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A fiery past: A comparison of glacial and contemporary fire regimes on the Palaeo-Agulhas Plain, Cape Floristic Region

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ABSTRACT

Landscape-level fire governs vegetation structure and composition in the contemporary Cape Floristic Region (CFR) and was key to the existence of Middle Stone-Age hunter gatherers on the Palaeo-Agulhas Plain (PAP). However, virtually nothing is known about Pleistocene fire regimes of the CFR. We characterized the fire danger climate of the PAP during the Last Glacial Maximum (LGM; 19–26 ka BP) based on palaeo-climate simulations and explored the severity and seasonality of fire danger weather along west-east and coastal-inland gradients across the PAP. We used knowledge of relationships between contemporary fire climate and contemporary CFR fire regimes to propose LGM fire regimes in relation to simulated LGM fire climate. We found that the severity of fire weather during the LGM across the PAP was significantly higher than present; mean fire danger index scores and the incidence of high fire danger days were greater, while the seasonality of fire weather was more pronounced, exhibiting summer-autumn fire regimes across the PAP. Although a more severe fire climate suggests potentially more frequent fires than present, slower fuel accumulation due to colder temperatures, reduced solar radiation and lower atmospheric CO₂ may have partly countered this effect. Our proposed LGM fire regimes predict the vegetation of the PAP to have been dominated by fire tolerant, largely Mediterranean-climate formations such as fynbos, renosterveld and grassland, but is unlikely to have provided a driver for mass seasonal east-west migration of large grazers on the PAP.

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1. Introduction

Fire is considered to have been a key selective force in the evolution of the megadiverse fynbos shrublands of the Cape Floristic Region (CFR) (Allsopp et al., 2014; Cowling, 1987). Based on molecular phylogenies of obligate post-fire flowering orchids (genus *Disa*), summer drought and its associated fire regime in the CFR have been estimated to date back to the Early Miocene (19.5 Ma BP) (Bytebier et al., 2011), while the oldest direct evidence for fire, in the form of fossil charcoal, in the region is in the Late Oligocene or Early Miocene (Roberts et al., 2017). A period of global cooling and drying, which followed the mid-Miocene climatic optimum (ca. 15 Ma BP), likely resulted in the spread of sparser and more flammable vegetation that supported a fire regime comparable to what is in existence today (Bytebier et al., 2011; Rundel et al., 2018). It is

furthermore known that humans have burnt fynbos since at least the start of the Holocene 12 ka BP to facilitate geophyte growth and hunting (Deacon, 1983; Marean et al., 2014). This special issue aimed to reconstruct the biophysical environment of the Palaeo-Agulhas Plain (PAP) during the Last Glacial Maximum (LGM), a strong glacial period of the Pleistocene (19–26 ka BP, Clark et al., 2009). Given the important role of fire in governing vegetation patterns within the CFR (Cowling and Holmes, 1992; Kraaij and van Wilgen, 2014; Stock and Allsopp, 1992) a basic understanding of fire incidence and seasonality on the PAP is fundamental to the reconstruction of the region's vegetation (Cowling et al., 2019), large mammal assemblages (Venter et al., 2019) and resource availability to early modern humans (Marean et al., 2015).

Palaeo-fire histories may be reconstructed based on sedimentary pollen or charcoal deposits (Bowman et al., 2009; Carcaillet et al., 2007; Leys et al., 2013) and radiocarbon-dating of plant-derived charcoal (Filion et al., 1991). A global review of changes in LGM-Holocene fire regimes showed that charcoal records are generally scant for the LGM and during the early phase of

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deglaciation, with no records from Africa south of 30°S (Power et al., 2008). Subsequently two studies of sedimentological micro charcoal were conducted on the Cape coastal lowlands, i.e. at Rietvlei (100 km west of George, spanning the last 16 ka BP) (Quick et al., 2015) and Vankervelsvlei (30 km east of George; spanning the last 100 ka BP) (Quick et al., 2016). Both suggested a regional and local fire signal over much of the last 100 ka BP, peaking around 6 and 47 ka BP and sometimes exceeding that associated with contemporary conditions. In such studies, charcoal concentrations are compared only in relative terms among different periods. Generally, higher charcoal concentrations (signifying elevated fire activity) occurred during drier periods when rainfall was more seasonal and when drought-tolerant vegetation, including fynbos, was more prominent than during wetter, less seasonal periods when Afrotemperate forest and thicket pollen increased. At Vankervelsvlei, fynbos elements were present throughout the 100 ka record, with ericaceous fynbos dominating during the last glacial period (Quick et al., 2016). This was largely replaced by asteraceous fynbos during the Holocene, associated with frequent fires (exceptionally high charcoal concentrations), warm conditions and marked drought episodes. More detailed knowledge of palaeo-fire regimes does not exist for the Cape coastal lowlands and is completely lacking for the currently submerged PAP.

The reconstruction of palaeo-fire regimes fundamentally relies on an understanding of the interactions among fire, climate, vegetation and land use (Bowman et al., 2009; Hu et al., 2006; Power et al., 2008). However, climate-fire relationships are complex, given feedbacks between climate and numerous other factors that influence the nature of fire regimes (Hu et al., 2006; Keeley and Syphard, 2016). These factors include ignitions, plant growth rates and thus fuel accumulation rates, vegetation type and thus fuel type, seasonality and frequency of dry conditions conducive to combustion, and more (Bowman et al., 2009; Keeley and Syphard, 2017; Seydack et al., 2007; van Wilgen et al., 2014). Feedbacks between these factors may furthermore affect fire regimes in opposing ways, which contribute to the complexity in climate-fire relationships and hence challenges in predictive fire regime modelling or hindcasting attempts (Keeley and Syphard, 2016). However, basic climate-fire regime relationships are evident in fire-prone ecosystems across the globe and these differ in nature between wooded and grassy ecosystems (Bradstock, 2010). Firstly, the seasonality of fires typically mirrors the seasonality of fire danger weather. This relationship is particularly obvious in ecosystems with a distinct dry season, e.g. summer-autumn fires in Mediterranean-climate (~winter rainfall) shrublands (Keeley et al., 2012) and winter-spring fires in summer rainfall grasslands, savannas and woodlands (Archibald et al., 2009; Bradstock, 2010; van Wilgen et al., 2000). Secondly, anomalously large burnt areas often follow multi-year droughts in wooded systems (Dimitrakopoulos et al., 2011; Keeley and Syphard, 2017; Kraaij et al., 2018; Williams, 2013), or multiple years of above average rainfall which increases horizontal fuel continuity in semi-arid grassy systems (Archibald et al., 2009; Keeley and Syphard, 2017; Syphard et al., 2017; van Wilgen et al., 2000). Thirdly, average fire frequency may be correlated with average annual rainfall through its control of plant growth (~fuel accumulation) rates in wooded systems (Bowman et al., 2009; Seydack et al., 2007), although this relation is dependent on the presence of a sufficiently long dry season (Archibald et al., 2009; Keeley, 2012). Fire frequency can usually not simply be predicted from climate due to opposing feedbacks of moisture on fuel accumulation and flammability (Bradstock, 2010; Keeley, 2012; Pausas and Paula, 2012). Lastly, relationships between ignition frequency and fire frequency, and ignition seasonality and fire seasonality, are equally vague in most ecosystems and further complicated by human influences (Archibald et al., 2009, 2013;

Keeley et al., 1999; Kraaij et al., 2013b; Syphard et al., 2017).

Based on such understanding of climate-fire (and to a lesser extent fuel-) relationships in the CFR, we took a novel approach to hindcasting the fire regimes of the PAP during the LGM. We characterized the fire danger climate of the region based on palaeo-climate simulations (Engelbrecht et al., 2019) and in particular explored the seasonality and severity of fire danger weather along longitudinal (west-east) and latitudinal (coastal-inland) gradients across the PAP. We used knowledge of relationships between contemporary fire climate and contemporary fire regimes in different parts of the CFR (Kraaij and van Wilgen, 2014) to propose LGM fire regimes in relation to simulated LGM fire climate. This approach was made possible by the availability of the paleo-climate simulations for the LGM PAP that were based on a regional climate model that predicts hourly weather patterns of precipitation, temperature, humidity and wind at spatial resolution high enough to capture topographic effects (Engelbrecht et al., 2019).

The contemporary CFR is characterized by summer-autumn fire regimes in the west where the climate is Mediterranean, grading into year-round rainfall and aseasonal occurrence of fires in the east (Kraaij et al., 2013a, 2013b; van Wilgen et al., 2010). Synoptic states commonly associated with fires in the west comprise easterly wave low pressure systems characterized by strong winds, convective activity and lightning in summer-autumn; with that in the east being hot, dry katabatic 'berg' winds that precede tropical temperate troughs in late autumn, winter and early spring (Southey, 2009). The severity of fire weather conditions and the frequency of lightning ignitions increase with distance from the coast, but neither of these gradients are associated with directional changes in the frequency of fires (Kraaij et al., 2013b; Kraaij and van Wilgen, 2014; van Wilgen et al., 2010). Important differences between LGM and contemporary climate of coastal regions of the CFR include reduced annual temperatures (-2 to -4 °C) (Cowling et al., 2019) and intensified westerly winds particularly in winter (Engelbrecht et al., 2019). Winter rainfall was furthermore higher than present ($+1$ mm/day) in the west, but lower than present (-1 mm/day) in the east. Drier LGM winters in the east were due to enhanced adiabatic northwesterlies and a rain shadow occurring southeast of the south-north aligned Cape Fold mountains under northward displacement of westerly frontal systems (Engelbrecht et al., 2019). Summer anomalies in wind, temperature and rainfall were less apparent throughout the domain (Cowling et al., 2019; Engelbrecht et al., 2019). We thus predicted the PAP fire climate during the LGM (i) to have been of lower severity (on account of colder and wetter conditions) towards the west, and (ii) to have reflected more of a winter fire regime (on account of drier, windier winters) towards the east, than under contemporary conditions.

2. Methods

We focused our analysis of fire weather in locations along the contemporary Cape south coast (Fig. 1) for which sufficiently detailed weather data existed to allow for computation of the McArthur forest fire danger index (Noble et al., 1980), and for which information was available (summarised by Kraaij and van Wilgen, 2014) about those regions' fire climate and recent fire regime (Table 1). The McArthur forest fire danger index (hereafter 'FDI') has been widely used in the CFR and in Australian shrublands and is considered a reasonable predictor of fire incidence in these systems (Bradstock et al., 2009; Kraaij et al., 2013b; van Wilgen et al., 2010). The six chosen locations represented longitudinal (west-east) and latitudinal (coastal-inland) gradients across the PAP, but little elevational variation (all locations were situated on the coastal plain).

We calculated daily FDI from daily measurements recorded at 14h00 (local time) of temperature, relative humidity, wind speed,

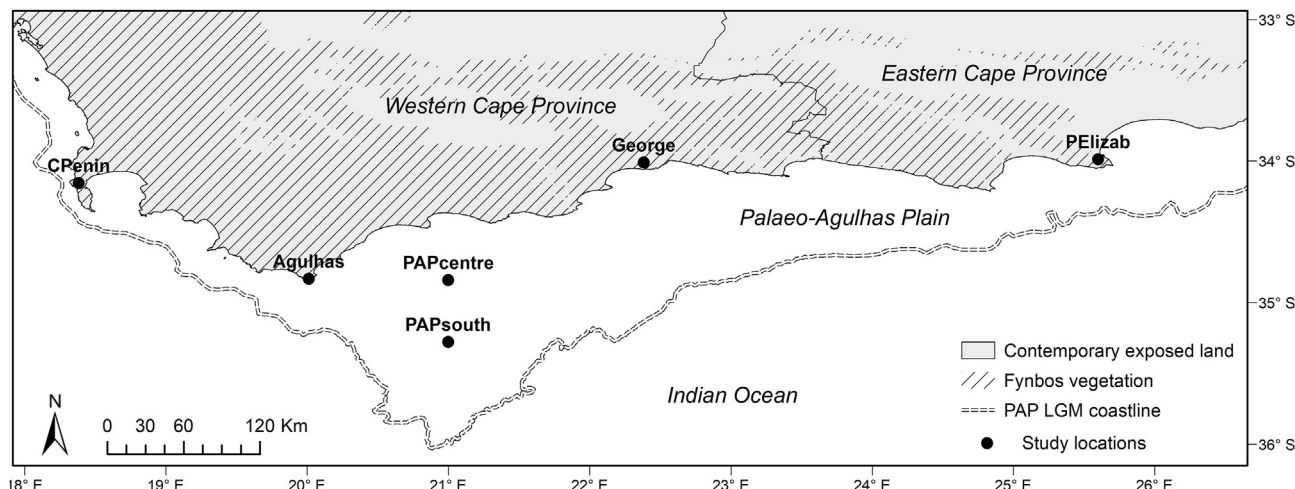


Fig. 1. Map of the Palaeo-Agulhas Plain (PAP) during the last glacial maximum (LGM) in relation to the current coastline of South Africa, and the locations for which fire weather was assessed in this study: CPenin, Cape Peninsula; Agulhas, Cape Agulhas; George; PELizab, Port Elizabeth; PAPcentre; and PAPsouth.

Table 1

Attributes of locations during contemporary (Con) and last glacial maximum (LGM) times for which fire weather (based on the McArthur Fire Danger Index, FDI) was assessed in this study. The distribution of these locations in the Cape Floristic Region (CFR) and on the Palaeo-Agulhas Plain (PAP) is shown in Fig. 1.

Location	Latitude Longitude	Elevation (masl)	CFR fire climate zone ^a	Fire return interval (years) ^a	Mean annual rainfall (mm)		Mean FDI		Number of days per year with FDI \geq high		Fire season	
					Con	LGM ^d	Con	LGM ^d	Con	LGM ^d	Con	LGM
Cape Peninsula (CPenin)	34.150°S 18.383°E	230	western coastal	14	357 ^b 767 ^c	954-1308	3.2 ^b 2.6 ^c	3.3-8.0	3 ^b 1 ^c	20-91	summer- autumn	summer- autumn
Cape Agulhas (Agulhas)	34.826°S 20.013°E	11	southwestern coastal	10	442 ^b 534 ^c	523-752	2.5 ^b 3.9 ^c	6.2-9.6	3 ^b 9 ^c	51-106	summer- autumn	summer- autumn
George	34.004°S 22.384°E	197	eastern coastal	15	714 ^b 1043 ^c	734-942	3.6 ^b 3.1 ^c	4.8-7.3	4 ^b 18 ^c	35-72	aseasonal (winter+)	summer- autumn
Port Elizabeth (PElizab)	33.983°S 25.600°E	60	far eastern coastal	8	580 ^b 494 ^c	355-492	4.5 ^b 3.3 ^c	8.4-10.5	5 ^b 9 ^c	79-110	aseasonal	summer- autumn
Centre of PAP (PAPcentre)	34.835°S 21.000°E					512-680		8.2-11.1		89-136		summer- autumn
South of PAP (PAPsouth)	35.272°S 21.000°E					588-838		4.3-7.8		21-68		summer- autumn

^a Kraaij and van Wilgen (2014)

^b This study 'Contemporary actual' series

^c This study 'Contemporary model' series

^d This study 'LGM models' series (range from different projections)

and rainfall (of the past 24 h) (cf. Kraaij et al., 2013b). Conditions at this time of day approximate daily maximum temperature, minimum relative humidity, wind at its strongest, and thus maximum daily FDI. This index also incorporates a drought factor and the Keetch Byram Drought Index (Keetch and Byram, 1968; Noble et al., 1980). For each of the six locations we calculated daily FDI spanning 30 years for three types of series:

- 'Contemporary actual', i.e. weather data actually observed during the past four decades (the exact dates of the series depended on the availability and completeness of weather records for the different locations);
- 'Contemporary model', i.e. data modelled for contemporary conditions (1981–2010) by the AMIPw simulation (Engelbrecht et al., 2019) but bias-corrected for rainfall and temperature as described by Cowling et al., (2019); and
- 'LGM models', i.e. data modelled for conditions during the LGM, obtained from the eight dynamically downscaled climate simulations (CCSIM4a, CNRM, FGOALS, GISS, IPSL, MIROC, MPI, and MRI) of Engelbrecht et al. (2019) that were

bias-corrected for rainfall and temperature as described by Cowling et al., (2019).

For each location and series type we then calculated mean monthly FDI and the mean number of days per month with at least moderate (FDI > 5) and at least high (FDI > 12) fire weather (respectively) to assess the seasonality and severity of fire danger weather and how this differed among locations and periods. We also computed mean monthly values for each of the input variables, i.e. maximum temperature, minimum relative humidity, wind speed at mid-day, and daily rainfall, to aid our interpretation of the FDI results.

3. Results & discussion

3.1. Modelled vs actual contemporary fire weather

The severity of fire danger weather was reasonably comparable between the actual (observed) series and the modelled contemporary series for each of the four locations along the current

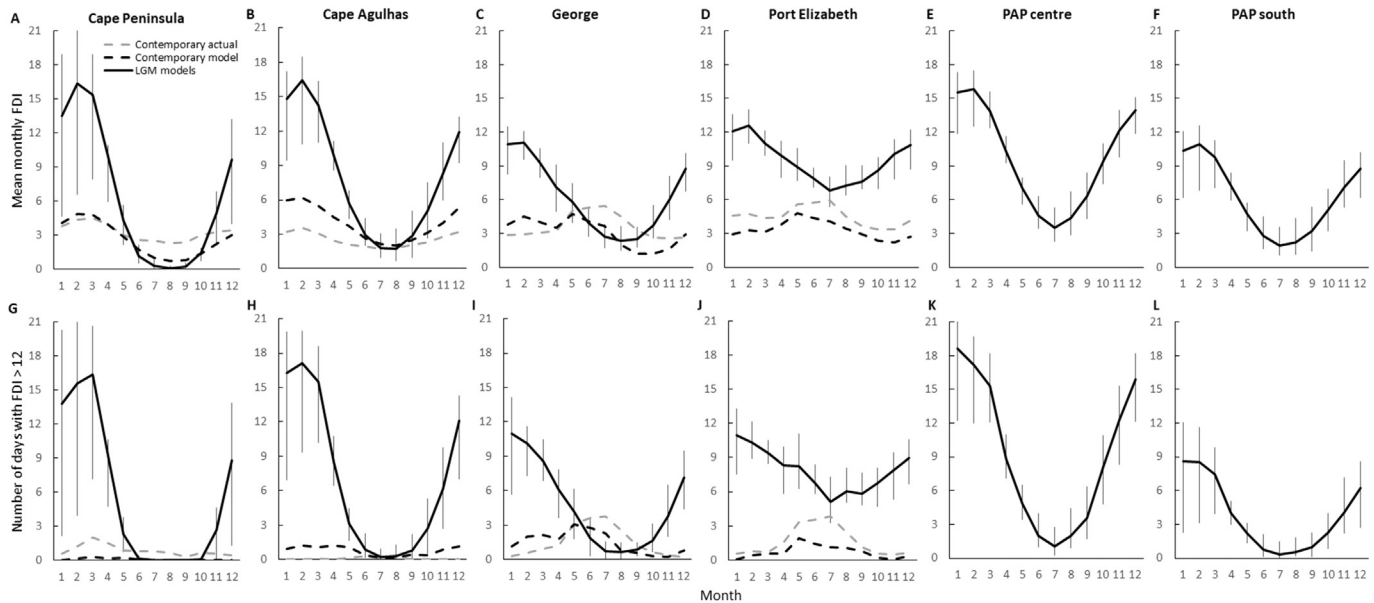


Fig. 2. Severity and seasonality of fire danger weather expressed as (A–F) mean monthly values of the McArthur forest fire danger index (FDI), and (G–L) the mean number of days per month with FDI being high or higher (i.e. FDI score > 12), at six locations across the Palaeo-Agulhas Plain (PAP) (see Fig. 1 for details) for different time series, i.e. contemporary actual; contemporary modelled; and last glacial maximum (LGM) modelled (mean \pm range of eight different simulations).

coastline (Fig. 2). The seasonality of fire danger weather was furthermore comparable between the actual and modelled contemporary series at Cape Peninsula and Cape Agulhas, both showing summer-autumn peaks, but less similar at George and Port Elizabeth where weak winter peaks in the actual series were more evident than in the modelled contemporary series. Overall we were satisfied with the accuracy of the modelled contemporary conditions to deem LGM simulations equally reliable.

3.2. Severity of LGM fire weather

Contrary to our predictions, the severity of fire weather during the LGM was significantly higher during the peak fire season than under contemporary conditions at all locations along the contemporary coastline but comparable or lower during the off-peak season (Fig. 2). Although the estimates of fire severity produced by the different simulations varied widely, even the lowest estimates of peak fire season severity during the LGM exceeded those of contemporary times. Not only was mean FDI during the fire season higher during the LGM and the seasonality of fire weather (the contrast between the peak and off-peak season) more pronounced at all study locations, but the number of days per annum with high or higher fire danger scores was almost an order of magnitude larger during the LGM than under contemporary conditions along the coast (Table 1; Fig. 2). The LGM series furthermore showed a decline in fire weather severity from north to south on the PAP (from Cape Agulhas to PAPcentre to PAPsouth) with increased proximity to the coast. This inland-coastal gradient was to be expected as it is also evident in contemporary CFR (Kraaij and van Wilgen, 2014).

Our interrogation of the weather variables that underpin FDI (Supplementary 1) confirmed the rainfall patterns reported by Engelbrecht et al. (2019) with LGM winter rainfall that was considerably higher than present at Cape Peninsula, comparable at Cape Agulhas, but lower than present at George and Port Elizabeth. Summer rainfall at all locations were comparable between the LGM and the present. Wind speeds were lower (or similar) than present at all contemporary locations. This is contrary to the intensified westerlies during LGM winters predicted by Engelbrecht et al. (2019)

over most of the southern African winter-rainfall area. Wind and rainfall anomalies can therefore not account for the increased severity in fire weather seen for the LGM. Summer conditions along the Cape coast were not considered in detail by Engelbrecht et al. (2019) or for various locations by Cowling et al., (2019). Our analyses showed that LGM daily maximum temperatures were 3–4 °C higher than present in summer (and 2–4 °C lower than present in winter), which would have contributed to the high severity of fire weather during LGM summers and more pronounced seasonality of LGM fire weather. In the west, the daily minimum relative humidity concomitantly showed greater seasonal contrast which would also have added to the pronounced seasonality of LGM fire weather. However, in the east, the present-day winter trough in minimum relative humidity (which partially accounts for a winter peak in FDI) were inverted during the LGM, when relative humidity peaked in winter, associated with comparatively low FDI. This result does not support the notion of enhanced adiabatic northwesterlies and a rain shadow along the Cape south coast during LGM winters due to northward displacement of westerly frontal systems (Engelbrecht et al., 2019). Overall, we conclude that the differences in severity of LGM and contemporary fire weather may be attributed to anomalies in temperature and associated relative humidity, rather than wind and rainfall influences.

To put the severity of fire weather during the LGM on the PAP in perspective, it was comparable with that of contemporary CFR inland mountainous locations such as the Cedarberg, Swartberg and Kamanassie Mountains where ca. 130 days per year, and ca. 25 days per month during peak season, have FDI rated high or higher (van Wilgen and Burgan, 2010; van Wilgen et al., 2010). Comparisons of fire weather severity among different regions globally are complicated by the use of different fire danger rating systems (Sirca et al., 2018), but a coarse comparison with other shrubland or forested ecosystems suggests that the fire weather severity predicted for the PAP are also high by contemporary international standards. For instance, the Sydney region of southeastern Australia has ca. 70 days per year with FDI rated high or higher (Bradstock et al., 2009) while the western US forest and plains regions have ca. 70 days per year when the likelihood of large fires is high (with an Energy Release Component index of 40–59, Brown et al., 2004).

3.3. Seasonality of LGM fire weather

The representations of fire weather produced by the eight different simulations of LGM climate were highly consistent in terms of fire weather seasonality (Fig. 2). Throughout the PAP summer-autumn peaks in fire danger weather were more evident during the LGM than presently. In the west the contrast between peak and off-peak was more pronounced during the LGM than presently, while in the east the contemporary aseasonality of fire weather (or mild winter peak) made way for distinct summer-autumn fire seasonality. In the west, the more pronounced Mediterranean climate of the LGM (colder and wetter winters; Table 1) clearly associated with pronounced summer fire weather. Although the Mediterranean climate is thought to have occurred as far as 30°E during the LGM (Cockcroft et al., 1987), the modelled LGM winter rainfall in the east was lower than contemporarily, with George and Port Elizabeth exhibiting aseasonal rainfall (Supplementary 1). Rainfall, therefore, cannot account for the summer seasonality of LGM fire weather in the east. In contemporary eastern coastal CFR, year-round rainfall in conjunction with hot and dry katabatic ('berg') winds in winter are associated with an aseasonal fire regime (Kraaij et al., 2013b). We suggest that the berg winds in winter that currently cause winter peaks in fire weather in the east were replaced in the LGM by colder katabatic winds in winter that descended over periglacial mountains (Boelhouwers, 1999) and hence did not result in elevated FDI in winter. However, significantly warmer than present summer temperatures associated with lower than present relative humidity, explain the more severe than present LGM summer fire weather in the east. Warmer than present summers during the LGM along the contemporary Cape south coast likely resulted from reduced southeasterly winds in summer (note seasonal trends in wind speed in Supplementary 1) that would have resulted in reduced upwelling and thus warmer sea surface temperatures. Generally, the more pronounced contrasts between summer and winter temperatures during the LGM (Engelbrecht et al., 2019) would also have contributed to the stark contrast between summer and winter FDI during the LGM.

The prominent summer-autumn seasonality of LGM fire weather across the PAP may cast uncertainty over the potential occurrence of extensive grasslands or savannas towards the east of the domain (Copeland et al., 2016), given that contemporary southern African grasslands and savannas typically exhibit summer rainfall and growth, with winter curing of grasses that fuel winter fire regimes (Archibald et al., 2009; van Wilgen et al., 2000). However, southern African savanna and grassland communities appear generally robust to deviations in fire season (Uys et al., 2004; van Wilgen et al., 2007). Furthermore, in contemporary south coast renosterveld and fynbos, C₃ and C₄ grass species may occur abundantly (Cowling, 1983; Kraaij, 2011). Here grasses, including C₄ species, are able to persist under all-year rainfall and largely summer-autumn fire regimes (Novellie and Kraaij, 2010) with particular ecotypes of C₄ species displaying cool season growth (Cowling et al., 1986). Fair abundance of C₃ and C₄ grasses on the PAP (and the existence of savanna-like woodlands in floodplains, Helm et al., 2018) can therefore not be ruled out, although the consistent and pronounced summer-dominated seasonality of LGM fire regimes across the east-west extent of the PAP are unlikely to have provided a driver for mass seasonal east-west migrations of large grazers on the PAP (as proposed by Copeland et al., 2016).

3.4. LGM fire regime

Major fire frequency shifts in response to millennial-scale climatic variation are evident in the global palaeo-record (Carcaillet

et al., 2001; Power et al., 2008). During the LGM in particular, charcoal records from other contemporary Mediterranean climate regions (Chile, Portugal and Spain) show less than present fire frequencies, although greater than present fire frequencies are evident for select southeastern Australian sites (Power et al., 2008). Our findings for the PAP of more severe fire weather and a more pronounced dry season may suggest a greater likelihood of fire and potentially more regular fires than present. However, fire frequency not only depends on fire climate but on atmospheric oxygen levels, the incidence of droughts, ignitions, and importantly, the nature and accumulation rate of fuels which are also dependent on climate (Keeley, 2012; Kraaij and van Wilgen, 2014). These factors were beyond the scope of this investigation of fire climate, focusing on the severity of fire weather, but we speculate about some of their potential influences and interactions.

Increased atmospheric oxygen can result in more frequent fires and fires not being restricted to the dry season (Scott and Glasspool, 2006); however, during the LGM atmospheric oxygen does not appear to have been considerably higher than currently (Stolper et al., 2019) and is unlikely to have changed fire incidence relative to contemporary regimes. Long-term droughts often precede unusually large or severe fires in wooded systems (Dimitrakopoulos et al., 2011; Keeley and Syphard, 2017; Williams, 2013), but fire frequencies have not been quantitatively linked to drought cycles in contemporary CFR, apart from recent evidence that extreme fires in the region of George followed an unprecedented 18-month drought (Kraaij et al., 2018). The 30-year span of our weather series did not permit rigorous assessment of long-term drought cycles. However, the severity of the worst 18-month droughts in our modelled time series was comparable or worse during the LGM than the present at most of our study locations (Supplementary 2), with worse droughts suggestive of potentially increased fire incidence. Lightning is not expected to have been limiting to the incidence of fire on the PAP during the LGM either, given that lightning does not control fire occurrence in contemporary CFR (Archibald et al., 2009; Kraaij et al., 2013b). Humans have furthermore provided ignitions in this landscape for tens of thousands of years (Wren et al., 2019; Deacon, 1983). We therefore contend that ignitions were unlikely to have limited the incidence of fire on the PAP during the LGM. Fuel accumulation rates may rather have limited fire frequency under LGM climate. Fynbos evolved under a Mediterranean climate and is a winter-growing flora (Cowling and Holmes, 1992). Although elevated winter rainfall would not have been limiting to plant growth (Cramer and Hoffman, 2015) during the LGM in the west, much reduced solar radiation and winter temperatures (3–4 °C less than present) may have been limiting (Hatfield and Prueger, 2015; Stock and Allsopp, 1992; Stock et al., 1992). Moreover, reduced atmospheric CO₂ (ca. 180 ppm) during the LGM (Bowman et al., 2009) may have depressed plant growth rates although this relationship appears to be species-dependent in fynbos (Hattas et al., 2005; Midgley et al., 1995). Fynbos shrubs tend to be less responsive than C₃ grasses to fluctuations in CO₂, with nutrient-deficiencies commonly overriding carbon limitations in shrubs, while C₃ grasses successfully invest elevated CO₂ into growth. Lower atmospheric CO₂ during the LGM could thus have had a depressing effect on grass growth and therefore fire frequency – a trend opposite to the 'grass-fire cycle' (D'Antonio and Vitousek, 1992; Kraaij et al., 2017). Slower fuel accumulation (cf. Seydack et al., 2007), and particularly of fine grassy fuels, may thus have partially countered potential positive effects of elevated fire danger weather on fire frequency.

Structurally, fine (microphyllous) fuels of medium stature, similar to current day ericaceous, asteraceous and grassy fynbos and renosterveld, are better adapted to survive and sustain (through high flammability, Burger and Bond, 2015; Calitz et al.,

2015) relatively short (<10 yr) fire return periods than taller, slow-maturing, mesophyllous proteoid fynbos (Kraaij and van Wilgen, 2014). The former is therefore likely to have dominated on the PAP if fires were more frequent than present. Furthermore, the proposed severity of LGM fire weather in conjunction with the lack of topography on the PAP (Cawthra et al., 2019) would have severely restricted the occurrence of fire sensitive forest and thicket (Geldenhuys, 1994). Accordingly, peaks in ericaceous and asteraceous pollen correspond with peaks in micro charcoal concentrations (and thus fire activity), while peaks in Afrotemperate forest and thicket pollen associate with lower charcoal concentrations in sedimentological records of the Cape coastal lowlands close to George (Quick et al., 2015, 2016).

3.5. Conclusions

Despite taking a very different approach to the reconstruction of paleo-fire regimes, our findings concur with other lines of evidence (molecular phylogenies and micro charcoal deposits, Bytebier et al., 2011; Quick et al., 2015; Quick et al., 2016) suggesting the presence of fire during the LGM in the CFR. Our results suggest potentially greater than present fire activity on the PAP during the LGM on account of a more distinct dry season (i.e. a fundamental requirement for regular fire, Archibald et al., 2013; Keeley, 2012) and the severity of fire weather during the warm dry summers greatly surpassing that associated with contemporary conditions. However, feedbacks between climate, atmospheric CO₂ and fuel accumulation may have partly countered this effect and warrant further investigation. Our proposed LGM fire regimes support the predominance of fire-prone and fire-dependent Mediterranean-climate vegetation on the PAP (Cowling et al., 2019). Although the proposed fire regimes could have sustained an abundance of C₃ and C₄ grasses particularly towards the east of the PAP, the pronounced and consistent summer-autumn peak in fire weather (and by implication fire season) could not have provided a driver for mass east-west migration of large grazers (Copeland et al., 2016). However, recurrent fire throughout the PAP, potentially at frequencies that exceeded that of contemporary regimes, should have been able to support considerable numbers and a diversity of medium to large herbivores (Venter et al., 2019) in this landscape. In terms of frequency and seasonality, such fire regimes could likewise have sustained an abundant supply of winter-growing geophytes, an important food source for Middle Stone-Age hunter gatherers on the PAP (Faltei et al., 2019; Singels et al., 2016).

Conflicts of interest

As authors we declare that this work has not been previously published and has not been submitted to another journal for publication; also that we do not have any financial or personal relationships with other people or organizations that could inappropriately influence our work.

Author contributions

All authors took part in the conceptualization of the study; TK and FE were responsible for data curation and formal analysis; RMC and JF were responsible for funding acquisition; TK wrote the original draft and RMC and JF contributed to the review and editing of subsequent drafts.

Declaration of competing interest

None.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2019.106059>.

References

- Allsopp, N., Colville, J.F., Verboom, G.A., 2014. Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press, Oxford.
- Archibald, S., Lehmann, C.E.R., Gomez-Dans, J.L., Bradstock, R.A., 2013. Defining pyromes and global syndromes of fire regimes. *Proc. Natl. Acad. Sci.* 110, 6442–6447.
- Archibald, S., Roy, D.P., van Wilgen, B.W., Scholes, R.J., 2009. What limits fire? An examination of drivers of burnt area in Southern Africa. *Glob. Chang. Biol.* 15, 613–630.
- Boelhouwers, J.C., 1999. Relict periglacial slope deposits in the Hex River Mountains, South Africa: observations and palaeoenvironmental implications. *Geomorphology* 30, 245–258.
- Bowman, D.M., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A., D'Antonio, C.M., DeFries, R.S., Doyle, J.C., Harrison, S.P., 2009. Fire in the earth system. *Science* 324, 481–484.
- Bradstock, R.A., 2010. A biogeographic model of fire regimes in Australia: current and future implications. *Glob. Ecol. Biogeogr.* 19, 145–158.
- Bradstock, R.A., Cohn, J.S., Gill, A.M., Bedward, M., Lucas, C., 2009. Prediction of the probability of large fires in the Sydney region of south-eastern Australia using fire weather. *Int. J. Wildland Fire* 18, 932–943.
- Brown, T.J., Hall, B.L., Westerling, A.L., 2004. The impact of twenty-first century climate change on wildland fire danger in the Western United States: an applications perspective. *Clim. Change* 62, 365–388.
- Burger, N., Bond, W.J., 2015. Flammability traits of Cape shrubland species with different post-fire recruitment strategies. *South Afr. J. Bot.* 101, 40–48.
- Bytebier, B., Antonelli, A., Bellstedt, D.U., Linder, H.P., 2011. Estimating the age of fire in the Cape flora of South Africa from an orchid phylogeny. *Proc. R. Soc. B* 278, 188–195.
- Calitz, W., Potts, A.J., Cowling, R.M., 2015. Investigating species-level flammability across five biomes in the Eastern Cape, South Africa. *South Afr. J. Bot.* 101, 32–39.
- Carcaillat, C., Bergeron, Y., Richard, P.J., Fréchette, B., Gauthier, S., Prairie, Y.T., 2001. Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *J. Ecol.* 89, 930–946.
- Carcaillat, C., Perroux, A.-S., Genries, A., Perrette, Y., 2007. Sedimentary charcoal pattern in a karstic underground lake, Vercors massif, French Alps: implications for palaeo-fire history. *Holocene* 17, 845–850.
- Cawthra, H.C., Cowling, R.M., Ando, S., Marean, C.W., 2019. Geological and soil maps of the Palaeo-Agulhas Plain for the Last Glacial Maximum. *Quart. Sci. Rev.* doi.org/10.1016/j.quascirev.2019.07.040. In this issue.
- Clark, P.U., Dyke, A.S., Shakun, J.D., Carlson, A.E., Clark, J., Wohlfarth, B., Mitrovica, J.X., Hostetler, S.W., McCabe, A.M., 2009. The last glacial maximum. *Science* 325, 710–714.
- Cockcroft, M., Wilkinson, M., Tyson, P., 1987. The application of a present-day climatic model to the late Quaternary in southern Africa. *Clim. Change* 10, 161–181.
- Copeland, S.R., Cawthra, H.C., Fischer, E., Lee-Thorp, J.A., Cowling, R.M., Le Roux, P.J., Hodgkins, J., Marean, C.W., 2016. Strontium isotope investigation of ungulate movement patterns on the Pleistocene paleo-Agulhas Plain of the greater Cape Floristic region, South Africa. *Quat. Sci. Rev.* 141, 65–84.
- Cowling, R., Holmes, P., 1992. Flora and vegetation. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 23–61.
- Cowling, R., Pierce, S., Moll, E., 1986. Conservation and utilisation of South Coast Renosterveld, an endangered South African vegetation type. *Biol. Conserv.* 37, 363–377.
- Cowling, R.M., 1983. The occurrence of C₃ and C₄ grasses in fynbos and allied

- shrublands in the South Eastern Cape, South Africa. *Oecologia* 58, 121–127.
- Cowling, R.M., 1987. Fire and its role in coexistence and speciation in Gondwanan shrublands. *South Afr. J. Sci.* 83, 106–112.
- Cowling, R.M., Potts, A.J., Franklin, J.F., Marean, C.W., 2019. Describing a drowned Pleistocene ecosystem: Last Glacial Maximum vegetation reconstruction of the Palaeo-Agulhas Plain. *Quart. Sci. Rev.* 105866 <https://doi.org/10.1016/j.quascirev.2019.105866>. In this issue.
- Cramer, M.D., Hoffman, M.T., 2015. The consequences of precipitation seasonality for Mediterranean-ecosystem vegetation of South Africa. *PLoS One* 10, e0144512.
- D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annu. Rev. Ecol. Systemat.* 63–87.
- Deacon, H.J., 1983. The peopling of the Fynbos region. In: Deacon, H.J., Hendey, Q.B., Lambrechts, J.J.N. (Eds.), *Fynbos Palaeoecology: a Preliminary Synthesis*. Council for Scientific and Industrial Research, Pretoria, pp. 183–204.
- Dimitrakopoulos, A.P., Vlahou, M., Anagnostopoulou, C.G., Mitsopoulos, I.D., 2011. Impact of drought on wildland fires in Greece: implications of climatic change? *Clim. Change* 109, 331–347.
- Engelbrecht, F.A., Marean, C.W., Cowling, R.M., Engelbrecht, C., Neumann, F.H., Scott, L., Nkoana, R., O'Neal, D., Fisher, E., Shook, E., Franklin, J., Thatcher, M., McGregor, J.L., Van der Merwe, J., Dedekind, Z., Difford, M., 2019. Downscaling Last Glacial Maximum climate over southern Africa. *Quart. Sci. Rev.* 226, 105879 <https://doi.org/10.1016/j.quascirev.2019.105879>.
- Faltein, Z., Esler, K., Midgley, G., Ripley, B., 2019. Atmospheric CO₂ concentrations restrict the growth of *Oxalis pes-caprae* bulbs used by human inhabitants of the Palaeo-Agulhas plain during the Pleistocene glacials. *Quat. Sci. Rev.* <https://doi.org/10.1016/j.quascirev.2019.04.017>. In this issue.
- Filion, L., Saint-Laurent, D., Despons, M., Payette, S., 1991. The late Holocene record of aeolian and fire activity in northern Québec, Canada. *Holocene* 1, 201–208.
- Geldenhuys, C., 1994. Bergwind fires and the location pattern of forest patches in the southern Cape landscape, South Africa. *J. Biogeogr.* 21, 49–62.
- Hatfield, J.L., Prueger, J.H., 2015. Temperature extremes: effect on plant growth and development. *Weather Clim. Extrem.* 10, 4–10.
- Hattas, D., Stock, W.D., Mabuse, W.T., Green, I.R., 2005. Phytochemical changes in leaves of subtropical grasses and fynbos shrubs at elevated atmospheric CO₂ concentrations. *Glob. Planet. Chang.* 47, 181–192.
- Helm, C., Cawthra, H., Cowling, R., De Vynck, J., Marean, C., McCrea, R., Rust, R., 2018. Palaeoecology of giraffe tracks in Late Pleistocene aeolianites on the Cape south coast. *South Afr. J. Sci.* 114, 1–8.
- Hu, F.S., Brubaker, L.B., Gavin, D.G., Higuera, P.E., Lynch, J.A., Rupp, T.S., Tinner, W., 2006. How climate and vegetation influence the fire regime of the Alaskan boreal biome: the Holocene perspective. *Mitig. Adapt. Strategies Glob. Change* 11, 829–846.
- Keeley, J., Syphard, A., 2016. Climate change and future fire regimes: examples from California. *Geosciences* 6, 37.
- Keeley, J.E., 2012. Fire in Mediterranean climate ecosystems - a comparative overview. *Israel J. Ecol. Evol.* 58, 123–135.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2012. Fire in Mediterranean ecosystems. In: *Ecology, Evolution and Management*. Cambridge University Press, Cambridge.
- Keeley, J.E., Fotheringham, C.J., Morais, M., 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284, 1829–1832.
- Keeley, J.E., Syphard, A.D., 2017. Different historical fire-climate patterns in California. *Int. J. Wildland Fire* 26, 253–268.
- Keetch, J.J., Byram, G.M., 1968. A Drought Index for Forest Fire Control. US Department of Agriculture, Forest Service, Asheville, North Carolina, USA, p. 32.
- Kraaij, T., 2011. The flora of the Bontebok National Park in regional perspective. *South Afr. J. Bot.* 77, 455–473.
- Kraaij, T., Baard, J.A., Arndt, J., Vhengani, L., van Wilgen, B.W., 2018. An assessment of climate, weather, and fuel factors influencing a large, destructive wildfire in the Knysna region, South Africa. *Fire Ecol.* 14, 4.
- Kraaij, T., Baard, J.A., Cowling, R.M., van Wilgen, B.W., Das, S., 2013a. Historical fire regimes in a poorly understood, fire-prone ecosystem: eastern coastal fynbos. *Int. J. Wildland Fire* 22, 277–287.
- Kraaij, T., Cowling, R.M., van Wilgen, B.W., 2013b. Lightning and fire weather in eastern coastal fynbos shrublands: seasonality and long-term trends. *Int. J. Wildland Fire* 22, 288–295.
- Kraaij, T., van Wilgen, B.W., 2014. Drivers, ecology, and management of fire in fynbos. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region*. Oxford University Press, Oxford, pp. 47–72.
- Kraaij, T., Young, C., Bezuidenhout, H., 2017. Growth-form responses to fire in Nama-Karoo escarpment grassland, South Africa. *Fire Ecol.* 13, 85–94.
- Lays, B., Carcaillet, C., Dezileau, L., Ali, A.A., Bradshaw, R.H.W., 2013. A comparison of charcoal measurements for reconstruction of Mediterranean paleo-fire frequency in the mountains of Corsica. *Quat. Res.* 79, 337–349.
- Marean, C.W., Anderson, R.J., Bar-Matthews, M., Braun, K., Cawthra, H.C., Cowling, R.M., Engelbrecht, F., Esler, K.J., Fisher, E., Franklin, J., 2015. A new research strategy for integrating studies of paleoclimate, paleoenvironment, and paleoanthropology. *Evol. Anthropol. Issues News Rev.* 24, 62–72.
- Marean, C.W., Cawthra, H.C., Cowling, R.M., Esler, K.J., Fisher, E., Milewski, A., Potts, A.J., Singels, E., De Vynck, J., 2014. Stone age people in a changing South African greater Cape Floristic region. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), *Ecology, Evolution, and Conservation of a Megadiverse Region*. Oxford University Press, Oxford, pp. 164–199.
- Midgley, G., Stock, W., Juritz, J., 1995. Effects of elevated CO₂ on Cape fynbos species adapted to soils of different nutrient status: nutrient and CO₂-responsiveness. *J. Biogeogr.* 22, 185–191.
- Noble, I.R., Bary, G.A.V., Gill, A.M., 1980. McArthur's fire-danger meters expressed as equations. *Austral Ecol.* 5, 201–203.
- Novellie, P., Kraaij, T., 2010. Evaluation of Themeda triandra as an indicator for monitoring the effects of grazing and fire in the Bontebok National Park. *Koedoe* 52, 1–5.
- Pausas, J.G., Paula, S., 2012. Fuel shapes the fire-climate relationship: evidence from Mediterranean ecosystems. *Glob. Ecol. Biogeogr.* 21, 1074–1082.
- Power, M.J., Marlon, J., Ortiz, N., Bartlein, P.J., Harrison, S.P., Mayle, F.E., Ballouche, A., Bradshaw, R.H., Carcaillet, C., Cordova, C., 2008. Changes in fire regimes since the Last Glacial Maximum: an assessment based on a global synthesis and analysis of charcoal data. *Clim. Dyn.* 30, 887–907.
- Quick, L.J., Carr, A.S., Meadows, M.E., Boom, A., Bateman, M.D., Roberts, D.L., Reimer, P.J., Chase, B.M., 2015. A late Pleistocene-Holocene multi-proxy record of palaeoenvironmental change from Still Bay, southern Cape Coast, South Africa. *J. Quat. Sci.* 30, 870–885.
- Quick, L.J., Meadows, M.E., Bateman, M.D., Kirsten, K.L., Mäusbacher, R., Haberzettl, T., Chase, B.M., 2016. Vegetation and climate dynamics during the last glacial period in the fynbos-afrotemperate forest ecotone, southern Cape, South Africa. *Quat. Int.* 404, 136–149.
- Roberts, D., Neumann, F., Cawthra, H., Carr, A., Scott, L., Durugbo, E., Humphries, M., Cowling, R., Bamford, M., Musekiwa, C., MacHutchon, M., 2017. Palaeoenvironments during a terminal Oligocene or early Miocene transgression in a fluvial system at the southwestern tip of Africa. *Glob. Planet. Chang.* 150, 1–23.
- Rundel, P.W., Arroyo, M.T., Cowling, R.M., Keeley, J.E., Lamont, B.B., Pausas, J.G., Vargas, P., 2018. Fire and plant diversification in mediterranean-climate regions. *Front. Plant Sci.* 9, 851.
- Scott, A.C., Glasspool, I.J., 2006. The diversification of Paleozoic fire systems and fluctuations in atmospheric oxygen concentration. *Proc. Natl. Acad. Sci. U. S. A.* 103, 10861–10865.
- Seydack, A.H.W., Bekker, S.J., Marshall, A.H., 2007. Shrubland fire regime scenarios in the Swartberg Mountain Range, South Africa: implications for fire management. *Int. J. Wildland Fire* 16, 81–95.
- Singels, E., Potts, A.J., Cowling, R.M., Marean, C.W., De Vynck, J., Esler, K.J., 2016. Foraging potential of underground storage organ plants in the southern Cape, South Africa. *J. Hum. Evol.* 101, 79–89.
- Sirca, C., Salis, M., Arca, B., Duce, P., Spano, D., 2018. Assessing the performance of fire danger indexes in a Mediterranean area. *IFOR. Biogeosci. For.* 11, 563–571.
- Southey, D., 2009. Wildfires in the Cape Floristic Region: Exploring Vegetation and Weather as Drivers of Fire Frequency. Department of Botany. MSc thesis, University of Cape Town, Cape Town, p. 82.
- Stock, W., Allsopp, N., 1992. Functional perspective of ecosystems. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 241–259.
- Stock, W., Van der Heyden, F., Lewis, O., 1992. Plant structure and function. In: Cowling, R.M. (Ed.), *The Ecology of Fynbos: Nutrients, Fire and Diversity*. Oxford University Press, Cape Town, pp. 226–240.
- Stolper, D.A., Bender, M.L., Dreyfus, G.B., Yan, Y., Higgins, J.A., 2019. A Pleistocene ice core record of atmospheric O₂ concentrations. *Science* 353, 1427–1430.
- Syphard, A.D., Keeley, J.E., Pfaff, A.H., Ferschweiler, K., 2017. Human presence diminishes the importance of climate in driving fire activity across the United States. *Proc. Natl. Acad. Sci.* 114, 13750–13755.
- Uys, R.G., Bond, W.J., Everson, T.M., 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biol. Conserv.* 118, 489–499.
- van Wilgen, B.W., Biggs, H.C., O'Regan, S.P., Mare, N., 2000. A fire history of the savanna ecosystems in the Kruger National Park, South Africa, between 1941 and 1996. *South Afr. J. Sci.* 96, 167–178.
- van Wilgen, B.W., Burgan, R.E., 2010. Adaptation of the United States Fire Danger Rating System to fynbos conditions. Part II. Historic fire danger in the fynbos biome. *S. Afr. For. J.* 129, 66–78.
- van Wilgen, B.W., Forsyth, G.G., De Klerk, H., Das, S., Khuluse, S., Schmitz, P., 2010. Fire management in Mediterranean-climate shrublands: a case study from the Cape fynbos, South Africa. *J. Appl. Ecol.* 47, 631–638.
- van Wilgen, B.W., Govender, N., Biggs, H.C., 2007. The contribution of fire research to fire management: a critical review of a long-term experiment in the Kruger National Park, South Africa. *Int. J. Wildland Fire* 16, 519–530.
- van Wilgen, B.W., Govender, N., Smit, I.P., MacFadyen, S., 2014. The ongoing development of a pragmatic and adaptive fire management policy in a large African savanna protected area. *J. Environ. Manag.* 132, 358–368.
- Venter, J.A., Brooke, C.F., Marean, C.W., Fritz, H., 2019. Large mammals of the Palaeo-Agulhas Plain: conceptual reconstruction of large mammal assemblages and their habitats. *Quart. Sci. Rev.* In this issue.
- Williams, J., 2013. Exploring the onset of high-impact mega-fires through a forest land management prism. *For. Ecol. Manag.* 294, 4–10.
- Wren, C.D., Botha, S., De Vynck, J., Janssen, M.A., Hill, K., Shook, E., Harris, J.A., Wood, B.M., Venter, J., Cowling, R.M., Franklin, J., Fisher, E.C., Marean, C.W., 2019. The foraging potential of the Holocene Cape south coast of South Africa without the Palaeo-Agulhas Plain. *Quart. Sci. Rev.* <https://doi.org/10.1016/j.quascirev.2019.06.012>. In this issue.