Title of the manuscript Fire hazard modulation by long-term dynamics in land cover and dominant forest type in Eastern and Central Europe

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Abstract

Wildfire occurrence is influenced by climate, vegetation and human activities. A key challenge for understanding fire-climate-human interactions is to quantify the mediating effect of vegetation on fire regimes. Here, we explore the relative importance of Holocene land cover, land use, dominant functional forest type, and climate dynamics on biomass burning in temperate and boreo-nemoral regions of Central and Eastern Europe over the past 12 ka BP. We used an extensive data set of Holocene pollen and sedimentary charcoal records, in combination with climate simulations and statistical modelling. Biomass burning was highest during the early Holocene and lowest during the mid-Holocene in all three ecoregions, but was more spatially variable over the past 3-4 ka BP. Although climate explained a significant variance in biomass burning during the early Holocene, tree cover was consistently the highest predictor of past biomass burning over the past 8 ka BP. In temperate forests, biomass burning was high at ~ 45% tree cover and decreased to a minimum between 60 to 70% tree cover. In needleleaf-dominated forests, biomass burning was highest at ~ 60-65% tree cover and steeply declined at > 65% tree cover. Biomass burning also increased when arable lands and grasslands reached ~15-20%, although this relationship was variable depending on land use practice via ignition sources, fuel type and quantities. Higher tree cover reduced the amount of solar radiation reaching the forest floor and could provide moister, more wind-protected microclimates underneath canopies, thereby decreasing fuel flammability. Tree cover at which biomass burning increased appears to be driven by warmer and drier summer conditions during the early Holocene, and by increasing human influence on land cover during the late Holocene. Our observations cover the full range of Holocene climate variability and land cover changes, and illustrate that during most of the Holocene percentages of land

cover are a key predictor of the probability of fire occurrence over timescales of centuries to millennia. We suggest that long-term fire hazard may be effectively reduced through land cover management, given that land cover has controlled fire regimes under the dynamic climates of the Holocene.

1 Introduction

Wildfires can have dramatic environmental, economic, and social impacts, as demonstrated by recent catastrophic fire events (Leverkus et al., 2019). However, fire is an integral part of many ecosystems and controls a range of evolutionary and ecological processes (Bond and Keeley, 2005; Bowman et al., 2009; Archibald et al., 2018). Fire regimes (i.e. fire frequency, size, intensity, severity, seasonality) are influenced by climate and vegetation properties (fuel moisture, availability, composition and structure) and vary both spatially and temporally (Bond and Keeley, 2005; van der Werf et al., 2010; Pausas and Paula, 2012; Archibald et al., 2018). A key challenge for understanding fire-climate interactions is to quantify the effect that vegetation properties have in mediating biomass burning. Overall, it has been hypothesised that along a fuel-load gradient, climate-induced fire hazard (ignition and spread) is lowest in both productive moist regions (with high fuel load provided by dense tree cover) and in unproductive arid systems (with low fuel load and dominant grass and shrub cover), and is highest in intermediate systems that have a mixed fuel load provided by tree, shrub and grass cover (Pausas and Ribeiro, 2013). Grasses and shrubs are implicated in positive fire-fuel feedbacks, whereas an increase in tree cover beyond a specific threshold can reduce fire hazard, thereby fostering a negative feedback on fire (Beckage et al., 2009; Frejaville et al., 2016). It has also been shown that plant functional traits (growth rate and architecture, leaf chemical composition and moisture content, litter decomposition) that determine flammability can mitigate climate-driven fire occurrence, leading to fire regimes other than those expected based solely on climate conditions (Girardin et al., 2013; Pausas and Ribeiro, 2013; Kloster et al., 2015; Rogers et al., 2015; Blarquez et al., 2015; Feurdean et al., 2017). For example, needleleaf trees with volatile compounds and resins, retention of dead biomass in crown, ladder fuels and slow litter decomposition rates promote fire hazard. Temperate broadleaf deciduous trees (with the exception of drought-adapted oaks) with high leaf moisture content and faster litter turnover, usually have a low ignition probability and less flammable fuel, although under very dry conditions fire may spread with high intensity once fuel has been ignited (Sturtevant et al., 2009; Rogers et al., 2015). Human activities, however, can also influence fuel load, composition and ignition patterns, thereby adding another level of complexity to fire regime variability and probability of occurrence. In this context, human activities are particularly relevant in Europe, where (i) a long history of human-driven decline in tree cover (often including the use of fire) is documented (Roberts et al., 2018), and (ii) forest extent has increased over the past few decades due to rural land abandonment, fire suppression, and carbon abatement programmes (Jepsen et al., 2015). While high tree cover may reduce the likelihood of fire spread, widespread plantations of highly flammable trees (e.g. *Pinus*) produced by modern forestry may increase the probability and impact of catastrophic fires for human health, economy and ecosystems (Frejaville and Curt 2017; Słowiński et al., 2019). In addition fire-promoting climatic conditions are also projected to increase in areas where natural fires were historically infrequent, e.g., in Central and Eastern Europe (Khabarov, et al., 2016). However, the levels of forest cover and prevailing dominant tree types that will reduce or augment climate-driven fire hazard in the European context has not yet been quantified.

A fundamental limitation for understanding fire-climate-vegetation interactions based on observations or modelling approaches is that they are rooted in the modern environment. Yet, present-day ecosystems and fire regimes carry the legacies of past anthropogenic impact and climates (Marlon et al., 2016; Vannière et al., 2016). Palaeoecological studies based on pollen, plant macrofossils and charcoal sedimentary records provide centennial-to-millennial data sets to decipher past vegetation and fire dynamics and associated drivers. This is particularly relevant in forested ecosystems, which are dominated by species that have long generation times and fire return intervals that exceed observational records (Whitlock et al., 2017). Establishing how land-cover changes influence fire regimes will be critical to infer the probability of future fire occurrence and its impacts (Pausas and Paula, 2012; Whitlock et al., 2017).

Here we explore interactions between fire, land cover, land use, and climate during the Holocene in major Central and Eastern European temperate and boreo-nemoral vegetation types. We use independent evidence of changes in fire, land-cover composition and climate with a statistical modelling approach (generalized additive models, GAM) to quantify percentages in land cover and tree-density associated with fire hazard.

2 Methods

2.1 Geographical location and charcoal site selection

To determine past biomass burned, we compiled a dataset comprising 117 sedimentary charcoal records from sites located in Central and Eastern Europe (Fig. 1; Supplement S1). Of these, 70 records are from peatlands (bogs and fens), whereas 47 records are from lakes. For each record we compiled metadata including geographical coordinates, elevation, depositional environment, and data source (Supplement S1). Sedimentary charcoal is the most common proxy to determine relative changes in biomass burning (Whitlock and Larsen, 2001). While progress has been made to determine charcoal source areas, the quantification of absolute burned area from charcoal records is still challenging (Adolf et al., 2018). We therefore interpret the charcoal signal as relative trends in biomass burning (see Marlon et al., 2016). Regarding the depositional environment, bogs provide a more local representation of past fire occurrence than lakes, because they are characterised by limited charcoal transport and post-fire transport or erosion (Conedera et al., 2009; Rius et al., 2011). However, peatlands are susceptible to burning, which may introduce hiatuses in the depositional environment. The overall climate of the study area is temperate with considerable variability across regions due to marine or continental influences: the northern and eastern part have long cold winters and short, warm summers, whereas the central and southern parts have relatively warm, wet winters and dry, hot summers. Climate conditions also vary along an elevation gradient in this region.

In terms of fire activity, natural ignition sources such as lightning strikes occur at low frequencies, i.e., < 5 flashes km^2/yr^1 and most fires are intentionally or accidentally ignited by humans (Christian et al., 2003). The average fire size is ~10 ha in eastern Europe, between 5 and 10 ha in southern Europe and < 5 ha in northern and central Europe (European Forest Fire Information System, (http://effis.jrc.ec.europa.eu). The number of fires per year is higher in northern, eastern and southern Europe (> 50 fires/yr) than in central Europe (1-50 fires/yr).

2.2 Charcoal records and regional composite of biomass burning

Spatio-temporal patterns in fire-land cover interactions were investigated using a geographical delineation of Central and Eastern Europe (CEE) based on modern environmental stratification (Metzger et al., 2005). We defined three ecoregions within the Central and Eastern European region: Continental (CON), Boreo-Nemoral (BNE), and Atlantic (ATL). The Boreo-Nemoral ecoregion includes 26 sites from the boreal and nemoral zones, the Continental ecoregion includes 72 sites from the Continental, Alpine (conifer belt) and Pannonian zones, and the Atlantic region includes 19 sites from the Atlantic zone (Fig. 1).

All age measurements of the charcoal records were converted to calibrated years before present by using either the depth-age models provided by the original publications, or new depth-age models established for this study (Supplement S1). Charcoal concentrations were transformed into charcoal accumulation rates or influx (CHAR) by multiplying concentrations (charcoal counts [pieces cm^{-3}] or charcoal areas [mm^2 cm^{-3}]) by sediment-accumulation rates [cm yr^{-1}] to account for variations in sedimentation among sequences. To allow comparison between and within charcoal records obtained from various depositional environments with different analytical methods and sampling resolution, we have applied the standardisation technique established by Power et al. (2008) and modified by Daniau et al. (2012) and Blarquez et al. (2014). The standardisation procedure included a min-max rescaling of CHAR values, followed by a Box-Cox transformation to homogenise within-record variance, and a subsequent Z-score transformation using a base period from 12 to 0.15 ka BP. This base period includes the entire dataset, but excludes the effect of post-industrial human impact on fire activity. For compositing charcoal records by ecoregions, transformed charcoal records from each ecoregion were pre-binned in 100-year bins to reduce the influence of high-resolution records on the composite charcoal record. Pre-binned charcoal time series were smoothed with a LOWESS smoother with a 500-year window half width. Confidence interval values (95%) were calculated by bootstrap resampling the binned charcoal series and calculation of the mean for each bin 1000 times (default settings). For numerical processing of the CHAR series we used the R paleofire package version 4.0 (Blarquez et al., 2014). CHAR composite anomalies (100-year time interval) relative to the Holocene average of the entire CEE region and the three ecoregions, represent regional trends in biomass burning; where zero Z-score values correspond to the mean charcoal influx over the base period; and positive/negative Z-score values represent greater-than-mean/lower-than-mean charcoal influx over the base period (Fig. 2).

2.3 Pollen-based regional composite of land cover classes

We used pollen-based land cover estimates at 200-year time intervals for the period 10.9 ka BP to present, based on the pseudobiomisation method (Fyfe et al., 2015) to quantify changes in land cover type. The pseudobiomisation approach groups pollen types into land-cover classes that are directly comparable to other land cover classifications (Fyfe et al., 2015). These land-cover estimates are available from the PANGAEA Database for the entire study area, as opposed to other pollen-based quantitative vegetation reconstructions restricted mainly to northwestern Europe (Fyfe et al., 2015). We extracted six land cover classes: total forest, closed needleleaf forest, closed broadleaf deciduous forest, heath/scrubland, natural grasslands and open pastures, and arable/disturbed land cover other than heathland. Needleleaf forests are represented by the sum of pollen taxa dominated by *Pinus*, *Picea, Abies*, *Larix,* whereas broadleaf forests by the sum of pollen of *Quercus*, *Fagus*, *Betula*, *Carpinus*, *Ulmus*, *Tilia, Acer, Corylus*, *Alnus, Betula* as the most common taxa. Heath/scrubland primarily includes *Calluna, Empetrum, Ephedra, Erica, Hippophaë, Juniperus* (Fyfe et al., 2015). The natural grasslands/open pastures land cover class is a sum of a mixture of herb taxa, including pasture-specific taxa, whereas arable/disturbed land is defined by the sum of herb taxa typically adapted to cultivated and high-disturbance environments. For a full list of pollen taxa assigned to each land-cover class see Fyfe et al. (2015). Throughout the text, we use the term 'grassland cover' to denote both natural and human-modified grasslands (pastures), and 'arable land cover' to denote arable and disturbed land, because it is not always possible to distinguish between natural and managed grasslands or between arable and other forms of disturbed open-land cover based on pollen analysis (Fyfe et al., 2015). For example, the large proportion of open land cover classes (pasture and disturbed taxa) during the early Holocene (pre-Neolithic) is likely to represent natural landscape openness. We distinguished the increase of arable/pasture cover from natural open-land cover from the Neolithic onwards based on the change in abundance, rather than on the absolute values (Fyfe et al., 2015). We assigned to each charcoal site the relative proportion of the six land cover classes from the nearest pollen site. We then generated composite estimates of land cover classes grouped by present-day ecoregions by spatially aggregating the averages of pollen records within the corresponding ecoregion.

2.4 Simulation of past climate conditions

Holocene climate conditions were derived from TraCE-21ka (Transient Climate Evolution over the last 21,000 years (Liu et al., 2009; He, 2011). This is a transient simulation of the last deglaciation phase (22 to 0 ka BP) using the fully coupled NCAR Community Climate System Model version 3 (CCSM3, Liu et al., 2009; He, 2011). Atmospheric and land model simulations were performed at the T31 (~3.75° x 3.75°) horizontal resolution and approximately 3° in the ocean and sea-ice models. The simulation output data (near-surface temperature and precipitation) was downloaded at monthly temporal resolution from earthsystemgrid.org. To remove systematic model biases, the climate simulation data was first bias-corrected using monthly climatologies between 1950 and 1980 from the Climate Research Unit (CRU TS 3.1) observational dataset (Harris et al., 2014). The bias correction was calculated with respect to the last 30 years of the TraCE-21ka simulation (representing pre-industrial conditions) as anomalies of the surface temperature and ratios of precipitation. The temperature anomalies were subsequently added, and precipitation ratios multiplied with the CRU data in order to obtain the bias-corrected climate.

We used the boreal summer (June, July, August, hereafter "JJA") surface temperature (JJA T) and precipitation minus potential evapotranspiration (JJA P-PET), as a proxy of peak summer dryness, which is a main driver of fire hazard. P-PET is a drought indicator that, opposed to P-AET (actual evapotranspiration), purely depends on atmospheric moisture demand independent of soil and vegetation, and reflects the atmospherically-driven intensity of drought conditions (Pidwirny, 2006). PET was calculated using the Thornthwaite model (Thornthwaite, 1948), which requires the surface temperature and average day length of each month as input variables. Surface temperature was taken directly from the bias-corrected TraCE-21ka data and the average day length for each month going back to 12 ka BP was calculated using the Earth's orbital parameter scheme in CCSM3. The resulting bias-corrected climate fields were subsequently interpolated to the same locations as the charcoal records using a bilinear interpolation. We generated composite climate estimates by spatially aggregating individual climate records at 100-year time intervals within the corresponding ecoregions.

2.5 Generalized Additive Models

We developed generalized additive models (GAMs) to explore the response of biomass burning to changes in percent land cover, dominant functional forest type, and JJA climate. GAMs have been show to provide robust statistical analyses of trends in palaeoenvironmental time series (Simpson, 2018). The predictor is the sum of smoothed functions of land cover and climate (Hastie and Tibshirani, 1990). We used the mgcv package to fit models with thin-plate spline predictors and a Gaussian-family error distribution to automatically determine the optimal level of smoothing for each term in the model and automatic term selection (Hastie and Tibshirani, 1990). We calculated Akaike Information Criterion (AIC) weights to identify the models that were best able to predict the observed changes in biomass burning (Wagenmakers and Farrell 2004). AIC weights are a normalized indicator of support for each model given the goodness of fit while penalising more complex models (Hastie and Tibshirani, 1990). We obtained AIC values using the AIC function in R and calculated AIC weights relative to the model with the lowest AIC score using the qpcR package (Wood, 2017). AIC values can only be compared across a common data set; we therefore fitted the GAMs and calculated AIC weights separately for each ecoregion (including land cover classes, JJA T and JJA P-PET). Visual inspection of plots produced by the gam.precheck R function showed that all selected models were well-fit (Supplement S2). We first explored the effect of JJA climate alone for the full period (12-0 ka BP) then constructed GAMs using JJA climate for the 12-8 ka BP and 8-0 ka BP separately to investigate the relationship between climate and fire without significant human impact (see section 2.3). We also restricted the GAMs including all predictors to the last 8 ka BP as the proportion of open land cover classes (arable and grassland cover) during this period should predominantly reflect the influence of human impact (see section 2.3).

3 Results

3.1 Biomass burning, land cover, and climate dynamics

The amount of biomass burning was highest during the early Holocene (between ~ 10.5 and 8 ka BP) over all of Central and Eastern Europe and within the three ecoregions, although the onset of this biomass burning increase was earlier (11 ka BP) in the CON ecoregion (Fig. 2A-D). The climate-model simulation indicates warmer-than-present summer temperatures (JJA T) and lower-than-present moisture availability (JJA P-PET) for the early Holocene across all three ecoregions (Fig. 2B-D). Biomass burning became lower-than-at present between ~ 8 and 4 ka BP in all ecoregions (Fig. 2B-D). The reduction in biomass burning accompanied a decrease in JJA temperature and an increase in summer moisture availability (around 8 ka BP) in all ecoregions (Fig. 2B-D). We found differences in trends in biomass burning among ecoregions over the past 3 ka BP. Biomass burning increased markedly at 3 ka BP in the BNE ecoregion, but this increase is less evident in the CON ecoregion, and occurs only around 1.5 ka BP in the ATL ecoregion (Fig. 2B-D). Climate simulations display generally cool, moist climate conditions in all ecoregions over the past 4 ka (Fig. 2A-D).

Pollen-based land cover reconstructions indicate that tree cover ranged between ~ 40-65% in CON, ~ 45-73% in ATL and ~ 55-80% in BNE ecoregions (Fig. 2B-D). Tree cover reached the maximum extent between ~ 9 and 5 ka BP in all ecoregions and was dominated by mixed broadleaf deciduous trees, while the abundance of needleleaf trees was highest between ~ 11 and 9 ka BP for all ecoregions and between 4 and 1 ka BP for the BNE ecoregion (Fig. 2B-D). Arable land cover ranged between ~ 5-17% in BNE, ~ 5-22% in ATL and ~ 10-25% in CON ecoregions, whereas grassland cover ranged between ~ 5-12% in BNE, ~ 10-22% in ATL and ~ 15-25% in CON ecoregions. Grassland cover reached the maximum extent over the past 1.5 ka in all ecoregions, whereas arable land cover reached the maximum extent over the past 4 ka in ATL and CON ecoregions and 1.5 ka in the BNE ecoregion (Figure 2B-D). Three-dimensional scatter plots of biomass burning and percentages of land cover classes show that locations with greater biomass burning tend to be consistently characterised by low broadleaf and high needleleaf tree cover in all three ecoregions (Fig. 3). Biomass burning also increases with arable and pasture cover, although percentages of the two land-cover classes at which biomass burning increases vary between ecoregions (Fig. 3).

3.2 Generalized Additive Models

When considering GAMs fitted with only climate predictor variables over the full time series (12-0 ka BP), the proportion of the deviance of biomass burning in the three ecoregions averages 48% (Table 1; Supplement S2). We therefore investigated into the drivers of biomass burning on the pre- and post-8 ka BP time periods separately. Climate alone explains a large proportion of the deviance of biomass burning for the 12-8 ka BP period (average 71.7%), when biomass burning increased with increasing temperature and P-PET in all ecoregions (Table 1; Appendix A1; Supplement S2). On the contrary climate alone explains a considerably smaller proportion of the deviance (average 48%) for the 8-0 ka BP period (Table 1; Supplement S2). Full model selections procedure (climate and land cover) for the 8-0 ka BP period illustrated that the inclusion of land cover fractions in the GAMs increased the deviance explained to 76.6% (Table 1; Supplement S2). Furthermore, AIC values and weights for the full model selection procedure for the 8-0 ka BP period showed that models including land cover perform better in comparison to the models including climate alone in all ecoregions (Table 2). Evaluation of AIC values and weights demonstrate that most of the explanatory power (including > 0.99 of the total cumulative AIC weight) comes from models that include broadleaf cover alone for the ATL and BNE ecoregions and the joint effects of total tree, broadleaf, heathland and arable cover for the CON ecoregion (Table 2, Supplement S2). When examining the fire-tree cover relationships we found that in the ATL and CON ecoregions, biomass burning was high at 45% tree cover declining strongly towards 60% tree cover (Fig. 4A). In the BNE ecoregion, biomass burning abruptly decreased as tree cover increased from its maximum of ~ 65% to 80% (Fig. 4A). When examining fire-human relationships, biomass burning increased when arable and grassland cover reached ~15-17% in the ATL and CON ecoregions, and at ~6-10% in the BNE ecoregion (Fig. 3 and Fig. 4DE). Biomass burning also increased for heathland cover greater than 12% in the ATL and CON ecoregions (Fig. 4F; Supplement S2).

4 Discussion

Understanding fire regime variability is typically based on recent estimates of vegetation and burned area obtained from remote sensing data as well as fire and vegetation models (Bistinas et al., 2014; Forkel et al., 2017). This may hinder our ability to recognise links and feedbacks between fire, vegetation and land-use shifts especially in ecosystems with species that have long generation times. Our study uses high-density millennial records of ecosystem history (vegetation, fire, climate, humans) and proposes a framework for testing the relationships between biomass burning, land cover, land use, and climate conditions in three distinct ecoregions from Central and Eastern Europe.

4. 1 The effect of tree cover and dominant functional forest type on fire

At the millennial scale considered here, we detected non-linear relations between biomass burning and percentages of tree cover (Fig. 4A). While we set up the GAMs with biomass burning as the response variable, we acknowledge that the relationship can be bi-directional: increased biomass burning can be a response to decreasing forest cover, but more frequent fires can also lead to a decrease in forest cover. Our findings are consistent with emerging evidence on fire-fuel-relationships that suggest a strong link between tree cover and fire hazard in modern environments (Hirota et al., 2011; Pausas and Paula 2012; Scheffer et al., 2012; Frejaville et al., 2016; van Nes et al., 2018). The shape of the fire-tree cover relationship could be explained by feedback mechanisms linking climate and fuel composition/ structure. Low biomass burning at high tree cover may have been driven by dense tree stands with reduced understorey, which created a cool and moist microclimate that lowers ignition potential and fuel flammability (Kloster et al., 2015). Radiative properties of the land surface at higher tree cover can decrease evaporation and/or enhance cloud formation, which in turn contributes to a moister local climate (Teuling et al., 2017). A reduction in tree cover allows the development of more understorey vegetation that provides a favourable fuel mix composed of fine herbs, shrubs and coarse woody debris that facilitates ignition, surface fire spread, as well as the transition from surface to crown fire (Pausas and Paula, 2012; Frejaville et al., 2016). Further, in open forests, radiation can penetrate deeper into the canopy, and the wind speed close to the ground is higher, which dries the understorey vegetation and litter, ultimately increasing flammability (Ryan, 2002).

The shape of the relationship between tree cover and biomass burning differs among the ecoregions associated with the dominant functional forest type (Fig. 3 and Fig. 4A). In ecoregions dominated by temperate forests (CON and ATL), biomass burning is high at 45% tree cover and declines towards ~ 60% (Fig. 4A). In the BNE ecoregion, where needleleaf trees dominate, the relationship is distinctly different: biomass burning decreases sharply as tree cover increases from 65% to its maximum of 80 (Fig. 4A). The pronounced shift in biomass burning in the BNE ecoregion resembles a system crossing a critical ecological threshold and transitioning to a new vegetation and/or fire regime state (Scheffer et al., 2012). The GAMs run separately on broadleaf and needleleaf forest type further demonstrate regional differences in the relationship between biomass burning and percentages of tree cover associated with the dominant functional forest type (Figs. 3, 4). Broadleaf cover had the most pronounced negative effect on biomass burning in the BNE and ATL ecoregions, and the second-most negative effect after total tree cover in the CON ecoregion (Fig. 4B; Table 1; Supplement S2). Contrastingly, biomass burning shows an increase rather than a decrease with increasing needleleaf cover, which is evident in the BNE ecoregion with a considerable proportion of needleleaf forests (Fig. 4C; Table 1). This finding is in line with the ecological inference that deciduous broadleaf trees have low ignition probability and rates of fire spread (Sturtevant et al., 2009). Fire occurrence in boreal forest systems is often augmented at higher tree cover (up to 75%) due to the high flammability of needleleaf biomass, in particular when it is exposed to dry, windy conditions (Scheffer et al., 2012; Rogers et al., 2015). Life history and morphological traits of the dominant species (relatively short life cycle, high relative growth rates, shallow roots, accumulation of dead biomass and slow litter decomposition) create a substantial amount of readily available dead fuel in boreal forests (Scheffer et al., 2012). Pollen records from Central and Eastern Europe additionally indicate shifts in the species composition within the needleleaf forest functional group (Giesecke et al., 2017) and consequently a change in fire-related vegetation traits. Abundant *Pinus diploxylon*-type pollen during the early Holocene indicates that *Pinus sylvestris* was the dominant needleleaf tree in all ecoregions at the time of high biomass burning. As a fire-resister, *Pinus sylvestris* could have withstood fire as a result of its fire-resistant morphological traits, i.e., thick insulating bark, deep roots, and a well-developed capacity for post-fire recovery (Groot et al., 2013; Rogers et al., 2015; Adámek et al., 2016; Feurdean et al., 2017; Carter et al., 2018; Bobek et al., 2019). *Picea abies* became the dominant needleleaf species in the CON ecoregion during the mid-Holocene and in the BNE ecoregion during the late Holocene (Giesecke et al., 2017), at times when biomass burning varied amount ecoregions, but was lower compared to the early Holocene maxima. As a fire-avoider, *Picea abies* does not have functional traits required for fire survival but boosts crown fires because its low branches create a ladder canopy structure and dead branches are retained in the crown.

4. 2 The impact of climate on fire via conditions conductive for fire and fuel quality

We found that climate, specifically warmer-than-present summer temperatures and increasing, but still lower-than-present, moisture content between 12-8 ka BP period exerted a positive control on biomass burning in all ecoregions (Table 1; Appendix A1; Supplement S2). Enhanced biomass burning with increasing temperature and moisture in the early Holocene in CEE is expected, as fuel builds up progressively following the cold and dry conditions with limited biomass that prevailed during the Lateglacial (Feurdean et al., 2014). These climatic conditions, coupled with the fact that biomass was primarily composed of needleleaf trees, likely created a positive feedback on biomass burning. The finding of low but increasing biomass burning with increasing fuel amount under climate conditions conductive for fire supports the notion that climate-induced fire hazard is lower in less productive systems (Pausas and Ribeiro, 2013).

In contrast, GAMs indicate that the importance of tree cover on biomass burning became stronger and the influence of climate less pronounced during the 8-0 ka BP period in all ecoregions (Tables 1, 2). For most of this period, biomass burning declined when temperature and moisture increased, suggesting low biomass burning under warmer and moister conditions. Such climate conditions also determined forest expansion, in particular broadleaf tree cover, with positive effects on fuel moisture and a dampening effect on biomass burning (see chapter 4. 1). Higher levels of burning over large areas in Europe during the early Holocene were generally associated with warmer summers and/or drier conditions, whereas a stronger effect of land cover for the mid- to late-Holocene was detected particularly at low-to-mid latitudes (Vannière et al., 2016; Dietze et al., 2018; Molinari et al., 2018).

Proxy data do not provide all climate variables (T, P-PET) and the monthly resolution available from climate models. Proxy-based climate datasets were used to check whether the model simulations depict general trends in past climate conditions. TraCE-21ka simulation and proxy-based climate reconstructions are generally in good agreement, with both indicating warm and dry climate conditions for the early Holocene and increased moisture availability during the mid-Holocene in all ecoregions, and cooler summer temperatures in the CON ecoregion (Davis and Brewer, 2009; Heiri et al., 2015; Veski et al., 2015; Tóth et al., 2015; Hájková et al., 2016; Diaconu et al., 2017; Marcisz et al., 2017). Although the climate simulation and most proxy-based climate reconstructions show cool and moist climate conditions throughout the late Holocene, proxy-based reconstructions indicate greater spatial and temporal climate variability (Davis and Brewer, 2009; Heiri et al., 2015; Tóth et al., 2015; Diaconu et al., 2017; Marcisz et al., 2017). On the one hand, this disagreement could be explained by the coarse resolution of the climate model. Further, the model does not account for changes in the length of individual months or seasons due to variations in Earth's orbit (e.g. Bartlein and Shafer, 2019). Therefore future work might rather analyse the monthly time series instead of seasonal averages. On the other hand, increasing human impact on the proxies used for climate reconstructions, such as the effect of water acidification and eutrophication on chironomid assemblages and deforestation on testate amoebae composition, could also be responsible for disagreement between proxy- and simulation-based inference of past climate conditions (Heiri et al., 2015).

4.3 The human impact in fire

The shape of fire-fuel relationship could have also been substantially altered by human activities (Pausas and Ribeiro, 2013). Humans likely altered the temporal and spatial structure of fuel availability and timing and frequency of ignitions since the early Holocene (Pfeiffer et al., 2013; Marlon et al., 2016; Vannière et al., 2016; Andela et al., 2017; Dietze et al., 2018), potentially even earlier (Kaplan et al., 2016). While ignitions tend to increase until population reaches intermediate density, human-caused change in land cover from forest to arable land and associated fuel limitation and landscape fragmentation may result in a decline in biomass burning (Pfeiffer et al., 2013; Andela et al., 2017). A contrasting position suggests that increasing population density exclusively reduces fire frequency and burned area through the impact of land conversion and landscape fragmentation on fuel availability and continuity (Knorr et al., 2014). Our results reveal that biomass burning mostly shows a positive response to increases in arable and grassland cover in all ecoregions. However, this relationship is variable and may illustrate a complex fire-human interaction (Figs. 3, 4). In the CON ecoregion, the most evident increase in biomass burning occurred after 3 ka BP (Fig. 2B), and is consistent with percentages in arable and grassland cover at which biomass burning shows positive responses in the GAMs (Figure 4DE). Historically, the onset of this rise in biomass burning corresponds to the Late Bronze Age to the Iron Age, periods characterized by the establishment of urban centres, farms, early industries and mining activities (Rösch, et al., 2014; Chapman, 2017). The sharp increase in biomass burning over the last millennium coincides with a marked population growth and renewed deforestation (Jamrichova et al., 2017; Marquer et al., 2017). It is therefore apparent that land-use intensification in the CON involved deforestation-related burning that accompanied creation of arable land, starting with the Bronze or Iron Age and reaching a maximum during the Early Modern period. In the ATL ecoregion, arable and grassland cover rose steadily from ~4 to 1.5 ka BP, but biomass burning remained constant during the same time (Fig. 2), which is consistent with percentages in arable and grassland cover at which biomass burning shows no responses in the GAMs (Fig. 4CD). This may suggest that the local intensification in land use between 4 and 1.5 ka BP did not involve major use of fire for deforestation (Fig. 2). If fire was primarily restricted to burning of agricultural waste, e.g., straw and chaff, to improve soil fertility and clean the land, this should have provided less biomass to burn than wood (Pfeiffer et al., 2013). However, the further increase in arable and grassland cover in the ATL ecoregion from ~1 ka BP onwards coincident with a rise in biomass burning may be explained by renewed deforestation activity at marginal sites during medieval times (Marquer et al., 2017). In the BNE ecoregion, we detected increases in biomass burning over the past 4 ka BP, while the rise in abundance of arable and grassland cover to values at which biomass burning shows the strongest positive responses only occurred over the past 2 ka BP (Fig. 2D). It therefore appears that the rise in biomass burning at 4 ka BP could be primarily related to the naturally or human-driven increase of the needleleaf component, and only after 2 ka BP to a perpetual use of fire for deforestation and agricultural activities (Fig. 2D). The relatively late occurrence of land conversion in the BNE ecoregion is probably due to the fact that broadleaf forests were edaphically more suited for conversion to arable fields and pastures than needleleaf forests (Roberts et al., 2018). It should be noted that inferences of fire regime from sedimentary charcoal have their limitations, in particular with respect to the cause of fires. Therefore, if humans significantly increased fire frequency since the prehistory (Vannière et al 2016) or earlier (Kaplan et al. 2016), the impact of post-deforestation mosaic landscape heritage and the land use on fuel amounts may have reduced the probability of large fires and consequently the amount of charcoal preserved in the depositional environments. Nevertheless, our fuel-fire relationship using pooled charcoal and pollen records reflects a regional pattern, and individual sites may more effectively depict small-scale alteration in land cover and burning pattern (Gavin et al., 2002).

4.4 Potential implications for fire-vegetation modelling

Global fire-vegetation models are useful tools for projecting future changes in fire regimes and assessing fire-vegetation interactions. Improving such models is an area of active development (Rabin et al., 2017) and typically utilises recent estimates of burned area and few land cover types obtained from remote sensing data and other vegetation-related products to evaluate the models (Bistinas et al., 2014; Forkel et al., 2017). However, this reliance on short-term data does not offer the full picture of fire-vegetation interactions, particularly as fire regimes and present-day ecosystems carry legacies of past anthropogenic activities (Vannière et al., 2016). The analysis presented here provides complementary evidence to evaluate fire-vegetation model development in several ways. Firstly, the fire-land cover relationships emerging from fire-vegetation models can be evaluated against the charcoal and pollen derived fire-land cover relationships attained here. Secondly, synthesized charcoal records provide data for fire model evaluation in regions where fire return intervals are significantly longer than the short time for which satellite data are available. Finally, the coherent time series presented here provide an independent test case, i.e., under different climates and with different, limited or no human influence, for fire models outside of the time period in which they were calibrated. Once we incorporate these aspects into fire-vegetation models, we can more accurately model changes through time, i.e., the past range of fire regimes (Pfeiffer et al., 2013; Forkel et al., 2017) and examine critical ecological transitions hypothesised to be mediated by fire-vegetation interactions (Scheiter et al., 2012).

5 Conclusions

Our results provide compelling evidence that land cover, especially percent of tree cover, was strongly related to biomass burning for most of the Holocene. Regional differences, however, were observed among major vegetation types. Specifically, in ecoregions dominated by temperate forests (the CON and ATL), biomass burning was high at 45% tree cover and declined towards ~ 60%. In the BNE ecoregion where needleleaf trees dominate, biomass burning was highest at ~ 60-65% tree cover and abruptly declines at tree cover >65%. The non-linear biomass-burning shift in the BNE ecoregion resembles a system crossing a critical ecological threshold and transitioning to a new state. Biomass burning showed a positive response when arable and grassland cover reached ~ 15-20%, but this relationship is regionally distinct and highlights the complex fire-human interactions that depend on land-use intensity in the different ecoregions. A higher tree cover reduces radiative energy influx to the forest floor and provides moister, more wind-protected microclimates, which decreases fuel flammability. The lower tree cover at which biomass burning is higher appear to be driven by warmer and drier summer conditions during the early Holocene, and increasing human influence on land cover during the late Holocene. Our records of past fire-fuel interactions indicate that tree cover is a first-order predictor of the probability of fire occurrence whatever the driver of fire dynamic. Our observations cover the full range of Holocene climate variability and therefore provide a long-term test of vegetation-climate-fire interactions. An important implication of this test is that effective mitigation of future fire hazard relies on regional scale land cover management. Information derived from such long-term fire-vegetation relationships can be used to improve fire-mitigation strategies and fire-vegetation models. Future work should also include an examination of post-fire vegetation responses to shifts in fire frequency and intensity i.e., a higher forest cover may lead to less frequent fires, but more frequent fires can also lead to a decrease in forest cover, and possible ways of fire hazard mitigation.

545 **Figure legends and embedded figures**

Figure 1. Map showing the distribution of main environmental zones in Central and Eastern Europe (Metzger et al., 2015). Filled triangles and circles show the location of charcoal and pollen records (Appendix S1). Orange rectangles denote the ecoregions analysed in this study: Atlantic (ATL), Continental (CON) and Boreo-Nemoral (BNE).

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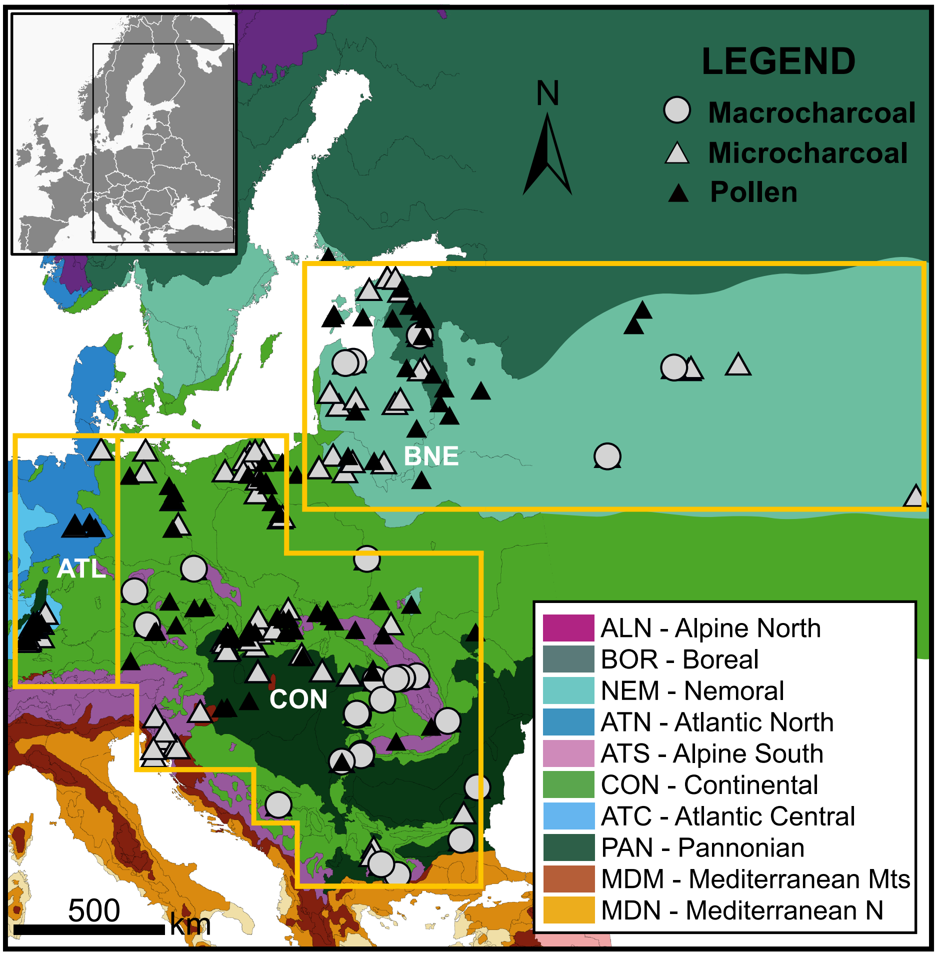


Figure 2. Holocene trends in biomass burning, climate, and land cover changes over all of Central and Eastern Europe (panel A) and in each of the ecoregions: Continental (B), Atlantic (C) and Boreo-Nemoral (D). Biomass burning is inferred based on charcoal influx (z-score values). Climate conditions (anomalies) represent average simulated seasonal summer (June, July, August (JJA)) temperatures and precipitation minus potential evapotranspiration (P-PET), from a global transient climate simulation. Relative abundance of needleleaf forests, broadleaf deciduous forests, grasslands, and arable land represents their pollen-based percentages in relation to the total land cover (Fyfe et al., 2015). We fitted a 500-year loess smoother for JJA P-PET, temperature and land cover classes for each ecoregion.

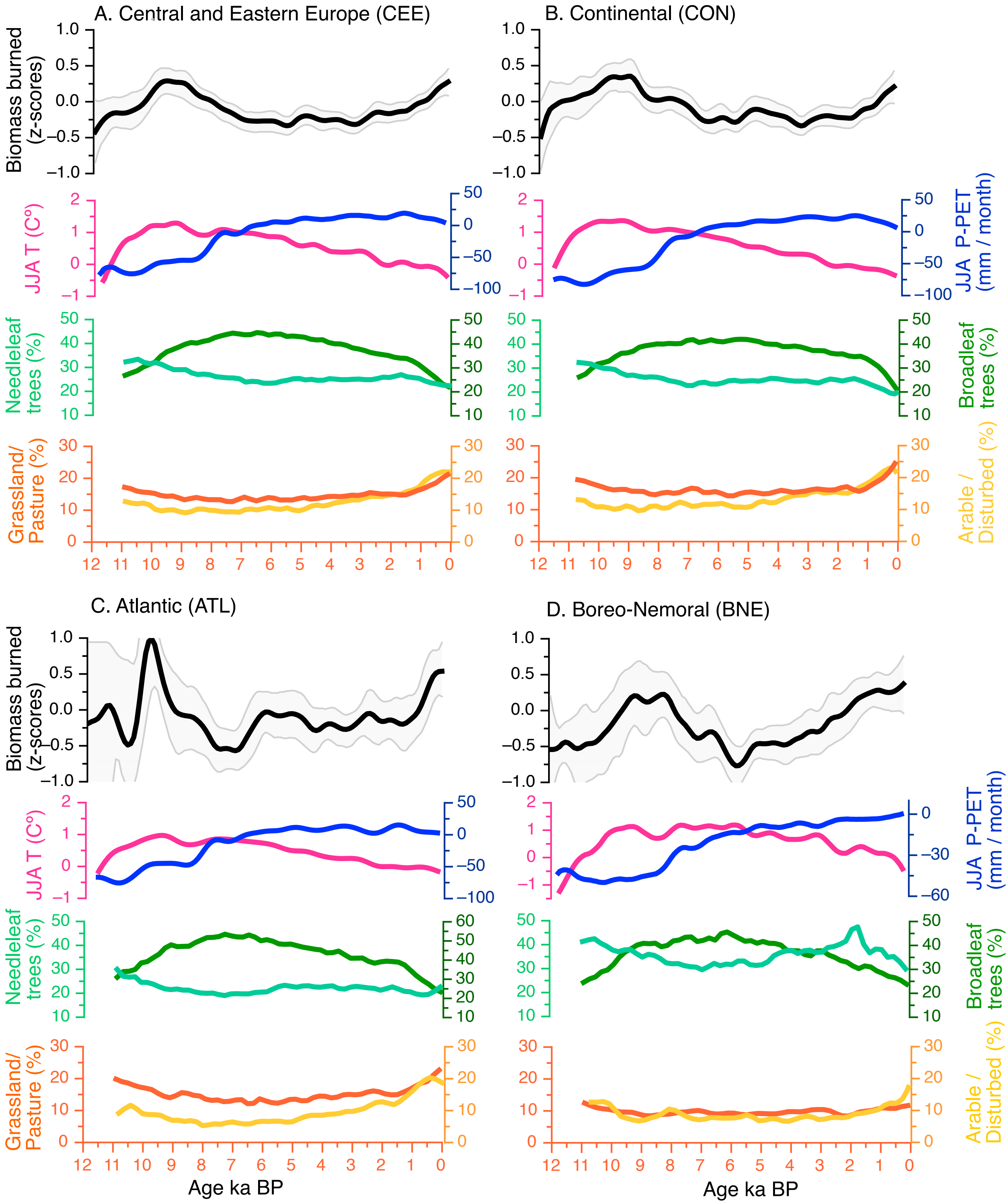

A. Central and Eastern Europe (CEE)
B. Continental (CON)
C. Atlantic (ATL)
D. Boreo-Nemoral (BNE)
Biomass burned (z-scores)
JJA T (C°)
JJA P-PET (mm / month)
Needleleaf trees (%)
Broadleaf trees (%)
Grassland/ Pasture (%)
Arable / Disturbed (%)
Age ka BP

Figure 3. Relationship between biomass burning, broadleaf tree cover, needleleaf tree cover, arable cover and grassland cover over the past 8 ka BP in the three ecoregions in Central and Eastern Europe. Biomass burning and land cover are determined as above. Locations with greater biomass burning tend to be consistently characterised by low broadleaf tree cover in the CON and ATL ecoregions, and by high needleleaf forest cover in the BNE ecoregion. In terms of land use, biomass burning increases with arable and pasture cover but the patterns and thresholds vary between ecoregions, reflecting complex fire-human interactions. The colour circles represent individual sampling points (n=80).

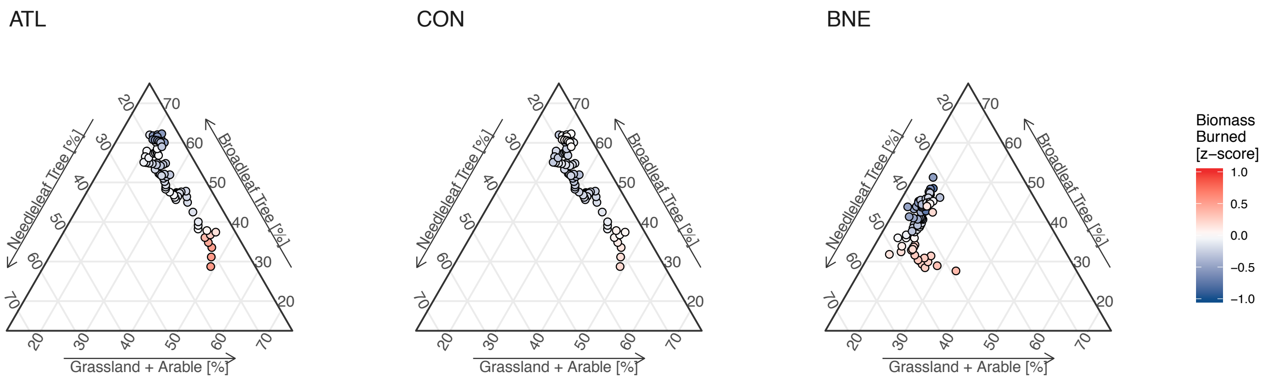
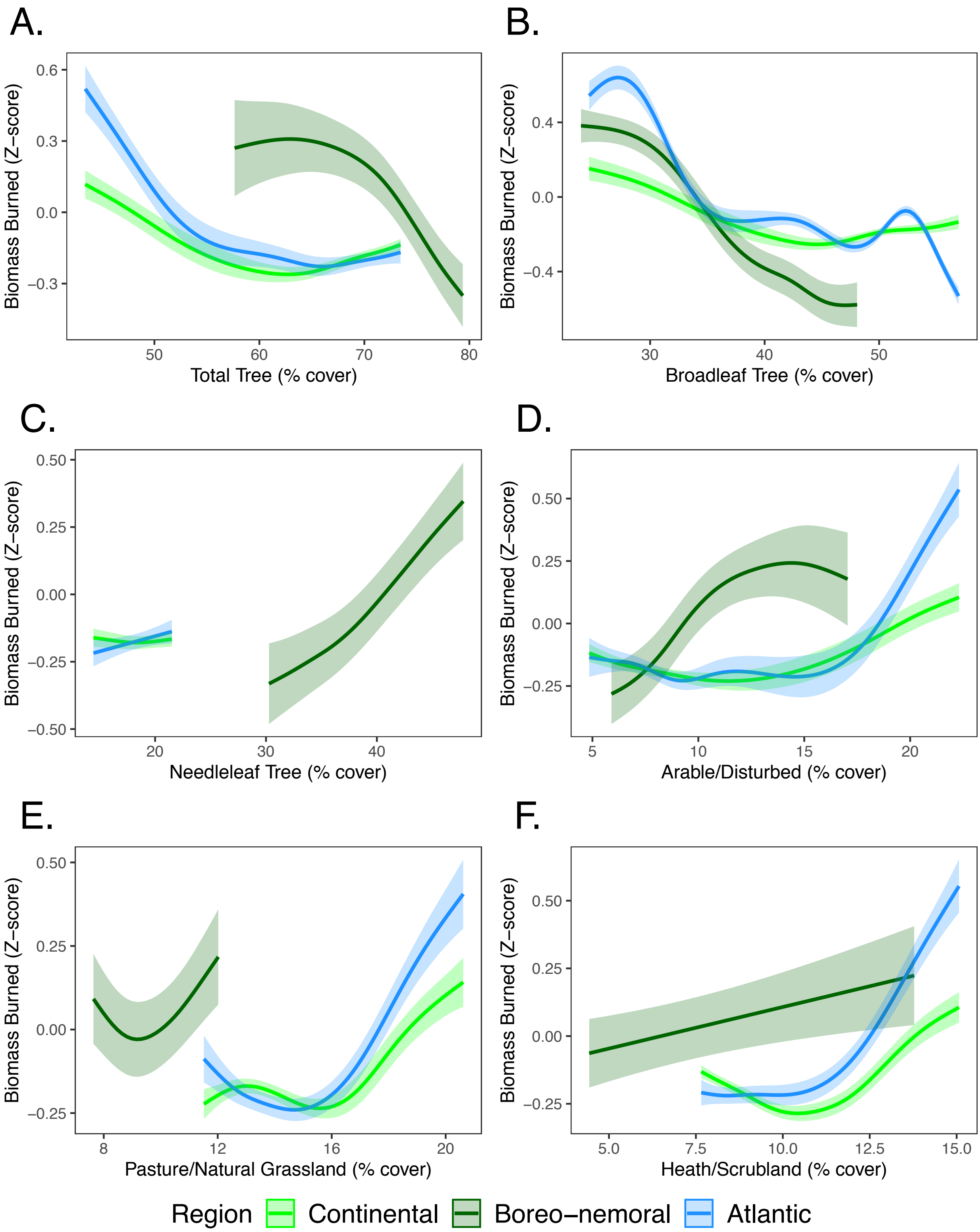


Figure 4. Fire-fuel type and load relationship in Central and Eastern Europe. The relationship between biomass burning, determined from z-score composite charcoal values and the main land-cover types, derived from percentages of pollen-based land cover classes. These relationships were developed from generalized additive models (GAMs) for each ecoregion. Total tree cover (A), broadleaf tree cover (B), needleleaf tree cover (C) arable/disturbed cover (D) pastures/natural grasslands cover (E) and heath/scrubland cover (F).


A.
B.
C.
D.
E.
F.
Biomass Burned (Z−score)
Total Tree (% cover)
Broadleaf Tree (% cover)
Needleleaf Tree (% cover)
Arable/Disturbed (% cover)
Pasture/Natural Grassland (% cover)
Heath/Scrubland (% cover)
Region
Continental
Boreo−nemoral
Atlantic

Tables

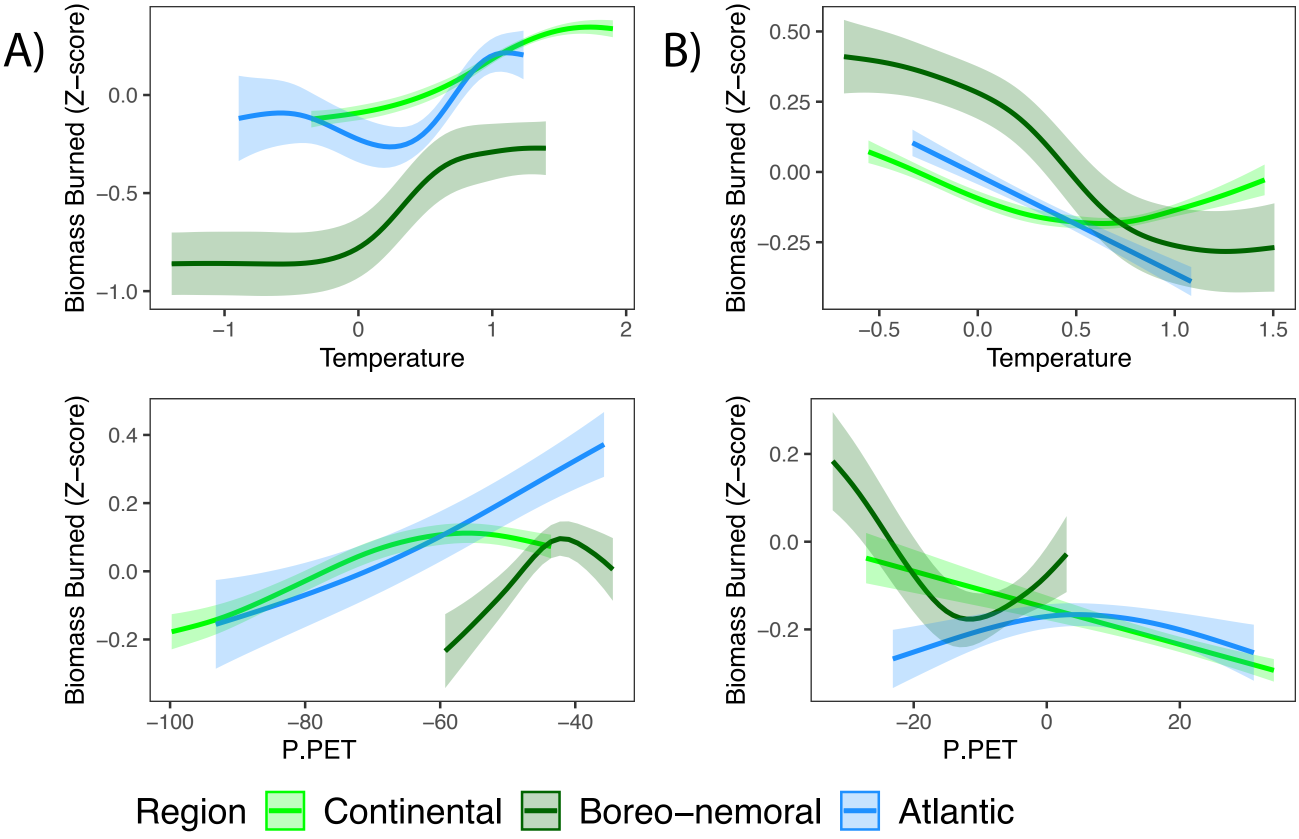
Table 1. Goodness of fit (deviance) and R squared adjusted for each ecoregion including climate conditions only for the following periods: 12-0 ka BP (n=119), the 12-8 ka BP (n=39), 8-0 ka BP (n=80).

Models	Deviance explained (%)	R sq (adj)
Continental (CON)		
Climate 12-0 ka	73.1	0.708
Climate 12-8 ka	87.4	0.854
Climate 8-0 ka	49.2	0.467
Climate and land cover 8-0 ka	79.6	0.765
Atlantic (ATL)		
Climate 12-0 ka	35	0.305
Climate 12-8 ka	52.7	0.470
Climate 8-0 ka	37.8	0.359
Climate and land cover 8-0 ka	76.7	0.707
Boreo-Nemoral (BNE)		
Climate 12-0 ka	37	0,334
Climate 12-8 ka	75	0.709
Climate 8-0 ka	60	0.571
Climate and land cover 8-0 ka	73.8	0.708
Mean of ecregions		
Climate 12-0 ka	48	
Climate 12-8 ka	71.7	
Climate 8-0 ka	48	
Climate and land cover 8-0 ka	76.6	

Table 2. Model selection results for generalized additive models of the effects of land cover and climate on biomass burning for the period 8-0 ka BP. Model selection metrics were obtained using the summary functions in the mgcv and qpcR packages in R. Lower values of Akaike Information Criterion (AIC) and higher values of AIC weights identify the models that were best able to predict the observed changes in biomass burning. Delta AIC values measure the relative performance of each model compared to the best model for that region; a delta AIC of > 2 between two models is typically considered to indicate a significant difference in explanatory power.

Models	AIC	delta AIC	Weights	Cumulative weight
Continental (CON)				
Total tree cover	-206.6704	0.0001	0.9197	0.9197
Broadleaf forest	-200.8468	5.8236	0.5001	0.9698
Heath/scrubland	-199.6713	6.9990	0.0277	0.9975
Arable/disturbed	-194.7156	11.9547	0.0023	0.9999
Pasture/natural grassland	-187.7218	18.9485	0.0000	1
Needleleaf forest	-145.1892	61.4812	0.0000	1
Climate	-144.9648	61.7055	0.0000	1
Intercept	-98.2406	108.4297	0.000	1
Atlantic (ATL)				
Broadleaf forest	-154.0558	0	1	1
Arable/disturbed	-94.8110	59.2448	0.0000	1
Total tree cover	-86.2392	67.8166	0	1
Heath/scrubland	-77.5731	76.4827	0	1
Pasture/natural grassland -	-64.3536	89.7022	0	1
Needleleaf forest	-33.5075	120.5483	0	1
Climate	-33.1322	120.9236	0	1
Intercept	0.1920	154.2479	0	1
Boreo-Nemoral (BNE)				
Broadleaf forest	-89.1985	0	1	1
Arable/disturbed	-45.2853	43.9131	2.91E-10	1
Needleleaf forest	-40.6312	48.5673	2.84E-11	1
Total tree cover	-36.7701	52.4284	4.12E-12	1
Pasture/natural grassland	-20.7741	68.4244	1.39E-15	1
Heath/scrubland	-19.4368	69.7616	0	1
Climate	-17.5311	71.6674	2.74E-16	1
Intercept	45.0892	134.2877	6.91E-30	1

Appendix A. Fire-climate relationship in the three ecoregions from Central and Eastern Europe for the 12-8 ka BP (A) and 8-0 ka BP (B), respectively. The relationship between biomass burning, determined from z-score composite charcoal values and simulated seasonal summer (June, July, August (JJA) temperatures and precipitation minus potential evapotranspiration (P-PET) was developed from generalized additive models (GAMs).



Supplement S1: Table S1. Metadata

Supplement S2. R code, plots, and descriptive information demonstrating the development of generalized additive models (GAMs) to explore the relationship between fire, land cover classes and climate for each region.

Data sets

Accessibility Statement

All essential input and output data will be made open-access and available online at paleofire.org.

Software and model code: R code, plots, and descriptive information demonstrating the development of generalized additive models (GAMs) are presented in Supplement S2 and at paleofire.org

Author contribution: AF, BV, and WF designed the study with contribution from TH, MF and DW. AF compiled site-based data with the help of GF. AF performed the analyses. DW, MF, AP, JL and CW developed the model codes and/or performed the modeling. All others provided data or carried out a minor component of data compilation or analysis. AF prepared the manuscript with significant contributions of BV, WF, SC, MP and input from all authors.

Competing interests: The authors declare that they have no conflict of interest.

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References

Adámek, M., Hadincová V., and Wild J.: Long-term effect of wildfires on temperate Pinus sylvestris forests: Vegetation dynamics and ecosystem resilience. Forest Ecology and Management, 380, 285-295, https://doi.org/10.1016/j.foreco.2016.08.051, 2016.

Adolf, C., Wunderle, S., Colombaroli, D., Weber, H., Gobet, E., Heiri, O., van Leeuwen, J. F. N C., Bigler, C., Connor, S.E., Galka, M., La Mantia, T., Makhortykh, S., Svitavska-Svobodova, H., Vanniere, B., Tinner, W.: The sedimentary and remote-sensing reflection of biomass burning in Europe. Global Ecology and Biogeography 27, 2, 199-212. DOI: 10.1111/geb.12682, 2018.

Andela, N., Morton, D. C., Giglio, L., Chen, Y., van der Werf, G. R., Kasibhatla, P. S., DeFries, R. S., Collatz, G. J., Hantson, S., Kloster, S., Bachelet, D., Forrest, M., Lasslop, G., Li, F., Mangeon, S., Melton, J. R., Yue, C., and Randerson, J. T.: A human-driven decline in 10 global burned area, Science, 356, 1356–1362, https://doi.org/10.1126/science.aal4108, http://science.sciencemag.org/content/356/6345/ 1356, 2017.

Archibald, S., Lehmann, C. E.R., Belcher, C. M, Bond, W. J., Bradstock, R. A., Daniau, A. L., Dexter, K. G., Forrestel, E. J., Greve, M., He, T., Higgins, S. I., Hoffmann, W. A., Lamont, B. B., McGlinn, D. J., Moncrieff, G. R., Osborne, C. P., Pausas, J. G., Price, O., Ripley, B. S., Rogers, B. M., Schwilk, D. W., Simon, M. F., Turetsky, M. R., Van Der Werf, G. R., and Zanne, A.: Biological and geophysical feedbacks with fire in the Earth system. Environmental Research Letters, 13, 033003, https://doi.org/10.1088/1748-9326/aa9ead, 2018.

Beckage, B., Platt, W.J., Gross, L.J.: Vegetation, fire, and feedbacks: A disturbance mediated model of savannas. American Naturalist, 174, 805–818. https://doi.org/10.1086/648458, 2019.

Bistinas, I., Harrison, S. P., Prentice, I. C., and Pereira, J. M. C.: Causal relationships versus emergent patterns in the global controls of fire frequency, Biogeosciences, 11, 5087–5101, https://doi.org/10.5194/bg-11-5087-2014.

Blarquez, O., Vannière, B., Marlon, J.R., Daniau, A.-L., Power, M.J., Brewer, S., and Bartlein, P.J.: Paleofire An R package to analyse sedimentary charcoal records from the Global Charcoal Database to reconstruct past biomass burning. Computers & Geosciences, 72, 255-261. https://doi.org/10.1016/j.cageo.2014.07.020, 2014. Blarquez, O., Ali, A.A., Girardin, M.P., Grondin, P., Fréchette, B., Bergeron, Y., and Hély, C.: Regional paleofire regimes affected by non-uniform climate, vegetation and human drivers. Scientific Reports, 5, 13356, https://doi.org/10.1038/srep13356, 2015.

Blarquez, O., Ali, A.A., Girardin, M.P., Grondin, P., Fréchette, B., Bergeron, Y., and Hély, C.: Regional paleofire regimes affected by non-uniform climate, vegetation and human drivers. Scientific Reports, 5, 13356, https://doi.org/10.1038/srep13356, 2015.

Bobek, P., Svitavská, H., Pokorný, P., Šamonil, P., Kuneš, P., Kozáková, R., Abraham ,V., Klinerová, T., Švarcová, M. G., Jamrichov,á E., Krauseová, E. and Wild J.: 2019: Divergent fire history trajectories in Central European temperate forests revealed a pronounced influence of broadleaved trees on fire dynamics. Quaternary Science Reviews 222, https://doi.org/10.1016/j.quascirev.2019.105865, 2019.

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D'Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., Swetnam, T. W., van der Werf, G. R., and Pyne, S. J.: Fire in the Earth System, Science, 324, 481–484, https://doi.org/10.1126/science.1163886, 2009.

Bond, W.J., and Keeley J.E.: 2005. Fire as a global herbivore: the ecology and evolution of flammable ecosystems Trends in Ecology and Evolution, 20, 387–94, https://doi.org/10.1016/j.tree.2005.04.025, 2005.

Conedera, M., Tinner, W., Neff, C., Meurer, M., Dickens, A.F., and Krebs, P.: Reconstructing past fire regimes: methods, applications, and relevance to fire management and conservation. Quaternary Science Reviews, 28, 555-576. https://doi.org/10.1016/j.quascirev.2008.11.005, 2009.

Chapman, J.: Climatic and human impact on the environment? A question of scale, Quaternary International https://doi.org/10.1016/j.quaint.2017.08.010, 2017.

Christian, H.J., Blakeslee, R.J., Boccippio, D.J., Boeck, W.L., Buechler, D.E., Driscoll, K.T., Goodman, S.J., Hall, J.M., Koshak, W.J., Mach, D.M., and Stewart M.F.: Global frequency and distribution of lightning as observed from space by the Optical Transient Detector. Journal of Geophysical Research Atmospheres, 108, ACL 4-1-ACL 4-15, https://doi.org/10.1029/2002JD002347, 2003.

Carter, V. A., Moravcová, A., Chiverrell, R. C., Clear, J. L., Finsinger, W., Dreslerová, D., Halsall., K., and Kuneš, P.: Holocene-scale fire dynamics of central European temperate spruce-beech forests. Quaternary Science Reviews, 191, 15-30, https://doi.org/10.1016/j.quascirev.2018.05.001, 2018.

Daniau, AL, Bartlein, P.J., Harrison, S.P., Prentice, I.C., Brewer, S., Friedlingstein, P., Harrison-Prentice, T.I., Inoue, J., Izumi, K., Marlon, J.R., Mooney, S., Power, M.J., Stevenson, J., Tinner, W., Andrič, M., Atanassova, J., Behling, H., Black, M., Blarquez, O., Brown, K.J., Carcaillet, C., Colhoun, E.A., Colombaroli, D., Davis, B.A.S., D'Costa, D., Dodson, J., Dupont, L., Eshetu, Z., Gavin, D.G., Genries, A., Haberle, S., Hallett, D.J., Hope, G., Horn, S.P., Kassa, T.G., Katamura, F., Kennedy, L.M., Kershaw, P., Krivonogov, S., Long, C., Magri, D., Marinova, E., McKenzie, G.M., Moreno, P.I., Moss, P., Neumann, F.H., Norström, E., Paitre, C., Rius, D., Roberts, N., Robinson, G.S., Sasaki, N., Scott, L., Takahara, H., Terwilliger, V., Thevenon, F., Turner, R., Valsecchi, V.G., Vannière, B., Walsh, M., Williams, N., and Zhang Y.: Predictability of biomass burning in response to climate changes. Global Biogeochemistry Cycles, 26, GB4007 https://doi.org/10.1029/2011GB004249, 2012.

Davis, B.A.S., and Brewer, S.: Orbital forcing and role of the latitudinal insolation/ temperature gradient. Climate Dynamics, 32, 143-165, https://doi.org/10.1007/s00382-008-0480-9, 2009.

Diaconu, A.C., Tóth, M., Lamentowicz, M., Heiri, O., Kuske, E., Tanţău, I., Panait, A., Braun, M., and Feurdean, A.: How warm? How wet? Hydroclimate reconstruction of the past 7500 years in northern Carpathians, Romania. Palaeogeography, Palaeoclimatology, Palaeoecology, 482, 1–12, https://doi.org/10.1016/j.palaeo.2017.05.007, 2017.

Dietze, E., Theuerkauf, M., Bloom, K., Brauer, A., Dörfler, W., Feeser, I., Feurdean, A., Gedminienė, L., Giesecke, T., Jahns, S., Karpińska-Kołaczek, M., Kołaczek, P., Lamentowicz, M., Latałowa, M., Marcisz, K., Obremska, M., Pędziszewska, A., Poska, A., Rehfeld, K., Stančikaitė, M., Stivrins, N., Święta-Musznicka, J., Szal, M., Vassiljev, J., Veski, S., Wacnik, A., Weisbrodt, D., Wiethold, J., Vannière, B., and Słowiński, M.: Holocene fire activity during low-natural flammability periods reveals scale-dependent cultural human-fire relationships in Europe, Quaternary Science Reviews, 201, 44-56, https://doi.org/10.1016/j.quascirev.2018.10.005, 2018.

Fréjaville, T., Curt, T., and Carcaillet, C.: Tree cover and seasonal precipitation drive understorey flammability in alpine mountain forests. Journal of Biogeography, 43, 1869-1880. https://doi.org/10.1111/jbi.12745, 2016.

Frejaville, T., and Curt, T.: Seasonal changes in the human alteration of fire regimes beyond the climate forcing. Environmental Research Letters. 2017 1;12(3):035006. https://doi.org/10.1088/1748-9326/aa5d23, 2017

Feurdean, A., Perşoiu, A., Tanţău, I., Stevens, T., Magyari, E.K., Onac, B.P., Marković, S., Andrič, M., Connor, S., Fărcaş, S., Gałka, M., Gaudeny, T., Hoek, W., Kolaczek, P., Kuneš, P., Lamentowicz, M., Marinova, E., Michczyńska, D.J., Perşoiu, I., Płociennik, M., Słowiński, M., Stancikaite, M., Sumegi, P., Svensson, A., Tămaş, T., Timar, A., Tonkov, S., Toth, M., Veski, S., Willis, K.J., and Zernitskaya V.: 2014. Climate variabilityand associated vegetation response throughout Central and Eastern Climate variability and associated vegetation response throughout Central and Eastern Europe (CEE) between 60 and 8 ka. Quaternary Science Reviews, 106, 206-224. http://dx.doi.org/10.1016/j.quascirev.2014.06.003, 2014.

Feurdean, A., Veski, S., Florescu, G., Vannière, B., Pfeiffer, M., O'Hara, R.B., Stivrins, N., Amon, L., Heinsalu, A., Vassiljev, J. and Hickler, T.: Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). Quaternary Science Reviews, 169, 378-390, https://doi.org/10.1016/j.quascirev.2017.05.024, 2017.

Forkel, M., Dorigo, W., Lasslop, G., Teubner, I., Chuvieco, E., and Thonicke, K.: A data-driven approach to identify controls on global fire activity from satellite and climate observations (SOFIA V1), Geoscientific Model Development, 10, 4443–4476, https://doi.org/10.5194/gmd-10-4443-2017, 2017.

Fyfe, R.M., Woodbridge, J., and Roberts N., 2015. From forest to farmland: pollen inferred land cover change across Europe using the pseudobiomization approach. Global Change Biology, 21, 1197–1212, https://doi.org/10.1111/gcb.12776, 2015.

Giesecke, T., Brewer, S., Finsinger, W., Leydet, M., and Bradshaw, R. H.: Patterns and dynamics of European vegetation change over the last 15,000 years. Journal of Biogeography, 44, 1441-1456, https://doi.org/10.1111/jbi.12974, 2017.

Girardin, M.P., Ali, A.A., Carcaillet, C., Blarquez, O., Hély C., Terrier, A., Genries, A. and Bergeron, Y.: Vegetation limits the impact of a warm climate on boreal wildfires. New Phytologist, 199, 1001-1011, https://doi.org/10.1111/nph.12322, 2013.

Grooth, W.J., Cantin, A.S., Flannigan, M.D., Soja, A.J., Gowman, L.M., and Newbery, A.: A comparison of Canadian and Russian boreal forest fie regimes. Forest Ecology Management, 294, 23-34, https://doi.org/10.1016/j.foreco.2012.07.033, 2013.

Hájková, P., Pařil, P., Petr, L., Chattová, B., Grygar, T.M., and Heiri, O.: A first chironomid-based summer temperature reconstruction (13–5 ka BP) around 49° N in inland Europe compared with local lake development. Quaternary Science Reviews, 141, 94-111, https://doi.org/10.1016/j.quascirev.2016.04.001, 2016.

Harris, I., Jones, P.D., Osborn, T.J., and Lister, D.H.: Updated high-resolution grids of monthly climatic observations – the CRU TS3.10 Dataset. International Journal of Climatology, 34, 623–642, https://doi.org/10.1002/joc.3711, 2014.

Hastie, T.J., Tibshirani R.J.: Generalized additive models, volume 43 of Monographs on Statistics and Applied Probability, Chapman & Hall/CRC, 1990.

He, F.: Simulating transient climate evolution of the last deglaciation with CCSM3. Ph.D.thesis, University of Wisconsin-Madison. http://www.cgd.ucar.edu/ccr/paleo/Notes/TRACE/he_phd_092010-1.pdf, 2011.

He, T., and Lamont, B. B.: Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora. National Science Review, 5, 237-254, https://doi-org.eres.qnl.qa/10.1093/nsr/nwy024, 2018.

Heiri, O., Ilyashuk, B., Millet, L., Samartin, S., and Lotter, A.F.: Stacking of discontinuous regional paleoclimate records: chironomid-based summer temperaturesfrom the Alpine region. The Holocene 25, 137–149, https://doi.org/10.1177/0959683614556382, 2015.

Hirota, M., Holmgre,n E., and Van Nes, Scheffer M.: Global resilience of tropical forest and savanna to critical transitions. *Science*, 334, 232-235, https://doi.org/10.1126/science.1210657, 2011.

Jamrichová, E., Petr, L., Jiménez Alfaro, B., Jankovská, V., Dudová, L., Pokorný P., ... and Syrovátka, V.: Pollen-inferred millennial changes in landscape patterns at a majorbiogeographical interface within Europe. Journal of Biogeography, 44, 2386–2397, https://doi.org/10.1111/jbi.13038, 2017.

Jepsen, M.R., Kuemmerle, T., Müller, D., Erb, K., Verburg, P. H., Haberl, H., Vesterager, J.P., Andrič, M., Antrop, M., Austrheim, G., Björn, I., Bondeau, A., Bürgi, M., Bryson, J., Caspar, G., Cassar, L.F., Conrad, E., Chromý, P., Daugirdas, V., Van Eetvelde, V., Elena-Rosselló, R., Gimmi, U., Izakovicova, Z., Jančák, V., Jansson, U., Kladnik, D., Kozak, J., Konkoly-Gyuró, E., Krausmann, F., Mander, Ü., McDonagh, J., Pärn, J., Niedertscheider, M., Nikodemus, O., Ostapowicz, K., Pérez-Sobaa, M., Pinto-Correia, T., Ribokas, G., Rounsevell, M., Schistou, D., Schmit, C., Terkenli, T.S., Tretvik, A.M., Trzepacz, P., Vadineanu A., Walz, A., Zhllima, E., and Reenberg, A.: Transitions in European land-management regimes between 1800 and 2010. Land Use Policy, 49, 53-64, https://doi.org/10.1016/j.landusepol.2015.07.003, 2015.

Kaplan, J.O., Pfeiffer, M., Kolen, J.C.A., and Davis, B.A.S.: Large Scale Anthropogenic Reduction of Forest Cover in Last Glacial Maximum Europe. PLOS ONE 11, e0166726, https://doi.org/10.1371/journal.pone.0166726, 2016.

Khabarov, N., Krasovskii, A., and Obersteiner, M.:2016 Forest fires and adaptation options in Europe. Regional Environmental Change, 16, 21-30, 1436-378 https://doi.org/10.1007/s10113-014-0621-0, 2016.

Kloster, S., Brücher, T., Brovkin, V., and Wilkenskjeld, S.: Controls on fire activity over the Holocene. Climate of the Past, 11, 781–788, https://doi.org/10.5194/cp-11-781-2015, 2015.

Knorr, W., Kaminski, T., Arneth, A., and Weber, U.: Impact of human population density on fire frequency at the global scale, Biogeosciences, 11, 1085–1102, https://doi.org/10.5194/bg-11-1085-2014, 2014.

Leverkus, A, B., Murillo, P.G., Dona, V.J., and Pausas, J.G.: Wildfire: opportunity for restoration? Science 363: https://doi.org/10.1126/science.aaw2134, 2019.

Liu Z., Otto-Bliesner B.L., He F., Brady E.C., Tomas R., Clark P.U., Carlson A.E., Lynch-Stieglitz J., Curry W., Brook E., Erickson D., Jacob R., Kutzbach J., and Cheng J.: Transient Simulation of Last Deglaciation with a New Mechanism for Bølling-Allerød Warming. Science, 325, 310-314, http://dx.doi.org/10.1126/science.1171041, 2009.

Marcisz, K., Gałka, M., Pietrala, P., Miotk-Szpiganowicz, G., Obremska, M., Tobolski, K., and Lamentowicz, M.: Fire activity and hydrological dynamics in the past 5700 years reconstructed from Sphagnum peatlands along the oceanic–continental climatic gradient in northern Poland. Quaternary Science Reviews, 177, 145-157, https://doi.org/10.1016/j.quascirev.2017.10.018, 2017.

Marlon, J. R., Kelly, R., Daniau, A.-L., Vannière, B., Power, M. J., Bartlein, P., Higuera, P., Blarquez, O., Brewer, S., Brücher, T., Feurdean, A., Romera, G. G., Iglesias, V., Maezumi, S. Y., Magi, B., Courtney Mustaphi, C. J., and Zhihai, T.: Reconstructions of biomass burning from sediment-charcoal records to improve data–model comparisons, Biogeosciences, 13, 3225–3244, https://doi.org/10.5194/bg-13-3225-2016, 2016.

Marquer, L., Gaillard, M.J., Sugita, S., Poska, A., Trondman, A.K., Mazier, F., Nielsen, A.B., Fyfe, R.M., Jönsson, A.M., Smith, B., Kaplan, J.O., Alenius, T., Birks, H.J.B., Bjune, A.E., Christiansen, J., Dodson, J., Edwards, K.J., Giesecke, T., Herzschuh, U., Kangur, M., Koff, T., Latałowa, M., Lechterbeck, J., Olofsson, J., and Seppä, H.: Quantifying the effects of land use and climate on Holocene vegetation in Europe. Quaternary Science Reviews, 171, 20-37, https://doi.org/10.1016/j.quascirev.2017.07.001, 2017.

McWethy, D. B., Higuera,P. E., Whitlock, C., Veblen, T. T., Bowman, D. M. J. S., Cary, G. J., ... & Perry, G. L. W.: A conceptual framework for predicting temperate ecosystem sensitivity to human impacts on fire regimes. Global Ecology and Biogeography, 22, 900-912, https://doi.org/10.1111/geb.12038, 2013.

Molinari, C., Lehsten, V., Blarquez, O., Carcaillet, C., Davis, B.A., Kaplan, J.O., Clear, J., Bradshaw, R.H.: The climate, the fuel and the land use: Long‐term regional variability of biomass burning in boreal forests. Global Change Biology, 24:4929-45, https://doi.org/10.1111/gcb.14380, 2018.

Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Mücher, C.A., and Watkins J.W.: A climatic stratification of the environment of Europe. Global Ecology and Biogeography, 14, 549-563, https://doi.org/10.1111/j.1466-822X.2005.00190.x, 2015.

Pausas, J.G., and Paula, S.: Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems Global Ecology and Biogeography, 21, 1074–82, https://doi.org/10.1111/j.1466-8238.2012.00769.x, 2012.

Pausas, J.G., and Ribeiro, E.: The global fire–productivity relationship. Global Ecology and Biogeography, 22, 728–36, https://doi.org/10.1111/geb.12043, 2013.

Pfeiffer, M., Spessa, A., and Kaplan J.O.: A model for global biomass burning in preindustrial time: LPJ-LMfire (v1.0). Geoscientific Model Development, 6, 643–685, https://doi.org/10.5194/gmd-6-643-2013, 2013.

Power, M.J, Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H.W., Carcaillet C., Cordova, C., Mooney, S., Moreno, P.I., Prentice, I.C., Thonicke, K., Tinner, W., Whitlock, C., Zhang, Y., Zhao, Y., Ali, A.A., Anderson, R.S., Beer, R., Behling, H., Briles, C., Brown, K.J., Brunelle, A., Bush, M., Camill, P., Chu, G.Q., Clark, J., Colombaroli, D., Connor, S., Daniau, A.L., Daniels, M., Dodson, J., Doughty, E., Edwards, M.E., Finsinger, W., Foster, D., Frechette, J., Gaillard, M.J., Gavin, D.G., Gobet, E., Haberle, S., Hallett, D.J., Higuera, P., Hope, G., Horn, S., Inoue, J., Kaltenrieder, P., Kennedy, L., Kong, Z.C., Larsen, C., Long, C.J., Lynch, J., Lynch, E.A., McGlone, M., Meeks, S., Mensing, S., Meyer, G., Minckley, T., Mohr, J., Nelson, D.M., New, J., Newnham, R., Noti, R., Oswald, W., Pierce, J., Richard, P.J.H., Rowe, C., Sanchez, Goñi, M.F., Shuman, B.N., Takahara, H., Toney, J., Turney, C., Urrego-Sanchez, D.H., Umbanhowar, C., Vandergoes, M., Vanniere, B., Vescovi, E., Walsh, M., Wang, X., Williams, N., Wilmshurst, J., and Zhang J.H.: Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. Climate Dynamics, 30, 887-907, https://doi.org/10.1007/s00382-007-0334-x, 2008

Pidwirny, M.: Actual and Potential Evapotranspiration. Fundamentals of Physical Geography, 2006, 2nd Edition.

Rius, D., Vannière, B., Galop, D., Richard, H.: Holocene fire regime changes from multiple-site sedimentary charcoal analyses in the Lourdes basin (Pyrenees, France). Quaternary Science Reviews, 30, 1696-709, https://doi.org/10.1016/j.quascirev.2011.03.014, 2011.

Rabin, S. S., Melton, J. R., Lasslop, G., Bachelet, D., Forrest, M., Hantson, S., Kaplan, J. O., Li, F., Mangeon, S., Ward, D. S., Yue, C., Arora, V. K., Hickler, T., Kloster, S., Knorr, W., Nieradzik, L., Spessa, A., Folberth, G. A., Sheehan, T., Voulgarakis, A., Kelley, D. I., Prentice, 5 I. C., Sitch, S., Harrison, S., and Arneth, A.: The Fire Modeling Intercomparison Project (FireMIP), phase 1: experimental and analytical protocols with detailed model descriptions, Geoscientific Model Development, 10, 1175–1197, https://doi.org/10.5194/gmd-10-1175-2017.

Roberts, N., Fyfe, R.M., Woodbridge, J., Gaillard, M.J., Davis, B.A., Kaplan, J.O., Marquer, L., Mazier, F., Nielsen, A.B., Sugita, S., and Trondman, A.K.: Europe's lost forests: a pollen-based synthesis for the last 11,000 years. Scientific reports. 158:716, https://doi.org/10.1038/s41598-017-18646-7, 2018.

Rogers, B.M., Soja, A.J., Goulden, M.L., and Randerson, J.T.: Influence of tree species on continental differences in boreal fires and climate feedbacks. Nature Geosciences, 8, 228-234. https://doi.org/10.1038/ngeo2352, 2015.

Rösch, M., Kleinmann, A., Lechterbeck, J., and Wick, L.: 2014 Botanical off-site and on-site data as indicators of different land use systems: a discussion with examples from Southwest Germany. Vegetation history and archaeobotany, 23, 121-133, https://doi.org/10.1007/s00334-014-0437-3, 2014.

Ryan, K.C.: 2002. Dynamic interactions between forest structure and fire behavior in boreal ecosystems. Silva Fennica, 36, 13–39, https://doi.org/10.14214/sf.548, 2002.

Simpson, G.L.: Modelling palaeoecological time series using generalized additive models. Frontiers in Ecology and Evolution, 6,149. https://doi.org/10.3389/fevo.2018.00149, 2018.

Scheffer, M., Hirota, M., Holmgren, M., Van, Nes E.H., and Chapin, III FS.: Thresholds for Boreal Biome Transitions. *PNAS*, 109, 21384–21389, https://doi.org/10.1073/pnas.1219844110, 2012

Scheiter, S., Higgins, S.I., Osborne, C.P., Bradshaw, C., Lunt, D., Ripley, B.S., Taylor, L.L., and Beerling, D.J.: Fire and fire-adapted vegetation promoted C4 expansion in the late Miocene. New Phytologist, 195, 653–666 https://doi.org/10.1111/j.1469-8137.2012.04202.x, 2012.

Słowiński, M., Lamentowicz M., Łuców D., Barabach J., Brykała D., Tyszkowski S., Pieńczewska A., Śnieszko Z., Dietze E., Jażdżewski K., Obremska M., Ott F., Brauer A., and Marcisz K.: Paleoecological and historical data as an important tool in ecosystem management. Journal of Environmental Management. https://doi.org/10.1016/j.jenvman.2019.02.002, 2019.

Sturtevant, B.R., Miranda, B.R., Yang, J., He, H.S., Gustafson, E.J., Scheller, R.M.: Ecosystems, 12, 445. https://doi.org/10.1007/s10021-009-9234-8, 2009.

Teuling, A.J., Taylor, C.M., Meirink, J.F., Melsen, L.A., Miralles, D.G., Van Heerwaarden, C.C., Vautard, R., Stegehuis, A.I., Nabuurs, G.J. and de Arellano, J.V.G.: Observational evidence for cloud cover enhancement over western European forests. Nature Communications, 8, https://doi.org/10.1038/ncomms14065, 2017.

Thornthwaite, C.W.: 1948. An approach toward a rational classification of climate. Geographical Review, 38, 55-94 https://www.jstor.org/stable/210739, 1948

Tóth M., Magyari, E.K., Buczkó, K., Braun, M., Panagiotopoulos, K., and Heiri, O.: Chironomid-inferred Holocene temperature changes in the South Carpathians (Romania). The Holocene, 25, 569–582, ttps://doi.org/10.1177/0959683614565953, 2015.

van der Werf, G., Randerson, J.T., Giglio, L., Collatz, G. J., Mu, M., Kasibhatla P. S., Morton, D.C., DeFries, R.S., Jin Y., and van Leeuwen T.: Global fire emissions and the contribution of deforestation, savanna, forest, agricultural, and peat fires (1997– 2009). Atmospheric Chemistry and Physics, 10, 11707–11735, https://doi.org/10.5194/acp-10-11707-2010, 2010.

van Nes, E.H., Staal A., Hantson, S., Holmgren, M., Pueyo, S., and Bernardi, R.E.: Fire forbids fifty-fifty forest. PLoS ONE 13(1): e0191027. https://doi.org/10.1371/journal.pone.0191027, 2018.

Vannière, B., Blarquez, O., Rius, D., Doyen, E., Brücher, T., Colombaroli, D., Connor, S., Feurdean, A., Hickler, T., Kaltenrieder, P., Lemmen, C., Leys, B., Massa, C., and Olofsson, J.: 7000-year human legacy of elevation-dependent European fire regimes, Quaternary Science Reviews, 132, 206–212, https://doi.org/10.1016/j.quascirev.2015.11.012, 2016.

Veski, S, Seppä, H., Stančikaitė, M., Zernitskaya, V., Reitalu, T., Gryguc, G., Heinsalu, A., Stivrins, N., Amon, L., Vassiljev, J., and Heiri O.: Quantitative summer and winter temperature reconstructions from pollen and chironomid data between 15 and 8 ka BP in the Baltic-Belarus area. Quaternary International, 388, 4-11, https://doi.org/10.1016/j.quaint.2014.10.059, 2015.

Wagenmakers, E.J., Farrell S. AIC model selection using Akaike weights. Psychonomic Bulletin & Review 11: 192-196, 2004.

Whitlock, C., Colombaroli, D., Conedera, M., Tinner, W.: 2017 Land-use history as a guide for forest conservation and management. Conservation Biology, 32, 84-97, https://doi.org/10.1111/cobi.12960, 2017.

Whitlock, C., Larsen, C.: 2001. Charcoal as a fire proxy. In Smol, JP, Birks, HJB and Last, WM., editors, Tracking environmental change using lake sediments. Volume 3: terrestrial, algal, and siliceous indicators. Kluwer Academic Publishers, 75-97, 10.1007/0-306-47668-1, 2001.

Wood, S.N.: 2017. Generalized Additive Models: An Introduction with R, Second Edition Chapman and Hall/CRC. https://doi.org/10.1201/9781315370279, 2017.