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The contribution of fire to the late Miocene spread of grasslands in eastern Eurasia (Black Sea region)

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Grasslands are globally extensive, but the processes governing their ecology and evolution remain unclear. The role of fire for the expansion of ancestral C₃ grasslands is particularly poorly understood. Here we present the first biomass combustion record based on late Miocene to Pleistocene (~10–1.9 Ma) charcoal morphologies (grass, herbs, wood) from the Black Sea, and test the extent of fire events and their role in the rise of open grassy habitats in eastern Eurasia. We show that a mixed regime of surface and crown fires under progressively colder and, at times, drier climates from the late Miocene to Pliocene (8.5–4.6 Ma) accelerated the forest to open woodland transition and sustained a more flammable ecosystem. A tipping point in the fire regime occurred at 4.3 Ma (mid-Pliocene), when increasingly cold and dry conditions led to the dominance of grasslands, and surface, litter fires of low intensity. We provide alternative mechanisms of C₃ plant evolution by highlighting that fire has been a significant ecological agent for Eurasian grasslands. This study opens a new direction of research into grassland evolutionary histories that can be tested with fossil records of fire alongside climate and vegetation as well as with dynamic vegetation models.

Grasslands have among the world's highest species diversity, harbor endemic and threatened plant and animal species, and provide critical ecosystem services¹. However, limited knowledge of the ecological processes governing grassland function and evolution has contributed to the loss of grasslands with cascading, negative consequences for biodiversity¹. Research on the evolution and expansion of grasslands reveal that the rise of this ecosystem was a long process occurring asynchronously across continents^{2–4}. For example, the ancestral C₃ savanna mosaic spread during the mid to late Cenozoic (~55–33 Ma), whereas C₄-dominated open habitats, better adapted to high temperatures, low water availability, and low CO₂ concentration, expanded during the late Neogene (~10–8 Ma)^{2,5}. In Europe, fossil plant records (pollen, macrofossils) show that open biome development started during the early to middle Miocene (~20 Ma), though full development occurred since the late Miocene (~10 Ma)⁴. In contrast, eastern Mediterranean phytolith remains (microscopic silica bodies abundantly produced in grass tissues and better preserved in drier environments) show that grass-dominated habitats were prevalent by the early Miocene (~20 Ma)⁶.

Several drivers have been put forward to explain forest loss and the expansion of an open grassy biome. Earlier hypotheses highlighted declining atmospheric CO₂ concentrations and temperatures and increased aridity and seasonality of precipitation as the main drivers of grassland spread^{5,7}. More recently, hypotheses have focused on the influence of local-scale factors such as fire and herbivores^{4,8,9}. The critical role of fire in the rise of the savanna mosaic has been confirmed from fossil pollen, charcoal, and leaf wax *n*-alkanes records in C₄-dominated grasslands in southern Africa¹⁰. However, whether variations in fire disturbances have contributed to the forest-grassland transition in Eurasian C₃-dominated grasslands remains unclear. The involvement of fire is likely because the ancestral transition from forest to open grassy biome occurred in C₃ species, but the rise of grasslands are explained based on processes that maintain tree-grass interactions in C₄-dominated ecosystems³. Furthermore, recent studies from non-forested ecosystems (grasslands, shrublands, savannas) question the view of climate as the only driver of vegetation, and increasingly emphasises the role of disturbance by fire and herbivores^{11,12}.

To test the hypothesis that fire contributed to the rise of C₃-dominated open habitats in eastern Eurasia, we used the charcoal morphology record of biomass burning from the Deep Sea Drilling Program (DSDP) 42B

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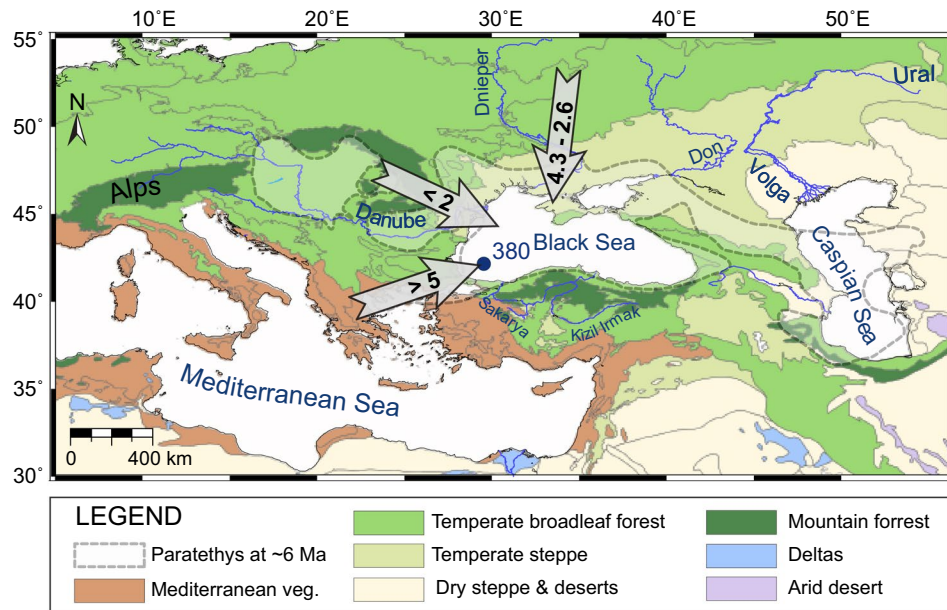


Figure 1. Sediment transport into the Black Sea. Major rivers draining into the Paratethys highlight major sediment transport routes²⁶. Arrows show the dominant direction of sediment transport into the Black Sea during the assigned ages¹⁶ whereas the bold numbers denote Ma. The location of DSDP Site 380/380 A in the Black Sea is indicated by the blue dot labelled '380', along with modern vegetation distribution in the entire region.

380 A core retrieved from the Black Sea. This 1075 m thick core represents the longest and most complete existing record of the late Miocene to Pleistocene (~10 to 1.9 Ma) Black Sea sedimentary and climatic history. Charcoal morphotypes (grass, forbs, wood) provide evidence of major changes in: i) the source of the fuel burnt (herbs vs. wood), ii) fire type (low intensity- surface vs. high-intensity crown fires), and iii) grassland community dynamics. Charcoal is one of the most robust proxy of past fire frequency and fuel type, however, the amount of charcoal does not reflect the fire history per se, but how charcoal resulting from fires is produced, transported, and incorporated into sediments¹³. Our study is the first approach to quantify the long-term extent of fires in temperate open habitats of Eurasia, providing a new view on the ecology and evolution of C_3 grasslands independent of the C_4 pathway.

Results and Discussion

Evidence for changes in sediment provenance and charcoal. Charcoal arriving in marine environments follows two main routes: atmospheric deposition in the case of smaller particles and riverine discharge for small and large particles alike^{14,15}. Today, the Danube provides 53% of the fresh water and sediment discharge into the Black Sea, the Dnieper and Don provide about 30%, and rivers flowing from the south and southeast ~4% (Fig. 1). However, source-to-sink analysis shows that the provenance of Black Sea sediments 1050–755 m below sea floor (mbsf) (~10–5 Ma) was predominantly from southerly to southwesterly sources such as the Balkan and Anatolian rivers (Fig. 2a)¹⁶. A transition to a northerly Russian Platform source with episodic delivery of sediments from the Danube occurred between ~5 and 4.3 Ma (755–708 mbsf), and sediments were sourced almost solely from the Russian Platform between ~4.3 and 2.6 Ma (708–651 mbsf). The influx of Danube-supplied sediment to the southwestern Black Sea began after ~4.3 Ma¹⁶, however, the final arrival of Danube sediments into the Black Sea took place during the Pleistocene i.e., 571 mbsf (~2 Ma)^{16–18}.

Evidence for changes in fire regimes and vegetation communities. The charcoal record of DSDP 42B 380 A shows an increase in total charcoal concentration from ~0–25 pieces/cm³ at the base of the core (1050 mbsf, ~10 Ma) to maximum values in the profile (~50–250 pieces/cm³) between 920 and 700 mbsf (~8.5–4.3 Ma), and a subsequent decline of charcoal abundance to minimum values in the record (~0–5 pieces/cm³) between 700 and 540 mbsf (~4.3–1.9 Ma; Figs 2c and S2). Poaceae and forb (herbs) charcoal morphotypes are co-dominant between 1050 and 920 mbsf (~10–8.5 Ma), herbaceous (70–90%) and woody charcoal (10–30%) are mixed between 920 and 750 mbsf (~8.5–5 Ma), and charcoal became almost exclusively of herbaceous type between 700 and 540 mbsf (~4.3–1.9 Ma; Figs 2c and S2). Charcoal became smaller in size from the base (~10 Ma) to ~4.3 Ma, and became larger again between ~4.3 and 1.9 Ma (Fig. 2). Peak charcoal concentrations of notably high magnitude and large particle size are at 850, 785, and 701 mbsf (~6.1, ~5.33, and ~4.3 Ma, respectively; Fig. 2c). The peak at ~6.1 Ma corresponds to Pontian flooding in the Paratethys, a time of marine ingress from the Mediterranean Sea¹⁹. The peak at ~5.33 Ma closely coincides with Pliocene flooding, when Atlantic waters invaded the Mediterranean Sea and briefly reached the Black Sea¹⁹. Only the peak at 701 mbsf corresponds to a change in sediment provenance (Fig. 2a,c).

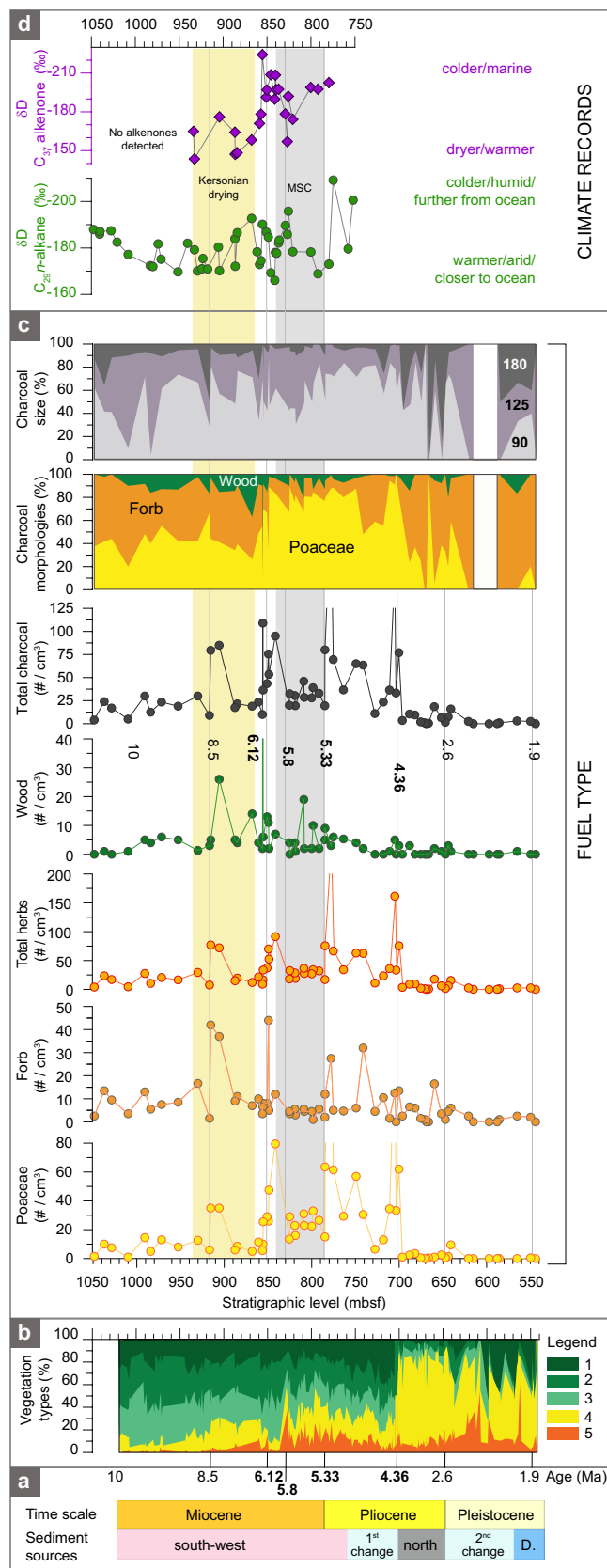


Figure 2. Biomass burning, fuel type, vegetation, and climatic conditions during the Miocene to early Pleistocene (~10–2 Ma). (a) Changes in sediment provenance;¹⁶ 'D' is Danube) are shown within the chronological framework of this study. (b) The relative abundance of five ecological groups based on the pollen record:²⁰ 1 = subtropical forest, 2 = warm temperate forest, 3 = coniferous forest, 4 = herbs, and 5 = steppe elements. (c) Biomass burning reconstructed from total charcoal concentrations and percentages and fuel type

and fire intensity based on charcoal morphologies (Poaceae, forbs, wood). Total herbs sums Poaceae and forb morphotypes. Poaceae and forb morphologies originate from burning by low-intensity surface fires, whereas wood morphology primarily originates from severe burning of the tree crown. Charcoal class size (90, 125 and 180 μm) is given in percentages. **(d)** Climatic conditions derived from the hydrogen isotopic compositions (δD) of C_{29} long-chain *n*-alkanes and C_{37} alkenones (an evaporation proxy) from the same DSDP core²⁴. 'MSC' denotes the Messinian Salinity Crisis.

The pollen-based vegetation reconstruction²⁰ indicates stepwise changes in main ecological groups (Fig. 2b). The percentages of herbs (Poaceae, Asteraceae, Brassicaceae, etc.) and steppe elements (*Artemisia* and *Ephedra*) were low (~10%) until 940 mbsf (~8.5 Ma), whereas those of subtropical, warm temperate and coniferous forests show an almost equal representation. The percentages of herbs (grasses and forbs) and steppic plants rose to ~20–30% between 940 and 700 mbsf (~8.5–4.3 Ma), coincidentally to the decline in all forest types (Fig. 2b). Herbaceous pollen percentages increased abruptly to ~80% at 700 mbsf (~4.3 Ma) and remained dominant until 540 mbsf (~1.9 Ma).

Two main patterns in the dynamics of the dominant fuel type burnt and the development of grass and forb habitats are apparent in the charcoal morphotype record from the Black Sea core (Fig. 2c). First, we recorded the greatest biomass burning and fire of high-intensity when mixed herbaceous and woody fuels were prevalent during the late Miocene (~8.5 Ma) to the early and middle Pliocene (~5.33–4.3 Ma). Biomass burning declined markedly and fire were of low-intensity from the late Pliocene to the early Pleistocene (~4.3–1.9 Ma) when fuel originated predominantly from herbaceous plants (Fig. 2b,c). Second, there is a strong association between increased biomass burning, particularly of grass (Poaceae) fuel, at ~8.5 Ma and the rise in dominance of grass and forb habitats as inferred from pollen records (Figs 2b,c and S2). The charcoal and pollen records thus provide strong evidence for a shift from mixed surface and crown fires during the transition from closed forests to open woodlands during the late Miocene and early Pliocene (~8.5–4.3 Ma) towards surface fires when open grassy biomes dominated during the Pliocene to early Pleistocene (~4.3–1.9 Ma).

The link between fire and vegetation turnover: implication for grassland expansion. Although grasslands are poorly competitive against trees, they tolerate soils with permanent or seasonal moisture deficits, temperature extremes, and disturbances by fires and herbivores, which otherwise limit the establishment and growth of woody plants²¹. It has been shown that the global tendency towards cool and arid conditions that characterised the late Miocene gave rise to an open biome^{22,23}, although the extension of grass-dominated habitats in the Mediterranean region has been demonstrated to occur as soon as the early Miocene⁴. The onset of the expansion of open habitat vegetation from ~8.5 to 5.97 Ma in the Black Sea region was concurrent with slightly enhanced biomass burning (Fig. 2b–d) and largely increasing evaporative conditions in the Black Sea basin, as indicated by the alkenone-based hydrogen isotopic (δD) record (an evaporation proxy) measured from the same core²⁴. The presence of carbonate nodules requiring strong climate seasonality show that evaporative conditions affected the entire circum-Black Sea region around 8.5 Ma^{25–28}. This part of the sedimentary sequence is primarily sourced from the Balkans and Anatolia, although charcoal fragments transported by water and air could have originated from the entire Black Sea region (Fig. 1). A pytholith-based vegetation reconstruction from Turkey indicates a C_3 -grass-dominated savanna mosaic at that time⁶. Similarly, stable carbon isotopic analyses ($\delta^{13}\text{C}$) of palaeosols from the Greco-Iranian region and pollen records from Bulgaria indicate the development of open vegetation in the late Miocene^{6,29}. Further support for the progressive drying of the late Miocene environment (~8–5.3 Ma) around the Black Sea and Eastern Mediterranean is found in the rise of large mammals adapted to open habitats^{30,31}. It is therefore probable that the warm and especially dry climatic conditions that prevailed during large intervals between ~8.5 and 5.97 Ma around the Black Sea may have led to the drying of fuels in the subtropical-warm temperate deciduous-coniferous forests and promoted mixed surface and crown fires. An increasing proportion of herbaceous plants in formerly closed forests may have provided a favorable fuel mix, i.e., fine herbs and coarse wood, therefore escalating ignition potential, flammability, and fire spread³².

Climatic conditions became increasingly dry and temperatures declined during the late Miocene to middle Pliocene (~5.97–4.3 Ma), especially in the northern Black Sea^{24,26,27,29}. Though fluctuating, biomass burning peaked and the more frequent fires likely promoted grassland expansion, accelerated the forest to open woodland transition and sustained a more flammable ecosystem (Figs 2b,c and S2). Studies of grass evolution in tropical savannas (C_4 -type) indicate that their fine fuels with rapid curing, low bulk densities, and fast regrowth rates led to frequent surface fires, and that woody species, adapted to infrequent fires, were unable to complete their life cycle^{5,9,33,34}. Sediment provenance analysis suggests continued sediment transport from the Balkan and Anatolian rivers (Fig. 1), thus areas increasingly covered by open vegetation, although this source becomes uncertain towards the later part of this interval, i.e., ~5.33–4.3 Ma (Fig. 2a). Pollen records from northern regions (i.e., the Ukrainian Plain) corroborate an increasingly cold and dry climate along a west-to-east gradient during this time, and vegetation dominated by forest-steppe and open xerophytic herbs²⁹. It is noteworthy that the sustained decline in biomass burning from ~5.8 to 5.33 Ma was coeval with the Messinian Salinity Crisis (Fig. 2d), a period characterised by a large disruption in the regional hydrological cycle, a major water level drop in the Mediterranean Sea³⁵, and enhanced northern hemisphere glaciation that culminated during the TG 20 and TG 22 glacial peaks³⁶.

A tipping point in the fire regime occurred at ~4.3 Ma and the new established fire regime lasted at least until the end of our record (~1.9 Ma, early Pleistocene). It is evident as a decrease in burning activity, the predominance of herbaceous charcoal fuel and the maximum extent of grassy vegetation (Figs 2b,c and S2). A regional differentiation in climate, vegetation, and fauna assemblages was apparent between ~4.2 and 2 Ma, when Central

and Eastern Europe (the major source feeding sediments into the Black Sea at that time) remained arid, while the Mediterranean region became more humid^{23,30,37}. We propose that low vegetation productivity and thus fuel availability of grassy vegetation limited the biomass burned yet, surface fires were perhaps frequent. Low amounts of burned biomass and/or frequent fires have been documented in modern low productivity grassy environments and during past dry and cold climatic periods of slow vegetation growth and fuel accumulation^{15,38–41}. Herbivores are also known to remove vegetation load, leading to reduced fuel availability and therefore biomass burned⁴². By ~15 Ma, ca. 25% of the world's mammals were typically hypsodont grazers and 35% of mixed diet⁴³, whereas hypsodont grazers rose to dominance in Eurasia from ~8 to 4.5 Ma^{23,37}. It is therefore probable that the observed decline in biomass burning may have also been a response to increased grazing pressure and reduced fuel availability.

We further tested whether periods of high fire occurrence coincided with increased representation of C_4 plants in the surrounding vegetation, as this vegetation type has a strong competitive advantage under frequent fires^{5,44}. In eastern Eurasia, C_3 plants dominated throughout the Neogene, whereas C_4 grasses were of little ecological importance^{6,7}. The $\delta^{13}C$ values of C_{29} long-chain n -alkanes from the same Black Sea record covering the period ~10–5 Ma are in the range of C_3 plant communities (–27 to –30‰; Fig. S2). This indicates that the enhanced late Miocene fire activity was associated with the dominance of C_3 grasses and further highlights that fire has been a significant ecological agent for C_3 plants in the Black Sea region. Simulated late Miocene vegetation scenarios for Africa, show that fire allowed both C_3 and C_4 grasses to expand into forests⁹.

Conclusion

We provide a unique charcoal morphotype record of the role of fire disturbances in the spread and evolution of temperate grassy ecosystems in Eurasia and identify mechanisms that controlled biomass burning in the Black Sea region over six million years. Results show that progressively colder and episodic dry climatic conditions from the late Miocene to middle Pliocene (~8.5–4.3 Ma) promoted fire activity, accentuated the forest-grassland transition, and sustained a more flammable ecosystem. A tipping point in the fire regime occurred at ~4.6 Ma, when the dominance of open grassy vegetation limited biomass productivity and fuel availability and connectivity, leading to surface, low intensity, but likely frequent fires. As the transition to this new vegetation state (grasslands) was associated to an abrupt shift in fire regime, it suggests thresholds in tree-grass cover which, when crossed, resulted in shifts in fire regime. Our results provide an alternative view on grassland ecology and evolution by showing that fire has been a significant ecological and evolutionary agent in temperate C_3 -plant-dominated open habitats in Eurasia. Critically, we provide a new framework for better understanding the evolution of temperate grasslands and testing new predictions using fossil charcoal records alongside those for climate and vegetation, as well as dynamic vegetation models.

Methods

The DSDP 42B 380 A core (42° 05.94'N, 29° 36.82'E) represents a 1075-m-thick late Miocene to Quaternary (~10 to 0.5 Ma) sedimentary record from the Black Sea⁴⁵. The construction of geochronological framework was performed through combined magnetostratigraphy and ⁴⁰Ar/³⁹Ar dating^{46,47} as well as novel biomarker geochemistry and pollen records^{24,48,49}. [See Fig. S1].

Charcoal-based reconstruction of biomass burning and grassland dynamics. We estimated changes in regional biomass burning in the Black Sea region by analysing sedimentary charcoal in 65 levels of approximately 2 cm³ each from the 1075–550 mbsf section, representing the late Miocene to the Pliocene (~10 to 1.9 Ma). Each sample was bleached and wet sieved to 90, 125, and 180 μm respectively, resulting in a total of 195 samples. Sedimentary charcoal pieces were categorised into three main morphotypes (grasses, forbs and wood). The size class and morphotype separation allows us to: a) better constrain the charcoal source area^{50,51}, where the finer particles (90 and 125 μm) are sourced farther away than the larger particles (180 μm), and b) provide additional information on the fuel source and fire severity, where grass and herb morphotypes primarily originate from low-intensity surface fires and wood from high-intensity crown fires^{51–56}. Crown fires also supply larger charcoal particles and in greater amounts than surface herbaceous fires^{51,57}. The remaining material was transferred to a Petri dish, counted, and examined under a stereoscope at 30–60X magnification. Opaque, rectangular particles were classified as charcoal, and some had preserved anatomical structures. The source of the main morphotype categories are: 1) grasses (Poaceae), 2) forbs resulting from the burning of herbaceous plants other than grasses, and 3) wood (ligneous material) following previously described methodologies^{51–56}. We note the rare occurrence of other morphologies such as roots (charcoal likely derived from roots, stolons, rootlets) and deciduous leaves. The resulting macroscopic charcoal counts are expressed as the concentration of total particles (particles/cm³) and the concentration of each charcoal morphotype by dividing the counts by the sediment volume (Fig. 2c). We calculated percentages of each charcoal morphotype and size using the sum of charcoal counts (Figs 2 and S2).

Theoretical functions and calibrations for the relationship between fire and charcoal production and deposition in sedimentary basins suggest that increased charcoal levels may correlate with fire severity (fuel consumption per fire episode)^{58,59}, and the size of the area burnt at the ecosystem scale^{13,60}. Distance from the fire source, charcoal transport and deposition can also affect charcoal accumulation [3,60]. Therefore our reconstructed rise in biomass burning integrates information about the increase in area burnt, severity of fire events but also the proximity of the fire source and transportation.

Pollen-based reconstruction of vegetation. To determine past vegetation dynamics we used a published pollen-based vegetation record from the same core²⁰. We extracted five main ecological groups following the classification of²⁰. These are: 1 = subtropical forests (*Buxus colporate* *Canthium*, Acanthaceae,

Sapindaceae, Sapotaceae, *Bombax*, Taxodiaceae, Arecaceae, *Engelhardia*, *Platycarya*, *Distylium*, *Hamamelis*, etc); 2 = warm-temperate forests (*Quercus*, *Carya*, *Pterocarya*, *Carpinus*, *Ulmus*, *Tilia*, *Alnus*, *Betula*, etc); 3 = coniferous forests (*Pinus*, *Picea*, *Abies*, *Tsuga*, *Cedrus*); 4 = herbs (Poaceae, Asteraceae, Brassicaceae, Lamiaceae, Chenopodiaceae, etc); and 5 = steppe elements (*Artemisia* and *Ephedra*).

Data Availability

The charcoal datasets will be made available online and deposited into PANGEA.

References

- Veldman, J. W. *et al.* Tyranny of trees in grassy biomes. *Science* **347**, 6221 (2015).
- Edwards, E. J. *et al.* The origins of C₄ grasslands: integrating evolutionary and ecosystem science. *Science* **328**, 587–91 (2010).
- Strömberg, C. A. E. Decoupled taxonomic radiation and ecological expansion of open-habitat grasses in the Cenozoic of North America. *Proc. Natl. Acad. Sci. USA* **102**, 11980–11984 (2005).
- Strömberg, C. A. E. Evolution of Grasses and Grassland Ecosystems. *Annual Review of Earth and Planetary Science* **39**, 517–544 (2011).
- Osborne, C. P. & Beerling, D. J. Nature's green revolution: the remarkable evolutionary rise of C₄ plants. *Phil. Trans. R. Soc. London Ser. B-Biological Sci.* **361**, 173–194 (2006).
- Strömberg, C. A. E., Werdelin, L., Friis, E. M. & Sarac, G. The spread of grass-dominated habitats in Turkey and surrounding areas during the Cenozoic: phytolith evidence. *Palaeogeogr Palaeoclimatol Palaeoecol.* **250**, 18–49 (2007).
- Cerling, T. E. *et al.* Global change through the Miocene/Pliocene boundary. *Nature* **389**, 153–158 (1997).
- Osborne, C. P. A. ecology and evolution: What drove the Miocene expansion of C₄ grasslands? *J Ecol.* **96**, 35–45 (2008).
- Scheiter, S. *et al.* Fire and fire-adapted vegetation promoted C₄ expansion in the late Miocene. *New Phytol.* **195**, 653–666 (2012).
- Hoetzel, S., Dupont, L., Schefuß, E., Rommerskirchen, F. & Wefer, G. The role of fire in Miocene to Pliocene C₄ grassland and ecosystem evolution. *Nat. Geosci.* **6**, 1027–30 (2013).
- Feurdean, A., Ruprecht, E., Molnár, Z. S., Hutchinson, S. M. & Hickler, T. Biodiversity-rich European grasslands: Ancient, forgotten ecosystems. *Biol. Conserv.* **228**, 224–232 (2018).
- Pausas, J. G. & Bond, W. J. Humboldt and the reinvention of nature. *J Ecol.* **00**, 1–7, <https://doi.org/10.1111/1365-2745.13109> (2018).
- Duffin, K. I., Gillson, L. & Willis, K. J. Testing the sensitivity of charcoal as an indicator of fire events in savanna environments: quantitative predictions of fire proximity, area and intensity. *Holocene* **18**, 279–291 (2008).
- Verardo, D. & Ruddiman, W. Late Pleistocene charcoal in tropical Atlantic deep sea sediments. Climatic and geochemical significance. *Geology* **24**, 855–857 (1996).
- Daniau, A. L. *et al.* Orbital-scale climate forcing of grassland burning in southern Africa. *Proc. Natl. Acad. Sci. USA* **110**, 5069–5073 (2013).
- de Leeuw, A., Morton, A., van Baak, C. G. C. & Vincent, S. J. Timing of arrival of the Danube to the Black Sea: Provenance of sediments from DSDP site 380/380A. *Terra Nova* **30**, 114–124 (2018).
- Maynard, J. R., Ardic, C. & McAllister, N. *Source to sink assessment of Oligocene to Pleistocene sediment supply in the Black Sea*. In N. C. Rosen, *et al.* (Eds), 32nd Annual GCSSEPM Foundation Bob F. Perkins Research Conference. New understandings of the petroleum systems of continental margins of the world Houston, Texas, 27 (2012).
- Olariu, C., Krezsek, C. & Jipa, D. C. The Danube River inception: Evidence for a 4 Ma continentalscale river born from segmented ParaTethys basins. *Terra Nova* **9**, 1–9 (2017).
- Krijgsman, W., Hilgen, F. J., Raffi, I., Sierro, F. J. & Wilson, D. S. Chronology, causes and progression of the Messinian salinity crisis. *Nature* **400**, 652–655.
- Popescu, S. M. *et al.* Pliocene and lower pleistocene vegetation and climate change at the European scale: long pollen records and climatostratigraphy. *Quat Int.* **219**, 152–167 (2010).
- Ellenberg, H. & Leuschner, C. Vegetation Mitteleuropas mit den Alpen. Eugen Ulmer KG, Stuttgart (2010).
- Herbert, T. D. *et al.* Late Miocene global cooling and the rise of modern ecosystems. *Nat. Geosci.* **9**, 843–847 (2016).
- Kaya, F. *et al.* The rise and fall of the Old World savannah fauna and the origins of the African savannah biome. *Nat Ecol Evol.* **2**, 241–246 (2018).
- Vasiliev, I. *et al.* Recurrent phases of drought in the upper Miocene of the Black Sea region. *Palaeogeogr Palaeoclimatol Palaeoecol.* **423**, 18–31 (2015).
- Vasiliev, I., Krijgsman, W., Langereis, C. G. & Panaiotu, C. E. Towards an astrochronological framework for the eastern Paratethys Mio–Pliocene sedimentary sequences of the Focșani basin (Romania). *Earth Planet. Sci. Lett.* **227**, 231–247 (2004).
- Vasiliev, I., Reichart, G. J. & Krijgsman, W. Impact of the Messinian Salinity Crisis on Black Sea hydrology — insights from hydrogen isotopes on molecular biomarkers. *Earth Planet. Sci. Lett.* **362**, 272–282 (2013).
- Vasiliev, I., Reichart, G. J., Krijgsman, W. & Mulch, A. Black Sea rivers capture drastic change in catchment-wide mean annual temperature and soil pH during the Miocene-to-Pliocene transition. *Glob Planet Change* **172**, 428–439 (2019).
- Popov, S. V. *et al.* Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeogeogr Palaeoclimatol Palaeoecol.* **238**, 91–106 (2006).
- Ivanov, D. *et al.* Miocene vegetation and climate dynamics in Eastern and Central Paratethys (Southeastern Europe). *Palaeogeogr Palaeoclimatol Palaeoecol.* **304**, 262–275 (2011).
- Eronen, J. T. *et al.* Distribution history and climatic controls of the Late Miocene Pliocene chronofauna. *Proc. Natl. Acad. Sci. USA* **106**, 11867–11871 (2009).
- Fortelius, M. *et al.* Evolution of Neogene mammals in Eurasia: environmental forcing and biotic interactions. *Annual Review of Earth and Planetary Science* **42**, 579–604 (2014).
- Pausas, J. G., Keeley, J. E. & Schwill, D. W. Flammability as an ecological and evolutionary driver. *J Ecol.* **205**, 289–297 (2017).
- Keeley, J. E. & Rundel, P. W. Fire and the Miocene expansion of C₄ grasslands. *Ecol Lett.* **8**, 683–90 (2005).
- He, T. & Lamont, B. Baptism by fire: the pivotal role of ancient conflagrations. Baptism by fire: the pivotal role of ancient conflagrations in evolution of the Earth's flora. *Natl Sci Rev.* **5**, 237–254 (2018).
- Flecker, R. *et al.* Evolution of the Late Miocene Mediterranean Atlantic gateways and their impact on regional and global environmental change. *Earth Sci Rev.* **150**, 365–392 (2015).
- Hilgen, F. J., Lourens, L. J. & Van Dam, J. A. The neogene period, in *The Geological Time Scale 2012*, eds Gradstein, F. M., Ogg, J. G. Schmitz, M. D & Ogg, G. M. Amsterdam: Elsevier BV), 947–1002 (2012).
- Fortelius, M. *et al.* Late Miocene and Pliocene large land mammals and climatic changes in Eurasia. *Palaeogeogr Palaeoclimatol Palaeoecol.* **238**, 219–227 (2006).
- Turner, R., Roberts, N. & Jones, M. D. Climatic pacing of Mediterranean fire histories from lake sedimentary microcharcoal. *Glob Planet. Changes* **63**, 317–324 (2008).
- Gil-Romera, G. *et al.* Holocene fire activity and vegetation response in South-Eastern Iberia. *Quat Sci Rev.* **29**, 1082–1092 (2010).
- Feurdean, A. *et al.* 12,000 years of fire regime drivers in the lowlands of Transylvania (Central-Eastern Europe): a data-model approach. *Quat Sci Rev.* **81**, 48–61 (2013).

41. Leys, B. A., Marlon, J. R., Umbanhowar, C. & Vanni re, B. Global fire history of grassland biomes. *Ecol Evol.* **00**, 1–22 (2018).
42. Gill, J. L. Ecological impacts of the late Quaternary megaherbivore extinctions. *New Phytol.* **201**, 1163–1169 (2014).
43. Zachos, J. C., Shackleton, N. J., Revenaugh, J. S., Palike, H. & Flower, B. P. Climate response to orbital forcing across the Oligocene–Miocene boundary. *Science* **292**, 274–78 (2001).
44. Lamont, B. B., He, T. & Downes, K. S. Adaptive responses to directional trait selection in the Miocene enabled Cape proteas to colonize the savanna grasslands. *Ecol Evol.* **27**, 1099–1115 (2013).
45. Shipboard Scientific Party. In: Ross, D. A. *et al.* (Eds), Initial Reports of the Deep Sea Drilling Project, Volume 42, Part 2. U.S. Government Printing Office, Washington, 483–488 (1978).
46. van Baak, G. C. *et al.* Messinian events in the Black Sea. *Terra Nova* **27**, 433–441 (2015).
47. van Baak, G. C. *et al.* Objective utilization of data from DSDP Site 380 (Black Sea). *Terra Nova* **28**, 230–231 (2016).
48. Popescu, S. M. Late Miocene and early Pliocene environments in the southwestern Black Sea region from high-resolution palynology of DSDP Site 380A (Leg 42B). *Palaeogeogr Palaeoclimatol Palaeoecol.* **238**, 64–77 (2006).
49. Grothe, A. *et al.* Black Sea desiccation during the Messinian Salinity Crisis: Fact or fiction? *Geology* **42**, 563–566 (2014).
50. Whitlock, C. & Larsen, C. Charcoal as a Fire Proxy, In: Smol, J. P., Birks, H. J. B., Last, W. M. (Eds), 1016 Tracking Environmental Change Using Lake Sediments. Terrestrial, Algal, and Siliceous Indicators. 1017 KluwerAcademic Publishers, Dordrecht, The Netherlands, 75–97 (2001).
51. Leys, B. A., Commerford, J. L. & McLauchlan, K. K. Reconstructing grassland fire history using sedimentary charcoal: Considering count, size and shape. *PLoS ONE* **12**, e0176445 (2017).
52. Enache, M. D. & Cumming, B. F. Tracking recorded fires using charcoal morphology from the sedimentary sequence of Prosser Lake, British Columbia (Canada). *Quat Res.* **65**, 282–292 (2006).
53. Enache, M. D. & Cumming, B. F. Charcoal morphotypes in lake sediments from British Columbia (Canada): an assessment of their utility for the reconstruction of past fire and precipitation. *J. Paleolimnol.* **38**, 347–363 (2007).
54. Jensen, K., Lynch, E., Calcote, R. & Hotchkiss, S. C. Interpretation of charcoal morphotypes in sediments from Ferry Lake, Wisconsin, USA: do different plant fuel sources produce distinctive charcoal morphotypes? *Holocene* **17**, 907–915 (2007).
55. Courtney-Mustaphi, C. J. & Pisaric, M. F. A classification for macroscopic charcoal morphologies found in Holocene lacustrine sediments. *Prog Phys Geogr.* **38**, 734–754 (2014).
56. Feurdean, A. *et al.* Broadleaf deciduous forest counterbalanced the direct effect of climate on Holocene fire regime in hemiboreal/boreal region (NE Europe). *Quat Sci Rev.* **169**, 378–390 (2017).
57. Tinner, W. *et al.* Long-distance transport of macroscopic charcoal by an intensive crown fire in the Swiss Alps-implications for fire history reconstruction. *Holocene* **16**, 287–292 (2006).
58. Higuera, P. E., Gavin, D. G., Bartlein, P. J. & Hallett, D. J. Peak detection in sediment charcoal records: impacts of alternative data analysis methods on fire history interpretations. *Int J Wildland Fire* **19**, 996–1014 (2011).
59. Higuera, P. E., Briles, C. E. & Whitlock, C. Fire-regime complacency and sensitivity to centennial-through millennial-scale climate change in Rocky Mountain subalpine forests, Colorado, USA. *J Ecol.* **102**, 1429–1441 (2014).
60. Higuera, P. E., Brubaker, L. B., Anderson, P. M., Hu, F. S. & Brown, T. A. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monograph* **79**, 201–219 (2009).

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Author Contributions

A.F. and I.V. conceived the paper; A.F. performed the charcoal analysis; I.V. draw the figures; A.F. and I.V. interpreted the datasets; A.F. led the writing with significant contribution from I.V.

Additional Information

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