Holocene climatic variability indicated by multi-proxy records from southern Africa’s highest wetland

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Holocene climatic variability indicated by multi-proxy records from southern Africa’s highest wetland
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Abstract
The eastern Lesotho Highlands observe climate patterns distinct from those of surrounding lower altitude regions, representing a niche environment with a unique biodiversity, leading to well adapted but restricted biomes. This study explores changes in the environmental composition of diatoms and pollen at southern Africa’s highest altitude wetland (Mafadi - 3390m.asl) through the Holocene. The palaeoenvironmental record for Mafadi Wetland indicates fluctuations between cold, wet conditions, prevalent between ~8,140-7,580 and ~5,500-1,100 cal. yr BP, and warmer, drier periods between ~7,520-6,680 and ~6,160-5,700 cal. yr BP. Marked climatic variability is noted from ~1,100 cal. yr BP with notably cold conditions at ~150 kyr BP. Inferred cold periods in the Lesotho Highlands are coincident with the 8.2kyr and Little Ice Age cold events identified from records in western Lesotho and South Africa. Variability exists between the moisture reconstructions presented in this study and those from adjacent lower altitude sites, which is hypothesised to reflect variations in the strength and extent of the Westerlies throughout the Holocene.

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Introduction

Southern Africa provides a valuable geographic setting for palaeoenvironmental and palaeoclimatic research owing to the large number of ocean-atmospheric driving forces (Chase & Meadows, 2007). Situated at the confluence of the Indian and Atlantic Oceans, and spanning the sub-tropics to mid-latitudes, a wide range of climates and biomes comprise the contemporary environment (Mucina & Rutherford, 2006). Throughout the Holocene, spatial variation in climate changes have been noted for a range of sites, indicating relative influences of climatic variables including the strength of the Westerlies and Easterlies, and the position of the Inter Tropical Convergence Zone (cf. Chase & Meadows, 2007; Chase et al., 2011, 2013, 2015; Nörström et al., 2014). This body of research has also raised debates concerning the extent to which Holocene climatic changes in the Northern Hemisphere are consistent in timing, extent and magnitude with those of the Southern Hemisphere. There has been substantial academic output covering past climatic and environmental reconstructions in southern Africa (Nørström et al., 2009), however, the late Quaternary environmental record remains uncertain and at best undefined for much of the Lesotho Highlands (Grab et al., 2005). The Lesotho Highlands offer a unique study region in southern Africa given their high altitude and variable topography, influencing local and regional climate, and consequently vegetation at such spatial scales. Furthermore, a palaeoenvironmental record from southern Africa’s highest wetland permits comparison with neighbouring lower altitude records and the exploration of palaeo-lapse rates and climate thresholds for biota.

The majority of Quaternary environmental reconstructions for the Lesotho region stem from the rich archaeological heritage (cf. Carter, 1976; Plug, 1993; Mitchell et al., 1994, 1998, 2011; Mitchell, 1996; Cain, 2009; Stewart et al., 2012). This archaeological work has included palaeoclimatic inferences (Mitchell et al., 1998), but the temporal resolution and quantification of past climates lacks detail. A variety of Quaternary periglacial and glacial studies from Lesotho’s eastern high mountain region have indicated colder, and possibly relatively wet conditions during the late Pleistocene (Harper, 1969; Grab, 2002a; Mills and Grab, 2005; Mills et al., 2009) and Holocene neoglacial episodes (Grab, 2000). However, the absence of age dates for many of these periglacial studies, the lack of consistent temporal
chronologies, and the disputed interpretation of geomorphological landforms have limited their palaeoenvironmental value (Boelhouwers & Meiklejohn, 2002).

The only published record analysing fossil pollen from a sedimentary sequence in the eastern Lesotho Highlands (Van Zinderen Bakker, 1955) is limited in its palaeoenvironmental value owing to the absence of a chronology, a low sampling resolution, and the examination of only five plant taxa. Although age dates are available for a few Holocene sedimentary sequences in eastern Lesotho (Hanvey & Marker, 1994; Marker, 1994, 1995, 1998), these lack analyses on pollen, diatoms or other environmental proxy markers and thus are of limited value for detailed environmental and climatic reconstructions. The only detailed Holocene palaeoenvironmental records for Lesotho stem from the western lowlands, based on charcoal assemblages and grazer tooth enamel in the Phuthiatansana-ea-Rhaba Bosiu basin (Esterhuysen and Mitchell, 1996; Smith et al., 2002; Roberts et al., 2013), sedimentary and phytolith records from an exposed sedimentary sequence in a gully of the Tsoaing Basin (Grab et al., 2005), and from central Lesotho, based on phytoliths and stable isotopes (Parker et al., 2011). Many of these studies explore palaeoenvironmental proxies extracted from archaeological excavations, and therefore are limited due to biases of material selection (Esterhuysen & Mitchell, 1996).

The eastern Lesotho Highlands are, furthermore, particularly well positioned for identifying late Quaternary synoptic climate fluctuations, and associated ecological changes in the alpine zone, a niche biome sensitive to climate change. The high altitude, relatively high latitude, and frequent occurrence of snowfalls produce a particularly marginal environment for plant growth. Not only are a very specific group of species able to survive the harsh environmental conditions, but any climatic changes can potentially lead to the extirpation of plant groups (Carbutt & Edwards, 2006; Inouye, 2008). While plants at lower altitudes may respond to atmospheric warming by upslope succession, those at the mountain summit habitat edge are unable to relocate altitudinally during such warming, and so may suffer heat stress (Parmesan & Yohe, 2003). Similarly, the contemporary sparse vegetation cover on the highest peaks of eastern Lesotho would have occurred further downslope during past colder or drier periods. Consequently, vegetation at the habitat edge is more sensitive to
climate changes, with more noticeable responses, than at lower altitude sites (Carbutt & Edwards, 2004).

This study presents a Holocene climate and environmental record based on diatom and pollen communities and sediment characteristics from southern Africa’s highest wetland (here termed Mafadi Wetland; see Figure 1). In so doing, we aim to address some of the knowledge gaps mentioned above and provide the highest resolution palaeoenvironmental record thus far for the alpine zone of southern Africa.

Study Region
Mafadi summit is located on the border between Lesotho and South Africa, and is the highest peak in South Africa and the third highest in Lesotho (3450m.asl). Immediately northwest of the summit (29°11′58″S, 29°21′04.1″E) is a bowl shaped depression, with a spring fed wetland. According to Schwabe (1995), the wetland is classified as a ‘bog’ — the highest in southern Africa at 3390m.asl (Figures 1 & 2). Mean annual temperatures at this site are estimated at ~4°C, varying from 9°C in January to -2°C in July, with extreme minimum temperatures reaching -18°C in winter (Grab, 1996; Grab 2002b). Annual precipitation is highly variable across the Lesotho Highlands, ranging between 740-1600 (Sene et al., 1998), with the Mafadi summit region likely receiving a median value of this.

Above ~3400m.asl, vegetation becomes increasingly sparse, and almost absent near the summit. The vegetation is broadly classified as alpine grassland (Carbutt & Edwards, 2004), comprising of Erica-Helichrysum heath, with shrubs and grasses notably dwarfed compared to those at lower altitude. The site is characterised by white patches where diatomite-rich sediments are exposed. The moist wetland conditions and the presence of diatomite, together with the geomorphology of the depression, make the site ideal for palaeoenvironmental work, as pollen and diatoms are well-preserved proxies.

Methods
A 1.2m sediment core (Figure 3) was extracted from the wetland in April 2014 (Figure 2), and subsampled in a pressure-sealed laboratory at a 3cm frequency. Six bulk organic material samples from relatively equally spaced depths throughout the core were sent for
Accelerator Mass Spectrometer (AMS) radiocarbon dating at Beta Analytic (Table 1). These dates were calibrated using the Southern Hemisphere SHCal13 model (Hogg et al., 2013). The BACON model (Blaauw & Christen, 2011) was used to interpolate dates for the remainder of the profile, which employs millions of self-adjusting Markov Chain Monte Carlo iterations. This model was selected given its improved performance of Bayesian over linear regression models, and the inclusion of information on sample thickness. No outliers were identified by the BACON model.

Palaeoenvironments were investigated using a range of analyses. At the broadest scale, sediment properties were used to determine moisture availability, demonstrated predominantly by relative changes in the percentage organic content, and the proportions of gravel- and sand-sized particles to silt- and clay-sized particles. Distinct variations in the skewness: kurtosis ratio indicate changes in depositional environment (Saarinen & Petterson, 2006; Masselink et al., 2014). Pollen was used to reconstruct past vegetation composition, biomes, and to study the presence and absence of indicator species for alternating wetland and grassland conditions in the Highlands region. At a local scale, diatoms were used to reconstruct the aquatic conditions and biodiversity within the wetland. Pollen preparation followed standard procedures outlined by Faegri et al. (1989). Once the pollen had been isolated and slides prepared, a minimum of 250 pollen grains were counted per sample at a magnification of 400x using an Olympus BX51 light microscope. Identification was made with reference to the African Pollen Database and the reference collection at the University of the Free State, South Africa. Diatom preparation was undertaken using the procedures outlined by Battarbee et al. (2001). A minimum of 300 diatom valves were counted per sample at a magnification of 1000x using an Olympus BX51 light microscope. Diatoms were identified through consultation with both local (Schoeman, 1973; Schoeman & Archibald, 1976; Harding & Taylor, 2011; Matlala et al., 2011) and international (Patrick & Reimer, 1975; Krammer & Lange-Bertalot, 1986; Snoeijjs & Balashova, 1998; Camburn & Charles, 2000; Kramer, 2002) literature. Sediment analyses involved determining the organic and carbonate content of each sample through loss-on-ignition (LOI) at 550 °C and 925 °C respectively (Heiri et al., 2001). The sediment particle size distributions for each sample, together with the mean, skewness and kurtosis, were measured using a Malvern Mastersizer 3000. The fluctuations in skewness indicate periods
in which a disproportionately large component of the particle size distribution comprises larger particles, which indicate drier conditions with less active weathering (Masselink et al., 2014). Fluctuations in kurtosis indicate periods with a flattened particle size distribution curve, indicating a broader spread of particle sizes. Important gradients in each of the datasets were explored using the indirect ordination technique of principal components analyses, while zones in the pollen data were designated using CONISS. All statistical analyses were undertaken using the code-based statistical platform R (Venables & Smith, 2015), and stratigraphic plots were produced using C2 (Juggins, 2007).

Results

The lithology, comprising high percentages of organic matter and consistently predominant peat, reflects a relatively stable shallow peatland environment throughout much of the period represented by the sediment core (Figure 3). The six AMS radiocarbon ages obtained constrain the profile to the mid- to early-Holocene with a basal calibrated date of 7,140 cal. yr BP. Sediments sampled at a depth of 7 cm are dated to 870 cal. yr BP, indicating that the profile most likely extends continuously to the present day at the surface.

The sedimentation rate, calculated by the BACON model, is averaged for the sequence at 100 yr cm\(^{-1}\) (0.01 cm/yr). There is a marked period of particularly slow sedimentation, which extends from 1,280 ± 30 cal. yr BP to 4,960 ± 30 cal. yr BP (Figure 4). During this period, only 18 cm of sediment accumulated, yielding a much slower sedimentation rate (mean 205 yr cm\(^{-1}\)), resulting in a lower temporal frequency of samples (as they were sampled at consistent depth) and generally less well-resolved profiles. Before and after this period of slow sedimentation, periods of consistent and comparatively more rapid sedimentation are noted (Figure 4). Interpolated dates from the BACON model are used throughout this paper to ensure consistent interpretation.

CONISS revealed four statistically significant pollen zones (Figure 5). Samples spanning a depth of 103-84 cm contained insufficient pollen for counting (<20 pollen grains counted across duplicate slides from each sample). The absence of pollen is, however, a ‘similarity’ between the samples, and thus while they could not be statistically clustered using CONISS, an artificial manually created zone MP5 is defined by including these samples for the
purpose of comparison with the other proxies. Zone MP5 extends from a depth of 103-84cm (~8,140-7,580 cal. yr BP). Zone MP4 covers the sequence from 81-72cm (~7,380-6,680 cal. yr BP), marking the terminal depth of samples containing sufficient pollen for counting. Zone MP3 includes seven samples, and extends from 71-62cm depth (~6,610-6,010 cal. yr BP). Zones MP1 and MP2 comprise larger sets of samples than zones MP3 and MP4, and are separated at a mean depth of 26.5cm (~1,080 cal. yr BP).

The sediment profile is dominated by silt-sized sediment particles (>40%), with relatively low percentages of organic matter through zones MP5-MP2 (>15%; Figure 6). The percentage of organic matter rapidly increases in zone MP1 (~1080 cal. yr BP to present), with a peak in the contemporary material (Figure 6). The percentage of sand-sized particles peaks in zone MP4 and at the termination of zone MP2 (Figure 6). The relationship between skewness and kurtosis reflect no statistically significant changes in sedimentation environment.

The pollen record is dominated by Poaceae (43.6%), Cyperaceae (23.5%) and Asteraceae (22.2%). Pollen grains from a total of 20 families, or genera where identification was possible, appeared with a frequency of more than 1% at any point throughout the profile. Due to morphological and environmental similarities, pollen counts from the plant families Chenopodiaceae and Amaranthaceae are summed to form a single group ‘Cheno-Am’ (Scott et al., 2012). These pollen grains are largely representative of the contemporary wetland environment, comprising semi-aquatic species, shrubs and herbs, and succulents (Figure 7). Occasional Podocarpus pollen grains were counted (<2% maximum occurrence; Figure 7). As Mafadi Wetland is situated above the tree-line, these would have been transported to the site by wind from adjacent forests at lower altitudes. The ratio of Asteraceae: Poaceae is presented (Figure 7) as a proxy for the strength of seasonality of precipitation, which in turn is argued to represent changes in the latitudinal extent and strength of the Westerlies (Coetzee, 1967; Norström et al., 2009). A ratio value >0.5 is interpreted as a seasonal shift to summer precipitation, and in the case of Lesotho, a decrease in snowfall; a value <0.5 suggests a proportional increase in winter precipitation (Norström et al., 2009). Such shifts in seasonality may occur during periods of increasing, decreasing or constant total precipitation, and are thus indicative only of the timing and not the quantity of precipitation.
(Coetzee, 1967). Principal Component 1 accounts for a statistically significant 29.1% (p >0.0001) of the variance of the pollen distribution in the samples, separating at extremes Poaceae, Indigofera and Apiaceae, which have the strongest negative scores (-1.65, -0.58 and -0.29 respectively), from Cyperaceae and Asteraceae, with the strongest positive scores (1.6 and 0.5 respectively).

The diatom record is dominated by *Staurosirella (Fragilaria) pinnata* (22.4%), *Aulacoseira ambiguа* (19.3%) and *Fragilaria construens* (19.0%). Due to similarities in both the morphology and ecological preferences, *Staurosirella (Fragilaria) pinnata* and *Fragilaria construens* are grouped together and named *Fragilaria pinnata/construens*. The diatom profile comprises cycles between periods dominated by the planktonic and facultative planktonic species *Aulacoseira ambiguа* and *Fragilaria pinnata/construens*, and periods with a larger selection of diatom species dominated by aerophilic, epiphytic, epipellic, epilithic and benthic groups, dominated by aerophilic *Eunotia praerupta* and *Pinnularia divergentissima* (Figure 8). Zone MP5, for which no pollen could be counted, demonstrates the highest proportion of *Fragilaria pinnata/construens* (Figure 8). Principal Component 1 accounts for a statistically significant 68.1% (p <0.0001) of the observed variance in diatom species distribution across the profile, and consistent with the observations made above, segregates at extremes *Fragilaria pinnata/construens* and *Aulacoseira ambiguа* with strong negative scores (-1.9 and -1.6 respectively) from *Eunotia praerupta, Eunotia bilunaris* and *Pinnularia borealis* with the strongest positive scores (1.9, 1.0 and 1.0 respectively).

**Discussion**

With a basal date of ~8,200 cal. yr BP, this sequence does not span the entire Holocene, but rather commences at a period coincident with the final disappearance of the Northern Hemisphere ice sheets (Mayweski et al., 2004). The very slow sedimentation rate of 100yr.cm$^{-1}$ is attributed to the particularly low temperatures at this site. Temperature would have been an important control in the sedimentation rate at such high altitude given the peat-dominated sediment, which required relatively mild temperatures to facilitate plant growth, and for sufficient humidity to develop peat (Van Zinderen Bakker, 1955; Meadows, 1988). The zones, based on the CONISS analysis on the pollen results, coincide with changes across all three of the proxies, indicating clearly defined climate and environmental shifts at
Mafadi Wetland. At present, grass and small shrub cover ceases mid-way up the slope between the wetland and Mafadi Summit (at ~3400 m.a.s.l), suggesting that the site is located in close proximity to the terminal altitude for vegetation cover in eastern Lesotho (Grab, 1996, 1999). Given the high altitude and radiocarbon AMS ages constraining the profile to the Holocene, sea-level changes are not of influence. Yet, this being the highest altitude wetland in southern Africa, provides an opportunity to discuss niche communities and threshold conditions associated with climate change through the Holocene.

**MP5: ~8,140-7,580 cal. yr BP**

Zone MP5 is marked by a complete absence of pollen (Figure 7). The sterile layer could be due to a number of factors, including: an absence of plants at the site during this period; the prevention of pollen being deposited onto wetland sediments (perhaps during periods of extended snow and ice cover); or an alkaline pH that would compromise the preservation of pollen grains (cf. Gasse & Van Campo, 1998; Grab et al., 2005; Metwally et al., 2014). The diatom composition almost entirely comprises planktonic *Aulacoseira ambigu*a, and facultative planktonic *Fragilaria pinnata/construens* (Figure 8). The habitat of these species suggests the presence of shallow standing water (Gasse & Van Campo, 1998; Sitoe et al., 2015), which does not support an inference of conditions too dry to support plants. *Fragilaria pinnata/construens* are common in alpine lakes of East Africa, and survive under conditions of substantial ice cover and cold water temperatures (Schmidt et al., 2004; Ohlendorf et al., 2000; Wang et al., 2013). The diatom composition does not suggest pH conditions markedly different from the remainder of the core, and thus it is unlikely that the pollen deteriorated under conditions of very high pH. It is thus inferred that this was a cold but wet period, with temperatures too low to sustain plant life, resulting in a climatic barrier to plant growth at the site during this time. The percentage composition of carbonates and organic material in the sediments is low during this period (Figure 6), further indicative of low rates of primary production. The large percentage of silt-sized particles further confirms wetland presence in this zone (Figure 6). The very cold period at the beginning of this zone, marked by the highest percentage of *Fragilaria* diatom species in the sequence (Figure 8), coincides with the relatively brief ‘8.2 kyr’ cold event (Mayewski et al., 2004; Alley & Ágústsdóttir, 2005; Chase et al., 2015).
MP4: ~7,520-6,680 cal. yr BP

Fossil pollen emerges at the start of this zone, dominated by Cyperaceae, suggesting at least localised wet patches (Figure 7). This is concurrent with a peak in Cheno-Am, Acanthaceae and the drought resistant Crassula and Aizoaceae, with relatively high percentages of Poaceae and Asteraceae, suggesting warmer, less moist conditions than in the preceding zone (Figure 7). This coincides with a decrease in the relative abundance of Aulacoseira ambiguа and Fragilaria pinnata/ construens as the zone commences, replaced by an increase in aerophilic diatoms (Eunotia praerupta, Pinnularia borealis and Pinnularia divergentissima, Figure 8) indicating a shift to shallow-water conditions, most likely associated with a drier climate. The relative decrease in Fragilaria species further concurs with the pollen-based inference of warming during this period. This warming may tentatively reflect the Holocene Altithermal (Wanner et al., 2015), but this signal is very weak as warming appears to have been insufficient to encourage a considerable up-slope shift in plant communities. The beginning of the zone is marked by an Asteraceae: Poaceae ratio of >0.5, interpreted as representing weak rainfall seasonality and a strengthening of the Westerlies, but shifts to <0.5 for the remainder of the profile, indicating the re-establishment of summer rainfall (Figure 7; Norström et al., 2009). This shift is concurrent with a brief decrease in Cyperaceae and Asteraceae, a decrease in the percentage organic content, and with an increase in the percentage of sand-sized sediment particles (Figures 6, 7). Paired with a second abrupt decrease in the proportion of planktonic and facultative planktonic diatoms, this is indicative of a dry period (Figure 8). The sustained population of planktonic Aulacoseira ambiguа (Figure 8), however, suggests the continued presence of at least discrete ponds of surface water during this dry period.

MP3: ~6,610-5,700 cal. yr BP

The pollen record for Zone MP3 is characterised by an overall increase in the relative abundance of Poaceae and decrease in the percentage of Asteraceae pollen (Figure 6). The Asteraceae: Poaceae ratio suggests a shift to more exclusive summer precipitation (Norström et al., 2009), while the relative decrease in Cyperaceae indicates a progressively more arid environment. The increase in the proportional number of pollen taxa counted would suggest a continuation of warming inferred for zone MP4. The diatom record is marked by a larger proportion of epiphytic diatoms, which remain relatively constant.
Throughout the zone (Figure 7), supporting inferences for moister wetland conditions than during the previous zone (~7,520-6,680). The proportion of benthic and planktonic, relative to aerophilic, diatoms fluctuates throughout the zone (Figure 7), indicating distinct wet and dry pulses, interpreted as changes from periods in which the wetland comprises shallow standing water (at least in ponds or flarks) to a drier wetland surface. The relatively low proportion of ice-tolerant *Fragilaria* species supports the inference of even milder conditions than that represented in zone MP4. This warming period coincides with the Holocene Altithermal (Neumann et al., 2014), although due to the altitude of the site, must necessarily be inferred as a ‘milder’ event rather than an objectively ‘warm’ event. A peak in the percentage organic composition of sediments is noted for the middle of this period, with the concurrent peak in Cyperaceae pollen suggesting a discrete wet period, during an otherwise dry phase (Figures 6, 7). The period of slower sedimentation commences at ~6,000 cal. yr BP and persists to the end of this zone, with a lithology comprising dark peat and organic rich clay (Figure 3).

**MP2: ~5,600-1,100 cal. yr BP**

The period of slow sedimentation continues throughout much of this zone. The first half of zone MP2 is marked by abrupt changes in pollen, diatoms and sediment properties leading up to peaks at ~4,500 cal. yr BP. This is coincident with the first of the Holocene neoglacial events (Jerardino, 1995). The remainder of the zone comprises a more consistent period relative to MP4 and MP3, with greater stability in all three proxies. This could be due to the lower temporal frequency of sampling, which does not facilitate the detection of more short-lived climate events. However, the consistent relative abundance of both pollen and diatom communities and the stability in their PC1 sample scores suggests that overall, the conditions were indeed relatively stable.

Poaceae dominates the pollen record for this zone, which following a considerable increase leading up to ~4,500 cal. yr BP, demonstrates little change in relative abundance until ~2,000 cal. yr BP (Figure 7). This results in a Poaceae: Asteraceae ratio of >0.5 (Figure 7), indicative of a more dominant summer rainfall regime with weakened Westerlies (Norström et al., 2009). The relative abundance of Cyperaceae and Asteraceae is very low (Figure 7). Compared to the contemporary environment, this would suggest a decrease in the wetland
extent, and a re-establishment of grassland conditions. However, the presence of large proportions of *Aulacoseira ambigua* suggests that water depth must have been sufficiently deep for planktonic species to flourish (Gasse & Van Campo, 1998; Sitoe et al., 2015). The decrease in Cyperaceae and Asteraceae pollen, therefore, may be in response to colder temperatures, which may have exceeded their cold tolerance. This hypothesis is supported by the proportional increase in *Fragilaria* species relative to the preceding two zones, which would suggest climatic conditions were suitable only to the more cold water, ice and snow tolerant species (Ohlendorf et al., 2000; Wang et al., 2013). Alternately, due to the bowl shaped topography of the wetland, a substantial surface water extent of the wetland, as supported by the presence of *Aulacoseira ambigua*, may possibly have forced these terrestrial plants to less suitable areas upslope, which only grass species can tolerate. Notably, the highest relative abundance of Apiaceae in the profile is observed in this zone (Figure 7). This is most likely because this semi-aquatic species has a greater cold tolerance, as evidenced by its common presence on Marion Island (Nyakata & McGeogh, 2008). While the relative abundance of *Fragilaria pinnata/construens*, and the comparable PC1 scores, are equivalent to zone MP5, the presence of pollen suggests that conditions were not as cold as during MP5, but is consistent with a period of cooling following the Holocene Altithermal (Figures 7, 8). The zone terminates with an increase in sedimentation rate, and a short-lived peak in Poaceae pollen following the relatively consistent percentage composition for a period of ~2,500 years (Figure 7). This is concurrent with the highest relative abundance of *Aulacoseira ambigua* in the profile (Figure 8), a spike which tentatively may indicate a short-lived increase in the expanse of shallow to deep standing water, yet is inferred from a single sample, with a resultant large margin of error.

**MP1: ~1,060 cal. yr BP - Present**

The pollen indicates more rapid moisture fluctuations in the first half of this zone, and fluctuations in the hydrology of the wetland, from one with shallow ponds to drier marshy conditions. During this period, aerophilic and benthic diatom species re-emerge (Figures 7, 8), likely a result of low-water levels caused by reduced rainfall. This period is also characterised by a shift in the Asteraceae: Poaceae ratio, indicating a decrease in rainfall seasonality and an increase in the strength of the Westerlies (Norström et al., 2009). The percentage organic matter increases during this zone, which, given no prominent shifts in
pollen composition in the second half of the zone, rather suggests a change in sediment accumulation, possibly associated with more year-round rainfall distribution. At ~820 cal. yr BP, a brief peak in the Asteraceae: Poaceae ratio is reflected in the pollen record (Figure 7), suggesting a short-lived increase in the strength of the Westerlies and a greater incidence of mid-latitude cyclones reaching the central plateau of South Africa, resulting in colder temperatures and winter rainfall. This inference is supported by a concurrent short-lived peak in *Fragilaria* species (Figure 8) indicating cooler conditions which are tolerated more readily by these species which proliferate in ice and snow conditions. Evidence for this cold event is contemporaneous with the beginning of the Little Ice Age (Tyson et al., 2000). From ~750 cal. yr BP, fluctuations in the environmental proxies stabilise with relatively constant proportions of Asteraceae, and a slight change to Poaceae pollen from Cyperaceae, indicating an overall drying. A decrease in aerophilic diatoms during this time would further support these inferences for a drying trend. This period witnesses a progressive increase in the total number of pollen taxa, reaching a maxima at ~591 cal. yr BP, which may indicate a slight amelioration of temperatures following the onset of the Little Ice Age. This is supported by a very low relative abundance of *Fragilaria* species from ~750 cal. yr BP to ~150 cal. yr BP (Figure 8). At ~150 cal. yr BP, a peak occurs in the Asteraceae: Poaceae ratio (Figure 7), indicating a short-lived increase in the strength of the Westerlies and associated increased incidence of mid-latitude cyclones. This is supported by the re-emergence of *Fragilaria* diatoms, both coincident with the end of the Little Ice Age (Tyson et al., 2000).

**Regional Comparison**

The distribution of plant species represented by the pollen record for Mafadi Summit is largely consistent with the contemporary regional vegetation including the ubiquitous bogs, comprising grasslands, sedges, and small herbs and shrubs. The few incidents of *Podocarpus* pollen are wind-derived from adjacent lower altitude regions in South Africa (Van Zinderen Bakker, 1955; Neumann et al., 2014). None of the diatom taxa recorded from the Mafadi Wetland samples were endemic to Lesotho, but rather the diatom flora represented were highly cosmopolitan. Two groups of species are worth comment due to their presence in similar environments elsewhere in the world. The first are the *Fragilaria* species, which, due to their tolerance for ice and snow cover, support inferences of colder temperatures in instances where they dominate the diatom profile. These are cosmopolitan species, which
appear in a range of high stress environments, but are dominant in high alpine wetlands and lakes in a range of locations, including Uganda (Panizzo et al., 2008; McGlynn et al., 2010), Switzerland (Lotter & Bigler, 2000; Ohlendorf et al., 2000), Canada (Karst-Riddoch et al., 2005), Finland (Shala et al., 2014) and Siberia (Westover et al., 2006). The second are the pair of planktonic *Aulacoseira ambigu*a and aerophilic *Hantzschia amphioxys*, which interchange throughout profiles to indicate periods of wet and dry conditions, at sites in South Africa (Finne et al., 2009), Mozambique (Sito e et al., 2015), Australia (Gell & Little, 2007), and Canada (Hargan et al., 2015). All of the diatom species identified at Mafadi Wetland have been previously recorded in Lesotho (Schoeman, 1973) and South Africa (Harding & Taylor, 2011). Such similarities within comparable environmental settings, environmental conditions, and environmental fluctuations elsewhere in the world demonstrate the value of this proxy for environmental reconstructions, and the global similarities in species. While the pollen record is specific to the vegetation of southern Africa, the dominant Poaceae, Cyperaceae and Asteraceae are common to wetland conditions globally, with shifts between Poaceae and Cyperaceae representing a cosmopolitan indicator of shifts between dry and wet conditions (Gasse & Van Campo, 1998).

**Comparison of Regional Temperature Reconstructions.** In addition to the proxy composition, it is valuable to explore the extent to which the climate and environmental reconstruction for Mafadi Wetland is consistent with those elsewhere in southern Africa and globally. This is of particular interest given the unique high altitude alpine niche environment represented in eastern Lesotho, which provides a setting for testing palaeoenvironmental lapse rates and topographic boundaries to synoptic climate scenarios. The Mafadi Wetland record reflects two colder events, indicated by a predominance of ice-tolerant *Fragilaria* species, extending from ~8,140-7,850 cal. yr BP and ~1,000-150 cal. yr BP. A short-lived cold period driven by a large meltwater pulse in the northern Atlantic Ocean, often assumed to have influenced climates only in the Northern Hemisphere, is the ‘8.2 kyr’ event (Mayewski et al., 2004; Alley & Ágústsdóttir, 2005). The very cold conditions which characterise the commencement of the Mafadi Wetland record from ~8,140-7,850 cal. yr BP coincides with this event. Isotope records from archaeological settlements in western Lesotho provide further evidence for markedly cold conditions over the same time period (Smith et al., 2002), while phytolith
records from Braamhoek indicate an increase in C\textsubscript{3} vegetation at 8,000 cal. yr BP (Finné et al., 2010). The Makapansgat speleothem record provides evidence for a cool event at 8,500 cal. yr BP (Holmgren et al., 2003), which may be synchronous with these events due to age uncertainties (Norström et al., 2009). In addition, evidence for the ‘8.2kyr’ event has most recently been reported for the southwestern Cape (Chase et al., 2015). It would thus seem that this cold event in the northern Atlantic, formed due to meltwater pulses, is detectable in southern Africa. This further suggests that associated ocean heat transport during this early Holocene deglaciation in the Northern Hemisphere impacted climate dynamics in the Southern Hemisphere.

The overall warming period associated with deglaciation continues until ‘optimal’ conditions at the Holocene Altithermal (Wanner et al., 2015). The timing of this event is unclear, with discrepancies for much of southern Africa, but it appears broadly to span the period ~7,500-6,500 cal. yr BP (Holmgren et al., 2003; Truc et al., 2013; Neumann et al., 2014; Wanner et al., 2015). There is no clear warm signal coinciding with this event at Mafadi Wetland, although a slight increase in plant and diatom species taxa numbers, and decrease in \textit{Fragilaria} species, is observed. This may reflect temperatures at this high altitude not reaching particular temperature thresholds required for less cold-tolerant taxa to establish themselves, with upslope range-shifts being limited by the extent of warming. However, a greater increase in pollen taxa representation occurs during the late Holocene, than for the period coinciding with the Holocene Altithermal. This may indicate that the rate of altitudinal temperature decrease (lapse rates) during this period may have been stronger than today due to fluctuations in the strength of the Westerlies, which would have resulting in persistent cold conditions at high altitudes (Grab, 1997). It is notable, given this hypothesis, that there was no clear indication for Holocene Altithermal conditions at the lower-altitude Braamhoek Wetland (Norström et al., 2009, 2014; Finné et al., 2010), yet pollen records from the similarly low altitude Drakensberg site at Mahwaqa Mountain suggests a clearly defined Holocene Altithermal maximum at 6,500 cal. yr BP (Neumann et al., 2014). Unfortunately the isotope records from the archaeological shelter sites in western Lesotho do not span this period.
Considerable discussion has concerned itself with, and provided evidence for, the Little Ice Age in southern Africa (cf. Talma et al., 1974; Herbert, 1987; Talma & Vogel, 1992; Tyson & Lindesay, 1992; Holmgren et al., 2003; Sundqvist et al., 2013; Zinke et al., 2014); a short-lived cold event that occurred between AD 1300-1800 (Tyson et al., 2000; Wanner et al., 2015). A peak in *Fragilaria* species and a decrease in pollen taxa diversity may be indicative of such an abrupt cold period at ~150 cal. yr BP, with cooling from ~1,000 cal. yr BP, for Mafadi Wetland. The second climate event during the last ~1,000 years is the Medieval Warm Period, which preceded the Little Ice Age, with warmer than contemporary conditions between AD 1000-1300 (Wanner et al., 2015). The only evidence in southern Africa for a Medieval Warm Period is derived from high resolution speleothem isotope records (Tyson et al., 2000; Holmgren et al., 2003). It is therefore interesting that the relatively mild conditions are inferred from a particularly low relative abundance of *Fragilaria* species and increase in pollen taxa diversity at Mafadi Wetland during this period.

**Comparison of Regional Moisture Reconstructions.** In terms of moisture, the reconstruction for Mafadi Wetland is in broad agreement with the sedimentologically derived results for eastern Lesotho by Marker (1994, 1995, 1998). Notably, however, when comparing the moisture inferences made in this study to those from lower altitude sites at Braamhoek and Mahwaqa Mountain, delays in the onset of dry and wet periods are noted. In particular, dry conditions commence consistently earlier at Mafadi Wetland than at Mahwaqa Mountain, located to the east (Neumann et al., 2014). This most likely is due to the influence of the Great Escarpment which restricts the transfer of moist air from the Indian Ocean to the Lesotho Highlands. Under regionally drying conditions, moisture will precipitate out at Mahwaqa due to orographic uplift, with limited moisture remaining for transport into the Lesotho Highlands. By contrast, moist conditions persist longer at Mafadi Wetland than at Braamhoek Wetland, located to the north (Norström et al., 2009, 2014; Finné et al., 2010). This is most likely due to the predominant role of the Westerlies in transporting moisture from the south-western region of the country, particularly in winter (Norström et al., 2009, 2014; Mills et al., 2012). A northward shift in the extent of the Westerlies would increase the likelihood of moisture transfer to the eastern Lesotho Highlands (Mills et al., 2012). Due to the lower latitude of Braamhoek wetland, the Westerlies would have less frequently
extended sufficiently far north to ensure moisture transport to this region (Norström et al., 2009).

Debate is still ongoing with regard to the existence of an African Humid Period in southern Africa (Chase et al., 2009; Burrough & Thomas, 2013). This event spans the period 14,500-5,500 cal. yr BP, and has been detected in a range of records from western and tropical Africa (Burrough & Thomas, 2013). Evidence from hyrax middens in Namibia for humid conditions during this period have raised hypotheses of such an event extending as far as 23°S (Chase et al., 2009), yet a review of palaeoclimatic records from southern Africa, with a particular focus on dryland conditions, is not in support of this view (Burrough & Thomas, 2013). The Mafadi Wetland record broadly suggests relatively wet conditions until ~6,500 cal. yr BP. This period is, however, marked by pronounced dry events. Precipitation reconstructions for other sites in eastern Lesotho indicate more consistent marked dry periods throughout this time period (cf. Marker, 1994, 1998; Grab et al., 2005). Evidence from pollen, diatom and sediment records presented in this study is, therefore, insufficient to determine whether the prolonged wet periods inferred for eastern Lesotho during this period are coincident with, or more substantive indicators of, an African Humid Period.

Debate on the Little Ice Age event in southern Africa focuses more on precipitation during this period, with a current understanding that dry conditions occurred in the summer rainfall zone (Lee-Thorp et al., 2001; Holmgren et al., 1999; Ekblom et al., 2008; Neumann et al., 2010), but wet conditions in the winter rainfall zone (Stager et al., 2012; Weldeab et al., 2013). Results from Mafadi Wetland would support this conjecture, with colder conditions contemporaneous with an increase in planktonic and facultative planktonic species, and an Asteraceae: Poaceae ratio indicative of a return to winter rainfall conditions. This would imply that the Westerlies which dominate the winter rainfall zone were strengthened during this period, yet not sufficiently to influence the interior plateau of South Africa, and thus supports Tyson and Lindesay’s (1992) original hypothesis. For the Medieval Climate Anomaly, a period of greater stability in precipitation is noted for central southern Africa from ~2,000 cal. yr BP to present (Burrough & Thomas, 2013). The results from Mafadi Wetland, for which a high temporal resolution of samples was achieved for this period, directly contradict these results, indicating impacts from rapid high amplitude fluctuations.
in precipitation throughout the period, as supported at a global scale (Wanner et al., 2015), and more recently noted for southern Africa (Norström et al., 2014; Chase et al., 2013).

**Conclusion**

This study presents a multi-proxy palaeoenvironmental reconstruction for the highest wetland in southern Africa, located at 3390m asl. This setting induces a niche environment for highly cold-resilient plant and diatom species. The severity of this cold environment is highlighted by the absence of pollen at the commencement of the sequence at ~8,140 cal. yr BP, and dominance of cold-tolerant *Fragilaria pinnata/construens* diatoms. The emergence of pollen in the MP4-MP1 subsamples suggests up-slope succession in terrestrial vegetation from ~7,520 cal. yr BP thereafter, indicative of a shift to warmer temperatures more typical to those today.

The pollen, diatom and sediment results indicate fluctuations between dry and wet conditions throughout the mid- to late-Holocene. Notable periods of wet conditions, inferred from an increased relative abundance of semi-aquatic pollen taxa and supported by the presence of an increased surface depth required to support planktonic and facultative planktonic diatoms, are detected between ~8,140-7,580 cal. yr BP, and between ~5,600-1,100 cal. yr BP. Periods of notably dry conditions, inferred from an increase in pollen from succulents and grasses, are reconstructed for ~7,520-6,680 cal. yr BP, ~6,160-5,700 cal. yr BP, and from ~1,000 cal. yr BP to present, and led to marked declines in water balance at Mafadi, as indicated by increased abundances of aerophilic diatoms. Pronounced cold events are identified at ~8,140 cal. yr BP and ~150 cal. yr BP, coinciding with the 8.2kyr (Smith et al., 2002; Mayewski et al., 2004) and Little Ice Age (Tyson, 2000; Wanner et al., 2008) events.

The use of a multi-proxy approach, exploring changes in pollen, diatoms and sediment characteristics, facilitated the corroboration of palaeoenvironmental inferences. This is particularly important in a climatically marginal environment, for which changes may, and do, result in the occasional absence of certain proxies, and hence known unknowns. This study therefore provides a detailed palaeoenvironmental reconstruction for an under-
researched region, which is of geographical and environmental significance to the broader southern African sub-continent.

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<table>
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<tr>
<th>Laboratory ID</th>
<th>^14C Age (yr BP)</th>
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<th>2σ calibrated age range (BP)</th>
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</table>
Figure 1: Topographic map indicating the location of the Mafadi Wetland site.

144x142mm (600 x 600 DPI)
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650x487mm (180 x 180 DPI)
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389x637mm (72 x 72 DPI)
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86x35mm (300 x 300 DPI)
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352x105mm (72 x 72 DPI)
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1728x768mm (72 x 72 DPI)
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1582x861mm (72 x 72 DPI)
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2278x968mm (72 x 72 DPI)