CHAPTER 17

Modern pollen-vegetation relationships in the Drakensberg Mountains, South Africa

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ABSTRACT: Contemporary pollen rain studies are conducted to determine pollen-vegetation relationships and develop modern analogues to facilitate palaeoreconstruction from fossil pollen assemblages. In this study, a two year modern pollen sampling campaign was conducted for eleven vegetation communities across a range of altitudes in the Drakensberg Mountains, South Africa. The aim was to compare pollen assemblage composition, diversity, and influx between vegetation communities, and investigate representivity of taxa. Despite a high degree of within and between community homogeneity, characteristic pollen taxa are suggested as indicative of particular communities. We highlight over- and under-representation of certain taxa within the vegetation communities and list ‘palynologically silent’ taxa – those that appear in the vegetation but are absent from the modern pollen spectra. From the resultant modern pollen assemblages, it is not possible to distinguish the grassland types, although the possibility does exist for the forest, shrubland and wetland communities. Arboreal *Celtis* and *Podocarpus* pollen types are diagnostic for the Afrotropical forest community, and *Leucosidea sericea* for the shrubland community which it dominates. We suggest that modern pollen analogues are feasible for the non-grassland Drakensberg communities and echo the sentiments of others that modern pollen rain-vegetation dynamics are a prerequisite to accurately constrain interpretation of fossil pollen spectra.

17.1 INTRODUCTION

The modern pollen-vegetation relationship underpins vegetation reconstructions from fossil pollen data, and yet foundational studies exploring this relationship are often lacking, particularly in the tropics and subtropics. Outside of temperate zones, traditional assumptions surrounding pollen representivity of anemophilous and zoophilous taxa have been challenged, and require further investigation to understand complex bias introduced by variable pollen production and dispersal (Watrin *et al.* 2007). Detailed studies of local pollen and parent vegetation can be used to determine pollen taphonomy, and explore representivity within the pollen rain. Few such small-scale studies exist for the African tropics and subtropics (e.g. Elenga *et al.* 2000; Henga-Botsikabobe *et al.* 2020; Julier *et al.* 2018; Marchant and Taylor 2000; Schüller *et al.* 2014), thereby limiting palaeoecological inferences and attempts to model vegetation from pollen data.

Southern Africa has an established tradition of palynological research, dating back to the pioneering efforts of van Zinderen Bakker (1950, 1951). Early palynologists often incorporated a few surface pollen spectra to support fossil pollen records (e.g. Cooremans 1989; Scott 1982a, b, 1989; Scott and Cooremans 1992; Scott *et al.* 1992), however, relatively few dedicated studies, particularly those with a temporal component, exist (Hill 1995). A recent modelling synthesis of modern pollen data from southern Africa pulled together a dataset of mostly surface soil samples

from 211 sites across the subregion (Sobol *et al.* 2019), showing strong bias towards savanna ($n = 67$) and grassland ($n = 53$) relative to the other seven biomes. More detailed local studies, which employ passive pollen traps to calibrate modern-pollen vegetation relationships, include those from the Winterberg (Meadows and Meadows 1988), Nuweveldberg (Sugden and Meadows 1989), and Cederberg (Meadows and Sugden 1990; 1991a;b), all in the winter rainfall zone. In the absence of such detailed contemporary pollen studies, Meadows (1989, p. 160) commented that the reconstruction of palaeovegetation communities is ‘largely guesswork’. Recent advances in the field include modelled estimates of relevant source area of pollen and relative pollen productivity undertaken in the Kruger National Park (Duffin and Bunting 2008) and Drakensberg Mountains (Duthie *et al.*, this volume). Despite these efforts, modern pollen–vegetation relationships in the subregion ‘remain poorly resolved relative to other parts of the world’ (Meadows 2015, p. 4).

In this paper, we present the results of a highly detailed modern pollen rain survey from the KwaZulu-Natal Drakensberg, comprising data from eleven vegetation communities and corresponding surface soil samples, in addition to seasonal pollen trap data spanning a two year period. The aim is to characterise the modern pollen rain produced by each vegetation community by (i) comparing pollen spectra, diversity and influx across the different vegetation communities; and (ii) determining which taxa are under- and overrepresented in the pollen assemblage. The research was carried out in the Cathedral Peak area of the northern KwaZulu-Natal Drakensberg Mountains (29°00’S, 29°15’E; Figure 1), in South Africa’s summer rainfall zone. This mountainous environment presents the opportunity to study a range of vegetation communities within a confined region due to the altitudinal gradient, ranging from open grassland to ericaceous scrub, closed woodland and forest. The broader Maloti-Drakensberg region is recognised as having the preservation potential for late Quaternary palynological studies due to the availability of high altitude polliniferous deposits (e.g. Fitchett *et al.* 2016; 2017; Lodder *et al.* 2018; Neumann *et al.* 2014; Norström *et al.* 2009; van Zinderen Bakker 1955).

17.2 MATERIALS AND METHODS

Sampling design was based on eleven vegetation communities from three altitudinal zones (Table 1; Figure 2), *viz.* the montane (1280–1829 m asl), subalpine (1830–2865 m asl) and the alpine belts (2866–3353 m asl) (Killick 1963). Selected communities represented either (i) the dominant community within a vegetation belt; (ii) communities which follow a particular successional pathway; or (iii) communities that characterise a distinct topographic or geomorphological feature within the altitudinal vegetation belt. Killick (1963) and Hill (1996) describe the species composition and abundance within each of these vegetation communities in detail.

Vegetation surveys were undertaken within each of the communities and species present and percentage aerial cover were recorded (Table 1). The percentage aerial cover was deemed more appropriate than the more conventional basal cover (Bradshaw 1981) as aerial cover is an estimate of the dominance of a particular species within the community. As the pollen is produced from the upper aerial part of the plant it was presumed that this measure would provide a better representation of the amount of pollen produced. Percentage aerial cover was measured as the proportion of the ground occupied by perpendicular projections onto it of the aerial parts of the individuals of a species under consideration (Kershaw and Looney 1985).

Meadows (1989) advocates for the collection of surface samples, and corresponding trap data, from as many plant communities as possible. Here, modern pollen rain was sampled passively using a modified version of the Oldfield pollen trap (Flenley 1973), which is easy to construct, transport, install and recollect in an inaccessible mountainous environment. Pollen traps were randomly installed within each community at a height of 1 m above the ground. The number of pollen traps placed in each vegetation community varied between 5–18 based on the

Figure 1. (a) Location map and (b) aerial photograph of the Cathedral Peak area of the KwaZulu-Natal Drakensberg, indicating the position of vegetation communities investigated relative to important topographic features.

Table 1. Distribution of pollen and vegetation samples among the eleven vegetation communities. Pollen traps were sampled on a seasonal basis across a two-year period, hence total pollen samples exceeds individual samples per community. Alpine communities were sampled using soils, while subalpine and montane communities used pollen traps.

Vegetation community (code)	Geographical position (GPS)	Elevation (m asl)	No. pollen samples	Total pollen samples (all seasons)	No. of vegetation quadrats	Quadrat size
Alpine						
Alpine grassland (AG)	–28.98; 29.13	3000	20	20	20	1 × 1 m
Alpine wetland (AW)	–29.01; 29.18	2965	20	20	20	1 × 1 m
<i>Erica Helichrysum</i> shrubland (EH)	–29.00; 29.18	3010	20	20	20	1 × 1 m
Subalpine						
<i>Leucosidea sericea</i> shrubland (LS)	–28.99; 29.26	1895	10	63	20	10 × 10 m
<i>Microchloa altera</i> grassland (MA)	–28.95; 29.22	1810	5	32	20	1 × 1 m
Subalpine fynbos (SF)	–29.01; 29.20	2690	10	37	20	10 × 10 m
Subalpine grassland (SG)	–28.99; 29.21	1975	25	175	60	1 × 1 m
Subalpine wetland (SW)	–28.99; 29.25	1890	6	31	25	1 × 1 m
Montane						
Afrotropical forest (AF)	–28.96; 29.22	1550	18	125	20	10 × 10 m
Highland sourveld (HS)	–28.93; 29.25	1350	5	32	25	1 × 1 m
<i>Protea</i> savanna (PS)	–28.95; 29.20	1545	18	115	20	10 × 10 m
Total			159	670	270	

size and complexity of the community (Table 1). The traps have proved successful collectors of pollen rain and, in some instances, provide a better reflection of the vegetation community prevailing in the catchment area than surface soil samples (Crowder and Starling 1980; Meadows and Sugden 1991b; Sugden 1990). Twenty surface soil samples were taken randomly from each vegetation community. A sample of approximately 100 g constituting the top 3–5 cm of the soil was collected, with overlying organic matter having been first removed. Samples were placed into paper bags, sealed and refrigerated to reduce bacterial and fungal growth, until the necessary laboratory techniques could be carried out (Hicks and Hyvärinen 1986).

Fieldwork was undertaken from June 1988 to June 1990, thereby gaining a full two years of modern pollen rain data. The traps were replaced on a tri-monthly basis until November–December 1989. A seventh sample of six months duration, December 1989 to June 1990, was collected to compare a six month sample with the usual tri-monthly samples. Two full years of data were not achieved for the subalpine fynbos and subalpine wetland communities (Table 1).

Figure 2. (a) 1 × 1 m quadrat used for aerial vegetation survey; (b) passive pollen trap; (c) subalpine grassland; (d) alpine grassland; (e) *Erica Helichrysum* shrubland; (f) alpine wetland; (g) subalpine fynbos; (h) subalpine wetland; (i) *Leucosidea sericea* shrubland; (j) Afrotemperate forest; (k) *Protea* savanna; (l) highland sourveld.

Pollen was extracted from the traps and soil samples using acetolysis (Faegri and Iversen 1989). Identification was achieved using a predominantly local pollen reference collection of *c.* 700 species (Hill 1992). Absolute counts of *c.* 500 on trap samples and *c.* 1000 on soil samples were performed on pollen grains and spores (hereafter collectively termed 'pollen' for brevity). Pollen influx values were calculated based on sample volume as grains/cm²/30 days (Berglund and Ralska-Jasiewiczowa 1986). R-rel values were calculated ($R\text{-rel} = \% \text{ mean abundance in pollen rain} / \% \text{ aerial cover of vegetation}$) (Davis 1963; Gosling *et al.* 2005) for each taxon in each community to understand the representivity of pollen taxa across the landscape. The Shannon-Wiener Index was calculated for each pollen sample and each vegetation community to determine how well the pollen assemblage captured vegetation diversity. The index ranges from 0–5, with most values falling between 1.5 and 3.5, and is a comparative index with higher values indicating higher diversity (Barnes *et al.* 1998). It should be acknowledged that many pollen taxa cannot be

distinguished below the family level and thus the diversity index was calculated at the taxonomic level of the identified palynomorphs. The multivariate structure of the pollen assemblage data was represented using non-metric multidimensional scaling (nMDS) using the software PRIMER v7 (Clarke and Gorley 2015). The data were 4th root transformed to down weight the dominant species and Bray-Curtis similarity matrix calculated. Vectors of important species were based on Pearson's rank correlation. A pollen diagram showing characteristic taxa for each community was plotted using C2 (Juggins 2007).

17.3 RESULTS

From a total of *c.* 700 pollen traps deployed over the two year period, 16 were lost or damaged by animals or fire. All 36 traps deployed in the alpine belt over two attempts were stolen, thus surface soil samples were relied upon as a substitute within this vegetation belt. Pollen assemblage count size varied with an average of 1120 grains counted per soil sample in the alpine communities (ranging from 965-1272 grains per sample), and an average of 560 grains counted per trap in the subalpine and montane communities (ranging from 207-3392 grains per sample). A complete list of all pollen taxa recorded together with potential parent vegetation based on vegetation survey data is provided in supplementary information and used to infer likely parent taxa, which are indicated in parentheses (Hill 1992; Table S1).

17.3.1 Characterisation of vegetation communities by pollen assemblage

A total of 25 characteristic taxa were designated on the basis of being recorded from at least 80% of the samples from a vegetation community, and at >3% abundance in one sample or more (Table S1). Asteraceae, Cyperaceae, Poaceae and Pteridophyta are ubiquitous and characteristic across all altitudinal zones and vegetation communities, and are therefore deemed to be of limited value as diagnostic taxa.

For pollen trap data, relative abundance data are averaged across the seven time intervals due to a focus on spatial rather than temporal assemblage variability. Spatial variability in the pollen assemblage, both between and within vegetation communities, is depicted according to relative abundance of characteristic taxa, pollen influx, and assemblage diversity (Figure 3a-c). Influx values are indicated for all subalpine and montane belt communities together with relative abundance data for each trap (Figure 3b-c). It is worth noting that while some vegetation communities were represented by a high number of samples (up to 25 traps or 20 soil samples), the *M. altera* grassland and highland sourveld contained only five traps each, which may contribute towards their apparent homogeneity.

17.3.1.1 Alpine belt

The alpine vegetation communities display a relatively high degree of homogeneity within each community, and all three are distinctive for the presence of bryophyte spores which are absent from other altitudinal zones (Figure 3a). Within the alpine grassland the diversity index ranged from 1.2–1.5 with an average of 1.4 (Figure 4), and the most abundant taxa are Poaceae and Cyperaceae. Similar to the alpine grassland, the alpine wetland is dominated by Poaceae and Cyperaceae. The consistent presence of Umbelliferae (Apiaceae) in the pollen assemblage distinguishes the alpine wetland from other communities across the altitudinal range. The alpine wetland diversity ranged from 1.6–2.2 with an average of 1.9 (Figure 4). Distinctive taxa within the *Erica Helichrysum* shrubland include Ericaceae and Thymelaeaceae. Diversity ranged from 1.1 to 1.9, with an average of 1.6 (Figure 4).

17.3.1.2 Subalpine belt

Aside from the subalpine fynbos, the other subalpine communities are relatively homogenous within individual communities.

Leucosidea sericea shrubland – *L. sericea* shrubland is distinctive for dominant *L. sericea* pollen (30–60%), and the presence of Ericaceae. Diversity ranged from 1.2–2, with an average of 1.7. Influx rates varied from 65 to 275 grains/cm²/month, with an average of 107 grains/cm²/month (Figure 3b).

Microchloa altera grassland – The *M. altera* pollen assemblage is fairly uniform, with the main distinction being the low presence of extra-local forest taxa *Celtis* (<5%) and *Podocarpus* (<5%), due to the close proximity of this community to the edge of an Afrotropical forest patch (<300 m). In the *M. altera* grassland, diversity varied from 2–2.1 with an average of 2.1 (Figure 4). Influx rates varied from 104 to 239 grains/cm²/month, with an average of 145 grains/cm²/month.

Subalpine fynbos – In the subalpine zone, the subalpine fynbos community displays a high degree of heterogeneity across the community, largely centred around variations in three taxa, viz. Ericaceae, Proteaceae and Scrophulariaceae (Figure 3b). In the subalpine fynbos, diversity ranged from 1.8–2.5 (average 2.3) (Figure 4). Influx rates varied from 101 to 269 grains/cm²/month, with an average of 172 grains/cm²/month.

Subalpine grassland – The subalpine grassland and *M. altera* grassland communities are similar, with the exception of forest taxa presence in the latter. In the subalpine grassland, pollen assemblage diversity ranged from 1.6 to 1.8, with an average of 1.7 (Figure 4). Influx rates varied from 118 to 409 grains/cm²/month, with an average of 199 grains/cm²/month (Figure 3b).

Subalpine wetland – As with subalpine grassland communities, the subalpine wetland pollen assemblage is Poaceae–Asteraceae dominated, and includes relatively high Cyperaceae (10–15%) and Pteridophyta (10–20%) frequencies. Diversity ranged from 1.8–2.1 (average 1.9) (Figure 4). Influx rates varied from 140 to 274 grains/cm²/month, with an average of 198 grains/cm²/month.

17.3.1.3 Montane belt

Afrotropical forest – In the montane belt, there is a high degree of heterogeneity across the Afrotropical forest community, particularly in the relative dominance of *Podocarpus* (5–40%) and *Celtis* (5–40%) (Figure 3c). This community displays a relatively strong arboreal pollen assemblage, muting the ubiquitous Asteraceae/Poaceae signal evident in other communities. The Afrotropical forest diversity varied from 1.8–2.5 (average 2.1) (Figure 4). Pollen influx was highly variable, ranging from 111 to 493 grains/cm²/month, with an average of 264 grains/cm²/month (Figure 3c).

Protea savanna – The *Protea* savanna is distinctive for its high level of Proteaceae pollen (15–50%). Pollen assemblage diversity varied from 1.7 to 2 with an average of 1.9 (Figure 4). Influx rates varied from 68 to 275 grains/cm²/month, with an average of 129 grains/cm²/month.

Highland sourveld – The highland sourveld is similar to the subalpine grassland community, with no distinctive characteristic taxa evident from the modern pollen data. In the highland sourveld, diversity varied between 1.5–1.6, with an average of 1.5 (Figure 4). Pollen influx varied from 94 to 185 grains/cm²/month (average 127 grains/cm²/month) (Figure 3c).

17.3.2 Representivity of the pollen assemblage

Where characteristic pollen taxa are recorded together with the corresponding parent vegetation type in the surrounding community, the relative frequencies of pollen and vegetation can be directly compared to provide an indication of the degree of correspondence between pollen rain and parent vegetation composition (Figure S1). The R-rel value can be used as an indicator of representivity, with values <1 indicating underrepresentation and values >1 indicating overrepresentation (Figure 5). Furthermore, we can plot pollen abundance against vegetation

(a) Alpine vegetation belt

(b) Subalpine vegetation belt

(c) Montane vegetation belt

Figure 3. Pollen diagram showing pollen assemblages with samples grouped by vegetation community in the (a) alpine belt; (b) subalpine belt; and (c) montane belt, along with total influx values for each trap. For the three alpine vegetation communities, pollen data are derived from surface soil samples rather than traps.

Figure 4. Boxplot showing diversity (Shannon-Wiener Index) of the pollen assemblages across each vegetation community. Communities are ranked according to species level diversity of the plots (triangle symbols), in order of decreasing diversity. For alpine grassland, alpine wetland, and *Erica Helichrysium* shrubland, pollen data are derived from surface soil samples rather than traps.

abundance using a R-rel reference line of 1 as a guide to over- and underrepresentation (Figure S2). Results show that for many taxa the representivity of the pollen type varies between vegetation communities.

In both the alpine and subalpine wetland communities, Cyperaceae is notably underrepresented, with a R-rel of 0.2–0.4 (Figure 5), whilst Poaceae is overrepresented. Some dominant taxa, such as Poaceae, are highly variable in their degree of representivity between communities (Figure S2). In general, Asteraceae appear to be overrepresented with the exception of the *Erica Helichrysium* shrubland where they are notably underrepresented (R-rel = 0.2) (Figure 5, S2). Based on high R-rel values exceeding 2 (Figure 5), Scrophulariaceae pollen appears to be highly overrepresented in all vegetation communities where it is recorded, with the exception of the *L. sericea* shrubland and subalpine wetland (Figure 5). Similarly, Crassulaceae are overrepresented in the alpine wetland and *Erica Helichrysium* communities (Figure 5).

Ericaceae pollen appears to be fairly representative of the vegetation cover in the subalpine fynbos and *L. sericea* shrubland, with a R-rel of 1.1–1.2 (Figure 5). However, in the *Erica Helichrysium* shrubland Ericaceae pollen is overrepresented with a R-rel of 1.7 (Figures 5, S2). *L. sericea* pollen abundance mirrors that of the parent vegetation in the *L. sericea* shrubland community, with a R-rel of c. 1.1 (Figures 5, S2).

When comparing aerial vegetation cover of *Celtis* with the pollen assemblage in the Afrotemperate forest, *Celtis* pollen is found to be overrepresented with a R-rel value of 1.7 (Figures 5, S2). *Podocarpus* pollen is underrepresented relative to the vegetation cover in the Afrotemperate forest, with a R-rel of 0.4 (Figures 5, S2). In the *Protea* savanna, Proteaceae pollen is underrepresented relative to the surrounding vegetation, with a R-rel of 0.6 (Figures 5, S2).

In the alpine grassland, Brassicaceae (*Heliothila*) pollen was absent, despite the parent taxon was recorded in the surrounding vegetation. These ‘palynologically silent’ taxa are

Figure 5. Bar chart showing R-rel (representivity) values of taxa represented in both pollen and vegetation. Asterisks indicate that the R-rel values were too high to show on the figure; For the alpine wetland Crassulaceae = 4.05, Poaceae = 3.35; for *Erica Helichrysium* Crassulaceae = 3.35; For Highland sourveld Asteraceae = 3.32; For *M. altera* grassland Hypoxidaceae = 5.06, Asteraceae = 4.43, Fabaceae = 3.52, for *Protea* savanna Scrophulariaceae = 3.60; for subalpine grassland Scrophulariaceae = 5.78, Asteraceae = 3.07; for subalpine wetland Asteraceae = 8.09, Poaceae = 3.99. For alpine grassland, alpine wetland, and *Erica Helichrysium* belt, pollen data are derived from surface soil samples rather than traps.

unrepresented in the pollen assemblage. For the *Erica Helichrysium* shrubland, this included Santalaceae (*Thesium*). In the alpine wetland community, all recorded vegetation types were represented in the pollen spectra, at least at family level. Afrotemperate forest appears to have the largest number of ‘silent taxa’, including *Ilex mitis*, Gesneriaceae (*Streptocarpus*), *Impatiens*, Apiaceae (*Conium*, *Sanicula*) and Vitaceae (*Rhoicissus*). In the *L. sericea* shrubland, such taxa included Sterculiaceae (*Hermannia*), Apiaceae (*Allipedia*), Malvaceae (*Hibiscus*), and Melianthaceae (*Melanthus*). Orchidaceae (*Disa*) pollen was absent from the *M. altera* grassland despite being recorded in the vegetation plots. In the subalpine fynbos, *Gunnera perpensa*, Melianthaceae (*Melanthus*), *Olea* and Primulaceae (*Lysimachia*) were absent from the pollen spectra, however, were recorded in the surrounding vegetation. Apiaceae (*Allepidea*) pollen was similarly absent from the subalpine grassland. Illecebracaceae (*Silene*) pollen was palynologically silent in both the subalpine grassland and wetland communities. Finally, Valerianaceae (*Valeriana*) pollen was recorded from the highland sourveld community but absent from the pollen spectra. In the *Protea* savanna, all plant taxa present were recorded in the pollen traps.

17.3.3 Multivariate analysis

The nMDS ordination plot depicts the distribution of the samples relative to vegetation community groupings (Figure 6). The ordination shows discrete clustering of samples within vegetation

Figure 6. Non-metric multidimensional scaling (nMDS) plot of pollen assemblage data, grouped by vegetation community.

communities, with Afrotemperate forest and *Erica Helichrysum* shrubland being the most distinctive. Overall, the alpine communities are clearly distinct from the other vegetation belts, illustrating the importance of altitude. The alpine grassland and alpine wetland communities cluster fairly closely together, albeit with no direct overlap. The *L. sericea* shrubland and sub-alpine fynbos show some degree of overlap. Subalpine grassland, subalpine wetland, subalpine fynbos, highland sourveld and *Protea* savanna cluster fairly closely together, but with very limited direct overlap of ordination space.

17.4 DISCUSSION

17.4.1 Modern pollen-vegetation relationships

The results provide an indication of the relative uniformity of each vegetation community. Furthermore, they allow us to assess whether these vegetation communities can be qualitatively distinguished by their modern pollen assemblages. Here we evaluate whether there is a distinctive pollen signal or are distinctive ‘indicator’ taxa that can be used to differentiate each community.

Overall, we find that the grassland vegetation communities are relatively difficult to be separated by their pollen assemblage, which can be attributed to the limited taxonomic resolution achievable in identifying grass pollen types (i.e. family level). This is supported by the diversity data, which show that the grassland pollen assemblages consistently underrepresent the diversity of their parent vegetation, when compared with other communities. One exception to this is the alpine grassland community, which the nMDS picks out as a separate cluster from other grassland types.

The alpine vegetation communities were easily distinguished from communities in other vegetation belts using nMDS. A combination of bryophytes and Crassulaceae (likely from the common *Crassula setulosa* or possibly the less common *Crassula natans*) in the pollen assemblage appears to be relatively characteristic of the alpine communities, in particular within the alpine wetland. The alpine wetland community was rather similar to the alpine grassland, with the only differences being a higher frequencies of bryophytes and Juncaceae (*Juncus* or *Lezula*), and the presence of Umbelliferae in the alpine wetland. Umbelliferae pollen appears to be restricted in its presence to the alpine wetland community, and therefore serves as a useful indicator taxon. van Zinderen Bakker (1955) recorded Umbelliferae frequencies of 2–8% in four wetland surface samples in Lesotho.

Scott (1982b) associates the Umbelliferae with damp conditions, however its source at Cathedral Peak is unknown as no members of the Umbelliferae family were recorded in the vegetation. Similar to the situation in the alpine belt, the subalpine wetland and subalpine grassland communities showed a high degree of overlap, with differences being higher Cyperaceae and Pteridophyta in the former, and higher Scrophulariaceae (*Selago*, *Zaluzianskya*, *Diascia*, *Manulea*, *Nemesia*, *Hebenstretia*, *Sopubia*, *Sutera*) and Ericaceae (*Erica* spp.) in the latter.

The *Erica Helichrysum* shrubland is distinctive in the pollen diagram and the nMDS for consistent, and sometimes relatively high, frequencies of Thymelaeaceae (*Passerina montana* or *Gnidia polystachya*), and dominated by high representation of Ericaceae, occasionally exceeding 80% abundance. In contrast, subalpine fynbos is dominated by a mix of Proteaceae (*Protea subvestita*), Ericaceae (*Erica* spp.) and Poaceae, with Rosaceae (*Cliffortia* or *Alchemilla*) and Scrophulariaceae (*Bowkeria* or *Halleria*) consistently recorded.

The *L. sericea* shrubland has a distinctive pollen signature, with pollen of the shrub *L. sericea* dominating the assemblage (40–60%), and relatively low Poaceae and Asteraceae frequencies compared with other communities. In the nMDS, however, this community showed a slight overlap with the subalpine fynbos community. Ericaceae is prominent in *L. sericea* shrubland, as are the Pteridophyta.

The Afrotemperate forest has a highly unique pollen signature, clearly observed in the nMDS, with relatively high arboreal pollen frequencies including *Celtis* (10–45%) and *Podocarpus* (10–40%). Sapindaceae pollen, probably from the tree *Allophylus melanocarpus*, is a good indicator for this community. The *Protea* savanna community can be distinguished by high Proteaceae pollen frequencies (20–50%). Although subalpine fynbos records high Proteaceae, the *Protea* savanna assemblage can be separated by a lack of Ericaceae pollen, and the two are clearly separated in the nMDS.

The above comparison highlights the challenges of pollen analytical research in a grass dominated environment, and the need for additional supporting proxies such as grass phytoliths to detect palaeovegetation change (e.g. Alexandre *et al.* 1997). With the potential for C₃/C₄ grass species migration with climate change along a clear altitudinal gradient (e.g. Roberts *et al.* 2013) it could be of some value to attempt to quantitatively distinguish C₃ from C₄ vegetation. Despite these challenges, the nMDS was able to clearly separate almost all vegetation communities sampled, with limited overlap between samples from different communities.

Those communities with a significant tree component i.e. Afrotemperate forest, *Protea* savanna and *L. sericea* shrubland, are more easily distinguished by their pollen assemblage. The *Erica Helichrysum* shrubland and subalpine fynbos, could be distinguished by their dominant fynbos elements, although the latter overlapped with *L. sericea* in the nMDS. The two wetland communities displayed a strong degree of overlap with the surrounding grassland vegetation, but with some distinctive taxa. The presence of less abundant but nevertheless useful aquatic and ‘damp habitat’ indicators (*sensu* Scott 1982b) such as Dipsacaceae (*Scabiosa drakensbergensis*) and Gunneraceae (*Gunnera perpensa*) may assist in distinguishing wetland pollen communities. In the subalpine wetland community, Cyperaceae and Pteridophyta were the only

pollen taxa to record higher abundances than in the surrounding subalpine grassland community. The reality is that fossil pollen preserving archives in these summer rainfall mountain environments tend to be restricted to wetland sediments (e.g. Fitchett *et al.* 2016 2017, Lodder *et al.* 2018, Neumann *et al.* 2014, Norström *et al.* 2009), thus the fossil pollen signal is usually overrepresented by local wetland taxa, usually excluded from the pollen sum. In the Cathedral Peak area, wetlands representing potential fossil pollen archives are present across a range of altitudes (e.g. Finch *et al.* 2021; Lodder *et al.* 2018), from the montane to sub-alpine to alpine (e.g., this study), although the depth and organic content of these sites is variable.

17.4.2 Representivity of taxa

The modern pollen-vegetation comparison allows for some general recommendations regarding interpretation of key taxa based on their relative representivity in the pollen assemblage. These are compared with existing information in the available literature.

Podocarpus – *Podocarpus* pollen is an important arboreal pollen type in southern African pollen records, and also constitutes an key component of Afromontane vegetation in across Sub-Saharan Africa (Gajewski *et al.* 2002; Verlhac *et al.* 2018; Vincens *et al.* 2006). Previous studies designate *Podocarpus* as a very well dispersed anemophilous pollen type (Hamilton 1972), that tends to be overrepresented within the pollen signal (Marchant and Taylor 2000; Schüller *et al.* 2014). In terms of dispersal, a West African biome-scale study (Verlhac *et al.* 2018) found *Podocarpus* pollen distribution to be similar to that of the parent plant, and identified this taxon as a good indicator of modern vegetation. Coetzee (1967) developed a guideline for interpreting *Podocarpus* pollen frequencies with 10–20% indicating close proximity of the parent vegetation, and frequencies exceeding 20% indicative of local presence of *Podocarpus* forest. Schüller *et al.* (2014) commented that such overrepresented taxa are ‘probably significantly less important components of the surrounding vegetation than indicated by the modern pollen-rain’ (Schüller *et al.* 2014, p. 710). In the Cathedral Peak area, *Podocarpus* pollen is likely derived predominantly from *Podocarpus latifolius*, and to a lesser degree from *Afrocarpus* (formerly *Podocarpus*) *falcatus* and *Podocarpus henkelii* (Killick 1963). Interestingly, our data suggest that *Podocarpus* pollen is underrepresented relative to the vegetation cover in the Afrotropical forest community (R-rel = 0.4), and indeed, with the exception of the *M. altera* grassland, *Podocarpus* pollen does not appear to be represented outside of the forest community. This is surprising given the prevalence of small *Podocarpus* forest patches which form a mosaic within the grassland community (Adie *et al.* 2017; Figure 1b)). The underrepresentation of *Podocarpus* within the forest community could be explained by (i) high pollen production by other taxa e.g. *Celtis*; and/or (ii) the size and complexity of the Afromontane forest community, which appears to be characterised by a heterogeneous pollen signal, with *Celtis* dominant in some areas and *Podocarpus* in others. Averaging *Podocarpus* abundance for both the pollen traps and the parent vegetation across such a heterogeneous community may explain these anomalous results.

Celtis – as with *Podocarpus*, *Celtis* pollen is restricted to the Afrotropical forest community, with the exception of the nearby *M. altera* community (<300 m upward of the forest boundary). Within the forest community, *Celtis* pollen is overrepresented (R-rel = 1.7), aligning with previous studies (e.g. Marchant and Taylor 2000), with *Celtis* being a very well dispersed taxon (Hamilton 1972; Verlhac *et al.* 2018). Previous studies found *Celtis* to be abundant pollen producers, present outside of the parent vegetation distribution (Watrin *et al.* 2007). Interestingly, studies from east and west Africa (e.g., Livingstone 1967; Verlhac *et al.* 2018) have shown *Celtis* to be characteristic of lower altitudes than *Podocarpus*, which is not the case in southern Africa.

Ilex mitis – it was found to be ‘palynologically silent’ in the Afrotropical forest community. As a highly distinctive pollen type, this is unlikely to have been missed during analysis. Hamilton (1972) commented that *I. mitis* has low to poor pollen dispersal capacity, while Marchant and

Taylor (2000) concluded that *Ilex mitis* pollen was representative of the density of the parent vegetation.

Cyperaceae – A surprising outcome of this study is that Cyperaceae pollen was found to be underrepresented in both wetland communities, with frequencies consistently below 20%. Cyperaceae pollen often dominates fossil pollen spectra due to the local nature of the taxon. Scott (1982b) and van Zinderen Bakker (1955) found Cyperaceae to be a dominant pollen taxon in modern surface samples, with high frequencies recorded. Lodder *et al.* (2018) investigated a 5000-yr sediment core retrieved from the subalpine wetland community at Cathedral Peak (Catchment VI), and recorded Cyperaceae abundance of 40–90% in the fossil assemblages, yet in the current study the modern pollen abundance for the same site remained <20% for the two year sampling period. The apparent underrepresentation of Cyperaceae pollen in the current study might be attributed to pollen trap height (1 m from the ground), above the parent vegetation, whereas the other modern sampling campaigns used surface samples. This inference is supported by relatively higher representation of Cyperaceae pollen in surface soil samples as compared with traps in the subalpine wetland (17% vs. 9%) (Hill 1992). In a comparison of surface and trap data from the Winterberg, Meadows and Meadows (1988) also found that sedges were more well represented in the surface samples than in the traps, which may be attributed to trap height. Irrespective of differences in apparent representivity between studies, Cyperaceae are ubiquitous across a range of habitat types and climate zones (e.g. Gajewski *et al.* 2002), and have limited applicability as a palaeoenvironmental indicator.

Ericaceae – The representivity of Ericaceae pollen varied from representative in the sub-alpine fynbos (R-rel = 1.1) and *L. sericea* (R-rel = 1.2) communities to overrepresented in the *Erica Helichrysum* shrubland (R-rel = 1.7). Marchant and Taylor (2000) and Schüler *et al.* (2014) designated Ericaceae pollen as overrepresented, although the dispersal characteristics of the pollen taxon are debated, ranging from poorly dispersed (due to large grain size; Verlhac *et al.* 2018), to moderately dispersed (Hamilton 1972), and well dispersed (Schüler *et al.* 2014). Dispersal is one facet of pollen representivity, but so too is pollen production, and to a lesser degree in modern samples, preservation.

Poaceae – The results indicate a wide degree of variability in the representivity of Poaceae pollen between different communities, with few obvious patterns apparent. The two wetland communities showed a high degree of overrepresentation of Poaceae pollen relative to vegetation cover. In the closed vegetation communities, Poaceae pollen varied from representative in the Afrotropical forest (R-rel = 1.0) to underrepresented in the *L. sericea* shrubland (R-rel = 0.7) and *Protea* savanna (R-rel = 0.6). Within open ecosystems and grassland communities, the degree of Poaceae representivity was highly variable. Previous studies have designated Poaceae pollen as a generally well dispersed taxon linked to its anemophilous pollination syndrome (Hamilton 1972), consequently often overrepresented within the pollen signal.

17.5 CONCLUSIONS

The original palynologists' dream was to develop a 'signature' modern pollen assemblage for each distinct vegetation community within the three recorded vegetation belts, *viz.* montane, subalpine and alpine, in the KwaZulu-Natal Drakensberg. With this achieved, the aim was to correlate, or cross-reference, dated fossil pollen spectra against these modern analogues to infer past vegetation communities, which could then be extended to interpret palaeoenvironments. As with any palaeoreconstruction proxy, the outcome is less straightforward and open to interpretation.

We identified eleven vegetation communities across the three altitudinal belts, undertook a vegetation survey, deployed pollen traps and/or collected surface soil samples. Modern pollen sampling was conducted over two years and influx values were calculated. Overall, a high degree of homogeneity exists both within and between communities with regards to modern pollen,

although characteristic taxa could be identified for certain communities. Dominant pollen taxa were often over- or underrepresented in comparison with the surrounding vegetation composition and abundance, taking cognisance of the taxonomic resolution. We note and justify these characteristic taxa and suggest reasons why they could prove useful as signature taxa during fossil pollen interpretation. Perhaps unsurprisingly, there appears to be little variation across the various grassland communities, greater opportunity exists to recognise the forest and shrubland types, and to distinguish the communities from different altitudinal vegetation belts, e.g. alpine communities.

The Drakensberg is a region with a high palynological potential, however it is imperative that any palaeoreconstruction be based on a sound understanding of the modern pollen processes. Therefore, contemporary pollen rain-vegetation relationships and modern analogues should be considered and refined. Thus, in conjunction with other palaeoecological proxies and dating methods, one is able to build a clearer picture of past environments in a mountainous region which has a high biodiversity and displays clear altitudinal and latitudinal gradients, imperative to improving our understanding of the past environments in southern Africa.

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