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RESEARCH PAPER

Climate change-induced shifts in fire for Mediterranean ecosystems

Enric Batllori[1]*, Marc-André Parisien[2], Meg A. Krawchuk[3] and Max A. Moritz[1]

[1]*Department of Environmental Science, Policy, & Management, University of California, Berkeley, California, USA,* [2]*Natural Resources Canada, Canadian Forest Service, Edmonton, Alberta, Canada,* [3]*Department of Geography, Simon Fraser University, Burnaby, British Columbia, Canada*

*Correspondence: Enric Batllori, Environmental Science Policy and Management, University of California Berkeley, 335 Mulford Hall, Berkeley, CA 94720, USA.
E-mail: enric.batllori@gmail.com

ABSTRACT

Aim Pyrogeographical theory suggests that fire is controlled by spatial gradients in resources to burn (fuel amount) and climatic conditions promoting combustion (fuel moisture). Examining trade-offs among these environmental constraints is critical to understanding future fire activity. We evaluate constraints on fire frequency in modern fire records over the entire Mediterranean biome and identify potential shifts in fire activity under an ensemble of global climate projections.

Location The biome encompassing the Mediterranean-type ecosystems (MTEs).

Methods We evaluate potential changes in fire over the 21st century in MTEs based on a standardized global framework. Future fire predictions are generated from statistical fire–climate models driven by ensembles of climate projections under the IPCC A2 emissions scenario depicting warmer–drier and warmer–wetter syndromes. We test the hypothesis that MTEs lie in the transition zone discriminating fuel moisture versus fuel amount as the dominant constraint on fire activity.

Results Fire increases reported in MTEs in recent decades may not continue throughout the century. MTEs occupy a sensitive portion of global fire–climate relationships, especially for precipitation-related variables, leading to highly divergent fire predictions under drier versus wetter syndromes. Warmer–drier conditions could result in decreased fire activity over more than half the Mediterranean biome by 2070–2099, and the opposite is predicted under a warmer–wetter future. MTEs encompass, however, a climate space broad and complex enough to include spatially varied fire responses and potential conversions to non-MTE biomes.

Main conclusions Our results strongly support the existence of both fuel amount and fuel moisture constraints on fire activity and show their geographically variable influence throughout MTEs. Climatic controls on fire occurrence in MTEs lie close to 'tipping points', where relatively small changes in future climates could translate into drastic and divergent shifts in fire activity over the Mediterranean biome, mediated by productivity alterations.

Keywords

Climate change, climate uncertainty, fire–climate relationship, fire shifts, Mediterranean biome, productivity, pyrogeography, spatially explicit models, warmer–drier syndrome, warmer–wetter syndrome.

INTRODUCTION

Fire is an ecological process that affects the structure and function of terrestrial plant communities over vast areas, and together with climate, plays a paramount role in shaping global biome distributions (Bond & Keeley, 2005; Bowman *et al.*, 2009). Mediterranean-type ecosystems (MTEs) are a paradigmatic example of fire-prone vegetation induced by seasonality, where occurrence of cool wet winters promotes ample biomass growth and extended summer drought favours the regular occurrence of wildfire. Several studies have reported changes in fire activity in MTEs and other ecosystems during recent

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decades (e.g. Piñol *et al*., 1998; Gillett *et al*., 2004; Westerling *et al*., 2006), and further changes at a global scale are expected (Scholze *et al*., 2006; Krawchuk *et al*., 2009). However, the direction (i.e. increase or decrease) and magnitude of projected changes in fire exhibit extraordinary diversity over the globe (e.g. Flannigan *et al*., 2009; Moritz *et al*., 2012), exacerbated by lack of consensus among projections of future climate. Climates of the MTEs may change dramatically over the next century (Klausmeyer & Shaw, 2009), and models to forecast potential alterations in fire activity across the entire biome are critical to understand its future.

MTEs are found on five continents and have been mapped as a distinct terrestrial biome: Mediterranean Forests, Woodlands and Scrub (*sensu* Olson *et al*., 2001). These areas include California and Baja California in the western United States and Mexico (CA), the Mediterranean Basin of southern Europe and North Africa (MB), central Chile in western South America (CH), the Western Cape region of South Africa (WC), and southwest and south Australia (AU). Although MTEs cover only 2% of the Earth's land area, they support 20% of known vascular plant species, high levels of species endemism, and are thus considered important biodiversity hotspots (Myers *et al*., 2000). Given fire's role in many ecosystem processes, and the tight coupling between fire and climate in MTEs, rapid changes in fire regimes threaten their ecological integrity under global change (Lavorel *et al*., 2007; Keeley *et al*., 2012).

In pyrogeographical theory, interactions between climate and fuels and their influence on fire occurrence (i.e. frequency) have been framed in a continuum of fuel amount to fuel moisture limitation (e.g. Meyn *et al*., 2007; Pausas & Bradstock, 2007; Bradstock, 2010; Krawchuk & Moritz, 2011). In this conceptual framework, fuel moisture limitation occurs where vegetation biomass is generally abundant, but a lack of conditions conducive to fire (i.e. flammability) limits its occurrence; drier conditions would lead to more fire. In contrast, fuel amount limitation occurs where weather conditions would regularly support fire, but there is insufficient biomass available to burn; drier conditions would lead to less fire. A growing body of evidence supports this framework and points to a varying sensitivity of fire to moisture-related variables along a productivity gradient (e.g. Westerling *et al*., 2003; Littell *et al*., 2009; Pausas & Paula, 2012).

The MTEs fall within a transition zone of productivity that discriminates between limitations of fuel moisture versus fuel amount. As such, it is unclear whether increases, decreases or a heterogeneous mixture of responses in fire activity will result from exposure to climate changes projected to occur over this century. We test the hypothesis that, while the magnitude of change in fire activity will vary across MTEs over time, a warmer–drier future would eventually lead to general decreases in burning, reflecting a shift to a fire environment with increasingly strong limitation from fuel amount. As a corollary test, we hypothesize that a warmer–wetter future would lead to increased productivity and thus more fire activity across most MTEs in the long run, because it would counteract the fuel moisture limitation associated with warmer conditions. We test this by examining potential shifts in fire occurrence across MTEs as a function of changes in key climate variables through a standardized global approach. Statistical models of fire occurrence based on modern observations of fire and climate provide a baseline from which future fire is estimated, using an ensemble of climate projections over the 21st century under IPCC (2007) AR4 mid-high A2 emissions levels. We use two ensembles of six global climate models (GCMs) that project warmer–drier versus warmer–wetter future climates (hereafter, 'syndromes'; Littell *et al*., 2011) to examine how the predicted changes in fire activity evolve through time, as changes in climate between the two syndromes become more extreme.

METHODS

The study region includes the terrestrial surface of the world's five MTEs regions, comprising the Mediterranean biome as defined by Olson *et al.* (2001). Our analysis builds upon an existing global framework (Moritz *et al*., 2012) that evaluates the relative probability of experiencing fire over a multi-decadal period. This framework permits model calibration over environments beyond the current extent of MTEs, allowing us to evaluate the possibility that future fire–climate relationships may take on characteristics of other biomes closer to the extremes of the fuel amount versus fuel moisture limitation continuum. Despite uncertainty in climate projections, the end-of-century exploration of diverging climatic syndromes provides novel and valuable information because climatic conditions become more extreme and contrasted and trade-offs in fire–climate relationships can then be better illustrated and evaluated, critical to anticipate potential future fire activity.

Our approach is climate based, where the dependent variable in the fire probability models is the presence of fire at a given pixel, and bioclimatic factors are the explanatory variables. The models describe the general fire–climate relationship in MTEs by characterizing the long-term proneness of MTEs to burning, and as such, are not designed to evaluate conditions that lead to fire in a particular year. Future events at local scale could strongly depend on other drivers not included in our approach (e.g. population density, land-use changes, invasive species), but consistent long-term projections of such drivers are unavailable at the biome level. Limitations of our approach are discussed below (see *Modelling framework considerations*).

Data

Geographic patterns of global fire activity were obtained through a consensus approach from two remotely sensed data sets: the European Space Agency Advanced and Along Track Radiometer (ATSR) World Fire Atlas for 1996–2006 (Mota *et al*., 2006), and the Moderate Resolution Imaging Spectroradiometer (MODIS) Collection 5 Climate Modeling Grid corrected active fire data from 2001–2007 (Giglio *et al*., 2006). We produced a dichotomous data set quantifying the presence or absence of fire at each location over the time span of the data (see Appendix S1 in Supporting Information). Despite the relatively short period

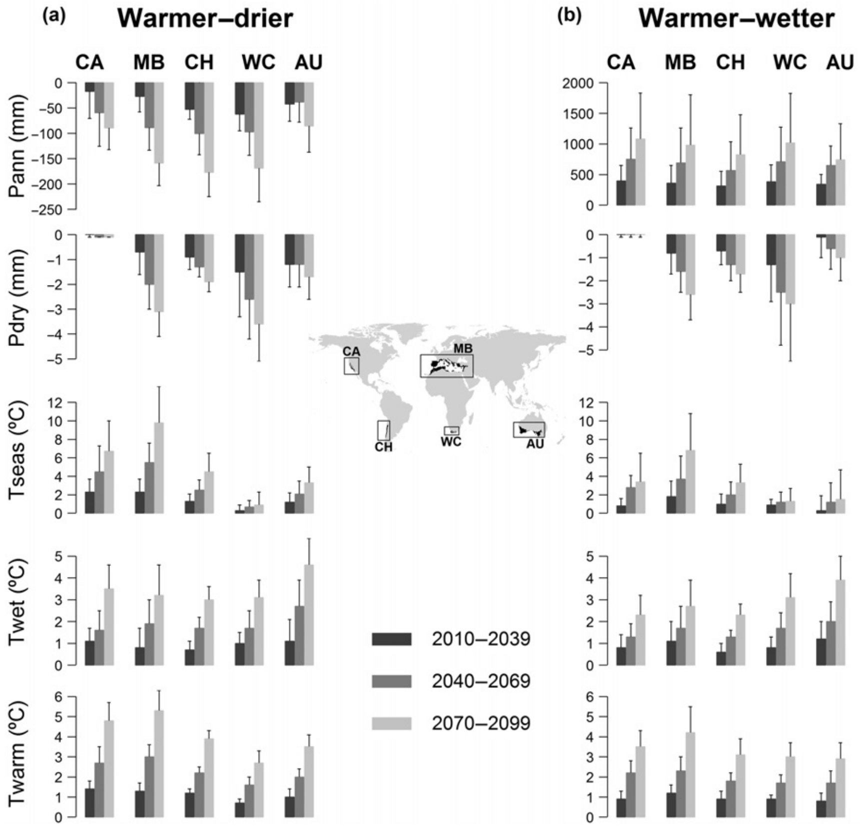

Figure 1 Summary of mean changes ± 1 SD (standard deviation) predicted for the five climate variables used in the fire probability models in each Mediterranean-type ecosystems region: CA – California and Baja California, MB – the Mediterranean Basin, CH – central Chile, WC – Western Cape and AU – southwest and south Australia. Syndromes of future climate consist of the ensemble of six Global Climate Models depicting warmer–drier (a) and warmer–wetter (b) conditions in each region over the century under IPCC (2007) AR4 A2 emission scenario. Pann – total annual precipitation, Pdry – precipitation of driest month, Tseas – temperature seasonality, Twet – temperature of wettest month, Twarm – temperature of warmest month. See Table 1 for variable descriptions.

covered by the data (12 years), they provide a measure of fire proneness that is adequate for the macroscopic scale of our study.

Temperature and precipitation climate variables were incorporated in the fire models as gridded representations of historical (i.e. baseline) and future climate data obtained from the GCM output of the World Climate Research Programme (WCRP) Coupled Model Intercomparison Project phase 3 (CMIP3) multi-model data set (Meehl *et al.*, 2007). From an initial suite of 16 GCMs, we selected 12 GCMs in each MTE to define the two climate syndromes: warmer–wetter and warmer–drier. Climate syndromes in each MTE were defined on the basis of projections of annual precipitation over the 21st century in each region (Fig. 1, see Appendix S2). The relative likelihood of the two syndromes of change cannot be ascertained because each GCM tends to capture climate dynamics better in some locations than others; in addition, it is unclear how performance metrics of GCMs relate to the reality of future outcomes (Knutti *et al.*, 2010). All spatial data used the World Geodetic System 1984 datum coordinate reference system and a pixel resolution of 0.5 degrees.

Modelling methods

Global fire probability models were developed using the MaxEnt v.3.3.3e software (Phillips *et al.*, 2006), as per Moritz *et al.* (2012). MaxEnt evaluates potential distribution from presence-only data (when the true absences are unknown), pertinent here because, globally, many fire-prone areas have not burned in the 12 years spanned by the fire data. Although numerous alternative techniques exist, MaxEnt performs well for many situations and diverse data sets (e.g. Hernandez *et al.*, 2006; Elith *et al.*, 2010).

We used five bioclimatic variables to build the fire probability models (Table 1; see Appendix S1): temperature seasonality (Tseas; standard deviation of monthly mean temperature), mean temperature of the wettest month (Twet), mean temperature of the warmest month (Twarm), total annual precipitation (Pann) and precipitation of the driest month (Pdry). Pdry and Twarm capture the fire season conditions, Pann and Twet are related to productivity, and Tseas reflects annual patterns in temperature affecting fuel moisture.

Biomass patterns and coarse-scale fuel accumulation rates are implicitly captured by the climatic variables in our models. There is a strong relationship between water availability and productivity in arid and sub-arid environments at the scale of our study (van der Werf *et al.*, 2008; Beer *et al.*, 2010; see Appendix S3), and fire probability models including a metric of vegetation biomass showed no significant differences from our climate-based approach (see Appendix S4). Therefore, we opted to exclude biomass metrics because of the challenge in predicting detailed future vegetation patterns (Cramer *et al.*, 2001). Similarly, we did not include ignition covariates in our models because there are currently no adequate projections of lightning

Table 1 Description of the independent variables used in the fire models and their relative importance (percent contribution) to the modelled fire probability. For each variable, values in the table correspond to averages of the ensemble of 100 model replicates produced for each of the six Global Climate Models depicting warmer–drier and warmer–wetter climate syndromes.

Variable name	Description (units)	Contribution (%) Warmer–drier	Warmer–wetter
Pann	Total annual precipitation (mm)	24.0	24.6
Pdry	Precipitation of driest month (mm)	20.8	16.3
Tseas	Temperature seasonality (SD)	15.3	17.0
Twet	Mean temperature of wettest month (°C)	12.0	14.5
Twarm	Mean temperature of warmest month (°C)	27.9	27.7

or human-caused fires ignitions (or proxies) that apply to all five MTEs.

Fire probability models were fitted to recent historical GCM reference period (1971–2000; hereafter 'baseline') and projected to future climatic conditions in the 2010–2039, 2040–2069 and 2070–2099 time periods for each GCM. Baseline models were developed on the basis of 100 bootstrapped replicates, each of them built on randomly sampled subsets of 1% of the global fire observations as training points. The remaining 99% of the fire records were used for model testing. This conservative approach avoids model over-fitting and minimizes effects of spatial autocorrelation in both fire and environmental covariates. Ripley's K function was used to determine the fraction of fire observations representing spatially independent samples. Models were fitted in Maxent using all feature types (i.e. linear, quadratic, product, hinge and threshold) and a regularization multiplier of 1 (Parisien & Moritz, 2009). For each GCM, the output of each of the 100 replicates were averaged to obtain baseline fire probability models. Similarly, model replicates were forced with future climate variables, and subsequently averaged, to generate future fire probabilities.

Model evaluation was performed using the area under the curve (AUC) statistic, which measures the ability of model predictions to discriminate fire presence from background points. AUCs were calculated from testing points (i.e. the 99% fraction of fire observations) for each of the 100 model replicates and subsequently averaged by GCM and, ultimately, by climate syndrome. A prevalence adjustment was applied to the AUC as per Phillips *et al*. (2006) by assuming that the prevalence equalled the proportion of fire presence pixels. The relative contribution of each covariate was assessed by estimating the change in model gain associated with each variable.

Data analysis

Predicted changes in fire probability by climate syndrome

Fire shifts, recognized as changes in fire probability over the century, were assessed by subtracting predicted future fire probabilities from those of baseline models for each GCM. For each MTE, we created maps of mean expected change by averaging estimates of change for the ensemble of predictions within the warmer–drier and warmer–wetter syndromes. The ensemble means, however, reveal nothing about uncertainty in the predicted direction of fire changes (increase or decrease) across GCM projections. Therefore, we also evaluated the level of agreement in expected change under both syndromes by mapping those areas where at least 66.7% ($\geq$ 4 out of 6) of the GCMs predicted either a decrease or an increase in fire probability. The remaining pixels were considered to have high uncertainty in the direction of fire change.

We produced maps of the most limiting factor (MLF), the variable with the strongest influence on model prediction, on a pixel-wise basis using the MaxEnt model output (*cf.* Elith *et al*., 2010). To compute MLF, a model was run by successively changing the values of each explanatory variable to its mean over the occurrence data; MLF corresponds to the variable causing the largest change in fire probability. MLF was obtained for each fire probability model built with each GCM, and the overall MLF at each pixel was the one that occurred most frequently. Pixels were considered 'tied' when there was no majority in the variables.

MTEs exhibit important north–south climate and productivity gradients (see Appendix S3). We therefore evaluated latitudinal patterns of future fire probability and the level of agreement among ensemble GCMs under warmer–drier and warmer–wetter syndromes for the 2070–2099 period. For each latitudinal band at a 0.5 degree resolution, we computed the proportion of pixels showing consistent directional changes in fire, along with the associated mean values of change.

Fire–climate relationships

The relationship between predicted fire probability and each independent variable was examined through response curves by generating a MaxEnt model for each variable of interest. Response curves for the five independent climatic variables were generated from baseline models at the global extent for each GCM and subsequently averaged by climate syndrome. The 'position' or climate space of each MTE was located on these fire response curves to analyse how their respective conditions vary from baseline to future time periods. In each MTE, we evaluated the baseline range of each variable (mean values of ensemble GCMs) via density distributions for all pixels in each region. Baseline climate conditions were then compared with the projected climate conditions in areas showing consistent directional fire changes (i.e. meeting $\geq$ 66.7% agreement criteria). Finally, projected climate conditions were compared to the interquartile range of baseline climate conditions from biomes found adjacent to MTEs: Desert and Xeric Shrublands, Temperate

Broadleaf and Mixed Forests, and Temperate Coniferous Forests (*sensu* Olson *et al.*, 2001). These biomes occupy different locations in the gradient between limitations of fuel amount and fuel moisture on fire activity. This comparison provides context for how changes in MTEs relate to conditions in adjacent biomes and insight into potential biome transitions under future climates. All data analyses were performed in R 2.12.2 (R Development Core Team, 2011).

RESULTS

Predicted changes in fire probability

Spatial patterns of baseline fire probability models for MTEs showed substantial variation both among and within regions (Fig. 2a) and were congruent with broad patterns of fire activity observed in those regions. In general, fire probabilities were high, and the lowest values were confined to the wettest and driest areas. Models provided good discrimination of fire-prone areas over the Mediterranean biome with average prevalence-adjusted AUC values corresponding to 0.92 (an AUC equal to 1 indicates perfect classification accuracy).

Comparison of warmer–drier and warmer–wetter syndromes revealed highly divergent changes in predicted future fire probability in MTEs (Fig. 2b & c). Despite the differences among the five MTEs in the GCMs depicting warmer–drier and warmer–wetter conditions (see Appendix S2), consistent trends in fire alterations among regions were apparent (Fig. 2). The projected direction of temperature-related changes, captured in our models by Twarm, Tseas and Twet, was similar between the two syndromes and among MTEs. The differences among ensemble GCMs were largely driven by variability in precipitation (Fig. 1).

All explanatory variables contributed substantially to fire probability estimates (Table 1). Evaluation of the most limiting factor demonstrated that precipitation-related variables had the most influence over baseline fire probabilities, and this will be amplified by the end of the century, especially under the warmer–drier syndrome (Fig. 3). Precipitation variables (especially Pann) were the most influential across 71% of MTEs' area in baseline conditions, rising to 86% by 2070–2099 under the

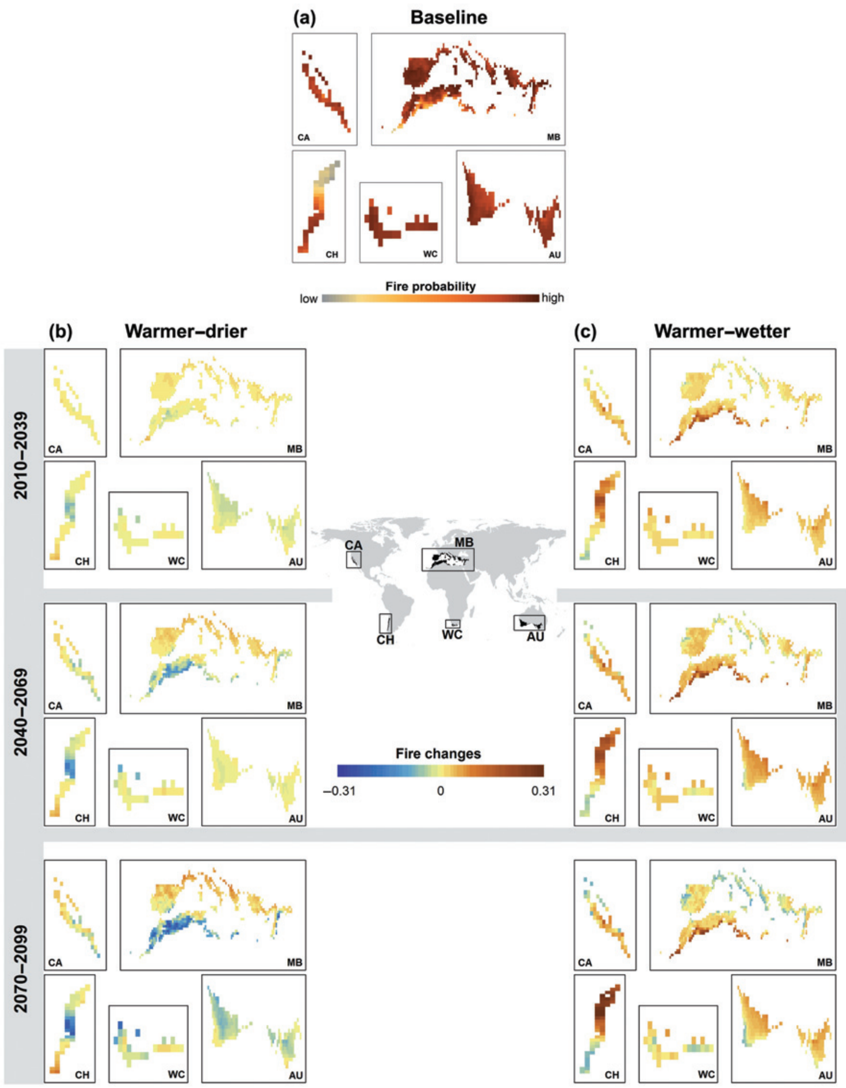

Figure 2 Mean fire probability of the baseline conditions (1971–2000) model (a) and the predicted changes in mean fire probability relative to the baseline conditions under warmer–drier (b) and warmer–wetter (c) syndromes of climate change in the five Mediterranean-type ecosystems (MTEs) for each time period (2010–2039, 2040–2069, and 2070–2099). The six Global Climate Models selected in each MTE depicting the two syndromes of change are listed in Table S1. CA – California and Baja California, MB – the Mediterranean Basin, CH – central Chile, WC – Western Cape, and AU – southwest and south Australia.

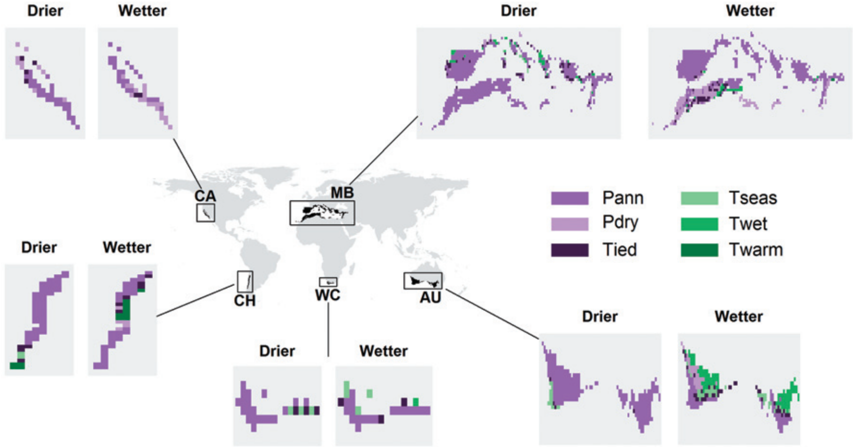

Figure 3 Maps of the most limiting factor (MLF) to fire probability under warmer–drier (Drier) and warmer–wetter (Wetter) climate syndromes for the 2070–2099 time period in the five Mediterranean-type ecosystems. The MLF was obtained from fire probability models built with the ensembles of six Global Climate Models per climate syndrome using a majority approach: the MLF that occurs the most frequently at each pixel is depicted. CA – California and Baja California, MB – the Mediterranean Basin, CH – central Chile, WC – Western Cape, and AU – southwest and south Australia. Pann – total annual precipitation, Pdry – precipitation of driest month, Tseas – temperature seasonality, Twet – temperature of wettest month, Twarm – temperature of warmest month. Pixels were considered 'tied' when there was no majority among variables.

warmer–drier syndrome; this remained stable at 73% under the warmer–wetter syndrome (percentages expressed as a mean of ensembles). Temperature-related factors exerted a lesser influence on fire probability and were most limiting for 22% of the MTEs' total area in the baseline conditions; by 2070–2099, their area dropped to 7 and 17% under drier and wetter conditions, respectively. The remaining area (7–9%) did not exhibit a dominant influence by variables included in our models.

Mean projected changes in fire activity were not distributed uniformly either among or within the five MTEs, and departures from current fire probabilities amplified over the study period (Fig. 4, see Appendix S5). The level of agreement in the direction of fire changes among ensemble GCMs was relatively high at the biome level under both syndromes, but some MTEs showed substantial portions of the landscape subject to large uncertainty. The warmer–drier syndrome led to an overall decrease in fire activity across 56% of the Mediterranean biome by the end of the century (2070–2099), whereas warmer–wetter conditions led to an overall increase across 65% of the biome. The CA and MB regions showed parallel trends over the century, dominated by increased probability of fire relative to baseline levels in both syndromes. However, areas showing reduced fire probability also gradually increased over the century, especially under the warmer–drier syndrome. In contrast, CH, WC and AU all exhibited patterns dominated by increases in fire under the warmer–wetter syndrome and decreases in fire under the warmer–drier syndrome.

Spatial patterns in the direction of predicted fire changes by 2070–2099 under both future climate syndromes exhibit pronounced, divergent latitudinal variation within the Mediterranean biome (Fig. 5, see Appendix S5). In the northern hemisphere (CA, MB) and under the warmer–drier syndrome, projected fire increases and decreases were concentrated at high and low latitudes of the biome, respectively, whereas the opposite patterns were predicted under the warmer–wetter syndrome. Areas exhibiting no agreement in the direction of change dominated the intermediate latitudes of MTEs under both syndromes. In the southern hemisphere, CH exhibited similar but reversed patterns in the direction of fire changes, as compared to MTEs of the northern hemisphere, which might be expected given their amphitropical positions and the broad latitudinal range of CH. More latitudinally restricted, WC and AU showed lower spatial variation in the direction of changes than the other MTEs; these regions mostly showed a single, contrasting direction of change under the two climate syndromes (Fig. 5, see Appendix S5).

Fire–climate relationships

The MTEs occupy a subset of the climate space used in global parent models from which the fire–climate relationships (response curves) were produced (Fig. 6, see Appendix S6 (a–h)). Only Pann and Twarm showed a unimodal response (Fig. 6), including highly sensitive zones (i.e. steep slopes) towards their extreme values. Taking MB under the warmer–drier syndrome as an example (Fig. 6a), areas of predicted fire decreases in 2070–2099 were those where decreased Pann relative to the baseline period occurred in a very sensitive zone of the response curves. By the end of the century, all variables showed characteristics more closely related to current desert-like and xeric environments adjacent to MTEs (Fig. 6, gold bars). At the other extreme, under a warmer–wetter climate (Fig. 6b), fire decreases emerge where disproportionately large increases in precipitation by the end of the century exceeded the threshold where conditions most conducive to fire currently occur. The fact that both increases and decreases occurred under both the warmer–drier and warmer–wetter syndromes suggests that multivariate trade-

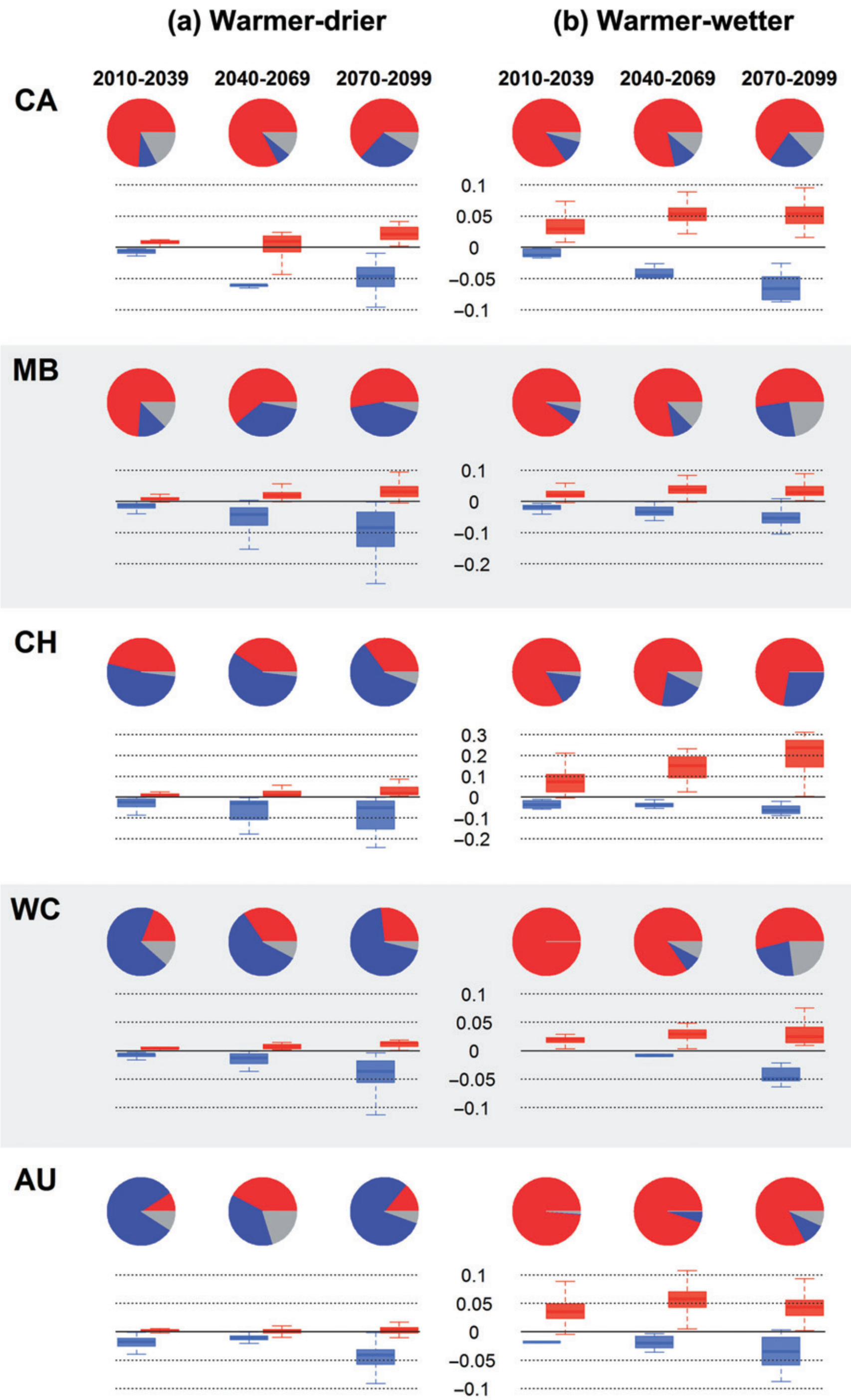

Figure 4 Change in fire probability from the baseline conditions under warmer–drier (a) and warmer–wetter (b) syndromes of climate change in the five Mediterranean-type ecosystems for each time period (2010–2039, 2040–2069, and 2070–2099). The pie charts represent the proportion of pixels in each of the following agreement classes in projected fire change: increase, decrease and low agreement. Box plots represent the values of mean change in fire probability in those areas where the level of agreement was met. In all cases, red and blue correspond to fire increase and decreases, respectively. Agreement is based on a ≥ 66.7% level (at least 4/6 Global Climate Models–GCMs–) among the ensembles of GCMs; grey corresponds to areas where the 4/6 level of agreement was not met. Note the differences in *y*-axis among study areas. CA – California and Baja California, MB – the Mediterranean Basin, CH – central Chile, WC – Western Cape, and AU – southwest and south Australia.

offs play a major role in controlling fire occurrence. For instance, areas exhibiting fire increases under a warmer–wetter syndrome occupy a climate space where, despite Twarm increases leading to less fire probability, associated increases in Pann were large enough to compensate for warming.

DISCUSSION

Our projections of fire activity over the 21st century reveal substantial heterogeneity among and within the five MTEs. The use of divergent, multi-GCM climate syndromes of warmer–drier and warmer–wetter futures provides a new understanding of drivers of region-specific fire changes and their sensitivity to climatic variation. Overall, our projections of fire activity suggest that fire increases reported for the last decades in some MTEs (e.g. Piñol *et al.*, 1998; Westerling *et al.*, 2006) may not continue through the upcoming century. We see support for our hypotheses of generally contrasted fire outcomes under the two climatic syndromes evaluated, reaffirming that parts of the MTEs lie close to a threshold discriminating fuel moisture

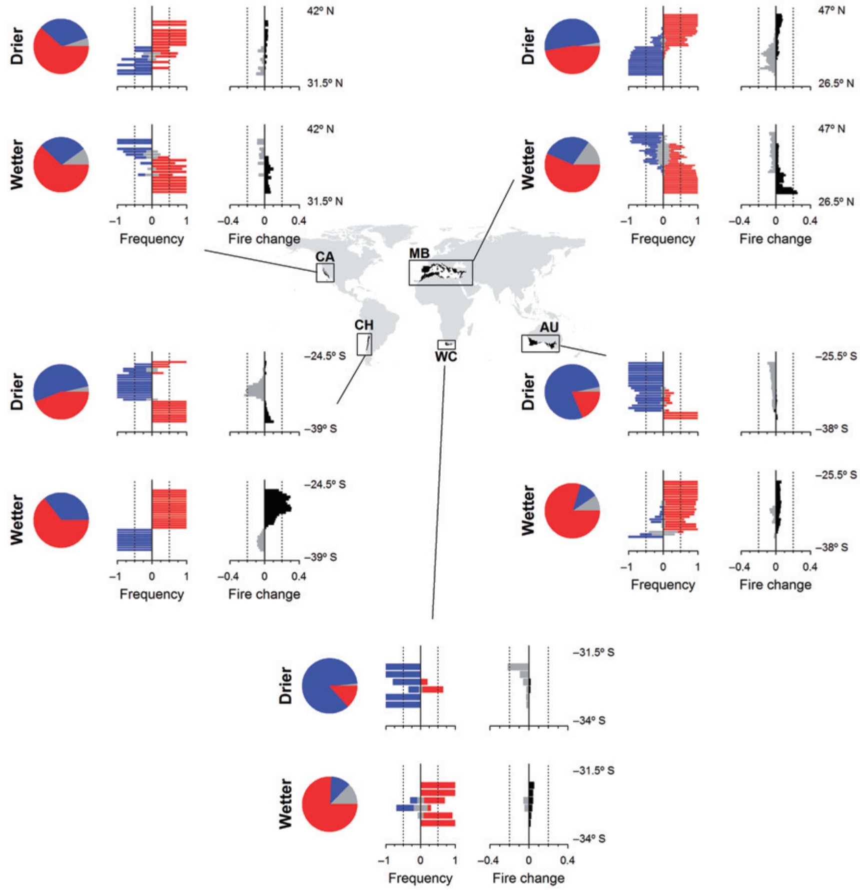

Figure 5 Latitudinal patterns of predicted changes in fire probability in the five Mediterranean-type ecosystems under warmer–drier (Drier) and warmer–wetter (Wetter) syndromes of climate change by 2070–2099. The pie charts represent the total proportion of pixels in the fire probability increase (red) and decrease (blue) agreement classes, as well as the no agreement class (grey). The bar plots show the frequency of pixels by agreement class (left bar plots) and the predicted mean fire probability changes (right bar plots) by 0.5° latitudinal band, where the black and grey bars represent mean fire probability increases and decreases, respectively. Agreement is based on a ≥ 66.7% level of among the ensembles of six Global Climate Models; grey corresponds to areas where the 4/6 level of agreement was not met. CA – California and Baja California, MB – the Mediterranean Basin, CH – central Chile, WC – Western Cape, and AU – southwest and south Australia.

versus fuel amount limitation (e.g. Bradstock, 2010). However, our models also show evidence that MTEs occupy a climate space sufficiently broad and complex to accommodate increases and decreases in fire under a given syndrome; these responses are spatially heterogeneous but have distinct amphitropic pattern. Regardless of whether future climates shift towards warmer–drier or warmer–wetter conditions, climate changes may promote sharp alterations of fire activity in MTEs, and parts of their distribution could move towards desert-like or temperate forest-like ecosystems. Our results thus strongly suggest that climatic controls on fire occurrence in the Mediterranean biome lie close to 'tipping points', making these ecosystems especially sensitive to change.

Climatic changes leading to warmer and drier climate over the 21st century have often been associated with increases in fire risk, fire occurrence or more extreme fire behaviour both at regional and global scales (e.g. Williams *et al.*, 2001; Pechony & Shindell, 2010; Carvalho *et al.*, 2011). Our fire projections under a warmer–drier future suggest that large parts of MTEs could experience substantial decreases in fire activity, even in the near term, whereas a warmer–wetter future may lead to more widespread increases in fire activity across MTEs. Such divergent fire responses to future variation in the amount of precipitation emphasize how much water availability drives productivity, and thus flammable biomass, in arid and sub-arid environments (van der Werf *et al.*, 2008; Bradstock, 2010) and, in turn, fire activity in large parts of the Mediterranean biome (e.g. Westerling *et al.*, 2003; Pausas & Paula, 2012). The primary importance of productivity gradients to fire incidence in some MTEs has been suggested in previous studies in Spain (Vázquez *et al.*, 2006; Pausas & Paula, 2012), California (Westerling *et al.*, 2003; Littell *et al.*, 2009) and in southern Australia (Pausas & Bradstock, 2007; Bradstock, 2010). Our study confirms these regional studies and provides a biome-wide illustration of how changing climate conditions might interact with fuel amount and fuel moisture constraints.

The observed unimodal responses of fire to its environment are in agreement with previous regional-to-continental (Parisien & Moritz, 2009; Bradstock, 2010) and global studies (e.g. Aldersley *et al.*, 2011; Prentice *et al.*, 2011). The shapes of modelled relationships illustrate how the climate space of fire in MTEs is restricted to a sensitive zone along steep sections of the fire–climate response curves for key environmental variables. Therefore, relatively small changes in climatic drivers of fire, such as annual precipitation, can yield substantial changes in fire activity. Portions of future MTEs could easily shift to fire environments more characteristic of current xeric or temperate forest biomes, as has occurred in the past (Colombaroli *et al.*, 2007).

Because regional climate changes in MTEs are expected to be large and spatially uneven (Klausmeyer & Shaw, 2009), they will inevitably entrain heterogeneous changes in fire occurrence, as

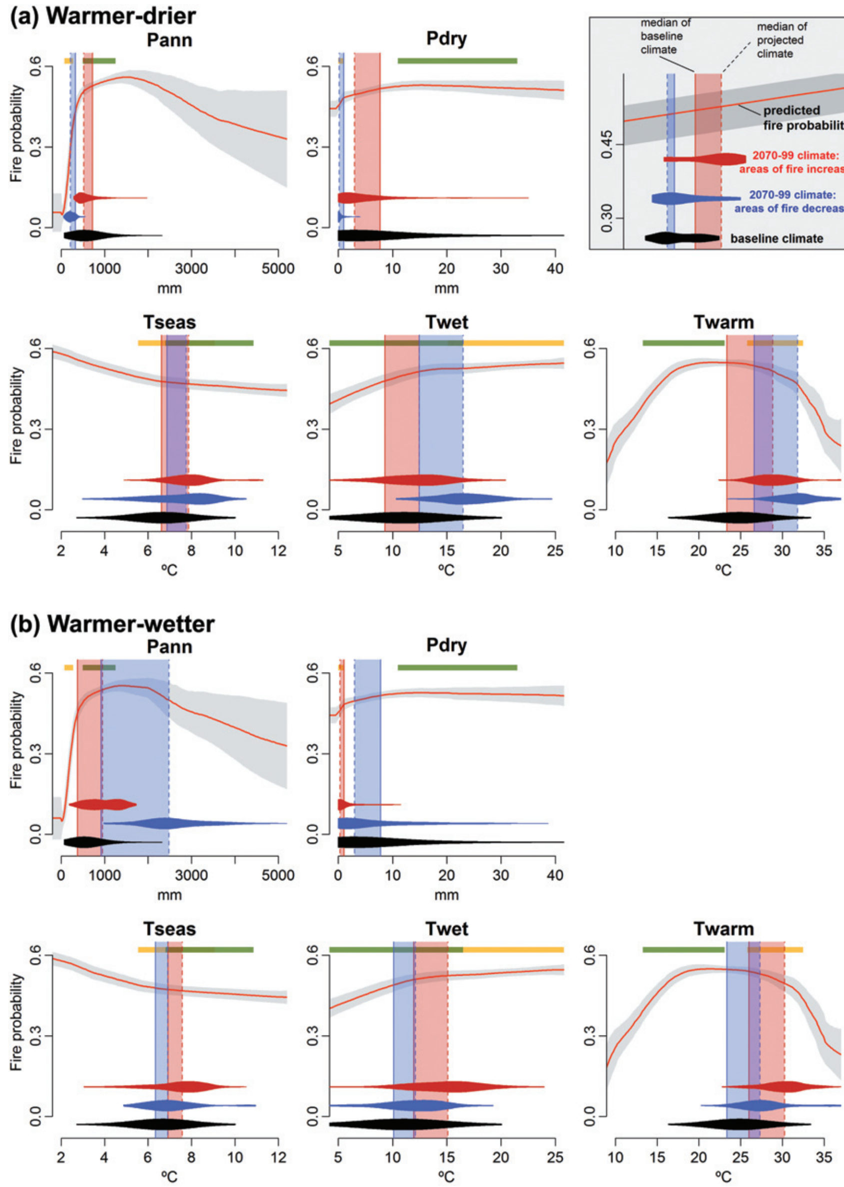

Figure 6 The response of predicted fire probability to each independent variable in the Mediterranean Basin (MB). The change in each variable from the baseline period (1971–2000) to 2070–2099 under warmer–drier (a) and warmer–wetter (b) climate syndromes is also shown. The solid red line indicates the mean predicted fire probability values from the ensemble of six Global Climate Models under each syndrome, whereas the grey shading represents the standard deviation among models. Projected climate shifts in areas representing agreement in predicted increases (red) or decreases (blue) in fire probability are depicted as follows (*see inset legend plot*): vertical solid lines correspond to the median of the baseline climate conditions and dashed lines correspond to the median by 2070–2099 period; the red and blue shading illustrates the median change among baseline and future time periods. The density distributions of baseline climate conditions for the MB are depicted by black violin plots, whereas red and blue violin plots depict the projected climate conditions in areas showing consistent fire probability increases and decreases by 2070–2099, respectively. Finally, the 25–75% percentile values of each variable in current Desert and Xeric Shrublands biome, as well as temperate forest biomes (Temperate Broadleaf and Mixed Forests biome, and the Temperate Coniferous Forests biome), is illustrated at the top of each subplot by gold and green horizontal bars, respectively. Pann – total annual precipitation, Pdry – precipitation of driest month, Tseas – temperature seasonality, Twet – temperature of wettest month, Twarm – temperature of warmest month.

our results suggest. The WC and AU regions, with a narrow latitudinal span, are poised to experience the most widespread reductions in the climate space that currently defines the Mediterranean biome (Klausmeyer & Shaw, 2009). Such regional geographic climate contraction, coupled with the extensive fire alterations predicted by our models in these areas, will have serious implications for native plants and animals. This impact could be further exacerbated by the fact that fire-induced changes may have a much greater impact on biological communities than the direct effect of climate changes (Bond & Keeley, 2005). Our models also predict spatially diverse fire changes in CH, CA and MB landscapes, with remarkable geographic separation between areas of projected fire increases and decreases by the end of the century.

Modelling framework considerations

This study provides the first opportunity for a detailed comparison of future fire probability shifts in the five MTEs of the world. We focus on fire probability as an estimate of fire frequency alterations, whereas changes in other parameters of a fire regime such as fire severity, seasonality, or fire type and behaviour were not assessed in our models. The spatio-temporal scale of our approach does not capture crucial processes for fire occurrence and behaviour that may be regionally important at finer scales, such as convection, extreme winds and ignition patterns (e.g. Honig & Fulé, 2012), all of which are subject to great uncertainty in future projections. At global scales, the effects of increased CO_2 on biomass production or alterations to land–atmosphere feedbacks represent other fire research questions that require more mechanistic approaches (e.g. DGVMs) and are beyond the scope of our evaluation.

Inter-annual climate variability plays a role on yearly fire activity (e.g. Prentice *et al*., 2011), as do feedbacks between changes in fuel structure and abundance or ecosystems flammability and fire regime (e.g. invasive species; Mack & D'Antonio, 1998). In MTEs, the influence of human activities such as land development, ignitions and fire suppression and the effect of different regenerative strategies (e.g. resprouters vs. seeders) on post-fire biomass regeneration may be key to future fuel patterns and availability. Plant life history strategies can be particularly relevant in MTEs, where fire has been a strong evolutionary pressure in shaping plant traits (Keeley *et al*., 2011), some of which could favour certain species through positive feedbacks between fire risk and community composition (Saura-Mas *et al*., 2010). Therefore, the results of our climate-based approach are contingent on how strong a role climate will eventually play. Overall, our analysis represents a spatially explicit characterization of the fire environment, and it covers a relevant time-scale over which climate operates to 'switch' fuel availability constraints that, in turn, affect the occurrence of fire (Meyn *et al*., 2007; Bradstock, 2010).

Our statistical, climate-based projections of future fire occurrence yield encouragingly similar results for specific MTEs when compared to other modelling approaches. For example, both our results and those reported by Lenihan *et al*. (2008), which are based on the MC1 Dynamic General Vegetation Model (DGVM) for California, predict reduced levels of fire activity by the end of the century under a warmer–drier syndrome. Therefore, results presented here reinforce the idea that 'top-down' statistical models based on fire observations can provide new insights and complementary information to analytical studies and complex mechanistic models at finer scales, as long as statistical models are based on meaningful environmental covariates and applied at relatively broad scales (Thuiller *et al*., 2008).

Overall, we found that fire activity in MTEs is highly sensitive to environmental changes and that productivity may be key to future fire occurrence in this biome. Climate–productivity–fire couplings appear certain to affect the resilience of some MTEs, which could result in shifts to alternative states vastly different from today (e.g. Scheffer *et al*., 2001; Staver *et al*., 2011). Our findings of heterogeneous fire changes across MTEs suggests that fire, land and conservation management strategies will need to be diverse and flexible to be relevant under future climate conditions.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web site.

Appendix S1 Fire and climate data preparation
Appendix S2 Ensemble of GCMs depicting the warmer-drier and warmer-wetter syndromes of climate change in each Mediterranean region.
Appendix S3 Patterns of productivity and precipitation in the Mediterranean biome.
Appendix S4 Comparison of baseline fire probability models based only on climate variables (i.e., the approach used in this study) and based on climate variables and net primary productivity as a metric of vegetation biomass.
Appendix S5 Spatial distribution of agreement in the direction of change in predicted fire probability in the five MTEs over the 21st century under warmer-drier and warmer-wetter climate syndromes.
Appendix S6 Fire–climate relationships (i.e., response of predicted fire probability to each independent variable) in CA, CH, WC, and AU.

BIOSKETCH

Enric Batllori is currently a post-doctoral researcher at the University of California, Berkeley. With a forest ecology background, his is broadly interested in ecosystem responses to disturbance under global change and its potential effects on landscape structure at multiple temporal and spatial scales. E.B., M-A.P., M.A.K and M.A.M conceived and designed the modelling framework. E.B and M-A.P. developed the fire probability models. E.B. analysed the data and led the writing. All authors contributed to results interpretation and writing.

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