ramifications for conservation and management of ecosystems like the CFR. In addition to added risk to residential areas and agriculture, a changing fire regime may lead to ecological changes in an ecosystem which is already stressed by climate change, habitat fragmentation, and land-use change (Hannah et al., 2005). A thorough understanding of the strength and nature of the relationship of vegetation dynamics (including fire) and inter-annual weather variability is vital to understanding how climate change may impact ecosystems like the CFR. Decision makers (reserve managers, conservation biologists, and policy-makers) need reliable information and models to develop effective management practices. This is especially important in the context of a changing environment, as managers must make decisions based on predictions of future changes.

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References

- Albert, J.H., Chib, S., 1993. Bayesian analysis of binary and polychotomous response data. Journal of the American Statistical Association 88, 669–679.
- Balling, R., Meyer, G.A., Wells, S.G., 1992. Climate change in Yellowstone National Park: is the drought-related risk of wildfires increasing? Climatic Change 22, 35–45
- Banerjee, S., Carlin, B.P., Gelfand, A.E., 2004. Hierarchical Modeling and Analysis for Spatial Data. Chapman & Hall/CRC, Boca Raton, 472 pp.
- Blamey, R., Reason, C.J.C., 2007. Relationships between Antarctic sea-ice and South African winter rainfall. Climate Research 33, 188–193.
- Bond, W.J., 1995. Fire and Plants. Chapman & Hall, New York.
- Bond, W.J., Midgley, G.F., Woodward, F.I., 2003. What controls South African vegetation—climate or fire? South African Journal of Botany 69 (1), 13.
- Brown, P.J., Manders, P.T., Bands, D.P., 1991. Prescribed burning as a conservation management practice: a case history from the Cederberg Mountains, Cape Province, South Africa. Biological Conservation 56, 133–150.
- Calvin, M., Wettlaufer, D., 2000. Fires in the Southern Cape Peninsula, Western Cape Province, South Africa January 2000. International Forest Fire News 22, 69–75.
- Clark, J.S., 2007. Models for Ecological Data. Princeton University Press, Princeton, NJ, 152 pp.
- Clark, J.S., 1988. Effect of climate change on fire regimes in northwestern Minnesota. Nature 334, 233–235.
- Cowling, R.M., Lombard, A.T., 2002. Heterogeneity, speciation/extinction history and climate: explaining regional plant diversity patterns in the Cape Floristic Region. Diversity and Distributions 8, 163–179.
- de Klerk, H., 2008. A pragmatic assessment of the usefulness of the MODIS (Terra and Aqua) 1-km active fire (MOD14A2 and MYD14A2) products for mapping fires in the fynbos biome. International Journal of Wildland Fire 17, 166–178.
- Duffy, P.A., Walsh, J.E., Graham, J.M., Mann, D.H., Rupp, T.S., 2005. Impacts of large-scale atmospheric-ocean variability on Alaskan fire season severity. Ecological Applications 15, 1317–1330.
- Esque, T.C., Schwalbe, C.R., DeFalco, L.A., Duncan, R.B., Hughes, T.J., 2003. Effects of desert wildfires on desert tortoise (Gopherus agassizii) and other small vertebrates. Southwestern Naturalist 48, 103–111.
- Forsyth, G.G., van Wilgen, B.W., 2007. An Analysis of the Fire History Records from Protected Areas in the Western Cape. CSIR Report CSIR/NRE/ECO/ER/2007/0118/C. Council of Scientific and Industrial Research, Stellenbosch South Africa
- Gan, J., 2006. Causasilty among wildfire, ENSO, timber harvest, and urban sprawl: the vector autoregression approach. Ecological Modelling 191, 304–314.
- Gelfand, A.E., Smith, A.F.M., 1990. Sampling-based approaches to calculating marginal densities. Journal of the American Statistical Association 8 (410), 398–409.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. Bayesian Data Analysis. Chapman & Hall/CRC, Boca Raton.
- Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7, 457–472.
- Gillett, N., Weaver, A., Zwiers, F., Flannigan, M., 2004. Detecting the effect of climate change on Canadian forest fires. Geophysical Research Letters 31, L18211.
- Goldblatt, P., Manning, J.C., 2002. Plant diversity of the Cape Region of southern Africa. Annals of the Missouri Botanical Garden 89, 281–302.
- Grau, H.R., Veblen, T.T., 2000. Rainfall variability, fire and vegetation dynamics in neotropical montane ecosystems in north-western Argentina. Journal of Biogeography 27, 1107–1121.
- Hannah, L, Midgley, G.F., Hughes, G., Bomhard, B., 2005. The view from the cape. Extinction risk, protected areas, and climate change. Bioscience 55, 231– 242.
- Hewitson, B.C., 2006. The Development of Regional Climate Change Scenarios for Sub-Saharan Africa. Final Report No. AF 07. Assessments of Impacts and Adaptations to Climate Change (AIACC), Washington, DC.
- Hewitson, B.C., Crane, R.G., 2006. Consensus between GCM climate change projections with empirical downscaling: precipitation downscaling over South Africa. International Journal of Climatology 26, 1315–1337.
- IPCC-WGII, 2001. Climate Change 2001: Impacts, Adaptation, and Vulnerability: Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.

- Kitzberger, T., 2002. ENSO as a forewarning tool of regional fire occurrence in northern Patagonia, Argentina. International Journal of Wildland Fire 11, 33–39.
- Klein, J., Moeschberger, M., 2003. Survival Analysis: Techniques for Censored and Truncated Data. Springer, New York.
- Köppen, W.P., 1931. Grundriss der Klimakunde. W. de Gruyter, Berlin.
- Latimer, A.M., Silander, J.A., Cowling, R.M., 2005. Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. Science 309, 1722–1725. Layser, E.F., 1980. Forestry and climatic change. Journal of Forestry 78, 678–682.
- Markham, C.G., 1970. Seasonality of precipitation in the United States. Annals of the Association of American Geographers 60, 593–597.
- Marshall, G.J., 2003. Trends in the southern annular mode from observations and reanalyses. Journal of Climate 16, 4134–4143.
- Mason, S.J., 1995. Sea-surface temperature—South-African Rainfall Associations 1910–1989. International Journal of Climatology 15, 119–135.
- McKenzie, D., Gedalof, Z., Peterson, D.L., Mote, P., 2004. Climatic change, wildfire, and conservation. Conservation Biology 18, 890–902.
- Midgley, G.F., Hannah, L., Millar, D., Rutherford, M.C., Powrie, L.W., 2002. Assessing the vulnerability of species richness to anthropogenic climate change in a biodiversity hotspot. Global Ecology and Biogeography 11, 445–451.
- Nicholls, N., Lucas, C., 2007. Interannual variations of area burnt in Tasmanian bushfires: relationships with climate and predictability. International Journal of Wildland Fire 16, 540–546.
- R Development Core Team, 2008. A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
- Reason, C.J.C., Jagadheesha, D., 2005. Relationships between South Atlantic SST variability and atmospheric circulation over the South African region during austral winter. Journal of Climate 18, 3339–3355.
- Reason, C.J.C., Rouault, M., 2005. Links between the Antarctic oscillation and winter rainfall over western South Africa. Geophysical Research Letters 32, L07705.
- Reason, C.J.C., Rouault, M., Melice, J.L., Jagadheesha, D., 2002. Interannual winter rainfall variability in SW South Africa and large scale ocean–atmosphere interactions. Meteorology and Atmospheric Physics 80, 19–29.

- Schulze, R.E., 1997. South African Atlas of Agrohydrology and Climatology. Technical Report. Report TT82/96, Water Resource Commission, Pretoria, South Africa.
- Schurr, F.M., Midgley, G.F., Reeves, G., Poschlod, P., Higgins, S.I., 2007. Colonization and persistence ability explain the extent to which plant species fill their potential range. Global Ecology and Biogeography 16, 449–459.
- Seydack, A.H.W., Bekker, S.J., Marshall, A.H., 2007. Shrubland fire regime scenarios in the Swartberg Mountain Range, South Africa: implications for fire management. International Journal of Wildland Fire 16, 81–95.
- Shlisky, A., 2007. Fire, ecosystems and people: threats and strategies for global biodiversity conservation. In: 4th International Wildland Fire Conference, Seville, Spain, p. 17.
- Smith, L., Hansen, S., 2003. Access to water for the urban poor in Cape Town: where equity meets cost recovery. Urban Studies 40, 1517–1548.
- Swetnam, T.W., Betancourt, J.L., 1990. Fire-southern oscillation relations in the Southwestern United States. Science 249, 1017–1020.
- Thompson, D.W.J., Solomon, S., 2002. Interpretation of recent southern hemisphere climate change. Science 296, 895–899.
- van Wilgen, B.W., 1981. Some effects of fire frequency on fynbos plant community composition and structure at Jonkershoek, Stellenbosch. South African Forestry Journal 118, 42–55.
- van Wilgen, B.W., 1992. Fire in South African Mountain Fynbos: Ecosystem, Community, and Species Response at Swartboskloof. Springer-Verlag, New York.
- van Wilgen, B.W., Bond, W.J., Richardson, D.M., 1991. Ecosystem management. In: Cowling, R.M. (Ed.), Fynbos—Nutrients, Fire and Diversity. Oxford University Press, Cape Town, pp. 345–371.
- Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S. Springer-Verlag, New York.
- Westerling, A.L., Hidalgo, H.G., Cayan, D.R., Swetnam, T.W., 2006. Warming and earlier spring increase western US forest wildfire activity. Science 313, 940-943