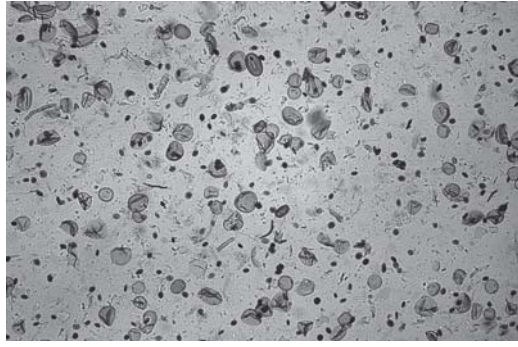Figure 6. Photomicrograph of a pollen slide made up from a takahē sign sample (X00/17/3; Upper Plateau Bog) showing dominance of single-pore grass pollen (taken under ×200 magnification).

Zone 2 (20–10 cm)—pine pollen horizon

Although *Nothofagus menziesii* and *Fuscospora* still dominate, there is a marked decline in *Nothofagus menziesii* pollen. At the same time, *Aristotelia*, *Coprosma*, and monolete fern spores (mostly *Blechnum* spp.) increase. The first trace of exotic Pinaceae pollen occurs in this zone.

Zone 3 (10–0 cm)

Nothofagus menziesii regains its former high levels, dominating the pollen sum. *Fuscospora* pollen declines towards the surface, as does *Aristotelia*, *Coprosma, Poaceae* (particularly small *Poa* type), Cyperaceae and monolete fern spores (*Blechnum* spp.). There is a notable increase of *Polystichum vestitum* spores and exotic pine pollen. *Histiopteris* and *Hymenophyllum* spores and Pinaceae pollen are more consistently present in this zone although at low abundances.

5.3.2 X00/4 Top of track up to the Lake Eyles hut

Zone 1 (47–15 cm)

Dominated by *Nothofagus menziesii* and *Fuscospora,* with *Celmisia* type, *Raoulia* type, *Coprosma, Bulbinella,* and Poaceae. Cyperaceae consists mostly of the *Eleocharis* type and some *Carex* type. At 30 cm, there is a marked decline in *Nothofagus menziesii* and *Fuscospora,* with a corresponding temporary decline in *Cyperaceae* and *Celmisia* type, and an increase in *Bulbinella* sp.

Zone 2 (15–0 cm) pine pollen horizon

Nothofagus menziesii dominates; *Celmisia* type is not recorded in this zone; *Coprosma,* Poaceae (particularly larger *Chionochloa* type) and *Myrsine* decline towards the surface. At the base of zone 2, there is a shift in the Cyperaceae pollen, from *Eleocharis* and *Carex* types to *Uncinia* type, although the latter eventually declines towards the surface. Pinaceae pollen is consistently recorded in this zone only.
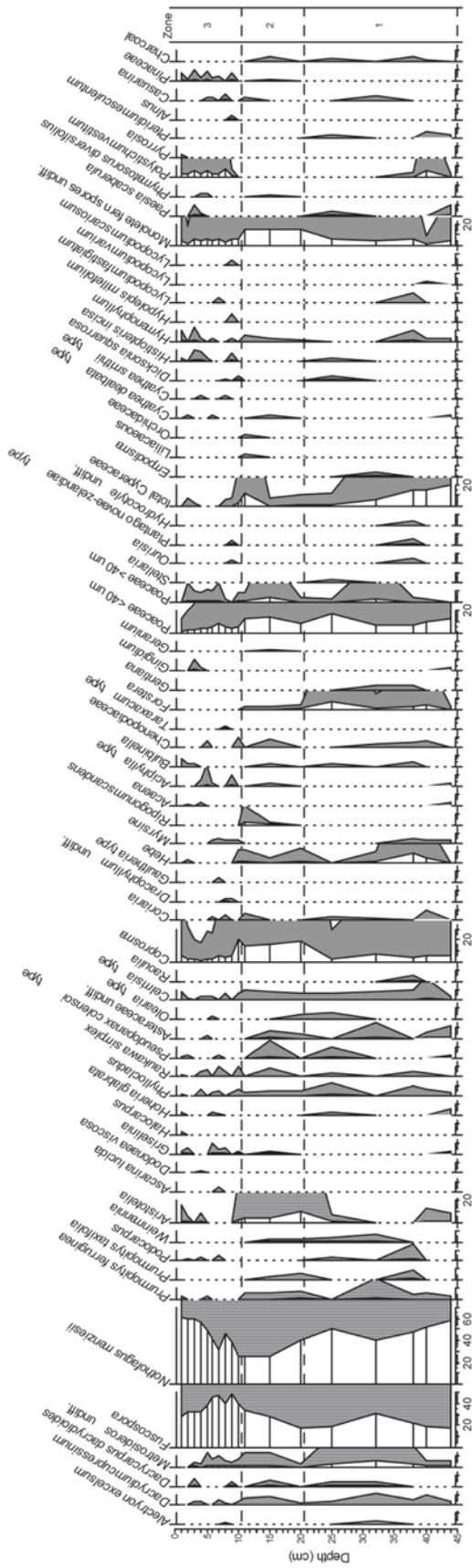
Figure 7.   Percentage pollen diagram for core X00/2 from Eyles Upper Plateau Bog, forest margin. Shaded curves represent ×10 exaggeration to highlight low values.
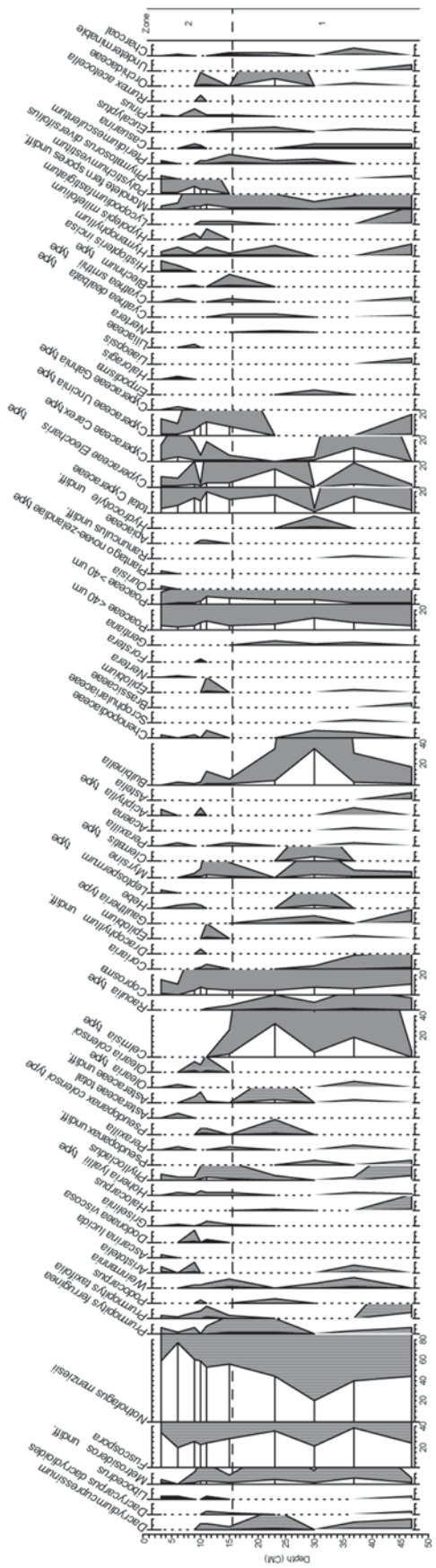
Figure 8.   Percentage pollen diagram for core X00/4 from top of Lake Eyles track below hut. Shaded curves represent ×10 exaggeration to highlight low values.

6. Conclusions

6.1 SURFACE POLLEN

It is evident from the surface pollen samples (Fig. 4) that the wind-dispersed *Fuscospora* pollen is highly over-represented, i.e. there is more pollen present in the sample than there are parent plants in the local vicinity. This is particularly evident from the samples above the tree line, which all show levels up to c. 40% of the pollen sum. In sites where *Nothofagus menziesii* was the dominant canopy tree, *Fuscospora* levels are lower than in exposed sites above the tree line, but still over-represented. *Nothofagus menziesii* is generally well-represented; where the tree dominates at a site, this is reflected in the high pollen levels. Most of other pollen types tend to be under-represented, including Poaceae (both small and large grains), Cyperaceae, fern spores etc., mostly because they are overwhelmed by large amounts of wind-dispersed pollen from the dominant canopy trees. However, even though mostly under-represented, often severely, most of the main species present in the vegetation are at least recorded as present in the pollen samples.

6.2 SIGN OF THE TAKAHĒ

Of the seven takahē sign samples, four contained sufficient pollen to make a representative pollen count. Three Chester Burn samples were virtually totally dominated by grass pollen. If it is assumed that fresh feeding sign represents recent local usage (Mills & Mark 1977), then this extraordinarily high percentage of grass pollen in the samples (which is unusual compared with surface moss samples normally collected for modern pollen studies), suggests whole flower heads were being eaten by the takahē. In addition, with the separation of grass pollen types, consistently more *Poa* type than *Chionochloa* type are represented. In contrast, the Ettrick Burn sample was almost entirely dominated by the ferns *Hypolepis millefolium* and *Polystichum vestitum* with some *Uncinia* spp. suggesting some part of these ferns and sedges must have been eaten. The two other winter takahē sign samples, although virtually devoid of pollen, did contain what looked like fern tissue under microscopic examination, as well as black rhizomatous fibres, which were visible to the naked eye. Although only based on a few opportunistically collected samples, the pollen and spore results from the takahē sign concur broadly with known observations of takahē diet (Mills & Mark 1977; Maxwell 2001), i.e. that in summer the takahē feed on grasses, and in winter on *Hypolepis millefolium.* However, I am not aware that *Polystichum vestitum* has been mentioned in the literature as a possible diet item for takahē, but the equally high number of spores from this fern in the Ettrick Burn sample may indicate takahē were utilising it in the same way as they do *Hypolepis millefolium*. The fern spores were all in remarkably good condition suggesting they are from relatively fresh material, not from old decaying spores that have been preserved in the soil for many years and inadvertently been ingested while grubbing other species among this fern.

6.3   FOSSIL POLLEN PROFILES

6.3.1   Pre-pine pollen horizon forest composition

In most pollen diagrams from the dry eastern parts of New Zealand, the sudden increase in abundance of *Pteridium esculentum* spores in conjunction with charcoal particles provides a distinct chronological marker for c. 1350 AD when vast areas of forest were burnt by early Māori settlers (McGlone & Wilmshurst 1999). In the Chester Burn cores, the *Pteridium esculentum* spore curve is not particularly clear, and reflects the remote situation and high rainfall of the Fiordland region, which spared it from being burnt. The trace levels of *Pteridium esculentum* in the Chester Burn pollen profiles may merely reflect this fern occurring as a seral element in clearings rather than any long-distance signal of deforestation in drier or lowland areas. An estimate can be made that the bottom of the cores are no older than 2000 years old, as regional pollen records from near Te Anau show *Fuscospora* beeches did not spread into Fiordland until after this time (Wilmshurst et al. 2002). However, to refine the chronology of the pollen records, several samples of peat from both cores need to be radiocarbon dated. Until dates are available, the following interpretation of the changes occurring in the forest structure before the European period remains provisional.

In the X00/2 pollen profile from Upper Plateau Bog, below the pine pollen horizon there is a distinct period of disturbance where pollen from the dominant canopy tree *Nothofagus menziesii* declines, indicating a more open canopy. At the same time there is a corresponding increase in seral taxa including *Aristotelia* (probably *A. serrata*), *Coprosma* spp., and ground ferns (mostly *Blechnum* spp.). As there are numerous possible causes for such disturbance (for example wind throw, snow damage, earthquake, insect attack, natural senescence) and few causal clues, no conclusion about what initiated the disturbance can be drawn. Nor can an estimate of its duration be made without better chronological control. However, before European settlement at least, the forest composition was dynamic, and any change in relatively short term (30 years) data from permanent vegetation plots (for example Burrows et al. 1999) should be considered within this context. In the X00/4 pollen profile, which is close to the tree line, there is also evidence of increased canopy openness at 30-cm depth, by increases in *Bulbinella, Clematis, Myrsine* and *Hebe*. As all these changes occur before any presence of pine pollen, it is assumed the changes are not related to deer browsing.

In both pollen profiles, some taxa are consistently more abundant in the pre-pine horizon zones, for example, all grasses, but particularly the smaller type which includes *Poa* spp., and *Microlaena avenacea* (a forest grass), sedges (including *Carex, Uncinia, Eleocharis* type), *Celmisia* and *Coprosma*. There are more sedges than grasses in the tree line core X00/4 and vice versa with the Upper Plateau Bog core X00/2, which may reflect differences with altitude of these two sites.

6.3.2   Post-pine pollen horizon and deer-browsing effects

The presence of Pinaceae pollen in most New Zealand pollen diagrams provides one of the earliest chronological markers for the onset of European settlement (e.g. see Wilmshurst 1997). Various species of pine were planted in New Zealand from the 1860s onwards (Adams 1915), with numerous plantations

established in the 1950s (closest plantations to the Murchison Mountains are on the Takitimu Range and Blackmount Hill areas). Pine pollen is produced in abundance, is transported long distances by wind, and is readily incorporated into soils and peat deposits on the landscape. This is highlighted by the pine pollen recorded in all the surface samples collected from the Chester Burn, despite the remote situation and prevailing westerly winds. Pine pollen is also recorded at relatively low levels in the Chester Burn fossil profiles in the upper zones, providing a useful temporal guide to interpreting changing vegetation composition. However, given the similarly low levels of Pinaceae pollen in both surface and upper fossil samples, the beginning of the pine curve is interpreted to denote post-1950s rather than representing scattered pine trees from the latter part of the 19th Century.

There are some distinct changes that coincide with the presence of pine pollen in the fossil profiles, and if we assume this is approximately taken to represent the 1950s, then these changes also coincide with peak deer numbers in the Murchison Mountains (Mills & Mark 1977) and may have been initiated by deer browsing. Of particular relevance to known takahē diet, compared with the zones below the pine horizon, are the following:

- In the tree-line core X00/4, there is a sharp decline in the abundance of *Celmisia*, all grasses (but particularly the larger grained *Chionochloa* type), and all sedges (although *Uncinia* type initially shows an increase). Many of the ferns become more abundant particularly *Histiopteris incisa, Hypolepis millefolium* and *Polystichum vestitum*, although the latter two species decline towards the surface. The pollen data from this tree-line core shows significant change over the last 50 years, which contrasts with the conclusions drawn from analyses of permanent-plot remeasurements (Burrows et al. 1999) that high altitude mountain/silver beech forests have not changed much in the last c. 30 years.

- In the Upper Plateau Bog core X00/2, there is a marked decline in the abundance of grass (mostly the small-grained *Poa* spp. and *Microlaena* spp.), sedges and *Celmisia*, whereas there are increases in *Histiopteris incisa* and *Polystichum vestitum*. *Hypolepis millefolium* spores are not common in this core. Although *Polystichum vestitum* is known to be browsed by deer (Wardle et al. 1971; Stewart et al. 1987) it may be browse resistant and able to withstand cropping because of starch storage protected in underground rhizomes. The remarkable increased abundance of this fern over the last 50 years may reflect its expansion into niches vacated by other deer-browsed dicot taxa.

Some taxa known to have been browsed by deer in Fiordland forests (e.g. Wardle et al. 1971; Stewart et al. 1987) also show periods of declining abundance in the pine horizon of both pollen records: e.g. *Coprosma* spp., *Griselinia littoralis, Pseudopanax colensoi* var. *fiordensis*, *Weinmannia racemosa* and *Aristotelia serrata* in addition to grasses. However, the abundances and possibly resolution are too low to reflect any detailed chronological analysis of browsing pressure. In a broader sense though, some increased abundances of relatively less browsed taxa seen in the pollen records, such as the ground ferns and *Uncinia*, may be reflecting a release from interspecific competition caused by the selective removal of more palatable taxa by deer (Allen et al. 1984; Mark & Baylis 1975). Many exclosure studies have shown *Uncinia* spp. to increase in forests where more palatable species

have been browsed out by deer, e.g. in the Murchison Mountains (Burrows et al. 1999); Urewera National Park (Allen et al. 1984); Aorangi Range, Wairarapa (Wardle 1967).

6.4 DEER IMPACTS, TAKAHĒ DIET, AND PALYNOLOGY

The rediscovery of the takahē in 1948 coincided with the time when invading deer were reaching peak numbers in the Murchison Mountains. Therefore, there are no detailed observations of the takahē diet before deer were present in the area, particularly within the forested habitats that are used during harsh winters. Since the takahē's rediscovery, observations on their dietary habits have identified that during the winter within the forests they rely on grasses, sedges and the starchy rhizomes of *Hypolepis millefolium*, particularly when deep snow has smothered their preferred alpine habitats (Mills & Mark 1977). Although Burrows et al. (1999) identified a trend of increasing abundance of *H. millefolium* on permanent plots in the Murchison Mountains over the last 30 years, the two pollen records in this study show that this fern has only spread relatively recently in the forests, and may have been stimulated directly or indirectly by selective deer browsing. This longer term perspective from the pollen records shows that takahē diet may have been quite different to dietary observations made since its rediscovery. Takahē may therefore be adapting their diet to suit a changing understorey composition induced since deer browsing. The decline in grasses and sedges may indicate that takahē relied more heavily on these and other plants such as *Celmisia* spp. before deer invaded the catchment.

High-resolution pollen analysis has highlighted the need to consider forest dynamics and the ecology of the takahē in a longer term perspective than short-term ecological observations can provide. The pollen data have shown not only that the forest has experienced some major perturbations in the canopy cover some time in the past, and changes likely to be induced by deer browsing, but has also thrown new light on perceptions of takahē diet. Beauchamp & Worthy (1988) already showed from widespread subfossil evidence that before takahē were reduced to their present relict population in Fiordland, these birds occupied lowland forests throughout New Zealand and were certainly not restricted to alpine habitats. They also imply that takahē could have fed on a wider, or different, range of food, and were more adaptable in their food habits than the present Fiordland population. Clout & Craig (1995) remark that takahē translocated to island habitats are capable of rapidly adapting to new foods; it would appear from the pollen records that this is probably what the birds have been doing in Fiordland in the last 50 years as the forest understorey has been modified by deer browsing. Using the recently abundant *H. millefolium* may be one of these adaptations, in the absence or declining abundance of other favoured ground ferns or bush grasses in the forest understorey. Perhaps a period of hunting pressure by Māori within the more easily accessible parts of the forests, the decline or extinction of natural avian predators, and the deer-induced loss of monocots in the forest understorey has modified takahē behaviour over time, and forced the birds into the monocot-rich alpine areas?

7. Suggestions of future beneficial work

High-resolution pollen analyses of the remaining cores collected from the Chester Burn (Table 1) would help to reveal the regional nature of (a) pre-1950s forest disturbance and (b) changes induced by deer browsing. The remaining cores are from different habitats to the forested ones analysed in this study. One of the remaining three cores is from a wetland surrounding a tarn above the tree line, and two are from large *Sphagnum* wetlands below the tree line dominated by grasses and sedges. These sites are common in the Murchison Mountains and provide large areas of potential winter feeding grounds for takahē. Fresh takahē sign was found on the Upper and Lower Plateau Bogs indicating they were also used in the summer. Pollen analysis of these cores would show if these habitats have also been modified by deer browsing in the past. Ample fresh deer sign was found at least on one of these wetlands at Heart Shaped Lake indicating they are used by deer as well as takahē.

Radiocarbon dating of the vegetation changes shown in the pollen profiles would provide a reliable chronological context and allow enhanced interpretation. For example, if the deposits are less than 900 years old, then the period of vegetation change before deer browsing could be considered in the absence of browsing pressures from moa and other extinct native birds. Scanning Electron Microscopy of the fossil grass pollen and comparison with fresh pollen samples would help determine which species of grass were formerly more abundant in the past (N.T. Moar, pers. comm.). Light microscopy alone is insufficient to provide such detailed information, but if vegetation restoration plans are to be considered, e.g. planting bush grasses in the forest, this may be of great importance and interest. Further observations could be made of takahē winter feeding behaviour to assess what other plant species takahē may be foraging for. Further work on faecal samples may provide useful complementary information about takahē diet and may be less invasive and time consuming than tracking birds.

8. Acknowledgements

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