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Title of the manuscript Fire risk 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-vegetation interactions is to quantify the effect vegetation has in mediating fire regime. Here, we explore the relative importance of Holocene land cover and dominant functional forest type, and climate dynamics on biomass burned in temperate and boreo-nemoral regions of Central and Eastern Europe over the past 12 ka BP years. We used an extensive data set of Holocene pollen and sedimentary charcoal records, in combination with climate simulations and novel statistical modelling. Biomass burned was highest during the early Holocene and lowest during the mid Holocene in all three ecoregions, but diverged more markedly over the past 3-4 ka BP. Although the climate was an important driver of fire hazard during the warm and dry early Holocene, tree cover was consistently the strongest predictor of past biomass burning. In temperate forests, biomass burned was high at ~ 45% tree cover and decreased strongly towards 60% tree cover. In needleleaf dominated forests, biomass burned was highest at ~60-65% tree cover and abruptly declined at >65% tree cover. Biomass burned also increased when arable lands and grasslands reached ~15-20%, although this relationship was highly dynamic depending on land use intensity throughout ignition and fuel type and availability. Our observations cover the full range of Holocene climate variability and land cover changes and illustrates that percentages of land cover is a key predictor of the probability of fire occurrence over timescales of centuries to millennia. We suggest that long-term fire risk 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

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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, area, 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; Higuera et al., 2009; van der Werf et al., 2010; Pausas and Paula, 2012; Archibald et al., 2018). A key challenge for understanding fire-climate-vegetation interactions is to quantify the effect that vegetation properties has 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 given 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 of 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; Archibal et al., 2009). It has also been shown that plant functional traits (growth rate and architecture, leaf chemical and moisture content, litter, bark thickness) 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, whereas temperate broadleaf deciduous trees with high leaf moisture content and lower litter accumulation, have a clear negative effect on ignition probability and fire spread (Rogers et al., 2015). Human activities can also influence fuel load, composition and ignition patterns, which is particularly relevant in Europe, where after a long history of human-driven decline in tree cover, forest extent has increased over the past few decades due to rural land abandonment and carbon abatement programmes (Jepsen et al., 2015; Roberts et al., 2018). While higher tree cover may reduce fire hazard, fire-promoting climatic conditions are also projected to increase in areas where natural fires were historically infrequent, e.g. Central and Eastern Europe (Khabarov, et al., 2016; Frejaville and Curt 2017). Widespread plantations of highly flammable

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trees (e.g. *Pinus*) by modern forestry may further increase the probability and impact of catastrophic fires for human health, economy and ecosystems (Słowiński et al., 2019). 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 with 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 (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 and climate during the Holocene in major Central and Eastern European vegetation types: temperate and boreo-nemoral. This study utilises independent estimation of evidence fire, land cover composition and climate changes with a novel statistical modelling approach (generalized additive models, GAM) to quantify percentages in land cover and tree-density associated to fire hazard probability.

2 Methods

2.1 Geographical location and charcoal site selection

To determine past biomass burned, we compiled a dataset comprising 117 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). 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

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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} /a^{-1} and most fires are intentionally or accidentally ignited by humans (Christian et al., 2003). The average fire size (fires <10 ha) is higher in eastern and southern Europe (5-10 ha), compared to northern and central Europe (<5 ha); 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 burned

Spatio-temporal patterns in fire-land cover interactions were investigated using a geographical delineation of Central and Eastern Europe based on environmental stratification (Metzger et al., 2005). We defined three ecoregions from 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 charcoal records were converted to a calibrated years before present (1950 CE) 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 (CHAR) by multiplying concentrations (charcoal counts [pieces cm^{-3}] or charcoal areas [mm^2 cm^{-3}]) by sediment-accumulation rates [cm a^{-1}] to account for variations in sedimentation among sequences. To allow comparison between and within charcoal records obtained from various depositional environments with different laboratory methods, 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 Z-score transformation using a base period from 12 to 0.15 ka BP. This period includes the entire dataset, but excludes the effect of recent human impact on fire activity during the post-industrial period. To reduce the influence of high-resolution

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charcoal records on the composite charcoal record, transformed charcoal records were bootstrap-resampled 999 times. Resampled charcoal time series were aggregated by ecoregion and smoothed with a 500-years loess smoother. We then calculated the mean and 90% confidence intervals of the aggregated records to obtain regional biomass-burned trends. For numerical processing of the CHAR series we used the R paleofire package version 4.0 (Blarquez et al., 2014).

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* among 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. This is 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

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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 ecoregion by spatially aggregating the averages of pollen records within the corresponding ecoregion. We then fitted a 500-year loess smoother for each land cover class.

2.4 Simulated-based regional composite of 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 (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) 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 ratios of the surface temperature (precipitation) from CRU. These ratios were then multiplied to all climate simulation fields of the interval 12 to 0 ka BP.

We focus here on the boreal summer (June, July, August, hereafter "JJA") surface temperature (JJA T) and precipitation minus potential evapotranspiration (JJA P-PET), as these parameters are most representative for fuel moisture during the major fire season (Thonicke et al., 2001). JJA P-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 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 within

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the corresponding ecoregions. Similar to vegetation and fire reconstructions, a 500-year loess smoother was fitted to the climate simulations.

2.5 Generalized Additive Models

We developed generalized additive models (GAMs) to explore the response of biomass burned to changes in percent land cover, dominant functional forest type, and JJA climate. GAMs are models with a linear predictor (here the composite pollen-derived regional land cover class abundance and simulated climate conditions) involving a sum of smooth functions of covariates (Hastie and Tibshirani, 1990). We used a Gaussian error distribution to fit models with the mgcv package (Hastie and Tibshirani, 1990). GAMs were estimated with thin plate regression splines using restricted maximum likelihood to automatically determine the optimal level of smoothing for each term in the model and automatic term selection. We calculated Akaike Information Criterion (AIC) weights to identify the models that were best able to predict the observed changes in biomass burned. AIC weights are a normalized indicator of support for each model given the evidence within each data set while penalising more complex models (Hastie and Tibshirani, 1990). We obtained AIC scores 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 restricted the GAMs analysis 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 Pollen-based regional composite of land cover). However, we also constructed GAMs on JJA climate for the 12-8 ka BP period to investigate the relationship between climate and fire without any significant human impact.

3 Results

3.1 Biomass burned, land cover, and climate dynamics

The amount of biomass burned was highest during the early Holocene (between ~ 10.5 and 8 ka BP)

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over all of Central and Eastern Europe and the three ecoregions, although the onset of this biomass increase was earlier (11 ka BP) in the CON ecoregions (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 burned showed lower-than-present values between ~ 8 and 4 ka BP in all ecoregions (Fig. 2B-D). The reduction in biomass burned accompanied the declining JJA temperature, although it remained warmer-than-present, and by a rapid rise in summer moisture availability (around 8 ka BP) in all ecoregions (Fig. 2B-D). We found differences in trends in biomass burned among ecoregions over the past 3 ka BP. Biomass burned increased markedly at 3 ka BP in the BNE ecoregion, but less evident in the CON ecoregion, and 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. 3A). 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).

3.2 Generalized Additive Models

Model selections based on AIC shows that climate alone explains a large proportion of the deviance of biomass burning in the three ecoregions in the time period between 12-8 ka BP (average 71%; Appendix A1, Supplement S2). However, climate alone explained a considerably smaller proportion of the deviance (average 48%) for the 8-0 ka BP period, whereas inclusion of land cover fractions in the GAMs increased the deviance explained to 76% (Supplement S2). Furthermore, the full model selection

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(climate and land cover) procedure for the 8-0 ka BP period shows that models including land cover are superior to model including climate alone in all ecoregions (Table 1). Evaluation of the models using AIC scores and weights shows 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 1, Supplement S2). When examining the fire-tree cover relationships we found that in ATL and CON ecoregions, biomass burned is high at 45% tree cover declining strongly towards 60% tree cover. (Fig. 3A). In the BNE ecoregion, biomass burned abruptly increases as tree cover declines from its maximum of 80% to 65% tree cover (Fig. 3A). When examining fire-human relationships, biomass burned increases when arable and grassland cover reached ~15-17% in ATL and CON ecoregions, and at ~6-10% in the BNE ecoregion (Fig. 3DE and Fig. 4). Biomass burned also increases for heathland cover greater than 12% in ATL and CON ecoregions (Supplement S2).

4 Discussion

Understanding fire-climate-vegetation interactions is typically based on recent estimates of vegetation and burned area obtained from remote sensing data as well as fire and vegetation models. This may hinder our ability to recognise links and feedbacks between fire and vegetation shifts especially in ecosystems with species that have long generation times. Our study uses high-density millennial records of ecosystem history (vegetation, fire, climate) and proposes a framework for testing how long-term changes in climate alone or in combination with land cover and dominant forest type influence biomass burned in three distinct ecoregions from Central and Eastern Europe.

4.1 Fire-climate relationship

We found that climate, specifically warmer-than-present summer temperatures and high moisture content, exerted a strong top-down control on biomass burned between 12-8 ka BP period in all ecoregions (Appendix A1; Supplement S2). This relationship is expected, as the early Holocene vegetation progressively recovered from the cold and dry conditions with limited biomass prevailing during the Lateglacial (Feurdean et al., 2014). However, the importance of land cover and human

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imprint on biomass burned become stronger post 8 ka BP in all ecoregions, as shown by higher significance levels of land cover models over models based on climate alone (Table 1). Warmer summers and/or drier conditions were generally associated with higher biomass burned over large areas in Europe, although a stronger effect of land cover was detected at mid to low latitudes (Vannière et al., 2016; Dietze et al., 2018; Molinari et al., 2018). Proxy-based climate reconstructions are fragmentary and mostly qualitative, which hampers their inclusion in the generalized additive models. However, proxy climate datasets were used to check whether the model simulations depict general trends in climate conditions. Simulated and proxy-based climate reconstructions are in general good agreement in indicating warm and dry climate conditions for the early Holocene and increased moisture availability during the mid-Holocene in all ecoregions, and cooler summer temperature 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). Though simulated and most proxy-based climate reconstructions show cool and moist climate conditions over 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). This could be partly explained by a greater human impact on the proxy-based climate reconstructions such as the effect of water acidification and eutrophication on chironomid taxa and deforestation on pollen on testate amoebae composition (Heiri et al., 2015; Mauri et al., 2017).

4.2 Fire-fuel relationship: the effect of tree cover composition

At the temporal scale considered here, we detected that biomass burned increases with declining percent tree cover (Fig. 3A). While the GAM models use biomass burned as the response variable, we acknowledge that the relationship can go in both directions: fire probability can increase when forest cover decreases, and frequent fires can lead to a decrease in forest cover. Yet our findings are consistent with emerging evidence on fire-fuel relationships that suggest a strong relationship 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). A lowering of the tree cover allows the development of understorey cover (herbs, shrubs and fine woody debris) and provides a favourable fuel mix of fine

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herb, shrubs and coarse woody debris that facilitates ignition and surface fire spread (Pausas and Paula, 2012; Frejaville et al., 2016). Open forests also have high penetration of radiation and wind to the ground surface to dry the understory vegetation and litter (Ryan, 2002).

However, the relationship between percent tree cover and biomass burned differs among the ecoregions (Fig. 3A and Fig. 4). In ecoregions dominated by temperate forests (CON and ATL), biomass burned is high at 45% tree cover and declines towards ~ 60% (Fig. 3A). In the BNE ecoregion, where needleleaf trees dominate, the relationship is distinctly different, biomass burned increases as tree cover declines abruptly from its maximum of 80% and is highest at 65% tree cover (Fig. 3A). The abrupt shift in 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 GAM models run separately broadleaf and needleleaf tree cover indicate that the regional divergence between biomass burned and percent tree cover is caused by different dominant functional forest type (Figs. 3, 4). Broadleaf cover had the most powerful negative effect on biomass burned in all three ecoregions (Fig. 3B; Table 1; Supplement S2). By contrast, biomass burned shows an increase rather than a decrease with increasing needleleaf cover evident in the BNE ecoregion with a considerable proportion of needleleaf forests (Fig. 3C; Table 1). This finding supports the ecological inference that deciduous broadleaf trees have a clear negative effect on fire hazard (Rogers et al., 2015).

Fire in boreal forest systems often increases also at higher tree cover (up to 75%) due to more flammable needleleaf biomass when exposed to dry, windy conditions (Scheffer et al., 2012; Rogers et al., 2015). Life history and morphological traits of the dominant species (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). Abundant *Pinus diploxylon*-type pollen indicates that *Pinus sylvestris* was the dominant needleleaf tree in all ecoregions during the Early Holocene. *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). *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). In contrast,

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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.

4.3 Fire-fuel relationship: the human impact

Human activities have 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). While past ignitions is assumed to increase with population density, human-caused change in land cover from forest to arable land and associated fuel limitation has resulted in a decline in biomass burned. Biomass burned mostly shows a positive response with increases in arable and grassland cover in all ecoregions, however, this relationship is dynamic and may illustrate a complex fire-human interaction (Figs. 3, 4). In the CON ecoregion, the most evident increase in biomass burned occurred after 3 ka BP (Fig. 2B), and is consistent with percentages in arable and grassland cover at which biomass burned shows positive responses in the GAMs (Figure 3DE). Historically, the onset of the rise in biomass burned 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). Further, the sharp increase in biomass burned over the last millennium coincides to a marked population growth and renewed deforestation (Jamrichova et al., 2017; Marquer et al., 2017). In the ATL ecoregion, while the rise in arable and grassland cover first occurs ~4 ka BP, biomass burned increased after 1.5 ka BP and may reflect local intensification in land use without major use of fire for deforestation (Fig. 2). Burning of agricultural waste, e.g. straw and chaff, to improve soil fertility and clean the land provides less biomass to burn than wood (Pfeiffer et al., 2013). In the BNE ecoregion, we detected increases in biomass burned over the past 4 ka BP, while the rise in abundance of arable and grassland cover to values at which biomass burned shows the strongest positive responses were only visible over the past 2 ka BP (Fig. 2D). It is therefore apparent that the rise in biomass burned at 4 ka BP could be primarily relate to the naturally or human-driven increase needleleaf component, and only after 2 ka BP to a sustained use of fire for deforestation and agricultural activities (Fig. 2D). Broadleaf forests were edaphically more suited to conversion to arable fields and pastures than needleleaf forests, leading to an increased of needleleaf forest over time (Roberts, 2018).

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 greater 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 in fire regimes (Pfeiffer et al., 2013; Forkel et al., 2017) and examine critical ecological transitions hypothesized to be mediated by fire-vegetation interactions (Scheiter et al., 2012).

5 Conclusions

Although the climate was an important driver of fire hazard during the early Holocene, in particular warmer and drier-than-present summer, our results provide compelling evidence that the land cover and the dominant forest types can override the direct effect of climate on biomass burned. Percent of tree cover was consistently the strongest predictor of past biomass burning, but regional differences were observed among major vegetation types. Specifically, in ecoregions dominated by temperate forests

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(CON and ATL), biomass burned was high at 45% tree cover and declined towards ~ 60%. In the BNE ecoregion where needleleaf trees dominate, biomass burned was highest at ~60-65% tree cover and abruptly declines at tree cover >65%. The abrupt shift in BNE ecoregion resembles a system crossing a critical ecological threshold and transitioning to a new state. Biomass burned shows a positive response when arable and grassland cover reached ~15-20%, but this relationship is dynamic and highlights the complex fire-human interactions that depend on land-use intensity. Our records of past fire-fuel interactions indicate that tree cover is a first-order predictor of the probability of fire occurrence. 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 risk relies on land cover management on a regional scale. Information derived from such long-term fire-vegetation relationships can be used to improve fire-mitigation strategies and fire-vegetation models.

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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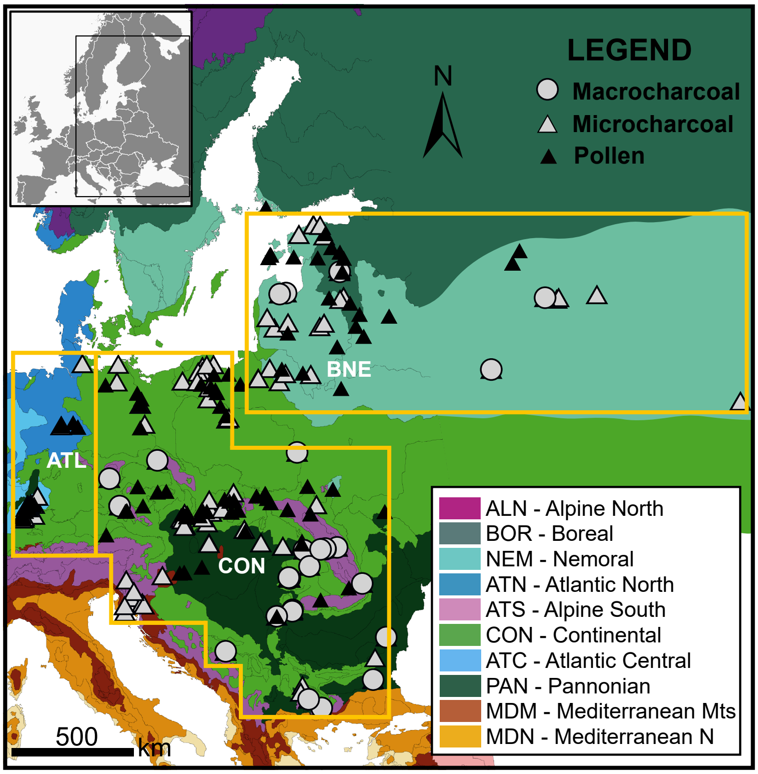

Figure 2. Holocene trends in biomass burned, climate, and land cover changes over all of Central and Eastern Europe (panel A) and in each of the ecoregions: Continental (B), Atlantic (C) and Boreo-Nemoral (D). Biomass burned is based on charcoal influx (z-score values). Climate conditions (anomalies) represent average simulated seasonal summer (June, July, August (JJA)) temperatures and

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precipitation minus potential evapotranspiration (P-PET), from a global transient climate simulation (Thornthwaite, 1948). 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).

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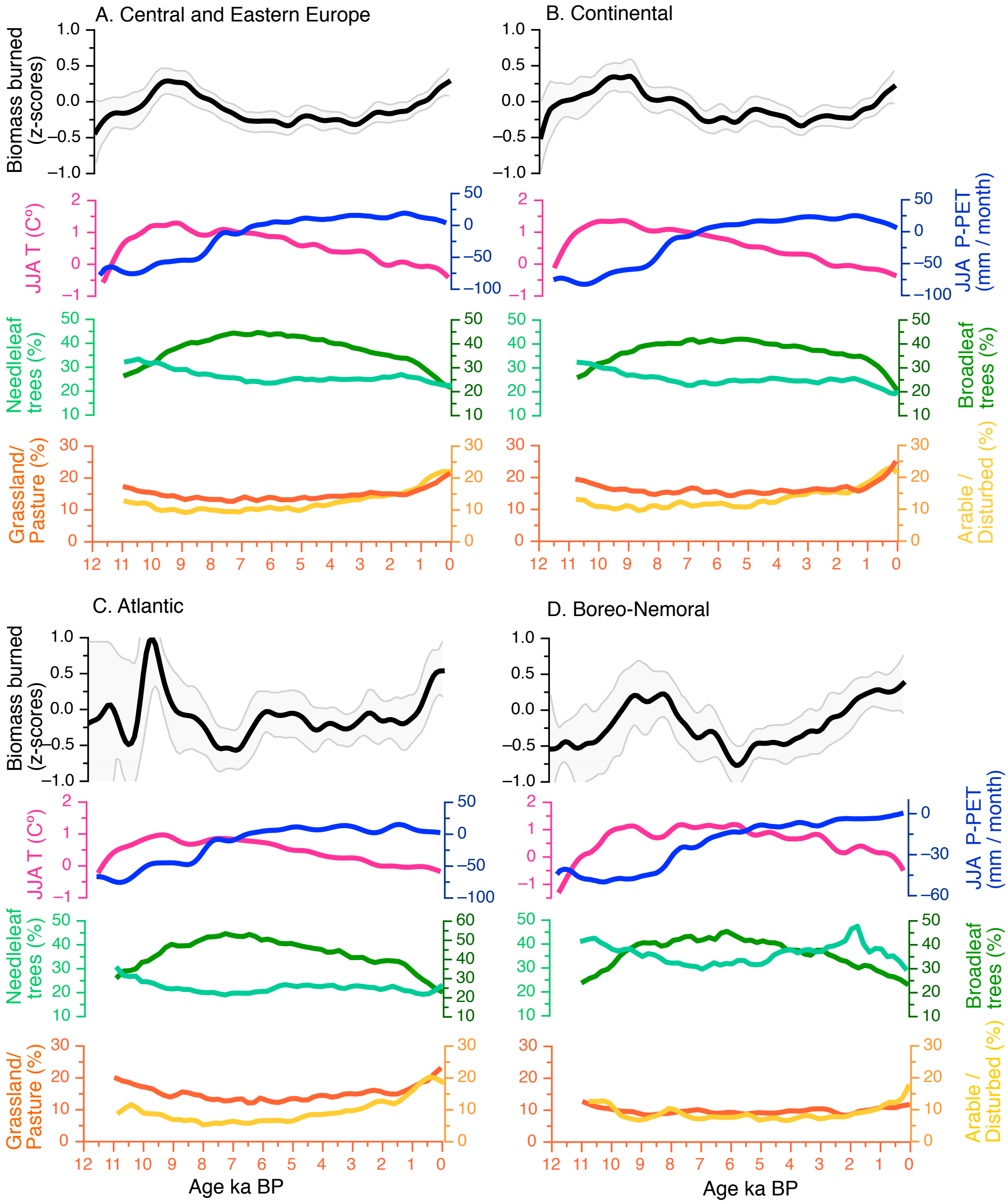

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Figure 3. Fire-fuel type and load relationship in Central and Eastern Europe. The relationship between biomass burned, determined from z-score composite charcoal values and the main land-cover types, derived from percentages of pollen-based land cover 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).

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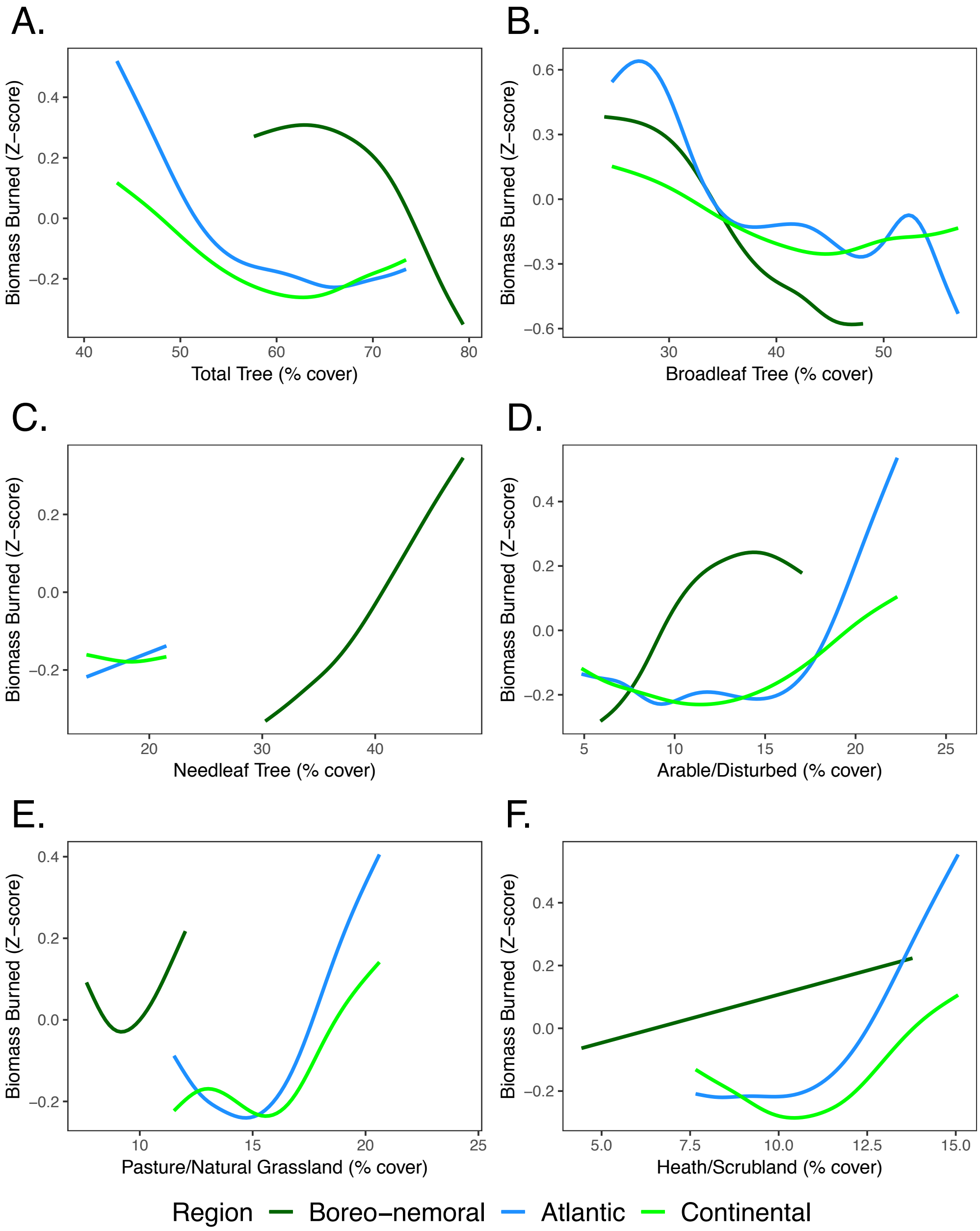

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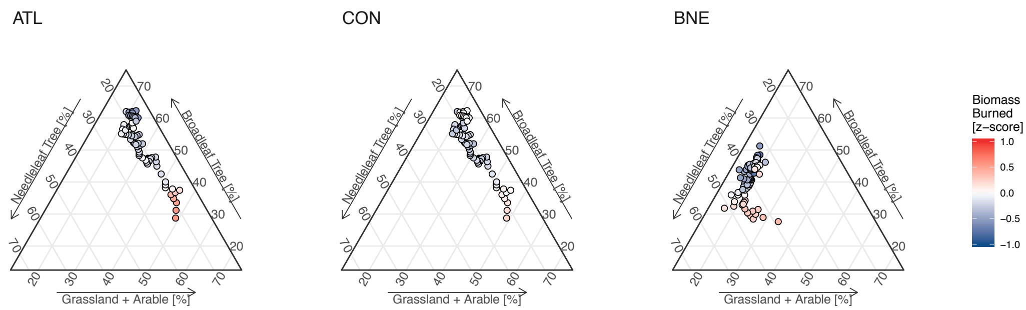
Figure 4. Relationship between biomass burned, broadleaf tree cover, needleleaf tree cover, arable cover and grassland cover in the three ecoregions in Central and Eastern Europe. Biomass burned and land cover are determined as above. Locations with greater biomass burned tend to be consistently characterised by low broadleaf tree cover in CON and ATL ecoregions, and by high needleleaf forest cover in BNE ecoregion. In terms of land use, biomass burned increases with arable and pasture cover but the patterns and thresholds vary between ecoregions, reflecting complex fire-human interactions.



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Tables

Table 1. Model selection results for generalized additive models of the effects of land cover and climate on biomass burned. 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 burned. 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
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
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

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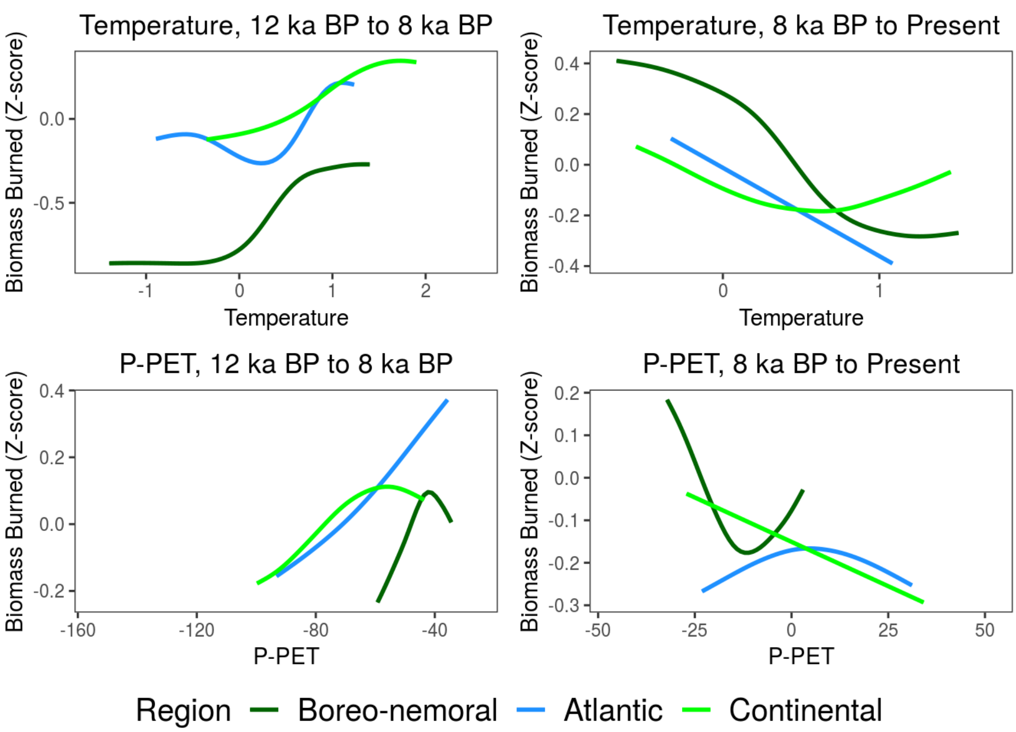
Appendix A. Fire-climate relationship in the three ecoregions from Central and Eastern Europe for the 12-8 ka BP and 8-0 ka BP period, respectively. The relationship between biomass burned, determined from z-score composite charcoal values and simulated seasonal summer (June, July, August (JJA) temperatures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



555 **Supplement S1:** Table S1. Metadata

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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 in suitable repositories (e.g. the Global Charcoal Database, Neotoma, Pangaea) upon publication.

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

Author contribution: AF, BV, and WF design the study with contribution from TH and MF. AF compiled site-based data and 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 BV, WF, SC, and input from all authors.

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

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