The optimum fire window: applying the fire-productivity

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hypothesis to Jurassic climate states

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18	Abstract
19	Present day fire frequency has been related to a productivity/aridity gradient on a regional and global
20	scale. Optimum fire conditions occur at times of intermediate productivity and aridity, whereas fire is
21	limited on the high productivity (moisture) and aridity (no fuel) endmembers. However, the current
22	global fire activity pattern is reinforced by the predominant burning of grasslands. Here we test the
23	intermediate fire-productivity hypothesis for a period on Earth before the evolution of grasses, the
24	Early Jurassic, and explore the fire regime of two contrasting climatic states: the Late Pliensbachian
25	(LPE) cooling Event and the Sinemurian-Pliensbachian Boundary (SPB) warming. Palaeo-fire
26	records are reconstructed from fossil charcoal abundance, and changes in the hydrological cycle are
27	tracked via clay mineralogy, which allows inference of changes in fuel moisture status. Large
28	fluctuations in the fossil charcoal on an eccentricity time scale indicate two modes of fire regime at
29	the time. Wildfires were moisture limited in a high productivity ecosystem during eccentricity minima
30	for both the SPB and LPE. During eccentricity maxima, fires increased, and an optimum fire window

was reached, in which greater seasonality in rainfall and temperatures led to intermediate states of

productivity and aridity. The LPE experienced more extreme climatic endmembers compared to the

SPB, with the fire regime edging closer to 'moisture limitation' during eccentricity minima, and more

pronounced seasonality during eccentricity maxima, explained by the overall cooler climate at the time. This study illustrates that the intermediate-productivity gradient holds up during two contrasting climatic states in the Jurassic. **Plain Language Summary** Fires are limited in year-round wet climates (tropical rainforests, too wet), and in year-round dry climates (deserts, no fuel). This concept, the intermediate-productivity gradient, explains the global pattern of fire activity. Here we test this concept for climate states of the Jurassic (~190 Myr ago). We find that the intermediate-productivity gradient also applies in the Jurassic, despite the very different ecosystem assemblages, with fires most frequent at times of high seasonality. **Key Points** The intermediate-fire productivity gradient can be applied to the Jurassic and be utilized to explain changes in biomass abundance, moisture availability, and fire activity. The terrestrial ecosystem surrounding the Cardigan Bay Basin was not year-round dry during the Sinemurian-Pliensbachian Boundary warming Event or the Late Pliensbachian Cooling Event and therefore fire was not aridity limited. Fire activity was strongly influenced by the ~100 kyr and 405 kyr eccentricity cycle during both climatic states, which led to two modes in the fire regime: productivity limited (minima) and the optimum fire-window (maxima).

1 Introduction

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64 The global distribution of fire at the present day follows the intermediate-productivity hypothesis. 65 This hypothesis suggests that fire activity increases non-linearly along a productivity gradient primarily controlled by biomass and fuel availability (Pausas & Bradstock, 2007; Pausas & Ribeiro, 66 67 2013). Climate drives fuel availability, structure, and moisture, which are the main determinants of the fire regime. Where the fire regime reflects the frequency, behaviour, type of fire, and the impact on 68 69 the ecosystem (Bradstock, 2010). Fire is either limited by high moisture in ecosystems with high biomass production, for example in tropical rainforests, or in high aridity and low biomass production 70 71 ecosystems, with disconnected fuel such as in deserts. This principle explains drought-driven fire 72 regimes and fuel-limited fire regimes (Pausas & Ribeiro, 2013). In humid regions fires are initiated by 73 seasonal aridity which leads to flammable conditions and lower fuel-moisture status. Rising 74 temperatures can lead to increased drought and flammability in high productivity ecosystems and 75 further accelerate this drought-driven increase in fire activity (Pausas & Ribeiro, 2013). In 76 unproductive arid regions it is biomass production that determines fire activity, as the fuel-moisture 77 status would not be limiting (Pausas & Ribeiro, 2013). The optimum window for wildfires is at 78 intermediate productivity levels, such as in the tropical savannahs of today, wherein biomass can 79 accumulate due to seasonal precipitation and fuel becomes available in the dry season when the fuel 80 moisture status decreases (Meyn et al., 2007; Pausas & Bradstock, 2007; Krawchuk & Moritz, 2011; 81 Pausas & Paula, 2012; Pausas & Ribeiro, 2013). 83 The intermediate-productivity concept provides an effective explanation for the distribution of fire on 84 a global and regional scale in the modern day where highest fire activity is found at intermediate 85 moisture availability (Meyn et al., 2007; Krawchuk & Moritz, 2011; Daniau et al., 2012). The

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94 95 observation of high fire activity in ecosystems that are of intermediate aridity and productivity is strongly driven by grass biomes today (Archibald et al., 2018), where >80 % of area burnt is in grasslands (van der Werf et al., 2006). Although the intermediate-productivity gradient hypothesis of the present day is strongly linked to the expanse of grassland habitats, it should not require the presence of grasses to explain the impact of climate and seasonality on fire frequency in other vegetation types. The crucial concept is that an optimum fire window exists when there is a sufficiently moist season that allows fuel growth which is followed by a drier season in which fuel moisture levels are lowered, allowing ignition and fire spread. Since fire has formed an important part of ecosystems and the Earth system since 420 Ma (Glasspool et al., 2004; Glasspool & Gastaldo, 2022), we therefore test whether the intermediate-productivity gradient has also existed and if the concept can also be applied in a world before the evolution of grasses.

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Here we look back at two contrasting climate events in the Early Jurassic, ~190 Myr ago, to assess what evidence there is for the existence of the intermediate-productivity fire gradient at such time

100 (Fig. 1). The first event, the Sinemurian-Pliensbachian Boundary event (SPB, is marked by global 101 warming, sea-level rise, increased humidity, and a negative carbon-isotope excursion (Ruhl et al., 2016; Haq, 2018; Deconinck et al., 2019; Storm et al., 2020). In contrast, the second event, the late 102 103 Pliensbachian Event (LPE) is marked by ~5 °C cooling in NW Europe, greater aridity, sea-level fall and a global positive carbon-isotope excursion (e.g. Korte et al., 2015; Ruhl et al., 2016; Haq, 2018; 104 Deconinck et al., 2019; Storm et al., 2020). We couple charcoal, clay and climate data to infer palaeo-105 106 fire and the hydrological regimes during both these time intervals. 107 108 2 Materials and Methods 109 Materials 110 The records from both time periods are taken from the Llanbedr (Mochras Farm) borehole, from sedimentary strata deposited in a relatively deep marine setting close to the shore in the Cardigan Bay 111 Basin (Wales, UK). These sediments show a strong regular orbital control in the limestone-mudstone 112 alternations (Ruhl et al., 2016), and an existing astrochronological framework provides an age model 113 114 for the Mochras borehole. In addition, input of terrestrial organic matter in the sampled section is relatively high (van de Schootbrugge et al., 2005; Riding et al., 2013), and thus provides ideal 115 material to study palaeo-fire regimes with a relatively high temporal constraint. 116

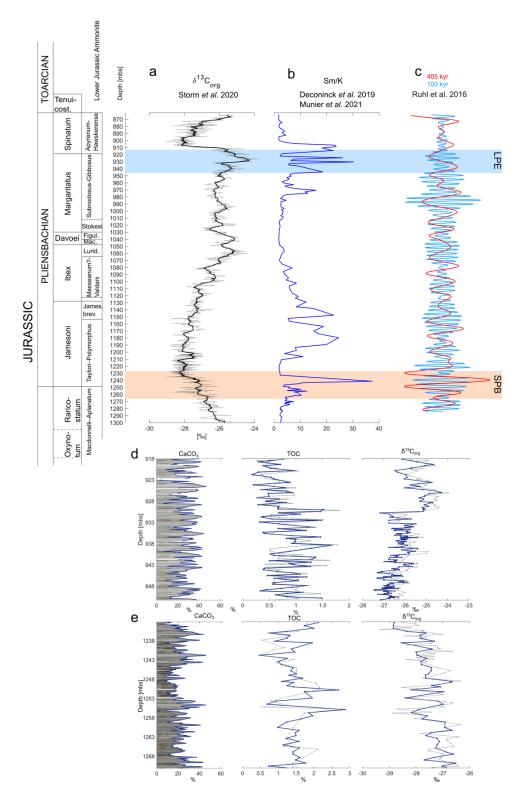


Fig. 1: Cyclostratigraphic framework of the latest Sinemurian–Pliensbachian of the Mochras core and the two intervals here studied. Red bar represents the interval (1271–1233 metres below surface (mbs)) of the SPB and the blue bar represents the interval of the LPE (951–918 mbs) (a) The $\delta^{13}C_{org}$ record from the Mochras core (Storm et al., 2020), shows the broad negative carbon-isotope trend around the SPB and the positive carbon-isotope excursion (CIE) in the Late Pliensbachian. (b) The

- smectite/kaolinite (Sm/K) ratio reflects changes in the hydrological cycle; data from Deconinck et al.
- 124 (2019) and Munier et al. (2021). Peaks in smectite indicate greater climatic aridity (Deconinck et al.,
- 2019; Munier et al., 2021). (c) Bandpass filters of the 100 kyr and 405 kyr cycle based on the Ca-
- elemental record in the depth domain from Ruhl et al. (2016). (d) The LPE interval is carbonate-rich
- and shows the metre-scale variations in CaCO₃ and TOC, next to the $\delta^{13}C_{org}$ positive shifts that marks
- the onset of the LPE. (e) The SPB interval contains relatively more clay and lithological couplets of
- alternating $CaCO_3$ and TOC-enhanced beds occurring on a metre scale. The $\delta^{I3}C_{org}$ shows the
- 130 negative trend of the long-negative limb of the SPB negative CIE.
- The Mochras core was drilled between 1967 and 1969 on the coast in NW Wales, UK. Preserved 1-m-
- length core slabs of the core are stored at the British Geological Survey National Core Repository at
- 133 Keyworth, United Kingdom. The Pliensbachian of Mochras shows alternating beds of pale grey
- limestone and dark brown to grey mudstone (Ruhl et al., 2016). These couplets occur throughout the
- Pliensbachian, but vary in thickness, from about 90 cm at the Sinemurian–Pliensbachian boundary to
- about 30 cm in the Late Pliensbachian age strata (latest Margaritatus and Spinatum zones) (Ruhl et al.,
- 137 2016). The lithological couplets are well expressed around the SPB and in the Margaritatus Zone
- 138 (Ruhl et al., 2016). For this study, samples were taken at an average sample spacing of 90 cm across
- the Sinemurian–Pliensbachian boundary (1272–1233 mbs (metres below surface)). In addition, data
- are utilized in this study that are published in Hollaar et al. (2021; 2023), from the Late Pliensbachian
- interval that is sampled at a 10 cm (951–934 mbs) and 30 cm (934–918 mbs) resolutions. The
- macrocharcoal data between 934–918 mbs are new and not previously published. An overview of the
- number of samples per stratigraphic interval and proxy can be found in SI Table 1.
- 144 Palaeolocation and provenance
- During the Early Jurassic, the Mochras site was situated in the Boreal realm of the Laurasian Seaway,
- which contained an island archipelago, and covers most of present-day NW and W Europe. The
- Mochras site was situated at a palaeolatitude of ~ 35° N (Torsvik & Cocks, 2017), just off the Welsh
- Massif, in a relatively deep marine setting, below storm base (Pieńkowski et al., 2021), but with a
- strong terrestrial influence (van de Schootbrugge et al., 2005; Riding et al., 2013; Xu et al., 2018;
- 150 Storm et al., 2020).
- 151 The Welsh Massif was likely the main detrital source to the Cardigan Bay Basin (Deconinck et al.,
- 2019), although other emergent areas in proximity likely also contributed (Deconinck et al., 2019).
- 153 The nearby Irish Massif, situated west of the Welsh Massif, also cannot be dismissed as a source of
- nutrients, terrestrial organic particles, clay and coarser mineral grains to the Cardigan Bay Basin
- 155 (Deconinck et al., 2019). Another possible source area is the emergent land of the Scottish Massif to
- the north of the Mochras Borehole and the London-Brabant Massif to the east of the Mochras
- 157 Borehole (van de Schootbrugge et al., 2005).

158 The multiple nearby landmasses contributing runoff to the here studied relatively deeper marine 159 depositional environment, allowed for the charcoal record presented in this study to reflect a regional 160 expression of likely multiple fires. It is important to note that one stratigraphic rock sample in this study represents a ~2 kyr average signal, which likely is more than the fire return interval at the time 161 162 op deposition. And thus represents an averaging of the overall fire signal. Therefore, the term 'fire 163 activity' here describes the overall occurrences as increases and decreases in wildfires across the 164 region. 165 Methods Mass spectrometry $\delta^{13}C_{org}$, TOC and CaCO₃ 166 Bulk organic carbon-isotopes, TOC and carbonate content were measured to track changes in the 167 carbon-cycle and changes in total organic matter in the studied interval. For the SPB interval (1271– 168 1233 mbs) 50 samples and for the LPE (918–951 mbs) 193 samples were processed for carbon 169 isotope mass spectrometry. Bulk rock samples were powdered using a pestle-a-mortar, weighed into 170 centrifuge tubes, and decarbonated using 3.3 % HCl. Following, the samples were transferred to a hot 171 172 bath (79 °C) for 1 h to remove siderite and dolomite. After this, the samples were centrifuged and the 173 liquid decanted, this step repeated until the samples were neutralized (on average 2 times). Finally, the 174 samples were oven-dried, re-powdered, and weighed (to measure CaCO₃ loss) and transferred into 175 small tin capsules for mass spectrometry (TOC and $\delta^{13}C_{org}$), at the University of Exeter, Penryn 176 Campus. 177 Charcoal quantification and palynofacies For the SPB interval, 54 samples were prepared for charcoal analysis and 42 for palynofacies at the 178 179 University of Exeter, Streatham Campus. For the LPE interval, an additional 50 macrocharcoal 180 samples were analysed, to compliment a total of 204 macrocharcoal samples for this interval. A total 181 of 162 samples for palynofacies and 200 microcharcoal samples are included in the LPE study 182 interval. Rock samples of 10–30 g weight were split into 0.5 cm³ fragments to minimize the breakage of the 183 organic particles whilst optimizing the surface area for palynological acid maceration. First, the 190 184 samples were treated with 10 % and 37 % HCl to remove carbonate. After this, hydrofluoric acid (40 185 186 % HF) was added to remove silicates from the sample. The samples were left to digest for 48 h, after which cold concentrated HCl (37 %) was added to avoid calcium fluoride precipitation. Each sample 187 188 was left to settle, after which it could be decanted and topped up with DI water, a step that was 189 repeated ~ 6 times in order for the sample to neutralize. After neutralizing, 5 droplets of the mixed residue were taken for the analysis of palynofacies (total 190 191 particulate organic matter) prior to any sieving. The remaining residue was sieved through a 125 µm sieve and a 10 μm sieve to retrieve the macroscopic fraction (> 125 μm) and microscopic fraction 192

193 (10–125 μm). Macroscopic charcoal (>125 μm) was quantified using a Zeiss Stemi microscope, with 194 a 10 x 4 magnification lens and top lighting from a 'goose necked' light source. The entire 195 macroscopic fraction was dispersed in a Petri dish filled with DI water and the number of charcoal particles counted and expressed per 10 g of processed rock (n/g). In some samples large clusters of 196 197 matrix were not digested by the acid, in which case they were taken out and dry weighed to deduce 198 the weight of the total processed rock. Charcoal particles are identified as opaque, black, angular, 199 reflective of light, with lustrous shine, elongated, lacking brown edges, and splintering during breakage, and often showing the anatomical structure of the plant preserved (SI Fig. 1 and SI Table 2, 200 201 Scott, 2000; Scott & Damblon, 2010). 202 Microscopic charcoal (10–125 μm) was analysed on a palynological slide. A known quantity of 125 203 μl of the microscopic fraction was mounted onto microscopic slides using glycerine jelly. A transmitted light microscope (Olympus (BX53)) with a 40 x 10 magnification was used to count the 204 charcoal particles. Four transects per slide were counted, one transect on the left, two in the middle, 205 206 and one on the right of the coverslip. These data were then scaled up to the known quantity of the total 207 sample (Belcher et al., 2005). Palynofacies were examined to record shifts in the type of organic 208 matter (terrestrial vs marine) and potential changes in organic matter preservation and/or terrestrial 209 runoff. Palynofacies were quantified using the optical light microscope and a minimum of 300 organic 210 particles per palynological slide was counted. The types of organic matter were roughly grouped after 211 Oboh-Ikuenobe et al. (2005): terrestrial palynomorphs (spores and pollen), marine palynomorphs (dinoflagellates, acritarchs, prasinophytes and foraminifera test linings), fungal remains, structured 212 213 phytoclasts (wood particles, parenchyma), unstructured phytoclasts (degraded plant remains), 214 charcoal, black debris (palynomorphs filled with pyrite) and amorphous organic matter (AOM: fluffy, 215 clotted and granular masses, colour ranging between almost colourless to yellow and pale brown). 216 XRD clay mineralogy A total of 55 samples were prepared for clay mineralogy spanning the SPB interval and 194 samples 217 for the LPE interval. About 5 g of bulk-rock sample was gently crushed and powdered with an agate 218 mortar, after which about 2–3 g of the powdered sample was decarbonated with a 0.2 M HCl solution. 219 The samples were left to settle for 95 min, after which the suspended clay sized fraction (< 2 µm) was 220 221 extracted with a syringe (following Stokes' law). The clay fraction was centrifuged and subsequently 222 smeared and oriented on glass slides. The samples were analysed by X-ray diffraction (XRD) using a 223 Bruker D4 Endeavour diffractometer (Bruker, Billerica, MA, USA) with Cu Kα radiations, LynxEye 224 detector and Ni filter under 40 kV voltage and 25 mA intensity at the Biogéosciences Laboratory, Université Bourgogne/FrancheComté, Dijon. Three runs were performed per sample to discriminate 225 226 the clay phases: (1) air-drying at room temperature; (2) ethylene-glycol solvation for 24 h; (3) heating at 490 °C for 2 h, following Moore & Reynolds (1997). Comparing the three diffractograms obtained, 227 228 the clay minerals were identified using their main diffraction (d0001) peak. The proportions of each

- 229 clay mineral on glycolated diffractograms was estimated with the MACDIFF 4.2.5 software
- 230 (Petschick, 2000). The identification of the clay minerals further follows the methods in Moore &
- Reynolds (1997) and Deconinck et al. (2019).
- 232 Statistical analysis
- 233 Orbital filters and the charcoal record
- The Pliensbachian of the Mochras core has a well-established astrochronological framework (Ruhl et
- 235 al., 2016; Hinnov et al., 2018; Storm et al., 2020; Hollaar et al., 2021; Pienkowski et al., 2021). Based
- on the existing cyclostratigraphy, the 100 kyr eccentricity cycle lies within the range of 3.2–10.2 m
- 237 (Ruhl et al., 2016; Hinnov et al., 2018), 6.3–4.8 m (Storm et al., 2020), and ~5.3 m (Pieńkowski et al.,
- 238 2021) for the here studied SPB and LPE intervals. These intervals each compromise \sim 7–8 short
- eccentricity cycles. No spectral analysis has been performed on the records presented here because of
- 240 the limited time span represented. Instead, we compare the charcoal and clay records visually with the
- 241 100 kyr and 405 kyr filters based on Ca and Ti (Ruhl et al., 2016; Hinnov et al., 2018). In SI Fig. 2 we
- overlay the 3.2 10 m filter (based on Ruhl et al., 2016) derived from the macrocharcoal record with
- the normalized dataset of the macrocharcoal record.
- 244 Pearson correlation
- A Pearson correlation was used to test for possible correlation between the charcoal abundance (both
- size fractions) and palynofacies and the significance using RMatlab2021. The p value tests the
- 247 hypothesis of no correlation against the alternative hypothesize of a positive or negative correlation,
- with the significance level at p = 0.05. See SI Fig. 3.
- 249 Wilcoxon test
- A Wilcoxon rank sum test was performed in RMatlab2023b to test the H0 hypothesis of equal means
- between the charcoal populations of the LPE and the SPB interval with the significance level at p =
- 252 0.05. The test is performed for the macrocharcoal and microcharcoal records separately.
- 253 PCA analysis
- 254 Principal component analysis (PCA) was performed to explore the potential correlation of charcoal,
- 255 clay mineralogy, palynofacies and mass-spectrometry records for the two studied intervals. This was
- executed in the software PAST on the normalized dataset (macrocharcoal, microcharcoal, TOC,
- 257 CaCO₃, δ^{13} C_{org}, S/I, Sm/K, K/I, phytoclasts).
- 258 3 Results
- The data presented here that cover the run-up to and onset of the SPB (1271–1233 mbs) show a \sim 1.8
- 260 % negative shift in δ^{13} C_{org} spanning the end of the negative CIE limb in the Mochras borehole and
- reaching most negative values. The results of the LPE interval which encompass the run-up and onset
- of the LPE (951 918 mbs), show a rapid positive shift in the δ^{13} C_{org} of ~1.8 % (between 930.8 –

930.4 mbs) (in agreement with Storm et al., 2020).

Large fluctuations are observed in the abundance of both macroscopic (>125 μ m) and microscopic (10–125 μ m) fossil charcoal for both CIEs. For the SPB, microcharcoal abundance fluctuates from $2x10^4$ – $4.2x10^5$ (mean $2x10^5$) particles per 10 g of sediment, and the number of macrocharcoal particles varies from 99–2327 (mean 787) particles per 10 g sediment (Fig. 2, SI Table 3). A similar trend is observed in both size fractions, with individual charcoal peaks fluctuating on a 2–4 m scale (Fig. 2). In the higher resolution LPE interval, metre-scale individual peaks of charcoal abundance are observed, with microcharcoal abundance fluctuating from $4.5x10^3$ – $4.3x10^5$ (mean $1.1x10^5$) particles per 10 g of sediment, and the number of macrocharcoal particles varies from 8–2276 (mean 376) particles per 10 g sediment (Fig. 3, SI Table 3). Longer term fluctuations in the macrocharcoal record are also observed, with bundling of peaks visible every ~4–5 m. Micro- and macro-charcoal are more abundant in the SPB compared to the LPE (Fig. 4). The outcome of the Wilcoxon signed rank test confirms a different median of the SPB and LPE macrocharcoal (H0 rejected, p<0.001) and microcharcoal (H0 rejected, p<0.001).

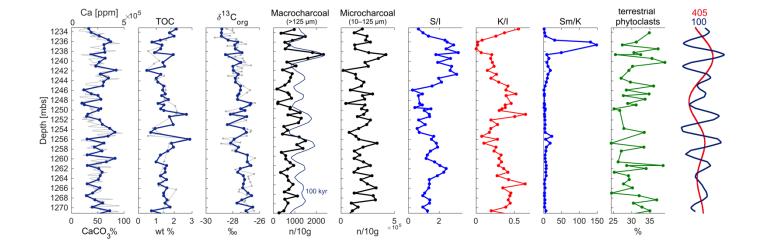


Fig. 2: The SPB studied interval showing all proxies of this study in context of the orbital filters (Ruhl et al., 2016). The $CaCO_3$, TOC and $\delta^{13}C_{org}$ (blue) data obtained for the present study are plotted over previously published data (light grey – Ruhl et al., 2016; Storm et al., 2020). The macrocharcoal abundance shows ~8 increases and decreases throughout the studied interval. These high-low intervals in the macrocharcoal record correspond to the 100 kyr filter (blue; and see SI Fig. 2). The majority of macrocharcoal peaks are mirrored in the microcharcoal fraction. Alternating phases of increase in the smectite/illite ratio (S/I) and the kaolinite/illite ratio (K/I) indicate swings in the hydrological cycle. This is further indicated by the smectite/kaolinite ratio (Sm/K). The percentage of terrestrial phytoclasts shows that the terrestrially sourced organic particles fluctuate around 30% in the studied interval. Finally, the bandpass filters of Ruhl et al. (2016) based on the Ca-elemental



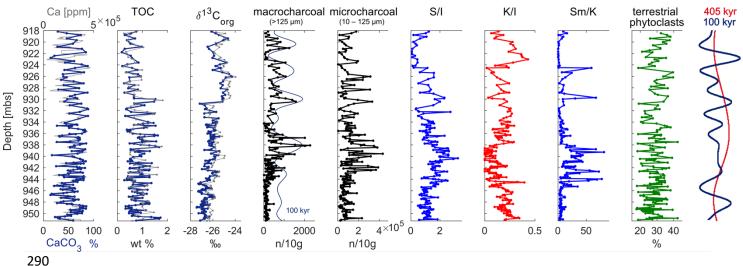


Fig. 3: Synthesis of the LPE interval showing all proxies considered in this study in context of the orbital filters (Ruhl et al., 2016). The $CaCO_3$, TOC and $\delta^{13}C_{org}$ (blue) from Hollaar et al. (2023) are plotted over independently generated data (light grey - Ruhl et al., 2016; Storm et al., 2020). The macrocharcoal abundance shows \sim 7 peaks throughout the studied interval. These 7 increases and decreases in macrocharcoal abundance correspond to the 100 kyr eccentricity (in blue, see SI Fig. 2). The majority of macrocharcoal peaks are mirrored in the microcharcoal fraction. Alternating phases of increase in the smectite/illite ratio (S/I) and the kaolinite/illite ratio (K/I) indicate swings in the hydrological cycle. This is further indicated by the smectite/kaolinite ratio (Sm/K). The percentage of terrestrial phytoclasts shows that the terrestrially sourced organic particles fluctuate around 30 % in the studied interval. Finally, the orbital filters of Ruhl et al. (2016) are placed next to the proxy records. This shows that the clay records shift dominance on a 405 kyr time scale. The peaks in the macrocharcoal record occur on a 100 kyr time scale.

The palynofacies of both intervals is typically marine (AOM>58%). The proportion of terrestrial vs marine organic matter remains relatively stable through both the SPB and LPE, varying between 24.4 and 39.1% (mean 30.7%), and 17.7 and 42.3% (mean 28.9%), respectively. Charcoal accounts for \sim 3.7% and \sim 4.5% of the total particulate organic matter, respectively for the SPB and the LPE intervals (SI Fig. 4). The abundance of macrocharcoal is not influenced by the percentage of terrestrial particulate organic matter through the SPB and LPE intervals (SPB r = -0.12, p = 0.42; LPE r = 0.06, p = 0.46) and nor is the microcharcoal abundance for the SPB interval (r = 0.07, p = 0.62). However, a very weak correlation exists between the percentage of terrestrial phytoclasts and microcharcoal abundance in the LPE interval (r = 0.16, p = 0.05). These results suggest that the preservation and/or

influx of terrestrial particulate organic matter is not the main driver of fluctuations in charcoal abundance.

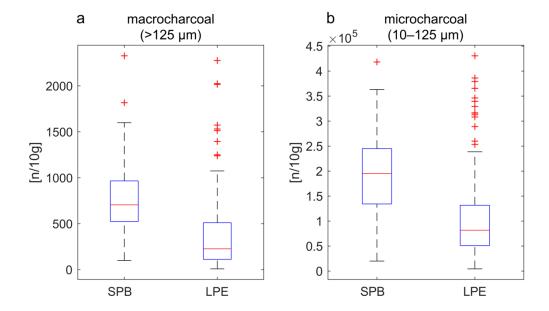


Fig. 4: Distribution boxplots of the macrocharcoal and microcharcoal abundance of the SPB and LPE studied intervals. (a) Average macrocharcoal abundance is higher in the SPB interval compared to the LPE interval, however, the absolute minimum and maximum are similar. (b) Average microcharcoal abundance is higher for the SPB compared to the LPE. The minimum number of microcharcoal particles is lower for the LPE, however, the maximum microcharcoal abundance is similar in both records.

The clay mineral assemblages of the SPB and LPE are dominated by illite, kaolinite and smectite (I-S R0), with smectite increasing in parallel with decreases of illite and kaolinite (SI Fig. 5). Low proportions of chlorite and sparse I-S R1 are present in the SPB record. Chlorite and I-S R1 are generally low in the LPE record but increase between 924–219 mbs (SI Fig. 5). Two smectite-enhanced phases occur for the SPB, at 1264–1255 mbs and 1245–1235 mbs. Both these phases are coeval with high charcoal abundance (both size fractions) (Fig. 2, SI Fig. 6). Additionally, the LPE interval encompasses two stratigraphic intervals rich in smectite; from 944–937 mbs and 931–924 mbs. Charcoal abundance (both size fractions) increases overall, and coevally with the S/I, over \sim 5 m scale fluctuations, and decreases at levels with high K/I (Fig. 3, SI Fig. 7). The 3.2–10.2 m orbital filter of the macrocharcoal records (interpreted as the 100 kyr eccentricity (Ruhl et al., 2016; Hinnov et al., 2018; Storm et al., 2020; Pienkowski et al., 2021)), indicates that the observed fluctuations in the macrocharcoal record occur with a 100 kyr periodicity (SI Fig. 2).

4 Discussion

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337 Charcoal transport and preservation 338 The charcoal records for both the SPB and LPE intervals do not appear to be linked to the terrestrial 339 influx of materials, as evidenced by the palynofacies. No parallel trends are observed between the abundance of terrestrial phytoclasts and the number of charcoal particles, which suggests that the 340 abundance of charcoal is not a reflection of preservation and/or runoff changes. Inferred sea level 341 changes during the LPE and the SPB could potentially have impacted the charcoal abundance record 342 and the clay mineralogy. Transgression and relative sea-level rise during the SPB has been extensively 343 recorded from the Boreal and Tethys regions, and from South America (e.g. Legarreta and Uliana, 344 1996; de Graciansky et al., 1998; Hesselbo & Jenkyns, 1998; Danisch et al., 2019; Silva et al., 2021). 345 The Late Pliensbachian is characterized by widespread regressive facies and inferred relative sea-level 346 347 fall, likely indicating a closer proximity to shore also in the Mochras borehole. Fossil wood in the 348 Mochras borehole has been shown to become more abundant at this time, suggesting a potential bias of higher terrestrial input from a nearby landmass (Ullmann et al., 2022). However, the mean 349 350 abundance of macrocharcoal and microcharcoal is higher during the SPB (mean of 787 and 2x10⁵ respectively) compared to the LPE (mean of 376 and 1.1x10⁵ respectively) in the Mochras borehole, 351 352 suggesting that the shore proximity did not impact overall charcoal abundance. Similarly, the 353 palynofacies analysis indicates that the mean abundance of terrestrial particulate organic matter during 354 the SPB (30.7%) is not higher compared to the LPE (28.9%). Hence, we take this as strong evidence 355 that the record of fossil charcoal records changes in wildfire activity. 356 Orbital forcing of the hydrological cycle and fire 357 Alternations in the dominance of smectite and kaolinite occur approximately every 10 m in both the LPE and SPB records. Kaolinite and smectite reflect hydrological changes in the palaeoenvironment 358 of the Cardigan Bay Basin (Deconinck et al., 2019; Munier et al., 2021). As the smectite and kaolinite 359 360 clay minerals are detrital in character and their abundance varies in opposition to one another (Fig. 2 and 3), these clays are likely derived from pedogenic weathering profiles (Deconinck et al., 2019). 361 362 Smectite preferentially forms under a hot and seasonally arid climate, similar to a monsoonal climate system or the winter-wet climate of the Mediterranean zone (Chamley, 1989; Deconinck et al., 2019). 363 364 Kaolinite is indicative of an accelerated hydrological cycle, increased runoff and a year-round wet 365 climate (Chamley, 1989; Ruffell et al., 2002) either via formation in strong weathering profiles or via 366 the physical erosion of kaolinite-bearing rocks (Chamley, 1989). At times of high smectite abundance, 367 fire activity is greatest as observed from the macro- and micro-scopic charcoal fractions (Fig. 2 and 368 3). Based on the astrochronological framework of the Mochras borehole (Ruhl et al., 2016; Hinnov et al., 2018; Storm et al., 2020; Pieńkowski et al., 2021) these alternations appear to occur in concert 369 with the 405 kyr long-eccentricity cycles (Fig. 2, Fig. 3). Eccentricity modulates the precession driven 370 371 changes in seasonal and latitudinal distribution of insolation (Imbrie & Imbrie, 1980; Berger et al.,

372 1989). One ~20 kyr precession cycle can represent a strongly seasonal extreme climate for ~10 kyr 373 and a weakly seasonal climate for the subsequent ~10 kyr. The geological record averages the 374 amplification or suppression of seasonality between years (SI Fig. 8). Eccentricity forcing modulates the amplitudes of these extremes in seasonality with periodicities of 100 kyr and 405 kyr. 375 In the Mesozoic, eccentricity maxima are commonly associated with dry climates that are disrupted 376 377 by short and intense periods of precipitation and storm activity in the boreal landmasses bordering the NW Tethys (Martinez & Dera, 2015). In contrast, eccentricity minima are characterized by a more 378 379 moderate seasonal contrasts and year-round wet conditions (Martinez & Dera, 2015). Eccentricity minima are linked to periods of enhanced runoff and weathering conditions as evidenced by high 380 kaolinite content, 87 Sr, 86 Sr, and negative shifts in δ^{18} O (Martinez & Dera, 2015). Therefore, we link 381 382 the observed smectite-rich intervals to eccentricity maxima and the kaolinite-rich intervals to eccentricity minima. Charcoal abundance is highest during the seasonal climate of the eccentricity 383 maxima for the SPB (Fig. 2 and 3), in agreement with the previous findings for the LPE (Hollaar et 384 385 al., 2021, 2023). 386 Both the LPE and SPB study intervals span two 405-kyr cycles (Ruhl et al., 2016; Hinnov et al., 2018; 387 Storm et al., 2020; Pieńkowksi et al., 2021). The relative abundance of smectite and the abundance of 388 charcoal both reach a peak during the maxima in the long eccentricity cycle, supporting the notion that orbitally driven changes in seasonal contrast led to high fire activity. Within these long-term 389 390 trends, the macrocharcoal record also shows ~ 5 m scale individual peaks or clusters in both the LPE 391 and SPB records (SI Fig. 2, Fig. 2 and 3). Based on the existing age model (Ruhl et al., 2016; Hinnov et al., 2018; Storm et al., 2020; Pieńkowksi et al., 2021) we derive that this is the expression of the 392 393 ~100 kyr eccentricity cycle in the macrocharcoal record. The bandpass filter representing the ~100 kyr 394 cycle in the Pliensbachian of the Mochras core (derived from the Ca and macrocharcoal records), captures the observed ~5 m oscillations in the fire record (SI Fig. 2, Fig. 2 and 3) (Ruhl et al., 2016; 395 Hinnov et al., 2018; Storm et al., 2020; Pieńkowski et al., 2021). 396 397 The Sinemurian-Pliensbachian transition is generally associated with an overall warm and humid climate (Korte & Hesselbo, 2011; Gómez et al., 2016), and enhanced levels of runoff and weathering 398 399 (Bougeault et al., 2017). The results presented here suggest that within this overall warm and humid 400 background, orbital forcing created year-round wet periods, that were not conducive to frequent fire, alternating with periods that remained warm but had a more seasonal climate, that allowed ignition 401 402 during the dry season. In contrast, the LPE, and the sediments of late Margaritatus ammonite 403 chronozone formed in an overall semi-arid climate with proposed lower runoff levels from the land into the sea (Deconinck et al., 2019; Hollaar et al., 2021; 2023). During the run-up of the LPE we 404 405 infer orbitally forced alternating climatic states of more extreme seasonality (high fire and smectite) 406 and a more equitable year-round wet climate (low fire and high kaolinite) (Hollaar et al., 2021; 2023)

407 acting within this overall semi-arid climate phase. Overall, kaolinite fluctuates in abundance in 408 opposition to smectite, reflecting hydrological changes from wet and hot to semi-arid and hot, in 409 agreement with high fire activity during a seasonal climate and fire suppression during a year-round 410 wet climate for both the LPE and the SPB. 411 Vegetation, fire and the intermediate fire-productivity gradient Fuel (vegetation biomass) and moisture status of the fuel, as governed by seasonal patterns in 412 precipitation and temperature, are the core factors that influence fire behaviour and fire regime 413 (Archibald et al., 2009; Cochrane & Ryan, 2009; Bradstock, 2010; Archibald et al., 2013; Bowman et 414 al., 2014; Archibald et al., 2018). Ecosystems with limited wildfire activity are generally associated 415 with either high precipitation and abundant primary productivity, or low productivity under strongly 416 417 arid conditions (Pausas & Paula, 2012). In contrast, high wildfire activity occurs in climates that are in the middle of the productivity gradient, where during moist periods plant growth is rapid and biomass 418 builds up forming a connected fuel structure. When followed by periods of drought the fuel moisture 419 content is lowered enabling fire ignition and spread (Pausas & Paula, 2012). Additionally, higher 420 sensitivity to fuel moisture levels in the tropical or mesic areas have been noted, where a small fall in 421 422 fuel moisture content can lead to more flammable conditions (Cochrane, 2003). Such that the mid 423 points in the intermediate fire-productivity gradient are further enhanced. The intermediate fire-424 productivity hypothesis (Pausas & Bradstock, 2007; Pausas & Ribeiro, 2013) conceptualizes this relationship between climate-vegetation-fire, where fire activity is plotted along an aridity and 425 426 productivity gradient (Fig. 5). The observed alternating modes of high and low fire activity, as inferred from the lower Jurassic fossil charcoal record, during the onset of the SPB and LPE, likely 427 428 indicates shifts in seasonality of the Cardigan Bay Basin hinterland and would place both the LPE and the SPB at intermediate productivity levels during maximum eccentricity forcing. The deep time 429 combined fire and hydrological records we present here are in agreement with the intermediate 430 431 productivity hypothesis of Pausas & Bradstock (2007) and indicate that even the very different plant functional types and different vegetation assemblages, e.g., a world without grasses, were still subject 432 to this overall fire-productivity gradient control. We indicated on Fig. 5 how these ecosystems without 433 434 grasses and other flowering plants may have looked in respect to typical Jurassic fuel types. We 435 suggest that both the LPE and the SPB switched between a state of low fire (either limited by climatic 436 aridity or the presence and presence and connectivity of fuel) and a state of high fire during which 437 seasonal contrast is high and an ideal 'fire window' exists in which biomass built up during the wet 438 season after which a fire-prone season followed (Fig. 5).

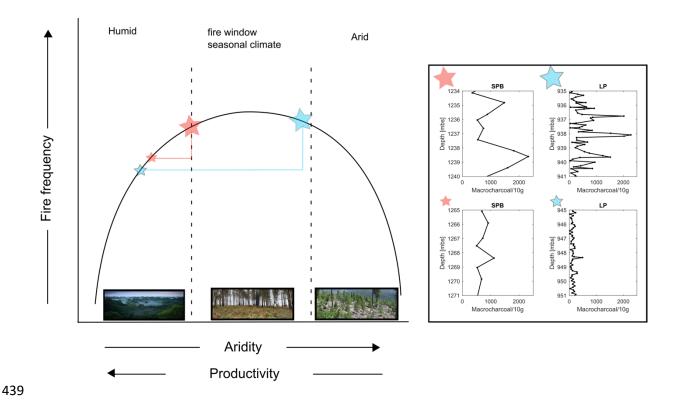


Fig. 5: The LPE and SPB fire records placed on the intermediate productivity gradient. The graph is adapted from Pausas & Bradstock (2007). Fire frequency is highest in the middle of the hyperbola, medium levels of aridity and productivity created a seasonal climate in which seasonal biomass growth was possible (productivity) and seasonally the fuel moisture limits were lower in a season of drought (aridity), this created the optimized 'fire window'. The SPB is plotted on this fire-productivity gradient in red: the small star indicates the eccentricity minimum state and the large star the eccentricity maximum state. The LPE is plotted on the fire-productivity gradient in blue, and again the small star indicates the eccentricity minimum and the large star the eccentricity maximum. The LPE has a larger range compared to the SPB, and experienced more fire suppression due to high humidity levels during eccentricity minima, and also was closer to a productivity limitation state during the eccentricity maximum.

The studied Early Jurassic time-interval likely had five distinct biomes; a seasonal dry (summerwet or subtropical) biome in the low latitudes, a desert biome in the subtropics, narrow latitudinal bands of a winterwet biome at low-mid latitude, and warm temperate and cool temperate biomes at mid- and high-latitudes, respectively (Rees et al., 2000; Willes and McElwain, 2014). The Cardigan Bay Basin was likely positioned within the winterwet biome at approximately 35 °N (Torsvik et al., 2017). It therefore would have sat within the bounds of the fire window of the intermediate fire-productivity hypothesis (Fig. 5). The winterwet biome in both the Sinemurian and Pliensbachian stages were dominated by conifers as the canopy tree, with a mid-canopy vegetation of cycads and tree-ferns, and an understory mixture of seed ferns, horsetails and ferns that likely flourished during wetter periods

460 (Rees et al., 2000; Slater et al., 2019; Bos et al., 2023). This is evidenced from sporomorph data from 461 the Mochras borehole that hosts abundant fossil pollen in the Sinemurian and Pliensbachian (>94%) 462 (Van de Schootbrugge et al., 2005). Additionally, nearby locations also show evidence of orbitally paced shifts in vegetation assemblages from sites at St. Audries Bay, UK and in NW Germany (Bonis 463 464 et al., 2010; Bos et al., 2023). During the 100 kyr eccentricity maxima in the UK pollen from the dry-adapted cheirolepidacean 465 conifers is found to be highly abundant (Bonis et al., 2010). Whilst, in Germany a mire-conifer 466 community is apparent with sporomorphs indicating variations in abundance of ferns and fern allies 467 occurring over a 405-kyr eccentricity cycle, with ferns most abundant during eccentricity maxima 468 (Bos et al., 2023). 469 470 Dry-adapted vegetation, such as the cheirolepidacean conifers likely thrived during more extreme seasonal droughts, maintaining their biomass. In contrast, ferns and fern allies, and mire-conifers as 471 472 humid-loving plants would grow rapidly during sustained, year-round, periods of rainfall (eccentricity 473 minima), likely inhabiting both open environments and colonising the understory of conifer forests. 474 Furthermore, they would also be able to build dense connected fuel loads during the wet-season of 475 eccentricity maxima, that were then easily dried during the annual dry-season. Ferns, when cured, 476 carry high intensity fires (Adie et al., 2011; Belcher and Hudspith, 2016) and during the Mesozoic 'fern prairies' have been linked to intensive surface fires (Harris, 1981; Van Konijnenburg-Van Cittert, 477 478 2002; Collinson et al., 2007, 2009). Hence, they are suggested to have functioned in a similar fashion 479 to support fires as grasslands and fern stands do today; Mesozoic fern prairies and savannahs therefore likely filled a similar ecological niche to grasses in the modern day (Belcher, 2013 and references 480 481 therein). Ferns are indeed a common feature of Mesozoic charcoal assemblages, showing their 482 association with fire throughout time (e.g. Collinson et al., 2000; Brown et al., 2012). In the present-day, temperature is an important regulator of fire occurrence. Whilst dead fuel moisture 483 (e.g. that of litter and cured herbaceous components) is primarily influenced by the variability in 484 relative humidity, live fuels are controlled by the combination of temperature and moisture 485 availability, where long periods of drought or heat wave extremes can strongly influence the 486 flammability of live fuels. Sea surface temperatures (TEX⁸⁶) during the Sinemurian and Pliensbachian 487 488 were at times apparently higher than 28 °C (Robinson et al., 2017). But high-resolution temperature reconstructions are lacking for the Early Jurassic. Orbital forcing of regional-global seawater 489 490 temperatures occurred throughout the Cenozoic (Westerhold et al., 2020), and likely also the 491 Mesozoic; however, the climate response to changes in orbital insolation is non-linear, and the mean 492 annual insolation is not impacted by precession (Rubicam, 1994). Therefore, the biomes of the SPB 493 not only existed in an overall warm world that was characterized by background orbitally driven

climate shifts across the moister side of the fire-productivity gradient, but superimposed on this live fuels were also responsive to extreme weather linked to periods of drought and heat.

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We propose that the overall humid climate of the SPB fits the high productivity scenario, in which the frequency of flammable conditions is the main factor controlling fire occurrences. No evidence was found to place the SPB on the productivity-limiting high-aridity side of the fire-productivity gradient, where fire frequency would have been mainly influenced by enhanced rainfall in an otherwise dry climate. These findings are in line with the presence of plant cuticle through the studied record, indicating the presence of vegetation throughout this time period and during both phases of high and low modes of fire activity. Hence, the SPB seems to conform to the humid and high productivity end of the aridity gradient (Fig. 5 red lines). Within these constraints (Fig. 5) the SPB is characterized by likely two states across the fire productivity gradient. The biome was situated at the wetter, low fire side of the fire-productivity gradient during eccentricity minima (Fig. 5), and at the seasonal, high fire end of the fire-productivity gradient during eccentricity maxima (but only for each precession halfcycle) (Fig. 5). The fluctuations detected in the present study for the SPB occurred over both long-eccentricity and short eccentricity timescales in the macrocharcoal record, showing longer phases of overall enhancement of fire (405 kyr eccentricity) and relatively abrupt shifts from low to high fire and back again (~100 kyr eccentricity). For this reason, the SPB is placed on a steep portion of the fire-

productivity gradient curve (Fig. 5). Overall, the mean charcoal abundance is relatively high, and no sustained periods of very low charcoal abundance are observed in the SPB record, which indicates that the climate never became too wet to fully limit fire activity at that time.

The Late Pliensbachian has been linked to a global cooling event, with a potential of 5–7 °C lowering in temperature inferred for the NW Tethys region (Korte et al., 2015). The atmospheric moisture holding capacity of a cooler climate is lower compared to a warm climate, in which a 1 °C cooling likely lowers the water holding capacity of air by 7% (Trenberth et al., 2005). The presence of terrestrial phytoclasts throughout confirms the presence of vegetation in the surrounding landmasses throughout this period. The mean abundance of charcoal for the LPE section is slightly lower than that of the SPB and the lowest charcoal abundances are coeval with a K/I enhancement, suggesting that during eccentricity minima environmental conditions moved further into the humid zone of the fireproductivity gradient (Fig. 5 blue line). Increasing eccentricity shifted the system to a more seasonal climate where the fire and clay records indicate the presence of a wet season that allowed for build-up of biomass followed by a dry season in which fire was able to be ignited and spread.

Conceptually, the relatively drier and cooler LPE climate would have resulted in conditions that are more arid, shifting to the biomass-limited part of the productivity/ aridity – fire frequency gradient

during eccentricity maxima, compared to the SPB (Fig. 5 blue lines). This is supported by the large fluctuations observed between low fire frequency and high fire frequency for the LPE and the fact that estimated high fire periods did not occur suddenly, but rather were sustained over a larger part of the cycle. Therefore, the phase of highest fire frequency operating in the seasonal 'fire window' as indicated in figure 5 for the LPE (blue lines) likely occurred for a larger part of the fire productivity gradient. Hence, conditions across the LPE occurred across a wider range of the productivity/aridity spectrum of the fire frequency gradient (Fig. 5 blue lines) compared to the SPB. There is no evidence that conditions ever became limited by aridity, and conditions during the LPE did not extend beyond the seasonal fire window into the arid part of the productivity/aridity spectrum of the fire frequency gradient.

Importantly, the Jurassic climate was overall warm and humid, about 5–10 °C warmer on global average compared to today (e.g., Rees et al., 2000; Sellwood & Valdes, 2008), with \sim 3.5–10 times the pre-industrial value of atmospheric pCO_2 during the Early Jurassic (e.g. Retallack, 2001; Beerling & Royer, 2002; McElwain et al., 2005; Berner, 2006; Steinthorsdottir & Vajda, 2015; Li et al., 2020). In this context, it may not be surprising that a relative cooling event in the Early Jurassic did not lead to the aridity and biomass-limiting conditions observed during the last glacial period, at latitudes of \sim 38 °C N (Daniau et al., 2007).

5 Conclusions

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The study of two different climatic 'background' states, at the LPE and the SPB, shows that fire activity was strongly modulated by orbital eccentricity cycles. The 405 kyr shifts in the record of wildfire prevalence reflect similar changes also in the hydrological cycle (based on clay mineralogy data) showing that high fire activity occurred during periods of high seasonal contrast and that fire activity was suppressed during periods of high year-round humidity, because the latter would have enhanced the fuel moisture levels and prevented frequent ignition and sustained fire spread. The fire record of both climatic events is limited by the high fuel moisture levels during eccentricity minima, but fires were more prevalent during times of increased seasonality, every precession half-cycle during eccentricity maxima. Hence, during both events fire activity was limited by fuel moisture content and not by productivity. Both the SPB and the LPE climate systems were therefore situated on the moisture-limited side of the intermediate fire-productivity gradient (Fig. 5). Due to the lower moisture-holding capacity of cold air, the overall higher seasonality of the Late Pliensbachian and the more sustained high fire-frequency periods (based on the charcoal record for the LPE) we place the LPE towards the higher end of the aridity gradient, within maximum seasonality and maximum fire frequency window of the fire productivity graph (Fig. 5). The SPB fire regime reflected a more humid climate that shifted abruptly between low fire frequency to high fire frequency within less extreme bounds on the aridity gradient. This research reveals that the intermediate-fire productivity hypothesis (Pausas & Bradstock, 2007) can also be applied to high-resolution deep time records, before the

565	evolution of grasses and that this hypothesis explains well the influence of orbital cycles within
566	different overall climate states, be they cooling or warming trends. The coupling of high-resolution
567	clay mineralogy and fossil charcoal records, combined with constraints on orbital forcing at such
568	time, allows for inferences on how Earth's natural climate state variability has driven shifts in
569	terrestrial productivity through the geological past.
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574	of Exeter.
575	Conflict of Interest
576	The authors declare no conflicts of interest relevant to this study.
577	Data Availability Statement
578	Supplementary data are available at the National Geoscience Data Centre at Keyworth (NGDC)
579	at https://doi.org/10.5285/1461dbe5-50a8-425c-8c49-ac1f04bcc271 (Hollaar, 2022) for the interval
580	934–918 m. b.s. All data presented for the interval 951–934 m. b.s. are available at the National
581	Geoscience Data Centre at Keyworth (NGDC) at https://doi.org/10.5285/d6b7c567-49f0-44c7-a94c-
582	e82fa17ff98e (Hollaar et al., 2021b). All data for the interval 1271–1233 mbs is deposited at the
583	University of Exeter: http://hdl.handle.net/10871/133255.
584	Supporting Information
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