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Understanding and modelling wildfire regimes: an ecological perspective

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Abstract

Recent extreme wildfire seasons in several regions have been associated with exceptionally hot, dry conditions, made more probable by climate change. Much research has focused on extreme fire weather and its drivers, but natural wildfire regimes—and their interactions with human activities—are far from being comprehensively understood. There is a lack of clarity about the 'causes' of wildfire, and about how ecosystems could be managed for the co-existence of wildfire and people. We present evidence supporting an ecosystem-centred framework for improved understanding and modelling of wildfire. Wildfire has a long geological history and is a pervasive natural process in contemporary plant communities. In some biomes, wildfire would be more frequent without human settlement; in others they would be unchanged or less frequent. A world without fire would have greater forest cover, especially in present-day savannas. Many species would be missing, because fire regimes have co-evolved with plant traits that resist, adapt to or promote wildfire. Certain plant traits are favoured by different fire frequencies, and may be missing in ecosystems that are normally fire-free. For example, post-fire resprouting is more common among woody plants in high-frequency fire regimes than where fire is infrequent. The impact of habitat fragmentation on wildfire crucially depends on whether the ecosystem is fire-adapted. In normally fire-free ecosystems, fragmentation facilitates wildfire starts and is detrimental to biodiversity. In fire-adapted ecosystems, fragmentation inhibits fires from spreading and fire suppression is detrimental to biodiversity. This interpretation explains observed, counterintuitive patterns of spatial correlation between wildfire and potential ignition sources. Lightning correlates

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positively with burnt area only in open ecosystems with frequent fire. Human population correlates positively with burnt area only in densely forested regions. Models for vegetation-fire interactions must be informed by insights from fire ecology to make credible future projections in a changing climate.

1. Introduction

Wildfire is in the news because of recent extreme fire seasons, notably in western North America, south-eastern Australia and the Mediterranean region, that have occurred under exceptionally hot and dry conditions made more probable by anthropogenic climate change (Abatzoglou *et al* 2019, Kirchmeier-Young *et al* 2019, Williams *et al* 2019, Bowman *et al* 2020, Abram *et al* 2021, van Oldenborgh *et al* 2021). The most newsworthy wildfires are, unsurprisingly, those that destroy (or threaten to destroy) human settlements. Tropical deforestation by deliberate burning is also widely reported. Media accounts often mention the large *number* of fires that are started accidentally or otherwise by people (although most are very small), and almost universally attribute the *cause* of a fire to the ignition event that started it rather than the conditions that allowed it to spread. The consequence of such skewed reporting is a widespread negative perception of fire: as if it were a malign human invention, generally a threat to ecosystems and biodiversity, universally (and increasingly) exacerbated by human activities.

This perception is almost entirely incorrect (Pausas and Keeley 2009, 2019, Doerr and Santin, 2016). Wildfire is a natural process with a long geological history; indeed, it is as ancient as plant life on land (Bowman *et al* 2009, Scott 2018). Many ecosystems and plant species are adapted to wildfire and depend on it for their persistence. Current increases in fire frequency in some regions are offset by continuing declines in others (Andela *et al* 2017, Forkel *et al* 2019). Some regions of the world have also experienced changes in fire severity (e.g. Parks and Abatzoglou 2020, Tran *et al* 2020) which will also have an impact on ecosystems and post-fire recovery, but increases in severity are not ubiquitous (Keyser and Westerling 2017). Globally, human population density has a negative relationship with burnt area (Bistinas *et al* 2014, Knorr *et al* 2014, 2016). Empirical analyses of remotely sensed burnt area data have contributed to overturning previous hypotheses about wildfire, such as the incorrect idea (Seiler and Crutzen 1980) that pre-industrial wildfire was an order of magnitude less extensive than contemporary wildfire (Hamilton *et al* 2018). Studies of past fire regimes based on sedimentary charcoal records (Marlon *et al* 2008, 2013, Harrison *et al* 2010) and atmospheric indicators in ice cores (Wang *et al* 2010) have also contributed to improved general understanding of the controls of biomass burning, including the insight that global wildfire as recently as the mid-nineteenth century was much more extensive than today. However, understanding of present fire regimes and fire-vegetation interactions—whether in remote, natural ecosystems or in densely settled and managed landscapes—remains far from comprehensive. This partial understanding is reflected in the fact that global, process-based models of vegetation that include fire and fire-vegetation interactions can reproduce the broad, global-scale patterns of burnt area but produce substantially different estimates of global burnt area and struggle to simulate other key aspects, such as fire season length and interannual variability (Hantson *et al* 2020).

Other strands of research on the ecology of fire have been making steady progress meanwhile and have produced an extensive and rapidly growing literature (see McLauchlan *et al* 2020 for a wide-ranging review). However, few insights from fire ecology have yet been incorporated in global, process-based fire-enabled vegetation or land-surface models, such as those used and evaluated in the Fire Modeling Intercomparison Project, FireMIP (Hantson *et al* 2016, Rabin *et al* 2017, Forkel *et al* 2019, Teckentrup *et al* 2019, Lasslop *et al* 2020, Hantson *et al* 2020). Fire ecology research has revealed associations between specific plant traits and wildfire regimes (Lloret *et al* 2005, Enright *et al* 2011, Hollingsworth *et al* 2013, Pausas 2015a, Pausas *et al* 2016), and pointed to the existence of positive feedbacks that can maintain sharp boundaries and allow abrupt transitions between vegetation types with different characteristic fire frequencies and plant traits (Ratnam *et al* 2011, Dantas *et al* 2016, Aleman *et al* 2020). In this paper, we summarize findings from recent empirical and theoretical research in fire ecology. We develop a simple conceptual framework based on these findings, illustrating key points with regional or global data analyses. We hope that this framework will facilitate improved understanding of the causes and consequences of wildfire in a global context, as well as improved realism in fire-enabled vegetation models.

2. Fire as a natural ecosystem process

Most biomes are adapted to fire to some degree. Tropical rain forests, most temperate deciduous forests and deserts are exceptions, since although they may be resilient to isolated sporadic fires which initiate gap dynamics they are not adapted to regular or intense burning. Fire return intervals range from one to two years in some tropical grasslands to hundreds

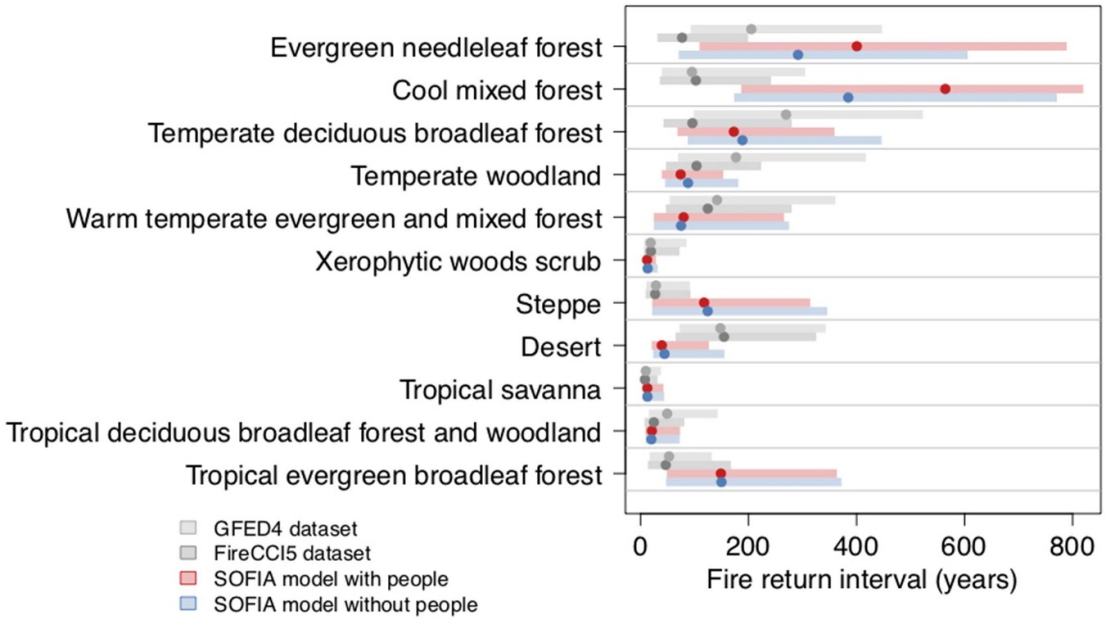


Figure 1. Assessment of actual and potential natural fire return intervals across different biomes, using the SOFIA model (Forkel *et al* 2019). SOFIA is an empirical model of monthly burnt area that accounts for climate, land cover and human influences on fire occurrence. Two simulations were made to investigate the impact of people on fire return intervals, one in which the model was run using all driving variables (SOFIA model with people) and one in which the human population density effect was removed (SOFIA model without people). The monthly burnt areas were aggregated to provide annual burnt area. The allocation to biomes is based on the Hengl *et al* (2018) potential natural vegetation map. Observed actual burnt area, based on the GFED4 (Giglio *et al* 2013) and FireCC51 (Chuvieco *et al* 2018) data sets, is shown for comparison.

of years in boreal forests. Some direct information on fire return intervals on these longer time scales can be obtained from sedimentary charcoal (Gavin *et al* 2007, Stivrins *et al* 2019) and tree-ring (Everett 2008, Kharuk *et al* 2016) records. Satellite remote sensing can provide spatially explicit information about fire regimes and has been used to create regional burnt area data sets (e.g. Finco *et al* 2012, García-Lázaro *et al* 2018). However, reliable global satellite-derived burnt area records are available only for the period since about 2000 CE, and thus only provide useful information about regions characterised by shorter fire return intervals. Furthermore, there are still substantial differences between remotely sensed burnt-area products derived by different methods and depending on the resolution of the satellite sensor used (Hantson *et al* 2016, Humber *et al* 2019, Roteta *et al* 2019). To estimate fire return intervals from these rather short records we rely on the approximation that annual burnt-area fraction is the reciprocal of fire return interval. This is true for the idealized case in which fires are randomly distributed within the grid cell, but leads to an overestimation of fire return intervals in ecosystems (e.g. boreal forests) where there has been little fire in the satellite observational record.

Remotely sensed data can provide information only about actual fire return intervals under the recently prevailing conditions of climate, land management and settlement. Inferring 'natural' fire regimes (i.e. the fire regime that would occur in the absence of human influence) is a challenge, and prone to error. Given the sensitivity of wildfire to climate change (Pausas and Keeley 2021), whether natural or anthropogenic, it is essentially impossible to estimate the natural fire regime today based on evidence from any period in the past.

An alternative approach to infer natural fire return intervals is via empirical models trained on remotely sensed data products. Figure 1 illustrates the considerable range of actual fire return intervals, as estimated from two such products (Giglio *et al* 2013, Chuvieco *et al* 2018), both within and between biomes. It also shows results from an empirical model that accounts for the effects of multiple climatic and land-use predictors, and for the influence of human population density (Forkel *et al* 2019). The model can be run with all predictors 'on' to provide an estimate of actual return intervals, and with the influence of population density 'off' to provide an estimate of natural return intervals (figure 1, SI figure 1 available online at stacks.iop.org/ERL/16/125008/mmedia). In biomes with short fire return intervals, such as tropical savanna and xerophytic woods and scrub, there is no net influence of human population (figure 1, SI table 1). In some biomes with long fire return intervals, such as evergreen needleleaf and cool mixed forests, the net effect of human population is to suppress fire and further lengthen the return interval. In temperate deciduous broadleaf forest and temperate woodlands, with moderate fire return intervals, the

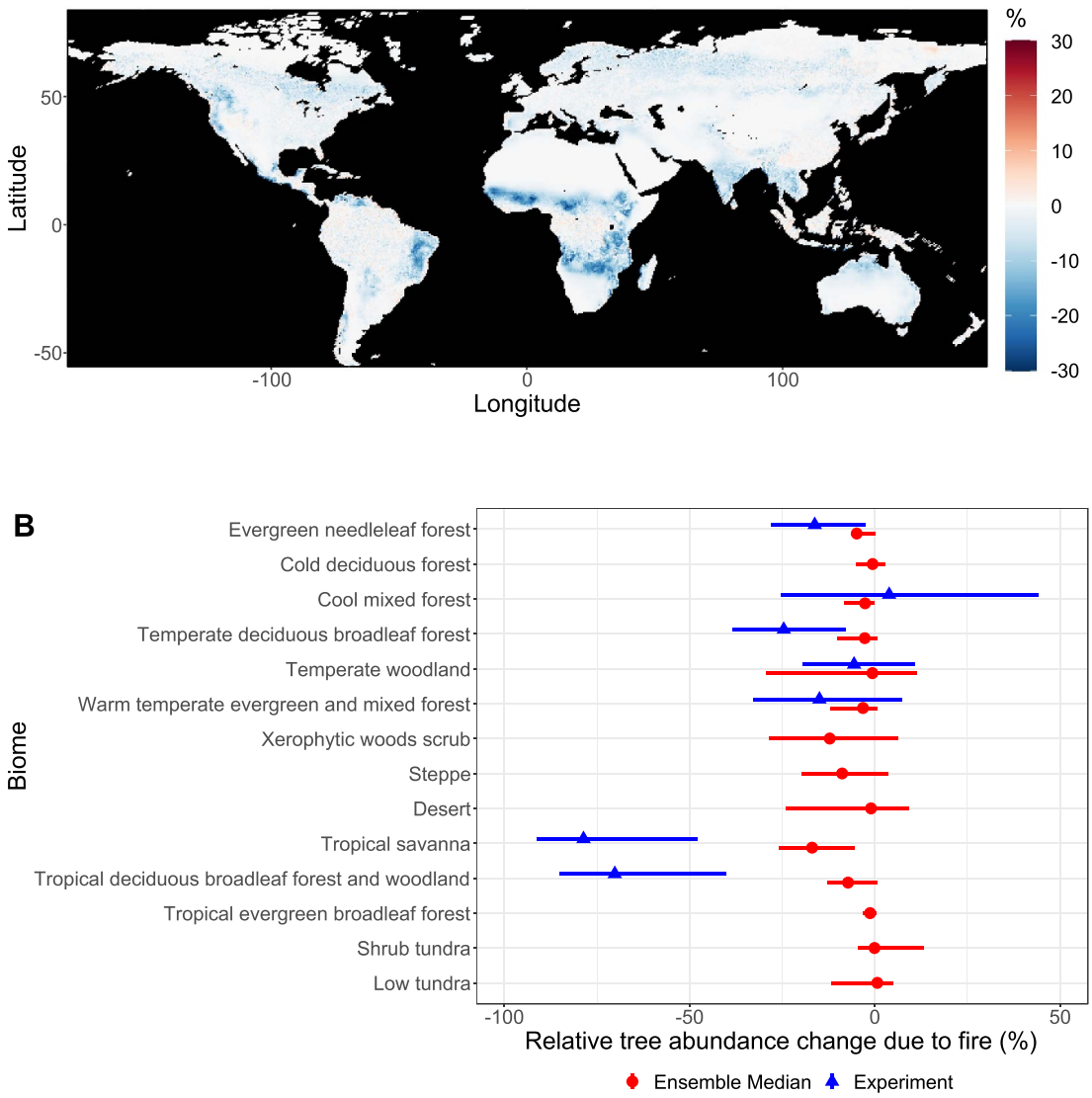


Figure 2. Changes in tree abundance as a result of fire. The top plot shows the absolute change in simulated tree cover as a result of fire for an ensemble of four global vegetation-fire models (LPJ-GUESS-SPITFIRE, LPJ-GUESS-SIMFIRE-BLAZE, and JSBACH-SPITFIRE, JULES-Inferno). The simulations are from the FireMIP project and consist of baseline experiments for the historical period and experiments in which fire was switched off (Rabin *et al* 2017, Lasslop *et al* 2020). The bottom plot shows the response of tree abundance to the presence of fire aggregated by biome from the same ensemble of four global vegetation-fire models (green circles) and from a meta-analysis of fire exclusion experiments (orange triangles). The simulation results shown represent tree cover change due to fire (averaged between 1993 and 2013) and are displayed as the median of the modelled values for each biome and the bars show the range between the minimum and maximum of the individual model results. The experimental data are from Pellegrini *et al* (2020) and Pellegrini *et al* (2021) and show changes in tree cover as a result of fire based on exclusion experiments (See SI table 2 for details). The allocation to biomes is based on the Hengl *et al* (2018) potential natural vegetation map.

net effect is to increase fire and shorten the return interval. Overall, the effects of human population are small compared to the intrinsic differences among biomes, and are of similar magnitude to the differences between alternative burnt-area data sets. Nonetheless, this comparison points to heterogeneity among biomes in their wildfire responses to human presence in the landscape.

Another counterfactual model experiment involves examining the nature of a 'world without fire' (Bond *et al* 2005). This requires the use of process-based models of vegetation and its interactions with fire. The limitations of process-based models can be circumvented, to some extent, by pooling results from an ensemble of models with different potential deficiencies and associated errors—an approach widely used in the climate modelling community (Hagedorn *et al* 2005, Parker 2013, Sanderson *et al* 2015, Merrifield *et al* 2020). The map in figure 2 shows the decrease in tree abundance due to fire, as simulated

by the average of four of the fire-enabled vegetation models that participated in FireMIP (Rabin *et al* 2017, Lasslop *et al* 2020) with fire turned on or off. Median, minimum and maximum values of modelled tree abundance changes are averaged across each biome, and shown in figure 2. These model results are supported by independent evidence for tree abundance changes derived from manipulative experiments (Pellegrini *et al* 2020, 2021). In most biomes where such experiments have been conducted, the observed changes overlap with the simulated changes. In tropical savannas and tropical deciduous broadleaf forests and woodlands, models consistently show reductions in tree abundance due to fire, and experiments show even greater reductions. Mapped biome shifts (e.g. Bond *et al* 2005, Martin Calvo and Prentice 2015, Lasslop *et al* 2020) suggest the expansion of tropical forests into savannas as the most prominent consequence of a world without fire, consistent with the geographic pattern of changes in tree cover shown in figure 2, although the extent of modelled biome shifts differs among models.

3. Plant adaptations and feedbacks to fire

Plant species are not passive recipients of fire regimes. Instead, species and fire regimes have co-evolved on a macroevolutionary time scale (Keeley *et al* 2011, 2012, Archibald *et al* 2018, Lamont *et al* 2019). Fire-prone ecosystems today include species possessing a variety of traits that promote their survival, reproduction and competitive success in different fire regimes (Keeley *et al* 2012, Enright *et al* 2014). The most common fire-related traits vary according to the mode of fire spread (surface or crown) and the typical fire return interval. Therefore, at least in a semi-quantitative sense, the natural fire regime of an ecosystem (to which plants are adapted) can be reliably inferred from the traits of the plants it contains. The following four examples provide illustrations of this.

- Ecosystems may be normally fire-free for three reasons, or combinations thereof (McLauchlan *et al* 2020): a lack of continuous fuel due to low productivity, e.g. deserts; climates where potential fuel is rarely dry enough to burn, e.g. tropical rain forests; or in a few (rare) cases, a lack of natural ignition sources (Keeley *et al* 2011, 2012). Plant species characteristic of (largely) fire-free ecosystems typically lack fire-adaptive traits and may be vulnerable to burning.
- In ecosystems characterized by relatively infrequent crown wildfires (fire return interval >10–25 years on average), many plant species show *resilience* to fire i.e. the population survives through enhanced recruitment even though individual plants die. This is facilitated through traits such as serotiny—possessing seeds that are only released when a fire occurs (Buma *et al* 2013, Lamont *et al* 2020)—and heat- or smoke-dependent germination, which enable regeneration from seed after a fire has occurred (Paula and Pausas 2008, Moreira *et al* 2010).
- In ecosystems characterized by relatively frequent surface fires (fire return interval <10–25 years on average), plants more often show *resistance* to burning, i.e. individual plants resist fire-induced mortality, through traits such as thick bark (which prevents cambial damage from overheating: Lawes *et al* 2011, Pausas 2015a); protected meristems; underground storage organs, allowing plants to resprout from the base (Pausas *et al* 2018, Corrêa Scanlon *et al* 2020); and umbrella-type (rather than conical) canopies that mean that leaves are able to survive the passage of ground fires (Pausas 2015b).
- In ecosystems subject to very frequent surface fires (fire return interval <5–10 years on average), only plants with underground meristems and predominantly below-ground biomass (e.g. grasses), ephemeral plants with fire-promoted germination, and occasional trees with thick bark can survive and thrive (Pausas *et al* 2015a, Pausas *et al* 2018, Simpson *et al* 2019).

Here we illustrate this by showing how the abundance of resprouting woody species changes with fire frequency across the European continent (figure 3, SI figure 3). This analysis shows that the frequency of resprouters (relative to non-resprouters) differs significantly along the gradient of fire return intervals, with resprouting species being the most common when the fire return interval is shorter and least common when fire return interval is longer. Resprouting allows individual plants to persist after fire and therefore is a strong response to frequent fires (Karavani *et al* 2018), while plants that cannot resprout will be excluded unless they have alternative survival mechanisms such as post-fire seeding. The ability to resprout has a significant impact on the speed of ecosystem recovery after fire (Calvo *et al* 2003, Casady *et al* 2009, Gouveia *et al* 2010, van Leeuwen *et al* 2010) and indeed on the trajectory of ecosystem change in response to climate (Baudena *et al* 2020). However, it is not usually included as a trait in global fire-enabled vegetation models, although the failure to account for this behaviour could have an important effect on simulated ecosystem development (Kelley *et al* 2014) and, through this, on fire regimes (Baudena *et al* 2020).

Some woody plants experiencing frequent fires also possess traits that increase flammability (Pausas *et al* 2017), such as deciduous bark or the presence of volatile secondary compounds. Likewise, some serotinous woody species in low-frequency, high-severity fire regimes possess flammability-enhancing traits such as the retention of lower branches, which allow fire to spread into the canopy where

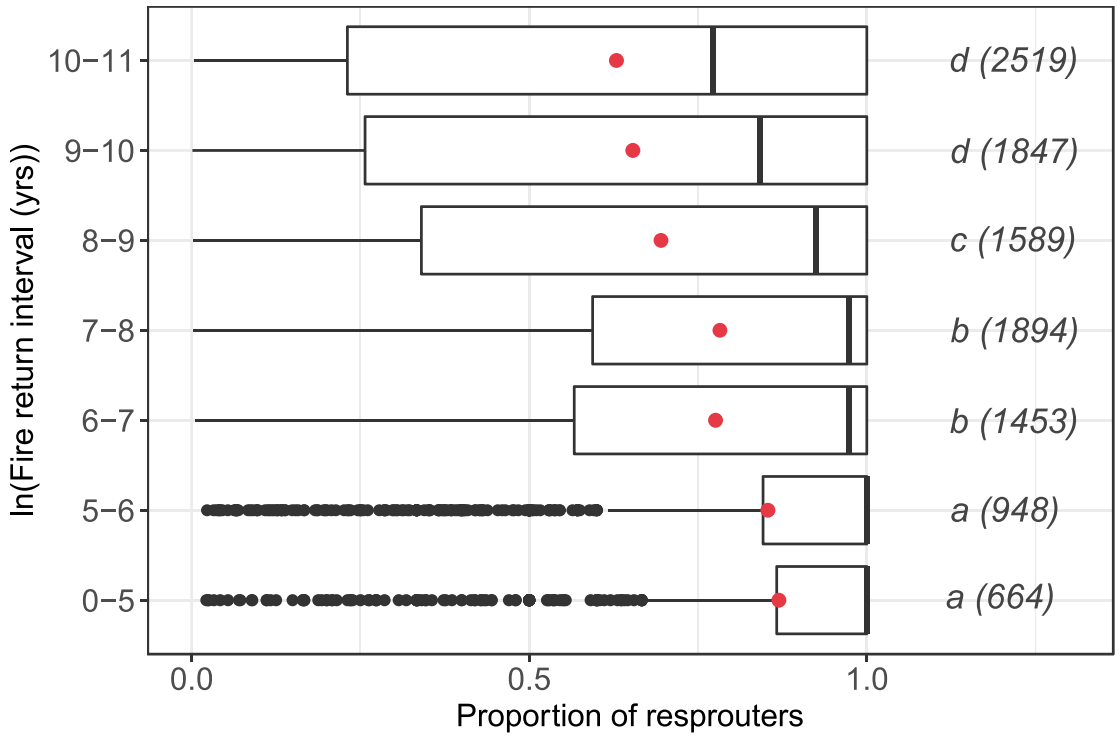


Figure 3. Changes in the relative abundance of resprouting woody plants as a function of fire return interval. The relative abundance information for 29 192 sites across Europe (SI figure 2) was derived from the sPlotOpen data base (Sabatini *et al* 2021). Information about species that resprout or do not resprout after fire was derived from the BROT (Tavşanoğlu and Pausas 2018) and TRY (Kattge *et al* 2020) databases, an extensive literature search and the authors' field knowledge (see SI table 3). Species that could not be classified as resprouters or non-resprouters are excluded from the analysis. The fire return interval was calculated using burnt area data from 2000 to 2020 from MODIS MCD64CMQ (Giglio *et al* 2018). This product does not sense small fires and thus underestimates total burnt area in individual grid cells. This and the short length of the record means that the fire return times should be considered as relative rather than absolute estimates of actual fire return times. Individual site values are shown as blue dots, the red dots show the mean, the black lines show the median, the boxes show the interquartile range of the relative abundance. The significance of median differences under different fire return intervals was assessed using the non-parametric Kruskall-Wallis test, where significantly different populations are indicated by different letters. The number of observations in each category is indicated in brackets.

heat-responsive seed-bearing structures are held (He *et al* 2012). While it is still debated whether these flammability-related traits are adaptive (see e.g. Bond and Midgley 1995, Bowman *et al* 2014, Prior *et al* 2017), it is clear that deciduous bark such as in some *Eucalyptus* species increase the build-up of fuel and therefore the probability of fire. Grasses show a large range in flammability; more flammable species are both adapted to and promote frequent burning (Simpson *et al* 2016, 2021, Cardoso *et al* 2018). Variations in flammability are also seen at the community scale. Closed canopy forests, for example, tend to resist the incursion and spread of fire from neighbouring flammable ecosystems by maintaining a shadier, more humid and relatively windless understorey from which flammable grass species are excluded and other accumulated fine fuels remain too wet to support fire spread (Hoffmann *et al* 2011, Oliveras *et al* 2016, Cardoso *et al* 2021). Grasslands in general burn more frequently than forests, and their frequent burning makes it hard for trees to dominate even if climatic conditions are suitable and there are nearby seed sources of tree species (Hoffmann *et al* 2012a, 2012b, Pausas and Bond 2020a). There is a universal threshold around 40% forest cover, below which fire frequency increases steeply (Archibald *et al* 2009, Staver *et al* 2011, van Nes *et al* 2018). The fire regime, in turn, impacts nutrient availability: frequent fires reduce plant and ecosystem nutrient contents and thereby the potential for biomass accumulation (Pellegrini *et al* 2021). Indeed, the emissions from frequent fires may lead to the redistribution of nutrients over a large area, thus increasing the spatial scale of nutrient recycling (Pausas and Bond 2020b).

Plant adaptations to wildfire thus tend to reinforce the fire regime with which they are associated through positive feedback mechanisms ('vegetation switches' *sensu* Wilson and Agnew 1992). These feedbacks can maintain persistent sharp boundaries between vegetation patches, for example between forest and grassland (Dantas *et al* 2013, Oliveras and Malhi 2016, van Nes *et al* 2018). Positive feedbacks can also cause sharp spatial vegetation transitions along continuous environmental gradients (Grimm 1983, Grimm and Jacobson 1992) and, analogously, abrupt temporal responses of vegetation to gradual changes in climate (deMenocal *et al* 2000, Zhao *et al* 2017). Some mathematical models of such systems

predict the co-existence of alternative stable states under identical environmental conditions (Accetino *et al* 2010, Staver and Levin 2012), and this concept has been widely invoked in interpretation of observed sharp forest-savanna boundaries (e.g. Staver *et al* 2011, van Nes *et al* 2018, Pausas and Bond 2020a). The extent of the climate space where such states co-exist is still debated. Veenendal *et al* (2018) suggested that it may be small, and that climatic and edaphic gradients primarily determine vegetation composition even in the presence of positive feedbacks, while several others (e.g. Staver *et al* 2011, Dantas *et al* 2016, D'Onofrio *et al* 2018) predict it to be a relatively widespread phenomenon. However, there is general agreement about the existence of positive vegetation-fire feedbacks, and their role in sharpening vegetation transitions in fire-prone regions.

4. The effects of fragmentation and ignition sources

The distinction between fire-prone and normally fire-free ecosystems, as determined by the traits of the plant species they contain, is crucial to understanding the ways in which different ecosystems respond to fragmentation. Fragmentation of some natural ecosystems has been found to promote fire, whereas in others fragmentation has been found to suppress fire (see e.g. Armenteras *et al* 2013, Alencar *et al* 2015 vs Parsons and Gosper 2011). The origin of this apparent paradox lies in the existence of two competing effects of fragmentation. On the one hand, in normally fire-free ecosystems, deforestation, logging and the creation of 'edges' by road-building promote drying of litter, and increase wind speed (compared to the forest interior), thereby increasing the chance that either a lightning strike or a human ignition will start a fire (Arienti *et al* 2009, Armenteras *et al* 2013, Cano-Crespo *et al* 2015, Armenteras *et al* 2017, Pausas and Keeley 2021). On the other hand, in fire-prone ecosystems the creation of clearings, paths, roads, and other barriers mainly act to interrupt fuel continuity and thus fire spread, leading to a reduction in burnt area (Gillson *et al* 2019). Figure 4 illustrates these differences in behaviour across three different biomes in South America. There is a positive relationship between fragmentation and burnt area in evergreen broadleaf forests, which are normally fire-free ecosystems, but fragmentation leads to decreased fire in savanna and cerrado.

These different effects of fragmentation on wildfire may also be relevant for understanding why potential ignition sources (human population density and the frequency of lightning) have been demonstrated (see e.g. Bistinas *et al* 2014, Knorr *et al* 2014, 2016, Andela *et al* 2017) to be generally poor predictors of wildfire. Figure 5, inspired by a similar graphic in Andela *et al* (2017), maps the spatial correlations between burnt area and human population density and between burnt area and lightning frequency. Burnt area is negatively correlated with human population almost everywhere. Exceptions, showing positive correlation between burnt area and population, are in densely forested regions, including tropical rain forests in Borneo and south-western Amazonia. For lightning, there is a positive correlation with burnt area over many fire-prone regions (notably tropical savannas) but no correlation (or even a negative correlation) with burnt area in dense forests. Examination of these spatial correlations with respect to population density (SI figure 4) and burnt area (SI figure 5) shows that positive correlations with population density occur in regions with high population but low burnt area. There is no interaction between lightning and population density, but significant positive correlations with lightning occur at high levels of burnt area.

We suggest the following explanation for these contrasting patterns. One key consequence of human population is vegetation fragmentation, which has opposite effects in fire-prone versus normally fire-free ecosystems. The widespread negative correlation between human population and burnt area primarily reflects the inhibition of fire spread by landscape fragmentation (including permanent cultivation). This correlation is observed even though fragmentation facilitates access, and therefore the chance of accidental human ignition. Fire suppression may also be a factor in regions where fire severity is limited by moist climates or discontinuous fuel (Balch *et al* 2017). The practice of slash-and-burn agriculture (now geographically restricted) is also considered to be incompatible with a large human population (Smith *et al* 2021). Lightning is an important ignition source, and in fire-prone ecosystems in relatively dry regions a higher lightning frequency is linked to more fire starts. However, in normally fire-free forest ecosystems, high precipitation levels mean that fuel is almost permanently wet so that lightning strikes are ineffective in starting fires. The negative correlation between lightning and burnt area in densely forested regions reflects their low flammability, and the fact that lightning is likely to be accompanied by rain in climates suitable for such forests.

The lack of a consistently positive correlation between fire starts and potential ignition sources is a serious problem for models that assume such a correlation exists. Venevsky *et al* (2002) introduced the concept that each person, on average, starts a given number of fires per unit time. This number propagates directly into the total number of modelled fires. Subsequent models have also adopted this concept but sometimes along with an additional function to describe fire *suppression* by people (see model descriptions in Rabin *et al* 2017). Teckentrup *et al* (2019) illustrated the large diversity of functions for human ignition and suppression that have been adopted in global fire-enabled vegetation models.

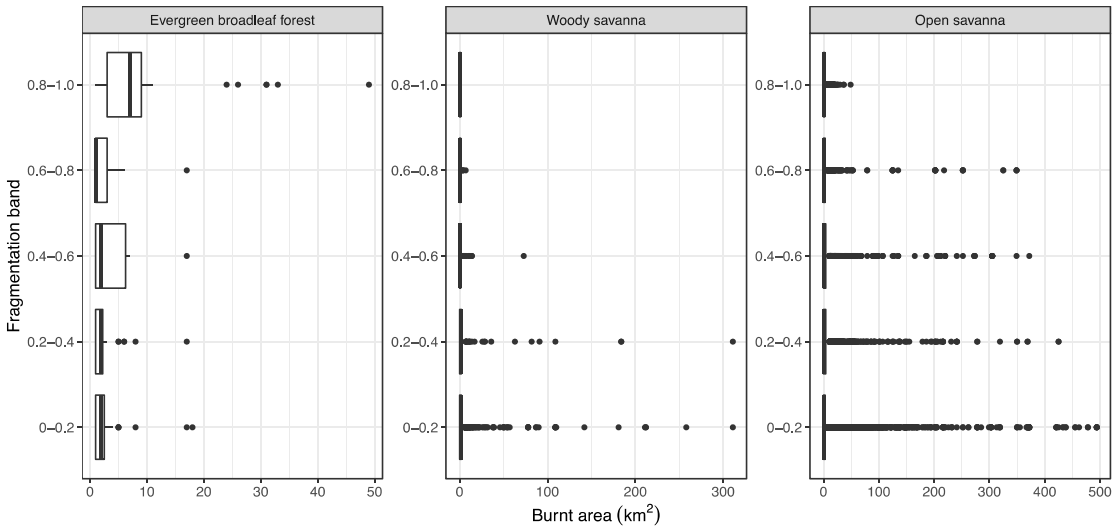


Figure 4. The relationship between vegetation fragmentation and burnt area in evergreen broadleaf forest, woody savanna and open savanna in tropical South America. Observed burnt area and vegetation fragmentation is based on the Global Fire Atlas (Andela *et al* 2019) and Hansen *et al* (2020) data sets at 1 km pixel resolution. Evergreen broadleaf forest (>60% evergreen woody vegetation, >2 m height), woody savanna (30%–60% forest cover, >2 m height) and open savanna (<30% forest cover, grassland and shrubland) is based on MODIS MCD12Q1 for 2012 (Friedl *et al* 2002) resampled at 1 km pixel spacing. The data for evergreen broadleaf forests are only from north of the equator. The scales for burnt area differ between the three biome types.

Given that the empirical basis for all these formulations is weak, there is a need for more rigorous testing of how potential ignitions relate to observed ignitions. Furthermore, it would be useful in a model development context to shift the focus away from potential ignition sources, to the physical and biological factors that influence the fuel loads and flammability of ecosystems and hence fire spread, and the way that these factors may be modified by human interventions. Indeed, how vegetation properties determine fuel loads and fuel drying is known to be a weakness of existing global models (Baudena *et al* 2015, Forkel *et al* 2019, D'Onofrio *et al* 2020).

5. Implications for biodiversity and ecosystem management

It is now generally accepted that universal fire suppression is neither possible nor desirable. Although biodiversity can be negatively impacted by fire in non-fire-adapted ecosystems, it is also expected to be negatively impacted by fire *suppression* elsewhere because the life histories of plants adapted to fire are intimately bound up with their fire regime (Driscoll *et al* 2010). Moreover, as is now widely recognized, zero-fire policies in some countries have increased the risks of uncharacteristically intense wildfires (Calkin *et al* 2015, Moreira *et al* 2020, Santos *et al* 2021) with potentially negative consequences for biodiversity, as well as for human habitation.

Globally, wildfire frequency has declined steeply since the late nineteenth century (Marlon *et al* 2008), a trend they explained by increased landscape fragmentation due to the widespread adoption of intensive agriculture. Other factors, such as the expansion of commercial forestry, improved forest management and deliberate fire suppression to preserve agricultural and timber resources may also have contributed to this decline. The (partly unintentional) role of human population in reducing fire frequency in fire-adapted ecosystems means that almost no place on Earth can now be said to have an entirely natural fire regime (Chuvieco *et al* 2021). Biodiversity conservation in some regions may require trying to mimic the natural fire regime through a combination of approaches, including prescribed burning (Kelly *et al* 2020).

Recent years have indeed seen a shift in wildfire management practices in regions where wildfires are important for maintaining natural resources and biodiversity (Hunter *et al* 2011, Huffman *et al* 2020). Nevertheless, adapting wildfire management to meet multiple objectives, including safeguarding habitation and infrastructure while conserving biodiversity, in a rapidly warming climate is a challenge for which we are still poorly equipped (Moritz *et al* 2014, Kelly *et al* 2020). The palaeorecord has shown that wildfire frequency is highly sensitive to temperature variations: even the relatively small-amplitude variations in global mean temperature over the last millennium are reflected in charcoal records all over the world (Marlon *et al* 2008). Model simulations of future fire risk under continued climate change do not project increases everywhere, but they do so consistently in some regions. However, the projections of climate change made using different climate models also show considerable divergence from one another and there are substantial regions where the projected changes in fire risk diverge even in sign (IPCC Land Report 2019). The evidence base for

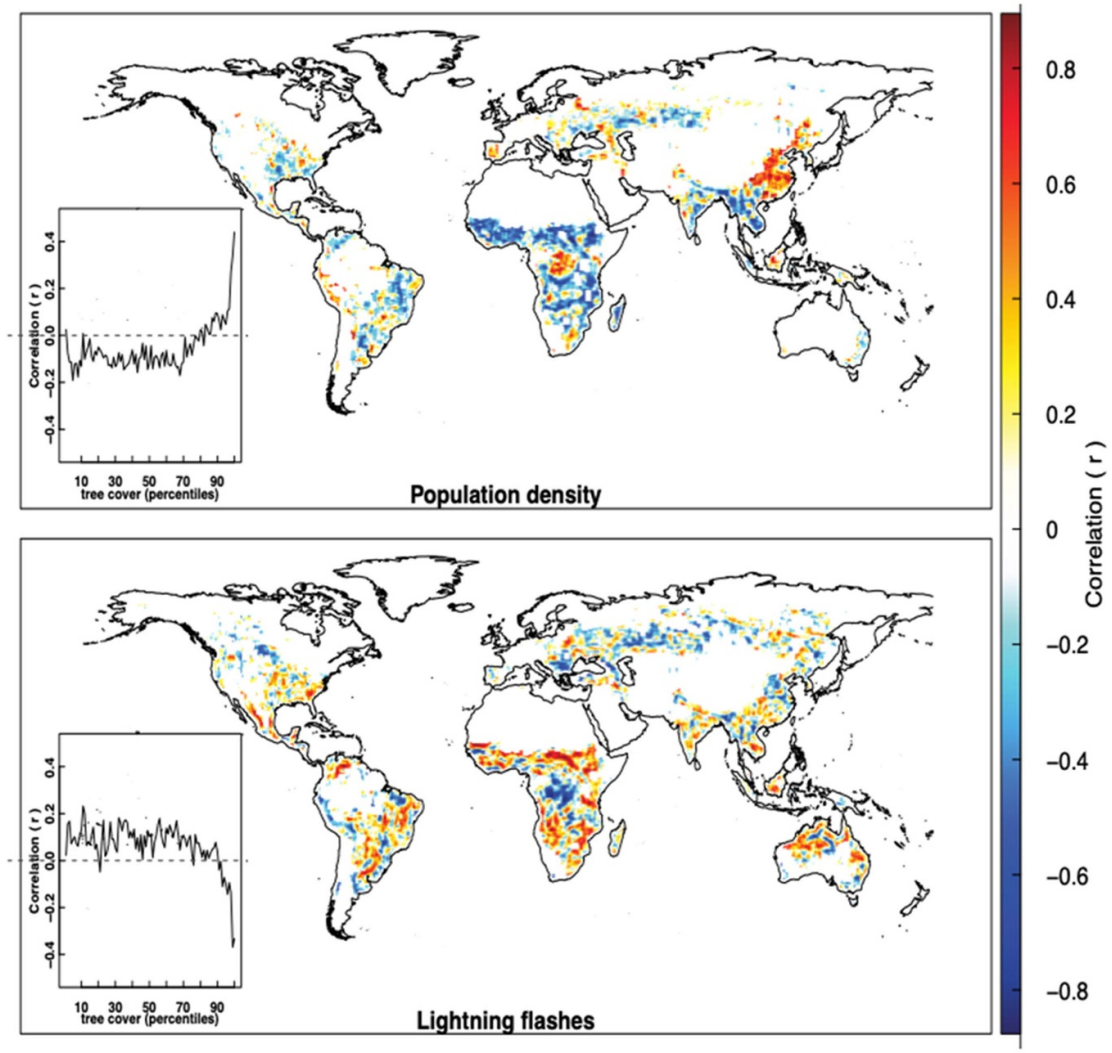


Figure 5. Mapped correlations between annual burnt area and human population (top panel), and between annual burnt area and cloud-to-ground lightning frequency (bottom panel) during 2010–2016 at 0.5° resolution. Burnt area data are from GFED4; population density data from HYDE 3.2; lightning data from Kaplan and Lau (2019). The insets show median correlation coefficients for grid cells classified into percentiles of tree cover, based on the MOD44B product at 250 m resolution. All correlations were calculated over a 5 × 5 mesh of individual 0.5° grid cells. For correlations and relationships with other potential drivers of burnt area, see supplementary information.

adaptation to future fire regimes is thus weak. The problem is compounded by the inability of current fire-enabled vegetation or land-surface models to distinguish different types of fire regime (see e.g. Rabin *et al* 2017)—yet transitions between them would have implications for biodiversity. Abrupt transitions in fire regime accompanied by large changes in vegetation composition have occurred in the recent geological past (Fordham *et al* 2020), and are likely to happen in the future, posing new challenges for biodiversity conservation as well as fire management.

6. Towards an ecosystem-centred framework for understanding fire

We have outlined a number of ways in which vegetation properties, either at plant or ecosystem level, shape fire regimes. Traditional approaches to linking vegetation and fire focus on the role of vegetation for fuel dynamics and fuel drying. While this is necessary, it is not sufficient. Most plants and ecosystems have co-evolved with fire. The behaviour of fire-adapted vegetation is very different from that of vegetation that experiences fire less often, in terms of both the response to anthropogenic fragmentation and the speed of ecosystem recovery after fire. Vegetation properties are diagnostic of fire regimes and can provide valuable insights into ecosystem resilience and guides to appropriate fire management. Although there are some remaining puzzles and data gaps, embedding current understanding of fire ecology into process-based fire models should help improve the ability to predict how fire regimes might change in the future. Thus, we advocate the adoption of an ecosystem-centred approach to modelling fire regimes, building on the insights this offers on the bi-directional interactions between vegetation and fire.

Data availability statement

All the data used in this analysis are publicly available as cited or are included in supplementary information.

All data that support the findings of this study are included within the article (and any supplementary files).

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Author contributions

SPH conceived the paper. ICP and SPH planned and led the mini-workshop and wrote the first draft. Figures were created by M Forkel (figure 1), M Forrest and AP (figure 2), YS, JH, KJS, AWC, MB and JGP (figure 3), RKN and KJB (figure 4) and ND (figure 5). All authors contributed to the discussions and to the final draft.

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