



Indirect interactions between climate and cropland distribution shape fire size in West African grasslands

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Received: 30 May 2022 / Accepted: 28 November 2022
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Abstract

Context Climate and land use changes often interact, yet our ability to predict their combined effects on biodiversity is currently limited. In particular, the combined effects of climate and land use on key ecosystem dynamics, such as disturbance regimes, that shape biodiversity across large spatial scales, are poorly understood.

Objectives We assess how indirect climate–land use interactions influence disturbance regimes by examining the mechanistic pathways by which climate and proximity to cropland interact to shape fire size in a West African grassland ecosystem, the W-Arly-Pendjari transboundary protected area complex.

Methods We use remotely sensed indicators of burned area, rainfall, cropland distribution, and vegetation dynamics to test two spatially explicit hypotheses about the interaction between climate and land use effects on fire dynamics.

Results We demonstrate that in areas where wet season grass production (which is driven by rainfall) is higher, fires are larger, but that this relationship depends on the distance to cropland. Close to cropland, environmental drivers of fire size (wet season grass production, and progressive loss of fire fuel during the fire season) have little effect on fire size, as fuel breaks induced by cropland limit fire size.

Conclusion Our results suggest that the extent to which climate factors control fire dynamics in this African grassland depends on the spatial distribution of land use. More broadly, considering the relative spatial distributions of interacting stressors may be key to improving predictions of their combined impacts on ecosystem functioning.

Keywords Fire dynamics · Fire size · Savannah · West Africa · Satellite remote sensing · Climate change-land use change interactions

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-022-01571-0>.

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Introduction

Climate change and land use change are major driving forces of biodiversity (*sensu* CBD 1992) change in the 21st century. Interactions between these two drivers—i.e. situations in which the response of biodiversity to climate change depends on the presence, type, or rate of land use change, and vice versa—have been observed across a range of species and ecosystems (Zhou et al. 2002; Bennett et al. 2015; Trisurat

et al. 2015; Kamp et al. 2016). Although the potential importance of such interactions has long been recognised (e.g. Hansen et al. 2001), it remains difficult to predict where and when they will occur (Côté et al. 2016; Schulte to Bühne et al. 2021). Such information is however vital to enable decision makers to appropriately prioritise resource allocation for biodiversity conservation, and to develop effective strategies that mitigate against the impacts of climate change on an increasingly anthropogenically modified planet.

A key reason for why predicting the effects of climate change–land use change interactions remains challenging is that relevant studies typically focus on the observed patterns of biodiversity under different climate and land use combinations, rather than elucidating the underlying pathways by which climate change can modify the effects of land use change on biodiversity, and vice versa (Schulte to Bühne et al. 2021). In addition, many climate change–land use change studies focus on the distribution of single species or the composition of communities (e.g. Conenna et al. 2017; Guo et al. 2018). However, many of the proposed mechanisms for land use change–climate change interactions on single species hinge on habitat availability and connectivity (e.g. Hansen et al. 2001; Driscoll et al. 2012; Oliver and Morecroft 2014), which are themselves shaped by ecosystem processes (sensu Pettorelli et al. 2018). So far, little has been done to clarify how climate change and land use change may interact to shape the larger-scale dynamics which give rise to ecosystem composition and structure.

A key group of climate change–land use change interactions that could ultimately affect ecosystem functioning relate to mechanistic pathways affecting disturbance regimes (Schulte to Bühne et al. 2021). Climate change directly alters the dynamics of disturbances such as fire and floods, with an increased frequency of heatwaves, droughts and extreme rain events leading, in some places, to an increase in the occurrence and/or intensity of fire and flood events (IPCC 2021). The standard trajectories of land use change—intensification of human land use and expansion into relatively pristine areas (e.g. Fuchs et al. 2015; Song et al. 2018)—are associated with significant levels of habitat loss or alteration, including removal of biomass (Thompson et al. 2011), canopy cover (Gibbs et al. 2010) and decreases in species diversity (Newbold et al. 2016), which are all

associated with the ecological processes and components that affect the response of ecosystems to disturbances (Johnstone et al. 2016). However, few studies have explored how climate change–land use change interactions could lead to “unpredictable”, non-linear changes in disturbance regimes, and we currently have no systematic understanding of the mechanistic pathways that shape the impacts of such interactions on disturbance regimes.

To address this issue, we investigate the effects of two potential mechanisms by which climate and land use could indirectly interact to shape the fire regime, specifically the size of individual fires, in an African grassland ecosystem. While not directly investigating the effects of *changes* in climate or land use on fire dynamics, elucidating the mechanisms by which these two factors interact will contribute to a better understanding of the pathways through which climate change and land use change may interact (Schulte to Bühne et al. 2021). To our knowledge, this is the first study identifying such interaction *mechanisms* in the context of fire disturbance at the landscape scale. Fire is an important disturbance agent in tropical grassland ecosystems (e.g. Laris and Wardell 2006) that promotes the coexistence of trees and grass (Sankaran et al. 2005; Baudena et al. 2010) and modifies the structure and composition of vegetation communities (Wiegand et al. 2006; Devineau et al. 2010; Lehmann et al. 2014). In particular, the spatio-temporal distribution of fires shapes the spatial configuration of the burned–unburned mosaic that characterises many grassland ecosystems (Laris and Wardell 2006; Laris et al. 2011), which influences the distribution of food and shelter for wild animals over the landscape (Sensening et al. 2010). The dominant limiting factors for fire dynamics—fuel, flammability, and ignition—have been shown to vary in time and space as a result of human activity, including different types of land use (Heyerdahl et al. 2001; van der Werf et al. 2008; Carcaillet et al. 2009). The effects of climate on grassland fire regimes are thought to be mainly driven by rainfall, which can alter the availability of fire fuel—e.g. by altering the productivity or the proportion of highly flammable grass species in the landscape (Govender et al. 2006; Devine et al. 2017)—or the flammability of any existing fuel (Govender et al. 2006).

Land use could interact with climate to alter grassland fire size in at least two different ways (Table 1;

Fig. 1). First, land use by farmers—including in the form of cropland, built-up areas and local grazing grounds—results in abrupt and continued loss of fuel volume and connectivity. This limits the size of any fire that eventually reaches these areas by creating fuel gaps, which act as fire barriers (Devineau et al. 2010; Ryan and Williams 2011), perhaps explaining the observation that fires tend to be smaller in landscapes more intensively used by humans (Archibald et al. 2013). Such agricultural land use is likely to block, or dominate, the effect of climatic drivers on fire regimes in African grasslands. Conversely, fire size could increase in some settings where the presence of cropland is associated with an increase in the number of people using nearby unconverted land. Where people have more access to land, this generally results in more ignition points because of the deliberate or accidental setting of fires (Eriksen 2007), although this relationship tails off at high population densities (Archibald 2016). If areas of

(highly fire-prone) savannah relatively close to intensive human land use have a higher density of ignition points, such areas could be expected to have larger fire extents overall when fuel and flammability conditions are more favourable, since many neighbouring small fires merge into a single burned area (Glasa 2009; Caillault et al. 2020), or more ignition events successfully lead to a significant fire in the first place.

To explore which, if any, mechanistic pathway is more likely to underpin interactions between climate variability and agricultural land use (specifically, using land to grow crops) in determining fire size, we investigate how differences in climate and the distribution of cropland shape fire size in the large W-Arly-Pendjari (WAP) transboundary protected area complex. The WAP is a 35,400 km² network of protected areas and hunting zones surrounded by croplands (Schulte to Bühne et al. 2017, Fig. 2A, B and C), and a cornerstone for wildlife conservation in West Africa. Given the (1) large rainfall gradient (Clerici

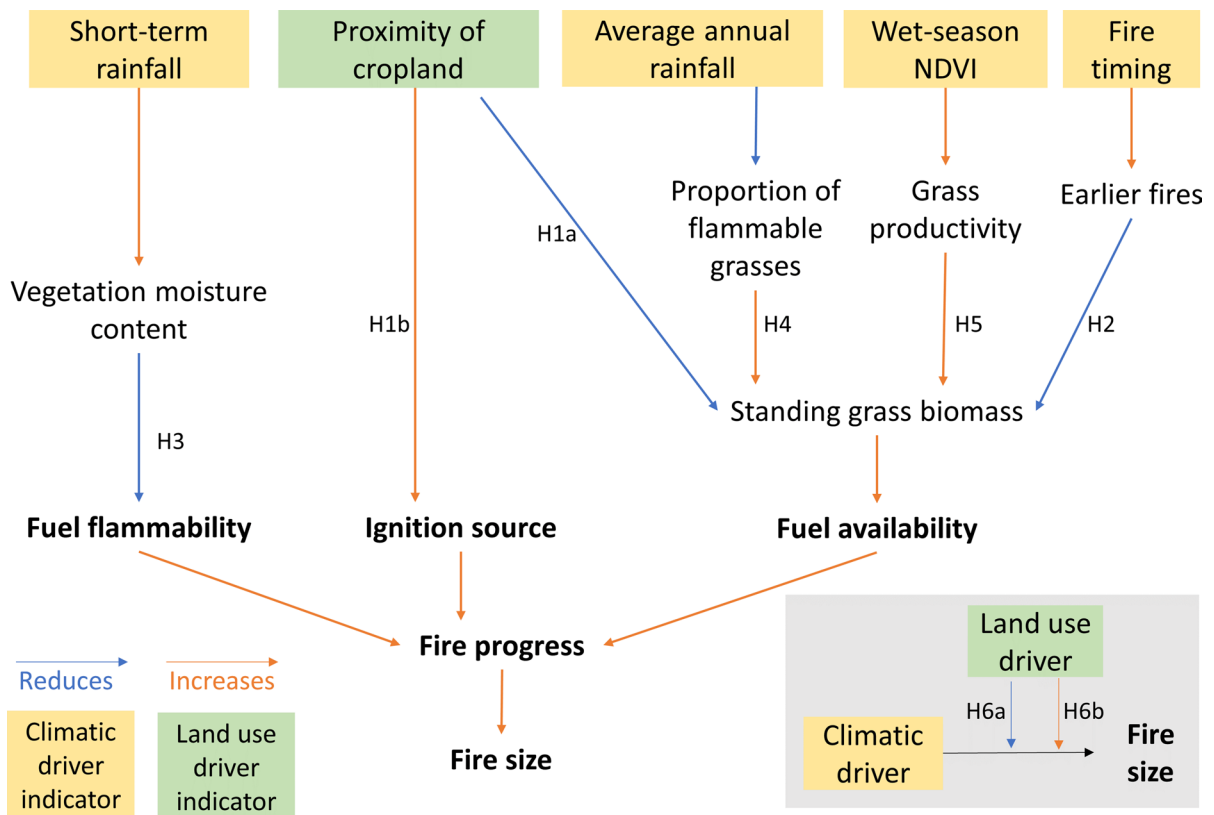


Fig. 1 Conceptual diagram of the hypothesised relationships between climate, land use, and their separate and combined effects on fire size in a West African savannah. See also Table 1 for a detailed explanation of each hypothesis

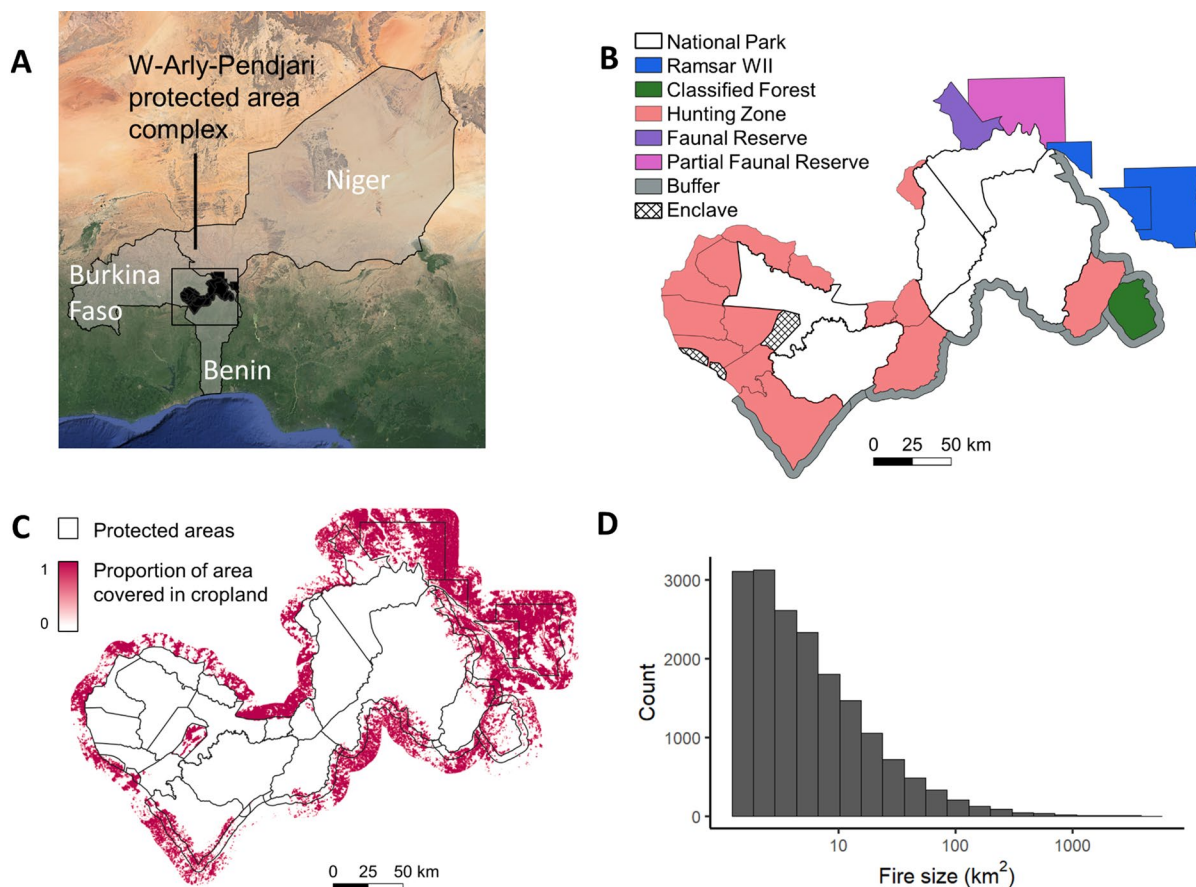


Fig. 2 Study site and context. **A** The W–Arly–Pendjari (WAP) transboundary complex spans three countries in West Africa and straddles the ecotone between desert and grasslands (habitat zones illustrated by Google Earth, 2019). **B** It is composed of protected areas with different designations, ranging from strictly protected IUCN Category II protected areas such as National Parks to areas where resource use is allowed in the form of hunting (e.g. Hunting Zones) or limited agriculture and other natural resource use (classified forests). Enclaves

represent pockets of human settlements and cropland within the protected area complex. Ramsar WII: Ramsar Wetlands of International Importance. **C** Distribution of cropland inside protected areas and within a 10 km buffer around protected areas. To aid visualization at this scale, coverage by cropland is presented as the percentage of each 500 m by 500 m pixel covered by cropland. **D** Distribution of fire size detected between 2000 and 2018, showing the strong right skew of fire sizes (i.e. many more small fires than large fires)

et al. 2007) and (2) large gradient in distances from cropland observed across the WAP (Schulte to Böhne et al. 2017), it is a useful study site to investigate how differences in climate may modify the effect of land use on fires (and vice versa). Because the presence of cropland is known to reduce the amount and connectivity of fuel available for fires, and because croplands are generally found near human settlements, we expect distance to cropland to affect fire size (H1). If cropland acts as a barrier for fire, fire size is expected to be larger for fires starting far away from cropland (H1a). However, if cropland increases

the accessibility of surrounding land to humans, fires are expected to be larger if they start closer to cropland (H1b). The importance of fuel for fire size implies that, as fuel is consumed by fires throughout the dry season, fuel availability and connectivity are progressively reduced, so fires are expected to be smaller later in the dry season (H2). In the short term, rainfall determines the moisture content of fuel, and thus alters flammability, so that fires are expected to be larger just after relatively dry periods (H3). In the long-term, rainfall levels affect vegetation composition in grasslands, with wetter areas having higher

tree coverage displacing highly flammable grass species, as well as higher coverage of perennial grasses, which dry out more slowly during the dry season and thus burn less well (Savadogo et al. 2007). Consequently, we expect fires to be smaller in very wet climatic zones (due to a lack of grass fuel), and larger in areas in drier climatic zones, where rainfall is sufficient to produce high grass biomass but where tree cover is limited (Archibald et al. 2009; H4). We also expect large fires to be more common after wet seasons with high primary productivity, since high primary productivity translates to high grass biomass, which is the most important fuel for grassland fires (H5, Hennenberg et al. 2006; Hoffman et al. 2012). Finally, we expect the effect of the distance to cropland to vary according to the climatic zone, wet-season primary productivity, and vegetation moisture content, as well as with the timing of fires (H6): If cropland simply acts as a fire barrier, fires should grow larger under otherwise suitable conditions (in drier climate zones, when wet-season primary productivity is high, when vegetation is dry and thus highly flammable, as well as early in the dry season) as the distance from croplands increases (H6a). However, if cropland is associated with a larger density of ignition points, fires are expected to grow larger close to cropland under otherwise suitable conditions (H6b).

Methods

Study site

The W-Arly-Pendjari (WAP) transboundary protected area complex consists of several contiguous protected areas (including National Parks, hunting zones, and protected forests) spanning ca. 35,400 km² across three West African countries (Niger, Burkina Faso, Benin; Fig. 2A). While buffer (“transition”) zones around the WAP are technically a part of the complex, we here focus on formally protected areas in which intensive land use (such as deforestation or agriculture) is largely prohibited. About 1 million people live within a distance of 40 km of the borders of the complex (permanent settlements within the WAP complex are limited to the enclaves, Fig. 2B, C), and the surrounding landscape is dominated by cropland (UNDP 2007, Fig. 2C). Key crops grown

around the study site include cotton (UNDP 2007), as well as millet, sorghum, yam, cassava, and maize (Konrad 2015; Houessou et al. 2013). The WAP sits at the border between the Sahelian and Sudanian zones; annual rainfall ranges from ca. 600 mm p.a. in the North to ca. 1000 mm in the South and falls during a single wet season (April–October); the average annual temperature across the whole complex is 28 °C (Almazroui et al. 2020), with a cold season from November through February. The vegetation is a mosaic of savannah with different tree-grass balances, ranging from grasslands to shrub and tree savannahs, as well as some woodlands (especially along temporary rivers) and closed-canopy gallery forests, e.g. around Pendjari River (UNDP 2007). Fires are common during the dry season and are inferred to be predominantly of anthropogenic origin, given the dearth of lightning during the fire season (CENAGREF 2014, 2015; BERD 2015). The fire regime in this region is characterised by frequent, cool and small fires, typical for savannahs (though some areas have frequent, intense, and large fires, Archibald et al. 2013). Previous studies on fire dynamics in West Africa have typically found that human decisions are at the core of fire dynamics (e.g. Laris 2011; Caillault et al. 2015), with fires intentionally being set for a variety of purposes, such as setting fires early to create fire breaks to protect agricultural lands from later (more damaging) fires, or to protect savannah from woody encroachment (Laris et al. 2016). However, these studies necessarily were situated in areas with a finer agriculture-savannah mosaic than the WAP, which is the largest continuous remaining savannah in West Africa. This means the WAP is a useful study site to observe the progression of fires in contexts where landscape fragmentation by agriculture is low or absent, and where fire progression (though not ignition) is largely not controlled by people.

Data

Fire size

Information about fire occurrence was derived from the MCD64A1 Burned Area product (Giglio et al. 2018), which provides monthly estimates of burn dates across the entire Earth’s land surface at a 500 m spatial resolution and has been used in previous studies of regional fire dynamics

in African grasslands (Mishra et al. 2016). We chose this dataset due to its long temporal coverage (2000-present), as well as its high temporal resolution (return frequency: 1 day), which allows inferring the progression of single fires over time through the landscape from their starting points. Due to its relatively coarse spatial resolution, the MCD64A1 Burned Area product has a higher risk of omitting small fires (e.g., Laris 2005), likely underestimating the total burned area in our study site. However, comparison of these data with the MODIS-derived active fire product demonstrates that the MCD64A1 product accurately reflects seasonal changes in fire activity across our study site (see Fig. S1A in Supplementary materials). Similarly, visual comparison of these data with a burned area map derived from Sentinel 2 imagery (with a resolution of 20 m) revealed that the MODIS-derived data does not systematically omit small fires during the beginning of the fire season (see Fig. S2 in Supplementary Material). Detection of these early fires is particularly important, as they could introduce fire breaks that influence sizes of later fires.

All fires between November 2000 and August 2018 that did not start on cropland were analysed (corresponding to 18 dry seasons). All burned pixels (1) that shared a boundary and (2) whose burn dates were close in time were treated as a single, unique fire event. “Close in time” was defined as the median temporal uncertainty (extracted from the MCD64A1 Burned Area product) of adjacent pixels plus an additional day. While we only considered fires that started inside the study site (and not on cropland), some of these fires expanded beyond the boundaries of the protected areas, and these burned areas were included in subsequent analyses to accurately reflect fire size. Fire size was quantified as the number of 500 m by 500 m pixels identified as belonging to a single fire event; this can easily be converted to square kilometres (which we have done in subsequent Figures). The detection accuracy of the MCD64A1 product tends to be higher when more than 50% of a MODIS pixel has been burned (i.e., more than 0.125 km², Tsela et al. 2014). Because of this, we discarded all fires smaller than 10 pixels, or 1.25 km² (as suggested by Hantson et al. 2015).

Fire timing

We also extracted the timing of each fire event with respect to the start of the fire season during which it occurred. Most fires (99.7%) started between October and April over the 18 fire seasons considered. No fires were ever recorded in the months of June to August, and there was no relationship between the onset of the fire season and the climatic zone (see Fig. S1B in Supplementary Materials). We thus chose August 1 as a cut-off to differentiate between fire seasons. The timing of each fire within a given fire season was then quantified as the number of days between the preceding August 1st and the start of the fire to control for the reduction in fuel availability as the dry season progresses. Thus, fire timing is a continuous variable, ranging from “early” fires which occur closest to the start of the new fire season on August 1, to “late” fires that occur closest to the end of the fire season on July 31st of the following year.

Fire starting zone(s)

We identified the likely location of fire ignition points as any area within a single fire event that was surrounded entirely by areas that burned on a later day (fire starting zones). Due to the spatial resolution of the MCD64A1 Burned Area product, it is not possible to determine whether such fire starting zones correspond to single ignition point, or several ignition points lit close together on the same day. However, we assume that fires spread from such neighbouring ignition points are likely to merge into a single fire front very quickly (as, e.g., wind direction will likely be very similar at similar times and at such small spatial scales), and hence it is reasonable to treat them as a single fire starting event. In addition, the density of fire starting zones, while low, overlaps with the range of ignition densities considered realistic in other West African contexts (Caillaud et al. 2020, Supplementary Materials, Annex 1, Table S1).

Short-term and long-term rainfall

Rainfall was quantified using the CHIRPS v2 dataset, which provides information on daily precipitation at a global scale from 1981 to the present at a 0.05° (ca. 5.5 km) spatial resolution (Funk et al. 2014). Validation of this dataset using ground

stations in the same climatic zone as the WAP indicated that CHIRPS v2 is among the best rainfall products for areas falling in the West African monsoon regime (including the WAP), with its high spatial resolution and long temporal record making it especially attractive for long-term analysis (Dembélé and Zwart 2016). All available layers between 2000 and 2018 were downloaded from <http://ftp.chg.ucsb.edu/pub/org/chg/products/CHIRPS-2.0/>. Vegetation can dry out within days (Biddulph and Kellman 1998; de Groot et al. 2005; Cardoso et al. 2018), so we calculated two indicators of short-term vegetation moisture content: (1) cumulative rainfall in the preceding week in the area covered by each fire, and (2) cumulative rainfall during the preceding day. To calculate cumulative rainfall in the preceding week for fires which burned over multiple days, we extracted the cumulative rainfall for the previous week for each day that the fire burned, and calculated an overall mean weighted by the relative area burned on each day. For 75% of fires, there had been no rainfall during the previous week. Similarly, we calculated the area-weighted mean cumulative precipitation during the preceding day; 91% of fires had not experienced any precipitation on the previous day(s). This suggests that the majority of fires occurs long after fuel has become flammable, or put differently, vegetation moisture content does not seem to be a key factor constraining the majority of fires in the study site. While short-term rainfall may affect the onset of the fire season, there is not enough variability in short-term rainfall to allow formally testing its effects on fire size throughout the entire fire season. As a result, short-term rainfall was not included in subsequent analyses.

The WAP spans a large gradient of climatic conditions, with mean annual precipitation ranging from ca. 600 mm in the North to ca. 1000 mm in the South. To characterise spatial gradients in long-term amounts of rainfall, we summed the precipitation received in each calendar year in each 5.5 km by 5.5 km pixel (i.e. original resolution of the rainfall data) and for each year between 2000 and 2017 and calculated the mean of these annual values for each fire. Where a fire spanned several CHIRPS v2 rainfall pixels, the mean of all annual precipitation sums was used.

Distribution of cropland

The distribution of cropland in and around the WAP and the 10 km buffer zone was mapped using Landsat 5 imagery from the U.S. Geological Survey (see Annex 2, Supplementary Material). While cropland expansion has occurred both inside and outside the protected areas (Schulte to Bühne et al. 2017), the majority has occurred outside. Across the entire study period considered, cropland has dominated land cover outside protected areas (Fig. 2B and C), whilst it has almost been absent inside protected areas. Thus, a constant land cover map represents a fair indicator of how far any given point in the study site is from the nearest cropland, especially on the spatial scales considered (several kilometers). To characterise how close each fire was to cropland when it started, we calculated the mean distance of the edge of the starting zone(s) of each fire to the edge of the closest cropland patch. Note that due to the coarser spatial resolution of the burned area data, this estimate has an error of up to 500 m.

Primary productivity

Wet season primary productivity was indexed using the normalised difference vegetation index (NDVI; Pettorelli 2013), which has been shown to be a good proxy for primary productivity and related ecosystem processes in grasslands (Zhang et al. 2016). Specifically, the small integral of NDVI curves has been used as a proxy for standing grass biomass (Olsen et al. 2015; Tian et al. 2016), which is the main fuel in savannah fires (though as they progress fires will also burn leaf litter and, depending on intensity, smaller shrubs and trees). To gauge primary productivity in the areas that subsequently burned, we downloaded all available MODIS MOD09A1 v.61 layers between 2000 and 2018 (Vermote 2015), which provide surface reflectance at a 500 m resolution, every 8 days, from the AppEEARS platform. From this surface reflectance data, we calculated the NDVI for each individual layer, resulting in a timeseries of NDVI values from 2000 to 2018 for each 500 m pixel. To correct for temporary drops in NDVI due to clouds, we deleted NDVI values that were more than 0.25 lower than the preceding value, replacing these with the mean of the preceding and succeeding NDVI value instead (Pettorelli et al. 2012). Since fires in the

wet season (May–September) are extremely rare (see above), we assume that such intense drops in NDVI are the result of cloud contamination rather than fire itself. We then smoothed the timeseries using a Savitsky-Golay filter with a third order polynomial (a relatively conservative filter). In grassland ecosystems, fires predominantly consume grass (Hoffman et al. 2012). We assumed that most plant growth occurs during the wet season (May–September) and calculated the small integral of the smoothed NDVI timeseries during the most recent growing season as an indicator of fuel available across a given fire (Jönsson and Eklund 2004). This index partially accounts for differences in NDVI due to background differences in vegetation (e.g. trees and shrubs tend to have higher NDVI than grass throughout all seasons, meaning that the magnitude of their seasonal response to elevated rainfall is smaller), isolating the part of the NDVI timeseries that is responding to seasonally elevated rainfall, which correlates with plant biomass production in savannahs (Olsen et al. 2015, Tian et al. 2016). Inspection of wet season NDVI values revealed a limited number of extremely small values, which corresponded to pixels overlaying large rivers (which likely have a large amount of surface water present). We removed fires with the smallest 1.5% of NDVI values from the analysis ($n=27$, or 0.02% of all observed fires).

Analysis

The distribution of fire size was strongly right skewed (i.e., large fires were rare, Fig. 2D). We log₁₀-transformed the response variable (fire size) and used a mixed effect, generalised linear model with an inverse Gaussian distribution with an additional log link function (inspection of diagnostic plots and stability of coefficient estimates showed that this resulted in a satisfactory model fit). We were interested in the effects of (1) distance to cropland, (2) time of fire onset (to account for the fuel loss during each dry season due to earlier fires), (3) average annual rainfall (a proxy for climatic zone), and (4) wet season NDVI (a proxy for primary productivity). Non-linear relationships are common in ecology, and we expected fire size to vary non-linearly with all of these predictors, thus we also included the second and third polynomial of all candidate variables in our analysis. All potential predictors (as well as their second and

third polynomials) were weakly correlated (with all correlation coefficients <0.5 ; see Table S2 in Supplementary Materials); however, wet season NDVI and average annual rainfall were moderately correlated (0.48). This prompted us to investigate the relationship between NDVI and precipitation in a given wet season, with the latter explaining around 42% of variability in the former in our study site (Supplementary Material, Annex 3). Fire season (starting on 1st August and ending on 31st July in the subsequent calendar year) was included as a random variable.

All predictor variables were standardised before testing to compare their effect size. Model selection was performed using the Akaike Information Criterion (Richards 2005), using a bottom-up stepwise selection procedure. Interactions between all variables were considered. Variables and their interactions were only included if they reduced the AIC by 2 or more. Diagnostic plots for our best model were generated by simulating model residuals using the R-package ‘DhARMA’ (Hartig 2019); these indicated that the distribution of residuals was concurrent with expectations.

Results

Seventeen thousand, five hundred ninety-eight fires with a size larger than 1.25 km² were observed in the WAP complex between November 2000 and August 2018, burning between 16,800 km² and 21,400 km² annually (i.e., between 47% and 60% of the entire study site).

Fire size was larger for fires which started at a larger distance from cropland, supporting the hypothesis that cropland creates a fuel break that blocks fire spread (H1a, Table 2; Fig. 3). There was no evidence that cropland increases the accessibility of nearby land and increases fire size through increasing ignition point density (H1b). Fires were larger early in the dry season, suggesting that the loss of fuel from early fires progressively limits fire size throughout the dry season (H2). Pre-fire short-term rainfall was universally low or absent across all fires (see Methods), suggesting that fire progression is not limited by vegetation moisture content during the majority of the fire season across the WAP (H3). Average annual rainfall was not retained in the best model, indicating that it does not explain variability in fire size, contrary to expectations

Fig. 3 Effects of environmental drivers on fire size in an African grassland, estimated using a generalised linear model with an inverse Gaussian distribution (see Methods for details). Only three drivers (of five tested) were found to affect fire size: distance to cropland, time of fire onset relative to the start of the dry season, and NDVI in the previous wet season (Normalized Difference Vegetation Index; a proxy for grass biomass production, and thus fuel production), as well as interactions between all three drivers (Table 2). The modelled relationship between fire size, time of fire onset, and wet-season NDVI is plotted for three distances to cropland (corresponding to the 10th, 50th and 90th quantile, or 0.4 km, 5.7 km, and 19.9 km respectively), including confidence intervals. We also plotted the observed sizes for fires that started closer than or at a short distance (0.4 km) in the top panel, and fires that started 19.9 km or further from cropland in the bottom panel. All other fires are plotted in the middle panel

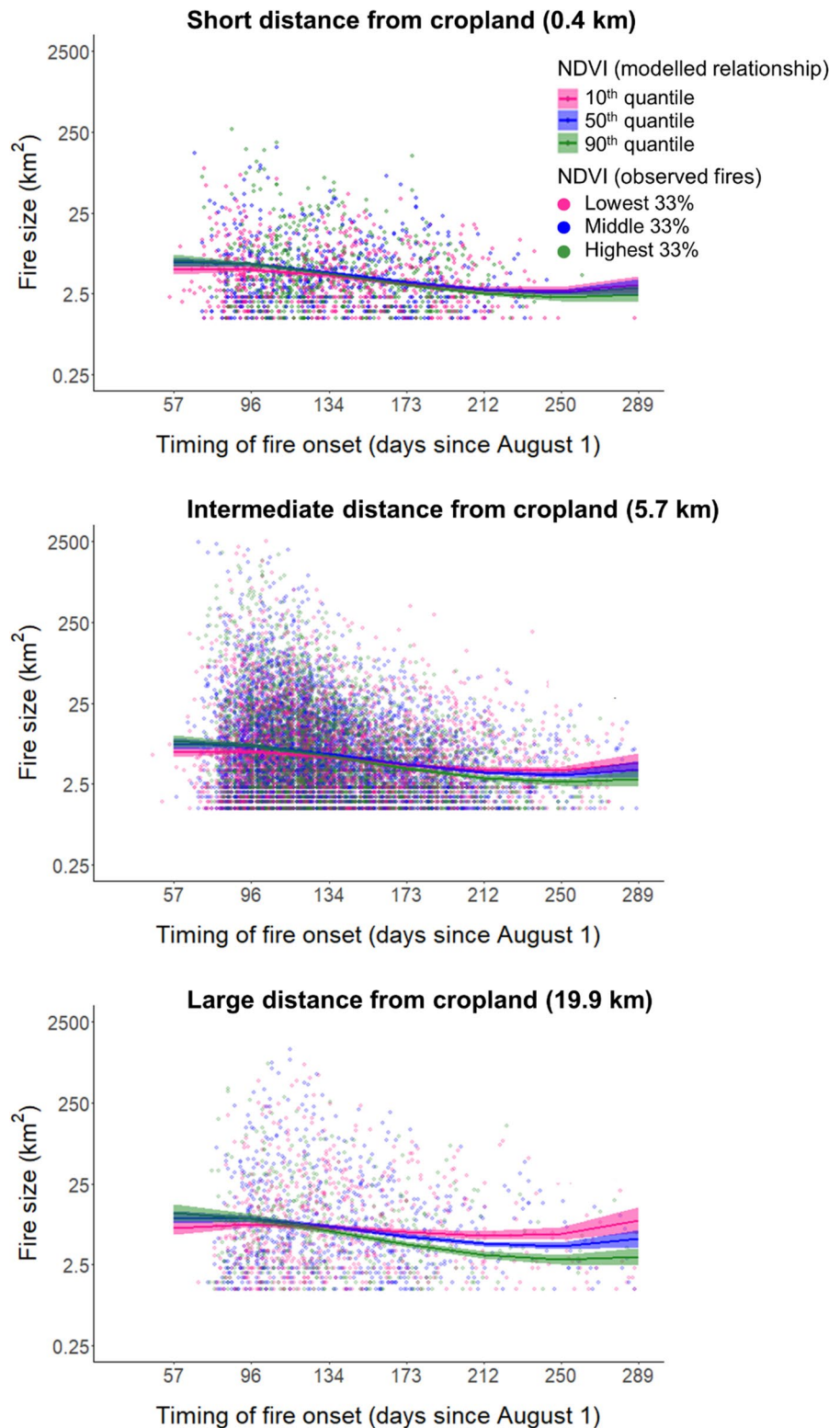


Fig. 4 Conceptual overview over environmental drivers of fire size in a West African savannah. Background wet season NDVI is the median of all wet seasons from 2000 to 2017

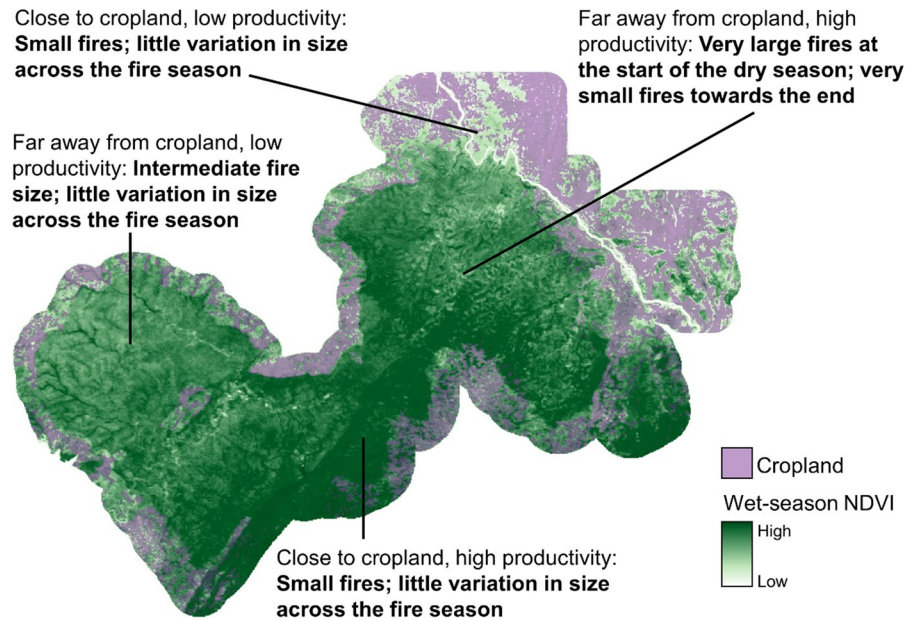


Table 1 Overview over hypotheses on effect of land use and climate effects on fire size in an African grassland

Hypothesis	Rationale	Supported
Effect of cropland (H1a): Cropland acts as a fuel break, limiting fire size	Crops replace more flammable grasses; after the harvest, ground may be bare altogether. People may control fires close to cropland	YES
Effect of cropland (H1b): Ignition events increase close to cropland, increasing fire size	Areas close to cropland are used by more people, increasing the chance of intentional or accidental fire ignition	NO
Effect of season (H2): Early fires reduce fuel availability, thus reducing fire size of any following fires	Areas rarely burn twice in one fire season, as fires consume the majority of flammable fuel	YES
Effect of short-term rainfall (H3): Vegetation moisture limits fire spread	Short-term rainfall increases vegetation moisture, reducing the flammability of fuel and thus its spread	NO
Effect of climate zone (H4): Wetter zones have proportionally less highly flammable grasses, which limits fire size	Woody plant species, and less flammable perennial grass species, occur at higher densities in areas that receive more rainfall, which reduces the cover of highly flammable grasses (especially annuals)	NO
Effect of grass biomass (H5): Grass biomass productivity produces fire fuel, increasing fire size	Grass biomass is the primary fuel of grassland fires	YES*
Interaction 1 (H6a): Cropland limits the effect of climate factors on fire size by acting as a fuel break	The fire break effect means only small fires can occur; this overrides any positive effect of climate on fire size	YES
Interaction 2 (H6b): Cropland amplifies the effect of climate factors on fire size by increasing ignition events	The high density of ignition events close to cropland means fires can spread better close to cropland when climate conditions are beneficial	NO

*Interaction with fire timing means this effect is visible only at the beginning of the fire season, when fuel availability is highest (size of later fires is strongly constrained by large earlier fires in areas with high grass biomass production.)

(H4). NDVI in the previous wet season, when considered alone, had a hump-shaped relationship with fire size, with largest fires occurring at intermediate levels of NDVI (Table 2, H5); however, it is necessary to consider the interactions between the effect of wet season

NDVI, timing of fire onset, and distance to cropland for a full understanding of its effects: Distance to cropland interacted with all other drivers of fire size, dampening their effects, as expected (H6a). As visible in Fig. 3, for fires that started close to cropland, wet season NDVI

Table 2 Coefficient estimates* based on the best model (identified by bottom-up stepwise AIC-based selection) predicting fire size in an African grassland. Our best model had modest predictive power ($R^2=7.6\%$)

Variable name	Coefficient estimate (standard error)	P-value
Intercept	0.30 (0.006)	< 0.01
Distance to nearest cropland patch	7.3 (0.39)	< 0.01
Distance to nearest cropland patch ²	- 2.71 (0.38)	< 0.01
Distance to nearest cropland patch ³	1.25 (0.38)	< 0.01
Time of fire onset	- 10.17 (0.36)	< 0.01
Time of fire onset ²	0.44 (0.37)	0.24
Time of fire onset ³	1.62 (0.37)	< 0.01
Wet season NDVI	- 0.66 (0.43)	0.13
Wet season NDVI ²	- 2.13 (0.37)	< 0.01
Wet season NDVI ³	- 1.22 (0.36)	0.01
Interaction between timing of fire onset and wet season NDVI	- 0.02 (0.003)	< 0.01
Interaction between time of fire onset and distance to nearest cropland patch	0.005 (0.003)	0.04
Interaction between wet season NDVI and distance to nearest cropland patch	- 0.008 (0.003)	0.02
Interaction between time of fire onset, wet season NDVI and distance to cropland	- 0.007 (0.003)	0.01

*Since the predictive variables were standardised, the size of the coefficient estimate is proportional to the effect size

NDVI normalized difference vegetation index

had little effect on the decline of fire size across the fire season: Fires were all similarly small (note that the smallest fire size detected by our method was 1.25 km²), and size declined even further throughout the fire season. However, for fires that started far away from cropland, wet-season NDVI did affect the change in fire size across the fire season. In areas with high wet-season NDVI, fires were very large at the beginning of the fire season, before declining over time. For intermediate NDVI, initial fires were smaller, and the decline was less pronounced. At low levels of NDVI, fires at the beginning of the fire season were relatively small and size did not decline across the fire season. This means that, at the end of the fire season in areas far away from cropland, fires had a significantly different size depending on NDVI, whereas in areas close to cropland, there was no such NDVI-dependent difference. Altogether, these results support the hypothesis that cropland can override the effect of other environmental drivers on fire size (H6a).

Discussion

By combining satellite remote sensing derived information about fire size, cropland distribution, rainfall

and primary productivity, we demonstrate that indirect climate–land use interactions operating at large spatial scales can significantly impact fire dynamics in African grassland ecosystems (Fig. 4). Specifically, croplands appear to reduce fire size directly through fuel break effects, dampening particularly the risk of very large fires early in the dry season. The strength of this effect depends, however, on the prevailing growth conditions for grass (the primary fuel of savannah fires) in the previous wet season: the fuel break effect of cropland is more important in regions with higher wet season NDVI, i.e. areas in which grass biomass is larger at the end of the wet season, especially during the start of the fire season. In low-growth regions, by contrast, fire size remains at intermediate levels throughout the fire season, and proximity to cropland reduces fire size comparatively less. These results suggest that the spatial configuration of agricultural land use (here: growing crops), which has so far been neglected by climate change–land use change interaction studies, may have a critical impact on the effects of these two global drivers on ecosystem-level biodiversity, with the impacts of human activities on disturbance dynamics (such as fires) superseding the impacts of climate change in highly-used landscapes.

The primary aim of this study was to elucidate a new mechanism by which differences in climate and land use interact and influence fire size, thereby contributing to a better understanding of the effects of global environmental change on disturbance dynamics in grasslands. Our findings expand our mechanistic understanding of fire dynamics, but there is clearly scope to improve the predictive power of models of individual fire size in these ecosystems. Given that we considered fires across a large area (ca. 35,000 km²) that were observed over a timespan of almost two decades, our model explained a reasonable, although limited, amount of the overall variability in fire size (Table 2). Comparable studies that report the explanatory power of models of fire size have been able to achieve higher explanatory power by limiting their analysis to a particular size class of fires (e.g. Perry et al. 2020), or estimating the shape of the fire size distribution (e.g. Hantson et al. 2015), rather than predicting the size of each individual fire. In this study, explanatory power was likely limited by a lack of data on other environmental factors that may influence fire size such as wind direction. Information about fire occurrence at higher spatial resolution than available from MODIS-derived products could also provide higher explanatory power, but only if the high temporal resolution and coverage of these products could be matched. In addition, there is currently no spatially explicit information available about the distribution of legal and illegal livestock grazing and fire management throughout the study site, or about the community composition and contiguity of different types of savannah vegetation, which could affect fuel distribution and ignition density, and thus would likely improve the explanatory capacity of our model.

Our results show that it is the spatial configuration of land use (and not simply the extent of land dedicated to a certain use) that influences fire size and determines to what extent fire seasonality and growth conditions interact. The WAP is an island of grassland vegetation on all sides surrounded by cropland (Fig. 2C), meaning that every large fire will eventually meet cropland (and then stop). Our results show that fires were larger further away from cropland in agreement with earlier findings that show that fires are smaller in areas with more intense human land use (Clerici et al. 2005; Archibald 2016). If the protected areas of the WAP had been less effective, and the same amount of cropland were instead scattered

throughout the WAP complex, fires would likely be overall smaller, shifting the fire regime more towards that prevailing in heavily human-modified landscapes (Archibald et al. 2013), and the effects of time of fire onset and wet season NDVI smaller than they presently are. In the WAP, protected area boundaries have so far contained the spread of cropland (Schulte to Bühne et al. 2017), creating a boundary zone where fire size is overall small and primarily controlled by the fuel break effect of cropland, and a core zone where fires tend to be larger and controlled by the timing of fire onset and growth conditions in the wet season. Land use distribution patterns vary significantly between landscapes, and, consequently, we can expect the extent to which they control ecosystem responses to climatic changes to vary significantly, too. This underlines the need to consider landscape configuration explicitly to improve our ability to predict the responses of ecosystem dynamics to combined land use change and climate change.

In contrast to observations in other grassland ecosystems (Laris 2013), fire size was large early in the dry season, and declined thereafter. The large size of early fires in the wetter parts of the study site is particularly surprising. Other studies in West Africa have found that early fires in mesic savannahs areas tend to be limited by residual vegetation moisture, and hence more fragmented (Laris et al. 2015), with short grasslands on upland burning earlier than other vegetation types, introducing fire breaks (Benoit 1999, Fig. S3A in Supplementary Materials). By contrast, the very large fires observed early during the fire season, especially in areas where NDVI in the previous wet season was high, indicate that fuel connectivity is generally high across the WAP, and not significantly limited by spatial mosaics of vegetation types with different drying-down times.

Another surprising effect was that climate zone (average annual rainfall) was not retained in the best model of fire size, since long-term rainfall affects the balance of flammable grass and non-flammable vegetation (trees and shrubs) in savannahs (Sankaran et al. 2008). Average annual rainfall and wet-season NDVI were correlated, with areas receiving higher amounts of rainfall in the long-term also displaying, on average, higher levels of wet season primary productivity; similarly, the amount of rainfall received in a given wet season explained a large part of the wet season NDVI. This

suggests that the main mechanism by which climate affects fuel availability in this study site is by altering grass biomass, rather than by changing the vegetation composition. Indeed, gallery forests (forests along topographic depressions with low flammability) appear to be very widespread in the more arid areas of the WAP (see Fig. S3B in Supplementary Material), and could limit fire size in these areas, meaning that annual rainfall does not exert a lot of control on the spatial differences in the grass-tree balance across this study site. This highlights the importance of vegetation horizontal structure (in addition to vegetation type, and amount of vegetation coverage) for understanding fire dynamics in grassland ecosystems, and again, suggests a key role for spatial patterns in landscapes for understanding the effects of climate change-land use change interactions at the ecosystem scale.

Our current ability to predict how global climate change will shape local climatic conditions across African grasslands remains limited (IPCC 2021). However, given that our analyses covered a gradient of wet season productivity across the WAP, it is possible to speculate on the most likely outcomes of opposing climate shifts in the core zone, where cropland does not affect fire size, based on the mechanism governing the interaction between the distribution of agriculture and rainfall-driven grass productivity shown in our analysis. If climate zones shift North, with drier grasslands becoming wetter, and producing more grass biomass during the wet seasons, fire size distribution will likely become more extreme, with very large fires early in the dry season, and small fires late in the dry season. If climate zones shift South, and wetter grasslands become drier, i.e. wet-season NDVI declines, fire size will remain at an intermediate level throughout the fire season. In areas where cropland expands in the future, any such changes will be smaller in magnitude than in areas that remain unconverted.

Research into stressor interaction effects on biodiversity is driven by an urgent need to become better at predicting biodiversity outcomes at management-relevant scales (Orr et al. 2020). Our results demonstrate that the spatial configuration of stressors and the ecological structures and processes which they affect play an important role in understanding such outcomes. Comparing stressor interaction mechanisms between landscapes with different relative spatial distributions

of global change drivers and biodiversity will be an important step towards improving predictive capacity.

Funding HSB was supported by a scholarship from the Grantham Institute, Imperial College London, UK. JAT was supported by UKRI Global Challenges Research Fund grant ES/P011306/1. NP and SMD were funded by Research England.

Data availability The dataset analysed in this study is available from the corresponding author upon request.

Declarations

Competing interest The authors declare that they have no competing interests.

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