Contents lists available at ScienceDirect

Global and Planetary Change

Research Article

# Multi-millennial reconstruction of fire return intervals from a fynbos – Afrotemperate forest ecotone in the Cape Floristic Region, South Africa: Paleoecological implications for present-day management[☆]

Stella G. Mosher[a,*], Mitchell J. Power[b,c], Lynne J. Quick[d], Brian M. Chase[e,f], Torsten Haberzettl[g], Thomas Kasper[g], Simon C. Brewer[b], David R. Braun[h], J. Tyler Faith[c,i,j]

[a] Department of Earth Science, Utah Valley University, Orem, UT, USA
[b] School of Environment, Society and Sustainability, University of Utah, Salt Lake City, UT, USA
[c] Natural History Museum of Utah, University of Utah, Salt Lake City, UT, USA
[d] African Centre for Coastal Palaeoscience, Nelson Mandela University, 6031 Gqeberha, South Africa
[e] Institut des Sciences de l'Evolution-Montpellier (ISEM), University of Montpellier, Centre National de la Recherche Scientifique (CNRS), EPHE, IRD, Montpellier, France
[f] Department of Environmental and Geographical Science, University of Cape Town, Rondebosch, South Africa
[g] Physical Geography, Institute for Geography and Geology, University of Greifswald, 17489 Greifswald, Germany
[h] Center for the Advanced Study of Human Paleobiology, George Washington University, Washington, DC 20052, USA
[i] Department of Anthropology, University of Utah, Salt Lake City, UT, USA
[j] Department of Archaeology, University of Cape Town, Rondebosch, South Africa

ARTICLE INFO

Editor: Shilong Piao

*Keywords:*
Fire history
Fire frequency
Paleofire
Eilandvlei
Conservation

ABSTRACT

In South Africa's highly biodiverse and fire-adapted Cape Floristic Region, fire is critical to maintaining ecosystem health and for the reproductive strategies of many endemic species. Ecological studies have identified fire return intervals (FRIs) of approximately 10–15 years. However, the short timescale of these observations, derived from anthropogenically impacted systems, means that the extent to which these FRIs are maintained over millennia, and how vegetation dynamics co-vary with fire frequency is poorly resolved. Here, we analyze a high-resolution macrocharcoal record from a lacustrine sedimentary archive to reconstruct fire return intervals over four millennia at a fynbos-afrotemperate forest ecotone along South Africa's southern Cape coast. We address variability in fire activity (i.e., more or less burning) and FRIs in relation to pollen-derived reconstructions of local vegetation change and regional shifts in moisture availability over the past 4200 years. We document a range of FRIs between 10.5 and 166 years. We find that FRIs shift towards longer intervals, fire activity decreases, and afrotemperate forest vegetation becomes more abundant during periods of increased moisture availability. Our historical (1890–2013 CE) FRI reconstruction is consistent with ~10–15 years between burns, but one must only look back a few centuries to see FRIs far outside the range of variability observed today. This suggests that our present-day ecological lens is not representative of the full range of natural variability experienced at this site over the past four millennia. This work provides long-term ecological context to land managers working towards the conservation and protection of fynbos.

## 1. Introduction

Paleoecological research can improve our understanding of the long-term variability in ecosystems over centuries to millennia – outside the range of historical, ecological knowledge encompassed by direct human observation (e.g., Birks, 2012; Willis and Bhagwat, 2010). However, despite a growing awareness of the value of paleo records (Barnosky et al., 2017; Dietl et al., 2015; Rick and Lockwood, 2013), applying such research to conservation and land management decisions remains a challenge (e.g., Gillson, 2021; Groff et al., 2023; Lyman, 2006). Previous work has argued that long-term records provide a broader perspective on what may be considered “natural” within an ecosystem (Willis and

---

[☆] This article is part of a Special issue entitled: ‘Fire’ published in Global and Planetary Change.

[*] Corresponding author at: Utah Valley University, Department of Earth Science, 800 W. University Pkwy, Orem, UT 84058, USA (S.G. Mosher).

16 December 2025; Accepted 11 January 2026

Birks, 2006), and can offer insights into historical variability (i.e., the temporal domain) to inform policymakers and land managers about climate and human-induced ecosystem impacts (e.g., Birks, 2012; Gillson, 2021; Kirsten et al., 2024). Paleoecology acknowledges that landscapes are not static – often experiencing dynamic shifts in composition and diversity over millennia. Therefore, paleoecological reconstructions can reveal ecological processes and responses over thousands of years, including periods of pronounced climatic changes and human-environment impacts, facilitating a more robust understanding of landscape evolution and history (e.g., Kirsten et al., 2024; Manzano et al., 2020; McWethy et al., 2010). These reconstructions can also shed light on biome resilience and ecological tipping points – wherein threshold conditions are reached that push the ecosystem non-linearly into a new state (Thomas, 2016). This is important because many ecological datasets, which typically provide a baseline range of ecosystem variability, are often temporally limited to only a few decades of observations in systems already heavily modified by human activity and may miss critical responses to long-term climate changes. Through the integration of deep-time paleoecology and modern-day conservation biology, inter-biome dynamics and ecosystem resilience can be better understood, and conservation and management plans can be established that account for long-term variability in climate-vegetation-fire interactions.

In South Africa's highly biodiverse and disturbance-adapted Cape Floristic Region (CFR), fire is a decisive force in maintaining ecosystem health and for the reproductive strategies of many endemic plants of the mediterranean shrublands of the Fynbos Biome (Cowling, 1987; Keeley, 2012). Because of its ecological importance, managing fynbos ecosystems means managing fire, a perspective that has guided historical efforts to prescribe and contain fires in the CFR. Since ~1970 CE, land management strategies have focused on prescribed burning to protect soil, ensure water flow, rejuvenate vegetation, and prevent harmful large-scale wildfires by reducing fuel build-up (van Wilgen, 2009). However, much of our present-day understanding of how fire operates in the CFR comes from historical, ecological studies extending back, at most, ~80 years. Furthermore, these studies come from protected areas that have already been altered by human activity or efforts to “protect” fynbos species (e.g., Kraaij et al., 2018; Kraaij et al., 2013; Kruger, 1984; van Wilgen et al., 2010), and that lack many large herbivores, such as hippopotamus (*Hippopotamus amphibius*), which were historically present in many wetland and fynbos-dominated areas (Skead, 2011) and would otherwise have removed burnable plant biomass from the system (Karp et al., 2024; Staver et al., 2021).

Fire return intervals (FRIs), or the time interval between fires at any given site (Bond and Keeley, 2005), are often indicated as a useful metric for managing ecosystems because they present a number, or range of numbers, that are considered appropriate for the ecological requirements of a particular plant community. In the CFR, these FRIs tend to range between 7 and 55 years, with the majority of fires re-occurring within a ~ 10–15 year interval (e.g., Kraaij et al., 2018; Kraaij et al., 2013; Kraaij and van Wilgen, 2014; Kruger, 1984; van Wilgen et al., 2010). Most fynbos plants are known to be resilient to fire and capable of surviving decadal to multi-decadal fire regimes with FRIs of 10 to 40 years (van Wilgen and Forsyth, 1992). In contrast, the CFR's moisture-loving and fire-adverse Southern Afrotemperate Forest Biome (hereafter refered to as afrotemperate forest) prefers sheltered topographical locations with protection from fire and high plant-available moisture (e.g., Cramer et al., 2019; Gillson et al., 2020; Mucina et al., 2006). Because of this, the afrotemperate forest is more sensitive than fynbos to drought and fire and therefore is expected to expand (contract) under wetter (drier) conditions and/or periods of reduced (increased) rainfall seasonality while the fire-adapted fynbos may contract (expand) under these conditions when fires may be less (more) frequent. However, despite the importance of fire in the CFR, little is known about the long-term range of variability in FRIs and how changes in fire frequency relate to inter-biome dynamics and ecosystem resilience. While many Holocene paleoecological reconstructions from the CFR focus on vegetation responses to changes in climate (e.g., du Plessis et al., 2020; Manzano et al., 2023; Quick et al., 2018; Valsecchi et al., 2013), none have explored variability in fire activity, magnitude, and FRIs at temporal scales relevant to the frequency of present-day CFR fires. In this paper, we first reconstruct fire activity, magnitude, and frequency at 2-year timesteps (median value) over ~4200 years from a sediment core extracted from a coastal, ecotonal fynbos-afrotemperate forest lake, Eilandvlei, along the southern Cape coast. We then explore variable FRIs alongside long-term inter-biome, fynbos–afrotemperate forest dynamics, which provide a lens through which ecosystem change and resilience can be evaluated.

The Eilandvlei fire history record provides the first long-term record of variability in FRIs at ecological-scale temporal resolution to address two questions: (a) *how does our historical, ecological understanding of FRIs in the CFR align with the natural range of variability in FRIs over four millennia?* And (b)*, if variations in FRIs are identified over time, how do they impact ecosystem resilience at this fynbos – afrotemperate forest ecotone?* This long-term record of fire captures variability in the CFR disturbance regime – shifting alongside changes in climate, vegetation assemblage, and human land-use histories, and improves our long-term perspective on fire regimes along the southern Cape coast.

## 2. Regional setting

### 2.1. Hydroclimate

South Africa contains a diversity of biomes and vegetation communities, which are in part a result of distinct seasonal rainfall regimes across the subcontinent (Fig. 1; Mucina and Rutherford, 2006). While the eastern and interior parts of South Africa receive summertime precipitation driven by the low-latitude tropical easterlies, the west coast experiences a contrasting winter rainfall regime driven by seasonal shifts in the mid-latitude temperate westerly winds (Tyson, 1986; Tyson and Preston-Whyte, 2000). These broad regions form the summer rainfall zone (SRZ) and winter rainfall zone (WRZ), respectively. In between the SRZ and WRZ is a narrow zone of year-round rainfall (YRZ) that receives precipitation from both these tropical and temperate moisture sources (Chase and Meadows, 2007; Tyson and Preston-Whyte, 2000). The southern Cape coast experiences a high degree of climate variability due to these tropical and temperate climate systems and the Agulhas Current, which brings warm water and moisture-laden air along the southern Cape coast (Chase et al., 2024; Chase and Quick, 2018; Engelbrecht and Landman, 2016). The 90,000 km$^2$ CFR is a product of the Mediterranean climate experienced by the WRZ, with winter rainfall (i.e., a cool growing season) critical for the development of the region's high levels of endemism and biodiversity found within the Fynbos Biome (e.g., Linder, 2003). Here, we focus on a coastal CFR site within a fynbos-afrotemperate forest ecotone, Eilandvlei, which is found in the YRZ (Fig. 1).

### 2.2. Fire regimes of the CFR

The CFR has been subdivided into six fire climatic zones (Kraaij et al., 2013; van Wilgen, 1984), which are distinguished by slightly variable FRIs, fire weather danger, and fire seasonality. Mean FRIs in fynbos shrublands range between 8 years in the far eastern coastal zone, and 16 years in the eastern inland zone (Kraaij and van Wilgen, 2014). Eilandvlei is located in the southwestern coastal zone, with average fynbos FRIs of ~10 years, and the majority of wildfires igniting between November and February when extreme summer conditions can elevate dangerous fire conditions (Kraaij and van Wilgen, 2014; van Wilgen, 1984). Most of what is known about fire in the CFR comes from studies of historical fires, extending back between 30 and 80 years (e.g., Brown et al., 1991; Forsyth and van Wilgen, 2008; Kraaij and van Wilgen, 2014; Seydack et al., 2007; van Wilgen et al., 2010), with more recent

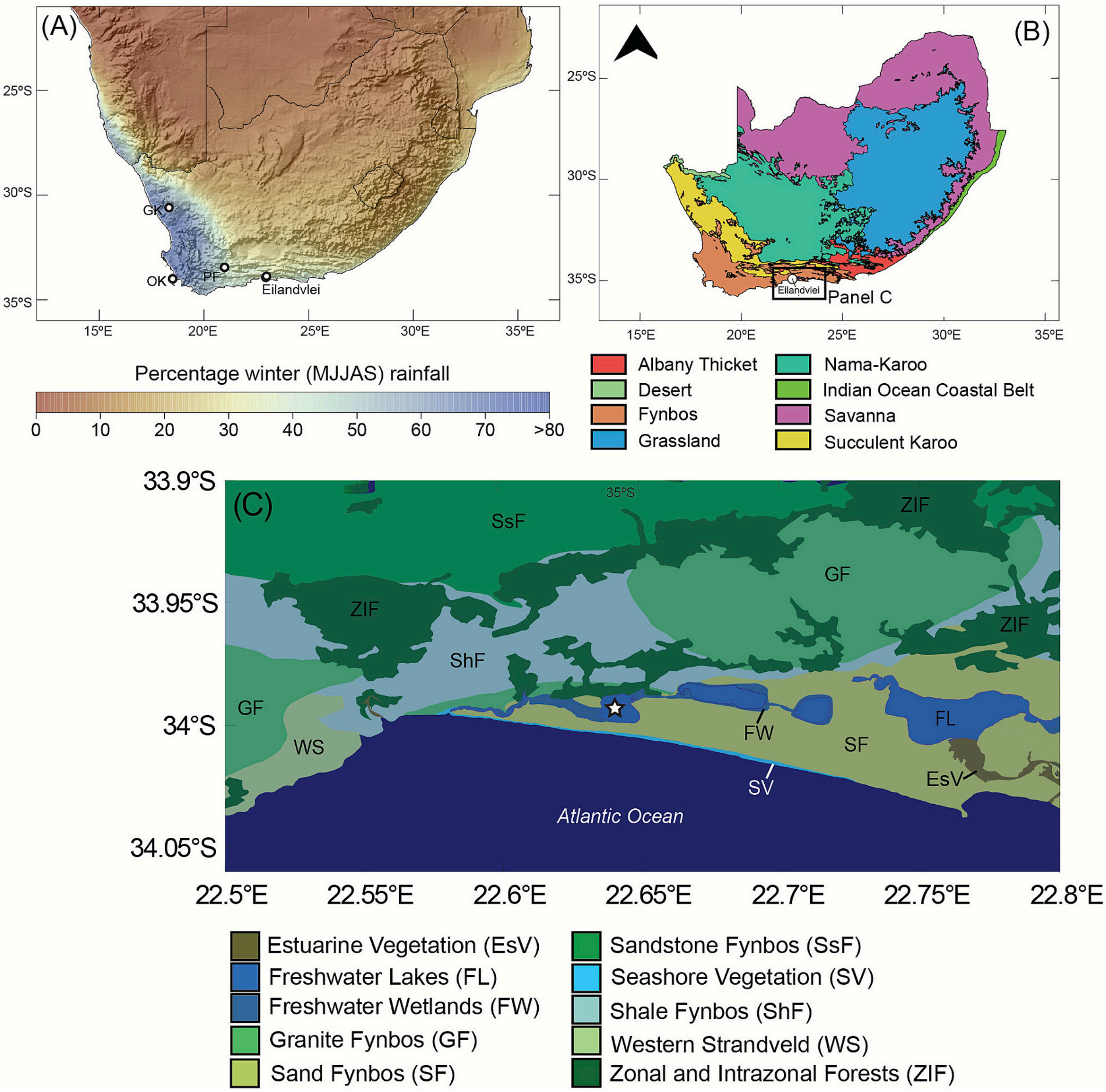

**Fig. 1.** (A) Map of southern Africa depicting seasonal rainfall gradients as percent winter rainfall received (May – September). Eilandvlei (study site) is shown in the YRZ along the southern Cape coast. Basemap sensu Chase and Meadows (2007). Eilandvlei is shown in relation to other paleoecological archives referenced in this text: (GK – Groenkloof; OK – Orange Kloof; PF – Papkuilsfontein). (B) Biomes of southern Africa (Mucina and Rutherford, 2006) with Eilandvlei's location. (C) Zoomed in panel of contemporary vegetation surrounding Eilandvlei (Mucina and Rutherford, 2006), highlighting the ecotonal location of Eilandvlei (white star) between fynbos and forest vegetation types.

developments via remote sensing and satellite-derived burnt area products (e.g., Andela et al., 2019; de Klerk et al., 2012; Xulu et al., 2021). These historical data suggest that fires broadly recur after 7–55 years (Kraaij and van Wilgen, 2014), though mostly within ~10–15 years (Forsyth and van Wilgen, 2008; Kraaij and van Wilgen, 2014; van Wilgen et al., 2010). Shorter FRIs occur locally in the far eastern coastal Tsitsikamma region (~7 years between fires; Kraaij et al., 2013) and the intensively managed southwest coastal lowland fynbos found in Bontebok National Park (~7.2 years between fires; Kraaij, 2010) while longer FRIs are in drier, inland areas along the eastern extent of the Swartberg Mountains (~21 years between burns; Seydack et al., 2007) where observations suggest that fuel accumulation rates are lower.

Fires generally increase in frequency along rainfall gradients increasing from west to east in the CFR (Kraaij et al., 2013) and from lower to higher altitudes (i.e., in the Swartberg mountains; Seydack et al., 2007), where lower altitude shrublands are drier and more fuel-limited than higher altitude sites, which are controlled primarily by fire weather and lightning occurrences rather than fuel availability. These linkages between fire and precipitation are non-linear, with fire peaking in seasonal environments that receive sufficient moisture to sustain fuel loads, yet undergo sufficient seasonal drying to permit ignition (e.g., Daniau et al., 2012; Karp et al., 2023). In areas with low rainfall and productivity, often referred to as “fuel-limited” systems, an increase in precipitation may result in an increase in fire activity as biomass (i.e., fuel) increases on the landscape (Mosher et al., 2024). Alternately, areas that experience very high moisture, typically >900 mm per year, may experience reduced fire despite high fuel loads and are known as “fuel-moisture-limited” systems (Karp et al., 2023).

Critically, our historical understanding of CFR FRIs is limited to observations of a landscape that has already been significantly impacted by human activity, and does not inform on the full natural range of variability during the Holocene or the long-term dynamics between climate, vegetation, and fire. In this paper, we seek to explore the dynamic interplay between fire and vegetation at Eilandvlei using high-resolution sedimentary records of fire alongside pollen-derived reconstructions of vegetation change over the past four millennia.

### 2.3. Study site

Located in the Wilderness Embayment, Eilandvlei (34°10”59′S, 22°44″43′E; surface area ~ 1.38 km$^2$; maximum depth ~ 6.5 m) is the westernmost of three lakes which are connected via small, historically natural channels which are now artificially kept open by land managers (Fig. 1). The Embayment started to form during the Pleistocene and has since experienced several marine transgression-regression cycles (Bateman et al., 2011; Cawthra et al., 2014). The Touw River is the primary freshwater source in the catchment and feeds into the Serpentine Channel about 3 km upstream from its mouth, though additional freshwater enters at Eilandvlei's northeastern shore from the Duiwe River. Both inflows originate in the Outeniqua Mountains to the north. This region has experienced four major geomorphological and hydrological shifts over the Holocene, ranging from a drowned paleo-valley to a marine embayment during the mid-Holocene sea-level high-stand, to a lagoon system, and finally to the present-day coastal lake and estuarine system since ~1200 cal yrs. BP (Fig. 1; Wündsch et al., 2018).

Annual rainfall along the southern Cape coast can be highly variable, ranging between 375 and 1475 mm (mean: 760 mm), and is relatively evenly distributed throughout the year (SAWS, 2017). Eilandvlei is located within the Knysna Afrotemperate Forest (Zonal and Interzonal Forests of Fig. 1C) – southern Africa's largest temperate forest type (Geldenhuys, 1991; Midgley et al., 1997; Mucina et al., 2006) – which is typically found in valleys sheltered from fire and containing high soil moisture. Fynbos and coastal thicket communities can be found on the coastal lowlands and dunes, as well as on the northern side of the embayment. Specifically, Knysna Sand Fynbos is found on the coastal flats, while to the north of Eilandvlei, Garden Route Shale Fynbos is found at the intersections between fynbos, scrub forest, and afrotemperate forest patches. Other dominant terrestrial vegetation groups include the Southern Cape Dune Fynbos along the lake's seaward barrier dunes, characterized by sclerophyllous shrubs and a restionaceaeous undergrowth, Cape Lowland Freshwater Wetlands along the Serpentine Channel to the west, and Granite Fynbos groups to the north towards the Outeniqua Mountains (Mucina and Rutherford, 2006). For a more detailed description of the contemporary vegetation refer to Quick et al. (2018).

The relative locations and dominance of these different vegetation assemblages are driven by ecological factors such as micro-climate, topography (Geldenhuys, 1994), geology (Coetsee et al., 2015), drainage (Cowling, 1984), and fire regimes, including frequency, seasonality, intensity, and size (e.g., Manders and Richardson, 1992; Power et al., 2017; Strydom et al., 2022; van Wilgen et al., 2010). Dynamics between climate, vegetation, soil type, and fire are recognized to drive alternating states, or periods of relative expansion or contraction between fynbos and afrotemperate forest vegetation, with fynbos better tolerating drier conditions or extended periods of drought (Cramer et al., 2019; Gillson et al., 2020; Prader et al., 2023; Slingsby et al., 2020).

## 3. Methods

### 3.1. Core extraction

The Eilandvlei core was extracted from 33°59′43” S; 22°38′24″ E as part of the 2013 RAiN field campaign (Haberzettl et al., 2014). Two long piston cores (EV13–3: 30.22 m and EV13–4: 9.86 m) were extracted from the profundal zone at a water depth of 6 m using a UWITEC system, and a short core (156 cm) was retrieved using a gravity corer. The cores were transported to the Friedrich Schiller University, Jena, Germany, and were split, photographed, and lithologically described following standard procedures. Geochemical variations and optical marker layers were used to correlate the overlapping cores and to build a composite record of 30.47 m (‘EV13’). To span the past 4200 years, a macro-charcoal (>125 μm) record was established from the top 9.6 m of the EV13 composite to encompass the potentially variable human impacts surrounding the regional arrival of pastoralist herders ~2000 cal yrs. BP (e.g., Bousman, 1998; Coutu et al., 2021; Schweitzer, 1974).

### 3.2. Chronology

Radiocarbon ages were produced by Beta Analytic Inc., Miami, and are reported as calibrated years before present (cal yrs. BP). The chronology applied here has been adapted from the original chronology used by Kirsten et al. (2018), Quick et al. (2018), and Wündsch et al. (2018) by re-calibrating $^{14}$C ages to the more recent marine (Marine20) and southern hemisphere (SHCal20) calibration curves in OxCal version 4.4 (Fig. 2; Bronk Ramsey, 2009; Heaton et al., 2020; Hogg et al., 2020). Bulk samples calibrated on the Marine20 curve were corrected for regional marine reservoir effects (Wündsch et al., 2016). The new EV13 age model was produced in R using the rbacon software package, version 3.2 (Blaauw and Christen, 2011; R Core Team, 2023) and reached a median basal depth of 8730 cal yrs. BP for the complete 30.47 m sequence. Here, we used the top 9.6 m of the EV13 sequence, extending back to a median age of 4260 cal yrs. BP (Fig. 2).

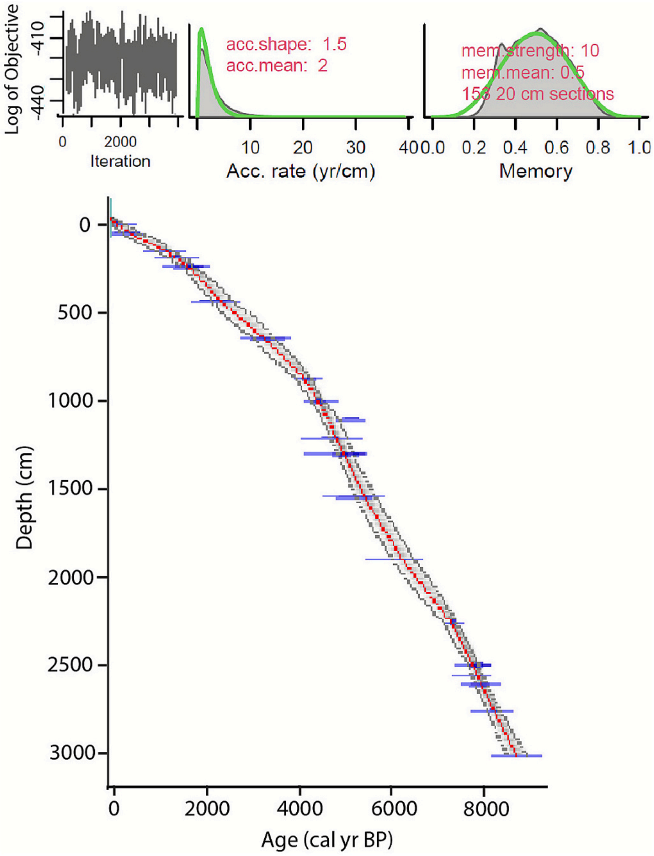

**Fig. 2.** *Re*-calibrated EV13 age-depth model using the Marine20 and SHCal20 calibration curves (Heaton et al., 2020; Hogg et al., 2020). The original age-depth model was produced by Wündsch et al. (2016). Blue lines represent 2σ probability-density function of the calibrated $^{14}$C ages. Gray areas demonstrate the 95% confidence interval, and the central red line illustrates the single best model using median ages at each depth. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 3.3. Charcoal analyses

Contiguous samples were processed for macroscopic charcoal (< 125 μm) fragments at 0.5 cm intervals through the uppermost 9.6 m of the EV13 sequence. Each 0.5 cm sample represented a median value of 2 years of deposition. Charcoal samples initially averaged 0.75 g per sample but were later reduced to 0.5 g at sample number 1142 due to exceptionally high charcoal counts. Samples were placed in 15 ml test tubes with 3 ml of sodium hexametaphosphate and were soaked for 24–72 h to assist in the deflocculation of clay-rich sediments. Volumetric displacement was measured, and samples were wet-sieved through nested 250 μm and 125 μm sieves to isolate charcoal size classes. In total, 1919 charcoal samples were counted from the EV13 sequence from both size classes. The results presented here are based on the sum of both size classes. See Mosher et al. (2025) for an analysis of variability in fire activity (i.e., more or less burning) at Eilandvlei alongside climate and anthropogenic changes.

Charcoal data were analyzed using CharAnalysis in MATLAB (Higuera et al., 2009). CharAnalysis permits the reconstruction of average charcoal influx (CHAR = # of particles cm$^{-2}$ year$^{-1}$) over each sample time interval. CHAR reconstructions provide two components: first, a slowly varying trend, referred to as the *background* component (often referred to as “fire activity” – periods of relatively more or less burning), representing long-term changes in fire that are related to variability in fuel types and amount, regional patterns of burning, changing climate conditions, and depositional environments; and second, short-term activity in fire, referred to as the *peaks* component, which are identified as pulses in CHAR that exceed the background component by a specified threshold (Clark and Royall, 1996). These *peaks* indicate one or more fire *episodes* during the time interval contained in the sample (Long et al., 1998). Charcoal peak magnitudes (# of particles cm$^{-2}$ peak$^{-1}$) are the sum of all CHAR values for each sample exceeding the final threshold value for each identified fire episode (Higuera et al., 2009). CharAnalysis also permits the reconstruction of fire frequency as the number of fire episodes per 100 years. This is calculated by smoothing the fire episodes detected such that variations in the number of fire episodes (i.e., frequency) over time can be visualized (Power et al., 2006). We use the terminology of fire return

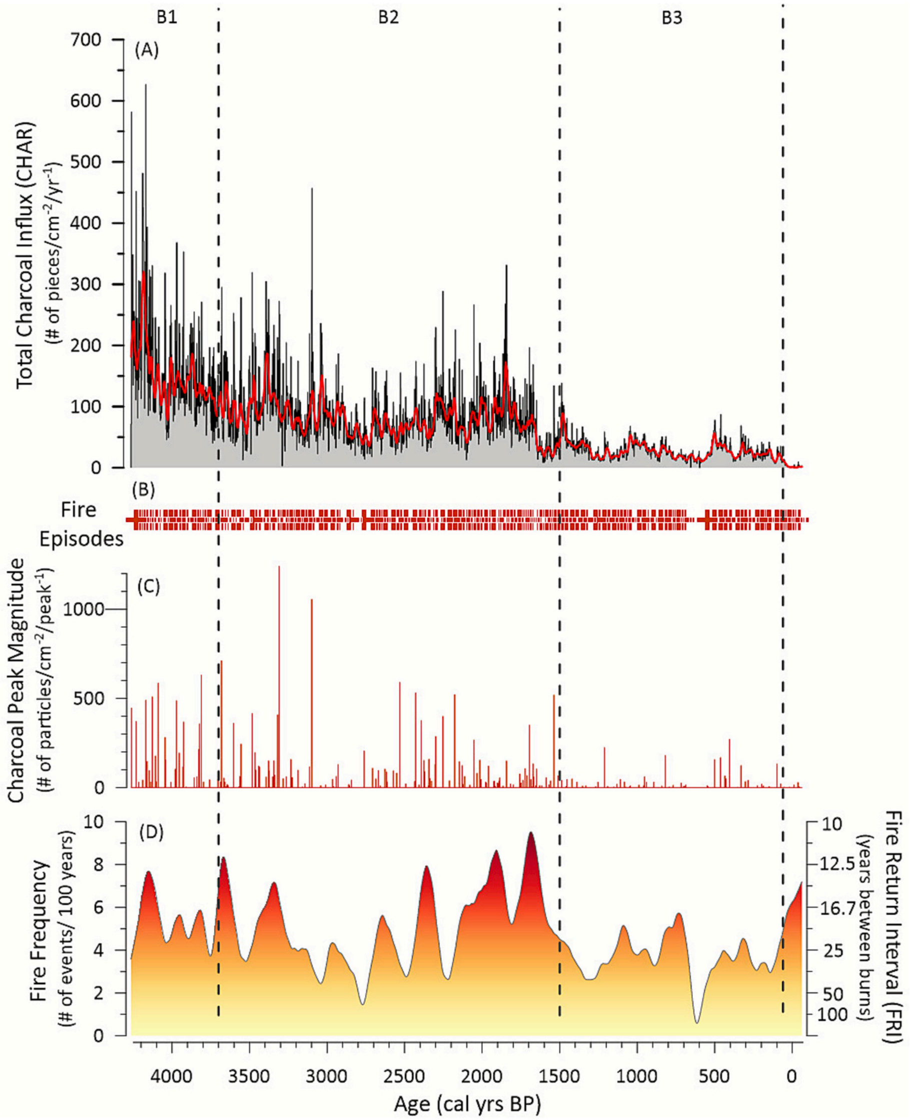

**Fig. 3.** Eilandvlei fire history reconstruction over the past 4200 years. A) Charcoal influx (CHAR; particles cm$^{-2}$ yr$^{-1}$), is interpreted as a metric of fire activity over time. B) Fire episodes (*peaks*) identified as one or more fires detected above background CHAR during the time interval represented by the sample (median value: 2 years). C) Charcoal peak magnitudes (# of particles cm$^{-2}$ peak$^{-1}$), which are calculated as the sum of all CHAR values exceeding the assigned threshold value for each fire episode identified in (B). D) Reconstruction of fire frequency (# of fires/ 100 years) and fire return intervals (FRIs; # of years between burns). Dotted lines depict CONISS period boundaries as identified in Quick et al. (2018).

intervals (FRIs; i.e., years between burns) in the text to match terms commonly used in other studies. We calculate FRIs as 100 years / the number of fire episodes detected. Both fire frequency and FRIs are shown in Figs. 3 and 4.

The suitability of fire history reconstructions for peak and frequency analyses are highly dependent upon the appropriateness of the sediment-charcoal record, and therefore, a signal-to-noise index (SNI) is used to quantify the suitability of the record and the robustness of the reconstruction – both over the entire record and within each zone (Kelly et al., 2017). Ideally, selected threshold parameters that result in an SNI of about 3 protect against over-interpreting a weak signal. SNI values <3 suggest limited separation of the signal (*peak*) and noise (*background*) components.

For the EV13 sequence, raw charcoal data was converted to CHAR using the median resolution of 2 years per sample (Mosher et al., 2025). This high-resolution temporal interval permitted multiple charcoal samples within an expected fire frequency interval (i.e., ~10–15 years in the CFR). The full record was smoothed using a LOESS smoother over a

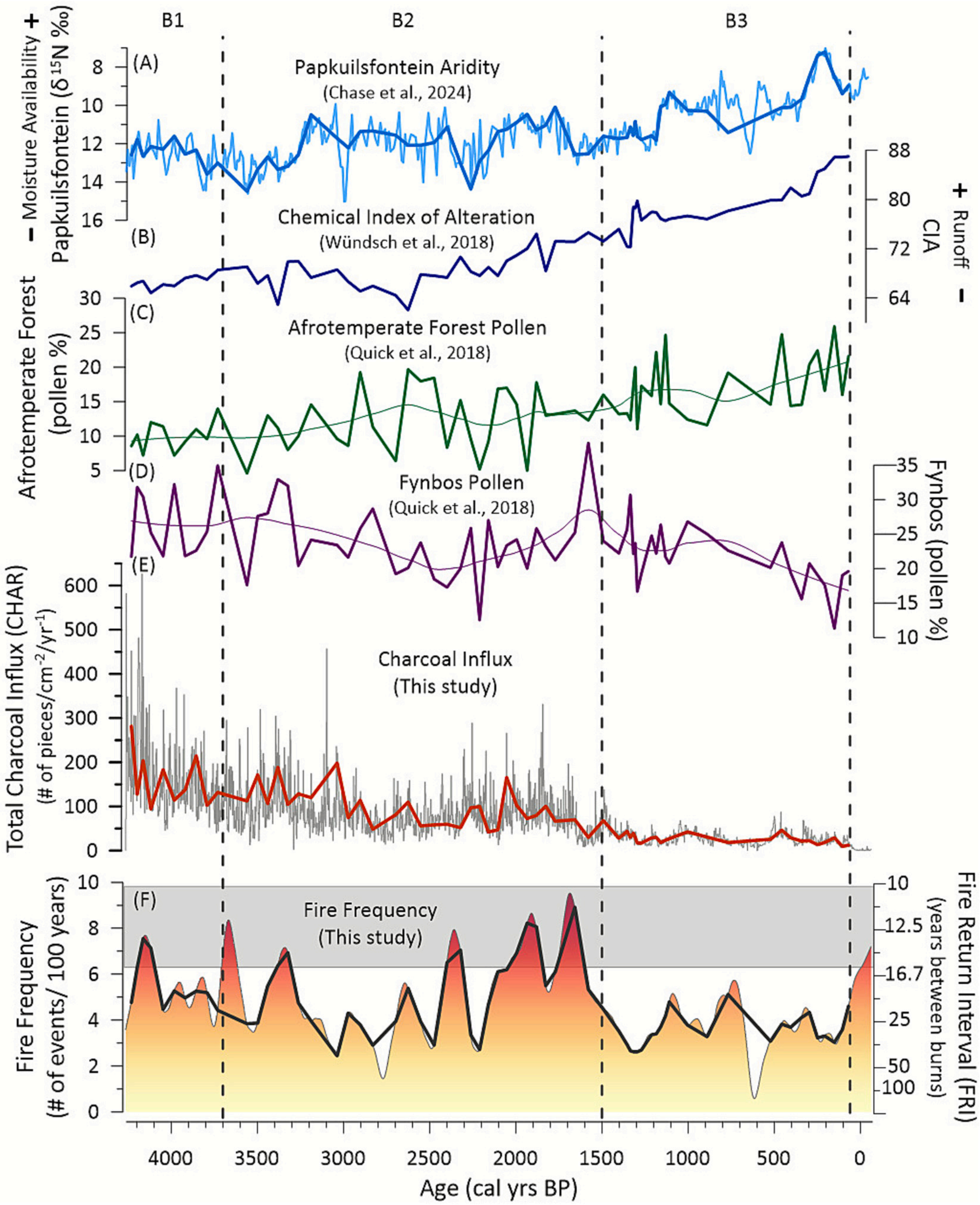

**Fig. 4.** Climate, vegetation, and fire frequency dynamics at Eilandvlei over the past 4200 years. A) $\delta^{15}N$ aridity reconstruction from Papkuilsfontein (Chase et al., 2024). Dark blue trend line reflects the upscaled $\delta^{15}N$ data at the resolution of the CIA and pollen records. B) Chemical index of alteration (CIA) data from Eilandvlei (Wündsch et al., 2018), interpreted as reflecting runoff into the lake. C) Afrotemperate forest pollen sum (%) (Quick et al., 2018) with LOESS smoother (span = 0.3). D) Fynbos pollen sum (%) (Quick et al., 2018) with LOESS smoother (span = 0.3). E) Raw charcoal influx from Eilandvlei (this study). Red trend line reflects the upscaled data CHAR at the resolution of the CIA and pollen records. F) Reconstruction of fire frequency (# of fires / 100 years) and fire return intervals (FRIs; # of years between burns) (this study). Black trend line reflects the upscaled FRI data at the resoltion of the CIA and pollen records. Horizontal gray shading demonstrates the envelope of historical varibility in CFR FRIs, with 10–15 years between burns. FRIs falling outside of this range reflect FRIs outside the historical range of variability. Vertical dotted lines depict CONISS period boundaries as identified in Quick et al. (2018), referred to in the text as B1, B2, and B3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

35-year window. This resulted in 17.5 samples per smoothing window and an SNI of 3.0751 (Kelly et al., 2017). SNIs for each zone are presented in the results. Peaks, or fire episodes, were detected using residuals ($CHAR_{peak} = CHAR_{interpolated} - CHAR_{background}$), with a locally defined threshold wherein the signal-to-noise distribution is determined by a Gaussian mixture model. Threshold values were evaluated at the 95th, 99th, and 99.9th percentiles of the noise distribution and final peaks were isolated using the 99th percentile. These parameters were selected for the final analysis because they produced the strongest signal-to-noise index. FRI, final peak detection, and peak magnitude data are provided in Appendix A.

### *3.4. Pollen and aridity reconstruction analyses*

Previously published pollen data from Eilandvlei were used to interpret the interplay between variations in fire activity, FRIs, and the relative abundances of fynbos and afrotemperate forest over the past four millennia (Quick et al., 2018). Taxa included within each ecological grouping are presented in Quick et al. (2018) and listed in Appendix B. Here, we refer to one partial pollen assemblage zone and two full pollen assemblage zones from the original publication (Quick et al., 2018), derived from CONISS (constrained incremental sum of squares) analysis (Grimm, 1987). We use a partial zone where our record does not extend back through the full zone denoted in Quick et al. (2018). Our fire history reconstruction documents ~500 years from the partial zone EV13 – B1 (full zone per Quick et al. (2018): 4700–3700 cal yrs. BP; our reconstruction: ~4260–3700 cal yrs. BP), and two complete zones: EV13 – B2 (3700–1500 cal yrs. BP) and EV13 – B3 (1500–60 cal yrs. BP). Hereafter these zones will be referenced in the text as B1, B2 and B3. We also discuss fire frequency during the historical era between 1890 CE (60 cal yrs. BP) and 2013 CE, though pollen data are not available for this portion of the record. Pollen data have been plotted on the updated EV13 age model and have been smoothed with a LOESS smoother (span = 0.3) to assist in the visualization of trends over time.

We also explore local and regional aridity using a Chemical Index of Alteration (CIA) record from Eilandvlei (Wündsch et al., 2018) as well as a high-resolution hyrax midden $\delta^{15}N$ reconstruction from Papkuilsfontein, ~182 km northwest of Eilandvlei along the southern flank of the Anysberg mountains (Chase et al., 2024). The CIA record is interpreted to reflect changes in runoff at Eilandvlei (Wündsch et al., 2018), while the Papkuilsfontein record highlights regional shifts in aridity related to larger-scale atmospheric-ocean dynamics along the southern Cape coast over the Holocene (Chase et al., 2024). The combination of these two records is appropriate for understanding local and regional trends in aridity and moisture availability experienced at Eilandvlei over the past four millennia.

The Eilandvlei CIA and pollen records are relatively lower resolution datasets than the Papkuilsfontein aridity and Eilandvlei charcoal influx (CHAR; Mosher et al., 2025) and FRI records. Therefore, for improved comparability in trends between proxies, the aridity and charcoal records were upscaled to the resolution of the CIA and pollen records. This was done by establishing continuous 1 cm sample intervals and averaging the values contained within each 1 cm window for the high-resolution proxies. Both the original, higher resolution data and the upscaled data are visualized for these proxies in Fig. 4.

We use Spearman's rank-order correlation coefficient to identify directional changes through time (i.e., increases or decreases) in fire activity, FRIs, and proxies of vegetation and climate change. Strength and direction of the relationship are reported as $R_s$, and significance as $p$. Raw data (not upscaled) were used for these statistical tests. The threshold for significance occurs when $p \leq 0.05$.

## 4. Results

### *4.1. B1 (~4260–3700 cal yrs. BP)*

This reconstruction only spans a portion of the full B1 period presented in Quick et al. (2018) – from around 4260 to 3700 cal yrs. BP. The average SNI for B1 is 3.42. Total charcoal influx (CHAR; # of particles cm $^{2}$ yr $^{1}$) is the highest of the record during start of B1 (Fig. 3A), generally decreasing throughout this zone ($R_s =$ 0.392; $p < 0.001$). Charcoal peak magnitudes are relatively consistent (Figs. 3B and C). Within B1, FRIs are shortest around 4150 cal yrs. BP with ~13 years between burns (Fig. 3D), and the longest FRIs occur towards the end of B1, with approximately 27 years between burns around 3750 cal yrs. BP. Similar to the decline in charcoal influx over B1, there is a weak but variabile shift towards longer FRIs through B1 ($R_s =$ 0.279; $p < 0.001$).

There are no clear directional changes in afrotemperate forest (Fig. 4C; $R_s = 0.382$; $p = 0.276$) or fynbos abundance through B1 (Fig. 4D; $R_s = 0.310$; $p = 0.383$). Regionally, moisture availability decreased modestly (Fig. 4A; $R_s =$ 0.319 $p = 0.02$) while locally, Eilandvlei experienced a slight increase in runoff to the lake (Fig. 4B; $R_s = 0.733$; $p = 0.01$).

### *4.2. B2 (3700–1500 cal yrs. BP)*

B2 spans between 3700 and 1500 cal yrs. BP, with an average SNI of 3.26. CHAR is generally much lower during B2 than in B1 (Fig. 3A), and there is a slight but variable decrease in fire activity through time ($R_s =$ 0.249; $p < 0.001$). While many fire episodes are identified (Fig. 3B), two fire episodes (around 3300 and 3100 cal yrs. BP) are detected with magnitudes larger than any other episodes identified in the full record (Fig. 3C), perhaps reflecting unprecedentedly large “mega-fires” (Linley et al., 2022). Following these potential “mega-fire” events, comparably small magnitudes are detected for several hundred years. FRIs are the shortest of the entire 4200 year record at around 1690 cal yrs. BP, with ~10.5 years between burns (Fig. 3D). FRIs are longest around 2770 cal yrs. BP with ~67 years between burns (Fig. 3D). Towards the end of B2, FRIs are generally short, with the period of ~1750–1600 cal yrs. BP encompassing FRIs of 11.5–10.5 years between burns. Throughout B2, FRIs are variable but generally shift towards shorter FRIs (more frequent fires) that again become longer into the beginning of B3 ($R_s = 0.314$; $p < 0.001$).

There are no significant directional changes in afrotemperate forest ($R_s = 0.344$; $p = 0.07$; Fig. 4C) or fynbos ($R_s =$ 0.095; $p = 0.623$; Fig. 4D) taxa during B2. Both regional moisture availabily (Fig. 4A; $R_s =$ 0.472; $p < 0.001$) and local runoff at Eilandvlei increase over this interval (Fig. 4B; $R_s = 0.590$; $p < 0.001$).

### *4.3. B3 (1500–60 cal yrs. BP)*

Fire activity is considerably lower during B3, with an average SNI of 2.82. This somewhat low SNI (< 3) suggests that the CharAnalysis algorithm may have some limitations in isolating discrete fire events from the background noise, with potential implications for the accuracy of the charcoal magnitude and FRI reconstructions (Kelly et al., 2017). The drop in FRIs identified ~620 cal yrs. BP corresponds with an interval of ~140 years during which no fire episdoes were detected (Fig. 3B).

The highest fire activity is around 1490 cal yrs. BP and the lowest is around 600 cal yrs. BP (Fig. 3A). Overall, there is a weak decline in fire activity over B3 ($R_s =$ 0.270; $p < 0.001$), continuing the long-term decline observed in preceding intervals. Among the fire episodes that are identified, the overall magnitudes are low, suggesting that fire activity was reduced and that fires were relatively small in size (Figs. 3B and C). Following the shortest FRIs during B2 around 1690 cal yrs. BP with about 10.5 years between burns, FRIs became longer into B3. During B3, shortest FRI is ~17.5 years between burns around 730 cal yrs. BP (Fig. 3D) and the longest FRI is ~166 years between burns around 610 cal yrs. BP – documenting a time of unexpectedly infrequent fires for a CFR system (Fig. 3D). FRIs do not exhibit any directional change over this period ($R_s =\ \ 0.059$; $p = 0.112$), though as described above, there may be some limitations to the fire history reconstrution during B3.

During B3, afrotemperate forest abundance increases (Fig. 4C; $R_s = 0.498$; $p = 0.01$) while relative fynbos abundance declines (Fig. 4D; $R_s =\ \ 0.575$; $p = 0.002$). Continuing the trend documented in zone B2, regional moisture availability ($R_s = 0.629$; $p < 0.001$) and local runoff ($R_s = 0.846$; $p < 0.001$) both increase across B3.

### 4.4. Historical era (1890 CE (60 cal yrs. BP) – 2013 CE)

The historical era captured by this fire reconstruction ranges from 1890 CE (60 cal yrs. BP) until the EV13 sedimentary sequence was cored in 2013 CE. The average SNI for this historical period is 3.53. Fire activity is generally very low, and decreases through time ($R_s =\ \ 0.493$; $p < 0.001$; Fig. 3A). Charcoal peak magnitudes are very low during this historical period (Fig. 3C). The longest FRI is ~20 years between fires at ~1890 CE (60 cal yrs. BP) and the shortest FRI is 13.8 years between fires at the top of the record around 2010 CE (  60 cal yrs. BP; Fig. 3D). FRIs generally shift towards shorter intervals beween fires across this historical era ($R_s = 1, p < 0.05$). Since around 1970 CE (  20 cal yrs. BP), when historical monitoring of CFR FRIs began, FRIs have ranged between about ~13.8 to 15 years between burns. Pollen and CIA data are not available for this topmost section of the EV13 sequence, but regional moisture avaialability increases over this zone ($R_s = 0.775$; $p < 0.001$; Fig. 4A).

## 5. Discussion

### 5.1. The long-term range of natural variability in FRIs

This long-term high-resolution FRI reconstruction is the first of its kind in the CFR, providing an opportunity to use paleoecological data to improve our understanding of present-day ecosystems. Reconstructed FRIs during the historical period of this record (1890–2013 CE) document ~13.8–20 years between fires, with shorter FRIs occuring towards the present (Fig. 3D). This is consistent with our present-day understanding of FRIs in the fynbos (~10–15 years between fires), validating the interpretation of this macrocharcoal reconstruction in observing FRIs over millennial timescales. Over our full reconstruction, this paleofire record reveals that the natural range of variability in fynbos FRIs at Eilandvlei is much larger than our historical understanding (Fig. 4F). Fire activity begins high and slowly drops over the course of the record (Fig. 3A; see Mosher et al., 2025 for further interpretation of Eilandvlei fire activity), but FRIs are variable throughout (Fig. 3D). The southwestern coastal zone, where Eilandvlei is found today, generally experiences FRIs of around 10 years (Kraaij and van Wilgen, 2014). The record thus highlights periods over the past four millennia that are at times similar to our present-day understanding of CFR fire (FRIs of ~10–15 years), while at others being markedly different (e.g., B3, with FRIs of 17.5 to 166 years), but no periods when FRIs are shorter than our historical understanding (Fig. 4F).

### 5.2. Inter-biome dynamics

The Eilandvlei pollen reconstruction documents variability in afrotemperate forest taxa relative to fynbos taxa over the full 4200-year record (Fig. 4; Quick et al., 2018). Throughout parts of the record, fynbos abundance decreases during periods with longer FRIs (Fig. 4). For example, strong directional changes in vegetation assemblages are identified in B3 from about 1500 to 60 cal yrs. BP. During this period, afrotemperate forest abundance increases and fynbos abundance decreases, and while there is no significant directional change in the length of FRIs throughout B3, FRIs are notably longer during B3 than during most of the preceding B2 period (Fig. 4). These trends support previous findings that in the absence of regular, high-frequency fires, fynbos may be encroached upon by the expanding afrotemperate forest (e.g., MacPherson et al., 2019; Manders and Richardson, 1992; Prader et al., 2023; Watson and Cameron, 2001). Additionally, this shift towards longer FRIs and decreased fynbos vegetation during B3 at Eilandvlei approximately coincides with a broader-scale, regionally significant shift towards increased moisture availability (Fig. 4A; Chase et al., 2024), and a decrease in overall fire activity (Mosher et al., 2025), supporting the importance of vegetation structure (van Wilgen et al., 1990) and fuel-moisture interactions (Karp et al., 2023) as critical factors influencing fire at Eilandvlei (Mosher et al., 2025).

In the CFR, questions of resilience and vegetational dynamics between and among the fire-dependent fynbos and fire-adverse afrotemperate forest communities, alongside changes in climate forcing and anthropogenic pressures, are of great interest (e.g., Cramer et al., 2019; Gillson et al., 2020; MacPherson et al., 2019; Prader et al., 2023). In some cases, these studies have documented stability between fynbos and afrotemperate forest vegetation, despite climate variability over the late Holocene (Gillson et al., 2020; MacPherson et al., 2019). In others, more dynamic responses to changes in climate were observed, both between the fynbos and afrotemperate forest, as well as within the fynbos ecological grouping (Prader et al., 2023). While these studies lack FRI reconstructions, micro- and macrocharcoal influxes reinforce our finding that low overall fire activity and increased afrotemperate forest abundance are closely related. At Orange Kloof, historical fire suppression since the 1930s CE appears to have resulted in afrotemperate forest expansion and fynbos contraction (Prader et al., 2023). Similarly, fynbos abundance is highest during periods of increased burning at Groenkloof (Gillson et al., 2020; MacPherson et al., 2018). Our study contributes to this understanding of vegetation dynamics and resilience by presenting a novel FRI dataset that permits a deeper exploration of how these seemingly opposing vegetation types respond to variability in fire frequency over long timescales.

In addition to these fynbos-afrotemperate forest dynamics, there are also within-biome changes identified in other key fynbos families (Quick et al., 2018). As moisture availability increases during B3, the Quick et al. (2018) reconstruction shows a decrease in Ericaceae pollen until ~1300 cal yrs. BP, after which Ericaceae remains relatively stable. Proteaceae is variable throughout B3 and Restionaceae declines from the start to end of B3. It may be that shifts in moisture availability, soil fertility, and the responses and effects of fire on these factors influences the abundance of plants with re-seeding or resprouting functional traits (Wüest et al., 2016). Increasing fire frequency has been shown to favor resprouting plants over re-seeders, which require longer intervals between fires to reach maturity and produce seeds (van Wilgen and Forsyth, 1992; Vilà-Cabrera et al., 2015), with negative impacts on plant diversity (Vlok and Yeaton, 1999). Changes in FRIs, fire seasonality, and fire intensity may influence the species diversity within these characteristic fynbos families. Future work increasing the temporal resolution of the pollen data, focusing on species abundance shifts over time, and exploring these paleoecological FRIs will be valuable in determining the importance of variable FRIs and overall fire activity at the afrotemperate forest-fynbos ecotone.

### 5.3. Implications for conservation and management

This fire history reconstruction from Eilandvlei documents a reduction in fire activity over the late Holocene (Fig. 3A) and a wide range of variability in FRIs, from ~10.5–166 years between burns (Fig. 3D). Though the top of the Eilandvlei core is consistent with our current understanding of historical FRIs of ~10–15 years between burns (Fig. 4.3D; Kraaij and van Wilgen, 2014), it only requires exploration of patterns a few centuries in the past to see FRIs far outside the range of variability that we experience today, suggesting that the timescale of our historical, ecological lens is not representative of the full range of natural variability experienced at Eilandvlei over the past four millennia.

More frequent fires (shorter FRIs), though not necessarily more overall burning (lower fire activity), may facilitate fynbos resilience in areas experiencing afrotemperate forest encroachment. However, high-frequency fires (< 10.5 years between burns) are not identified in this reconstruction, suggesting that routine burning for the sake of other conservation goals (e.g., promoting forage for large herbivores; Mentis and Tainton, 1984; Smith et al., 2011; Watson and Chadwick, 2007; Watson et al., 2005) may be inconsistent with typical FRIs over both historical and paleoecological timescales.

Along biome boundaries, ecosystem responses to shifts in climate, vegetation assemblage, and fire are especially pronounced and often highly sensitive to change. By integrating multi-millennial scale records into our understanding of long-term ecology, we can better understand how these vulnerable systems may respond to changes in climate and disturbance (both anthropogenic and "natural"). Future climate conditions in the CFR are predicted to be up to 20% drier along the southern Cape coast (IPCC, 2022), and Mediterranean systems worldwide are expected to experience an increase in burnt area, fire frequency, and fire severity under all RCP scenarios by 2050 (Sayedi et al., 2024). We may therefore expect to see rapid shifts in rainfall amount and/or seasonality, vegetation distribution, and fire activity along the southern Cape coast, with implications for overall fire activity and FRIs experienced at the fynbos-afrotemperate forest ecotone around Eilandvlei.

## 6. Conclusions

This paper presents the first high-resolution, continuous reconstruction of fire return intervals from the CFR, spanning four millennia from a fynbos-afrotemperate forest ecotone. We find that FRIs have varied over the past four millennia, ranging from as frequent as one fire every 10.5 years to as infrequent as one fire every 67 years, and possibly as infrequent as one fire every 166 years. Periods of more frequent fire activity align with our present-day understanding of approximately 10–15 years between burns – based on historical, ecological studies conducted in ecosystems already heavily impacted by anthropogenic activities. The large range in FRIs documented here suggests that this fynbos-afrotemperate forest ecotone may have experienced dynamic boundary shifts across the late Holocene, alongside changes in climate conditions, vegetation assemblage (i.e., fuel), and fire activity over millennial-, centennial-, and decadal- timescales. During periods of increased moisture availability, the afrotemperate forest expands at the expense of the fynbos, fire activity decreases, and FRIs become generally longer (i.e., during much of B3) in comparison to periods of increased aridity. Importantly, we also find that our present-day range of variability in fynbos FRIs (~10–15 years between burns) is not consistently maintained over millennial timescales and is not representative of the natural range of variability experienced at Eilandvlei. This record highlights how paleoecological datasets can benefit our understanding of ecosystem dynamics and resilience by offering a window into the long-term range of variability within an ecosystem in response to changes in climate and human activities.

## CRediT authorship contribution statement

**Stella G. Mosher:** Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Mitchell J. Power:** Writing – review & editing, Writing – original draft, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization. **Lynne J. Quick:** Writing – review & editing, Supervision, Resources, Investigation. **Brian M. Chase:** Writing – review & editing, Supervision, Resources, Formal analysis. **Torsten Haberzettl:** Writing – review & editing, Supervision, Resources, Investigation, Funding acquisition, Conceptualization. **Thomas Kasper:** Writing – review & editing, Visualization, Software, Resources. **Simon C. Brewer:** Writing – review & editing, Methodology. **David R. Braun:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **J. Tyler Faith:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Acknowledegments

This study was funded by the National Science Foundation (NSF CNH-S: 1826666). Extraction of the EV13 sedimentary archive was funded by the German Federal Ministry of Education and Research (BMBF) and collected as part of the collaborative project 'Regional Archives for Integrated Investigations' (RAIN, grant no: 03G0862B). The International Association of Wildland Fire is thanked for funding related to the communication and dissemination of this research. The Geological Society of America and the University of Utah Undergraduate Research Opportunity Program funded student lab opportunities related to this project. We thank Topher Lloyd, Siena Popiel, Eugene Kneller, Amy Harvey, Eliza Pehkonen, and Emily Adler for their laboratory assistance. We also thank two anonymous reviewers for their helpful edits and suggestions that improved this manuscript.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2026.105307.

## Data availability

Data have been included in Appendix A.

## References

Andela, N., Morton, D.C., Giglio, L., Paugam, R., Chen, Y., Hantson, S., van der Werf, G. R., Randerson, J.T., 2019. The Global Fire Atlas of individual fire size, duration, speed and direction. Earth Syst. Sci. Data 11, 529–552.

Barnosky, A.D., Hadly, E.A., Gonzalez, P., Head, J., Polly, P.D., Lawing, A.M., Eronen, J. T., Ackerly, D.D., Alex, K., Biber, E., Blois, J., Brashares, J., Ceballos, G., Davis, E., Dietl, G.P., Dirzo, R., Doremus, H., Fortelius, M., Greene, H.W., Hellmann, J., Hickler, T., Jackson, S.T., Kemp, M., Koch, P.L., Kremen, C., Lindsey, E.L., Looy, C., Marshall, C.R., Mendenhall, C., Mulch, A., Mychajliw, A.M., Nowak, C., Ramakrishnan, U., Schnitzler, J., Das Shrestha, K., Solari, K., Stegner, L., Stegner, M. A., Stenseth, N.C., Wake, M.H., Zhang, Z., 2017. Merging paleobiology with conservation biology to guide the future of terrestrial ecosystems. Science 355, eaah4787.

Bateman, M.D., Carr, A.S., Dunajko, A.C., Holmes, P.J., Roberts, D.L., McLaren, S.J., Bryant, R.G., Marker, M.E., Murray-Wallace, C.V., 2011. The evolution of coastal barrier systems: a case study of the Middle-late Pleistocene wilderness barriers, South Africa. Quat. Sci. Rev. 30, 63–81.

Birks, H.J.B., 2012. Ecological palaeoecology and conservation biology: controversies, challenges, and compromises. Intern. J. Biodiver. Sci. Ecosyst. Servic. Manage. 8, 292–304.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6, 457–474.

Bond, W., Keeley, J., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends Ecol. Evol. 20, 387–394.

Bousman, C.B., 1998. The chronological evidence for introduction of domestic stock into Southern Africa. Afr. Archaeol. Rev. 15, 133–150.

Bronk Ramsey, C., 2009. Bayesian analysis of radiocarbon dates. Radiocarbon 51, 337–360.

Brown, P.J., Manders, P.T., D.P., B, Kruger, F.J., Andrag, R.H., 1991. Prescribed burning as a conservation management practice: a case history from the Cederberg Mountains, Cape Province, South Africa. Biol. Conserv. 56, 133–150.

Cawthra, H.C., Bateman, M.D., Carr, A.S., Compton, J.S., Holmes, P.J., 2014. Understanding late Quaternary change at the land–ocean interface: a synthesis of the evolution of the wilderness coastline, South Africa. Quat. Sci. Rev. 99, 210–223.

Chase, B.M., Meadows, M.E., 2007. Late Quaternary dynamics of southern Africa's winter rainfall zone. Earth Sci. Rev. 84, 103–138.

Chase, B.M., Quick, L.J., 2018. Influence of Agulhas forcing of Holocene climate change in South Africa's southern Cape. Quat. Res. 90, 303–309.

Chase, B.M., Boom, A., Carr, A.S., Reimer, P.J., 2024. Tropical forcing and ENSO dominate Holocene climates in South Africa's southern Cape. Quat. Sci. Rev. 330, 108563.

Clark, J.S., Royall, P.D., 1996. Local and Regional Sediment Charcoal evidence for Fire Regimes in Presettlement North-Eastern North America. J. Ecol. 84, 365–382.

Coetsee, C., Bond, W.J., Wigley, B.J., 2015. Forest and fynbos are alternative states on the same nutrient poor geological substrate. S. Afr. J. Bot. 101, 57–65.

Coutu, A.N., Taurozzi, A.J., Mackie, M., Jensen, T.Z.T., Collins, M.J., Sealy, J., 2021. Palaeoproteomics confirm earliest domesticated sheep in southern Africa ca. 2000 BP. Sci. Rep. 11, 6631.

Cowling, R.M., 1984. A syntaxonomic and synecological study in the Humansdorp region of the Fynbos Biome. Bothalia 15, 175–227.

Cowling, R.M., 1987. Fire and its role in the coexistence and speciation in Gondwanan shrublands. S. Afr. J. Sci. 83, 106–112.

Cramer, M.D., Power, S.C., Belev, A., Gillson, L., Bond, W.J., Hoffman, M.T., Hedin, L.O., 2019. Are forest-shrubland mosaics of the Cape Floristic Region an example of alternate stable states? Ecography 42, 717–729.

Daniau, A.L., Bartlein, P.J., Harrison, S.P., Prentice, I.C., Brewer, S., Friedlingstein, P., Harrison-Prentice, T.I., Inoue, J., Izumi, K., Marlon, J.R., Mooney, S., Power, M.J., Stevenson, J., Tinner, W., Andrič, M., Atanassova, J., Behling, H., Black, M., Blarquez, O., Brown, K.J., Carcaillet, C., Colhoun, E.A., Colombaroli, D., Davis, B.A.S., D'Costa, D., Dodson, J., Dupont, L., Eshetu, Z., Gavin, D.G., Genries, A., Haberle, S., Hallett, D.J., Hope, G., Horn, S.P., Kassa, T.G., Katamura, F., Kennedy, L.M., Kershaw, P., Krivonogov, S., Long, C., Magri, D., Marinova, E., McKenzie, G.M., Moreno, P.I., Moss, P., Neumann, F.H., Norström, E., Paitre, C., Rius, D., Roberts, N., Robinson, G.S., Sasaki, N., Scott, L., Takahara, H., Terwilliger, V., Thevenon, F., Turner, R., Valsecchi, V.G., Vannière, B., Walsh, M., Williams, N., Zhang, Y., 2012. Predictability of biomass burning in response to climate changes. Glob. Biogeochem. Cycles 26, GB4007.

Dietl, G.P., Kidwell, S.M., Brenner, M., Burney, D.A., Flessa, K.W., Jackson, S.T., Koch, P.L., 2015. Conservation paleobiology: leveraging knowledge of the past to inform conservation and restoration. Annu. Rev. Earth Planet. Sci. 43, 79–103.

Engelbrecht, C.J., Landman, W.A., 2016. Interannual variability of seasonal rainfall over the Cape south coast of South Africa and synoptic type association. Clim. Dyn. 47, 295–313.

Forsyth, G.G., van Wilgen, B.W., 2008. The recent fire history of the Table Mountain National Park and implications for fire management. Koedoe 50, 3–9.

Geldenhuys, C.J., 1991. Distribution, size and ownership of forests in the southern Cape. S. Afr. Forest. J. 158, 51–66.

Geldenhuys, C.J., 1994. Bergwind fires and the Location Pattern of Forest Patches in the Southern Cape Landscape, South Africa. J. Biogeogr. 21, 49–62.

Gillson, L., 2021. The role of palaeoecology in conserving African ecosystems. In: Runge, J. (Ed.), Palaeoecology in Africa. CRC Press, London, pp. 397–410.

Gillson, L., MacPherson, A.J., Hoffman, M.T., 2020. Contrasting mechanisms of resilience at Mesic and semi-arid boundaries of fynbos, a mega-diverse heathland of South Africa. Ecol. Complex. 42, 100827.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13, 13–35.

Groff, D.V., McDonough MacKenzie, C., Pier, J.Q., Shaffer, A.B., Dietl, G.P., 2023. Knowing but not doing: Quantifying the research-implementation gap in conservation paleobiology. Front. Ecol. Evol. 11.

Haberzettl, T., Baade, J., Compton, J., Daut, G., Dupont, L., Finch, J., Frenzel, P., Green, A., Hahn, A., Hebbeln, D., Helmschrot, J., Humphries, M., Kasper, T., Kirsten, K., Mäusbacher, R., Meadows, M., Meschner, S., Quick, L., Schefuß, E., Wündsch, M., Zabel, M., 2014. Paleoenvironmental investigations using a combination of terrestrial and marine sediments from South Africa - the RAIN (Regional Archives for Integrated iNvestigations) approach. Zentralbl. Geol. Paläontol. Teil 2014, 55–73.

Heaton, T.J., Köhler, P., Butzin, M., Bard, E., Reimer, R.W., Austin, W.E.N., Bronk Ramsey, C., Grootes, P.M., Hughen, K.A., Kromer, B., Reimer, P.J., Adkins, J., Burke, A., Cook, M.S., Olsen, J., Skinner, L.C., 2020. Marine20—the Marine Radiocarbon Age Calibration Curve (0–55,000 cal BP). Radiocarbon 62, 779–820.

Higuera, P.E., Brubaker, L.B., Anderson, P.M., Hu, F.S., Brown, T.A., 2009. Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-Central Brooks Range, Alaska. Ecol. Monogr. 79, 201–219.

Hogg, A.G., Heaton, T.J., Hua, Q., Palmer, J.G., Turney, C.S.M., Southon, J., Bayliss, A., Blackwell, P.G., Boswijk, G., Bronk Ramsey, C., Pearson, C., Petchey, F., Reimer, P., Reimer, R., Wacker, L., 2020. SHCal20 Southern Hemisphere Calibration, 0–55,000 years cal BP. Radiocarbon 62, 759–778.

IPCC, 2022. Climate change 2022: Impacts, adaptation, and vulnerability. In: Pörtner, H.-O., Roberts, D.C., Tignor, M., Poloczanska, E.S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V., Okem, A., Rama, B. (Eds.), Contribution of Working Group 2 to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, NY.

Karp, A.T., Uno, K.T., Berke, M.A., Russell, J.M., Scholz, C.A., Marlon, J.R., Faith, J.T., Staver, A.C., 2023. Nonlinear rainfall effects on savanna fire activity across the African Humid Period. Quat. Sci. Rev. 304, 107994.

Karp, A.T., Koerner, S.E., Hempson, G.P., Abraham, J.O., Anderson, T.M., Bond, W.J., Burkepile, D.E., Fillion, E.N., Goheen, J.R., Guyton, J.A., Kartzinel, T.R., Kimuyu, D.M., Mohanbabu, N., Palmer, T.M., Porensky, L.M., Pringle, R.M., Ritchie, M.E., Smith, M.D., Thompson, D.I., Young, T.P., Staver, A.C., 2024. Grazing herbivores reduce herbaceous biomass and fire activity across African savannas. Ecol. Lett. 27, e14450.

Keeley, J.E., 2012. Fire in Mediterranean climate ecosystems - a comparative overview. Israel J. Ecol. Evol. 58, 123–135.

Kelly, R.F., Higuera, P.E., Barrett, C.M., Hu, F.S., 2017. Short Paper: a signal-to-noise index to quantify the potential for peak detection in sediment–charcoal records. Quat. Res. 75, 11–17.

Kirsten, K.L., Haberzettl, T., Wündsch, M., Frenzel, P., Meschner, S., Smit, A.J., Quick, L.J., Mäusbacher, R., Meadows, M.E., 2018. A multiproxy study of the ocean-atmospheric forcing and the impact of sea-level changes on the southern Cape coast, South Africa during the Holocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 496, 282–291.

Kirsten, K.L., Forbes, C.J., Finch, J.M., Gillson, L., 2024. The application of paleoenvironmental research in supporting land management approaches and conservation in South Africa. Sustainabil. South. Afr. Ecosyst. Global Change 313–333.

de Klerk, H.M., Wilson, A.M., Steenkamp, K., 2012. Evaluation of satellite-derived burned area products for the fynbos, a Mediterranean shrubland. Int. J. Wildland Fire 21, 36–47.

Kraaij, T., 2010. Changing the fire management regime in the renosterveld and lowland fynbos of the Bontebok National Park. S. Afr. J. Bot. 76, 550–557.

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, pp. 47–72.

Kraaij, T., Baard, J.A., Cowling, R.M., van Wilgen, B.W., Das, S., 2013. Historical fire regimes in a poorly understood, fire-prone ecosystem: eastern coastal fynbos. Int. J. Wildland Fire 22, 277–287.

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, 1–12.

Kruger, F.J., 1984. Chapter 10: Effects of Fire on Vegetation Structure and Dynamics. In: de Booysen, V., Tainton, N.M. (Eds.), Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Berlin, pp. 219–244.

Linder, H.P., 2003. The radiation of the Cape flora, southern Africa. Biol. Rev. Camb. Philos. Soc. 78, 597–638.

Linley, G.D., Jolly, C.J., Doherty, T.S., Geary, W.L., Armenteras, D., Belcher, C.M., Bliege Bird, R., Duane, A., Fletcher, M.S., Giorgis, M.A., Haslem, A., Jones, G.M., Kelly, L.T., Lee, C.K.F., Nolan, R.H., Parr, C.L., Pausas, J.G., Price, J.N., Regos, A., Ritchie, E.G., Ruffault, J., Williamson, G.J., Wu, Q., Nimmo, D.G., 2022. What do you mean, 'megafire'? Glob. Ecol. Biogeogr. 31, 1906–1922.

Long, C.J., Whitlock, C., Bartlein, P.J., Millspaugh, S.H., 1998. A 9000-year fire history from the Oregon Coast Range, based on a high-resolution charcoal study. Can. J. For. Res. 28, 774–787.

Lyman, R.L., 2006. Paleozoology in the service of conservation biology. Evolution. Anthropol.: Iss. News, Rev. 15, 11–19.

MacPherson, A.J., Gillson, L., Hoffman, M.T., 2018. Climatic buffering and anthropogenic degradation of a Mediterranean-type shrubland refugium at its semi-arid boundary, South Africa. The Holocene 28, 651–666.

MacPherson, A.J., Gillson, L., Hoffman, M.T., 2019. Between- and within-biome resistance and resilience at the fynbos-forest ecotone, South Africa. The Holocene 29, 1801–1816.

Manders, P.T., Richardson, D.M., 1992. Colonization of Cape fynbos communities by forest species. For. Ecol. Manag. 48, 277–293.

Manzano, S., Julier, A.C.M., Dirk, C.J., Razafimanantsoa, A.H.I., Samuels, I., Petersen, H., Gell, P., Hoffman, M.T., Gillson, L., 2020. Using the past to manage the future: the role of palaeoecological and long-term data in ecological restoration. Restor. Ecol. 28, 1335–1342.

Manzano, S., Quick, L.J., Chase, B.M., Hoffman, M.T., Gillson, L., 2023. Long-term vegetation response to rainfall seasonality and fire in the heathlands and shrublands of the Cape Floristic Region (SW South Africa). Glob. Planet. Chang. 220, 104014.

McWethy, D.B., Whitlock, C., Wilmshurst, J.M., McGlone, M.S., Fromont, M., Li, X., Dieffenbacher-Krall, A., Hobbs, W.O., Fritz, S.C., Cook, E.R., 2010. Rapid landscape transformation in South Island, New Zealand, following initial Polynesian settlement. Proc. Natl. Acad. Sci. 107, 21343–21348.

Mentis, M.T., Tainton, N.M., 1984. The effects of fire on forage production and quality. In: de Booysen, P.V., Tainton, N.M. (Eds.), Ecological Effects of Fire in South African Ecosystems. Springer-Verlag, Berlin, pp. 246–254.

Midgley, J.J., Cowling, R.M., Seydack, A.H.W., Van Wyk, G.F., 1997. Forest. In: Cowling, R.M., Richardson, D.M., Pierce, S.M. (Eds.), Vegetation of southern Africa. Cambridge University Press, Cambridge, pp. 278–299.

Mosher, S.G., Power, M.J., Quick, L.J., Haberzettl, T., Kasper, T., Kirsten, K.L., Braun, D.R., Faith, J.T., 2024. Examining the effects of climate change and human impacts on a high-resolution, late Holocene paleofire record from South Africa's winter rainfall zone. Quat. Sci. Adv. 14, 100194.

Mosher, S.G., Power, M.J., Chase, B.M., Quick, L., Haberzettl, T., Kasper, T., Braun, D.R., Faith, J.T., 2025. Evaluating climatic and anthropogenic drivers of fire activity over four millennia at Eilandvlei, southern Cape coast, South Africa. Quat. Sci. Rev. 366, 109520.

Mucina, L., Rutherford, M.C., 2006. The Vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Mucina, L., Geldenhuys, C.J., Rutherofrd, M.C., Powrie, L.W., Lötter, M.C., 2006. Afrotemperate, Subtropical and Azonal Forests, the vegetation of South Africa, Lesotho and Swaziland. Strelitzia 19, 584–614.

du Plessis, N., Chase, B.M., Quick, L.J., Haberzettl, T., Kasper, T., Meadows, M.E., 2020. Vegetation and climate change during the medieval climate Anomaly and the Little Ice Age on the southern Cape coast of South Africa: Pollen evidence from Bo Langvlei. The Holocene 30, 1716–1727.

Power, M.J., Whitlock, C., Bartlein, P., Stevens, L.R., 2006. Fire and vegetation history during the last 3800 years in northwestern Montana. Geomorphology 75, 420–436.

Power, S.C., Anthony Verboom, G., Bond, W.J., Cramer, M.D., 2017. Environmental correlates of biome-level floristic turnover in South Africa. J. Biogeogr. 44, 1745–1757.

Prader, S., Gillson, L., Chase, B.M., Hoffman, M.T., 2023. Late-Holocene fynbos-forest dynamics in Orange Kloof, Table Mountain National Park, South Africa. The Holocene 33, 592–604.

Quick, L.J., Chase, B.M., Wündsch, M., Kirsten, K.L., Chevalier, M., Mäusbacher, R., Meadows, M.E., Haberzettl, T., 2018. A high-resolution record of Holocene climate and vegetation dynamics from the southern Cape coast of South Africa: pollen and microcharcoal evidence from Eilandvlei. J. Quat. Sci. 33, 487–500.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rick, T.C., Lockwood, R., 2013. Integrating paleobiology, archeology, and history to inform biological conservation. Conserv. Biol. 27, 45–54.

SAWS, 2017. Rainfall Data from the Weather Stations 0012661 7 (George WO), 0014123 3 (Knysna), and 0028776 9 (George Witfontein). South African Weather Service, Pretoria.

Sayedi, S.S., Abbott, B.W., Vannière, B., Leys, B., Colombaroli, D., Romera, G.G., Słowiński, M., Aleman, J.C., Blarquez, O., Feurdean, A., Brown, K., Aakala, T., Alenius, T., Allen, K., Andric, M., Bergeron, Y., Biagioni, S., Bradshaw, R., Bremond, L., Brisset, E., Brooks, J., Brugger, S.O., Brussel, T., Cadd, H., Cagliero, E., Carcaillet, C., Carter, V., Catry, F.X., Champreux, A., Chaste, E., Chavardès, R.D., Chipman, M., Conedera, M., Connor, S., Constantine, M., Courtney Mustaphi, C., Dabengwa, A.N., Daniels, W., De Boer, E., Dietze, E., Estrany, J., Fernandes, P., Finsinger, W., Flantua, S.G.A., Fox-Hughes, P., Gaboriau, D.M., Gayo, E., Girardin, M.P., Glenn, J., Glückler, R., González-Arango, C., Groves, M., Hamilton, D.S., Hamilton, R.J., Hantson, S., Hapsari, K.A., Hardiman, M., Hawthorne, D., Hoffman, K., Inoue, J., Karp, A.T., Krebs, P., Kulkarni, C., Kuosmanen, N., Lacourse, T., Ledru, M.-P., Lestienne, M., Long, C., López-Sáez, J.A., Loughlin, N., Niklasson, M., Madrigal, J., Maezumi, S.Y., Marcisz, K., Mariani, M., McWethy, D., Meyer, G., Molinari, C., Montoya, E., Mooney, S., Morales-Molino, C., Morris, J., Moss, P., Oliveras, I., Pereira, J.M., Pezzatti, G.B., Pickarski, N., Pini, R., Rehn, E., Remy, C.C., Revelles, J., Rius, D., Robin, V., Ruan, Y., Rudaya, N., Russell-Smith, J., Seppa, H., Shumilovskikh, L., Sommers, W., Tavsanoglu, Ç., Umbanhowar, C., Urquiaga, E., Urrego, D., Vachula, R.S., Wallenius, T., You, C., Daniau, A.-L., 2024. Assessing changes in global fire regimes. Fire Ecol. 20, 1–22.

Schweitzer, F.R., 1974. Archaeological evidence for Sheep at the Cape. South Afr. Archaeol. Bull. 29, 75–82.

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.

Skead, C.J., 2011. Man's Influence on the Incidence of the Larger Mammals, Historical Incidence of the Larger Land Mammals in the Broader Western and Northern Cape. Centre for African Conservation Ecology, Nelson Mandela University, Port Elizabeth.

Slingsby, J.A., Moncrieff, G.R., Rogers, A.J., February, E.C., 2020. Altered ignition catchments threaten a hyperdiverse fire-dependent ecosystem. Glob. Chang. Biol. 26, 616–628.

Smith, R.K., Ryan, E., Morley, E., Hill, R.A., 2011. Resolving management conflicts: could agricultural land provide the answer for an endangered species in a habitat classified as a World Heritage Site? Environ. Conserv. 38, 325–333.

Staver, A.C., Abraham, J.O., Hempson, G.P., Karp, A.T., Faith, J.T., 2021. The past, present, and future of herbivore impacts on savanna vegetation. J. Ecol. 109, 2804–2822.

Strydom, T., Kraaij, T., Grobler, B.A., Cowling, R.M., 2022. Canopy plant composition and structure of Cape subtropical dune thicket are predicted by the levels of fire exposure. PeerJ 10, e14310.

Thomas, Z.A., 2016. Using natural archives to detect climate and environmental tipping points in the Earth System. Quat. Sci. Rev. 152, 60–71.

Tyson, P.D., 1986. Climate Change and Variability in Southern Africa. Oxford University Press, Cape Town.

Tyson, P.D., Preston-Whyte, R.A., 2000. The Weather and Climate of Southern Africa. Oxford University Press, Cape Town.

Valsecchi, V., Chase, B.M., Slingsby, J.A., Carr, A.S., Quick, L.J., Meadows, M.E., Cheddadi, R., Reimer, P.J., 2013. A high resolution 15,600-year pollen and microcharcoal record from the Cederberg Mountains, South Africa. Palaeogeogr. Palaeoclimatol. Palaeoecol. 387, 6–16.

Vilà-Cabrera, A., Saura-Mas, S., Lloret, F., 2015. Effects of fire frequency on species composition in a Mediterranean shrubland. Écoscience 15, 519–528.

Vlok, J.H.J., Yeaton, R.I., 1999. The effect of overstorey proteas on plant species richness in south African mountain fynbos. Divers. Distrib. 5, 231–222.

Watson, L.H., Cameron, M.J., 2001. The influence of fire on a southern Cape mountain forest. South. Afr. For. J. 2001, 39–42.

Watson, L.H., Chadwick, P., 2007. Management of Cape mountain zebra in the Kammanassie Nature Reserve, South Africa. S. Afr. J. Wildl. Res. 37, 31–39.

Watson, L.H., Odendaal, H.E., Barry, T.J., Pietersen, J., 2005. Population viability of Cape mountain zebra in Gamka Mountain Nature Reserve, South Africa: the influence of habitat and fire. Biol. Conserv. 122, 173–180.

van Wilgen, B.W., 1984. Fire climates in the southern and western Cape Province and their potential use in fire control and management. S. Afr. J. Sci. 80, 358–362.

van Wilgen, B.W., 2009. The evolution of fire and invasive alien plant management practices in fynbos. S. Afr. J. Sci. 105, 335–342.

van Wilgen, B.W., Forsyth, G.G., 1992. Regeneration strategies in Fynbos Plants and their Influence on the Stability of Community Boundaries after Fire. In: van Wilgen, B.W., Richarson, D.M., Kruger, F.J., van Hensbergen, H.J. (Eds.), Fire in South African Mountain Fynbos: Species, Community and Ecosystem Response in Swartboskloof. Springer-Verlag, Heidelberg, pp. 54–80.

van Wilgen, B.W., Higgens, K.B., Bellstedt, D.U., 1990. The role of vegetation structure and fuel chemistry in excluding fire from forest patches in the fire-prone Fynbos shrublands of South Africa. J. Ecol. 78, 210–222.

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.

Willis, K.J., Bhagwat, S.A., 2010. Questions of importance to the conservation of biological diversity: answers from the past. Clim. Past 6, 759–769.

Willis, K.J., Birks, J.B., 2006. What is natural? The need for a long-term perspective in biodiversity conservation. Science 314, 1261–1265.

Wüest, R.O., Litsios, G., Forest, F., Lexer, C., Linder, H.P., Salamin, N., Zimmermann, N. E., Pearman, P.B., Anten, N., 2016. Resprouter fraction in Cape Restionaceae assemblages varies with climate and soil type. Funct. Ecol. 30, 1583–1592.

Wündsch, M., Haberzettl, T., Meadows, M.E., Kirsten, K.L., Kasper, T., Baade, J., Daut, G., Stoner, J.S., Mäusbacher, R., 2016. The impact of changing reservoir effects on the 14C chronology of a Holocene sediment record from South Africa. Quat. Geochronol. 36, 148–160.

Wündsch, M., Haberzettl, T., Cawthra, H.C., Kirsten, K.L., Quick, L.J., Zabel, M., Frenzel, P., Hahn, A., Baade, J., Daut, G., Kasper, T., Meadows, M.E., Mäusbacher, R., 2018. Holocene environmental change along the southern Cape coast of South Africa – Insights from the Eilandvlei sediment record spanning the last 8.9 kyr. Glob. Planet. Chang. 163, 51–66.

Xulu, S., Mbatha, N., Peerbhay, K., 2021. Burned Area Mapping over the Southern Cape Forestry Region, South Africa using Sentinel Data within GEE Cloud Platform. ISPRS Int. J. Geo Inf. 10.