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Contrasting human influences and macro-environmental factors on fire activity inside and outside protected areas of North America

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Abstract

Human activities threaten the effectiveness of protected areas (PAs) in achieving their conservation goals across the globe. In this study, we contrast the influence of human and macro-environmental factors driving fire activity inside and outside PAs. Using area burned between 1984 and 2014 for 11 ecoregions in Canada and the United States, we built and compared statistical models of fire likelihood using the MaxEnt software and a set of 11 key anthropogenic, climatic, and physical variables. Overall, the full model (i.e. including all variables) performed better (adjusted area under the curve ranging from 0.71 to 0.95 for individual ecoregions) than the model that excluded anthropogenic variables. Both model types (with and without anthropogenic variables) generally performed better inside than outside the PAs. Climatic variables were usually of foremost importance in explaining fire activity inside and outside PAs, with anthropogenic variables being the second most important predictors, even inside PAs. While the individual contributions of anthropogenic variables indicate that fire activity decreased as a function of increasing human footprint, the anthropogenic effects were often substantially greater than those of physical features and were comparable to or even greater than climatic effects in some densely developed ecoregions, both outside and within PAs (e.g. Mediterranean California, Eastern Temperate Forest, and Tropical Wet Forests). Together, these results show the pervasive impact of humans on fire regimes inside PAs, as well as outside PAs. Given the increasing attractiveness of PAs, the implications for adaptive fire management beyond the concept of naturalness in the PAs are discussed. Our assessment of human-altered fire activity could serve as an indicator of human pressure in PAs; however, we suggest that further analysis is needed to understand specific interactions among fire, human pressures, and the environmental conditions at the scale of PAs.

Significance statement

Protected areas (PAs) are critical for maintaining habitat integrity, species diversity, and ecosystem health. Untangling the biophysical and anthropogenic drivers of fire regimes within PAs is crucial for developing effective strategies to preserve and manage

biodiversity and ecosystem functions. Our study reveals the large influence of humans on fire activity in and outside of PAs. Even in PAs with minimal human activity, human influence on fire is pervasive and reduces fire activity. Our assessment of human-altered fire activity could be used as an indicator to measure the effectiveness of PAs in meeting conservation goals.

Introduction

Effectively managed protected areas (PAs) have been recognized as critical instruments in nature-conservation policy [1]. The International Union for Conservation of Nature defines a PA as a distinct geographic unit that is recognized and managed for the long-term conservation of nature along with the associated ecosystem services and cultural values. However, PAs are under threat globally because of cumulative stresses from land-use changes, resource extraction, recreational activities, invasive species, and climate change [1–5]. In consequence, the effectiveness of PAs in achieving their conservation goals is questioned across the globe [6].

Essential to maintaining the ecological integrity of PAs is the preservation of key natural disturbance regimes such as wildfire [7, 8]. Fires play a vital ecological role in many ecosystems. The fire regime, typically described in terms of fire frequency, size, intensity, seasonality, type, and severity, shapes species distributions and maintains the structure and function of fire-prone plant communities [9]. When fire regimes are altered beyond their natural ranges of variability, ecosystems can become less resilient to other disturbances [10]. However, fires are often perceived as socially and economically unwanted disturbances. Driven by safety policies and regulations, active suppression of fires in PAs has led to the reduction of fire's ecological benefits [11, 12]. In an era of rapid land-use and climate change, reconciling the management of PAs with the reality of wildfire is a major challenge [13, 14]. Untangling the biophysical and anthropogenic drivers of fire regimes within PAs is therefore a prerequisite to developing effective strategies to preserve and manage biodiversity and ecosystem functions [15–17].

Environmental controls on fire regimes in North America are relatively well understood. Natural variability in fire activity is the outcome of interactions among climate, weather, fuel structure and composition, topography, and ignition sources [18, 19]. Variation in these top-down and bottom-up interactions across ecosystems generates spatial heterogeneity in fire regimes [20, 21]. Climate and weather exert top-down controls at broad spatial scales, whereas other factors, such as fuel and topography, are typically considered bottom-up influences that operate at finer spatial scales [22–24].

The nature of anthropogenic controls on fire regimes in recent decades is less clear than that of biophysical factors [25, 26]. Historical human-fire relationships (e.g. deliberate burning performed by aboriginal peoples) and the lack of a purely natural baseline of fire activity have frustrated efforts to disentangle modern anthropogenic influences from natural ones [27, 28]. Humans influence fire regimes in ways that can amplify fire activity (e.g. through the

introduction of ignitions or invasive annual grasses) or dampen it (e.g. fire suppression, land-management activities that alter fuel structure and continuity, or the conversion to non-flammable land cover) [29, 30]. As a result, the influence of humans on fire activity is not always linear and it varies at broad geographic scales (e.g. among sub regions). Despite numerous studies showing that the human influence on fire is strong and ubiquitous in North America, its net effect on fire activity remains unclear [31–35].

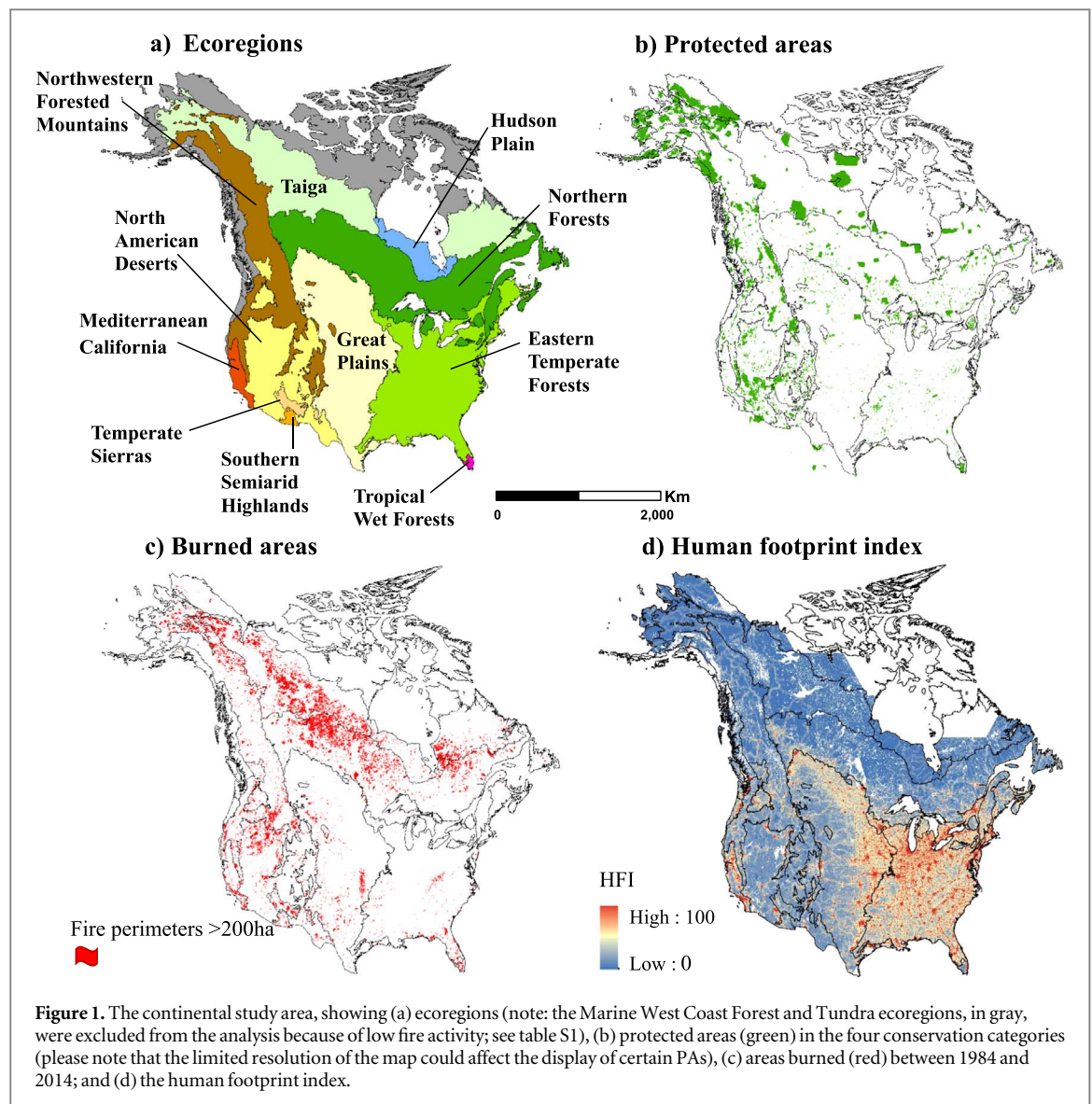
An important yet untested and unquantified assumption is that fire activity in PAs represents an important contrast to fire activity in other landscapes that are subject to a heavier anthropogenic footprint. PAs vary in management intensity and remoteness from human activities [36], and no PA is altogether free from anthropogenic influences [36–38]. However, PAs have been viewed as the best natural baseline from which to measure and monitor change or departures in fire regimes induced by humans [39, 40]. The degree to which fire regimes in PAs are influenced by human activities versus environmental drivers at the continental scale remains largely unexplored.

This study aims to contrast the drivers of fire activity in PAs versus non-PAs across a range of ecosystems in North America. Using data from the 1984–2014 period, we applied a modeling approach to (i) determine whether the proportion of burned area is different in PAs and non-PAs, (ii) assess the relative importance of human, climatic and physical influences on fire activity, and (iii) evaluate and compare human influence on fire activity inside and outside PAs.

Material and methods

Study area

The study area consisted of the United States (excluding Hawaii and the Caribbean islands) and Canada (excluding the high Arctic zones). This area covers roughly $18 \times 10^6 \text{ km}^2$ (figure 1) and encompasses extreme variation in geology, landform, climate, vegetation, land use, and anthropogenic activities. Adopting an ecoregion-based approach to assess subcontinental variability in fire regimes, we subdivided the study area into 13 ecoregions [41], subsequently excluding the Marine West Coast Forest and Tundra ecoregions from analysis because of their very low fire activity (table S1 is available online at stacks.iop.org/ERL/14/064007/mmedia). The remaining 11 ecoregions analyzed here ranged in extent from $3 \times 10^6 \text{ km}^2$ (Taiga) to $22 \times 10^3 \text{ km}^2$ (Tropical Wet Forests). For most ecoregions, climatic conditions within PAs were similar to those outside PAs (table S3).



Data

Protected areas

Polygon data delineating the network of PAs were obtained from the World Database on PAs (WDPA; [42]). We selected the four highest conservation categories of the WDPA: category Ia, Strict Nature Reserve; category Ib, Wilderness Area; category II, National Park; category III, Natural Monument or Feature (figure 1(c)). These categories are recognized by international bodies such as the United Nations and by many national governments, including those of Canada and the United States, as the global standard for defining and recording PAs. Similar to Batllori *et al* [43], we excluded PAs with area $<10 \text{ km}^2$ and removed nonvegetated and noncombustible PAs (e.g. urban parks, rivers, wetlands, marine parks). PA polygons were rasterized in a binary 1 km grid map representing PAs and non-PAs (assigned values of 1 and 0, respectively). The prevalence of PAs among ecoregions (excluding the Marine West Coast Forest and Tundra ecoregions) ranged from 2.41% (Great

Plains) to 48.96% (Tropical West Forests), with an overall average of 13.9% (figure S1).

Burned area

We used polygon data describing burned area extent for the United States and Canada for the period 1984–2014. The US data were obtained from the Monitoring Trends in Burn Severity project [44], whereas the Canadian data were obtained from the Canadian Forest Service National Fire Database [45]. A small fraction of both datasets represented prescribed burns ($<2\%$ of the total area burned across the study area). Burned areas smaller than 200 ha were excluded from analysis because they have been inconsistently reported over space and time; they similarly represented a small fraction of the total area burned ($<7\%$). For the purpose of the analysis, polygons were converted to a 1 km grid map of burned and unburned pixels (assigned values of 1 and 0, respectively). Total burned area and percent burned area were summarized by ecoregion and protected status.

Table 1. Explanatory variables used in the models. Mean values by ecoregion and protection status are available in table S2. All variables were converted to a 1 km raster map for the data extraction and modeling.

Variable	Description (units)
Climate normals (1981–2010)	
CMD	Hargreave's climatic moisture deficit (mm)
DD < 18	Degree-days below 18 °C (degree-days)
MAP	Mean annual precipitation (mm)
RH	Mean annual relative humidity (%)
Enduring landscape features	
SAR	Surface area ratio, a measure of surface roughness (dimensionless)
HLI	Heat load index, an index calculating the southwestness of a slope (dimensionless)
TPI	Topographic position index computed with a 2 km window (dimensionless)
PNF	Percent nonfuel at a 1000 km ² moving window size. Nonfuel classified as urban, barren lands, water, snow, and ice (%)
Human influence	
HFI	Human footprint, an index of human influence for the year 2004. Calculated with a 100 km ² moving window (dimensionless)
RLV	Roadless volume calculated with a 10 000 km ² moving window (dimensionless)
LPD	Population density for the year 2000 (logged number of people km ⁻²)

Climatic data

Gridded climate data were generated with the ClimateNA version 5.10 software package (available at <http://tinyurl.com/ClimateNA>). The software uses historical weather station data and an elevation adjustment to calculate more than 50 monthly, seasonal, and annual climate variables across North America [46]. From these variables, we selected four climate variables that are known to influence fire activity at the continental scale in North America: mean annual precipitation; mean annual relative humidity; the Hargreave climatic moisture deficit, an annual integrative measure of energy and moisture (precipitation–potential evapotranspiration); and degree-days below 18 °C (DD < 18).

Enduring landscape features

Four variables were used to describe the enduring landscape features, those components of the landscape that vary little, if at all, over the time scale of the study. Three of these variables described topography and were derived from a digital elevation model at 1 km resolution. The surface-area ratio, a measure of surface roughness, and the heat-load index, a measure of potential sun exposure, were computed with Geomorphometry and Gradient Metrics Toolbox 2.0 [47]. The topographic position index was used to describe the relative position along a valley-to-peak gradient; this metric was computed with a 2 km window. The fourth variable was the percent permanent nonfuel; this metric was derived from the global land cover for 2005 [48] and quantified the area occupied by nonflammable land cover types, including open water, glaciers, barren ground, and urban areas.

Human influence

While land and fire management practices vary substantially inside and outside PAs, explicit data describing these differences are not available at the NA

scale. Instead, three anthropogenic variables were used as proxies for human activities across the study area. The human footprint index (HFI) is a global dataset (at 1 km resolution) that represents anthropogenic effects on the basis of nine factors, including human density, human land use and infrastructure (built-up areas, nighttime lights, land use/cover), and human access (coastlines, roads, railroads, navigable rivers). HFI values were obtained from the Wildlife Conservation Society and the Columbia University Center for International Earth Science Information Network [49]. The HFI has been widely used to evaluate anthropogenic influences on fire regimes in NA [32, 34]. HFI is also an adequate variable to measure human pressure and habitat modification within PAs on a continental to global scale [5]. Roadless volume (RLV) is a metric of isolation that is based on distance from roads [50]. High values of this metric indicate a low level of human influence. RLV was summarized using a 10 000 km² moving window average. The population density (LPD; log10-transformed) was obtained from the Center for International Earth Science Information Network [51]. High values of LPD are concentrated in urban areas; as such, this variable effectively separates urban from vegetated and flammable area.

Variables selection

We built two types of models of fire activity using burned area as a response variable and a pool of 11 explanatory variables divided into three categories representing climatic, physical and anthropogenic factors for 11 ecoregions covering most of North America (table 1). Similar to the study by Parisien *et al* [32], the initial dataset contained 34 explanatory variables based on their ability to predict fire activity in the study area. However, the number of variables has been reduced to 11 in order to minimize the degree of correlation (table S2). Correlations were computed

between each pair of variables to identify those correlated at $|r| > 0.7$ across the study area. Because we were primarily interested in human influences on fire activity, LPD and HFI were retained in spite of correlations $|r| > 0.70$ (table S2). In addition, the lightning variable was excluded because it was poorly related to the area burned in almost all areas, as seen in Parisien *et al* [32].

Modeling

A systematic random sampling scheme was applied as follows. Within each ecoregion, each 1 km pixel was assigned one of the four following categories: PA burned, PA unburned, non-PA burned, non-PA unburned. The category with the smallest number of pixels was used to define the number of observations for model building that were randomly sampled within each of the other categories. As such, the same number of observations outside and within PAs was used to model fire probability in each ecoregion. The number of observations (i.e. pixels) used in the model calibration varied from about 800 in the smallest ecoregion (Tropical Wet Forests) to more than 51 000 in the largest ecoregion (Northern Forests). For each sampled pixel, we extracted the entire suite of explanatory variables. All data extractions and sampling were conducted in the R statistical environment [52].

We used MaxEnt 3.3.3k to build two types of presence-only models for each ecoregion. All 11 explanatory variables, including three measures of human influence, were used to build the first model (termed the full model). The second model (referred to as the NoAnthro model) was built using only climatic and physical (i.e. enduring landscape features) variables. Comparison of these two models for PAs and non-PAs in each ecoregion allowed us to statistically contrast the influence of macro-environmental and human factors driving fire activity and its geographic variation. The MaxEnt software package is one of the most popular machine learning tools for species distribution and environmental niche modeling [53] and has been extensively used to make spatial predictions in fire modeling studies [32]. According to the sampling design described above, MaxEnt extracted a sample of background locations (i.e. pixels describing the environment of the entire area of interest) that were then contrasted with the sample of presence locations (i.e. burned pixels). Classification accuracy of the model with MaxEnt is represented with the receiver operating characteristic area under the curve (AUC). The AUC is a common evaluation metric for binary classification problems. AUC values range between 0.5 and 1, where 0.5 denotes accuracy no better than if samples were randomly selected, and 1 indicates perfect classification accuracy. MaxEnt settings were selected following the method in Parisien *et al* [32]. To compare both model types for PAs and non-PAs, and to avoid overfitting the models, we used 50 model

replicates with 30% of presence localities randomly set aside as test data. Then we opted for a regularization value of 4 and did not use the ‘hinge’ feature, which tends to produce unrealistic (i.e. overfit) responses. Model evaluation was performed on each of the 50 model replicates, and the values generated were subsequently averaged for each ecoregion and protection status. We used an adjusted area under the receiver operating characteristic curve (AUC) to account for the portion of the study area covered by fire in the PAs and non-PAs. In a presence-only framework, as in this study, it is impossible to achieve an AUC value of 1 because absences (i.e. false positives) are unknown. The maximum achievable AUC (AUC max) in a presence-only framework is equal to $1 - a/2$, where a is the proportion of the analysis area covered by fire (i.e. the prevalence). The adjusted AUC value is calculated as follows: $1 - \text{AUC max} + \text{AUC original}$.

Variable importance was calculated for the full PA and non-PA models in each ecoregion as the model gain associated with each variable. The contributions were also grouped by each of the three main categories of drivers: climatic, physical, and anthropogenic. In addition, to better interpret how human influences vary across the continent and with protection status, the relation between fire activity and the HFI variable was plotted using response curves from the results of the full model. The response curve was constructed for a variable of interest by keeping all other variables at their average values.

Results

Fire activity by ecoregion and protection status

Burned area varied dramatically across the study area (figure 2(a); table S1). Most of the fire activity occurred in two large northern forested ecoregions: the Taiga and Northern Forests (58.94% of the total area burned). The second-highest concentration of fire activity occurred in the western United States, in Mediterranean California, North American Deserts, and Temperate Sierras ecoregions (13.21% of the total area burned). Proportionally, the smallest ecoregions, located in the southern US, were the most affected by fire: Tropical Wet Forests (44.24%), Temperate Sierras (19.45%), Mediterranean California (18.12%), and Southern Semiarid Highlands (17.29%). By comparison, the two largest ecoregions, Taiga and Northern Forests, had 16.03% and 12.85% of their area burned, respectively.

Burned area also varied with protection status (figure 2(b); table S1). Overall, the proportional area burned in PAs was greater than in non-PAs (26.60% versus 13.74% on average). Fires burned disproportionately more area in PAs compared to non-PAs in six ecoregions: Eastern Temperate Forests, Great Plains, Mediterranean California, Northwestern

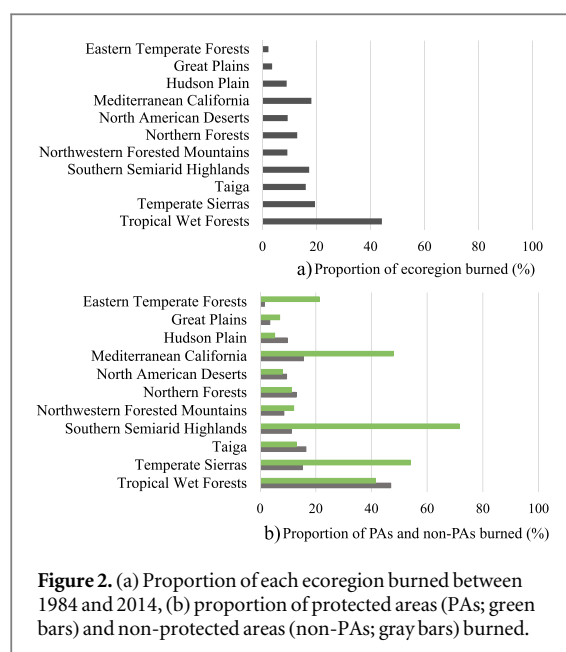


Figure 2. (a) Proportion of each ecoregion burned between 1984 and 2014, (b) proportion of protected areas (PAs; green bars) and non-protected areas (non-PAs; gray bars) burned.

Forested Mountains, Southern Semiarid Highlands, and Temperate Sierras (figure 2(b)).

Models of fire activity and contribution of variables

Across all 11 ecoregions, the full model usually performed better (adjusted AUC values ranged from 0.71 to 0.95) than the NoAnthro model (adjusted AUC values ranged from 0.75 to 0.94; table 2). With few exceptions, models performed better for PAs than for non-PAs. Across all 11 ecoregions, climatic variables had the highest explanatory power (average 55.9% for non-PAs, 58.9% for PAs), followed by anthropogenic (27.8% for non-PAs, 23.1% for PAs) and physical (16.3% for non-PAs, 18.0% for PAs) variables (figure 3).

The relative contribution of climatic, physical, and anthropogenic variables in describing fire activity varied among ecoregions, and often by protected status (figure 3). The climatic category was the most important (>50% contribution to model fit) for 7 of the 11 ecoregions, both outside and inside PAs (Great Plains, Northwestern Forested Mountains, Northern Forests, Southern Semiarid Highlands, Temperate Sierras, North American Deserts, and Taiga). The anthropogenic category was the most important in only a few instances: the Tropical Wet Forests ecoregion both outside and inside PAs (54.2% and 42.9%, respectively), the Mediterranean California ecoregion outside the PAs (46.0%), and the Eastern Temperate Forest outside the PAs (37.9%). In three ecoregions, the anthropogenic category was more important inside than outside the PAs (Taiga, Southern Semiarid Highlands, and Temperate Sierras). For most ecoregions, the physical variables were the least important predictors. Exceptions to this were the Hudson Plain ecoregion (inside PAs, 53.6%) and where they were the second-most important (Mediterranean California,

36.9%; Northwestern Forested Mountains, 27.1%). The relative contribution of each individual variable by ecoregion and protection status is available in figure S2.

The probability of fire usually decreased as a function of increasing HFI both inside and outside the PAs, the exception being the PAs of the North American Deserts ecoregion, where the relation between HFI and area burned was positive (figure 4). Overall, the individual contribution of HFI to the full model tended to be lower inside than outside the PAs, except in the Temperate Sierra ecoregion. The highest individual contributions of HFI were observed for non-PAs in the Tropical Wet Forests, Mediterranean California, and Eastern Temperate Forests ecoregions (32.6%, 28.1%, and 17.5%, respectively).

Discussion

Are the drivers of fire different inside and outside PAs?

Contrasting the macro-environmental and human drivers of fire activity inside and outside PAs in NA can be complicated. Our results confirm the dominance of climate as the main top-down driver of fire activity in all ecoregions, whether directly through effects on weather conditions, or indirectly by controlling productivity and dominant vegetation types [54–57]. However, our approach also reveals that human influence on fire activity is ubiquitous across the study area, even within PAs. The full model consistently performed better than the NoAnthro model both within and outside of PAs. Our results support previous claims that there are few purely natural fire regimes in North America [57–59]. This said, we were surprised that the influence of humans on fire activity in PAs was so pronounced, as some studies have shown that fire regimes are more ‘natural’ in PAs [39]. Although the drivers of fire in PAs are often similar to those in non-PAs, we found important differences between PAs and non-PAs in certain ecoregions (e.g. Mediterranean California, Eastern Temperate Forest, and Hudson Plain).

The human influence on the fire activity varied geographically for PAs, as well as for non-PAs. At the spatiotemporal scale of this study, anthropogenic effects were often substantially greater than those of enduring physical features and were comparable to or even greater than climatic effects in some densely developed ecoregions, both outside and within PAs (e.g. Mediterranean California, Eastern Temperate Forest, and Tropical Wet Forests). This contrast in the spatial distribution of human-altered fire regimes has been particularly well documented at the NA scale [58] and is highlighted in our study as well (figure S3). In Mediterranean California, high population density, dense road networks, and wildland–urban interfaces have been identified as recurring sources of human-caused ignition, with a strong effect on fire size, frequency and seasonality [27, 32]. In the eastern United

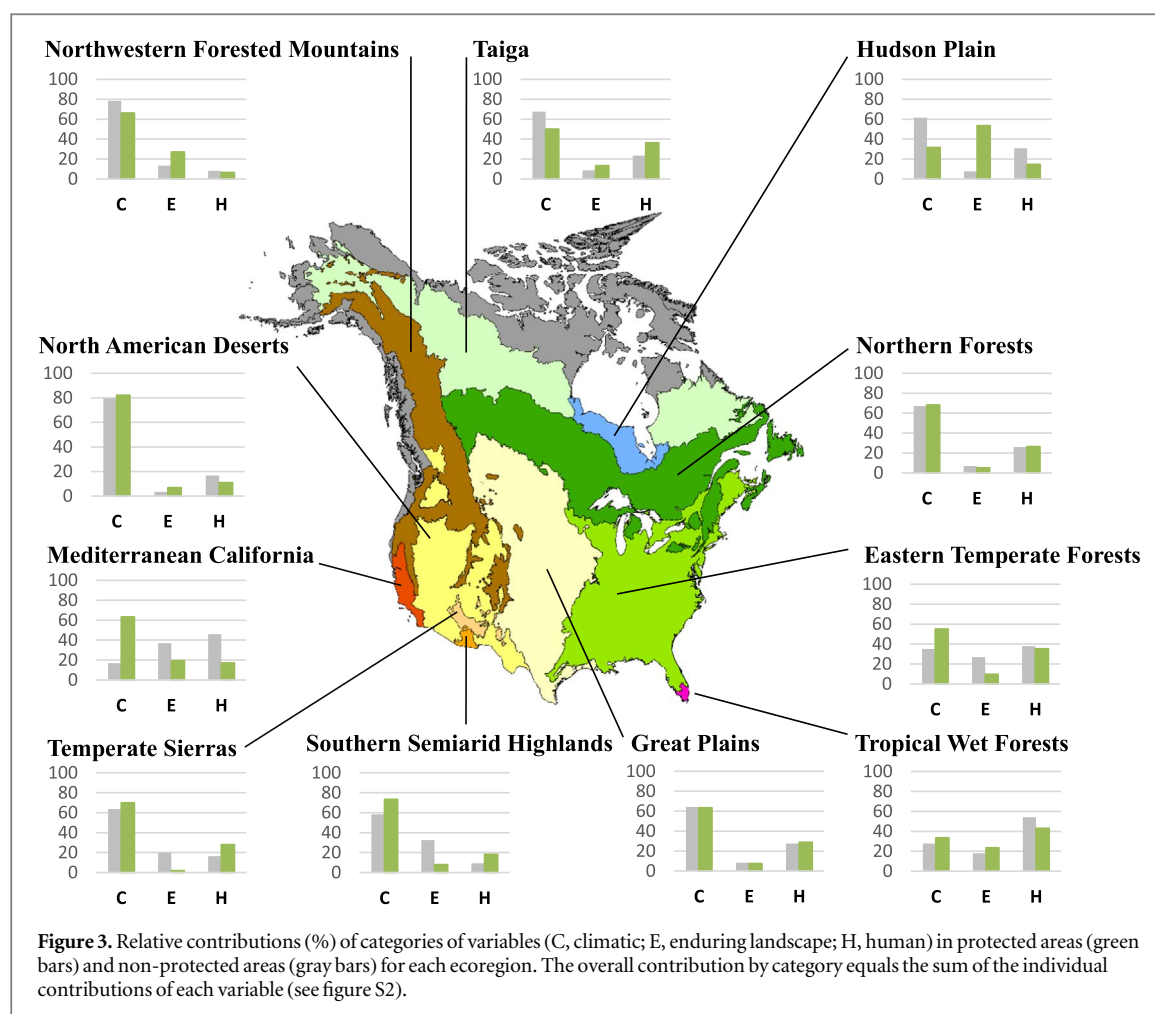


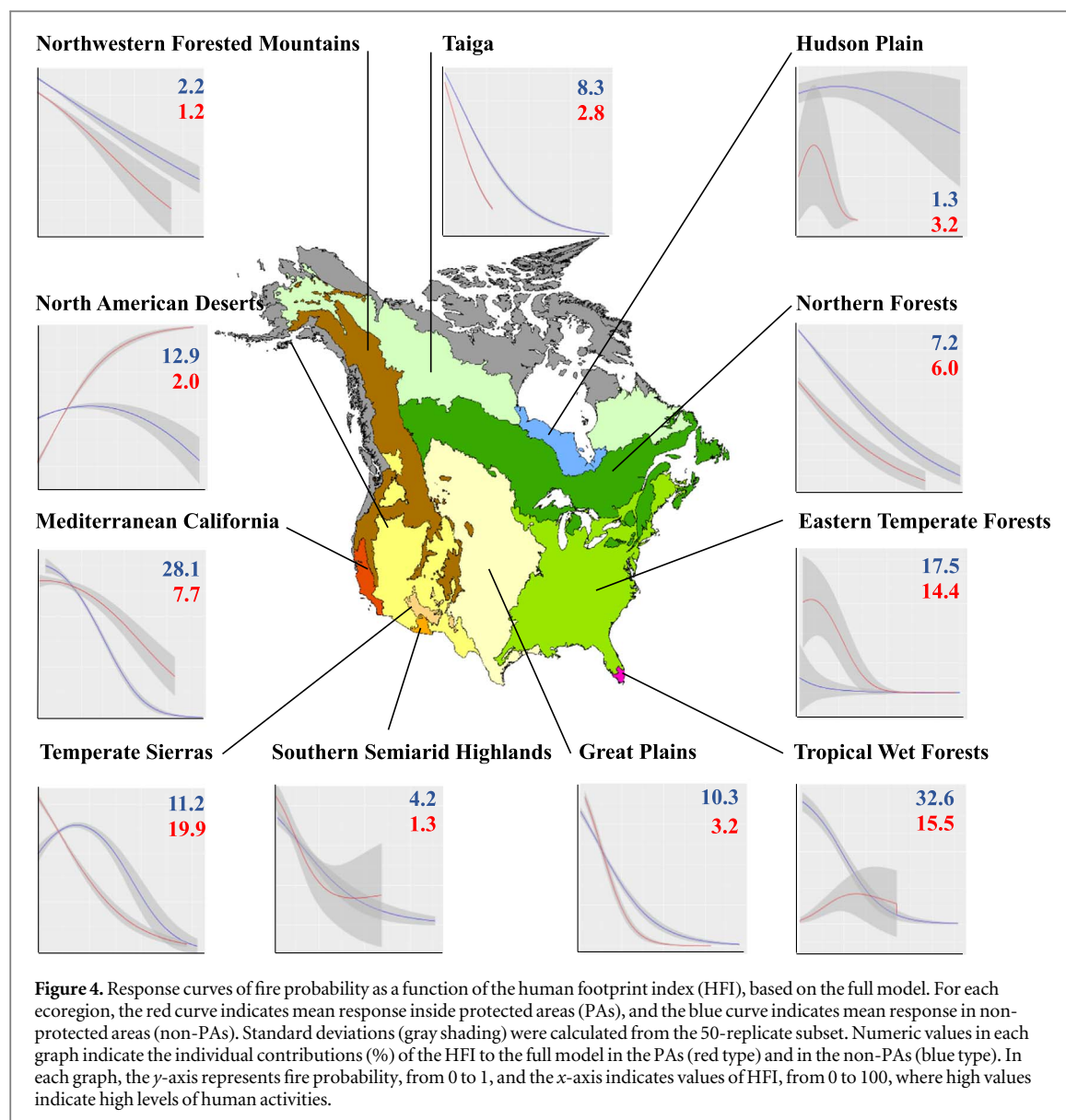
Table 2. Model performance by ecoregion and protection status estimated using the adjusted area under a receiver operating characteristic curve (AUC). Bold text indicates the best model among the four possible cases when differences were greater than 0.01.

Ecoregions	Full model		NoAnthro model	
	Non-PAs	PAs	Non-PAs	PAs
Eastern temperate forests	0.802	0.948	0.846	0.938
Great plains	0.804	0.852	0.768	0.797
Hudson plain	0.870	0.714	0.856	0.833
Mediterranean california	0.862	0.894	0.818	0.860
North american deserts	0.790	0.850	0.754	0.823
Northern forests	0.864	0.888	0.870	0.870
Northwestern forested mountains	0.816	0.841	0.804	0.829
Southern semiarid highlands	0.886	0.926	0.846	0.845
Taiga	0.851	0.840	0.831	0.808
Temperate sierras	0.850	0.876	0.803	0.856
Tropical wet forests	0.912	0.905	0.833	0.760

States, including Florida, fire regimes have been greatly affected by a combination of active fire suppression and human ignition, often for the purpose of reducing fuels through prescribed burning [57]. In contrast, the influence of humans on fire activity remains low in the northwest ecoregions and in Canada because most of the annual area burned comes from natural sources [58, 60].

How does this affect the burned areas?

Our study further reveals that human influence, as measured with the HFI, showed a negative relationship with burned area across most of Canada and the United States. Despite the fact that human activities introduce fire ignitions [57], our results suggest that humans, via fire suppression, diminished current fire activity in the study area. A notable exception to the



typical HFI–fire relationship occurred in the North American Deserts ecoregion, where PAs showed increasing fire activity with increasing human activity. This pattern is consistent with the findings of Parks *et al* [39] who suggested that the fire surplus observed in the PAs of this ecoregion were due to the spread of flammable non-native grasses, the prevalence of human ignitions, and the lack of natural ignitions.

For most ecoregions, climatic conditions within PAs were similar to those outside PAs (table S2), which suggests that much of the discrepancy in the burned areas can be attributed to different land uses, fire management practices, and ignitions. In some ways, our study allows us to describe continental-scale patterns in human-induced fire deficits and surpluses. The most human-altered ecoregions (Eastern Temperate Forests, Great Plains, Mediterranean California, Southern Semiarid Highlands, Tropical Wet Forests, and Temperate Sierras) have higher proportions of burned area within the PAs compared to non-PAs.

This difference likely reflects less burnable area (e.g. agricultural and urban areas) and perhaps more effective fire suppression outside the PAs. Fire suppression also affects PAs. In northern and less-developed ecoregions (e.g. those in boreal forests), where fuel limitation is low, human influence has a smaller yet still significant effect on fire activity, even in PAs; this pattern is consistent with other recent studies [32, 61]. Results from studies in the western United States and Canada suggest that many PAs (for example, Jasper National Park, Canada, Yellowstone National Park, USA) are in a fire deficit, due in large part to intense fire suppression activities [61–63]. Southern regions of the boreal forest also likely experience fire deficits because intense fire suppression aims to protect populated places and natural-resource values (e.g. timber, mines, energy [64]). In contrast, large expanses of non-forested regions have experienced a fire surplus, presumably because of introduced annual grasses and the prevalence of anthropogenic ignitions [39, 63].

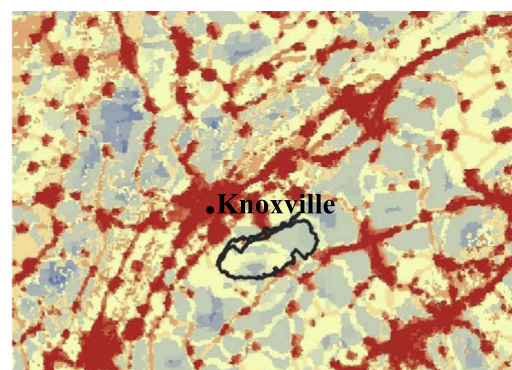
Implications for adaptive fire management

Canada and the United States have a long history in the designation and management of PAs: the first national park in Canada was designated in 1885 (Banff) and in the US in 1872 (Yellowstone). A century later, with millions of visits each year (figure 5; [65]), the fire management of North America's PA network is more complicated than perhaps was first anticipated. An increasing human footprint inside and surrounding PAs [2–5] potentially brings more human-caused ignitions. At the same time, increasing human activities multiply the public assets (including facilities for tourism and recreation) that may be at risk from fire, amplifying the need for fire suppression [66]. From both perspectives, an increase in extent and intensity of human development could not only diminish the conservation value of PAs, but also disrupt the natural fire regime inside PAs.

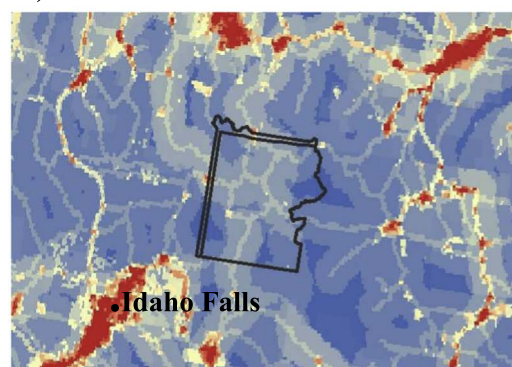
Achieving a balance between the conservation of fire-dependent ecosystems and increased human development requires careful management of fire regimes in PAs. Following nearly a century of fire exclusion from some areas, restoring natural fire regimes in PAs is likely to require a sustained effort from park managers [67]. However, managers still struggle with how best to restore fire as a natural ecological process and conserve inherent ecosystem resilience [68]. One widely used approach for setting fire management goals is the assessment of historical range of variability (HRV), a concept that focuses on quantifying the range of variation that a set of ecological patterns or processes may naturally exhibit over a given historical period (e.g. range of mean annual burned or mean fire frequency) [69]. However, implementation of HRV to restore a natural fire regime on the ground can be complex and not always successful or desired [70, 71]. Results from Kruger National Park in South Africa, suggest that a natural fire policy, in which all lightning-ignited fires were allowed to burn freely while all other fires were prevented, suppressed, or contained, had little if any effect on the extent of area burned or on the variability in fire intervals [72]. Other results from well-documented histories of fire management in western US National Parks, suggest that HRV may not adequately reflect ecosystem resilience to future fire activity [71, 73].

In an era of rapid change, both anthropogenic and climatic, it is likely that future social-ecological and environmental conditions lie beyond the HRV in the PAs [74]. Instead of aiming for conditions based on the past, some studies have advocated for a more adaptive approach based on the restoration of landscape heterogeneity, in terms of vegetation structure and composition, bounded by potential socio-ecological thresholds in order to enhance ecosystems resilience over a range of possible future conditions [71, 75, 76]. The concept of thresholds and tipping points have become increasingly relevant in the context of environmental management, as stressor–response relationships are better understood

a) Great Smoky Mountains National Park



b) Yellowstone National Park



c) Banff National Park

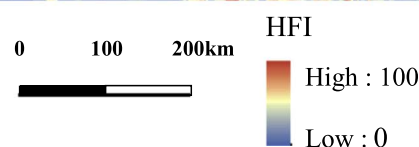
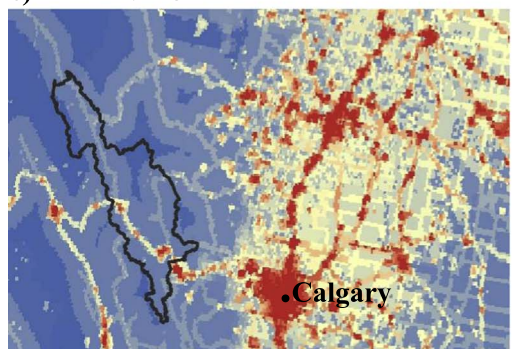


Figure 5. High-resolution map of the human footprint index (HFI) in and around the three most frequently visited national parks in North America [65]. The values of HFI range from 0 to 100, where high values indicate high levels of human activities. (a) Great Smoky Mountains National Park (11×10^6 visitors annually), (b) Yellowstone National Park (4.1×10^6 visitors annually), (c) Banff National Park (3.1×10^6 visitors annually), where visitor numbers are for the year 2017; park boundaries are indicated by gray polygons.

[77]. Consequently, further research is needed to identify future fire regimes, as well as human footprint thresholds prospectively to inform decision-making in fire management.

The concept of naturalness was once considered the key guiding principle when making conservation-related decisions in PAs and wilderness ecosystems

[68, 78]. However, given the rise in anthropogenic stressors and climate change, this principle is now debated as to whether and how we should intervene in wilderness to achieve the multiple goals and values of conservation and, at the same time, increase ecosystem integrity and resiliency [70, 79]. Our results highlight that human-altered fire regimes are ubiquitous in the PAs across NA and suggests that management solutions beyond the concept of naturalness are required. Contrasting the anthropogenic and environmental drivers of fire inside and outside PAs, as we did it in this study, can therefore provide valuable information for determining whether and to what degree humans have altered the fire regime, and in which environmental conditions. We suggest that the degree to which fire regimes are altered within PAs could serve as an indicator of human pressure in PAs and that information could be used as a proxy to measure the effectiveness of PAs and could support the selection of adaptive fire management strategies.

The wide range of ecosystems covered in this analysis provides some guidance for developing adaptive fire management strategies. For example, the contrasting results between the remote PAs in the Taiga and California (figure 4) implies different fire management objectives. For instance, in the northern Taiga, where the human footprint inside and outside PAs is low, the level of human intervention required in PA management will be minimal, whereas in highly populated California, PAs may require a higher level of human intervention to achieve multiple conservation goals and values. At the same time, conservation objectives, land-management plans, scenery values, level of human activities and societal goals are unique for each PA. Fire management within PAs may therefore require a case-by-case representation of land-use objectives and its influence on fire dynamics and vegetation dynamics, so as to capture the uniqueness of each PA. Thus, it remains crucial to measure and restore fire regimes at the PA scale, which accommodates socio-ecological values; as well as the need for landscape heterogeneity to increase future resilience [71].

Limitations and conclusions

This study focused on just one attribute of a fire regime—area burned. Further analyses would be needed to examine the potential effects of human activities on other fire regime attributes, such as fire frequency, seasonality, or severity [80]. Although we evaluated the human influence on area burned regardless of the ignition source, we acknowledge that human ignitions are distinct from natural ignitions in terms of their environmental drivers. However, it is difficult to disentangle the effect of ignitions on regional fire regimes, given that naturally ignited (i.e. lightning) fires are still affected by anthropogenic factors (e.g. fire suppression, land-cover change). In the United States, human-caused ignitions are responsible for four times as many large fires as lightning, and human-related

ignitions have more than tripled the length of the wildfire season [57, 58], though this varies among ecoregions. Unfortunately, high-quality consistent data on seasonality and ignition sources were not available across the continent. Similarly, data on fire-management policies and conservation guidelines, as well as their associated on-the-ground actions, were not available at the PA level. Integrating this information into our analytical models would allow us to better tease out the other myriad human influences on fire in PAs. This could, however, provide an interesting future arena of research.

Human activities threaten the effectiveness of PAs in preserving key natural ecosystem functions across the globe [8], including natural fire regimes. Our findings suggest a need for further analysis to understand specific interactions among fire, human pressures, and the environment at the scale of PAs. As countries aim to expand their terrestrial PAs network to meet the Aichi Target 11 by 2020 [81], this knowledge is needed to not only manage and restore the resilience of fire-dependent ecosystems, but also to include socio-ecological drivers in achieving conservation goals. In a world of rapid changing climate and expanding human pressures, where historical conditions would become progressively less meaningful to ecosystem maintenance and where it will be increasingly difficult to prevent human impacts (direct or indirect) on PAs, it is imperative to develop adaptive fire management strategies in PAs. Ultimately, meeting the conservation goals in fire-prone ecosystems will require ongoing monitoring and adaptive management of fire regime attributes in response to climate change, integrated with the cumulative effects of land-use change and increasing human pressures.

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References

- [1] Hoffmann S, Beierkuhnlein C, Field R, Provenza A and Chiarucci A 2018 Uniqueness of protected areas for conservation strategies in the European union *Sci. Rep.* **8** 6445

- [2] Radeloff V C, Stewart S I, Hawbaker T J, Gimmi U, Pidgeon A M, Flather C H, Hammer R B and Hesters D P 2010 Housing growth in and near United States protected areas limits their conservation value *Proc. Natl Acad. Sci. USA* **107** 940–5
- [3] Geldmann J, Joppa L N and Burgess N D 2014 Mapping change in human pressure globally on land and within protected areas *Conserv. Biol.* **28** 1604–16
- [4] Schulze K, Knights K, Coad L, Geldmann J, Leverington F, Eassom A, Marr M, Butchart S H M, Hockings M and Burgess N D 2018 An assessment of threats to terrestrial protected areas *Conserv. Lett.* **11** e12435
- [5] Jones K R, Venter O, Fuller R A, Allan J R, Maxwell S L, Negret P J and Watson J E 2018 One-third of global protected land is under intense human pressure *Science* **360** 788–91
- [6] Leverington F, Costa K L, Pavese H, Lisle A and Hockings M 2010 A global analysis of protected area management effectiveness *J. Environ. Manage.* **46** 685–98
- [7] Joppa L N, Loarie S R and Pimm S L 2008 On the protection of ‘protected areas’ *Proc. Natl Acad. Sci. USA* **105** 6673–8
- [8] Parrish J D, Braun D P and Unnasch R S 2003 Are we conserving what we say we are? Measuring ecological integrity within protected areas *BioScience* **53** 851–60
- [9] Bond W J and Keeley J E 2005 Fire as a global ‘herbivore’: the ecology and evolution of flammable ecosystems *Trends Ecol. Evol.* **20** 387–94
- [10] Keeley J E, Pausas J G, Rundel P W, Bond W J and Bradstock R A 2011 Fire as an evolutionary pressure shaping plant traits *Trends Plant Sci.* **16** 406–11
- [11] Parsons D J, Graber D M, Agee J K and Van Wagtenonk J W 1986 Natural fire management in national parks *J. Environ. Manage.* **10** 21–4
- [12] Pereira P, Mierauskas P, Úbeda X, Mataix-Solera J and Cerda A 2012 Fire in protected areas—the effect of protection and importance of fire management *Environ. Res. Eng. Manage.* **59** 52–62
- [13] Halpin P N 1997 Global climate change and natural-area protection: management responses and research directions *Ecol. Appl.* **7** 828–43
- [14] North M P, Stephens S L, Collins B M, Agee J K, Aplet G, Franklin J F and Fulé P Z 2015 Reform forest fire management *Science* **349** 1280–1
- [15] Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L and Holling C S 2004 Regime shifts, resilience, and biodiversity in ecosystem management *Annu. Rev. Ecol. Syst.* **35** 557–81
- [16] Coneder M, Tinner W, Neff C, Meurer M, Dickens A F and Krebs P 2009 Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation *Quat. Sci. Rev.* **28** 555–76
- [17] Swetnam T W, Allen C D and Betancourt J L 2009 Applied historical ecology: using the past to manage for the future *Ecol. Appl.* **9** 1189–206
- [18] Pechony O and Shindell D T 2010 Driving forces of global wildfires over the past millennium and the forthcoming century *Proc. Natl Acad. Sci.* **107** 19167–70
- [19] Parisien M A and Moritz M A 2009 Environmental controls on the distribution of wildfire at multiple spatial scales *Ecol. Monogr.* **79** 127–54
- [20] Lertzman K and Fall J 1998 From forest stands to landscapes: spatial scales and the roles of disturbances *Ecological Scale* ed D L Peterson and V T Parker (New York: Columbia University Press) pp 339–67
- [21] Bélisle A C, Leduc A, Gauthier S, Desrochers M, Mansuy N, Morin H and Bergeron Y 2016 Detecting local drivers of fire cycle heterogeneity in boreal forests: a scale issue *Forests* **7** 139
- [22] Mansuy N, Gauthier S, Robitaille A and Bergeron Y 2011 The effects of surficial deposit–drainage combinations on spatial variations of fire cycles in the boreal forest of eastern Canada *Int. J. Wildland Fire* **19** 1083–98
- [23] Parisien M A, Parks S A, Krawchuk M A, Flannigan M D, Bowman L and Moritz M A 2011 Scale-dependent controls on the area burned in the boreal forest of Canada, 1980–2005 *Ecol. Appl.* **21** 789–805
- [24] Mansuy N, Boulanger Y, Terrier A, Gauthier S, Robitaille A and Bergeron Y 2014 Spatial attributes of fire regime in eastern Canada: influences of regional landscape physiography and climate *Landscape Ecol.* **29** 1157–70
- [25] Bowman D M, O’Brien J A and Goldammer J G 2013 Pyrogeography and the global quest for sustainable fire management *Annu. Rev. Environ. Resour.* **38** 57–80
- [26] Bowman D M *et al* 2009 Fire in the Earth system *Science* **324** 481–4
- [27] Taylor A H, Trouet V, Skinner C N and Stephens S 2016 Socioecological transitions trigger fire regime shifts and modulate fire–climate interactions in the Sierra Nevada, USA, 1600–2015 CE *Proc. Natl Acad. Sci. USA* **113** 13684–9
- [28] Moritz M A, Morais M E, Summerell L A, Carlson J and Doyle J 2005 Wildfires, complexity, and highly optimized tolerance *Proc. Natl Acad. Sci. USA* **102** 17912–7
- [29] Syphard A D, Radeloff V C, Keeley J E, Hawbaker T J, Clayton M K, Stewart S I and Hammer R B 2007 Human influence on California fire regimes *Ecol. Appl.* **17** 1388–402
- [30] Knorr W, Kaminski T, Arneith A and Weber U 2014 Impact of human population density on fire frequency at the global scale *Biogeosciences* **11** 1085–102
- [31] Hantson S, Pueyo S and Chuvieco E 2015 Global fire size distribution is driven by human impact and climate *Glob. Ecol. Biogeogr.* **24** 77–86
- [32] Parisien M A, Miller C, Parks S A, DeLancey E R, Robinne F N and Flannigan M D 2016 The spatially varying influence of humans on fire probability in North America *Environ. Res. Lett.* **11** 075005
- [33] Mann M L, Batllori E, Moritz M A, Waller E K, Berck P and Flint A L 2016 Incorporating anthropogenic influences into fire probability models: effects of human activity and climate change on fire activity in California *PLoS One* **11** e0153589
- [34] Radeloff V C, Hammer R B, Stewart S I, Fried J S, Holcomb S S and McKeefry J F 2005 The wildland–urban interface in the United States *Ecol. Appl.* **15** 799–805
- [35] Hawbaker T J, Volker C, Radeloff V C, Stewart S I, Hammer R B, Keuler N S and Clayton M K 2013 Human and biophysical influences on fire occurrence in the United States *Ecol. Appl.* **23** 565–82
- [36] Sanderson E W, Jaiteh M, Levy M A, Redford K H, Wannebo A V and Woolmer G 2002 The human footprint and the last of the wild: the human footprint is a global map of human influence on the land surface, which suggests that human beings are stewards of nature, whether we like it or not *AIBS Bull.* **52** 891–904
- [37] Tesfaw A T, Pfaff A, Kroner R E G, Qin S, Medeiros R and Mascia M B 2018 Land-use and land-cover change shape the sustainability and impacts of protected areas *Proc. Natl Acad. Sci. USA* **115** 2084–9
- [38] Joppa L N, Loarie S R and Pimm S L 2009 On population growth near protected areas *PLoS One* **4** e4279
- [39] Parks S A, Miller C, Parisien M A, Holsinger L M, Dobrowski S Z and Abatzoglou J T 2015 Wildland fire deficit and surplus in the western United States, 1984–2012 *Ecosphere* **6** 275
- [40] Alvarado S T, Silva T S F and Archibald S 2018 Management impacts on fire occurrence: a comparison of fire regimes of African and South American tropical savannas in different protected areas *J. Environ. Manage.* **218** 79–87
- [41] Omernik J M 1987 Ecoregions of the conterminous United States *Ann. Assoc. Am. Geogr.* **77** 118–25 (https://archive.epa.gov/web/ecoregions/web/html/na_eco.html)
- [42] International Union for Conservation of Nature 1994 *Guidelines for Protected Area Management Categories* (Gland, Switzerland: World Conservation Union (IUCN))
- [43] Batllori E, Miller C, Parisien M A, Parks S A and Moritz M A 2014 Is US climatic diversity well represented within the existing federal protection network? *Ecol. Appl.* **24** 1898–907
- [44] Eidenshink J, Schwind B, Brewer K, Zhu Z L, Quayle B and Howard S 2007 A project for monitoring trends in burn severity *Fire Ecol.* **3** 3–21

- [45] Canadian Forest Service 2017 *Canadian Wildland Fire Information System: Canadian National Fire Database* (Edmonton, Alberta: Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre) (<http://cwfis.cfs.nrcan.gc.ca/ha/nfdb/>) (Accessed: 10 May 2016)
- [46] Wang T, Hamann A, Spittlehouse D and Murdock T N 2012 ClimateWNA—high-resolution spatial climate data for western North America *J. Appl. Meteorol. Climatol.* **51** 16–29
- [47] Evans J S, Oakleaf J, Cushman S and Theobald D 2014 An ArcGIS Toolbox for Surface Gradient and Geomorphometric Modeling, version 2.0-0. (<https://arcgis.com/home/item.html?id=63ffcecf3b2a45bf99a84cdaedefacfc>) (Accessed: 6 June 2016)
- [48] Friedl M A, Sulla-Menashe D, Tan B, Schneider A, Ramankutty N, Sibley A and Huang X 2010 MODIS Collection 5 global land cover: algorithm refinements and characterization of new datasets *Remote Sens. Environ.* **114** 168–82
- [49] Wildlife Conservation Society—WCS, and Center for International Earth Science Information Network—CIESIN—Columbia University 2005 *Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic)* (Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC)) (Accessed: 10 May 2016) (<https://doi.org/10.7927/H4M61H5F>.)
- [50] Watts R D, Compton R W, McCammon J H, Rich C L, Wright S M, Owens T and Ouren D S 2007 Roadless space of the conterminous United States *Science* **316** 736–8
- [51] Center for International Earth Science Information Network—CIESIN—Columbia University 2017 *Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 10* (Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC)) (Accessed: 06 May 2016) (<https://doi.org/10.7927/H4DZ068D>)
- [52] R Development Core Team 2016 *R A Language and Environment for Statistical Computing* (Vienna: R Foundation for Statistical Computing)
- [53] Phillips S J, Anderson R P and Schapire R E 2006 Maximum entropy modeling of species geographic distributions *Ecol. Modell.* **190** 231–59
- [54] Krawchuk M and Moritz M 2012 Fire and Climate Change in California: Changes in the Distribution and Frequency of Fire in Climates of the Future and Recent Past (1911–2099) *Report CEC-500-2012-026* (Sacramento, CA: California Energy Commission)
- [55] Collins B M, Omi P N and Chapman P L 2006 Regional relationships between climate and wildfire-burned area in the Interior West, USA *Can. J. For. Res.* **36** 699–709
- [56] Flannigan M D, Wotton B M, Marshall G A, De Groot W J, Johnston J, Jurko N and Cantin A S 2016 Fuel moisture sensitivity to temperature and precipitation: climate change implications *Clim. Change* **134** 59–71
- [57] Nagy R C, Fusco E, Bradley B, Abatzoglou J T and Balch J 2018 Human-related ignitions increase the number of large wildfires across US ecoregions *Fire* **1** 4
- [58] Balch J K, Bradley B A, Abatzoglou J T, Nagy R C, Fusco E J and Mahood A L 2017 Human-started wildfires expand the fire niche across the United States *Proc. Natl Acad. Sci. USA* **114** 2946–51
- [59] Syphard A D, Keeley J E, Pfaff A H and Ferschweiler K 2017 Human presence diminishes the importance of climate in driving fire activity across the United States *Proc. Natl Acad. Sci. USA* **114** 13750–5
- [60] Stocks B J, Mason J A, Todd J B, Bosch E M, Wotton B M, Amiro B D and Skinner W R 2002 Large forest fires in Canada, 1959–1997 *J. Geophys. Res. Atmos.* **107** FFR 5-1–12
- [61] Chavardès R D, Daniels L D, Gedalof Z E and Anderson D W 2018 Human influences superseded climate to disrupt the 20th century fire regime in Jasper national park, Canada *Dendrochronologia* **48** 10–9
- [62] Van Wagtenonk J W 2007 The history and evolution of wildland fire use *Fire Ecology* **3** 3–17
- [63] Balch J K, Bradley B A, D'antonio C M and Gómez-Dans J 2013 Introduced annual grass increases regional fire activity across the arid western USA (1980–2009) *Glob. Change Biol.* **19** 173–83
- [64] Robinne F N, Parisien M A and Flannigan M 2016 Anthropogenic influence on wildfire activity in Alberta, Canada *Int. J. Wildland Fire* **25** 1131–43
- [65] National Geographic Staff 2017 *Top 10 Most Visited National Parks* (Washington: National Geographic) (<https://nationalgeographic.com/travel/national-parks/most-visited-parks-photos/>) (Accessed: 10 June 2018)
- [66] Calkin D E, Thompson M P and Finney M A 2015 Negative consequences of positive feedbacks in US wildfire management *Forest Ecosystems* **2** 9
- [67] Parsons D J and Botti S J 1996 Restoration of fire in national parks ed Colin C Hardy and Stephen F Arno *The Use of Fire in Forest Restoration. Gen. Tech. Rep. INT-GTR-341* (Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station) vol 341, 29–31
- [68] Parsons D J 2000 The challenge of restoring natural fire to wilderness *Wilderness Science in a Time of Change Conf.: Wilderness Ecosystems, Threats and Management* vol 5 (Missoula, MT, 23–27 May 1999) ed David N Cole (Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station) pp 276–82
- [69] Keane R E, Hessburg P F, Landres P B and Swanson F J 2009 The use of historical range and variability (HRV) in landscape management *Forest Ecol. Manag.* **258** 1025–37
- [70] Christensen N L 2005 Fire in the parks: a case study for change management. In the George Wright forum 2005 Jan 1 *George Wright Soc.* **22** 12–31
- [71] Moritz M A, Hurteau M D, Suding K N and D'antonio C M 2013 Bounded ranges of variation as a framework for future conservation and fire management *Ann. NY Acad. Sci.* **1286** 92–107
- [72] Van Wilgen B W, Govender N, Biggs H C, Ntsala D and Funda X N 2004 Response of savanna fire regimes to changing fire-management policies in a large African national park *Conserv. Biol.* **18** 1533–40
- [73] Schoennagel T, Balch J K, Brenkert-Smith H, Dennison P E, Harvey B J, Krawchuk M A and Turner M G 2017 Adapt to more wildfire in western North American forests as climate changes *Proc. Natl Acad. Sci. USA* **114** 4582–90
- [74] Batllori E, Parisien M A, Parks S A, Moritz M A and Miller C 2017 Potential relocation of climatic environments suggests high rates of climate displacement within the North American protection network *Glob. Change Biol.* **23** 3219–30
- [75] Keeley J E and Stephenson N L 2000 Restoring natural fire regimes to the Sierra Nevada in an era of global change *Wilderness Science in a Time of Change Conf.: Wilderness Ecosystems, Threats and Management* vol 5 (Missoula, Montana: USDA Forest Service, Rocky Mountain Research Station) pp 255–65
- [76] Biggs H C and Rogers K M 2003 An adaptive system to link science, monitoring and management in practice *The Kruger Experience: Ecology and Management of Savanna Heterogeneity* ed J T du Toit, K H Rogers and H C Biggs (Washington, DC: Island Press) pp 59–80
- [77] Kelly R P, Erickson A L, Mease L A, Battista W, Kittinger J N and Fujita R 2015 Embracing thresholds for better environmental management *Philos. Trans. R Soc. B* **370** 20130276
- [78] Hobbs R J *et al* 2010 Guiding concepts for park and wilderness stewardship in an era of global environmental change *Front. Ecol. Environ.* **8** 483–90
- [79] Cole D N 2012 Beyond naturalness: adapting wilderness stewardship to an era of rapid global change *Int. J. Wilderness* **18** 9–14
- [80] Whitman E, Batllori E, Parisien M A, Miller C, Coop J D, Krawchuk M A, Chong G W and Haire S L 2015 The climate space of fire regimes in north-western North America *J. Biogeogr.* **42** 1736–49
- [81] Venter O, Fuller R A, Segun D B, Carwardine J, Brooks T, Butchart S H, Di Marco M, Iwamura T, Joseph L, O'Grady D and Possingham H P 2014 Targeting global protected area expansion for imperiled biodiversity *PLoS. Biol.* **12** e1001891