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TITLE: Long-term vegetation response to rainfall seasonality and fire in the heathlands and shrublands of the Cape Floristic Region (SW South Africa).

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Abstract

Mediterranean environments are biodiversity hotspots in which strongly seasonal winter rainfall regimes and fire play major roles in driving ecosystem dynamics. Global predictions forecast unreliability of winter rainfall and increases in summer rainfall that are expected to result in major changes in community structure. Mediterranean systems are difficult to model, and although ecophysiological responses can be studied at observational timescales, a long-term understanding is necessary to address uncertainties and refine predictive models at landscape scales. Here we provide a ~1100 year-long multi-proxy palaeoecological reconstruction of vegetation, fire and sedimentological change at a site adjacent to a multi-annual rainfall manipulation experiment designed to test plant population and community responses to altered seasonal regimes in the Greater Cape Floristic Region hotspot (southwestern Africa). We use this data to test (i) whether long-term vegetation dynamics are controlled by changes in rainfall seasonality and (ii) whether centennial-scale landscape dynamics can be predicted from ecological responses at observational timescales. We conclude that at the research site vegetation dynamics correlate with centennial-scale seasonality fluctuations, with transitions between two ecologically distinct fine-leaved shrub communities. These transitions can be predicted from different responses to experimental manipulations of summer rainfall. Enhanced seasonality influences the competitiveness of taxa in relation to different nutrient acquisition strategies. Our results demonstrate the potential for ecophysiological research to interpret palaeoecological reconstructions and scale up the results of observational research to answer long-term questions about environmental change.

1. Introduction

Mediterranean-type ecosystems occur in regions characterized by winter rainfall in the Mediterranean basin, Africa, Australia and North and South America. In these ecosystems, the spatio-temporal distribution of precipitation affects vegetation at plant population (Moore *et al.*, 2020) and community levels (van Blerk *et al.*, 2021a,b). In many Mediterranean ecosystems, rainfall seasonality and fire interact to influence major patterns of vegetation, which consist mainly of shrublands and open woodlands (Cowling *et al.*, 2004; Bergh *et al.*, 2014).

The Cape Floristic Region spans over 90,000 km², framing the southwestern tip of the African continent, broadly coincident with that region of South Africa where >~40% of the rainfall falls during the winter months. A flora of about 9000 species of which ~70% are Cape endemics assemble into floristically and ecologically distinct vegetation types, including the Fynbos, Succulent Karoo, Albany Thicket and Afrotropical Forest biomes (Bergh *et al.*, 2014). Within the Fynbos Biome, distinct vegetation types can be identified, differentiated by gradients in water availability (fynbos to fynbos thicket) and soil nutrients (fynbos to renosterveld) (Rebello *et al.*, 2006; Bergh *et al.*, 2014). The development of the winter-rainfall Mediterranean climate and associated summer fire regimes were important in shaping the evolution, distribution and radiation of vegetation c. 6-10 million years ago (Dupont *et al.*, 2011). Although there are some pockets of Afrotropical Forest in ravines, the shrubby Fynbos and Succulent Karoo biomes dominate the GCFR (Bergh *et al.*, 2014; Cowling, 2014; Potts *et al.*, 2015a; Lechmere-Oertel & Cowling, 2016). The Succulent Karoo is an arid, fire-sensitive sparse shrubland biome composed mainly of succulents (Aizoaceae and Crassulaceae) and Asteraceae shrubs that occurs in low (< 300 mm per year) rainfall areas. Fynbos and renosterveld vegetation types are distinct fire-adapted, fine-leaved shrublands comparable to the Mediterranean basin heathlands and shrublands respectively. Fynbos is primarily characterized by heaths (Ericaceae), an evergreen broadleaved component (Proteaceae) and a reed-like element (mostly Restionaceae). Renosterveld, on the other hand, is typically dominated by the fine-leaved Asteraceae *Elytropappus rhinocerotis* (commonly known as renosterbos, from which the vegetation type derives its name. Compared with fynbos, renosterveld is typified by the co-occurrence and greater diversity of succulents and semi-succulents, grasses and bulbs (Bergh *et al.*, 2014).

Fynbos-renosterveld boundaries have been widely researched under the assumption that they are mostly determined by soil-type (Bergh *et al.*, 2014; Cowling, 2014; Potts *et al.*, 2015a; Lechmere-Oertel & Cowling, 2016). Fynbos typically occurs on sandstone derived, coarse-grained, nutrient-poor soils. Renosterveld is dominant in finer-textured and deeper, richer soils. These are often shale derived, but can also occur on granites, dolerites, silcrete, alluvium and limestone (Rebello *et al.*, 2006), as well as very occasionally on quartzites (Cowling *et al.*, 2004). Fynbos may occur on soils derived from nutrient rich parent materials, but only after the soils have been leached of much of their nutrients by higher rainfall rates (>500 mm/yr; Cowling & Holmes, 1992).

The establishment of a Dutch colony in the mid-17th century in what is today the city of Cape Town, preceded an intensification of landscape use in the GCFR. In the last 300 years, European agriculture and livestock farming radiated into the hinterland, having the most impact in low-lying, fertile areas, with crop cultivation largely eradicating the natural renosterveld vegetation (Forbes *et al.*, 2018a). Elsewhere, grazing and burning likely exceeded pre-European levels (Forbes *et al.*, 2018a).

The role of fire-vegetation-climate feedbacks in determining the relative dominance of different vegetation types in the CFR requires further investigation. Global change projections for Mediterranean-type ecosystems include extreme climatic events, unreliable winter rainfall

and increases in summer rainfall (Tadross *et al.*, 2005; Hewitson & Crane, 2006). In particular, changes in seasonality are expected to result in major shifts in community structure (Klausmeyer & Shaw, 2009; Parra & Moreno, 2018; Pausas *et al.*, 2016). In combination with climate and human altered fire regimes, the mid- to long-term ecological future of Mediterranean ecosystems is difficult to predict and model. Most models, including DGVMs, tend to focus on the relationships between forests and grasslands and perform poorly on shrubby ecosystems (Pausas, 1999; Canelles *et al.*, 2019). Observational data and instrumental records can be used to assess and inform models, however data from these sources rarely span more than a few decades, are costly to produce and are unavailable for many parts of the world. In this context, palaeoecological data series are invaluable as they extend the timescales of observation and provide a centennial to millennial-scale framework against which patterns of vegetation change dynamics can be examined in relation to human, environmental or combined forcings. Such studies are particularly valuable at ecotones where ecological communities are at an environmental or ecological limit (Forbes *et al.*, 2018a; MacPherson *et al.*, 2018; Macpherson & Gillson, 2019; Gillson *et al.*, 2020)

To this end, we developed a palaeoecological study at a site where fynbos, renosterveld and succulent karoo vegetation was present, and that was adjacent to a multi-annual rainfall manipulation experiment designed to test plant population and community responses to altered seasonal regimes (van Blerk *et al.*, 2021a, 2021c). Here we present a high-resolution multi-proxy reconstruction of centennial palaeoecological change and results from the TraCE21ka climate model simulation (Liu *et al.*, 2009; He *et al.*, 2013) from the highly biodiverse Greater Cape Floristic Region (GCFR) of South Africa. We use these data to test (i) whether long-term vegetation dynamics are controlled by changes in rainfall seasonality and (ii) whether centennial landscape dynamics can be predicted from ecological responses at observational timescales.

2.1 The Winter Rainfall Shrublands of the Greater Cape Floristic Region (GCFR)

Material and Methods

2.2 Study Site Description

The research site lies at the boundary between the present winter and year-round rainfall zones (*sensu* Chase & Meadows, 2007), in a contact zone between fynbos and renosterveld vegetation that potentially maximizes the sensitivity of the palaeoecological archive (Cowling & Potts, 2015; Potts *et al.*, 2015b; Birks, 2019). The study site is located on the Drie Kuilen Private Nature Reserve, about 20 km north of the town of Montagu in the Western Cape province of South Africa (Figure 1). Quartzitic sandstones of the Table Mountain Group dominate the high-lying areas while at lower elevations in the region, shales and siltstones of the Bokkeveld Group are common. The area is semi-arid with a mean annual rainfall of between 300-400 mm, 56% of which falls in winter (van Blerk *et al.* 2021b). Mean annual temperature is 13°C. Above about 1000 m, on sandstones of the Table Mountain Group, the vegetation is dominated by North Langeberg Sandstone Fynbos while Matjiesfontein Shale Renosterveld occurs on the soils derived from the Witteberg and Bokkeveld shales in the subjacent valleys (Rebelo *et al.*, 2006). However, floristic elements of both vegetation types intermingle at the location where the core was extracted. Common Renosterveld elements such as *Elytropappus* spp. and species of Aizoaceae occur in a mosaic landscape with patches dominated by representatives of typical fynbos species in the families Ericaceae, Restionaceae and Proteaceae. The area was used for domestic livestock production from the 1790s to 2001, when it was proclaimed a Nature Reserve. A small, abandoned homestead is situated about 1.2 km north of the coring site. Signs of anthropogenic disturbance, including sheet and gully erosion of the main river channel are evident in the valley where the site is located.

2.3 Coring, Sedimentological Analysis and Chronological controls

A seasonal wetland located at 1080 m asl (S-33.60532, E20.06149, Figure 1c, white star) in a 200 m wide valley between two ridges of the Waboomsberg mountains and drained by an ephemeral stream was identified for study (Figure 1). The sediment was extracted using a vibracorer with a 7 cm diameter core tube, which was pushed into the sediment until reaching the bedrock at a depth of 96 cm. The core was transported to the Palaeoecology Laboratory at the Department of Biological Sciences, University of Cape Town, South Africa, where it was cut open and the exposed face was cleaned. The sediment core was measured and photographed. Further visual description pertaining to textural changes and Munsell colour chart evaluations were performed. The cores were stored at 4°C and form part of the sedimentary archive of the institution. Magnetic Susceptibility was measured on dried, 1.5 cm³ samples using a Bartington MS2 / MS3 system. Organic Matter and carbonate concentrations in the sediments were analysed through loss on ignition at 450 °C and 900 °C (Heiri *et al.*, 2001). In addition, the dried bulk density of the sediment was calculated.

Three bulk sediment samples were chosen for radiocarbon dating. Radiocarbon ages were provided by Beta Analytic (Miami, Florida) and were calibrated using the SHCal20 calibration curve (Hogg *et al.*, 2020). The age at the top of the core was assigned to AD2019, when the core was extracted. Thereafter, Bayesian age-depth modelling using the R package Bacon v.2.3.9.1 was performed (Blaauw & Christen, 2015). For clarity of interpretation, ages are presented as calibrated years AD.

2.4 Palynology and Anthracology

A total of 27 one-cm³ samples were taken along the core at 4 cm intervals. At the start of the processing, a known concentration of *Lycopodium* spores was added to calculate palynomorph concentrations (Stockmarr, 1971). Pollen and Non-pollinic palynomorphs were extracted following a modification of the classical method of sequential elimination of carbonates, humic acids and silicates using HCl, NaOH and HF respectively (Bennett & Willis, 2001). In addition, samples were sieved through a 150 µm mesh to recover macro remains (>150 µm). Acetolysis was not used due to the low proportion of organic material in the sediment. Processed samples were stored in glycerol and aliquots mounted on semi-mobile light microscopy slides.

Pollen grains were identified and counted using a light transmission microscope under 400x and occasionally 1000x magnification. A pollen sum of a minimum of 200 intact pollen grains from terrestrial plants (excluding Cyperaceae) that showed no signs of taphonomic or diagenetic impact (airborne *sensu* López-Merino *et al.*, 2016) was employed. Pollen identification followed the works of Chevalier *et al.* (2021), Scott (1982) and Van Zinderen Bakker (1953) and was supported by the reference collection held at the Plant Conservation Unit, Department of Biological Sciences at the University of Cape Town. High resolution taxonomical identifications of Asteraceae, a key element in the GCFR shrublands (Bergh *et al.*, 2014), was undertaken to better refine vegetation reconstructions. This was based on preliminary analysis performed on the aforementioned reference collections and further literature (Blackmore *et al.*, 1984; Wortley *et al.*, 2007, 2008, 2009; Punt & Hoen, 2009; Robinson *et al.*, 2016). Pollen type nomenclature follows the mainstream terminology used by the seminal works of Prof. Louis Scott (University of the Free State, i.e. Scott, 1982), whereas botanical nomenclature, including taxa authors, (omitted in the main body of the text for clarity) follows Manning & Goldblatt (2012). Reworked pollen grains (*sensu* López-Merino *et al.*, 2016) appearing amongst intact grains were identified to the finest taxonomical level possible following the same reference works and counted separately. In a similar fashion, non-pollen palynomorphs (NPP) such as indeterminate fungal remains, coprophilous fungal spores, algal cysts or bryophytes spores were

also recorded and identified according to the standard NPP taxonomy and nomenclature (Gelorini *et al.*, 2011; van Geel *et al.*, 2011; Geel, 2014) but not included in the pollen sum.

Microcharcoal particles in the samples were measured (longest possible diameter) and counted into three size classes: 10-50 μm , 50-100 μm and larger than 100 μm . *Lycopodium* spores were used for calculating concentrations. A minimum sum of 200 items comprising both microcharcoal particles and *Lycopodium* spores were counted per sample (Finsinger & Tinner, 2005). Macrocharcoal remains were identified and counted in the over-150 μm fraction recovered from the palynomorph preparation using a stereomicroscope at 20x magnification.

2.5 Multivariate analysis

Percentages were calculated for each palynomorph based on the pollen sum. Zonation of the palynological spectrum was performed by constrained incremental sum of squares (CONISS) cluster analysis, based on Cavalli-Sforza distances on square root transformed percentages. Only taxa achieving a minimum of 2% in any given sample were included in the analysis. This selection of taxa was subjected to further multivariate analysis to summarize its variability using detrended correspondence analysis (DCA) and principal component analysis (PCA). Pollen diagrams were plotted using Tilia and Tilia Graph 2.6.1 (Grimm, 1991).

2.5 TraCE21-ka climate model data and Northern Hemisphere temperature anomaly

To compare our results with general circulation model simulations, we used data from the TraCE21ka experiment (Liu *et al.*, 2009; He *et al.*, 2013). TraCE21ka used the Community Climate System Model ver. 3 (Collins, 2006). This is a global coupled atmosphere – ocean – sea ice – land general circulation model that has a latitude – longitude resolution of $\sim 3.75^\circ$ in the atmosphere and $\sim 3^\circ$ in the ocean and includes a dynamic global vegetation module. The simulation includes transient orbitally-forced insolation changes and changes in the atmospheric concentrations of carbon dioxide, methane and nitrous oxide, as well as the evolution of ice sheets and their meltwater contributions to the ocean. The climate data have been regridded using bilinear interpolation to a spatial resolution of $2.5^\circ \times 2.5^\circ$ (latitude/longitude; Fordham *et al.*, 2017). The data used in this study were derived from simulations for the region 32.5S - 35S and 17.5E-22.5E. Northern Hemisphere temperature anomaly as reconstructed by Moberg *et al.* (2005) was chosen as a temperature change correlate.

3. Results

3.1 Chronology and Sedimentology

The 96 cm Erica Kuil core spans the last 1100 years, with a basal age of AD 900 (Figure 2). The sedimentation rate appears to be regular throughout the sequence, although a sharp contact at 92 cm marks the onset of the deposition of clays with varying concentrations of sand (Figure 3). Analyses of magnetic susceptibility, bulk density and organic matter content present generally stable values for the lower 90 cm of the core. The top 5 cm, corresponding with pollen zone EK-4, is markedly different from the rest of the core. Fibrous plant remains are abundant, translating into higher organic matter content and lower bulk density. Magnetic susceptibility values peak at the top of the core. Carbonate content is negligible throughout the core (Figure 3).

Table 1. Radiocarbon ages and calibration information for the Erica Kuil core

Sample code	Average depth (cm)	Measurement method	^{14}C age BP	1 sigma error	Calibration data (Hogg <i>et al.</i> , 2020)	95.4 % (2σ) cal age range	Relative area under distribution	Median probability (cal BP)	BC/AD (2σ)
Present	0	-	-	-	-	-	-	-69	2019
Beta-577528	39	AMS	270	30	SHCal20	147-218 269 – 324	0.444011 0.513498	284	1667

						408 - 436	0.042491		
Beta-577529	72	AMS	1030	30	SHCal20	799-871 879-891 896-934 943-957	0.54884 0.042268 0.341977 0.06987	865	1086
Beta-525661	96	AMS	1150	30	SHCal20	13735-14027	1	1010	941

3.2 Palynology and Anthracology

A total of 114 palynomorphs were identified in the Erica Kuil sequence: 71 terrestrial pollen taxa (included in the sum), two aquatic pollen taxa, four ferns, five bryophytes, eight saprotrophic fungal spores, seven coprophilous fungal spores, ten algal palynomorphs and 17 NPPs. Figure 4 summarises the most significant and abundant taxa, while a complete pollen diagram is included in Supplementary Information. Selection of taxa representing $\geq 2\%$ of the assemblage in any given sample yielded a list of 18 taxa that accounts for a minimum of 70.7% of the total sum (top sample, at 0.5 cm depth) and an average of 95.6% of the total pollen sum. CONISS zonation derived from this selection produced four zones EK1-EK4, described below.

Zone EK-1 (96-75 cm, cal. AD 902-1083)

The onset of the Erica Kuil sequence is characterized by high values of *Stoebe/Elytropappus* type, reaching a maximum of 65.8%. Sustained, low values of *Helichrysum* type and Ericaceae contrast with decreasing percentages of arid affinity taxa, such as Aizoaceae, *Macledium/Dicoma*, *Senecio/Othonna* type, Anthemidoideae and Calenduleae type. Micro and Macrocharcoal concentrations are consistently low.

Zone EK-2 (75-40 cm, cal. AD 1083-1590)

This zone presents lower values of *Stoebe/Elytropappus* type, oscillating between 20.5 and 39.5%. *Helichrysum* type presents a sequence maximum at 70.5 cm (31.1%) and an average background of $\sim 16.5\%$. Proteaceae, *Metalasia* type and *Clutia* are most prevalent in this zone. Restionaceae increase and then decline smoothly, with a maximum of 20% towards the middle of Zone EK-2. The representation of Aizoaceae ranges between 1% and 8.4% without abrupt changes. Anthemidoideae and *Senecio/Othonna* type present similar dynamics, being more prevalent towards the middle of the zone. Other arid-affinity taxa (*Gazania*, *Calenduleae* type) occur sporadically. Cyperaceae acquire importance in this zone, coeval to a rise in bryophytes (mostly *Phaeoceros*, refer to Supplementary Information for complete pollen diagram). Algae, predominantly Chrysophytes peak at the bottom of this zone, reaching values above 320% of the pollen sum. Taxonomically indistinct fungal remains (Fungi, in Figure 4), present background values of *ca.* 61.9%, with a peak at 60.5 cm. The palaeoanthracological record is consistent among size classes, presenting an escalating trend and a maximum at 50.5 cm where, for instance, macrocharcoal particles reach 279 particles/cm³. The charcoal signal decreases towards the top of the zone.

Zone EK-3 (40-5 cm, cal. AD 1590-1950)

In this zone the values of *Stoebe/Elytropappus* type pollen are high, consistently over 50% with sustained maxima between 36.5 and 32 cm ($\sim 63\%$) and 20.5 and 8.5 cm ($\sim 60\%$). The values of *Helichrysum* type are stable between 7-9 %, but present a peak at 12.5 cm, where they reach 18.5 %. Restionaceae, present at lower abundances than in the previous zone, average values of $\sim 8\%$, with a minimum of $\sim 5\%$ at 14.5 cm. Proteaceae is present at consistently low

percentages (less than 4%). Aizoaceae peak between 30 and 20 cm, with a subsequent decline to 3.4%. *Senecio/Othonna* type and Calenduleae type present similar trends, although their percentages are lower. Cyperaceae values are low (2-5%). Algae, bryophytes, indeterminate fungal remains and coprophilous fungi present low and stable values, negligible in comparison with adjacent pollen zones. Erosion indicators such as *Glomales* and *Hyphae* become prevalent in this zone for the first time, reaching values of 21.6% and 1.4% respectively. The anthracological record presents a stable trend with a maximum at 28.5 cm of 175 particles/cm³ and further increasing values towards the end of the zone.

Zone EK-4 (5-0 cm, cal. AD 1950-2019)

The top zone of the Erica Kuil sequence presents a markedly different pollen spectrum. *Stoebe/Elytropappus* type pollen drops abruptly to values of ~20%. Conversely, Restionaceae, Cyperaceae, and *Helichrysum* type peak in this zone, which also registers rises in *Erica*, *Clutia*, and *Senecio/Othonna* type. The presence of Proteaceae is marginal, decreasing towards the top of the zone. The Asteraceae types Astereae (*Felicia* type), *Metalasia* type, *Calenduleae* type, *Gazania*, and Anthemidoideae disappear from the pollen spectrum. The central section of this zone registers the highest levels of fungal spores (401%), coprophilous fungi (568%) and erosion indicators *Glomales* (16.9%) and *Hyphae* (531%). Fungal remains and coprophilous fungal spores decrease significantly in the top sample, however, the recession of the erosion indicators is less pronounced.

3.3 Multivariate analysis

Following the recommendation by Smilauer & Leps (2014) an exploratory DCA was performed. Given that the first axis was shorter than 2 units (DCA axis = 1.443 < 2), PCA was chosen to summarize the variability of the dataset. The first two components of the PCA explain 82.5% of the variance in the dataset (PC1: 66.9%, PC2: 15.6%). Factor loadings for PC1 oppose *Stoebe/Elytropappus* type and marginally Aizoaceae with positive loadings against Cyperaceae, Restionaceae and *Anthospermum*. For PC2, Cyperaceae, *Stoebe/Elytropappus* type present positive loadings, whereas Restionaceae, Proteaceae and *Anthospermum* have negative ones (Figure 5).

3.4 Simulated precipitation seasonality, winter precipitation and temperature anomaly.

GCM simulated records of precipitation seasonality (coefficient of variation – the variation in monthly precipitation totals over the course of the year) and winter precipitation (June, July and August) precipitation were obtained from the TraCE-21ka climate modelling experiment (He et al., 2013; Liu et al., 2009). Results indicate phases of relatively low precipitation seasonality from ~AD 900 - AD 1050 and ~AD 1600 - AD 1960 with phases of increased seasonality between ~AD 1050 – AD 1600 and after AD 1950 (Figure 6b). Increased rainfall seasonality generally corresponds to periods of increased winter rainfall. Temperature anomaly was obtained from Moberg *et al.* (2005) which evidence Northern Hemisphere anomalously hot and cold phases, namely the medieval climate anomaly (MCA; AD 950-AD 1250; Figure 6a) and Little Ice Age (LIA; AD 1300-1850; Figure 6a).

4. Discussion

4.1 Rainfall seasonality drives palaeoecological change in shrublands of the GCFR

Stoebe/Elytropappus type dominance between AD 900-1100 (Zone EK-1)

Stoebe/Elytropappus type dominates the early pollen assemblages. It is accompanied by the presence of Ericaceae as well as succulents (*Senecio/Othonna* type, Aizoaceae) and other Asteraceae (*Calenduleae* type, *Macledium/Dicoma*, Anthemidoideae) of karroid affinity (Bergh et al., 2014), which decrease towards the top of the zone. This Asteraceae-dominated

community developed in the context of relatively low rainfall seasonality, as simulated by the TraCE-21ka model (He et al., 2013; Liu et al., 2009, Figure 6b). It also occurred under a historically low incidence of fire (Figures 3 and 6g), which is typically attenuated under drier, less seasonal rainfall regimes (Keeley *et al.*, 2011). In the context of temperature changes of the last millennia (Moberg *et al.*, 2005) this phase is consistent with the warmest temperatures of the Medieval Climate Anomaly (MCA; AD 950-AD 1250; Figure 6a). While the MCA has not consistently appeared as a significant feature of regional records (Nicholson *et al.*, 2013; Nash *et al.*, 2016; du Plessis *et al.*, 2020), a less seasonal precipitation regime under warmer conditions would conform to the general models of late Holocene climate dynamics proposed by Tyson (1999).

The *Stoebe/Elytropappus* pollen type is produced by a taxonomically complex group of species from the *Stoebe* clade (Gnaphalioideae, Asteraceae), which includes among others *Stoebe* *ssp.*, *Elytropappus* *ssp.*, and *Seriphium* *ssp.* (Bergh, 2012; Koekemoer, 2016, 2019; Smissen *et al.*, 2020). Several of these are present today in the region, notably *E. adpressus* and *E. rhinocerotis* (SANBI, 2003) and are common either as part of fynbos or as dominant species within renosterveld respectively (Mucina & Rutherford, 2006). *Stoebe/Elytropappus* are generally unpalatable to domestic livestock, and if combined with limited grass cover, their dominance may explain the absence of grazing indicators (e.g. coprophilous fungal spores).

It is possible that the Asteraceae-rich assemblage which dominates Zones EK 1 (and EK3, see below, Figures 5 and 6d) represents a form of Asteraceous fynbos. This expression of fynbos is characterized by Asteraceae, non-Ericaceae ericoids, and succulent shrubs as opposed to more mesic fynbos with higher abundances of Ericaceae, Proteaceae and Restionaceae (Campbell & Werger, 1988; Campbell, 1985). Asteraceous fynbos occurs at the drier end of fynbos distribution, presenting higher restioid and lower grass and succulent cover than renosterveld (Rebello *et al.*, 2006). This is consistent with the prevalent soil type at the Erica Kuil site.

This pollen spectrum shares characteristics of xeric fynbos and renosterveld, in the co-occurrence of fynbos elements, succulents, *Stoebe* clade taxa and other Asteraceae of karroid affinity (Bergh *et al.*, 2014). This combination of taxa may reflect either local vegetation or pollen influx from both sandstone fynbos and shale renosterveld adjacent (currently <2 km) to the site. The presence of Restionaceae, which is a diagnostic character of fynbos is also lowest during the *Stoebe/Elytropappus* dominated phases (Figure 4), which could be consistent with an expansion and greater dominance of Renosterveld elements in this phase. This could be consistent with van Blerk *et al.* (2021b), who show that Renosterveld benefits more than fynbos from reduced summer drought and less seasonal rainfall. However, the fynbos discrimination value of 5% Restionaceae groundcover defined by Rebello *et al.* (2006), cannot be reliably assessed without pollen-vegetation calibration studies, which are to date unavailable.

Fynbos development is driven by an increase of rainfall seasonality (AD 1100-1600, Zone EK-2)

The increase in fynbos pollen taxa (Restionaceae, Ericaceae and Proteaceae) in Zone EK-2 is concurrent with a simulated increase in rainfall seasonality driven by increased winter rainfall as simulated by the TraCE21-ka climate model (He *et al.*, 2013; Liu *et al.*, 2009, Figure 6b, c). This transition is exemplified in the results of the multivariate analysis, where the loadings of Restionaceae and *Stoebe/Elytropappus* type taxa are inversely loaded for both PC1 and PC2 (Figure 5). This is an important factor as the percentage of Restionaceae is a defining characteristic distinguishing fynbos from other distinct Asteraceae-dominated vegetation types (Rebello *et al.*, 2006). During this period, there is also a higher incidence of fire as indicated by charcoal abundance (Figures 3 and 6g), suggesting an intensified fuel-controlled fire regime,

consistent with the shorter fire return intervals that maintain fynbos. This greater fire frequency reflects greater biomass and precipitation seasonality mediated by enhanced winter rainfall.

Community level responses at experimental timescales through rainfall seasonality manipulation predict this trend. At the research site, different post-fire responses to manipulated rainfall seasonality had differential impacts on renosterveld and fynbos communities (van Blerk *et al.*, 2021b). Under accentuated summer drought tighter nutrient conservation strategies would afford fynbos taxa a competitive advantage over renosterveld at a community level (van Blerk *et al.*, 2021a). Further mechanisms of post-fire competitive exclusion by seedling shading due to a more frequent fire regime probably explains fynbos resilience over 500 years. During this phase, the parallel dynamics of Restionaceae, Ericaceae and Proteaceae, which shade and outcompete each other in post-fire fynbos succession (Hoffman *et al.*, 1987; Rutherford *et al.*, 2011) likely reflect a dynamic mosaic pattern at the landscape scale, as is observed at the site today. The expansion of fynbos under enhanced seasonality may suggest the retreat of renosterveld and its replacement by fynbos, in accordance with the findings of van Blerk *et al.* (2021a).

Stoebe/Elytropappus type rebounds under decreased rainfall seasonality at the expense of fynbos (AD 1600-1950, Zone EK-3)

From AD 1600 onwards, a decrease in seasonality, promoted by reduced winter rainfall (Figure 6b and 6c) underpins a rebound of *Stoebe/Elytropappus* type and a decrease of fynbos elements (Proteaceae, Restionaceae). This recovery is predicted by differential effects of attenuated summer drought on productivity and community structure (van Blerk, 2020). At the experimental site, renosterveld elements were overall more responsive to experimental rainfall manipulation on higher nutrient soils (van Blerk *et al.*, 2021b). In particular, *Elytropappus rhinocerotis* was found to be more responsive to summer moisture supply displaying a positive growth response compensation in more nutrient rich soils (van Blerk *et al.*, 2021a). Conversely, growth responses of fynbos taxa appear insensitive to summer rainfall compensation, likely because they exercise a stricter control on growth as an adaptation to low nutrient availability (van Blerk *et al.*, 2021a). Therefore, it is likely that the source of *Stoebe/Elytropappus* type established as a dense continuum, outcompeting fynbos elements and particularly the smaller, more mesic, shrub component such as *Clutia* or *Helichrysum* type.

At the site, *Elytropappus rhinocerotis* dominates the colluvium that overlays the contact between the quartzitic sandstones from the Cape Group and the shales of the Bokkeveld Group. However, *E. adpressus*, which is also common at the mountains surrounding the research site (BOL SM20-7) and grows preferentially on sandstone slopes (Manning & Goldblatt, 2012) could be responsible for the increase in the *Stoebe/Elytropappus* type pollen signal. Taking the top pollen sample as a correlate of the present vegetation, zones EK 1 (see above) and EK3 represent phases where *Stoebe/Elytropappus* type are more abundant than at present. This may indicate either the development of renosterveld, asteraceous fynbos dominated by *E. adpressus* or a non-analogue community that substitutes typical fynbos vegetation under less seasonal rainfall regimes.

Increased aridity inferred from a decrease in winter rainfall and an increase in precipitation seasonality between AD 1700-1800 (Figure 6c) coincides with increased fire occurrence, as indicated by higher concentrations of micro and microcharcoal particles (Figures 4 and 6g). Leaf succulent and karroid affinity taxa (Aizoaceae, *Senecio/Othonna* type and Calenduleae) also expanded under these drier conditions. It is possible that in this instance, post-fire recovery occurred under an aridity regime beyond the recruiting tolerance of fine-leaved

renosterveld and fynbos taxa, and as a result succulents took over the vacant space. The presence of the mycorrhizal *Glomales* and *Hyphae* further suggests denudation and drought.

20th century anthropogenic transformations and the development of restioid fynbos from 1950 to present (Zone EK-4)

During the 20th century, the relationship between vegetation and climate dynamics is complicated by increasing human impact. In the first half of the twentieth century, despite lower seasonality, *Stoebe/Elytropappus* type abundance declines and fynbos dominance returns. From the mid-twentieth century human impact becomes the controlling factor on the local environmental dynamics, indicated by co-occurring increases in fire and herbivory indicators. In conservation terms, this suggests that burning and herbivory were unusually high in the latter half of the twentieth century, when agriculture in the Western Cape became more intensive (Forbes *et al.*, 2018b) and continued following the designation of Drie Kuilen as a nature reserve, when domestic herbivores were replaced by indigenous ungulates at similar densities.

Fynbos dominance returns but in a different, restioid, form, suggesting dramatic shifts in vegetation composition and structure. Around the research site, abandoned homesteads and hydraulic infrastructures such as earthen dam walls exist in the mountain areas, while abandoned plough fields are present in the lowlands. Consequently, combined increases in grazing (fungal spores), burning (charcoal) and erosion indicators (Figures 4, 6 e and 6f), reflect a transition towards unpalatable restioid fynbos dominated by reed-like Restionaceae and Cyperaceae. There is no evidence of increases in *Stoebe/Elytropappus* type, in contrast to findings from another nature reserve in the Western Cape where increases in grazing and burning was accompanied by increases in *Elytropappus* (Forbes *et al.*, 2018b). It is not clear whether this is due to a difference in ecology of the dominant *Elytropappus* species or the competitive interplay between fynbos and renosterveld elements, as mediated by changes in seasonality and soil type. Nonetheless, the abandonment of local agricultural activities in the last decades, and its declaration as a Private Nature Reserve in 2001 seem to be directing the system towards a proteoid-restioid fynbos mosaic state, as evidenced by the values of PC2 (Figure 5).

5. Conclusions

The dynamics of Mediterranean type ecosystems in the CFR are complex, involving the interplay between climate, fire and vegetation. Understanding these dynamics will be critical in informing the conservation and management of these systems in the light of global change. While increasing temperatures are predicted throughout southern Africa, changes in rainfall are highly uncertain and spatially heterogeneous (Altwegg *et al.*, 2014). A tendency towards drier summer conditions (Tadross *et al.*, 2005) would be exacerbated by higher temperatures, which together would reduce plant available moisture. Insights from palaeoecology can help in exploring the resilience of fynbos to climate change and in identifying possible trajectories of vegetation change into the future. Such studies provide important information on the feedbacks between changing seasonality, fire and land-use that can improve understanding of resilience and provide insight into possible future change (Forbes 2018, MacPherson *et al.* 2018, 2019, Gillson *et al.* 2020).

Transitions between distinct fynbos and an Asteraceae-rich community dominated by *Stoebe/Elytropappus* type occur in the last millennium at the research site. These vegetation

dynamics correlate with centennial seasonality fluctuations as simulated by the TraCE21-ka climate model (He et al., 2013; Liu et al., 2009). Enhanced seasonality was associated with fynbos dominance while attenuated seasonality was associated with a more Asteraceous community that could reflect a greater dominance of Renosterveld elements. These transitions can be predicted from different responses of fynbos and renosterveld vegetation to experimental manipulations of summer rainfall, which show that enhanced seasonality, afforded by an increase in winter rainfall would favour a fynbos rather than a renosterveld dominance at this site in relation to different nutrient acquisition strategies (van Blerk, 2020). Our findings suggest that either a sparser asteraceous fynbos, renosterveld or a no-analogue community can develop in mountain sites at the expense of more typical expressions of fynbos in relation to precipitation seasonality, aridity and fire.

Our results demonstrate the potential for future joint ecophysiological and palaeoecological research to interpret long-term vegetation reconstructions enhanced by climate simulations. These results are particularly interesting because they provide a cross-scale link between observational data and long-term ecology and can, potentially, open avenues to inform future scenarios of landscape change in terms of observed responses to experimental manipulations. However, further pollen-vegetation calibration studies are needed to determine ecological affinities with more precision. This will be key to interpret palaeoecological results in terms of ecosystem service provision and management and conservation recommendations.

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Figures

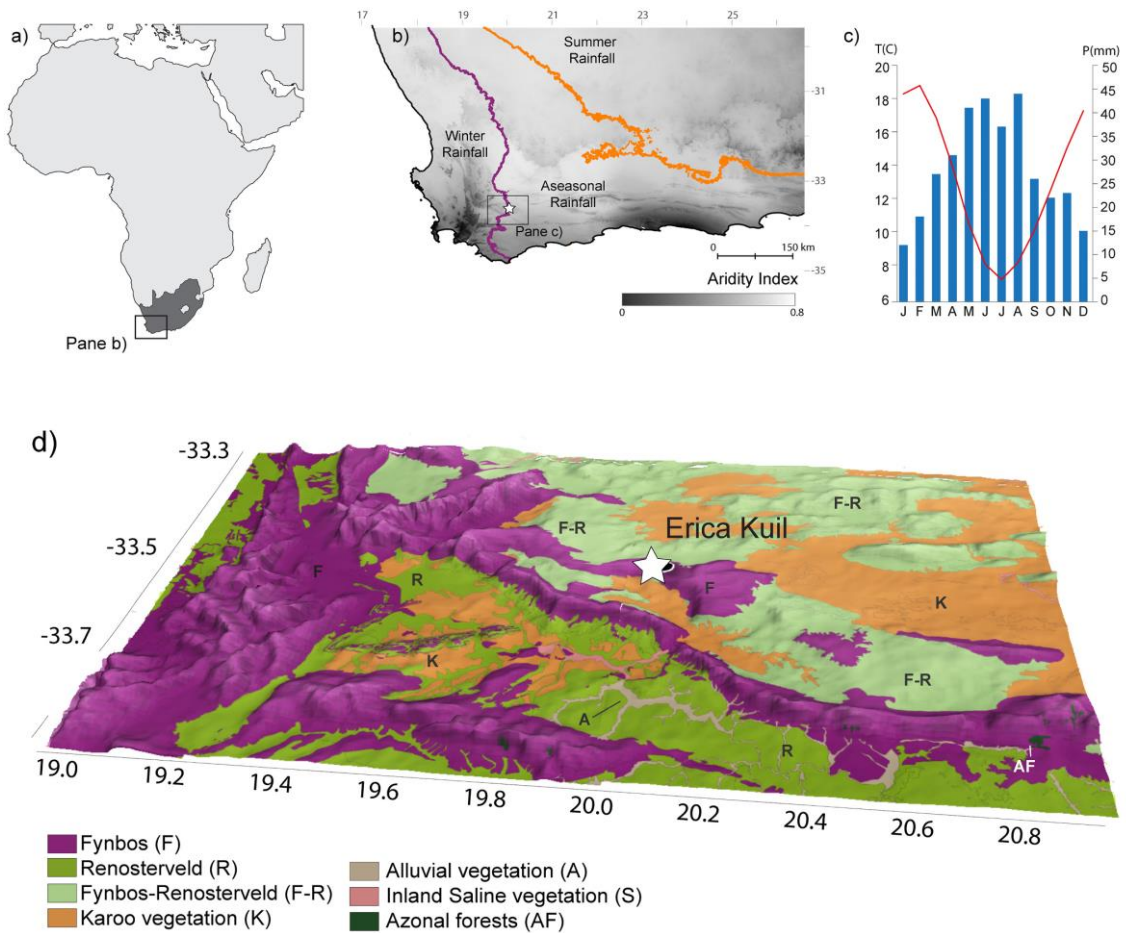


Figure 1. The Erica Kuil site. a) Climate diagram including mean monthly temperature (C) and precipitation (mm) derived from the Worldclim 2.1 dataset for the Erica Kuil site (Fick & Hijmans, 2017). b) Aridity index across southwestern South Africa, including seasonality of rainfall, and general location of the Erica Kuil site (white star), at the boundary between the winter and year-round (aseasonal) rainfall zones. c) Map of vegetation biomes/bioregions around the Erica Kuil study site. Classifications according to (Mucina & Rutherford, 2011); the coring site is located with a white star.

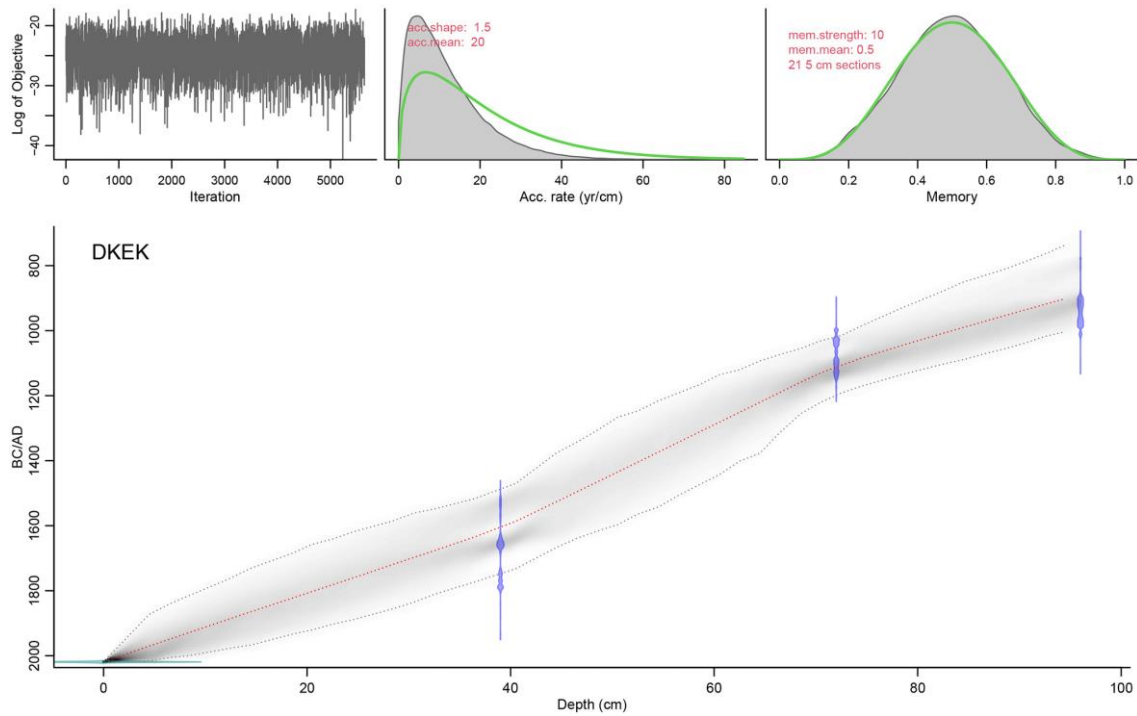


Figure 2. Bayesian age-depth model for the Erica Kuil core.

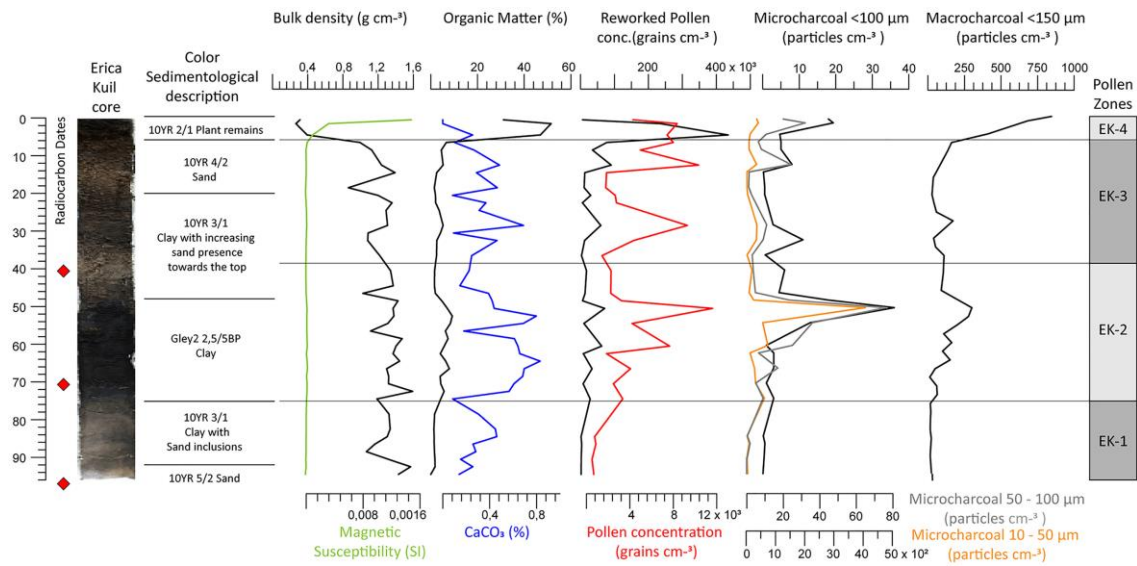


Figure 3. Erica Kuil core sedimentology, including sedimentary log, color, textural description, bulk density, magnetic susceptibility, organic matter and carbonate content, pollen, micro and macrocharcoal concentrations. Pollen zones EK 1-4 correspond to CONISS zonation (see Figure 4).

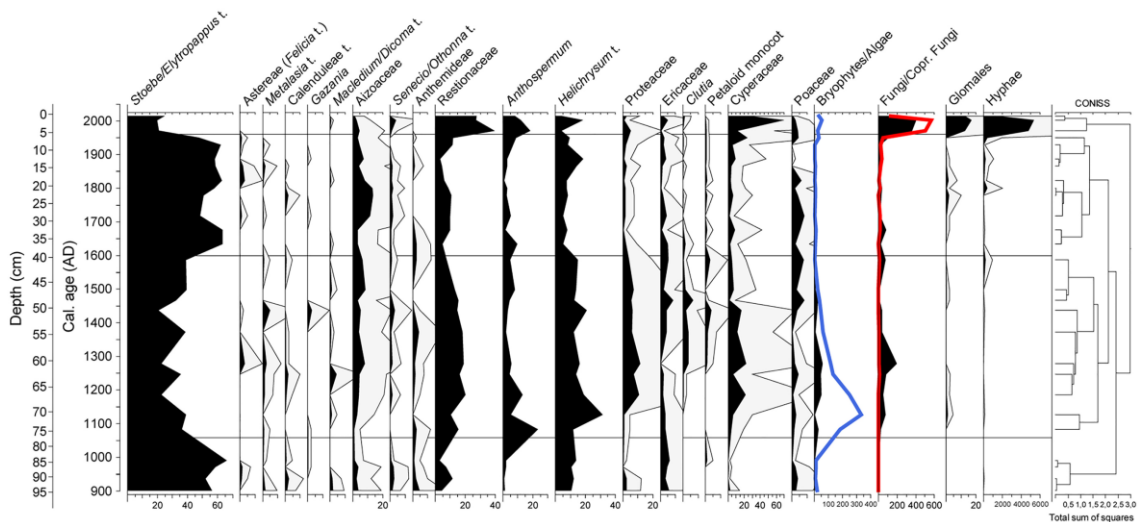


Figure 4. Erica Kuil summary pollen diagram, including taxa above 2%. Dendrogram represents CONISS pollen zonation.

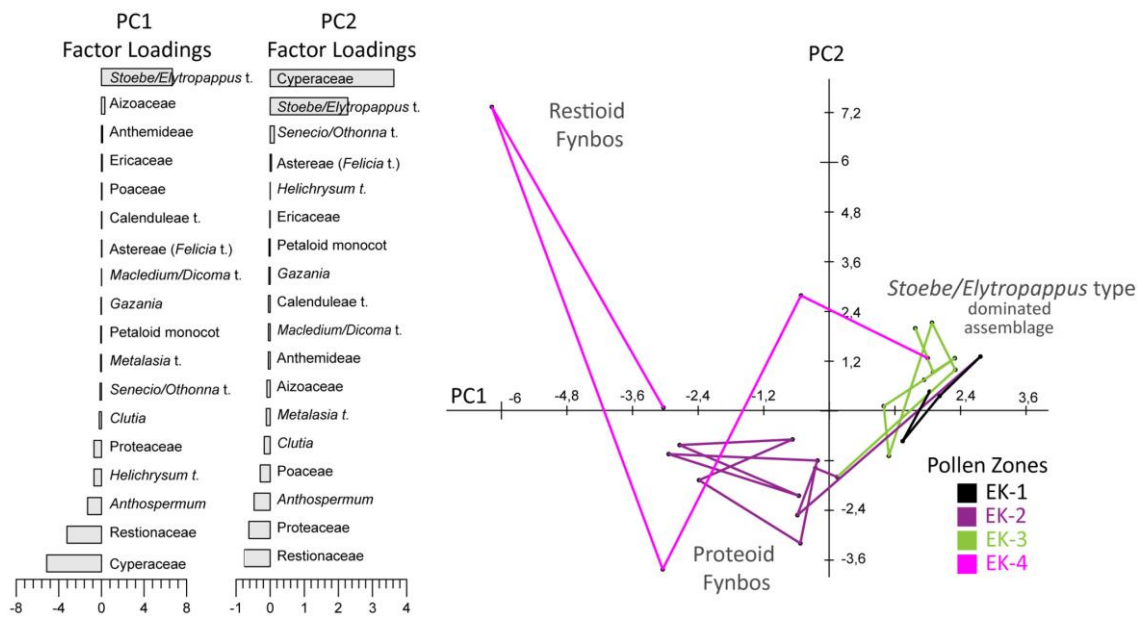


Figure 5. Principal component analysis for the Erica Kuil pollen dataset: factor loadings for PC1 and PC2 (left), PC1 and PC2 biplot (right), pollen zones EK 1-4 correspond to CONISS zonation (see Figure 4).

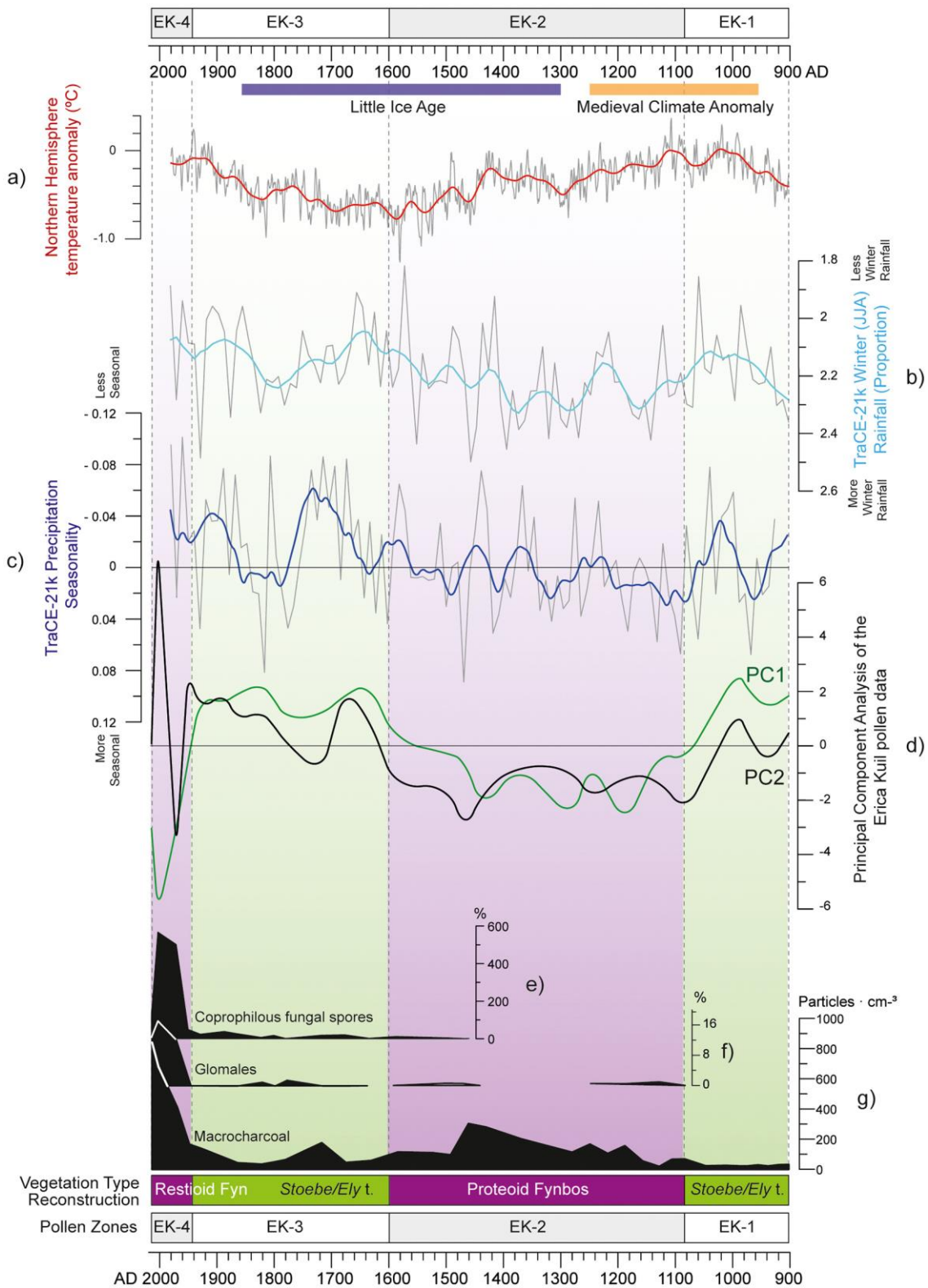


Figure 6. Palaeoecological changes after the Erica Kulil sequence. a) Northern Hemisphere temperature anomaly (°C), relative to the 1961-1990 average. b) TraCE-21k Winter (JJA) rainfall. c) TraCE-21k Precipitation Seasonality. d) PC1 and PC2 from the principal component analysis of the Erica Kulil pollen dataset (see Figure 5). e) Coprophilous fungal spores (%), a grazing indicator. f) Glomales (%), an erosion indicator. g) Macrocharcoal concentration (particles·cm⁻³), and indicator of fire incidence.

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