A palaeoecological investigation of long-term stand-scale ecological dynamics in semi-open native pine woods:

Contributing to conservation management in east Glen Affric

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Submitted for the degree of Doctor of Philosophy

December 2006

Statement of Originality

I hereby confirm that this research was carried out by the undersigned and that all research material has been duly referenced and cited.

Helen Shaw December 2006

Acknowledgements

As with all PhDs, this thesis would not have been possible without support. Forest Research and the University of Stirling funded this research project, via a project developed and supervised by Dr Richard Tipping with Dr Patrick Osborne and Dr Jonathan Humphrey. The Inverness Field Club provided an additional bursary to help towards the fieldwork costs of the modern pollen study. I am grateful for this and for the interest that they showed in my work. NERC funded 15 radiocarbon dates for use across my peat cores. I am grateful to Dr Charlotte Bryant at the NERC RCL for providing the dates. Alex Will, Helen MacGregor, Jo McKenzie, Sue Bowen, Phil Sansum and Richard Tipping helped with fieldwork. Althea Davies provided support and tips on laboratory preparation, help and advice in developing my skills in identifying pollen grains, and especially, company during long hours at the microscope. Andrew Tyler and Stuart Bradley carried out the ^{210}Pb detection on my samples. Bill Jamieson and Jo McKenzie helped with cartography. Kate Howie gave some statistical support. John MacArthur assisted with computer software. Dr Philip Wookey and Dr Andrew Tyler provided support during the latter stages of writing up this thesis. Many thanks go to all of the above people for help, guidance and useful discussions. Thanks should also go to my current employers, The International Centre for the Uplands-Cumbria; work has been a huge distraction to the writing up process, but they have also been supportive of me.

Much of the recent development in the subject of pollen-vegetation relationships has been achieved via researchers working together in networks and programmes. The NorFA (Nordic Council of Advanced Studies) sponsored POLLANDCAL network (www.geog.ucl.ac.uk/ecrc/pollandcal) co-ordinated by M.-J. Gaillard (University of Kalmar, Sweden) has, since 2001, provided a forum for collaboration and sharing between researchers and research students from many countries and academic institutions. The modern pollen study presented as part of this thesis, contributes to, and has benefited greatly from, the work and support of the members of the POLLANDCAL network. Special thanks go to Shinya Sugita (University of Minnesota, USA) for developing the models that form the basic research approach of the network and to Jane Bunting and Dick Middleton for translating these models into an easily useable software package (the HUMPOL suite of programs). I am grateful to all in the network; their generous support, fruitful discussions, and words of encouragement have meant a great deal to me in the otherwise lonely path through this research. I am especially grateful to Marie-José Gaillard for welcoming me as a late-comer into the network and to Jane Bunting for support and advice.

I am grateful to friends, especially to Sandra Pratt and Jo McKenzie for long hours on the telephone discussing pollen, PhDs, writers block and life in general, to Michael Grant and Jo McKenzie for reading and commenting on some of my chapters, to Sue Bowen, Hannah Bishop, Shona Webster and Danny Paterson for company, friendship and laughs in the office.

Most of all my heartfelt thanks to Alex Will, for unfailing support, for changing jobs and moving house so that I could study for the PhD, for braving the midges and for providing muscle and company on many fieldwork trips, for cooking, and plying me with cups of tea whilst writing up, for believing in me when things got tough, and just generally being fantastic – Thank you!

Abstract

This thesis investigates past structure and dynamics of native Caledonian pine woodland, representing part of the western fringes of the northern European boreal woodlands. The biogeographical extent and Holocene history of the Scottish pine woods are well studied, yet questions remain at finer scales. This thesis is concerned with two factors over the recent Holocene oceanic period; (i) the long-term ecology *within* the woods; the spatio-temporal dynamics, the canopy structure, and community composition and continuity; and (ii) the former extent of the woods, especially the temporal pattern of the inferred easterly contraction in woodland over recent history. The importance of these factors - to ecologists, challenged with understanding the theories of equilibrium and non-equilibrium processes in long-lived woodland communities - and to conservation managers - challenged, by policy directives, with implementing the restoration and expansion of native woodlands - is discussed.

Equally the identification and quantification of ecological detail over ecologically relevant temporal and spatial scales is an important challenge for palaeoecology.

The thesis therefore applies fine spatial resolution pollen analyses over a network of sites, within, and at the western edge of, the extant woodland zone in east Glen Affric. Correlation between these individual site histories develops a detailed view of the grain and extent of woodland within the landscape, previously missing from western pine woods.

Careful attention is paid to the interpretive potential and limitations of fine resolution palaeoecology; especially with regard (i) to techniques that can identify and spatially quantify stand-scale structure and community composition via reference to modern analogues; and (ii) to defining chronologies and elucidating rates and patterns of temporal change. The opportunities and limitations of the technique are explored and discussed, to ensure an understanding of the rigour and potential of the palaeoecological contribution to ecological research and to provide an evidence base for conservation.

The application of ^{210}Pb dating using the CRS and CIC models is explored. The CRS model is confirmed as suitable for peat deposits, but its use may mask fluctuations in peat sedimentation rate, which may be illustrated by the CIC model. The value of multiple ^{14}C assays for each core and a need for a new approach to chronologies for application to fine-scale palaeecological studies is discussed.

The relevant source area around the small basins in this semi-open pinewood is tentatively confirmed at 20 m from the pollen source. Tentative pollen productivity estimates for five key taxa in this ecosystem are presented.

The temporal stability of native woodland in Glen Affric is confirmed to the eastern part of the extant woodland zone; but challenged to the west, where the open and semi-open landscape has a long history. Woodland diversity decreased over the last *c.* 200 years, and past woodland also shows a greater ground flora diversity. The western extent of the Caledonian woodland in this landscape may have changed little in the last *c.* 4000 years.

Fluctuations, some clearly cyclical, in heath, and in woodland, communities are identified in the pollen record. The former may be aligned to changes in grazing regime or climatic shifts; and the latter to autochthonous shifts important in the maintenance of suitable edaphic conditions for the continuity of woodland. Former woodland is confirmed as likely to have been open in structure and mixed in tree species composition. The results presented here suggest that some caution should be applied to use of the term Caledonian, or native ‘pine’ forest: ‘Caledonian forest’ may better reflect the heterogeneity of past forests, particularly the importance, and persistence, of birch.

The implications for conservation management and restoration are discussed. It may be difficult to establish a sustainable woodland to the west of the extant stands, and any pine woodland here may need to be mixed with stands of broadleaved trees to maintain or restore soil structure and ecological function. The landscape to the west may have been open for several thousands of years, and consideration of this is required when managing for the future to prevent loss of biodiversity.

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1 Introduction and background to the research

1.1 Introduction and layout of thesis

Much attention has been paid to the past structure and spatio-temporal dynamics of European lowland woodland (e.g. Kirby 2003; Birks 2005; Evans *et al*. 2006; Mitchell 2005), after a challenge to our understanding of them by Vera (2000). Similarly the past structure and dynamics of European boreal and upland woodland is subject to discussion (Kuuluvainen 2002), and forest structure of the extreme west oceanic boreal *Pinus sylvestris* woodland in Scotland is largely untested (Bennett 1995). With claims that, under oceanic climate conditions, forest may not be the natural climax (Fenton 1997; Fenton 2001) and challenges to climax theory itself well established in the ecological literature (e.g. Botkin 1990), there is a need to investigate the dynamics and structure of the Scottish pine woods in greater detail.

Palaeoecology has been a fundamental tool in setting the scene for woodland ecology by providing information on ranges and dominance of tree taxa in the past; especially at the large scale of the biome or ecosystem. However, palaeoecological investigations can be designed to interpret finer scale ecological patterns and events (e.g. Segerstrom *et al.* 1994), and should be fundamental as an evidence base for achieving conservation aims via restoration and landscape ecology (e.g. Barber 1993; Walker 1983; Davis 1994; Birks 1996; Huntley 1996; Delcourt and Delcourt 1998; Tipping *et al.* 1999). Although calls for an interlinkage between ecology and palaeoecology are not new, palaeoecology has struggled to be widely accepted and deployed for this purpose. Advances in palaeoecology, linked with a new political impetus to improve the ecological evidence base for biodiversity conservation (see below), provide a renewed opportunity to embed palaeoecology into ecological thinking, and into the decision-making process of nature conservation.

The overarching aim of this thesis is therefore **to use palaeoecology to investigate the long-term stand-scale structure and dynamics of an upland boreal forest on the western edge of its European range; and, to identify the relevance of this information to conservation management.**

This thesis focuses on the extant native pine forest in east Glen Affric. The area is designated as a National Nature Reserve, recognised for containing one of the most *"remarkable relicts"* of native *Pinus sylvestris* left in Scotland (Salwan 1998), and proclaimed as an "*epitome of beauty*" (Weild 2001). The pine forest in this area has survived the late-Holocene pine decline (Froyd 2001), and more recent human driven impacts; whereas the area to the west of the Glen has not. The woodlands are currently managed with the aim of restoration and expansion, and the development of natural processes. Understanding the finer scale dynamics of this relict woodland, and the factors influencing its current extent, composition, structure and function may be key to achieving sustainable woodland into the future.

This introductory review chapter sets the scene by presenting a general summary of the gaps in ecological and conservation knowledge and related research questions resulting from deficiencies in the availability and/or resolution of data on temporal dynamics (Section 1.2). This is followed by a brief review of the contributions of palaeoecology to the ecological debate, together with a critique of the problems and the potential for overcoming these (Section 1.3), leading to a rationale for the thesis and the development of general aims in Section 1.4.

Chapter 2 summarises information on the ecology, status, and Holocene history of native pine woods (Section 2.1) and of Glen Affric (Section 2.2). Specific aims of the thesis, drawn from the examination of the history and ecological management assumptions of the case study area are then defined in section 2.3.

Chapter 3 discusses research design and introduces the sites used in the study. The research design highlights the need for close attention to temporal and spatial quantification of data. The testing of these aspects formed a major part of the research.

The following three chapters then present three aspects of the research contributing to the analyses:

Chapter 4 presents the chronological study, which defines the temporal grain and extent of the analysis.

Chapter 5 presents the research addressing modern pollen-vegetation relationships and the pollen source area for the woodlands of Glen Affric, which defines the spatial grain and extent possible in the analysis of palaeoecological data.

Chapter 6 presents the palaeoecological analysis and the historical vegetation reconstruction in the landscape in east Glen Affric.

Chapter 7 then discusses the study as a whole and draws conclusions from the study, examines the detail in which the study has managed to address issues of landscape history and dynamic vegetation structure, and draws conclusions for management planning, for further use of pollen analysis and for future developments of pollen analysis as a tool.

1.2 Research needs requiring a temporal perspective

Since 1992 international, European and UK legislation has existed to protect individual species, biodiversity, specific valued natural habitats and natural resources in a wide range of protected areas and via a range of management interventions (Anon 1992; Anon 1995; DOE October 1994; Hearn 1997). Obligations for biodiversity conservation were recently strengthened by an agreed commitment to reduce significantly the rate of biodiversity loss by 2010 (COP 2002). In the UK this has highlighted the need for, and driven a commitment to, a better evidence base upon which to plan for biodiversity management (Defra 2003).

Fundamental gaps in the ecological evidence base upon which nature conservation legislation and management interventions are designed are now well documented (e.g. BRWG 2001; Lake 2001; O'Connell and Yallop 2002; Defra 2003; Sutherland *et al.* 2006; Gaston *et al*. 2006). These limit our confidence in the outcomes of management practice (Pullin *et al*. 2004). Several of the identified gaps generate research questions that explicitly or implicitly require ecological information over long temporal scales to aid future management planning. Some examples of key research needs *requiring a temporal perspective*, as identified by a range of authors from academic and policy backgrounds, are presented in Table 1.1.

The knowledge gaps and questions in Table 1.1 fall into four main categories, these are to some extent nested and hierarchical in the levels of ecological knowledge that they address. All are relevant to the fourth, nature conservation category, particularly to landscape-scale ecology and to the creation or restoration of native woodland via concepts of rewilding[1], which shapes the long-term plan for the management of Glen Affric (see http://www.treesforlife.org.uk/tfl.contents2.html).

These data gaps and questions form a call for the clarification of many fundamental assumptions. The issues are expanded below in relation to ecological theory and the special case of woodland conservation and rewilding principles. The need for long-term ecological research to examine these questions is highlighted.

1.2.1 Ecosystem stability versus ecosystem dynamics

The climax community concept (Clements 1936), or equilibrium paradigm, has long been debated by ecologists (e.g. Gleason 1927; May 1977; Botkin 1990). Despite this, most conservation policy relies on theories of stability (Ingerson, 2002; Wallington *et al*. 2005). Within Europe the principal legislative directive is to restore land to a state termed *favourable condition*, which in EU legislation is measured by an increasing or stable (desirable) population or habitat (Gaston *et al*. 2006). A corollary of this is that any move away from this condition must be seen as failure of conservation management. For this reason the concept of favourable condition has recently been challenged as an unrealistic or unhelpful concept within nature conservation (Perry 2002; Adams 2003) as the concept cannot respond to theories of non-equilibrium dynamics. Non-equilibrium ecology (e.g. Levin 1999) recognises that ecosystems, communities and species may naturally shift, spatially and temporally, due to changes in climate, climate variability, or other impacts, thus creating non-linear shifts in community structure and composition (e.g. Webb 1981).

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[1] Rewilding is a concept that is much used and poorly defined (e.g. Kirby *et al* 2006). I have taken the meaning of rewilding as the reinstatement of natural ecological dynamics and processes over a landscape scale (*sensu* Taylor 2004). Natural processes being those predominated by drivers such as climate change and fluctuation, autochthonous ecological processes and stochastic processes with little manipulation by humans.

Table 1.1: Examples of research questions relevant to conservation and requiring a temporal perspective. Notes in italics are direct quotes and non-italics are slightly paraphrased

Question or Gap	Date and source
Non-equilibrium ecology: dynamics and function	
Defining and measuring agents of change	(BRWG 2001) p10
Landscape ecology, habitat fragmentation and land use change Visions for biodiversity and landscape, analysis of viable options Species ecology at landscape scales	(BRWG 2001) p10
What are the thresholds for biodiversity	(BRAG 2006)
“Research to understand underlying mechanisms and processes of change.”	(BRAG 2006)
“How should we manage landscape mosaics for the conservation of diverse taxa operating on different spatial scales?”	(Sutherland *et al*. 2006)
“Research should attend to all levels of ecological organization and to multiple spatio-temporal scales”	(Wallington *et al*. 2005)
“Management of environmental change requires knowledge of ecological processes and species’ functional response to change.”	(Wallington *et al*. 2005)
“Not much contemporary ecological research seems to be targeted at understanding natural system dynamics at the scales at which they function and are encountered by a manager,”	(Baskerville 1997)
Determining what is a fully functioning ecosystem	(BRAG 2006)
What effect does biodiversity loss have on ecosystem functionality and at different scales within the ecosystem?	(BRAG 2006)
Concepts and scales of naturalness and ecological thresholds	
“What are the lag times between habitat fragmentation and the loss of species of different taxonomic and functional groups?”	(Sutherland *et al*. 2006)
“Temporal scale: diversity-stability relationships.” Long-term studies of natural and anthropogenic change in ecosystems >10years are needed	(BRAG 2006)
“Do the ecological systems, communities and species that are the focus of conservation effort occur with sufficient size, with appropriately functioning ecological processes, and with sufficiently natural composition structure and function to persist over the long term?”	(Parrish *et al*. 2003)
Structure of habitats	
“What overall number, age structure and spatial distribution of trees are necessary for the long term survival of dependant species?”	(Sutherland *et al*. 2006)
Conservation management and rewilding	
“How can we best measure favourable conservation status for each of the species and habitats in the EU Habitats Directive?”	(Sutherland *et al*. 2006)
What are the ecological consequences of wilding (using natural processes) as a long-term conservation strategy?	(Sutherland *et al*. 2006)
“Inadequate knowledge, much of it of a very fundamental nature, has been and remains a major problem in resource management. This is further exacerbated by managers' unwillingness to accept and incorporate major new knowledge when it does emerge from scientific efforts. We simply do not know nearly as much about forest ecosystems as we, and especially foresters, thought that we did. And resource managers are not happy when new knowledge challenges fundamental assumptions, threatens on-going programs, and runs counter to professional values”	(Franklin 1997)

Thus, over time and space, change can be expected rather than stasis (Wallington *et al*. 2005) and there is a consequent need to understand the triggers, thresholds and dynamics of change in order to manage for conservation. Conservation areas need to be large enough to encompass a mosaic of patches (Franklin 1993) in order to sustain species within their range and ecological capabilities, as shifts in ranges outwith reserve boundaries may lead to extinctions (Huntley and Webb 1988). Maintaining small static ecosystems in favourable condition for species on the edge of their range is probably not the best use of management resources (Tilman 1994).

Despite claims from an American perspective, that policy and reserve management is not closely linked with ecological science (Baskerville 1997), landscape scale conservation and landscape ecology has developed in recognition of, and response to, this shift in ecological thinking, encompassing the need to incorporate ecosystem shifts into management of the natural environment (Poiani *et al*. 2000). In the UK, this is especially so for upland areas, where a decrease in the traditional pressures upon resources, and a corresponding shift towards the use of landscape for recreation has allowed the expansion of nature reserves and a search for new direction in landscape management.

At present, however, plans for the future of these larger reserves may still be based firmly around an assumption of restoring a stable ecosystem. Patch dynamics can be incorporated into a favourable condition model via prescription of spatio-temporal cyclical shifts in vegetation between two states - for example, the model of woodland and open parkland suggested by Vera (2000) - thus maintaining favourable condition at the landscape scale.

The arguments over equilibrium and non-equilibrium dynamics in ecology (above) may not *per se* cause a problem with setting such targets. An assumption of some form of quasi-stability (over, for example, the feasible *c*. 100 year planning scale of most woodland management) may still be realistic. As is often the case in scientific discussion, some entrenchment on either side can be seen (Wallington *et al*. 2005; Ingerson 2002). Wallington - who provides a thorough and up-to-date review of the subject - argues for a balanced approach;

and notes from Pickett (1992) that "*a landscape may be in compositional equilibrium even though individual patches may be in a variety of states, and individual patches change state through time*". Thus, the new paradigm can accommodate a stable end-point as a special state of a mosaic of communities in equilibrium at the landscape scale.

Development of Biodiversity Action Plan (BAP) and Habitat Action Plan (HAP) targets at the landscape scale currently tends to set a target for expansion of favoured communities, thus aiming to shift the balance of patches in the landscape mosaic towards a particularly valued community; for example *Pinus* woodland in the Scottish boreal zone. However, many of the current prescriptions are based upon assumption, using recent vegetation description to define ecological dynamics, and using ecological modelling and regional pollen analysis to define potential expansion. There is currently little tested spatio-temporal ecological knowledge at scales relevant to conservation managers (Baskerville 1997), and as Baskerville observes: *"system state, system structure, and system function have become thoroughly confused with what an element of a local system looks like now"*. Without a fuller understanding of the likely shifts of patches around the landscape, it is difficult to make accurate prescriptions of favourable condition. Any decline in the favoured community's extent may be seen as failure when it may be a quite natural fluctuation, or as a natural fluctuation, when in fact it has crossed an ecological threshold which confers loss of resilience and beyond which it ceases to function.

1.2.2 Concepts of naturalness as drivers of nature conservation in woodlands

Despite the growing acceptance of the non-equilibrium model within ecology, there is still a general acceptance of equilibrium ecology inherent within nature conservation policy. This has led to two main approaches to nature conservation interventions: either (i) the deliberate halting of ecological progression by constant controlled cultural disturbance (as, for instance, in the continued prescriptive management of extensive agricultural landscapes): or, (ii) the removal of management, in an assumption of allowing progression towards a stable climax ecosystem; the "natural" trajectory assumed under the equilibrium model.

Concepts of naturalness, which form key criteria in the determination of conservation potential, are thus primary criteria for most native woodland conservation[2] (Margules and Usher 1981). Traditionally, palaeoecology has supported this perception of native woodland as the natural climax. Interpretations at the broad regional scale are of the post-glacial development of woodland ecosystems throughout the UK. Palaeoecological syntheses have demonstrated that different arboreal taxa developed dominance in geographical zones, based on climatic or edaphic factors. These syntheses have produced maps showing potential woodland communities for climatic and edaphic zones (Birks *et al*. 1975; Birks 1977; Bennett 1989; Tipping 1994) prior to human impact, with loss of climax community woodland over much of the UK due to human land uses including forestry, culturally-controlled grazing and farming development since the Neolithic (Birks 1989).

The evidence, from pollen analysis, for a heavily-wooded past is further supported by present day ecological manipulations; which normally demonstrate that tree species regenerate in response to grazing suppression in a landscape. This supports the scenario that, when freed from human interference, native woodland is the natural climax community.

However, this supposed confirmation of the equilibrium model - that of succession to climax woodland as supported by grazing experiments and by regional pollen data - is challenged by the non-equilibrium model. In this non-equilibrium model "*what was considered a highly predictable, universal process is actually highly contingent on history and context*" (Cook 1998), therefore, it is consistent to argue that observations of early rapid regeneration can be considered a response to a system that has been held in a homogenous state by over-grazing to the extent that much of the original heterogeneity is lost. When such a landscape is freed, wholesale, from that scale of disturbance the recovery appears uni-directional. The non-equilibrium model suggests that in a naturally functioning ecosystem, heterogeneity would have been greater and the outcomes of manipulation of any one area may have been a more varied mosaic (e.g. Vera 2000).

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[2] with the exception of culturally-maintained coppiced woodland

Although definitions of ‘ancient’ within woodland surveys only imply a continuance of woodland since the historical period of AD 1600 (Peterken 1981) and AD 1750 for Scotland (Smout 2000), there is a pervading presumption (see for example Balfour 1977), that these ancient woodlands are linked intrinsically to the wildwood of the past (*sensu* Rackham 1976; Rose 2002). Where this has been tested in finer scale palaeoecological detail the results are often surprising and reveal episodes of clearance or manipulation that could have substantially altered the woodland structure and function (e.g. Mitchell 2001; Mitchell and Cole 1998; Segerstrom 1997; Segerstrom and Bradshaw 1994).

This point is important, as existing woodland areas defined by modern ecological description may express very different species composition from the original wildwood; as Ratcliffe (1984) states “*the culminating effect of a human population of 54 million on an island measuring only 230,000km^2 has been to leave very little truly natural vegetation*”. Many woodlands, even those classified as ancient and semi-natural (Peterken 1981; Peterken 1996; See section 2.1.3.1 for a more detailed description of these terms), have almost certainly been manipulated and managed intensively over many centuries. These same altered, and possibly degraded, woodlands are now used to measure and classify community composition and thereby to create prescriptive objectives of favourable condition for restoration planning. Thus, ecosystem planners are using a concept of stability as an end point, yet measuring the success of achieving that end point against a description of vegetation from potentially, and in most cases certainly, degraded woodland communities.

There is therefore an inherent weakness in using present day ecological survey information; the communities described and used as a benchmark for assessment of favourable condition for natural woodland are changed, not natural, and in most cases almost certainly degraded. This matters because community composition may confer resilience or sustainable function to ecosystems. Community composition can control edaphic (e.g. Crawford 2000) or other environmental factors and create micro-climates or micro-niches. Loss of diversity or changes in community composition may cause little change at first, but this may be followed by rapid shifts in structure, function and biodiversity as ecological thresholds (May 1977) are crossed. Understanding trajectories of change over long temporal scales is therefore extremely important to prevent wastage of conservation effort.

The non-equilibrium paradigm may at first seem to render the future of ecosystems impossible to predict, therefore removing the need for a focus on past community composition, naturalness and diversity. This has lead to claims (reviewed in Swetnam *et al*. 1999) that since change is predicted to be chaotic and *unpredictable* the past is of little importance to understanding and managing future ecosystems, especially as landscapes are now so altered by human impact. However, to some extent the 'jury is still out' regarding details of the non-equilibrium model. The acceptance of *quasi-stable* states is possible within the 'new paradigm' (Wallington *et al*. 2005). This should render some predictive capabilities of management possible, given a fuller understanding of the spatio-temporal aspects of ecosystem dynamics and process and community composition called for in Table 1.1. The adoption of a more detailed historical perspective is however, far more likely to provide a true understanding of the nature and context of *change*, to highlight degraded states and resilient states and to help to support and develop an understanding of functional integrity or resilience conferred by community diversity. It can therefore be argued that the historical perspective to understanding naturalness in community composition and diversity is still vitally important, but has far more resonance with an understanding of the *process* and dynamics of change than the reinstatement of an ecological community from a specific era (Willis *et al*. 2005). This is important to rewilding principles discussed below.

1.2.3 Restoring and recreating forests and woodlands by rewilding principles

Despite the ecological divergence from climax theory, and the understanding of process, the concept of rewilding has become a fashionable option for areas such as Scotland where opportunities exist for large-scale forest regeneration[3] (Akroyd 2004; Taylor 2004; Taylor 2005). Rewilding is an emotive cultural activity that involves the collaborative working of many

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[3] Mainly due to socio-economic factors and past land abandonment, which leave vast tracts of Highland Scotland open to new land uses.

experts, non-experts and amateur botanists (e.g. The Carrifran Wildwood group http://www.carrifran.org.uk/), and despite the acknowledgement of process within the concept, to the majority of representatives within all of these groups rewilding means trees; the reinstatement of the wildwood and the development of a self-sustaining woodland ecosystem.

However a recent hypothesis in lowland environments throughout Europe (Vera 2000) has suggested a *naturally* more open structure for woodlands. This challenges, not for the first time (Rose and Harding 1986), the concept of an original dense wildwood. In Vera's view, an open structure to woodland is natural, resulting from community cyclicity between woodland and grassland due to disturbance under completely natural grazing regimes. Similarly, in Scottish upland environments, suggestions of naturally open landscapes exist (e.g. Breeze 1992; Crawford, 2000; and see Chapter 2). Bennett (1995) identifies that, although we can be assured of the *presence* of pine woodland in the earlier Holocene, our understanding of the detailed structure of this woodland is limited based upon present pollen analysis. In addition, the concept of an open blanket bog climatic climax has been proffered (Fenton 1997), with woodland envisaged as being more patchy and existing only on free-draining slopes and drier outcrops.

Achieving the correct density of woodland could be vital to any long-term landscape management for biodiversity conservation. Many ground flora species associated with woodlands are deemed to be ancient woodland indicator species, assuming that they indicate a longevity of woodland at the site. Yet the ecological needs of these species in terms of continuity of forest cover may be misunderstood. For example, the valued bryophytes and lichens may have survived for centuries in semi-open woodland and be incapable of surviving in a shadier closed-canopy situation (Rose 2002; Rose and Harding 1986). Our understanding of the temporal habitat requirements of these important groups as indicators of a long history of woodland cover has been challenged by evidence from fine scale pollen analysis (e.g. Segerstrom 1997).

Since modern-day landscapes are degraded they may make poor measures for biodiversity objectives. The short life-span of humans and of scientific monitoring projects renders it impossible to understand the full life-cycle of woodlands without recourse to history. The overarching question for conservation management is encompassed in the quote from Parrish *et al.* (Parrish *et al*. 2003) in Table 1.1: "*Do the ecological systems, communities and species that are the focus of conservation effort occur with sufficient size, with appropriately functioning ecological processes, and with sufficiently natural composition structure and function to persist over the long term?*". To fully understand the long-term we must study these ecological relationships and interactions over the long-term, rather than using a space-for-time analogy on far from natural landscapes.

1.3 Investigating woodland ecology over long time periods

Woodland ecology over long time periods can be investigated via ecological modelling, written histories, or palaeoecology.

Ecological modelling is being applied widely to woodland planning (e.g. Bell 2003; Hope 2003; Hope *et al*. 2006; Humphrey 2003). However, parameters used in the models are based on modern ecological observation and therefore require temporal validation (Hope 2003; Hope *et al*. 2006).

Archival analyses, where these are available, can be utilised to explore factors such as past human impact, and to describe past vegetation. The accuracy and quantity of the documents and maps used in historical analyses decrease rapidly with increasing time from the present. Data soon become patchy and qualitative. Historical analyses become extremely limited beyond the 400 year timeframe (hence the selection of woodland continuity since AD 1600 as a criterion for ancient woodland (Peterken 1996)). A combination of present day vegetation description and historical analysis can help to define the longevity of any presently identified community. In woodland, this method has been used to distinguish a group of ancient woodland indicator species (AWIs), which only occur in woodland with a continuity of history (of at least 400 years, see above). The accuracy of the assumptions of AWI species is, however, challenged by pollen analysis (Segerstrom and Bradshaw 1994) and the *c.* 400 year span of historical analysis still limits our understanding to the life of a single generation of trees.

Palaeoecological analyses use pollen, plant or insect remains preserved in lake or peat sediments to derive vegetation history by proxy methods. Palaeoecology is limited in the detail it can provide to species that leave detectable remains. It is also limited by problems of quantification of past vegetation abundance from the abundances of fossil remains. Nevertheless, palaeoecology remains the only method of determining vegetation history over longer timescales and therefore plays a key role in providing information on the dynamics of long-lived species such as trees. Of the various palaeoecological tools, pollen is the most widely used. Plant macrofossil remains can be extremely useful, but can provide sporadic evidence; whilst non-pollen palynomorphs tend to give climatic signals, e.g. chironomids and testate amoebae, but can indicate presence of vegetation types by proxy e.g. insect remains (Whitehouse 2006). Pollen is ubiquitous in the environment and readily preserved in anaerobic sediments; and, the nature of the sediment types sampled for pollen mean that in most cases a continuous temporal record can be expected. Although there have been criticisms of the accuracy of interpretations from palaeoecology (Vera 2000), it remains the only tool that can allow a consistent level of ecological detail to be elucidated throughout the thousand-year-plus timeframes necessary to understand the ecology of taxa that have life-spans in excess of 300 years.

1.3.1 Contributions and potential of palaeoecology to issues in woodland ecology.

Palaeoecology has struggled in the past to demonstrate relevance at ecological scales (Section 1.1); partly due to poorly-resolved spatial and temporal reconstructions in early work (Heyerdahl and Card 2000), which was preoccupied with questions of a different scale; and probably partly due to slow uptake of new research development in conservation management, and across disciplines (*sensu* Wallington *et al*. 2005). Wallington *et al*. state. with reference to Hobbs (1998) that "*It is difficult for managers and policy makers to know which theories are important, and how much uncertainty is associated with current ecological knowledge*". This is no less true for palaeoecology, which has produced a vast body of work on the spread and potential cover of woodlands, but is still dogged by controversy regarding the complexities and uncertainties over the interpretation of pollen diagrams (Davis 2000; Vera 2000).

Notable exceptions; as reviewed for example in Birks (2005), have bridged the gap. However, the research needs outlined in Section 1.1 above suggest that palaeoecology needs to routinely demonstrate *and test* finer resolution reconstructions. Reconstructions at this palaeoecological "*micro-scale*" (Delcourt *et al*. 1983) fit between the scales of the traditional regional pollen analyses and the present day analyses of ecological data (Foster *et al*. 1990), thus allowing the interpretation of landscapes in a "*hierarchy of space-time domains*" (Delcourt *et al*. 1983). Such fine-scale reconstructions determine past woodland composition, structure and dynamic processes at the missing scale required by woodland managers[4] (Baskerville 1997).

1.3.2 The development and contribution of spatially precise pollen records

Fine spatial scale pollen analysis was first developed by Tauber (1965), who recognised that there was a relationship between basin size and pollen source area. This has been used as the basis for selection of sites for local vegetation reconstructions. Notable refinements (e.g. Jacobson and Bradshaw 1981; Prentice 1985; Sugita 1994) have modelled the relationship more precisely; and, with caveats discussed further in Section 3.1, have derived pollen source area estimates of between 20-30m (Jackson and Wong 1994) to between 50-100m (Sugita 1994) around small (<5m diameter) hollows under woodland canopies.

However, Turner *et al*. (1993; *and references therein*) note the importance of defining scale by two different measures; 'grain' and 'extent'. Analysis from one pollen site homogenises landscape detail at either the stand, or the regional scale, dependent on basin size (above and Section 3.1). A network approach using several small hollow pollen analyses provides a method of obtaining stand scale 'grain' within a landscape 'extent' (e.g. Bradshaw 1988; Davies and Tipping 2004; Bradshaw and Zackrisson 1990), and, therefore, with the application of secure chronologies, defining patch scale dynamics. This type of study should be

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[4] Scales relevant to conservation managers are defined by Baskerville as scales of thousands of hectares over decades and centuries.

capable of distinguishing random small-scale processes (mosaic shifts) from widespread responses to external factors such as climatic variation, or stochastic influences.

Thus in ideal situations a network approach can allow both patch scale dynamics and the larger regime shifts to be recognised. This can aid planning by developing an understanding of the processes that affect biodiversity (Delcourt and Delcourt 1998).

In addition to providing stand-alone vegetation and process based reconstructions of former woodland, the results from palaeoecological studies of this kind should be capable of being plugged-in to the validation of models of landscape ecological processes, and thus be embedded into decision making for conservation. Without this process-based historical context and understanding, any management decisions are likely to be based upon an inadequate evidence base, and models will remain without temporal evidence for validation.

1.3.3 Problems in palaeoecology

Despite many improvements in the palaeoecological method, there continue to be challenges that require recognition (Davis 2000). Vera (2000) claims that pollen analysis has not been good at identifying openness in vegetation and, due to a concentration on the collection of data about tree species; has overestimated tree cover in past landscapes. This view has been refuted (Mitchell 2005; Svenning 2002), but still requires further testing. Pollen analysts are increasingly aware that quantification of data is an important issue (e.g. http://www.ecrc.ucl.ac.uk/pollandcal/). Accuracy must, and is, being constantly (and site-specifically) tested by reference to modern analogues (e.g. Sugita *et al.* 1999; Brostrom 2002; Brostrom *et al.* 1998; Nielson 2003; Bunting *et al.* 2004; Brostrom *et al.* 2005; Mazier *et al.* 2006).

The current structure of the pine woods forming the basis of this study tends towards openness. Models have illustrated that openness can have profound effects on pollen source area (Bunting *et al.* 2004); investigations cited in Section 1.2.2 above concluding a 20-30m pollen source area for small hollows assume a closed canopy. The pollen source area for small hollows in native pine woods therefore requires further clarification. Additionally, a major chronological problem (Hunter 1998) is particularly associated with interpreting stand scale dynamics across a range of cores as deriving a secure and precise chronology for each core is key to the ability to make inter-core correlations.

Contributions to the attempts to address these technical issues also therefore form a major part of this thesis.

1.4 Thesis rationale

Our knowledge of four broad ecological problems requiring temporal research methods is limited and is important for landscape ecology and for restoration of woodland ecosystems. These problems are:

1. What is the size and natural extent of community patches within the landscape and how does this fluctuate, or change, through time?
2. How does the balance of the mosaics of community patches or stands change through time? What is the consequence for ecosystem function of shifts in community?
3. What is the community composition of the patches, and how stable is that community over time?
4. What was the structure of former woodlands - how open were woodland stands in the past?

Palaeoecological techniques applied to suitable scale analyses should be capable of providing answers to these questions but require quantitative and site-specific clarification of their interpretive capacities and limitations.

In Scotland, where opportunities for rewilding and woodland restoration are greatest a fine resolution palaeoecological study has been carried out within the western oak woods (Sansum 2005); whilst the eastern pine woods are the subject of an on-going palaeoecological study by Pratt (*pers. comm.*) and have formerly been studied at the stand scale (O'Sullivan 1973; O'Sullivan 1977). This thesis will concentrate on the native Caledonian pine woods of Scotland in an upland area possibly to the western extreme of their range in Glen Affric. The east of the glen contains one of the largest and most valued relict pine woodland areas in Scotland (Forestry-Commission 2003). The area is managed for conservation and the restoration/regeneration and expansion of woodlands at the landscape-scale by the Forestry Commission in line with European directives (Section 1.2).

In Glen Affric full Holocene fine spatial scale vegetation records are already available to the west, but reveal historical detail in a currently unforested area where woodland was all but lost *c.* 4000 cal. BP (Davies 2003; Davies 1999). Detailed reconstructions *within* extant pine woodland, and the dynamics and fluctuations of the mosaic of open and wooded communities in the landscape, have yet to be carried-out. This thesis will explore this detail within the extant pine woods where a previous study has revealed temporal continuity (Froyd 2005; Froyd 2001), but not resolved spatial detail. It will attempt to make a contribution to the ecological evidence required in management strategies for the future of these habitats and landscapes, But will also be concerned with applying quantitative techniques to the pollen data and assessing the associated uncertainty within the interpretations (*sensu* Hobbs 1998; Section 1.2.1)

This chapter has summarised the general ecological questions still unanswered in landscape ecology that require a spatio-temporal perspective to their resolution. The role of palaeoecology in answering these questions has been examined, and some general aims for the contribution of this project to the method and debate are raised. The next Chapter will refine these issues in relation to native pine woods and the case study area.

2 The Native pine woods of Scotland and the case study area

2.1 Introduction

Scots Pine (*Pinus sylvestris* L.) has an impressive geographical range across Europe (Steven and Carlisle 1959; Rodwell and Cooper 1995; Willis *et al*. 1998). It is mainly a tree of continental climates. In the UK therefore, especially in the oceanic climate pervading towards the west, and at altitude, the species is at the physiological limits of its climatic range. Despite this, pine woodland is typical of much of the original upland vegetation that colonised the Scottish Highlands as post-glacial woodland developed between *c.* 8000 and *c.* 5000 BP (Tipping 1994). These woodlands now form one of five native types classified by the forestry commission in Scotland[5].

Scottish Pine woods have long been recognised as valuable and worthy of conservation for native species biodiversity (Anon 1995; Anon 1992) and a range of other socio-economic and cultural factors (Forestry-Commission 1994; Balfour 1977) including their emblematic visual nature in the Scottish landscape (Miles and Jackman 1991). In 1959 the seminal book *The Native Pine Woods of Scotland* brought the perilous preservation state and conservation need of pine woodlands to the attention of foresters (Steven and Carlisle 1959). The authors noted the reduced range from that of historical times and the pressures on regeneration of these woodlands from grazing by high numbers of deer. They also highlighted the presence of a distinctive flora and fauna associated with these woods, and proclaimed the much used quote "*to stand in them is to feel the past*" (p. *v*.) stating that it would be a "*national loss*" to allow them to disappear. These findings have fuelled most of the conservation work on native or semi-natural pine woodlands in Scotland since that time.

Native, or semi-natural Pine woodland, conforming to the NVC class W18 *Pinus sylvestris-Hylocomium splendens* woodland (Rodwell 1991) is now protected under European

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[5] There are 5 formal Native Woodland Habitat Action Plans (NWHAPs) which are being implemented in Scotland; Native pine woodlands; Upland oakwoods; Wet woodland; Upland mixed ashwoods; Wood pasture. In addition two proposed NWHAPs have yet to be officially adopted; Lowland Mixed Broadleaves; Scottish Upland Birchwoods http://www.forestry.gov.uk/pdf/UKHAPReportingpaperJan62006.pdf/$FILE/UKHAPReportingpaperJan62006.pdf

legislation by the European Habitats Directive (Anon 1992) implemented through the UK Biodiversity Action Plan (Anon 1995). The key requirements of the legislation for the protection of Caledonian Forest set out in the 1995 UK Pinewood biodiversity action plan (http://www.ukbap.org.uk/UKPlans.aspx?ID=6) are: to maintain existing relict pine woods, and to regenerate and expand the pinewood, creating favourable areas for regeneration. To achieve this objective a 35% expansion in pine woodland is targeted within the next 20 years.

Despite this clarity of conservation vision, in practice, there are still gaps in the evidence base that require scientific research, especially into ecological dynamics at the landscape scale (Bell 2003; Ferris and Purdy 2003; Ferris *et al*. 2000; Hope 2003); and a wide recognition that site specific historical knowledge will help with the development of management plans (Bennett 1995; Cameron 1995; Rodwell and Cooper 1995). This review chapter will summarise current research knowledge and management assumptions for the Native Pine woods of Scotland. Native Pine woods have been the subject of a great deal of study in the last few decades reported via three major conferences in 1977 (Bunce and Jeffers 1977), 1995 (Aldhous 1995) and 2006 (Humphrey 2006). Therefore issues in this review focus on the ecological and conservation questions highlighted in Chapter 1 and their relevance to native pine woods. The case study area of east Glen Affric is introduced in Section 2.2 and the main aims of this thesis in relation to the case study area are outlined in Section 2.3.

2.1.1 The present extent and biodiversity of native pine woodland

The largest extant populations of native pine woodland occur at Abernethy and Rothiemurchus in Speyside, Glen Tanar and Mar in Deeside, and Glen Affric and Glen Strathfarrar within the Strath Glass group, west of the Great Glen. Other smaller woodlands also exist for example in the Black Wood of Rannoch and Loch Maree. All are recently mapped in the Caledonian Pinewood Inventory (Forestry-Commission 1998) and the UK status of EC habitats report (Jackson and McLeod 2000) where the estimated current area of this woodland is listed as 25440 Ha. The majority of these pine woods are listed in Steven and Carlisle’s 1959 monograph. Their list comprises 35 sites in eight main groups; these groups and major pinewoods are displayed in Table 2.1 with geographic zones according to the Native Pinewood Inventory and Forestry Commission (2003). The location of the major pinewoods and those mentioned in this text are displayed in Figure 2.1 below. Some smaller areas have been added by the Caledonian Pinewood Inventory (Forestry-Commission 1998), which now lists 84 separate pine woods and provides maps of their locations.

Table 2.1: The major *Pinus sylvestris* woodland groupings in Scotland according to Steven and Carlisle (1959) and their biochemical groupings (Forestry Commission 2003).

Pinewood Group	Some example pine woods within the group	Biochemical grouping
The Speyside Group	Abernethy, Rothiemurchus, Glenmore, Glen Feshie	East Central
The Deeside Group	Glen Tanar, Ballochbuie, Mar	North East
The Rannoch Group	Black Wood of Rannoch, Old wood of Meggernie	South Central
The Strath Glass Group	Glen Affric, Glen Cannich,Glen Strathfarrar	North Central/South Central
The Northern Group	Assynt	North
The Great Glen Group	Glen Moriston, Glen Loyne, Barisdale	South West / North Central
The Wester Ross Group	Loch Maree, Loch Clair	North West / North Central
The Southern Group	Glen Orchy, Glen Falloch	South West / South Central

NVC W18 *Pinus sylvestris – Hylocomium splendens* woodland (Rodwell 1991) is a community found on leached and podsolised acidic soils in the highlands of Scotland. (Hall *et al.* 2004). The poor competitive abilities of *Pinus* are thought to limit its spread where conditions are suitable for other woodland types. *Pinus* is the dominant tree within W18 communities, but some *Betula* is often present, and in addition *Sorbus aucuparia, Ilex aquifolium and Juniperus communis* can form a scattered understorey (Rodwell 1991). Rodwell defines *Pinus sylvestris-Hylocomium splendens* woodland strictly, preferring to see the inclusion of other arboreal taxa as a mosaic of NVC classes; but notes other, wider, definitions e.g. Steven and Carlisle (1959) list associations with *Alnus glutinosa, Populus tremula* and *Salix* sp.. *Quercus petraea* can also occur but is seen as a gradation into *Quercus-Betula-Dicranum* woodland or *Quercus-Betula-Oxalis* woodland on better soils (Rodwell 1991).

Five sub-communities are identified (Rodwell 1991; Hall *et al*. 2004). These are defined by a variety of factors which currently exert control over the dominance of associated species (Hall *et al*. 2004). There is a general east-west divide across Scotland (McVean 1964), probably linked to oceanicity (Birse 1980). With W18a *Erica cinerea-Goodyera repens* sub-community, W18b *Vaccinium myrtillus-V. vitis-idaea* sub-community and W18c *Luzula pilosa* sub-community occurring mainly in the east; whilst W18d *Sphagnum capillifolium/quinquefarium-Erica tetralix* sub-community and W18e *Scapania gracilis* sub-community occur in the wetter west of Scotland (Averis *et al*. 2004).

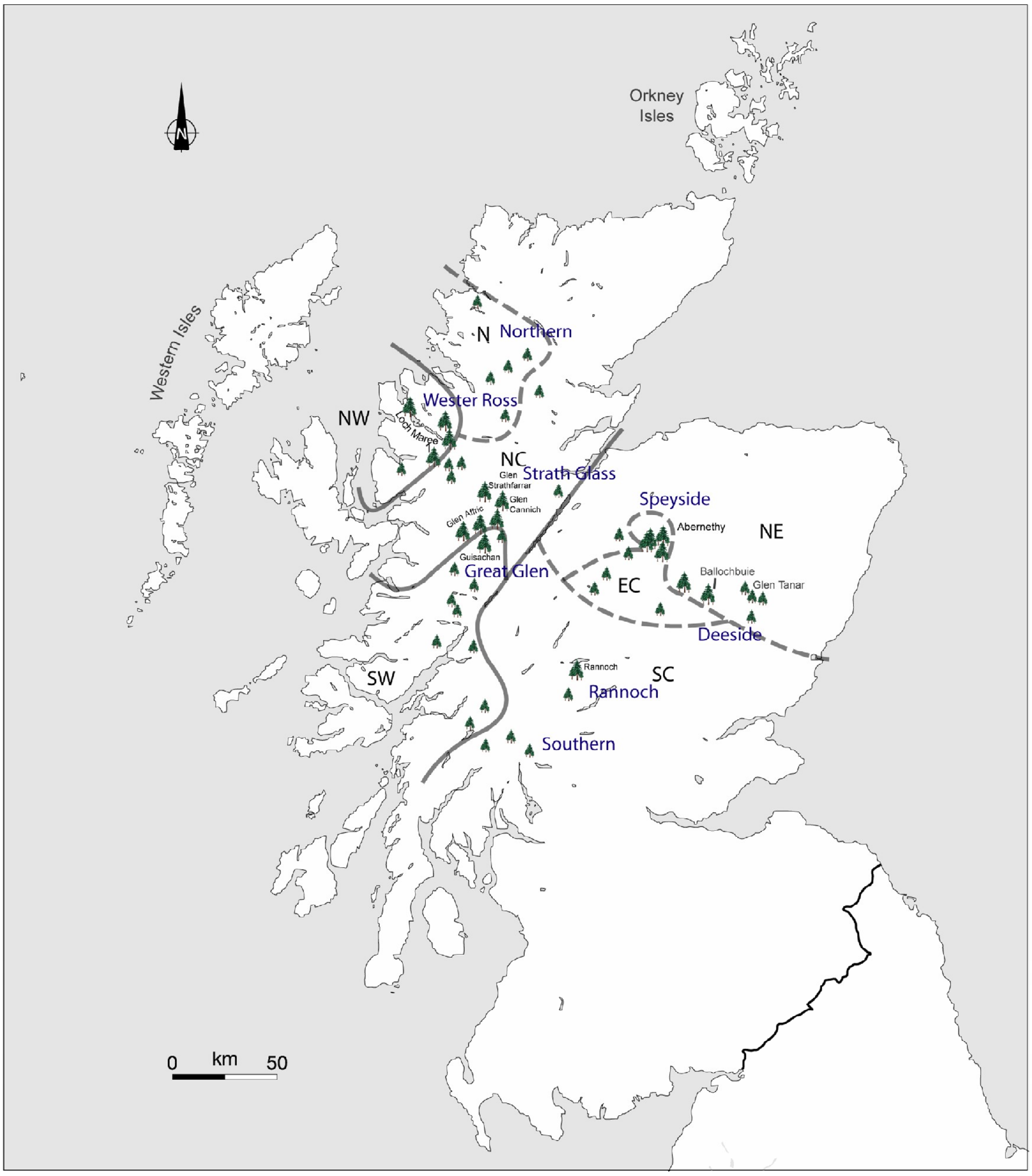

Figure 2.1: Map of the major pine woodlands groups in Scotland and their geographical separation defined by biochemical markers. For clarity only the major pinewoods and pinewoods refered to in this text are labelled. For a full list see the Caledonian Pinewood Inventory (Forestry-Commission 1998).

The dominance of grazing can also effect the understorey with *Deschampsia* being indicative of heavy grazing and denser shade, and *Vaccinium* with lighter grazing regimes, grading into *Calluna* where the canopy is more open (Rodwell and Cooper 1995). The differing tolerances of the Ericales to shade conditions means that there is likely to be some shift in dominance of the ground flora during the life cycle of a forest stand.

Although ground flora is limited, generally to species such as *Melampyrum pratense, Potentilla erecta*, *Trientalis europaea*, *Luzula pilosa*, *Oxalis acetosella* and *Galium saxatile,* several characteristic species of conservation value occur in association with W18 woodland. These include; *Goodyera repens, Listera cordata*, *Pyrola minor*, *P. media, P. rotundifolia*, *Moneses uniflora*, *Orthilia secunda* and *Linnaea borealis* (Hall *et al*. 2004). Of these *Linnaea borealis* is subject to a species action plan (http://www.ukbap.org.uk/UKPlans.aspx?ID=413). In addition to higher plants the pine woods are also important for many lichens (Coppins and Coppins 2006) and animal species (Averis *et al*. 2004).

Native pine woods can be very open: Rodwell defines as W18 any area with >*c*. 25% canopy cover and, where this is less, identifies a gradation into Ericoid heath communities and mire communities, especially to the west (Rodwell 1991). This may demonstrate that the classification of woodland and heath as separate entities is due to a classification construct rather than any ecologically meaningful cutoff in function.

Many of the ground flora species understood to be associated with semi-natural pine woodland also occur in similar floras within the heathland communities (Bunce 1977; Gimingham, 1964). For example *Listera cordata* is also associated with H21 *Calluna vulgaris-Vaccinium myrtillus-Sphagnum capillifolium* heath (Rodwell 1991)**,** whilst *Linnaea borealis* is also found in heaths associated with the shelter of rocks etc (Anon 1999). Similarly, some of the lichen species are associated with dead trees, which can remain upright in the environment for many centuries, and also with heath where some *Bryoria* species can maintain themselves on the woody stems of *Calluna vulgaris* as well as the trunks of *Pinus* (J Hope *pers. comm.*).

In addition to the description above, based around the NVC classification system (Rodwell 1991) a soils based classification has been introduced (Pyatt 1994; Pyatt *et al*. 2001; Pyatt *et al*. 2003), this is described in Section 2.2 in relation to Glen Affric.

2.1.2 The past extent and history of the pine woods – current knowledge

The contribution of pollen analysis to our understanding of the long-term dynamics of pine woods has been reviewed extensively (e.g. Bennett 1989; Birks 1989; Gear and Huntley 1991; Tipping 1994; Willis *et al*. 1998). A brief summary of the main interpretive developments from palaeoecological analysis is given below; focussing on highlighting the finer resolution, ecological scale data gaps.

2.1.2.1 Post-glacial pine invasion and pinewood maximum

Pinus invaded areas of the UK soon after the retreat of ice from last glacial cycle and was present throughout the UK by *c.* 11200 cal. BP and was locally dominant by *c.* 10000 cal. BP (Willis *et al*. 1998). The presence of *Pinus* at Loch Maree (Birks 1972), at an early date of *c.* 8500 cal. BP, indicates that *Pinus* woodland developed from more than one source (Birks 1989); possibly spreading across from a refugium, off the coast of Ireland (Bennett 1995) as well as spreading northwards through England (Huntley and Birks 1983). A more recent study from four Scottish Lochs (Froyd 2005; Froyd 2001; Froyd and Bennett 2006) has confirmed the early presence of *Pinus* in Scotland from multiple origins, or refugia. This multiple origin for post-glacial *Pinus* is also supported by chemical and genetic analysis, which defines three distinct genetic populations of *Pinus* native to Scotland (Kinloch *et al*. 1986).

The pine wood range quite rapidly retracted northwards in the UK, as deciduous trees such as *Quercus,* and *Ulmus glabra* began to invade and compete for space. By approximately 7000 years BP, *Pinus* woodland only remained in Scotland. *Pinus* is easily out-competed on better soils and favourable climatic conditions, and consequently geographically in the UK it only really survived the later Holocene in Scotland where competition with other species such as oak and ash was lessened. In Scotland pollen data demonstrates that *Pinus* underwent a rapid range expansion from *c.* 7500 BP (Tipping 1994), this coincided with a period of warmer and drier climate. However there is an alternative suggestion that this range expansion could be, at least partly, due to a shift in woodland dominance triggered by selective resource use by early human settlers and may also be coincident with the removal, by hunting, of many of the wild herbivores (e.g. Willis *et al*. 1998; Bennett 1995). During the range expansion *Pinus* reached the far north of Scotland to Sutherland and Caithness, (Bennett 1995; *and references therein*) and perhaps to Orkney (Bunting 1995).

Isochrone maps (Birks 1989) and reviews of pollen analysis (Tipping 1994) illustrating geographic extents for woodland in Scotland show the pine woods as occupying a central location in the highlands of Scotland, flanked to the north by more open heathland, and to the west by the western oakwoods in the zones of higher rainfall. However, these zones, in reality, illustrate potential extents of pine woods rather than actual extents. The maps are regional in nature and there are problems in determining whether the pollen data should be interpreted as indicating local scattered trees or a more widespread extent (Bennett 1995; and see Section 1.3.3). As Tipping (1994) acknowledges, the data used has barely begun to exploit the full potential of pollen analysis in defining vegetation history. The use of lake sediments for many of these studies possibly renders them incapable of depicting fine stand scale events in the woodlands, or of depicting structure and canopy cover.

In addition, although evidence from preserved tree stumps in peat, as well as pollen analysis, has been interpreted as indicating that pine woods may have formed a dense canopy in the past (Bennett 1984; Steven and Carlisle 1959), more recent studies challenge this evidence and have demonstrated that the actual age range of stumps is wider than first presumed (Bridge *et al*. 1990). The concentration of stumps may present a biased record due to episodes of increased preservation during periods of accelerated peat accumulation (Dubois and Ferguson 1985; Bridge *et al*. 1990). Bridge *et al.* therefore hypothesise that indications are for a sustained and sparse population of *Pinus* in their study site at Rannoch Moor. This scattered sparse structure for woodland is supported elsewhere (e.g. Fossitt 1996).

2.1.2.2 Pine Decline: event timing and drivers

Whether a dense canopy cover, or an open mosaic landscape, the pinewood maximum between *c.* 7500-4400 BP was followed by a well documented ‘pine decline’ event (e.g. Bennett 1984; Birks 1989; Birks 1972; Birks 1975; Gear and Huntley 1991). This event is evident in pollen data, and also in the occurrence of *Pinus* tree stumps within peat deposits. At first, this decline was thought to be synchronous and climatically controlled as it coincides with a marked increase in oceanicity of the climate. However the rate, spatio-temporal pattern, and drivers of this decline have more recently been subject to debate (e.g. Bennett 1995).

A stepped pattern of decline now seems more likely. The first areas to suffer the decline in trees were the northernmost ranges and into the Northern Isles and the Outer Hebrides (Fossitt 1996; Bunting 1996; Tipping 1994). In these areas *Pinus* may have dominated for little more than one generation of trees. The Pine decline was also more marked to the west of Scotland. Eastern pine woods suffered less from the pine decline than western ones, although some areas to the west are demonstrated to have maintained their pine populations, whilst other areas succumbed to the invasion of blanket bog; perhaps due to topographic controls on edaphic processes (O'Sullivan 1977; Birks 1996). Recently, Froyd (2001) presented confirming evidence, using pollen and pine stomata from four small lakes, that the pine decline was not synchronous, and that pine populations remained in pockets on some steeper slopes throughout the later Holocene.

Pine wood development and maximum coincided with a period of climatic optima for the species in the warmer drier conditions of the hypsithermal interval, together with a possible selective removal, by humans, of other more competitive tree species (Willis *et al*. 1998). The pine decline event coincides with two possible major driving forces; the post-hypsithermal onset of oceanic conditions (Crawford *et al*. 2003), and the onset of, or increase in, human activity, with clearing of trees, development of agriculture and use of fire regimes. The most likely scenario now accepted for the destruction of the pine woodlands is a combination of these factors acting to positively enforce each other (e.g. Davies 2003; Davies 1999).

The pine decline phenomenon has been the subject of a great deal of focus for palynologists, and is important in detecting the interplay between human and environmental impacts. It illustrates that conditions since *c.* 4400 BP have possibly been very different edaphically as well as in respect of human influence and Holocene climatic variation. For example, in Scotland the paludification of soils results in the development of blanket bog and heathland formation (Crawford 2001). An oceanic climate may increase the feedback between pine reduction and the paludification of soils which in turn may cause increased pine decline through lack of suitable edaphic conditions for regeneration (Crawford 2001; Crawford *et al*. 2003).

Whilst understanding these expansive losses of pine woods in the mid-Holocene, is important, there is no doubt that pine woodland did survive in some areas, even though the finer spatial details are uncertain. Equally important therefore is an understanding of how, where and why pine woods did survive in some areas. An examination of the ecological functioning of the remaining pine woods through the last few thousand years since the pine decline is required to provide a relevant information base for current and future issues of pine woodland sustainability (Birks 1996).

2.1.2.3 The Highland pinewood landscape since c. 4000 BP

Following from the pine decline event, whether synchronous or not, pine woodland did not regain its foothold, many areas of the north-western Highlands, having succumbed to blanket bog (O'Sullivan 1977). Pollen diagrams from Loch Sionascaig, and, and Loch Maree (Birks 1972), demonstrate disturbed vegetation or blanket bog formation after *c.* 4000 BP. More recent pollen analyses also demonstrating continued forest decline are Dubh-Lochan and Reidh-Lochan (Froyd 2001) and sites in west Glen Affric (Davies 2003; Davies 1999). Some exceptions are Loch an Amair in east Glen Affric (Froyd 2001), Loch Clair (Pennington *et al*. 1972) and to the eastern pine woods around Abernethy, e.g. Loch Garten and Loch a Chnuic (Birks 1970; O'Sullivan 1974; O'Sullivan 1977), where almost continuous forest is confirmed until *c.* AD 1800.

It is by no means clear what cover extent of pinewood survived into early prehistory (Fenton 1997); partly due to a general continued reliance on poorly spatially resolved pollen analyses, and partly due to less secure dating of the more recent sediments. The gradual and geographically variable reduction in woodland as evidenced by pollen analysis continued from *c.* 4000 BP into the first millennium AD (Armit and Ralston 2003). Although McVean (1964) proposes a steady decrease in woodlands from 500 BC to historical times, the decrease may have been much earlier. Historical accounts, which noted the presence of pine wood in many areas, with Ptolemy first using the phrase Caledonian Forest in the 2nd Century AD (Steven and Carlisle 1959), must be interpreted with extreme caution (Breeze 1992; Armit and Ralston 2003). It is likely that Scotland was already very open in Roman times.

Scotland is not as well served by historical written records as the rest of the UK. Historical maps (e.g. Bleau 1654; General Roy 1750; and Timothy Pont in the 1580-90s) illustrate expanses of pine woodland or at least scattered trees. Although these records demonstrate something of the extent and existence of forest in Scotland at these times, they cannot account for the deeper temporal resolution and the records are surprisingly sparse, and lack detail of woodland structure, even in the more recent period of *c.* 250 years. The accuracy of some of these accounts has also been questioned. The financial rewards of forestry exploitation were high, as were the political ones, as timber was exploited for battle ships etc. It may be that descriptions of timber resources in distant glens were exaggerated, either by the map makers themselves, or by locals; as mapping of the remoter glens may have relied on local descriptions rather than site visits. In addition, the concentration on the mapping of timber sources may mean that scant attention was paid to other tree species.

Forestry records also show widespread exploitation of pine woods developing in Scotland in the 18th and 19th Centuries, with some forestry activities as early as the 1600s (Smout *et al.* 2005). This exploitation was heavier in the east, where valuable timber resources existed, and less heavy to the west where the timber quality was in general poorer, and the extraction of wood in any quantity more problematic.

The evidence for continuous forest cover since *c.* 4000 BP is therefore limited. Even when relict status is confirmed by regional scale pollen analysis it must be remembered that there may be considerable variation in site histories at a local scale (*sensu* Bradshaw and Zackrisson 1990; Segerstrom and Bradshaw 1994; Segerstrom 1997; Section 1.2.3). In addition, the focus on *Pinus* as the major tree species may be questionable. Local scale analysis has revealed possible differences in diversity and quantitative balance in the species mix in past forests, which may have been key to the maintenance of edaphic conditions suitable for forest regeneration (O'Sullivan 1977). Additional fine spatial resolution work in extant pine woods is therefore required.

Although in 1977 (O'Sullivan 1977) and again in 1995 (Bennett 1995) the need for finer scale pollen analysis in native pine woods was realised and called for, in fact the attempts at quantification were still in their infancy. Few pollen diagrams at the fine scale proceeded in Scotland after the work of O’Sullivan (1973; 1974; 1977). Kerslake (1982) examined pollen data from Scottish loch islands and compared these with regional scale diagrams. However, it seems that during the 1990s researchers were generally using pollen data as a proxy for climate change rather than for the detection of small-scale vegetation patterns. The recent work of Davies (1999) and Smith (1998; 1996) has begun to develop the use of fine spatial scale approaches in the Highlands of Scotland, however studies within extant pine woods were limited (O'Sullivan 1977), and remain so (Wilson 2001).

2.1.3 Planning and management assumptions for future pine woodland

2.1.3.1 Definitions of naturalness and presumed naturalness of the present native pine woodlands

It must be remembered that the phytosociological classifications and descriptions described in Section 2.1.1 above comprise information from surveys of current woodlands. The NVC and other phytosociological classifications do not have a long temporal dimension to their analysis of community groupings. In fact many discussions argue for more mixed communities in the past (e.g. McVean 1964; Atherden 1992; Rodwell and Cooper 1995), the NVC acknowledges this possibility (Rodwell 1991) and, where tested pollen analysis confirms this supposition (Section 2.1.2.3). Others claim that there is evidence for the selective removal of less valuable tree species by humans (Worrell and Mackenzie 2003), thus for instance, leaving an increased *Pinus* dominance in some areas. In contrast where the other more valuable timbers have been removed *Betula* can often form the only tree colonising (Worrell and Mackenzie 2003).

Notwithstanding this uncertainty and lack of detailed temporal data, the EU Habitat Action Plan (Anon 1992) describes these woodlands as "relict indigenous forests dominated by self-sown *Scots Pinus sylvestris*". Whilst Balfour (1977), uses the term "continuous forest" to refer to these woodlands, assuming woodland presence, although altered by human impact, has been sustained in the landscape since Boreal times. It is therefore worth contemplating here, the meaning and context of the terms 'semi-natural', 'native' and 'ancient' with regard to native pine woods.

Smout *et al.* (2005) define two terms; "semi-natural", denoting a self sown, naturally regenerating woodland, and "ancient" as "directly descended on the same site from the original 'wildwood' of early prehistory". Whilst native tends to be used to describe the woodland comprising taxa that colonised the UK soon after the last ice retreat and before loss of the land bridge that connected the UK to the European continent.

Despite a clarification of the meaning of these terms there may still be considerable flexibility and assumptions made in their application. Atherden (1992) considers that the work of McVean and Ratcliffe (1962), Burnett (1964), and Bunce (1977), "*confirm the native status of these sites*" [6] (p.77). The ancient or relict status of much semi-natural native woodland in Scotland is defined by continuity in the documentary historical archive, going back to the sixteenth century (Atherden 1992); but often, due to lack of historical data, only back to Roys Military Map of 1750 (Smout *et al.* 2005). This definition of 'ancient' requires that woodland may be confirmed as having existed for little more than *c.* 300-350 years; i.e. the lifetime of a

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[6] although 'native' is now understood to refer to species that are original colonisers of a landscape PETERKEN, G. (1981) *Woodland conservation and management,* London, Chapman and Hall., the context of the use of the word native by Atherden above seems likely to refer to a link with ancient woodland as a continuous presence on a site.

mature pine tree. This definition uses a combination of ecological survey, invoking the space for time analogy, and the, sometimes limited, historical record predominantly from regional scale pollen analysis. It is important to recognise therefore, that at the time of these early and influential studies into native pine woods, and even in the more recent Caledonian pinewood inventory (Forestry-Commission 1998), the relict status, and continuity, of these woodlands may not have been confirmed in any great detail (Gimingham 1977).

At first this may seem to indicate that the past does not matter in future planning for native pine woods (Section 1.1.3), especially if newly planted stands can take on the same form as older stands. However, extant stands, both semi-natural and planted, are understood to be degraded and in need of restoration and expansion and may be much altered, or even be "*dysfunctional*" (Taylor 2005). Thus, semi-natural stands may be confused with older planted stands, not so much due to the *enrichment* of the planted, but the *impoverishment* of the natural. Equally, any enrichment of planted stands may be due to an inheritance of biodiversity from the former vegetation composition of that site. An understanding of the trajectory of change, i.e. gradual losses and gains in diversity are important in recognising the possibilities of either extinction debt, or restoration potential in either stand type. For example, in Glen Affric there is likely to be a drastic reduction in suitable habitat for the lichen *Bryoria furcellata* over the next 50–100 years as newly regenerating woodland will create large areas where the shade is too great for this species (J Hope in Humphrey *et al*. 2004).

2.1.3.2 Pine wood and heathland landscape structure and dynamics

Within the woodland landscape, mosaic structures are recognised as important. The gradations between heathland and W18 woodland outlined above can be due to seral or edaphic factors (Rodwell 1991), and these can be moderated by grazing and browsing pressures (Hall *et al*. 2004). Some separation of woodland communities is likely over longer time-periods due to geological and topographic landscape features. For example, edaphic variations between alluvial deposits at stream margins, where soils are richer, in flat, low lying valley bottoms where drainage is impeded and on rocky slope outcrops where rankers can occur can be seen to affect the associated vegetation communities (Pyatt *et al*. 2001) and these broad edaphic factors may persist. However, seral and edaphic factors may not always be separate. Crawford (2000) proposes that small changes in canopy cover triggered perhaps by human influence, or by climatic deterioration, can trigger larger changes by affecting the soil moisture regime, these changes favour the growth of heathland communities in which *Calluna* plays a large part. Equally soil structure can be maintained by a mix or cyclicity with broadleaved woodland. It is possible that the maintenance of soil structure may have previously relied on a greater mix of tree species (Miles 1985; Miles 1986), which may have now been broken down by the segregation of woodland into near monocultures by human use (McVean 1964; McVean and Ratcliffe 1962). This has been proposed for the eastern pine woods in sites around Abernethy (O'Sullivan 1977). Additional work determining the recent (over several generations of trees) dynamics and cyclicity of woodland areas that have survived may help elucidate useful ecological information for conservation management practice (O'Sullivan 1977).

Crawford’s model (above) identifies the spread of *Calluna* as a possible driver of a breakdown in *Pinus* community via the effect of triggered edaphic processes on regeneration. *Calluna* is however, not itself in equilibrium, as the shrubs soon become tall and eventually unable to support themselves. The resultant spread leaves open ground available for other species to colonise (Gimingham 1964), either as the successional stage in the regeneration of woodland, or to other heathland dominants. As *Pinus* regenerates neither under its own canopy, or under the canopy of a dense cover of *Calluna* it is possible that surviving pine woods have relied in the past on some form of cyclicity, with regeneration over a mosaic of space in the landscape.

2.1.3.3 Pine wood renewal

The problem of regeneration of pine woods has been the major focus in management planning; the current, perhaps apparent, lack of regeneration is considered a major threat to pinewood sustainability. This is mentioned in detail by Steven and Carlisle (Steven and Carlisle 1959) who sum up (p300) that the establishment of younger missing age classes is the *central* *problem* in ensuring a future for these woodlands due to large deer numbers and failing regeneration of trees along with reduced ground flora diversity. They advocate the building up, over a century of a "*reasonable balance of age classes*" comprising an irregular mosaic of stands, noting the sparsity of *Pinus* trees in some areas. This structure of a pine wood as a mosaic of stands with open space for regeneration is important. Pine woodlands do not conform to a traditional gap-phase model of successional dynamics (McVean 1964). *Pinus* is described as gregarious and currently tends to regenerate as almost even aged cohorts in patches in the landscape. However, some stands are poorly stocked and tree structure indicates that they may always have been so. Evidence for this open structure in the past is suggested in palaeoecological analysis (Bridge *et al*. 1990).

The main factor thought to be affecting regeneration in the pine woods is the high numbers of grazing animals (Palmer and Truscott 2003). Studies have demonstrated that exclusion zones tend to recruit more *Pinus* seedlings, indicating a link between grazing density and regeneration. Deer numbers have been kept abnormally high in the recent past over much of the Highlands for hunting purposes. However, reduction in grazing increases *Calluna* dominance, which can also have a negative effect on regeneration. Recent studies also conclude that fire may need to play a larger part in the future management for *Pinus* regeneration (Bruce and Servant 2003; Hancock *et al*. 2005). The interplay between these different factors may be important as illustrated in Sweden where a historical monitoring study has confirmed the complex combined roles of climate, fire and grazing on woodland dynamics (Engelmark *et al*. 1998).

Despite concluding that the main problem for the pine woods is the lack of regeneration, Steven and Carlisle do note regeneration in some areas. In some places this is correlated with the exclusion of high numbers of grazing animals, although in others this does not seem to be the case. It must be remembered that this survey was carried out with the view of a forester, using language evocative of ensuring resource use, such as "well stocked stands". More recently Cameron *et al.* (2000) measure the temporal loss of pine wood through historic aerial photos from Glenfeshie (1946 and 1988) and Bollochbuie (1965 and 1997) and demonstrate an overall loss of trees when balancing recruitment against loss of older specimens. This study however, using aerial photography probably incorporates a bias as trees under 20 years old are not recorded. Consequently, approximately half of the recruitment within the *c.* 40 year period of the aerial photographs may not be recorded. When making judgements about stocking levels quantified patterns of regeneration required over any temporal period to maintain these remnants of former woodland seem unclear. Further information on the temporal scale of regeneration is presented by Edwards and Mason (2006) who examined age classes of *Pinus* through dendrochronology and determined, as did (Zackrisson *et al*. 1995) in Sweden, that regeneration may come in pulses of up to *c.* 100 years apart, and may require the breakdown of the current stand before it can start. It may be that our understanding of regeneration cycles in pine woodlands is limited by the short timescales of our studies in relation to natural cycles.

The regeneration process is complex and includes successional processes triggered by climate variability, soil structure and edaphic change, ground flora structure and impacts of grazing. Longer term studies can help to ensure that predictive models used in management are more robust (Hester *et al*. 1996).

2.1.4 Summary

The extent to which forest cover remained dominant after 4000 years BP is debatable (O'Sullivan 1973). In addition, the canopy structure and composition of this original Caledonian woodland remains unclear at the stand scale. Concepts of an expansive Scottish wildwood in more recent times have been criticised as largely a mythical romanticised image (Smout Dickson 1993; Dickson *et al*. 1985; Breeze 1992). Environmental and climatic change over recent millennia render the concept of the pre 4000 BP pine woodland questionable as a baseline trajectory for current and future management planning (Dickson 1993; Tipping *et al*. 1999). The consequence may be to reinstate a failing woodland (Fenton 1982; Fenton 1997; Crawford 2000; Crawford 2001; Fenton 2001; Crawford *et al*. 2003). Restoring ecological function rather than a past static woodland community is important to achieve sustainable woodlands (Gimingham 1977).

Ecological function over relevant timescales is not well understood. Recent pinewood dynamics and woodland community fluctuations over several generations of trees require more thorough investigation in order to appreciate potential pine woodland sustainability into the future (Fenton 1997). Some cyclicity in particular, may be important in the maintenance of soil structure and ecological function (Miles 1985; 1986; 1988). Evidence for cyclicity is tentatively recorded in pollen diagrams from Abernethy (O'Sullivan 1973) and a pilot study pollen diagram from Glen Affric (Wolff 2003; Wolff and Tipping 1999). However, pollen analysis in Scotland has, with these few exceptions, continued to concentrate on regional scales, on events from the mid-Holocene woodland maximum or on human impact (Tipping *et al*. 1999). Spatially detailed studies from within extant pine woods have been limited (Tipping 1994).

Despite the impact of range reductions and edaphic changes, *Pinus* still survives in relict continuous stands. In some areas of Scotland, including in Glen Affric (Froyd 2005; Froyd 2001; Froyd and Bennett 2006) the continuity has been confirmed. Detailed spatio-temporal studies of the structural history of these stands and their continuity in the face of environmental adversity is of particular interest for understanding future ecosystem functioning through fine scale pollen analysis.

Modelling investigations are continuing to shed new light on the complex processes and trajectories of future woodlands (Bell 2003; Hope 2003; Hope *et al*. 2006). Validation of the resultant range maps (Hope *et al*. 2006) and the previous real extent of woodland can only be gained via historical analysis (Hester *et al*. 1996). More palynological detail from additional, spatially defined pollen and palaeoecological analyses can assist in this (Bennett 1995), by giving a longer term view than available from ecological survey or written record (O'Sullivan 1977). Obtaining and refining this spatial detail through palaeoecological analysis in the Glen Affric pine woods will be the focus of this thesis.

2.2 The study area – east Glen Affric

2.2.1 Geography and geology of Glen Affric

2.2.1.1 Location

Glen Affric lies north of the Great Glen in the parish of Kilmorack. The glen forms the largest, and most southerly, of four glacially sculpted glens in the Beauly catchment, which drains to the sea at the Beauly Firth to the north-east (Figure 2.2). The glen runs approximately west-south-west to east-north-east with a steep sided, narrow entrance to the north-east. This study is confined to the north-east of the glen where pine woodland still dominates. The area contains a large 1045 hectare forest reserve (Figure 2.3).

2.2.1.2 Topography

The east of Glen Affric is centred around two lochs, Loch Affric to the south-west, which then flows through to Loch Beinn a Mheadhoin (dammed as a reservoir since the 1940s) and into the River Affric to the north-east and onwards to the River Glass and the Beauly Firth (Figure 2.2). The entrance to the Glen from the north-east is narrow and steep with a gorge and waterfall leading out of the catchment. These steeper valley sides continue alongside Loch Beinn a Mheadhoin, with rocky outcrops predominant here, whilst the glen opens out to the west alongside Loch Affric with shallower sloping ground from the loch side to the surrounding steeper mountains. The glen is flanked by high mountains on the north and west to heights of over 600 m. Several Munros mark the end of Loch Affric, some with heights of over 1100 m. Through these is a pass, via Athnamulloch through to Kintail and the west coast, which has a long history of use as a droving road (Haldane 1999).

2.2.1.3 Geology

The underlying rocks in Glen Affric are those of the Moine succession; originally clastic sediments, these have been metamorphosed into schists and psammites by the Caledonian orogeny (Peacock *et al*. 1992), and now form a heavily foliated, nutrient poor, and metamorphosed sedimentary series of quartz-feldspar-granulite, mica schist, semi peletic schist and mixed schists (Pyatt 1994; and Geological Survey 10 mile map North Sheet (1979)). Loch Affric and Loch Beinn a Mheadhoin are situated in ice sculpted basins (Peacock *et al*. 1992).

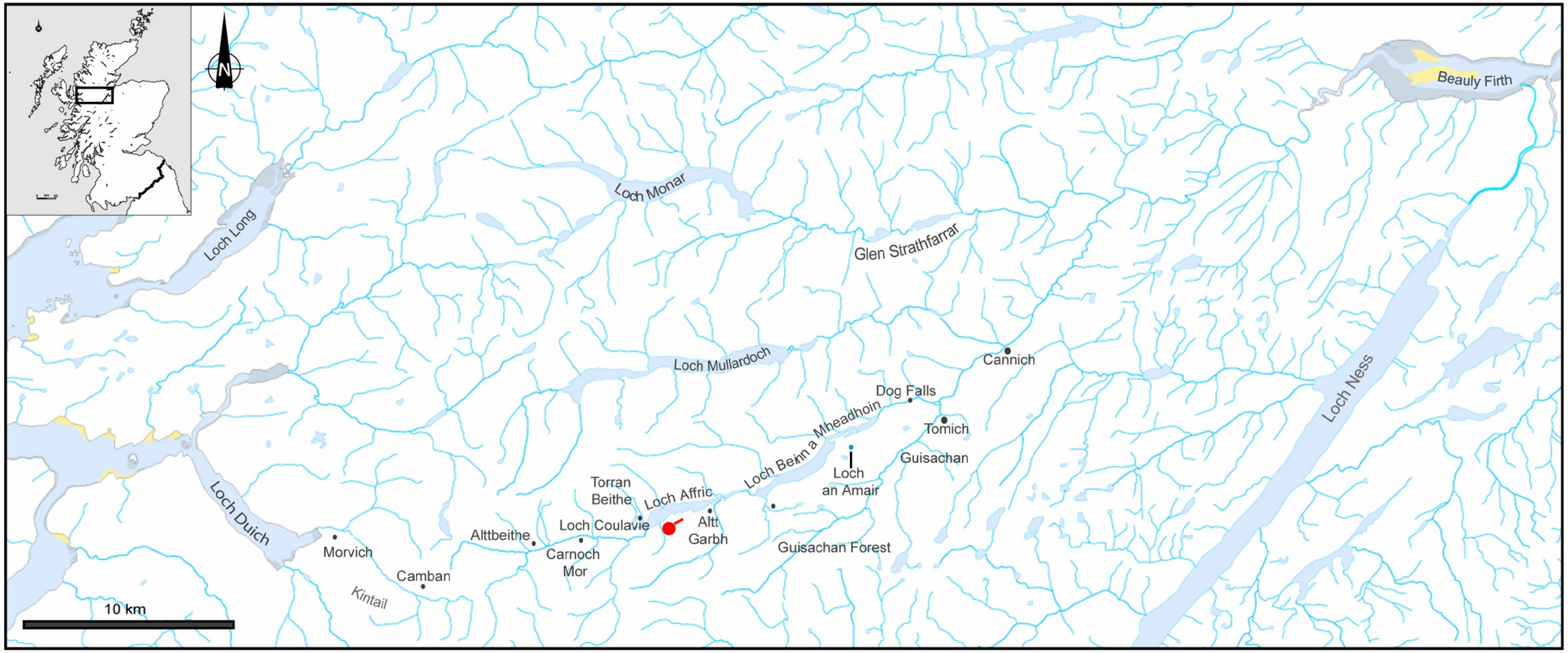

Figure 2.2: Map of Glen Affric and surrounding area including the location of pollen sites and places mentioned in Section 2.2. Red dot represents the viewpoint of the photograph in Figure 2.4, and the red line the direction of view.
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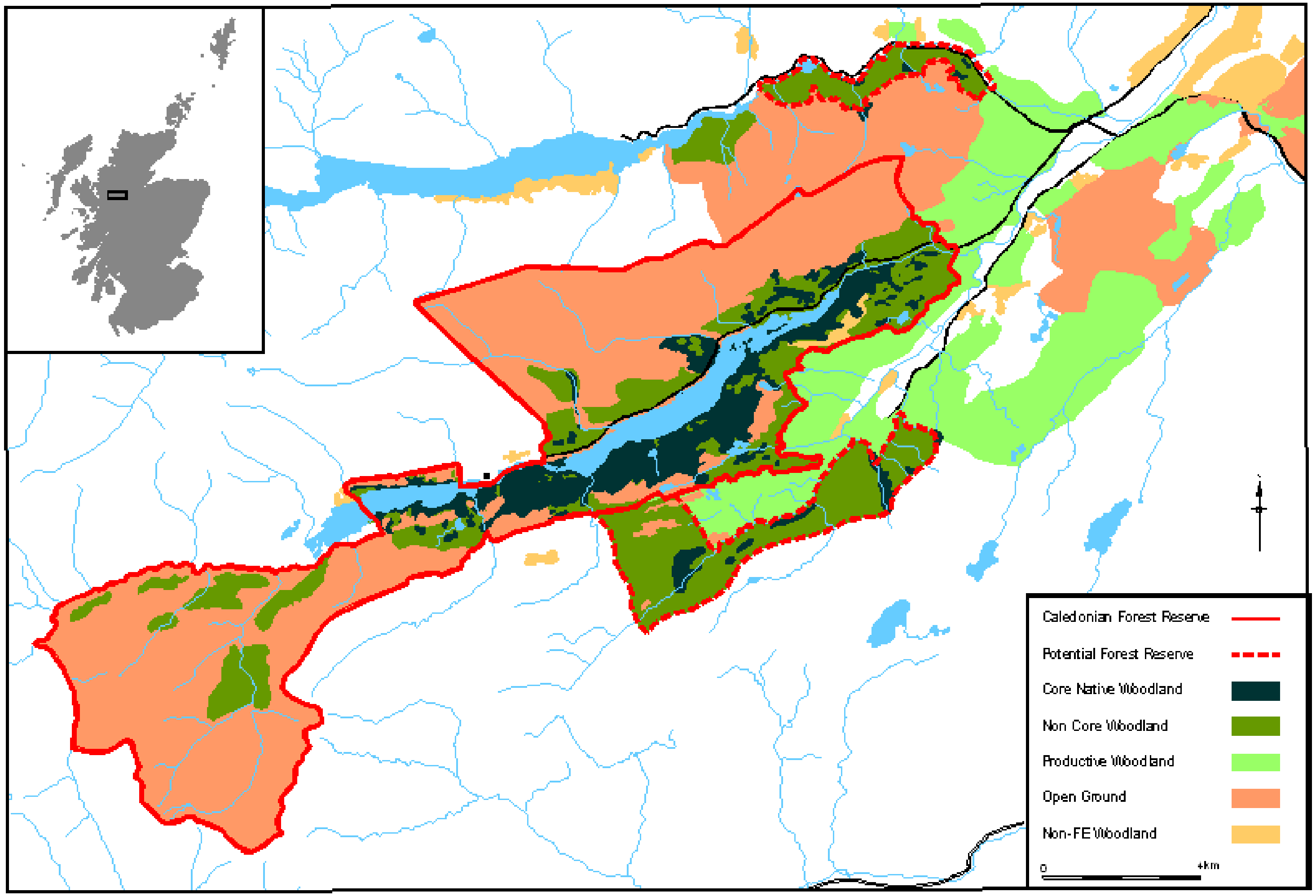

Figure 2.3: The extent of the forest reserve area in Glen Affric. Redrawn from Forestry Commission Management Plan Map

The impact of the last glaciation is evident in the typical glacial till and moraine deposits on the hillslopes beside these lochs. Extensive glacial drift overlies the bedrock, with fluvial sand and gravels at valley bottoms and slopes covered with a stoney lateral moraine (Pyatt 1994). The landscape is undulating and hummocky with many small lochans in addition to the two main lochs. Peat is widespread to the west and on poor draining substrates; there are also areas of more free draining sands and gravels situated at stream outflows and slope bases as alluvial fan deposits.

2.2.1.4 Soils

The west of the glen is predominantly undulating and covered with blanket peats (Steven and Carlisle 1959). Areas of alluvial free draining sand and gravel deposits are generally overlain by podsols. To the east, some brown earths are present. The steeper slopes beside Loch Beinn a Mheadhoin, especially those facing north, often contain rankers (soils less than 30cm deep) associated with rock outcrops (Pyatt 1994; Pyatt *et al*. 2003). Brown earths are restricted to the lower forest zone and more commonly the southern facing, warmer, areas. Some more basic flushes exist among the acidic rock, and these create microhabitats of vegetation interest. These form areas where the growth of *Alnus* is more likely. A study into the differing vegetation on different soils has been carried out in Glen Affric using the Ecological Site Classification Model (Pyatt 1994; Pyatt *et al*. 2003). Pyatt finds that the soil composition is complex and that two or three site types can occur on any one hectare in a repeating pattern. The current soils maps for this area do not illustrate this scale of detail.

2.2.1.5 Climate

The climate in Glen Affric is oceanic, a high rainfall gradient exists with rainfall at 1600 mm per year to the east increasing to 3800 mm per year in the mountains to the west of the glen (Hope *et al*. 2006). The topographic nature of the area, and the geographical position, create zones of alpine and sub-alpine temperature regime. The Glen also experiences a high wind regime and this is identified as having the largest natural effect on forest stands. The area is therefore monitored continuously for wind speed and direction at two weather stations (Quine 2003).

Evidence for climatic change within the historical period, is present in the Statistical Accounts for Scotland entry for the Parish of Kilmorack (Anon 1791-99), the entry reads;

> "Climate – In no respect has this country undergone a greater change than as to climate. About 20 years ago, the farmers, without a coat upon them, were obliged to yoke their labouring cattle, even in the month of March, about three or four o'clock in the morning, as neither the ploughman nor the cattle could stand the heat of the day after six or seven. But how great the reverse; no sight more common now, in the latter end of April, and the beginning of May, than a ploughman, with his body wrapt up in a great coat, and his hands muffled up in worsted mits to save him from the frosty air. Showers and snow are not unusual in June, even in the dog-days; but although our seasons have thus varied, we have on the whole less frosts and snow throughout the year than formerly."

Whilst in the 1834-45 account (Fraser 1841 p363) the climate is said to be humid and mild, with temperatures in the winter not dipping below 24^0 Fahrenheit (-4.5^0C) for "*some past years*" and some rapid and frequent pressure changes observed from the barometer. This account however, also mentions that on the north side of Loch Beinn a Mheadhoin on the mountain Maum Soule lies the largest area of perennial snow in Britain, something which no longer occurs in the present climate.

The glen has been the subject of a palaeoecological climate change research project (Tisdall 2000), which has demonstrated climate fluctuation throughout the Holocene by reference to changes in precipitation and temperature inferred from lake level changes and mire development (Tisdall 2003a; Tisdall 2003b). A mid-Holocene variability is found from 6330 cal. BP after a prolonged period of stability. From 6330 cal. BP the climate cooled, at first in conjunction with a period of low precipitation, but then followed, from 5200 cal. BP by a period of warmer climate with increased precipitation. 4800 cal. BP then marked the onset of a period of cooling. The changes are thought to be related to atmospheric and oceanic circulation patterns (Tisdall 2003a). In the last *c.* 1000 years the record is difficult to interpret due to humification changes associated with the acrotelm (Tisdall *pers comm*.).

2.2.2 Current vegetation and woodland in east Glen Affric

2.2.2.1 The vegetation types and the vegetation mosaic

The vegetation in east Glen Affric comprises a mosaic of semi-natural pine woodland conforming to the NVC class W18 (Rodwell 1991). Within the Glen, these stands encompass the full range of canopy cover discussed by Rodwell, with some very open stands grading into heath with scattered trees, and some stands well stocked with a canopy cover of over 70%. Age structure of the stands within the woodland is variable, but individual stands tend to be even aged and either in the older ages classes or in the younger ones (Steven and Carlisle 1959; Edwards and Mason, 2006). Younger age classes have regenerated since the exclusion of grazing; leading to the presumption that grazing was formerly limiting pine regeneration (see section 2.1.3.3 and 2.2.3.3 below).

Interspersed with the Pine woodland, sometimes in discrete patches and sometimes in more intimate mixture, are broadleaved trees, predominantly birch and rowan, but with some *Alnus* by stream sides, wet flushes and alluvial deposits. The current control on the distribution of these species is edaphic (Pyatt 1994; Pyatt *et al*. 2003). These broadleaved communities mainly conform to the NVC classes W17; *Quercus – Betula – Dicranum*, W11; *Quercus – Betula –Oxalis* and W4; *Betula- Molinia* woodland although the current role of *Quercus* is somewhat limited. Some larger areas of these vegetation classes exist to the east. From the Benavean Power station building alongside the road and into the glen at the Loch Beinn a Mheadhoin dam are stands of *Betula*, with a more luxuriant ground flora including *Primula vulgaris*, *Oxalis acetosella* and *Viola sp*.. Whilst, on the slopes above Dog Falls at the head of Loch Beinn a Mheadhoin, brown earths support mixed woodland with *Betula*, and a sparse presence of *Quercus* and *Ulmus glabra*. *Pinus sylvestris* also occurs in this area; as does one of the oldest ‘granny pines’ noted in the glen. Aspen, *Populus tremula*, is also present in small patches especially at Coille na Ruighe where the organisation Trees for Life have fenced an exclosure for the regeneration of this species (http://www.treesforlife.org.uk). There is some *Juniperis communis* and *Ilex aquifolium*, but these are rare. Rowan, *Sorbus aucuparia*, and various species of willow, *Salix* sp., also occur throughout the glen and hazel, *Corylus avellana*, is present in pockets to the east on the richer soils.

In addition to the mosaic structure, there is also a general trend of denser woodland to the east alongside Loch Beinn a Mheadhoin and scattered woodland further to the west thinning out to open land alongside Loch Affric and becoming treeless further to the west (see the photogrph in Figure 2.4). Although a few scattered groups of *Pinus* do exist there now, and may have always contributed to the mix (Davies 2003).

The native woodland zone runs alongside the lochs Affric and Beinn a Mheadhoin, further to the south and east are some plantations with stands of *Larix* and *Picea*. The current layout of the main vegetation units is displayed in Figure 2.5.

Figure 2.4: Photograph of Glen Affric looking to the north-east from the south side of Loch Affric, showing the grading of pine woodland into open heathland. (The NHP site used in this study is in the woodland to the left of the photo (See chapter 3)).

2.2.2.2 Biodiversity

Glen Affric has a long history of management for conservation, and has, consequently, been the subject of scientific survey. The area was examined in some detail by Steven and Carlisle (1959), and since then the area has been assessed both under the NVC survey scheme and the Ecological Site Classification (ESC) scheme of Pyatt (1994; 2001). Surveys have also been carried out by Fenton (Fenton 1982) and the organisation Trees for Life; useful inventories can be located on their web site (http://www.treesforlife.org.uk/).

These surveys highlight the value of Glen Affric for biodiversity especially for ground flora and fauna, and particularly for some lichens and mosses. New species of national importance are being found through continuing surveys (Coppins and Coppins 2006; and see the trees for life web site http://www.treesforlife.org.uk/). In addition to biological diversity Glen Affric may be important for genetic diversity within Scots Pine as the genetic strain found in the Glen differs from that found elsewhere in Scotland (Kinloch *et al*. 1986). This may implicate the pine woods in a long history of isolation from other pine wood communities.

The Glen Affric area and the SSSI contain some rare and protected plant species associated with the presence of ancient pine woodland. In particular Creeping Ladies Tresses (*Goodyera repens*), Twinflower (*Linnaea borealis*), and Lesser Twayblade (*Listera cordata*), although see section 2.1.1 for challenges to this association.

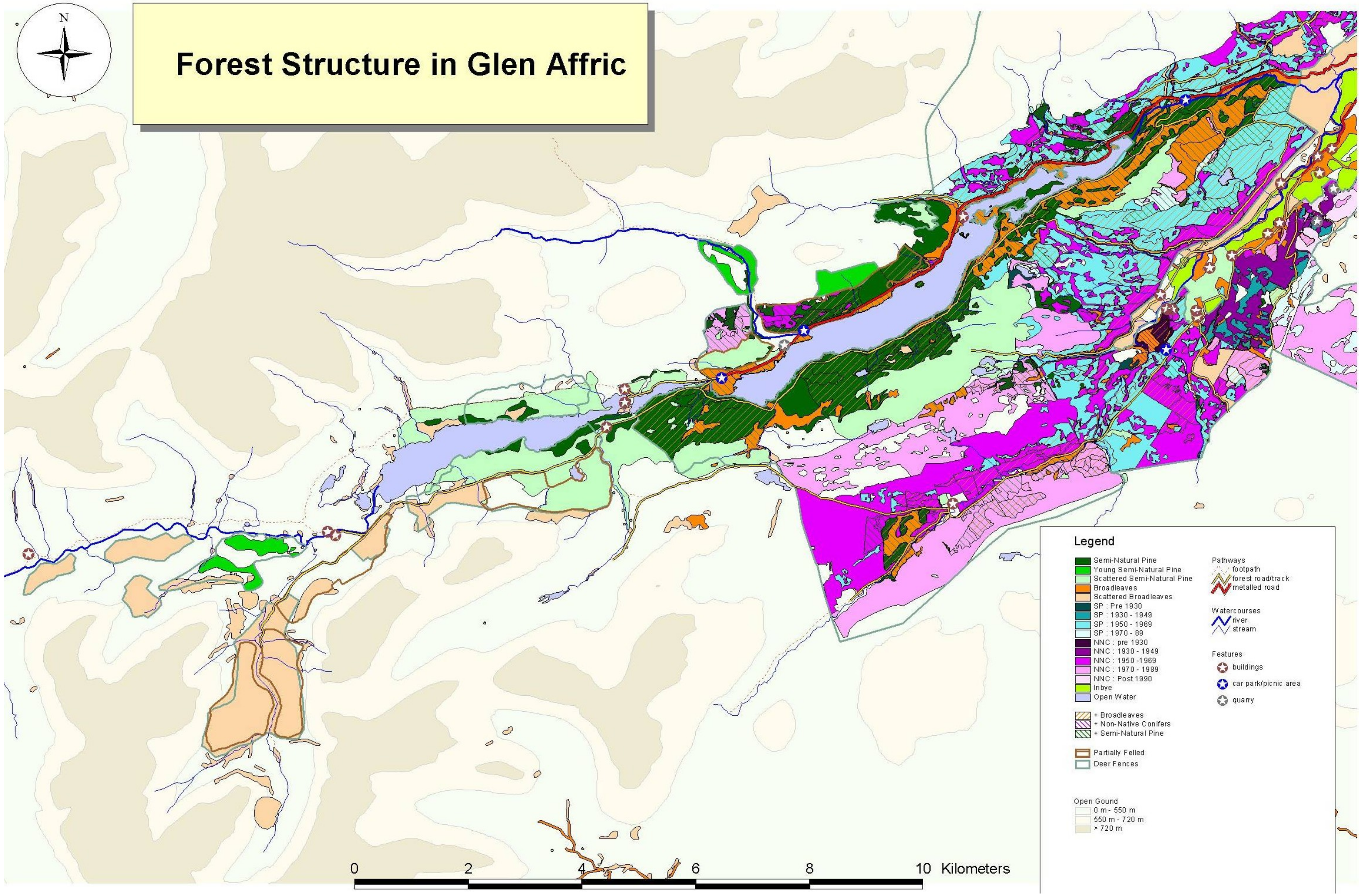

Figure 2.5: Map of the east Glen Affric study area showing vegetation types. Map created by Joe Hope

2.2.3 Factors affecting recent and current woodland structure and regeneration

2.2.3.1 Geography

Topography, soils, and climate are all thought to have an influence on vegetation in Glen Affric. Bell (2003 p32) identifies three altitudinal zones in Glen Affric. The Alpine zone, the sub-alpine zone and the Forest zone; the latter, below 550 m is the one concentrated on in this study. Bell describes this zone as moorland with the potential for closed-canopy woodland. (Bell 2003 p37). Pyatt (1994; 2003) has tested the ESC model (see Section 2.2.2.1) and found that soil variation affects vegetation communities whilst Quine (2003) identifies wind as the major disturbance agent in the Glen. Past climate and vegetation studies of west Affric (Davies 1999; Tisdall 2000) have identified that climate as well as human influence was likely to have been key to vegetation change. The woodland in west Affric was however, always different, and more mixed and *Quercus* dominated than the woodland to east, which forms the extant relict stand. The climatic variation, particularly the gradient in rainfall between west and east, may drive edaphic processes and prevent westward spread of *Pinus*. The presence of *Pinus* in the near surface of the pollen site at Torran Beithe (Davies 2003) together with the purported forestry activity in the Glen indicates that the ecotone may have been nearer to the head of Loch Affric in the past. This requires testing.

2.2.3.2 Human impact

Historical and archaeological records are rare from the glen beyond *c.* 250 years ago. There is some evidence of sheilings, and the presence of an ancient droving route. However, the Statistical Accounts for Scotland 1791- 1799 p406 note that there were, at that time, as yet no sheep farms in the parish of Kilmorack; although there were some sheep on each holding and black cattle were sent to market every year. By the time of the 1834-45 account (Fraser 1841; http://stat-acc-scot.edina.ac.uk/link/1834-45/Inverness/Kilmorack/) the rich pasture of the county is said to have been occupied by thousands of black-face and cheviot sheep although this account is for the whole parish and therefore does not always distinguish between lowland and upland areas.

Prior to the last *c*. 300 years human influence is likely to have been patchy, although evidence shows that Affric has been occupied by humans since at least 4000 BP, it is likely that occupation was limited to certain more favourable sites, such as alluvial fan deposits where soil nutrients were replenished (Davies 1999). These occur to the head of Loch Affric and may have occurred around Loch Beinn a Mheadhoin prior to the building of the hydro dam.

In the last 300 years Affric has been used variously for forestry, as well as subsistence farming, ranch style farming and hunting. The area was held as estate lands of the Clan Chisolm from the 15th Century to 1858. There was some forestry usage during these times, with sketchy records of tree felling as far back as 1560 (Smout 2006). The Statistical accounts for 1791-99 (p408) state that wood is the only manufacturing industry within the glen with "*many thousands of fir-trees cut annually in Lovat's the Chisholm's and Struie's woods*", again this refers to the whole Kilmorack parish taking in Glens Cannich and Strathfarrar. Caution must be used when assuming levels of forestry in any one of the glens.

In 1858 when the Chisolm Clan Chief died there were 6 tenants, no cattle and 30,000 sheep on the Affric estate, and from the 1860s to 1950 the Estate was used for sporting pursuits and the population of deer was maintained at high levels (Forestry Commission 1995). In 1951, the Forestry Commission purchased the estate, at this time little regeneration was occurring, and the Forestry Commission sought to recoup the purchase price by marketing the remaining timber. During 1951-1962, 33,000m^3 of timber was harvested from Glen Cannich, Glen Affric and Guisachan; again, it is unclear what proportion was harvested from each glen.

In 1959 the Annual Excursion of Foresters visited the Pine woods of Affric, following publication in 1957 of Stevens and Carlisle's book The Native Pine woods of Scotland. This formed a turning point in the management of Affric, which shifted focus from aims of commercial forestry to that of native woodland restoration in 1960. The first areas were fenced in 1962 to prevent further damage from grazing, and encourage regeneration. It is likely that some areas were also planted to kick-start the regeneration process. It is therefore difficult to assess if the current young pine trees are natural regeneration or a result of early management intervention.

2.2.3.3 Grazing pressure and pinewood age structure and regeneration

The pine woods were described in Steven and Carlisle (1959 p181) as being overall of uneven age structure, tending into groups of more similar age and with some very old trees and few young ones below 80 years. The authors describe a few groups of regenerating trees between 40 and 10 years in age, and some current regeneration. They also note that the regeneration on bogs is stunted and the young trees here are yellow in colour.

This lack of regeneration with age classes skewed towards older generations of trees is understood to correlate with changes in land use first for widespread sheep grazing and later for increased deer numbers for hunting purposes. Management planning of Glen Affric assumes a lack of woodland regeneration in many areas is due to grazing (Bell 2003; Bell 2003; Humphrey 2003; Pyatt *et al*. 2003; Quine 2003). In many areas exclusion fences were erected and regeneration recommenced; perhaps confirming the role of grazing in prevention of regeneration. However, Huntley (1991) claims that in many pine wood areas this assumption may be "*illusory*", and, in the case of Glen Affric two points (Section 2.1.3.3) are worth consideration:

1. Pine woodland has previously been found to regenerate in pulses lagging 20-30 years behind climatic change, and with a cycling of as much as 100 years between pulses (Zackrisson *et al*. 1995);
2. The forestry commission did kick start the process of regeneration by planting in the 1960s (Fowler 2002), it is possible that some of the regeneration we see today stems from this planting.

It is by no means clear how much regeneration there needs to be to maintain the woodland. Zackrisson *et al*. (1995) demonstrate, in north Swedish boreal forest, that 100-year pulses of regeneration are adequate for pine wood survival whilst Edwards and Mason (2006), from a dendrochronological study of four Scottish pine woods including Glen Affric, highlight the need to examine pine woodland regeneration dynamics in terms of 300 year cycles.

Additionally, although some woodland to the east has a closed canopy structure, the assumption that woodland should be maintained in a dense canopy structure does not seem to be supported by the presence of 'granny pine'[7] structural forms to many individual trees.

As mentioned above, Fenton proposes that the treeless habitats may be natural climatic and edaphic climax communities in many parts of Scotland (Fenton 1997), this is supported by evidence of stepped climatic change in the Glen (Tisdall 2003a; and Section 2.2.1.5). Some areas to the west of the glen are open wet moorland communities and may therefore have a limited scope for tree regeneration, which tends to favour the drier soils. The amount of open space that should remain at any time within the pinewood zone where edaphic factors are conducive to regeneration is not clear. Some open space is to be expected, but patch size, scale and longevity all require some clarification. A modelling project is attempting to do this (Hope 2003; Hope 2003; Hope *et al*. 2006).

2.2.3.4 Pine wood history

That the Glen Affric pine woods are presumed part of a relict larger forest degraded by human impact is not confirmed by evidence and requires further analysis. The Glen Affric pine woods have been subject to a full Holocene lake core pollen analysis which has identified local presence of *Pinus sylvestris* early in the Holocene, and continuously throughout the last *c.* 8000 years (Froyd 2005; Froyd and Bennett 2006). The woodland here may however be on the edge of its western range, and gives an opportunity to test the theories of a climatic deterioration (Fenton 1997; and Section 2.1.5 above).

Despite the supposition described in section 2.2.2, there is no real evidence to support the presumption of wider woodland extent in the more recent past. Regional pollen diagrams for Scotland indicate that Glen Affric is within the potential pine woodland range (Tipping 1994) and therefore have contributed to the logical interpretation that this area was once forested following successional processes after ice retreat, from approximately 7500 to 5000 years ago.

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[7] This is the term given to *Pinus* trees In Scotland that have a branched trunk and widespread canopy such as that of trees formed in open wood pasture where canopy spread is not limited by crowding as in denser forest.

This has been supported more locally since by Davies (Davies 1999; Davies and Tipping 2004) whose local scale work to the west of the glen demonstrated that this area was indeed wooded but with a dominance of broadleaved tree species rather than pine, and with that woodland canopy diminishing after *c.* 4000 BP. This contrasts with a study by Froyd (2001; 2005) who carried out a pollen analysis to the east alongside Loch Beinn a Mheadhoin. This study demonstrated an interesting longevity of woodland or, at least, scattered Pine trees, within the catchment of Loch an Amair, including very early Scots Pine presence prior to that expected at around 7500 BP and a continued presence of *Pinus* trees through to the present day stand.

These studies raise interesting, and unresolved questions about the relationship between the forested east and unforested west after the *c.* 4000 BP pine decline. Froyd (2001; 2005) clearly demonstrates that the pine decline is not synchronous over the Highlands as previously thought, and that woodland or trees have remained in Glen Affric throughout the latter part of the Holocene, thus supporting the relict theory for the east Affric woodland. Davies (1999; 2003) demonstrates that the findings from Loch an Amair cannot be extrapolated throughout the glen as she finds evidence of classic pine decline *c.* 4400 BP at her site and increasingly open moorland thereafter. Davies also raises questions about the assumptions of pine wood dominance in an area so close to the east-west boundary and suggests a possibly complex pattern of woodland composition.

Preliminary local scale palynological studies within the existing pine woods indicate that woodland may be cycling naturally in Affric (Fitzgerald 2001; Wolff 2003; Wolff and Tipping 1999), however this information is limited in both spatial and temporal extent, being studies from short, or incomplete, cores from single sites.

Presence of human occupation in Glen Affric from *c.* 4000 BP is suggested to the west (Davies 1999). In addition, there is an old drover's route running through the glen to the south of the lochs from Morvich and Kintail to the sea. Davies surmises that the human occupation of the glen would have been limited to the more fertile land, in pockets of alluvial soils. It is still therefore debatable how much disturbance and influence humans have had to the east of Glen

Affric and if the *restoration* goal in Affric is completely warranted on grounds of naturalness. Furthermore considerable patch scale dynamics are indicated; and the extent of openness in pine woodland is not confirmed. Under the circumstances it is possible that the continuance of structural openness and dynamics may be essential for the future to sustain a healthy forest and maximise potential biodiversity.

2.2.3.5 Pine wood ecotone

Currently woodland canopy and *Pinus* are contained to the east of Glen Affric; to the west an open blanket bog community is dominant, with tree presence gradually diminishing westward. The reason for this gradient is unclear. The landscape scale pollen analysis from Loch an Amair (Froyd 2001) demonstrates that woodland and *Pinus* have been present in the east Glen Affric landscape since the early Holocene escaping any possible *Pinus* decline at *c.* 4400 BP (section 2.1.2.2). The local scale pollen diagram from Torran Beithe (Davies 2003) does however show a significant decline in *Pinus* at *c.* 4100 cal. BP. However, the presence of *Pinus* pollen and stomata in the Torran Beithe pollen diagram until *c.* 490 cal. BP, together with information from Roy's military survey map, of trees in Glen Affric in 1750, indicates recent receding of the woodland eastward possibly due to recent human intervention. Davies (2003) however, postulates that the low *Pinus* and arboreal pollen percentages at the Torran Beithe site meant that the wider landscape was relatively treeless since *c.* 2000 cal. BP. In addition *Pinus* was never dominant to the west (Davies 1999). The change in edaphic factors between east and west of the glen could also indicate that the gradation into open heath represents an ecotone, with some western *Pinus* populations resisting the *Pinus* decline for longer on areas of more suitable and freer draining substrate such as Torran Beithe. This hypothesis would lead to the view that the current stands in Glen Affric are of pine woodland at the edge of its western climatic range.

2.2.4 Conservation management requirements

Part of the management work in the Glen Affric reserve is implemented and guided by the 'Trees for Life' organisation, who plant trees cultivated from native local seed sources. Due to its perceived naturalness Glen Affric also forms a case study area for native woodland research and has been the subject of a variety of studies into the potential for future forest and the best practice for management of native pine woodlands (see Bell 2003) including modelling the natural dynamics of woodlands through time. The modelling approach will aim to use the Glen Affric example to add information about natural structure into forest plan and design models by examining patterns and dynamics of natural processes (Bell 2003). The modelling tool requires further information on ecological process over timescales suitable for tree species to validate the outcomes (Hope 2003).

Many assumptions and ideas require further analysis, indeed as Quine observes (2003) "There is little local evidence on which to base a view of the natural forest". Patch size, species mix within communities, and past and future extent of woodland all require validation. Palaeoecological work of the type undertaken in this study will contribute to ecological modelling and management of the woodlands.

2.3 Aims and objectives of this study in relation to Glen Affric and native pine woodlands in Scotland

The overarching aims of this thesis in relation to Glen Affric are therefore:

- To provide a pollen based reconstruction of the woodland history in the extant forest zone; and,
- To investigate the former westward extent of the pine woodland.
- To contribute to management tools in development by the Forestry Commission by providing information on the history of the extant pine woods for ecological understanding and for input for a model to predict the effects of forest design and management in Glen Affric
- To contribute to the development of a more quantified approach to fine spatial scale palaeoecology in semi-open woodland landscapes.

Specific questions for investigation and testing in this thesis are

- What is the history, structure and longevity of the current breakdown and opening of woodland to the west?

- What is the stand scale longevity and variation within the existing and purported relict woodland alongside Loch Beinn a Mheadhoin?
- What are the differences in species composition between present and past stands?
- Is there evidence of *Pinus* and *Betula* as mixed stands or in patterns of temporal cyclicity?
- What is the former structure of the ground flora and how has this changed through time?

3 Research strategy, methods, and sites selected

3.1 Research Design

Several factors influence the scale and precision possible in an interpretation of vegetation history and ecology through pollen analysis and therefore require consideration in the research strategy:

1. Site selection: basin size, type and substrate, which affect ecological and spatial interpretations via;
    a) The source of fossil pollen and associated depositional bias,
    b) The source area for pollen and associated scale of vegetation reconstruction.
2. A quantifiable relationship between pollen and vegetation.
3. The chronological precision and chronological controls;
    a) The derivation of chronologies
    b) The choice of a suitable temporal resolution (both grain and extent)
4. Taxonomic precision in pollen identification.

3.2 Spatial considerations of site selection

The type of vegetation reconstruction potential from any pollen analysis is dependent on site conditions in and around the basin of deposition. Conditions *in* the basin affect the taxonomic and preservational bias of the pollen assemblage whilst conditions *surrounding* the basin, and basin size, affect the pollen source area according to a model proposed by Jacobson and Bradshaw (1981; see Figure 3.1) and therefore the potential for spatial precision of the interpretation.

3.2.1 Choice of fossil pollen source

The pollen exine is highly resistant to decay especially in anaerobic and or acidic conditions. The main substrates for fossil pollen are lake sediments, peats, mor-humus and soils, each of which suffers from its own unique forms of depositional and diagenetic bias.

Soil can form a problematic substrate for palaeoecological study. The aerobic preservation environment of soils can lead to exine damage, rendering identification more difficult, or to differential decay in less resistant pollen. These factors can result in bias in the vegetation reconstructions (see for example Cushing 1967; Davidson *et al.* 1999). In addition, the microbial and biological activity in aerobic soils can lead to considerable reworking of the sediment, leading to insecure stratigraphies. Soil pollen is probably best used only in areas where peat and other wet deposits are not available.

Lake deposits can give highly accurate temporal scales through annually laminated, or varved, sediments; however, the temporal precision can be misleading. Pollen within each layer can be deposited from reworked sediment or differentially mixed in the water column before deposition (Jacobson and Bradshaw 1981). Lakes also tend to have a large surface area, which acts to trap pollen from a wide source area, and through which surface mixing takes place (Sugita 1993).

Peat deposits have been used for pollen analysis since Von Post's original work in 1916 (Jacobson and Bradshaw 1981). Peat provides an anaerobic depositional environment where mixing and reworking are likely to be minimal. Recent studies in New Zealand have found that moss cushions give a more accurate reflection of surrounding vegetation than lake sediments, which contain reworked pollen and spores (Wilmshurst and McGlone 2005). It seems therefore that peat deposits will be more suitable for local scale studies and will be used for this analysis.

3.2.2 Testing the pollen source area

As highlighted in Chapters 1 and 2, valuable examples of spatially precise pollen analysis exist. The approach to their reconstruction is to use pollen derived from small hollows or basins within woodlands to attain local-scale palaeoecological reconstructions according to the model relating pollen source area and basin size (Jacobson and Bradshaw 1981; Figure 3.1; Section 1.3). The selection of small hollows as a source of pollen is therefore standard for 'stand-scale' studies.

However, the degree to which the small hollow approach may detect stand scale openness or quantitatively define canopy cover is questionable (Section 1.3). In cultural landscapes the open land component of the vegetation may not be visible in a pollen interpretation (Broström 2002). It is unclear what differences there may be in a semi-natural boreal forest landscape.

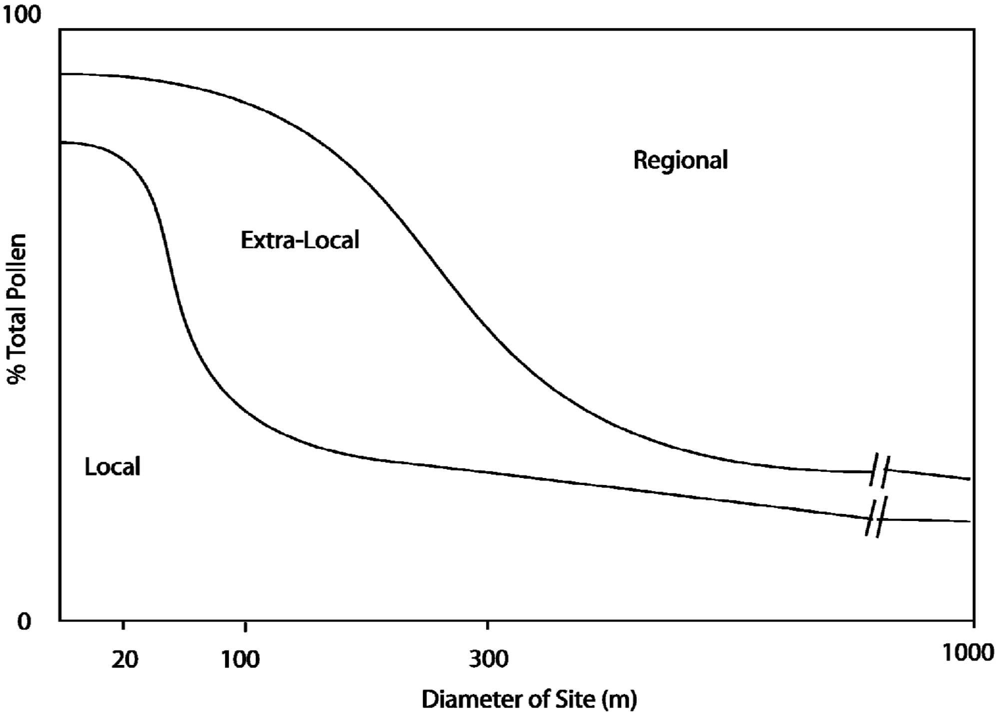

Figure 3.1: The relationship between the size of basin and the relative proportions of pollen from the local, extra-local and regional vegetation in a closed canopy landscape (redrawn from Jacobson and Bradshaw 1981) demonstrating that pollen source area is related to basin size.

Unlike in cultural landscapes, where the agricultural environment comprises low pollen producers, in Scotland studies have shown that the bog surface itself contains many taxa that are themselves high pollen producers (Fossitt 1994). These taxa often additionally form the matrix of ground flora in the surrounding landscape, and this is certainly the case in Glen Affric. The extent to which flora from the basin surface can influence the pollen interpretation in these environments is unclear. This has lead Jacobson and Bradshaw (1981) to suggest that bog surface taxa may be a confounding factor in the accuracy of reconstructions from peat deposits. In the case of local scale studies, however, the dominance of the basin surface vegetation may be less important, as the basin surface is small and the local vegetation is the object of study. Thus high pollen production may help to determine woodland canopy cover, via a high NAP input. This may vary from the situation in cultural landscapes where pollen production may be low due to grazing pressures or low pollen producing taxa.

To reconstruct the dynamics of the semi-natural woodlands of Glen Affric it is important to be able to understand and evaluate the pollen source area and quantify arboreal canopy cover in a landscape in which the variation in vegetation types between woodland and open land is subtle. The relationship between pollen and vegetation in these semi-open landscapes therefore requires further testing and such testing is the subject of Chapter 5.

3.2.3 Multiple site selection

This study in Glen Affric is concerned with determining not only woodland variation, but also any waxing and waning of stand presence within the landscape.

To achieve the aims of this thesis the pollen analysis must identify stand scale changes in forest structure across the landscape. To gain this detailed landscape interpretation several separate pollen analyses are required (Section 1.3) and the analyses should form a network of sites. This approach relies not only on the determination of pollen source area and quantitative vegetation reconstructions, but also on secure chronologies as discussed below.

The network approach to sampling peat deposits from small hollows forms a tried and tested research design for deriving stand-scale palaeo-histories of woodlands. However, two major areas are problematic for pollen analysis using a network of sites:

1. The quantification and testing of pollen-vegetation representation and pollen source area in open canopy woodlands and the ability to recognise and define scales of openness
2. The ability to correlate between cores by developing a secure chronology in recent peat.

These aspects of the study are therefore dealt with more fully in separate chapters (Chapter 4 and 5) contributing to the palaeo-historical interpretation in Chapter 6. The remainder of this chapter introduces the sites selected for study in this thesis and outlines the basic methods used in the research. Specific research methods are outlined in the relevant research chapters.

3.3 Sites selected

Two major aspects of investigation guided the location of sites within Glen Affric (Section 2.3):

- To gain information on the possible east-west ecotone alongside Loch Affric and
- To gain information about the longevity and variation within the existing, and purported relict, woodland stands alongside Loch Beinn a Mheadhoin.

The perfect sampling site would be a distinct small hollow under 20m in diameter (Jacobson and Bradshaw 1981), with no inflow or outflow, and in a peat which stayed wet year round to maintain the optimal anaerobic conditions for pollen preservation (Section 3.1). Although Glen Affric contains much peat and many small hollows and blanket bogs, the realities of the field are of course different from the ideal. Much of the land in Glen Affric is steeply sloping and many of the hollows and depressions are fed by burns and are interlinked by channels and overlying blanket peat deposits. In addition, smooth bottomed basins are non-existent, with most basins highly variable in depth due to the nature of the rocky glacial moraine deposits. The peats were similarly highly variable in texture and humification, raising some concerns over the possibility of variable accumulation rates.

Eight cores (Figure 3.2) and a further 22 surface samples were collected and analysed (further surface samples were collected but pollen yields were low and therefore these sites were not used in the analysis).

The eight sites selected for fossil pollen analysis are shown on the map in Figure 3.2. Sites were selected in areas forming three main clusters along an ENE/WSW transect through the lower forest zone within east Glen Affric. Cluster 1 comprises NHP, PB, and BEAT and is located in the region to the west where the stands become sparse. This cluster should enable some investigation of the possibilities of recent eastward retraction in woodland. Cluster 2 comprises two sites; one on a hillslope (ANI); and, one in a wetter flush area (ARC), where currently there is a trend towards W17 woodland comprising abundant *Vaccinium myrtillus* under a *Betula* canopy with some *Alnus* by the streamside flush. The longevity of the *Betula* dominated stand and the history of any dynamics with *Pinus* is of interest here. Whilst further to the east Cluster 3, comprising CLH CLP2 and CLKH, is in a zone of brown earths where woodland is mixed and a few *Quercus* occur. The history of *Quercus* and the longevity of the mixed woodland, and any fluctuations in arboreal taxa abundance are of interest here.

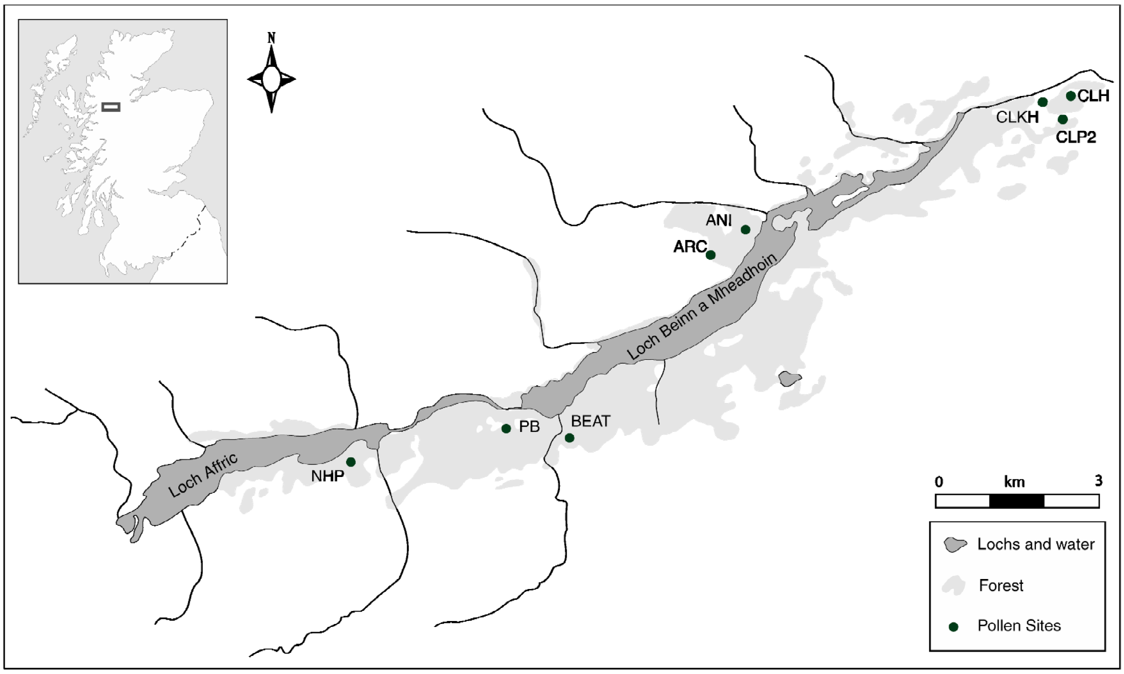

Figure 3.2: Map of Glen Affric showing the location of sites used for pollen core analysis

For all core sites basins were surveyed using an Eikelkamp corer to examine maximum depth on a metre transect. Basin diameter was also recorded.

Vegetation abundance was quantified around each site for use in the analysis of modern analogues. Percentage herbaceous and Ericaceous cover was recorded to 20 m in 1, 2, 3, 4, 5, 5-10 and 10-20 m diameter rings. Tree cover was recorded and approximate position marked within these rings and additionally to 50 m in 10 m ring increments. Methods for the study of pollen-vegetation relationships are discussed further in Chapter 5.

3.4 Core collection and description

The eight cores for historical analyses were taken using a 100 cm Russian Sampler. The top *c.* 30 cm was found to be inadequate via this method; firstly, a larger sample volume was required for ^{210}Pb dating; and secondly, the lack of compaction in the top layer leads to a loosely packed sample in the Russian corer. It is unclear if the sampler is recovering the topmost sediments as the sediments could be extruded upwards in the sampling chamber thus producing temporal sampling errors in the surface layers. The top 50cm was also therefore extracted from a second hole within *c.* 10 cm lateral distance of the first with a modified golf hole corer (Tyler *et al.* 1996). This method gave sufficient sediment for ^{210}Pb assays as well as ensuring a more reliable stratigraphy to the topmost sediment.

Surface sediments were collected using a short golf-hole corer for the additional 23 modern analogue samples with only the top 1-2 cm (depending on compaction) sub-sampled for modern analogue analysis. Cores were described prior to sub-sampling using the modified Troels-Smith method of classification (Aaby and Berglund 1986). Compaction, humification, colour and texture of the sediment were all recorded along with any visible wood or charcoal fragments.

Loss on ignition was not recorded due to insufficient material in the surface sediments after bulk sampling for ^{210}Pb chronologies. Collection of monolith tin samples was considered; however, their use is very destructive to the sampling area with digging required (Sansum 2005) and their use in a site of National Nature Reserve and SSSI status was not considered appropriate.

3.4.1 Site and Core descriptions

3.4.1.1 Cluster 1

NHP

This site at NH17441 22153 (Figure 3.4) is the most westerly sampled (Figure 3.2). It is a small peat filled oval basin 12 metres by 9 metres in diameter situated between small vegetation covered rock outcrops on a slope beside Loch Affric. Currently the site is within a woodland stand comprising mature pine trees (see photograph in Figure 3.3). The site is in a small open glade: 2 trees occur within 10 metres of the site, 21 trees within the 10-20 metre radius, and 164 trees within 50m radius (all mature *Pinus sylvestris*). Ground vegetation is dominated by Poaceae with some Cyperaceae in the basin flushes and *Vaccinium myrtillus*/*Calluna* *vulgaris*/*Empetrum nigrum* on the rocky outcrops. *Sphagnum* occurs within the basins whilst *Hylocomium* occurs on the rock outcrops under the *Vaccinium* and *Empetrum*.

The woodland becomes patchy to the west of this stand (see the photograph in Figure 2.4). This site is therefore selected to investigate the dynamics of a possible ecotone at this current east-west transition into open moorland.

The basin has an uneven and variable rocky floor, and the maximum depth is consequently variable. Peat directly overlies this rock. A maximum depth of 170 cm was recorded with the Eikelkamp corer. Cores were taken with the modified Golf Hole Corer to 47 cm and with the Russian type sampler from 28 to 128 cm. A stratigraphic description of the core is given in Table 3.1. There are no obvious discontinuities in the stratigraphy; a visual examination demonstrates a gradual increase in humification with depth. An age depth curve (Section 4.3.4.1) predicts that the topmost 100 cm of the core represents a time-span of *c*. 0-2850 years.

Table 3.1: Description of the peat stratigraphy for the NHP core.

Depth Interval (cm)	Colour	Brief description	Troels-Smith classification
0-1	Green	Non-humified fresh *Sphagnum* and Cyperaceae	Tb^{0}3 Th^{0}1
1-3	Yellow Brown	Non-humified *Sphagnum* and Cyperaceae	Tb^{0}3 Th^{0}1
3-7	Mid brown	Poorly humified Roots/*Sphagnum*	Th^{1}3 Tb^{1}1
7-13	Brown	Gradually more humified peat with some fibrous plant matter	Th^{1}2 Sh+ Dh^{1}2
13-28	Gradually darker	Gradually more humified peat with decreasing fibrous plant matter	Th^{2}1 Dh^{2}2 Sh1
28-68	Dark Brown	Humified amorphous peat with frequent red root Fragments	Dh^{3}2 Sh2
68-72	Dark Brown	Humified amorphous peat with wood fragments at 70 cm	Sh^{3}3 Dh^{3}1/2 Dl^3+
72-89	Dark Brown	Humified amorphous peat	Sh3 Dh^{4}1
89-112	Dark Brown	Humified amorphous peat wood fragment at 89 cm	Sh3 Dh^{4}1
112-117	Dark Brown	Humified amorphous peat	Sh3 Dh^{4}1
117-128	Dark Brown	Humified amorphous peat	Sh4

Figure 3.3: Photograph of the NHP site – pine trees in the surrounding stand looking to the west from the basin.

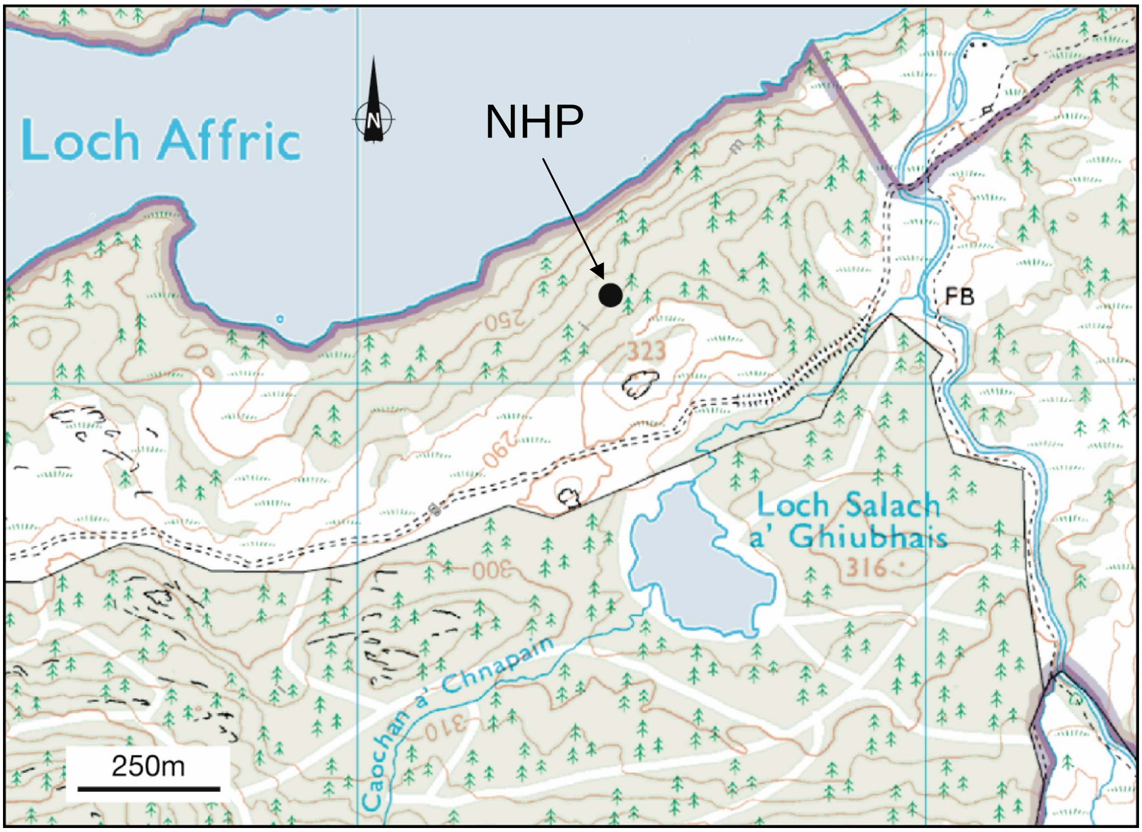

Figure 3.4: Map detail and location of the NHP site – for wider location map see Figure 3.2.
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PB

This site at NH19791 23041 (Figure 3.5) is situated to the east of NHP, but still towards the westerly extreme of the study area (Figure 3.2) and at an altitude of approximately 250 m. The basin is a peat filled depression *c.* 24 metres in diameter with a raised slope surrounding in a horseshoe shape. The basin is situated above, and drains into the Pollan Buidhe, a larger bog complex with a stream running through it at NH197 231. Currently the site is within a degenerating woodland stand comprising mature pine trees and some snags. There are just six mature *Pinus* trees within 20 metres of the core location, and 36 mature *Pinus* trees within a 50 m radius. *Betula* is present; with one tree within 20 m and eight trees within 50 m. Ground vegetation is dominated by *Calluna* (see photograph in Figure 3.6), which covers the surrounding slopes and has invaded the basin surface together with *Molinia* and *Deschampsia flexuosa*. *Sphagnum* and *Hylocomium* occur in patches under the *Calluna*. *Vaccinium myrtillus, E. tetralix*, *E.cinerea* and *Empetrum* all occur in small patches under the dominant *Calluna* canopy; *Myrica gale* is also present and *Potentilla erecta* was the only other herbaceous species evident at the time of sampling.

The peat in this basin is compacted and solid, with very little moisture content. A stratigraphic description is presented in Table 3.2.

Table 3.2: Description of the peat stratigraphy for the PB core

Depth Interval (cm)	Colour	Brief description	Troels-Smith classification
0-2	Fresh Green	Non-humified sedge some Sphagnum	Tb^{0}2 Th^{0}2
2-10	Red-brown	Part humified sedge strands and rootlets	Th^{1}3 Tl^{0}1
10-30	Dark red-brown	Gradually darker and more humified but still with sedge and rootlets	Th^{2}2 Sh2
30-39	Dark brown	Darker brown gradually more humified	Th^{3}1Sh3
39-135	Dark brown	As above: sticky dark fine textured matrix with some sedge fragments	Sh4 Dl+ Th^3+
40		Dark charcoal band	
70-72		Wood Fragments	
80-84		Wood Fragments	
98-99		Wood Fragments	
112-114		Wood Fragments	
123-125		Wood Fragments	

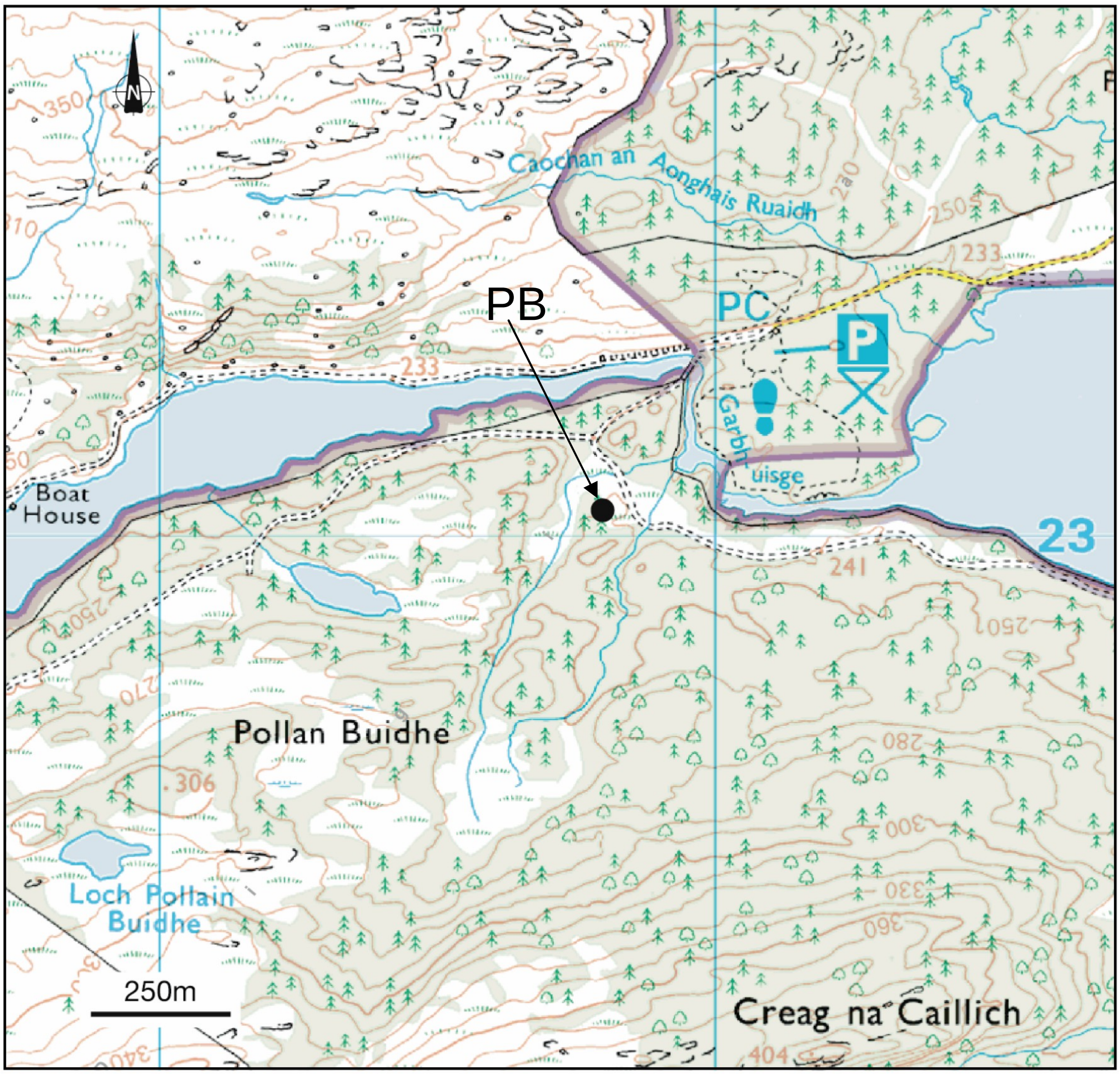

Figure 3.5: Map detail of the PB site – for wider location context see Figure 3.2
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Figure 3.6: Photograph of the PB site – set in a *Calluna* dominated basin, with scattered pine trees in the surrounding stand. This view looks to the north from the basin.

BEAT

This site at NH 21150 22630 is to the east of PB and NHP (Figure 3.2), towards the west end of Loch Beinn a Mheadhoin on a north facing slope at an altitude of approximately 250 m (Figure 3.7). The site is a peat-filled flush 12 by 20 m in diameter. The flush drains to the north into a larger sloping bog complex in semi-natural woodland to the east of the Allt an Laghair. Currently the site is within a mixed woodland stand comprising mature *Pinus* and *Betula* trees. There are two mature *Pinus* trees and one *Betula* within the 4-5 metre radius of the core, and 23 mature *Pinus* trees within a 50m radius and 87 mature *Betula*. Some young regeneration is also recorded. A single *Salix* stands to the south-east, 20 metres from the sample point. Ground vegetation surrounding the site is dominated by *Calluna* with other Ericales contributing to the diversity as an under-storey. *Pteridium* is also frequent around the site. *Sphagnum* dominates the basin surface accompanied by Poaceae and some Cyperaceae (Figure 3.8). *Potentilla erecta* is frequent on the basin surface and the wood horsetail, *Equisetum sylvatica,* is also present.

The peat in this basin to *c.* 65 cm is fibrous and uncompacted, then gradually more humified to depth. The surface of the basin remains wet throughout the year. A stratigraphic description is presented in Table 3.3. The chronology accepted for this core is subject to a large shift in accumulation rate at 67 cm (Section 4.5.4). The ^{14}C assays at 46 and 67 cm return dates possibly biased by modern carbon. The 100cm base of the sampled depth does, however, return a secure ^{14}C assay of 1975± 25BP. The full basin depth is approximately 260 cm.

Table 3.3: Description of the peat stratigraphy for the BEAT core.

Depth Interval (cm)	**Colour**	**Brief description**	**Troels-Smith classification**
0-1	Green	Fresh green non-humified *Sphagnum*/Cyperaceae	$Tb^0 2$ $Th^0 2$
1-6	Yellow-brown	Non-humified *Sphagnum*	$Tb^0 2$ $Th^0 2$ $Tl^0 +$ $Dl^0 +$
6-11	Yellow-brown to mid-brown	Loose barely humified *Sphagnum*/Cyperaceae peat and fine roots	$Tb^1 1$ $Th^1 1$ $Tl^1 +$ Sh1
11-46	Mid-brown	Poorly humified amorphous peat matrix with abundant fine roots and fibrous plant material Some large wood fragments at 13 and 37 cm	$Tb^1 1$ $Th^1 1$ $Tl^1 +$ $Dl^1 +$ Sh1
46-100	Red-brown	As above but redder brown gradually more humified with less fibrous material in the matrix	$Tb^2 1$ $Th^2 1$ $Tl^2 +$ Dl+ Sh2

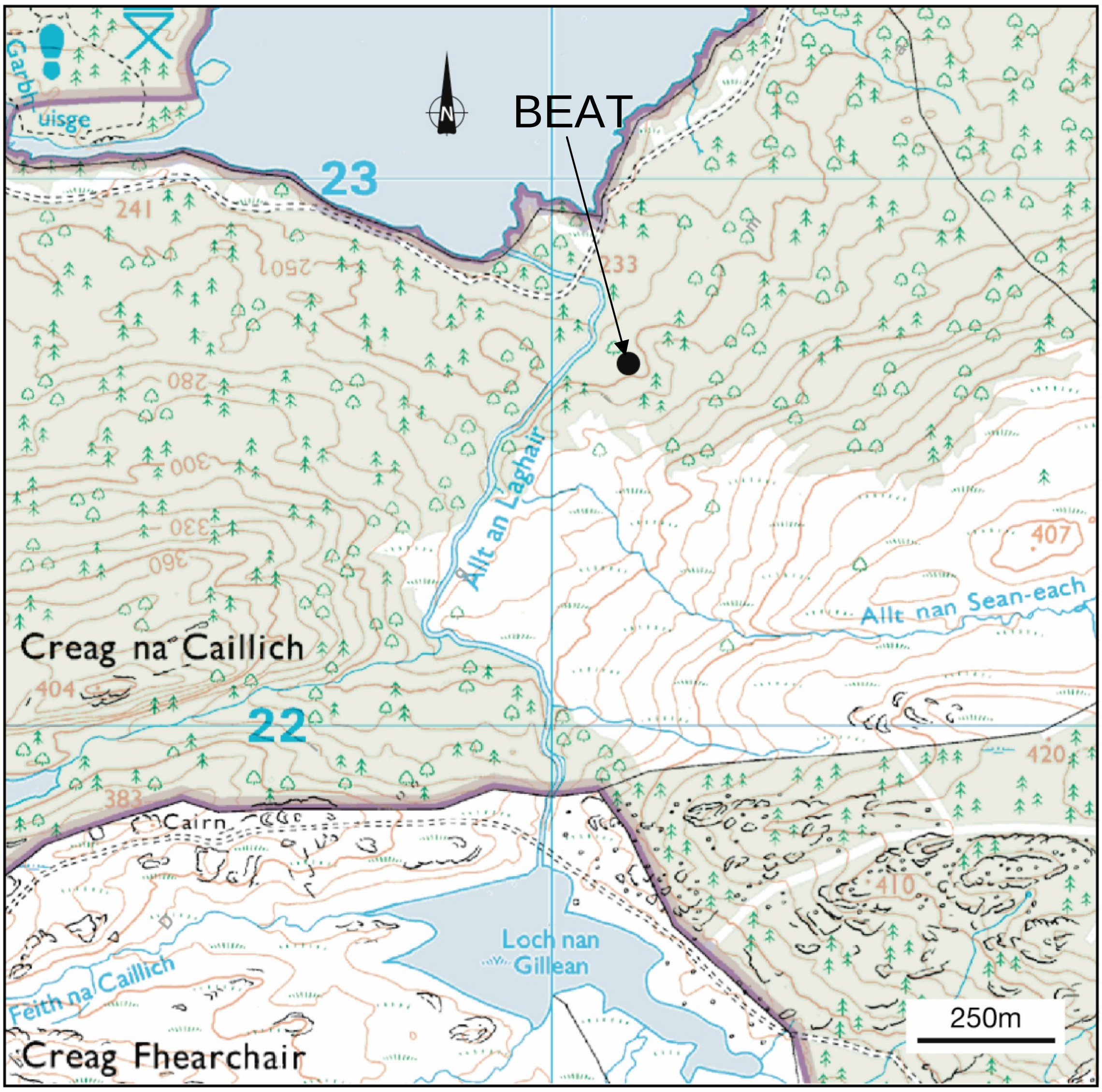

Figure 3.7: Map detail of the BEAT site – for wider location context see Figure 3.2

Figure 3.8: Photograph of the BEAT site – a flush surrounded by Pine and Birch woodland

3.4.1.2 Cluster 2

ANI

ANI is a broad Poaceae-rich flush site at the base of the south facing slopes beside Loch Beinn a Mheadhoin at grid reference NH 24239 26328 (Figure 3.2 and 3.9). The flush is *c*. 20 m X *c*. 28 m in diameter and is situated between the base of a steep bedrock slope and a stream: the Allt na h-Imrich. A bedrock outcrop high above the site has some *Pinus* trees on its crest, but immediately surrounding the basin is a mature *Betula*-dominated open woodland with some *Alnus* and *Sorbus aucuparia*. The ground flora of the flush is dominated by Poaceae, but the surrounding vegetation mosaic is of hummocks created by tree stumps, or possibly in some cases wood ant nests. These hummocks are covered in *Vaccinium myrtillus* (see photograph in Figure 3.10). *Calluna* is very sparse within the surrounding 20 m. *Potentilla erecta* and *Anemone nemorosa* are frequent plants.

Basin depth is variable, but not more than 125 cm. The core sampled was to 122 cm. A core sediment description is presented in Table 3.4.

Table 3.4: Description of the peat stratigraphy for the ANI core.

Depth Interval (cm)	Colour	Brief description	Troels-Smith classification
0-1	Green	Fresh green *Sphagnum* some Cyperaceae	Tb^{0}3 Th^{0}1
1-2	Yellow-green	Yellow *Sphagnum* and Cyperaceae	Tb^{1}3 Th^{1}1
2-9	Yellow-brown	Gradually darker and more humified fibrous with rootlets	Tb^{1}3 Th^{1}1 Dl^0+
9-19	Brown	Solid dark humified peat with rootlets	Sh2 Tb^{2}1 Th^{2}1 Dl^0+
19-29	Dark brown	Dark humified peat more fibrous and less solid than above. Wood fragments at 29 cm	Sh1 Tb^{2}1 Th^{2}2 Dl^0+
29-52	Dark brown	Gradually darkening and more humified with wood fragments at 40-42 cm	Sh 2Tb^{3}1 Th^{3}2 Dl^0+
52-122	Dark brown	Dark humified Cyperaceae peat with wood fragments some mineral flecks at base	Sh2 Tb^2+ Th^{2}2 Dl^0+

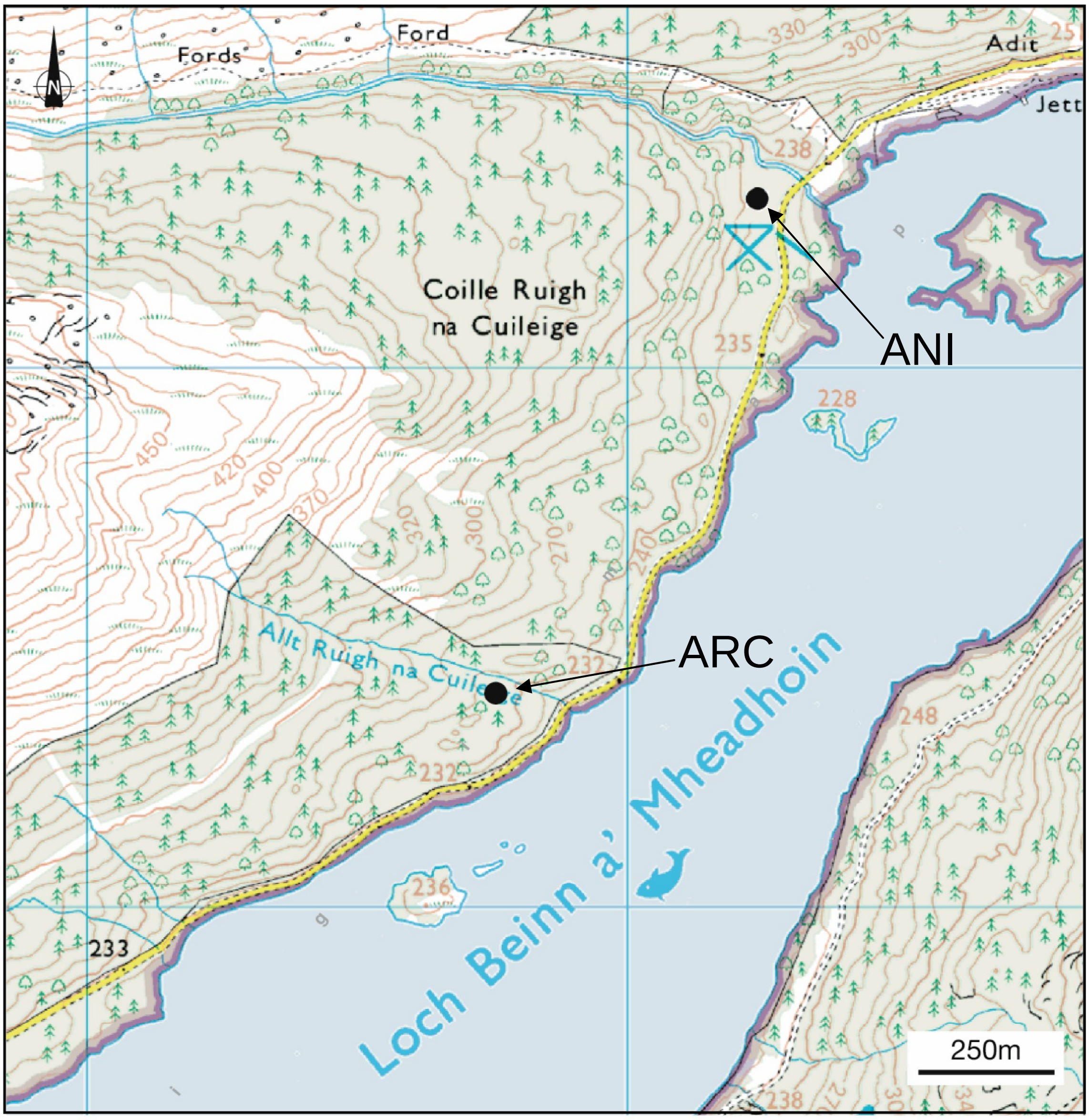

Figure 3.9: Map detail of the ANI and ARC sites – for location see Figure 3.2
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Figure 3.10: Photograph of the ANI site – a flush surrounded by birch with *Vaccinium* dominant in the ground flora.

ARC

The ARC pollen core is taken from Coille Ruigh na Cuileige on the south facing slopes of the hillside above Loch Beinn a Mheadhoin at grid reference NH23786 25360 (Figure 3.2 and 3.9). The site is currently surrounded by mixed woodland with *Betula* dominating the semi-open canopy. The basin is a small depression just 1.1m deep at its deepest point and measuring 6.5 metres by 12.5 metres in diameter situated between hummocky outcrops of *Vaccinium*-covered free draining moraine (Figure 3.11). There are one pine tree and 20 birch trees within a 20 m radius of the sample point, and 14 Pine and 72 Birch within 50 m. In addition, there are some scattered young regenerating pine and birch trees. The surface of the basin is dominated by Poaceae, with some *Vaccinium*, and the surrounding vegetation is dominated by *Vaccinium*, with Poaceae, with some Cyperaceae and *Juncus*. *Potentilla* and *Oxalis* are frequent herbs.

Coring recovered sediment to 85 cm only, due to an irregular base to the peat hollow. The sediment stratigraphy is described in Table 3.5.

Figure 3.11: Photograph of the ARC site – *Betula* and *Vaccinium* in the surrounding stand looking to the north from the basin.

Table 3.5: Description of the peat stratigraphy for the ARC core.

Depth Interval (cm)	Colour	Brief description	Troels-Smith classification
0-1	Green	Green non-humified *Polytrichum* and *Hylocomium*	$Tb^0 4$
1-2	Yellow-green	Non-humified *Polytrichum* and *Hylocomium*	$Tb^0 4$
2-6	Yellow/brown	Slightly humified fibrous moss peat	$Tb^1 4$
6-8	Yellow/brown	As above possible charcoal band	$Tb^1 4Dl+$
8-48	Yellow-brown	Slightly humified moss peat gradually darker and more humified. Wood fragments at 9-10 and 38 cm	$Tb^2 4Dl+$
48-68	Mid brown	Humified moss peat, some wood fragments	$Tb^3 4Dl+$
68-85	Dark Brown	Humified Cyperaceae peat with wood fragments and large charcoal fragments at 60 cm	$Th^1 4Dl+$

3.4.1.3 Cluster 3

CLH

This site, at NH29571 28135, is a small peat-filled depression only *c.* 84 cm deep and 4 m across situated adjacent to the flush site of CLP2 (Figure 3.2 and Figure 3.13). Currently the site is within a mature area of semi-open woodland (see photograph in Figure 3.12). One *Pinus* and one *Betula* tree occur within 10 m of the coring point. A further 10 *Pinus* and 10 *Betula* are present within 20m and 38 *Pinus* and 11 *Betula* within 50 m, together with several small saplings. Vegetation on the basin surface is dominated by Poaceae and Cyperaceae, and *Sphagnum* occurs under this ground flora layer. The surrounding vegetation has a luxuriant growth of *Calluna*, interspersed with Poaceae/Cyperaceae flushes.

A peat stratigraphy is presented in Table 3.6 and shows a gradual shift from *Sphagnum* peat at the surface to amorphous well humified peat. Some mineral inwashing occurs at the base of the core.

Figure 3.12: Photograph of the CLH site – *Pinus* in the surrounding stand looking to the west from the basin.

Table 3.6: Description of the peat stratigraphy for the CLH core.

Depth Interval (cm)	Colour	Brief description	Troels-Smith classification
0-1	Green to brown	Non-humified *Sphagnum* with *Betula* leaves and some Cyperaceae	Tb^{0}3 Th^{0}1
1-24	Red-brown	Poorly humified with rootlets and some wood fragments	Tb^{1}1 Th^{1}1 Tl^{1}1 Sh1
24-31	Dark-brown	Amorphous peat with wood fragments	Sh^{3}3 Dl^{2}1
31-45	Dark-brown	Amorphous peat with roots	Sh^{3}2 Tl^{2}1
45-67	Dark-brown	Amorphous peat with wood fragments	Sh^{3}3 Dl^{2}1
67-85	Darker-brown	Amorphous peat with wood fragments	Sh^{4}3 Dl1
85-88	Dark-brown	Amorphous peat with wood fragments, some mineral grains at base	Sh^{4}4 Dl+

CLKH

This site, at NH29398 28306, is a wet, steep-sided hollow between rock outcrops in the woodland above Dog Falls (Figure 2.2, 3.2 and 3.13). The basin measures approximately 20m across from north to south, but opens to a wide continuous grassy flush through a narrow opening to the east. The nature of the surrounding rock outcrops indicates, however, that this basin should behave effectively as a small hollow for pollen recruitment. The hollow surface lies well below the surrounding vegetation, which is present on rock outcrops (Figure 3.14). The basin is deep; containing 4.62 m of peat with a very wet, fibrous and uncompacted stratigraphy. The surrounding arboreal vegetation is mixed, and the canopy cover is light. The site lies within a mature area of semi-open woodland. Four small *Betula* trees are present on the basin surface within 10 m of the coring location. One *Pinus* and eight further *Betula* trees occur within 10 – 20 m of the coring point, and these are accompanied by single *Quercus*, *Corylus* and Juniper trees/bushes.

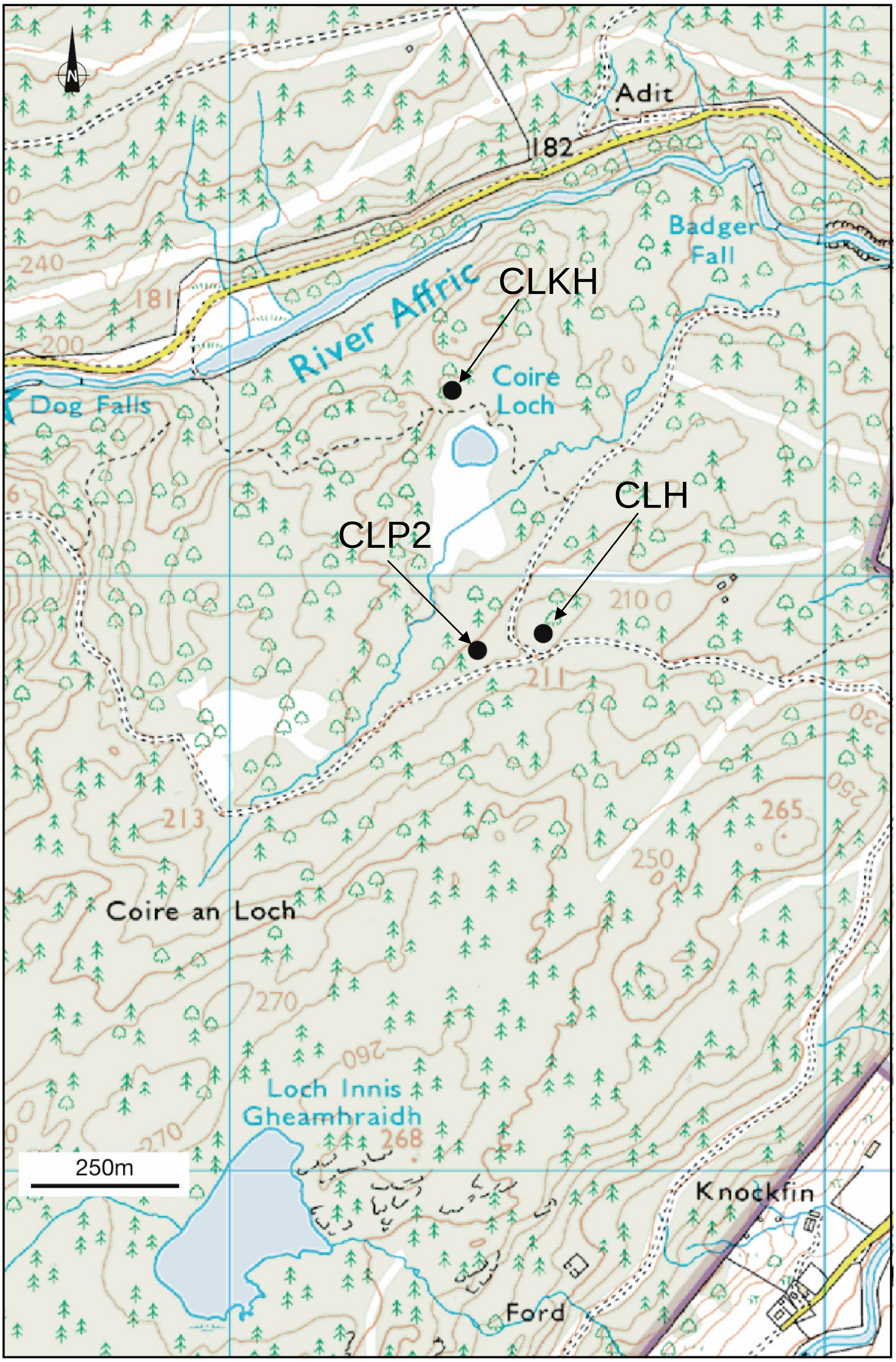

Figure 3.13: Map detail of the CLH, CLP2 and CLKH sites – for wider location context see Figure 3.2
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A further 20 *Pinus* and 10 *Betula* are present within 50m together with several small saplings. Vegetation on the basin surface is dominated by *Sphagnum* and *Polytrichum commune*. Some Poaceae and Cyperaceae occurs but is not dominant. The surrounding vegetation above the basin hollow has a luxuriant growth of *Calluna*.

A peat stratigraphy for the top 100 cm sampled for pollen analysis is presented in Table 3.7. The peat is fibrous and barely humified to below 30 cm.

Table 3.7: Description of the peat stratigraphy for the CLKH core.

Depth Interval (cm)	**Colour**	**Brief description**	**Troels-Smith classification**
0-2	Green to yellow-brown	Non-humified *Sphagnum* and *Polytrichum* with *Betula* leaves and some sedges	Tb^{0}4 Th^{0}+
2-9	Brown	Brown non-humified *Sphagnum*, and rootlets in wet humified matrix	Tb^{0}3 Tl^{0}1
9-15	Yellow - brown	Non-humified *Sphagnum*, and rootlets in wet humified matrix	Tb^{1}3 Tl^{0}1
15-31	Light brown to mid brown	Gradually darker more humified peat with wood fragments Significant wood fragments at 17-18 cm	Sh1 Dl^{1}1 Tb^{1}1 Tl+
31-42	Dark brown	Humified peat Significant wood fragments at 39-42 cm	Tb^{2}1Sh3 Dl^{1}+
42-100	Dark brown	Humified peat with small wood fragments rootlets towards base Significant wood fragments at 49 and 69 cm	Dl^{2}1 Dh^{2}+ Sh3

Figure 3.14: Photograph of the CLKH site – looking down into the basin from the Calluna covered slope

CLP2

This site, at NH29482 27904, is a small peat-filled depression only *c.* 72 cm deep within an undefined flush situated on gently sloping ground above the Coire Loch area (Figure 3.2 and 3.13). Currently the site is within a woodland stand comprising pole-stage pine trees. The site is in a small open glade where 8 *Pinus* and 15 small *Betula* trees occur between 20 and 30 metres distance from the site and a further 70 trees and 25 saplings occur between 30 and 50m away together with 70 *Betula*. Ground vegetation is dominated by Poaceae and Cyperaceae. *Sphagnum* occurs under these Cyperales. A photograph of the basin flush showing the trunks of pole-age and young pine trees is presented in Figure 3.15.

A sediment stratigraphy is presented in Table 3.8. The core is barely humified to depths of over 35 cm and there are grains from mineral inwashing at the base of the core.

Table 3.8: Description of the peat stratigraphy for the CLP2 core.

Depth Interval (cm)	**Colour**	**Brief description**	**Troels-Smith classification**
0-2	Green to brown	Non-humified *Sphagnum* with *Betula* leaves and some sedges	Tb^{0}3 Th^{0}1
2-7	Yellow-brown	Barely humified fibrous *Sphagnum*, and rootlets	Tb^{1}3 Tl^{0}1
7-35	Mid brown	Gradually more humified, still fibrous *Sphagnum* peat Wood fragments at 14-16 cm	Tb^{2}2 Tl^{1}1 Sh1Dl+
35-42	Brown	Gradually darker and more humified	Sh2 Tb^{3}2 Dl+
42-50	Brown	As above with wood fragments	Sh2 Tb^{3}1 Dl+
50-68	Darker brown	Gradually more humified	Sh4
68-72	Dark brown	As above with some mineral grains, increasing to base	Sh4

Figure 3.15: Photograph of the CLP2 site – a wet grassy flush with pine trees in the surrounding stand.

3.4.2 Sites selected for surface sampling

Additional sites selected for modern analogue study to allow local quantification of data for pollen-vegetation relationships and for defining the relevant source area for pollen were collected by the same method as the peat cores (by use of a modified golf-hole corer; Section 3.2.3) and the surface 1-2 cm was taken from the centre of the core surface for pollen preparation. The 29 sites used for surface sampling are introduced in Chapter 5 which presents results and analysis of the modern pollen and vegetation data. Site locations are shown in Figure 5.3.

3.5 Temporal scale

Chronological considerations include choice of temporal span and sampling resolution designed around the scale of the ecological questions posed on the data and the choice of validation methods used to determine the chronologies.

Core depth, and sub-sampling slice thickness and interval, determine the temporal extent and resolution of the final pollen diagram and vegetation reconstruction. A major problem for pollen analytical studies is that pollen preparation is often carried out prior to determining a chronology. This is due to the constraints of time and funding for chronological investigations discussed further in Section 4.6. This necessitates the use of age ‘guestimates’ to assist the estimation of the temporal scale for sub-sampling. The description of the research design therefore presents the strategy in the order in which it was necessary to carry it out; e.g. choice of time span and interval, then determination of chronologies. The limitations of this strategy are discussed in Section 4.6.

3.5.1 Choice of time span

Choices made to sample the whole core to the maximum depth of the basin or to concentrate effort on a particular time period or zone of interest are normally constrained by project time limitations. The selection of a network approach for this thesis necessitates collecting data from several cores and sampling effort was concentrated on a shorter time-period to allow a greater number of cores to be analysed.

A full Holocene record from a single lake site in Glen Affric demonstrates continuity of *Pinus* within this landscape since 8300 cal. BP (Froyd 2005; Froyd and Bennett 2006), whilst in west Affric the Pine population is demonstrated to have receded approximately 4400 cal. BP (Davies 1999). This study does not aim to repeat an examination of the temporal fluctuations of Holocene pine woodland. Instead, it aims to elucidate information on pattern and process within the current woodland by backcasting an ecological analysis over several generations of trees. In addition, it aims to explore the possible recession of woodland away from the west of the Glen (Section 2.3). The temporal span and resolution of the analysis must therefore be designed to encompass several generations of tree cover, to enable identification of any cyclical patterns in woodland cover, or major shifts in ground flora.

Pinus trees in Glen Affric can live to *c.* 300-400 years or more (Steven and Carlisle 1959; Edwards and Mason 2006). Therefore, to assess any cyclicity between *Pinus*, *Betula* and open space, a time-span of 1000-2000 years (representing 3-4 generations of trees) should be a minimum requirement to determine cyclical dynamics from vegetation shifts.

Previous pollen analyses in Glen Affric (Wolff 2003; Wolff and Tipping 1999) had recovered age estimates from extrapolation of ^{14}C assays of *c.* 1000 – 1500 years accumulation at 100cm depth. This was taken as a rough first approximation for age estimates of the cores in this study. Peats studied were from basins with different basal depths, and a consideration was given to sub-sampling based on this; but as there was no reason to assume that all of the small basins and hollows contained full Holocene records, this was not considered a strong indicator of peat age at depth (R. Tipping *pers. comm.*).

3.5.2 Sample intervals

Studies from pollen traps have determined that annual pollen rain records the climatically driven fluctuations in pollen productivity of the surrounding plants and can distort or detract from the quantification of plant abundance in the pollen record (Hicks 2001). In contrast, many coarser scale studies may amalgamate pollen records from many years and therefore miss out on the depiction of some small local scale fluctuations in plant abundance. In this study, an attempt was made to compromise between these temporal representations. A pollen sample representing just a few (3-6) years in each sample should help to converge scales between ecology and palaeoecology, whilst ensuring that any highly productive years for pollen are smoothed and therefore do not affect the interpretation (Hicks 1985).

Taking the crude age estimate of 100cm = 1000-2000 years, a sub-sampling strategy of a sample every 2 cm or 20-40 years was considered appropriate to determine a fine temporal resolution relevant to changes in woodland and ground flora cover in Glen Affric. In practice, the higher compaction of peat at depth in the core means that the surface layers will represent less time per centimetre of depth than the deeper sediments. This could affect the sample resolution and the temporal representation within the sub-sample.

Since the age-depth model is not expected to be linear, a staged reduction in sub-sample slice thickness was implemented after examination of the cores. A 1-2 cm sample was therefore taken from the surface to ensure several years representation in the uncompacted peats, a 1 cm slice was taken at each sample to 10 cm and a 0.5 cm slice at each sample point to 50cm followed by a 0.3 cm slice from 50-100 cm. The exact impact of this on the grain and extent of the subsampled chronologies was not known until after the pollen counting and preliminary analysis was completed.

3.5.3 Sub-sampling

Cores were sub sampled using a razor and fine spatula cleaned with distilled water between each sub-sample. A *c.* 1cm^3 sample of peat was taken every 2cm and prepared using standard pollen extraction techniques outlined below.

Sub-samples were stored in clean glass vials boxed and sealed from light and refrigerated until prepared for pollen extraction.

3.5.4 Determining chronologies

Chronologies are less precise for peat than for varved lake sediments but age estimates can be derived from a variety of methods and markers; these are introduced and reviewed by Lowe and Walker (1997).

Radiocarbon age estimates are used regularly in pollen analysis. These become unsuitable in recent stratigraphies due to contamination by modern and ‘bomb’ carbon (Lowe and Walker 1997). The linking of palaeoecology and ecology requires not just a shift in the spatial resolution of data, but a shift in the temporal resolution, as the recent history of extant woodlands becomes a more pressing focus than that of early Holocene woodland development. The Lead isotope ^{210}Pb has a half-life of 22.56 years and can be used for dating recent sediments. However, the methods are less standardised. In addition, the use of these two methods requires extrapolation between a chronological series (from the ^{210}Pb data) and individual sample ages at depth (from ^{14}C assays). This can be problematic. The chronological models and methods are therefore presented as a separate chapter (Chapter 4) to allow a fuller discussion of the complexities and implications.

3.6 Pollen preparation and analysis

3.6.1 Pollen extraction

Pollen was prepared from both surface and core sub-samples using standard acetolysis methods (Moore *et al*. 1991); HF was not used on any of the samples as they were organic peat sediments with minimal mineral inwashing in a few basal samples from CLP2 and CLH only. *Lycopodium* spores were added to enable absolute and influx counts to be calculated in addition to percentage data (Stockmarr 1971). *Lycopodium* does occur in Glen Affric, however, the spores from the tablets are separable from the fossil or fresh spores, due to the degradation of fossil spores by double acetolysis (A. Davies *pers. comm.*).

Slides were prepared using additional silicone oil to dilute the pollen preparation where necessary. Cover-slips were applied, and sealed with clear nail varnish prior to counting.

Modern samples were prepared by the same method. Surface samples were taken from the top of a bog of similar type to those used for the core analysis. Sub-samples were of larger volume (2-4 cm^3) to account for lack of humification and compression of the peat. Single surface samples were used; amalgamation of surface samples was not carried out, as differences between the modern sites should reflect those in the core profile (Hjelle 1998).

3.6.2 Pollen counting

Pollen and spores were counted using an Olympus 400 microscope at x400 magnification; with difficult grains identified under oil immersion at x100 magnification and/or the use of phase contrast (Moore *et al.* 1991). In addition to pollen, *Pinus* stomata were counted to assist with defining local *Pinus* presence (Parshall 1999) using a key published by Sweeney (2004). Microscopic charcoal present on pollen slides was counted in four size classes[8] to provide evidence of vegetation burning (Cayless and Tipping 2002). SCPs were counted to identify peaks for verification of ^{210}Pb data (Chapter 4), and diatoms were counted to infer surface wetness of the peat.

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[8] Charcoal size classes were 10-25 µm; 26-50 µm; 51-75 µm; 75-100 µm and >100 µm

3.6.3 Pollen identification and taxonomic precision

Pollen was identified with reference to Moore *et al*. (1991), and the pollen reference collection at the University of Stirling. A total land pollen sum of in excess of 500 grains was counted in each sub-sample. The sum of land pollen included Cyperaceae and Ericaceae as the surrounding ground vegetation is predominantly blanket bog/wet heath. Pollen nomenclature follows Bennett (1994), plant nomenclature follows Stace (1991).

Taxonomic precision is also a standard problem for pollen analysis. Some plant species have very similar pollen morphologies, and in some cases such as Cyperaceae and Poaceae, it is not possible, under standard microscope counting, to identify to a greater taxonomic detail than the genus or family. Table 3.9 identifies all trees native to Scotland according to Smout (2003) and demonstrates the taxonomic groupings possible in the identification of pollen from these species. The pollen taxonomy of species and groups of vegetation found in Glen Affric is explored further in Tables 5.1-5.4 and Section 5.5.1 of Chapter 5. In some cases choices must be made to split or converge taxonomic groups; where subtle differences in identification can lead to further splits down to species level, but with the possibility of a high degree of error. Two important pollen distinctions are key to vegetation interpretation in Glen Affric and methods employed to distinguish between them are discussed in Section 3.5.3. These are

Myrica gale* and *Corylus avellana

Both of these taxa are currently present in the glen, although the distribution of *Corylus* is limited to rare occurrences on the brown earths to the east, whilst *Myrica* tends to be present in the heath vegetation to the west, especially in association with *Erica tetralix* and *Narthecium ossifragum* on shallow poorly drained peat substrates (see Section 2.2.2).

The distinction and variation between these two taxa are difficult; both are trizonoporate. The separation from *Betula* is confident, due to the distinct vestibulum in the *Betula* grains. However, the *Corylus*/*Myrica* distinction is less assured. Separation of these types was made by reference to several texts (Blackmore *et al*. 2003; Edwards 1981; Punt *et al*. 2003). The most helpful feature was found to be the distinction based on porus construction with *Myrica* having a sexine distinct in the mesoporium and an endoaperture larger than the ectoaperture. The distinction between these two pollen types is however likely to be subject to error (Edwards 1981; in Punt *et al.* 2002).

Grains were recorded as *Myrica gale*, *Corylus avellana* or Coryloid for uncertain distinctions.

Ericales

Calluna is relatively easy to separate within this group, however, other pollen taxa in this family are morphologically similar. The distinction between *Vaccinium*, *Empetrum* and *Erica* is important to the identification of ground flora types. Ericales with the exception of *Calluna* are likely to be underrepresented but could be key to the separation of W18 and W17 woodland where *Betula* predominates.

Pollen of the Ericales was determined to species level where possible using the special key in Moore *et al.* (1991; p87-90) as well as Oldfield (1959). A summary of the main distinguishing features is outlined below.

Calluna is easily distinguishable from shape of the tetrad, which occurs in one plane or in a loose and irregular tetrahedral arrangement, with irregular colpi. Other grains have a less coarse exine structure.

Pyrola is identified by a regular triangular arrangement of the tetrad with clear colpi.

Empetrum nigrum type, which includes *Empetrum nigrum* and *Empetrum hermaphroditum,* has a triangular obtuse form, and the inner walls of the tetrad are thicker and tend to stain darker. This combined with the psilate grain surface has a property that makes the grain reflect light that is hard to describe but aids identification.

Vaccinium, which includes *Vaccinium myrtillus* and *V. vitis-idaea* and possibly *V. uliginosum* has a triangular globular form to the tetrad, sometimes lobed, but with a thin walled exine and a clear colpus with a porus.

Erica tetralix and *E. cinerea* tend to have lobular tetrads with clear costae to the colpi. The *E. tetralix* tetrad is commonly lobed whilst *E. cinerea* is a large tetrad >45µm.

In some pollen grains a confident identification could not be made. These were recorded in the following categories

"Ericaceae undiff" – for those taxa that could be keyed out beyond the separation of *Calluna* and other Ericas.

"Erica undiff" – for those taxa where *Erica tetralix* and *Erica cinerea* could not be distinguished.

"Erica/*Vaccinium"* for those taxa where Ericas and *Vaccinium* could not be distinguished.

Table 3.9: Tree and Shrub Species native to Scotland (data according to Smout (2003 appendix 1a)); together with information on their current presence in Glen Affric and the Pollen group and known representivity of the pollen taxa

Common Name	Latin Name	Known in Glen Affric	Pollen Type
Common Alder	*Alnus Glutinosa*	yes	*Alnus* glutinosa
Ash	*Fraxinus excelsior*	yes	*Fraxinus excelsior*
Aspen	*Populus tremula*	yes	*Populus*
Downy Birch	*Betula pubescens*	yes	*Betula*
Silver Birch	*Betula pendula*	yes	*Betula*
Dwarf Birch	*Betula nana*		*Betula*
Blackthorn	*Prunus spinosa*		
Bird Cherry	*Prunus padus*		*Prunus padus*
Wild Cherry (gean)	*Prunus avium*		
Elder	*Sambucus nigra*		
Wych Elm	*Ulmus glabra*	yes	*Ulmus glabra*
Hawthorn	*Crataegus monogyna*		
Hazel	*Corylus avellana*	yes	*Corylus avellana* problems distinguishing from *Myrica gale*
Holly	*Ilex aquifolium*	yes	Ilex
Juniper	*Juniperis communis*	yes	*Juniperis*
Pendunculate Oak	*Quercus robur*	yes	*Quercus*
Sessile Oak	*Quercus petraea*	yes	*Quercus*
Scots Pine	*Pinus sylvestris*	yes	*Pinus sylvestris*
Dog Rose	*Rosa canina*		Rosa/Rosaceae
Guelder Rose	*Viburnum opulus*		
Rowan	*Sorbus aucuparia*	yes	*Sorbus aucuparia*/Rosaceae
Rock Whitebeam	*Sorbus rupicola*		
Goat Willow	*Salix caprea*	yes	*Salix*
Grey Willow	*Salix aurita*	yes	*Salix*
Eared Willow	*Salix cinerea*	yes	*Salix*
Woolly Willow	*Salix lanata*		*Salix*
Downy Willow	*Salix lapponum*		*Salix*
Tea-leaved Willow	*Salix phylicifolia*		*Salix*
Mountain Willow	*Salix arbuscula*		*Salix*
Whortle-leaved Willow	*Salix myrsinites*		*Salix*
Dark Leaved Willow	*Salix myrsinifolia*		*Salix*
Net Leaved Willow	*Salix reticulata*		*Salix*

4 Chronological controls derived for the eight Glen Affric peat cores

4.1 Introduction and background

The aim of this chapter is to provide chronologies for the eight peat cores to aid the interpretation of the vegetation histories developed in later chapters. As well as dating specific horizons and shifts in vegetation in the individual cores, the chronologies will enable spatio-temporal woodland dynamics to be investigated across the network of eight cores. The precision and accuracy of chronologies is therefore especially relevant to the network approach. Additionally, chronologies may allow some tentative attempt at deriving pollen influx data in addition to percentage calculations. Pollen influx data may be crucial to improved quantitative pollen-vegetation reconstructions (Hicks 2001; Rasanen 2001).

The dating of recent sediments requires a complex suite of dating mechanisms or tools, as no single method is capable of providing accurate dates over the range of *c.* 1000s of years to present. The traditional method of deriving dates for Holocene pollen sequences is via ^{14}C assays. However, three factors preclude the use of this method in recent (last *c.* 300 years) of sediment accumulation; (i) the dilution of the atmospheric ^{14}C by the burning fossil fuels in the last *c.* 200 years; (ii) the nuclear industrialisation effect in the last 50 years (Lowe and Walker 1997); and (iii) the long half-life of *c.* 5700 years for the ^{14}C isotope. In this study, where the emphasis of the investigation is on the later Holocene woodland, the last 300 years forms an important component in the interpretation of vegetation dynamics. Additional methods of deriving dates for near surface sediments therefore form a necessary and integrated part of this thesis.

The various methods available to derive recent peat sediment chronologies include:

1. ^{14}C assays. Chronological markers for the earlier parts of the cores in this study are determined by ^{14}C assays which are routine (e.g. Lowe and Walker 1997).

2. Assays of the isotope ^{210}Pb: This radionuclide has a half-life of *c.* 22.1 years and is therefore useful for determining sediment dates in the last *c.* 150 years (Lowe and Walker 1997). Despite much recent use there is, however, some uncertainty surrounding the use of ^{210}Pb dating in peat deposits. Unlike ^{14}C assays, where universal and tested protocols exist, the use of ^{210}Pb is less standardised, and the criteria for selecting

appropriate models for deriving age from the decay curve is still open to question. Dates derived from ^{210}Pb assays can be variable depending on the chronological model used. Additional supporting methods of analysis are therefore recommended (Turetsky *et al*. 2004).

3. Assays of the isotope ^{137}Cs: Emitted in quantity into the atmosphere since atomic weapons testing in the 1940s (Lowe and Walker 1997), peaks in ^{137}Cs can be correlated with the Chernobyl event in 1986, and global fallout from atomic weapons testing in the early 1960s. However, this isotope is mobile in the peat column, can be taken up by plants in nutrient poor systems (P. Wookey *pers comm*.), and therefore may lack precision.

4. Spheroidal carbonaceous particles (SCPs): These can help corroborate ^{210}Pb evidence. SCPs appear from the 1860s, rise in the 1960s to a peak at 1977 followed by a fall in the surface sediments due to the decline of coal consumption in recent years (Yang *et al*. 2001). When found in sufficient quantities these can form stratigraphic markers to constrain dates. However, the original chronologies for the SCP peaks were determined by correlation with ^{210}Pb chronologies; therefore, there is some circularity in logic when using the presence of SCPs to verify ^{210}Pb chronologies.

5. Exotic marker pollen grains of known planting date (Belyea and Warner 1994): For tree taxa, which form the only possible exotic marker in the Glen Affric cores there may be some unknown delay between planting date and the initiation of pollen production in the plants.

6. Variations in the influx of pollen grains (Hicks 1974; Middeldorp 1982). This may be useful in discovering hiatuses, or major changes in sediment accumulation, but since pollen influx can vary over time, arguments for dates derived by this method quickly become circular. This method may be useful in determination of the location of rates of change between assays in dated peat.

7. Analysis of tephras: A distinct tephra horizon can form a precise data line and therefore help constrain chronologies. These were not found, however, in the Glen Affric cores and are therefore not discussed further here.

Results for ^{14}C chronologies in the deeper, older sections of peat are presented in Section 4.2. Surface chronologies for this thesis are principally established from the detection of decay patterns in the radioisotope ^{210}Pb. Given the lack of clarity regarding ^{210}Pb chronological models a fuller account of the ^{210}Pb analysis will be given than for ^{14}C age estimates, where methods are now standard. ^{210}Pb chronologies are presented in Section 4.3. Without the analysis of tephras other methods for deriving dates are less assured, nevertheless the methods listed above can provide some corroborating evidence for the ^{210}Pb assays. Where available these will be discussed in Section 4.4. The results from the various methods are then combined for each site to produce a final core chronology in Section 4.5. Discussion of the chronological evidence for the Glen Affric peat cores and the application of these data to the network of pollen-vegetation histories is presented in Section 4.6.

4.2 Radiocarbon chronologies

Radiocarbon assays were obtained through application to the NERC radiocarbon facility. Fifteen dates were allocated by the NERC Radiocarbon Laboratory Steering Committee (allocation no 1078.0404) across the eight peat cores in this study. Peat sub-samples were taken from the cores at various intervals defined by the need to date particular vegetation changes, and the need to determine a meaningful stratigraphy by extrapolating between the combined ^{14}C and ^{210}Pb dates.

Sub-samples were taken from 1 cm thick slices of peat using a clean razor blade. The samples were trimmed so that only the inner section of peat from the core was used in the analysis to prevent risk of contamination. Samples were immediately wrapped in clean aluminium foil before placing each individual sample in a clean, labelled, plastic bag. Samples were stored in the fridge until delivery to the radiocarbon laboratory.

The samples were prepared at the NERC Radiocarbon Laboratory in East Kilbride and the ^{14}C analyses were carried out at the SUERC AMS facility.

4.2.1 Results from the radiocarbon assays

Data from the NERC ^{14}C assays are presented in Table 4.1 together with calibrated dates derived using OXCAL v3.10 (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) with IntCal04 atmospheric data from Reimer *et al.* (2004).

Table 4.1: Results of Radiocarbon assays for eight sites in Glen Affric with calibrated age ranges using OXCAL v3.10.

NERC Code	Sample Code	Depth cm	*14C Enrichment*		*Conventional Radiocarbon age*		*Carbon content*	*d13C PDB*	*Calibrated Age 2 d Calibrated using OXCAL*	
			% modern	+/- 1d	(years BP)	error +/- 1d	(% by weight)	‰ +/- 0.1	Upper limit/ Lower Limit (Age in Years Cal. BP)	Midpoint
SUERC-3955	NHP/69	68.5-69.5	70.63	0.23	2793	26	98.1	-28.4	2965 - 2795	2880
SUERC-3956	NHP/89	88.5-89.5	75.11	0.21	2299	23	35.4	-28.1	2355 - 2185	2270
SUERC-3957	PB/71	70.5-71.5	62.52	0.22	3773	28	53.9	-28.1	4240 - 4080	4160
SUERC-3958	PB/93	92.5-93.5	57.94	0.22	4384	30	55.2	-26.8	5040 - 4860	4950
SUERC-3952	BEAT/49	48.5-49.5	98.34	0.26	135	21	49.1	-26.8	275 - 5	145
SUERC-3953	BEAT/68	67.5-68.5	97.03	0.29	242	24	50.6	-28.4	425 - -5	210
SUERC-3954	BEAT/99	98.5-99.5	77.73	0.24	2024	25	45	-29.4	2050 - 1895	1975
SUERC-3967	ANI/55	54.5-55.5	74.00	0.24	2418	26	54.6	-29.1	2690 - 2350	2520
SUERC-3966	ANI/69	68.5-69.5	71.34	0.21	2713	23	48.6	-27.9	2855 - 2760	2810
SUERC-3971	ARC/45	44.5-45.5	98.37	0.26	132	21	55.6	-29.2	275 - 10	145
SUERC-3968	ARC/69	68.5-69.5	93.36	0.28	552	24	54.9	-28.6	635 - 520	580
SUERC-3963	CLKH/65	64.5-65.5	98.39	0.29	131	24	48.3	-26.9	275 - 10	145
SUERC-3961	CLKH/93	92.5-93.5	98.94	0.26	85	21	52.3	-28.9	260 - 30	145
SUERC-3964	CLH/73	72.5-73.5	73.44	0.18	2480	20	41.1	-29.1	2715 - 2460	2590
SUERC-3965	CLP2/65	64.5-65.5	71.22	0.23	2726	26	55.3	-27.4	2850 - 2780	2815

4.2.2 Discussion

The two assays on the NHP core reveal calibrated age ranges of 2965-2795 at 69 cm and 2355-2185 at 89 cm thus demonstrating a possible inversion in the peat or a source of error in one, or both, of the two assays. An inversion of peat was considered, but the stratigraphy is a simple gradation to more humified peat at depth at this site (see section 3.3). Evidence of inversions in peat chronologies caused by slope failure in peat sediments may not be obvious from limited dates (Ashmore *et al*. 2000) and is therefore not testable here. The sample at 69 cm, however, has an abnormally high carbon content of 98.1% by weight (Table 4.1) in contrast to an average of 53.2% for all fifteen samples across the eight cores. The NHP core contained large quantities of micro-charcoal (see the NHP Pollen diagram A1.1c), and it is considered that this may have biased the ^{14}C assay at this depth in the core, perhaps with contamination from wood fragments from burnt older material. This date is therefore rejected in further analyses.

The assays from 49 cm and 65 cm at BEAT and both of the assays at CLKH contain a high percentage of modern carbon, rendering them unsuitable for determination of precise ages. The CLKH core shows a remarkably rapid accumulation history. The ^{14}C assay at 93 cm depth reveals an age range of 260-30 cal. BP with a midpoint of 145 cal. BP. Potentially this means that one metre of peat has accumulated in little over 300 years at this site. The top two assays at the BEAT site return date ranges of 275-5 cal. BP and 41- -5 cal. BP respectively; again indicating that this site may be rapidly accumulating in the surface layers. The ^{14}C assay at 99 cm for the BEAT site however, demonstrates a much older peat with an age range of 2050-1895 cal. BP and a midpoint of 1975 cal. BP. The possibility of a break in peat accumulation cannot be ruled out in this core and will be discussed further in Section 4.6.

The ^{14}C assays from the other six cores from Glen Affric have returned age ranges that imply remarkably different accumulation rates. The most slowly accumulating peat are at sites PB with an age range estimate at 93cm of 5040 – 4860 cal.BP; ANI, with an age range estimate of 2855 – 2760 cal. BP at 69cm; and CLP2, with an age range estimate of 2850 - 2780 cal. BP at 65 cm. Assuming a steady accumulation rate in the PB core, this would equate to 53 years per 1 cm of peat accumulation, but this will be greater at depth in relation to any more rapid surface accumulation. In comparison, the ARC core has an age range of just 635-520 cal. BP at 69 cm returning an accumulation rate of just 8 years per 1 cm. There seems no particular justification for rejecting any of the ^{14}C assays, apart from the NHP assay at 69 cm (see above); therefore, marked differences in accumulation rates are accepted for the sites. These accumulation rates seem consistent with peat condition, with visibly denser, more humified peat, displaying older stratigraphies, and fibrous and uncompacted or wetter peat displaying younger stratigraphies (see Chapter 3 for peat descriptions).

The time-depth relationships and the variation in peat accumulation rates between cores will be discussed subsequently, in the light of the combined results of dating methods in Section 4.5.

4.3 ^{210}Pb Isotope chronology

As outlined above and in Chapter 3, ecologically relevant applications of pollen analysis are especially reliant on dating of the more recent sediments (Oldfield and Appleby 1984). The isotope ^{210}Pb is a convenient tool in the dating of more recent sediments. First introduced by Goldberg in 1963, ^{210}Pb is now beginning to be more routinely used in palaeoecological studies. However, unlike ^{14}C assays there are no standardised methodologies for deriving chronologies from the results of ^{210}Pb assays. Although several models have been proposed and tested (Oldfield and Appleby 1984; Oldfield *et al.* 1995; Olsson 1986; Robbins 1978) no formalised conclusions or protocols are agreed. Simple conditions for the choice of age model have been suggested by Appleby and Oldfield (1983), however many papers present results without a full discussion of methods and assumptions used.

Peat may pose particular problems in ^{210}Pb age model application. There is a potential for vertical mobility of ^{210}Pb in the peat profile (Urban 1991; Urban *et al.* 1990) and model assumptions may fail due to variations in peat accumulation rates through time. The models currently used to derive chronologies from ^{210}Pb assays were first associated with lake sediments. Variations in accumulation rate for peat may contradict the steady accumulation rate assumptions of some models. Conley (2004) reviews the use of ^{210}Pb in relation to coastal sediments and advises caution as the differing models for deriving a chronology can produce differing results; especially under variable sediment accumulation rates. Care is therefore needed in the interpretation and application of the results of ^{210}Pb chronologies.

A summary of the background theory and the models for deriving chronologies from ^{210}Pb assays is outlined below. Section 4.3.2 then outlines the methodology and approach used in this study followed by a presentation of the results in Section 4.3.4., and discussion of results in Section 4.3.5.

4.3.1 Background to the method

The lead isotope ^{210}Pb is a short-lived radioisotope with a half-life of approximately 22.26 years. It is a daughter nuclide produced as part of the uranium series decay chain. The gas radon escapes from the earth as part of the U-series decay and this radon quickly undergoes further decays, through a series of very short-lived isotopes, to ^{210}Pb. The solid products of the decay of radon, including ^{210}Pb, rain out of the atmosphere to be embedded in sediments at an assumed constant rate. The ^{210}Pb that is incorporated into the sediments then decays to ^{210}Bi. Assuming a constant rate of supply of ^{210}Pb to the sediment, the decay curve of ^{210}Pb with increasing sediment depth can be determined. A chronology can then be established as a function of the ^{210}Pb half-life of 22.26 years. In theory ^{210}Pb should provide a dating mechanism for the last 150 years (Lowe and Walker 1997); in practice, this radioisotope is useful for dating the last c100 years of sediment or approximately 5 half-lives, as the errors associated with older sediments are large (Conley 2004). ^{210}Pb assays therefore assist in dating the most recent peat layers, which cannot be accomplished by ^{14}C assays (Section 4.2).

The ^{210}Pb method has been used to establish chronologies in lake sediments. However, the models developed for establishing chronologies in these sediments have some major caveats when applied to peats. In lakes, the water column interrupts the atmospheric deposition of ^{210}Pb into the sediment, reworking of sediment can occur at the sediment-water interface, and incorporation of eroded material in runoff can add minerals containing uranium, and therefore an additional source of ^{210}Pb (Olsson 1986). These problems should not occur for peat, especially where sediments are highly organic.

Some of the models assume a constant sedimentation rate, which may not be true for peats as sedimentation rate will vary with the growth rates of the peat-forming plants and these may be influenced by climatic fluctuations, as well as by changes in the growth rates of different taxa as any changes occur in species dominance over time. In addition to growth rates, the peat structure differs in humification and compression from the underlying substrate. This will influence the measured sedimentation rate through time.

There have also been suggestions that ^{210}Pb may be, in some situations, mobile within the sediment column (Urban 1991; Urban *et al.* 1990). Differences between age models from hummock and hollow profiles in the same bog have been noted (Belyea and Warner 1994).

Sansum (2004) reasons that this is likely to be less of a problem in seasonally wet small hollows, which tend not to have a hummock and hollow formation, and similarly, this should be the case in Glen Affric. Due to the terrain however, it was necessary to use some samples from sloping sites and sites of differing wetness, the comparison of ^{210}Pb assays from these differing substrates may therefore be of intrinsic interest.

4.3.1.1 Models for deriving ^{210}Pb chronologies

Three models, originally developed for lake sediment, have been used to derive chronologies from ^{210}Pb profiles.

1. The Constant Flux: Constant Sedimentation Rate (CF:CS) model
2. Constant Initial Concentration (CIC) model
3. Constant Rate of Supply (CRS) model

The CF:CS model derived by Robbins (1978) allows the sedimentation rate (r) to be derived from the equation:

$$C = C(o)e^{-km/r} \qquad \text{Equation 4.1}$$

Where C is the unsupported ^{210}Pb in the sediments; C(o) is the ^{210}Pb unsupported at the sediment water interface (or the peat surface); m is the cumulative dry sediment mass and k is the inverse log of the ^{210}Pb half life; the radioactive decay constant: 0.03114yr^{-1} (Robbins 1978; Oldfield and Appleby 1984).

The CF:CS model therefore allows the sedimentation rate r, to be derived from the regression slope –k/r from a plot of Ln unsupported ^{210}Pb against the cumulative dry-mass of sediment. As this model derives from a linear equation it assumes both the ^{210}Pb flux, and the dry-mass sedimentation rate are constant (Oldfield and Appleby 1984).

In reality, sedimentation rates vary with porosity and with mass accumulation rates (Boer *et al.* 2006 p.270). In the case of peat deposits this is analogous with; (i) peat structure, which can vary due to compaction or the character of peat produced by differing species in the peat-forming vegetation; and (ii) peat growth rates, which can vary over time due to climatic fluctuations.

Reduced compaction of the surface layers is normal and therefore some non-linearities are expected. Additional non-linearities in ^{210}Pb profiles include non-monotonic curves of ^{210}Pb against depth and strongly kinked curves (Oldfield and Appleby 1984; *and references therein*). Models 2 and 3 above overcome some of the problems of the CF:CS and provide alternative methods of treating non-linear profiles (Oldfield and Appleby 1984).

The Constant Rate of Supply (CRS) model, (Robbins 1978; Oldfield and Appleby 1984) assumes that cumulative residual unsupported ^{210}Pb, denoted A, beneath sediments (x) with an age of t varies with the formula:

$$\mathrm{A(x) = A(o)e^{-kt}} \qquad \text{Equation 4.2}$$

Where $A_{(o)}$ is the total of the residual unsupported ^{210}Pb in the sediment column and k is the radioactive decay constant for ^{210}Pb.

Equation 4.2 assumes a constant net rate of supply of ^{210}Pb from the lake water (or atmospheric deposition in the case of peat deposits) to the sediment, and, that this supply is independent of any changes in the net dry sedimentation rate.

The Constant Initial Concentration (CIC) method (Robbins 1978; Oldfield and Appleby 1984) assumes a constant initial unsupported ^{210}Pb concentration regardless of the net dry-mass sedimentation rate to derive Equation 4.3 and 4.4.

$$\mathrm{C = C(o)e^{-kt}} \qquad \text{Equation 4.3}$$

Equation 4.3 can be rearranged to:

$$t = \frac{1}{k} \ln \frac{C(o)}{C} \qquad \text{Equation 4.4}$$

Where C is the sample ^{210}Pb concentration; C(o) is the unsupported ^{210}Pb at the sediment water interface (or peat surface); and t and k are the same as Equation 4.2.

Again, this model was developed for lake sediments. Oldfield and Appleby (1984 p.101-102) observe that constant initial concentration is suitable for lakes in three main cases. Firstly, where ^{210}Pb is bound to particles in the water column and therefore reaches the sediment-water interface as a constant concentration in respect of these particles. Secondly, where ^{210}Pb is derived from autochthonous material and changes in sedimentary rates will again proportionally increase the input of ^{210}Pb. Thirdly, where a constant sedimentation rate applies and all sediments have the same initial concentration.

Since peat growth does not rely on the accumulation of particles from the water column, the first two assumptions above are likely to be violated in peat deposits. Thus in peat deposits, where variation in growth rates is not linked to ^{210}Pb particle adsorption, the concentration of ^{210}Pb into the sediment may be diluted in rapid growth years and the CIC model is, arguably, comparable to the CF:CS model in lacking suitability in peat deposits.

Non-linear profiles can, however, be divided into linear sections before applying the CIC model to overcome the problem of differing accumulation rates (Brugam 1978); although, this leads to problems of a possibly unrealistic stepped age-depth profile at section boundaries (Oldfield and Appleby 1984).

4.3.1.2 Choice of models

The CF:CS model is based upon a regression equation and is therefore only applicable if the plot of ln^{210}Pb against depth is linear, which is rarely the case in peat deposits. Appleby and Oldfield (1983), by reference to the plot of unsupported ^{210}Pb concentration against depth, discuss model choice between the CIC and CRS models in relation to lake sediments. The authors conclude that a non-monotonic profile favours the CRS model (see also Appleby and Oldfield 1986, where the authors conclude that when sediments have a non-monotonic profile for the plot of unsupported ^{210}Pb concentrations the CRS model is the only feasible chronology), whilst a monotonic decline with depth favours the CIC model. In relation to peat, however, Appleby *et al.* (1997) and Appleby and Oldfield (1992) reject the CIC model because peat deposits undergo organic decay thus losing mass and volume with depth even where the growth rate may have been stable.

The CRS model is therefore likely to be the model of choice for the Glen Affric peat cores. Plots of ln^{210}Pb and ^{210}Pb against depth are first applied to the data to investigate the nature of the curve and confirm applicability. As there is still some uncertainty over model choice, where the curves are monotonic the CIC model is compared to the CRS in this study.

4.3.2 ^{210}Pb preparation and detection methods

The top *c.* 20-30 cm of each core was prepared for ^{210}Pb dating, with the aim of covering the maximum period for ^{210}Pb chronology of *c.* 100-150 years. Sub-samples were taken at either 1 or 2 cm thick intervals using material from the golf hole corer (section 3.4). The decision on sub-sample thickness was made dependent on the compaction and density of the peat as there was a requirement to balance the need to maintain an adequate mass of sample to detect ^{210}Pb without excess error, with the derivation of fine scale chronologies. Compact sites were therefore sampled at 1cm intervals whilst the tops of cores and loosely compacted peat were sampled at 2 cm intervals.

The peat was oven dried at 95°C overnight and ground using a mixermill. The powder was then compressed using a mechanical press to *c.* 8 tonnes pressure and sealed into a 40 mm lidded plastic Petri dish with epoxy resin. Wet and dry mass of the uncompacted samples were recorded, as were the mass and thickness of the compacted pellet. Samples were left for at least two weeks to equilibrate.

Determination of ^{210}Pb activity along with other radioisotopes was carried out by Dr Andrew Tyler and Stuart Bradley using the University of Stirling Gamma Ray detector. Unsupported ^{210}Pb was determined by obtaining an average of ^{214}Pb, ^{214}Bi, ^{226}Ra and ^{243}Th and subtracting this average from the total ^{210}Pb activity. ^{226}Ra is subject to detection errors and since all of these isotopes should be in equilibrium it is assumed that the average of these 4 isotopes gives a better indication of the unsupported ^{210}Pb fraction than measurements of ^{226}Ra which can be subject to large errors. The specific activity of the isotope ^{137}Cs was also counted directly at the same time.

4.3.2.1 Data presentation

For each core results for supported, total and unsupported ^{210}Pb in Bq kg^{-1} are plotted against depth in Figure 4.1 together with the ^{137}Cs concentration data.

A table of ^{210}Pb inventory results and CRS derived ages for each site is then presented (Tables 4.2-4.9). CIC and CF:CS models were tested, but did not provide meaningful results for most cores. As expected from the discussions in Section 4.1.2 above, the CF:CS model failed to take account of lack of compaction in surface sediments, delivering a linear chronology, which is considered an unlikely descriptor of the peat age-depth curve. While the CIC model sometimes returned chronologies that started in the future, probably again due to the lack of surface compaction. Where the ^{210}Pb concentration was monotonic, the CIC model was applied as a comparison.

4.3.3 ^{210}Pb Results

Figure 4.2 shows plots of ln^{210}Pb as supported, unsupported and total concentrations together with ^{137}Cs all in Bq kg^{-1} against depth for the eight Glen Affric peat cores.

The trends in Figure 4.2 demonstrate declines in unsupported ^{210}Pb with depth for most cores although all demonstrate a classic reversal in concentrations in the surface sediments (Oldfield and Appleby 1984) with the exception of the PB core. In peat deposits from small diameter basins this is considered likely to be due to a lack of compaction which can cause an infiltration of atmospheric fall-out to below the peat surface or an overestimation in ^{226}Ra in the fresh peat layers (Belyea and Warner 1994).

Disregarding surface fluctuations, cores trending towards a monotonic decline with depth are PB, CLH, and NHP, and to a lesser extent, CLP2, which declines monotonically over just four sub-samples after steady concentration in the top 6 cm. ANI and ARC cores decline non-monotonically with depth although only showing concentration inversions in the top three sub-samples. BEAT and CLKH both show concentration inversions with depth, which possibly indicate problems with the peat stratigraphy.

Equilibrium between supported and unsupported ^{210}Pb (the meeting of the lines of the ^{210}Pb supported and unsupported activity in Figure 4.1) would be expected at *c.* 150 years (Reinikainen *et al.* 1997). BEAT and CLKH cores do not reach equilibrium between supported and unsupported ^{210}Pb within the sampled depths of 28 cm for BEAT and 24 cm for CLKH. The BEAT and CLKH cores also have a lower overall ^{210}Pb activity than the other cores. Within the remaining six cores, equilibrium occurs at varying depths from 11 to 22 cm demonstrating variable accumulation rates as expected from the ^{14}C age-estimates.

The non-linearity of ^{210}Pb with depth is also tested using plots of ln^{210}Pb concentrations against depth (Appleby and Oldfield 1983; Appleby and Oldfield 1986) in Figure 4.2; none of the cores display linearity, all having a non-monotonic or curved form. The topmost samples of each core often show depressed ^{210}Pb activity, and basal samples are subject to large errors. Ignoring these outlying data points, NHP, PB and CLH demonstrate a reasonably monotonic decline in ^{210}Pb with depth, whilst the other five cores display a non-montonic declines.

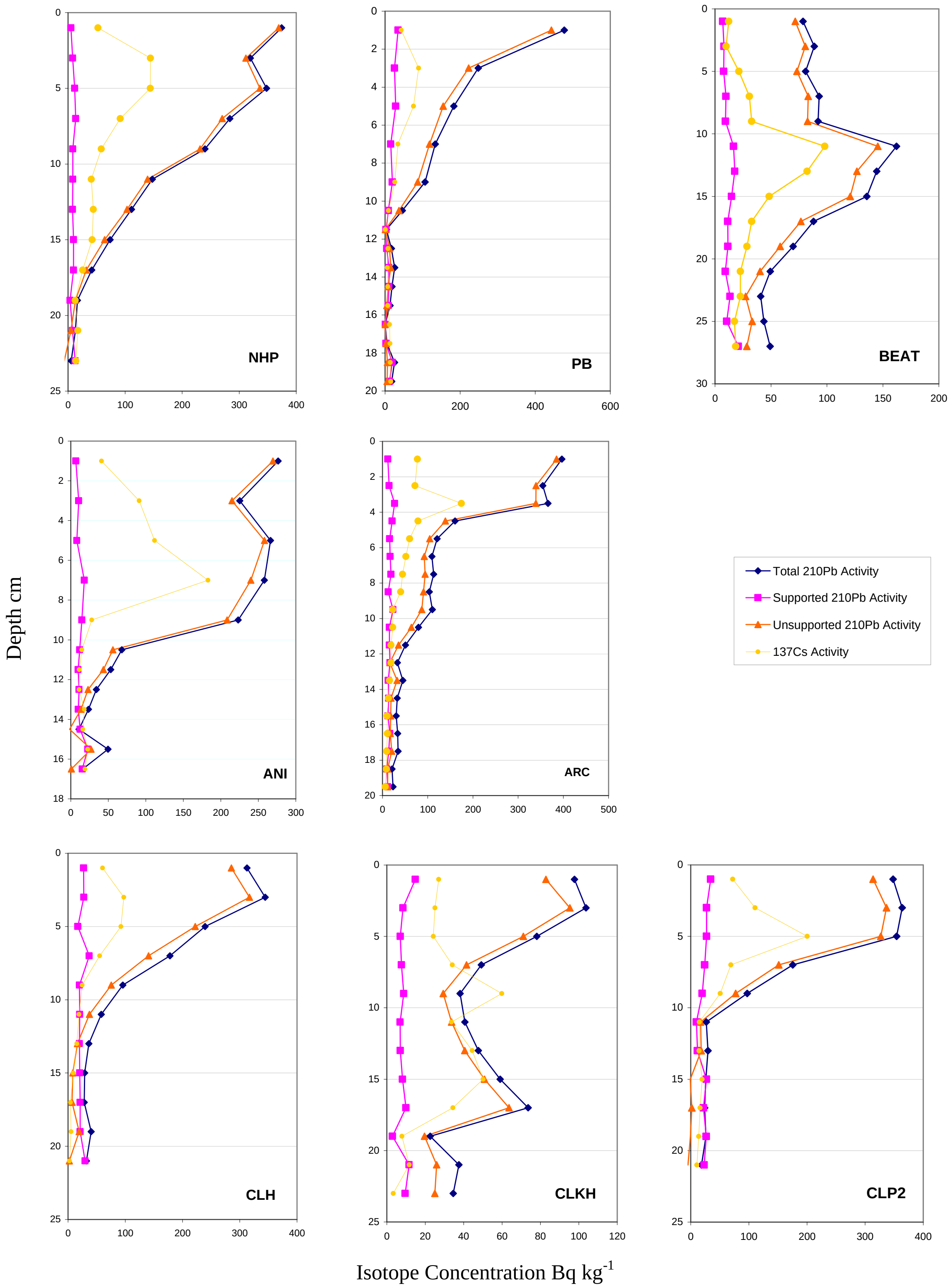


Figure 4.1: Plot of ^{210}Pb and ^{137}Cs activity (Bq kg^{-1}) with depth (cm) for the eight Glen Affric peat cores. ^{210}Pb activity is presented as; the total activity, the supported activity and the unsupported activity (see legend)

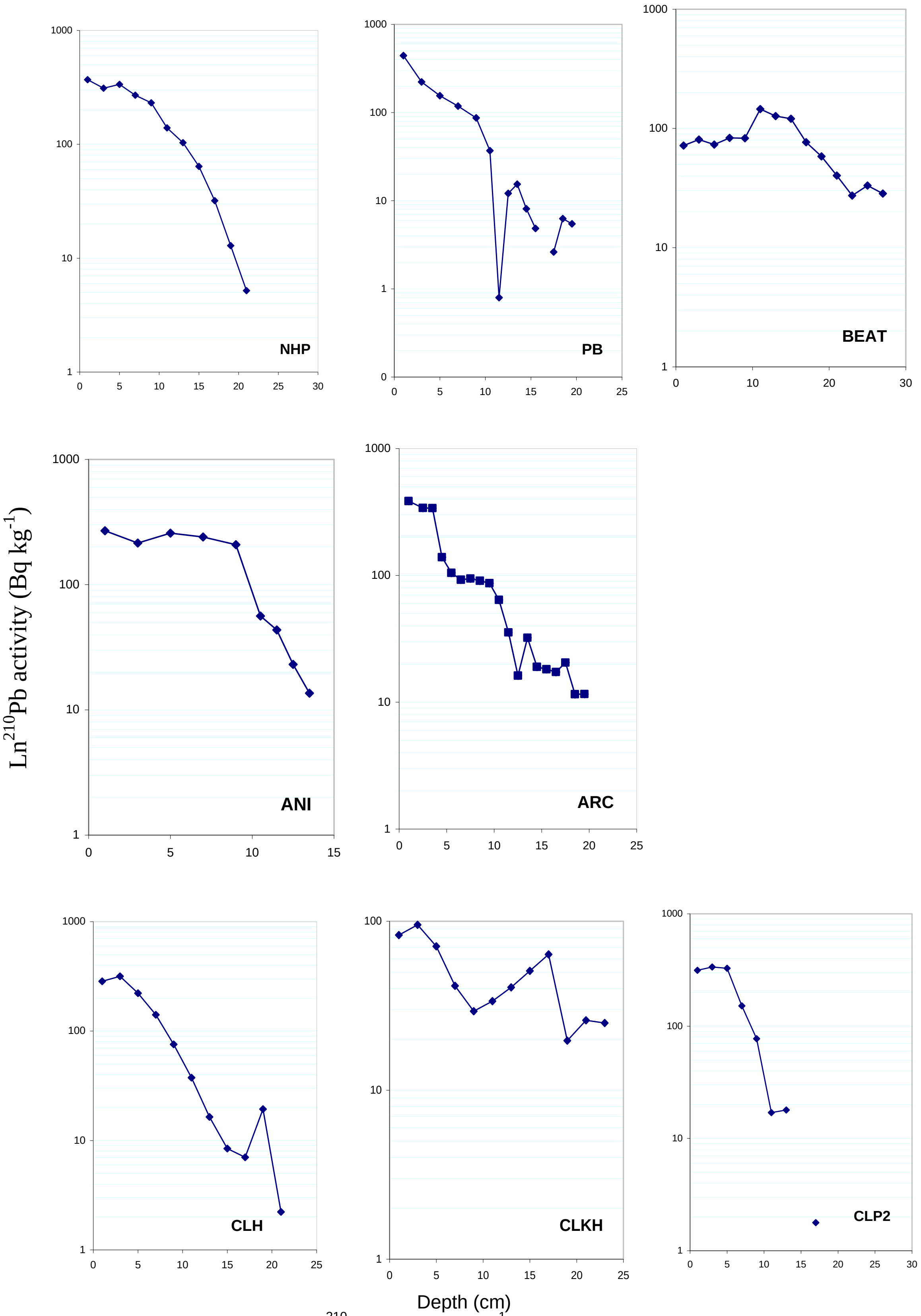


Figure 4.2: Plot of the ln unsupported ^{210}Pb activity (Bq kg^{-1}) with depth for the eight Glen Affric peat cores. x axis = depth cm; y axis – ln ^{210}Pb activity Bq kg^{-1} from top left Cores are: NHP, PB, BEAT, ANI, ARC, CLH, CLKH, and CLP2

4.3.4 ^{210}Pb chronologies for Glen Affric cores

4.3.4.1 NHP ^{210}Pb results

The NHP core was sampled at 2 cm intervals to 28 cm. The equilibrium between supported and unsupported ^{210}Pb is reached between 19 and 21 cm; therefore, dates are not derived below this level. The curve for NHP activity against depth in Figure 4.2 is monotonic below the surface 3 cm and therefore the CIC model results are displayed for comparison. The CIC model indicates a much more rapid accumulation at the surface than other models, with a depth of 5 cm representing the year 2002 as opposed to the 1980s from the CRS model. The inversion in activity level at the top of the core may cause this anomaly as evidenced by the inversion in dates of AD 2000 to AD 2002 between 3 and 5 cm. The ^{137}Cs peak is present as one broad and undefined peak from 9 cm to 3 cm with a maximum between 5 cm and 3 cm (Figure 4.2; Table 4.2). The inception of the ^{137}Cs peak at *c.* 9cm is likely to indicate the fallout maximum from nuclear testing in 1963 as this peak inception shows remarkably good agreement with the CRS date of 1968 at 8 cm. While the top section of the peak coincides well with the 1986 Chernobyl event correlating well with the CRS age estimates at this level of between 1980 and 1991. The ^{137}Cs peak does not support the suggested rapid accumulation rate at the top of the core derived from the CIC model and supports the rejection of this model.

Table 4.2: ^{210}Pb data and chronological models for NHP. Blue shading denotes depth below which supported and unsupported ^{210}Pb are in equilibrium: Yellow shading indicates presence of increased ^{137}Cs levels.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	374.3	9.4	6.2	368.1	35.3	8.2	7	1998	0.8	0	2005
4	319.7	10.9	10.8	308.9	36.6	19.7	14	1991	0.7	6	1999
6	348.1	12.6	12.9	335.2	44.0	32.9	25	1980	0.5	3	2002
8	283.7	12.3	13.2	270.5	38.8	46.2	37	1968	0.4	10	1995
10	240.0	9.4	9.1	230.9	22.9	60.9	53	1952	0.7	15	1990
12	147.9	10.5	8.6	139.2	15.5	83.0	69	1936	1.5	31	1974
14	111.3	11.4	8.1	103.1	12.7	99.6	90	1915	4.9	41	1964
16	73.7	13.3	12.3	61.4	11.1	118.3	116	1889	22.1	58	1947
18	41.7	25.2	11.1	30.5	12.7	135.7	146	1859	133.6	80	1925
20	16.5	29.9	4.1	12.4	5.5	157.6	178	1827	860.0	109	1896
22	13.0	129.0	4.7	8.3	17.1	177.5					
24	5.7	282.0	6.6	-0.9	17.0	196.8					
		Total	**107.9**	**1867.4**							

The CRS model displays larger errors in age in deeper samples in agreement with results from Beylea and Warner (1994). The date of AD 1859 at 18 cm is however consistent with an age of 150 years at *c.* 19 cm: the point of equilibrium between supported and unsupported ^{210}Pb (Reinikainen *et al.* 1997). The date at 20 cm is likely to be erroneous due to large errors on the ^{210}Pb detection.

4.3.4.2 PB ^{210}Pb results

The PB core was sampled at 2 cm intervals to 10 cm and at 1 cm intervals from 10 cm to 20 cm. The dates derived from models are presented in Table 4.3. The equilibrium between supported and unsupported ^{210}Pb was reached at *c.* 11 cm; therefore, dates derived below this level are likely to be subject to large errors. The unsupported activity curve for PB core declines smoothly. The CIC model is therefore applied and compared with the CRS model.

The ^{137}Cs peak is present as a broad and undefined increase between 3 cm and 6 cm depth; the CRS model returns age-estimates of 1963 at the ^{137}Cs peak inception (*c.* 6 cm) and between 1976 and 1989 (*c.* 3 cm) at the top of the peak. Although the ^{137}Cs peak is not well defined this again shows a remarkable alignment with the known ^{137}Cs atmospheric enrichment dates. The CIC model also produces age-estimates in broad agreement with the ^{137}Cs peak and, additionally, returns a closer match than the CRS model with the age expected at the level where supported-unsupported ^{210}Pb equilibrium is reached at *c.* 11 cm. At this depth the CIC model returns an age-estimate of AD 1843 whilst the CRS model predicts AD 1906. The curve of the CIC chronology for PB core follows the shape of the ^{210}Pb curve with depth in Figure 4.3, whereas the curve of the CRS model smoothes the chronology. Although the CRS model chronology is more acceptable for a peat stratigraphy (Appleby and Oldfield 1992; Appleby *et al.* 1997), research on lake sediments has indicated that the CRS model can be subject to errors due to smoothing of the age-depth curve around periods of irregularity in the sedimentation rate. The CIC model, using Equation 4.4, may indicate anomalies in the stratigraphy between 10 and 12 cm (*c.* 100 years (CRS) or 150 years (CIC)). This anomaly is worthy of further investigation as it coincides with a decrease in *Pinus* pollen percentages despite a number of trees surrounding this basin with possible ages of in excess of 300 years (as measured by C. Edwards of Forest Research via tree ring counts during a field trip of the conference on the Native Pine Woods of Scotland held at Drumnadrochit 14th-16th June 2004). The use of information from the CIC model will be discussed further in relation to this core in Section 4.5.3 and Chapter 6, and may indicate value in the use of both CRS and CIC modelling approaches in order to highlight any irregularities in the age-depth curve smoothed by the CRS model.

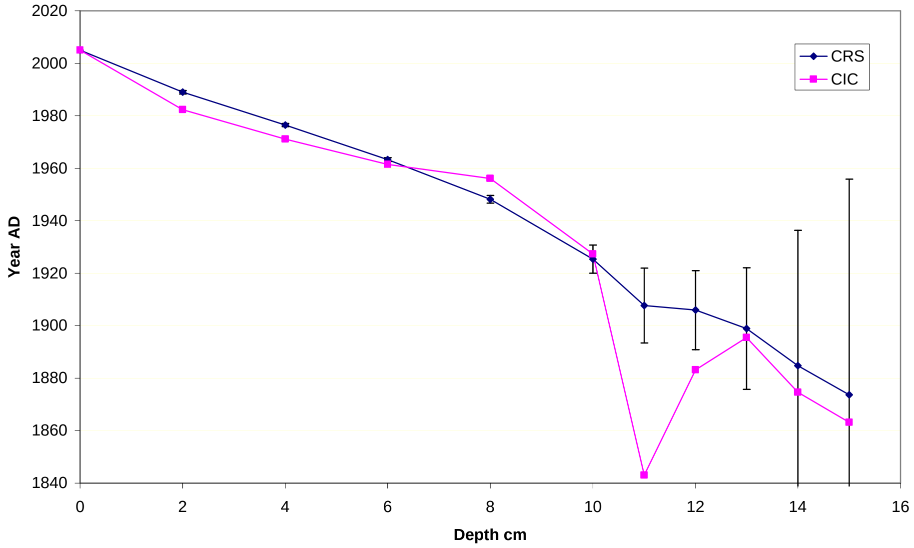


Figure 4.3: Linear interpolations derived from ^{210}Pb assays for the PB core using the CIC and CRS models.

Table 4.3: ^{210}Pb data and chronological models for PB core. Blue shading denotes depth below which supported and unsupported ^{210}Pb are in equilibrium: Yellow shading indicates presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bq kg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	477.6	10.07	0.7	476.95	48.10	14.22	16	1989	0.64	0	2005
4	248.2	14.81	13.2	235.03	36.76	30.02	29	1976	0.55	23	1982
6	183.2	13.83	17.2	166.05	38.78	47.15	42	1963	0.76	34	1971
8	133.6	15.50	10.7	122.94	20.80	63.25	57	1948	1.44	44	1961
10	106.7	19.26	2.6	104.09	21.17	79.05	80	1925	5.37	49	1956
11	45.9	23.76	3.5	42.42	12.93	88.24	97	1908	14.24	78	1927
12	3.6	63.23	0.5	3.08	2.44	95.93	99	1906	15.02	162	1843
13	16.9	36.42	6.2	10.74	14.77	102.23	106	1899	23.18	122	1883
14	25.4	30.65	9.6	15.79	20.72	109.65	120	1885	51.69	109	1896
15	18.5	54.72	10.3	8.22	22.97	117.20	131	1874	82.12	130	1875
16	13.2	27.22	7.5	5.75	15.42	125.26	142	1863	89.80	142	1863
17	0.0	0.00									
18	5.4	44.33									
19	25.3	29.48									
		Total	**115**	**1205**							

4.3.4.3 BEAT ^{210}Pb results

The BEAT core was sampled at 2 cm intervals to 30 cm. The model-derived dates are presented in Table 4.4. The equilibrium between supported and unsupported ^{210}Pb was not reached at 30 cm and the ^{210}Pb assays produce a definite non-monotonic curve. The CIC model is therefore not applicable for the BEAT core according to the criteria from Section 4.3.1.2. The CRS model produces a chronology that demonstrates a rapid accumulation rate in the BEAT profile, with a date of *c.* AD 1900 at 28 cm depth; this young age is supported by the lack of an equilibrium between supported and unsupported ^{210}Pb within the 30 cm depth of core analysed, and by a low total unsupported ^{210}Pb in Bq kg^{-1} (Table 4.4). However, the CRS model age-estimates between 16cm (AD 1962) and 10 cm (AD 1990) provide a broad agreement with the ^{137}Cs peak between these depths. Again, as with NHP and PPB cores above the ^{137}Cs peak shows evidence of an homogenised peak of the 1963 nuclear weapons testing maximum and the 1986 Chernobyl accident. Again, as in the PB core, the CRS model provides a credible but smoothed chronology, and the CIC model provides an unrealistically young chronology, although the shape of the CIC curve may be a better indicator of periods of more and less rapid accumulation within the core (Figure 4.4).

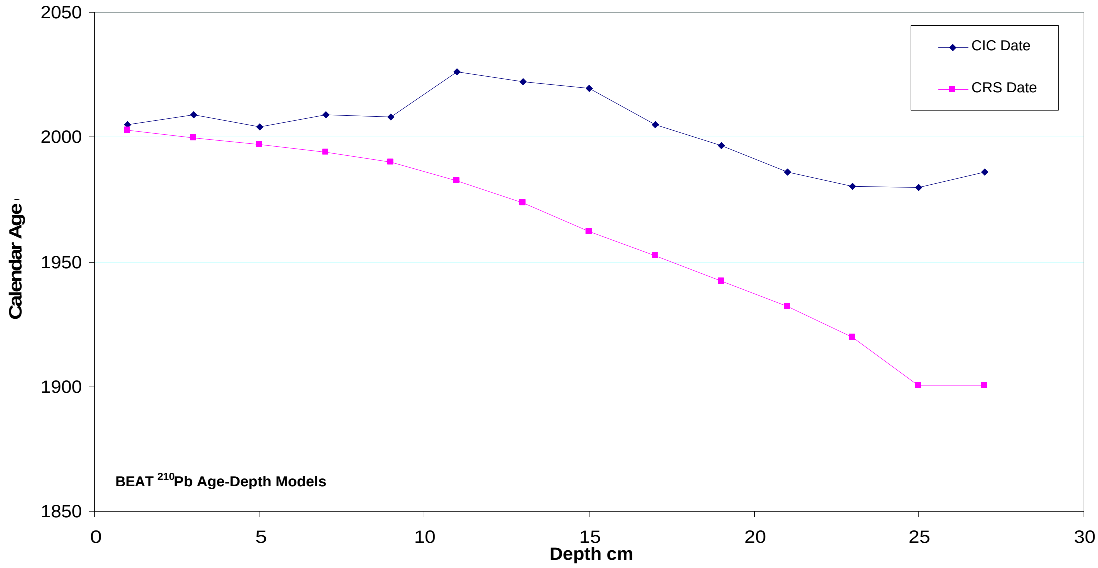


Figure 4.4: Linear interpolations derived from ^{210}Pb assays for the BEAT core using the CIC and CRS models.

Table 4.4: ^{210}Pb data and chronological models for BEAT core. Note no blue shading: no equilibrium reached between supported and unsupported ^{210}Pb at base sample depth: Yellow shading indicates presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	78.7	20.80	6.1	72.55	17.71	4.01	2	2003	0.93	n/a	n/a
4	88.7	13.05	6.9	81.75	14.19	7.83	5	2000	0.86	n/a	n/a
6	81.0	13.74	10.7	70.27	11.17	11.84	8	1997	0.79	n/a	n/a
8	93.1	14.42	11.3	81.79	13.54	17.44	11	1994	0.71	n/a	n/a
10	92.1	13.65	12.2	79.97	12.99	23.96	15	1990	0.64	n/a	n/a
12	162.2	10.33	21.6	140.60	17.56	34.29	23	1982	0.52	n/a	n/a
14	144.6	10.46	21.2	123.33	15.39	45.41	32	1973	0.47	n/a	n/a
16	135.7	13.01	21.8	113.88	17.98	57.99	43	1962	0.58	n/a	n/a
18	88.0	15.10	15.8	72.20	13.67	69.37	53	1952	0.86	n/a	n/a
20	69.8	20.66	14.3	55.46	14.60	81.09	63	1942	1.46	n/a	n/a
22	49.5	44.44	9.2	40.23	22.00	90.78	73	1932	2.41	n/a	n/a
24	40.8	35.80	7.2	33.61	14.62	99.54	85	1920	2.84	n/a	n/a
26	43.7	60.23	10.4	33.24	26.51	110.06	105	1900	19.70	n/a	n/a
28	49.3	50.63	9.3	39.96	25.50	119.55	105	1900	25.76	n/a	n/a
		Total	**178**	**1039**							

4.3.4.4 ARC ^{210}Pb results

The ARC core was sampled at 1 cm intervals to 20 cm. The CRS chronology is presented in Table 4.5. The curve of unsupported ^{210}Pb activity against depth for this site is non-monotonic (Figure 4.1), and therefore the CIC method is rejected. The CRS model produces a credible age estimate at 10 cm correlating with the top of the ^{137}Cs peak of AD 1991; the peak is therefore likely to be due to the Chernobyl accident in 1986; the slight age discrepancy, could be some upwards movement of the ^{137}Cs via uptake by nutrient limited plants on the basin surface (Section 4.3.1.2). The ^{137}Cs 1963 peak is not distinct, however there is some increase in the ^{137}Cs levels from *c.* 8 cm and this supports the age-estimate of AD 1958 by the CRS model, again demonstrating broad agreement between the evidence from these isotopes. Equilibrium between supported and unsupported ^{210}Pb activity occurs at *c.* 19 cm. This is coincident with a CRS derived age estimate of AD 1849, which is as expected for the 150-year age of the equilibrium point, although errors around the age determinations at this depth are large (Table 4.5).

Table 4.5: ^{210}Pb data and chronological models for ARC core. Blue shading denotes depth below which supported and unsupported ^{210}Pb are in equilibrium: Yellow shading indicates presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	396.71	11.56	11.7	385.02	45.90	14.35	7	1998	0.8	n/a	n/a
3	354.46	10.83	17.7	336.74	48.58	24.18	14	1991	0.7	n/a	n/a
4	366.08	17.07	16.3	349.77	64.46	33.47	25	1980	0.5	n/a	n/a
5	160.37	19.58	10.3	150.11	31.62	43.74	30	1975	0.5	n/a	n/a
6	120.74	19.01	10.1	110.66	23.28	55.70	35	1970	0.4	n/a	n/a
7	109.35	34.05	12.9	96.43	37.26	65.36	40	1965	0.5	n/a	n/a
8	113.21	17.04	5.2	107.96	19.29	75.00	47	1958	0.5	n/a	n/a
9	103.50	18.13	10.7	92.83	18.82	83.97	54	1951	0.6	n/a	n/a
10	110.27	20.01	10.9	99.35	22.08	94.65	64	1941	0.9	n/a	n/a
11	79.45	21.35	11.2	68.29	16.97	105.29	74	1931	1.2	n/a	n/a
12	50.96	22.03	12.3	38.70	14.21	114.91	80	1925	1.3	n/a	n/a
13	32.77	32.24	13.7	19.12	10.59	124.07	84	1921	1.0	n/a	n/a
14	44.95	23.08	11.3	33.63	11.87	133.46	93	1912	2.6	n/a	n/a
15	32.75	34.42	10.9	21.81	12.31	142.44	100	1905	5.1	n/a	n/a
16	30.42	28.01	12.3	18.14	9.31	152.28	107	1898	8.9	n/a	n/a
17	33.52	41.76	9.8	23.72	14.03	162.08	121	1884	24.0	n/a	n/a
18	34.43	32.86	14.8	19.67	31.60	169.05	138	1867	111.7	n/a	n/a
19	21.00	49.86	9.2	11.81	10.56	177.61	156	1849	362.2	n/a	n/a
		Total	**219**	**1999**							

4.3.4.5 ANI ^{210}Pb results

The ANI core was sampled at 2 cm intervals to 10 cm then at 1 cm intervals to 17 cm. The model-derived dates are presented in Table 4.6. The curve for this site is non-monotonic (Figure 4.1), and therefore the CRS model should be more secure. ^{137}Cs increases to a peak at 7 cm followed by a decline, with possibly a small further peak at 3 cm (Figure 4.1). CRS age estimates at these depths are slightly younger than expected for the 1963 and 1986 ^{137}Cs enrichment events; however, there is broad agreement and the difference could be due to mobility of ^{137}Cs in the peat. The equilibrium between supported and unsupported ^{210}Pb activity occurs at 15 cm. At the equilibrium point the CRS model predicts an age of AD 1896, which is younger than that of the 150 years expected; although this is within the limits expected in the lower part of the ^{210}Pb curve, when considering the large errors in determination of unsupported ^{210}Pb (A. Tyler *pers. comm.*). The age-depth curve of the CIC model (Figure 4.5) indicates that there may be a change in peat accumulation rate at *c.* 12 cm, leading possibly to young CRS age-depth estimates at this level, via smoothing in the CRS model.

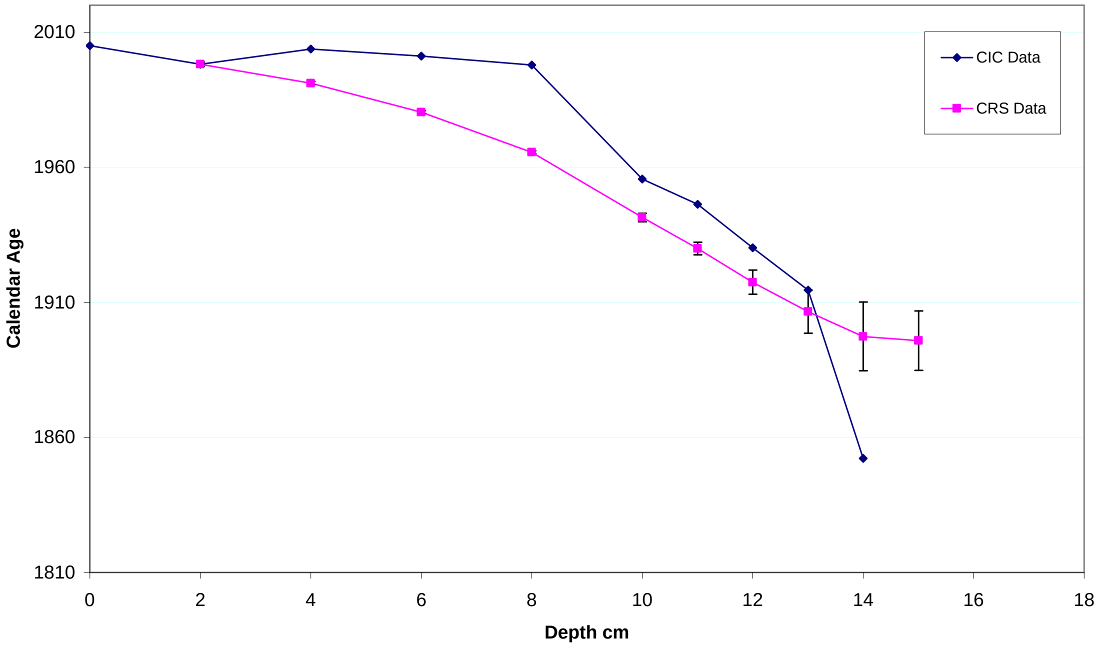


Figure 4.5: Linear interpolations derived from ^{210}Pb assays for the ANI core using the CIC and CRS models..

Table 4.6: ^{210}Pb data and chronological models for ANI. Blue shading denotes depth below which supported and unsupported ^{210}Pb are in equilibrium: Yellow shading indicate presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	276.4	6.569	6.1	270.21	20.75	13.31	7	1998	0.8	n/a	n/a
4	225.4	10.65	7.0	218.37	27.77	26.62	14	1991	0.7	n/a	n/a
6	266.2	5.131	6.7	259.55	18.09	37.57	25	1980	0.5	n/a	n/a
8	258.1	6.189	18.0	240.02	15.97	49.31	39	1966	0.5	n/a	n/a
10	223.2	12.89	6.7	216.48	29.87	62.38	64	1941	1.6	n/a	n/a
11	68.0	17.26	9.8	58.17	13.72	73.45	75	1930	2.3	n/a	n/a
12	53.3	20.97	9.9	43.37	11.40	83.52	88	1917	4.5	n/a	n/a
13	34.2	29.22	7.8	26.32	10.27	93.60	98	1907	8.0	n/a	n/a
14	23.5	27.02	7.4	16.16	13.53	104.19	108	1897	12.7	n/a	n/a
15	10.8	30.41	8.5	2.32	10.92	115.32	109	1896	11.0	n/a	n/a
16	49.6	20.19	12.9	36.70	11.74	126.37	159	1846	187.7	n/a	n/a
17	15.951	30.58	6.1	9.90	5.95	136.55				n/a	n/a
		Total	**107**	**1398**							

4.3.4.6 CLH ^{210}Pb results

The CLH core was sampled at 2 cm intervals to 22 cm. The ^{210}Pb data and derived chronology is presented in Table 4.7. The ^{137}Cs peak is broad and undefined, with an increase from 8 cm to a sustained peak between 5 and 3 cm. The CRS model returns age-estimates with the start of AD 1963 at 6 cm and AD 1980 at 4 cm. The agreement between the age-estimate of the CRS model and the ^{137}Cs marker horizons is again remarkable and helps to validate the ^{210}Pb age-estimates. Equilibrium is reached between supported and unsupported ^{210}Pb activity at 13 cm. The curve of ^{210}Pb with depth (Figure 4.1) for this site has a smooth decline from 3 cm; at the equilibrium-point (13 cm) the CRS models predicts an age of AD 1897, whereas the CIC model predicts AD 1908. The CIC model also under-predicts surface age and returns an age at 3 cm of 2008 due to the inversion of ^{210}Pb concentration with depth at the top of the core (Figure

4.2). The CIC model is therefore rejected for this core, despite the non-monotonic curve of ^{210}Pb with depth.

Table 4.7: ^{210}Pb data and chronological models for CLH. Blue line denotes depth below which supported and unsupported ^{210}Pb are in equilibrium. Yellow shading indicates presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	312.5	10.84	29.4	283.1335	36.29224	9.50	9	1996	0.8	0	2005
4	344.4	10.42	28.7	315.6445	35.88736	24.56	25	1980	0.5	-3	2008
6	239.4	9.678	21.7	217.672	23.26039	44.97	42	1963	0.7	8	1997
8	177.9	12.71	34.9	143.0525	23.94279	64.48	63	1942	2.0	22	1983
10	95.6	19.56	23.6	72.034	23.92772	82.26	82	1923	5.6	44	1961
12	58.1	24.85	22.9	35.199	17.64405	98.59	98	1907	12.4	67	1938
14	36.4	22.36	22.6	13.7925	8.529716	115.83	108	1897	18.6	97	1908
16	29.0	18.91	26.0	3.045	5.583952	132.39	111	1894	20.5	146	1859
18	28.3	20.72	22.1	6.27	10.53047	149.77	117	1888	29.4	122	1883
20	40.4	29.09	19.8	20.664	16.61641	169.07	156	1849	300.8	84	1921
22	32.1	31.59	23.5	8.588	10.81665	191.04	156	1849	164.1	112	1893
		Total	**275**	**1119**							

4.3.4.7 CLKH ^{210}Pb results

The CLKH core was sampled at 2 cm intervals to 24 cm. ^{210}Pb data and chronological models are presented in Table 4.7. The equilibrium-point between supported and unsupported ^{210}Pb was not reached at this depth. The total unsupported ^{210}Pb activity is also much lower than other cores at 593 Bq kg^{-1}, indicating that the equilibrium point may be well below the deepest sub-sample analysed at 24 cm. This agrees with the ^{14}C age-estimates in Section 4.5.8 and the stratigraphy presented in Chapter 6, which demonstrate that CLKH is a rapidly accumulating peat. The ^{210}Pb concentration with depth is non-monotonic and the CIC model is therefore rejected according to the criteria set out in Section 4.3.1.2. This profile is strongly kinked, with an inversion of ^{210}Pb concentration with depth to a second peak at 17 cm (Figure 4.2). This core is the only core out of the eight sampled in Glen Affric to show two ^{137}Cs peaks; the first rising from 19cm to a peak at 15cm; and the second peaking at 9 cm. The ^{137}Cs peaks show a broad agreement with the ^{137}Cs enrichment events, although the age-estimates at the peaks are slightly older than expected. In other cores the ^{137}Cs age markers have correlated with slightly younger CRS derived age-estimates, possibly due to uptake by plants in the growing peat. The older profile predicted in this core is consistent with a downward migration of ^{137}Cs in the peat. The stratigraphy of this core, which is fibrous and in a very wet hollow, may be consistent with this downward migration.

Table 4.8: ^{210}Pb data and chronological models for CLKH. Note no blue line: no equilibrium reached between supported and unsupported ^{210}Pb at base sample depth: Yellow cells indicate presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	21.8	90.0	7.7	90.0	23.7	6.7	5	2000	0.9	n/a	n/a
4	27.3	95.4	8.3	95.4	29.0	14.9	12	1993	0.7	n/a	n/a
6	22.4	72.3	5.8	72.3	17.6	22.2	18	1987	0.6	n/a	n/a
8	32.0	41.8	7.4	41.8	20.0	27.6	23	1982	0.6	n/a	n/a
10	28.3	29.3	8.8	29.3	20.7	34.3	26	1979	0.6	n/a	n/a
12	59.6	33.1	7.5	33.1	28.3	37.7	30	1975	0.6	n/a	n/a
14	31.0	40.6	7.0	40.6	14.8	42.8	36	1969	0.6	n/a	n/a
16	25.9	53.2	5.8	53.2	15.3	50.5	47	1958	0.9	n/a	n/a
18	21.5	64.6	9.0	64.6	15.8	60.4	67	1938	2.4	n/a	n/a
20	22.3	19.7	2.9	19.7	7.7	64.8	78	1927	3.1	n/a	n/a
22	16.0	26.2	11.3	26.2	7.5	71.2	99	1906	10.3	n/a	n/a
24	27.3	26.8	7.8	26.8	9.9	75.6	99	1906	8.2	n/a	n/a
		Total	**89**	**593**							

4.3.4.8 *CLP2 ^{210}Pb results*

CLP2 was sampled at 2 cm intervals to 22 cm. The ln ^{210}Pb profile is monotonic apart from the surface points (Figure 4.2), however, the slope is steep reducing from *c.* 336 Bq kg^{-1} at

5 cm to *c.* 76 Bq kg^{-1} at 11 cm (Figure 4.2). A major ^{137}Cs peak occurs at 5 cm but a small barely defined peak may also occur at 9 cm (Figure 4.1). The overall ^{137}Cs peak from 9 cm is too broad to correlate well with the CRS derived age-estimates (Table 4.8); at 9 cm the CRS model derives an age-estimate of *c.* AD 1930, whilst at 5 cm an age-estimate of *c.* AD 1980 is predicted; this is consistent with some downward mobility of ^{137}Cs in the core profile. The equilibrium point is reached at *c.* 15 cm at a date of between 1867 AD and AD 1848 using the CRS model and AD 1917 and AD 1887 with the CIC model. The CIC model predicts ages that are too young, both in comparison with the ^{137}Cs peak and the equilibrium-point. The interruption to the curve of ^{210}Pb with depth at 0-5 cm (Figure 4.1) causes the CIC model to return negative ages between 2 and 5 cm. The CIC model is therefore rejected.

Table 4.9: ^{210}Pb data and chronological models for CLP2. Blue shading denotes depth below which supported and unsupported ^{210}Pb are in equilibrium: Yellow shading indicates presence of a ^{137}Cs peak.

Depth to base of sample (cm)	^{210}Pb activity Bqkg^{-1}	^{210}Pb activity Bqkg^{-1} ± 2 Sigma error	^{210}Pb Supported Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1}	Unsupported ^{210}Pb Bqkg^{-1} ± 2 Sigma error	Cumulative dry sample weight g	CRS age	CRS date	CRS Age ± 2 Sigma Error	CIC age	CIC date
2	348.2	13.93	34.4	313.8	50.1	15.68	9	1996	0.8	0	2005
4	363.8	9.394	27.8	336.0	34.2	28.85	23	1982	0.5	-2	2007
6	354.3	10.16	27.2	327.1	37.7	46.44	48	1957	0.8	-1	2006
8	175.6	12.78	20.7	154.9	25.9	63.63	72	1933	2.6	23	1982
10	97.1	13.81	20.8	76.3	14.1	82.87	100	1905	9.7	45	1960
12	26.8	24.47	8.1	18.6	6.6	97.46	113	1892	17.5	91	1914
14	29.7	22.7	9.1	20.5	6.7	113.22	138	1867	78.6	88	1917
16	25.9	24.58	18.0	8.0	6.7	129.58	157	1848	249.9	118	1887
18	23.8	25.84	19.3	4.5	8.1	147.44	178	1827	844.3	136	1869
20	26.3	40.74	21.6	4.6	10.7	163.86	268	1737	198317.8	135	1870
22	18.5	42.71	18.2	0.3	9.2	177.76	268	1737	128894.1	223	1782
		Total	**225**	**1265**							

4.3.5 Discussion

4.3.5.1 Comparisons of the models

The plot of unsupported ^{210}Pb with depth is not linear for any of the samples and therefore the simple CF:CS model was not considered appropriate. Despite an almost monotonic curve for some samples, the CIC model did not produce age-depth models in agreement with that expected from the ^{137}Cs or equilibrium points apart from at the PB core. Although these are tentative dating controls, the indicated rejection of the CIC model is in agreement with Appleby and Oldfield (1992) and Appleby *et al.* (1997). The CRS model in agreement with these authors does produce the most parsimonious age predictions for all of the Glen Affric peat cores.

However, where the CIC model was attempted the differences between the models were marked and the suitability of each model is still, to some extent, unclear. The smoothing of the CRS age-depth curve by use of $A_{(o)}$ - the total of the residual unsupported ^{210}Pb in the sediment column - may produce age-depth relationships that miss important fluctuations, which could indicate hiatuses or marked fluctuations in accumulation rate. Reinikainen *et al.* (1997) also find significant age differences derived from use of different models and quote from Carroll *et al.* (1995) questioning the use of the CRS method on sediments with varying accumulation rates. The CRS age-depth curves for cores with strongly non-monotonic relationships of ^{210}Pb with depth must therefore be used with caution and the evidence from these cores demonstrates that there may be some value in plotting the CIC age depth curve using Equation 4.4 to determine the shape of any changes in accumulation rate (e.g. see the PB core in Section 4.3.4.2.).

BEAT and CLKH both demonstrate a lower total unsupported ^{210}Pb activity in the sediment column as well as not reaching an equilibrium between supported and unsupported ^{210}Pb at the depths sampled. BEAT and CLKH are the wettest sites sampled, with fibrous and uncompacted peat to depths of *c.* 60 cm or more. A first assumption may be to conclude that the extreme surface wetness has increased mobility of ^{210}Pb in the peat: Beylea and Warner (1994) call for further testing of ^{210}Pb to determine the specific microhabitats where post depositional mobility of peat is problematic. Urban *et al.* (1990) stress that "Dates based on ^{210}Pb should be verified by other techniques, especially when the inventory of ^{210}Pb is less than that expected from local rates of deposition". However, the lower total unsupported activities may not invalidate the age-depth models at these sites as the equilibrium point is not reached, and it is likely that these are fast accumulating peats, therefore diluting the ^{210}Pb concentration in each depth increment.

4.3.5.2 Core differences and accumulation rates

As discussed above, BEAT and CLKH both return ^{210}Pb chronologies demonstrating very young peat sediments at depth. Other cores also display differences in accumulation rates from 4 years per cm at BEAT through to 10 years per cm at CLP2.

The correlation with ^{137}Cs was problematic as the peaks of ^{137}Cs tended to be broad, but also because in comparison the ^{210}Pb-derived ages at the ^{137}Cs peaks were consistently underestimating the peat age. The alternative scenario is that ^{137}Cs is especially mobile in an upwards direction in the peat (although this is not impossible in an area with a fluctuating water table). However, not all of the peat cores from Glen Affric that exhibited this problem came from wet sites. It is therefore considered more likely that ^{210}Pb underestimated age near to the peat surface due to problems with the lack of compaction of peat and the assumptions of the models of a steady accumulation rate.

4.4 Supplementary dating techniques

Supplementary dating techniques are presented in this section prior to establishing the whole core chronologies in Section 4.5. Methods attempted were the counting of SCPs and the planted exotic *Picea* pollen, both of which were routinely counted on pollen slides.

Picea was planted in Glen Affric from 1890 and the discovery of a convincing appearance and presence of *Picea* pollen in the top peat samples would have provided a good corroboration of ^{210}Pb dating. In reality, the presence of *Picea* was very limited in the pollen record and the dating evidence from *Picea* counts was therefore inconclusive. This supports the assumption that small peat hollows record only the local vegetation, especially as the purpose of this study was to work in the presumed relict area of woodland where *Picea* does not have a local presence. The *Picea* pollen presence is presented in pollen diagrams in Chapter 6, but is not presented here as no meaningful dating horizon could be derived from the sparse grains present.

SCPs are formed from high temperature combustion of fossil fuels and are deposited from fall-out of flyash from coal and oil combustion (Wik and Natkanski 1990), which has the ability to travel long distances in the atmosphere from the original combustion source (Yang *et al.* 2001). SCPs have been used to derive independent dating of specific levels in peat and lake sediments. A dated curve of SCP peaks has been produced by Rose *et al*. (1995) and an examination and calibration of peaks in SCP levels for Scotland carried out by Yang *et al.* (2001). Yang *et al.* demonstrate the commencement of an SCP profile at *c.* AD 1860 and two changes in the profile of the curve; with the initiation of increase representing AD 1960; and the fall in the curve to current lower SCP concentrations in the late 1970s. SCPs can be counted by two methods; the concentration method, where the SCP content is concentrated from a specific volume of sediment; and the routine counting of particles along with pollen on microscope slides (Hendon and Charman 2004; R. Tipping *pers. comm*.).

For the Glen Affric cores, the counting of SCPs was carried out alongside the pollen in the prepared pollen slides. Concentration data was obtained by the standard method for pollen of comparing with the count of marker grains (in this case *Lycopodium* spores) of which a known volume had been added to the original sample preparation. SCP concentrations are presented in Figure 4.6. The concentrations are in most cases low, and caution should be applied to obtaining meaningful results of peaks which are developed from the counting of a very few particles.

4.4.1 Supplementary dating results

SCPs are shown to appear from the 1860s (Yang *et al.* 2001) and the SCP appearance in the Glen Affric cores tends to be below the depth of that date derived from ^{210}Pb age estimates for the cores (Section 4.4).

In addition, in the NHP core an early peak in SCPs at 18 cm is not supported by the ^{210}Pb chronology. It is considered unlikely that the peak represents the 1960 increase (Rose *et al.*

1995), as the compaction from this site is high and the ^{210}Pb and ^{14}C age-estimates indicate a rapidly decreasing age with depth at this site. The NHP site shows a lack of *Pinus* pollen prior to 20 cm but the site is now in a wooded area. It is possible that more SCPs reached the site in the early more open conditions and the site became more protected from atmospheric fall-out as the woodland developed. The woodland cover and nature of small hollows is concluded, by Sansum (2004), to be the reason for not finding high SCP concentrations in peats to the west of Scotland.

The curve for SCPs in the CLP2 core also shows a discrepancy with the ^{210}Pb dates, as in this core minor SCP presence occurs below the predicted AD 1860 level from the ^{210}Pb chronology. It is not impossible that some downward movement of SCPs occurs in accumulating sediment. In reality, the concentration is derived from just 2 grains counted on the pollen slide and is subject to very large errors. As the CLP2 core suffered from a short ^{210}Pb curve inaccuracies in the ^{210}Pb date cannot be ruled out however.

Because, in contrast to Sansum (2004), SCP peaks do exist in the Glen Affric cores it may have been appropriate to carry out a more detailed analysis by the concentration method (Rose *et al*. 1995); this was prevented however, by the need to utilise the full volume of core material at each level in the destructive process of analysis for ^{210}Pb dating.

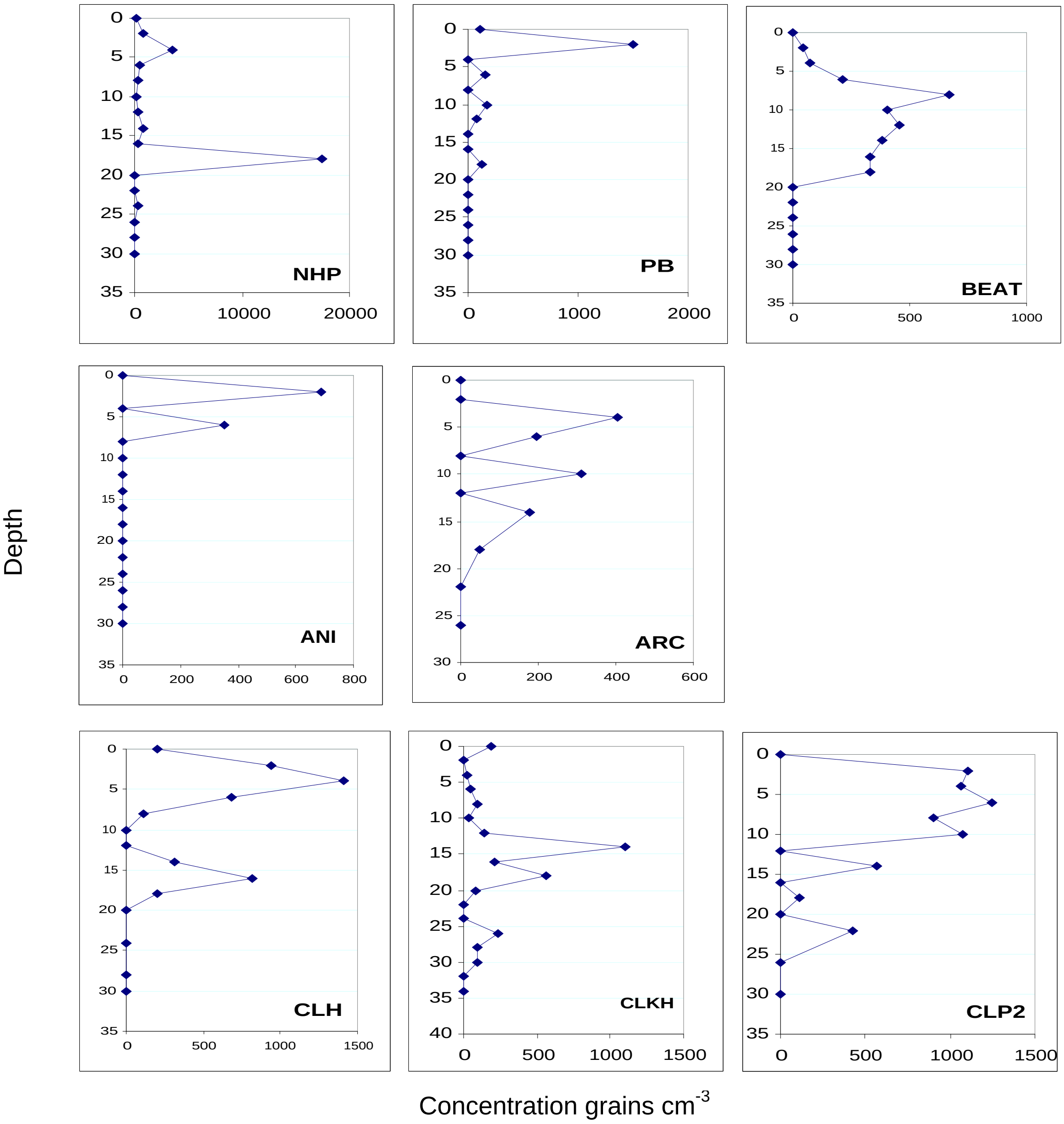


Figure 4.6: Plot of SCP concentrations (particles cm^{-3}) against depth (cm) for the eight Glen Affric peat cores

4.4.2 Discussion

As outlined in the introduction to this chapter, the purpose of utilising several chronological methods is both to corroborate between uncertain results and to correlate between older and younger sediments in more detail than available from a limited number of ^{14}C derived age-estimates. Chronologies derived from ^{210}Pb assays in Section 4.3 provide an age-depth model for the last 100-150 years and although other corroborating evidence from SCP and exotic pollen markers has proved limited, ^{137}Cs has provided some additional support for the chronologies. A major limiting factor however is that these corroborating methods only provide information about the near surface sediments. Thus, although they assist in deriving confident ^{210}Pb chronologies, they cannot provide data to link the deepest ^{210}Pb derived ages with the youngest ^{14}C derived ages.

4.5 Combining age estimates to derive chronologies

Any chronological model involves interpolation and extrapolation between two or more data points. The choice of age-depth model for this extrapolation is not straightforward. Several age-depth models using multiple ^{14}C assays over a number of cores have been tested (Bennett and Fuller 2002) and modelled (Telford *et al.* 2004a) including polynomial, cubic spline, linear interpolation and Bernstein polynomials. Errors associated with fitting age-depth models can be 100s of years in comparison with the 10s of years achieved for radiocarbon age determinations (Bennett, 1994).

In cores concentrating on more recent time-periods, there is an additional need to extrapolate between the ^{210}Pb chronologies and the ^{14}C age estimates. A challenge always arises in this extrapolation, especially in the 150-300 year time horizon in that the sediments are too old for ^{210}Pb dating and too young for ^{14}C dating (Russell *et al.* 1993). Anchored interpolations between ^{210}Pb and ^{14}C dates are often used, assuming a linear sedimentation rate (e.g. Russell *et al.* 1993; Francis and Foster 2001). However, this approach can lead to sudden changes in accumulation rate at the *c.* 150 year base of the ^{210}Pb chronology at the point where the age-depth curve changes direction to join the available ^{14}C age-estimate. Anchored linear interpolations do not account for the probability of gradual increases in compaction with depth, whilst other more complex models may achieve this, but will smooth the age-depth curve between known data points and also may limit the ability to model shifts in accumulation rate.

The challenge of interpolation between data points is exacerbated in many studies by the low number of ^{14}C assays available (Bennett 1994; Bennett and Fuller 2002). This is especially true in the dating of recent sediments from small hollows, which may be more prone to hiatuses and shifts in accumulation rate (Jacobson and Bradshaw 1981). This is an important issue; as temporal definition may be especially critical in these site types due to the nature of interpretation being sought, which is normally an attempt at the merging of ecological and palaeoecological debate and therefore requires a fine temporal and spatial precision to the analysis (Dumayne-Peaty 1999). These challenges are no less true of the Glen Affric cores interpreted in this thesis.

With funding allocated for 15 radiocarbon assays over the eight cores it was necessary to opt between the selection of assays at depth levels of particular vegetation shifts (R. Tipping *pers. comm.*), or the systematic spatial spread of age-estimates by depth.

Due to the time management issues surrounding obtaining data within a three year study ^{210}Pb age-estimates were not available until after the ^{14}C assays had been chosen and so could not be used to constrain the choice of depth for the assays. Thus for several of the cores, the returned ^{14}C age-estimates are considerably older than 300 cal. BP years and therefore the temporal gap between extrapolated points is much greater than the ideal *c.* 150 years. In addition, the selection of assays to date particular vegetation features in the pollen spectra meant that the opportunity to obtain assays from the bases of the pollen spectra was lost. This necessitates extrapolation below the depth of the lowest available ^{14}C assay, which is problematic.

The topmost sediments are obviously less compacted than those at depth and compaction may be assumed to increase with depth in the surface layers. Additionally, possible changes in tree cover as well as the effects of a warming climate in recent decades may all have had an effect on peat growth and formation, and it is possible that surface peat layers have accumulated at a different rate than those in the past. These factors create a difficulty in establishing the best method of interpolation between the surface ^{210}Pb dated peats and the ^{14}C dated horizons at depth.

Any modelled shift in sediment accumulation may be constrained by the depth level of the available assays rather than the actual depth of any accumulation rate shift. As Bennett and Fuller (1994) observe, any age-depth model "*cannot be right*" as changes in sedimentation rate do not fit neatly against locations chosen for radioisotope dates. They observe that possibly 100s of radiocarbon age determinations would be required to attempt to date synchronous events with precision across cores. Despite the preference for a realistic age-depth model that takes stratigraphic core compaction into account, Bennett and Fuller (p.425) observe that linear interpolations are "*not necessarily a bad choice*", whilst Telford *et al*. (2004a) observe that although smoothing splines can bypass noise incorporated into a dating model by avoiding passing through every point, when dates few, and are selected based on possible shifts in stratigraphy, linear interpolation may be the most appropriate model.

Bennett and Fuller tested several different age-depth curve models using a known marker horizon of *Tsuga canadensis*. This test approach is not available in the small basins of Glen Affric, where the local pollen signal does not record exotic markers in adequate numbers to base an interpretation. Additionally, since the rationale behind the small hollow approach is to test the scale of vegetation shifts assuming any single dateable shift across cores would lead to a circularity of argument. There is, therefore, no independent method by which to test the integrity of the chronological models. Any model choice will therefore be somewhat arbitrary. The approach to fitting a model curve is outlined below based on a number of logic assumptions.

4.5.1 Approach to chronological data combination

Logical assumptions for the determination of age-depth curves for Glen Affric peat cores are listed below:

1. The shape of the chronological age-depth curve is likely to be concave. This is because peat is likely to undergo very little compaction or decomposition in the surface layers, with rapid peat accumulation, followed by a period of rapid increase in age with depth as both decomposition and compression acts upon the peat substrate. Therefore, a polynomial should give a better fit where it is possible to use one.

2. Since all peat deposits can be assumed to have formed in the current post-glacial, extrapolations to the recorded basal depth of the peat basin cannot display ages greater than *c.* 10,000 years cal. BP. Basal ages have a good probability of being in the region of 7000-6000 cal. BP, or younger on sloping sites. This is assumed from supporting evidence in west Glen Affric where Tipping *et al.* (2003) found that it is likely that the near-complete ground cover of peat occurred by *c.* 6000 cal. BP whilst inception in the deepest parts of basins began at *c.* 10200-9480 cal. BP (p51). This factor should constrain polynomials, which can be too flexible to be realistic (Bennett and Fuller 2002).

3. Linear interpolations form the simplest model, but where two radiocarbon ages are close together, and the resultant slope between them is shallow, it may not be the most parsimonious solution to apply an extrapolation of this shallow slope below the oldest radiocarbon age. If a polynomial curve presents an extrapolated age-depth curve that returns a basal age in agreement with the *c.* 7000-6000 age range found by Tipping *et al.* (see above - assumption 2), then the polynomial curve will be accepted. If the polynomial seems wildly inaccurate, then the linear interpolation will be accepted.

4. ^{14}C ages from peat which show near surface ages and possible modern contamination must possess age ranges at the older end of the spectrum of radiocarbon age distribution. Assuming no inversions of the peat stratigraphy, these are constrained to older radiocarbon age spectra because they fall below the equilibrium point for ^{210}Pb, which signals *c.* 150 years of peat formation.

5. Where the midpoint in the calibrated radiocarbon age falls into "*radiocarbon plateaux*" (Telford *et al.* 2004b) a choice is made to select the midpoint of a suitable or likely age range within a radiocarbon peak to either side of any plateaux in consultation with the data from the OxCal calibration curve.

4.5.2 NHP combined age-depth models

Combined ^{210}Pb and^{14}C age-depth models for the NHP core are presented in Figure 4.8.

The ^{14}C assay at 69 cm is rejected (see Section 4.2). This leaves just one radiocarbon assay at 89 cm with which to interpolate and extrapolate and model the chronology from the ^{210}Pb assays. The radiocarbon calibration curve in Figure 4.7 indicates that the midpoint is an unlikely age estimate for the ^{14}C assay at 89 cm. At the 2s age-range there is an 86.7% probability that the age estimate lies between 2355 and 2305 cal. BP. The midpoint of this spectral peak is therefore used in the modelled chronologies.

The basin depth at the NHP site is *c.* 165 cm. Extension of a linear extrapolation between the basal ^{210}Pb age and the midpoint ^{14}C age returns a basal peat age estimate of *c.* 3000 BC (4950 cal. BP). A 2-term polynomial model returns a basal peat age estimate of *c.* 5800 BC (7750 BP), which is in agreement with the peat inception to the west of Glen Affric (Tipping *et al.* 2003). A 3-term polynomial returns a basal peat age estimate of *c.* 4200 BC (6150 cal. BP).

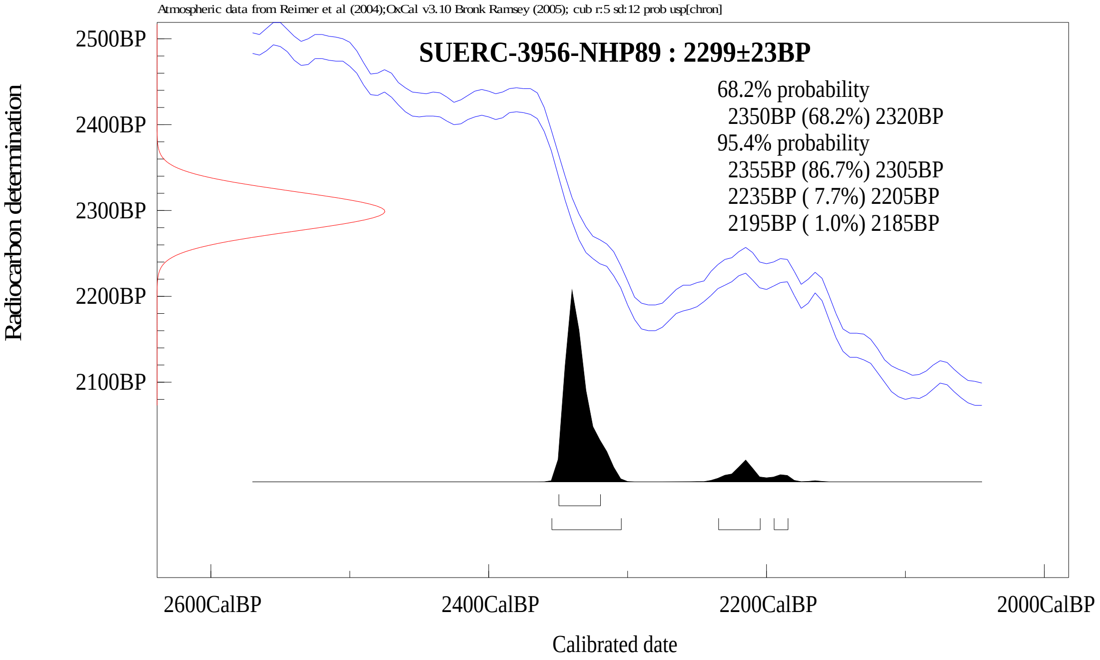


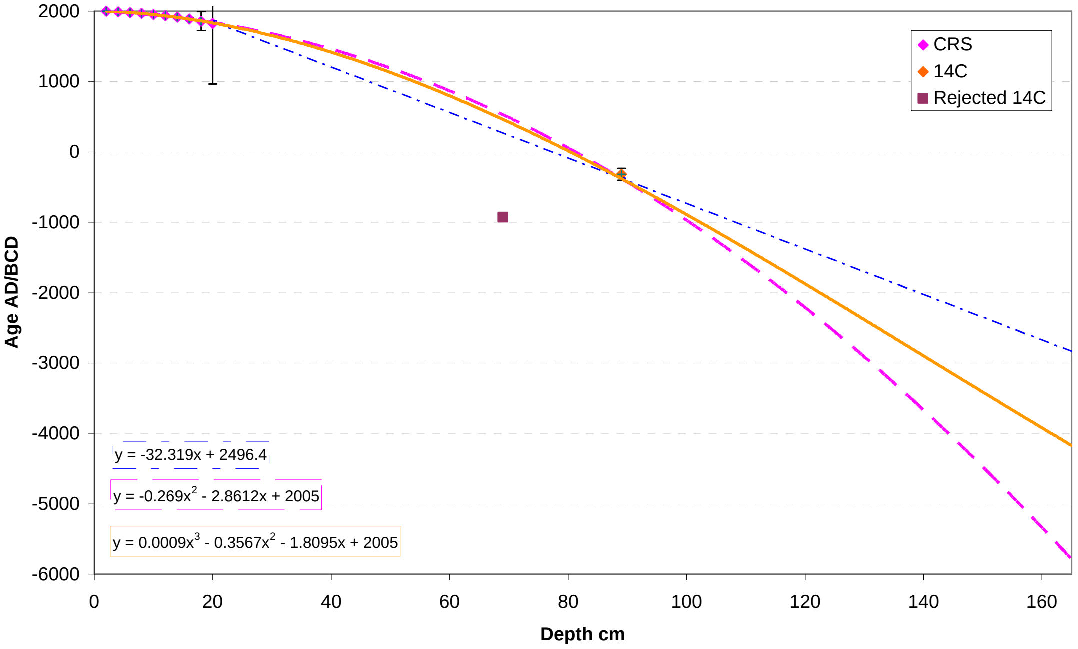
Figure 4.7: Plot of calibrated age-range probabilities for radiocarbon age-determination for the assay from NHP at 89 cm. Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al*. 2004).

Figure 4.8 presents three possible interpolations based on 2nd and 3rd order polynomials and a linear extrapolation from the basal ^{210}Pb age-estimate to the ^{14}C age-estimate. This illustrates the problem of age determinations with few assays to provide constraints. It is not possible to make an assured judgement on the best fit of any of the age-depth curves; each provides a credible alternative.

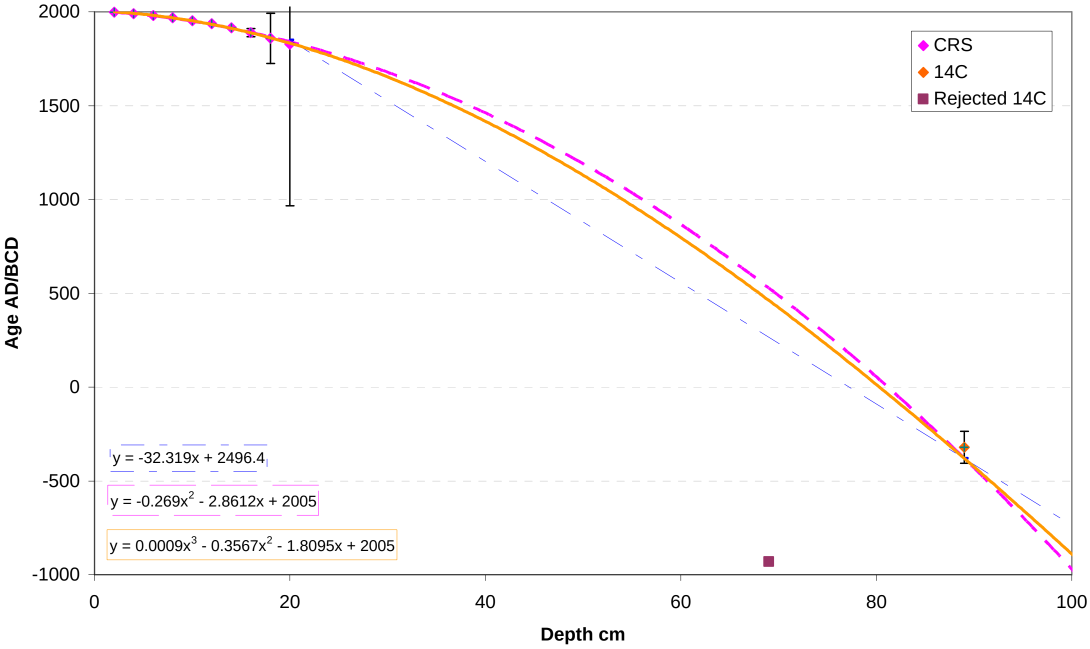
The basin at NHP is 165 cm deep. Equation 4.5, the 3rd-order polynomial, predicts a basal peat age-estimate of *c.* 6000 cal. BP. This correlates reasonably with previously published age estimates for peat inception (Tipping *et al*. 2003; see Section 4.5.1); and is therefore accepted as evidence to select the 3rd-order polynomial as the chronological model for the NHP core. The chronology is therefore modelled by Equation 4.5 as shown in Figure 4.8:

$$y = 0.0009\text{x } X^3 - 0.3567\text{x } X^2 - 1.8095\text{x } X + 2005 \qquad \text{Equation 4.5}$$

Although the different models in Figure 4.8 predict basal age-estimates for the NHP core that are *c.* 3000 years apart, the core was only sampled for pollen to 100cm. Figure 4.8b displays the relevant depth span for the NHP core. Extrapolations from the ^{14}C assay at 89 cm to 100 cm results in predicted age difference of *c.* 240 between the different models of which the 3rd-order polynomial is the midpoint.



a)



b)

Figure 4.8: Exploration of age-depth models for the NHP core using combined ^{210}Pb and ^{14}C data The pink long-dash line represents a 2-term polynomial through the CRS data points. The orange short-dash line represents a 3-term polynomial through the CRS data points. The blue dash-dot line represents a linear interpolation from basal ^{210}Pb age to the ^{14}C age estimate. Associated model equations are presented. The lines are extrapolated through to the maximum depth of the basin in Figure 4.8a to illustrate the correlation with predicted peat inception of Tipping *et al*. (2003). Pollen was sampled to 100 cm only and the age-depth curves over the depth of the pollen samples is illustrated in Figure 4.8b.

4.5.3 PB combined age-depth models

Combined ^{210}Pb and^{14}C age-depth models for the PB core are presented in Figure 4.9. CRS and CIC ^{210}Pb-chronological models both exhibit a steady, almost linear age-depth curve until 10 cm from where they diverge markedly (Figure 4.3). The CRS model returns a date of AD 1906 at 11 cm (the equilibrium point between supported and unsupported ^{210}Pb), this may indicate that the CRS age estimate is too young. The CIC model age estimate is AD 1843 at 11 cm (see discussion in Section 4.3.4.2).

Calibrations of the radiocarbon assays show no major plateaux at the midpoint of the predicted age-ranges and therefore the midpoint is accepted as a justified age estimate for both assays.

The 2-term polynomial combining the ^{14}C age-estimates and the ^{210}Pb CRS model produces a steady decline with depth, but smoothing between the age estimates means that the 2-term polynomial misses data points on the ^{210}Pb curve, and the two ^{14}C assays. The basin depth for PB core is *c.* 162 cm. The 2-term polynomial exceeds 10,000 BP at this depth (Figure 4.9a) and does not therefore provide a realistic age-depth curve. The 3rd order polynomial is too flexible (see Figure 4.9a), and is also rejected.

The CRS model does not reach the expected age estimate at the equilibrium depth between supported and unsupported ^{210}Pb. However, a 2-term polynomial plotted on the CIC data produces a smooth curve to the equilibrium point and interpolates well with the ^{14}C age-estimate at 71 cm (Figure 4.9b and Equation 4.6).

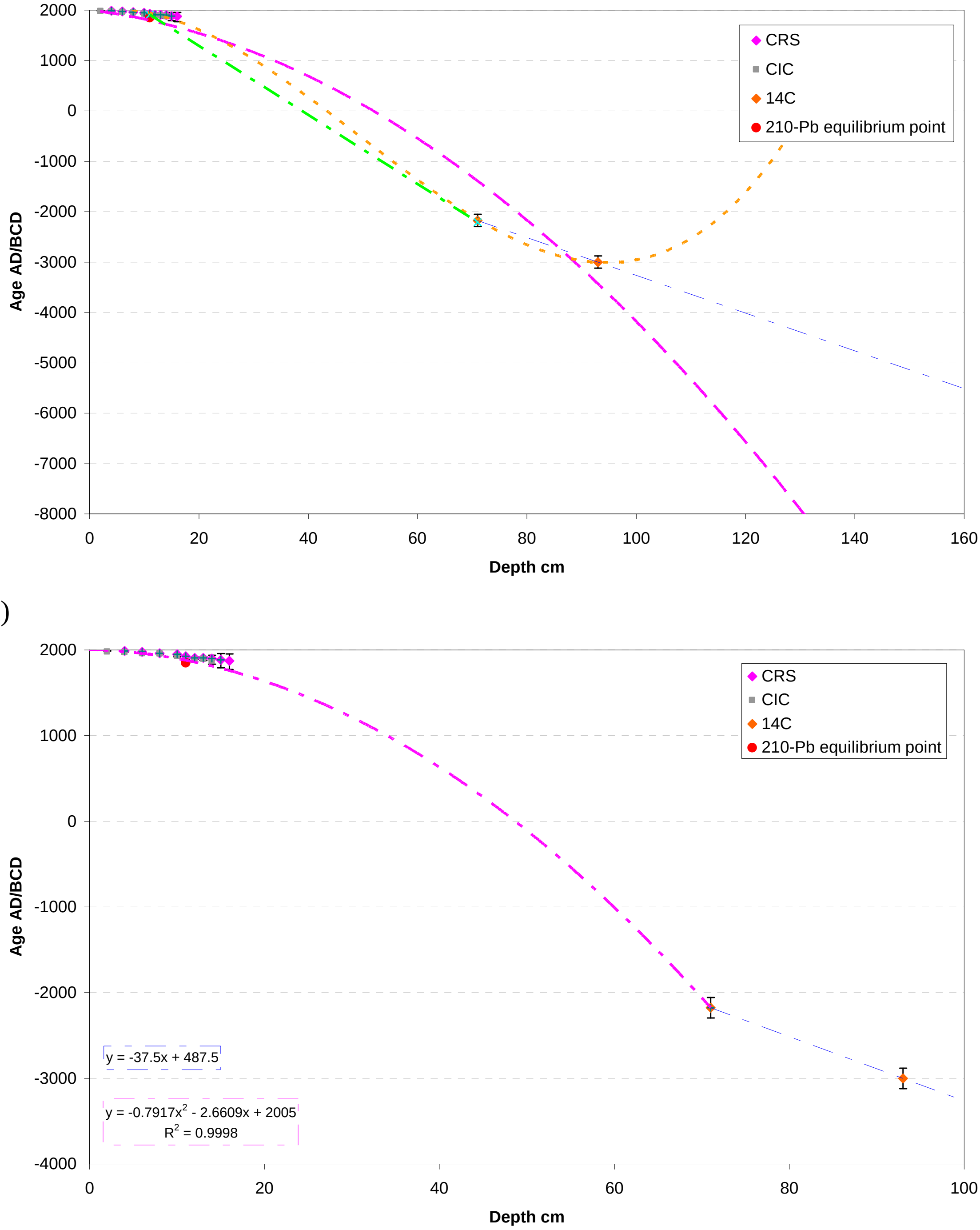
The extrapolation of the above curve, does not account however, for the second ^{14}C age-estimate at 93 cm. The shallow trajectory of the interpolation between the two ^{14}C age-estimates requires a change in peat accumulation rate. Pollen accumulation data in Chapter 6 show an increase in pollen accumulation between *c.* 30 cm and *c.* 6 cm in the PB core. This is followed by a decrease in total pollen accumulation to rates matching the top 30 cm. This is consistent with a change in accumulation rate and provides supporting evidence for accepting a change of age-depth model to a linear interpolation between 71 cm and 93 cm in the PB core.

Extension of a linear extrapolation between the two ^{14}C age estimates returns a basal peat age estimate of *c.* 5500 BC (7550 cal. BP; see Figure 4.9a). This is in agreement with the *c.* 7600-6000 cal. BP estimates for peat inception (Tipping *et al.* 2003).

A 2nd-order polynomial between the ^{210}Pb and ^{14}C assay at 71 cm (Equation 4.6), followed by the linear interpolation and extrapolation between the two ^{14}C assays (Equation 4.7) therefore provides a viable age-depth model for this core. This model is presented in Figure 4.9b with an extrapolation of the linear ^{14}C interpolation to 100 cm depth.

$$y = -0.7917 \text{x } X^2 - 2.6609 \text{x } X + 2005 \qquad \text{Equation 4.6}$$

$$y = -37.5 \text{x } X + 487.5 \qquad \text{Equation 4.7}$$



a)

b)

Figure 4.9: a) Exploration of age-depth models for the PB core using combined ^{210}Pb and ^{14}C data; and **b)** selected age depth model for the PB core.
a) The pink long-dash line represents a 2nd -order polynomial through the CRS data points. The orange short-dash line represents a 3rd-order polynomial through the CRS data points. The green dash-dot line represents a linear interpolation from basal ^{210}Pb age to the ^{14}C age estimate. The blue dash-dot line represents a linear interpolation and extrapolation through the ^{14}C age estimates. The lines are extrapolated through to the maximum depth of the basin. Pollen was sampled to 100 cm only.
b) The accepted age-depth model for the PB core incorporating a 2nd-order polynomial between the ^{210}Pb and first ^{14}C assay and a linear interpolation between ^{14}C assays.

4.5.4 BEAT age-depth models combined

Combined ^{210}Pb and^{14}C age-depth models for the BEAT core are presented in Figure 4.11. The CRS model is the only viable model for this core due to the non-monotonic nature of the ^{210}Pb assays (Section 4.3.4.3). The equilibrium point between supported and unsupported ^{210}Pb was not reached at this core, which shows evidence of rapid accumulation in both the ^{210}Pb and ^{14}C age-estimates and the stratigraphy.

Three radiocarbon assays are available for this core. The assays at 49 cm and 67 cm return young ages with large associated errors. The radiocarbon calibrations displayed in Figure 4.10 show major plateaux between peaks in the probability spectrum. The calibrated age range at 49 cm of 275-5 cal. BP comprises three separate age-range probabilities at 2s (275 cal. BP 170 cal. BP 37.8%): 155 cal. BP 55 cal. BP (41.6%): 45 cal. BP 5 cal. BP (16.0%)). The basal ^{210}Pb age-estimate at 28 cm for the BEAT core is AD 1900 (50 cal. BP). An extrapolation of the ^{210}Pb CRS curve to 49 cm returns an age estimate of *c.* AD 1660 (290 cal. BP). Assuming a steady decline in the age-depth curve the ^{210}Pb data constrains the age-estimate to the radiocarbon probability peak of 275-170 cal. BP (37.8%). This seems the most realistic age range for the ^{14}C assay at 49 cm. The midpoint of this age range is therefore used in the model calculations.

The calibrated age range for the radiocarbon assay at 67 cm shows four defined peaks of age probability (425 BP – 410 BP (1.3%) : 320 BP – 275 BP (61.2%) : 175 BP – 150 BP (27.7%): 10 BP - -6 BP (5.2%)). With a probability of 61.2% the age range of 320-275 BP is accepted as the likely age estimate for the ^{14}C assay at 67 cm. Given acceptance of the ^{210}Pb age-estimates and the ^{14}C age-estimate at 49 cm the younger spectral peaks in the calibration curve would be impossible without inferring an inversion of the peat. The midpoint of the 320 – 275 cal. BP probability spectra is therefore used in the age-depth models.

The calibration at 99 cm shows no major plateaux in the calibration spectra, and therefore the midpoint is accepted as a justified age estimate.

Polynomial models interpolated through the CRS and ^{14}C chronologies are not realistic; the 2nd order polynomial does not follow the ^{210}Pb curve, or agree with either ^{14}C assay. The 3rd order polynomial fits the data well (illustrated by the blue continuous line in Figure 4.11). However, the basin depth for BEAT core is *c.* 262 cm and both the 3rd, and 2nd -order polynomials, when extrapolated to this depth, exceed 10,000 cal. BP (the post-glacial age limit for peat inception), and are therefore unrealistic models.

The best explanation of the data is likely to be a linear interpolation. A choice is required between;

1. rejecting the ^{14}C assays at 49 cm and 67 cm as too young and extrapolating from the oldest ^{210}Pb age estimate at 28 cm to the ^{14}C assay at 99 cm (illustrated by the green short-dash line in Figure 4.11); or
2. assuming that the lower spectrum of the ^{14}C calibrated age ranges at 49 cm and 67 cm are secure. Thus justifying the application of a 2-term polynomial to the CRS and first two ^{14}C assays (solid orange line in Figure 4.9); followed by a linear interpolation between the ^{14}C age estimate at 67 cm and the ^{14}C age estimate at 99 cm (broken orange line in Figure 4.11).

Reference to the pollen concentration data for BEAT in Chapter 6 (Middeldorp 1986) supports evidence for a shift in peat accumulation rate at 67 cm demonstrating a marked increase in the pollen concentration at this depth. Comparing a median pollen concentration per cm from the samples above and below the 67 cm core depth, the pollen concentration below 67 cm is 11 times greater than above 67 cm. The rapidity of the pollen concentration increase after 67 cm may indicate a hiatus followed by rapid accumulation in the surface layers. However, an estimate of peat accumulation from 0-67 cm using the 2-term polynomial of CRS and 49 cm and 67 cm ^{14}C age estimates in Figure 4.9 returns a peat accumulation rate of 5.6 years per cm. If the median pollen concentration per cm is taken as a crude indicator of sediment accumulation (Hicks 1974), then the accumulation rate from 67 cm to 99 cm should be in the region of 56 years per cm (11 times smaller than the top sediments). The linear interpolation between the oldest midpoint age-estimate for the ^{14}C assay at 67 cm (as determined from the spectral peak in Figure 4.8) returns the equation 4.8. This equation returns a sediment accumulation rate of 52 years per cm. This is in agreement with the expected increase in accumulation predicted by the pollen concentration increase. This indicates that the peat system is likely to have undergone a rapid shift in peat accumulation rate at 67 cm, probably due to a shift in climate and vegetation (Chapter 6), and that this shift in accumulation rate, rather than a hiatus in peat accumulation is responsible for the shift in age-depth trajectory. The age-depth estimate for BEAT is therefore modelled by Equation 4.8 to 67 cm and Equation 4.9 from 67 to 100 cm.

$$y = -0.0474x\ X^2 - 2.3817x\ X + 2005 \qquad \text{Equation 4.8}$$

$$y = -52.188\ x\ X + 5151.6 \qquad \text{Equation 4.9}$$

Extension of the linear extrapolation (Equation 4.9) to 262 cm; the basal peat for this basin, returns an age estimate of 8520 BC or 10470 cal. BP. This would indicate that the basin at BEAT may hold a full Holocene sediment sequence, although further changes in sediment accumulation rate can of course not be ruled out.

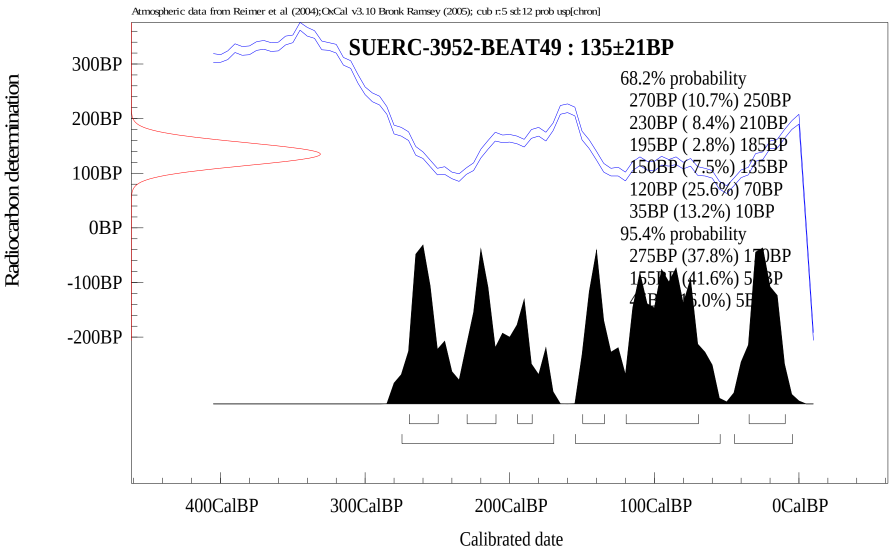


Figure 4.10: Plot of calibrated age-range probabilities for radiocarbon age-determination for the assay from BEAT at 67 cm. Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al.* 2004).

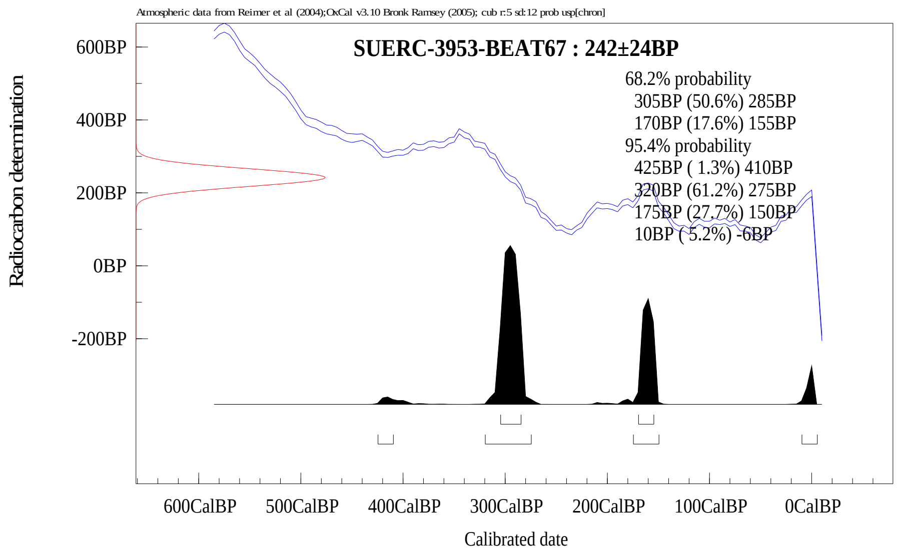


Figure 4.10 continued: Plot of calibrated age-range probabilities for radiocarbon age-determination for the assay from BEAT at 67 cm

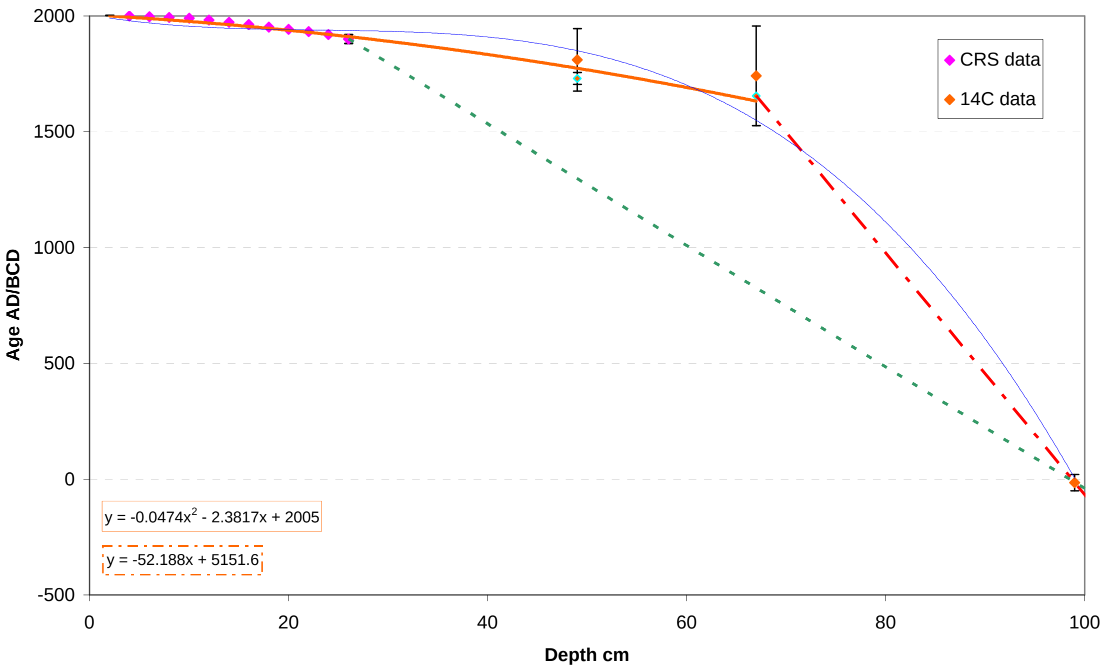


Figure 4.11: Exploration of age-depth models for the BEAT core using combined ^{210}Pb and ^{14}C data The blue continuous line represents a 3rd-order polynomial through the CRS model age-estimates and ^{14}C assays. The orange solid and dash-dot lines represent a 2nd-order polynomial between the ^{210}Pb and first two ^{14}C age-estimates followed by a linear interpolation between the ^{14}C assay at 67 cm and the assay at 99 cm. Relevant associated line equations are presented. The maximum depth of the basin was 262 cm the linear extrapolation is not shown to this depth. Pollen was sampled to 100 cm.

4.5.5 ANI combined age depth models

Combined ^{210}Pb and^{14}C age-depth models for the ANI core are presented in Figure 4.12. The CRS model returns a date of AD 1897 at 14 cm (the equilibrium point between supported and unsupported ^{210}Pb), this may indicate that the CRS age estimate is too young. The CIC model was rejected for this analysis (Section 4.3.4.5). However, the CIC model estimates an age of AD 1852 at 14 cm, displaying a rapid decrease in peat accumulation rate from 10 cm. Examination of the pollen concentration diagram in Chapter 6 shows a marked rise in pollen concentration between 10 cm and 20 cm depth in the ANI core with a peak at 18 cm. This supports the possibility of a rapid decrease in peat accumulation rate leading to an increased pollen concentration per centimetre, which is not modelled well by the CRS model.

The chronological model derived from a 3rd order polynomial of the CRS data to 10 cm and the supported-unsupported ^{210}Pb equilibrium point age-estimate of 150 years (Reinikainen *et al.* 1997) records this possible change in accumulation rate, whereas the CRS model alone does not (Figure 4.12). However, the CIC model underestimates the surface age (Figure 4.12). A polynomial that models the data-points from the CRS model ^{210}Pb age estimates to 10 cm, where the possible change in direction commences, followed by a data-point of AD 1855 at the equilibrium depth of 14 cm is therefore selected; this is displayed as the pink dashed line in Figure 4.12, together with the associated polynomial equation (Equation 4.10).

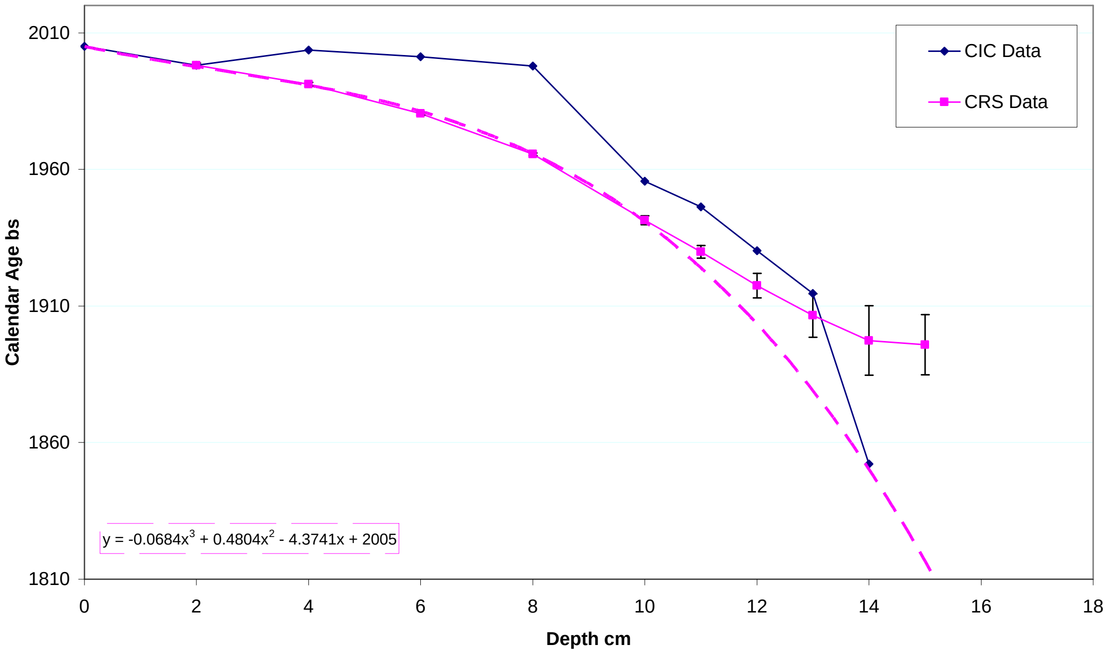


Figure 4.12: Interpolations between the age-estimates derived from ^{210}Pb data using the CIC and CRS models for the ANI core. The pink dashed line represents an extrapolation via a polynomial through the CRS model.

Radiocarbon assays at 55 cm and 69 cm constrain the age estimates at depth. The Calibration spectra for the 55 cm assay (Figure 4.13) demonstrate an 80.5% probability that the age range lies between 2500 cal. BP and 2350 cal. BP. Therefore the midpoint of this spectral peak is used in the analysis. Similarly, calibrations from the assay at 69 cm show no major plateaux and therefore the midpoint is accepted as a justified age estimate.

The 2nd-order polynomial for the CRS curve (pink dashed line in Figure 4.14) produces a steady decline with depth, but smoothing between the age estimates means that the 2nd-order polynomial does not follow the ^{210}Pb curve, or agree with either ^{14}C assay. Whilst a smoothed interpolation can be useful with many data points (Telford *et al.* 2004a), the pollen accumulation data suggests shifts in peat accumulation rate around the depths of the ^{14}C assays. The simplest approach using the available data appears to be; (i) a polynomial interpolation between the ^{210}Pb assays; followed by (ii) the linear interpolation between, the AD 1855 equilibrium-point from the ^{210}Pb dataset, and the younger calibration spectral peak of the ^{14}C assay at 55 cm (shown as a dot-dash blue line in Figure 4.14); and (iii) a second linear interpolation at 55 cm, between the ^{14}C assay at 55 cm and the assay at 69 cm, with an extrapolation of this line to 100cm, the base pollen sample. This model produces shifts in slope consistent with the fluctuations in pollen concentration.

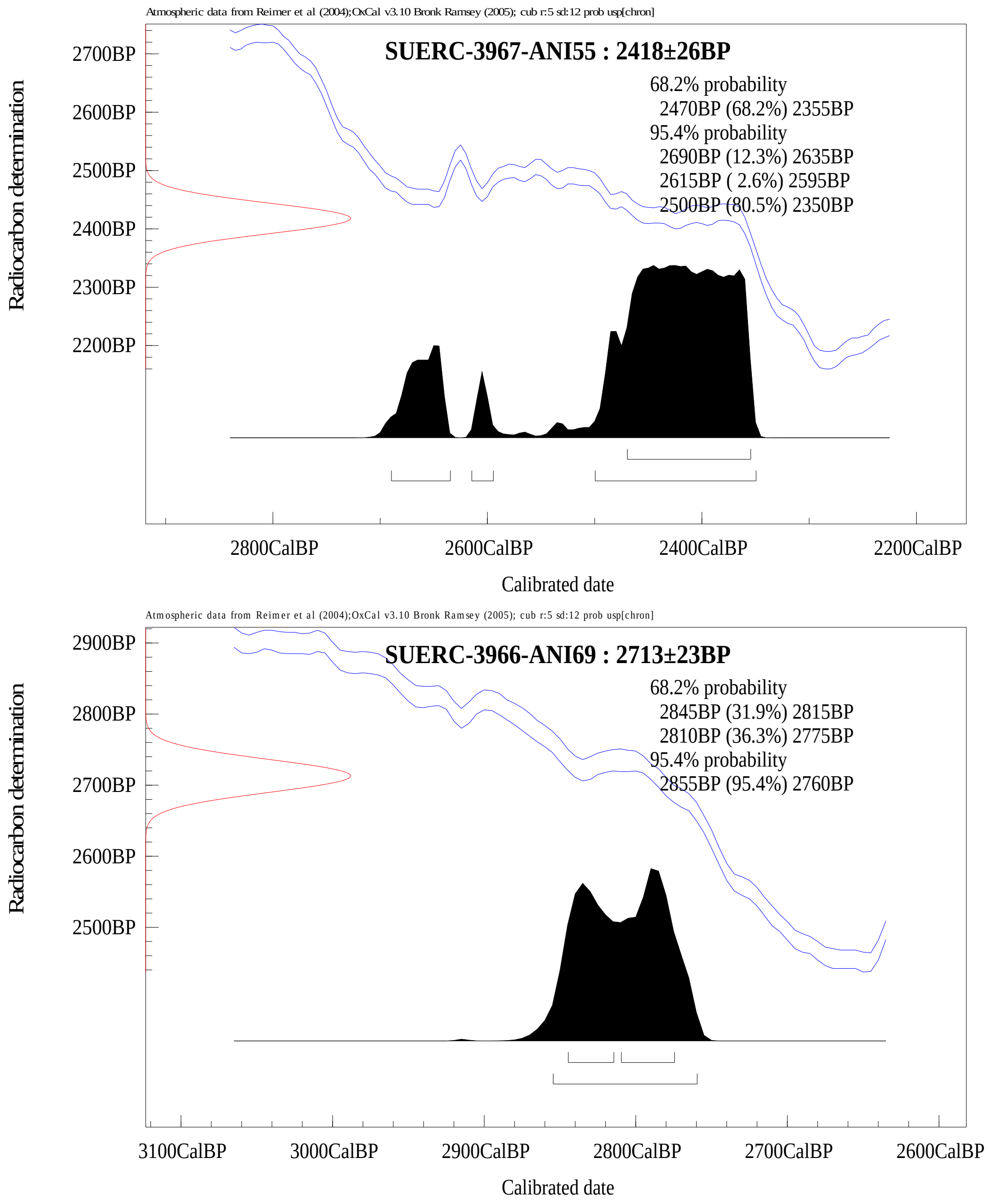


Figure 4.13: Plot of age-range probabilities for radiocarbon age-determinations for the assays from ANI at 55 cm (top) and 69 cm (bottom). Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al.* 2004).

In summary the age-depth curve selected for the ANI core is complex and comprises three curves.

A 3rd order polynomial to 10 cm to extrapolate between the ^{210}Pb assays to 10 cm and the ^{210}Pb equilibrium point at 14 cm: Equation 4.10

$$y = -0.0684x\,X^3 + 0.4804x\,X^2 - 4.3741x\,X + 2005 \qquad \text{Equation 4.10}$$

A linear interpolation between the ^{210}Pb equilibrium point and the midpoint from the 2500-2350 cal.BP spectral peak of the 55 cm ^{14}C assay: Equation 4.11

$$y = -56.707x\,X + 2643.9 \qquad \text{Equation 4.11}$$

A linear interpolation between the two ^{14}C assays at 55 cm and 69 cm including a linear extrapolation beyond the lowest ^{14}C assay to the base of the pollen samples at 100 cm and a estimated age of *c.* 2300 BC (4300 cal. BP): Equation 4.12

$$y = -27.5x\,X + 1037.5 \qquad \text{Equation 4.12}$$

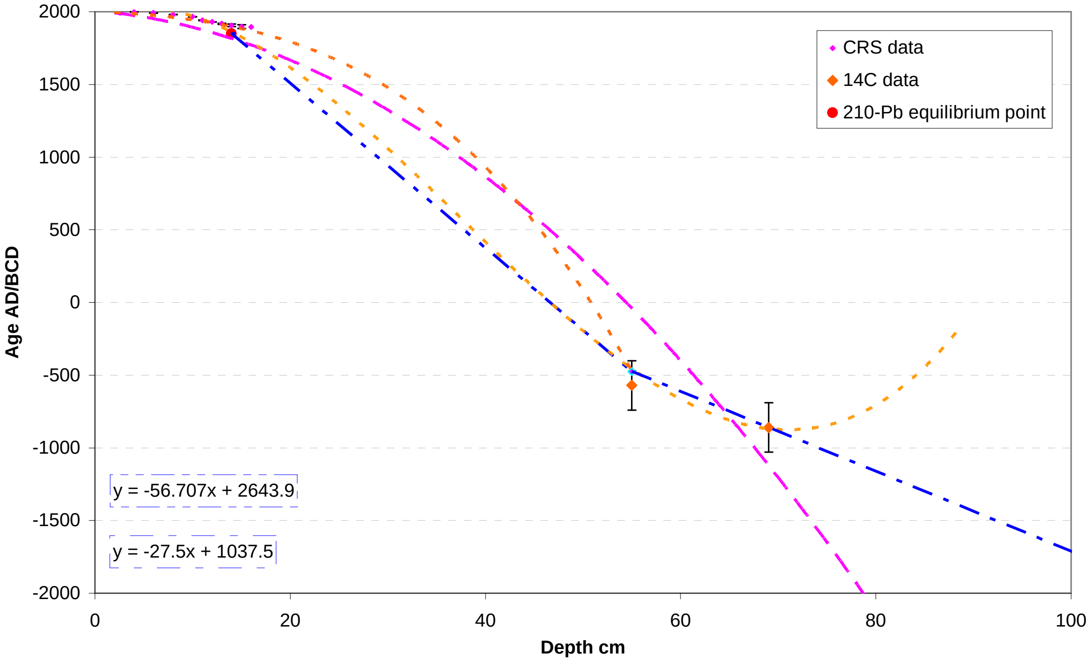


Figure 4.14: Exploration of age-depth models for the ANI core using combined ^{210}Pb and ^{14}C data
The pink long-dash line represents a 2-term polynomial through the CRS data points. The orange short-dash line represents a 3rd order polynomial through the CRS and ^{14}C data points. The blue dash-dot line represents linear interpolation and extrapolation between basal ^{210}Pb and ^{14}C age-estimates. Relevant associated line equations are presented. The lines are extrapolated through to the basal pollen sample at 100 cm.

4.5.6 ARC combined age-depth models

Combined ^{210}Pb and ^{14}C age-depth models for the ARC core are presented in Figure 4.16. The CRS model is used for interpolations between ^{210}Pb and ^{14}C assays. The equilibrium point between supported and unsupported ^{210}Pb is taken as approximately 19 cm (Section 4.3.4.4).

However, unsupported ^{210}Pb at this level is measured at 7.9 Bq kg^{-1} and supported ^{210}Pb is 15.3±18.0 Bq kg^{-1}; therefore, the equilibrium may not actually be reached. The young age estimates of the radiocarbon assays at 45 cm and 69 cm support that the equilibrium may be below this depth.

The calibrated 2s radiocarbon age-range estimate at 45 cm is 275-10 cal. BP. The midpoint falls at 145 cal. BP, which is near to the radiocarbon plateau (Figure 4.15). The calibrated age-range for the assay at 45 cm comprises three peaks at 2s: 275 BP-185 BP (34.9%): 155 BP- 55 BP (44.8%): and 45 BP-10 BP (15.6%). A midpoint based on the older spectral peak (275 BP-185 BP (34.9%)) seems more likely given trajectory of accumulation signalled by the ^{210}Pb data.

The calibration curve for the older radiocarbon assay at 69 cm displays two probability spectra (Figure 4.15b) and the midpoint falls in a plateau between these peaks. There is a slightly higher probability that the true age estimate lies within the range of the younger peak (565 BP – 520 BP (57.1%)).

A 3rd order polynomial through the CRS and ^{14}C spectral midpoints provides a smooth age-depth curve through the data and extrapolates to a basal age of AD 1070 (880 cal. BP) at *c.* 85 cm (Equation 4.13).

$$y = -0.0016x\, X^3 + 0.0995x\, X^2 - 7.8981x\, X^3 + 2005 \qquad \text{Equation 4.13}$$

Equation 4.13 predicts a much younger basal age than the *c.* 7600-6000 cal. BP estimates for peat inception (Tipping *et al.* 2003). However Tipping *et al.* found that peat inception was younger in some areas. The ARC core is from a very small hollow on the steep slope of the north side of Loch Beinn a Mheadhoin and may therefore have a justifiably later date for peat inception (Tipping *et al*. 2003).

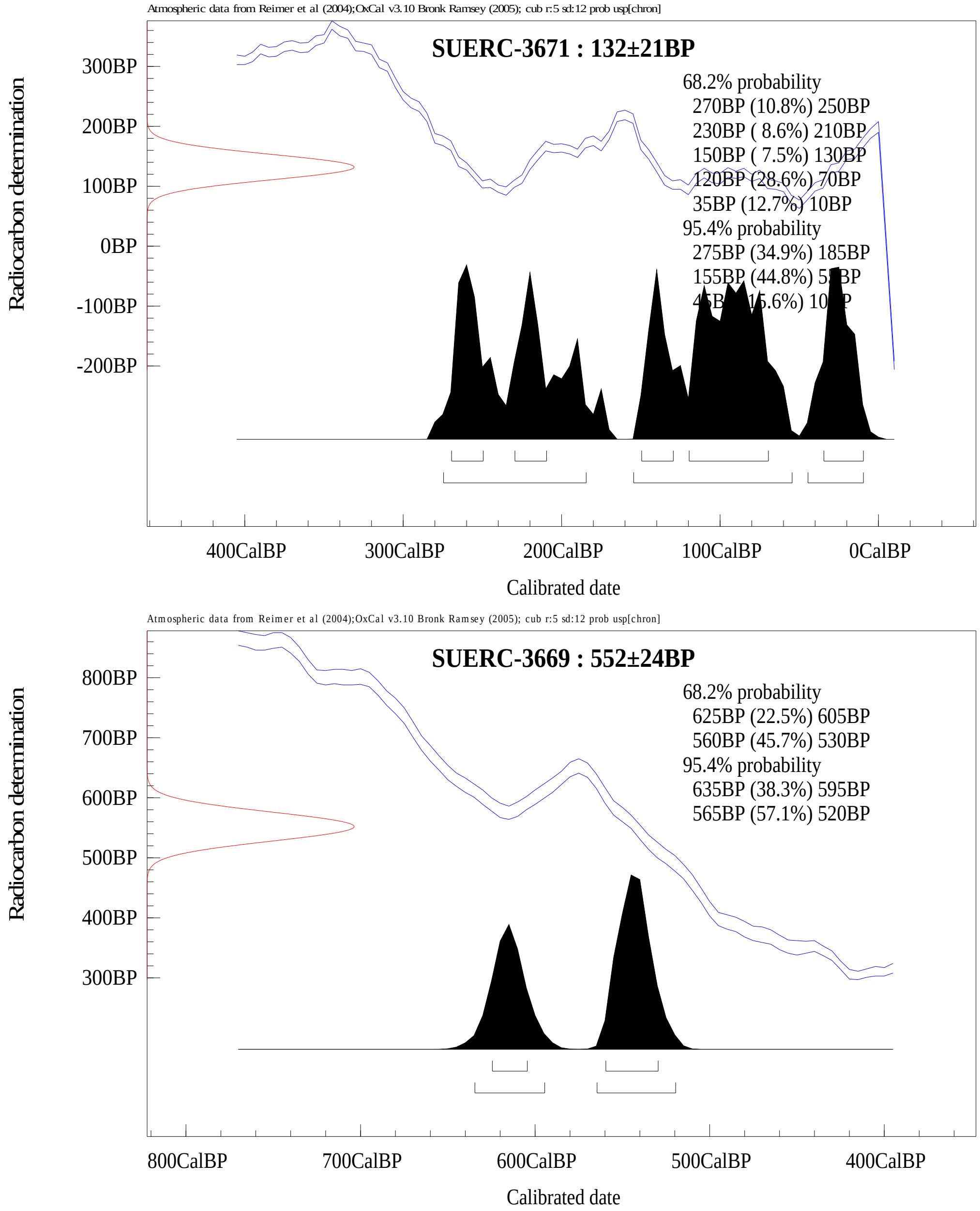


Figure 4.15: Plot of age range probabilities for radiocarbon age determinations for the assays from ARC at 45 cm (top) and 69 cm (bottom). Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al.*,2004).

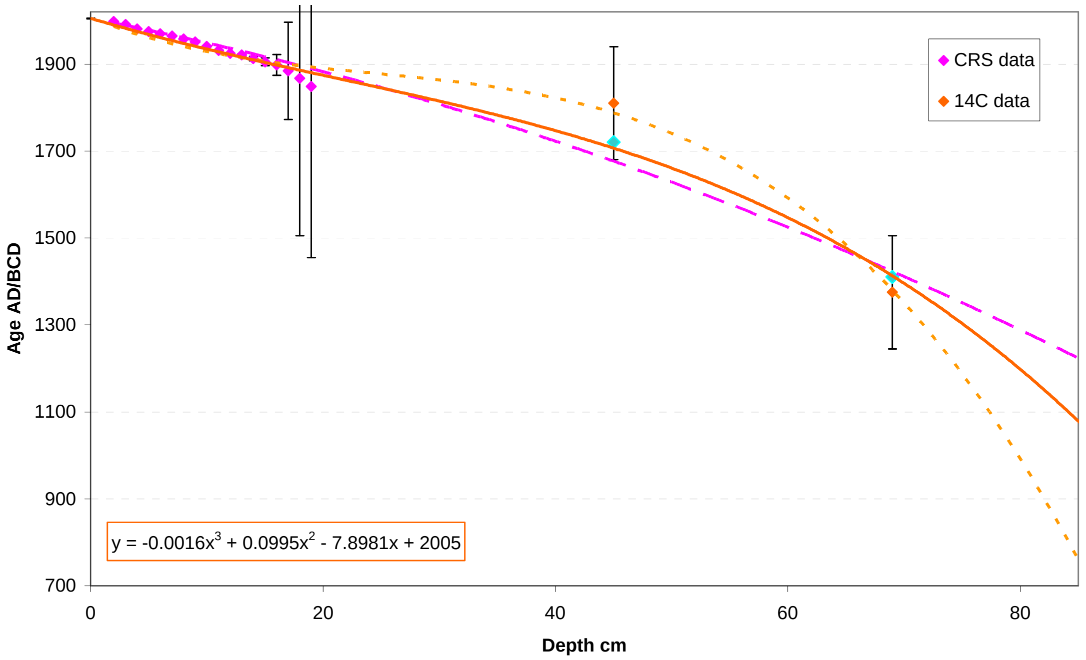


Figure 4.16: Combined age-depth models for the ARC core.
The pink long-dash line represents a 2-term polynomial through the CRS data points. The orange short-dash line represents a 3-term polynomial through the CRS and ^{14}C data points. The relevant associated model equation is presented. The lines are extrapolated through to the maximum depth of the basin at 85 cm. Pollen was sampled to base.

4.5.7 CLH combined age-depth models

Combined ^{210}Pb and ^{14}C age-depth models for the CLH core are presented in Figure 4.18. The CRS model is used for interpolations between the ^{210}Pb and ^{14}C assays. The equilibrium point between supported and unsupported ^{210}Pb is reached approximately at *c.* 13 cm

This core has one radiocarbon assay at 73 cm. The calibrated 2s age-range estimate for the assay is 2700-2490 cal. BP. The midpoint falls at 2600 cal. BP. The calibration curve in Figure 4.17 shows that there is a high probability of this being a true estimate of age and so the midpoint is accepted in the chronological models.

Both the 2-term and 3-term polynomial provide smooth age-depth curves through the CRS and ^{14}C midpoint. The curves extrapolate to a basal ages at *c.* 88 cm of 2720 BC (4670 cal. BP) and 1220 BC (730 cal. BP). This illustrates the problem faced with few age determinations. It is not possible to securely accept or reject either age depth curve or indeed any linear extrapolation between data points. However, the pollen concentration diagram in Appendix 1 (Figure A6.2) demonstrates an increase in pollen concentration at *c.* 40 cm, possibly indicating a decrease in peat accumulation rate. The 3rd order polynomial produces a curve that provides a slightly more defined shift to a steeper slope at around 40 cm, this curve would account more readily for the change in pollen concentration and is therefore arbitrarily chosen as the accepted model.

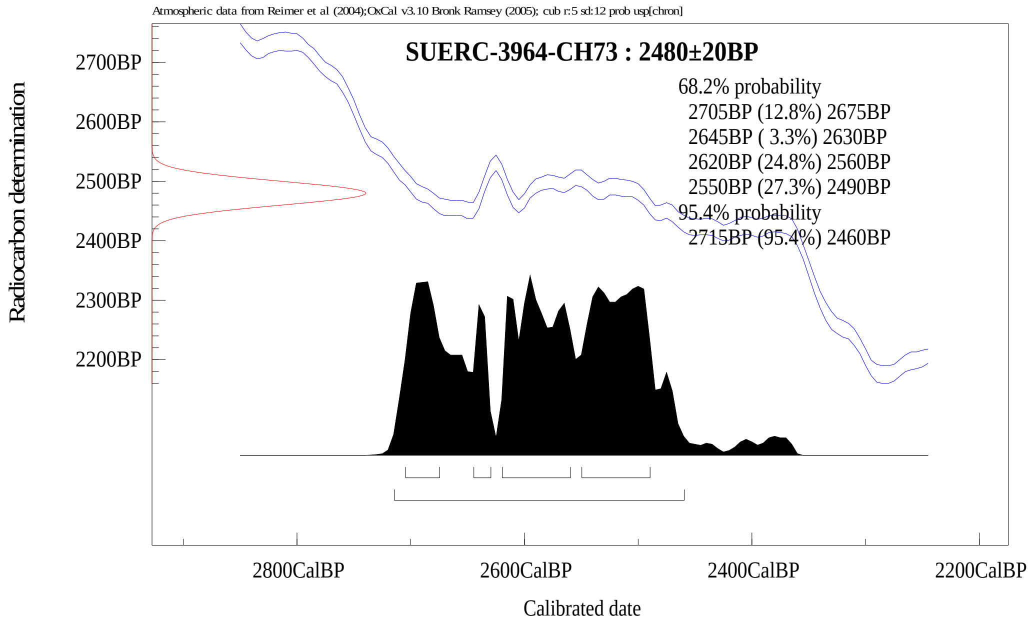


Figure 4.17: Plot of age range probabilities for radiocarbon age determination for the single assay from CLH at 73 cm. Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al.* 2004).

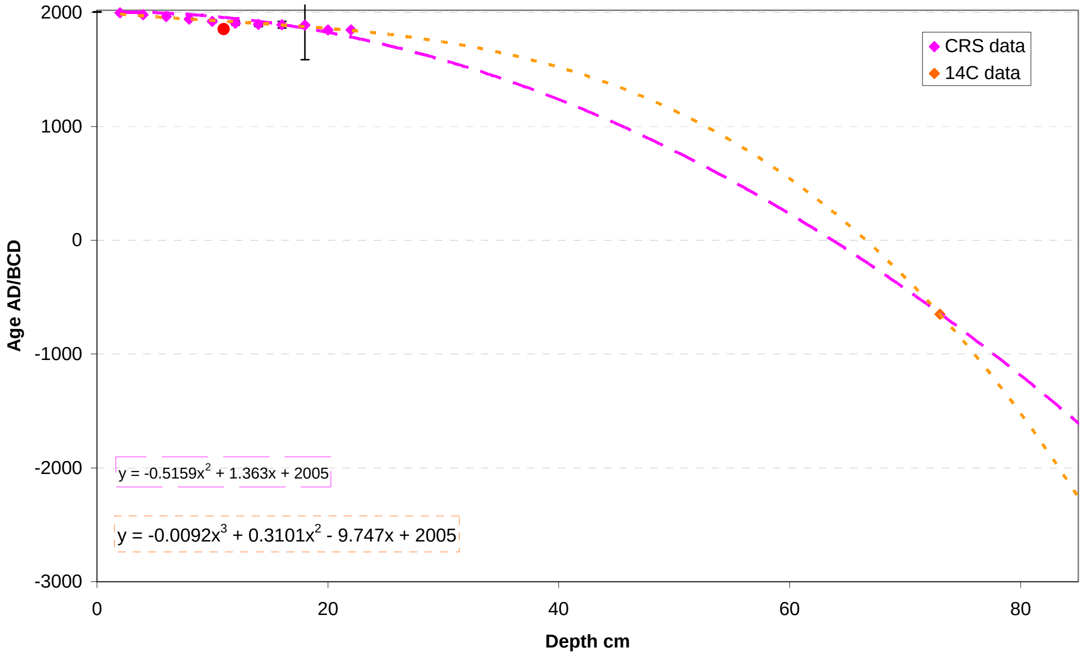


Figure 4.18: Exploration of age-depth models for the CLH core using combined ^{210}Pb and ^{14}C data The pink long-dash line represents a 2nd order polynomial through the CRS data points. The orange short-dash line represents a 3rd order polynomial through the CRS and ^{14}C data points. The relevant associated model equation is presented. The lines are extrapolated through to the maximum depth of the basin at 84 cm. Pollen was sampled to base.

4.5.8 CLKH combined date models

The CLKH core, as with the BEAT core demonstrates a rapid accumulation rate. The CRS model is used to determine a ^{210}Pb chronology (Section 4.3.4.7); however, the equilibrium point was not reached at a depth of 28 cm. Two radiocarbon assays return young age range estimates of 275-10 cal. BP (midpoint 140 cal. BP (AD 1810)) at 65 cm and 255-35 cal. BP (Midpoint 145 cal. BP (AD 1805)) at 93 cm. The radiocarbon calibration curves show plateaux in radiocarbon age at the midpoints of these ranges (Figure 4.19). Given an assumption of a steady decline in age with depth the ^{210}Pb data constrain the likely ^{14}C calibration curve for the 65 cm assay to the age-ranges below *c.* 150 years before 2005 (*c.* 100 cal. BP). Table 4.10 shows the 2s age-ranges and their probabilities. The age estimate is also constrained at 65 cm by the estimate at 93 cm, which must be older. Acceptance of the 155-55 BP (44.3%) age-range at 65 cm and the 255-225 BP (19.6%) age-range at 93 cm allows a chronological curve to be modelled for the data.

Table 4.10: ^{14}C calibrated age-range probabilities for the CLKH core from OxCal v.3.10.

^{14}C calibrated age-range probabilities for the CLKH core	
65 cm	93 cm
275BP-185BP (35.0%)	255BP-225BP (19.6%)
180BP-170BP (1.0%)	135BP-115BP (13.3%)
155BP-55BP (44.3%)	75BP-35BP (35.3%)
45BP-10BP (15.2%)	

CLKH was the deepest basin sampled in this study, extending to 450 cm in depth. A 3rd order polynomial curve fitted through the CRS and ^{14}C data points returns an age at 450 cm of 8000 BC (9950 cal. BP). If this age-depth model is correct, the CLKH basin holds a full Holocene peat sequence. This is likely as the basin is in a wet flush between outcrops of bedrock and would have always been a low-lying area prone to wetness. The 3rd order polynomial is therefore accepted as the age-depth curve for this core, although the accuracy of the extrapolation cannot be confirmed. Figure 4.19 plots the age-depth model to the 100 cm depth of the basal pollen sample. The age-depth is modelled by Equation 4.14

$$y = -0.0001x\ X^3 + 0.0183x\ X^2 - 3.7167x\ X + 2005 \qquad \text{Equation 4.14}$$

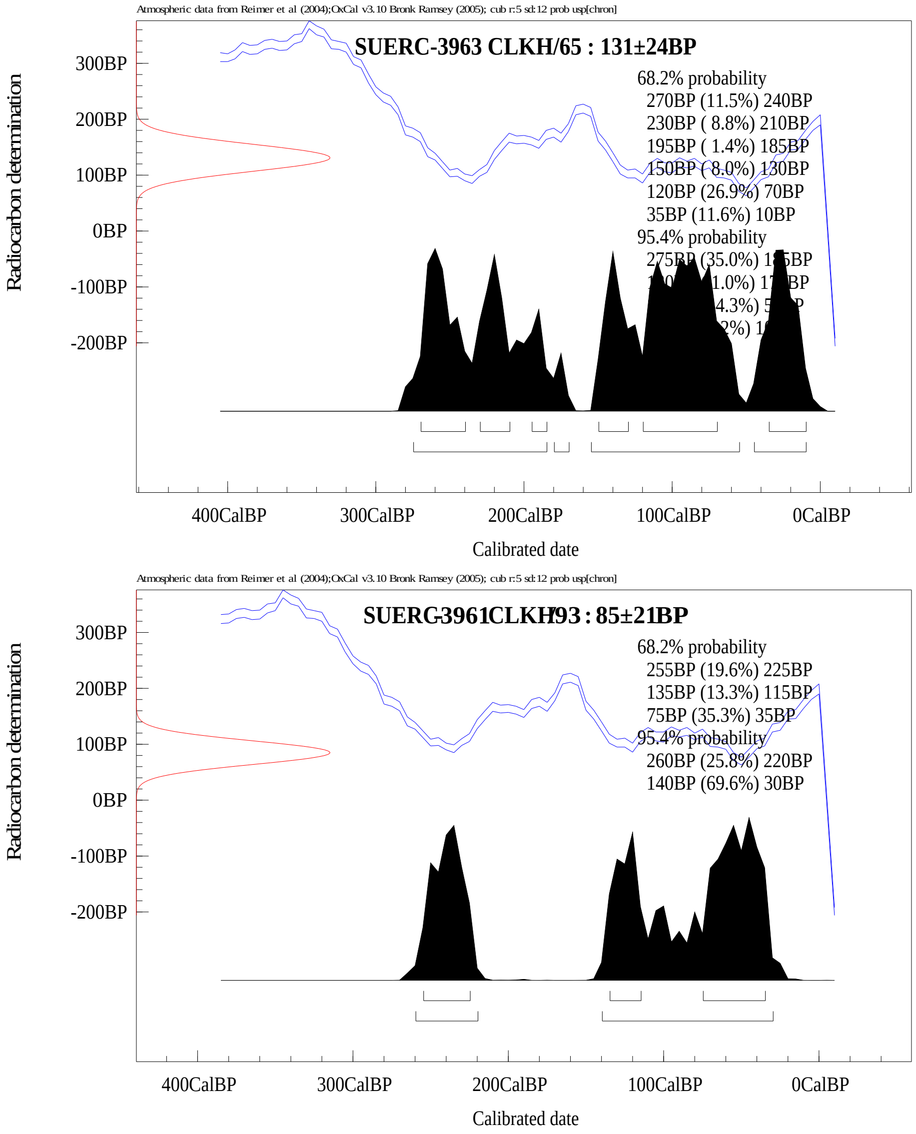


Figure 4.19: Plot of age range probabilities for radiocarbon age determinations for the assays from CLKH at 65 cm (top) and 93 cm (bottom). Plotted using OxCal v.3.10. (Bronk Ramsay 2005; Bronk Ramsey 2001; Bronk Ramsey 1995) and IntCal04 data from (Reimer *et al.* 2004).

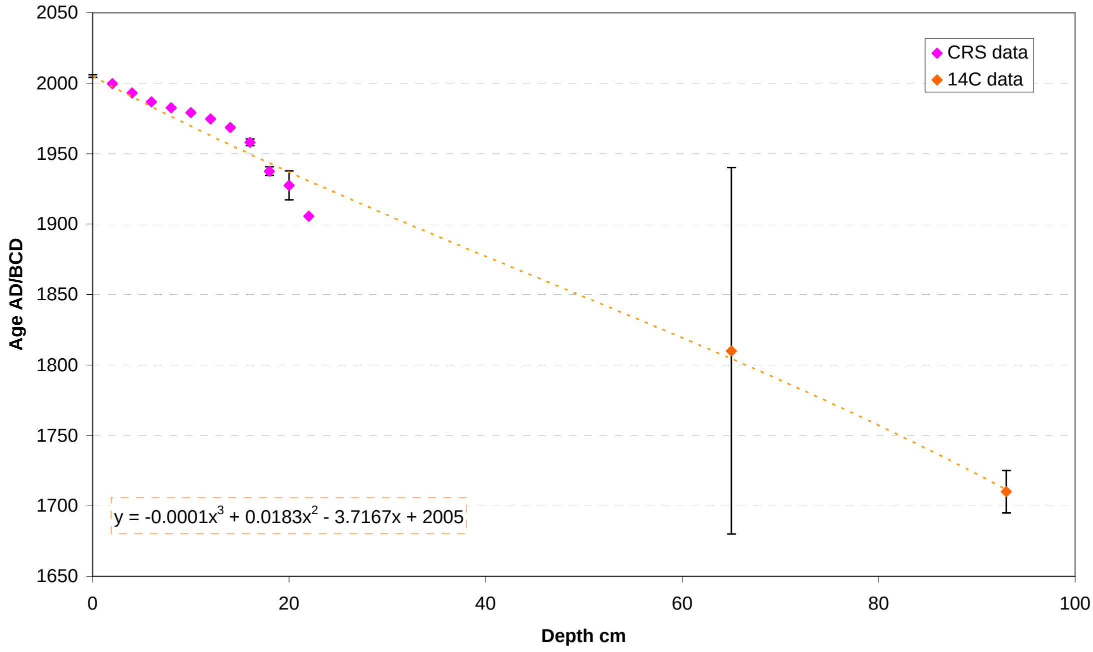


Figure 4.20: Age-depth model for the CLKH core using combined ^{210}Pb and ^{14}C data
The orange short-dash line represents a 3rd order polynomial through the CRS and ^{14}C data points. The associated model equation is presented. The maximum depth of the basin is 450 cm. Pollen was sampled to100 cm.

4.5.9 CLP2 combined age-depth models

Combined ^{210}Pb and ^{14}C age-depth models for the CLP2 core are presented in Figure 4.21. The equilibrium point between supported and unsupported ^{210}Pb is reached approximately at *c.* 15 cm, which corresponds to a CRS age-estimate of *c.* 1850.

This core has one radiocarbon assay at 65 cm. The calibrated 2s age-range estimate for this assay is 2870-2765 cal. BP. The midpoint falls at 2820 cal. BP. There is one broad peak in the ^{14}C probability spectrum (not shown) and there is no reason not to accept the midpoint as a secure age estimate.

Both the 2-term and 3-term polynomial provide smooth age-depth curves through the CRS and ^{14}C midpoint data. The curves extrapolate to a basal ages at *c.* 76 cm of 1910 BC (3970 cal. BP) and 2370 BC (4430 cal. BP) respectively. As with the CLH core, this illustrates the problem faced with few age determinations. It is not possible to securely accept or reject either age-depth polynomial or the linear extrapolation between data points (blue dashed line in Figure 4.21). The pollen concentration in the CLP2 core fluctuates but does not provide a meaningful method of choosing between models.

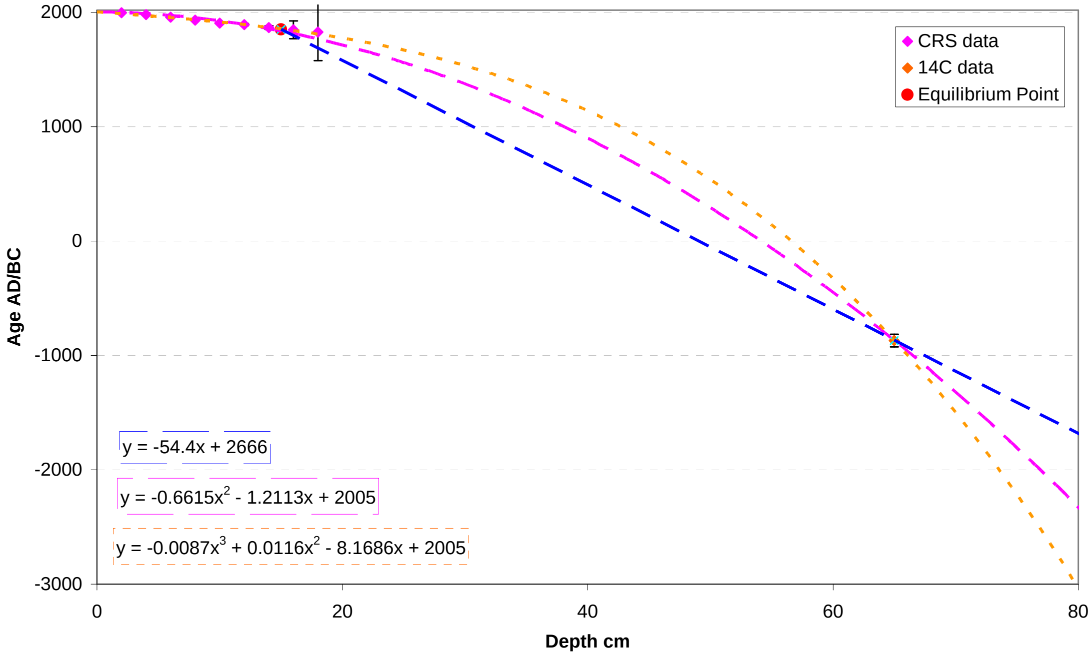


Figure 4.21: Exploration of age-depth models for the CLP2 core using combined ^{210}Pb and ^{14}C data The pink long-dash line represents a 2-term polynomial through the CRS and ^{14}C data points. The orange short-dash line represents a 3-term polynomial through the CRS and ^{14}C data points. The blue long dash line represents a linear interpolation. The associated model equations are presented. The lines are extrapolated through to the maximum depth of the basin at 82 cm. Pollen was sampled to base.

In the absence of meaningful model choice the 2nd-order polynomial, which falls midway between the 3rd-order and linear interpolation is accepted. The age-depth model for CLP2 is described by Equation 4.15.

$$y = -0.6615x\, X^2 - 1.2113x\, X + 2005 \qquad \text{Equation 4.15}$$

4.5.10 Core correlations

The age-depth models for the Glen Affric cores demonstrate the differences in accumulation histories between cores. This was unpredictable as cores did not adhere to the general model of one metre of sediment representing between 1000 and 2000 years, as determined by other studies in the east of Glen Affric (Wolff 2003; Wolff and Tipping 1999; R Tipping *pers comm*).

Although any interpretation of the data at sub-hundred year intervals is likely to have an uncertain precision, one of the aims of this thesis is to correlate across cores. An attempt is therefore made to achieve this, although it is accepted that there will be some potentially large errors associated with the chronology. Each core was sub-sampled for pollen to one metre; or to the basal sediment if this was less than one metre (ARC – 86 cm; CLH – 82 cm; CLP2 – 76 cm). Figure 4.22 illustrates and compares the time-period represented by each pollen diagram and the temporal distances between pollen samples in each core.

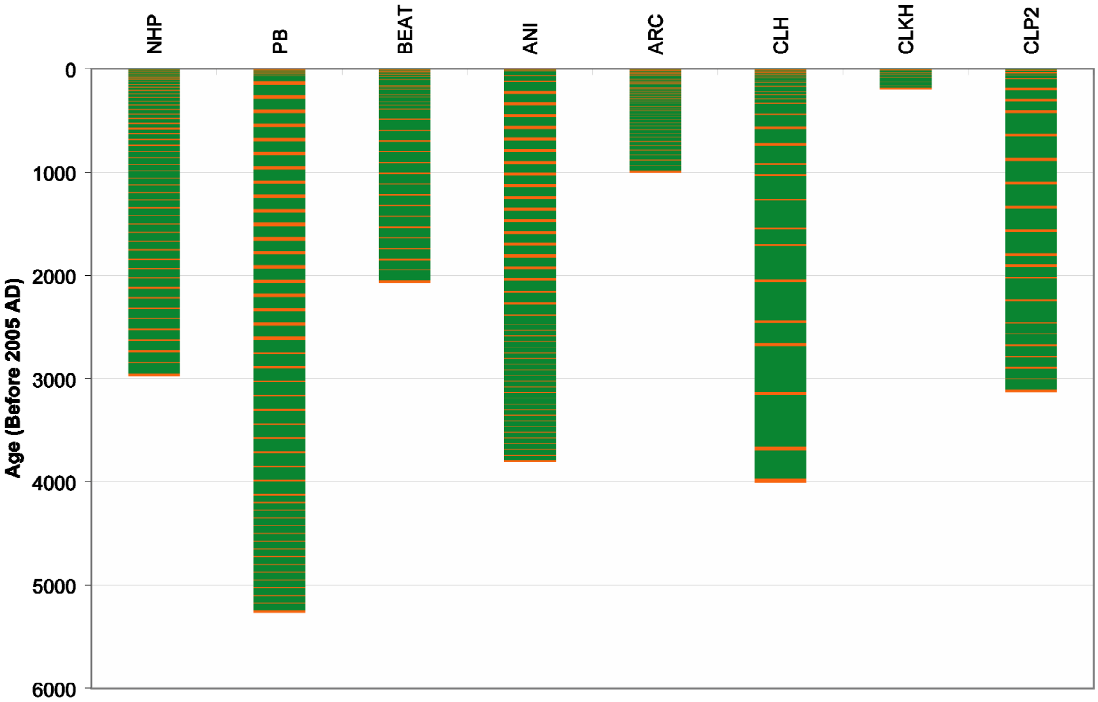


Figure 4.22: Comparison of estimated age-depth representations a cross section of the eight pollen cores from Glen Affric sampled for pollen analysis. Sections represent 100 cm of peat accumulation with the exception of; ARC (85 cm), CLP2 (72 cm), and CLH (84 cm).
Orange lines represent sub-samples and green areas are gaps between sub-samples.

4.6 Chronologies: discussion and conclusions

4.6.1 ^{14}C chronologies

The ^{14}C assays returning young sediment ages in CLKH and BEAT are supported by the evidence from ^{210}Pb ^{137}Cs and SCPs. The ^{14}C age-estimates for these cores lack precision, but there is no reason to believe that they are erroneous; young ages for these cores are therefore accepted.

The cores that display greater age with depth have a denser peat structure that the CLKH and BEAT cores and therefore age-estimates from these basins are also supported by the evidence.

A major problem in the determination of secure chronologies is the limitation on dating controls due to funding constraints. This thesis relies on secure chronologies in order to correlate across cores in the network. Extrapolations beyond the lowest ^{14}C date are used, but are limited in reliability. In addition the connection between the basal ^{210}Pb date and the uppermost ^{14}C date is several hundred years for some cores, identifying hiatuses and changes in sedimentation rates in these extrapolated areas of the age-depth curve is not possible. Any cross core correlations are therefore tentative.

4.6.2 Applicability of ^{210}Pb chronologies and success of models

According to Reinikainen (1997) the equilibrium between unsupported and supported ^{210}Pb is reached at approximately 150 years. In the Glen Affric cores the model dates at ^{210}Pb equilibrium returned ages ranging from approximately 100 to 150 years. In cores where younger CRS model age-estimates were predicted the CIC age-estimate and the pollen concentration data were examined. In some cases, the CIC curve provided evidence of a shift in sedimentation rate that was supported by the pollen concentration data. This may demonstrate merit to examining the results of the CIC model and using the curve form as a comparative measure with the CRS model to check for accumulation rate fluctuations.

The CF:CS model does not seem suitable for peats in Glen Affric as it produces a straight-line age-depth model, which is likely to be unrealistic in surface sediments due to factors of compaction and decomposition.

The derivation of dates for the peat cores is not an end in itself, but is a tool for the improved analysis of pollen data and the tighter application of that data to questions of ecological consequence. The importance of the chronologies, in the case of Glen Affric, is to allow correlation across the networks of sites at common age levels. In this application a high precision and accuracy is required (Veski *et al.* 2005). Although the ^{210}Pb age-estimates correlate well with ^{137}Cs peaks there is still some uncertainty surrounding the use of the CRS and CIC models in peat deposits. The data from Glen Affric demonstrate however, that the CRS provides a good basic smoothed age-depth model, which may be capable of being improved upon by reference to the CIC model and pollen accumulation data.

4.6.3 Supplementary dating

Supplementary dating tools were not successful in this study. This is likely to be mainly due to the nature of small hollow recruitment and/or below canopy recruitment of particles. This has limited the use of *Picea* as an exotic marker grain and, also, hampered the use of SCP analysis. Although further SCP analysis by the concentration method (Yang *et al.* 2001) may be of benefit, this would entail the collection of further core material as the core material already collected was destroyed during preparation for ^{210}Pb assays. This is therefore beyond the scope of this study.

4.6.4 Combined chronologies

Shifts in accumulation rate in each core have introduced some complexity to the modelling of the age-depth curve. It is difficult to assess the success of the chronological modelling as there are no supporting independent means of verifying the chronologies. However, a logical approach has been taken utilising all available data. Pollen data has proved useful in some of the cores, in providing some measure of pollen concentration data in the sediments to corroborate and verify acceptance of the selected combined-age-depth models. For example, the comparison of shifts in pollen concentration with the shifts in slope of the age-depth model in the BEAT core has allowed the acceptance of the hypothesis for a marked shift in sedimentation rate at 67 cm rather than an hiatus.

4.6.5 Conclusions

The data presented highlights the uncertainties of age-depth models, which can be of the order of 100s of years (Bennett and Fuller 2002). Extrapolation from the basal ^{14}C age-estimate to the basal pollen sample at 100 cm are possibly subject to larger errors.

These large errors create problems for the interpretive aims of this study. Firstly, the uncertainties limit the analysis of rates of ecological change within cores. Secondly, the uncertainties limit the ability to correlate between cores at the ecological scale of 20-50 years. Thirdly, the uncertainties limit the ability to derive and use pollen influx data for use in the quantification of the pollen-vegetation relationship.

The limits to the validity of these interpretations could only be resolved by an increased number of ^{14}C assays, the securing of which is beyond the financial scope and timetable of this thesis. However, the chronological controls for this study are reasonably standard for current pollen analyses and the attention paid to them in this chapter highlights and supports the view of Telford *et al*. (2004a), that many more ^{14}C age determinations are needed per core especially to provide a "*serious attempt at determining the ages of synchronous events*" Bennett and Fuller (2002).

The following chapter concentrates on the spatial quantification of pollen data and the representation and interpretation of vegetation from the pollen data. This subject has developed new modelling methodology in recent years. However, in terms of the type of study attempted in this thesis, dating controls need to continue to develop a similar innovation and rigour in the coming years to allow a true integration or palaeoecology with ecology.

5 Quantifying pollen-vegetation relationships in Glen Affric

Introduction

Planning for woodland restoration has aspirations that move beyond the desire to recreate the past. Current management aims visualise future woodland that is resilient and self-sustaining (Chapter 1). Historical analysis of past woodlands is still relevant to future ecosystem planning, but needs to respond by investigating and providing information on the ecological functionality and dynamics of woodland over ecological timescales, and at the landscape scale, in order to provide a useful evidence base. In pursuit of this aim, palaeoecology must be capable of better quantifying past woodland both in terms of canopy cover and in terms of species mix (Chapter 1).

Desire for, and development of, tools for deriving quantified plant abundance from pollen abundance or percentage data has been hoped for since von Post (1916). Early attempts at quantification comprised simple proportional relationships between pollen and plant abundance for individual taxa (Davis 1963; Anderson 1970). Progress in this, recently reviewed (Parsons and Prentice 1981; Schwartz 1989; Davis 2000), has been advanced by new models (Parsons and Prentice 1981; Prentice and Parsons 1983; Sugita 1994; Sugita 1998), and by the development of accessible computer programmes for applying these more complex models to pollen and vegetation data (e.g. Bunting and Middleton 2005).

This Chapter presents the modern analogue study in Glen Affric, which is used to aid interpretation of the core data in Chapter 6. Chapter 5 begins by introducing and outlining the problems in the reconstruction of vegetation at the local scale from pollen analyses, and by outlining the numerical approaches used to clarify the pollen-vegetation relationship for the Glen Affric data prior to interpretation of past vegetation from the fossil pollen datasets. Section 5.2 discusses the background to the methods applied to the research in Glen Affric and Sections 5.3-5.7 present the results of the vegetation survey and pollen count data, and the numerical analysis of the pollen-vegetation relationship derived from these. The Chapter then concludes with Section 5.8; a discussion of the correction factors, source area, cut-off values, and comparative measures selected for use in the interpretation of the pollen cores in Chapter 6.

5.1 Literature review and aims

Local stand scale pollen source areas are predicted for pollen from small diameter basins within woodlands (Jacobson and Bradshaw 1981; Figure 3.1); however, most studies have assumed or tested this under a continuous closed canopy (e.g. Anderson 1970; Prentice 1985; Bradshaw and Webb 1985; Jackson 1991; Jackson and Wong 1994; Calcote 1995; Jackson and Kearsley 1998). Several studies have demonstrated some doubt over the ability of small hollow sites to detect openness. Although Prentice (1978) demonstrated that the Non-Arboreal Pollen (NAP) component of the pollen spectrum could become substantial in areas extensively cleared of trees, evidence shows that open sites also contain a substantial amount of far-travelled pollen (Prentice 1988). Small basins with diameters and openings of just a few metres display wider source areas for pollen than samples from moss polsters under the woodland canopy (Prentice 1985). When canopy cover is removed around a small basin pollen site, the source area may change and vegetation interpretations become more complex (Sugita *et al.* 1999). This may render small patchy openings in forest cover invisible.

In 1970 Oldfield observed that it is unclear if pollen spectra from local trees can be distinguished from that created by distant vegetation (Oldfield 1970). This problem was still being highlighted by Davis in 2000 (Davis 2000), and despite much work on small hollow pollen representation, the problem is still not satisfactorily resolved; especially for studies in semi-open landscapes. Recent work in Sweden and Norway, and France has begun to address the source area issue in patchy open areas (e.g. Broström *et al.* 1998; Mazier *et al.* 2006; Court-Picon *et al.* 2006; Court-Picon *et al.* 2005; Hjelle 1997; Hjelle 1999; Hjelle 1998; Brostrom *et al.* 2004; Brostrom *et al.* 2005). Most, if not all, of these studies on pollen representation and source area are implemented in more open environments than that of Glen Affric, and have used sediments from lakes or from moss polsters. It may, therefore, be difficult to extrapolate these findings to small peat filled basins. In Southern Sweden Broström (2002) demonstrates that the occurrence of large openings may be missed in the fossil pollen record; especially if they are smaller than the grain of the source area for each basin. This may be less of a problem in small hollow sites; however, an additional problem in terms of investigating the extant pine woods in

Glen Affric is that these current studies of openness are primarily investigating known cultural landscapes, where the ground flora may differ markedly from that of woodland in open sites. In contrast in semi-natural landscapes where there may be little difference between ground flora under the semi-open canopy and in the open moorland (as described in the NVC for native pine woods in Chapter 2), analysis of bog deposits on Scottish islands (Fossitt 1994) has demonstrated a significant long distance transport component to the arboreal pollen rain. However, these island environments are extremely open and have high wind regimes, so again are not good analogues for the semi-open patchy vegetation in Glen Affric.

Pinewood reconstructions have on the whole, lacked spatial definition, this has limited our ability to determine the structure, extent and canopy cover of woodland *within* the defined areas of *potential woodland* derived from pollen regional pollen isochrones (Bennett 1995; and see Section 2.2).

In a Scottish context, the representivity of arboreal pollen has been the subject of several pollen-vegetation comparisons. Semi-quantitative analysis has been carried out in the eastern pine woods by O’Sullivan (1973) who found that the quantity of *Pinus* was high in sites with canopy cover, but also high in sites with no immediate canopy thus confirming the influence of extra-local arboreal pollen in open sites. Despite this, a general modal percentage interval for each vegetation sample category was found, although the *Betula* curve was less assured (O'Sullivan 1973). A series of transects through Bankhead Moss in Fife (Caseldine 1981; Caseldine and Gordon 1978) revealed a rapid decline in AP values away from a *Betula* woodland and similar declines are noted by other early studies (Turner 1964; Tinsley and Smith 1974). However, these transect studies test attenuation from a single woodland pollen source and do not test the stand scale openings *within* a forest, or the random factors of openness within a semi-open landscape. These past analyses have concentrated on either ground flora taxa or tree taxa, and have rarely combined these (Evans and Moore 1985). Additionally, these studies were too early to take advantage of the more recent developments in analysing and modelling pollen-vegetation relationships.

More recently Davies and Tipping (2004) drew conclusions on pollen source area by comparing the pollen signal from four small basins in the west of Glen Affric during the Holocene, but without recourse to any quantification. Whilst Bunting has applied modern techniques, including deriving source area and pollen productivity estimates, from non-arboreal pollen species in Assynt; but at a limited spatial extent (Bunting 2003) and the analysis did not include *Pinus* or *Betula*.

Quantified research on the pollen productivity and pollen source area for small hollows in patchy open pine woods is therefore, largely untested. Given the characteristics of long distance transport in *Pinus* pollen, a factor possibly exacerbated by an open stand structure, and given that the structure of former pine woodlands is still open to debate (see Section 2.2), understanding the effect of regional and extra-local *Pinus* pollen influx on the pollen spectra from small hollows is extremely important to spatially precise vegetation reconstructions.

The varied and sometimes open canopy structure in the Glen Affric landscape provides an opportunity to test the degree to which the pollen spectra in patchy woodland conform to the original theoretical models of pollen influx into small forest hollows. A modern pollen-vegetation comparison within the area of study may be essential to determine a quantified vegetation reconstruction (Birks and Gordon 1985), and to develop confidence in the use of the interpreted data as evidence in conservation planning.

The main aims of the modern pollen analyses in this study are;

- to define the relevant source area for pollen in small basins in semi-open pine woodland;
- to explore the extent to which stand scale openness can be detected within and between woodland from small peat basins;
- to explore the ability of pollen analysis to detect mixed species woodland stands from monocultural ones at the local-scale;
- to determine the ability to reconstruct patch scale differences in the ground flora and especially the species mix of the heathland vegetation;

- to determine locally-relevant pollen-correction factors for the dominant vegetation types in Glen Affric for application to the fossil data sets.

5.2 Numerical approaches to pollen-vegetation relationships

Numerical approaches to the pollen-vegetation relationship comprise both quantitative and comparative techniques based on regression and ordination (Birks and Gordon 1985). Additionally, semi quantitative approaches, using ranking of data or binary adjustment of presence absence data such as Indices of Association (Davis 1984; Hjelle 1997) prove useful tools for understanding the representivity of rare taxa. Although all of these techniques elucidate useful information, each carries individual problems and assumptions. Quantitative and semi-quantitative approaches tend to be useful for subsets of data, such as key taxa or rare pollen types, whilst the comparative approach concentrates on the whole assemblage. Comparisons between the results of several methods of data analysis can therefore be useful (Birks and Gordon 1985) and this is the approach taken in this thesis. A background to the methods of analysis used in the results sections of this chapter is outlined below.

5.2.1 Background theory for quantification of the pollen-vegetation relationship.

5.2.1.1 Development of pollen-vegetation calibration

The first attempts at quantifying the pollen-vegetation relationship proposed and tested a simple proportional relationship between pollen and vegetation to derive a pollen calibration for abundance data (Equation 5.1) (Fagerlind 1952; Davis 1963):

$$Y_{ik} = a_i \bullet X_{ik} \qquad \text{Equation 5.1}$$

Where the absolute pollen loading Y of a specific taxon $_i$ at a specific site $_k$ is equal to a species-specific constant a_i multiplied by the absolute abundance of the vegetation X of the taxon $_i$ around the site $_k$. Therefore deriving Equation 6.2:

$$a_i = Y_{ik} / X_{ik} \qquad \text{Equation 5.2}$$

Pollen analysts routinely derive percentage data. Absolute values for pollen data rely on secure chronological controls beyond the scope of extrapolation from ^{14}C assays. Equation 5.3 uses proportional values for pollen and vegetation.

$$R_i = P_{ik} / V_{ik} \qquad \text{Equation 5.3}$$

Where P_{ik} is the proportion of a specific taxon $_i$ at a specific site $_k$; and V_{ik} is the proportion of vegetation i at site k. R_i then represents the ratio of the pollen proportion to the vegetation proportion; called the R-value.

Davis used Equation 5.3, the R-value approach, to highlight the problems of proportional data: She demonstrated the Fagerlind effect, which shows that the relationship between pollen proportion and vegetation proportion is not linear; as an increase in the proportion of one taxon can affect the proportion of another, whose actual concentration, or pollen influx, remains unchanged (Fagerlind 1952).

A consequence of the Fagerlind effect is that R-values derived from proportional data are site specific and will vary through time and space. Indeterminacy in site-independent R-values is removed by assigning a reference taxon with a standard R-value of 1 to one taxon (R_1) (Davis 1963). All other R-values are then adjusted relative to the standard taxon (Equation 5.4) and assigned an R_{rel} value (Davis 1963; Anderson 1970; Birks and Gordon 1985). For proportional data as long as the proportionality remains between the absolute pollen loading onto site x and the absolute plant abundance into site x the R_{rel} values remain unchanged (Birks and Gordon 1985).

$$R_{(rel)ik} = R_{ik} / R_{i(1)} \qquad \text{Equation 5.4}$$

The R-value approach is site and taxon specific and has been criticised due to the high site-to-site variations. Birks and Gordon (1985) review criticisms of the R-value approach and conclude that early methods of application were at fault, rather than the theory behind R-values. The problems are summarised below:

- R-values can only be accurate if all of the vegetation contributing pollen to the site is measured – the pollen source area of Davis's original data was probably too small.
- There are large errors associated with deriving R-values from a small number of sites.
- Since the vegetation surrounding the site will have distance weighted effect on the pollen productivity this will affect the proportionality between plant abundance and pollen abundance. Applying a distance weighting to the vegetation data before R-value calculation would account for this.

Further testing of the R-value model has produced realistic results in closed canopy woodland where the source area is local (Bradshaw 1981). However, in reality a subset of the pollen counted is nearly always from a regional background plant community beyond that measured in the vegetation community around a pollen sample site. Parsons and Prentice (1981) demonstrated that it was possible to group sites via a PCA, based on similar R-value characteristics. Thus open sites could be identified and separate R-value correction factors applied. However more flexible model-options, which amalgamate a range of pollen and vegetation values and identify a background term in addition to a pollen correction factor, were being developed.

Anderson (1970) progressed Equation 5.1 by the inclusion of a background pollen loading term y_{i0} which denotes the amount of pollen contributed to the sample from beyond the measured vegetation For absolute pollen deposition he proposed Equation 5.5

$$Yik = ai \bullet Xik + yi0 \qquad \text{Equation 5.5}$$

This equation derives a_i and y_{i0} from the regression slope and intercept from a range of sites, and therefore produces a_i as a taxon specific rather than site-specific term for the pollen correction factor.

The analogous model for vegetation proportions (Equation 5.6) has been widely used (Birks and Gordon 1985; *and references therein*). Again the Fagerlind effect is ignored

Equation 5.6 is therefore a first approximation, for use with proportional pollen data. As with the simpler R-value model above there are problems with proportional data, but Equation 5.6 has been demonstrated to work providing there are no individually dominant pollen taxa (Birks and Gordon 1985).

$$U_{ik} = r_i \bullet v_{ik} + y_{i0} \qquad \text{Equation 5.6}$$

The incorporation of a background term is useful, in that for any vegetation-sampling radius around the site, pollen from beyond this source is accounted for. However, y_{i0} is regressed from a number of sites and may have high residual variation. In addition, it is unclear how y_{i0} may vary over sites with a steep gradient in vegetation cover, or through time if vegetation structure or composition changes drastically in the regional environment. Increases in pollen productivity, in the vicinity of, or on, the sample basin have the ability to affect the background component in two ways. Firstly the amount of pollen transported into the basin can be altered by structural components of the surrounding vegetation (Jacobson and Bradshaw 1981; Birks and Gordon 1985 p.186; *and references therein*). Secondly, any increased pollen rain from local vegetation may act to decrease the proportion of background pollen via the Fagerlind effect. On a regional scale, for example this could affect attempts to apply the regression models before and after the pine decline in Scotland, whilst on a local scale the background could vary spatially, or change temporally as sites fluctuate in canopy cover between closed and open woodland stands. Site and regional specific testing is therefore required. This may be especially relevant in the varied canopy cover around the small hollow sites in the context of Glen Affric.

5.2.1.2 Extended R-value analysis

Various methods of combining R-values are described by Birks and Gordon (1985) and include summing the pollen and vegetation proportions before applying Equation 1 to the sums, or deriving the arithmetic mean of all of the R values, or the geometric mean of the R-values. None are wholly adequate. Parsons and Prentice (Parsons *et al.* 1980) applied the maximum likelihood method to the R-value equation to derive more effective results through the modelling of pollen counts by a multinomial distribution (Birks and Gordon 1985).

The development of this maximum likelihood method (the Extended R-Value approach) to incorporate the background pollen component has since been developed to include 3 sub-models (Prentice and Parsons 1983; Sugita 1994) each with their own assumptions, which correct for the Fagerlind effect by an iterative process.

The basic equation of the ERV model is Equation 5.7

$$P_{ik} = a_i \text{ X } v_{ik} \text{ X } f_k + z_i \qquad \text{Equation 5.7}$$

Where P_{ik} is the pollen deposition (percentage) and v_{ik} is the plant abundance (percentage) for taxon i at site k. a_i and z_i are the pollen productivity and pollen background term, which, as with the R-value approach, are expressed relative to a taxon set at unity, whilst f_k is a site specific factor which varies with parameters of all the values for taxa at site k and compensates for the Fagerlind effect (Broström 2002).

These Extended R-value (ERV) models derive pollen taxon-specific Pollen Productivity Estimates (PPEs) and a background component (Z). In addition, the ERV calculation at any radius of plant abundance produces a Maximum Likelihood (ML) score, which, when plotted with ML scores for all vegetation radii, allows the determination of the Relevant Pollen Source Area, or RSAP (see below); determined as the radial distance at which the ML score reaches an asymptote (Sugita 1994).

5.2.1.3 Relevant Pollen Source Area (RSAP)

Equation 5.5 (Andersen 1970) and the ERV models determine a background pollen component contributed to the site from beyond the sampled vegetation unit and a pollen productivity estimate. The values for these, change with vegetation sampling distance from the pollen site.

The Relevant Source Area for Pollen (RSAP) determines the radius at which vegetation should be surveyed to determine the best fit of any R-value analysis (Sugita 1994; Sugita 1993; Prentice 1985). To gain a pollen productivity estimate with low variation across sites the background pollen component should be reasonably constant representing an homogenised regional background. RSAP can be determined by testing the correlation between vegetation and pollen (abundance or proportions) at various radial distances from the pollen sites; the RSAP is taken as the point at which the correlation statistic does not improve (Sugita 1994).

A further complication arises in the above model from the characteristics of pollen transport and ring source area. The area of the ring source increases with distance from the site. Consequently, in a correlation between vegetation and pollen, larger proportions of vegetation further from the site will contribute more to the vegetation dividend in the proportional equation (Equation 6.1) or to the slope (Equation 6.5). It is however fair to assume that plants further from a site may actually contribute less pollen. Pollen transport may be considered to follow a typical leptokurtic distribution of pollen from source vegetation (Davis 2000). A distance weighting function is required to adjust for this (Davis 2000; Prentice 1985; Sugita 1994).

5.2.1.4 Distance weighting of vegetation

Plants should contribute less pollen to the site of deposition with increasing distance from the site (Davis 2000). Plant abundance must therefore be distance weighted so that vegetation further from the site contributes less to the V_{ik} term in the R-value equations. Several distance weightings have been used. The Prentice-Sugita models (Sugita 1994; Sugita 1993; Prentice 1985) use distance weighting based on Sutton’s (1953) equations for the atmospheric dispersal of small particles (Nielsen and Sugita 2005). More recently wind roses have been applied to directionally weight dispersion in modelled pollen deposition studies (Bunting and Middleton 2005). Dispersion may also be affected by a range of complex and interacting factors, including topography, reviewed by Jackson and Lyford (1999). Many are still being tested on theoretical models (e.g. Eklof *et al.* 2005) and will not be considered further here in the complexities of the real landscape of Glen Affric.

More simplistic models of distance weighting have also been applied; commonly 1/d (Prentice and Webb 1986) and $1/d^2$ (Webb *et al.* 1981; Schwartz 1989; Calcote 1995) and some comparisons between methods made (Nielsen and Sugita 2005). Distance weighting in many of these studies is applied to lake samples with a regional pollen source area. Nielsen and Sugita (2005) for example test in ring increments of 20 m to a radius of 2500 m using vegetation cover derived from GIS data and small lake sites. It is less clear how well any distance-weighting function applies to local pollen assemblages at the spatial scale considered in the core analysis of this thesis. Jackson and Kearsley (1998) found that distance weighting did not improve the fit between pollen and plant abundance within 120 m of a small hollow pollen site within woodland, whilst Bunting (2003) found that distance weighting was applicable to ground flora at very small radii. The leptokurtic distribution of pollen from a herbaceous plant in the ground flora five metres from a pollen sample area, will however have a very different scale of distribution than a tree at the same distance from the site. It may be necessary to apply different weighting to ground cover and tree cover or taxon specific vegetation weighting. Some exploration and comparison of these latter simple distance-weighting models with unweighted data will be applied to assess their relevance to the small local scale basins in the Glen Affric landscape.

5.2.1.5 *Quantifying vegetation from pollen proportions: Inverse ERV analysis*

The RSAP, pollen productivity estimates and background term can be used in an Inverse-ERV equation to adjust pollen percentages from core data and to gain a more quantified vegetation reconstruction. The adjustment of pollen data by this method can highlight the dominance, in the vegetation, of taxa with low pollen productivity. This approach may also be useful in determining the fluctuations in pollen percentage data that represent underlying vegetation change from those which merely reflect the Fagerlind effect.

One problem still to some extent remains – interpreting whether the pollen comes from sparse vegetation local to the site, or abundant vegetation at a distance (Davis 2000). Modelling the possible vegetation patterns from any given pollen spectrum is a method of analysing the range and probabilities of possible vegetation patterns. The multiple scenario approach is currently being developed (e.g. Fyfe 2006) and will provide a useful future tool for local scale pollen studies.

The regression ERV and inverse-ERV models can only be applied to a subset of data from key taxa where there is some statistical significance to the correlation between pollen and vegetation. Many taxa appear in such low quantities in the pollen record that they cannot be analysed by these methods. Indices of Association and the Point Biserial Correlation Coefficient outlined below allow some measure of the pollen-vegetation association in rare taxa and the comparative approach outlined in Section 5.2.3 allows analysis of variation within the whole multivariate dataset.

5.2.2 Semi-quantitative methods for rare pollen types: Indices of Association (IOA) and the Point Biserial Correlation Coefficient (R_{pb})

For some pollen data the individual taxon count may be extremely limited to one or two grains per sample. In some cases these grains derive from important indicator taxa such as the cereal type grasses which may indicate human influence (Behre 1981). In other cases, the rare pollen taxa come from plants that are not native in the surrounding landscape and may indicate far travelled pollen influx. Some debate surrounds the use of these grains, for example Bunting (2003) finds that small numbers of *Hordeum*-type pollen and other taxa, understood to be indicators of human activity, can be present in the pollen record when there is no evidence of the plant in the surrounding landscape. Bunting therefore cautions against placing too much weight on these taxa as human-indicators. It is helpful therefore to gain a more detailed quantitative insight into the representivity of these rare pollen taxa.

Indices of Association (IOA) have been used to determine association between plants and pollen for rare pollen taxa (Davis 1984; Hjelle 1998). IOA are defined by equations 5.8-5.10.

$$A = B_0 (P_0 + P_1 + B_0)^{-1} \quad \text{(Indices of association) Equation 5.8}$$

$$U = P_1 (P_1 + B_0)^{-1} \quad \text{(under-representation) Equation 5.9}$$

$$O = P_0 (P_0 + B_0)^{-1} \quad \text{(over-representation) Equation 5.10}$$

Where B_0 is the number of samples where pollen is present and the associated plant taxon is present within a defined radius. P_0 is the number of samples where the pollen is present but associated plant taxon is not present within the defined radius, and P_1 is the number of samples where the pollen is not present but the plant is present within the defined radius (Bunting 2003).

IOA reduce the data to a binary presence-absence format before analysis. However, whilst this is valid for rare-type pollen data, due to a high counting error around low pollen counts, this data reduction also includes a loss of information on vegetation abundance. Although subject to errors in fieldwork collection, vegetation surveys may still provide relatively accurate abundance data for rarer taxa.

A point biserial correlation coefficient can be used when one set of data is in binary format and the other variable is continuous (Kent and Coker 2001). Kent and Coker observe that the Point Biserial method is underused in plant ecology. It does not seem to have been used in pollen studies. The method will be used in this study and results compared with the IOA method. This may be a helpful tool in assessing the significance of the association gained under the IOA score.

To obtain the point biserial correlation coefficient R_{pb} the continuous data variable is first partitioned into two sets based on the presence or absence in the binary data variable. R_{pb} is then obtained by Equation 5.10

$$R_{pb} = \frac{| Mp - Mq |}{Sx} * \surd(PxQ) \quad \text{Equation 5.11}$$

Where Mp is the mean of the values of the continuous variable when the binary variable is present; and Mq is the mean when the binary variable is absent. | Mp – Mq | is the absolute difference between means regardless of sign, p and q are the proportions of observations in each group respectively, and Sx is the standard deviation of all the continuous variable observations (Kent and Coker 2001 p141).

A theoretical incidence outlined below indicates the value of the R_{pb} as an addition to the IOA analysis:

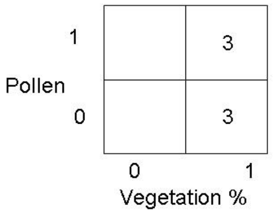
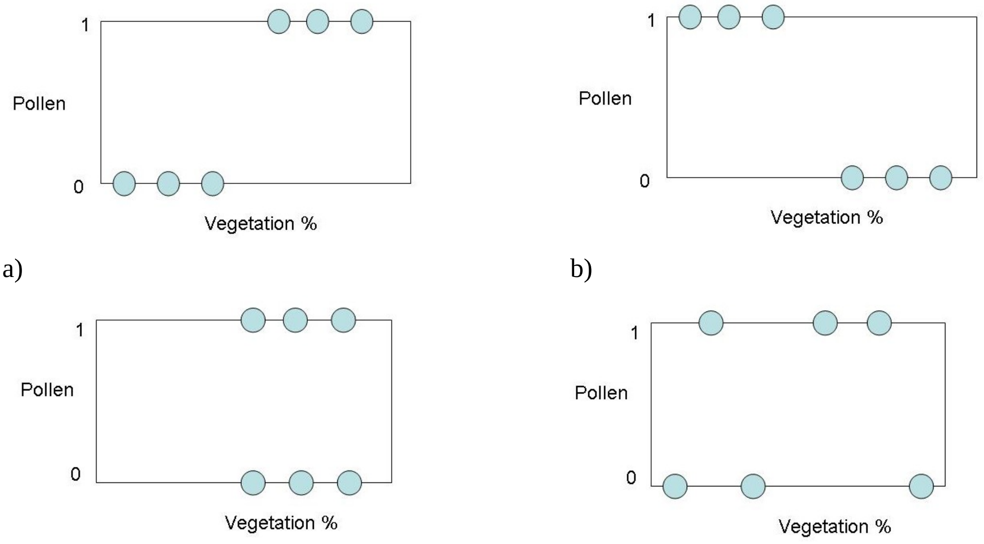


Figure 5.1: Theoretical values for pollen and vegetation from six pollen cores. All contain the vegetation of the theoretical taxon but three core samples contain the the associated pollen and three do not. For use in testing the relevance of the Point Biserial Correlation Coefficient: R_{pb} (see text for explanation).

Consider six pollen sites; three contain pollen taxa a, and three do not. They all contain vegetation taxa a, in various abundance values listed in Table 5.1. such that the data can be plotted in a binary matrix as Figure 5.1. The resultant IOA score would be: A = 0.5; U = 0.5 O = 0.

However this situation causes a loss of information as whilst there is no significance between counts of 1 or two pollen grains, vegetation can be more accurately measured, such that for the same pollen count various vegetation percentages may be recorded in a plot of binary pollen data and continuous vegetation date as illustrated in Figure 5.2. for the four sites in Table 5.1.



a) b)

c) d)

Figure 5.2: Model values for vegetation percentages for use in the R_{pb} example (see text for details)

The IOA and R_{pb} values for the four situations a-d in Figure 5.2 are presented in Table 5.1. IOA results for all of the pollen-vegetation values above are equal. Showing a weak association (A = 0.5). However, the R_{pb} can be used to provide valuable additional information on the significance of the relationship. It can be seen that situation a and b are both significant associations of pollen and vegetation, whilst situations c and d demonstrate a considerably more random relationship, whilst the same IOA values are returned for these situations the R_{pb} demonstrates that the relationship is not significant.

Table 5.1: Comparison of results from IOA and R_{pb} analysis on theoretical pollen values. (see text for details).

Pollen Count	Situation a Vegetation %	Situation b Vegetation %	Situation c Vegetation %	Situation d Vegetation %
0	1	7	9	9
0	3	9	7	7
0	4	10	10	3
1	7	1	9	4
2	9	3	8	1
1	10	4	10	10
IOA and R_{pb}				
A	0.5	0.5	0.5	0.5
U	0.5	0.5	0.5	0.5
O	0	0	0	0
R_{pb} (Kent and Coker)	0.174	- 0.174	0.029	0.039
R_{pb} (no negative)	0.174	- 0.174	0.029	0.039
t	0.92 *	(|t|) 0.92*	0.15 (ns)	0.2 (ns)

5.2.3 Comparative analysis

Simple comparisons between data can be made from a traditional pollen diagram approach with samples grouped on the y-axis according to a single or simple set of criteria such as arboreal cover. This approach is used for the Glen Affric data by ranking the tree cover data. Pollen and vegetation data are, however, complex and multivariate and visualisations of more complex variance is best achieved with ordination techniques (Bennett and Hicks 2005). Birks and Gordon (1985) identify the value in ordination as that of allowing clearly displayed visualisations of the multivariate pollen data, whereas some more recent studies use Redundancy Analysis (RDA) (Hicks and Birks 1996) and permutation testing (Mazier *et al.* 2006) to allow further statistical analysis by testing the fit of the datasets to a set of environmental variables.

Comparisons can be made between the fit of modern pollen and vegetation data by plotting modern pollen data with vegetation data and by plotting fossil pollen passively on the modern pollen (Hicks and Birks 1996). In a perfect one to one relationship between all pollen and vegetation taxa the sample position or each site based on the pollen data should plot in the same position as the vegetation data from the same site. Consistent directions of difference between pollen data and vegetation data may therefore highlight bias and indicate expected adjustments using R-values; whereas inconsistent variation between sites should indicate high variance in R-values between sites. The advantage of the comparative method of ordination between modern and fossil pollen is that fossil pollen plots with no modern analogues can be clearly identified as outliers in these plots.

Ordination techniques also provide information on shifts in pollen spectra through time. Stratigraphic pollen data can be plotted in an ordination and shifts of pollen zones in ordination space indicate possible shifts in vegetation state.

Ordination can, however, result in widely ranging scores for the first axis based mainly on differences in pollen productivity (Bennett and Hicks 2005). Although pollen percentage data is constrained by it’s proportionality (Bennett and Hicks 2005), in principle the data analysis is simply showing, in a clearer, multivariate format, the variation visible in a traditional percentage pollen diagram. This percentage data is already demonstrated above, to be skewed by the Fagerlind effect (Fagerlind 1952) and to be biased towards taxa with high pollen productivity. The same problems apply therefore to any visualisation through use of ordination as apply to the original pollen datasets identified by von Post and many since as problematic for interpretation.

5.3 Numerical analysis methods selected for the Glen Affric dataset

From the above discussion of modern analogue methods it can be seen that a combination of analytical methods may be appropriate to determine the pollen vegetation relationship. Birks and Gordon recommended this approach in 1985 and since then many techniques have undergone a substantial development and refinement. However, problems still arise. Firstly, the ERV method can only be carried out on subsets of the full taxonomic dataset as statistical significance in the ML method can only be obtained when sites outnumber taxa by a factor of 3 (Bunting *pers. com.*). Secondly, the ERV method constrains the data analysis so that the variation in R-value with site-specific factors is minimised. Thirdly, many taxa are too rare to be used in the regression analysis models and information can only be gained from simpler comparison of ranks or indices of association. Comparative techniques can be powerful visual aids, and have developed to include testing of variance and distance between data, and between the fit with environmental variables, however, the technique may benefit from application to transformed pollen data and this will be tested here.

Numerical analysis of the key pollen types in the Glen Affric data will therefore comprise the following:

- Ranking of pollen diagram and comparisons of ranked pollen and vegetation data
- Determining source area for pollen via the asymptote of the r^2 correlation coefficient and the Maximum Likelihood method
- Deriving pollen correction factors from the R-value, slope and intercept, and ERV model methods

- Additional analysis will provide an examination of the pollen-vegetation association between rare pollen types via Indices of association and the R_{pb}.

Pollen and vegetation data from the full spectrum of taxa are compared through ordination methods to identify the degree of separation possible between pollen data from sites of different vegetation content. Separate and combined ordination is compared and pollen is plotted passively on the vegetation ordination.

5.4 Methods

5.4.1 Site selection

Various pollen sources are used for modern pollen analysis, ranging from pollen trap data to surface samples from peat or lake cores. As discussed in Chapter 3 substrate type will confer some depositional bias to the pollen sample (e.g. Bradshaw 1981; Wilmshurst and McGlone 2005). Given this it is advisable to select surface samples from a "similar sampling situation" (Hicks 1985; Hicks *et al.* 1998; Fossitt 1994) to that of the fossil data. Modern pollen samples were therefore selected from the surface of small peat hollows and flushes in east Glen Affric to maximise the similarity to pollen spectra from the fossil records. Random site selection methods have been utilised by some researchers and whilst this has some benefit in statistical analysis, the method was not chosen for this study, as this requires the use of moss polsters rather than peat hollow surfaces, which may not be randomly distributed. Instead, in this study sites were selected throughout the Glen to ensure that key community differences are represented in the analysis.

5.4.2 Sample collection

The pollen sub-sample was taken from a point source. Some studies use a large volume of surface peat substrate amalgamated from several surface samples in a defined area (Hicks *et al.* 1998; Bunting 2003). This method smoothes and averages the pollen spectra. Problems occur with this approach; it may be difficult to identify abnormal spikes in pollen taxa due to over-representation via flower heads or insect remains within the sub-sample (Hjelle 1997). The smoothed data does not match that available in the fossil record. It is not possible to amalgamate samples in the fossil record due to possible variation in age structure throughout horizontal sections of peat. Using peat surface samples from a point source at the basin surface thus allows as far as possible, matched conditions with those of the fossil record. This approach was therefore adopted here.

5.4.3 Vegetation surveys

Site locations were mapped using a hand held GPS system (Garmin Etrex 12 Channel GPS) recording an accuracy of approximately 3-10 m. Site conditions, slope and surface wetness were recorded subjectively to give some approximate background information.

Source Area Considerations

An inadequate source area for the pollen-vegetation calibration is highlighted as one of the major reasons for the failure of initial efforts to calibrate modern pollen data with surrounding vegetation (Birks and Gordon 1985). Where possible, modelling of the pollen-vegetation relationship prior to vegetation sampling is recommended (Hicks *et al.* 1998). Although this can now be achieved through the HumPol suite of programmes (Bunting and Middleton 2005) this was not available for the Glen Affric study at the time of vegetation survey design. The Humpol approach attempts to model pollen-vegetation relationships using known estimates of pollen productivity and fall speed. Datasets of pollen productivity estimates are not available for Scotland, since these estimates are regionally specific, using estimates from other regions may lead to false assumptions of relevant pollen source. Pollen productivity estimates will also vary between small hollow and larger lake sites. Where pollen source area models are not available Hicks *et al.* (1998) recommend arbitrary or intuitive selection of ring source areas. The use of several ring sources for each site can then allow testing of the RSAP by plots of the r^2 and ERV Maximum Likelihood scores (Sugita 1994; 1998).

Several studies have confirmed that there is a correspondence between pollen samples from small hollows and forest vegetation within 20-50 m of the sample point (Andersen 1970; Bradshaw 1981; Heide and Bradshaw 1982; Bradshaw 1994; Calcote 1995). In addition, work on non-arboreal vegetation has indicated a very small relevant pollen source area for most herbaceous taxa (Evans and Moore 1985; Bunting 2003). These estimates of source area were used to determine the sampling radii in the Glen Affric survey. Vegetation cover data was therefore collected in concentric rings around the sample point in 1 metre increments to 5 m (to allow a detailed understanding of pattern and source area in the herbaceous vegetation (*sensu* Bunting 2003; Hjelle 1997) then from 5-10 m, and 10-20 m. Tree presence was recorded at 10 m increments to 50 m.

Measuring Plant Abundance

Various methods of deriving vegetation cover are used throughout the literature of pollen-vegetation calibration studies including stem density, biomass estimates, area cover, wood volume, or basal area of trees (Jackson 1994). Jackson discusses a measure of pollen source strength, which is dependent on various factors including tree age and is a measure of pollen productivity of the vegetation. However, the complexities and assumptions behind this in terms of pollen production of tree and herb taxa in Glen Affric are not known and therefore a simpler approach is favourable. For arboreal taxa, basal area is often used as an easier measure than canopy cover. Anderson (1970) found a relationship between canopy cover and basal area, However this is not always the case (Jackson 1994; *and references therein*), and studies using basal area of trees tend to concentrate on comparisons of cover between tree taxa.

A different approach to recording arboreal vegetation was taken in Glen Affric. Firstly, because fieldwork reconnaissance demonstrated a limited relationship between basal area and crown spread in the varied structural habits of the trees. Secondly, because as this study aimed to identify openness, and to determine pollen vegetation relationships between ground flora and arboreal taxa a comparative measure of vegetation cover between trees and ground flora was required. The basal area was therefore rejected for use in the Glen Affric surveys, instead an estimate of canopy cover was attempted, but the topography of Glen Affric made the collation of data from every tree extremely time consuming, and beyond the limits of the fieldwork budget. A measure of tree area cover was therefore gained by approximating an average crown area for each species and multiplying this by the number of trunks. It is accepted that this is a somewhat arbitrary measure, however, this method gives a first approximation of cover comparative with ground flora taxa within a realistic fieldwork timetable. The sources of error in pollen counting are likely to far outweigh any error in canopy cover calculations.

Each site was divided into rings and each resultant circle was divided into quarters by compass bearing and data collected in the four resultant quadrats per ring. Ground-flora vegetation cover was estimated as percentage cover area of each quadrat, thus allowing subsequent conversion to absolute cover. All trees within 50 m were identified and mapped for approximate location within each quadrat.

Information about each site is presented in Table 5.2. Each site is given a unique code of three or four letters/numbers and a map reference by GPS (Garmin Etrex 12 Channel GPS) recording an accuracy to approximately 3-10 m. Table 5.2 presents a visual assessment of tree and ground flora dominants and slope and aspect of the site. Site slope and wetness of the peat surface is given as a rough visual estimation. Wetness is measured for the basin surface only (see table legend for details); since edaphic conditions are extremely variable at the micro-scale this estimation does not give indication of the surrounding substrate, but will be used solely to make some comparisons regarding the nature of pollen recruitment.

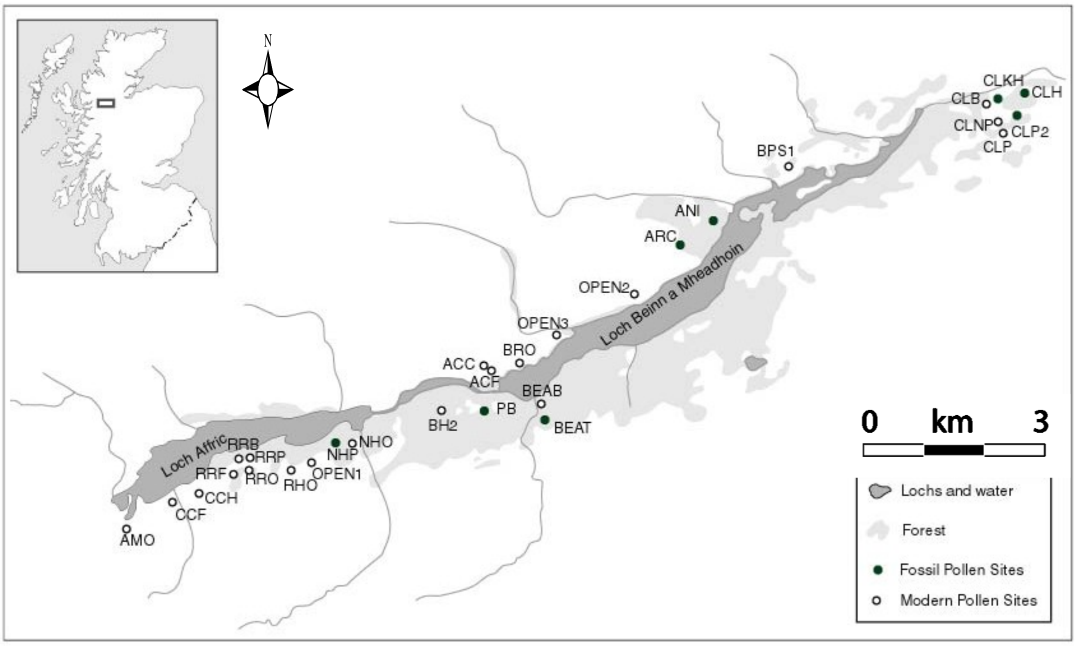


Figure 5.3: Glen Affric showing location of all sites used in this study for core analysis and modern pollen analogues

Table 5.2: Summary site data and descriptions for the Modern Analogue sites in Glen Affric. Field layer vegetation and tree cover are estimated from the vegetation surveys, moisture is estimated from the visual content and squeeze test in the peat core surface sediments (1=water dripping from peat sample; 2=water when peat squeezed; 3=no water only dampness to touch). Slope is arbitrarily estimated by eye.

Site Code	**Map reference**	**Visual Vegetation Description**		**Moisture** **1=wet** **2=moist** **3=dry**	**Slope** **Steep** **Shallow** **Flat**
		Arboreal vegetation	**Predominant Field layer**		
CCH	NH15276 21206	Open	Poaceae/Cyperaceae	2	Shallow
OPEN2	NH15330 21440	Open	Poaceae/Cyperaceae	3	Flat
OPEN3	NH21572 24124	Open	Poaceae/Cyperaceae	3	Flat
RHO	NH18851 22750	Open	*Calluna* Heath	3	Shallow
RRO	NH16030 21618	Open	*Calluna* Heath	3	Shallow
NHO	NH17557 22101	Open	*Calluna* Heath	2	Shallow
OPEN1	NH17138 21817	Open	*Calluna* Heath	3	Flat
CCF	NH 14907 21086	Open	*Calluna* Heath	1	Shallow
BRO	NH20617 23554	Near Pine	*Calluna* Heath	2	Flat
BEAB	NH21050 22780	Near Pine	*Calluna* Heath	2	Flat
BPS	NH27320 27748	Under Pine	*Vaccinium* Heath	3	Flat
BPS1	NH27320 27748	Under Pine	*Vaccinium* Heath	3	Flat
NHP	NH17441 22153	Under Pine	Poaceae/ *Vaccinium*	2	Steep
RRP	NH16007 21634	Under Pine	Heath	2	Flat
PB	NH19791 23041	Near Pine	*Calluna*	3	Flat
CLNP	NH28971 28236	Mixed canopy	Poaceae	2	Flat
CLP	NH29071 28136	Mixed canopy	Poaceae/Cyperaceae	2	Shallow
CLP2	NH29482 27904	Mixed canopy	Poaceae/Cyperaceae	2	Shallow
BEAT	NH21150 22630	Mixed canopy	Poaceae/Cyperaceae	1	Steep
CLH	NH29571 28135	Mixed canopy	Poaceae/Cyperaceae	2	Flat
BH2	NH19015 22832	Near Mixed	*Calluna* Heath	2	Flat
ANI	NH24239 26328	Under Birch	*Cyperaceae - Vaccinium* Heath	3	Steep
ARC	NH23786 25360	Under Birch	*Vaccinium* Heath	1	Steep
RRB	NH15921 21612	Under Birch	*Vaccinium* Heath	3	Flat
RRBW	NH15981 21622	Under Birch	*Vaccinium* Heath	3	Flat
RRBF	NH15995 21632	Under Birch	*Vaccinium* Heath	2	Shallow
CLB	NH29111 28173	Under Birch	Poaceae/Cyperaceae	3	Flat
RRF	NH15850 21770	Near Birch	Poaceae/Cyperaceae	1	Flat
CLKH	NH29398 28306	Near Birch/Pine + Oak + Hazel	Poaceae/Cyperaceae	1	Flat
ACC	NH20038 23404	Near Birch	Poaceae/Cyperaceae	2	Steep
ACF	NH20183 23422	Near Birch	Poaceae/Cyperaceae	1	Steep
AMO	NH14450 21150	Near Birch	Poaceae/Cyperaceae	1	Flat

5.4.4 Pollen counting

Pollen was counted to 500 land pollen grains. (A lesser pollen sum was counted in two sites due to low pollen concentration in the sample). A known quantity of *Lycopodium* spores were added to the pollen preparation and counted on the pollen slides to allow determination of concentration data in addition to percentage data. Influx data can be important to pollen-vegetation calibrations, however, to derive influx data chronologies must be secure (Hicks 2001; Hicks and Birks 1996). The timescale for accumulation of surface peat or vegetation for each site is not clear. Various studies (e.g. Rasanen *et al*. 2004) have attempted to estimate accumulation rates for moss polsters or surface samples, but have developed differing conclusions. An attempt was made to measure the surface growth of the basins in Glen Affric, but failed to find conclusive results. Influx data is therefore insecure.

5.4.5 Numerical analysis methods selected for the Glen Affric dataset

Most simple statistical and mathematical functions were carried out using the mathematical functions in Microsoft Excel or by using the statistics toolpack in Microsoft Excel. Regression analysis is carried out using Least-Squares Linear regression.

Pollen percentage and accumulation data were calculated in Tilia and pollen diagrams created using TiliaGraph (Grimm 1991).

ERV analysis was carried out using the HumPol Suite of programmes (Bunting and Middleton 2005).

Ordination was implemented in Canoco for Windows V.4.5 (ter Braak and Smilauer 1997-2003). Cluster Analysis was carried out in PAST PAlaeontological STatistics package (Hammer 2001).

5.5 Results of the modern pollen analogue study in Glen Affric

5.5.1 Taxa recorded in the vegetation surveys and surface pollen samples

This Section introduces the data from the site vegetation surveys and the surface pollen datasets. The aims of this section are:

To identify opportunities and constraints on the analysis of pollen data by;

- identifying plant taxa that occur where the corresponding pollen taxa are not recorded;
- identifying pollen taxa that occur where the corresponding plant taxa are not recorded;
- identifying fossil pollen taxa from the eight cores that do not appear in the surface samples;

and to identify opportunities for further analysis and quantification of pollen data by;

- identifying the key pollen taxa for use in Regression and ERV analysis;
- identifying appropriate taxa for IOA and Point-Biserial Regression analysis.

5.5.1.1 Vegetation types present

Overall, 59 species or taxa of higher plants are recorded in the vegetation surveys from the 29 sites in Glen Affric. Table 5.3 lists the plant taxa recorded within the 20 m (and 50 m for trees) radius of the sample sites and lists the corresponding pollen taxa for each plant. The third column in Table 5.3 shows the number of site surveys where each taxon was recorded. Common Cyperaceae and Poaceae species are identified to species level in the vegetation data but the list of species within these families is not exhaustive. A total cover for Poaceae and Cyperaceae is also presented in Table 5.3; these totals for the families are used in all further analysis as it is not possible to differentiate the pollen of these taxa to species level under the ordinary light microscope.

The main tree taxa are *Pinus sylvestris* and *Betula*, (likely to be both *Betula pubescens* and *Betula pendula*). *Sorbus aucuparia* is frequent, occurring in ten of the 29 sites, whilst *Alnus glutinosa* and *Quercus* are rare, occurring in only three and one site respectively. Canopy cover is quite open, with a maximum canopy cover estimate of 59%. Shrub taxa are rare, with infrequent occurrences of *Corylus*, *Juniper*, *Salix*, and *Myrica gale*.

Calluna vulgaris, is the most abundant Ericoid shrub, but at some sites, *Vaccinium myrtillus* is abundant. *Erica tetralix* occurs in 18 of the 29 sites whilst *E. cinerea* is recorded in only two sites. *Erica* is always infrequent where it occurs. Poaceae and Cyperaceae are abundant at some sites, especially on the basin surface; *Potentilla erecta* is a frequent herbaceous species, most other herbaceous species are found relatively infrequently across the sites and are generally sparse where they occur.

Pteridophyte taxa were also recorded, including *Blechnum spicant* and *Pteridium aqulinum*. However further visits to the sites throughout the summer revealed, sometimes large, cover changes in these taxa. The data may therefore be unreliable and are not considered further in the pollen-vegetation correlations.

Some species share common pollen taxa; the 59 plant taxa are represented by 43 pollen taxa. Five taxa (*Juncus* sp., *Dactylorhiza* sp.) have no equivalent pollen type likely to survive the pollen preparation process (Moore *et al.* 1991).

Table 5.3: Plant taxa recorded in Glen Affric vegetation surveys, together with the number of sites where each plant taxon is present, and a maximum and mean vegetation cover percentage. Corresponding pollen taxon are also listed for each plant taxon.

Plant Taxon	Corresponding Pollen taxon	Number of sites where taxon is recorded in the vegetation within 20m (50m for trees)	Maximum Percentage cover (as a percentage of total area)	Mean Percentage cover
Alnus glutinosa	*Alnus glutinosa*	3	0.4	0.0
Betula pendula/pubescens	*Betula*	19	38.5	7.6
Pinus sylvestris	*Pinus sylvestris*	21	58.5	11.2
Quercus petraea	*Quercus*	1	0.3	0.0
Sorbus aucuparia	*Sorbus aucuparia*	10	2.3	0.1
Corylus avellana	*Corylus*/Coryloid	1	0.2	0.0
Juniperis communis	*Juniper*	1	0.04	0.0
Myrica gale	*Myrica gale*/Coryloid	6	23.8	1.9
Salix spp.	*Salix*	3	0.4	0.0
Arctostaphylos uva-ursi	*Arctostaphylos uva-ursi*	5	3.3	0.3
Calluna vulgaris	*Calluna vulgaris*	27	71.2	33.3
Empetrum nigrum	*Empetrum*	12	20.9	2.0
Erica cinerea	*Erica cinerea*	2	4.2	0.2
Erica tetralix	*Erica tetralix*	18	16.0	3.3
Vaccinium sp	*Vaccinium*	23		
Vaccinium vitis-idaea	*Vaccinium*	11	21.8	1.5
Vaccinium myrtillus	*Vaccinium*	21	69.2	12.3

Table 5.3 continued:

Plant Taxon	Corresponding Pollen Taxon	Number of sites where taxon is recorded in the vegetation within 20m (50m for trees)	Maximum Percentage cover (as a percentage of total area)	Mean Percentage cover
Cyperaceae	Cyperaceae	21	78.3	19.2
Carex pauciflora	Cyperaceae	1	2.0	0.1
Carex echinata	Cyperaceae	6	13.2	1.0
Eriophorum angustifolium	Cyperaceae	15	29.6	3.9
Carex nigra	Cyperaceae	5	3.4	0.3
Eriophorum vaginatum	Cyperaceae	1	20.6	3.0
Carex pulicaris	Cyperaceae	11	0.6	0.0
Scirpus cespitosus	Cyperaceae	8	60.7	7.7
Poaceae	Poaceae	29	86.1	26.0
Molinia caerulea	Poaceae	18	86.1	11.4
Festuca vivipara	Poaceae	1	0.9	0.0
Deschampsia flexuosa	Poaceae	2	10.6	0.7
Deschampsia cespitosa	Poaceae	1	0.6	0.0
Lysimachia nemorum	*Anagellis arvensis* type	2	1.1	0.0
Anemone nemorosa	*Anenome nemorosa*	1	14.2	0.5
Achillea millefolium	*Anthemis* type	1	6.2	0.2
Asteraceae	Aster type	1	0.5	0.0
Crepis sp.	*Cichorum intybus* type	1	0.2	0.0
Drosera anglica / D. rotundifolia	*Drosera anglica / D. rotundifolia* type;	3	1.5	0.1
Equisetum spp.; *E.sylvaticum*	*Equisetum*	3	1.3	0.0
Galium saxatile	*Galium* type	8	2.7	0.3
Geum	*Geum*	1	0.2	0.0
Juncus effusus	*Juncus* (no pollen)	17	15.1	2.0
Juncus squarrosus	*Juncus* (no pollen)	4	1.9	0.1
Lotus corniculatus	*Lotus*-Type	1	0.5	0.0
Luzula multiflora	*Luzula* (no pollen)	7	5.7	0.4
Melampyrum pratense	*Melampyrum*	4	1.3	0.1
Narthecium ossifragum	*Narthecium ossifragum*	13	9.5	1.4
Oxalis acetosella	*Oxalis acetosella*	4	10.5	0.4
Pinguicula vulgaris	*Pinguicula*	2	0.1	0.0
Plantago lanceolata	*Plantago lanceolata* type	1	1.2	0.0
Dactylorhiza sp.	Pollen unlikely	3	0.8	0.0
Polygala serpyllifolia	*Polygala*	5	5.0	0.3
Potentilla erecta	*Potentilla* type	24	6.8	2.4
Pyrola media / Pyrola rotundifolia	*Pyrola* type	2	0.5	0.0
Ranunculus sp	*Ranunculus* type	1	0.3	0.0
Euphrasia spp.	*Rhinanthus* type	1		
Rumex acetosa	*Rumex acetosa*	2	2.8	0.1
Succisa pratensis	*Succisa*	4	3.7	0.2
Trientalis europaea	*Trientalis europaea*	5	2.8	0.2
Trifolium pratense; *T. repens*	*Trifolium*	1	0.5	0.0
Viola riviniana	*Viola canina-Viola riviniana*	6	0.7	0.0

5.5.1.2 Pollen types present

Surface pollen sample counts from Glen Affric yielded 63 pollen taxa and 12 spore taxa. These taxa are listed in Table 5.4, which also shows the number of sites in which the pollen taxa and corresponding source plant taxa are present, and identifies rare and common pollen taxa.

There are six key pollen taxa found consistently throughout the sites in this study; *Pinus sylvestris*, *Betula*, *Calluna vulgaris*, Poaceae, Cyperaceae, and *Potentilla*-type. Several other types including *Vaccinium* and *Erica* sp. also appear regularly but in lower percentages. Overall there are 28 pollen taxa where plant taxa presence is recorded in at least one of the local vegetation surveys. Table 5.4 shows that 35 of the pollen taxa counted in the surface samples have no corresponding plant taxa in the vegetation surveys surrounding the sample sites. The third column of Table 5.4 lists the possible source plant taxa found in other surveys in the wider Glen Affric landscape. These other surveys range from general lists in the management plan to transect and quadrat surveys in defined locations (e.g. Trees for Life surveys in Coille Ruigh). These lists therefore give only a general indication of vegetation presence in the landscape, but help to separate those pollen taxa likely to be of extra-local, landscape scale origin, from those likely to be deposited by long distance pollen transport mechanisms. Many of the pollen taxa that do not have local plant presence are represented by just one or two grains over the 29 pollen samples and may have a regional source; e.g. *Fagus*, and the cereal grains, *Avena*, *Hordeum* and *Secale*. It is possible that some types may be present in the vegetation of the Glen, but not yet recorded in surveys.

Also recorded in Table 5.4 are the number of samples that contain both the pollen or the plant for each taxa. IOA analysis (Section 5.3.9) can be carried out on those taxa where both the pollen and the plant are present in at least one sample. Regression analysis relies on a more frequent presence of both pollen and plant. Table 5.4 lists the suitability of each taxon to regression and IOA analysis based on presence and frequency of plant and pollen taxa. 16 taxa and 2 additional pollen groups (*Erica* undiff and Ericaceae undiff) are suitable for analysis using IOA.

Table 5.4: List of pollen taxa found in the Glen Affric surface samples, together with information on the presence of corresponding plant taxa in the vegetation surveys. The last column indicates the suitability of each taxa for further analysis by Regression or IOA techniques based on plant and pollen presence and abundance across the sites.

Pollen Type	**Associated Vegetation Types within 20m surveys of the sample sites (50m for trees)**	**Associated vegetation types in other Glen Affric species lists and surveys**	**Presence in other surveys**	**No of Site surveys containing taxa (this study only)**	**No of samples containing pollen taxa**	**Maximum Pollen %**	**Minimum Pollen %**	**Suitable for IOA and R_{pb} or regression or ERV**
Alnus glutinosa	*Alnus glutinosa*	*Alnus glutinosa*	CMJ	3	16	1.7	0	IOA
Betula	*Betula pendula; Betula pubescens*	*Betula pendula; Betula pubescens*	WCMJ	19	29	78.7	1.7	Linear regression
Fagus	/	/	/	None	5	0.3	0	No
Fraxinus	*Fraxinus excelsior*	*Fraxinus excelsior*	MJ	None	8	0.8	0	No
Picea	/	/	/	None	18	2.2	0	No
Pinus sylvestris	*Pinus sylvestris*	*Pinus sylvestris*	WCMJ	21	29	78.8	7.5	Linear regression
Quercus	*Quercus petraea*	*Quercus petraea*	MJ	1	7	0.6	0	IOA
Sorbus aucuparia	*Sorbus aucuparia*	*Sorbus acuparia*	WCMJ	10	7	2.5	0	IOA
Sorbus aria	*Sorbus aria*	/	/	None	1	0.2	0	No
Ulmus	*Ulmus glabra*	*Ulmus glabra*	MJ	None	4	0.4	0	No
Coryloid	*Corylus avellana/Myrica gale*	*Corylus avellana/Myrica gale*	MJ	/	7	2.2	0	No
Corylus/Coryloid	*Corylus avellana*	*Corylus avellana*	MJ	1	4	0.8	0	IOA
Myrica gale/Coryloid	*Myrica gale*	*Myrica gale*	WC	6	20	6.9	0	IOA
Salix	*Salix* spp.	*Salix* spp.	WCMJ	3	5	2.5	0	IOA
Calluna vulgaris	*Calluna vulgaris*	*Calluna vulgaris*	WCMJ	27	29	49.9	0.7	Linear regression
Empetrum nigrum	*Empetrum nigrum*	*Empetrum nigrum*	WCMJ	12	8	2.5	0	IOA
Erica cinerea	*Erica cinerea*	*Erica cinerea*	WCM	2	3	4.5	0	IOA
Erica tetralix	*Erica tetralix*	*Erica tetralix*	WCM	18	10	1.6	0	IOA
Erica undiff	*Erica cinerea / Erica tetralix*	*Erica cinerea / Erica tetralix*	WCM	/	12	8.7	0	IOA
Ericaceae undiff	*Erica/Vaccinium/Empetrum*	*Erica/Vaccinium/Empetrum*	WCM	/	13	6.9	0	IOA + Linear regression
Vaccinium undiff	*Vaccinium myrtillus; Vaccinium vitis-idaea*	*Vaccinium myrtillus; Vaccinium vitis-idaea*	WCMJ	23	13	1.4	0	IOA + Linear regression
Erica/Vaccinium	*Erica/Vaccinium*	*Erica/Vaccinium*	WCM	23	2	2.7	0	IOA

Table 5.4 Continued:

Pollen Type	Associated Vegetation Types within 20m surveys of the sample sites (50m for trees)	Associated vegetation types in other Glen Affric species lists and surveys	Presence in other surveys	No of Site surveys containing taxa (this study only)	No of samples containing pollen taxa	Maximum Pollen %	Minimum Pollen %	Suitable for IOA and Rpb or Linear Regression and ERV (LR-ERV)
Allium type				None	1	0.2	0	No
Androsaceae elongata type				None	1	23	0	No
Apiaceae		*Conopodium majus*	W	None	2	0.2	0	No
Artemisia				None	2	0.4	0	No
Aster type	Asteraceae undiff	*Antennaria dioica, Bellis perennis, Solidago virgaurea*	WC	1	1	0.2	0	
Avena Triticum type				None	3	0.6	0	No
Brassicaceae				None	2	0.4	0	
Circaea				None	1	0.4	0	
Cyperaceae	Various sp.	Various sp.	WCMJ	21	27	41.9	0	Linear regression
Drosera intermedia-type				1	1	0.2	0	
Filipendula				None	3	0.4	0	
Galium	*Galium saxatile; Galium palustre*	*Galium saxatile; Galium palustre*	WC	8	2	2.1	0	IOA
Hordeum type				None	4	0.4	0	No
Lactuceae sativa type				None	1	0.4	0	No
Lactuceae undiff	*Crepis* sp.			1	1	0.2	0	No
Lilliaceae				None	2	0.7	0	No
Narthecium ossifragum	*Narthecium ossifragum*	*Narthecium ossifragum*	WC	13	1	0.2	0	IOA
Nyssia cf				None	1	0.3	0	No
cf. *Morus nigra*				None	1	0.2	0	No
cf. *Muscari*				None	1	0.2	0	No
Oxalis	*Oxalis acetosella*		W	4	1	0.2	0	No
Parietaria cf				None	2	0.7	0	No
Pedicularis	*Pedicularis palustris*	*Pedicularis palustris*	WC	None	3	0.5	0	No
Plantago lanceolata	*Plantago lanceolata*	*Plantago lanceolata*	W	1	17	4.2	0	IOA
Plantago coronopus				None	1	0.2	0	No

Table 5.4 Continued:

Pollen Type	Associated Vegetation Types within 20m surveys of the sample sites (50m for trees)	Associated vegetation types in other Glen Affric species lists and surveys	Presence in other surveys	No of Site surveys containing taxa (this study only)	No of samples containing pollen taxa	Maximum Pollen %	Minimum Pollen %	Suitable for IOA and Rpb or Linear Regression and ERV (LR-ERV)
Poaceae	Various sp.		WCMJ	29	29	32.5	1.7	No: Linear regression
Potentilla-type	*Potentilla erecta*	*Potentilla erecta, Fragaria vesca*	WC	24	19	8.5	0	Yes + Linear regression
Primula veris type	*Primula vulgaris*	*Primula veris* type	W	None	1	0.2	0	No
Pyrola	Pyrola media; Pyrola rotundifolia	*Pyrola media; Pyrola rotundifolia*	WCM	2	4	0.5	0	IOA
Ranunculus acris - type	*Ranunculus acris*	*Ranunculus acris*	W	None	8	0.6	0	No
Ranunculus type	Ranunculus sp	*Ranunculus lingula, Ranunculus flammula, Ranunculus repens*	W	1	6	0.4	0	IOA
Rosaceae-undiff		various		/	3	0.4	0	No
Rumex acetosa		*Rumex acetosa*	w	2	10	0.8	0	No
Rumex acetosella	Rumex acetosella	*Rumex acetosella*	w	None	4	0.6	0	No
Sambucus nigra				None	1	0.2	0	No
Saxifragia granulata cf				None	1	0.2	0	No
Secale cereale				None	1	0.4	0	No
Stachys				None	1	0.2	0	No
Stellaria holostea				None	1	0.2	0	No
Sucissa	*Succisa pratensis*	*Succisa pratensis*	W	4	1	0.2	0	IOA
Urtica	*Urtica dioica*	*Urtica dioica*	W	None	9	2.2	0	No
Adiantum capillus-veneris	/							
Blechnam spicant	*Blechnam spicant*							
Diphasiastrum								
Dryopteris filix-mas type								
Equisitem								
Huperzia selago								
Isoetes								
Lycopodium clavatum	*Lycopodium clavatum*							
Polypodium								
Pteridium aquilinum	*Pteridium aquilinum*							
Pteropsida								
Sphagnum	*Sphagnum*							
Woodsia								

Table 5.5 lists the pollen taxa from surface samples not found in either the site vegetation surveys or any of the wider plant lists for Glen Affric together with likely source plant species. Possible sources are speculated for some taxa in the last column of the Table. *Picea* is likely to have come from local planted sources in Glen Affric, but in areas that have not attracted vegetation surveys. *Fagus* is likely to have a regional source, perhaps from the Cannich area or beyond. Of particular interest are the cereal grains of *Hordeum*-type and *Avena Triticum* type, which are often taken as indicators of local agricultural land use.

Table 5.5: List of pollen taxa found in modern pollen samples in Glen Affric but not in Glen Affric vegetation surveys; together with the likely corresponding plant taxon and possible source of the taxon to the pollen record..

Pollen Group	**Pollen Type**	**Possible Plant taxa**		**Possible source**
		Latin Name	**Common Name**	
Tree	*Fagus*	*Fagus sylvatica*	Beech	Possibly in the lower Glen
Tree	*Picea*	*Picea abies*	Spruce	Local plantations
Tree	*Sorbus aria*	*Sorbus aria*	Whitebeam	Not local
Herb	*Allium* type	Various		
Herb	*Androsaceae elongata* type	Various		
Herb	*Artemisia*			
Herb	*Avena Triticum* type	Various *Avena/Triticum*	Various cereals	Not local
Herb	Brassicaceae	Various		
Herb	*Circaea*	Various		
Herb	*Drosera intermedia*	*Drosera intermedia*		Likely to be local
Herb	*Filipendula*	*Filipendula vulgaris;* *Filipendula ulmaria*	Meadowsweet	Could be local, but not well represented in Scotland
Herb	*Hordeum* type	Various	Barley/Cereals	Possibly lower Glens to west or east
Herb	*Lactuceae sativa* type	Lactuca sp. Mycelis muralis		
Herb	Lilliaceae	Various		
Herb	*Morus nigra* cf.		Mulberry	Possible misidentification
Herb	*Muscari* cf.		Hyacinth	Possible misidentification of other Liliaceae
Herb	*Nyssa* cf		Dogwood	Possible misidentification
Herb	*Parietaria* cf		Pellitory	Possible misidentification
Herb	*Plantago coronopus*	*Plantago coronopus*	Buckthorn Plantain	Coastal
Herb	*Sambucus nigra*	*Sambucus nigra*	Elderberry	
Herb	*Saxifraga granulata* cf	Saxifraga sp.	Various Saxifrage	
Herb	*Secale cereale*	*Secale cereale*	Rye	Not local
Herb	*Stachys*	Various Lamiaceae		
Herb	*Stellaria holostea*	*Stellaria holostea*	Stitchwort	Possibly Local
Spore	*Adiantum capillus-veneris*	*Adiantum capillus-veneris*	Maidenhair fern	
Spore	*Dryopteris filix-mas* type	*Dryopteris sp.*	Common male fern	Possibly Local
Spore	Isoetes	Isoetes	Quillwort	Possibly Local
Spore	*Lycopodium clavatum*	*Lycopodium clavatum*	Clubmoss	Local
Spore	*Woodsia*	*Woodsia*		Possibly Local

Table 5.6 lists the plant taxa from Table 5.2 found in the vegetation samples around the 29 surface pollen sites that do not have associated pollen taxon presence in the surface pollen counts. Some of these plants produce pollen that does not survive well, whilst others produce

viable pollen but the lack of surface presence may indicate under-representation in the Glen Affric landscape. The last column in Table 5.6 indicates if these pollen taxa are found in the eight core samples. Some taxa are present in the fossil samples although not present in the surface samples. *Juniperis* is present in only three sub-samples across three out of the eight cores; *Arctostaphylos* and *Drosera* also show a low presence. *Melampyrum* and *Rumex acetosa* show a more common presence in the cores than in the surface. This could indicate that the surface samples are not recording all rare-type taxa consistently, or could indicate a wider, more abundant presence of these taxa in the previous vegetation. These taxa are examined further in Section 5.6.3 and compared with records of over and under-representation at other sites.

Table 5.6: List of plant taxa and species present in the surface vegetation surveys in Glen Affric that have no associated pollen found in the surface samples.

Pollen Group	Latin Name	Common Name	Pollen Type	No of fossil cores / no of sub-samples where present
Shrub	*Juniperis communis*	Juniper	Juniper	3/3
Heath	*Arctostaphylos uva-ursi*	Bearberry	*Arctostaphylos uva-ursi*	4/9
Herb	*Lysimachia nemorum*	Yellow pimpernel	*Anagellis arvensis* type	0/0
Herb	Anemone nemorosa	Wood anemone	*Anenome nemorosa*	5/17
Herb	*Achillea millefolium*	Yarrow	*Anthemis* type	5/11
Herb	*Drosera anglica*	Great sundew	*Drosera rotundifolia* type	2/5
Herb	*Drosera rotundifolia*	Round-leaved sundew	*Drosera rotundifolia* type	See above
Herb	*Geum*	Avens	*Geum*	7/20
Herb	*Juncus effusus*	Soft rush	Pollen unlikely	0/0
Herb	*Juncus squarrosus*	Hard rush	Pollen unlikely	0/0
Herb	*Lotus corniculatus*	Common birds-foot trefoil	*Lotus*-type	0/0
Herb	*Luzula multiflora*	Heath woodrush	Pollen unlikely	0/0
Herb	*Melampyrum pratense*	Common cow-wheat	*Melampyrum*	7/46
Herb	*Pinguicula vulgaris*	Common butterwort	*Pinguicula*	0/0
Herb	*Dactylorhiza maculata*	Heath spotted orchid	Pollen unlikely	0/0
Herb	*Dactylorhiza fuschii*	Common spotted orchid	Pollen unlikely	0/0
Herb	*Polygala serpyllifolia*	Milkwort	*Polygala*	0/0
Herb	*Euphrasia* spp. *Euphrasia officianalis*	Eyebright	*Rhinanthus* type	0/0
Herb	*Rumex acetosa*	Common sorrel	*Rumex acetosa*	8/56
Herb	*Trientalis europaea*	Chickweed wintergreen	*Trientalis europaea*	0/0
Herb	*Trifolium pratense*	Red clover	*Trifolium*	0/0
Herb	*Trifolium repens*	White clover	*Trifolium*	0/0
Herb	*Viola riviniana*	Common dog violet	*Viola canina-Viola riviniana*	0/0

5.5.1.3 Discussion

As expected in a pine wood and moorland ecosystem there are a few key pollen taxa that dominate the pollen record, and the landscape, including the major tree taxa, *Pinus* and *Betula*, together with Poaceae, Cyperaceae, *Calluna* and to a lesser extent *Potentilla*, which forms a frequent herb. These six key taxa are suitable for analysis and development of pollen correction factors using the ERV model.

Tables 5.1 – 5.4 above demonstrate the remarkably small number of taxa that have a regular presence in both the pollen and plant record with only 28 out of 94 (pollen and/or plant) taxa showing vegetation and pollen presence and possible association in these surface samples.

Some of the pollen taxa with no corresponding vegetation presence are likely to be from a regional or long distance plant source (Table 5.5). However many pollen taxa are associated with plant taxa in the wider Glen Affric surveys and species lists. This may indicate limitations of the small hollow approach. It is difficult to be certain of local source for many rare taxa.

Equally, however, this lack of association between plant and pollen taxa for many rare types may indicate the limitations of the survey techniques for modern pollen analysis. Two problems may occur:

1. Limitations in the vegetation survey. **-** Whilst the pollen sample represents possibly between one and five years of pollen deposition, the plant survey for each site was carried out in one site visit. It is possible that small plant taxa were missed, especially under denser Ericoid canopy cover, but also likely that some rarer herb taxa were missed due to changes in the cover and visibility of taxa during the growing season, or due to patchy and variable distribution through time.

2. Limitations in the pollen count data. – Whilst a sum of 500 TLP is often taken as a standard pollen count (R. Tipping *Pers. Comm.*) this may not be a high enough count to establish the presence of rare-type pollen taxa. Higher counts may need to become routine in order to establish openness and reconstruct ground flora communities.

5.5.2 Simple rank correlations and ratios of modern vegetation and surface pollen data for some key taxa

This section begins the quantitative analysis of the pollen-vegetation relationship by ranking the arboreal canopy cover and presenting a standard pollen diagram for the surface samples with sites displayed in rank order according to the degree of canopy cover of *Pinus* and *Betula*. The non-parametric Spearman Rank Correlation is applied to the pollen and vegetation data to test the relationship between key taxa (Birks and Gordon 1985; Hjelle 1997). The aims of this section are:

- To rank vegetation data according to canopy cover for *Pinus* and *Betula* and total arboreal canopy.
- To present the pollen diagram from the Glen Affric surface pollen dataset with sites ordered according to rank of arboreal cover to test for the relevance of a traditional visual interpretation of pollen data.
- To test the correlation between ranks of vegetation cover and pollen percentage for key taxa using the Spearman Rank Correlation Coefficient.
- To compare and correlate ratios of *Pinus*/*Betula* and Cyperales/Ericales in the pollen and the plant data in order to test the ability of pollen to generate semi-quantitative data on the comparative abundance of key taxa.

5.5.2.1 Ranking and ratios of arboreal cover

Total tree cover, and tree cover of *Pinus* and *Betula* to 50 m radius around each site are ranked and the scores presented in Table 5.7. The relative pine/birch percentage ratio is also displayed in Table 5.7 to distinguish mixed stands from single species stands. Sites are ordered in the table so that sites with a high cover of *Pinus* woodland are displayed at the top of the table, whilst sites with a high cover of *Betula* are displayed at the base. Using this ranking, open sites are displayed in the middle rows of Table 5.7, these sites are colour coded in yellow.

There are seven, woodland, or semi-open woodland, sites containing almost-pure stands of *Betula* or *Pinus*; NHP, RRP, NHO and PB are all almost pure *Pinus*, whilst ANI, ACC and RRF are dominantly *Betula* stands. CLNP, CLP and CLH also have a high proportion of *Pinus* dominance, but canopy cover does include some *Betula*. CLB and RRB have a high *Betula* dominance but with some *Pinus*. The other sites are mixed woodland stands apart from the five sites in the centre of the Table; CCH, OPEN1, OPEN2, OPEN3 and RRO, these sites are totally open, with no canopy cover to 50 m. Five sites; RHO, CCF, AMO, BRO and BH2, have very limited local tree cover, perhaps falling into the 'moorland with scattered trees' definition of Rodwell (1991) rather than the open woodland definition. In addition, the limited tree cover around CCF, AMO, and BH2 comprises a high proportion of young trees.

Table 5.7: List of modern pollen sites in Glen Affric together with the rank for tree cover around each site to 50m radius. The table is ordered according to a mix of tree cover rank and rank of *Pinus* as a percentage of *Betula* so that denser *Pinus* sites are at the top of the table and dense *Betula* sites at the base with mixed sites and open sites towards the centre.

Rank total tree cover	**Site**	**Site description**	***Pinus* as percentage of pine and *Betula***	**Rank *Pinus* cover**	**Rank *Betula* Cover**	**Total Estimated Canopy Cover m^2**
1	NHP	pine	100	1	20	4592
4	CLNP	pine	80	4	12	3053
6	CLP	pine	86	5	14	2755
5	CLH	pine	86	3	13	2827
7	BEAB	pine/birch	62	6	9	2444
3	CLP2	pine/birch	66	2	5	3762
10	BPS1	pine/birch	66	7	11	2238
12	PB	semi-open pine	92	8	18	1528
14	RRP	semi-open pine	100	9	20	1400
17	NHO	semi-open pine	100	10	20	1148
16	CLKH	semi-open pine/birch	72	12	15	1281
21	BH2	open/pine	100	15	20	358
22	BRO	open/pine	100	17	20	252
24	RHO	open pine/birch	62	19	19	102
25	CCH	open	N/A	22	20	0
25	OPEN3	open	N/A	22	20	0
25	OPEN2	open	N/A	22	20	0
25	OPEN1	open	N/A	22	20	0
25	RRO	open	N/A	22	20	0
23	CCF	open birch	0	22	17	140
20	AMO	semi-open birch/pine	32	18	16	426
19	ACF	semi-open birch	0	22	10	825
18	RRF	semi-open/birch	5	20	8	1046
15	CLB	semi-open birch	22	16	7	1389
13	ANI	semi-open birch	1	21	3	1416
9	ACC	birch	0	22	2	2250
11	ARC	birch/pine	32	14	6	1822
8	BEAT	birch/pine	36	11	4	2080
2	RRB	birch	19	13	1	3730

5.5.2.2 Ranked pollen diagram

Figure 5.4 presents a summary percentage pollen diagram for the surface pollen samples in Glen Affric. Pollen data for each taxon are displayed as a percentage of TLP. A full pollen diagram and pollen diagram of concentration pollen data for the surface samples is provided in Figure 5.5 at the end of Section 5.5.1 The sites are displayed on the y axis of the pollen diagram in the same order as the vegetation data in Table 5.7. The colour coded woodland types in Table 5.7 are labelled as zones at the end of the pollen diagram in Figure 5.1.

Pinus pollen percentages are highest in the pine dominated sites, with values for *Pinus* pollen consistently over 50%, this is similar to the results of studies at Abernethy (O'Sullivan 1973) where closed and semi-open sites produced *Pinus* pollen percentages of >60% and open sites below 40%[9]. *Betula* pollen percentages are also generally higher at the *Betula* dominated sites (Figure 5.1); values for *Betula* pollen are consistently over 35% in these sites. However whilst *Betula* pollen percentages remain low in the open and *Pinus* dominates sites the *Pinus* pollen percentages are high at over 50% in one open site (OPEN1). This site has no *Pinus* trees within a 50 m radius, although there are some *Pinus* trees just beyond that radius. *Pinus* pollen percentages also occur up to c. 50% in some sites of semi-open woodland or mixed stands e.g. RHO, BRO and AMO. The relationship between total arboreal cover and total arboreal pollen (AP) is less clear (see Section 5.6.2.3). In particular, NHP, which ranks highest for woodland cover (see Table 5.7), has a high herbaceous pollen total, and correspondingly depressed AP total; mainly due to the surface peak in Poaceae pollen. However, this is consistent with the vegetation data, as the NHP sample is taken from a Poaceae rich flush with sparse trees to 20 m and a denser stand beyond this distance.

Calluna pollen percentages are low (>10% TLP) in the sites with denser tree canopy cover. BH2 a semi-open site has a high *Calluna* percentage at *c.* 50% TLP. In the open sites, apart from OPEN2 where the *Calluna* reaches *c.* 30% TLP, Poaceae and Cyperaceae consistently show higher percentages than *Calluna*.

Pollen from heath taxa other than *Calluna* generally has a low percentage. Some sites, notably ANI, ARC, RRB, BPS1 and NHP have a considerable *Vaccinium* cover surrounding the sampling point, yet *Vaccinium* is a sparse pollen taxon. This is consistent with findings from other studies that *Vaccinium, Empetrum* and *Erica* are underrepresented pollen types (e.g. Caseldine 1981; Tallis 1997).

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[9] *but in O’sullivan’s study the Land Pollen sum excluded mire surface taxa*

Herbaceous taxa are mainly present as rare types and are sparse in the surface pollen diagram. Of particular interest are the single grains of *Avena Triticum*-type and *Hordeum*-type pollen in samples CLP RHO CLB, and CLP2, RHO, RRBF and RRBW respectively. Glen Affric is currently managed for conservation and growing of domestic crops will not have taken place in the glen in the last *c*. 60 years and probably, if at all, for a considerable period before this. The position of the glen means that pollen from crop plants is likely to be limited in source to sites in the Cannich and Guisachan areas to the south and south-east or from Kintail to the west; each several kilometres distant. This infers that any low-percentage counts of these important anthropogenic indicator-type taxa must be interpreted with caution. Similar results and conclusions were found in Assynt by Bunting (2003).

Generally, there are low percentages of spores, apart from *Sphagnum*. *Sphagnum* percentages are higher in the more open sites. *Equisetum* is also present more consistently than other species, but occurs more frequently in open and *Pinus* dominated sites. Diatoms occur in ten of the 29 sites; these sites are among the wetter flush sites. Diatoms are not identified to taxon or species and so their analysis in this study is limited, although the inference of surface wetness may be important.

Pinus stomata also occur consistently in sites with *Pinus* in the canopy with the exception of BEAB and BH2. These sites have a lower cover of *Pinus* trees and in addition, the *Pinus* occurs at a greater distance from the pollen sample point. *Pinus* stomata do have occurrences in some of the more open or *Betula* dominated sites. Apart from OPEN1 these sites always have some *Pinus* presence.

The relationship between pollen percentage and plant cover for key taxa and pollen groups is tested by rank correlation in Section 5.6.2.3 below.

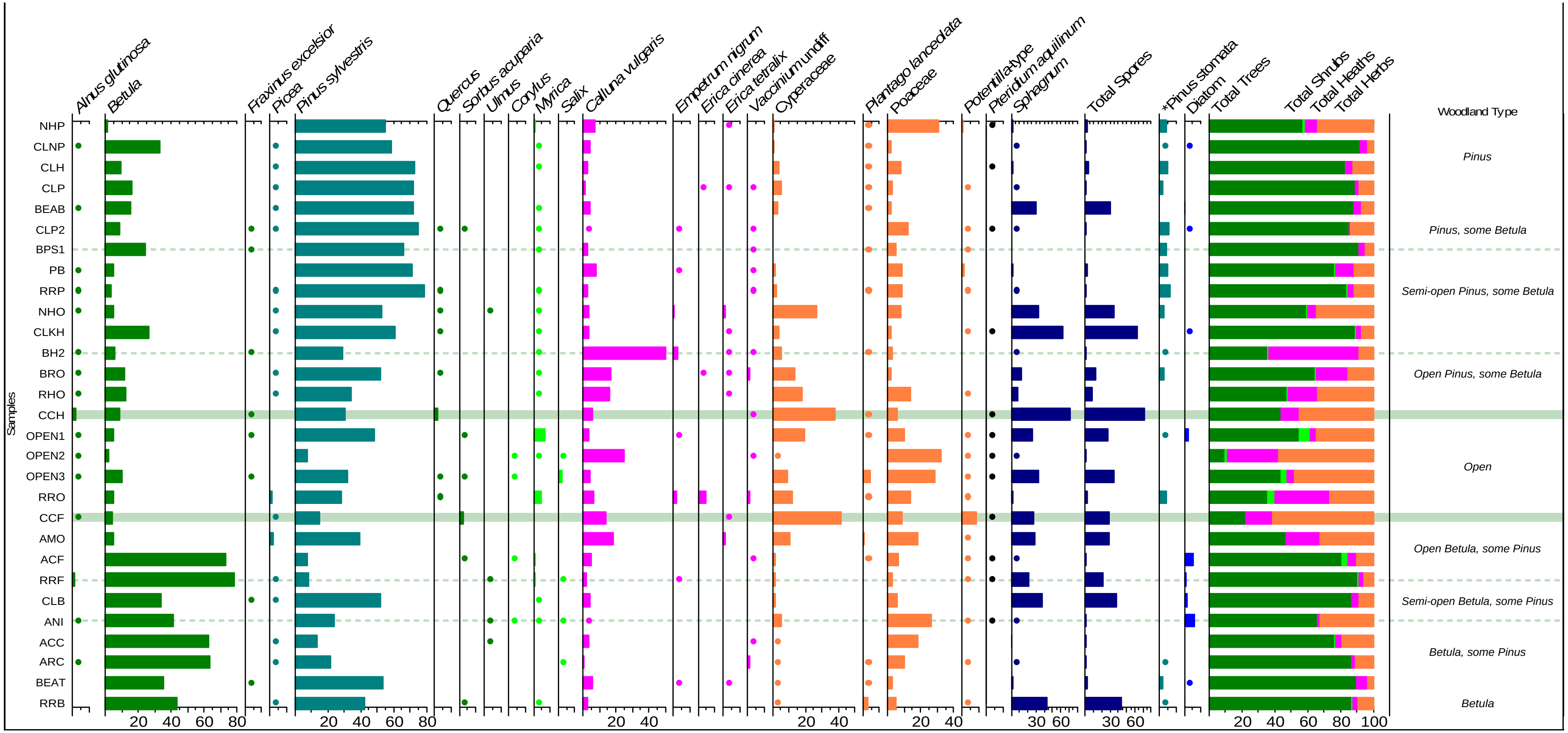


Figure 5.4: Pollen diagram of selected pollen taxa for the 29 surface samples 29 sites in Glen Affric used to determine and quantify pollen-vegetation relationships. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Grain counts of taxa <1% are expressed as + symbols.

5.5.2.3 Testing of rank correlation for key taxa

The relationship between key pollen and vegetation taxa and groups is tested using Spearman Rank Correlation between the key pollen taxa and vegetation taxa (Birks and Gordon 1985; Hjelle, 1997). The correlation coefficients Rs and significance levels are displayed in Table 5.8. Correlations are made on all key taxa with vegetation cover to 20 m radius around the sites, and for trees to 50 m. Correlations are made between the absolute cover of the plant taxa, and the pollen as a percentage of TLP. In the final column, a correlation is made between plant and pollen percentage as a percentage of the key taxa group; which comprises *Pinus*, *Betula*, *Calluna*, Poaceae, Cyperaceae and *Potentilla*.

5.5.2.4 Results

All rank correlations between pollen TLP and vegetation cover within a 20 m sampling radius are significant with the exception of *Potentilla* and the NAP total. Rs for *Calluna* is significant to 95% level, whilst the correlations for all other key taxa are very significant (P=>0.001).

Pinus, *Pinus* stomata, *Betula* and Arboreal totals are all tested for correlation with vegetation sampled to a 50 m radius. *Betula* and *Pinus* both show slight increase in the significance of the correlation at this sampling distance. The correlation between *Pinus* stomata and *Pinus*, however, shows a slight decrease in the significance of the correlation, as does the arboreal total.

Table 5.8: Table of Rs: the Spearman Rank Correlation Coefficient for correlations between pollen and vegetation for key taxa and groups of taxa. The significance level indicated by *= p=0.05, **= p=0.01, ***= p=0.001. N/A: vegetation data not available.

Taxa	Rs (20m) pollen % TLP and vegetation as cover abundance	Rs (50m) pollen % TLP and vegetation as cover abundance	Rs (20m) vegetation cover % and pollen % as a % of total key vegetation types
Arboreal total	0.69***	0.65***	N/A
NAP total	0.24 (ns)	N/A	N/A
Heath Total	-0.006 (ns)	N/A	N/A
Pinus	0.82***	0.84***	-0.21 (ns)
Pinus stomata	0.72***	0.66***	N/A
Betula	0.77***	0.79***	-0.01 (ns)
Calluna	0.36*	N/A	0.69***
Poaceae	0.49**	N/A	0.57***
Cyperaceae	0.65***	N/A	0.69***
Potentilla-type	-0.1 (ns)	N/A	

5.5.2.5 Discussion

The sites selected to examine the pollen-vegetation relationship in Glen Affric show a gradation of canopy cover for *Pinus* and *Betula* (Table 5.7) and this gradation is evident via a visual inspection of the pollen diagram (Figure 5.4). Similar results were found by Caseldine (1981), and by other researchers although these studies were based on a transect away from a woodland stand and so differ from the situation in Glen Affric where woodland may surround the sites beyond the 50 m sampled radius at a variety of distances and directions.

The visual confirmation of the interpretation of woodland types in the pollen diagram is supported by the statistical significance of the rank correlations, which give confidence to the interpretation of fossil pollen data. The decrease in the significance of R_s at 50 m vegetation sample radius for *Pinus* stomata is consistent with results from other studies where stomata are found to be linked to vegetation cover within 20 m of the sample point (e.g. Dunwiddie 1987).

Simple percentage data presented above suggest that in general it is possible to make distinction between open and closed woodland at the stand scale in these small hollow sites, even in sites with an open or semi-open canopy. In addition, it is possible to determine heath dominated ground vegetation from Poaceae or Cyperaceae rich herb floras. However, the fluctuations in percentages of *Pinus* pollen and to some extent *Calluna* do not always match the fluctuations in vegetation and a substantial presence of these species occurs in each sample of the pollen diagram regardless of presence or absence within 50 metres radius of the sampling site.

Critical pollen percentages (Davis and Jacobson 1985) have been used to assess the local presence of trees; for *Pinus sylvestris* critical thresholds of 20% (Bennett 1984), or more recently 5% (Froyd 2001), have been suggested as a cut-off point for interpreting *Pinus* presence in the landscape. However, these values demonstrate the importance of consideration of scale in relation to conclusions about cut-off values. Bennett and Froyd are working at the landscape or local catchment scale for small lake sites, and are trying to elucidate the *appearance* of *Pinus* in the landscape. The source area for pollen recruitment into small lakes used in their studies will be much larger than that for this current stand-scale study in Glen Affric. Sugita (1994), determined that meaningful interpretations and pollen vegetation relationships could be gained from a small basin approach even if the local pollen comprised only *c.* 40% of the total pollen loading into the site. These initial results in Glen Affric confirm this approach and indicate a *c.* 50% cut-off value for *Pinus* pollen to interpret and reconstruct local woodland cover. whilst values of between 50% and 20% TLP may be attributable to trees lying within the wider catchment, but not within the local stand area, or to single trees within a 20 m proximity of the sample site.

What is less clear is the relationship between open and closed woodland at wider landscape scales. For example RRB is a site surrounded by a small dense stand of *Betula* and limited *Pinus* within the open landscape alongside Loch Affric. Similarly, RRP is within a small stand of *Pinus* in an open landscape matrix. These sites have a high arboreal pollen content of a similar proportion to that found at CLB, or CLNP, which are sites from the east end of the Glen surrounded by woodland well beyond the 50 m stand scale. Whilst background arboreal pollen can be high in open sites, as expected, background NAP pollen seems to have little effect on the pollen spectra from closed sites. Therefore, although it is possible to identify small stand scale openings (for example as around NHP where a patch opening to 20 m is identifiable by a reduction to 50% in the AP), and it is possible to identify woodland cover in the surrounding stand, it is difficult to distinguish between small isolated woodland remnants and wider landscape scale woodland. This demonstrates the need for the network approach.

In addition to the problems of spatial extrapolation, interpretation of community composition may also be limited by the sparseness of most indicative herbaceous taxa in the pollen record. Section 5.6.1, and the pollen diagram in Figure 5.1, demonstrate that for many taxa it is not possible to test a correlation between plant abundance and pollen occurrence. The next section will examine the rare type pollen for association with vegetation and will determine via this analysis, groups of pollen with similar productivities prior to the determination of pollen correction factors.

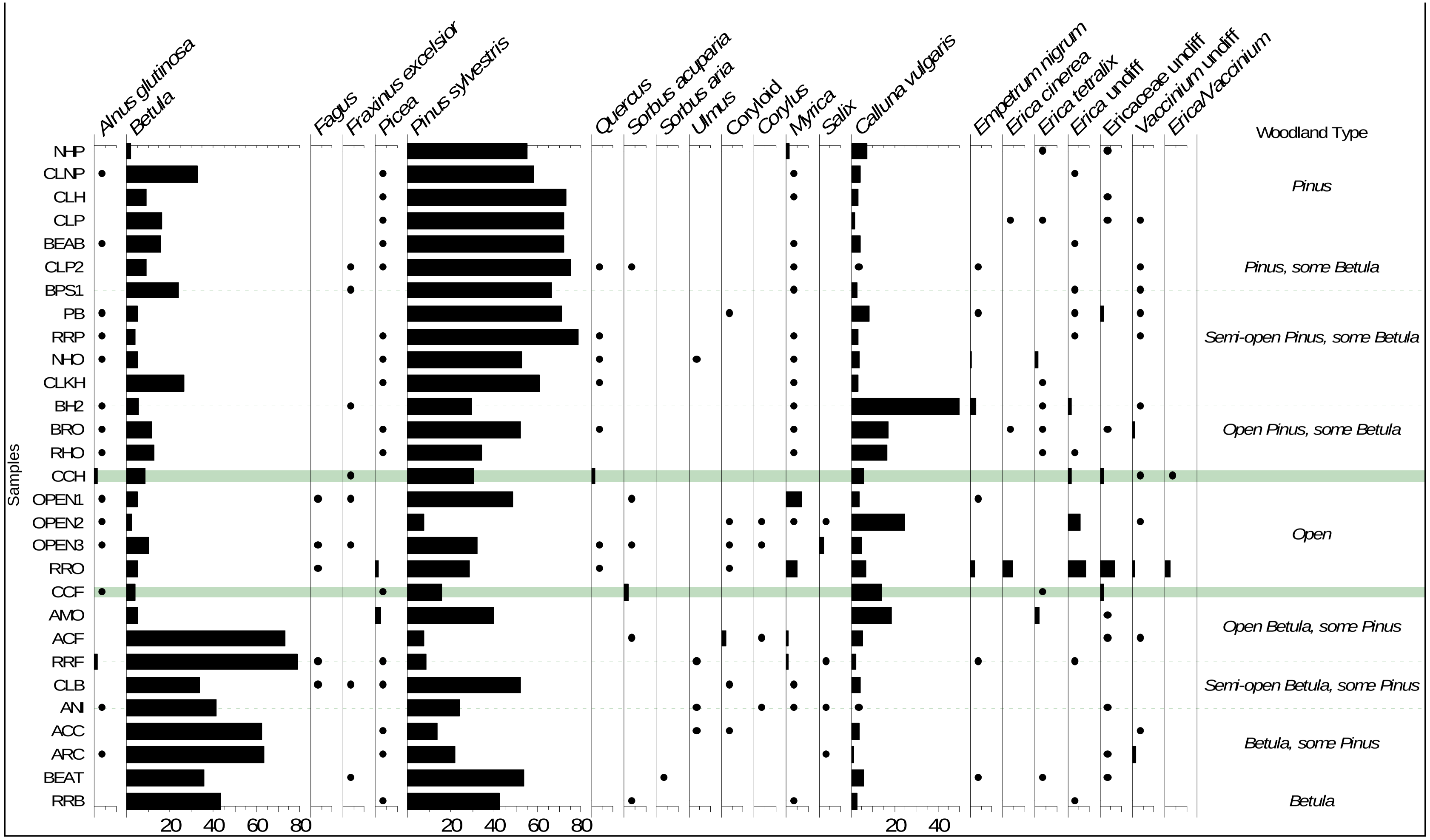


Figure 5.5: a) Trees, shrubs and heaths Pollen diagram for all palynomorphs in surface pollen samples. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Grain counts of taxa <1% are expressed as + symbols

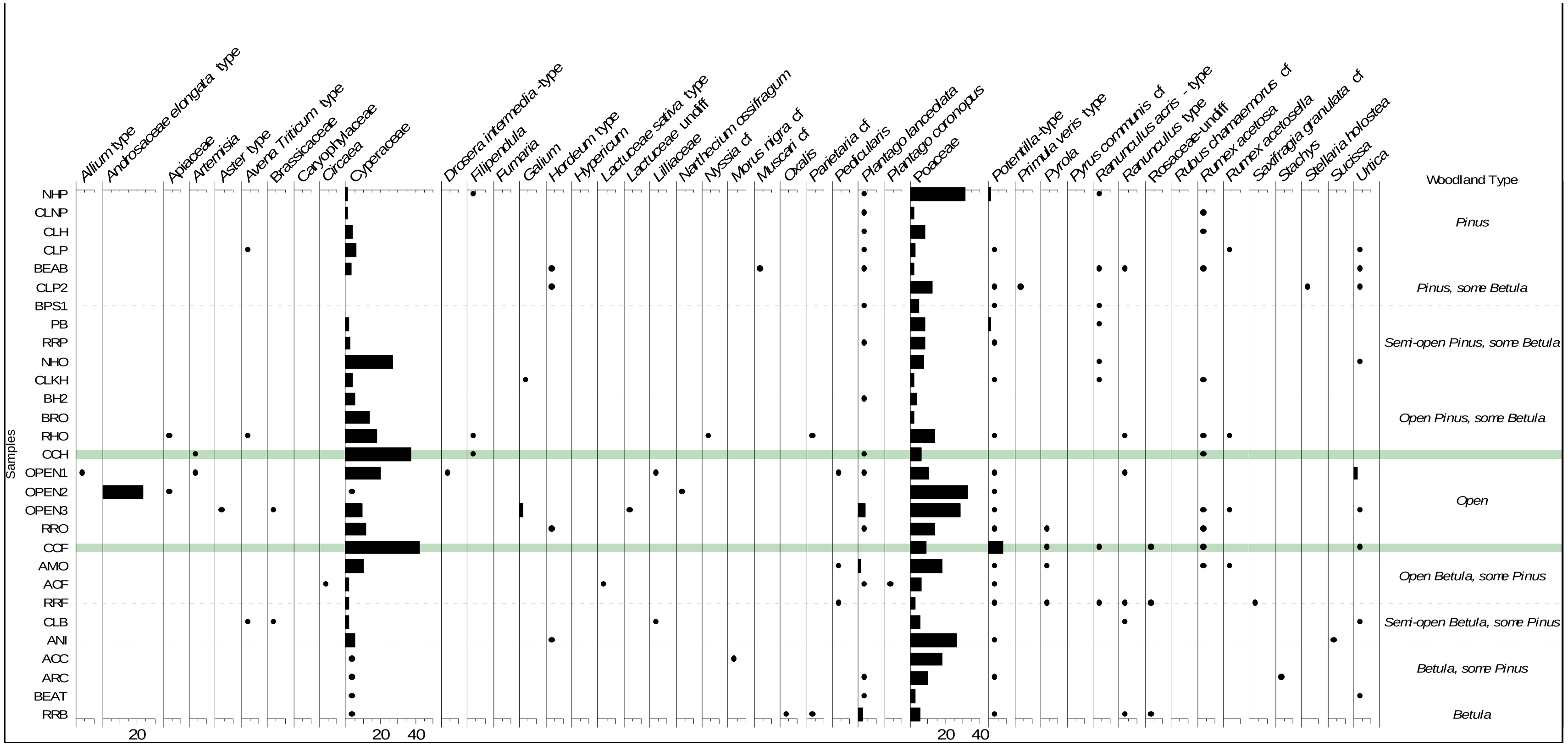


Figure 5.5: Continued: b) Herb taxa. Pollen diagram for all palynomorphs in surface pollen samples Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Grain counts of taxa <1% are expressed as + symbols

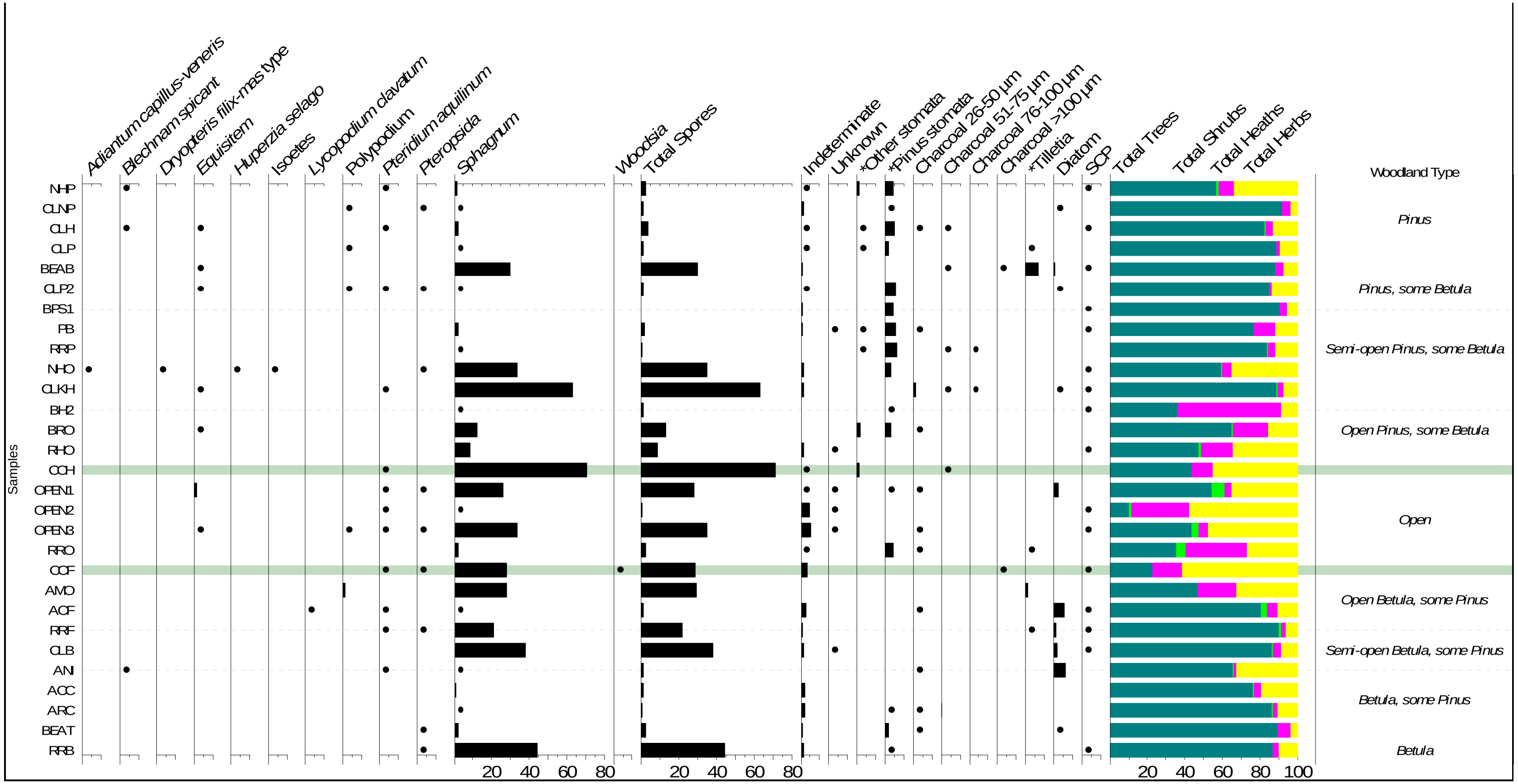


Figure 5.5: Continued: c) Spores, other palynomorphs and group totals. Pollen diagram for all palynomorphs in surface pollen samples. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Grain counts of taxa <1% are expressed as + symbols

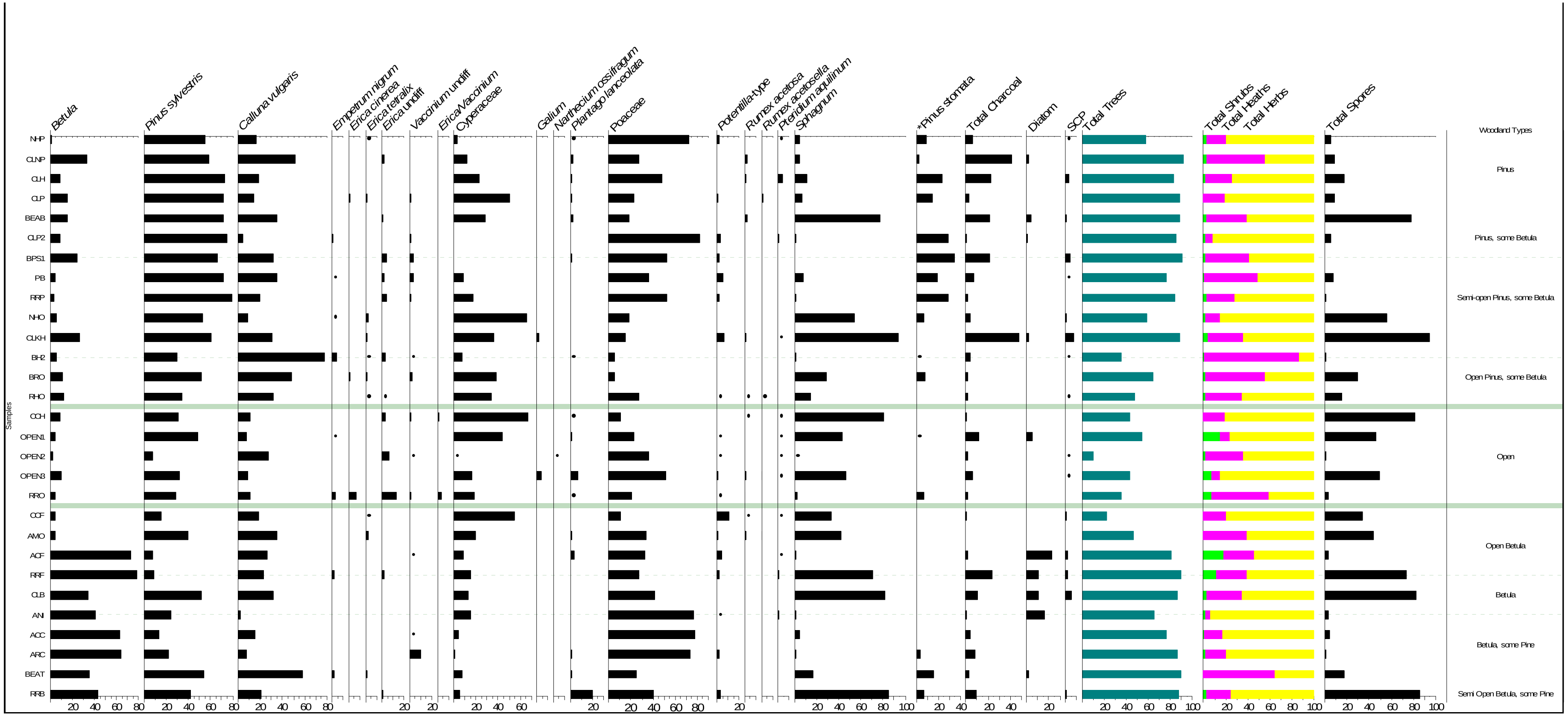


Figure 5.6: Pollen diagram of selected taxa for modern sites in Glen Affric. Tree Pollen as a percentage of TLP and al other taxa as a percentage of NAP.

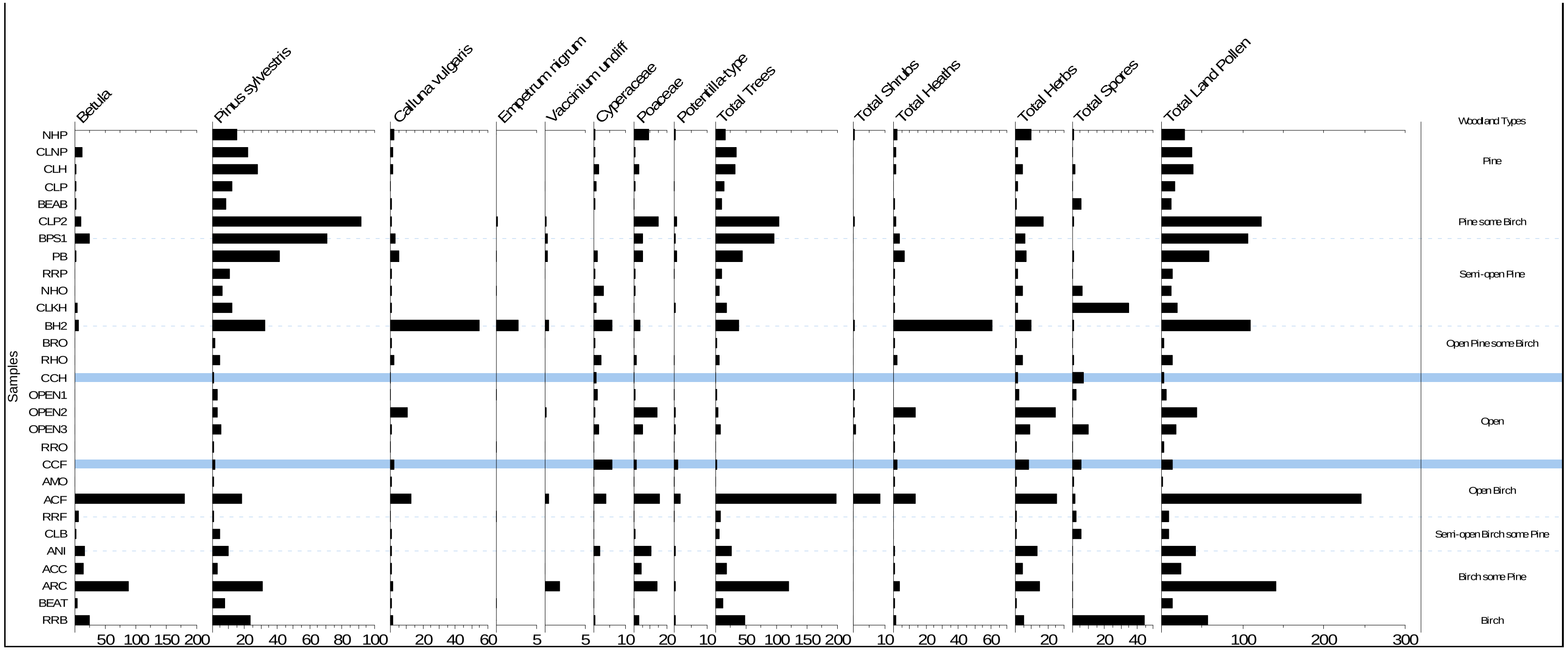


Figure 5.7: Pollen diagram for selected taxa from modern sites in Glen Affric. Pollen expressed as concentration data (cm-^{3}). For all taxa and groups, concentration is displayed as concentration x 10^{-3}. Note change of scale on some axis. Zones are determined by reference to Table 5.7

5.5.3 Representation of rare types by Indices of Association and the point biserial correlation coefficient

This section presents the results of the association analysis of pollen and vegetation data. Numerical data methods in this section are introduced in Section 5.3.9. The aims of this section are:

- To examine the over and under-representation of rare taxa and to compare this with other studies.
- To separate rare taxa into groups based on over and under-representation for group regression analysis.

5.5.3.1 Results

Results from the IOA and the Point-Biserial Correlation Coefficient R_{pb} for the Glen Affric dataset are presented in Table 5.9. IOA scores provide a measure of association; however, cut-off scores for determination of strength of association are somewhat subjective. Cut-off values used in other studies for delimiting strength of association from the IOA scores are presented in Table 5.10 together with cut-off values selected for use on the Glen Affric dataset.

Taxa where the R_{pb} is marked as N/A are those where that pollen taxa was found in every surface sample; the Point-biserial method cannot calculate an R_{pb} when there are no binary absence data. These taxa are suitable for least squares regression the results of which are presented in Section 5.6.4.3 below.

Comparisons of the results of the IOA analysis for Glen Affric with the results of other IOA analysis; in Norway (Hjelle 1997); Northern Scotland (Bunting 2003); and, France (Mazier *et al.* 2006); are presented in Table 5.11.

The strongest association is found between plants and pollen of the Asteraceae family. The R_{pb} correlation coefficient is highly significant as out of the 29 sites, only one site contains the plant and this same site is the only sample to contain Asteraceae pollen. In contrast Bunting (2003) finds no association for Asteraceae. Other strongly associated taxa in the Glen Affric dataset are Poaceae, *Calluna*, *Pinus* Stomata, *Erica*/*Vaccinium* as a combined count, and

Cyperaceae. Poaceae is also strongly associated in the results of all other studies listed in Table 5.10 whereas Cyperaceae and *Calluna* show variation.

Pinus pollen and *Pinus* stomata both fall into the associated category. *Pinus* pollen is capable of long distance transport and so should be over-represented. The O value of 0.31 supports this and shows that although *Pinus* Pollen is associated it tends towards over-representation; whilst, in contrast, *Pinus* stomata although categorised as an associated taxon has a high U score thus tending to under-representation. This demonstrates the value of interpreting *Pinus* presence through a combination of the results of counts of *Pinus* pollen and *Pinus* stomata. *Pinus* stomata and vegetation also show a significant R_{pb} correlation indicating that where the *Pinus* canopy is denser, stomata are more likely to be present.

Other associated taxa are *Betula*, *Erica* undiff. (encompassing both *E. cinerea* and *E. tetralix*) and *Potentilla*-type. *Potentilla* is also found to be an associated type in the Pyrenees (Mazier *et al*. 2006), although a strong association for this taxon is found in the Norway and Northern Scotland studies (Table 5.11).

Weakly associated types in the Glen Affric study can be separated into three groups. *Sorbus*, and *Myrica*, which have high O values and therefore tend to over-representation, and *Vaccinium*, *Erica tetralix* and *Empetrum nigrum*, which have slightly higher A and U values and so tend to be weakly associated or under-represented in the vegetation. Some of these taxa have contrasting values at other sites, with *Vaccinium* showing association or strong association between pollen and plant presence, whilst *Myrica gale* shows under-representation in the Pyrenees samples (Table 5.11) rather than the tendency to over-representation shown in the Glen Affric sites.

Alnus glutinosa, Quercus, Plantago and *Rumex* are over-represented occurring in the pollen record more frequently than in the vegetation. For Plantago and Rumex this is in agreement with the findings of Bunting (2003) in Assynt but not with those of Hjelle (1997) in the cultural landscape of western Norway, although the heathland samples from the Norway dataset show similar results.

Several taxa were unsuitable for analysis, as they did not have a presence in both the pollen and plant record (Section 5.5.1 and Tables 5.3 – 5.6). *Melampyrum* is locally present in some of the sample sites and appears regularly in the fossil record in the eight Glen Affric cores; it is found to have a good association in Norway (Hjelle 1997), but, in contrast, no pollen is found in the surface samples from Glen Affric. *Viola* sp. are found by Hjelle to be absent from the pollen record in Norway despite local presence in the field and, similarly, lack pollen presence in Glen Affric.

Table 5.11 also contains the A, O and U values from the Norway, France and Scotland datasets for taxa which appear in Glen Affric, but were not suitable for IOA analysis. These data may be useful in the interpretation of pollen from these taxa in the fossil record, although the lack of agreement in category of association between some taxa in the Glen Affric dataset and the other studies compared in Table 5.11 indicates that any use in interpretation should be treated with caution.

Table 5.9: Indices of Association and the Point Biserial Correlation Coefficient applied to taxa in Glen Affric present in both plant and pollen data. (A) – Indices of Association; (U) – Taxon is under-represented by pollen data; (O) – Taxon is over-represented by pollen data. When U and O both = 1 there is no association.

	A	U	O	R_{pb}	t	Sig. level *=p=0.05 **=p=0.001 for 27 df
Strongly Associated Types	**A>0.75**					
Aster type	1.00	0.00	0.00	0.98	27.50	**
Poaceae	0.97	0.00	0.03	n/a	n/a	n/a
Calluna vulgaris	0.93	0.00	0.07	n/a	n/a	n/a
Erica/Vaccinium	0.89	0.04	0.07	0.22	1.19	not sig
Cyperaceae	0.78	0.00	0.22	0.22	1.19	not sig
Associated Types	**A=0.5-0.75**					
Pinus sylvestris	0.69	0.00	0.31	n/a	n/a	n/a
Erica undiff.	0.65	0.17	0.25	0.20	1.08	not sig
Betula	0.59	0.00	0.41	n/a	n/a	n/a
Pinus stomata	0.64	0.30	0.13	0.51	3.08	**
Potentilla-type	0.54	0.38	0.21	0.16	0.83	not sig
Weakly Associated	**A<0.5; O is high; U is high**					
Sorbus aucuparia	0.25	0.33	0.71	0.38	2.15	*
Myrica gale	0.24	0.17	0.75	0.21	1.12	not sig
Salix	0.14	0.67	0.80	0.01	0.03	not sig
Vaccinium undiff.	0.42	0.52	0.23	0.12	0.64	not sig
Erica tetralix	0.40	0.56	0.20	0.21	1.11	not sig
Empetrum nigrum	0.33	0.58	0.38	0.09	0.46	not sig
Under-Represented Types	**A<0.5; O=0; U is high**					
Drosera intermedia-type	0.33	0.67	0.00	n/a	n/a	n/a
Oxalis	0.25	0.75	0.00	0.01	0.07	not sig
Over-Represented Types	**A<0.5; O is high; U=0**					
Rumex acetosa	0.18	0.00	0.82	0.25	1.34	*
Quercus	0.14	0.00	0.86	0.33	1.81	*
Alnus glutinosa	0.06	0.00	0.94	0.17	0.88	not sig
Plantago lanceolata	0.06	0.00	0.94	0.16	0.82	not sig
No Association	**A=0 O is high; U is high**					
Corylus	0.00	1.00	1.00	0.07	0.39	not sig
Erica cinerea	0.00	1.00	1.00	n/a	n/a	n/a
Gallium	0.00	1.00	1.00	0.12	0.63	not sig
Lactuceae undiff.	0.00	1.00	1.00	n/a	n/a	n/a
Narthecium ossifragum	0.00	1.00	1.00	0.11	0.58	not sig
Pyrola	0.00	1.00	1.00	0.10	0.54	not sig
Ranunculus type	0.00	1.00	1.00	0.16	0.82	not sig
Succisa	0.00	1.00	1.00	0.05	0.24	not sig

Table 5.10: Cut-off points for IOA from different studies and cut-off points selected for the Glen Affric dataset used in Table 6.6 above.

	Bunting (2003)	**Mazier *et al.* (2006)**	**Glen Affric Dataset**
Strongly Associated Taxon	A>0.75	A>0.65	A>0.75
Associated Taxon	A=0.5-0.75	A=0.5-0.65	A=0.5-0.75
Over Represented	A<0.5; O is high; U=0	A<0.5; O is high; U=0	A<0.5; O is high; U=0
Weakly Associated	A<0.5; O is high; U is high	A<0.5; O is high; U is high	A<0.5; O is high; U is high
Under-Represented		A<0.5; O=0; U is high	A<0.5; O=0; U is high
Unassociated	A=0 O is high; U is high	A=0 O is high; U is high	A=0 O is high; U is high

Table 5.11: Comparison of Indices of Association between the Glen Affric dataset and published datasets from Hjelle (1999), Bunting (2003) and Mazier *et al.* (2006). SAT = Strongly Associated Taxon; AT = Associated Taxon; WAT = Weakly Associated Taxon; ORT = Over-Represented Taxon; URT = Under-Represented Taxon; NA = No Association. IOA scores are highlighted in bold red where their IOA score disagrees with that from Glen Affric. Additional Results from Taxa not in the Glen Affric IOA dataset are presented at the base of the table.

Pollen Type	**Glen Affric**			**Hjelle (1997)**									**Bunting (2003)**				**Mazier *et al*. (2006)**			
				Norway									**Assynt-Coigach, Northwest Scotland**				**Pyrenees Mountains (France)**			
				Comb	**Meadow Pasture Dataset**				**Heath Dataset**				**Open landscape with patchy woodland**				**Grazed pasture vegetation**			
	A	**U**	**O**		**A**	**U**	**O**		**A**	**U**	**O**		**A**	**U**	**O**		**A**	**U**	**O**	
Strongly Associated Types A>0.75																				
Asteraceae	1	0	0										**0**	**1**	**1**	**UT**				
Poaceae	0.97	0	0.03	SAT									0.86	0	0.14	SAT	0.96	0.01	0.03	SAT
Calluna vulgaris	0.93	0	0.07		**0.09**	**0**	**0.91**	**ORT**	1	0	0	SAT	0.81	0	0.19	SAT	**0.58**	**0.12**	**0.38**	**AT**
Erica/Vaccinium	0.89	0.04	0.07																	
Cyperaceae	0.78	0.00	0.22		**0.39**	**0.13**	**0.58**	**WAT**	1	0	0	SAT	0.62	0.27	0.20	AT	0.73	0.1	0.2	SAT
Associated Types A=0.5-0.75																				
Pinus sylvestris	0.69	0.00	0.31																	
Erica undiff	0.65	0.17	0.25																	
Betula	0.59	0.00	0.41																	
Pinus stomata	0.55	0.45	0.00																	
Potentilla-type	0.54	0.38	0.21	**SAT**	0.61	0.1	0.35	AT	**1**	**0**	**0**	**SAT**	**0.97**	**0**	**0.03**	**SAT**	0.67	0.16	0.23	AT
Weakly Associated A<0.5; O is high; U is high																				
Sorbus	0.25	0.33	0.71														**0.11**	**0.89**	**0**	**URT**
Myrica gale	0.24	0.17	0.75										**0.6**	**0.32**	**0.17**	**AT**				
Vaccinium-type	0.42	0.52	0.23		**0.6**	**0.64**	**0.94**	**AT**	**0.87**	**0.07**	**0.07**	**SAT**	**0.78**	**0.05**	**0.19**	**SAT**				
Erica tetralix	0.40	0.56	0.20														0.16	0.82	0.44	WAT
Empetrum nigrum	0.33	0.58	0.38																	
Salix	0.14	0.67	0.80																	

Table 5.11 continued:

Pollen Type	Glen Affric				Hjelle (1997)								Bunting (2003)				Mazier *et al*. (2006)			
					Norway								Assynt-Coigach, Northwest Scotland				Pyrenees Mountains (France)			
				Comb	Meadow Pasture Dataset				Heath Dataset				Open landscape with patchy woodland				Grazed pasture vegetation			
	A	U	O		A	U	O		A	U	O		A	U	O		A	U	O	
Under-Represented Types A<0.5; O=0; U is high																				
Drosera intermedia-type	0.33	0.67	0.00																	
Over-Represented Types A<0.5; O is high; U=0																				
Rumex	0.18	0.00	0.82	**SAT**	**0.78**	**0.02**	**0.21**	**SAT**	0.13	0	0.81	ORT	0.09	0	0.91	ORT	**0.28**	**0.25**	**0.69**	**WAT**
Quercus	0.14	0.00	0.86														0.08	0	0.92	ORT
Alnus glutinosa	0.06	0.00	0.94																	
Plantago lanceolata	0.06	0.00	0.94	**SAT**	**0.7**	**0.01**	**0.29**	**SAT**	0.42	0	0.58	ORT	0.19	0	0.81	ORT	0.06	0	0.94	ORT
No Association A=0 O is high; U is high																				
Corylus	0.00	1.00	1.00																	
Erica cinerea	0.00	1.00	1.00																	
Galium	0.00	1.00	1.00		**0.51**	**0.17**	**0.43**	**AT**	**0.83**	**0**	**0.17**	**SAT**					**0.72**	**0.22**	**0.1**	**SAT**
Asteraceae (Lactuceae)	0.00	1.00	1.00	**SAT**									0.3	0.67	0.25					
Narthecium ossifragum	0.00	1.00	1.00										0.38	0.4	0.5					
Pyrola	0.00	1.00	1.00																	
Ranunculus acris-type	0.00	1.00	1.00	**SAT**	**0.69**	**0.12**	**0.24**	**AT**	0	1	1	NA	**0.3**	**0**	**0.7**	**ORT**	**0.2**	**0.2**	**0.79**	**WAT**
Succisa pratensis	0.00	1.00	1.00		**0.52**	**0.17**	**0.42**	**AT**	**0.8**	**0.2**	**0**	**SAT**	**0.5**	**0**	**0.5**	**ORT**				

Table 5.11 continued:

Pollen Type	Glen Affric			Hjelle (1997)									Bunting (2003)				Mazier *et al*. (2006)			
				Norway									Assynt-Coigach, Northwest Scotland				Pyrenees Mountains (France)			
				Comb	Meadow Pasture Dataset				Heath Dataset				Open landscape with patchy woodland				Grazed pasture vegetation			
	A	U	O		A	U	O		A	U	O		A	U	O		A	U	O	
Additional data from other Taxa not in Glen Affric IOA Dataset																				
Apiaceae				**SAT**									0.1	0	0.9	**ORT**	0.23	0.44	0.71	**WAT**
Geum													0.38	0	0.67	**ORT**				
Brassicaceae																	0.06	0	0.94	**ORT**
Cirsium-type													0.2	0.67	0.67	**WAT**				
Fagus																	0.38	0	0.62	**ORT**
Filipendula													0.13	0.33	0.86	**WAT**				
Polygala				**URT**													0.03	0.97	0.50	**WAT**
Primula veris													0.25	0.5	0.67	**WAT**				
Pteridium aquilinum				**WAT**									0.11	0.8	0.8	**WAT**	0.2	0.61	0.71	**WAT**
Rubiaceae													0.4	0	0.6	**WAT**				
Stellaria-type																	0.33	0.47	0.53	**WAT**
Trifolium				**SAT**													0.06	0.93	0.80	**WAT**
Urtica dioica																	0.05	0	0.95	**ORT**
Achillea-type													0	1	1	**NA**				
Anagallis																	0	1	1	**NA**
Centaurea jacea/nigra																	0	1	1	**NA**
Fabaceae													0	1	1	**NA**				
Fabaceae																	0	1	1	**NA**
Ilex																	0	1	1	**NA**
Labiatae																	0	1	1	**NA**
Lotus-type				**WAT**													0	1	1	**NA**
Pedicularis													0	1	1	**NA**				
Pteropsida													0	1	1	**NA**				

5.5.3.2 Discussion of association of rare types

Taxa which appear as pollen in all of the sites and as vegetation in all of the sites fall into the SAT groups; e.g. Poaceae and *Calluna*. However, testing for over-representation of these taxa would require more sample sites where these taxa are not present in the vegetation to test if they still appear in the pollen record. *Pinus* and *Betula* also appear in all of the pollen samples and most of the vegetation. They both show some over-representation as expected for these highly dispersed taxa. The point-biserial correlation is not appropriate to these taxa. These frequent taxa are better suited to examination by correlation.

For other common types within the SAT and AT categories, e.g., Cyperaceae, *Erica* and *Potentilla* although over 50% of the samples that contained pollen also contained vegetation in the surrounding sites the R_{pb} was not significant. This demonstrates that there was not a consistent difference in the quantity of vegetation when pollen was present, to that when pollen was absent. The R_{pb} also demonstrates that the measure of association for these taxa may not be significant. The R_{pb} therefore provides useful supplementary information to the IOA analysis.

The only strongly associated rare type taxon in the Glen Affric dataset is *Aster*-type, this taxa also shows a very significant value of R_{pb} this is because it only has one occurrence in the plant and one occurrence in the pollen data, and these occur in the same site.

In the AT category the R_{pb} value for *Pinus* Stomata is also very significant. This helps to clarify the A and U values for this taxon. The significant R_{pb} indicates that although several of the sites with *Pinus* trees have no stomata present, thus resulting in a positive U value, these sites tend to have a lower abundance of *Pinus* in the vegetation than those with stomata present.

Many taxa traditionally used in the interpretation of pollen diagrams demonstrate either no association, or, a high over-representation e.g. *Rumex*, *Plantago*. Comparison with the results from other studies in Table 5.11 reveals some disagreement in the degree of over-representation between studies. The lack of association between many rare pollen taxa traditionally used by pollen analysts as indicator species is important. For example *Plantago lanceolata* is generally interpreted as a ruderal species or one of grazed landscapes that indicate human agricultural or pastoral activity. This is confirmed by the strong association in the pasture samples from Norway (Table 5.11). However, in heathland vegetation from Norway, and Scotland and in the samples from the Pyrenees *P. lanceolata* shows a high over-representation, which agrees with a previous Scottish study at Bankhead Moss in Fife (Caseldine 1981). Cultural and environmental indicator taxa must therefore be treated with caution when present in low numbers in the pollen record (Bunting 2003; Mazier *et al*. 2006).

Mazier *et al*. (2006) also compared IOA analysis across datasets and discovered variation. Variation can be due to several factors:

1. Vegetation sampling technique varies between the studies (Mazier *et al*. 2006): This could affect the likelihood of detecting rare herbaceous taxa in the vegetation community.
2. Vegetation sampling radius differs between studies: High over-representation indicates an inadequate source area (Bunting 2003).
3. Total pollen counts vary between the studies: Increasing pollen count levels could increase the chance of finding rare pollen taxa and therefore increase the association for some taxa. The pollen counts over the studies compared in Table 5.11 varied from >400 grains (Mazier *et al*. 2006) to *c*. 1-2000 grains (Hjelle 1997).
4. A pollen taxon could represent different plant species in different areas (Hjelle 1997; Bunting 2003; Mazier *et al*. 2006): Different plant species with different pollen dispersal characteristics are grouped under the same pollen taxon due to lack of differentiation to species-level (e.g. *Ranunculus*-type is variously Ranunculaceae or *Ranunculus acris*-type).
5. A weak association may indicate far travelled pollen but may also indicate the mismatch in the temporal sampling scale between vegetation survey (usually a discrete point in time) and pollen survey, (with sub-sample representing several years pollen accumulation).

5.5.3.3 Conclusions on use of IOA and the point biserial method

The different results between studies may indicate site specific pollen dispersal factors for IOA as for R-value analysis (*sensu* Bradshaw 1981). Testing the association between plant and taxon can add weight to some of the fossil pollen interpretations, but for many taxa, with low or no association it merely highlights difficulties of interpreting detailed ecological information from the fossil pollen sequences.

This part of the Glen Affric modern study contributes to a growing dataset of evidence for pollen-vegetation relationships, but the lack of association for many taxa highlights a requirement for further study with larger datasets. Improvements might also be gained by seasonal and yearly vegetation surveys, representing the temporal span of the pollen sample, and by larger pollen counts to incorporate more rare taxa. In a three year study, collection of vegetation for the three years and pollen sampling in the third year would be an appropriate course of action, but would be time consuming.

The point-biserial correlation coefficient method highlights the lack of significance in the association scores for many taxa and provides a useful additional tool for the analysis. The lack of significance for many of the R_{pb} correlations for taxa in Glen Affric also highlights the need for increased datasets in the study of modern pollen-vegetation relationships.

In total, 19 taxa were suitable for IOA analysis out of a total of 63 pollen and 94 plant and pollen taxa present in the dataset. Of these 19 taxa five displayed a significance to the relationship defined by the IOA analysis. Although limited, the method does allow definition of the possible limits of pollen-vegetation interpretations based on rare pollen types. The herbaceous taxa data can be interpreted with an understanding of ecological life-histories and inferences of community groupings where presence of indicative taxa may confirm the likelihood of local presence of others. However, this approach assumes some longevity of community groupings, which argues against the non-equilibrium theory in ecology and therefore these arguments soon become circular when pollen investigation is testing community dynamics.

The information gained on the relationship between pollen and vegetation for rare types will prove useful in the fossil pollen interpretations and could be used to weight taxa in the ordination analyses in Section 5.7.

5.5.4 Relevant pollen source area and pollen correction factors for key taxa

This section uses ratio, regression and maximum likelihood approaches to determine pollen source area, pollen correction factors and background pollen loading for key taxa and pollen groups. The aims of this section are;

- To test the relevant pollen source area around small hollows in relatively open-canopy *Pinus* dominated woodland.
- To test for differences in RSAP between open and closed canopy sites.
- To determine PPEs (a) and background components (z) for the pollen of key taxa for use in the ordination analysis and fossil pollen study.

5.5.4.1 Regression analysis

Linear least squares regression and Pearsons product moment correlation is applied to key taxa at each vegetation sampling radius. r^2 values are plotted against ring source distance for each taxon. The point at which the r^2 plot reaches an asymptote defines the RSAP for that pollen taxon (Sugita 1994).

Distance weightings 1/d and $1/d^2$ and unweighted vegetation are compared. Pollen taxa as percentage TLP, NAP/AP and percentage of key taxa group are compared for key taxa in figures 5.9 – 5.13. The background pollen factor (intercept) and pollen correction factor (slope) are displayed for each taxon for the selected pollen-vegetation model in Table 5.12.

The key taxa group was limited to *Pinus*, *Betula*, *Calluna*, Poaceae, and Cyperaceae. The herbaceous taxa *Potentilla* was present in several samples, and an attempt was made to carry out the regression with the inclusion of this taxon. However, *Potentilla* showed no significant correlation between pollen and vegetation and so was removed from the analysis. Regression and correlation of *Pinus* stomata is also implemented. Regressions are compared using both plant abundance *sensu* ERV model 3 (Sugita 1994) and plant presence as a proportion of the cover of the key taxon group ERV models 1 and 2 (*sensu* Prentice and Parsons 1983) and Equation 5.5.

The linear regression method does not correct for the Fagerlind effect as the more powerful Extended R-value (ERV models of Prentice and Sugita (Prentice and Parsons 1983; Prentice 1985; Prentice and Webb 1986; Sugita 1994; Sugita 1998; and see Section 5.2). However, the application of a regression on the data from individual taxa allows an examination of residuals, and outliers and the examination of pollen source areas for individual taxa. This may be important when developing correction factors for both tree and ground flora taxa.

Regression and correlation of key taxa and *Pinus* stomata based on pollen percentages and vegetation cover are presented for unweighted and distance weighted vegetation data (1/d and 1/d^2) as it is not clear whether distance weighting is applicable to vegetation within a local source area (Section 5.1.2.4).

5.5.4.1.1 Pinus stomata – regression and correlation results

The presence of high pine pollen values shows association and correlation with pine presence local to the sampling site. However, with pollen percentage values up to *c.* 50% TLP where no local *Pinus* trees are present *Pinus* stomata can be key to distinguishing local presence of *Pinus* (e.g Froyd 2005). r^2 values for correlation between *Pinus* stomata (as a percentage of TLP) and *Pinus* cover data to each ring radius are presented in Figure 5.8 for three different distance weightings.

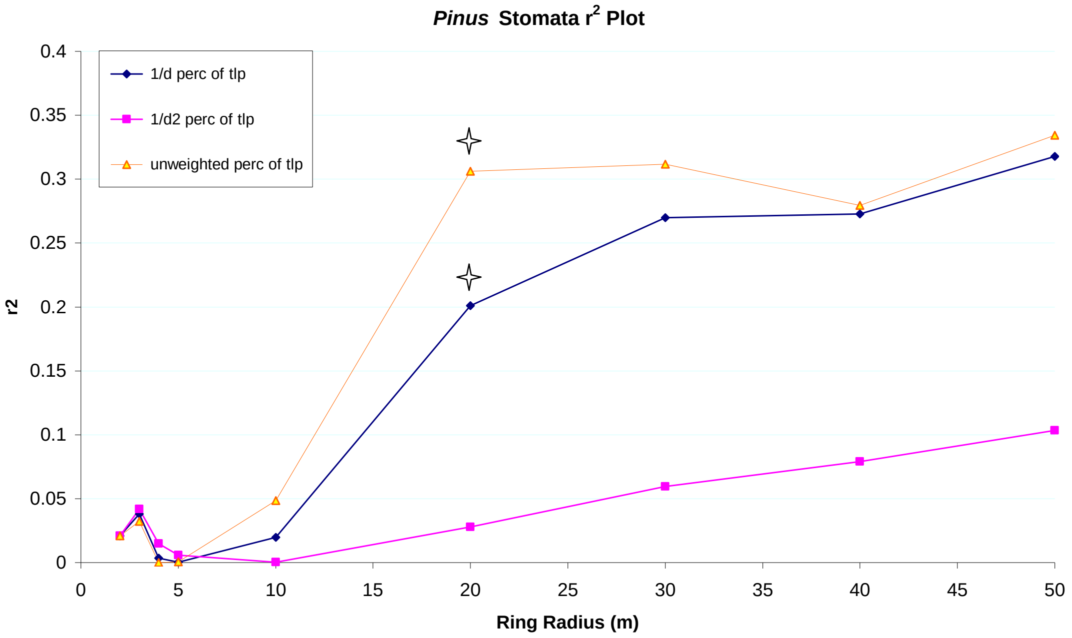


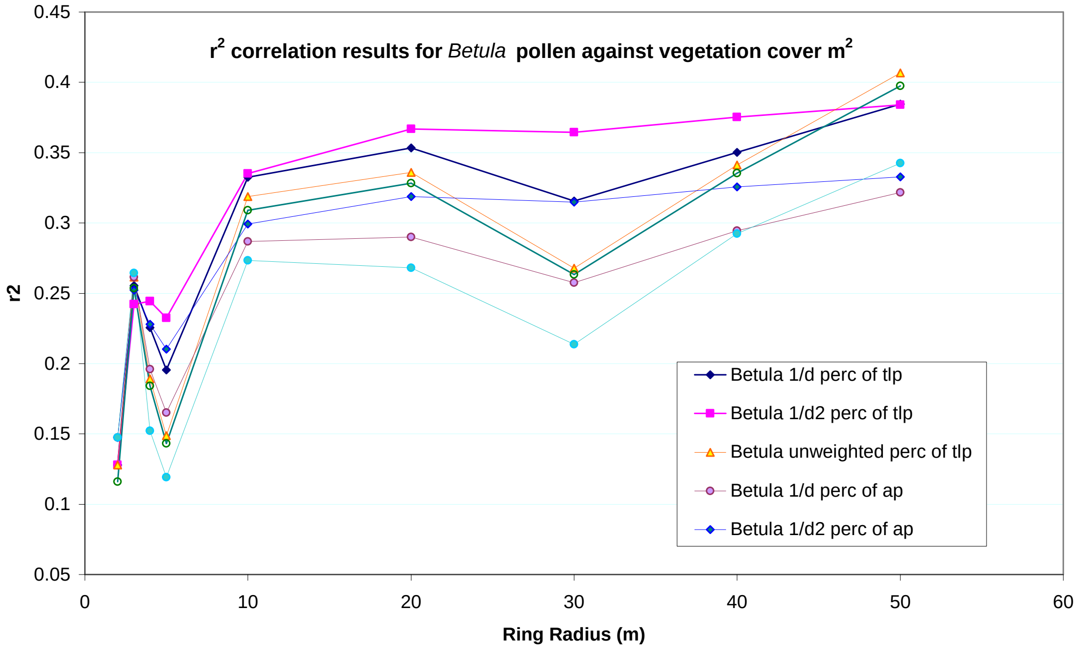
Figure 5.8: Plots of r^2 for *Pinus* Stomata data (stomata as a % of TLP) against *Pinus* cover under three distance weightings (see legend) from the modern pollen samples in Glen Affric. Stars indicate the point at which the correlation is significant.

The $1/d^2$ distance weighting is presumed to be the most similar to the leptokurtic pollen dispersal curve (Calcote 1995; Section 5.2.1.4). In the small sampling radii of Glen Affric however, the rapid attenuation with distance that is bestowed upon the vegetation data by the small ring radii may not be appropriate, especially for tree taxa. The $1/d^2$ distance weighted regressions do not produce a significant r^2 between stomata and vegetation at any of the sampled radii. Stomata correlations against the unweighted and 1/d distance weighting are significant from the 20 m radius. Both curves show a change of direction and flattening from the 20 m radius, and may show an asymptote. However, it is unclear if there may be further increases in r^2 at larger vegetation sampling radius and the $1/d^2$ does indicate this possibility as an asymptote is not reached. The erratic nature of the curve within the 5 m radius of the sample site is probably due to an inappropriate sampling radius for arboreal taxa, which may be smaller than the overhanging tree canopy. The small initial radii were selected to test the RSAP in the ground flora.

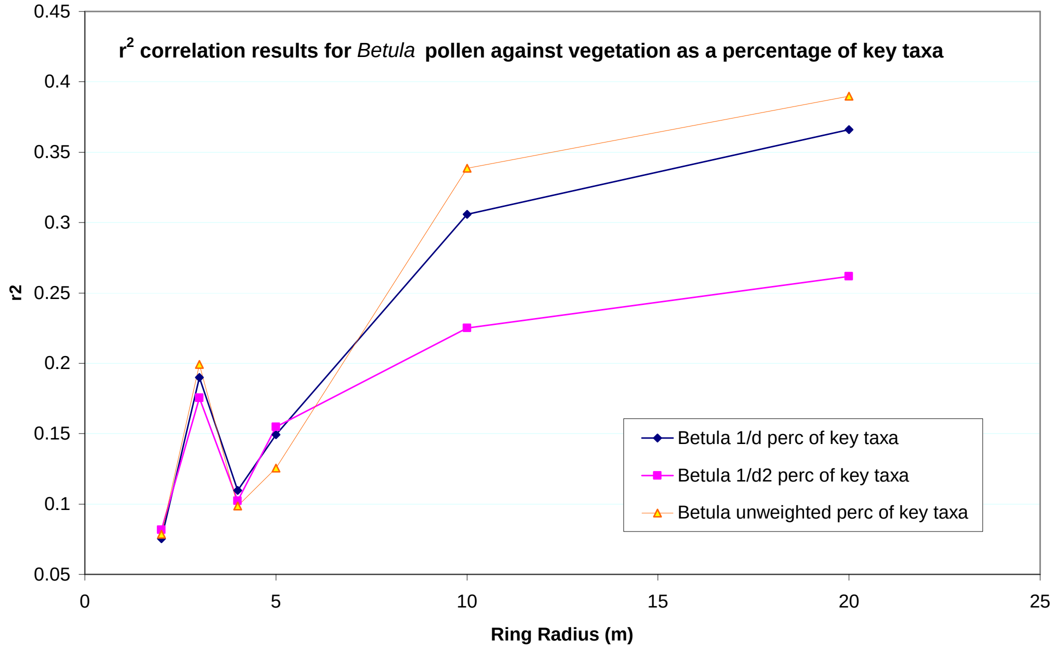
5.5.4.1.2 Betula – regression and correlation results

Figure 5.9 shows various r^2 plots for *Betula*. In all variations of the pollen-vegetation correlation, a significant correlation between the pollen and vegetation abundance surrounding the sample site is gained at 10 m. *Betula* presence as $1/d^2$ dwpa against pollen as a percentage of TLP returns the highest r^2 values and, therefore, the most significant regression results when correlated against vegetation cover. However, when correlated against the proportion of vegetation from the key taxa group $1/d^2$ is the least significant correlation. Between 30-50 m the change in r^2 ($1/d^2$ weighting, and 1/d weighting) for *Betula* is less than 0.01 therefore the Relevant Pollen Source Area for *Betula* in the sites in Glen Affric is likely to be between 40 and 50 m.

Several correlations show a dip to a lower r^2 value at 30 m; this is less evident on the $1/d^2$ distance weighted curve. The dip is probably due to a sampling anomaly. A range of vegetation cover at each radius is required to smooth out data points. It is possible that a distance 30 m from the basin centre may constitute a radius of increased tree growth around these small basins.



a)



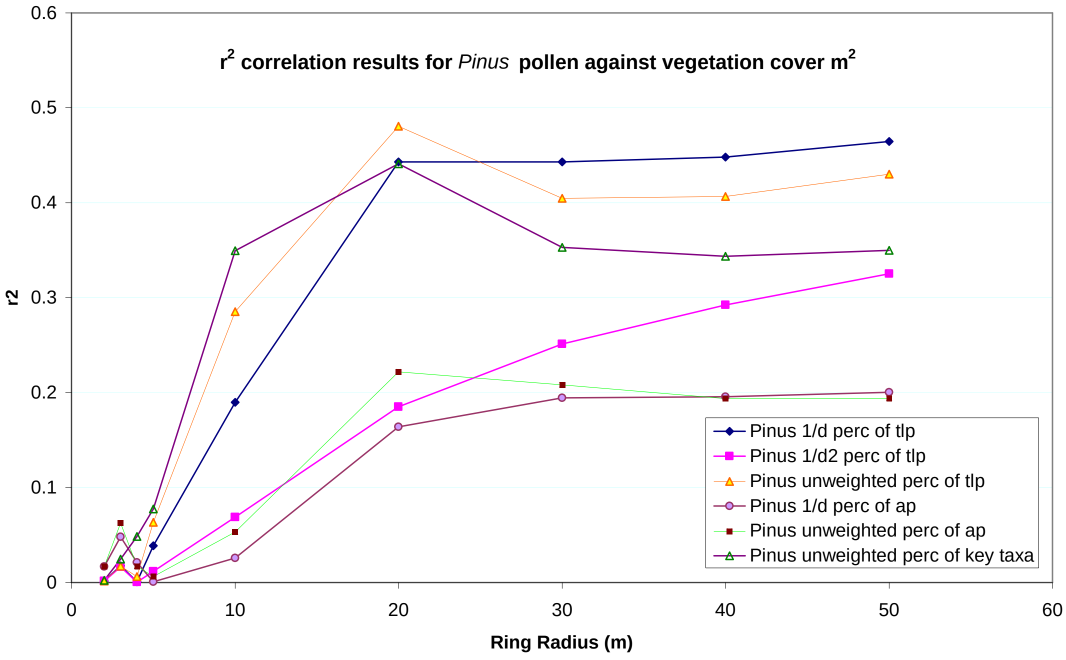
b)

Figure 5.9: Plot of associated r^2 values against distance for three different distance weightings against TLP and AP pollen percentages. For vegetation as cover in m^2 (a) and as a percentage cover of total area (b).

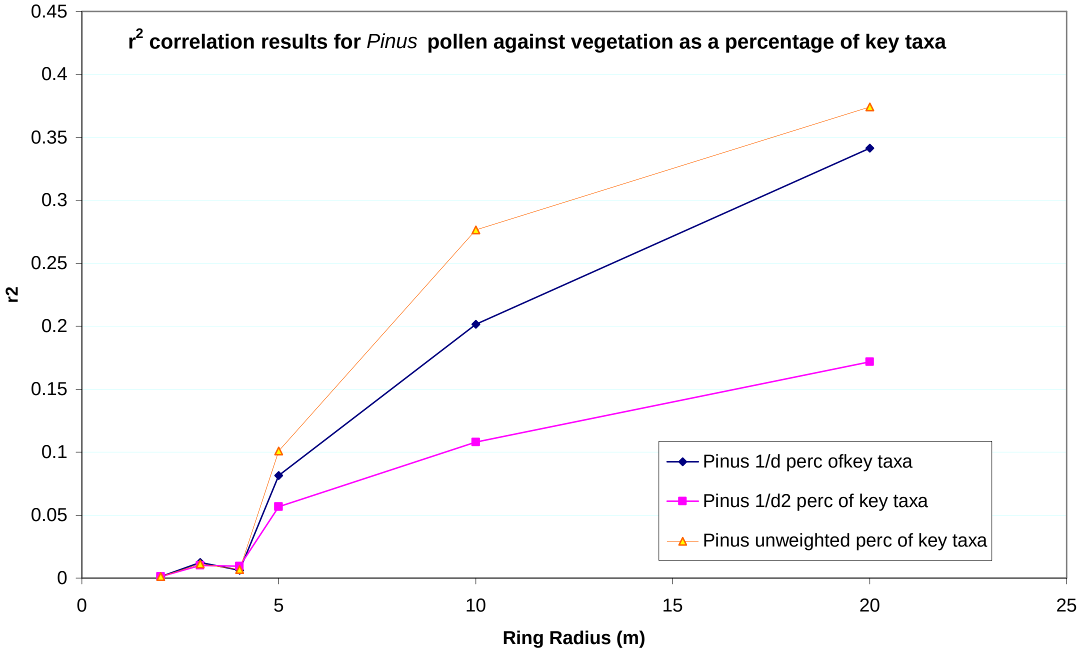
5.5.4.1.3 Pinus sylvestris – regression and correlation results

Figure 5.10 shows various r^2 plots for *Pinus*. In all variations of the pollen-vegetation correlation using TLP% as the pollen variable consistent significance between the pollen and vegetation abundance surrounding the sample site is gained at 10 m. For correlations using AP% the correlations are significant at the 20 m radius and the significance of the correlation at all radii is less than that for the TLP% correlations. *Pinus* presence as 1/d dwpa against pollen as a percentage of TLP returns the highest r^2 values and therefore the most significant regression results when correlated against vegetation cover, however when correlated against the proportion of vegetation from the key taxa group the unweighted vegetation data has a slightly higher r^2 value. All correlations in Figure 5.10a show an asymptote at 20 m radius. This RSAP seems small for *Pinus*, which is expected to have a high background component within the pollen spectrum. However, this is in agreement with the findings in Section 5.5.2, where the NHP site has the greatest *Pinus* canopy cover, but a relatively low *Pinus* pollen percentage. This correlates with *Pinus* canopy being present mainly in the 30-50 m radius around the site. The Relevant Pollen Source Area for *Pinus* in the sites in Glen Affric is therefore likely to be between 20 m and 50 m, but with a high intercept or background component. This infers that once the immediate canopy opens around a small basin, it may be difficult to assess the presence of a stand of trees just beyond the 20 m source area, from a more open local background with scattered *Pinus* in the wider environment.

As with the *Betula* curves several correlations show a dip to a lower r^2 value at 30 m, this is less evident than for *Betula* and not evident on the 1/d distance weighting which shows the smoothest curve and asymptote.



a)



b)

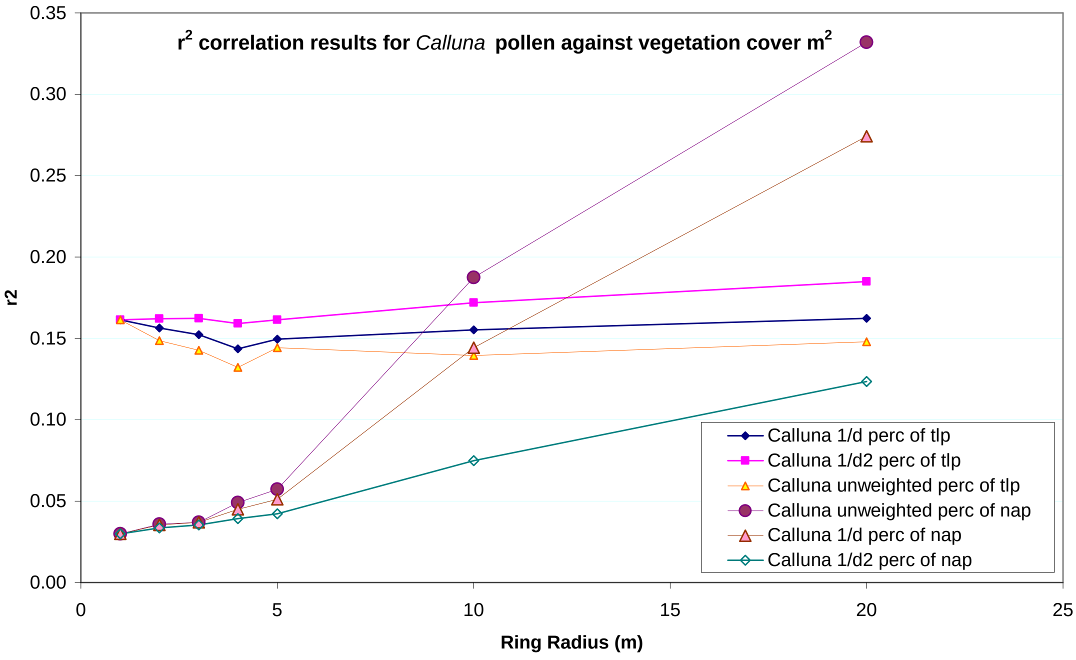
Figure 5.10: Plot of associated r^2 values against three distance weightings and for significant regressions against *Pinus* as TLP and AP. For vegetation as cover in m^2 (a) and as a percentage cover of total area (b).

5.5.4.1.4 Calluna – regression and correlation results

Plots of r^2 against different vegetation sample radii for *Calluna* are presented in Figure 5.11. Figure 5.11 demonstrates a notable difference between the r^2 plots from NAP% and TLP% correlations for all distance weightings. The reason is not clear, but could be due to the suppression of the dominance of *Calluna* in TLP percentages whereas *Calluna* is one of the more dominant pollen taxon in the NAP percentages.

Defining the relationship between *Calluna* and vegetation surrounding the sample sites is therefore problematic. Bunting (2003) finds that *Calluna* has a relevant pollen source area of three metres when plotted as a percentage of NAP, however her data tested the correlation to 5 m. Wider vegetation source radii may have produced the rapid increase in r^2 demonstrated for vegetation against NAP correlations in Figure 5.11. If the NAP percentage correlations are accepted then the source area for *Calluna* exceeds 20 m around the pollen sample point. This is not in agreement with other authors. However, Evans and Moore (1985) note problems in defining the *Calluna* source area and note a high background value for their study which measures the correlation at 1 m radius. This highlights a problem of the RSAP model, in that it is possible that there may be several small asymptotes within a still rising curve. Data which has modelled RSAP to wider sampling radii tends to have much larger ring source areas, less detailed vegetation cover measures, and regional pollen signals (e.g. Nielsen and Sugita 2005). It is possible, although speculative, that the structure of the vegetation surrounding the sample sites influences this pattern, with a very local RSAP provided by the immediate pollen rain (equivalent to a trunk space model in a tree canopy) and a larger RSAP at a greater distance from the above canopy component. The small, perhaps false, asymptote at 3-5 m may be caused by a ‘blind-spot’ in the pollen source where the plants are too close for above canopy transport, but local pollen transport mechanisms are shaded out by plants closer to the basin.

An improved fit is possible by removing outliers. The BH2 site has a very high percentage of *Calluna* pollen, with high absolute pollen counts (Figure 5.7) and may therefore represent an abnormal pollen loading. However, the reasons for removing any outlier other than BH2 is unclear, for this reason it was not considered justified in this study. Tallis (1997) finds that *Calluna* can be present even in sites with no local plant presence and estimates a background pollen rain for this taxon of 15-20%.



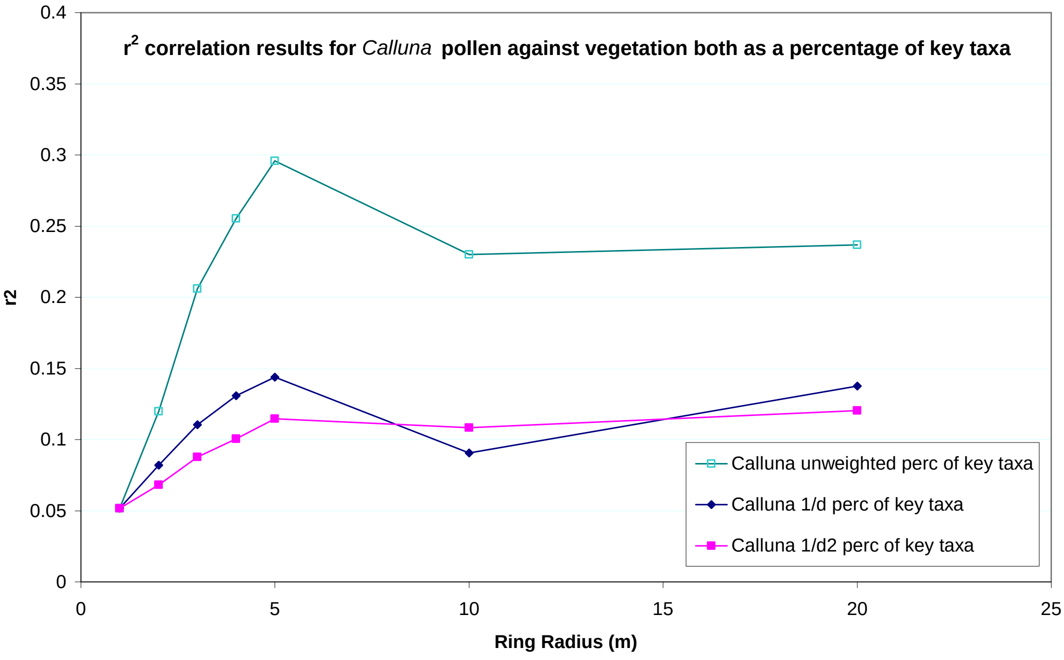


Figure 5.11: Plot of *Calluna* r^2 values against three distance weightings. Top graph is against vegetation abundance, bottom graph is against vegetation as a percentage of total vegetation for the groupings (TLP, NAP and Key Taxa).

5.5.4.1.5 Poaceae – regression and correlation results

Plots of r^2 for Poaceae in Figure 5.12, as with the *Calluna* plots, show a marked variation between the curves of NAP% and TLP%. The correlations with pollen as TLP% are not significant. The only significant pollen vegetation correlations when using plant abundance are those of pollen as NAP% against vegetation.

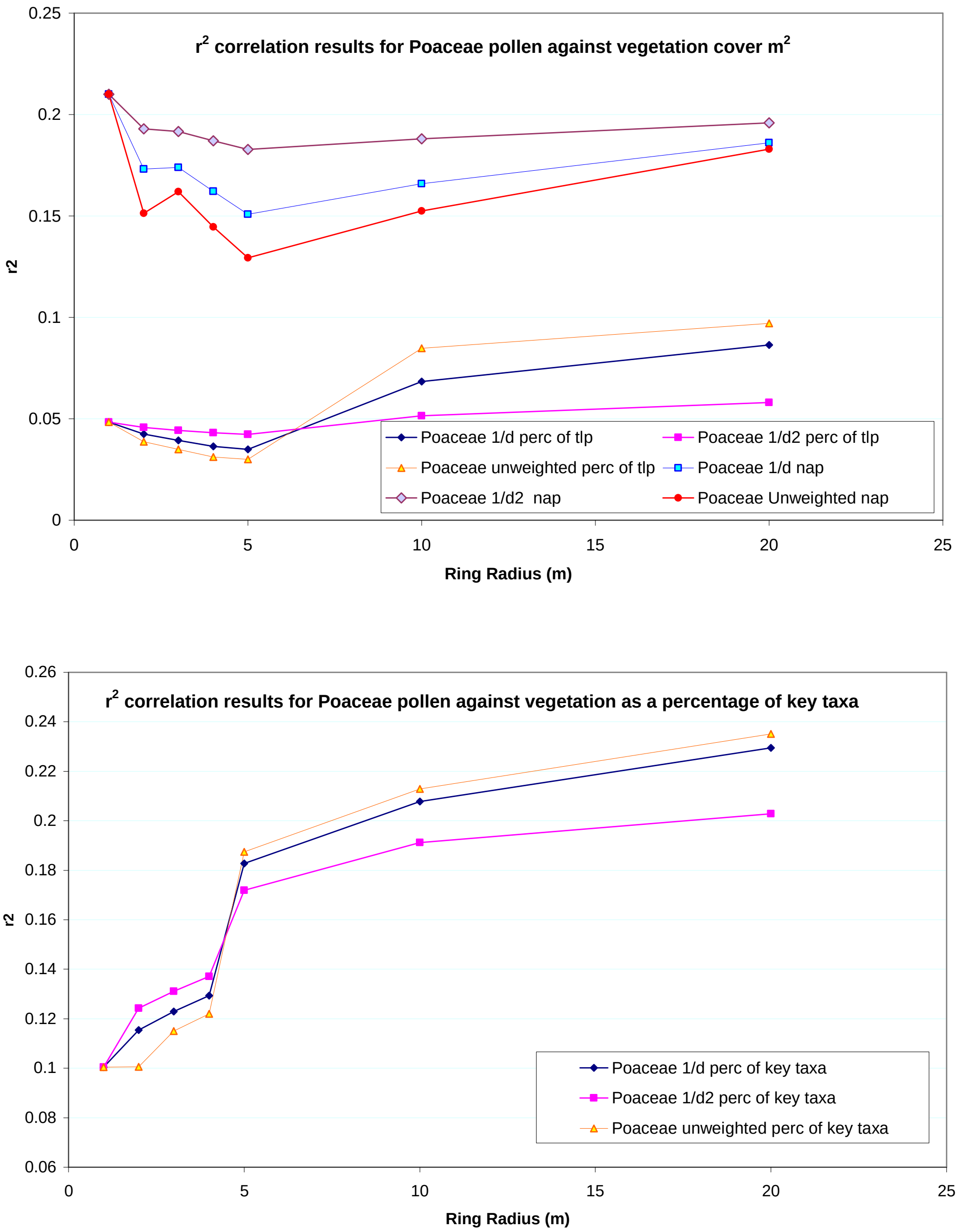
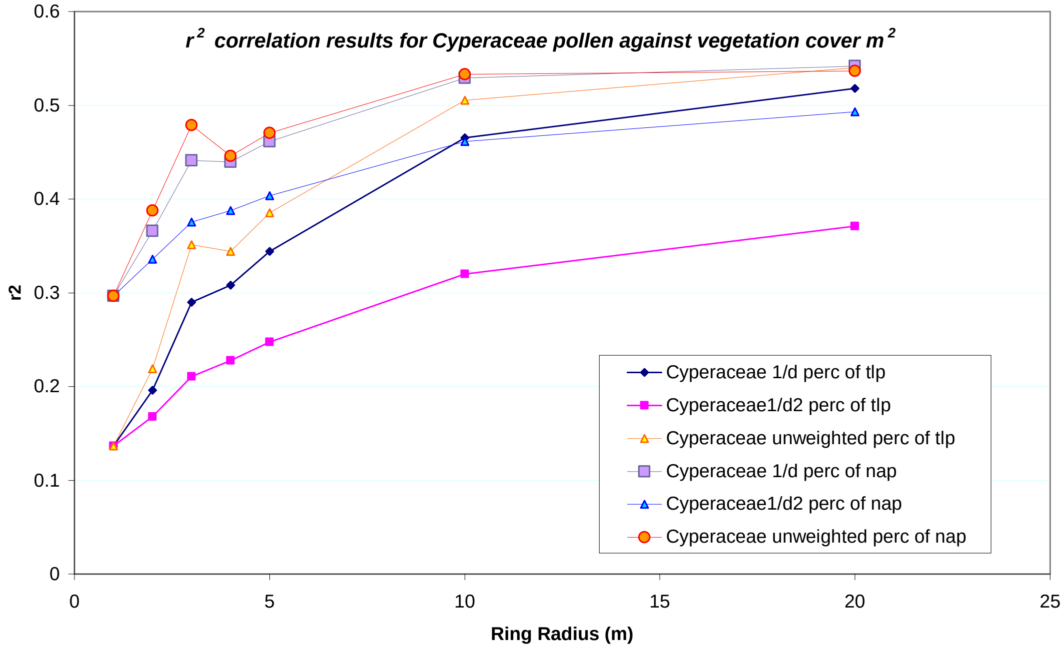


Figure 5.12: Plot of Poaceae r^2 values against three distance weightings and pollen as AP and NAP percentages (see legend). r^2 plots for for vegetation as cover in m^2 (a) and as a percentage cover of total area (b).

All of the correlations of pollen and vegetation as percentage values of the key taxa group are significant from the 5 m radius. There is little difference in r^2 between the different vegetation weighting models.

5.5.4.1.6 Cyperaceae – regression and correlation results

Plots of r^2 results from correlations between Cyperaceae pollen and vegetation are presented in Figure 5.13. Correlations against vegetation as cover data approach an asymptote consistently after the 10 m sampling radii. However, the plots of pollen and vegetation as a percentage of the key taxa group do not reach an asymptote. As with Poaceae and Cyperaceae, there is more difference between the models of pollen percentage than between the distance weighting parameters.



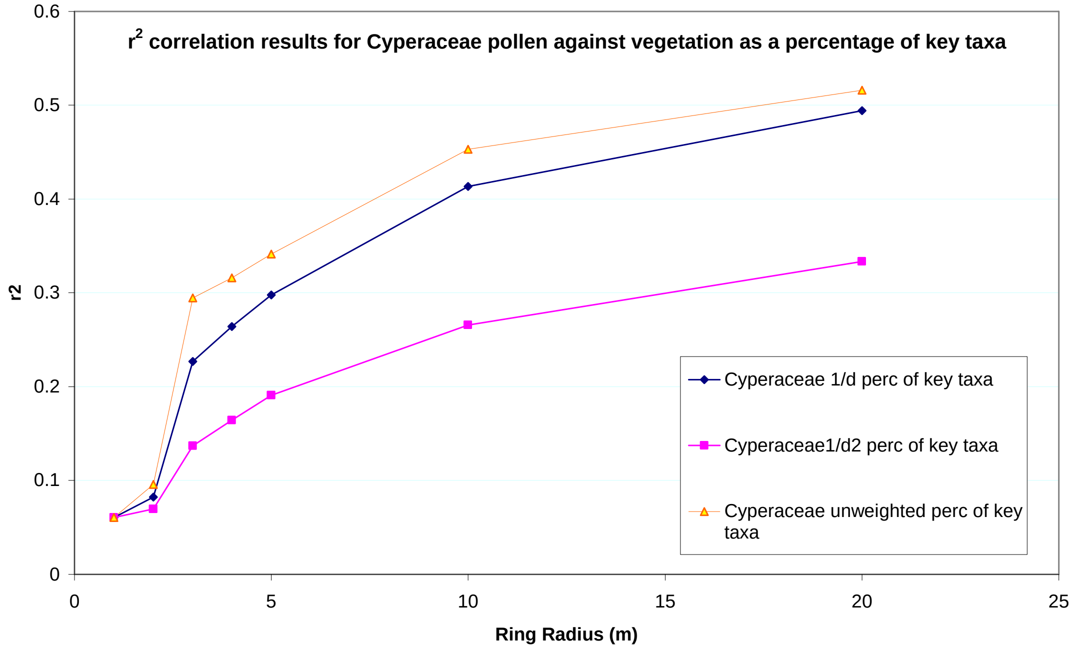


Figure 5.13: Plot of Cyperaceae r^2 values against three distance weightings and pollen as AP and NAP percentages (see legend). r^2 plots for vegetation as cover in m^2 (top) and as a percentage cover of total area (base).

5.5.4.1.7 RSAP, pollen productivity and background terms from the Anderson model.

There was little consistency of model approach in the correlations between vegetation and pollen data, with some taxa correlating more significantly with distance weighted vegetation and some with unweighted vegetation cover. An unweighted correlation between pollen and vegetation, as percentages of the key taxa group, may deliver the best compromise as this model seems to fit reasonably well for all taxa with all correlations showing a significant r^2 at 20 m. Whilst this value does not demonstrate an asymptote at 20 m for all taxa, the shift to a shallower curve from the 10 m radius demonstrates that it is likely to be close to the asymptote for most taxa analysed. Table 5.12 displays the correlation, and regression slope and intercept values for the five key taxa using the correlation between pollen key taxa percentage and unweighted vegetation key taxa percentage.

Table 5.12: Sample of significant regression and correlation statistics for key taxa based on correlations of pollen and vegetation as a percentage of the key taxa group.

	Ring Radius (m)						
	1	**2**	**3**	**4**	**5**	**10**	**20**
Betula							
Covariance		110.13	212.12	159.64	187.72	263.78	234.54
Pearson		0.28	0.45	0.31	0.35	0.58	0.62
R^2		0.08	0.20	0.10	0.13	0.34	0.39
Slope of line		0.38	0.51	0.33	0.36	0.69	**0.89**
Intercept		21.64	19.38	19.99	18.55	13.44	**13.11**
r^2 difference			0.12	-0.10	0.03	0.21	0.05
p<0.05		not sig	**sig**	not sig	not sig	**sig**	**sig**
p<0.01		not sig	not sig	not sig	not sig	**sig**	**sig**
Pinus							
Covariance		-8.30	-32.47	27.11	137.92	145.33	159.24
Pearson		-0.03	-0.11	0.08	0.32	0.53	0.61
R2		0.00	0.01	0.01	0.10	0.28	0.37
Slope of line		-0.07	-0.17	0.12	0.36	0.93	**1.15**
Intercept		46.18	46.79	45.36	42.21	38.37	**34.84**
r^2 difference			0.01	0.00	0.09	0.18	0.10
p<0.05		not sig	not sig	not sig	not sig	**sig**	**sig**
p<0.01		not sig	not sig	not sig	not sig	**sig**	**sig**
Calluna							
Covariance	54.43	65.22	85.28	98.53	104.96	95.32	54.43
Pearson	0.23	0.35	0.45	0.51	0.54	0.48	0.23
R2	0.05	0.12	0.21	0.26	0.30	0.23	0.24
Slope of line	0.11	0.22	0.29	0.31	0.34	0.29	**0.27**
Intercept	6.76	4.48	2.31	1.40	1.27	1.05	**0.59**
r^2 difference		0.07	0.09	0.05	0.04	-0.07	0.01
p<0.05	not sig	not sig	**sig**	**sig**	**sig**	**sig**	**sig**
p<0.01	not sig	not sig	not sig	**sig**	**sig**	**sig**	**sig**
Poaceae							
Covariance	123.36	119.24	124.46	124.11	146.46	132.80	135.88
Pearson	0.32	0.32	0.34	0.35	0.43	0.46	0.48
R2	0.10	0.10	0.11	0.12	0.19	0.21	0.24
Slope of line	0.10	0.10	0.11	0.12	0.15	0.19	**0.20**
Intercept	7.50	7.87	7.92	7.76	7.34	6.66	**6.20**
r^2 difference		0.00	0.01	0.01	0.07	0.03	0.02
p<0.05	not sig	not sig	not sig	not sig	**sig**	**sig**	**sig**
p<0.01	not sig	not sig	not sig	not sig	not sig	not sig	not sig
Cyperaceae							
Covariance		99.62	108.83	160.79	160.08	166.83	180.30
Pearson		0.25	0.31	0.54	0.56	0.58	0.67
R2		0.06	0.10	0.29	0.32	0.34	0.45
Slope of line		0.09	0.13	0.26	0.28	0.29	**0.36**
Intercept		5.91	5.00	2.25	1.80	2.24	**1.39**
r^2 difference			0.04	0.20	0.02	0.03	0.11
p<0.05		not sig	not sig	**sig**	**sig**	**sig**	**sig**
p<0.01		not sig	not sig	**sig**	**sig**	**sig**	**sig**

5.5.5 Discussion of correlation and regression

Correlation and regression is only suitable for taxa where presence in both the vegetation and the pollen is common. In most sites, the five key taxa *Pinus*, *Betula*, *Calluna*, Poaceae and Cyperaceae comprise over 90% of the pollen TLP sum and these five taxa are suitable for analysis. Additional analyses were attempted on *Empetrum*, *Erica*, *Vaccinium* and *Potentilla*. However, the results were not significant and are not shown. There are therefore relatively few taxa in the Glen Affric dataset where this analysis can assist in deriving species specific estimates of RSAP, background pollen loading and pollen productivity estimates (see Section 5.5.3).

For the key taxa and *Pinus* stomata a Relevant Pollen Source Area of 20 m around each sample site is assumed for the Glen Affric sites from the plot of the r^2 values against ring source area. This is probably an underestimate of the true source area, as although the plots level out at a 20 m radius from the pollen site the asymptote is not completely reached, especially for *Calluna*. Further survey data beyond the 20 m ring source area for ground flora would clarify this, but obtaining suitable ground flora survey data for these additional radii was beyond the scope of fieldwork for this thesis. The curve towards an asymptote presumed at this distance is supported, however, by data from some sites, e.g. NHP, where pinus pollen is reduced, and woodland is, in the main, at least 20 m from the coring point (Section 5.5). A 20 m source area will therefore be accepted as a working model for this thesis.

The significance of the correlations was variable not only between taxa, but within taxon. Within taxon r^2 differences were larger for different measures of vegetation cover than for different distance weighting models. NAP percentages may provide a closer correlation with plant abundance than TLP percentages for ground flora, whilst TLP percentages provide a closer correlation for arboreal taxa than AP percentages. This probably reflects the over-representation of the tree taxa in the pollen record and the open canopy and patchiness of the Glen Affric woodlands. Correlations of percentage arboreal vegetation cover do not account for open space in the canopy as does cover data.

From this testing of the correlation for individual taxa five taxa are selected for ERV analysis; *Pinus*, *Betula*, Poaceae, Cyperaceae, and *Calluna*. Data is examined as a five taxa group and a separate analysis of ground flora taxa against NAP percentages.

5.5.6 ERV analysis

The use of plant abundance, and therefore sub-model 3 is appropriate for small pollen source areas (Sugita 1994; Calcote 1995; and see Section 5.2.1). However, in the case of the Glen Affric data correlation results presented above may indicate a suitability of the pollen and vegetation percentage or proportion data for which ERV models 1 and 2 may be more suitable.

All three models are therefore tested on the datasets. Analyses were performed in the programme POLERV, part of the MOSAIC suite (Bunting and Middleton 2005).

Analyses were run for totals of the main taxonomic groups (Trees and Shrubs, Heaths, Cyperales and Herbs) for ring sources to 20 m radius. Only data for tree presence was collected beyond 20 m. Figure 5.14 shows the plots of Likelihood Function Score (LFS) from the analysis using ERV sub-model 3. Model runs were performed for all sites for unweighted, 1/d and $1/d^2$ distance weightings; and repeated with the five sites that are completely open to 50 m removed from the analysis. The Relevant Source Area for Pollen (RSAP) is defined as the distance beyond which the LFS ceases to decrease (Nielson 2003). The RSAP might be expected to be lower under the woodland canopy. The results in Figure 5.14 demonstrate only a subtle difference in slope; with the LFS between 10 and 20 m decreasing by *c.* 120 for the full sample analysis but *c.* 50 m for the analysis with open sites removed. LFS are not comparable between sets of analyses, but the shape of the curve is comparable. Although neither score has reached an asymptote, the shape of the curves is similar between site groupings and the trajectory confirms a likelihood of a RSAP for the pollen groups of little more than 20-30 m in both site groupings.

Analyses using tree taxa only using vegetation to 50 m radius and ERV sub-model 3 were attempted. The analysis of all 29 sites failed. Analyses run using a subset of the sites, both as open sites removed, and open and sites with scattered trees removed, were successful and results of the LFS plots for each source distance are presented in Figure 5.15. Data shows an approach towards an asymptote between 20 and 50 m radius but the LFS is still decreasing at 50 m.

The model was run for the five key taxa to 20 m vegetation sample distance for unweighted data (Figure 5.16) as this showed the most significant regression in Section 5.5.4. All model outputs demonstrate a similar LFS curve. Table 5.13 shows the PPE and background estimates from the sub-model output. These values vary between sub-models.

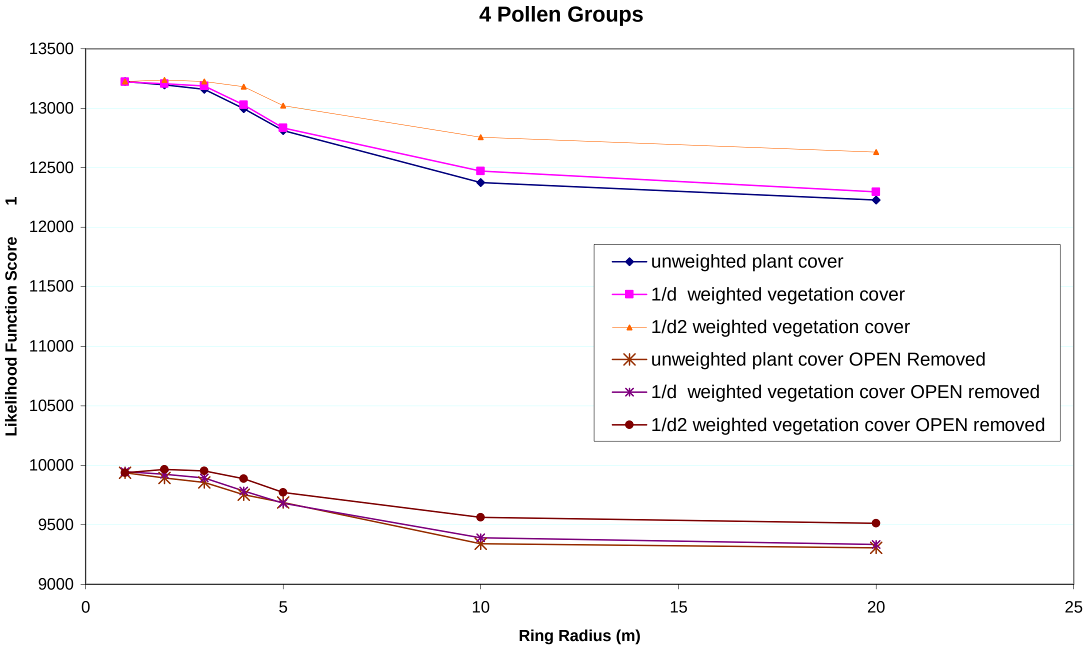


Figure 5.14: Plot of likelihood function scores estimated using the POLERV sub-model 3 for four pollen groups: trees and shrubs; heaths, Cyperales, and herbs. The three plots in the uppermost section of the graph are for all sites at various distance weightings (see legend). The three plots in the lower section of the graph are run with the five most open sites removed (CCH, OPEN1-3, and RRO. Note LFS scores are not comparable between sets of analyses but the shape of the curve is comparable.

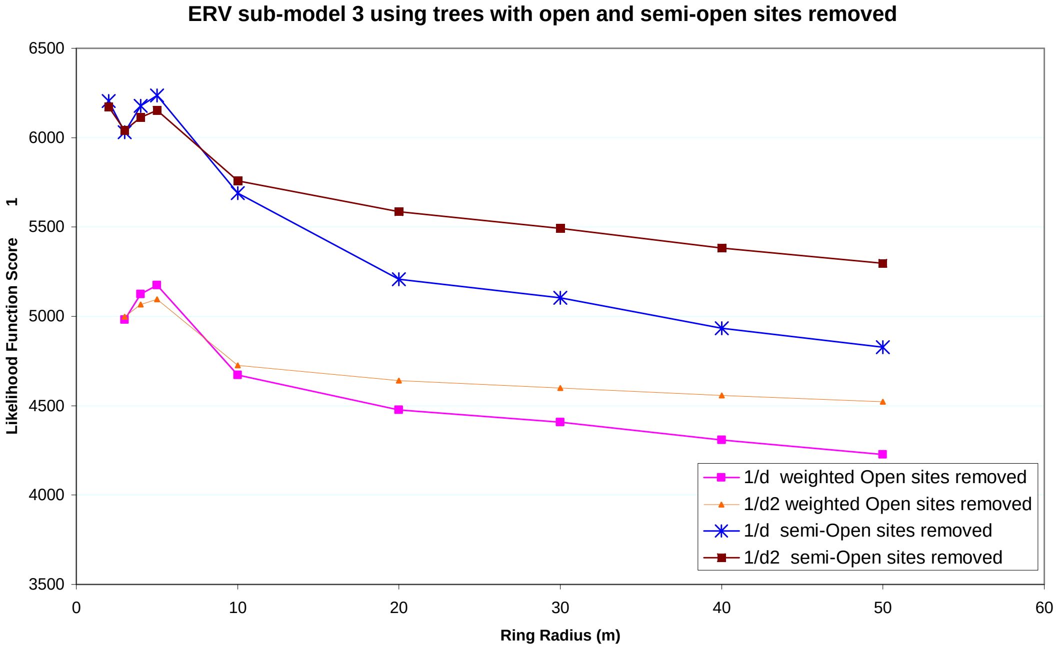


Figure 5.15: Plot of likelihood function score for various distance weightings for four main tree taxa. *Pinus*, *Betula*, *Alnus glutinosa* and *Sorbus aucuparia.* Note plots are for open sites removed (CCH, OPEN1-3 and RRO) or for closed woodland (ACF, AMO, BH2, BRO, CCF, NHO, RHO additionally removed). Analysis of all sites failed convergence in the POLERV programme.

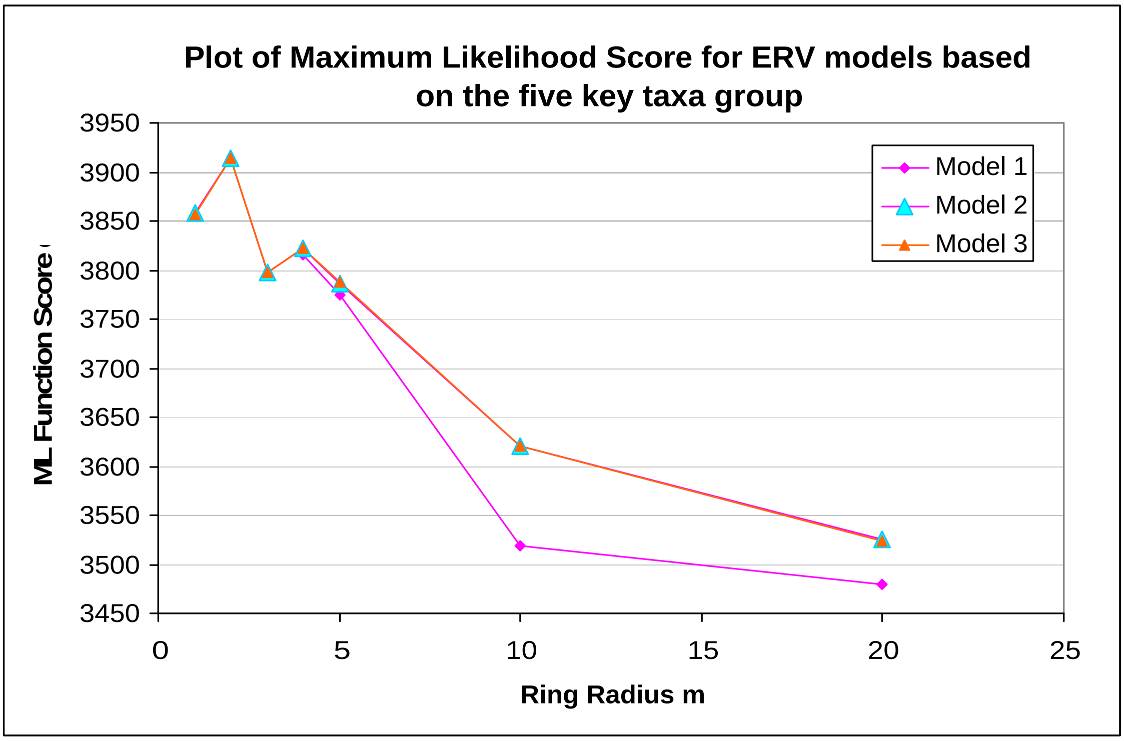


Figure 5.16: Plot of MLS for ERV models based on the five key taxa group using the three ERV models (see text for group details).

Table 5.13: PPE and background estimates from the analyses of five key taxa for Glen Affric using unweighted vegetation data to 20m ring source area and sub-models 1-3. Calculations carried out using PolERV in the HumPol suite of programmes (Bunting and Middleton 2005).

	Poaceae	Calluna	Cyperaceae	Pinus	Betula
Sub-model 1					
Alpha	1	1.5012	4.2397	76.125	45.756
Alpha sd	0	0.0307	0.8507	22.457	13.543
z	0.0832	0.0524	0.022	0.2948	0.0821
z sd	0.0056	0.0017	0.0035	0.0216	0.0068
Sub-model 2					
Alpha	1	2.0621	2.6247	34.345	18.066
Alpha sd	0	0.1815	0.1897	1.0593	0.4279
z	0.7679	0.2078	0.2558	2.0437	0.6156
z sd	0.058	0.0502	0.0462	0.1605	0.0682
Sub-model 3					
Alpha	1	1.9646	2.4815	33.012	17.166
Alpha sd	0	0.1704	0.1781	1.0395	0.4072
z	69.735	18.931	23.395	191.72	57.963
z sd	5.3087	4.5781	4.2256	15.088	6.3924

5.5.6.1 Discussion of ERV modelling

The ERV models, as with the Anderson model demonstrate an approach towards an asymptote at *c.* 20 m.

This may show a limitation of the ERV model in testing the source area and pollen productivity in semi-open environments where a test for openness is important. The ERV model requires a range of vegetation and pollen values and examines a best fit for these via a maximum likelihood method, it corrects for the Fagerlind effect and is therefore an improvement on the R-value and Regression models. However, as with the R-value model the ERV model cannot operate when there are several sites with zeros for the vegetation taxa. Removing sites from the analysis to gain PPE and background values for closed sites does not remove the problem of interpreting openness in the pollen record via application of a PPE and background.

5.6 Comparative analysis

5.6.1 Ordination of vegetation data

Principal Components Analysis (PCA) was performed on vegetation data recorded around the sample sites in Glen Affric. In Figure 5.17, cover data for trees to 50 m and ground flora to 20 m is combined and adjusted to a percentage of total cover before ordination. Data is square root transformed, and centred by samples and species.

Axis 1 (Figure 5.17) accounts for 34.3% of the variation; *Pinus* woodland and *Betula* woodland separate well from open-land vegetation on this axis. Axis 2 accounts for 25.1% of the variation and demonstrates a negative correlation with *Pinus* and a positive correlation with *Betula*. Axis 2 also separates Poaceae rich vegetation associated with a herb flora from *Calluna* dominated vegetation associated with a species poor heath flora.

The domination of *Pinus* and *Betula* in Figure 5.17 is expected as these large tree species dominate the percentage cover data. Figure 5.18 and 5.19 present the same ordination data, but with *Betula* and *Pinus* as supplementary species; *Betula* and *Pinus* are displayed on the ordination axis but have no influence on the eigenvalues. The separation of *Calluna* from Poaceae dominated vegetation is clearer through the suppression of the dominant arboreal taxa. Four groupings emerge; a Poaceae dominated herb rich grouping with *Succisa*, *Polygala*, *Achillea* and *Plantago* etc; A *Vaccinium* dominated grouping with *Melampyrum* etc; A *Calluna* dominated species poor grouping; and a grouping of Cyperaceae associated with *Erica tetralix*, *Narthecium ossifragum* and *Myrica Gale.*

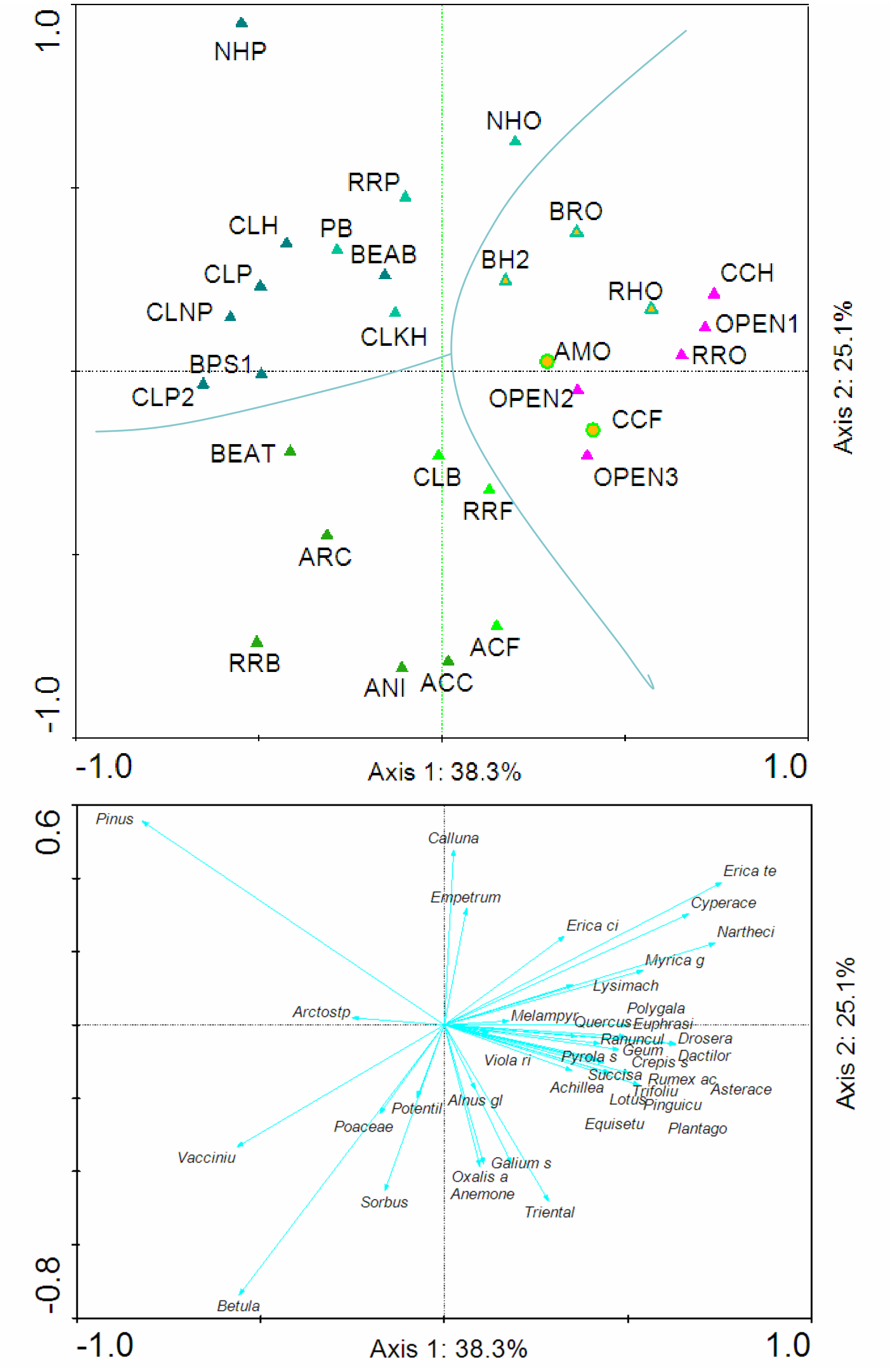


Figure 5.17: PCA of all vegetation cover data to 50m for trees and 20m for ground flora. a) sample scores and b) species scores. Vegetation sites are colour coded according to groups defined by previous ranking in Table 5.2.

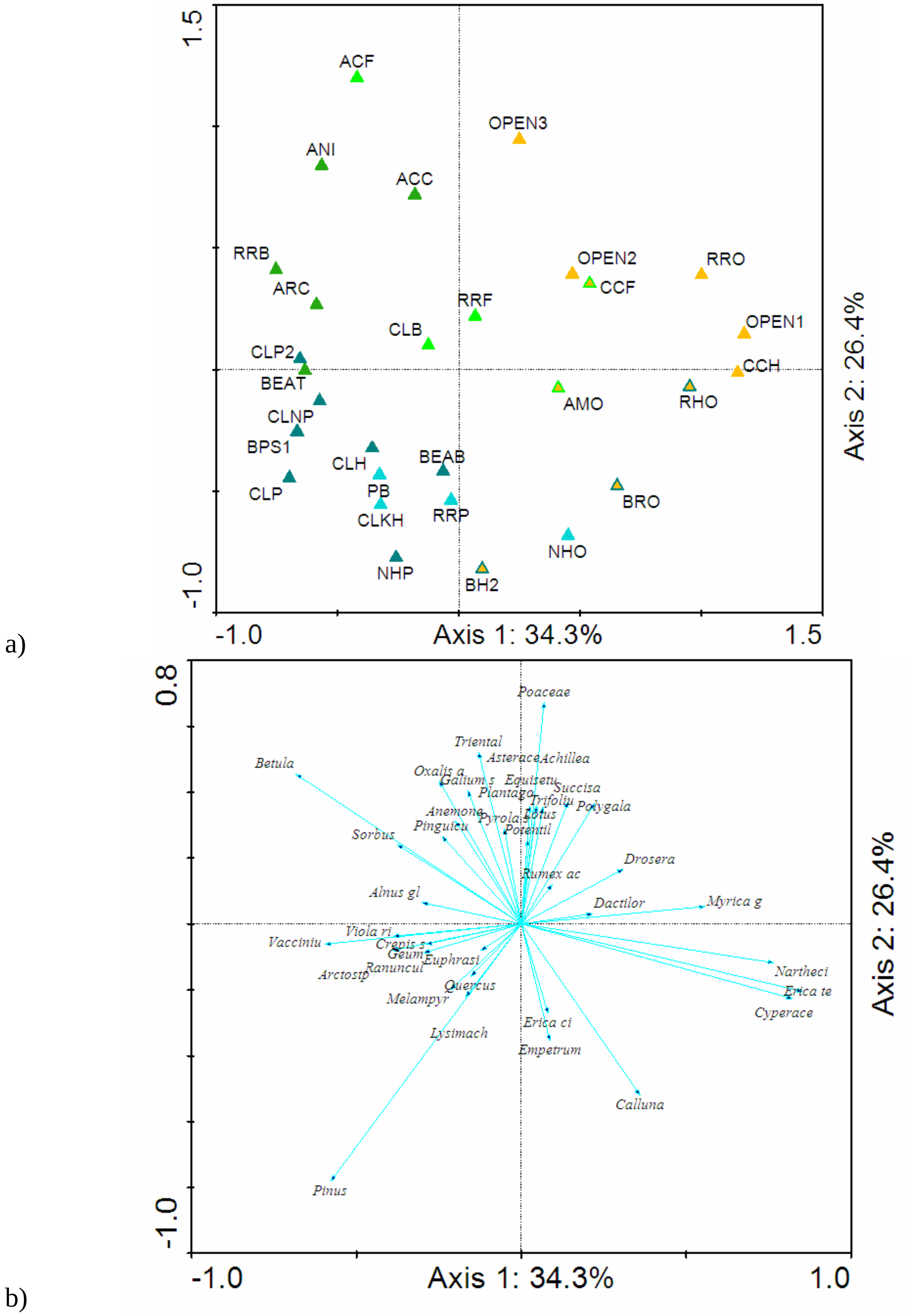


Figure 5.18: PCA of vegetation surrounding the pollen sample sites for all arboreal and non-arboreal taxa as percentage of total cover. a) sample scores and b) species scores. Vegetation sites are colour coded according to groups defined by previous ranking in Table 5.2.

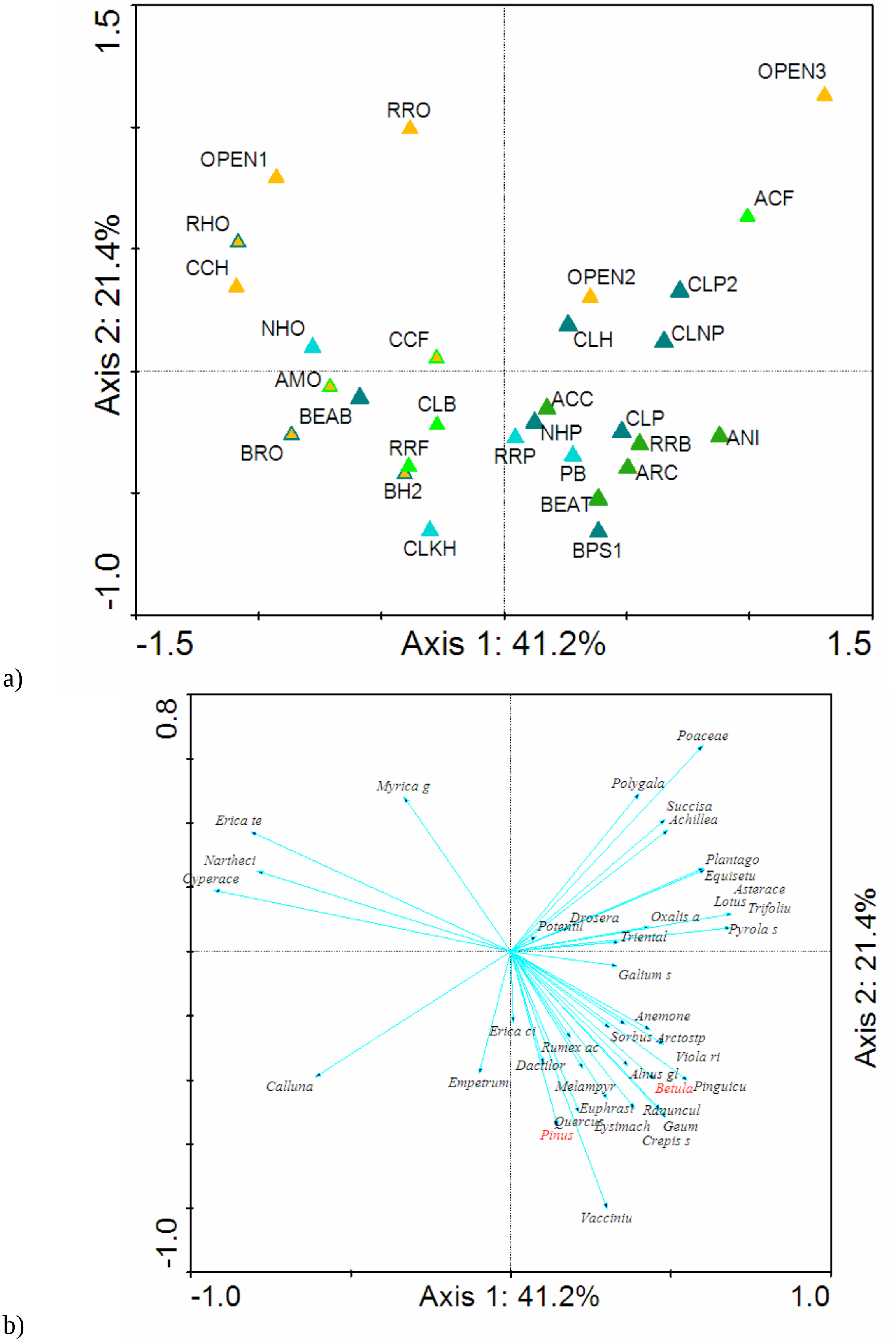


Figure 5.19: PCA plot of vegetation surrounding the pollen sample sites. *Pinus* and *Betula* are presented as passive samples to assess the impact of the ground flora on the ordination. a) sample scores and b) species scores. Vegetation sites are colour coded according to groups defined by previous ranking in Table 5.2.

PCA was a useful tool in the determination of open and closed woodland and in identifying ground flora sub-communities. Identification of the gradation of *Pinus* dominance in these woodland areas will be a key factor in the pollen analysis. Ordination produces clusters based upon *Pinus*, *Betula*, heath and Cyperales. Plots of ground flora only with main tree taxa as passive species allows the identification of difference between the ground flora of open land from that under the canopy cover. The vegetation sites in Glen Affric do show some differences and trends. The ability to identify and interpret these differences from the pollen signal is now tested, as this will be important in defining the scope of pollen analysis in this and other studies.

5.6.2 Ordination of pollen and vegetation

A PCA ordination plot of pollen percentage data is plotted in Figure 5.20. Axis 1 accounts for 37% of the variation and separates *Pinus* and open sites from *Betula* dominated sites indicating that where *Betula* is close to a site *Pinus* domination of the pollen record is suppressed slightly more than when the site is not surrounded by a canopy. Axis 2 accounts for 24.0% of the variation and is predominantly related to openness. The division between *Pinus* dominated sites and open sites in the top left hand quarter of the graph is remarkable, given the high levels of *Pinus* pollen in open sites. The presence of ACC, ARC and ANI as positively correlated with Axis 2 can be accounted for by their relatively open ranking (Table 5.2). Axis 3 (Figure 5.20 c-d) accounts for 13.3% of the variation and separates Cyperaceae, species poor moorland, from the Poaceae dominated sites. It describes the relationship between *Calluna*, Cyperaceae, Poaceae and more herb rich sites associated with the *Betula* woodland. This pattern is consistent with that found in the PCA groupings from the vegetation data (Figure 5.17 and 5.18) where Cyperaceae is associated with a species poor heathland community including *Erica tetralix* and *Narthecium ossifragum*, whilst Poaceae is associated with a more herb rich community. Each of these can be separated from a *Calluna* dominated community.

The PCA plots of pollen data with Pinus and Betula suppressed in Figure 5.21 demonstrate the ability of pollen data to reconstruct ground flora based on subtle changes in taxa and species. Axis 1 of the PCA separates woodland sites from open sites based on ground flora and rare tree species alone as *Pinus* and *Betula* are plotted as passive species in this ordination. This can be compared with the ordination of vegetation data with *Pinus* and *Betula* suppressed in Figure 5.19, where similarly modern vegetation under the canopy is highlighted as different to that of the open heathland communities. This gives confidence to the ground flora anaylsis based on comparative community descriptions.

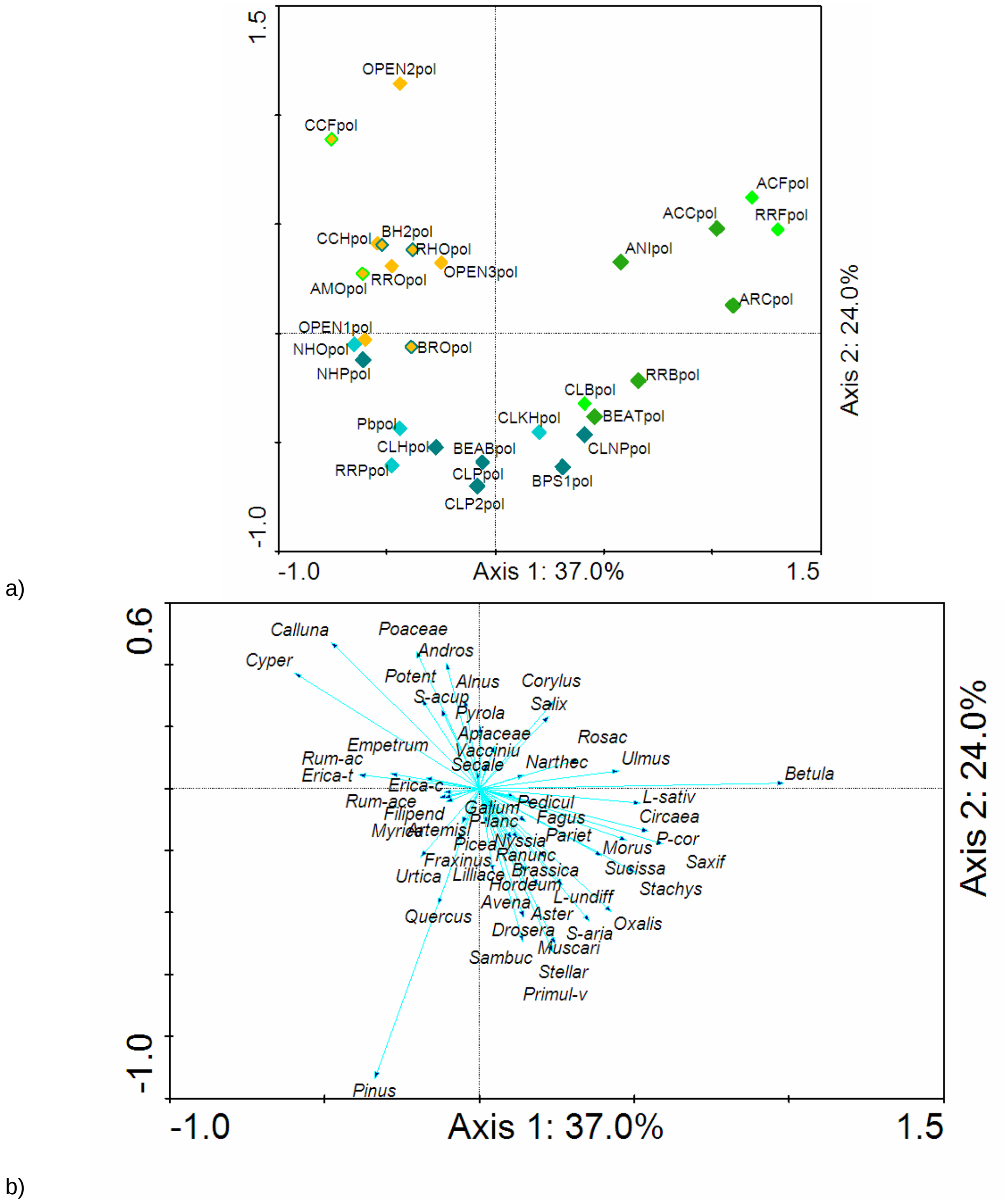


Figure 5.20: PCA ordination of pollen percentage data (pollen as a percentage of TLP). Plotted as axis 1 and 2: a) sites, b) species: and axis 1 and 3: c) sites, d) species.
Sites are labelled and colour coded (Orange – open sites; orange with green/turquoise outer line open-scattered trees Betula/Pinus dominated respectively; Light (semi-open) and dark (closed canopy) green and turquoise Betula/Pinus dominated respectively)

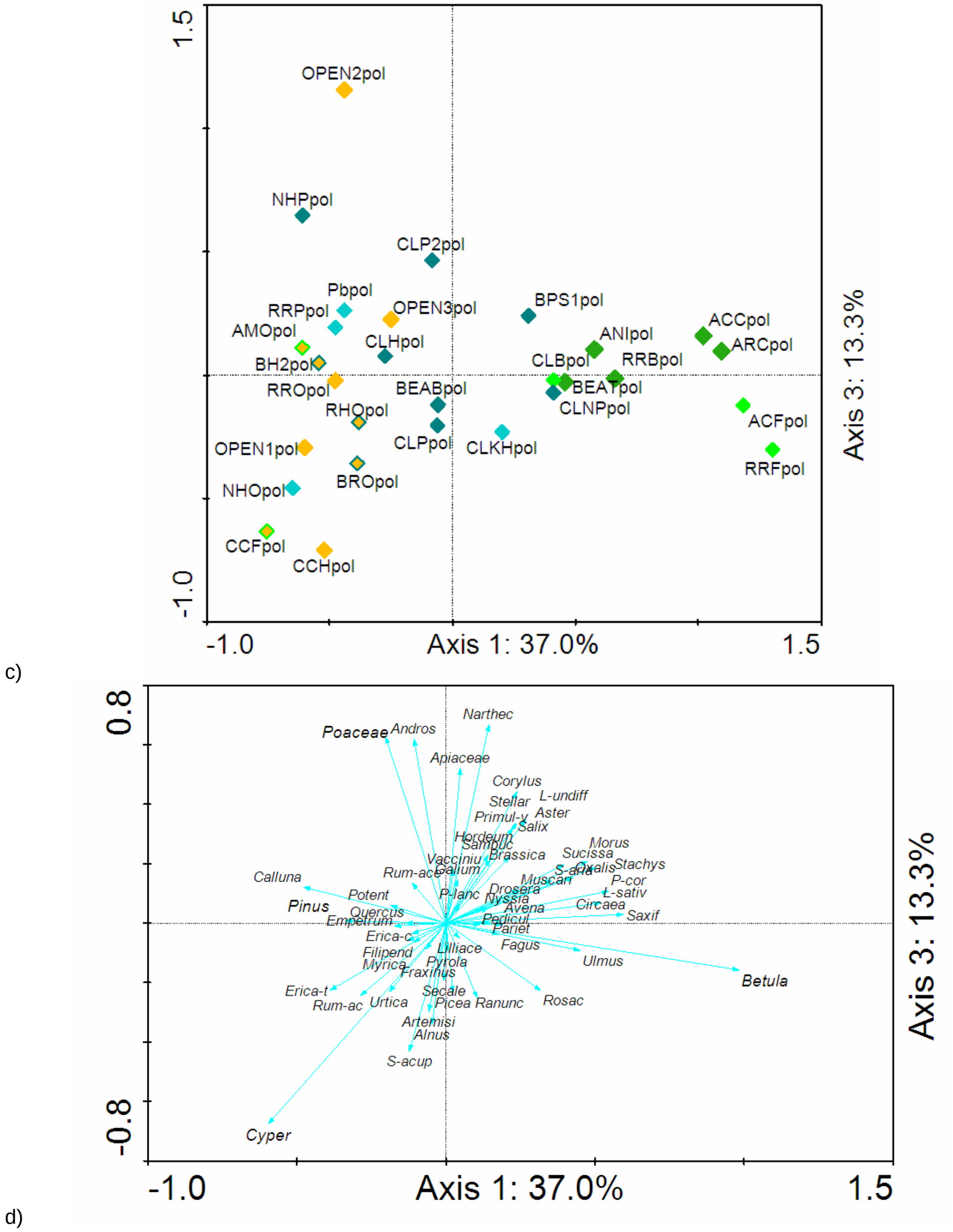


Figure 5.20 continued. Plots of axis 1 and 3. c) sites, d) species

Figure 5.22, however, plots PCA plots combined pollen and vegetation percentage data on the same ordination. This illustrates some of the differences between these datasets and highlights the well recognised problem that pollen from anemophilous arboreal taxa are over-represented in the pollen record. By combining the two data sets, the distance and direction of separation between pollen data and vegetation data can be examined. If the correlation between pollen and vegetation was a 1:1 relationship then the pollen and vegetation data signals should overlay each other on a PCA. The bias of the pollen samples, plotted with the vegetation samples, is towards the negative eigenvalues of axis 1 and 2, correlation with the *Pinus* in the species ordination plot (Figure 5.22b).

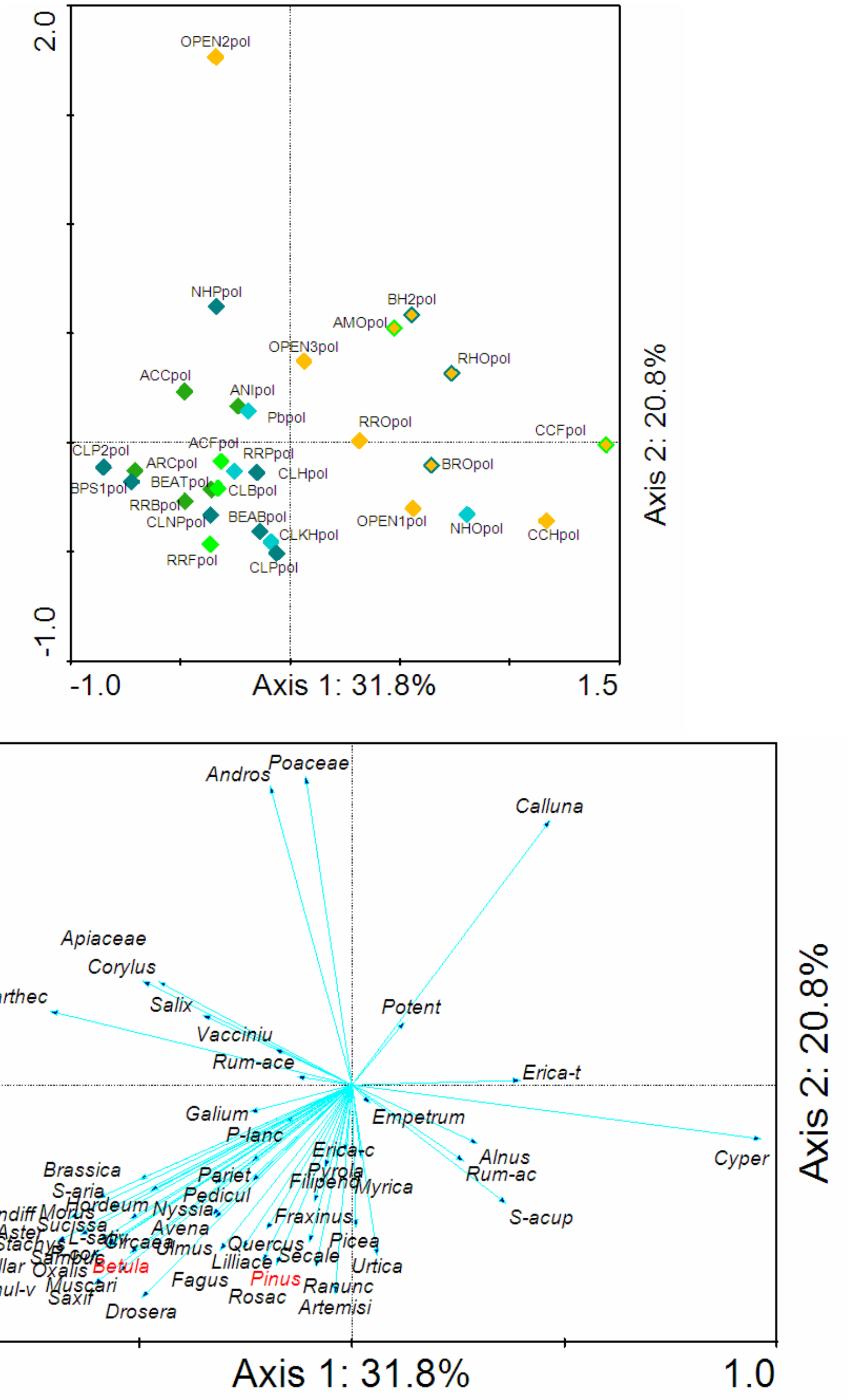


Figure 5.21: PCA of pollen data (pollen as a percentage of TLP) with *Pinus* and *Betula* pollen (labelled in red) plotted passively to determine underlying patterns in the ground flora.

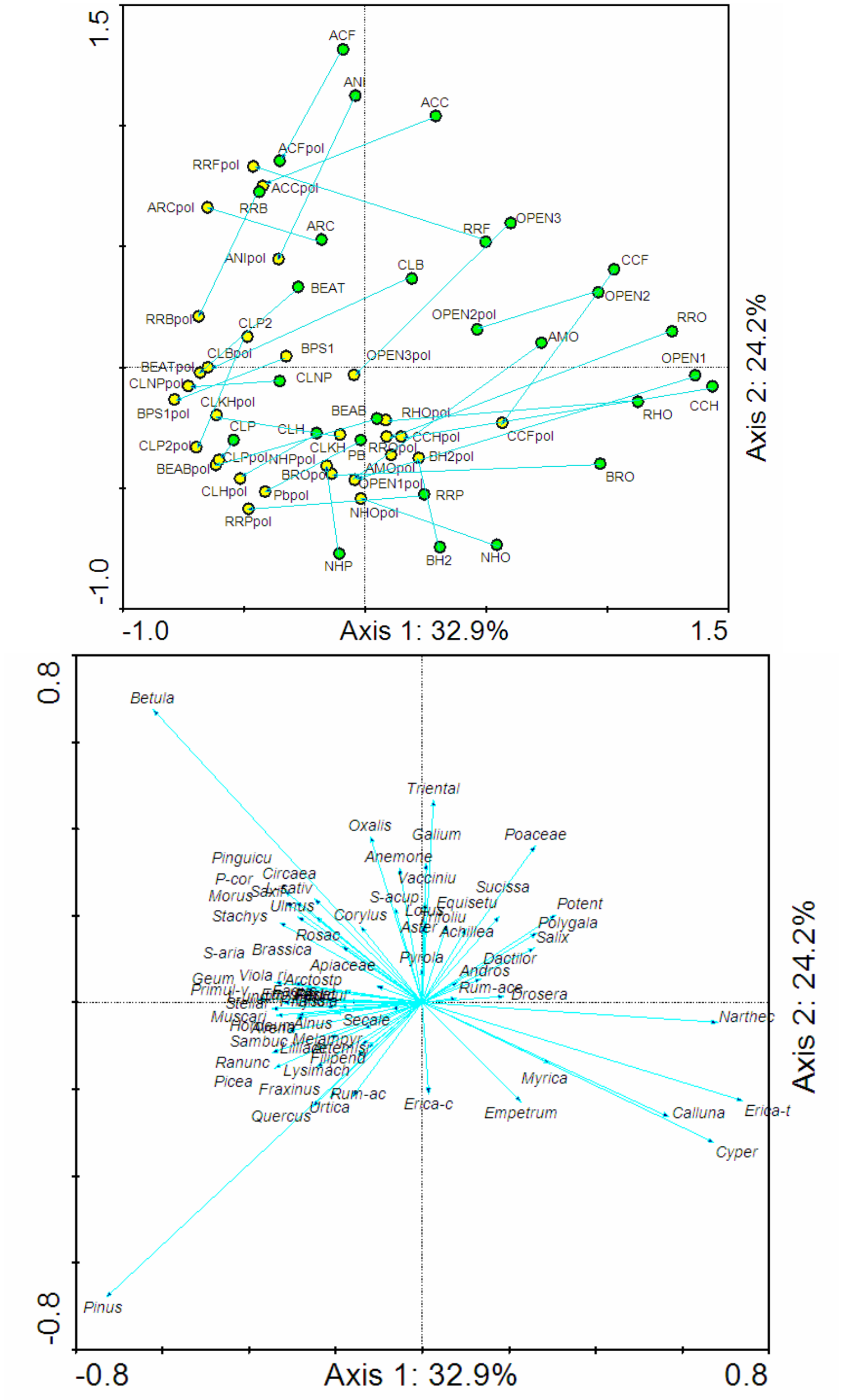
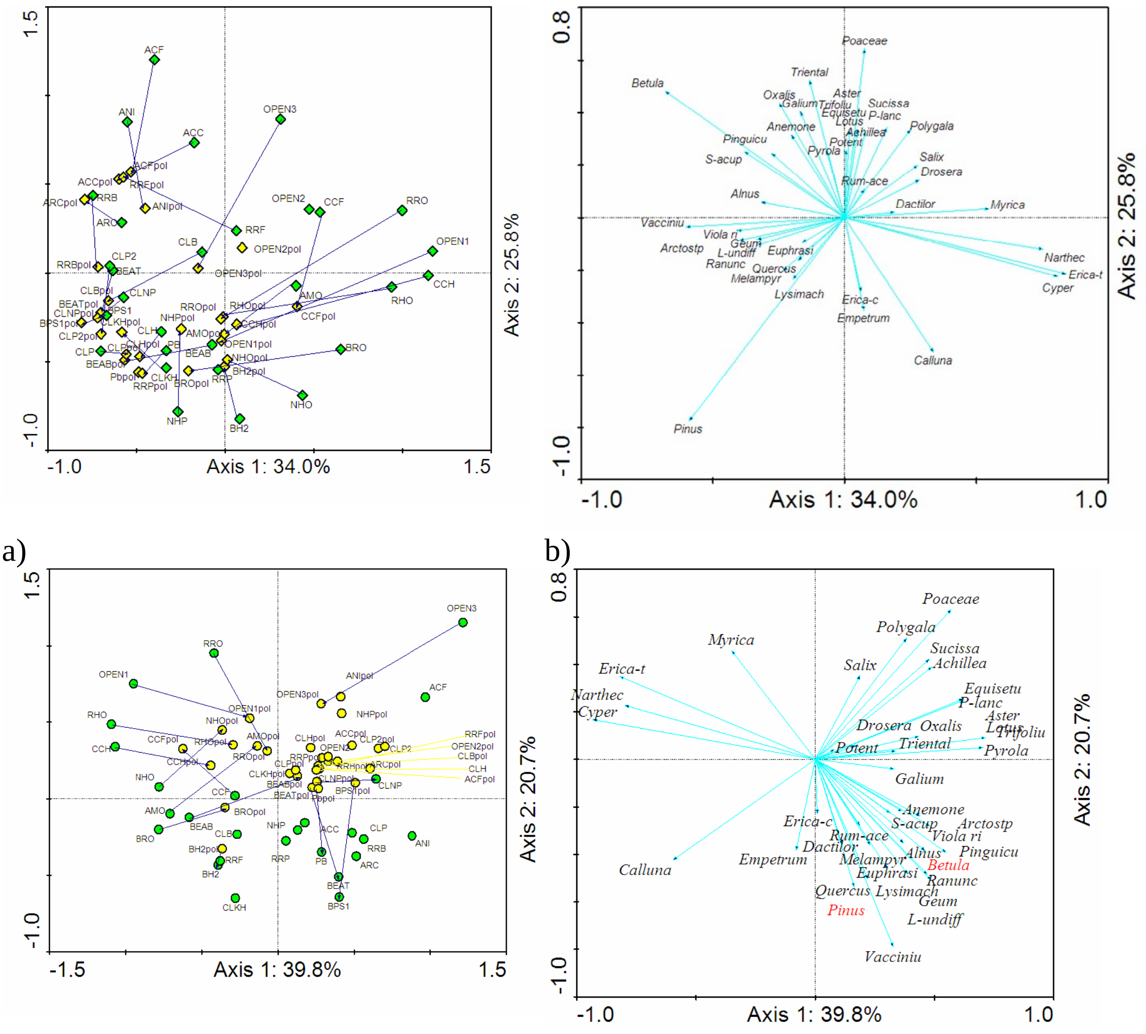


Figure 5.22: PCA of combined Pollen (as percentage TLP) and vegetation proportions Yellow sites represent vegetation samples green sites with the suffix pol represent pollen samples. Arrows show the distance between pollen and vegetation sample from the same site.

A second plot in Figure 5.22, where the pollen samples are plotted passively on the vegetation sample plot also demonstrates this problem. In Figure 5.23 c-d, the same passive plot of vegetation samples with pollen samples is implemented, but with *Pinus* and *Betula* plotted as passive species that do not contribute to the eigenvalues. This plot of Figure 5.23 shows that in comparison the pollen spectra from other taxa are suppressed and limit the detail of interpretation as the pollen samples all plot in a central cluster in the ordination space. However, although the distinctions are more subtle, the *Erica tetralix*, species poor moorland pollen samples do plot on the top left of the ordination plot, together with the vegetation samples of that type.



a)

b)

c)

d)

Figure 5.23: PCA of combined Pollen (as percentage TLP) and vegetation proportions. In contrast to Figure 5.22 Pollen samples in this ordination are suppressed and sit passively within the vegetation correlation. a-b) show all data and c-d show samples ordinated with Pinus and Betula suppressed. Green dots represent vegetation samples yellow dots with the suffix pol represent pollen samples. Arrows show the distance between pollen and vegetation sample from the same site.

5.7 Discussion

5.7.1 Discussion of modern vegetation analysis

Visual survey defined four main community types in Glen Affric, *Betula* dominated and *Pinus* dominated woodland; and Heath dominated and Cyperales dominated open land. Ranking and ratios of Pine/Birch highlight the mixed nature of most of the woodland stands in Glen Affric around the sampling points selected. These simple methods of ranking data also prove powerful in dividing the dataset manually into simple but meaningful clusters. Cluster analysis methods, however, although highlighting some useful differences - for example, *Vaccinium* dominated ground flora - do not, in general, define easily meaningful clusters in the continuum type vegetation community in Glen Affric. An increased number of sites may have allowed for identification of meaning in the cluster groupings.

PCA ordination was a useful tool in determination of open and closed woodland and in identifying ground flora sub-communities. Identification of the gradation of *Pinus* dominance in these woodland areas will be a key factor in the pollen analysis. Ordination produces groupings based upon *Pinus*, *Betula*, heath and Cyperales. Plots of ground flora only with main tree taxa as passive species allows the identification of difference between the ground floras of open land from that under the canopy cover. The vegetation sites in Glen Affric do show some differences and trends. The ability to identify and interpret these differences from the pollen signal will be important in defining the scope of pollen analysis in this and other studies.

5.7.1.1 Openness

This modern analogue study in Glen Affric has helped confirm some basic assumptions about pollen interpretations of canopy openness from small hollow sites (Jacobson and Bradshaw 1981). Even under the semi-open canopy in Glen Affric it is possible to interpret sites with woodland cover from open glades thus dispelling some continuing concerns over interpretations of woodland openness through pollen analysis (Vera 2000). Although ranking and regression of *Pinus* and *Betula* pollen and vegetation data demonstrate the ability to interpret canopy openness surrounding the pollen sites, the cut-off value for interpretation of open glades within the 20-30 m radius of the pollen site is high at *c.* 50% AP. This indicates that a large proportion of the pollen is background pollen from beyond the 50 m source area.

5.7.1.2 Relevant pollen source area for trees

The plot of regressions at increasing vegetation-sampling distance, and the plot of LFS scores from the ERV model both appear to approach an asymptote at *c.* 20 m radius from the pollen source; however, the limited sampling area may hide further increases in r^2 or LFS score at wider sampling radii. This assumption is supported by the high percentages of *Pinus* and arboreal pollen in sites with no woodland cover to 50 m or beyond. Bunting (2003)found an asymptote at a *c.* 2 m sample radius for herbaceous pollen types in Assynt, yet in the Glen Affric datasets the apparent asymptote at 2 m then rises again between 10 and 20 m radius for Poaceae Cyperaceae and *Calluna*. It is unclear if this is an inadequacy in the sampling radius, but given the significant regression between pollen and vegetation abundances at these low sampling radii, this could also demonstrate a feature of the regression model, in that several different RSAPs may exist at differing sample radii with different values for z (the background pollen proportion).

The ability to make meaningful reconstructions when a background pollen percentage is high was highlighted by Sugita (1994). However, the ability to detect openness may be constrained by the model characteristics in that it does not cope well with zero values for vegetation. This makes it difficult to test the effect, on PPE and background, of sites with no vegetation present within the sampled radius. A greater vegetation sample radius may stabilise the background component. However, this would reduce the ability of sites to determine local scale vegetation reconstructions.

5.7.1.3 Woodland composition

The current woodland in Glen Affric is dominated by *Pinus* and *Betula*, and consequently the pollen diagrams demonstrate the same species dominance. Although other tree taxa such as *Alnus* glutinosa and *Quercus* are present in the Glen, they are not abundant. Historically these, and other species such as *Populus tremulus*, may have been more widespread, but current conditions mean that it is not possible to test this scenario palynologically from modern analogue data. It was also difficult to find peat basins in areas where monodominance of *Pinus* was widespread, as on the south side of Loch Beinn a Mheadhoin becuase the drier slopes that favour this taxon in the present landscape (Pyatt 1994) lack suitable sample sites.

5.7.1.4 Ground flora composition and source area

The detection of heath and grassland surrounding the sampling sites is also consistent to the 20 m radius measured. Rank correlations and regressions of *Calluna*, Poaceae and Cyperaceae all demonstrate moderate correlations that are statistically significant although the correlations are generally weaker than those for trees. The plots of r^2 against distance from source for *Calluna* do not reach an asymptote at the 20 m radus. This is somewhat unexpected as previous studies have revealed a very small relevant pollen source area for ground flora (Bunting 2003; Hjelle 1998), but see above discussion on the possibility of multiple RSAPs dependent on sampling structure. Although the correlations and abundances of these three key taxa are significant, for other taxa the interpretation is more complex. The representation of *Vaccinium*, *Empetrum nigrum*, *Erica tetralix* and *Erica cinerea* in the pollen record is limited as the signal for these anemophilous species tends to be masked by *Calluna* dominance in the pollen record. Small percentages or single grains of these pollen types could be indicative of abundant local vegetation. It is for these taxa that PPEs would be most useful but, an increased number of sites and larger pollen counts may be required to fully understand their contribution to the pollen record. Although *Vaccinium* is locally dominant at some sites, it is possible that *Vaccinium myrtillus* was once more widespread in the ground flora. There is some suggestion from ecologists that *Calluna* dominance is facilitated by high levels of grazing (e.g. Rodwell 1991), and that also the dominance between *Calluna* and *Vaccinium* varies through the life-cycle of the woodland due to the degree of canopy shading (Gimingham 1964; Gimingham 1949). The ability to recognise and quantify *Vaccinium* or other Ericoid dominance over that of *Calluna* is therefore important, but may also be limited. It is likely however that any increase in the percentage of these grains is indicative of a marked increase in the presence of the vegetation. In addition, the examination of community assemblage data in the ordination analysis in Section 5.6 may be useful here. *Erica tetralix* tends to become more frequent in open sites with a high Cyperaceae contact and some other notable taxa such as *Narthecium ossifragum*, which are indicative of wetter sites with poor surface drainage. Sites with these ground flora characteristics group together in the PCA analysis even when the indicative taxa are only present as occasional rare types.

What is surprising is the extent to which it is possible to identify and define subtle changes in the ground flora within a landscape where superficially this is similar to that under the woodland canopy.

5.7.1.5 Herbaceous species

In general herbaceous species other than Poaceae and Cyperaceae are not abundant in the Glen Affric vegetation and this is reflected in the pollen diagrams. Samples from OPEN1 OPEN 2 and OPEN 3 were taken from areas of high floristic diversity to ensure that there was a modern equivalent to this analogue occurring in the past; these sites do include a higher diversity in the pollen records.

5.7.1.6 Human activity

In addition to the mapping of the stand dynamics of semi-natural vegetation in the extant woodlands of Glen Affric, there is a need to assess the relative impact of human activity on the woodlands through time. Although purported to be natural, little is known about the likely human impacts on the Glen Affric woodlands in prehistory. The study by Froyd (2006) demonstrates continuance of woodland, but with little spatial precision or detail (Section 2.2), whilst the study in west Glen Affric infers human interference as a contributor, together with climatic change, to the demise of woodland to the west (Davies 2003; Davies 1999; Davies and Tipping 2004). Anthropogenic indicator pollen taxa are used to infer human influence on the landscape (Behre 1981), these taxa include *Hordeum*, *Triticum* and *Avena* (Behre 1981). Pollen from these taxa occur in the surface samples of Glen Affric and therefore caution in their use at low counts as anthropogenic indicators is advised.

5.7.1.7 Application to core data

The use of the results of regression and ERV analysis to adjust the fossil pollen assemblages is more tenuous. Not least due to the limited taxa for which a regression was possible. In terms of tree taxa, only *Pinus* and *Betula* are present in sufficient quantities to implement regression analysis. Fossil pollen results presented in the next chapter show evidence of more widespread presence of *Alnus* and possibly *Quercus*. The correction factors derived from the modern dataset may therefore not be relevant for application to reconstruction from fossil pollen (Schwartz 1989).

5.7.2 Conclusions

This study provides information on realistic constraints to the interpretation of pollen data and the development of secure vegetation reconstructions. The number of taxa where there is a correlation between plant and pollen presence is few, but comparative analyses demonstrate some ability to make inferences of taxa presence by the use of indicative taxa for a particular community. However, this must be limited in terms of studies assessing community stability through time, as arguments for a particular species assemblage in the past inferred from indicator taxa quickly become circular.

The analysis presents some first tentative PPEs for Scotland relevant to the important issue of interpretation of pollen spectra from local sites in semi-open *Pinus* woodland. The variation between sites and in taxa mean that more sites, larger pollen counts and wider radius vegetation surveys are required as further work. However, these PPEs will assist the interpretation of pollen spectra and vegetation history in Glen Affric as presented in the next Chapter.

6 Historical vegetation reconstructions

6.1 Introduction and organisation of chapter

This Chapter presents the results and develops vegetation reconstructions from the eight cores introduced in Chapter 3. Chronologies were derived from ^{14}C and ^{210}Pb assays for each core and developed in Chapter 4. Chapter 5 defined the scope of the reconstruction by reference to modern pollen and vegetation data.

The core sites are located in three clusters (Figure 3.2) The results are presented and discussed as groups of cores based upon these clusters. Firstly, each core in the cluster is described individually. Secondly, as far as possible within the limits of the chronological controls, all cores in the cluster are compared to establish spatio-temporal commonalities and differences in the pollen spectra; and finally, a correlation and comparison is made between all eight cores across the Glen in Chapter 7.

6.2 Presentation of data and results

Summary percentage pollen diagrams showing key taxa and taxa of particular interest for the interpretation are presented for each core. Pollen percentages are calculated as a percentage of total land pollen (TLP); land pollen includes Cyperaceae, as this is present in the wider landscape rather than limited to discrete basin surfaces. Full percentage pollen diagrams of all recorded palynomorphs, and summary influx, concentration and percentage of NAP diagrams, are presented in the Appendix and referred to where these aid clarification of the interpretation.

Pollen diagrams are divided into zones and sub-zones marking major and minor changes in the pollen stratigraphy interpreted from stratified cluster analysis implemented via CONISS (Grimm 1987).

Analysis of palynological richness was carried out using Psimpoll and diagrams plotted to establish periods of high and low diversity (Birks and Line 1992).

Adjusted pollen percentage data using output from regression and ERV analysis is applied to pollen data from the ANI and ARC cores in cluster 2 where it may aid the interpretation of subtle cyclical processes between *Pinus* and *Betula*. Otherwise, the simpler cut-off value of 50% TLP is used to denote local presence of *Pinus* as pollen productivity estimates may not be appropriate due to differing background vegetation and a lack of true modern analogues.

Site descriptions, including site location, basin size, and stratigraphy are presented in Chapter 3.

6.3 Cluster 1 pollen cores; NHP, PB and BEAT

6.3.1 NHP pollen core

A summary TLP percentage pollen diagram for NHP core is presented as Figure 6.1 and a detailed extract of cyclicity between *Calluna* and other Ericales is presented in Figure 6.3. A full TLP percentage pollen diagram for all taxa, as well as summary diagrams for concentration, influx, and percentage NAP data, is presented in Appendix 1.1 as Figures A1.1 - A1.4. A comparative analysis with modern samples was performed via a passive PCA ordination plot of NHP samples onto the modern pollen plot (Figure 5.19; Chapter 5) and is presented in Figure 6.4. Pollen correction factors were not used on the data, as, apart from the two peaks in AP and the pollen spectrum from the recent *c.* 200 years of peat accumulation, arboreal taxa were rare and interpreted as non-local; whilst the local heath vegetation probably included *Empetrum* and *Vaccinium* for which there is no PPE estimate available in the modern data set.

6.3.1.1 Summary of main features of diagram and main zone changes

NHP is divided into five zones, of which three are divided into associated sub-zones. These are listed in Table 6.1 together with summary descriptions of the major patterns of change in pollen spectra.

Table 6.1: Zone and sub-zone boundaries and summary pollen descriptions for the NHP core. Zone boundaries are defined by CONISS (Grimm 1987). For details of the chronological model see Chapter 4.

Zone	Depth cm	Chronological Model	Description
NHP5b	0-13	AD 2004-1920	***Pinus* - Poaceae** Pinus % high with stomata; Cyperales high; *Calluna* decreased but *Erica* and *Vaccinium* is still present. Poaceae percentages increase rapidly to top of core.
NHP5a	13-19	AD 1920-1850	***Pinus* – Cyperales** *Pinus* rapid increase to 40% TLP by end of sub-zone, with stomata; decrease in *Calluna* possibly an effect of *Pinus* rise. Influx diagram shows steady *Calluna* values. Charcoal reduced from previously high values to under 10% of TLP plus charcoal.
NHP4	19-29	AD 1850-1765	***Calluna* -Poaceae** *Pinus* values remain low from end of last sub-zone, at under 10%. Stomata appear at end of sub-zone. *Alnus* becomes sparse from the beginning of this sub-zone, and *Betula* decreases to consistently under 5% TLP. *Calluna* rises to over 60% TLP. Poaceae percentages show slight increase. Charcoal disappears at end of zone.
NHP3c	29-39	AD 1765-1445	***Calluna* Heath** *Calluna* dominant but decreasing at zone boundaries. Ericales present with small peak in *Empetrum* mid sub-zone. Cyperaceae peaks at zone boundaries to 20% TLP. Arboreal pollen percentages low at under10% TLP
NHP3b	39-51	AD 1445 -1105	***Calluna* - *Pinus*** *Pinus* increase to *c.* 30% TLP accompanied by sparse stomata; Decrease in Pinus to centre of sub-zone correlated with increase in charcoal. Subtle decrease in *Alnus* and *Betula.* Fluctuations in *Calluna* and other Ericales; increase in Cyperales from centre of sub-zone.
NHP3a	51-57	AD 1105-910	***Calluna* Heath** Decrease in *Empetrum*, small increases in *Erica tetralix* and *Vaccinium* Beginnings of increase in *Pinus* pollen; but no stomata present. Charcoal high as a percentage of TLP, but influx data reveal a defined peak at start of zone.
NHP2	57-71	AD 910-400	***Empetrum* Heath** High values of *Empetrum* peak at over 50% at lower zone boundary. Arboreal values are low at under 15% TLP. Charcoal levels remain high, influx data shows two defined peaks in charcoal values.
NHP1c	71-83	AD 400-90 BC	***Calluna* Heath** Decline in *Pinus* to under 10% TLP, with low values of arboreal pollen to under 20% TLP. *Betula* also slightly declines in TLP values. *Calluna* values remain dominant but decrease at end of zone mainly due to *Empetrum* rapid increase in TLP at this point. Small increase in Cyperales. Charcoal shows rapid increase in smaller size fractions and some overall increase.
NHP1b	83-93	90-525 BC	***Calluna* - *Pinus*** *Pinus* levels increase to *c.* 25% with stomata also present; *Calluna* values remain high peaking at 90 cm. Other Ericales present. Low Cyperales values at under 5% for Cyperaceae and Poaceae. Charcoal decreased from previous sub-zone.
NHP1a	93-100	525-850 BC	**Cyperales and Ericales** *Pinus* and arboreal pollen values are low at under 10% TLP. Ericales dominant; *Calluna* between 40 and 50% TLP with *Empetrum* and *Vaccinium* pollen present. Cyperales peak with Cyperaceae over 15% and Poaceae over 10%. Charcoal peak present, but only smaller size fractions.

6.3.1.2 Interpretation of NHP local vegetation history

NHP zones 1-4 and associated sub-zones are mainly defined by shifts in ground flora (Figures 6.1 and A1.1b). Throughout the 4 zones, spanning *c.* 2650 years from 850 BC to AD 1800, arboreal pollen percentages are consistently lower than those in all but two of the modern analogue sites, and these are sites lying in the currently open western end of the Glen (CCF and OPEN2, see Chapter 5). The local, and probably extra-local, landscape around the NHP basin was therefore, largely devoid of extensive woodland, containing just scattered trees or localised stands.

Two short phases; *c.* 500 – 50 BC, and *c.* AD 950-1200, do show increases in AP pollen percentages (to >40% TLP) and *Pinus* pollen (to *c.* 30% TLP). The presence of local *Pinus* trees is confirmed in these two periods by the presence of *Pinus* stomata (Fossitt 1994; Parshall 1999; and Chapter 6). *Pinus* pollen percentages in these phases are less than in any modern sample with trees present (see Figure 5.4). This probably indicates, therefore, woodland phases characterised by sparse scattered local *Pinus* trees, rather than canopy-forming woodland.

Despite low woodland density, arboreal diversity is likely to have been a little higher in the landscape throughout NHP1-4 than in the present landscape, with *Alnus* and *Betula* in low but consistent percentages. *Alnus* pollen percentages are higher than in any modern sample, indicating, at least some increased extra-local presence. *Quercus,* at 2% TLP in sub-zone 1a. may also represent sparse local trees: *Quercus* is found at *c.* 2% TLP in the CLKH core (Section 6.5.3), where one local tree stands within 20 m of the site. The presence of these taxa at least in the extra-local landscape is therefore likely.

For *Betula*, which increases to *c.* 20% TLP, an interpretation of local presence of this taxon is supported. Quantitative investigations into pollen source and loading into small woodland hollows has demonstrated that *Betula* can have a background pollen loading of 10-15% (Bradshaw and Webb 1985; Mitchell 1988). The modern analogue study presented in Chapter 5 provides similar estimations for Glen Affric, with a regression intercept of 13.5% for a plot of pollen against vegetation within the 20 m ring source area. A regression plot of *Betula* pollen and vegetation demonstrates that, for the surface samples, when *Betula* pollen is over 12% TLP the tree is always present within 20 m radius, and for 50 m radius, the background pollen loading reduces to 11.1%.

However, single grains of *Fraxinus*, *Sorbus aucuparia* and *Ulmus glabra* may present no assured interpretation. Whilst *Quercus*, *Fraxinus* and *Ulmus* are found elsewhere to be low pollen producers (Andersen 1970), single grains from these taxa, and from *Fagus*, all occur in the modern samples from Glen Affric (Table 5.4), despite no local tree presence. All except Fagus are present in the Glen (Table 5.4). However, especially given the lack of canopy surrounding the basin (Bunting *et al.* 2004), it is not possible to distinguish between an extra-local or local pollen source for these trees although for *Fagus* a regional source is likely.

Whatever the uncertainties for these more peripheral taxa on woodland mix, *Pinus* was certainly locally present during this phase, and accompanied, almost certainly given the modern evidence, by *Betula*. Sub-zone NHP1b spans some 500 years of peat accumulation, which would form a suitable timescale for the development and decline of a single stand of trees. This woodland phase is illustrated well by PCA (Figure 6.4). Samples from 88, 86 and 84 cm plot as outliers from the majority of samples from NHP zone 1, and are aligned with the location of plots from modern samples where present day stands of mixed woodland exist. Increases in *Pinus* and *Betula* pollen are also evident in both the concentration and the influx data (See appendix Figures A1.2 and A1.3), helping to support the interpretation.

The woodland phase of NHP1b, coincides with a decrease in charcoal. Small charcoal fragments are abundant in relation to pollen throughout the diagram. The influx data (Figure A1.2) defines discrete peaks in charcoal, three of which occur in sub-zones 1a and 1c, but none in sub-zone 1b.

The percentage of pollen from heath taxa is high throughout zone 1, at *c.* 50-70% TLP, indicating a heathland-dominated ground flora surrounding this small basin. *Calluna* is probably over-represented here. *Calluna* is shown to have a relevant pollen source area beyond the 20 m defined for other key taxa (Chapter 6). In contrast, modern pollen data from Glen Affric indicates that other Ericales may be under-represented in the pollen record. Relationships are not clearly significant between Ericales and plant presence (Bradshaw 1981; Hjelle 1997; and Section 5.5.3). However, individual sites with high cover of *Vaccinium myrtillus*, such as ANI, ARC RRB, and to some extent NHP, all contain low percentages of these taxa in the modern pollen record. Even a small percentage of *Vaccinium* may be indicative of its dominance in the local vegetation cover. *Vaccinium* pollen is consistently present throughout the NHP1 zone at *c.*

2% TLP, possibly becoming sparse in sub-zone 1c, although the consistent *c.* 3% TLP of the undifferentiated Ericaceae pollen in this sub-zone may be due, at least in part, to *Vaccinium*. *Empetrum nigrum* is present in the lower part of sub-zone 1a and peaks again in sub-zone 1b and at the top of NHP1c (see below) possibly indicating a drying of the basin surface (Tallis 1997). Any inference of increased dry conditions must be moderated however, by the presence of *Erica tetralix*, which also appears in the same pollen spectra. Since this plant prefers wetter conditions, there may be some indication of local heterogeneity in surface wetness.

Cyperales, both Poaceae and Cyperaceae, show a decline from a few percent TLP to under 1% at the onset of the woodland phase in NHP1b. This decline is also evident in the influx diagram, and is thus likely to present a real shift in presence, rather than one due to the Fagerlind effect.

Herbaceous taxa are not well represented in this zone, or in the pollen diagram as a whole indicating a species-poor heathland, as found today. Herbaceous taxa appear as single grains, including *Hordeum*-type, *Melampyrum*, *Potentilla*-type, *Plantago lanceolata* and *Ranunculus acris*-type. Little local vegetation interpretation can be gained from individual grains (see Section 5.5.3). However rarefaction, which provides a measure of palynological richness (Birks and Line 1992), does demonstrate that sub-zones 1a and 1c have a higher palynological richness (Figure 6.2), and therefore possibly a higher diversity, than is present in the *Pinus* phase in sub-zone 1b (Figure 6.1 and A1.1b). Although it is possible that the shift to woodland in NHP1b was a response to the cessation of natural fires, the development of the *Pinus* stand in sub-zone 1b is not likely to be to a closed woodland. It seems unlikely, therefore, that the stand development would cause a loss of biodiversity in the ground flora via changes in light levels.

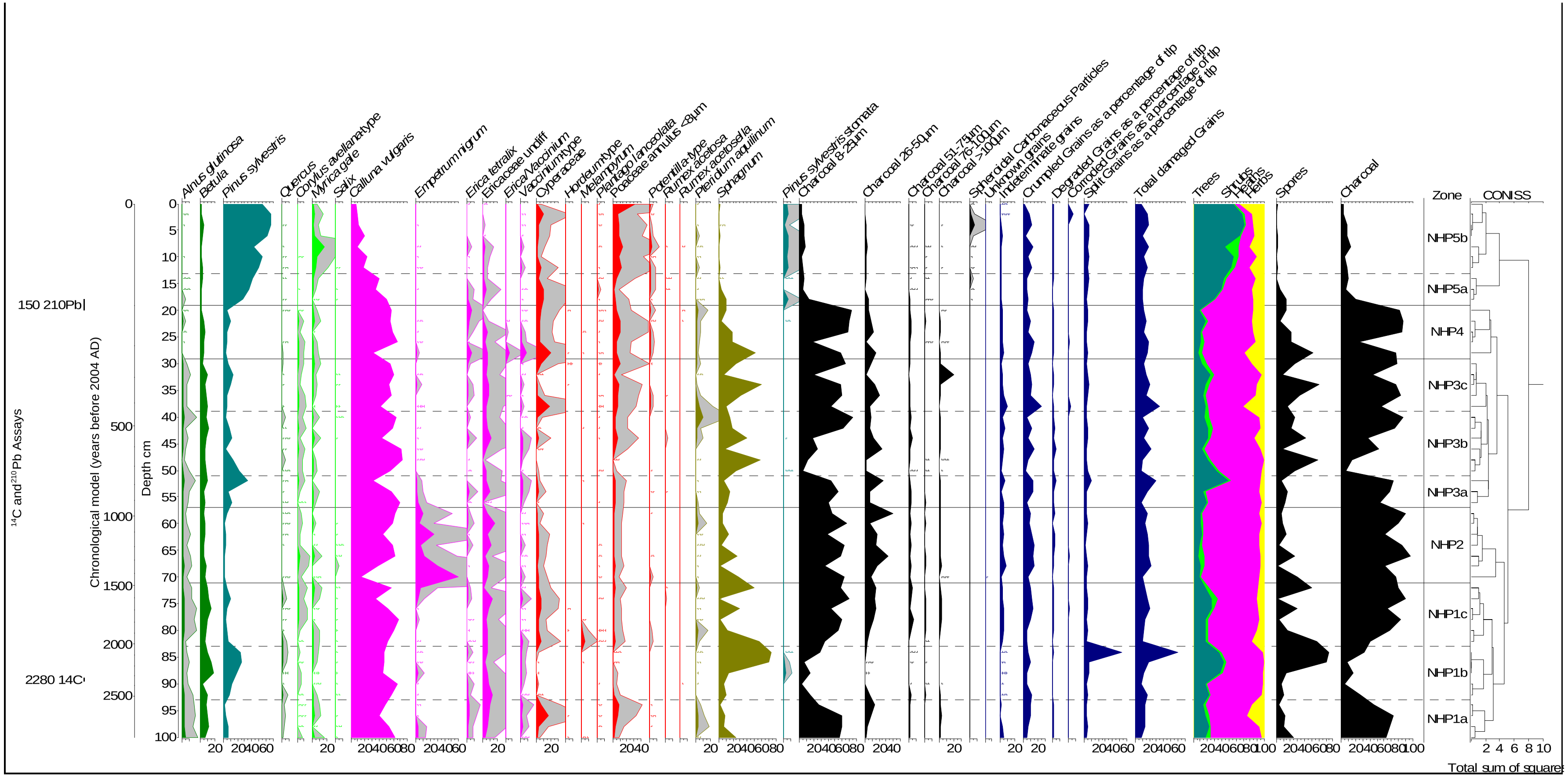


Figure 6.1: Pollen Diagram for selected taxa and palynomorphs from the NHP core. All land pollen taxa as a percentage of TLP; other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates and modelled chronology displayed. Note the 14C assay at 67 cm is not used in the chronological model.

NHP2 71-57 cm **(*c.* AD 620 – 1130)**

This zone depicts an open environment in a continuation from zone NHP1c with total AP percentages reduced further, to <15%. The absence of *Pinus* stomata indicates that *Pinus* trees continued to be absent from the immediate locality. Furthermore, *Pinus* pollen percentages are under 5% TLP throughout zone NHP2 indicating a strong probability of a restricted tree presence even in the extra-local landscape (regression analysis in the modern pollen predicts a background *Pinus* pollen percentage in open sites of *c.* 30% (Section 5.5.4). *Betula* and *Alnus* pollen continue to be present in the pollen record in low percentages, but lower than NHP1, whilst *Quercus* pollen decreases from 1 or 2% to a few grains. These values are unlikely to indicate local presence. The wider landscape may still hold pockets of more mixed woodland, but this zone is likely to represent the most open phase spanning a *c.* 500 year period in the landscape history.

The lower NHP2 zone boundary is marked by a decrease, then a recovery in *Calluna* pollen percentages (Figure 6.2). This decrease coincides with a sharp and remarkable increase in *Empetrum* pollen to values over 50% TLP. *Empetrum* is a limited pollen producer (Tallis 1997; and Chapter 5) and pollen percentages of this magnitude can often be attributed to a pollen-laden insect or a flower head in the sample (Moore *et al.* 1991). However, high *Empetrum* values are sustained over the whole zone, rather than a single sub-sample, and therefore represent a large increase in this taxon in the vegetation local to the site. This may also support the interpretation of an open environment as *Empetrum* does not tolerate shade (Ingrouille 1995). A high *Empetrum* pollen percentage can also be an indicator of severe drying of the bog surface (Tallis 1997). Although, in contrast Ingrouille (1995) notes that this species is confined to damp habitats and in addition, *Empetrum hermaphroditum* in present-day Fennoscandia is found across a broad spectrum of soil water conditions (P. Wookey *pers. comm.*).

Tallis (1997) found that significant *Empetrum* peaks in several Pennine cores correlated to 2700 BP, whilst other peaks were linked with the medieval warm period (AD 1100-1250) and to gully erosion. The linkage to gully erosion also implicates possible changes in peat accumulation rates. The peak in *Empetrum* at 69 cm is also the depth of the rejected ^{14}C assay

(Age Range: 2970-2800 cal. BP; see Section 4.2.1); whilst the accepted chronological model estimates the *Empetrum* peak to span from AD 440-AD 1000. Given the chronological uncertainties the *Empetrum* peak could fit well with the early stages of the Medieval Warm Period in Scotland, but equally could be a response to an earlier, or more localised event.

Acceptance of the ^{14}C assay at 69 cm together with the assay at 89 cm would have invoked interpretation of a peat inversion. The presence of wood fragments at 70 cm, after the inferred decline in woodland around the site, may demonstrate some ground disturbance at this level, which could provide a driver for a rise in *Empetrum*. The alternative scenario of an earlier *Empetrum* occurrence driven by some form of disturbance of the peat at this level cannot therefore be ruled out.

Another possibility is that the *Empetrum* peak is aligned to a period of sustained disturbance by fire; Gimingham (1964) notes that *Empetrum nigrum* can form a green appearance on burnt strips of hillsides together with *Vaccinium myrtillus* and it is possible that the *Empetrum* pollen is linked with the evidence from charcoal of continued burning around the site.

Herbaceous species in this zone are more diverse, Poaceae remains at a steady 3% TLP, whilst Cyperaceae decreases slightly from 4% to 1 or 2% TLP at the top zone boundary. *Plantago lanceolata and Potentilla*-type are perhaps more evident at the base of the zone than the top, whilst single grains of *Ranunculus acris, Filipendula*, *Fumaria*, and *Rumex acetosa* are present toward the top of the zone where the rarefaction analysis (Figure 6.2) shows an increase in palynological richness. *Melampyrum* is limited in this zone, despite the large peak in charcoal at 66 cm (*c.* AD 730) evident in the influx diagram (Figure A1.3). *Hordeum* grains are not present but some of the taxa found are indicative of disturbed ground, for example *Fumaria* although single grains make extremely tentative evidence (Chapter 5).

NHP3a-c: 57- 29 cm **(*c.* AD 1130 – 1770)**

This zone is divided into three sub-zones reflecting periods of subtle change and possible cyclicity in the heathland community; a detailed extract of the NAP pollen percentage and influx data is therefore provided as Figure 6.3 a) and b).

AP percentages remain low, but *Pinus* begins to increase to the upper NHP3a sub-zone boundary rising to *c.* 35% TLP. This peak also coincides with the appearance of a few *Pinus* stomata at 50 and 44 cm, indicating once more a local presence of *Pinus*, again probably as an open stand. This tree presence is short-lived (perhaps lasting little more than 200 years) as by the middle of sub-zone NHP3b AP and *Pinus* pollen percentages are reduced again.

At the base of zone NHP3a heathland taxa increase with *Calluna*, *Erica*, and *Vaccinium* all showing small percentage increases. *Empetrum* decreases here from the previously high percentages, with the overall depiction one of increasing diversity in heathland cover surrounding the site following a dry, perhaps disturbed, period of *Empetrum* domination. Fluctuations can be seen between *Calluna* and other Ericales with small peaks of *Vaccinium*, *Erica*, and *Empetrum* occurring between the *Calluna* peaks; these changes are highlighted in detail in an extracted pollen diagram in Figure 6.3. Gimingham (1964) notes that cyclicity between these taxa is normal on an undisturbed heather moor. However, charcoal also occurs in peaks throughout these sub-zones and perhaps burning helps to drive these subtle changes.

Herbaceous taxa and palynological richness decline during the period of *Pinus* presence in NHP3a-b; the pattern of *Pinus* increase and decrease in richness is similar to that in NHP1b (Figure 6.1). At the top of NHP3c *Hordeum*-type grains appear, again with some other herbaceous indicators including *Plantago lanceolata*. These taxa also coincide with a small peak in charcoal of the largest size class (>100µm). Although human impact cannot be concluded, it also cannot be ruled-out as a driver of these subtle changes. The cycling of heathland species, with charcoal episodes and with some evidence of ruderal herbs could well be envisaged as a result of a cycle of burning and grazing over this period.

NHP4: 29-19 cm **(*c.* AD 1770–1850)**

The base of this zone shows a near disappearance of *Alnus* from the fossil record, whilst *Pinus* pollen percentages remain low at under 10%, with stomata also absent. The depiction continues to be of a continued open landscape surrounding the locality of the pollen site, and in the extra-local to sub-regional landscape.

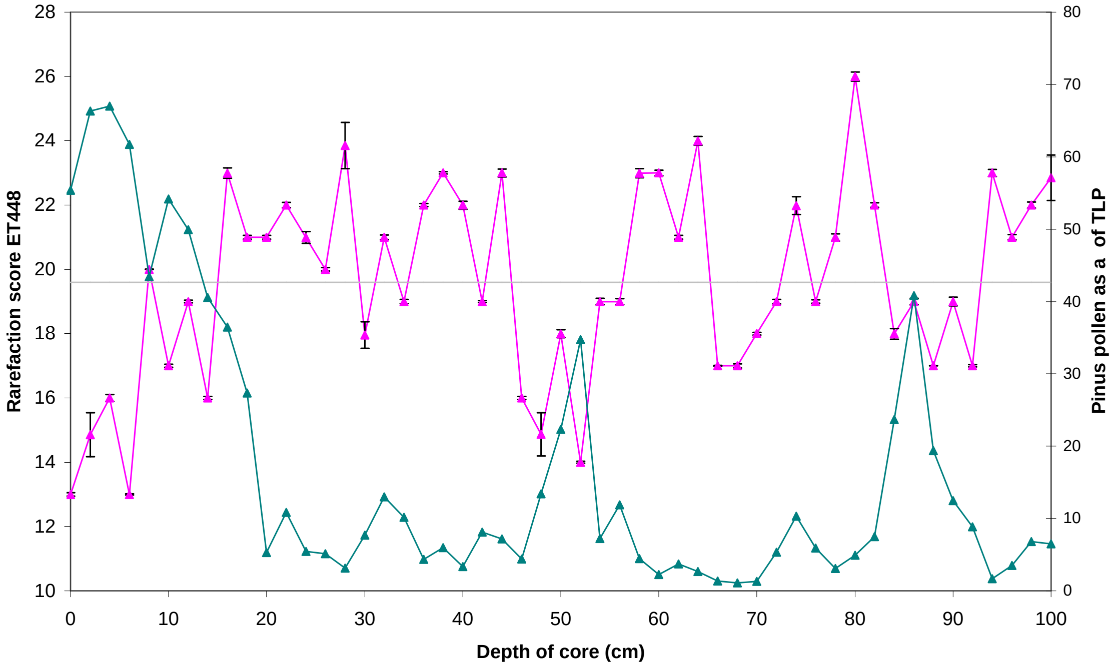
Calluna and other Ericales still form a major part of the ground flora during this period, although total herbaceous percentages increase slightly at the start of the zone, mainly due to a Cyperaceae peak. Palynological richness is above average and *Hordeum*-type grains still appear at some levels. Charcoal peaks in the influx diagram indicate possibly two distinct fire episodes during NHP4.

NHP5: 19-0 cm **(*c.* AD 1850–2005)**

The beginning of this zone is characterised by significant increases in *Pinus* pollen percentages and the consistent appearance of *Pinus* stomata (Figure 6.1). This indicates a marked expansion in *Pinus sylvestris* woodland in the locality of the sample area. Other tree taxa disappear in this zone apart from a few grains of *Quercus* and *Sorbus aucuparia,* which persist until the surface centimetres.

A decrease in *Calluna* TLP percentages is, in real terms, probably less significant as confirmed by the influx data (Figure A1.3). Poaceae pollen increases substantially to >30% TLP at the top of the diagram, whilst *Sphagnum* decreases at the lower boundary. This fluctuation indicates a change in the flora on the surface of the basin. Low values of *Vaccinium* still occur, indicating a domination of the ground flora surrounding the basin. This zone is characterised by a Poaceae-dominated flush system developing between the *Vaccinium/Calluna* heath-dominated raised ground.

The development of *Pinus*, and change in ground flora in this zone, again coincides with a disappearance of charcoal and a decrease in palynological richness from *c.* 20 cm depth (estimated age; AD 1830). Given that *Pinus* is likely to have been present as young trees for *c.* 10 years or more prior to pollen production, a regeneration phase around NHP can be envisaged *c.* AD 1810-1820. The statistical accounts of Scotland indicate some land abandonment at this time in favour of intensive sheep farming (http://stat-acc-scot.edina.ac.uk/link/1834-45/Inverness/Kilmorack/). The period between land abandonment and sheep stocking is not clear, but is likely to have been short. The climate was also reported as variable at this time, with the 1791 statistical accounts reporting a past warm period, and present (at the time of the report) cold one. Whilst the 1834-45 accounts reported a then current warm period which had been with them for "*some past years*" (Section 2.2.1.5). Thus, several drivers of change are possible but it does seem likely that the forest regenerated in the presence of grazing, although the extent to which grazing was shepherded and managed, or indeed woodland was planted, during this period is not clear. What is also difficult to reconcile is the map evidence from 1665 (Bleau and van der Krogt 2006) and 1750 (Roy's military map) both of which show the presence of woodland in this part of Glen Affric. However, given the likely inaccuracies in the map data (Smout 2005) and the presence of woodland at BEAT not far to the east, this early map evidence gives little reason to question the pollen interpretations.



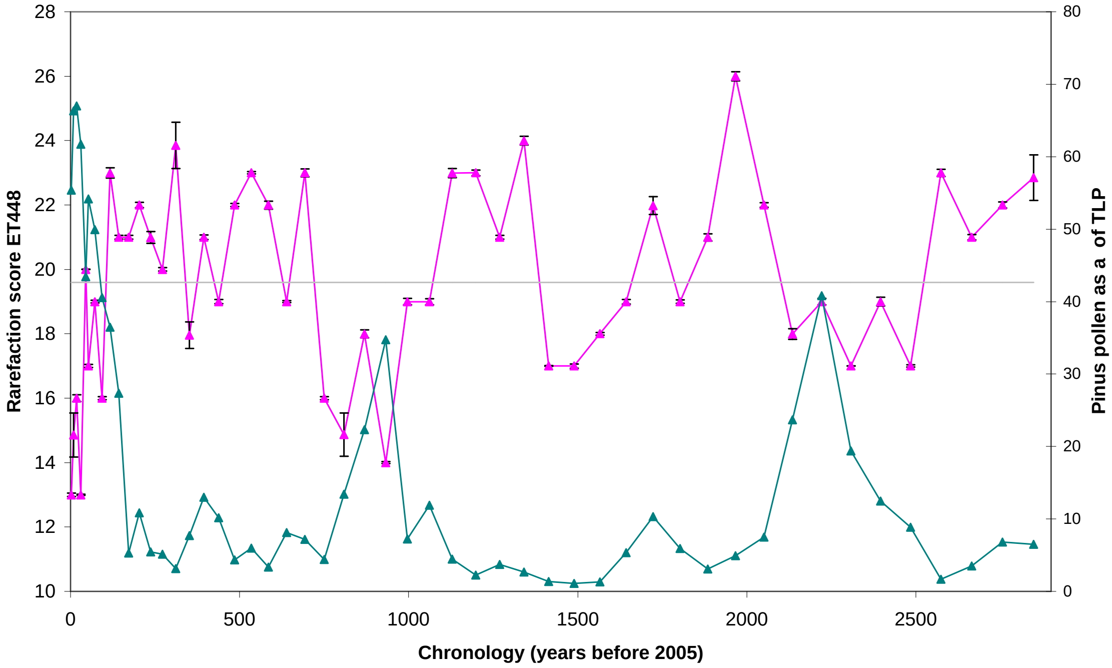


Figure 6.2: Palynological richness for the NHP core (ET_{448}) Expected number of pollen taxa for a normalised pollen count of 448 grains per sample, (pink line) compared with *Pinus* percentage fluctuations (green line). Against depth (top graph) and chronology (bottom graph).

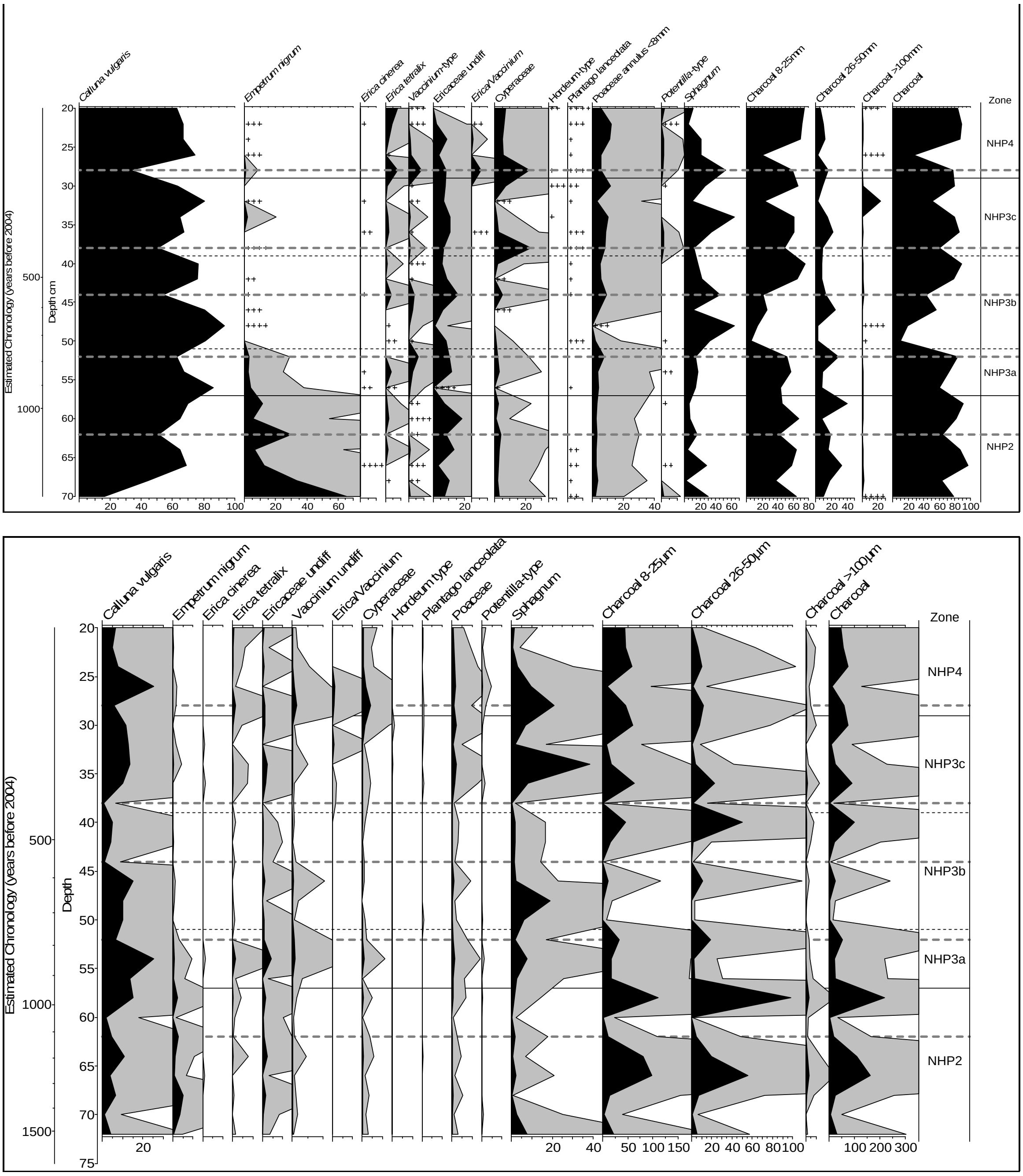


Figure 6.3: Selected stratigraphic evels of NHP pollen diagram in more detail

a) NHP selected stratigraphic levels and taxa to show cyclicity in Ericales (Taxon as a percentage of NAP)

b) NHP selected stratigraphic levels and taxa to show cyclicity in Ericales (Influx data)

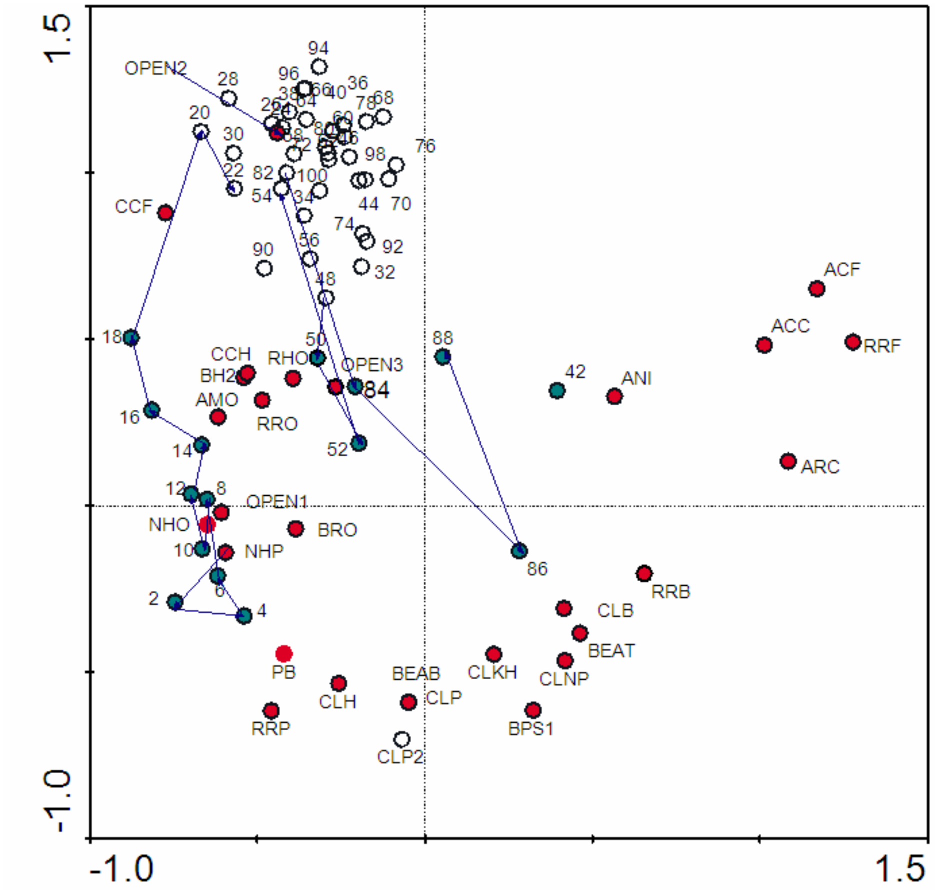


Figure 6.4: PCA ordination of modern pollen samples from Figure 5.19 with sites from the NHP core plotted as passive samples (numbers refer to depth of sample) to demonstrate where the samples from the NHP core correlate with modern analogues. The passive plot ensures that the NHP samples do not influence the axes. The lines between sample points demonstrate periods when vegetation composition is shifting at NHP.
Axis 1= 36.6% of the variance Axis 2 = 24.1%.

6.3.2 PB pollen core

6.3.2.1 Summary of main features of diagram and main zone changes

PB is divided into four zones, each divided into 2 sub-zones, marking major and minor changes in the pollen stratigraphy. These are listed in Table 6.2.

Table 6.2: Zone and sub-zone boundaries and summary pollen descriptions the PB core.

Zone	Depth (cm)	Chronological Model	Description
PB4b	0-5	AD 1970-2004	***Pinus – Calluna*** Increase in *Pinus* % TLP with decrease in *Calluna*, possibly due fluctuations in pollen productivity of *Pinus*.
PB4a	5-21	AD 1600-1970	***Pinus – Calluna*** Increase and then decrease in *Pinus* % TLP. Stomata appearing and becoming constant. Low arboreal species diversity. Charcoal not present. Lower pollen concentrations in this zone.
PB3b	21-27	AD 1350-1600	***Calluna - Poaceae*** Slight increase in *Pinus* % and sparse stomata, although influx data remains low. Decrease in *Calluna* at start of zone with a peak in Poaceae.
PB3a	27-49	20BC- AD 1600	***Calluna -Charcoal*** *Pinus* under 20% TLP; with *Calluna* at *c.* 60% TLP Low arboreal %. Charcoal peak at 40 cm coincident with charcoal peak visible in the stratigraphy. *Empetrum* levels fluctuating throughout zone. Pollen concentrations high in this zone. *Calluna* decrease at top of zone evident in influx diagram.
PB2b	49-55	500-20 BC	***Calluna - Charcoal*** *Pinus* under 20% TLP; with *Calluna* at *c.* 60% TLP *Quercus* levels fluctuating and *Alnus* decreasing. Some *Hordeum*-type grains at zone boundary. Large charcoal peak (evident on the influx diagram). Small peak in damaged grains and increase in pollen concentration.
PB2a	55-73	2250-500 BC	***Calluna –Empetrum*** *Pinus* decreasing to *c.* 20% TLP disappearance of stomata apart from presence at 58-64 cm; *Corylus*, *Alnus* and *Betula* all decreasing slightly. *Calluna* percentages increasing. *Empetrum* peak at start of zone. *Potentilla* significant in this level. Charcoal peak at start of zone and continued low presence of charcoal throughout zone. Increasing pollen concentration.
PB1b	73-83	2620-2250 BC	***Pinus – Betula*** Slight decrease in *Pinus*, stomata still present. Indications of continued mix to woodland composition, but *Ulmus* disappearing. *Calluna* increasing.
PB1a	83-100	3260-2620 BC	***Pinus – Betula with Ulmus*** *Pinus* values at 50% TLP+ *Pinus* stomata present: Indications of mixed woodland: *Ulmus* present throughout sub-zone. Low ground flora percentages, including *Calluna;* Cyperaceae peaking at sub-zone boundary.

6.3.2.2 Interpretation of PB pollen zones

PB1a-b: 100- 73 cm **(*c.* 3260 – 2620 BC)**

The oldest zone; PB1 is divided into two sub-zones (Figure 6.6). Sub-zone 1a (3260-2620 BC) is dominated by arboreal pollen at >60% TLP. *Pinus* is definitely present in the local landscape at the start of the zone as stomata are present to 98 cm. Between 96 cm and 94 cm, stomata disappear from the record. This could indicate a loss of trees from the very local (*c.* 20-30 m radius) of the site for a brief period. However, an extra-local mixed species woodland is still depicted by the high *Pinus* pollen and AP percentages. Sub-zone 1b marks the beginning of a gradual decline in the woodland, with AP values decreasing to below 60% TLP although with some recovery mid sub-zone. *Calluna* percentages rise at this point, but reference to the influx diagram (Figure A2.3) confirms this AP decrease. Palynological richness fluctuates, but is generally high, which is unusual for woodland phases (see NHP rarefaction results above) and supports the interpretation of a mixed and still fairly open woodland around this site over the *c.* 1400 years spanned by the zone.

Major taxa in the ground flora fluctuate in zone 1, *Calluna* percentages increase throughout the zone, with small peaks in pollen percentages associated with the disappearance of stomata at 96 cm and with a reduction in Cyperaceae pollen, and with *Sphagnum* spore percentages, which are initially high but decrease dramatically from >40% to under 15% TLP at 96 cm. This shift may indicate a change to drier conditions; also supported by a peak in *Empetrum*, However, this peak in *Empetrum* may precede the decrease in *Sphagnum* and Cyperaceae possibly demonstrating heterogeneity in the edaphic conditions. The temporal sample resolution at this depth is poor making it difficult to assess the temporal span and order of these subtle changes.

Charcoal increases from the 1a-1b sub-zone boundary may also provide supporting evidence for a change in environmental conditions. At 82 cm the micro-charcoal percentage curve presents a small but sharp rise in the smaller size classes (Figure 6.6). However, the influx data rise is less assured and the increase in the percentage calculation may be relative to a decline in pollen concentration. (Figures A2.2 and A2.3).

PB2a-b: 73- 55 cm **(*c.* 2250– 20 BC)**

Pinus pollen percentages decrease in sub-zone 2 to <20% TLP by the end of sub-zone 2a. *Betula* decreases slightly, but other arboreal taxa - *Quercus*, *Alnus*, *Corylus* - remain steady until the end of sub-zone 2a, depicting a continued presence in the extra-local or regional landscape. *Pinus* stomata make a brief appearance at 64 and 62 cm. Given the low *Pinus* pollen percentages this is possibly due to a single *Pinus* tree growing nearer to the site over a *c.* 200 year period. In addition, *Sorbus aucuparia* may be present, with a small but consistent number of grains appearing over this zone. By the end of sub-zone 2b the breakdown of woodland appears more complete, with levels of AP consistently at *c.* 20% TLP, a value which demonstrates open heathland in the modern pollen study (Chapter 5). The breakdown of the diversity of the extra-local woodland is also depicted as *Quercus* becomes a sparse contributor to the pollen record.

A phase of *Empetrum* growth, probably on the basin surface (Pardoe 1996) marks another fluctuation in ground flora at the base of sub-zone 2, continuing the fluctuations in ground flora evident in zone 1 (see above). The *Empetrum* peak is significant for this taxon (Tallis 1997), rising to *c.* 15% TLP, and sustained over 4 sub-samples representing possibly 400 years of peat accumulation. This event coincides with an exceptional peak in charcoal percentages (to *c.* 80% of pollen plus charcoal at 70 cm); this charcoal increase is evident as one of three large peaks in the influx data across zones 2 and 3. The *Empetrum* rise can be an indicator of disturbed ground and gully erosion episodes (Tallis 1997), although on this site, which is on flatter ground and protected from inwash from surrounding small slopes by a bank the likelihood of this kind of erosive episode is probably slight.

Calluna percentages continue to increase in zone PB2a but small concurrent increases in Poaceae and *Potentilla*-type pollen indicate that the heathland was likely to be interspersed with grassy patches at least on the basin surface. This is supported by the increase in variety of ground flora in the zone, including *Galium*, *Geum*, Ranunculaceae and *Succisa*.

The lack of woodland in this zone may be linked to an increase in palynological richness (Figure 6.5), which is concurrent with fluctuations in charcoal.

PB3a-b: **55 - 21** cm **(20 BC-AD 1600)**

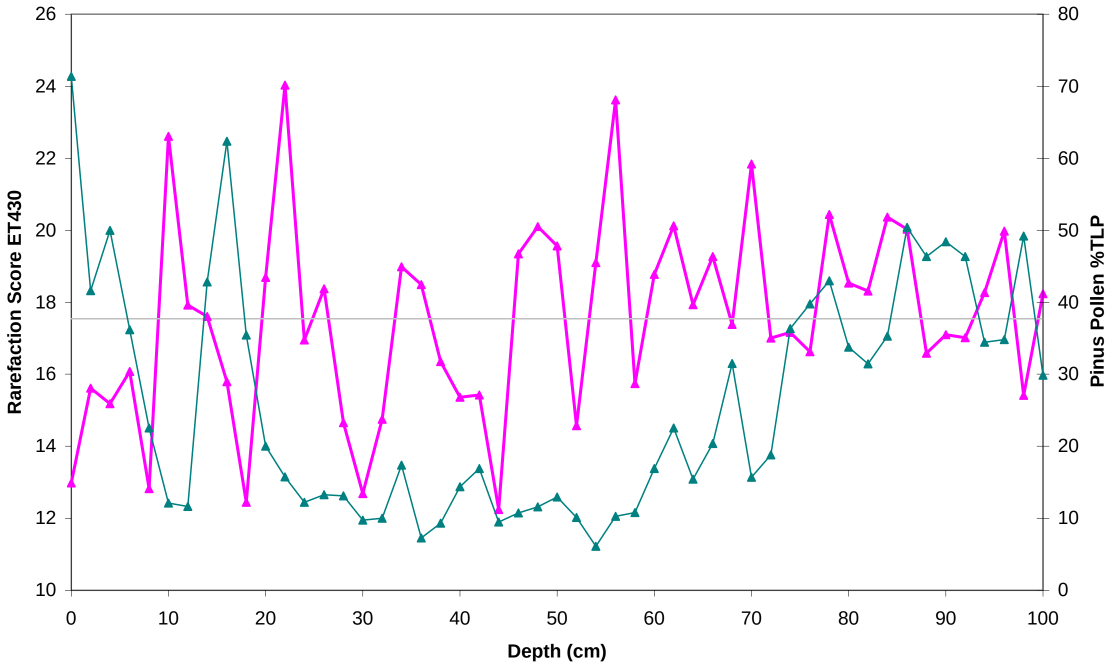
In this zone low arboreal percentages are maintained. Pine stomata do not appear throughout sub-zone 3a and *Alnus* is reduced to insignificant levels together with *Quercus*. *Sorbus aucuparia* and *Ulmus* are represented by a few grains. The depiction is of a sustained open landscape over a period of 1600 years.

Heathland is dominant in the landscape in sub-zone PB3a, with *Calluna* at >60% TLP. Correlated with this, the presence of discrete peaks in other Ericaceous pollen taxa demonstrate several, possibly cyclic, fluctuations between *Empetrum* and *Vaccinium*, and *Calluna*. Some Poaceae and limited Cyperaceae probably represent a mosaic of communities at the micro-scale on the basin surface, and perhaps some surrounding damp flushes in the landscape, these creating some areas for herbaceous taxa such as *Potentilla* and *Pyrola* to flourish.

Sub-zone 3b marks a change in this landscape. Poaceae begins to increase, with some increase in Cyperaceae, while *Calluna* decreases together with *Empetrum*. *Myrica* and *E. tetralix* also both peak in this sub-zone. These factors all indicate a change in the surface conditions of the basin, and possibly the wider landscape. The sub-zone is also marked by a cessation in charcoal influx.

PB4a-b: **21- 0** cm **(*c.* AD 1600-2004)**

Pinus pollen percentages rise sharply in zone PB4a, accompanied by stomata, probably indicating the development of the contemporary senescing stand of *Pinus*. The diversity of other woodland taxa and the palynological richness of the zone decreases sharply (Figure 6.5 and 6.6). The following marked decrease in arboreal taxa at 10 cm (*c.* AD 1900) does not fit well with the probable age of the current local stand of trees around this basin. Preliminary coring has indicated an age of *c.* 400 years for one of the trees (C. Edwards *pers. comm.*). The CIC ^{210}Pb data (Section 4.3.2.4) shows a marked dip in activity at *c.* 10 cm and this, in consideration of the pollen data, may demonstrate a disruption of the stratigraphy. However, the palynological richness is also high over this level, and *Pinus* influx values do not demonstrate the same decrease as the percentage values (Figure A2.3). It seems, therefore, that the decrease in *Pinus* as a percentage of TLP may be due to the Fagerlind effect given the increase in the pollen influx of other taxa.



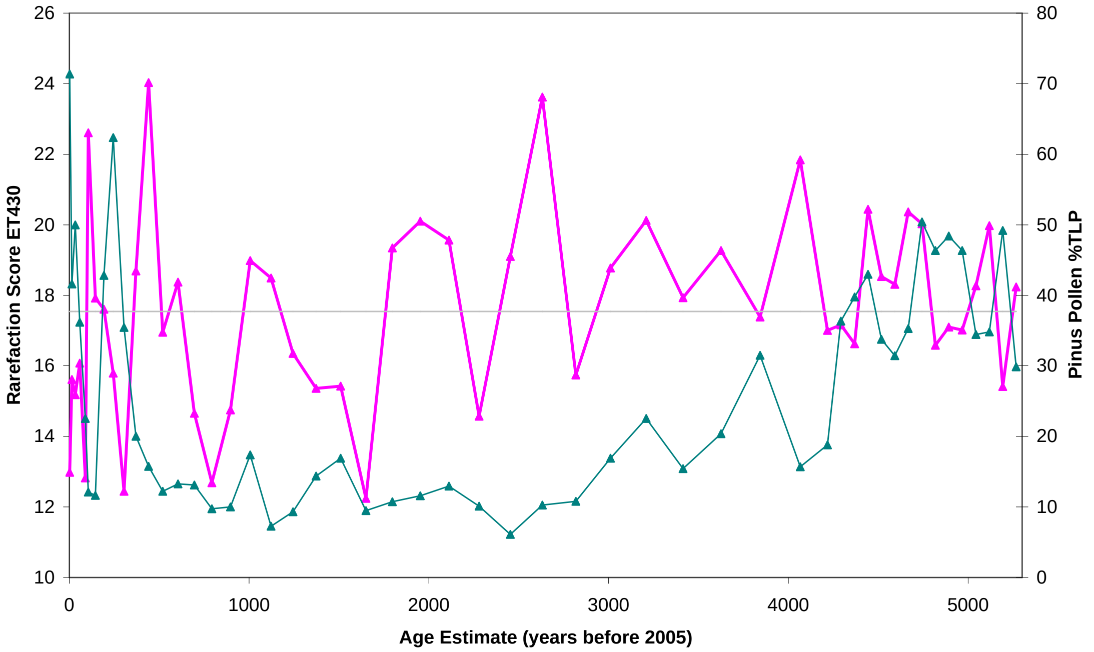


Figure 6.5: Results of rarefaction analysis on the PB core (ET_{430}) Expected number of pollen taxon for a normalised pollen count of 430 grains per sample, (pink line) compared with *Pinus* percentage fluctuations (green line). Against depth (top graph) and chronology (bottom graph).

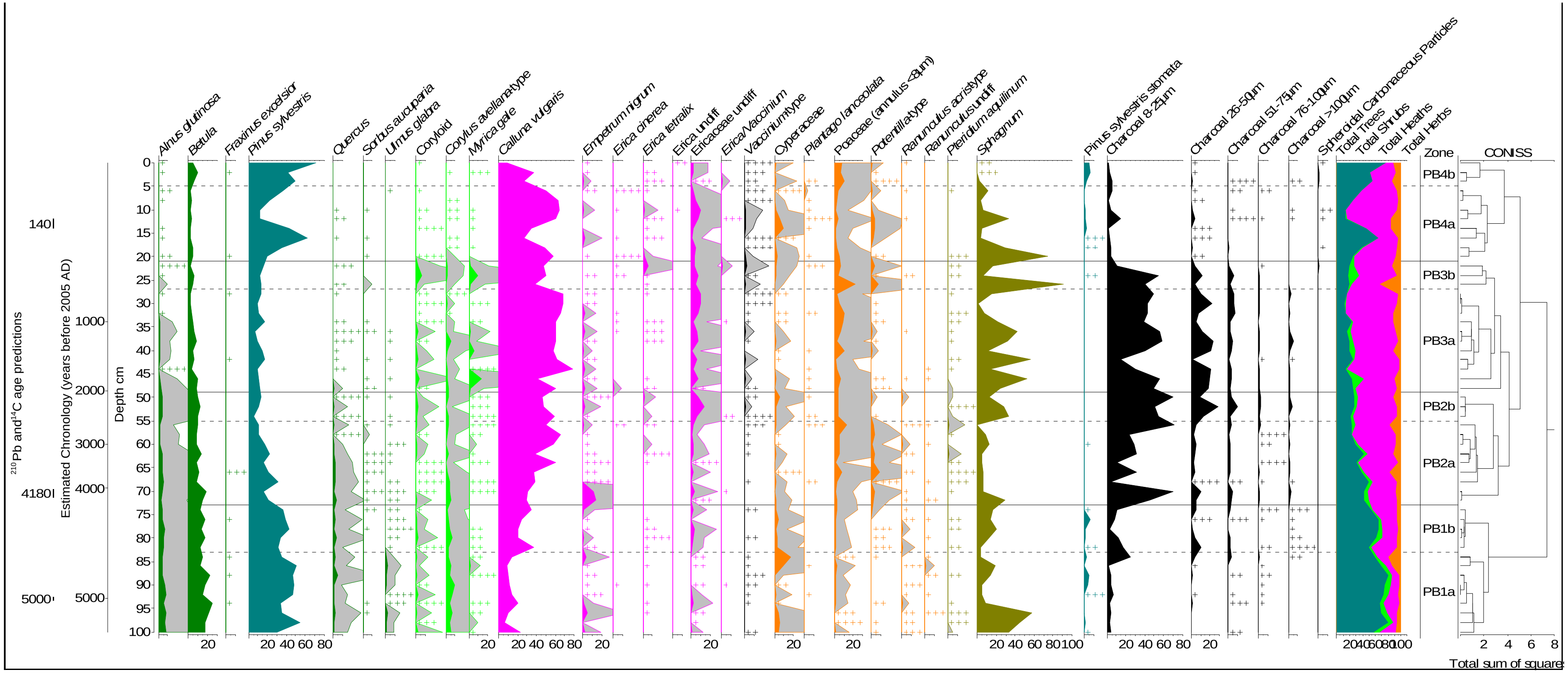


Figure 6.6: Pollen Diagram for selected taxa and palynomorphs from the PB core. All land pollen taxa as a percentage of TLP: other taxa as a percentage of TLP+ Group. Left axis against depth with age estmates and modelled chronology displayed.

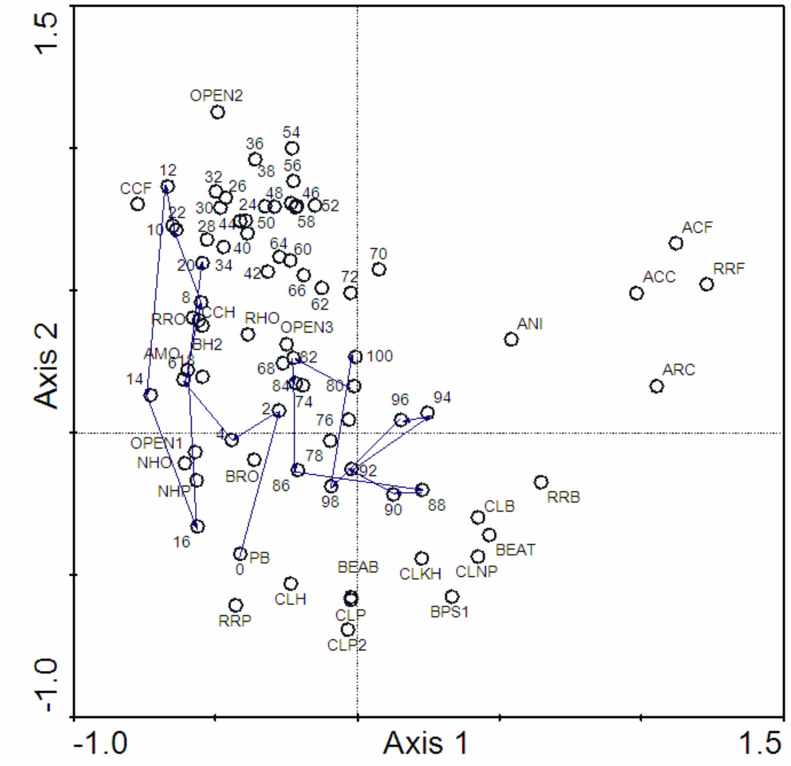


Figure 6.7: PCA ordination of modern pollen samples from Figure 5.19 with sites from the PB core plotted as passive samples (numbers refer to depth of sample) to demonstrate where the samples from the PB core correlate with modern analogues. The passive plot ensures that the PB samples do not influence the axes. The lines between sample points demonstrate periods when vegetation composition is shifting at PB.

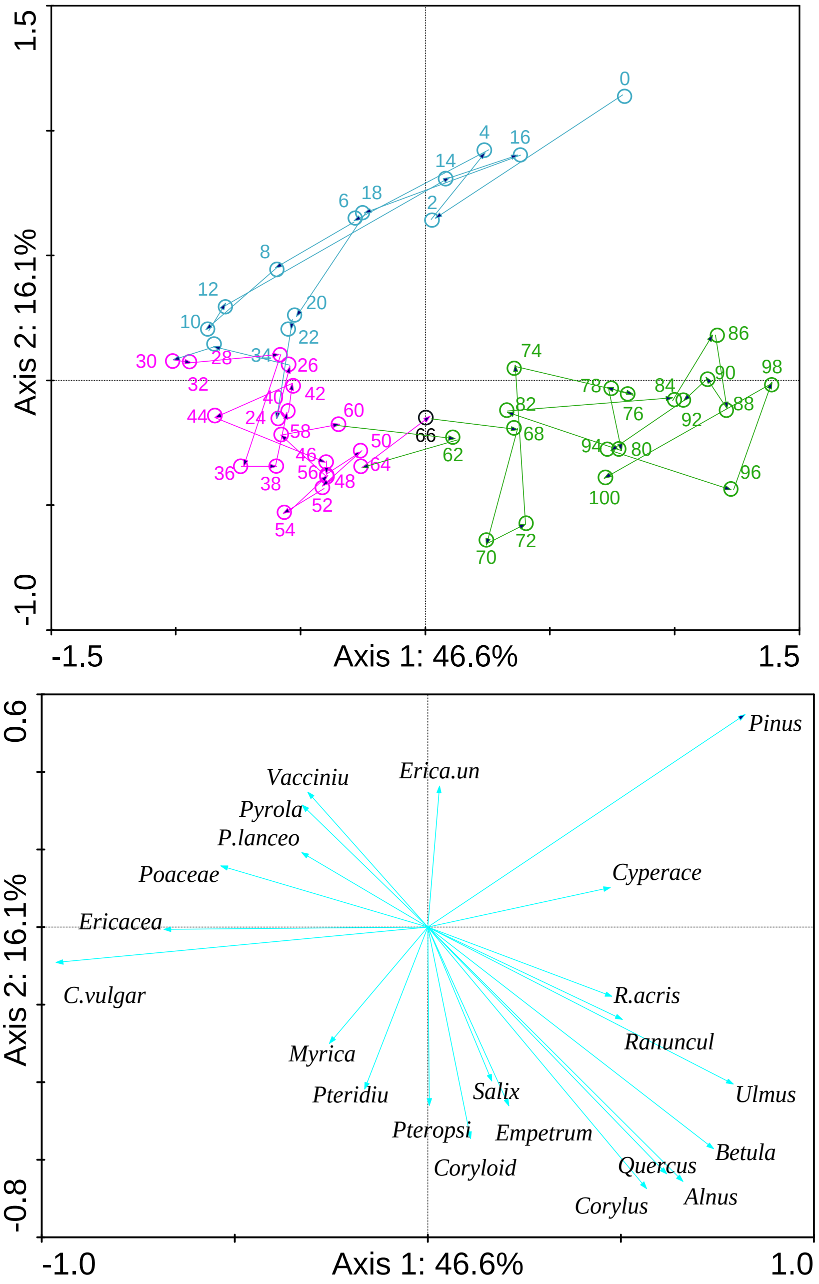


Figure 6.8: PCA ordination of PB percentage pollen data using all data including spores but not *Sphagnum*. The numbers of samples refer to sample depth. These are joined in sequence by lines to illustrate major shifts in vegetation composition.
Axis 1 46.6%, Axis 2 16.1%

6.3.3 BEAT pollen core

6.3.3.1 Summary of main features of diagram and main zone changes

A summary pollen percentage diagram is presented in Figure 6.9. BEAT is divided into three zones, each divided into associated sub-zones, marking major and minor changes in the pollen stratigraphy; these are listed in Table 6.3. The zones mark a closed phase of *Betula* and mixed broadleaved woodland, a short open phase dominated by Cyperaceae and then *Calluna*, and a current mixed woodland phase where *Pinus* is co-dominant with *Betula*. These phases are clearly defined in the PCA plots in Figure 6.11 and 6.12 in which BEAT pollen data are plotted as passive samples on the modern pollen data from Figure 5.19.

6.3.3.2 Interpretation of BEAT pollen zones

BEAT1a-c: 67- 100 cm (70 BC - AD 1630)

Pollen concentration is high in this zone and peat is accumulating slowly. The high AP percentages at 70-80% TLP - apart from a small dip to 50% TLP at 78 cm (AD 1080) - indicate a continuous woodland canopy. However, whilst *Betula* pollen percentages are high at >40% TLP, *Pinus* pollen percentages remain low at *c.* 20% TLP, which is well below the cut-off point for ascribing local presence (Chapter 5). In addition, *Pinus* stomata do not appear in this zone. The presence of *Alnus* at *c.* 10% TLP at the base of sub-zone 1a, and small peaks in *Quercus, Sorbus aucuparia* and *Corylus avellana* pollen percentages, probably indicate the likelihood of some individual trees from these taxa amongst a *Betula*-dominated broadleaved woodland, with *Pinus* present only in the wider landscape.

Key ground flora taxa are present in modest percentages, probably suppressed by the high AP productivity under the woodland canopy. *Calluna*, Cyperaceae and Poaceae occur between 5 and 10% TLP throughout the zone. *Calluna* increases together with *Erica tetralix* at 76 cm. *Succisa* is present at the base of sub-zone 1a, whilst *Gallium* presents small peaks in sub-zones 1b and 1c correlated with small charcoal peaks. Diversity, as indicated by palynological richness, fluctuates in this zone, but is generally higher that in the more recent pollen spectra (see trend line in Figure 6.10).

BEAT2a-b: 37-67 cm (AD 1630-1850)

The transition to this zone is marked by a rapid shift in pollen concentration, a marked and sudden decrease in woodland pollen taxa, together with a marked and sudden increase in Cyperaceae. The possibility of a hiatus in peat accumulation is, rejected however, by the chronological model presented in Section 4.3.4.3. The increase in Cyperaceae may well indicate a change in the hydrological conditions of the basin, and this is supported by the appearance of numerous diatoms in the samples above 67 cm (Figure A3.1c).

Table 6.3: Zones, sub-zones and associated vegetation descriptions for BEAT core.

Zone	Depth cm	Chronological Model	Description
BEAT3b	0-19	AD 1940-2003	***Pinus – Betula*** Arboreal pollen percentages remain high, dominated by *Pinus* and with a loss of arboreal diversity. Stomata are present throughout the zone. Ground flora cover is low and diversity reduced. *Sphagnum* increases and diatoms remain present in low values. Towards the top of the zone *Alnus* disappears from the record and the limited charcoal grains present before this zone disappear.
BEAT3a	19-37	AD 1850-1940	***Pinus – Betula*** Arboreal pollen recovers dominance in this zone rising to 80% TLP at the start of the zone. The lower zone boundary is marked by a peak in *Pinus* pollen to >60% TLP accompanied by a small rise in stomata. *Betula* also recovers to >40% TLP and in this zone *Pinus* and *Betula* percentages fluctuate in turn. Ground flora percentages are low, with *Calluna* ad Poaceae as co-dominants and Cyperaceae low but rising slightly in the middle of the zone. Other herbaceous taxa are poorly represented, in quantity and variety. Diatoms are present through the zone.
BEAT2b	37-51	AD 1760-1850	***Pinus – Calluna*** *Pinus* percentages are high at the start of the sub-zone *c.* 60% TLP but rapidly dip mid sub-zone to *c.* 25% TLP before rising once more. Stomata are continuously present, but rise and dip coincident with the pollen percentages. *Betula* remains low from lower zone boundary at <10% TLP and *Alnus*, *Quercus* and *Corylus* are all sparse in this zone. Cyperaceae is reduced significantly from previous zone to <5% TLP and *Calluna* increases to a peak of *c.* 60% mid sub-zone. But diatoms continue into this sub-zone. *Hordeum* is not present but *P.lanceolata* and *R.acris* type grains continue to be present in low numbers.
BEAT2a	51-67	AD 1630-1760	***Pinus* – Cyperaceae** *Pinus* percentages remain low at the start of this subzone, but peak by the end of the sub-zone to *c.* 60% TLP. *Pinus* stomata appear sparsely at the base of the sub-zone, and increase % rapidly to a peak of *c.* 20% TLP plus stomata at upper sub-zone boundary. *Betula* percentages remain high then dip rapidly at upper zone boundary to <10% TLP. Cyperaceae increases rapidly to >50% TLP at start of sub-zone and then decreases, but percentages remain significant at over 20% throughout the sub-zone. Diatoms also appear in this sub-zone at up to 5% of pollen plus diatoms. *Hordeum* type pollen appears in the sub-zone at *c.* 1% or a few grains as does *Plantago lanceolata* and *Ranunculus acris* type. *Calluna* increases slightly, and *E.tetralix*, *Empetrum* and *Vaccinium* also appear as single grains.
BEAT1c	67-79	AD 1030-1630	***Betula – Alnus*** Continuing *Betula* dominance with levels rising from brief dip at lower sub-zone boundary. *Pinus* is at background pollen levels of <20% TLP. *Alnus* recovers from dip at lower sub-zone boundary to *c.* 5% TLP. *Calluna* and *E tetralix* return to previous levels after their brief peak at 78 cm. Poaceae remains a co-dominant in the ground flora.
BEAT1b	79-91	AD 400-1030	***Betula - Alnus - Gallium*** *Betula* remains dominant from previous sub-zone, however percentages dip briefly to *c.* 30% TLP at 88 cm and decline to upper sub-zone boundary. *Pinus* pollen percentages rise slightly to *c.* 30% TLP, but no stomata are present. *Quercus* decreases from previous sub-zone to a few grains per sample. Poaceae remains constant at 7-10%TLP and *Potentilla* is also a constant presence in low percentages. *Gallium* appears at 2-3% TLP throughout the sub-zone. *Calluna* percentages remain low from previous levels but rise at end of the sub-zone together with a small peak in *Erica tetralix*.
BEAT1a	91-100	AD 70BC-400	***Betula – Alnus*** *Betula* is dominant with values >40% TLP and rising to the end of the zone, whilst *Pinus* is low with under 20% TLP throughout this sub-zone. *Alnus* rises and then steadily decreases through the sub-zone to <10% TLP. *Corylus* is also present as low percentages: 5-7%.TLP Ground flora cover is low at under 20% TLP, comprising mainly Poaceae, *Potentilla* and *Succisa*. *Calluna* is not well represented, and is likely to be background pollen. But a few grains of *Erica tetralix* and *Vaccinium*-type may demonstrate local presence.

The indications of possible climatic change at a broader scale are inconclusive. Although the previously *Betula*-dominated woodland fails rapidly, several ground flora taxa maintain a presence including the Ericales and also *Pteridium aquilinum,* which prefers the drier brown earths. *Hordeum*-type pollen also appears from 67 cm and charcoal peaks continue from sub-zone 1c. Although the *Hordeum* may not indicate local presence, two small peaks at *c.* 2% TLP may be a more convincing indicator than single grains. It is still problematic, however, to infer definite human land use from these data, as some wild Poaceae species produce pollen grains of similar size classes to *Hordeum*-type, and these tend to prefer wet conditions.

Whatever the drivers of woodland breakdown and hydrological change, they were short-lived. At 62 cm (AD 1675), *c.* 40 years later, *Pinus* woodland had invaded the site, confirmed by the presence of *Pinus* stomata in the middle of sub-zone 2a. *Pinus* pollen percentages also increase sharply over *c.* 100 years to a peak of *c.* 60% TLP at 48 cm (AD 1780) and decline together with stomata by AD 1820 in sub-zone 2b, indicating *c.* 150 years of *Pinus* woodland. During this phase of opening of the woodland canopy *Calluna* rather than Cyperaceae was the dominant ground flora.

BEAT3 a-b: 37- 0 cm (AD 1850-1940)

The decline in *Pinus* woodland in the middle of sub-zone 2b was immediately followed by a new regeneration of woodland. *Pinus* stomata demonstrate the continued local presence of this species, but an increase in *Betula* demonstrates the regeneration of the present mixed woodland phase in the last *c.* 150 years. During this period diversity, as defined by palynological richness (Figure 6.10) decreases and *Alnus* pollen disappears indicating the disappearance of this taxon from the landscape by the end of sub-zone 3b; and pollen from ground flora remains suppressed by that from the woodland canopy.

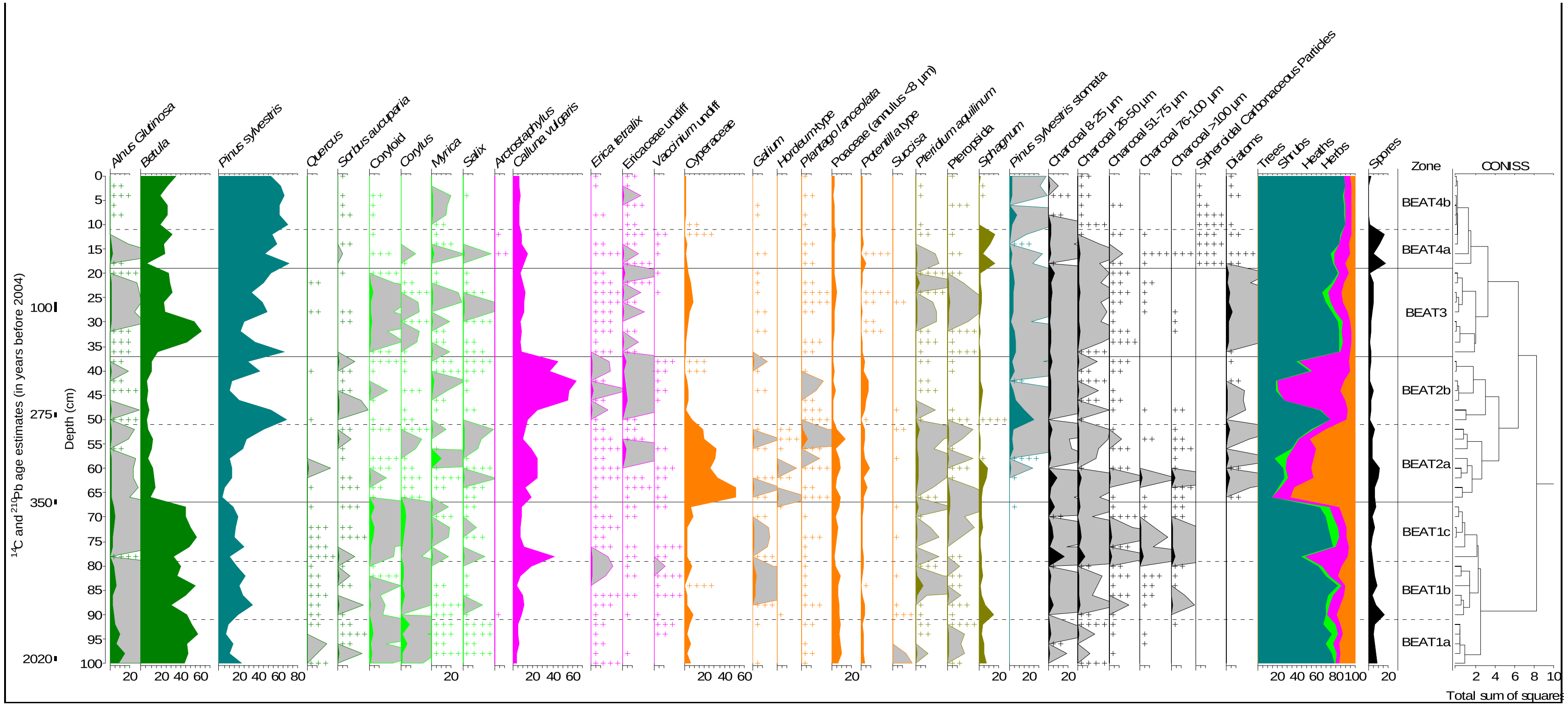


Figure 6.9: Summary Pollen Diagram for selected taxa and palynomorphs from the BEAT core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

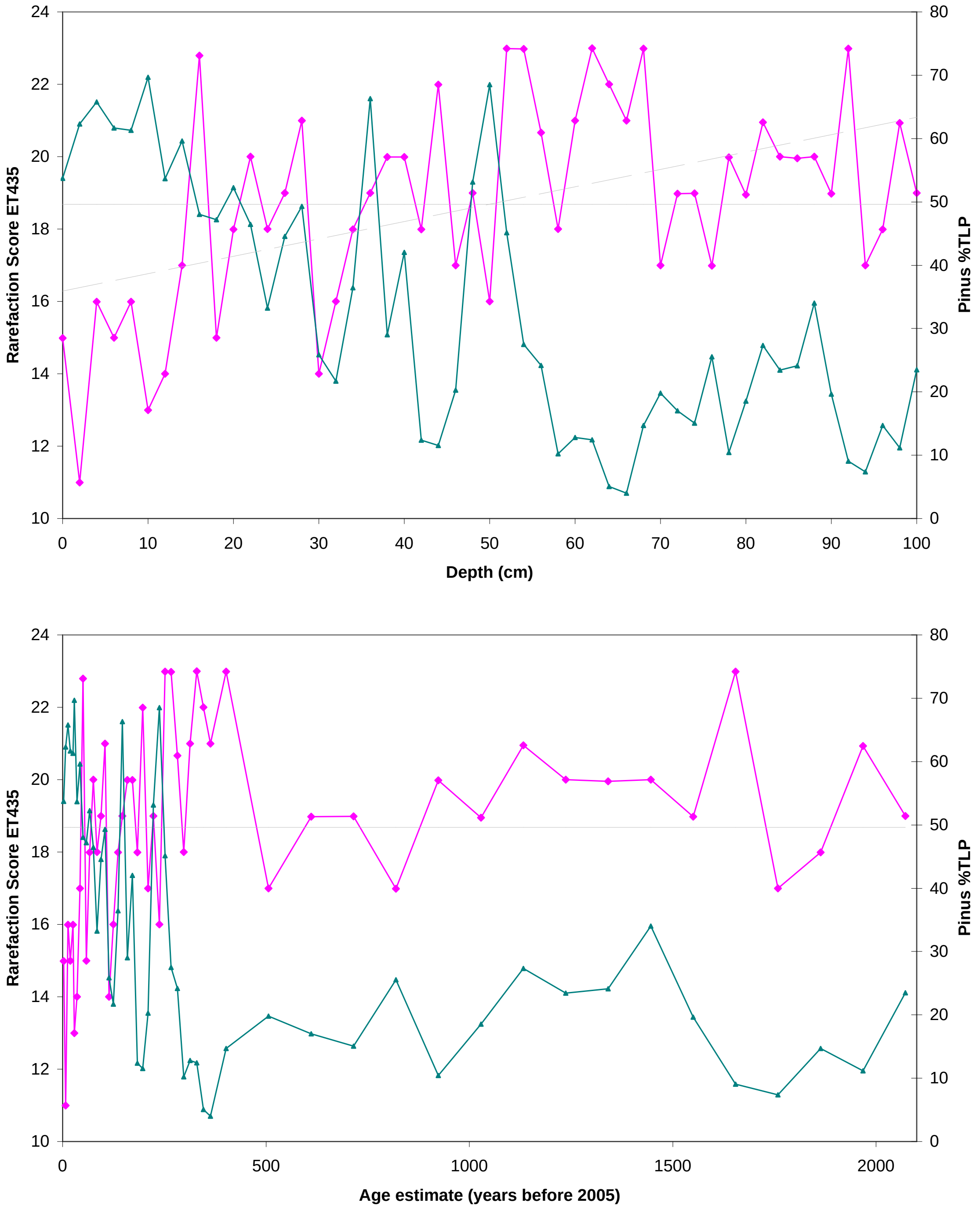


Figure 6.10: Palynological richness for the BEAT pollen samples (ET_{435}) Expected number of pollen taxon for a normalised pollen count of 435 grains per sample, (pink line) and *Pinus* pollen %TLP (green line) against depth (top) and age estimate (bottom). The grey horizontal line represents and average value for rarefaction over all of the samples, and the grey dashed line represents a linear regression, which demonstrates the trend to lower palynological richness in the recent samples.

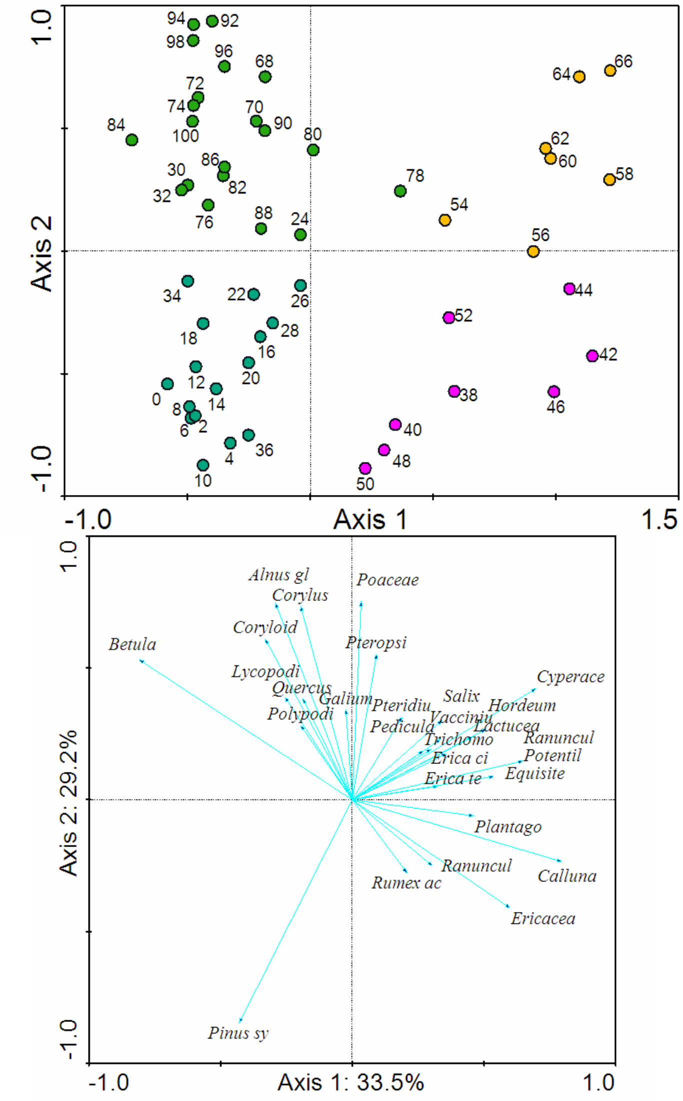


Figure 6.11: PCA ordination of pollen % TLP for the BEAT core samples and species

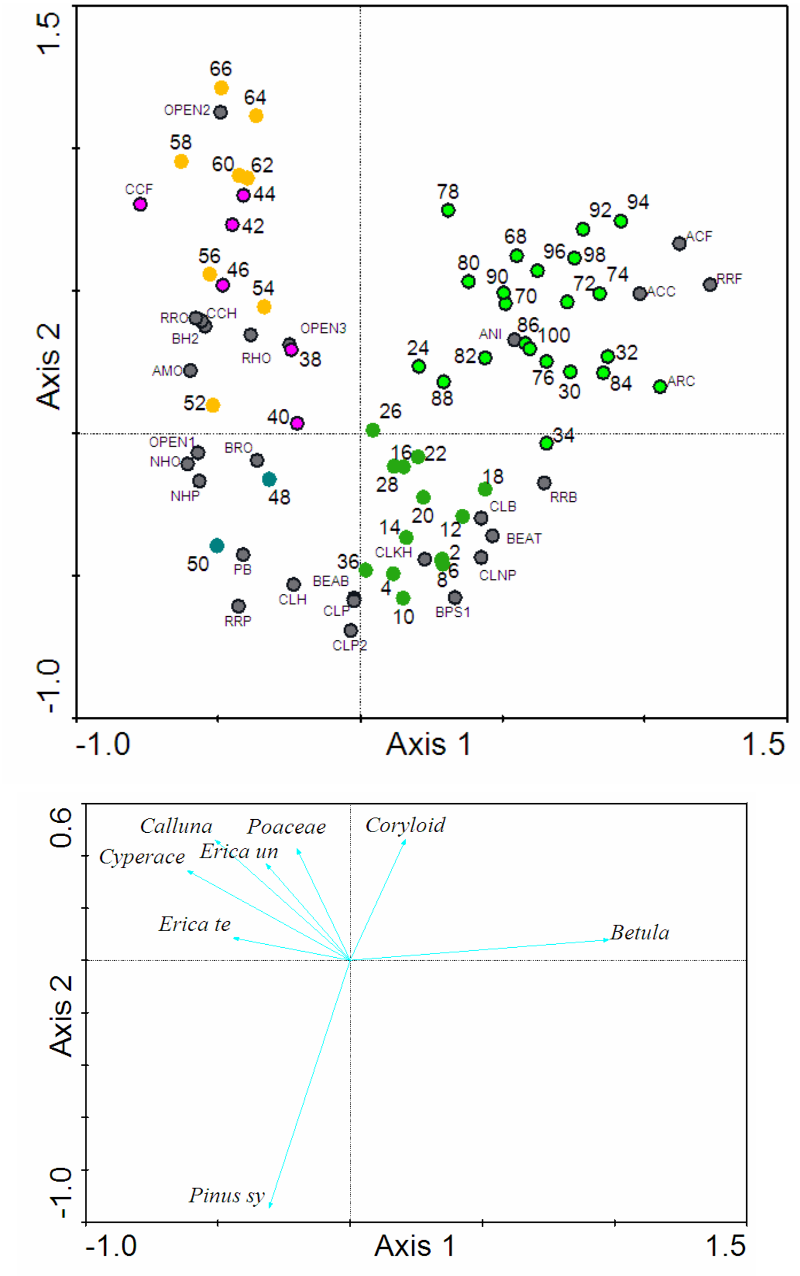


Figure 6.12: PCA ordination of modern pollen samples from Figure 5.19 with samples from the BEAT core plotted as passive samples (numbers refer to depth of sample) to demonstrate where the samples from the BEAT core correlate with modern analogues. The passive plot ensures the BEAT samples do not influence the axes. The lines between sample points demonstrate periods when vegetation composition is shifting at BEAT.

6.3.4 Discussion of Cluster 1: NHP, PB and BEAT cores

The three cores in cluster 1 at the western end of the extant native pinewood zone in east Glen Affric are compared in this section. As discussed in Chapter 4, chronological models for the cores may be subject to large errors. In addition, due to the large differences in peat accumulation rates inferred from the ^{14}C age estimates, each core represents a different temporal grain and extent[10]. Although part of the aim of this thesis was to correlate micro-scale events across cores the opportunity to do this in any quantified way is limited by this variation in temporal resolution. A comparison made for the *Pinus* pollen percentages from the three cores plotted against time demonstrates this well (Figure 6.13). Temporal errors plotted on these data points show approximate uncertainties as illustrated by the different linear models applied to the cores in Chapter 4, and the estimated magnitude of errors estimated by Telford (2004a), and Bennett and Fuller (2002). In the context of this uncertainty it is difficult to assess the synchronicity between any regeneration events beyond some basic observations. A descriptive approach will therefore be taken here.

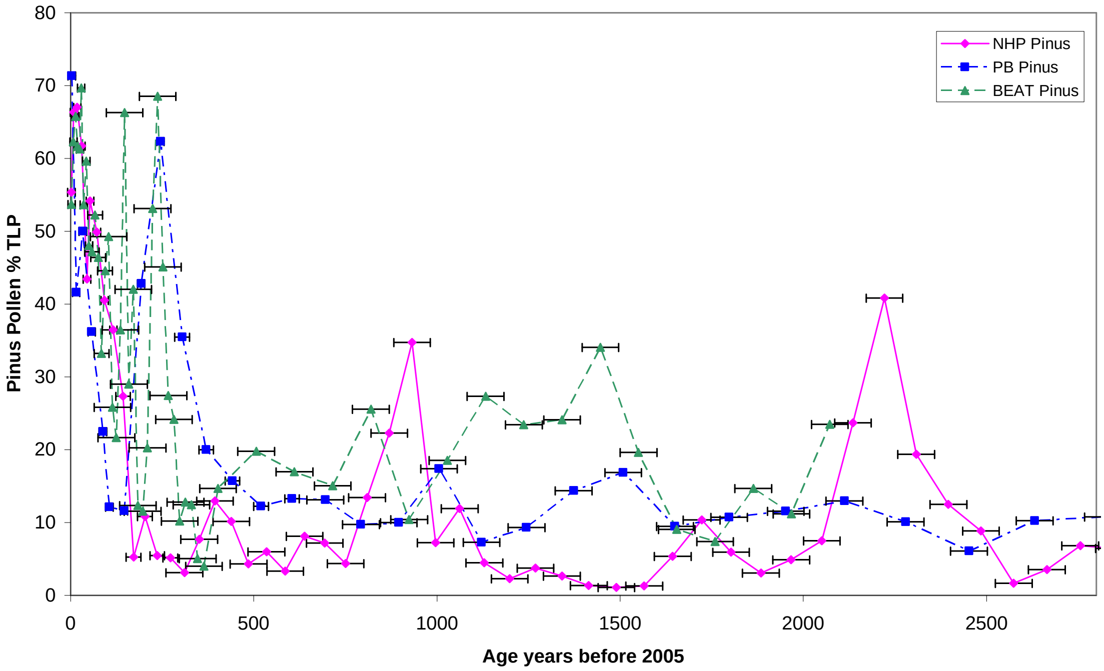


Figure 6.13: Plot of *Pinus* pollen, as percentage TLP, against estimated chronology for the pollen sequences in the three cores of cluster 1 in Glen Affric. Horizontal error bars estimate uncertainty at a nominal 50 years to illustrate the associated problems of uncertainty in correlation across cores.

The PB core provides an earlier history of the site spanning *c.* 5000 years, whilst NHP provides *c.* 3000 years of history, and BEAT provides *c.* 2000 years. Although the PB core illustrates that *Pinus* was present in this landscape between *c.* 5500 and 4000 BP, the woodland in this phase was more diverse than the current woodland (Figure 6.6), with *Betula* and possibly

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[10] See Chapter 1 for a discussion of 'grain' and 'extent'

Alnus and *Quercus* present and a higher overall plant diversity indicated (Figure 6.5). The breakdown of woodland illustrated in this diagram begins in zone PB2 at *c.* 4500 cal. BP. The decline of the woodland from *c.* 4500 cal. BP correlates with the now well documented pine decline postulated by Bennett (1984), but is possibly slow to complete, with remnants of woodland or scattered trees remaining in the landscape until *c.* 2,500 cal. BP, from whence an open phase lasting >2000 years begins.

At *c.* 2,900 cal. BP, the commencement of a record from the NHP core, the landscape portrayed here is similarly open. Although remnant patches of woodland in the landscape are evident from the likely local phase of woodland around this site from *c.*500 – 50 BC, the ephemeral and open nature of this landscape at the western end of the current woodland zone is clear (Figure 2.4 and Section 6.3.1). The findings from these two sites form a link between the previous work (Section 2.2.3.4) from a local scale peat deposit in West Affric (Davies 2003; Davies 1999) and the landscape scale small lake deposit at Loch an Amair (Froyd, 2001). The presence of a possible signal of the Mid-Holocene pine decline at PB is interesting. This pushes the boundary of this feature eastward into a tightly defined zone between the east and west extent of Loch Affric and given the extent of openness at NHP to the west of PB *c.* 3000 years ago, probably pushes this boundary into an even more tightly defined zone.

Both human impact, through grazing and fire, and climate change, have been suggested as drivers of the Mid-Holocene pine decline, and teasing out the relative contribution of either has been problematic. The interpretations from these local pollen analyses unfortunately remain unclear.

The general increase in charcoal must be treated with caution. The accumulation rate at PB was very slow during this phase, as evidenced by the long timescale represented (*c.* 5500 years in one metre of peat). The pollen concentration data (Figure A2.2) demonstrates a marked increase in pollen accumulation rates in this zone continuing into zone 3. A tentative extrapolation of the available ^{14}C and ^{210}Pb assays derives the influx diagram in Figure A2.3, which demonstrates that the general charcoal increase may be an artefact of slow accumulation rates. Influx data for charcoal actually demonstrates three significant, but separated, peaks at 70 cm, 52 cm and 38 cm. This effect of slow peat accumulation on charcoal abundance is also seen at NHP, however, the evidence here is for a greater number of fire episodes.

Fluctuations in the ground flora, however, may indicate small climatic shifts; or could be driven by grazing. Inference of widespread climatic change (*sensu* Anderson *et al.* 1998) is not possible from these extremely localised signals (Tallis 1997). Equally, evidence for human impact is limited, with two *Hordeum*-type grains at 96 cm and 52 cm, and only limited *Plantago lanceolata* grains (Figure 6.6) throughout this first woodland phase. The findings of the modern pollen study in Chapter 5, and Bunting, (2003), do not support the inference of human impact (*sensu* Davies 1999; 2003) from these sparse herbaceous indicator taxa.

The lack of a clear herbaceous indicator signal is exacerbated by the over-representation of *Pinus* and *Calluna*, ensuring that whether under arboreal or heathland dominance, the palynological richness of the landscape remains poorly defined at pollen counts of *c.* 500 TLP grains (Chapter 7).

What is clear is that, at PB, by 56 cm (*c.* 3300 cal. BP) fragmentation of the former mixed woodland is complete. This at a time when three *Hordeum* grains are apparent in the pollen record, together with *Plantago lanceolata* and a small peak in Ranunculaceae. The fragmentation and presence of *Hordeum*-type grains immediately predates a significant charcoal peak evident in the influx data in Figure A2.2, perhaps indictaing merely a response to a more combustible heathland flora, but perhaps attributable to human activity.

Whatever the reason for the woodland breakdown, throughout the past *c.* 3000 years the pollen diagrams from the NHP and PB sites depict a surrounding landscape that remained open and heath-dominated. There were probably trees or stands of woodland scattered in the landscape, although they seem to have been sparse[11]. Incursions of woodland did occur, and these seem linked with suppression of fire.

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[11] Tallis (1997) recorded 28% AP and shrub pollen in open sites in Wales despite there being no trees within a kilometre of his site.

The BEAT site, a little further eastward, has some difficulties regarding the chronology, but assuming the model chosen has some validity, the *c.* 2000 years of woodland history show a slightly different trajectory, with some open phases, but much more short-lived ones. Again, a more diverse woodland is inferred in the past.

The current woodland stands at the three sites, dominated for the most part by *Pinus*, show a modern origin to their structure and composition and at NHP and PB infer a recent incursion onto heathland and a loss of diversity.

6.4 Cluster 2 pollen cores: ANI and ARC

6.4.1 ANI pollen core

6.4.1.1 Summary of main features of diagram and main zone changes

ANI is divided, using CONISS, into six zones, each divided into associated sub-zones marking major and minor changes in the pollen stratigraphy. Major features in the pollen zones are summarised in Table 6.4. A summary pollen diagram is presented in Figure 6.14 and full pollen diagrams and concentration, influx and pollen as a percentage of NAP are presented in the Appendix.

6.4.1.2 Interpretation of ANI pollen zones

ANI1a-c: 79-100 cm (1715-1135 BC)

The arboreal pollen percentages, at over 60% TLP, are consistent with the presence of a woodland canopy (Chapter 5). The woodland is probably a mixed community dominated by a series of fluctuations between *Betula* and *Pinus*, but with *Quercus* and *Corylus avellana* also present. *Pinus* stomata presence indicates the local presence of *Pinus* trees in sub-zones ANI1a and 1c. However, in sub-zone 1b, although *Pinus* pollen peaks to just over 50% TLP, there are no supporting *Pinus* stomata, thus indicating that *Pinus* woodland was present in the surrounding extra-local landscape, but not within *c.* 20 m of the basin (Dunwiddie, 1987). *Ulmus* in such low counts is likely to have been a sparse tree in the wider woodland only, whilst a few percent of *Sorbus aucuparia* in sub-zone ANI1c (a tree with low pollen dispersal abilities) is likely to represent some local presence.

Table 6.4: Zone and sub-zone boundaries and summary pollen descriptions for ANI core.

Zone	Depth (cm)	Estimated Date	Description
ANI6	0-11	AD 1925-2004	***Betula* – *Poaceae*** *Betula* increases to >40% and *Pinus* decreases to *c.* 20%. Poaceae increases and *Calluna* decreases.
ANI5c	11-19	AD 1570-1925	***Pinus* invasion** Increase in *Pinus* to a peak of *c.* 60% at 18 cm with decrease in *Betula* to <20% followed by a decrease in *Pinus* and increase in *Betula* once more towards the top of the zone. *Calluna* increases slightly to *c.* 15% accompanied by small peak in *Vaccinium*; Poaceae peaks and decreases. Pollen concentration and possibly influx levels increase markedly in this sub-zone.
ANI5b	19-31	AD 890-1570	**Mixed woodland phase** Continuing mixed woodland from previous sub-zone with an increase in *Betula*.
ANI5a	31-37	AD 550 - 890	***Pinus* increase and charcoal peak** Increase in *Pinus* to >40% *Betula* decreasing then rising again at sub-zone boundary. Charcoal peak to 30% group + TLP.
ANI4	37-55	475 BC-AD 550	***Betula* –Poaceae** A decrease in *Pinus* percentages coincides with an increase in *Betula* percentages with *Betula* reaching *c.* 70% of TLP in a peak at 44 cm.. Little change in ground flora dominance occurs from the previous zone, a slight increase in *Calluna* percentages from *c.* 2% to *c.* 5% corresponds to a slight decrease in Poaceae percentages, but the influx data shows that Poaceae pollen quantities actually remain steady whilst *Calluna* increases. A high diversity of spores is maintained from the previous zone.
ANI3	55-67	805-475 BC	***Pinus - Poaceae*** The start of this zone marks a rapid increase in *Pinus* percentages together with the appearance of stomata. *Betula* percentages decrease from the start of the zone, with the rise in *Pinus*, but the influx data shows that *Betula* values actually remain slightly higher than in the previous zone. Ericales continues to remain low with Poaceae still dominating the ground flora. Two *Hordeum*-type grains are present at 64 cm and 60 cm. Plantago increases to *c.* 2% TLP at the end of the zone. Spore diversity increases in this zone, but *Sphagnum* decreases from the previous zone.
ANI2	67-79	1135-805 BC	***Betula – Poaceae*** *Pinus* values are <20% TLP with no stomata. *Betula* values are steady at *c.* 40% TLP, then rise at upper sub-zone boundary. Ericales continues to be sparse, and as in the previous zone *Vaccinium* occurs as single grains. Poaceae continues to dominate the ground flora with *Potentilla* and *Succisa* and an increase in diversity of herb taxa. *Sphagnum* peaks to 30% TLP plus spores in the middle of the sub-zone.
ANI1c	79-89	1410-1135 BC	***Pinus-Betula* Cyclicity** Fluctuation in *Betula*/Broadleaf taxa and *Pinus* with stomata indicating presence of *Pinus* in the locality. Ericales are sparse in this zone. One *Vaccinium* grain occurs at 88 cm. Poaceae percentages increase from *c.* 10% to 20% TLP and *Potentilla* type pollen increases from a few grains to >2% TLP with some *Succisa* also present.
ANI1b	95-89	1575-1410 BC	***Pinus-Sphagnum*** *Pinus* increasing to peak at start of sub-zone but with no accompanying stomata. *Betula* rises at the end of the sub-zone to *c.* 70% TLP, with *Pinus* values decreasing again to under 20%. Poaceae is still dominant in the ground flora although reduced in value from sub-zone 1a. *Potentilla* decreases temporarily to the top of the sub-zone. *Sphagnum* peaks at *c.* 35% of TLP plus spores.
ANI1a	95-100	1715-1575 BC	**Mixed woodland phase** Arboreal pollen values are >60% TLP in this zone. Broadleaf species are dominant at the start of the zone with *Betula* and *Alnus* dominant, but decreasing to top of sub-zone as *Pinus* increases. One *Pinus* stomata occurs at 96 cm. Ericales are in low percentages and Poaceae is dominant in ground flora and rising to peak in zone to 30% TLP.

Ericales are limited throughout the ANI1 zone, with *Calluna* at less than 4% TLP, and other Ericales not present apart from one *Vaccinium* pollen grain at 86 cm and two unidentified Ericales at 96 cm. The majority of the non-arboreal pollen input is from Poaceae (Figure A.4), with values to *c*. 30% TLP in sub-zone 1a and c, accompanied by *Potentilla*, sparse *Ranunculus acris* and, in sub-zone 1c, *Succisa,* indicating a herb-rich grass-dominated ground flora similar to that found today.

A rise in *Sphagnum* spores in sub-zone 4b, where Poaceae decreases to <10% TLP may indicate a fluctuation in wetness of the basin, causing the local failure in *Pinus* regeneration for a few centuries discussed above. However, this is unlikely to have caused a major failure of wider *Pinus* regeneration in the landscape as the surrounding topography is sloping and free draining. In addition, the increase in *Sphagnum* alone is not a secure indicator of change in wetness as *Sphagnum* spore production can vary erratically (Tipping, *pers. comm*.). A subtle increase in Cyperaceae at the start of this zone may add some support for increasing wetness, but is tentative at these low percentages.

ANI2: 67-79 cm (1135-805 BC)

This zone marks a decrease in *Pinus* pollen percentages and the disappearance of *Pinus* stomata. The woodland returns to a period of *Betula* domination in the surrounding stand, perhaps with local *Alnus*, which increases percentage slightly here, and is probably present by the wetter stream margins. Some *Corylus* is also consistently present. Fluctuating low percentage values of *Quercus* indicate some presence in the wider woodland, and perhaps in the stand; the modern sample in Glen Affric, with a single *Quercus* tree present (CLKH), presented little more than a few grains of *Quercus* pollen in the associated surface pollen sample (Section 6.5.3 and Chapter 5).

The ground flora of the site is depicted as a continuing Poaceae-dominated grassland, with associated herb flora. *Calluna* and Ericales values remain low although a few grains of *Vaccinium* and undifferentiated Ericaceae appear. Given this taxon's tendency to under-representation (Chapter 5), this could indicate local presence of *Vaccinium*, perhaps on the freer-draining slopes of the south facing hillside or on hummocks above the basin surface as in the present-day situation. *Potentilla*-type pollen remains at *c.* 2-3% TLP, and *Succisa* appears as a prominent herb. *Rumex acetosa*, *Plantago lanceolata* and *Ranunculus acris* all appear in this zone, possibly with the basin surface forming an open glade within the *Betula*-dominated woodland.

ANI3: 55-67cm (805-475 BC)

This zone is secured at it's boundaries by ^{14}C assays at 69 cm and 55 cm (Chapter 4). The zone shows a reinvasion of the local site by *Pinus* trees, supported by higher *Pinus* pollen percentages increasing to over 40% TLP together with *Pinus* stomata. Percentages of *Pinus* pollen at *c.* 40-50% are not high given the local presence of *Pinus*; the woodland therefore probably had an open canopy structure. Associated decreases in *Betula* pollen percentages are not supported by the influx data (Figure A4.2) indicating a mixed woodland canopy and further evidence for a mixed woodland in the surrounding landscape continues from previous zones, with *Alnus*, *Quercus*, and *Sorbus aucuparia* all present in the pollen record in low percentages and *Corylus avellana* also still sparsely present.

The ground flora matrix remains constant with Poaceae dominant. The small peaks in *Succisa* disappear in this *Pinus*-dominated zone, whilst *Plantago lanceolata*, *Ranunculus acris* type and *Hordeum*-type pollen all occur in low percentages or single grains (Figure A4.4). As evidence for human impact however, this low occurrence of grains is not conclusive (Tipping 1994; Bunting 2003; and see chapter 6). Charcoal does rise in two small peaks at the end of ANI3, but charcoal appears in very low quantities in the ANI core, with mainly smaller size fractions, giving little local evidence for fire, either human or naturally ignited fires.

ANI4: 37-55 (475 BC-AD 550)

The changes in pollen spectra at the beginning of this zone mark a return to *Betula*-dominated woodland. *Pinus* pollen percentages remain low in zone ANI4, decreasing to under 10% at 44 cm and *Pinus* stomata are not present possibly indicating a temporary reduction in *Pinus* in the surrounding landscape. *Alnus*, *Sorbus aucuparia*, *Corylus avellana* and *Quercus* remain a constant presence in the surrounding landscape; *Alnus* possibly continuing to be present only in the riparian zone; whilst *Sorbus aucuparia* may have some local presence, with a small rise in pollen percentages towards the end of the zone. Evidence of *Ulmus* pollen becomes more sparse; however, it was never a significant component of the pollen spectrum at this site. An increase in *Salix* pollen also strengthens the interpretation of a mixed and diverse woodland.

A small rise in *Calluna* percentages may indicate some increase in this taxon on the surrounding slopes, and *Vaccinium* grains become more frequent which may indicate some increased, but localised, spread; perhaps onto the degrading stumps from the former pine woodland (see section 6.4.1). A Poaceae dominated ground flora remains on the basin however, with *Succisa* pollen, which disappeared for most of zone 3, now returning in the record, accompanied by *Melampyrum* and *Plantago lanceolata*, and some *Oxalis acetosella* (although distinction from *Quercus* is highly tentative) and a richer Pteridophyte diversity; all indicating a damp, herb-rich ground-flora.

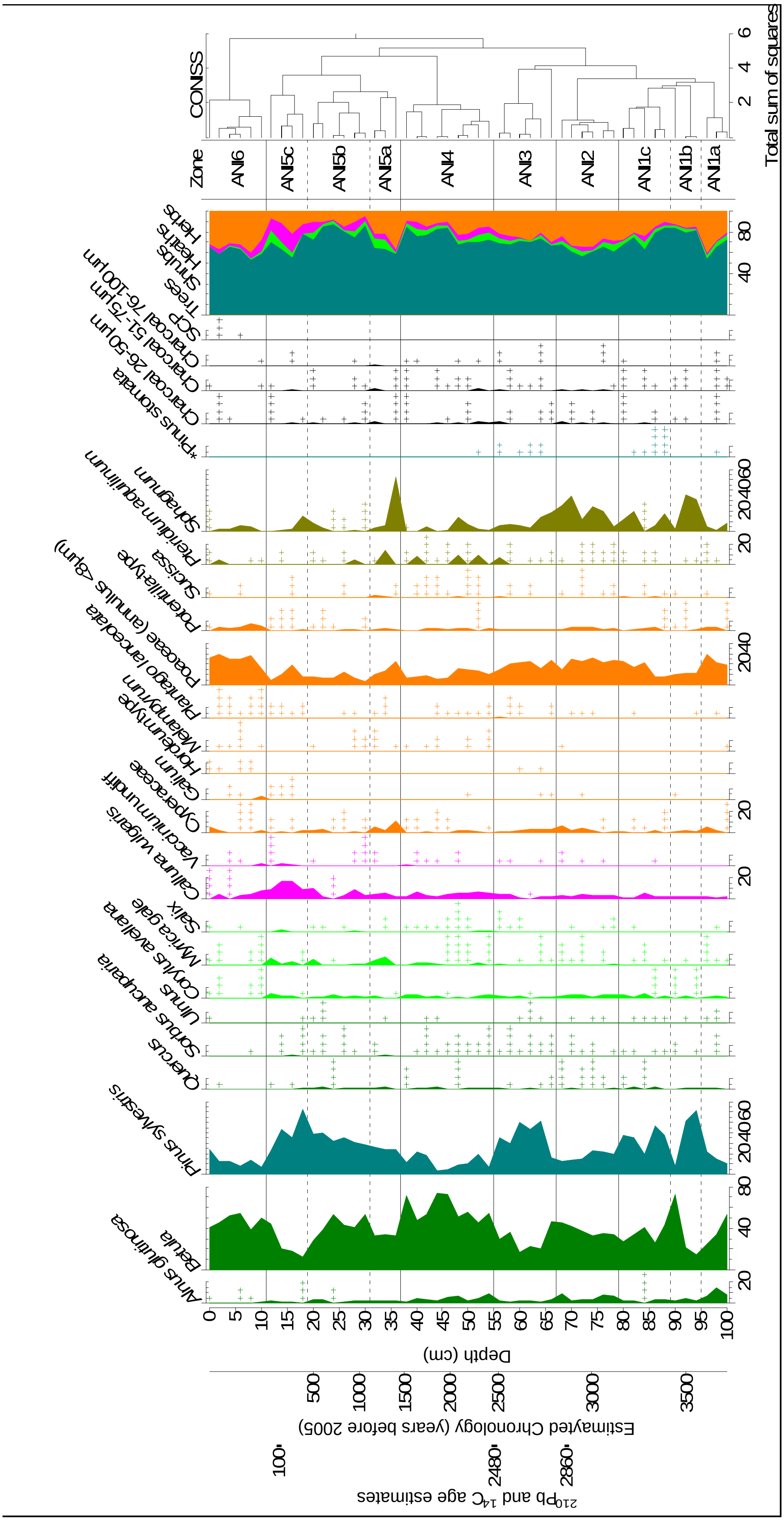

Figure 6.14 Pollen Diagram for selected taxa and palynomorphs from the ANI core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

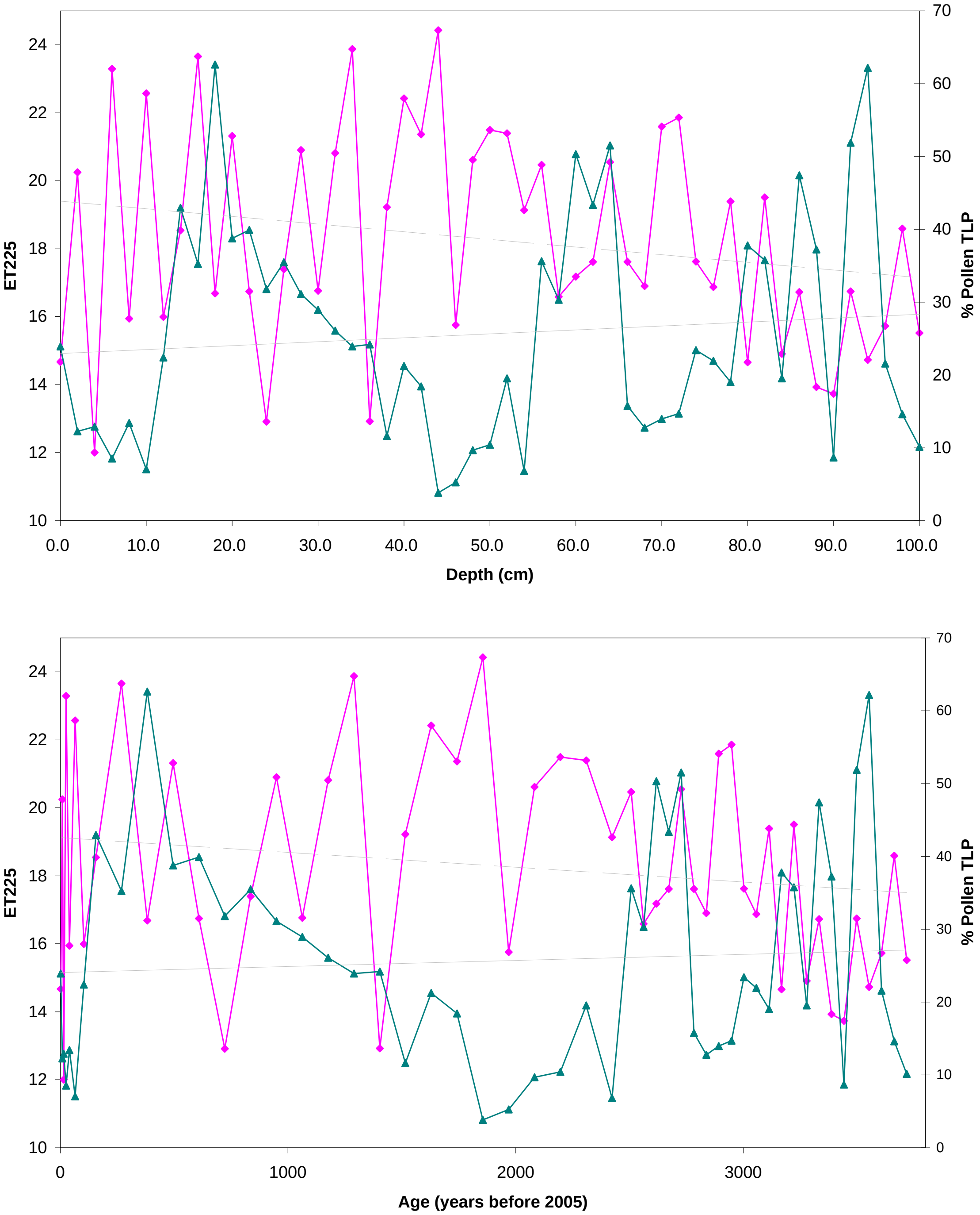

Figure 6.15: Palynological richness for the ANI pollen samples (pink line) and *Pinus* pollen %TLP (green line) against depth (top) and age estimate (bottom). The grey dashed line represents a regression, which demonstrates the trend to higher palynological richness in the recent samples, in contrast to the solid grey line which shows a downward trend in the contribution of *Pinus* pollen

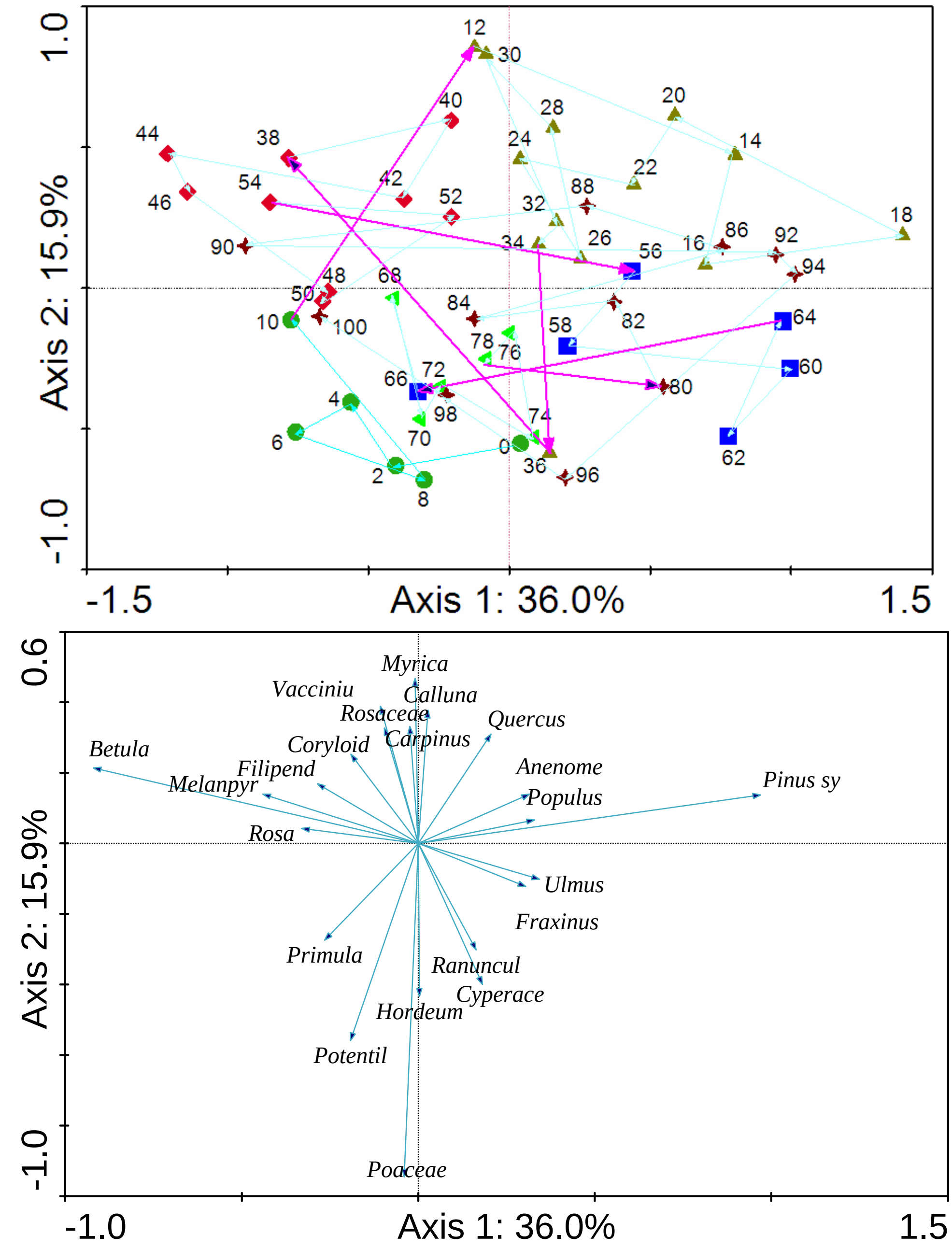

Figure 6.16: PCA ordination of pollen % TLP for the ANI core samples and species

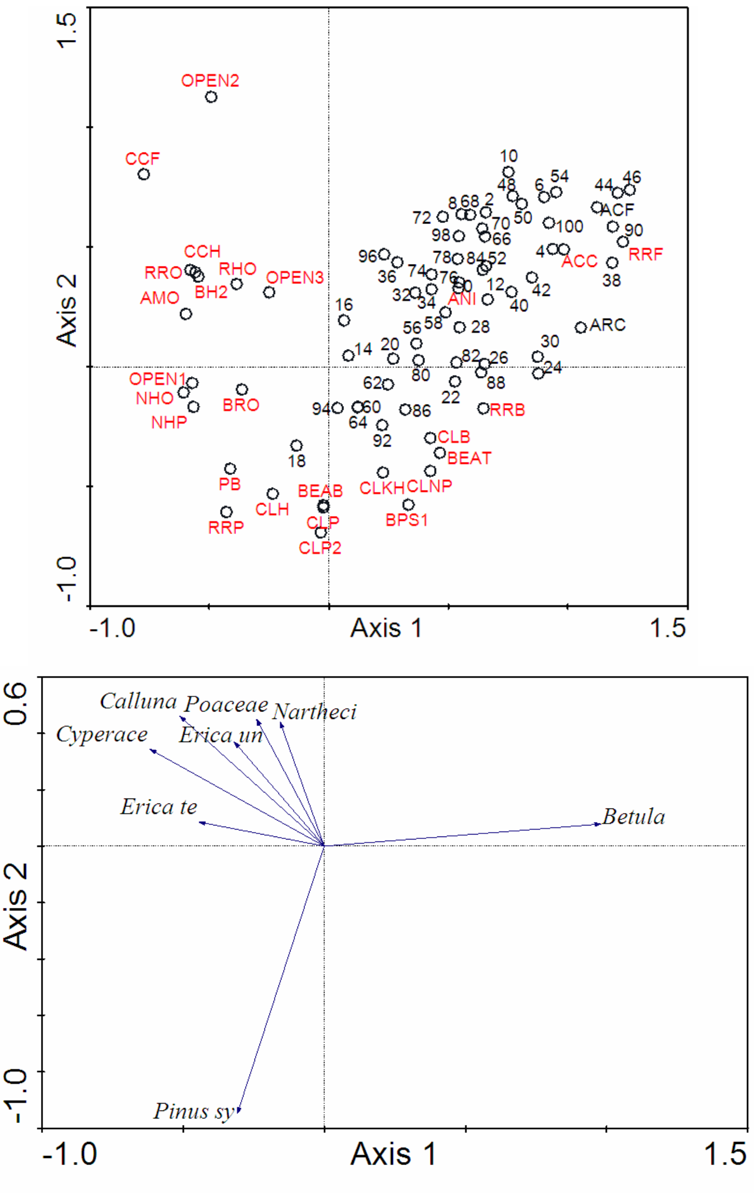

Figure 6.17: PCA ordination of modern pollen samples from Figure 5.19 with samples from the ANI core plotted as passive samples (numbers refer to depth of sample) to demonstrate where the samples from the ANI core correlate with modern analogues. The passive plot ensures that the ANI samples do not influence the axes.

ANI5: 11-37 cm (AD 550 - 1920)

A brief decrease in arboreal pollen and increase in herbaceous pollen define sub-zone ANI5a. These changes are associated with a charcoal peak at 34 cm, and, additionally, a *Sphagnum* peak, which could indicate increased wetness. Distinction is unclear, but the charcoal is mainly in the smaller size classes and probably not of local origin (Patterson *et al.* 1987). Arboreal pollen percentages recover into sub-zone 5b, where cyclicity of dominance between *Betula* and *Pinus* are seen again. *Betula* then reduces in to <20% TLP in sub-zone 5c, but the corresponding peak in *Pinus* pollen percentages to 60% TLP at 18 cm is not supported by stomatal presence. The depiction therefore, is of a failure of the local *Betula* woodland and the increased visibility in the pollen record of an extra-local *Pinus* stand, possibly on the hillslope to the north-west of the site, and possibly on the drier knolls of the surrounding flush system, which does show evidence of tree stumps in the present environment (see section 3.2.2).

This zone also marks a slow decline in woodland diversity, with *Quercus*, *Alnus*, *Corylus avellana* and *Sorbus aucuparia*, all decreasing, or disappearing, together with *Pinus*; so that by the end of ANI5c, when *Betula* pollen percentages rise again to over 40% the woodland is a more impoverished community than earlier in the site's history.

This zone also depicts slight changes in the ground flora, with *Vaccinium* and *Empetrum* presence inferred by sparse grains (Tallis 1997; and chapter 6), and *Calluna* increasing in sub-zone 5c. The ground flora is still, however, Poaceae-dominated and relatively herb rich, with *Succisa* present at the start of the zone, and Ranunculaceae, *Plantago lanceolata* and *Potentilla,* which, although still present, begins to fluctuate in coincidence with some fluctuations in *Sphagnum*; perhaps tentatively indicating changes in basin conditions. Support for a change in basin conditions to possibly drier phases of slow accumulation is found in the concentration and influx data which increases substantially in sub-zone 5c (Figure A 4.2 and A4.3).

ANI6: 0-11 cm (AD 1920-2004)

The recent stand history in ANI6 is of a dominant *Betula* woodland with limited woodland diversity in comparison with the past zones. *Sorbus aucuparia* pollen is present in the surface centimetres, but *Alnus*, *Quercus* and *Corylus* all disappear from the pollen record; although *Alnus* and *Sorbus aucuparia* remain in the current woodland as single trees.

Poaceae dominance of the ground flora increases in this zone to *c.* 30% TLP. *Calluna* levels decrease and *Vaccinium* also decreases to a few grains from an initial *c.* 3% TLP peak. The current landscape contains abundant *Vaccinium* a few metres from the site (see) despite the low pollen count for this taxon. Since Poaceae and herbaceous taxa remain high through this zone the previous peaks probably therefore represent some encroachment onto the basin surface, probably on a former hummock within the Poaceae-dominated flush.

6.4.2 ARC pollen core

6.4.2.1 Summary of main features of diagram and main zone changes

ARC is divided, using CONISS, into five zones, each divided into associated sub-zones marking major and minor changes in the pollen stratigraphy. Major features in the pollen zones are summarised in Table 6.5. A summary pollen diagram is presented in Figure 6.18 and full pollen diagrams and concentration, influx and pollen as a percentage of NAP are presented in the Appendix.

Table 6.5: Zone, and sub-zone descriptions for ARC core.

Zone	**Depth** cm	**Estimated Date**	**Description**
ARC5c	0-4	AD 0-1970	Arboreal values remain high but diatoms disappear from record.
ARC5b	4-15	AD 1970-1900	Increasing arboreal percentages occur, but with low *Pinus* values and no stomata. *Betula* percentages remain high throughout zone indicating development of current stand structure. Cyperaceae levels decreased from zone 4, but diatom abundance is still high throughout sub-zone 5a and 5b with a *Sphagnum* peak in sub-zone 5a.
ARC5a	15-23	AD 1900-1880	
ARC4	23-33	AD 1850-1880	Decreasing *Betula* and *Pinus* % TLP and absence of *Pinus* stomata. A substantial peak in Cyperaceae, and abundant diatoms indicate a wet shift. Charcoal peak at lower zone boundary is coincident with a *Pinus* pollen decrease.
ARC3	33-45	AD 1780-1850	*Pinus* phase with high pollen percentages (50-60% TLP)with stomata present. Low *Calluna* and Ericales values as *Pinus* woodland develops.
ARC2b	45-57	AD 1625-1780	Decreasing *Betula* to *c.* 20% TLP at the top of zone with increasing *Pinus* and peak in *Calluna* and Ericales. Possibly a cycling of woodland structure.
ARC2a	57-65	AD 1450-1625	Increasing *Betula* to 50% of TLP by end of sub-zone; decreasing *Calluna* percentages likely to be due to swamping of signal by *Salix* peaking at *c.* 40% (evident from influx diagram). Small increase in *Alnus*.
ARC1b	65-75	AD 1120-1450	Sharp peak in *Sphagnum* correlated with a rise in diatoms to high levels; possibly an indicator of increased wetness (with *Sphagnum* also peaking here). *Pinus* pollen decreasing through zone with stomata still present indicating local presence of *Pinus* trees. *Calluna* and Ericales increasing, probably as stand opens out in maturity. Small charcoal peak at end of sub-zone correlates with *Pinus* decline.
ARC1a	75-84	AD 710-1120	*Pinus* at over 40% at start of zone although dipping to *c.* 25% before increasing again. Stomata constantly present. *Betula* and *Alnus* both present but at low percentages. Local open *Betula*/*Pinus* woodland near to the site. Low herbaceous pollen signal includes *Vaccinium*. Likely to be local to the site and therefore limiting ground flora input to the pollen record.

6.4.2.2 Interpretation of ARC pollen zones

ARC1a-b 65-84 cm (AD 710-1450)

Pinus-dominated woodland surrounded the sample site at this time with *Betula* also an important taxon, but there is limited presence of other arboreal species. Moderately high *Pinus* percentages and *Pinus* stomata presence support the local presence of *Pinus*, but *Betula* pollen percentages, at *c.* 30% TLP (Figure 6.18), are also likely to indicate some local presence. The position of the samples on the PCA of the ARC pollen data, plotted against modern pollen data in Figure 6.20, show the woodland to be similar to the mixed, birch-pine and pine-birch stands than the *Pinus*-dominated NHP and RRP sites.

The reduction in AP percentages in sub-zone ARC1b indicates the breakdown of the woodland, which is complete by 70 cm. This is illustrated well by the position of sample 70 adjacent to AMO and OPEN3 (two of the most open modern sites (Chapter 6)), in the PCA plot.

Woodland diversity is low throughout the zone, with *Quercus*, and *Corylus* occurring only as single grains.

Cyperales are characterised by low pollen percentages in this zone, but are present as visible macro remains in the peat stratigraphy. Pollen from these taxa is likely to have come from the small hollow, whilst the *Vaccinium* and *Empetrum* pollen, although limited to one or two percent of TLP, is probably a significant part of the surrounding ground flora on the drier rock outcrops surrounding the site. Increases in *Calluna* in sub-zone 1b may indicate an invasion of the site during the opening of the maturing *Pinus* woodland (Rodwell 1991), which shows evidence of decline in sub-zone 1b (above).

The basin surface conditions at this time were likely to have been wetter than the surrounding hillslopes where woodland grew. This is supported by the presence of diatoms and *Sphagnum* - both indicators of wet conditions - together with the *Vaccinium* and *Empetrum* as dryland indicators.

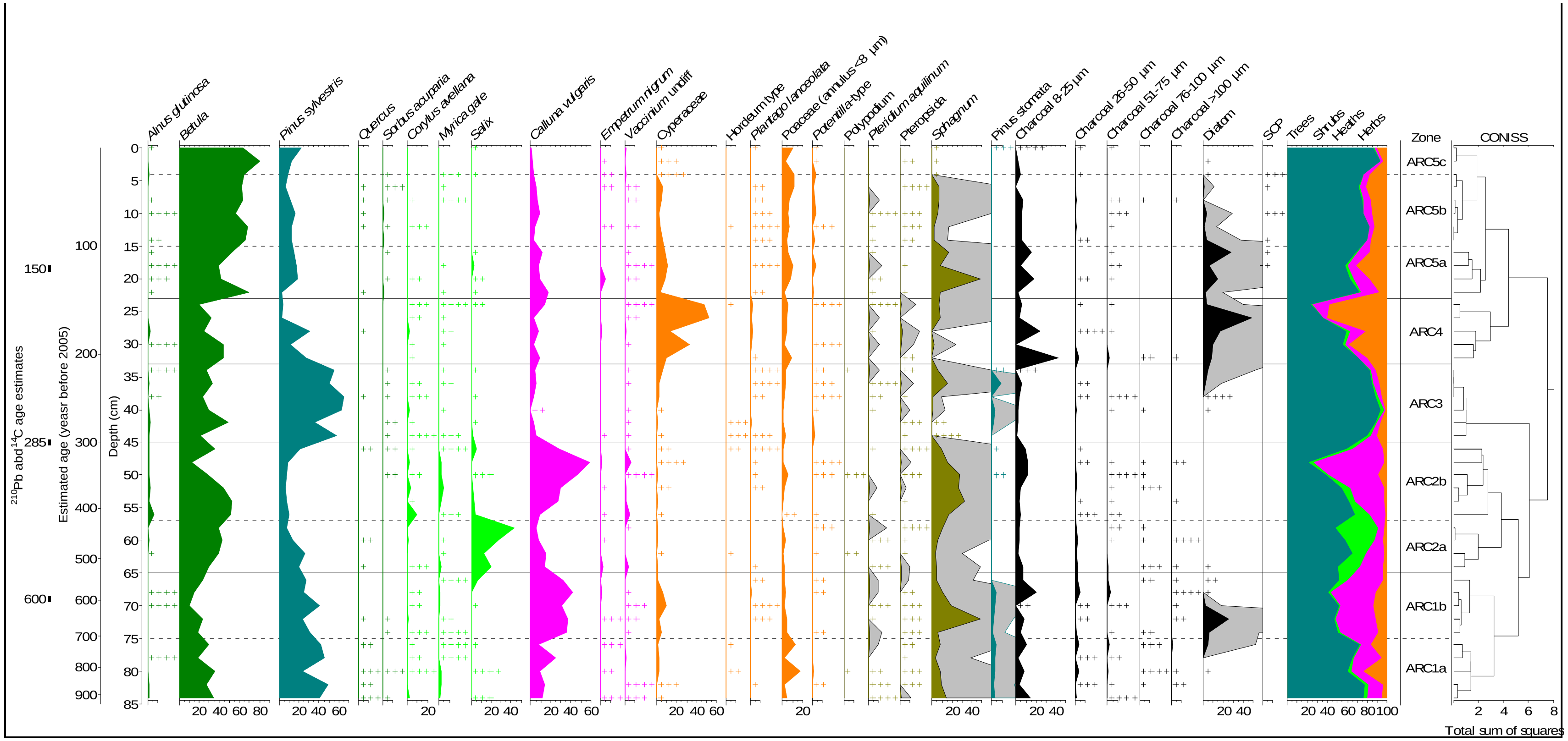

Figure 6.18: Pollen Diagram for selected taxa and palynomorphs from the ARC core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

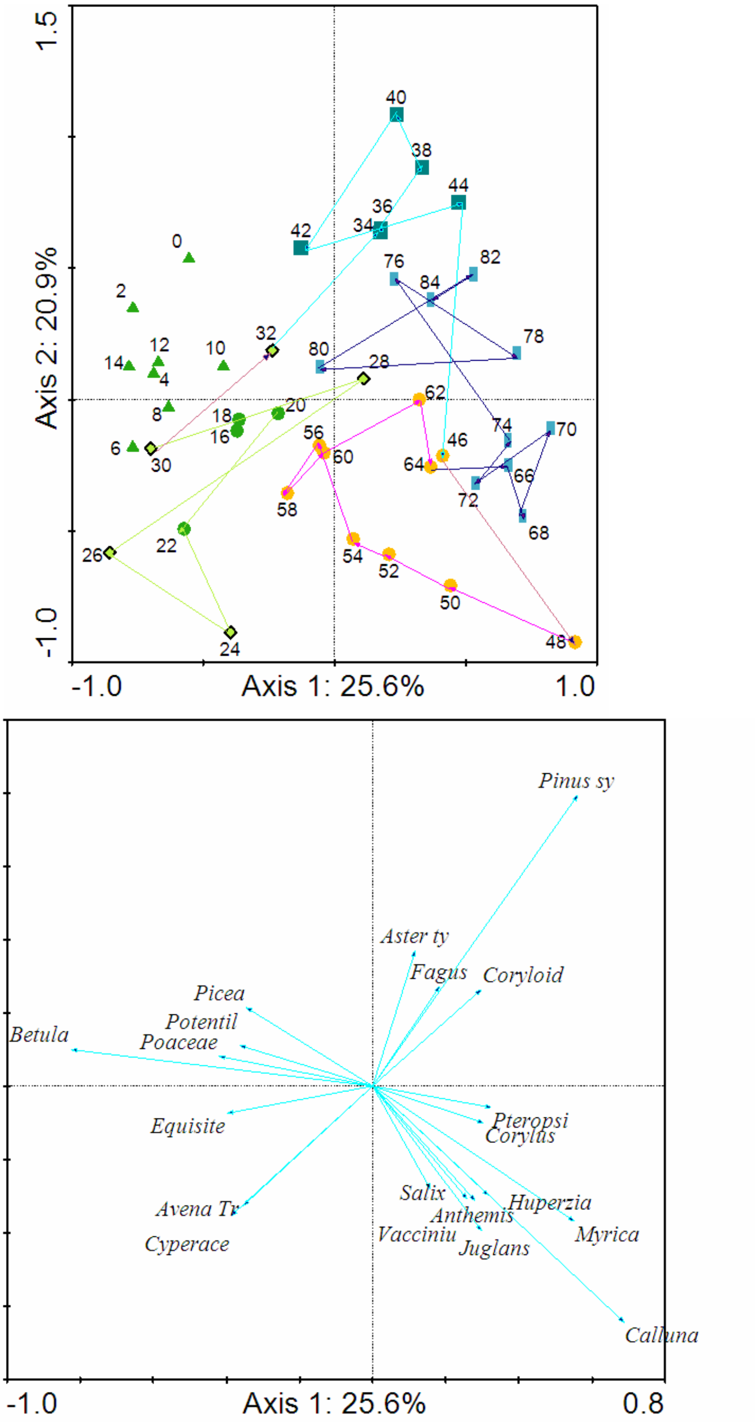

Figure 6.19: PCA ordination of pollen % TLP for the ARC core samples and species

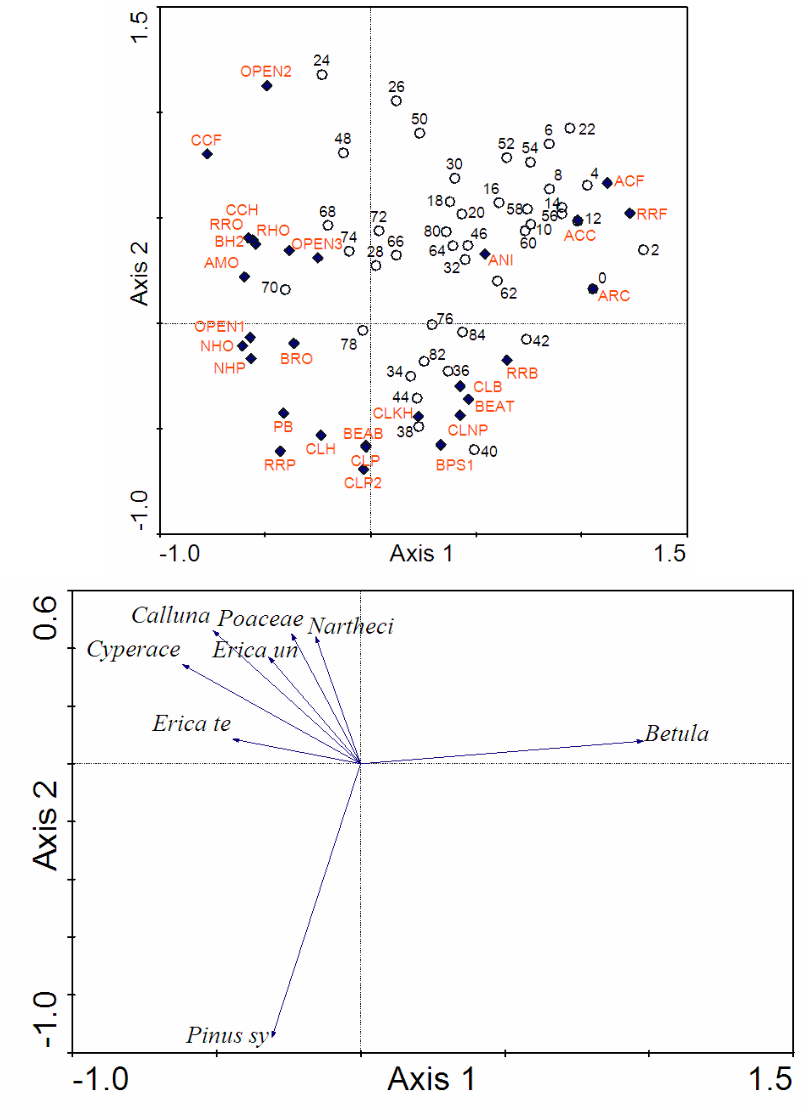

Figure 6.20: PCA ordination of modern pollen samples from Figure 5.19 with samples from the ARC core plotted as passive samples (numbers refer to depth of sample) to demonstrate where the samples from the ARC core correlate with modern analogues. The passive plot ensures that the ARC samples do not influence the axes.

ARC2a-b: 45- 65 cm (AD 1450 – 1780)

This zone is characterised by a rise in *Betula*, which replaces *Pinus* in stand dominance. *Pinus* pollen as percentage TLP is reduced in the locality of the site, but the influx data (Figure A5.3) demonstrate that the reduction in *Pinus* pollen is greater in sub-zone 2b, with influx values in zone 2a actually slightly higher than zone 1 below[12].The PCA plot of samples against modern pollen sites (Figure 6.20) confirms that the woodland from this zone plots near to the more open *Betula* woodland of ACC and ANI. Woodland diversity is still limited in this zone, with other arboreal pollen taxa at low percentages, with the exception of a large peak in *Salix* to

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[12] Although this may be due to a general decrease in peat accumulation causing increased pollen accumulation not counteracted for in the chronological model (Figure A5.3)

>40% TLP at 62 cm which becomes a sustained increase over the whole of sub-zone 2a and reduced but still present in sub-zone 2b. This is likely to indicate the development of local *Salix*, possibly as a small tree or large shrub overhanging the sample site.

Ground flora remains similar to zone a. A reduction in Poaceae and Cyperaceae from low percentage TLP in zone 1 to single pollen grains is constant throughout the zone. However, the *Calluna* fluctuation evident in the percentage data is not supported by the influx data (Figure A5.3), which shows this to be an artefact of increased *Salix* input to the pollen record. *Calluna* influx actually increases steadily within this zone. A single *Hordeum*-type grain appears at 64 cm after a small charcoal peak at the end of zone 1. Other herbaceous indicators are low, however, and the charcoal increase occurs only in the smaller size fractions and therefore may not indicate local fire. Therefore, again, evidence for human impact local to this site is not supported. A large *Sphagnum* peak in sub-zone 2b indicates the continued existence of a wet flush site among the dryer heathland, although as diatoms are not present in this zone a widespread increase in surface wetness is probably not inferred.

ARC3: 33- 45 cm (AD 1780-1850)

This sub-zone is marked by a resurgence of *Pinus* woodland local to the site, supported by *Pinus* stomata and high *Pinus* pollen percentages. The *Betula* pollen percentage increases at the start of the zone and continues at levels that indicate some *Betula* in the woodland mix (*c.* 30% TLP). As in lower zones other arboreal taxa are rare or absent, indicating a *Pinus*-dominated woodland carpeted with *Vaccinium* heath. A few grains of *Hordeum*-type pollen, together with *Plantago lanceolata*, *Potentilla*, *Gallium* and Ranunculaceae indicate some diversity to the herb flora, especially in the small flushes and hollows containing Poaceae and Cyperaceae. Again, the evidence for human impact is limited; given the sparse occurrences of these pollen taxa, and the evidence for limited correlations between herbaceous pollen taxa and vegetation presence in Chapter 5.

ARC4: 23 - 33 cm (AD 1850-1880)

This zone depicts the breakdown of *Pinus* woodlands and a small regeneration of *Betula*. *Pinus* stomata disappear from the record at this point, and *Pinus* pollen percentages reach a low of <5% TLP at 28 cm. This change in woodland structure coincides with a peak in charcoal to 40% of TLP plus charcoal at the lower zone boundary; although this charcoal peak is limited to the 10-25 µm size range and compared to other sites (NHP and PB) may be an unremarkable peak. A large increase in Cyperaceae pollen indicates some invasion of the bog surface by this taxon, likely to imply a wet phase, as this shift is also supported by a substantial (*c.* 40% TLP + diatoms) peak in Diatoms and a corresponding peak in *Sphagnum* by the end of the zone.

The presence of *Avena*-*Triticum*-type grains in this zone (Figure A5.4), and one *Hordeum*-type grain at the top of the zone, provide some possible evidence of human impact in the landscape. Although *Avena*-*Triticum*-type grains also appear in the modern record, and so may indicate the possibility of longer distance pollen transport from the lower altitude, more fertile, areas of Guisachan or Cannich; *Plantago lanceolata* also increases here, but again is inconclusive evidence of human impact at these low pollen percentages.

ARC5a-c: 0 - 23 cm (AD 1880-2004)

The onset of *Betula* woodland is marked by a rise in *Betula* pollen in zone 5. Cyperaceae values are reduced from zone 4, and Poaceae values increase by a few percent, whilst *Calluna* remains in low percentages and *Vaccinium* presence is still confirmed by a few grains. The samples from this zone plot near to ACC and ACF and RRF on the Modern PCA diagram, indicating a woodland that is open and *Betula*-dominated. *Potentilla* and *P. lanceolata* both appear as evidenced by sparse grains, but diversity is reduced from previous zones and the current woodland is depicted. Basin conditions may have changed slightly into sub-zone 4c, marked by the disappearance of diatoms at the lower sub-zone boundary, but, generally, little change from the present environment is inferred.

6.4.3 Discussion of Cluster 2: ANI and ARC cores

The overall feature of these two diagrams is the stability of a diverse woodland cover for most of the last *c.* 4000 years. Axis 1 of the PCA plot of ANI pollen percentages demonstrates that the main shifts between vegetation in the diagram were between *Pinus* or *Betula* domination of the woodlands. *Pinus* was present locally to the basin until *c.* 1500 years ago, but high pollen percentages in more recent peat from this core support its continued presence in the wider landscape. The PCA of the ANI pollen samples plotted passively on the modern pollen samples in Figure 6.16 demonstrates both the stability and the openness of this woodland over time. Most of the core samples plot near to the current ANI sample and to the ACC and RRF sites, which are grassy herb rich flush sites with *Betula* in the current landscape (Chapter 5). Apart from some cyclicity in tree dominance the PCA plot therefore depicts a stable woodland canopy over at least 3,700 years, but one that remained mixed, with alignments to current W17 woodland rather than W18 (*sensu* Rodwell 1991).

Within this site Pocaceae, has for the past *c.* 5000 years, been the dominant ground flora on the flush surface, with the presence of Ericales, mainly *Vaccinium,* inferred as a perhaps more minor vegetation component. These currently develop on hummock microhabitats (tree stumps and perhaps wood ant mounds) and it is easy to infer the continuance of this vegetation structure in the past, with stumps available from the successive episodes woodland development and senescence. The *Calluna* was always a limited element of the plant cover at this site, and was probably confined to the higher slopes above the basin. Little evidence of human disturbance is available and little evidence of grazing, although the reduction in Poaceae throughout zone 5 may be due to this.

The ARC site produces a shorter history of the vegetation, but demonstrates the value of the consequent increased temporal resolution. From this core the identification of a possibly cyclical breakdown and renewal of canopy cover within the last *c.* 900 years is possible and a perhaps *c.* 200 year periodicity can be seen. The ARC core is from a hillslope basin rather than a stream-side flush, and the difference between the ground flora, between this core and ANI, is sustained over time, indicating some support for the ESC site classification. There is, unfortunately, little opportunity to examine the independence or synchronicity of the stand scale fluctuation between the cores, given the uncertainties over dating (Section 4.6 and 6.3.4). However some dynamic species cycling is inferred in each site.

6.5 Cluster 3 pollen cores: CLH, CLKH and CLP2

6.5.1 CLH pollen core results

6.5.1.1 Summary of main features of diagram and main zone changes

This pollen diagram, from a short, *c.* 84 cm core to the east of Glen Affric, depicts a landscape dominated by woodland, with AP at >70% TLP throughout the core which spans possibly 3,700 years of peat and pollen accumulation. A summary of the main shifts in the pollen diagram is presented in Table 6.6. The pollen percentages of group totals for trees, shrubs, heaths and herbs, in the summary percentage TLP diagram in Figure 6.22, demonstrate very little fluctuation or change. However, a shift in species dominance of arboreal taxa occurs during sub-zone CLH2b, defining two distinct phases in the arboreal vegetation history surrounding this small basin, which is also subtly evident in the balance of heaths and herbaceous taxa.

Table 6.6: Zones, sub-zones descriptions for CLH core.

Zone	Depth cm	Estimated Date	Description
CLH2d	0-5	AD 1965-2005	***Pinus*-Poaceae** *Pinus* peaks at *c.* 70% TLP demonstrating the maturing of the stand. Dominance shifts from *Calluna* to Poaceae and a small peak in *Convallaria*
CLH2c	5-22	AD 1845-1965	***Pinus-Calluna*** Little difference from CLH2b, but slight shift in ground flora. Spores increase in diversity including *Equisetum* and *Selaginella*
CLH2b	22-38	AD 1580-1845	***Pinus-Calluna*** *Pinus* at *c.* 40% TLP is now the only woodland dominant. *Betula* at *c.* 20% TLP may be background only or a small presence in the local woodland. *Potentilla* peak and high number of individual herbaceous grains may indicate some openness, or light canopy cover.
CLH2a	38-50	AD 1150-1580	***Betula-Pinus* shift** *Betula* gives way to *Pinus* woodland with *Betula* decreasing to 20%TLP and *Pinus* increasing to *c.* 50% TLP supported by stomata presence. *Alnus* disappears from the pollen record. Spore numbers decrease and ground flora dominance shifts from Poaceae to Cyperaceae
CLH1b	50-66	AD 70-1150	***Betula-Pinus*** *Betula* decreases to 40% TLP and *Pinus* pollen increases with sparse presence of stomata, indicating a shift to local presence. Poaceae is receding and Cyperaceae increasing in the ground flora
CLH1a	66-84	AD 1780 BC-70	***Betula – Poaceae* and spores** *Betula* pollen percentages at >55% TLP and evidence of some mix of species in the woodland with a low % presence of *Alnus*, *Quercus* and *Corylus* and some *Sorbus aucuparia*. *Pinus* pollen occurs at under 20% TLP and no stomata are present; therefore *Pinus* is lacking local presence. Poaceae is dominant in the ground flora but percentages are depressed by high AP percentages

6.5.1.2 Interpretation of CLH pollen spectra

CLH1a-b: 50 – 84 cm (1780 BC- AD 1150)

The base of this zone, and of the core, is marked by the presence of some mineral grains (Table 3.6); and corroded pollen grains and spores comprise a significant part of the pollen spectrum (Figure A6.1). The area at this eastern end of the glen is currently characterised edaphically by the presence of brown earths (Pyatt 1994). The slow accumulation rate of the peat, the mineral grains and the high spore presence attest to this in the history of the area. *Betula*-dominated woodland characterises the early part of this sequence, persisting - assuming a secure chronology - over perhaps 2,500 years. This is remarkable for a *Betula*-dominated woodland. The taxon usually represents a pioneer species and regeneration under its own canopy is unusual (Burnett 1964). In addition, the continuous presence of low, but probably significant, TLP percentages of *Alnus* in this zone, is another indication that the woodland canopy structure may require careful interpretation. The sampling resolution is coarse in this basin, at *c.* 200 years between each pollen spectrum in the basal sediments, which were considerably older than estimated when selecting the sampling strategy (Section 3.2). Given that a continuity in *Betula* dominance is unusual for this pioneer taxon, it is possible that the sampling resolution masks fluctuations in the presence of this taxon (see the temporal difference between ARC and ANI cores in Figure 4.22), or, that there was a high extra-local presence, with a mosaic of gap phases, but an overall steady state of canopy cover within the landscape. The presence of continuous *Alnus* signal however may help to provide evidence that infers stability, as local opening and closing of the canopy should create fluctuations in the pollen percentages of this taxon. Although, as it is not possible to decipher the detailed vegetation history from the resolution available, any suggestion of dynamics (or lack of it) is little more than theory or conjecture.

An alternative proposal is that the age-depth chronology is over-estimating the antiquity of the basal samples from this core. A comparison can be made between the pollen concentration data and the influx pollen data, derived as a consequence of the application of the chronological model to this data (Figures A6.2 and A6.3). On reflection, the application of the chronological model accepted in Section 4.5.7 attenuates the influx data at depth. The lower total pollen influx values in zone 1, in comparison with those in the more recent peat in zone 2, may indicate that the chronological model is indeed predicting older sediments than is realistic. However, alternatively, the lower total pollen influx could be accounted for by loss of pollen, which may be inferred by the preserevation state and high spore counts. Several other curves could be envisaged (Section 4.5.7). However, even if a linear interpolation is made between the ^{210}Pb supported and unsupported equilibrium point and the ^{14}C assay, the basal peat would be predicted as *c.* 1000 years younger, but the span of zone 1 still depicts dominance of *Betula* pollen for over 1000 years. When compared to the *c.* 100 year life-span assumed in most pioneer stages for this taxon, the chronological uncertainty becomes less relevant to the argument for an exceptionally long period of stasis in the history of the *Betula* around the CLH core.

Despite this *Betula* dominance and initially low (<20% TLP) *Pinus* pollen percentages, *Pinus* stomata occur sparsely in zone 1. The inconsistent appearance of these grains is unusual, and could indicate, given the low pollen percentages, a single tree at the edge of the *c.* 20m source area. Given the temporal spacing of the samples in this pollen core the growth and senescence of a few trees over time and between sub-samples is also possible.

The evidence for other broadleaved taxa in the local woodland is tentative, but a consistent low percentage value of *Quercus* may indicate some local presence, as this taxon is found to be under-represented in the CLKH core where it occurs presently in the glen, and this under-representation of *Quercus* is found in other palynological studies (Anderson 1970; Bradshaw 1981). *Sorbus aucuparia* and *Fraxinus excelsior* also occur in sub-zone 1a as single grains. The pollen from these taxa are known to be under-represented (Bradshaw 1981) and to suffer from post depositional deterioration (Havinga 1984), their presence, in a zone where pollen corrosion is high and spore taxa are present in quantity may indicate pollen survival from a more abundant pollen loading, and therefore, local presence of these taxa. A single pollen grain of *Populus* is also present at 74 cm (*c.* 750 BC). *Populus tremula* is a very low pollen producer and is sparse in the glen at present, but thought to have been more widespread (http://www.treesforlife.org.uk/tfl.aspen_info_resource.html). *Corylus avellana* and *Salix* pollen are also present.

During this phase of woodland and *Betula* dominance, palynological richness is high (Figure 6.22). Fluctuations occur, but may be less frequent in the earlier sediments depending on the acceptance of the chronological model (compare the plots of palynological richness against depth and against chronology in Figure 6.21).

The ground flora of the woodland is characterised sparsely, as expected when arboreal taxa dominate the pollen spectrum. The pollen diagram of NAP percentage data (Figure A6.4) illustrates that Poaceae was dominant. The base of sub-zone 1a shows a peak in *Succisa* and this, together with the presence of *Salix pollen*, may indicate damp site conditions. However, pollen from *Filipendula*, a tall herbaceous taxon, also appears here as single grains along with *Plantago lanceolata* and *Potentilla*, perhaps indicating a mosaic of habitat patches dependent upon differing shade levels.

CLH2a-d: 0 – 50 cm (AD 1150-2004)

The start of this zone marks a shift in dominance of *Pinus* over *Betula*. *Betula* dominance was already receding by the end of zone CLH1 and *Pinus* increasing, but the consistent and abundant *Pinus* stomata present from 46 cm to the top of the CLH core indicate that this woodland shifted in composition substantially, to be dominated by a local *Pinus* canopy. The shift in taxa also affects the Lycophytes and Pteridophytes, which show a reduction in quantity and diversity, and in the ground flora where the NAP percentage diagram (Figure A6.4) clearly shows a shift from Poaceae to *Calluna*. The palynological richness of the samples declines in correlation with *Pinus* pollen increase; however, some herbaceous taxa remain in the pollen record as sparse grains, although evidence of local plant presence cannot be deduced.

As with the *Betula* phase the *Pinus* woodland shows a remarkable stability over perhaps 1000 years around the CLH basin. *Pinus* pollen percentages are high enough at *.c.* 0-60% TLP, to infer some local and extralocal input, and consistent enough to infer little obvious sign of disturbance. The shift between the two stable states in CLH is illustrated well by the PCA plot in Figure 6.23.

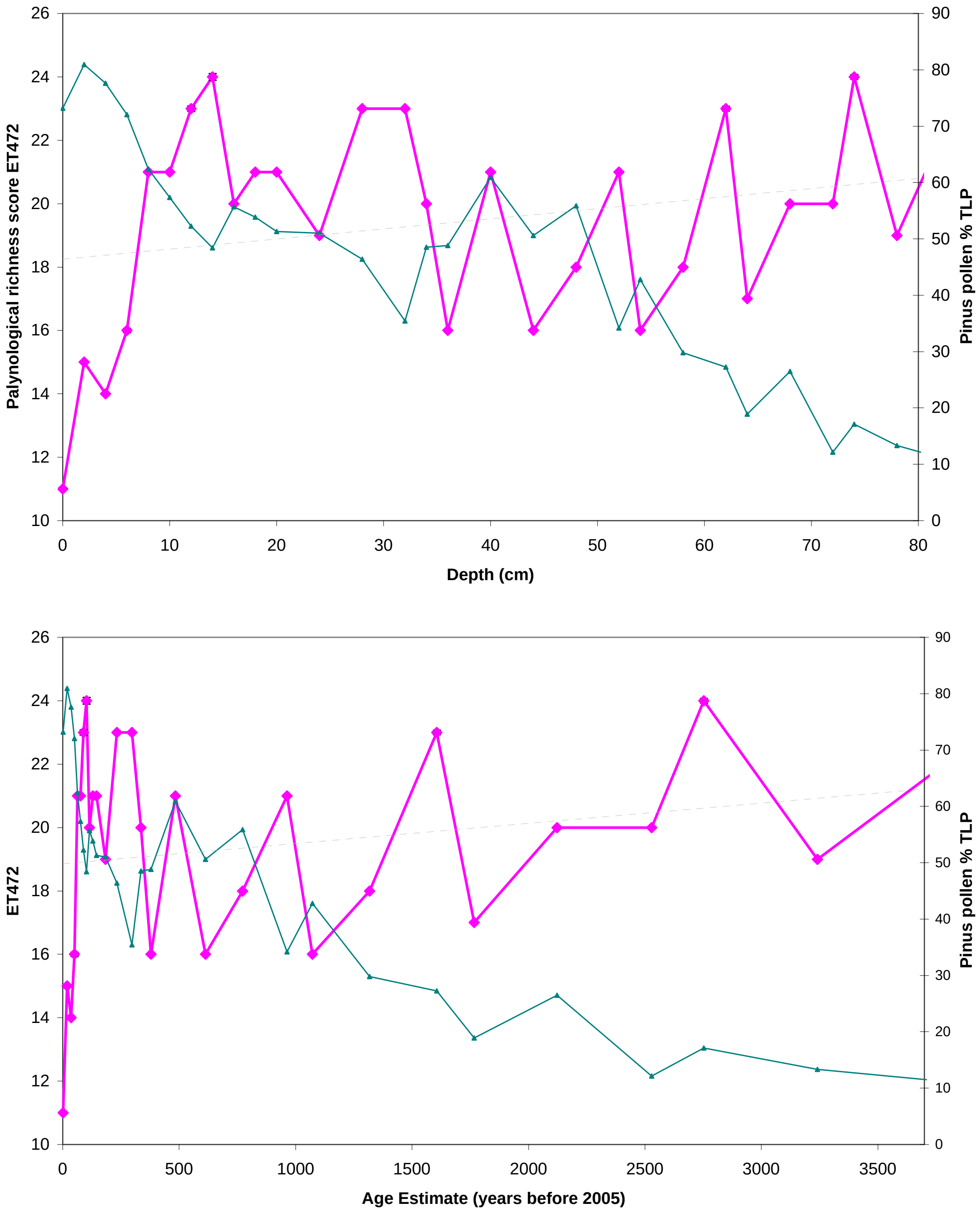


Figure 6.21: Palynological richness of the CLH core (ET_{472}) Expected number of pollen taxon for a normalised pollen count of 472 grains per sample, compared with *Pinus* pollen as % TLP; against depth (top); and age estimate (bottom). Palynological richness score (pink line) and *Pinus* pollen (green line). Grey trend line demonstrates the reduction in palynological richness towards the present.

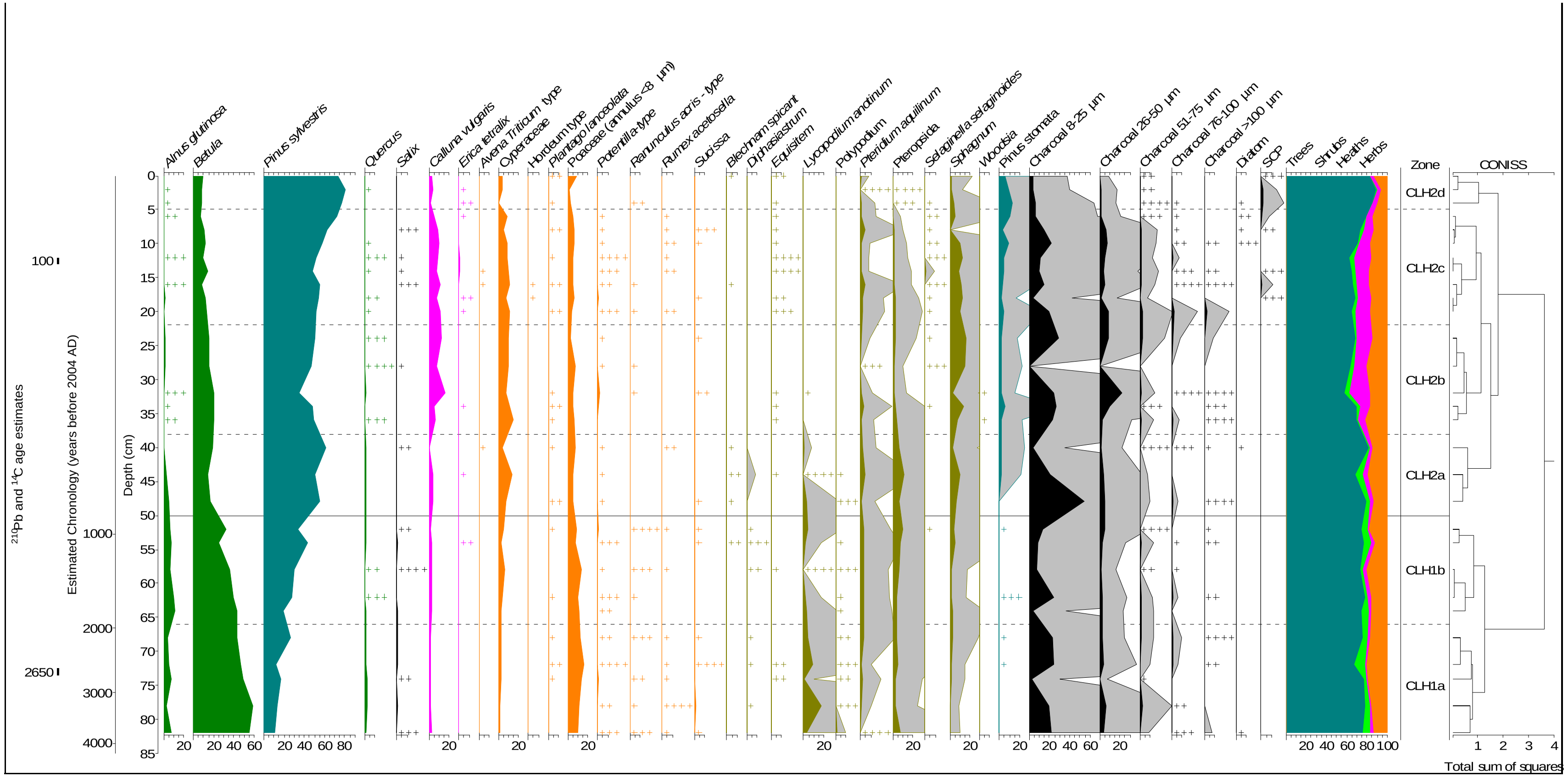


Figure 6.22: Pollen Diagram for selected taxa and palynomorphs from the CLH core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

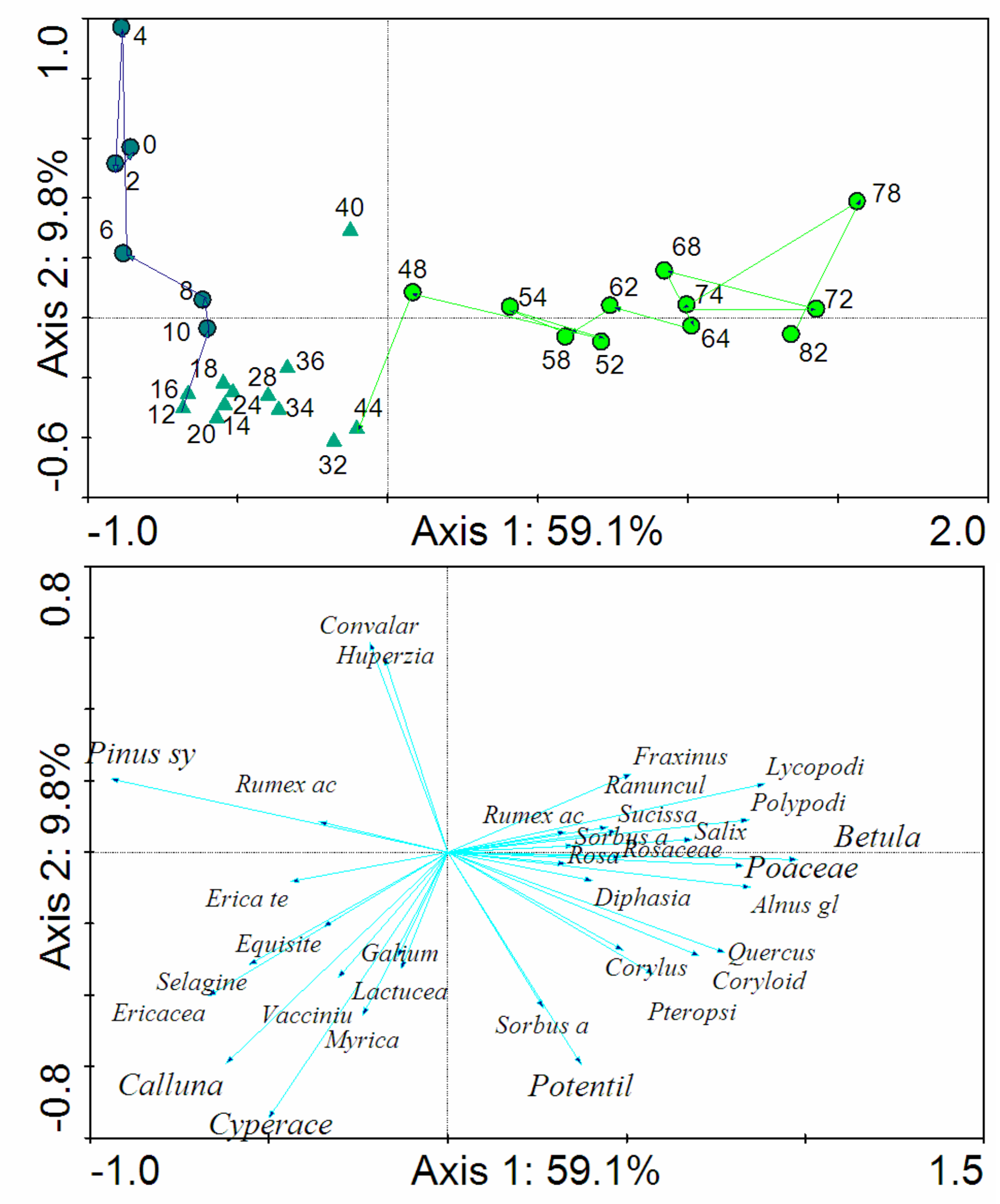


Figure 6.23: PCA ordination of pollen % TLP for the CLH core samples and species

6.5.2 CLP2 pollen core

6.5.2.1 Summary of main features of diagram and main zone changes

As with the CLH core, this core presents a picture of a woodland canopy, continuous, at the landscape scale, over the last *c.* 3000 years. The arboreal dominance of the landscape has fluctuated a little more than at CLH and since the cores are located within 150 metres of eachother, this demonstrates the fine resolution ability of the palynological interpretations. As with the CLH core, zonation is based on subtle vegetation features rather than bulk changes in vegetation composition. A summary of the main changes is provided in Table 6.7 and a summary pollen diagram in Figure 6.25.

Table 6.7: Zones, sub-zones descriptions for CLP2 core.

Zone	Depth (cm)	Estimated age	Description
CLP2-3b	0-5	AD 2004-1980	***Pinus* – *Betula* – Poaceae** *Pinus* stomata occur and the local stand is identifiable with some *Betula.*
CLP2-3a	5-12	AD 1890-1980	***Pinus* - Poaceae** *Pinus* pollen increases; although no stomata occur this is within the time span of current woodland. Poaceae pollen increases sharply and *Calluna* decreases
CLP2-2e	12-19	AD 1740-1890	**Woodland breakdown** Loss of *Pinus* stomata may indicate loss of local *Pinus* woodland. Slight increase in *Betula* and small peak in *Sorbus aucuparia* may indicate some local regeneration phase.
CLP2-2d	19-28	AD 1450-1740	***Pinus* – *Calluna*** *Pinus* continues to be present. *Calluna* pollen increases, and *Alnus* pollen increases slightly.
CLP2-2c	28-40	AD 900-1450	***Pinus* – *Cyperaceae* – *high diversity*** *Pinus* continues to be present. Pteridophytes and Lycophytes reduce and Cyperaceae and *Salix* increase by a few percent TLP
CLP2-2b	40-49	AD 355-900	***Pinus* – *Vaccinium*** *Pinus* stomata indicate a return to local *Pinus* tree dominance. *Vaccinium* becomes important with pollen at 2-3% TLP
CLP2-2a	49-59	AD 370 BC-355	***Mixed woodland* – Ericales** *Pinus* pollen percentages increasing but with no *Pinus* stomata so likely to be extra-local. Ericales increasing indicating an opening of the local stand.
CLP2-1b	59-65	370 - 870 BC	***Betula* peak** Peak in *Betula* to 80%TLP over single spectrum may be a catkin. No *Pinus* stomata and decrease in *Pinus*.
CLP2-1a	65-70	1320 – 870 BC	***Pinus* mixed woodland and Pteridophytes** *Pinus* percentages are modest at *c.* 30% TLP but stomata are also present indicating local *Pinus* trees. Woodland is mixed *Betula* is probably co-dominant. Pteridophyte and Lycophyte spores are abundant. Diatoms indicate wet site conditions

6.5.2.2 Interpretation of CLP2 pollen zones

CLP2 3a-b: 59 – 70 cm **(1320-870 BC)**

The base of the zone, and the core, is marked by some mineral grains and abundant spores (Table 3. 8) indicating, as for CLH core, development in an area where brown earths and soils are dominant. *Pinus* stomata occur at the base of the zone, (Figure 6.25) with modest *Pinus* pollen percentages (decreasing to *c.* 30% TLP) indicating perhaps local dominance but with the trees not in sufficient abundance in the extra-local environment to produce a large background pollen loading to the site.

This interpretation is supported by the evidence for mixed extra-local woodland from the low but consistent percentages of other arboreal taxa such as *Quercus*, *Alnus* and perhaps *Corylus avellana*. The high levels of Coryloid-type are also likely to be due to *Corylus avellana*, as when separated (Section 3.5.3), the majority of grains are assigned to *Corylus*, and, in addition, *Myrica gale* is a poor pollen producer (Janssen 1984; Birks 1989). The presence of *Polypodium* spores in this zone may be linked to local *Quercus* presence, as the first is often an epiphyte of the latter (Rose 1974; Sansum 2005), and therefore may provide some additional confirmation of localness.

The transition into sub-zone 1b is marked by a reduction in *Pinus* due to the eventual loss of stomata and a marked decline in the pollen percentages of this taxon in the pollen record at 62 cm (*c.* 620 BC). *Betula* peaks sharply at this level although the relationship between this pollen peak and the dynamics of the woodland is difficult to establish. The peak is related to a large peak in the pollen concentration in the profile, indicating either a protracted period of slow sediment accumulation, or perhaps more likely, a *Betula* catkin entering the peat here. *Pinus* pollen concentrations do reduce in the concentration diagram independent of the *Betula* rise (Figure A7.2). Other broadleaved taxa remain from sub-zone 1a indicating continued landscape presence.

Ground flora in zone 1 is not dominated heavily by any of the three main taxa; *Calluna*, Cyperaceae or Poaceae. A small peak in Cyperaceae does occur in sub-zone 1a (to >15% TLP), whilst Pocaceae is a little more dominant in sub-zone 1b. The zone is marked by a high diversity of dicotyledonous taxa, with *Succisa*, *Plantago* and Lilliaceae forming small percentage peaks. The basin itself is likely to have been wet at this point, as evidenced by the presence of abundant diatoms (Figure A7.1c). There is some evidence of fire presence with small peaks in charcoal from all the size classes; two peaks occur in sub-zone 1b and may be associated with the shift in woodland at this time. However, little information on the natural or human origin of these fires is available.

CLP2 2a-d: 12–59 cm (370 BC – AD 1740)

This zone is marked at is base by a reduction in charcoal, a reduction in Lycophytes and Pteridophytes and the disappearance of diatoms. Pollen preservation quality increases and *Sphagnum* spore presence increases slightly. This perhaps indicates the development of a true peat from a small muddy hollow.

Pinus pollen increases to >50% TLP in sub-zone 2a but all other arboreal pollen taxa demonstrate slight percentage decreases, and *Pinus* stomata are not present indicating an extra-local pollen source. This may therefore mark an opening of the local canopy.

The open character of the vegetation is supported by increases in *Calluna* and Ericales (Figure 6.25), however reference to the NAP pollen percentage diagram indicates more clearly that Poaceae was also a co-dominant at this time. It is possible that *Myrica gale* was present locally here, although any interpretation between *Corylus* and *Myrica* pollen grains may be somewhat insecure.

The opening may have lasted 6-700 years (between 58 and 48 cm depth), the driver of this sustained open period is not clear. Diversity increases after a dip at 58 cm (Figure 6.24) and some grains of *Hordeum*-type appear, and one grain of *Avena*-*Triticum*-type. However, evidence of human impact from these single grains is far from conclusive (Chapter 6), and evidence from charcoal suggests the cessation of fires during this period.

Sub-zones 2c and 2d show little change in *Pinus* pollen dominance, although stomata become sparse in sub-zone 2d. In 2c *Alnus* and *Betula* pollen percentages decrease, and *Salix*, perhaps *Myrica*, and Cyperaceae increase. This could be an indicator of a short phase of wetter site conditions. *Alnus*, although a tree of wetter conditions can suffer from water-logging (McVean 1953; McVean 1956; *In* Sansum, 2005). Given the topography of the area, it is possible that *Alnus* was driven temporarily from local wetter micro-sites, whilst *Pinus* remained on the drier knolls. The local breakdown of *Pinus* canopy in sub-zone 2d, may be unrelated to the subsequent reappearance of *Alnus* pollen, as the two taxa occupy different niches.

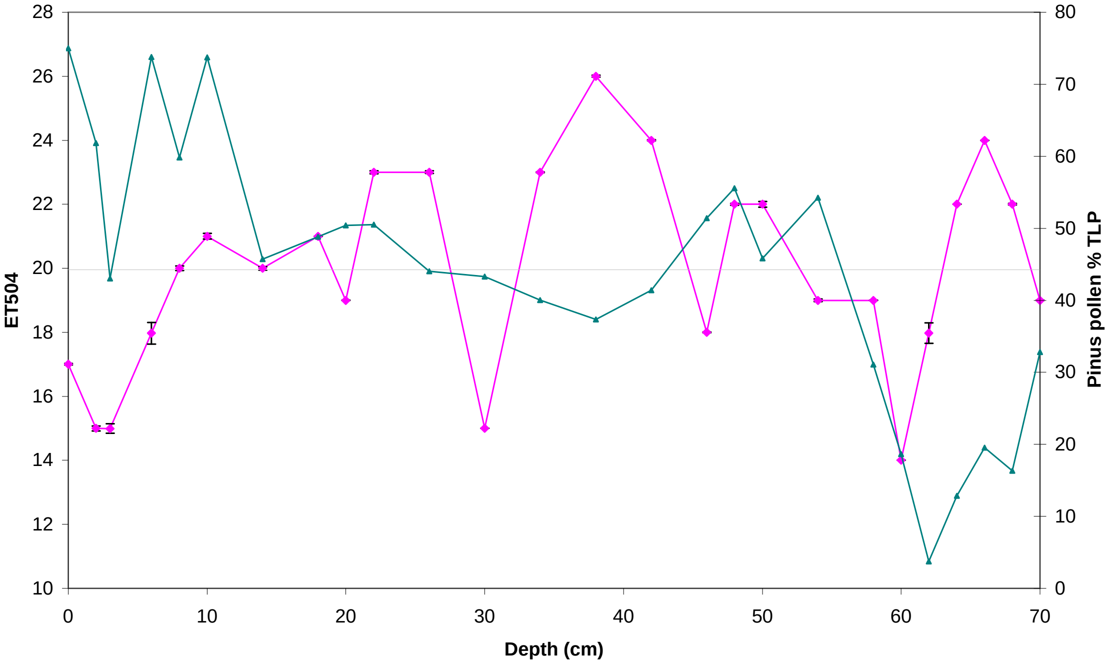
During sub-zone 2e *Alnus* and *Betula* pollen percentage decrease once again and the end of zone 2 marks the end of *Alnus* presence in the locality. Despite the high *Pinus* pollen percentages (*c*. 40% TLP) these represent extra-local tree presence. The surrounding open area of the basin was probably subject to some local regeneration of *Sorbus aucuparia* indicated by an increase in the pollen percentages here, for this poorly dispersed pollen taxon.

In general, a shift towards wetter conditions again, is suggested by the *Sphagnum* peak together with a peak in *Salix* and the presence of single *Drosera intermedia* grains at the zone boundary.

CLP2 3a-b: 12–59 cm (1740 - AD 2004)

Following from the open, wet phase of sub-zone 2e, zone 3 depicts an increase in *Pinus* once more, but with *Pinus* stomata only appearing in sub-zone 3b; the surface 0-5 cm sediments. Since all *Pinus* trees currently surrounding this basin are present beyond the 20 m ring source area it may be that their presence constitutes an extra-local interpretation in terms of *Pinus* stomata and the increase in surface sediment may be consistent with the appearance of some faster growing young *Pinus* near to the basin. A small increase in *Betula* in sub-zone 3b also reflects the current presence of Betula trees around the site.

The modern vegetation phase in zone 3 is also marked by an increase in Poaceae and a decrease in *Calluna* and palynological richness (Figure 6.24), perhaps indicating a recent change with the protection of the area from grazing pressure.



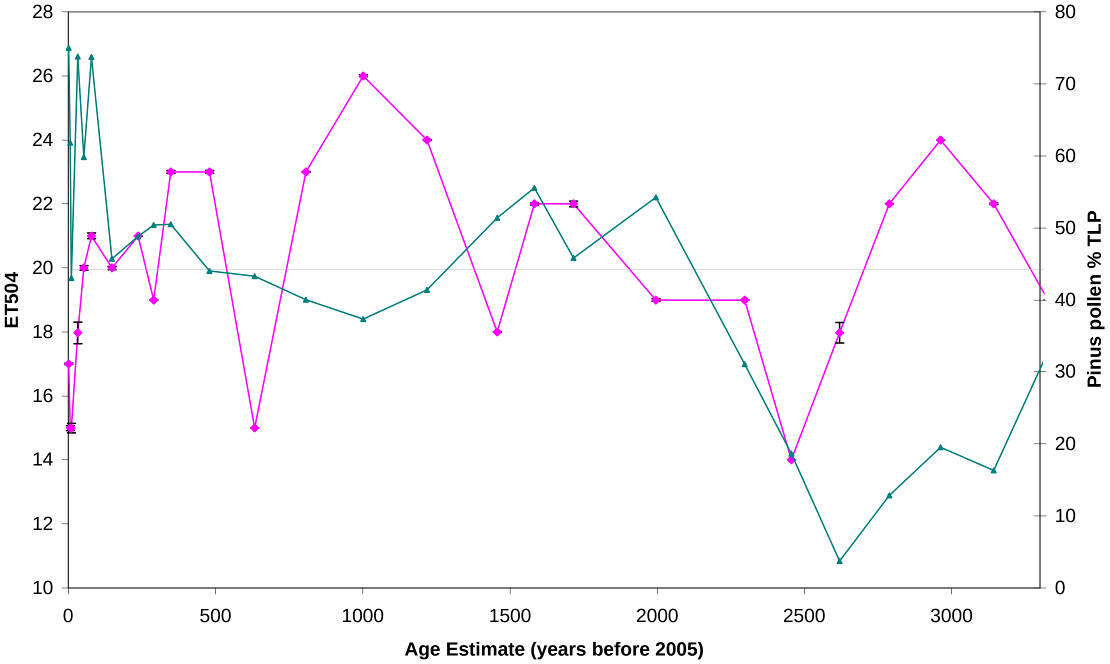


Figure 6.24: Palynological richness for the CLP2 pollen samples (pink line) (ET_{504}) Expected number of pollen taxon for a normalised pollen count of 504 grains per sample, and *Pinus* pollen %TLP (green line) against depth (top) and age estimate (bottom). The grey line represents the average richness score

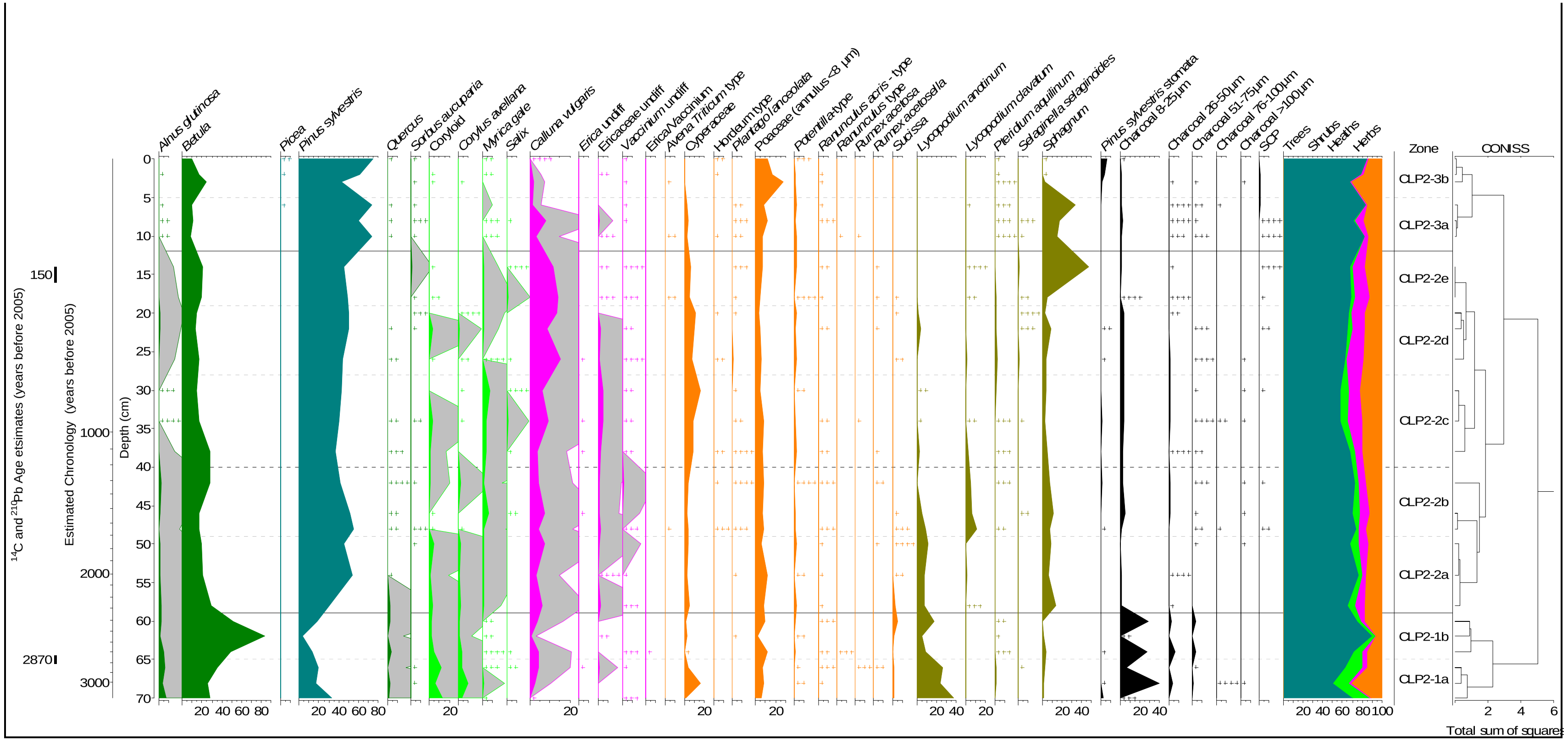


Figure 6.25: Summary Pollen Diagram for selected taxa and palynomorphs from the CLP2 core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

6.5.3 CLKH pollen core

The chronology for this site shows a limited age with depth and a rapid peat accumulation. The age at 100 cm, the basal pollen sample, is estimated as just AD 1720 (Chapter 4), thus limiting the historical information that can be gained form this core. A very brief description and intepretation will therefore follow.

6.5.3.1 Interpretation of CLKH pollen zones

The CLKH core depicts a relatively steady arboreal presence in the pollen record at 60-80% TLP (Figure 6.26) and therefore infers *c.* 300 year stability in woodland canopy cover. Despite this high AP % the site is actually characterised by an open canopy, one with patches of woodland and scattered trees. The high AP dominance in this pollen record could be a product of the low pollen productivity of the basin surface, which is predominantly *Sphagnum*.

CLKH 1a-b: 64 – 100 cm (AD 1810-1780)

This basal zone from *c.* 300 to 200 years ago depicts the presence in the surrounding stand of *Alnus, Betula* and *Pinus*. Poaceae may have been a little more dominant than at present, and *Plantago lanceolata* occurs as a steady 1-2% TLP. *Hordeum*-type grains and one *Avena Triticum*-type grain occurs in this zone. One small peak in charcoal at *c.* 96 cm is present across all of the size classes and therefore may indicate local firing, but whether by natural or human agency is not discernable. *Sphagnum* spores are not an abundant feature of the base of this core, but a peak in *Potomageton* may indicate rather more pond-like conditions in the hollow itself. A shift in pollen concentration at the basal pollen sample may also indicate changed conditions (Figure A8.3). This would not, given the topography of the site, necessarily indicate any change in the surrounding edaphic conditions.

CLKH 2a-b: – 32-64 cm (AD 1810-1900)

The boundary to zone 2 is marked by an increase in AP and *Pinus* pollen percentages and a reduction in *Alnus*. By the middle of the zone *Quercus* pollen reaches steady low (1-2% TLP) values and probably indicates the development of the present single oak tree at the site. This indicates that just 1-2%TLP of *Quercus* pollen can depict a sparse local tree presence, but, in the absence of modern evidence, it may still be impossible to interpret past the current dilemma of pollen analysts; that of the difference between sparse local presence or abundant distant presence of a taxon (Davis 2000).

CLKH 2a-b: – 32-0 cm (AD 1900-2004)

Little changes from the previous zone here, except that pine stomata, although still scarce, become consistently present; perhaps indicating the maturing of the current local *Pinus* population. *Alnus* becomes scarce. Juniper is not evident in the pollen record despite tree presence, and the sparse *Myrica* grains, given the presence of *Corylus avellana*, could be a misidentification. Palynological richness is reduced (Figure 6.27), and *Plantago lanceolata* and *Potentilla* become sparse from a former constant 1-3% TLP presence.

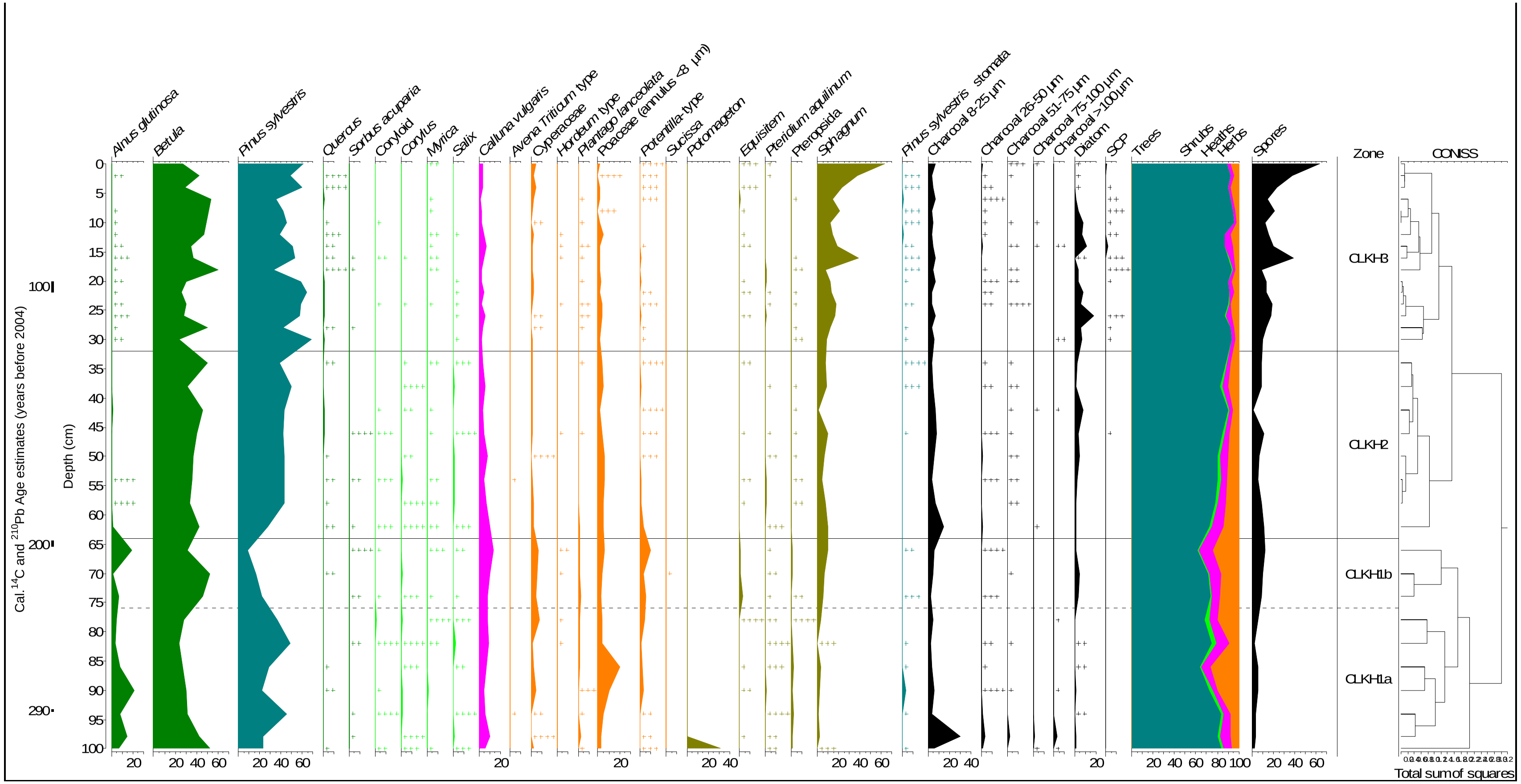


Figure 6.26: Pollen Diagram for selected taxa and palynomorphs from the CLKH core. All land pollen taxa as a percentage of TLP other taxa as a percentage of TLP+ Group. Left axis against depth with age estimates displayed.

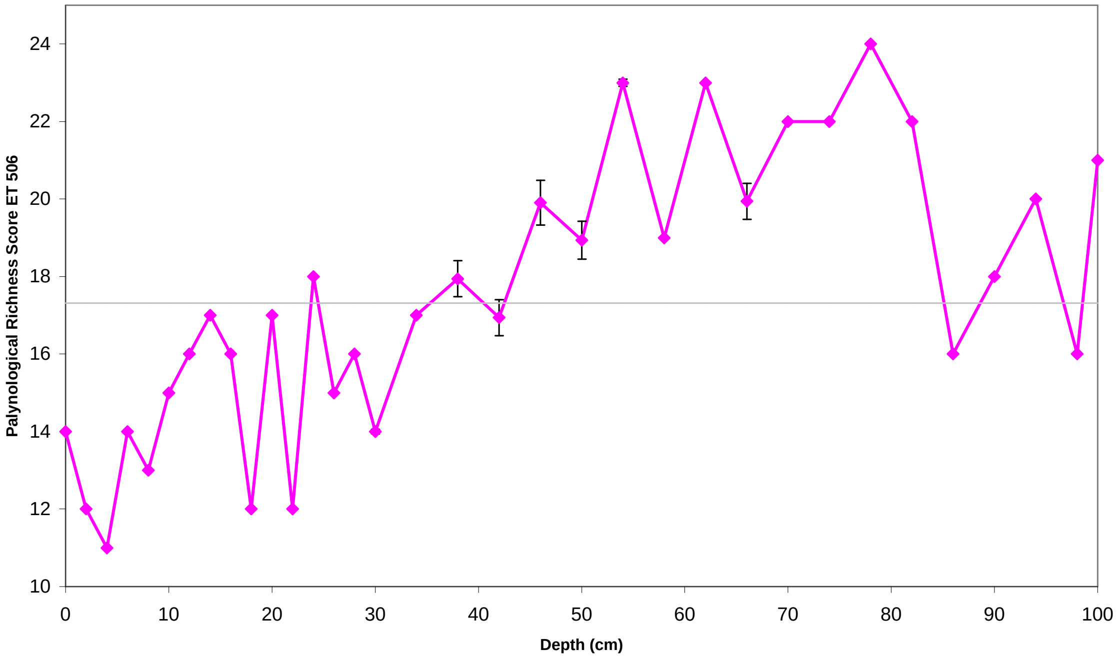


Figure 6.27: Plot of palynological richness for CLKH (ET_{506}) Expected number of pollen taxon for a normalised pollen count of 506 grains per sample.

6.5.4 Discussion of Cluster 3 CLH, CLP2 and CLKH cores

This eastern-most cluster of sites in the study demonstrates the stability of the woodland in this area. Although the pollen core from the CLKH basin returns a very short site history, the CLH and CLP2cores illustrate *c.* 4000 and *c.* 3000 years of woodland history respectively.

All three cores show little fluctuation in the dominance of the arboreal taxa, with AP values consistently >60% TLP. Over the temporal spans of CLP2 and CLH this is remarkable. The woodland shows little evidence of drivers of change, from either human or natural forces. Charcoal presence is low, and tends to be in the smaller size classes inferring landscape rather than local fire episodes (Blackford 2000). There is certainly no evidence of a regular pattern of firing.

The sub-sampling resolution on these cores was coarser than expected and so some subtleties of ground flora shifts, or brief canopy openings may not have been detected; however, the data fits well with that of Froyd (2006) for this eastern part of the glen, although the woodland may always have been quite mixed.

6.6 Summary of core results

Overall, the data from the eight sites show a clear spatial pattern of woodland. An open landscape, to the westernmost core sites, is gradually graded into stable woodland to the sites of the easternmost cores. The openness in the west has been stable, apart from a few minor episodes of woodland, or perhaps more accurately, of scattered trees in a heathland matrix, over the last *c.* 4000 years. Whilst to the east the canopy, at the landscape scale, has also been stable, although the cores with higher sampling resolution hint at some internal, cyclical dynamics and short episodes of canopy breakdown at the stand scale, whilst shifts from *Betula* to *Pinus* dominance or cyclity between these taxa is apparent in some cores.

What seems clear is that over the last *c.* 200 years there has been an expansion of woodland westward, which should be an interesting finding in terms of the ability to expand the native pine wood and achieve policy and management goals for the woodlands here. However, what is also clear is that this expansion has been accompanied by a reduction in biodiversity, and a reduction in arboreal diversity, as well as a loss of openness, which may all have implications for conservation management and our understanding of the Caledonian pine woodlands.

These implications and the successes and problems involved in the development of interpretations in this study are discussed in the next and concluding chapter.

7 Discussion and conclusions

The discussion sections within the individual research chapters address specific technical and interpretive aspects of the work presented there. This chapter will evaluate the work presented in Chapters 3-6 in relation to the development of the broad and detailed aims of the thesis outlined in Chapters 1 and 2 respectively. The discussion falls into three parts;

(1) an examination of the scope and effectiveness of the methodology, especially the spatial and temporal resolution obtained, and the application of developments in palaeoecology;

(2) a consideration of the development of the ecological history of the Caledonian native pine woodlands, and especially that of the east Glen Affric woodlands;

(3) a consideration of the implications for future conservation management

7.1 Methods and interpretation

This thesis set out to be deliberately analytical and critical of the techniques used. Part of the reasons outlined in Chapter one for the poor uptake of evidence-based knowledge and research by practitioners concerned the difficulties in understanding the limitations and assumptions - the “uncertainties” - of ecological knowledge (Hobbs 1998; and Section 1.3.1).

For Scottish boreal woodlands, which may have been of open structure in the past, the ability of pollen analysis to determine fine-scale ecological histories required further testing and the objective outlined in Chapter 1 was:

- *To contribute to the development of a more quantified approach to fine spatial scale palaeoecology in semi-open woodland landscapes.*

Palaeoecology has recently been criticised for its limitations (Vera 2000), however, an obvious strength within the discipline is its ability to be self-critical (e.g. Davis 2000) and to continue to develop, test, and validate the results of analysis (e.g. Broström 2002; Broström *et al.* 1998; Broström *et al.* 2005; Bunting *et al.* 2005; Bunting and Middleton 2005; Gaillard *et al.* 1994a; 1994b; Sugita 1998; Sugita 1994; Sugita *et al.* 1999). Whilst this is not unique to palaeoecology, it nonetheless affirms the relevance of the discipline. Self-criticism, rather than invalidating conclusions, helps to validate and give confidence in their application.

Several aspects of the palaeoecological technique have been examined, tested, and critically evaluated, during the course of this research; these include the temporal and spatial scale of the analyses, the opportunities for quantitative and qualitative vegetation reconstructions using modern analogue techniques, and the application of these to a network approach. These aspects are discussed below.

7.1.1 Time

The notion of grain and extent (Section 1.3.1) in relation to planning the temporal scale of this research is highlighted in Chapter 3, and chronological models developed and discussed in some depth and complexity in Chapter 4. The selection of a standard core length and sub-sample resolution failed, probably unsurprisingly, to provide a standard temporal grain and extent across the cores, with some cores having a short temporal spacing between sub-samples over a short overall time-span, and some having temporal spacing of a hundred years or more over a time-span of several millennia. In many ways, however, the resultant temporal scales proved serendipitous as the longer-than-expected span of cores NHP and PB - *c.* 5000 and 3000 years, respectively - towards the western extremity of the current woodland, enabled interpretation of openness through to the classic ‘pine decline’ *c.* 4000 years BP (Bennett 1984; Section 6.3.4). These cores demonstrated, just kilometres from a previously analysed site (Froyd 2002), that the woodland in Glen Affric had, during the mid- to late Holocene, always been spatially limited (Section 6.3.4 and 6.5.4), whilst stand-scale fluctuations in a broadly ‘stable equilibrium landscape’ have been the pattern over equally extensive periods of time to the east (Section 6.4.3, and 6.3).

In those sites with a longer temporal sequence, the grain, or resolution, of the analysis was compromised (Section 4.6.4). However, the presence of multiple temporal scales may also have worked to the advantage of the analysis. For example, in the pollen diagrams from cluster 2 - ANI and ARC - temporal scales allow an interpretation over *c.* 3700 years and *c.* 1000 years, respectively, with associated resolution of *c.* 50-80 years, and 10-20 years, respectively. Within these sites, not only the continuity of woodland can be identified (ANI, Section 6.4.1.), but the finer stand scale cyclicity and regeneration can be seen (ARC, Section 6.4.2). Of course, in an ideal situation, each core would be sampled at micro-time-scales over its whole length, but, within time-limited periods of research, the deliberate selection of a variety of temporal scales (analogous to the "*hierarchy of nested scales*" of Delcourt and Delcourt (1983), see Chapter 1), may be important in extracting maximum detail from the data. Either of the two cores in cluster 2 would be impoverished in their interpretation without the opportunity of comparison with the other[13].

In general, however, the unintended expansive temporal resolution of many of the cores created difficulties in interpreting shifts in ground flora composition. The areas of shifting dominance between Calluna and other Ericales in PB and NHP are particularly worthy of further analysis through closer sub-sampling. This may provide a unique 'real-time' insight into the processes of shifting dominance of these taxa, with changing canopy cover and grazing regime, observed in modern ecology (Gimingham 1964; Gimingham 1949; Gimingham 1988; Gimingham *et al.* 1981).

An additional problem, especially relevant to the reconstruction of ground flora communities, is in the temporal representivity of each pollen spectrum (Section 3.4). When attempting to analyse fine scale vegetation change, the palynologist is in pursuit of the perfect balance, between merging years of pollen accumulation, and the separating of fine-temporal-scale vegetation shifts (Hicks 1985). In the cores covering several thousands of years of peat accumulation, the rate of change in temporal representivity, caused by both the accumulation and compaction of peat, is high[14]. This implies that, despite efforts to use thicker slices at the top of the core, the surface samples may represent only one or two years of peat accumulation, whilst the basal samples may represent 20 years or more. There may be several separate problems generated by this; (i) the modern analogue interpretations may be subject to

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[13] This is illustrated by examination of the cores to the western end of the study area; where cluster 1 reveals a long history of openness as discussed above, but lacks finer temporal resolution with samples at 60-120 years spacing. Although openness is defined in these cores some short phases where *Pinus* stomata are revealed in just one level (e.g. 50 cm at NHP and 60 cm at PB) may mask short periods of regeneration which would be better identified with a finer temporal scale.

[14] If, as was done for this study, no hiatuses are presumed.

productivity errors; (ii) rare taxa may be better represented in basal samples due to the amalgamation of several years of flowering; and (iii) the identification of palynological richness (Birks and Line 1992); and thus interpretations of higher past diversity may be flawed by (ii).

Although several studies have attempted to examine surface peat growth and pollen productivity (Cundill 1998; Cundill 1991; Cundill 1986), there seems to be no satisfactory single measure of peat accumulation, and the Glen Affric cores suggest a high variation[15].

Lastly, as identified in Chapter 4, the accuracy and precision of the chronological models also impacts strongly on the network approach. The aims of this thesis included the identification of, and differentiation between, landscape-scale canopy change, and internal stand-scale cyclicity and stand regeneration/replacement phases. This requires the correlation of peaks and breakdowns in pollen taxon dominance across cores, yet the errors surrounding modelled chronologies can be of the order of 100s of years (Section 4.6.5). The attempt to identify and correlate periods of high *Pinus* dominance and high diversity in Figure 6.13 for cluster 1 demonstrates that the separation of local, from widespread, events was not possible with any certainty. This requires a precision of chronology that perhaps is just not available at present. The critical analysis of the chronological models used in this study, presented in Chapter 4, is certainly in agreement with that of other authors (Bennett 1994; Bennett and Fuller 2002; Telford *et al.* 2004a; 2004b), and suggests that development in the merging of ecology and palaeoecology (*sensu* Davis 1994) routinely requires an increased number of radiocarbon dates per core. Given the importance of temporal precision to the ability to analyse the results of any pollen analysis with rigour, this perhaps highlights the need for the costs of these assays to be built into the overall project costs at an early stage.

The need for rangefinder dates to ensure the palynological investigation is only carried out on secure stratigraphies is key, and reiterated here. In hindsight, a certain wasted effort was associated with the sampling and pollen counting of the CLKH core (Sections 4.5.8 and 6.5.3).

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[15] A test experiment of peat growth in Glen Affric carried out in the first year of this research aimed to test this by placing plastic markers in the peat and measuring growth a year on. This largely failed due to some ground disturbance and some loss of the markers under vegetation growth. However the results of this type of study are probably routinely required.

However, additional problems are associated with selection of sample levels for further assays, and are worthy of discussion. The palynologist is faced with a dilemma as the selection of sub-samples for assays can be based on two regimes (Section 4.1). (i) the regular spacing of assays at depth, or (ii) selecting levels based on vegetation shifts (Telford *et al.* 2004b). This study strongly suggests merit in choosing assay levels based upon shifts in the pollen concentration data. Application of shifts in slope to the chronological models (Section 4.6) based on shifts in pollen concentration rates was partially successful in smoothing pollen influx data (Chapter 6 and Appendix 1). Further smoothing is likely with increased assays. Accurate influx data are, in turn, important in the quantification of vegetation (Hicks 2006; Hicks 2001; Hicks 1985) and their use is illustrated in Chapter 6, in illuminating detail for some of the pollen percentage fluctuations from the cores.

7.1.2 Space

Grain and extent is also important to spatial scale (Section 1.3.2), and provided the rationale underpinning the small basin network approach. Key to this is defining the spatial resolution of the vegetation interpretation, both for key taxa, and for the pollen assemblage. The small basin approach is tested here in a semi-open environment (Chapter 5), whereas previous studies have used a less quantitative approach, or have been applied to the identification of attenuation in pollen signal away from a spatially-defined area of woodland in a transect approach (e.g. Turner 1964; Setion 5.1), which may not produce comaparable results (Jackson and Wong 1994). This study was probably novel for Scotland, in attempting to determine RSAP and PPEs (Chapter 5) for small basin deposits in a semi-open environment.

In spite of predicted changes in source area for pollen via modified emphasis of above-canopy pollen transport mechanisms as a consequence of an open canopy, the small basin approach does seem to provide the opportunity for local vegetation reconstructions, even in semi-open and open environments. The suggested Relevant Source Area for Pollen (RSAP) for woodland, of *c.* 20 m (Calcote 1995), is tentatively confirmed as a workable model for this semi-open woodland in Glen Affric, by reference to the asymptotes in both the simple, single taxon regression, and the key taxa Extended R-Value (ERV) analysis in Chapter 5. Supporting confirmation also comes from the ranking of data and pollen in Section 5.5.2. However, further testing at extended ring-source radii is required. When comparing the asymptote from ground flora with that found by Hjelle (1997) and Bunting (2003) extending the sampling radius to 20 m highlights that there may be a possibility that the asymptote is scale specific (Section 5.5.6.1), and this requires further testing.

7.1.3 Quantitative and qualitative reconstructions

- *What is the former structure of the ground flora and how has this changed through time?*

The large background pollen component derived from a regression at the 20 m vegetation sample radius, and the uncertainties over the RSAP highlighted by both the asymptote plot, and the variation in residuals in taxon plots under linear regression (Chapter 5), indicate that, without further testing, use of the calculated pollen productivity estimates (PPEs), from and within Glen Affric, may be susceptible to large errors (A. Broström; A. B. Nielson, *pers. comm*.). Hence, a comparative, less formal approach is used in the interpretation of the fossil data in this study (R. Fyfe *pers. comm*.). This is perhaps a disappointment and quantitative reconstructions of the key taxa are still a goal for further work on this data set.

However, an additional problem of the development of PPEs for species poor woodland such as native pine woodland is that the application of the method is probably limited to just five key taxa (Chapter 5). Testing of the Indices of Association (IOA) method for analysis of the pollen-vegetation relationship of rare pollen taxa therefore became important (Section 5.2.2 and 5.5.3). The Point Biserial Correlation Coefficient (Section 5.5.3) applied, probably for the first time, to pollen data, may prove a useful additional tool in the understanding of rare taxa representivity. The ability to test the regression using this method highlights various problems and possibilities for testing of the pollen-vegetation relationship of these rare taxa. The lack of significant correlation for many pollen-plant relationships tested under the IOA analysis is highlighted by the use of the R_{pb}. Testing of the plot of r^2 for R_{pb} regressions at different source areas is also possible. The application of this method to other data sets for comparison would be of interest. The extent to which the lack of significant correlation between plant and pollen taxa for rare pollen types is a product of time or space is difficult to establish and may be worthy of further testing (Section 5.5.3.3).

Whilst expanding the ring source area for vegetation may be possible by reference to forest maps and aerial photographs for trees and for key ground flora (e.g. Nielsen and Odgaard 2004; Nielsen and Sugita 2005), these methods will lack the detail of ground vegetation surveys, and therefore, will not resolve the issues of the sporadic coincidence of pollen with plant within the rare taxa. Given the dominance of the key taxa in the pollen data, a greatly increased pollen count is recommended for future local-scale studies. In addition, determining chronological control over the surface sample (Section 7.1.2) to ensure a suitable number of years of pollen accumulation in modern pollen spectra, may be key to achieving successful regressions. In the context of the current study, for example, I suspect that the current lack of significance between plant and pollen amongst the rare taxa in the Glen Affric surface samples is a product of too low a pollen count, and a lack of temporal accumulation in the surface samples (Section 7.1.1).

Many inferences drawn from pollen analysis confined to the standard 500 TLP count may be similarly limited in the scope for interpretation, especially in terms of the inferences of human impact. In Estonia Poska *et al*. (2004), when developing a correlative study of human impact across Estonian pollen analyses, rejected 370 out of the 400 sites so far studied, for a lack of secure chronology, and a lack of rigorous sampling technique; all counts under 1000 pollen grains were omitted.

PCA analysis (Section 5.2.3; 5.6 and Chapter 6) as a comparative approach (Birks and Gordon 1985) between pollen spectra as communities has been successful in Glen Affric, and has helped to determine mixed from pure stands in past woodland phases. It provides a good method of illustrating shifts between vegetation states. However, testing of the fit of these analyses has been implemented through RDA and Monte Carlo permutation testing on other data sets. This relies on additional environmental data, such as information on management regimes, which was not available for, and may not be relevant to the more natural current conditions in Glen Affric. However, understanding the patterns in the pollen spectra from heavily grazed and exclosed areas of the pine wood could be an interesting objective for further testing of the data. Cluster analysis of the modern vegetation set produced very little consistency and so this was not attempted in the current study.

In spite of these limitations, the interpretations were strengthened by the modern comparison data set, which determined some cut-off values for *Pinus* and *Betula*, highlighted problems with *Calluna* pollen loading, and confirmed agreement with other studies on the use of *Pinus* stomata. The interpretations also highlighted where caution should be applied to traditional indicator taxa in the pine wood environment. Understanding the limitations of the data set may constrain, but also strengthens thevalidity of the interpretation, and may help to provide some guidelines for interpretation of other, similar pollen analyses.

7.1.4 The network approach

The network approach has enabled a detailed landscape history to be reconstructed, and differences and similarities between contrasting areas of the extant woodland to be assessed. Single fine-spatial-resolution pollen analyses would not have identified the variation in past tree cover between east and west, or the differences in woodland dynamics and structure between some areas. The extreme localness of the interpretations does limit, however, the ability to correlate between cores and therefore may miss fine-grained and multiple-stand states in other locations. The analysis of pollen can never produce datasets over a vast number of point sources as can be achieved in the application of computer modelling approaches. This may limit the aims of this project, to link with computer simulations (P. Osborne *pers. comm.*). It is anticipated, however, that the newly developing models within the POLLANDCAL network will allow some development of this in the near future. The published REVEALS model is suitable for reconstructions around large lakes, however models in development include LOVE (Sugita in press) and GIS landscape reconstructions (Fyfe 2006), which are applicable to small basins. The development of site-specific PPEs will be advantageous in applying these models to the Glen Affric vegetation reconstructions, although further chronological controls may be required (Section 7.1.1).

In terms of less mechanistic correlations, the analyses were driven, to some extent, by the ability to find suitable sites (Section 3.2). A large area of extant native pine woodland to the south of Loch Beinn à Mheadhoin was not sampled due to a lack of perceived suitable substrate on the steeper slopes where *Pinus* is currently abundant. The development of chronological models for the sites, when the results of the ^{14}C and ^{210}Pb assays became available nearer to the end of the project, revealed that even shallow basins can hold deposits representing several thousands of years of peat accumulation. Given this, it seems that it may be possible to utilise shallow sites in areas of *Pinus* woodland that were not sampled as part of the work programme for by this thesis. A suite of sites within this zone would provide a useful addition to the current network and test the mono-dominance of *Pinus* is this area. This would provide a contrast to the findings from mixed woodland sites and would assist in the testing of the ESC model (Pyatt 1994; Pyatt *et al.* 2001).

7.1.5 Ecological function

Whilst this study supports and reaffirms the conclusions of other studies, that pollen analysis can contribute to our knowledge of the past history and dynamics of vegetation (Segerstrom 1997; Segerstrom and Bradshaw 1994; Segerstrom and Emanuelsson 2002; Segerstrom *et al.* 1996), difficulties in determining autochthonous vegetation change from impact-driven change (Birks and Gordon 1985) still remain. The modern analogue study revealed just how tenuous the interpretation of vegetation is from most herbaceous pollen, thus limiting the ability to identify human impact (see also Bunting 2003 and Section 5.7.1).

Some information can be gained from the comparative analysis of communities rather than individual species, and from an examination of the diversity of a pollen spectrum, via rarefaction. Any inference of this nature, however, negates, through the danger of circularities to the argument, the ability to examine the longevity of communities; a key aim of this thesis. In addition, the analysis of palynological richness, which in this and other studies (A. Davies *pers.*

comm.) decreases in the last *c.* 200 years, may be an artefact of the subsample resolution. Many aspects of a palaeoecological study thus still require a degree of informed guesswork in the interpretation. Care should be taken to avoid circularities of argument, or, when they are used, to acknowledge them and make them explicit. It is only via this open approach that we may find solutions to interpretive problems and avoid unnecessary criticism.

Where information on possible drivers of change is available, for example from insights on environmental and human drivers reported in the Statistical Accounts of Scotland (Section 2.2.1.5) these often indicate multiple possible drivers (e.g. the shift to woodland at *c.* AD 1810 around the NHP basin (Section 6.3.1). Teasing out these subtleties may indicate a requirement to return to the application of multiproxy studies (Seppa and Bennett 2003) and larger more-integrated projects (e.g the Ystad project Berglund 1991).

7.2 Recent woodland history of Glen Affric

Despite the limitations outlined in Section 7.1, the development of a palaeo-dataset, of eight fine-spatial resolution sites, in the extant woodland of Glen Affric, and the opportunity to compare this with 29 surface pollen samples and associated vegetation datasets, provides a unique opportunity to look, in some detail, at the internal workings of a Scottish boreal woodland over the last *c.* 2-5000 years.

The aims for the thesis were:

- To provide a pollen-based reconstruction of the woodland history in the extant forest zone; and,
- To investigate the former westward extent of the pine woodland.
- To contribute to management tools in development by Forestry Research (Bell 2003) by providing information on the history of the extant pine woods for ecological understanding and for input for a model to predict the effects of forest design and management in Glen Affric

And questions forming the basis for the investigation were:

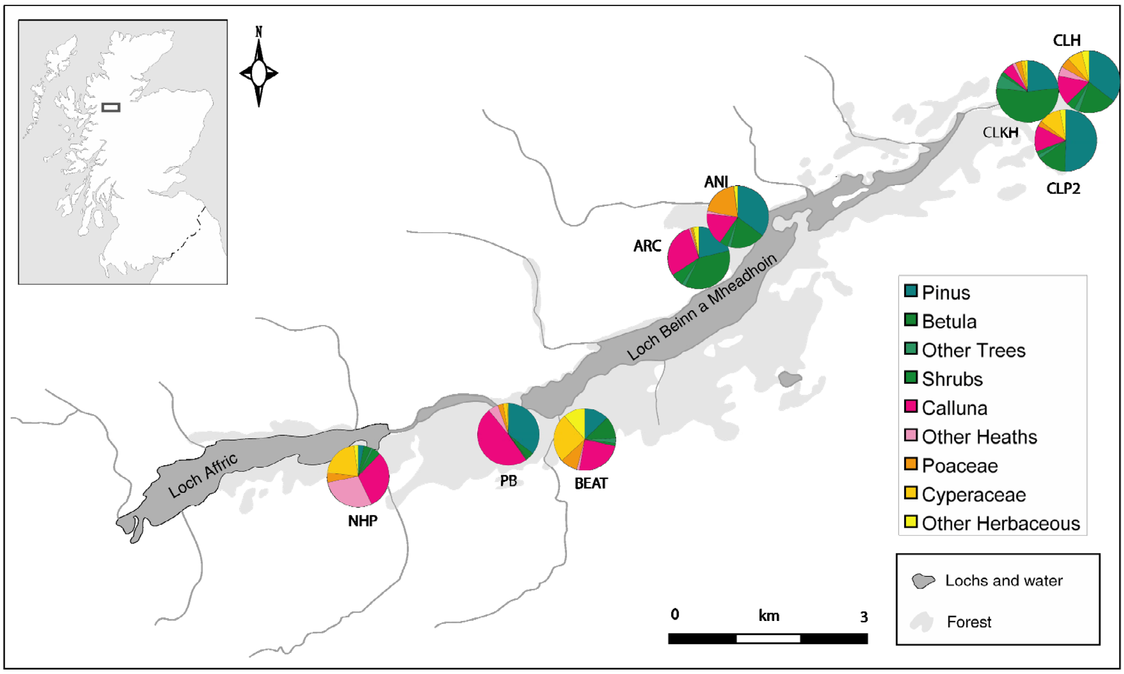
- What is the history structure and longevity of the current breakdown and opening of woodland to the west?

- What is the stand scale longevity and variation within the existing and purported relict woodland alongside Loch Beinn a Mheadhoin.
- What are the differences in species composition between present and past stands
- Is there evidence of *Pinus* and *Betula* as mixed stands or in patterns of temporal cyclicity?

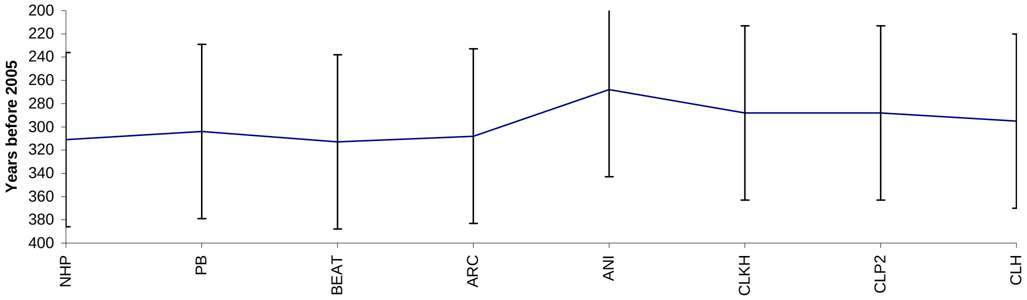
7.2.1 Spatial extent of woodland

- *What is the history, structure and longevity of the current breakdown and opening of woodland to the west?*

The former westerly extent is an important feature of these woodlands as they are generally regarded as having undergone an eastward retraction. The timing of this retraction has been unclear (Chapter 2) and has been purported to be recent. The 1725 map by Joseph Avery, shows the extent of the woodland at this time is not very different to the present, despite the activity of various logging companies (Smout *et al.* 2005). Blaeu’s Atlas Maior, from *c.* 1665 (Bleau and van der Krogt 2006) also shows Loch Affric and highlights trees to the east of the Loch and a small patch towards Allt Beithe, but none to the loch-side. Whilst the accuracy of the depiction of trees on these large-scale historic maps of Scotland is of question, there is a remarkable coincidence between the pollen and map evidence. Similar correlations between present and past extent of woodland were found via historical study in Assynt (Noble 1997). Although it is difficult to correlate accurately across cores given the chronological constraints previously discussed (Chapter 4 and Section 7.1.1), the continuity of the openness at NHP and PB, prior to the current stands, and the continuity of the woodland at the easternmost sites allow an approximate correlation across cores to illustrate site conditions before the present stand developed. Figure 7.1 shows the percentage pollen at each site for major taxa and groups at approximately 300 years before present (present being year AD 2005) and demonstrates the openness to the Glen Affric lochside. This pollen study extends the pattern of woodland presence in the landscape of Glen Affric back to the *c.* 4000 year time period, and a match with the classic ‘pine decline event’ that has recently been found not to be present in the east of the Glen (Froyd 2006; Section 6.3.4). Apart from small fluctuations and incursions of woodland the pattern and extent of woodland in the glen remained remarkably stable from 300 years to *c.*5000 years before present.



a)



b)

Figure 7.1a): Map of Glen Affric showing, in pie chart form, the percentage of pollen from the major arboreal and non-arboreal pollen taxa to show the major differences between east and west of the Glen at approximately 300 years cal. BP (The sampling resolution was such that the age range of samples was actually from 265 to 315 years before present (see 7.1b above). The errors surrounding the chronological models are also wide - see the comments in Section 7.1.1 and Chapter 4 regarding accuracy of the chronology).
Fig 7.1b): Midpoint age and error for the eight samples shown in the pie charts above.

Two classic hypotheses emerge; (i) that the extent of woodland is climatically controlled; and (ii) that the woodland has been degraded over long time periods by human activity.

In the case of Glen Affric the management hypothesis is interesting, as it would imply some tightly defined management boundary, stable for 4 millennia. Whilst this is not impossible, Peterken, (1986) discusses the concept of woodland fluctuation around core areas, and it is possible that the woodland in Glen Affric has always been range limited, and varied in cover and compostion from east to west. In fact, pollen analyses from Davies (1999; 2003) demonstrate that the composition of the woodland graded to broadleaved mixes, when present in the past, to the far west of the Glen, and that any *Pinus* domination was short-lived between *c.* 7000 and 4000 years ago. Human land use is inferred in these records, and the possibility of a management boundary cannot be ruled out at the NHP and PB site locations, especially in the light of the charcoal evidence, which is far more abundant in the past at these range-edge sites than within the extant pine woods. The cessation of a burning record in both of these sites occurs at or about the time of the Highland Clearances and so could mark the cessation of *c.* 4000 years of land use. However a natural shift in fire patterns with changing climate probably cannot be ruled-out and it is entirely possible that human land use and woodland reduction are entirely coincidental with ecological site factors being drivers of an open community structure to the west as well as making the area more conducive to settlement.

What is equally important to the ecological history of Glen Affric is the continuity of woodland to the east of the Glen. Whatever balance between climate or human influence took place to the west, to the east woodland has demonstrated continuity in the landscape over eight millennia (Froyd 2005). By means of the pollen analyses presented in this thesis, this continuity is confirmed at the stand scale from the mid- to recent Holocene, and the structure and composition of the woodland is described in some detail (Chapter 6).

7.2.2 Woodland structure

- *What is the stand scale longevity and variation within the existing and purported relict woodland alongside Loch Beinn a Mheadhoin*

The woodland structure to the east is characterised by a continuity in canopy cover (Core ANI), with some internal stand-scale cyclicity and opening inferred (Core ARC). This structure has remained remarkably stable over time (Section 6.4.3 and Section 6.5.4), and therefore the implication is that it should remain so into the future (in the absence of any major environmental change drivers – an increasingly unlikely scenario; see Houghton *et al*. (2001), SEPA (2006)). Possible signs of recent reduction in diversity require some further testing, but the evidence shows that *Pinus* may have become a more important part of the woodland mix over recent centuries.

The comparison between the east and west of the Glen illustrates that landscape patches can be variable over long time-periods. Linkages between landscape patches are often important (Jongman *et al.* 1998). This has implications for the findings in Glen Affric. The landscape to the west has been found to have been considerably more open in the past than now, and the evidence from BEAT is that there may have been a gradation in the permanence of woodland cover from east to west. For species such as the rare ‘woodland’ lichens and bryophytes (Hope 2003; Coppins and Coppins 2006; see Section 2.1.1), it must be deduced whether their survival is due to the openness of the landscape (Hope 2003), or, if it is in spite of the openness and due to the patchy survival of trees within the landscape acting as a bridge to the isolated patches. This will have profound implications for the management of the landscape for these species into the future. Evidence from the west in this study does not fully support the view that wide-scale or dense tree cover is a prerequisite for these species’ survival, or that these species are a consistent indicator of ancient woodland. This possible inconsistency in the identification of, and understanding of the ecology of, ancient woodland indicator species has been previously observed in other palaeoecological studies (Edwards 1986; Day 1991; Segerstrom 1997; Willis 1993; Segerstrom and Bradshaw 1994).

7.2.3 Main findings on woodland cyclicity

- *Is there evidence of Pinus and Betula as mixed stands or in patterns of temporal cyclicity?*

Comparisons of the cyclicity among stands in the same clusters is limited by the chronological controls (Section 7.1.1) but still contributes greatly to our knowledge of the fine-scale functioning of these extant Caledonian woodlands. The cyclicity and community diversity had been postulated, but not previously tested in these North Central (Table 2.3) woodlands. Both show a marked correlation in this study with the previous findings of O’Sullivan in Abernethy (O'Sullivan 1974; O'Sullivan 1973), thus contributing to the body of work, and expanding the opportunity to understand the differences and similarities between Caledonian woodland areas.

What does seem clear within the cyclicity, is that the regeneration of woodland has taken place within small stand-scale patches to the east, whilst overall in this area, a consistent canopy cover was maintained, and, contrastingly regeneration has been onto open moorland to the west in recent centuries. These regeneration episodes were always in the presence of grazing pressure. This supports theories from Zackrisson (1995) and Edwards (2006) that pulses of regeneration may be adequate to maintain the current stand structure (Section 2.1.3.2 and 2.2.3). It would be useful to understand more about the control over grazing imposed by past differences in management during the historical period from the east to west of the Glen.

7.2.4 Main findings on community structure, stability and change

- *What are the differences in species composition between present and past stands*

The space-for-time ecological classifications are critiqued in Chapters 1 and 2 of this thesis. However, in reality, Rodwell (1991), McVean (1964 p564) Burnett (1964) and others have always postulated a more mixed woodland in the past. McVean supposed that the pine woods were always subsidiary to birch, and this thesis provides some support for that view, contributing a reconstruction from *inside* the woodland as called for by Bennett (1995; and Section 2.1.2). Furthermore the *Betula* dominated, possibly, comparatively, species rich woodland may have been more stable, and as discussed in Section 2.1.2.2, may confer resilience by maintenance of soil structure (Crawford 2000; Crawford 2001; Crawford *et al.* 2003). Some support can be seem for this view from the cyclicity between pine and birch observed in the cores to the east of Glen Affric. Here soil structure has maintained a less podsolised condition (Pyatt 1994), and woodland has been demonstrated to be relatively closed in canopy structure, and variable in species composition, with *Pinus* never dominant for long periods (clusters 2 and 3, Chapter 6). This of course is difficult to separate from the climatic drivers of change between the east and the west of the Glen, which is subject to a high rainfall gradient (Section 2.2.1.5).

This however does indicate that we need to be careful about image versus substance in biodiversity enhancement and preservation. Perhaps this is a reason to accept the, sometimes blighted, name of 'Caldonian' woodland rather than pine woodland – woods were and should be about more than native pine (Balfour 1977). This thesis may support, therefore, the view and activites of the organisation Trees for Life in Glen Affric in the planting of mixed broadleaved woodland, although, given the probable ability of the woodland to regenerate itself (see above), the need for sustained planting may be questionable.

7.3 Contribution to conservation management

- *To contribute to management tools in development by Forestry Research (Bell 2003) by providing information on the history of the extant pine woods for ecological understanding and for input for a model to predict the effects of forest design and management in Glen Affric*

Hobbs (1997) observes that "*In its present condition, landscape ecology has little to offer those wishing to plan and manage the landscape of the future*" (*In* Hope 2003 p83), whilst Hope (2003) concludes that the limitations to modelling development in the UK are the acquisition of baseline data at landscape scales and the detailed understanding of ecological process. This thesis contributes some relevant baseline data of use to these subject areas. It shows that, at the landscape scale, processes aligned to both climax, and non-equilibrium states can exist (Worrell and Mackenzie 2003). However, this information can only be a modest part of a larger interdisciplinary framework of conservation management.

The question remains how to deal with this spatial arrangement in the core area of native pinewood into the future? It is possible that some of the core area can be expected to maintain a permanent woodland cover, as it has done for the last 3000 years. However other areas may be less stable, and a cyclicity between Pine and Birch may be important. The expansion possibilities outside of the core area to the west may be climatically and edaphically more limited, at least in the long-foreseeable future. Systems with a long history of degradation can develop a resilience in that state (Suding *et al.* 2004). *Pinus* expansion may rely on a shift in soils structure, which could take many hundreds of years (Section 7.2.4). Current management plans in Glen Affric rely on expansion of the forest zone to achieve policy driven management objectives (Chapter 1 and Section 2.1.3). The likelihood of stable woodland in this expanded zone may be limited.

The possible importance of a gradation in canopy cover to the west should therefore be examined. It is commonly assumed that woodland must contain a mix of patches at various life stages to maintain itself sustainably. However, key pulses of regeneration and decline in the west may be normal, but may be difficult to manage from a short-term policy perspective without express recognition of this process. We should probably guard against too much more regeneration in this area to ensure some open space for the future and prevent an even aged stand developing over the whole east Affric landscape (Hope 2003).

7.4 Conclusions

This thesis contributes to a body of work using fine resolution palaeoecology to bridge the scales between Holocene palaeocology and present-day ecological survey. It demonstrates the role that palaeoecology can play in determining past histories of interest to ecology, and confirms the ability of palaeoecological investigation to determine openness at the stand scale in upland semi-open woodland containing *Pinus sylvestris*.

It identifies former structure and extent of a woodland and links some of the assumptions of modern ecological classifications with a temporal test of these factors.

It suggests caution in assumptions that the woodland is currently degraded, and highlights the possible need to maintain some openness to the west of the extant woodland zone.

Further work to expand and strengthen the palaeoecological interpretation should include:

- An expansion of the ring source area for testing pollen-vegetation relationships and determingin RSAP and PPEs.
- Application for further radiocarbon age estimates
- Modelling and correlation across cores using POLLANDCAL models currently being developed.

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Appendix 1: Pollen diagrams

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1. Pollen Diagrams: NHP core

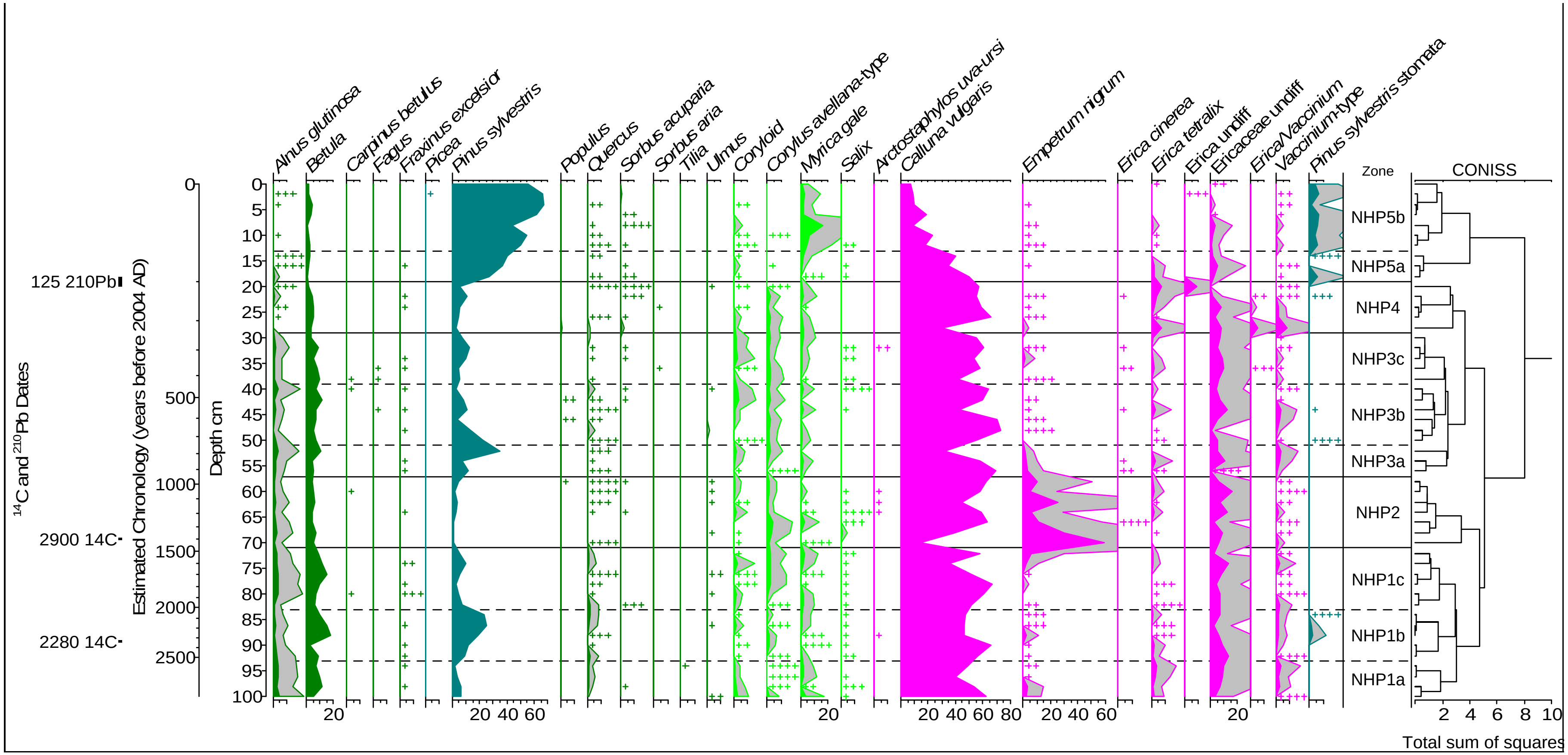


Figure A1.1: NHP pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

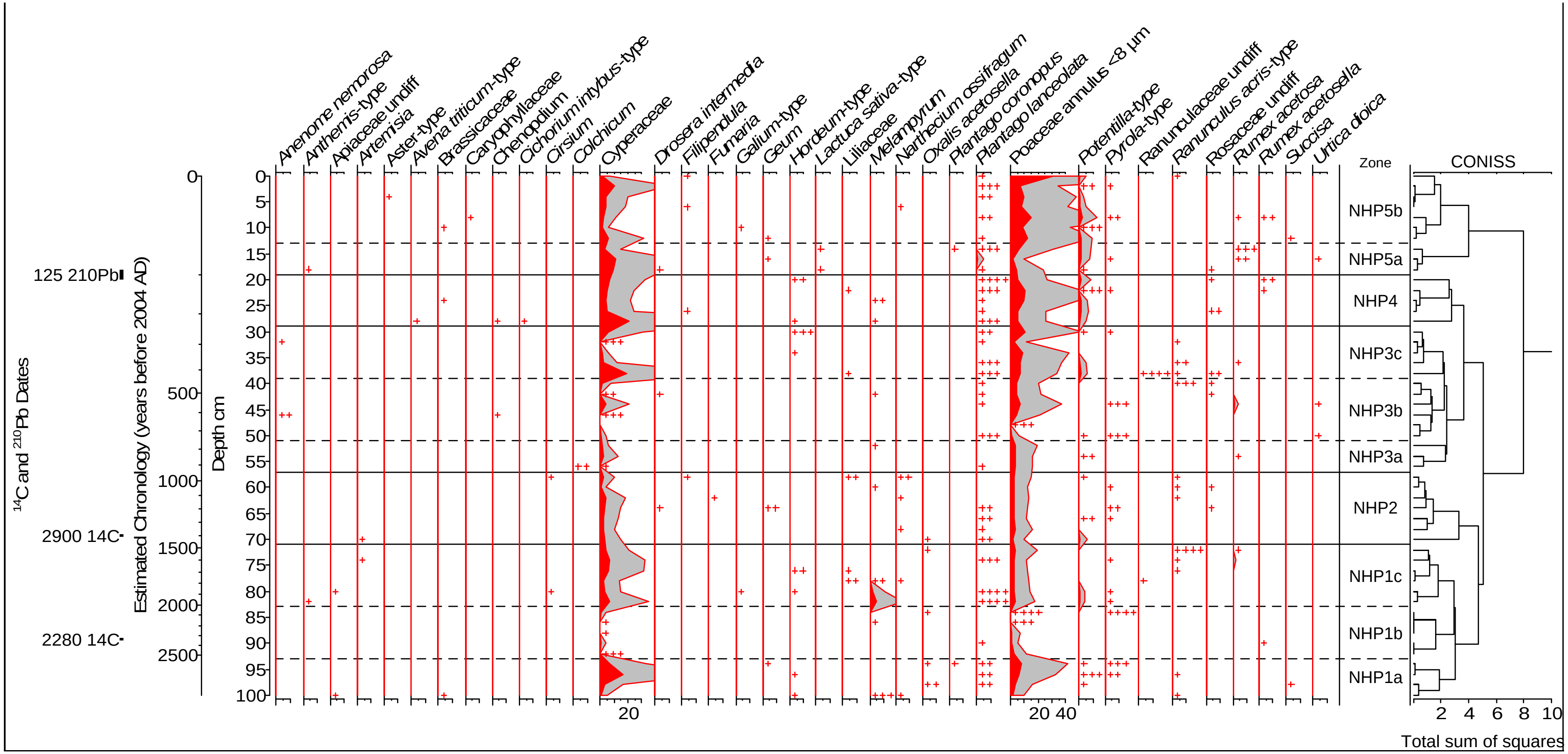


Figure A1.1: NHP pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS {Grimm, 1987 #1458}, used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

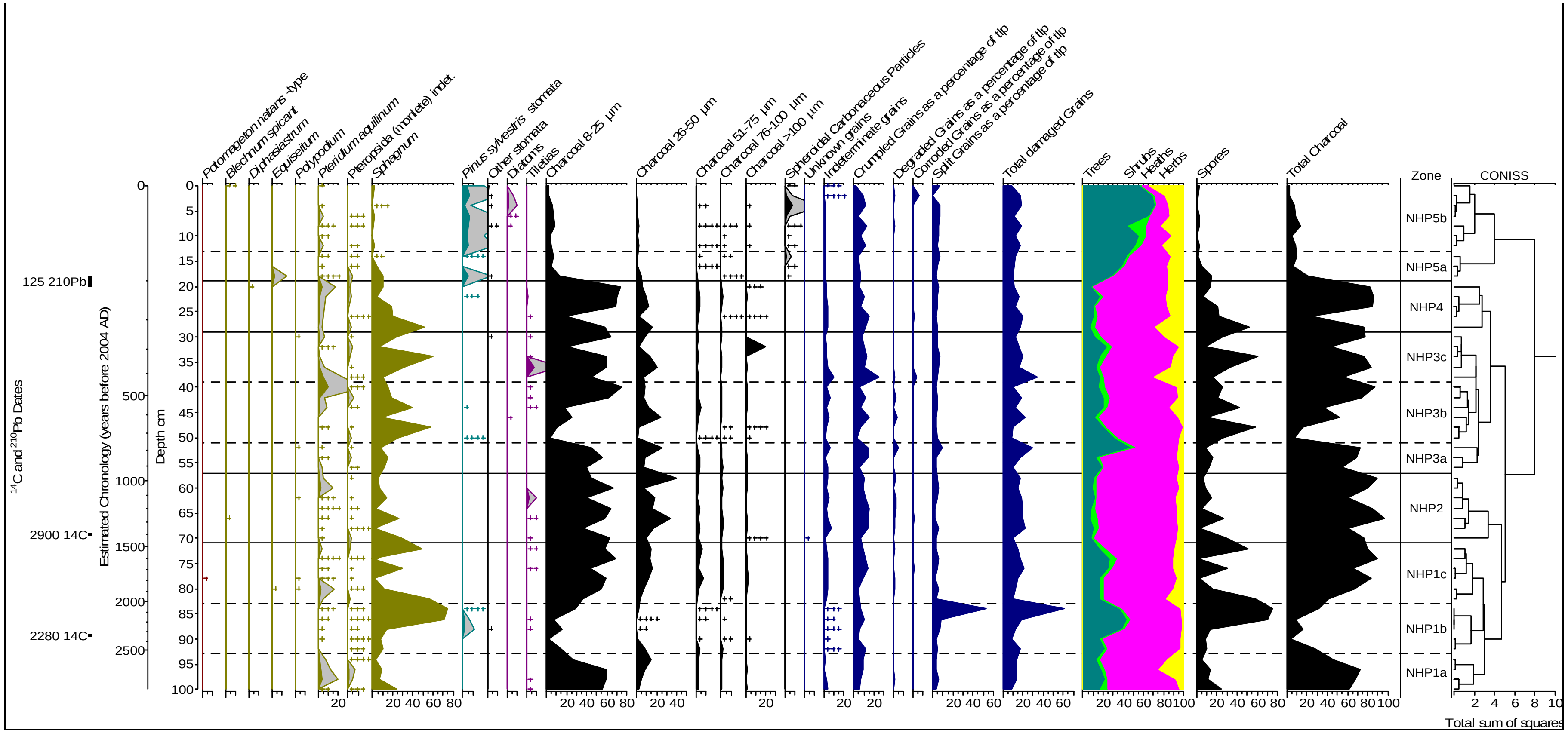


Figure A1.1: NHP pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

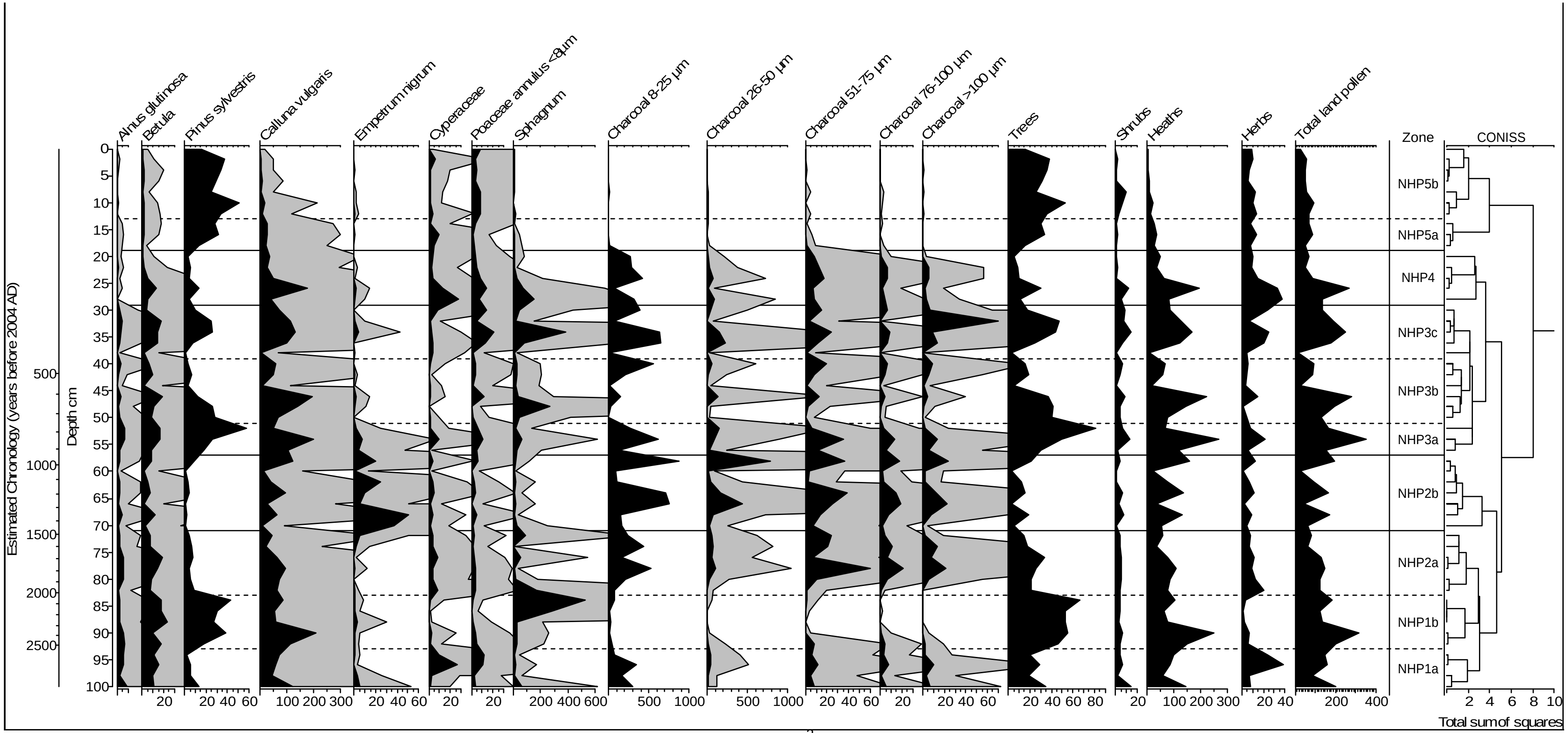


Figure A1.2: NHP summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A1.1

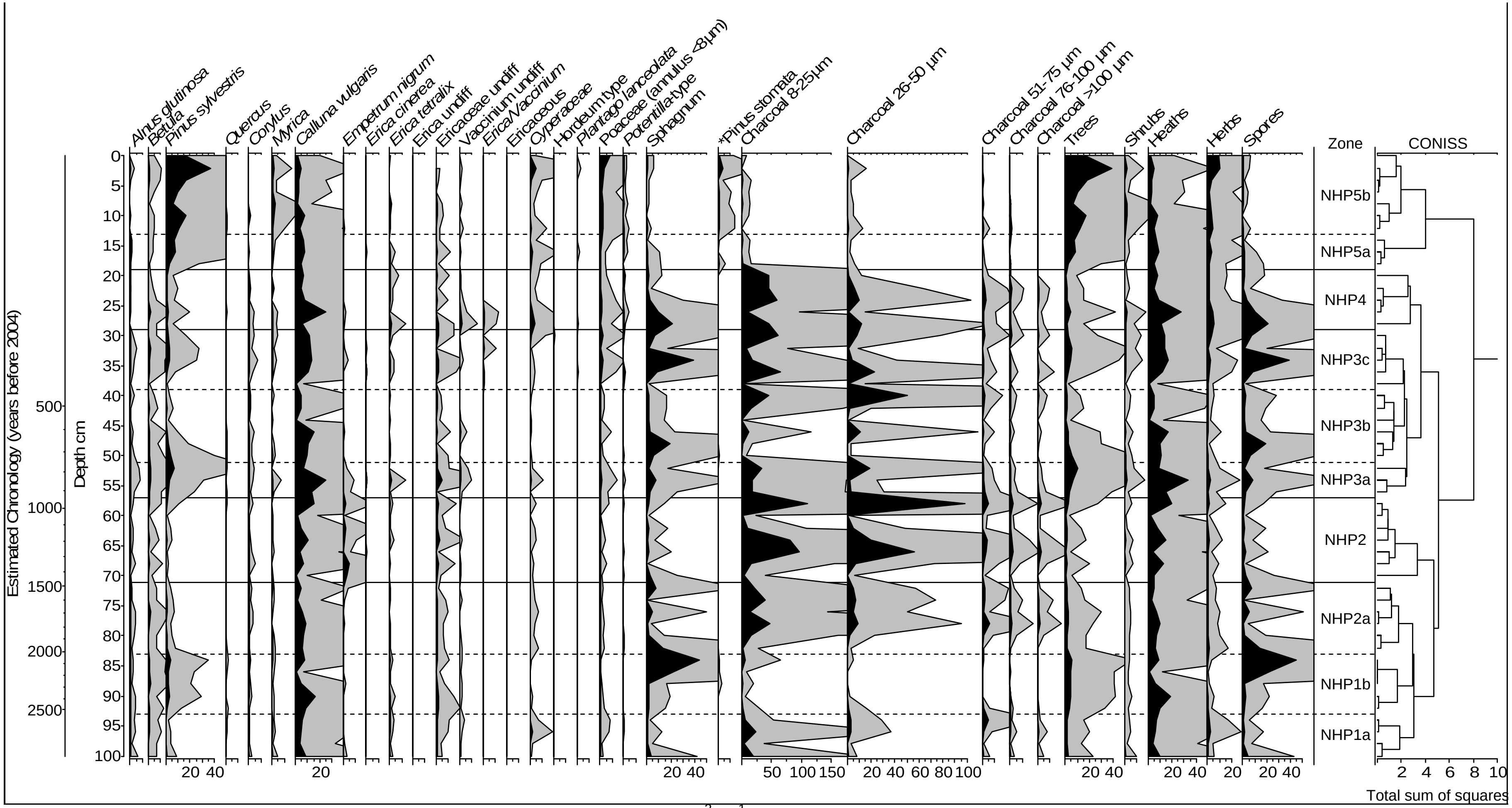


Figure A1.3: NHP summary pollen diagram. Pollen influx data in grains per cm^{-2} yr^{-1}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A1.1

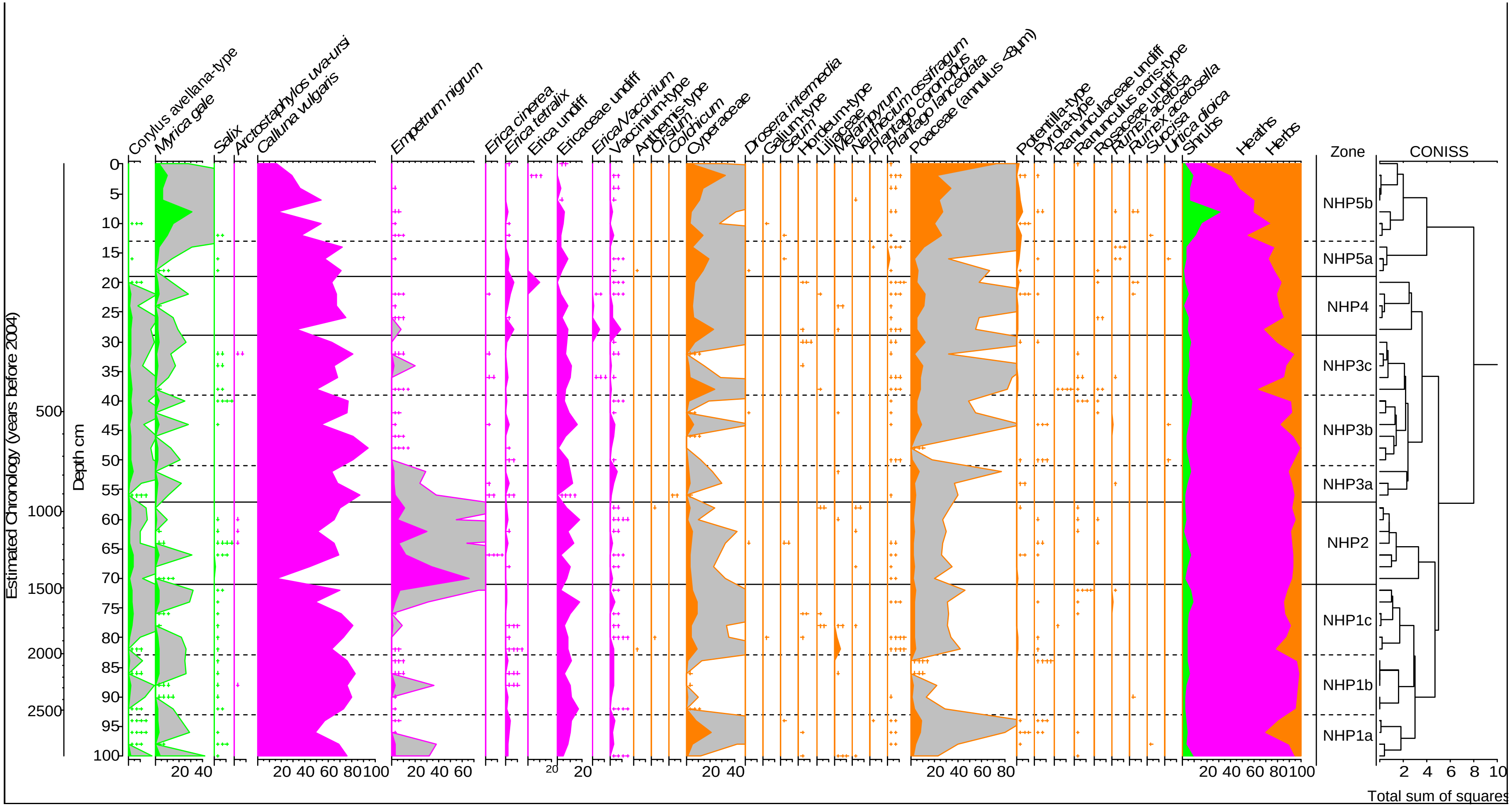


Figure A1.4: NHP non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Exaggeration factor x 10. Zonation and chronology as for Figure A1.1

2. Pollen Diagrams: PB core

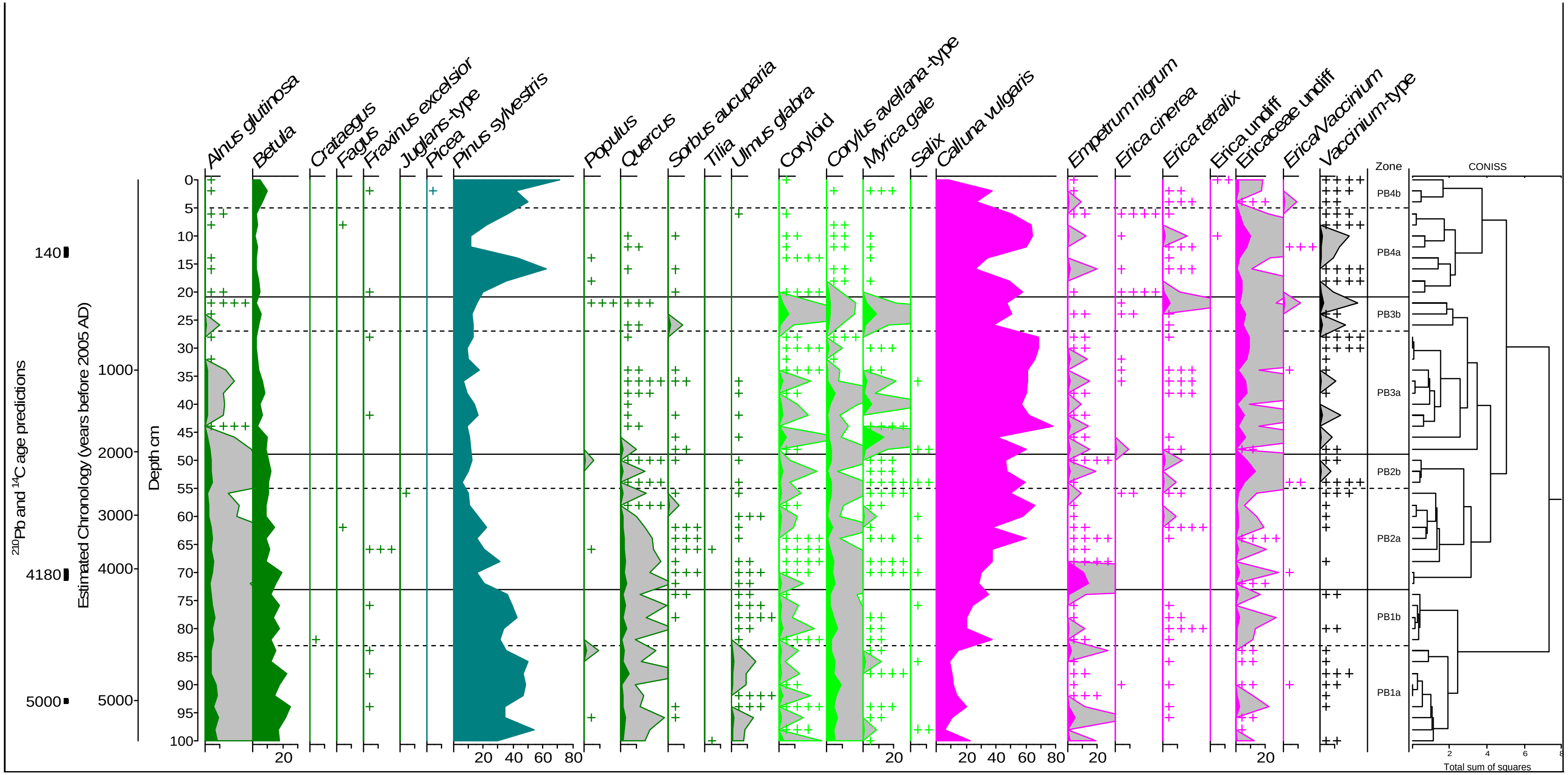


Figure A2.1: PB pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

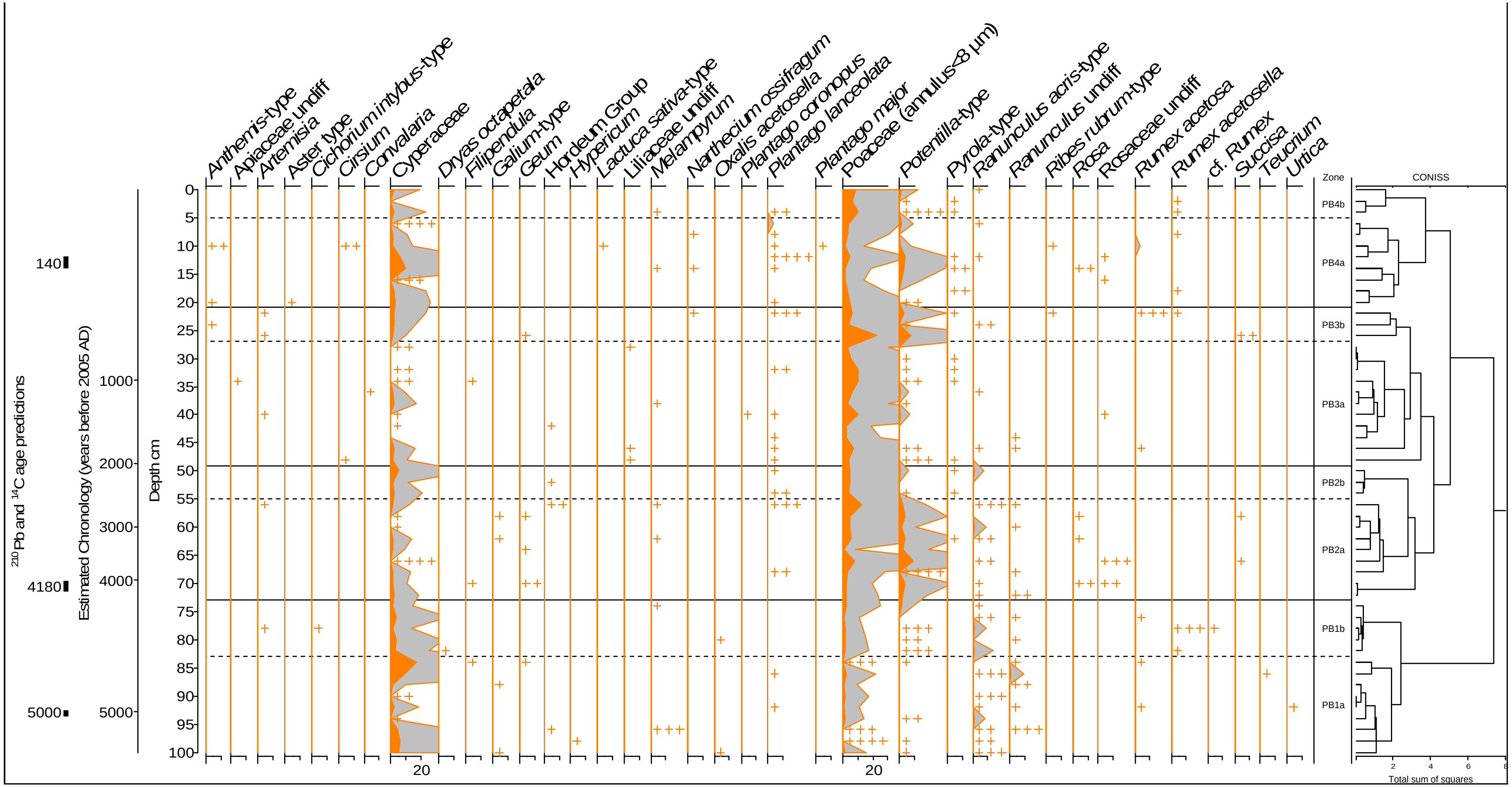


Figure A2.1: PB pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

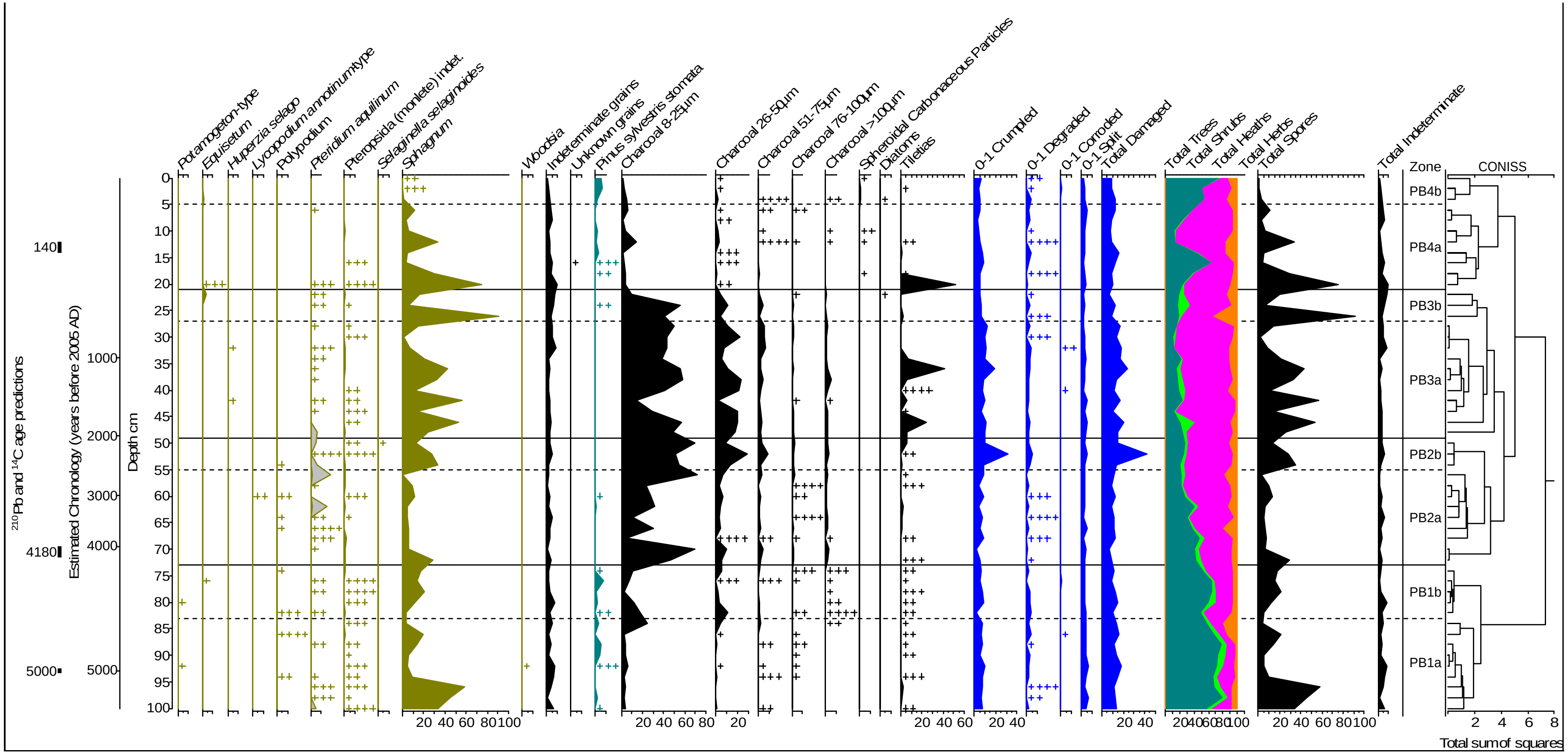


Figure A2.1: PB pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

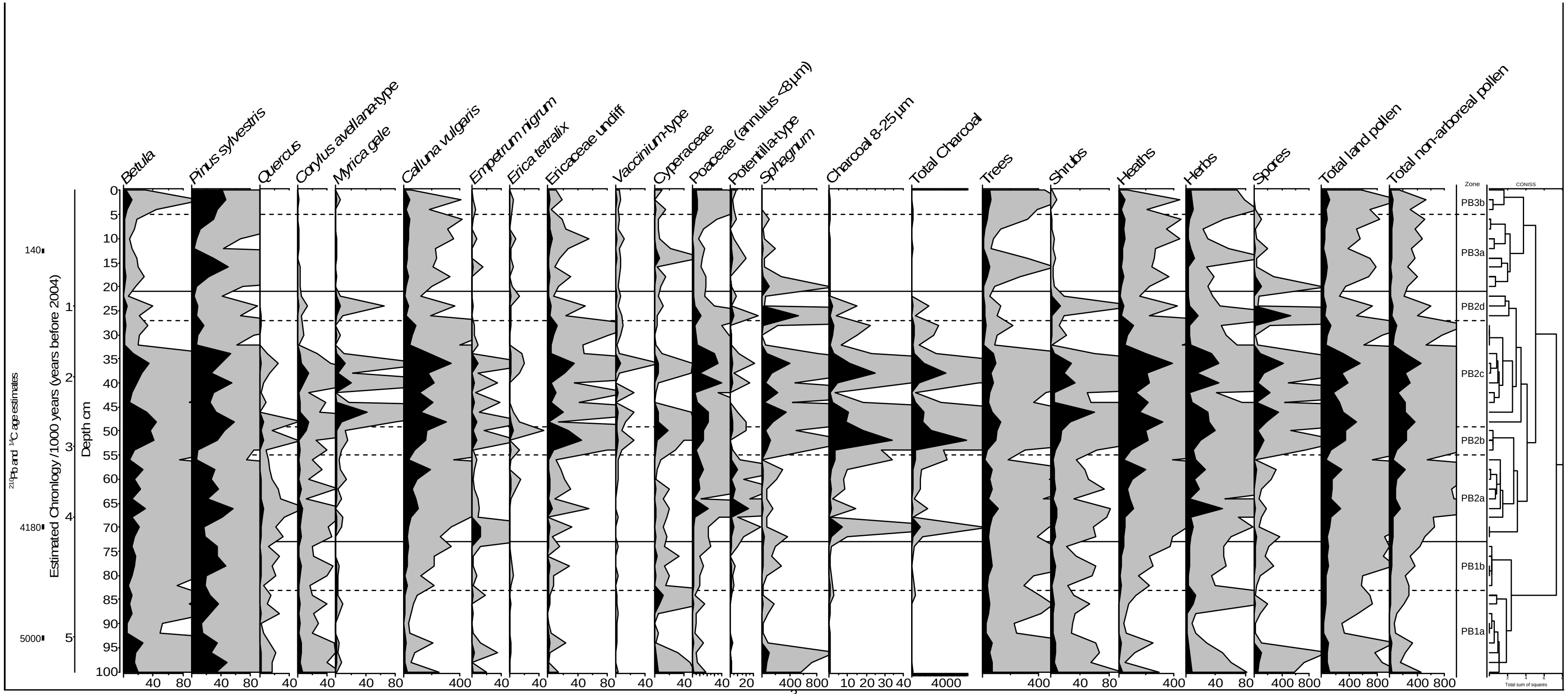
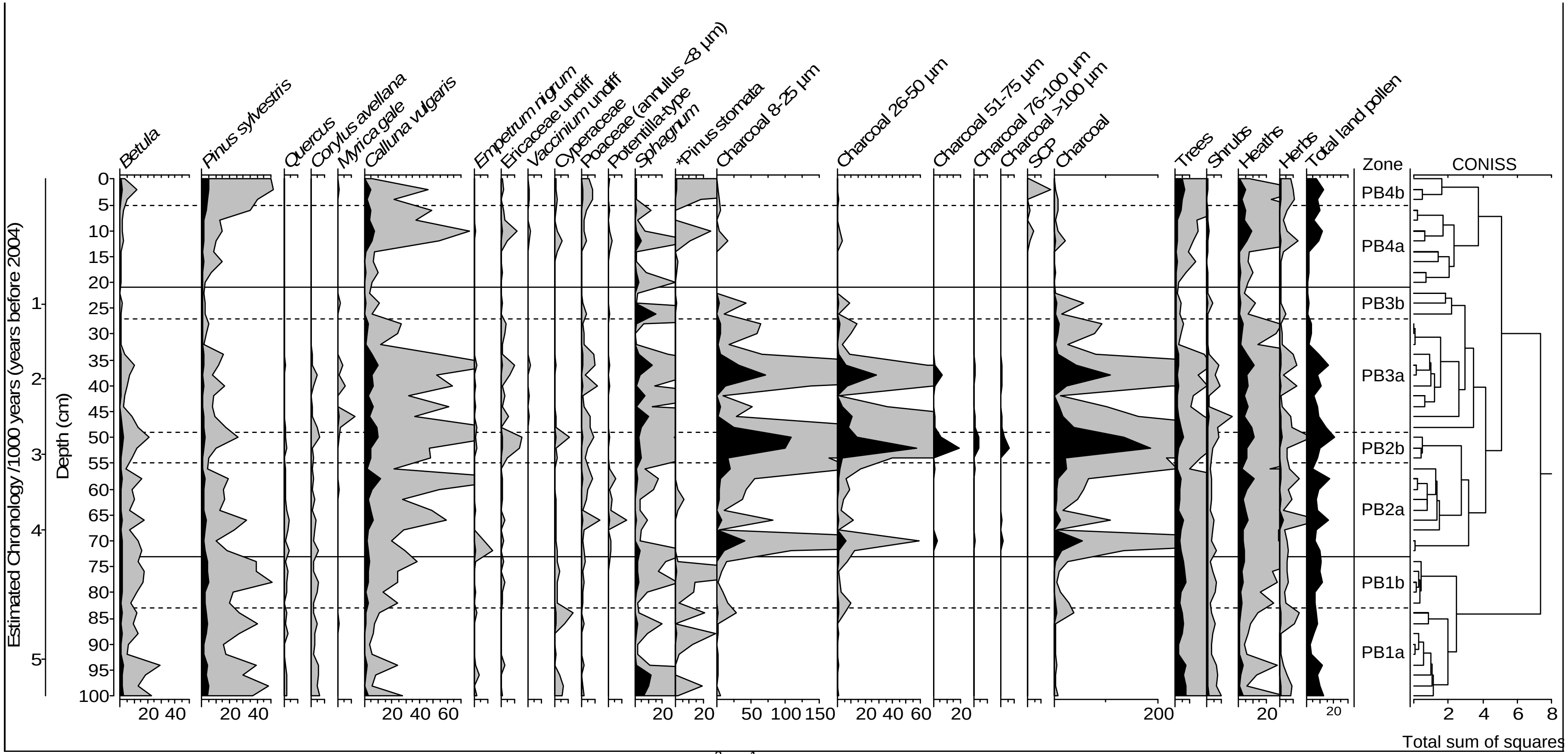


Figure A2.2: PB summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A2.1



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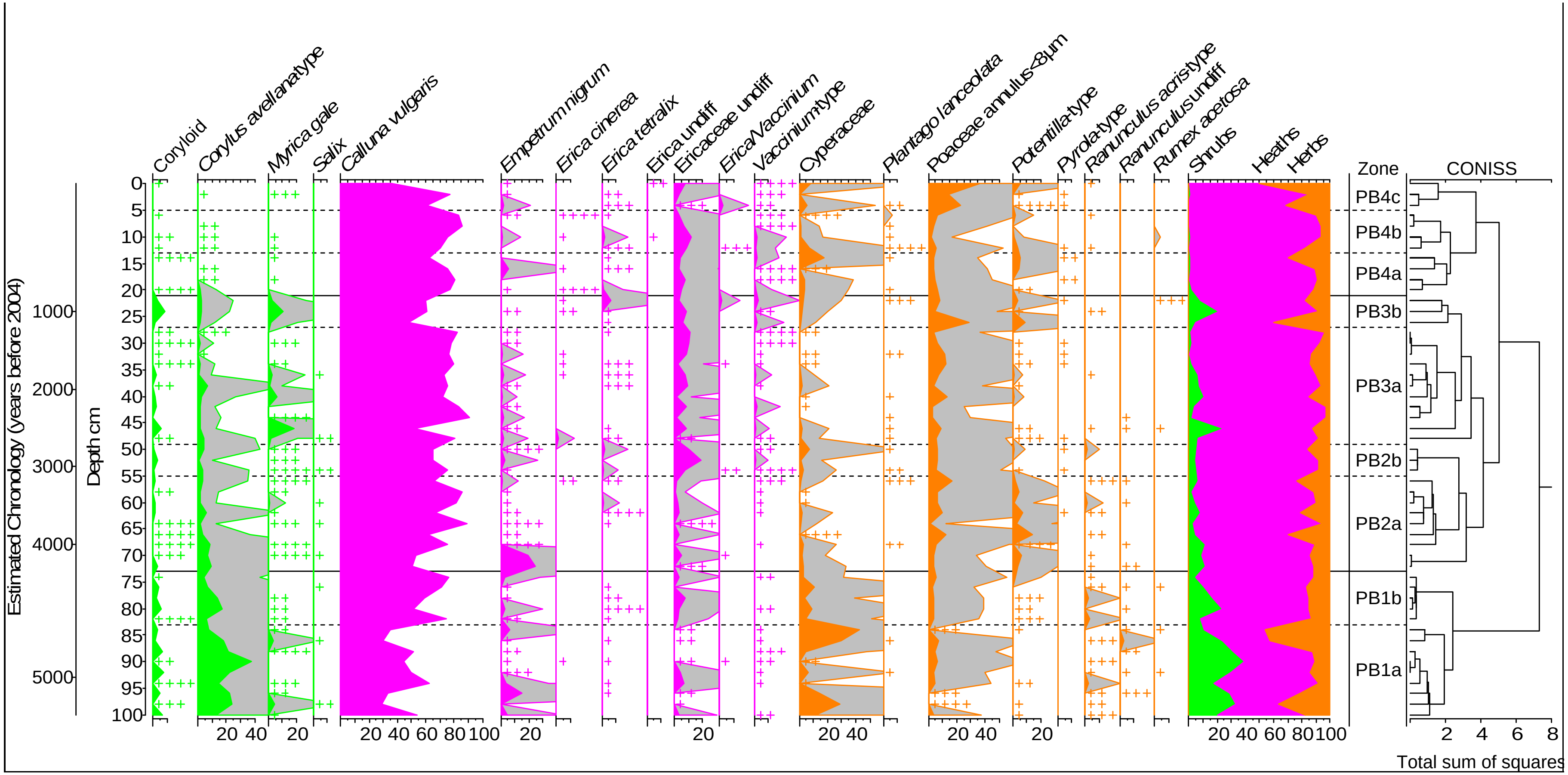
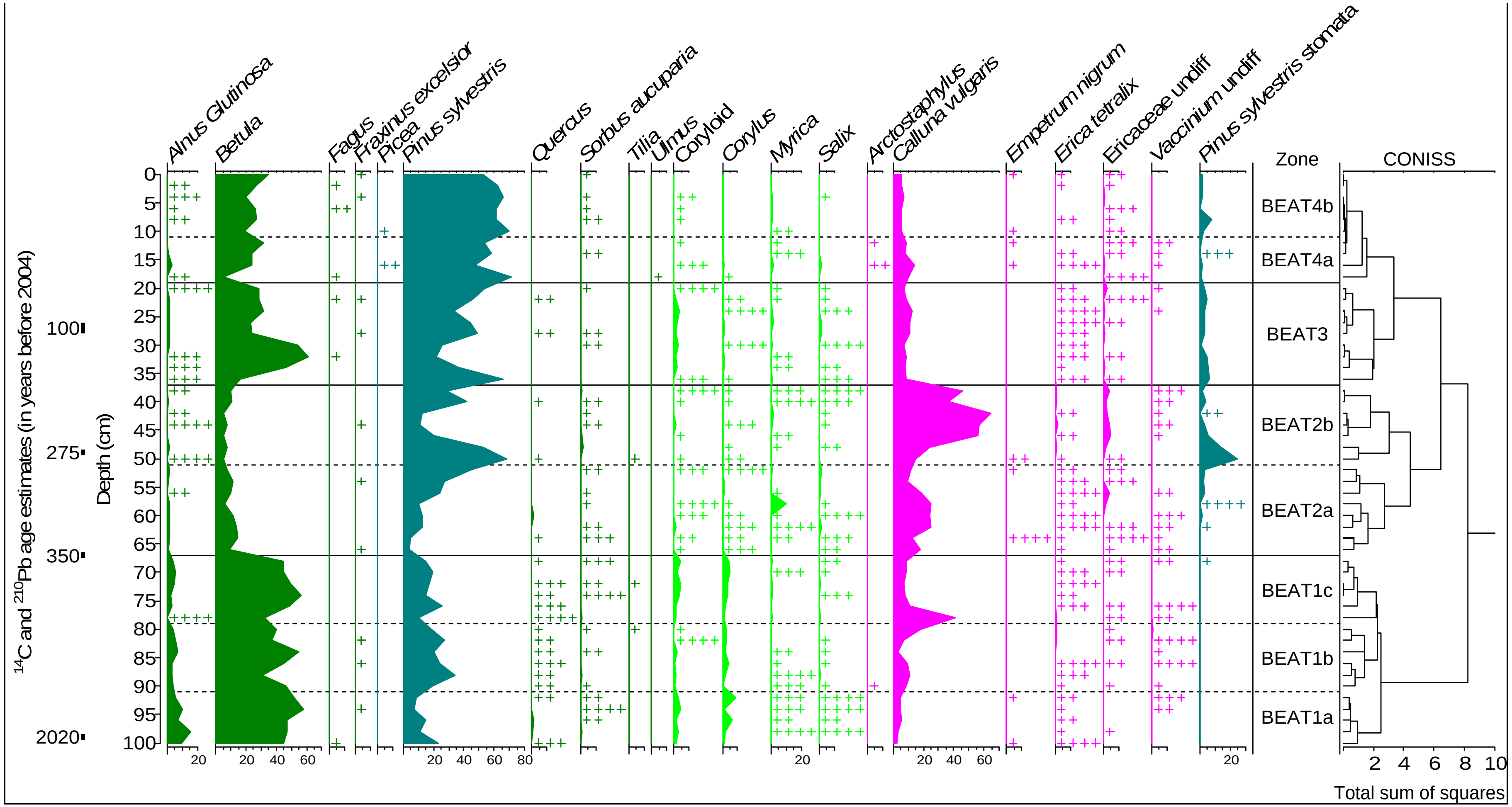


Figure A2.4: PB non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Exaggeration factor x 10. Zonation and chronology as for Figure A2.1

8 Pollen Diagrams: BEAT core



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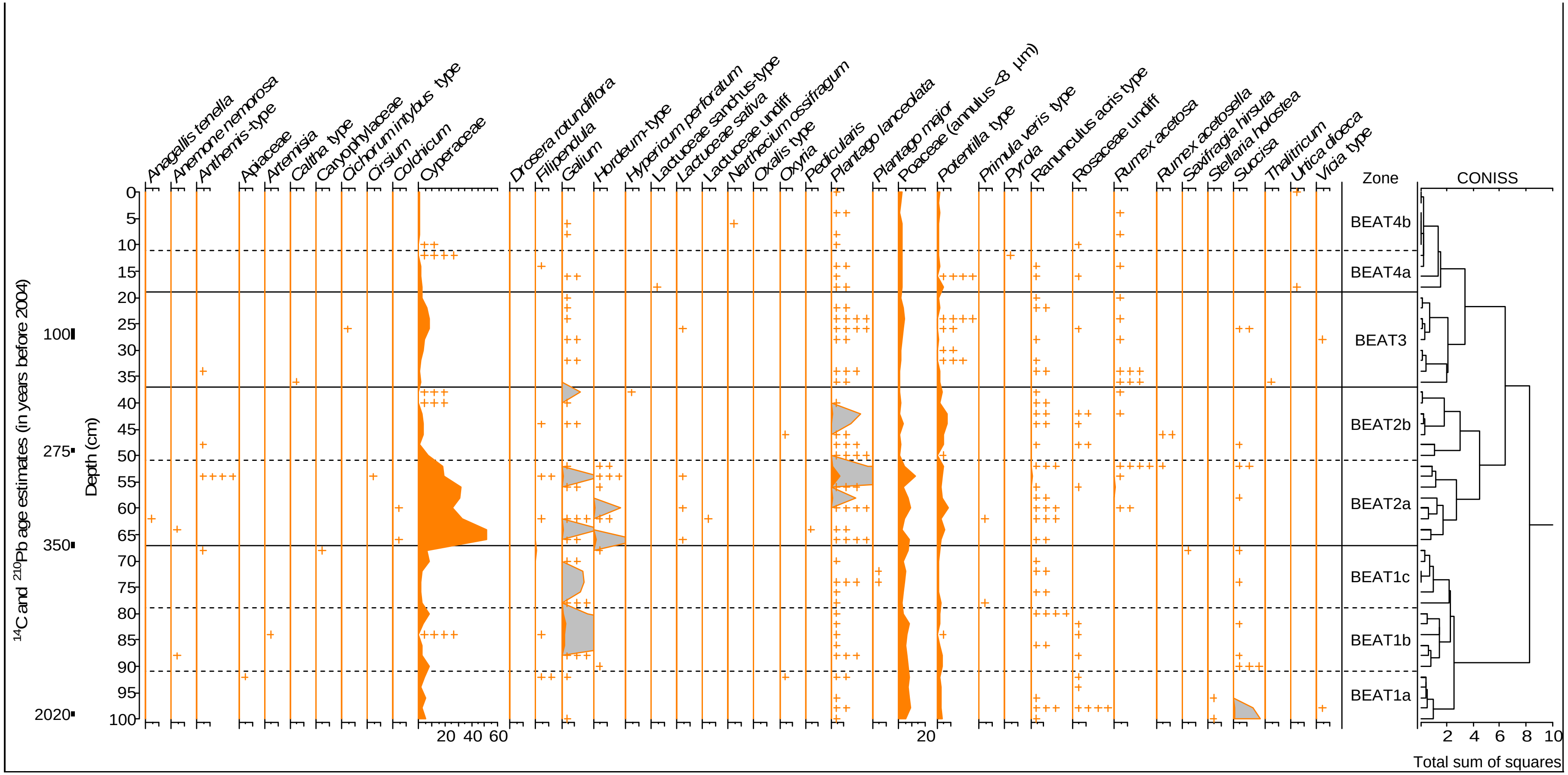

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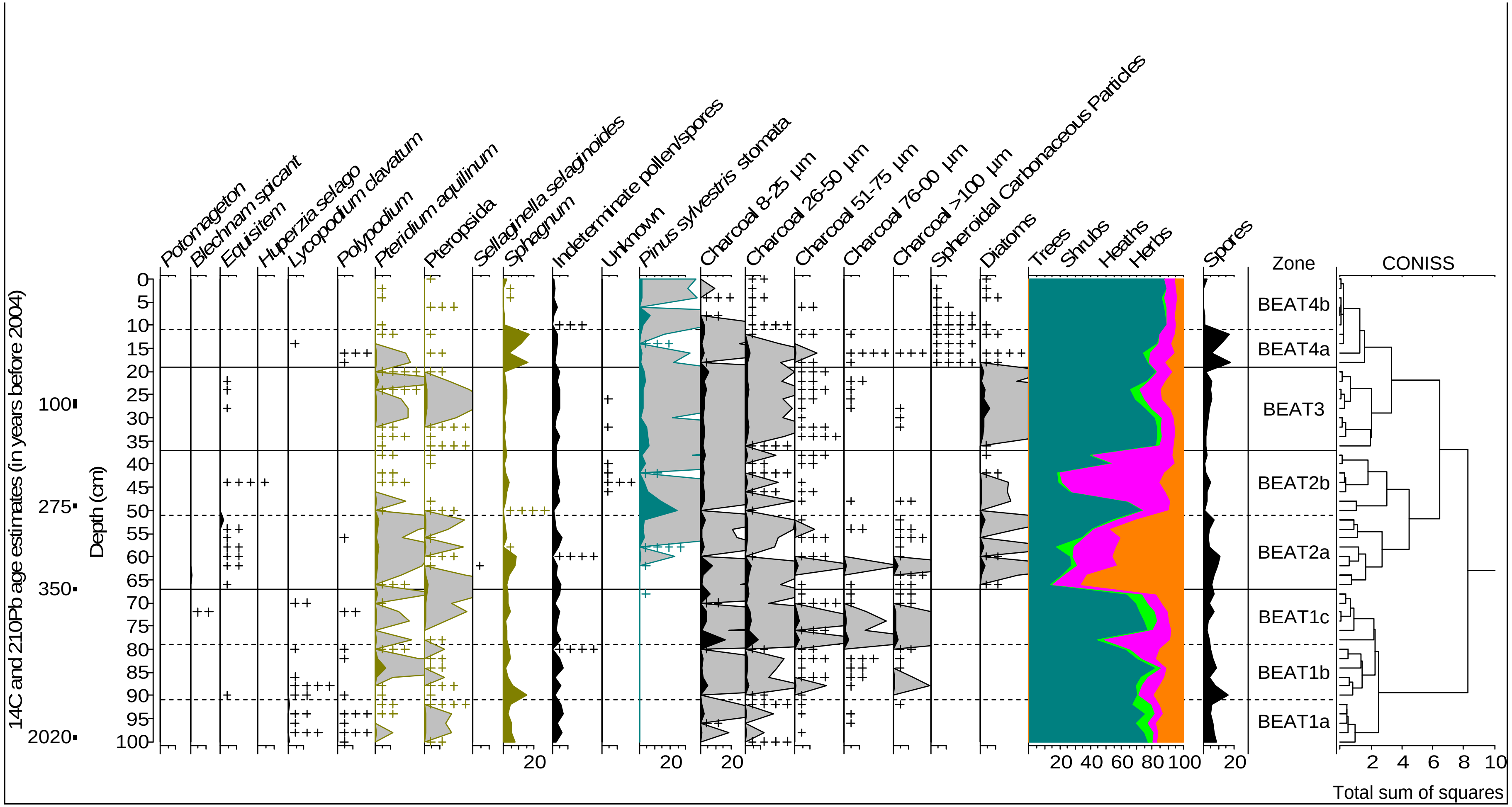
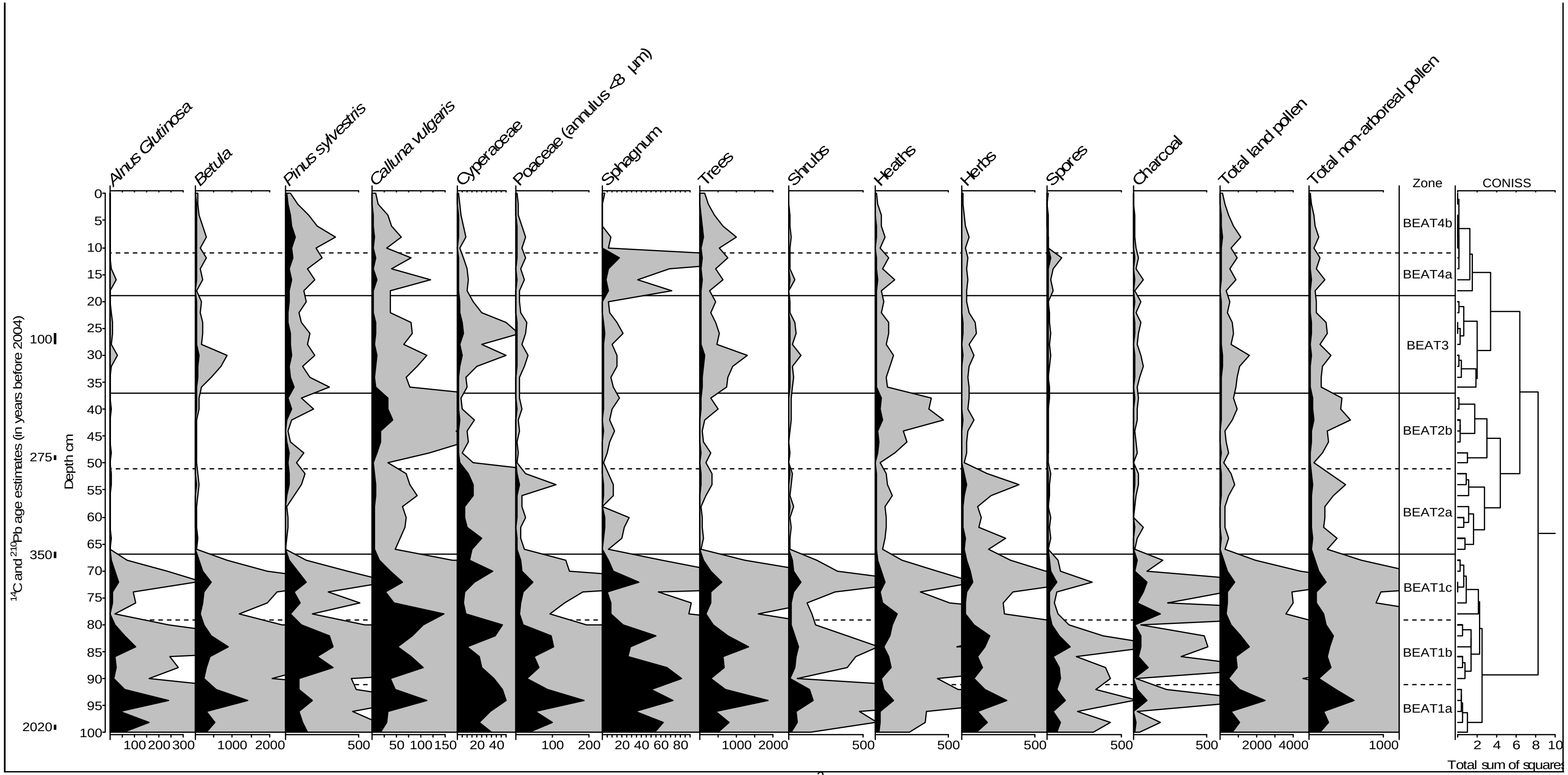


Figure A3.1: BEAT pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).



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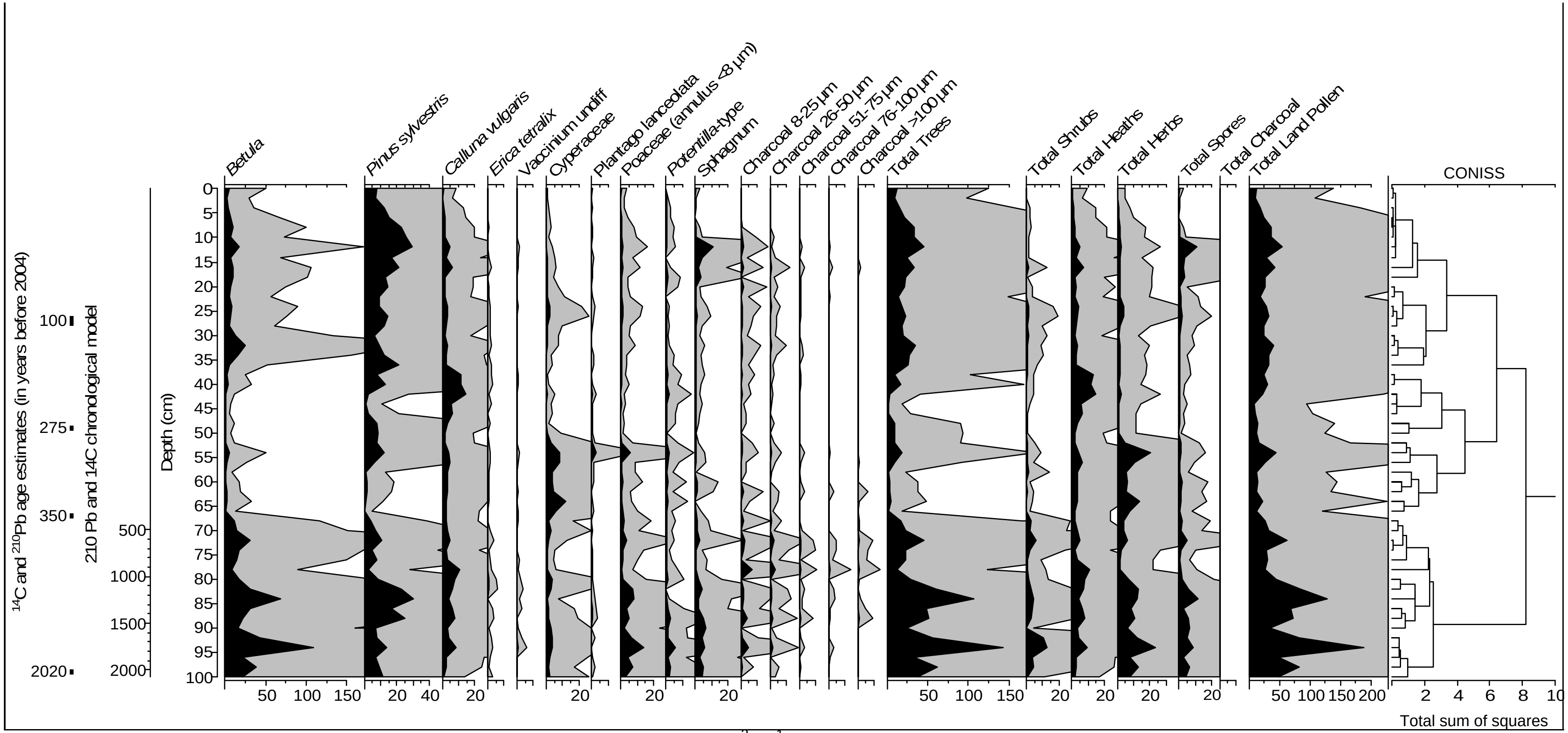

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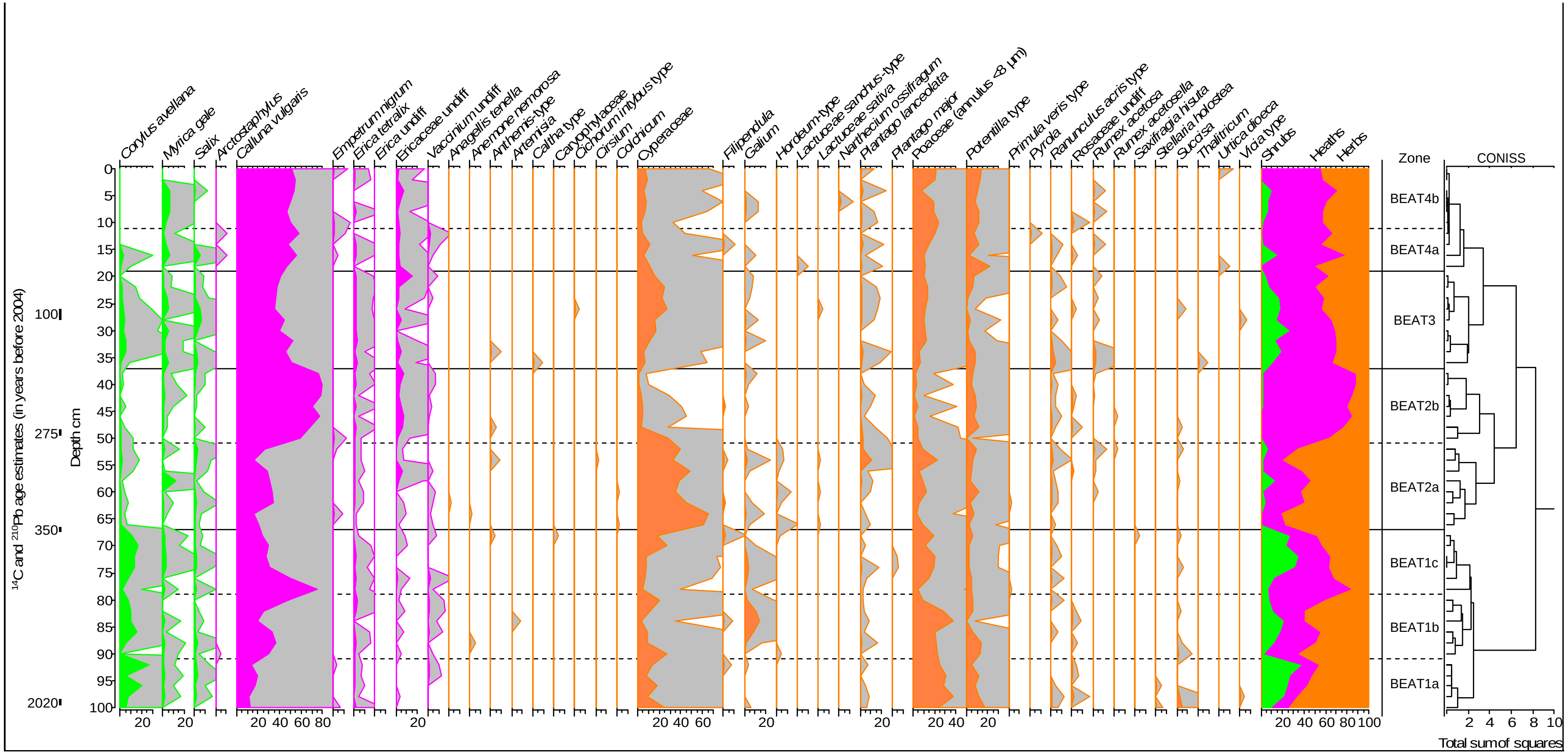

Figure A3.4: BEAT non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Exaggeration factor x 10. Zonation and chronology as for Figure A3.1

9 Pollen Diagrams: ANI core

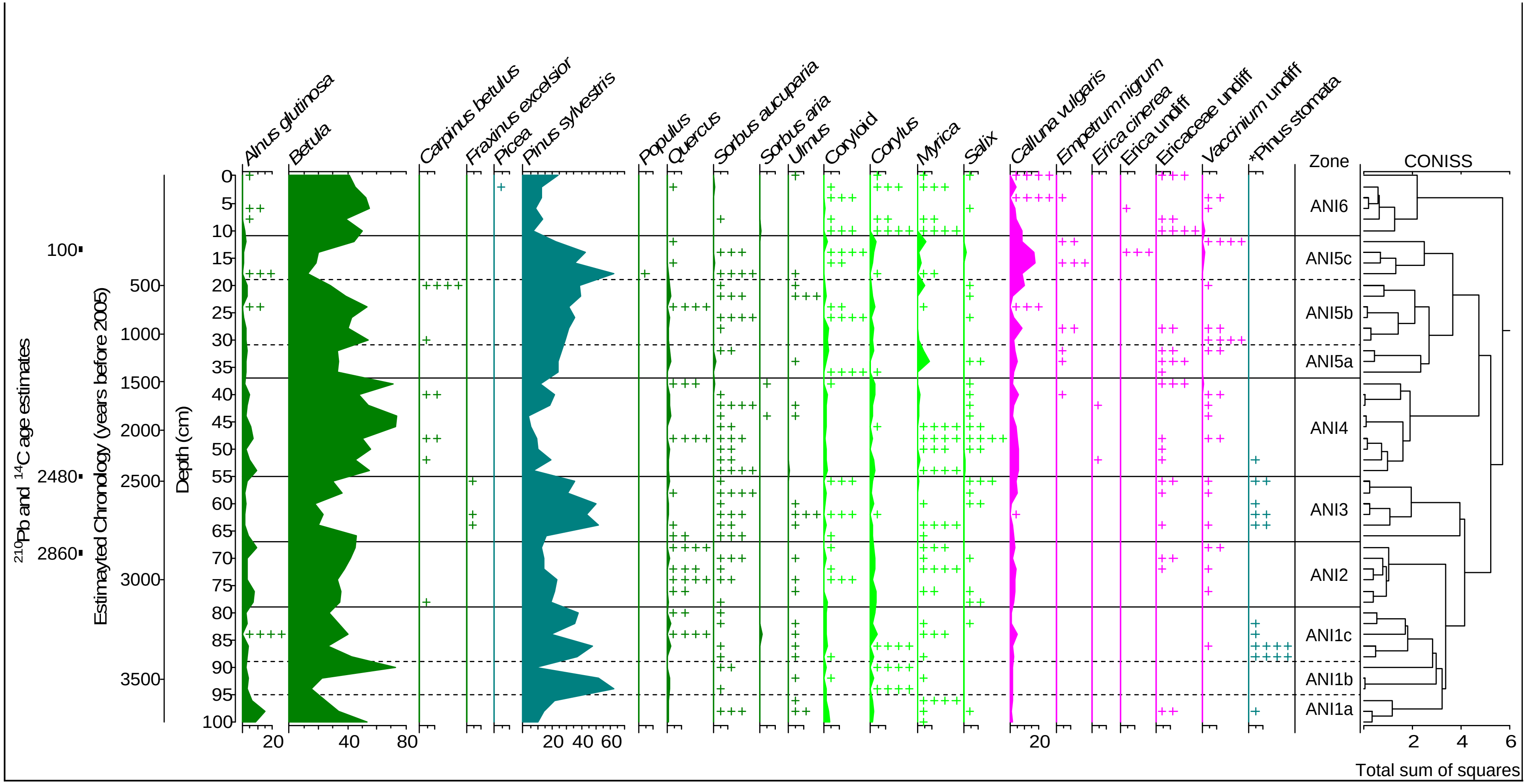

Figure A4.1: ANI pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

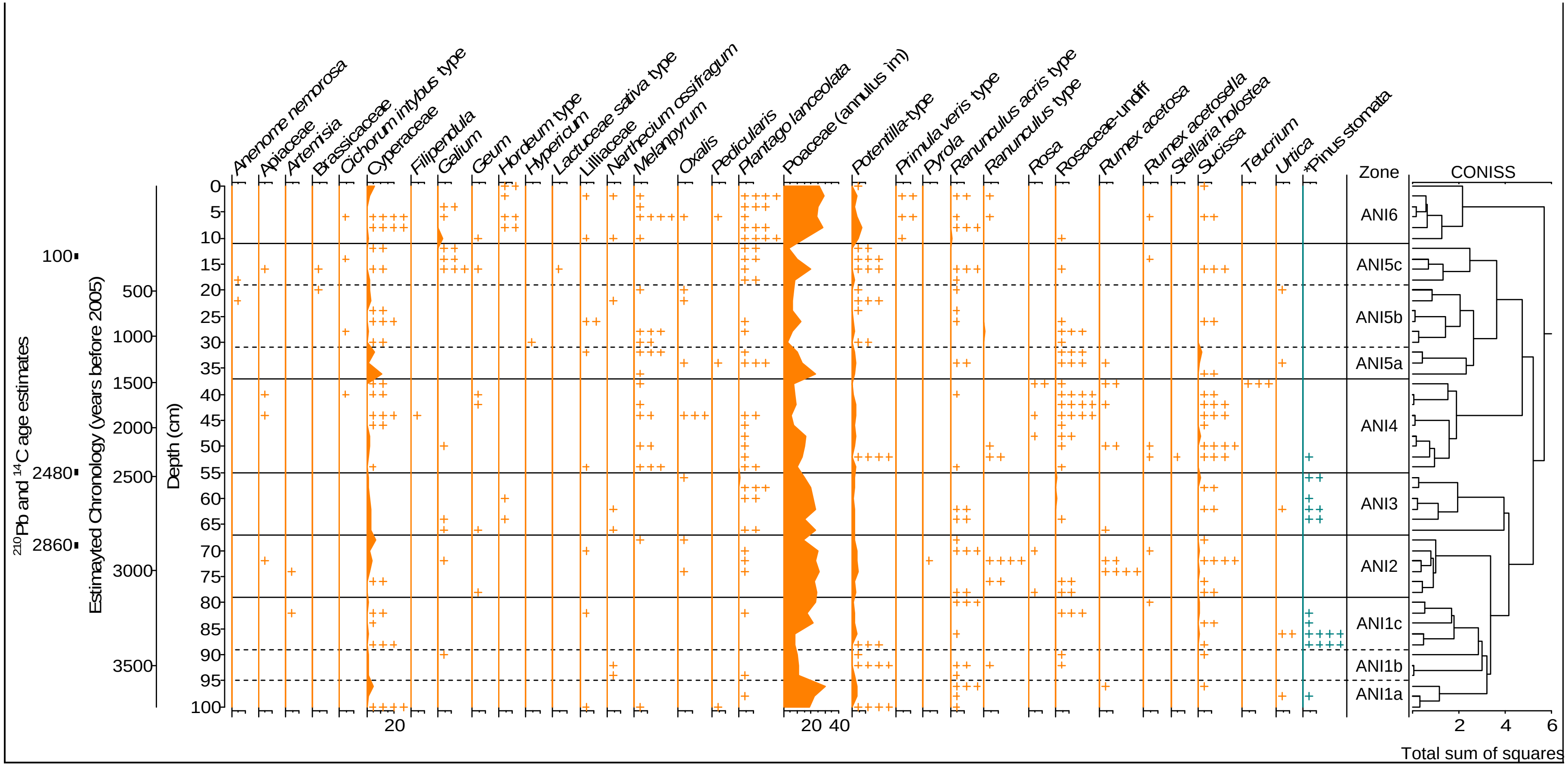

Figure A4.1: ANI pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

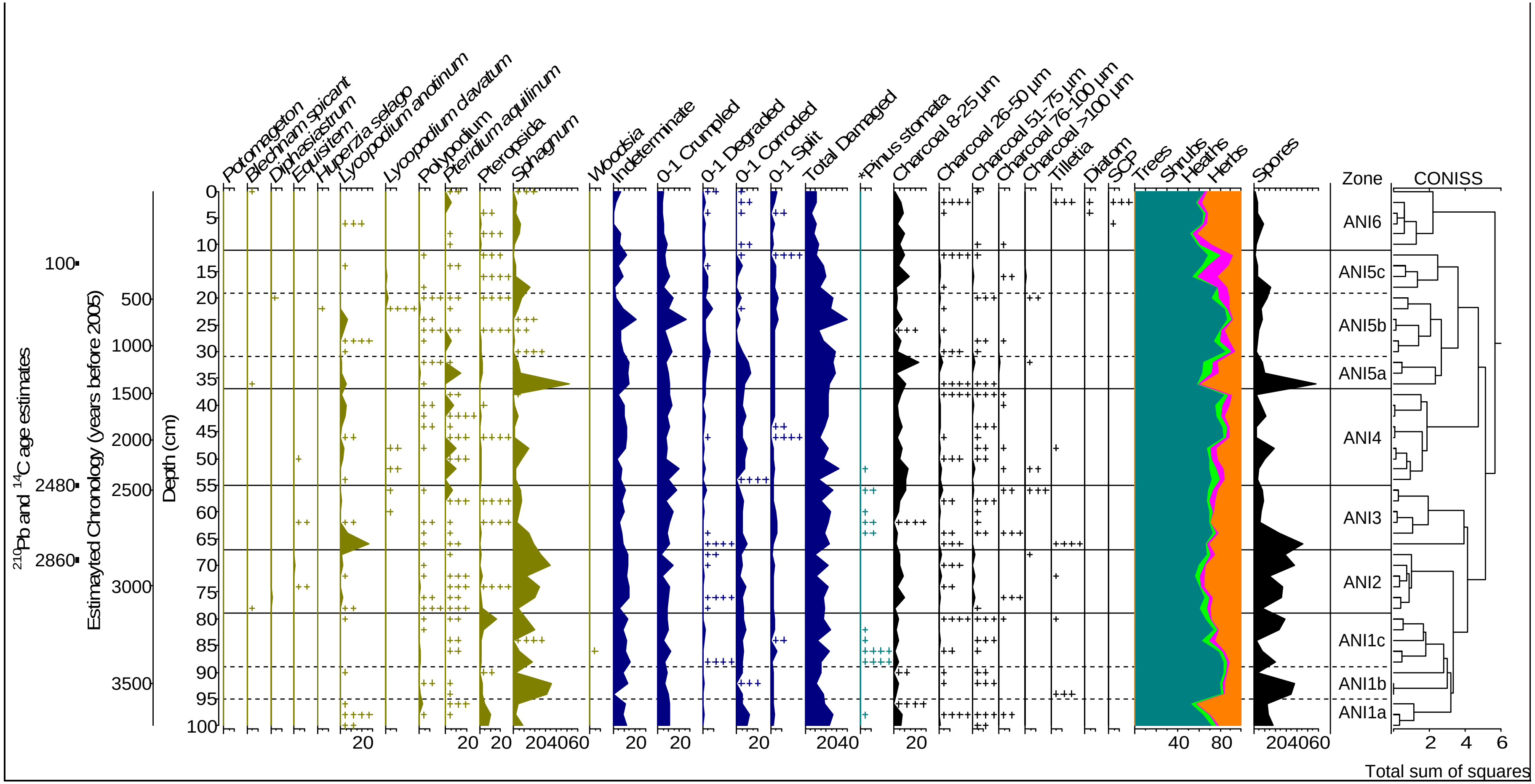

Figure A4.1: ANI pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

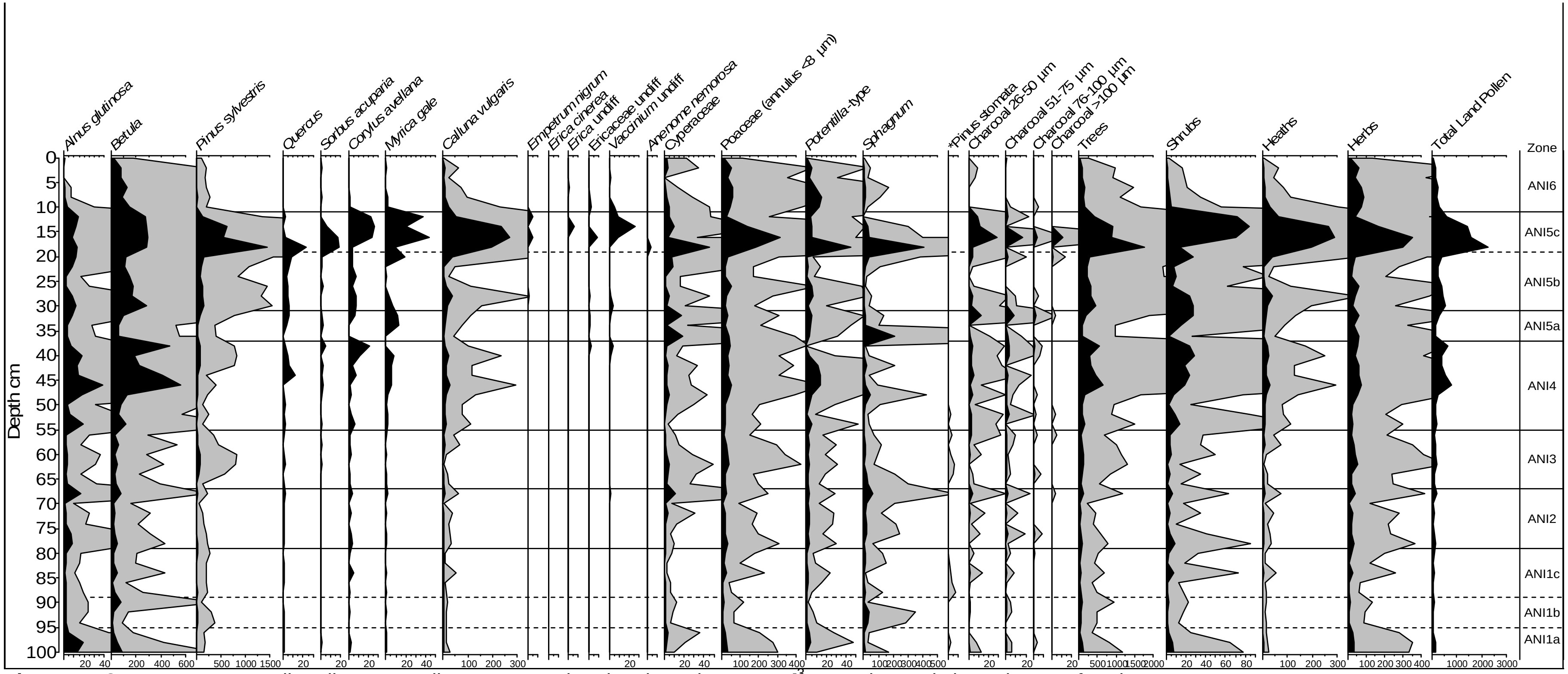

Figure A4.2: ANI summary pollen diagram. Pollen concentration data in grains per cm^{-3}. Zonation and chronology as for Figure A4.1

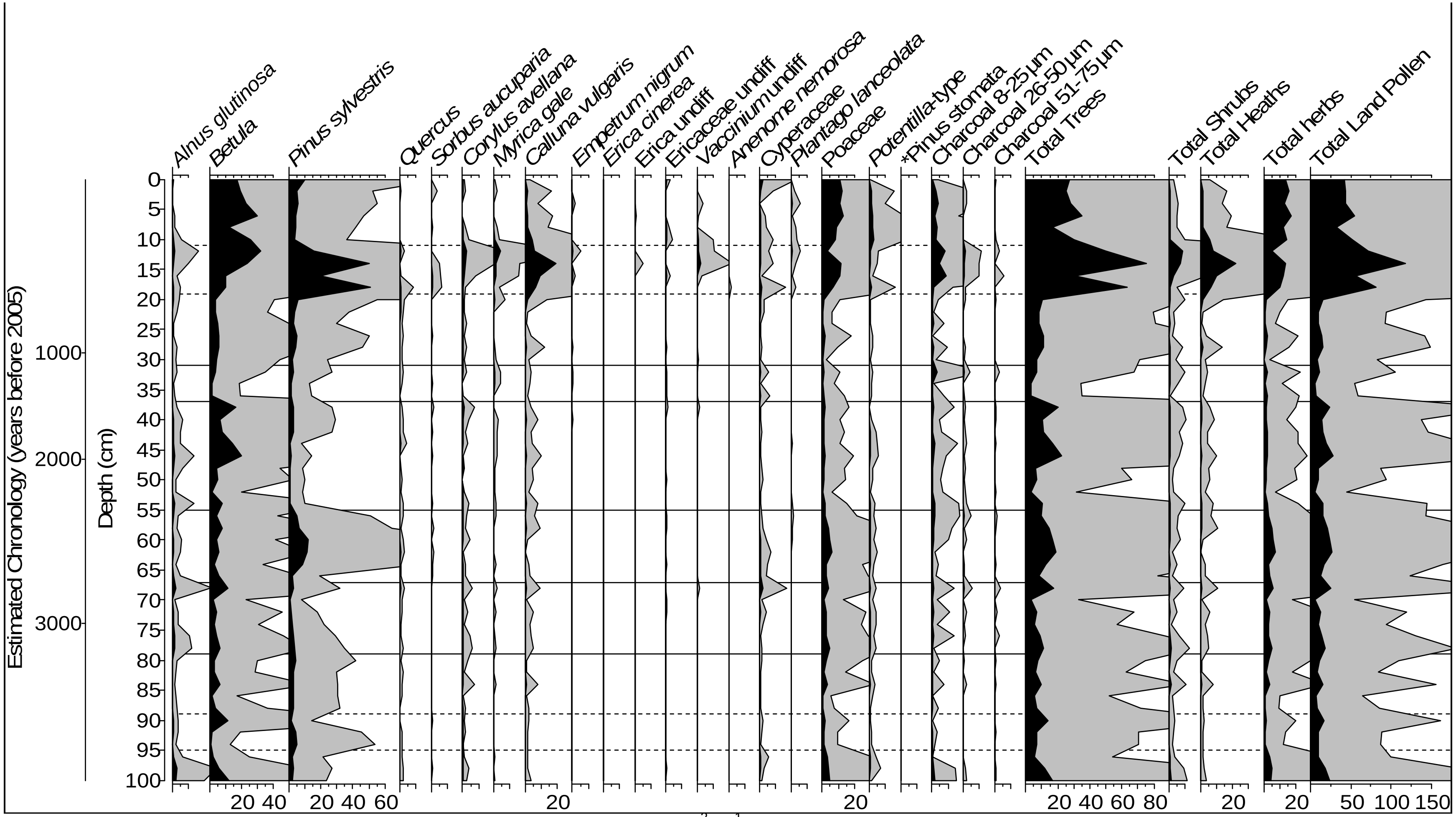

Figure A4.3: ANI summary pollen diagram. Pollen influx data in grains per cm^{-2} yr^{-1}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A4.1

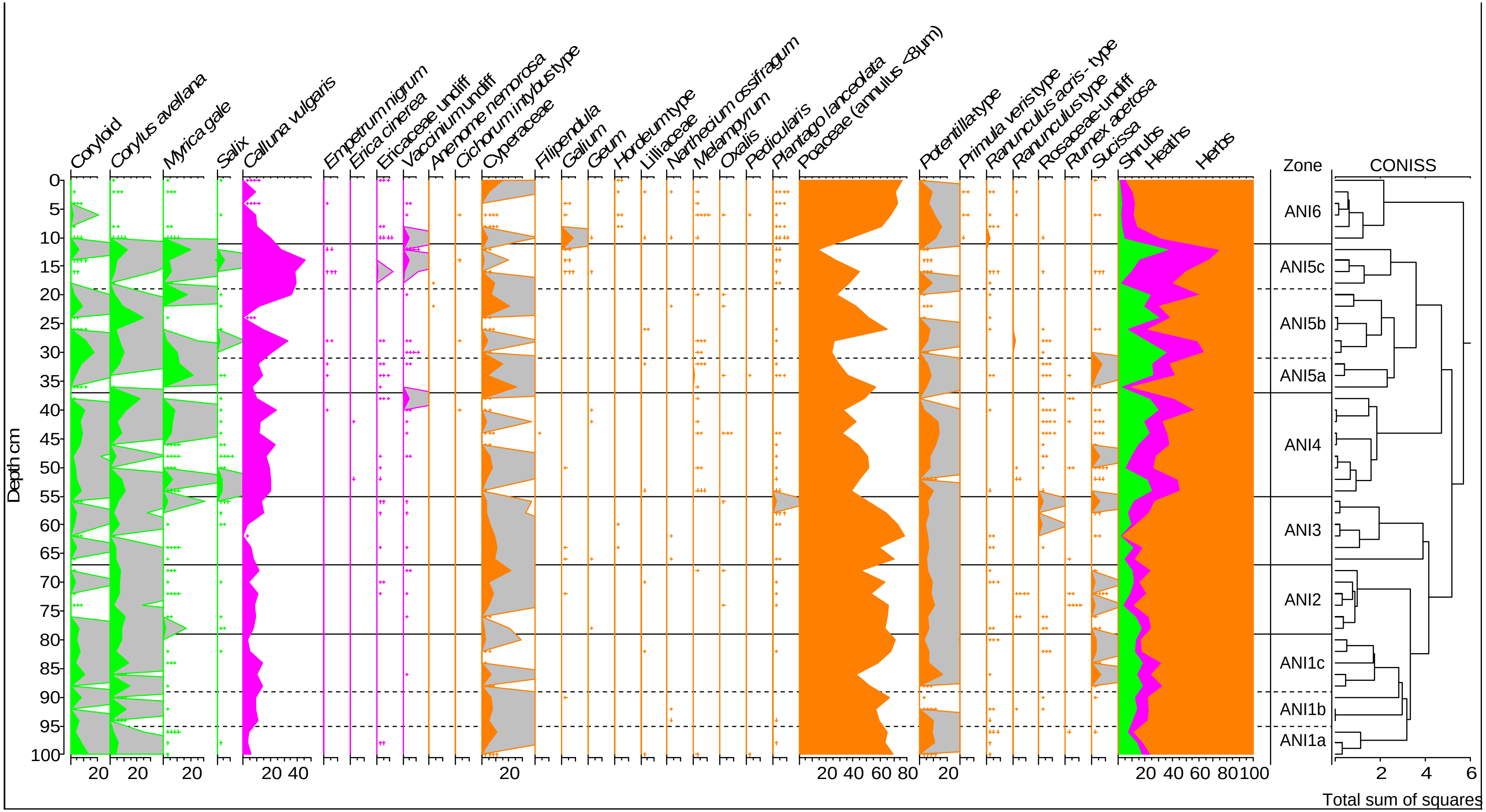

Figure A4.4: ANI non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A4.1

10 Pollen Diagrams: ARC core

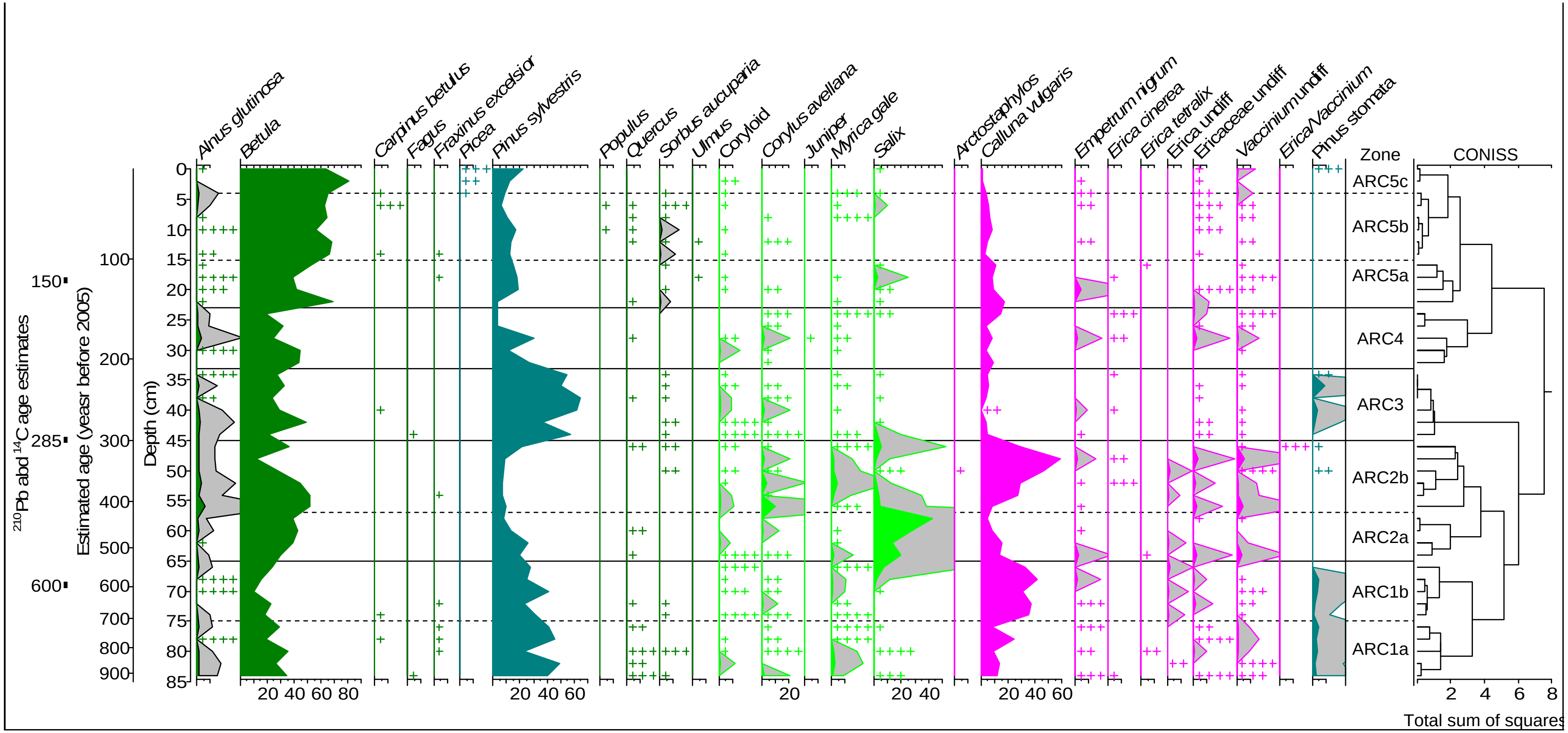

Figure A5.1: ARC pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

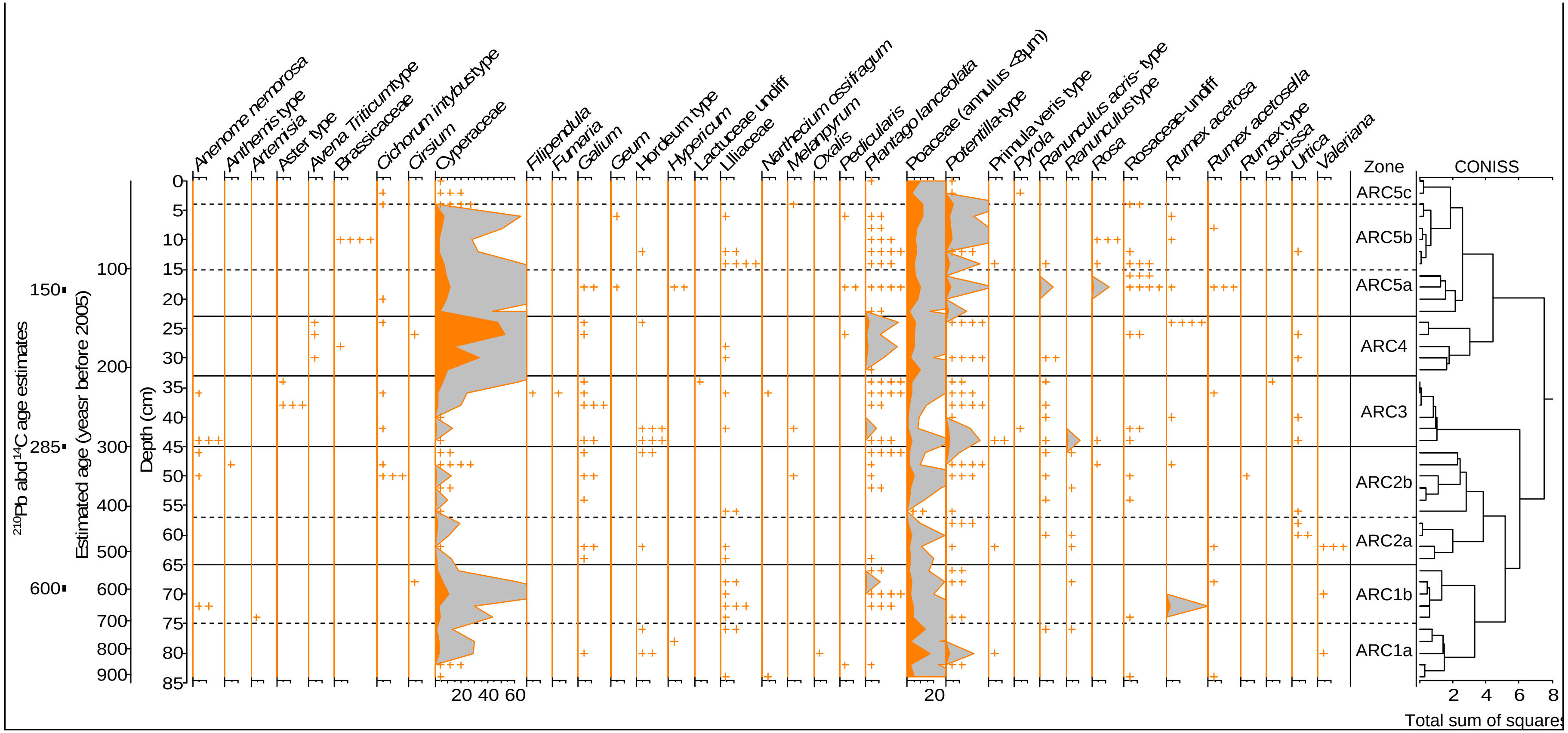

Figure A5.1: ARC pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

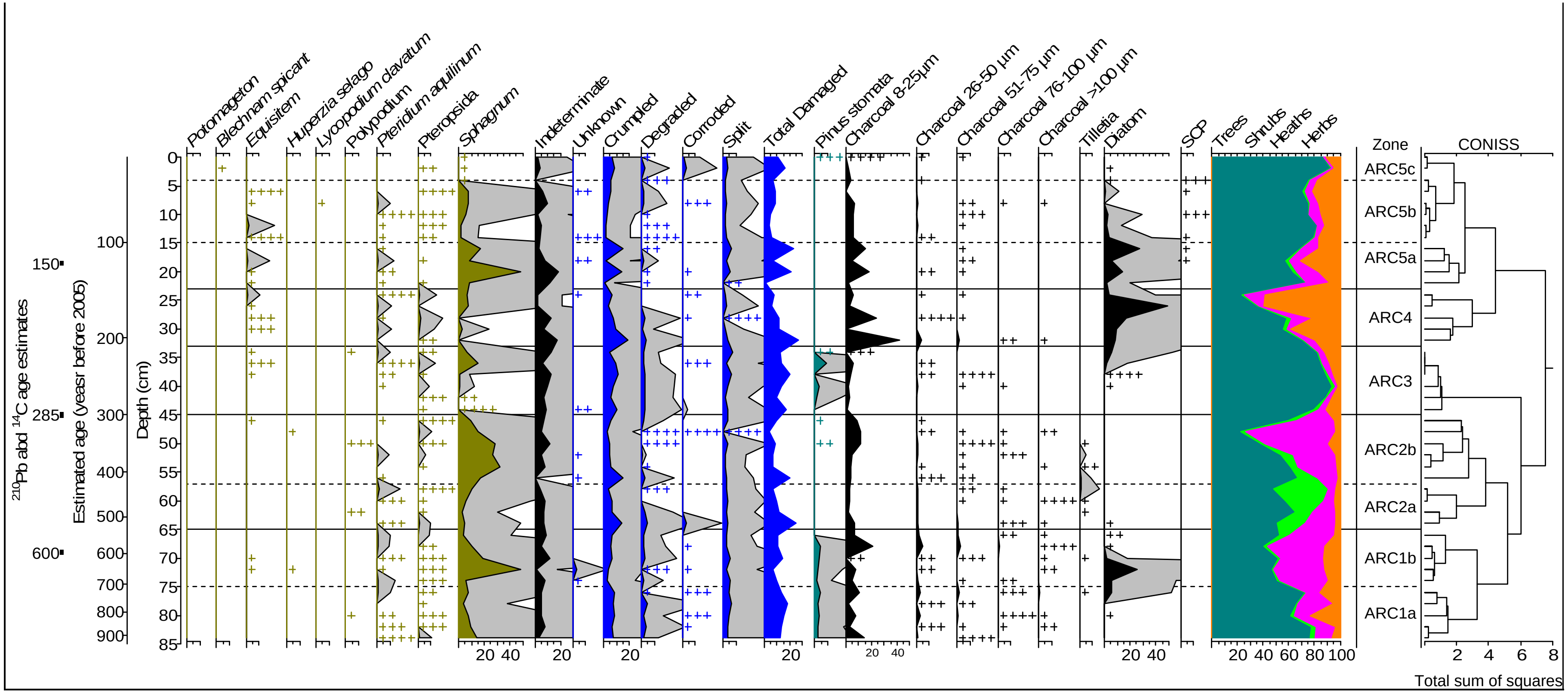

Figure A5.1: ARC pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

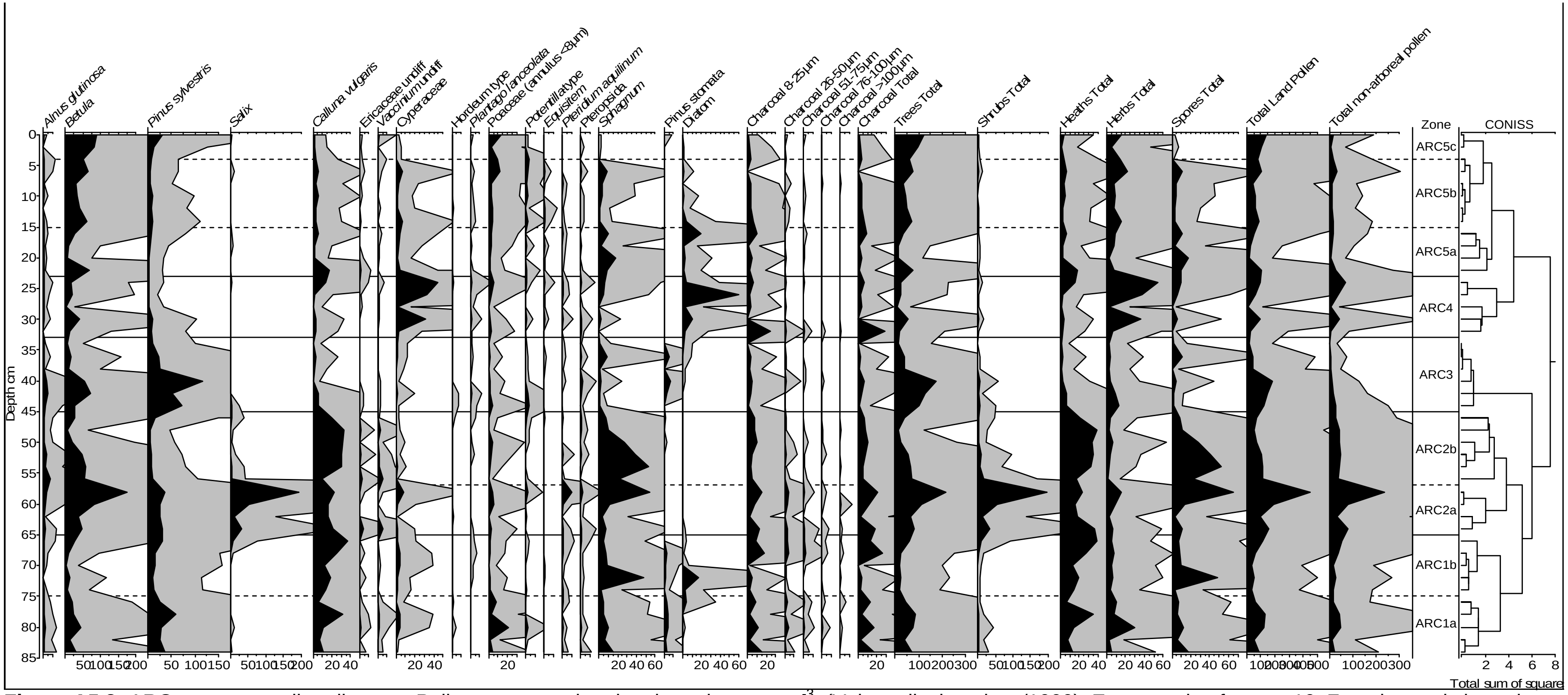

Figure A5.2: ARC summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A5.1

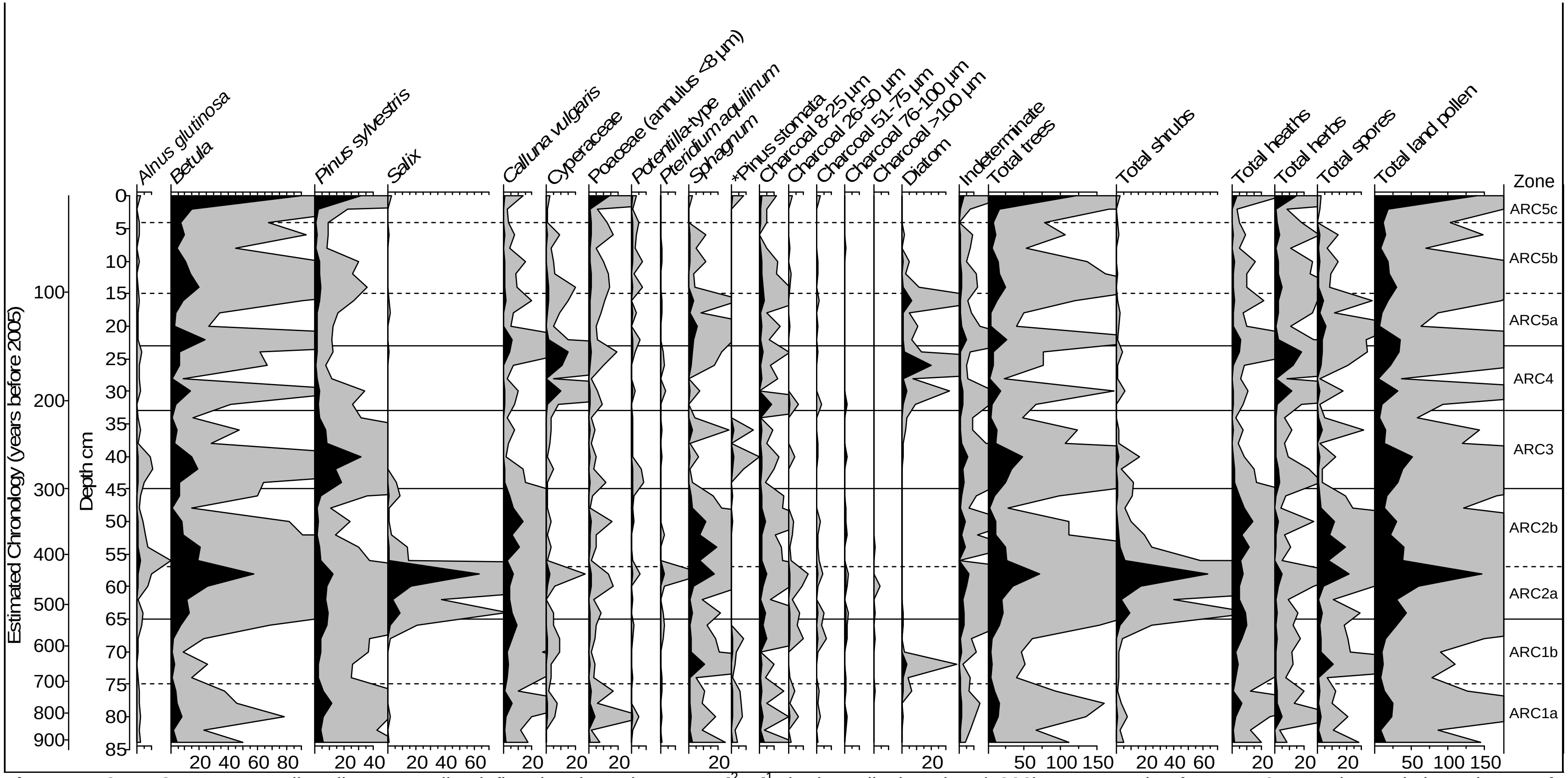

Figure A5.3: ARC summary pollen diagram. Pollen influx data in grains per cm^{-2} yr^{-1}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A5.1

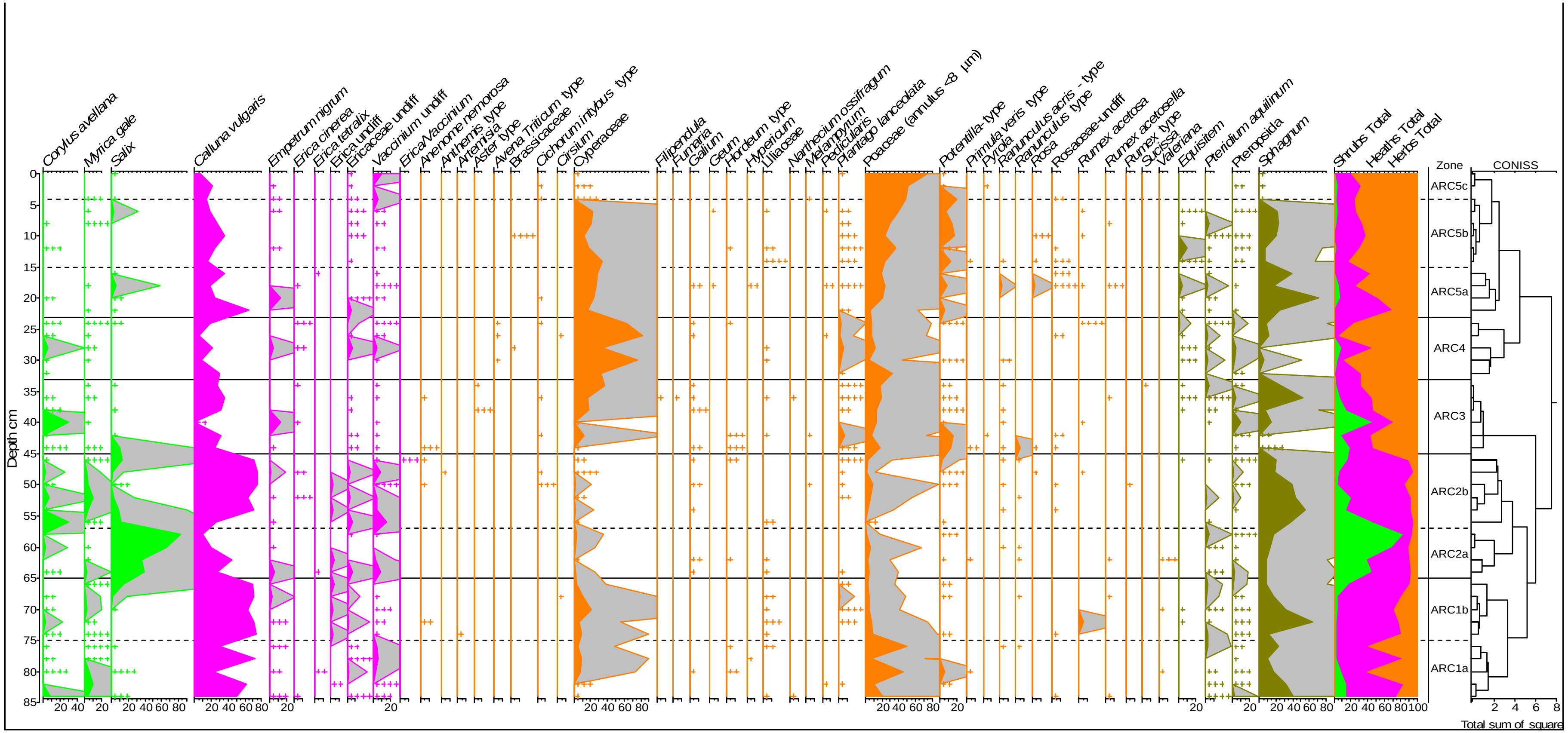

Figure A5.4: ARC non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Exaggeration factor x 10. Zonation and chronology as for Figure A5.1

11 Pollen Diagrams CLH core

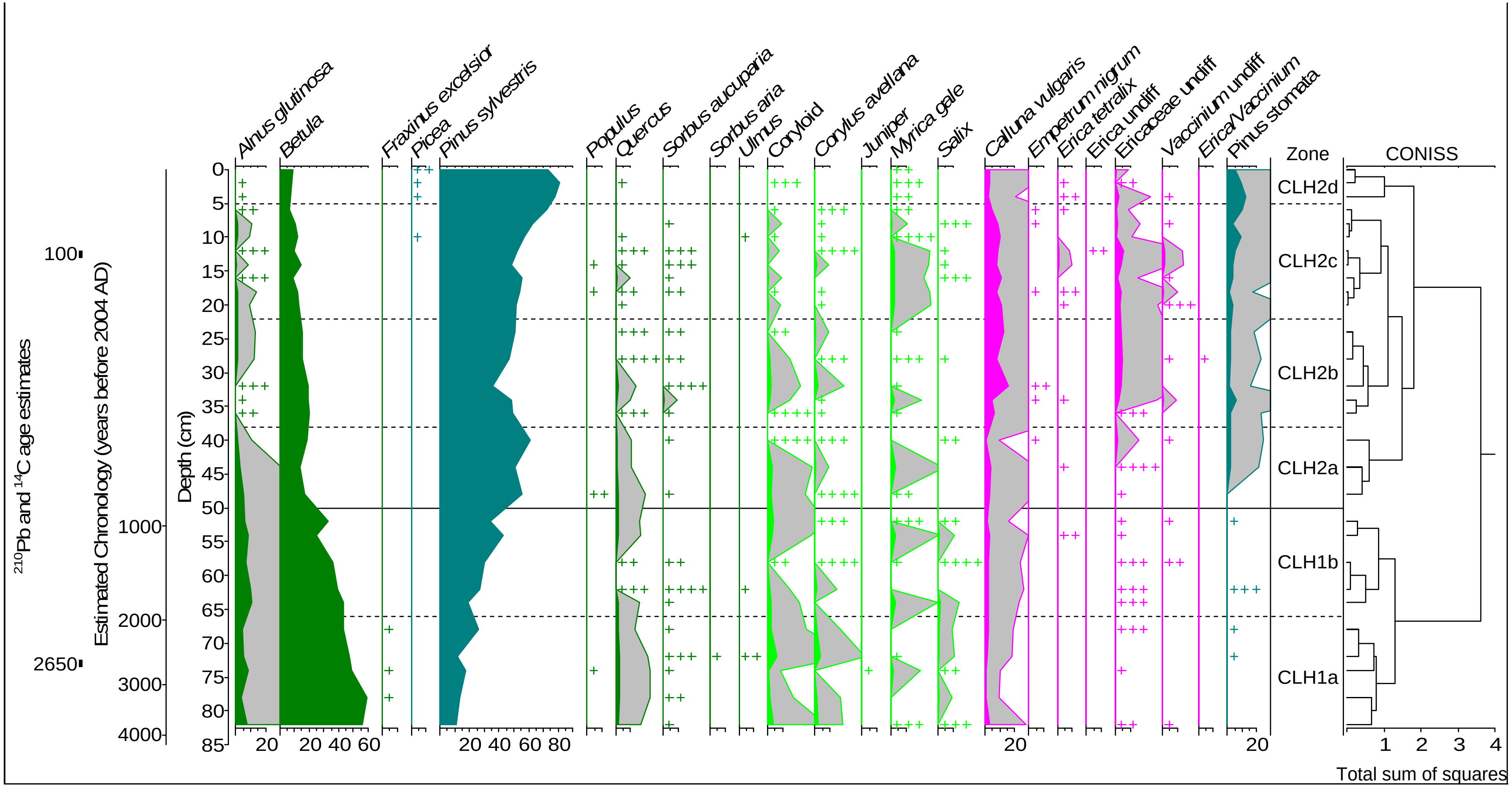

Figure A6.1: CLH pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

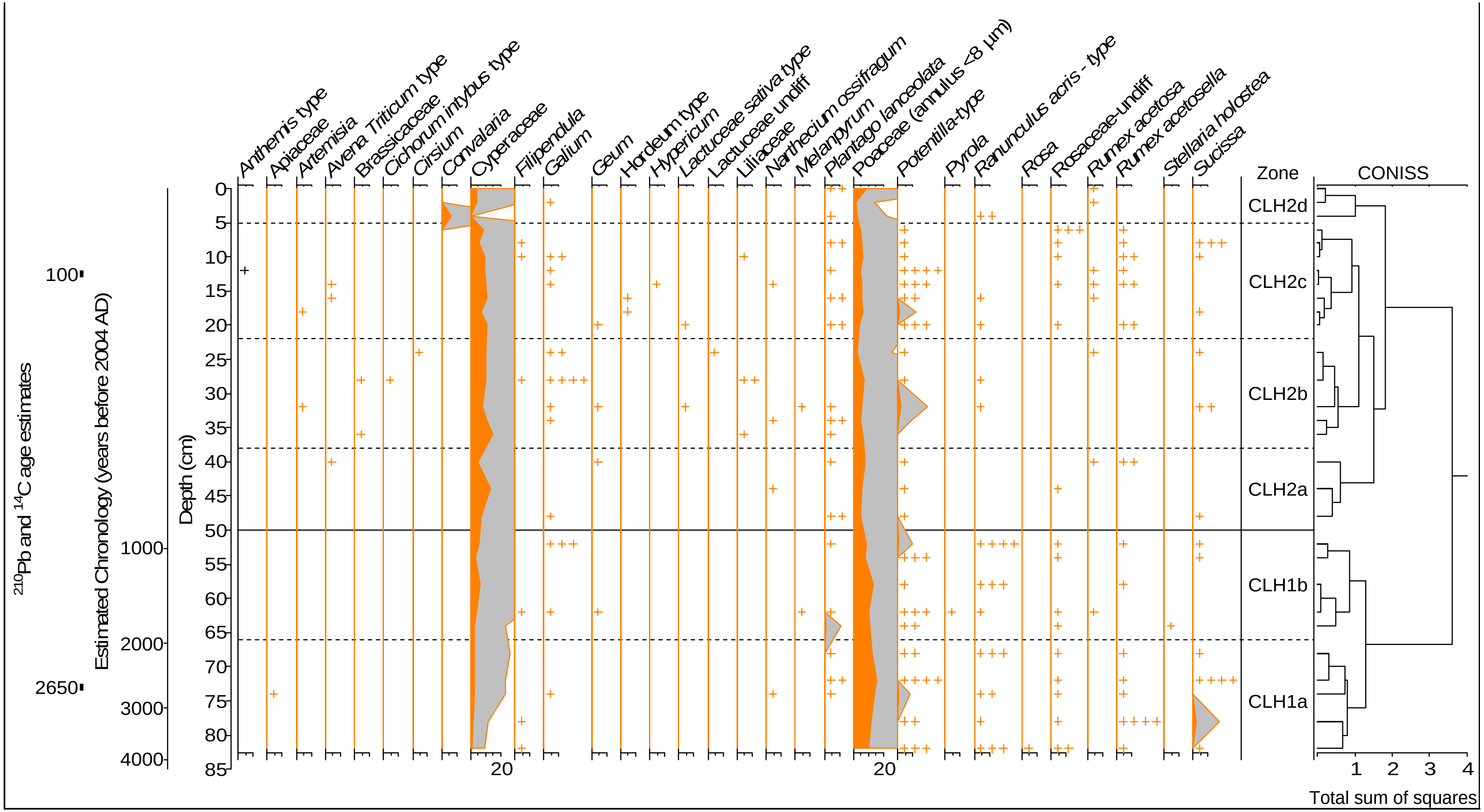

Figure A6.1: CLH pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

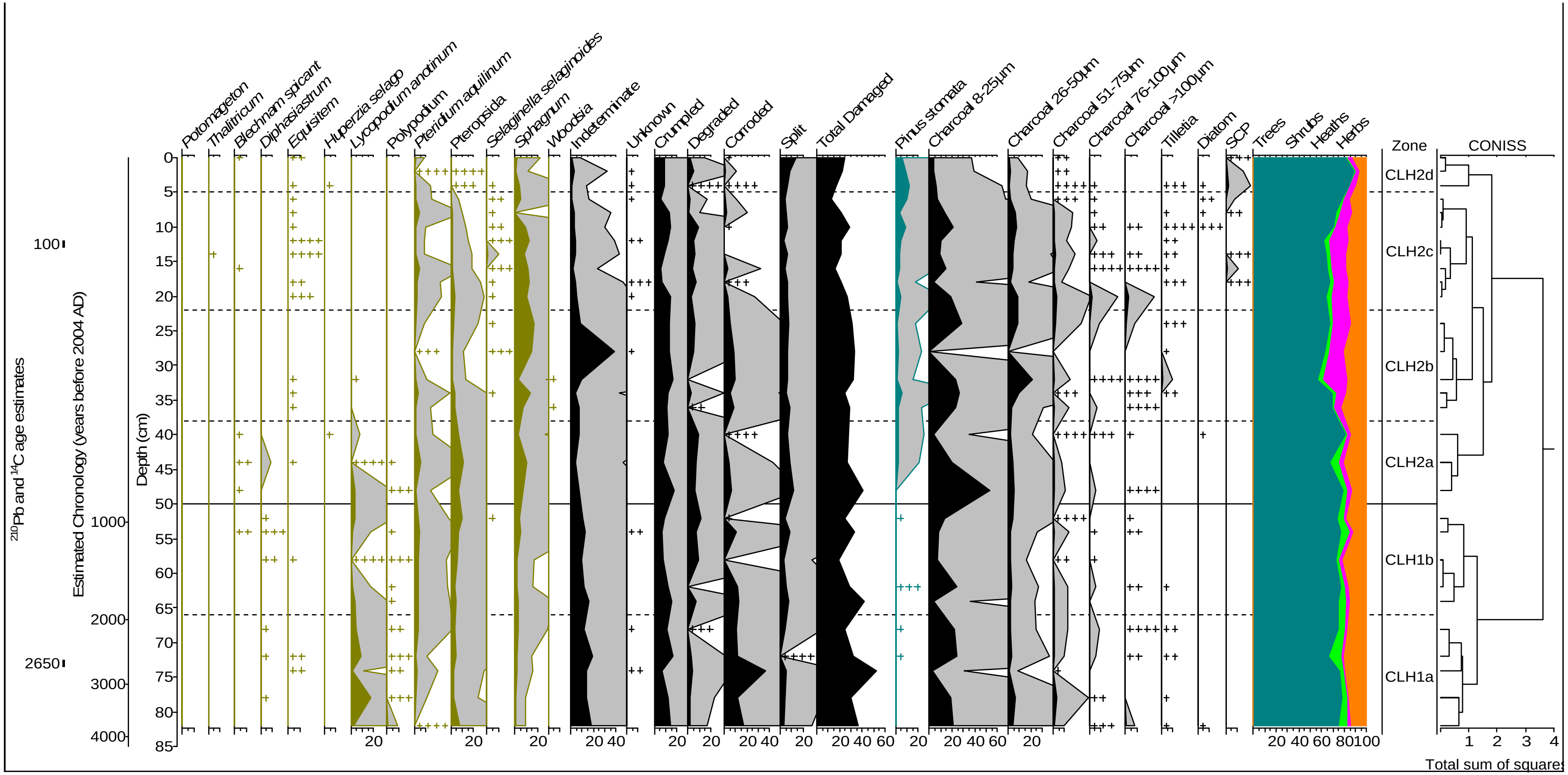

Figure A6.1: CLH pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

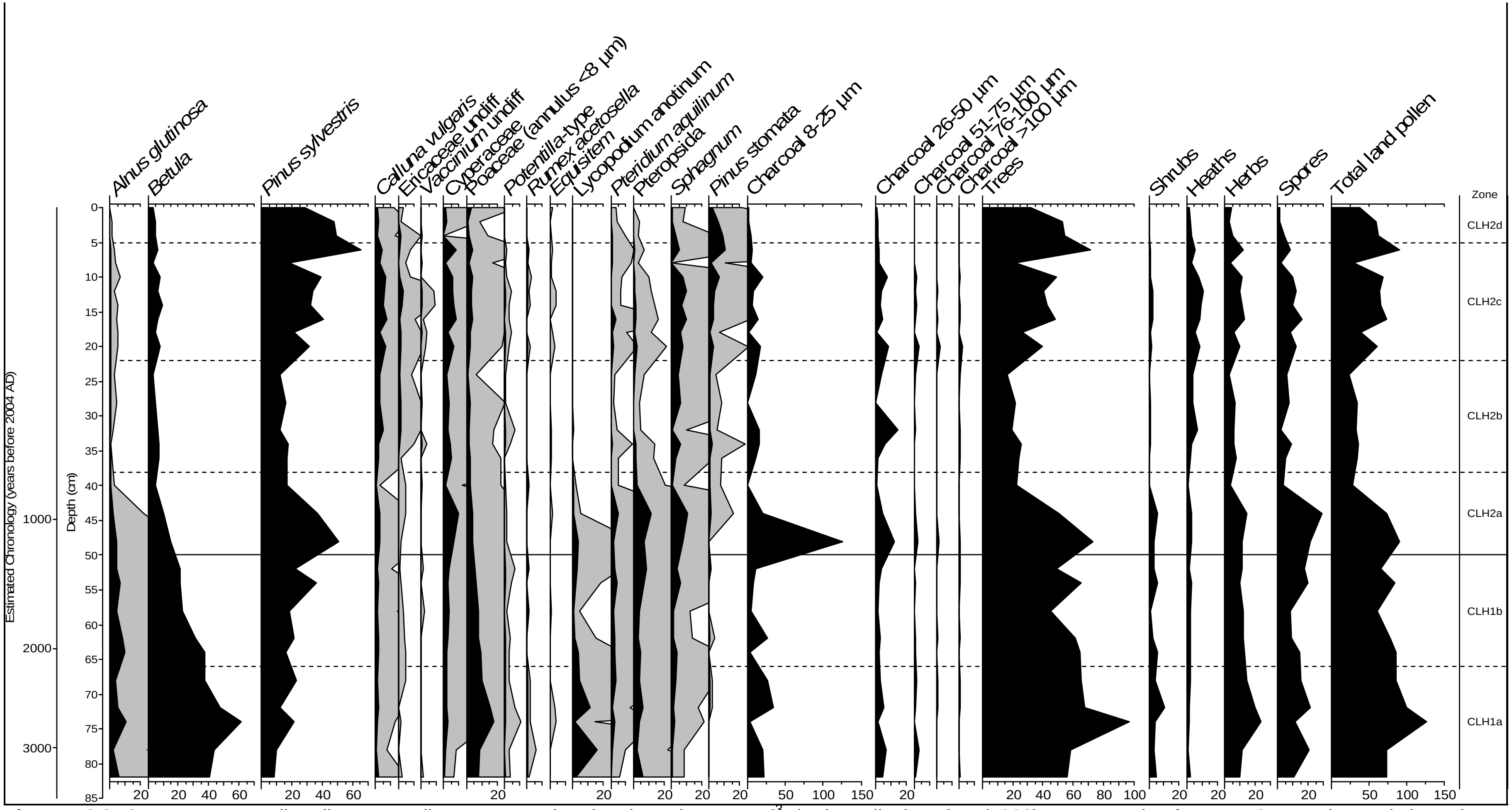

Figure A6.2: CLH summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A6.1

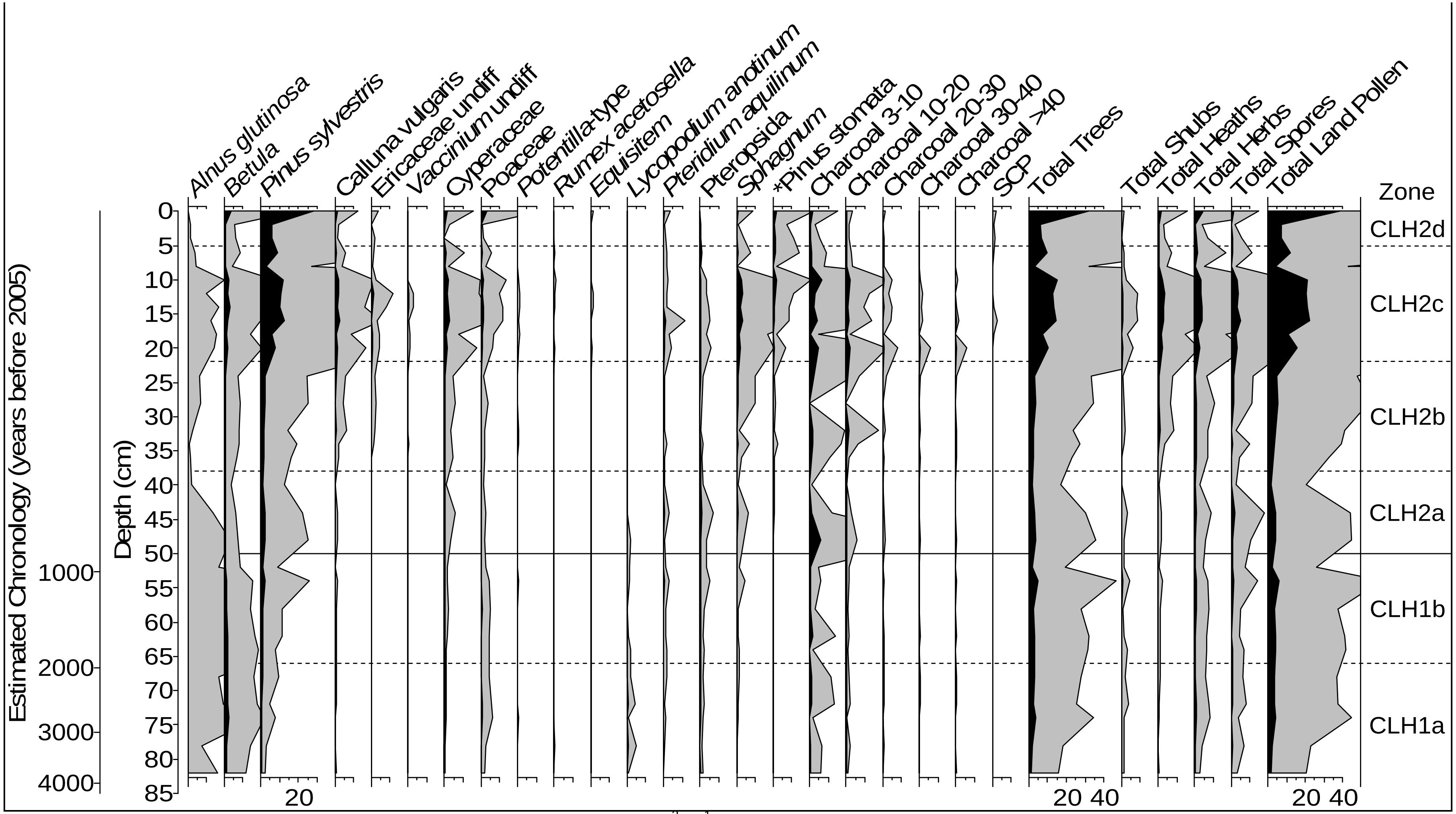

Figure A6.3: CLH summary pollen diagram. Pollen influx data in grains per cm^{-2} yr^{-1}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A6.1

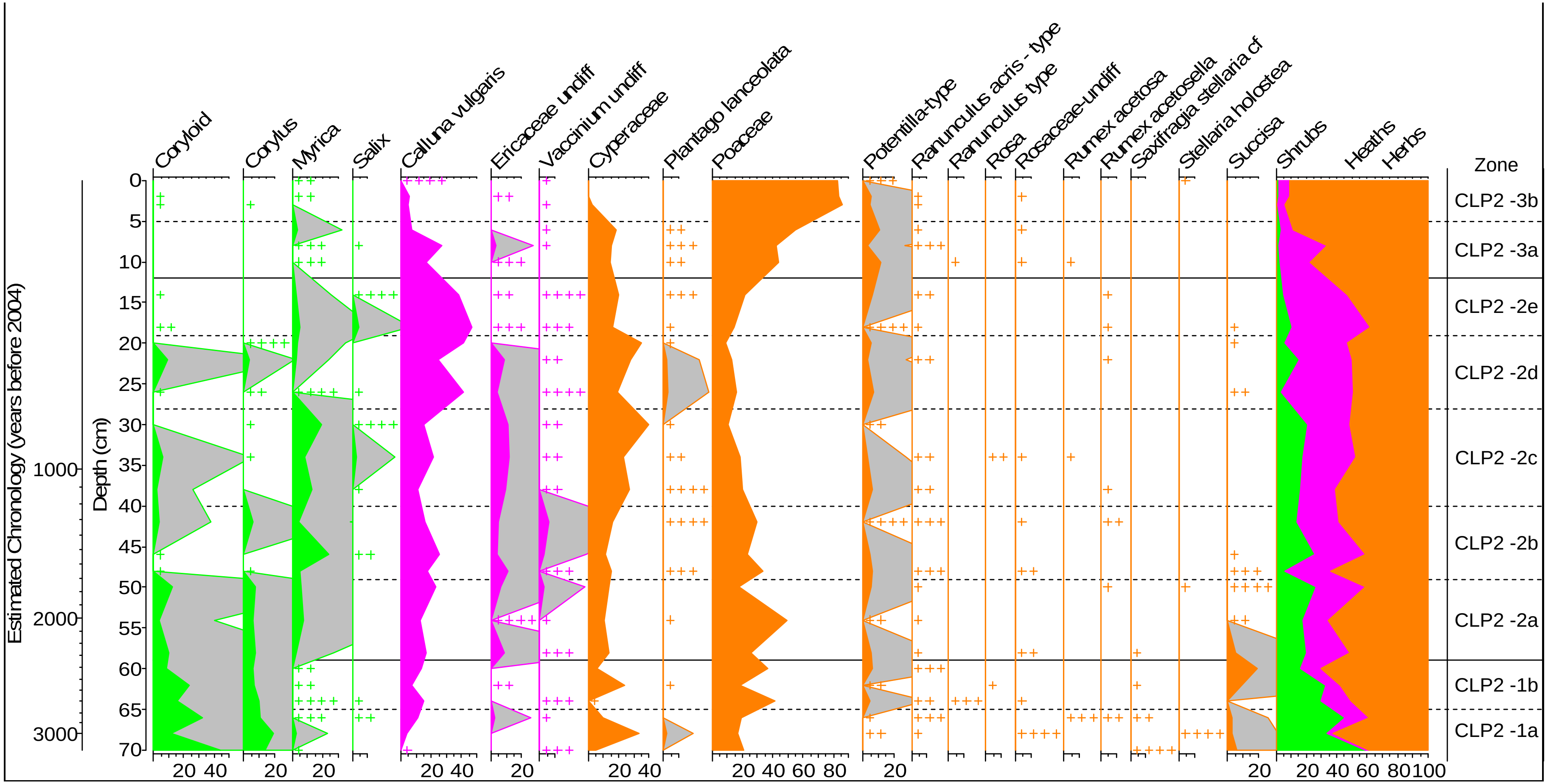

Figure A6.4: CLH non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Zonation and chronology as for Figure A6.1

12 Pollen Diagrams CLP2 core

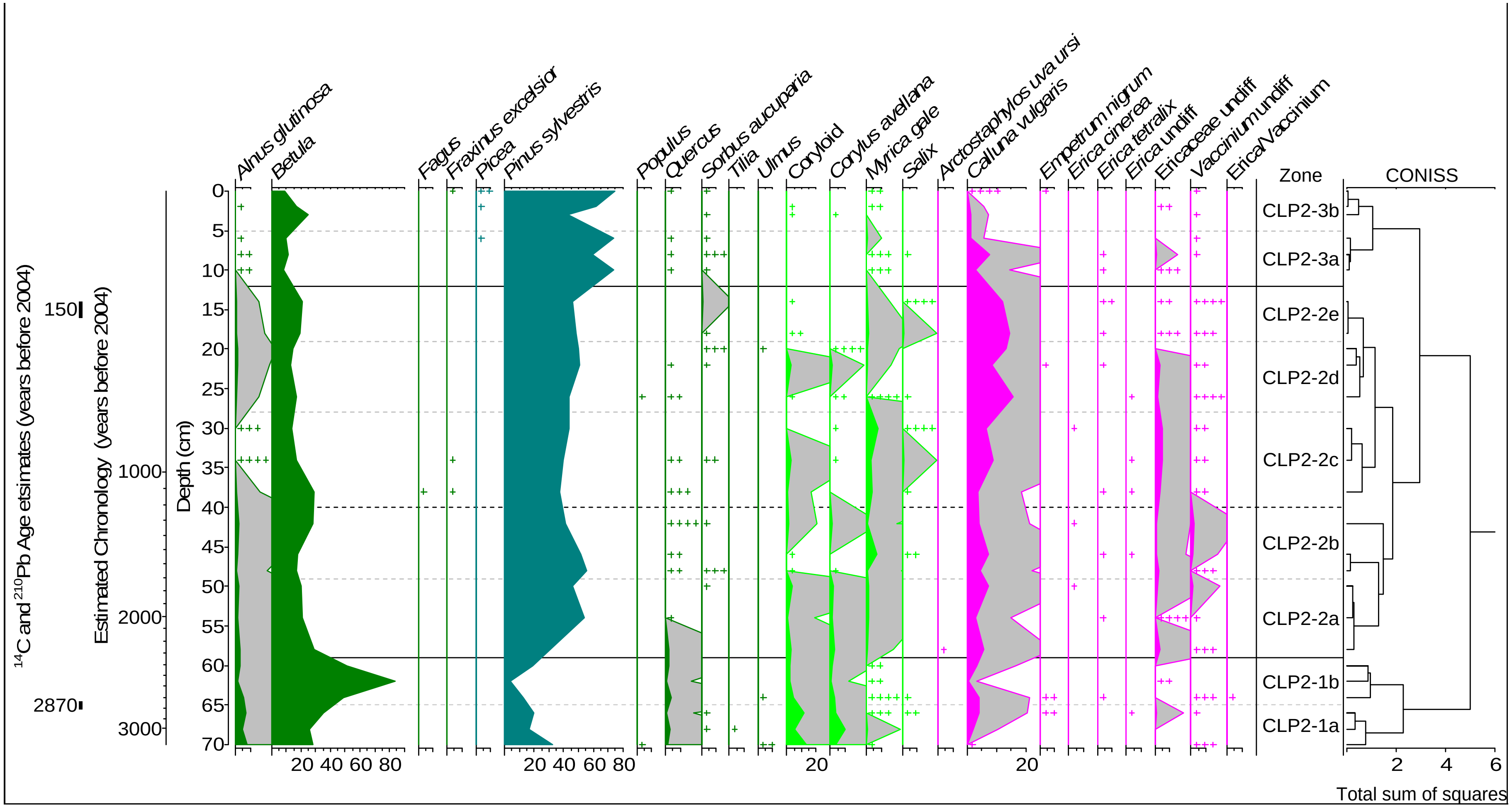

Figure A7.1: CLP2 pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

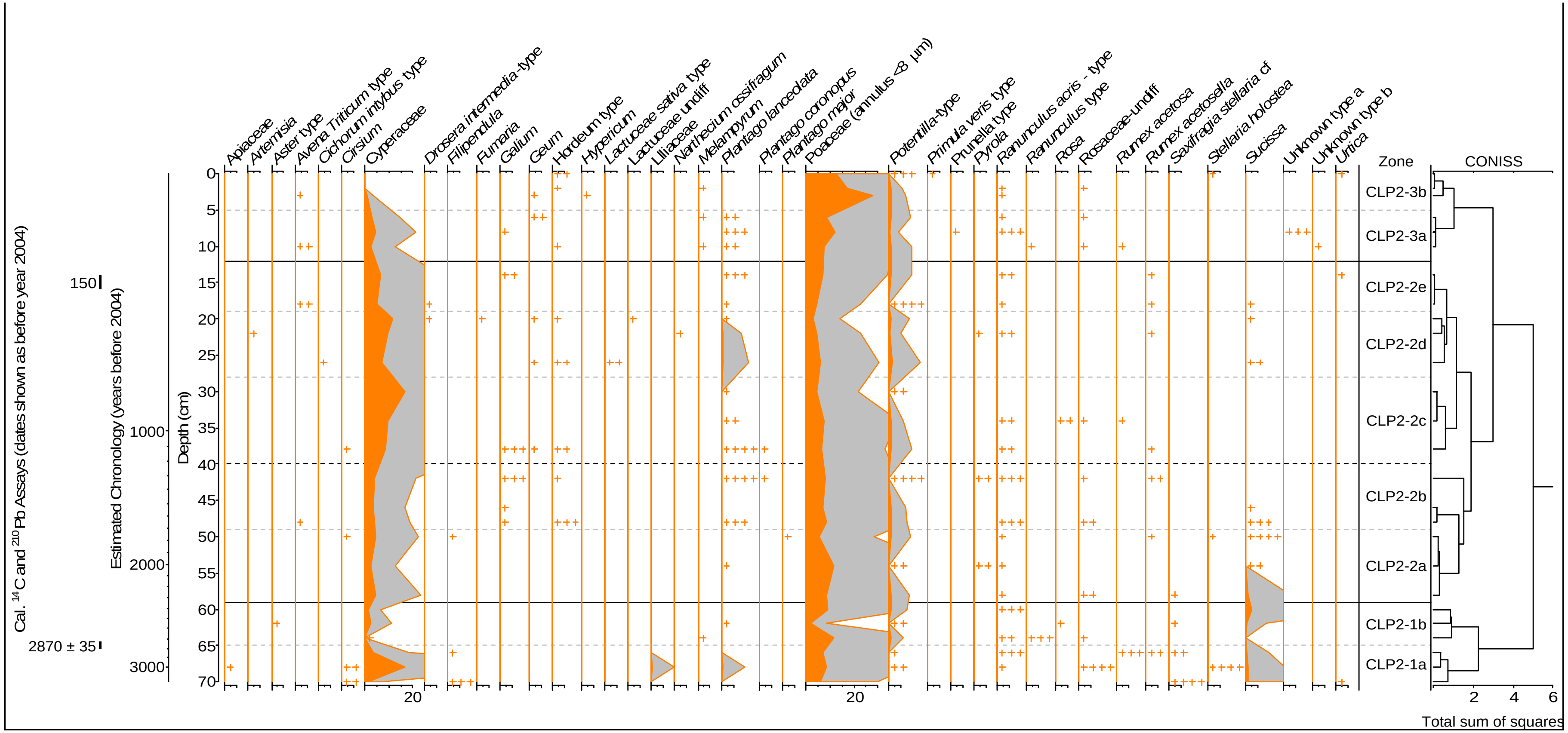

Figure A7.1: CLP2 pollen diagram: **b)** Cyperales and herbaceous taxa Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

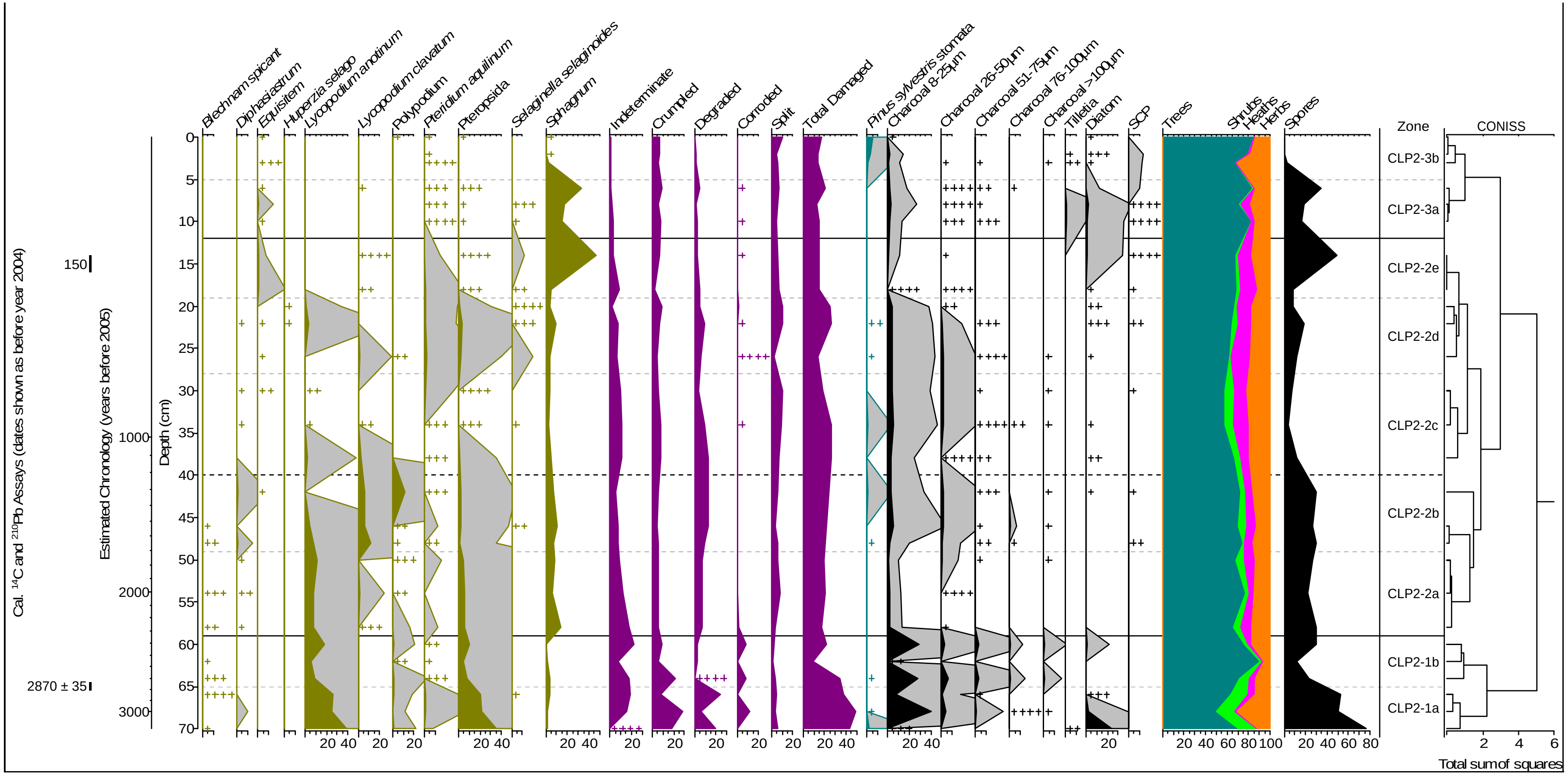

Figure A7.1: CLP2 pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

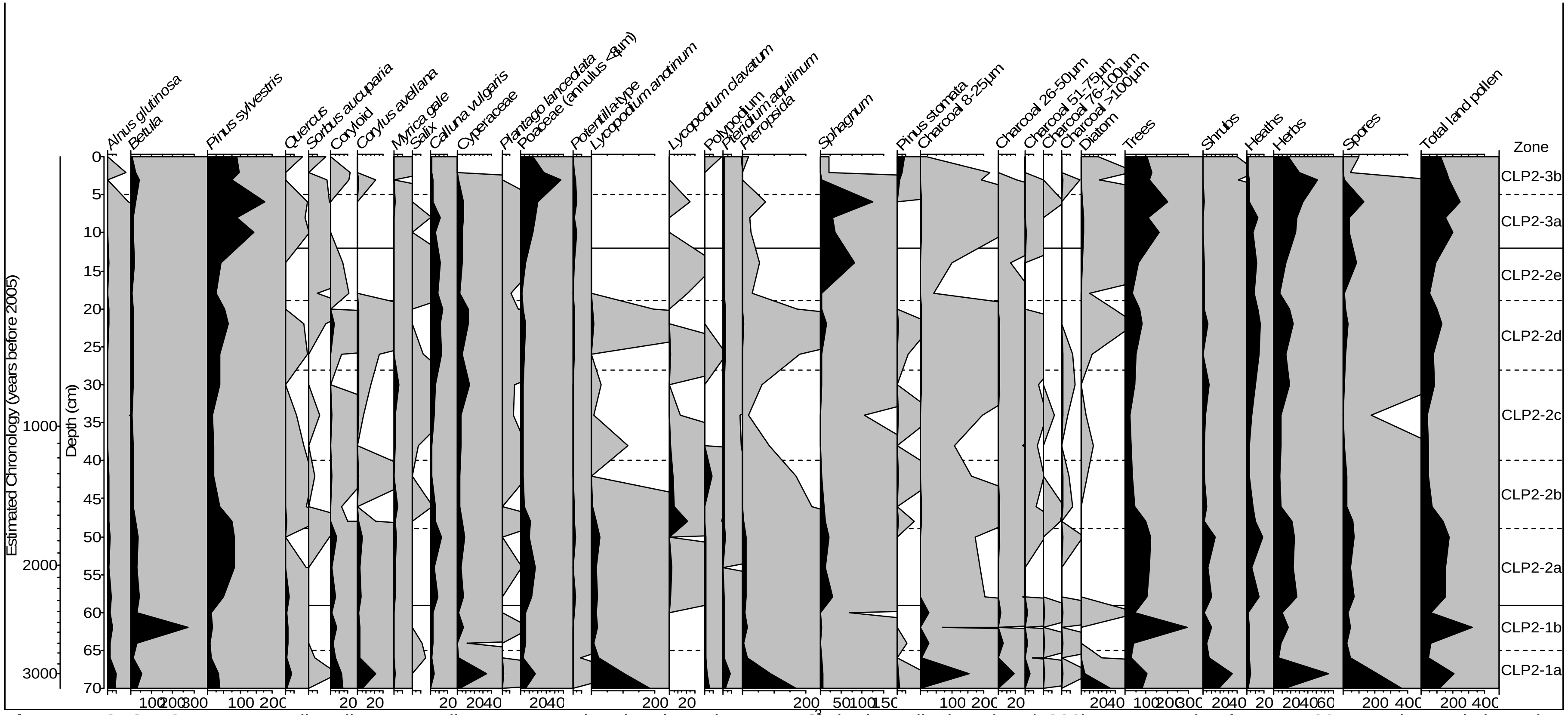

Figure A7.2: CLP2 summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 100. Zonation and chronology as for Figure A7.1

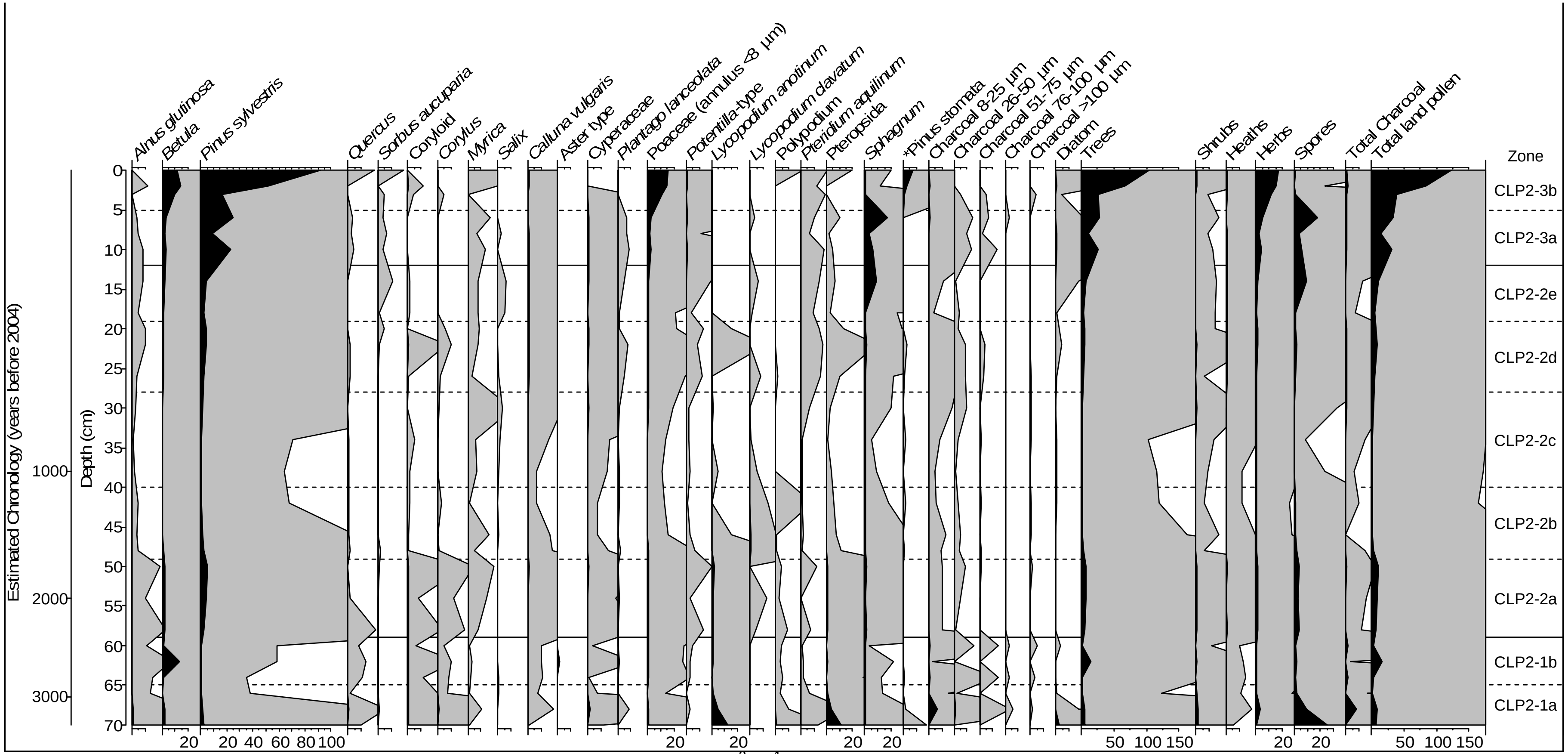

Figure A7.3: CLP2 summary pollen diagram. Pollen influx data in grains per cm^{-2} yr^{-1} (Values displayed as /1000). Exaggeration factor x 100. Zonation and chronology as for Figure A7.1

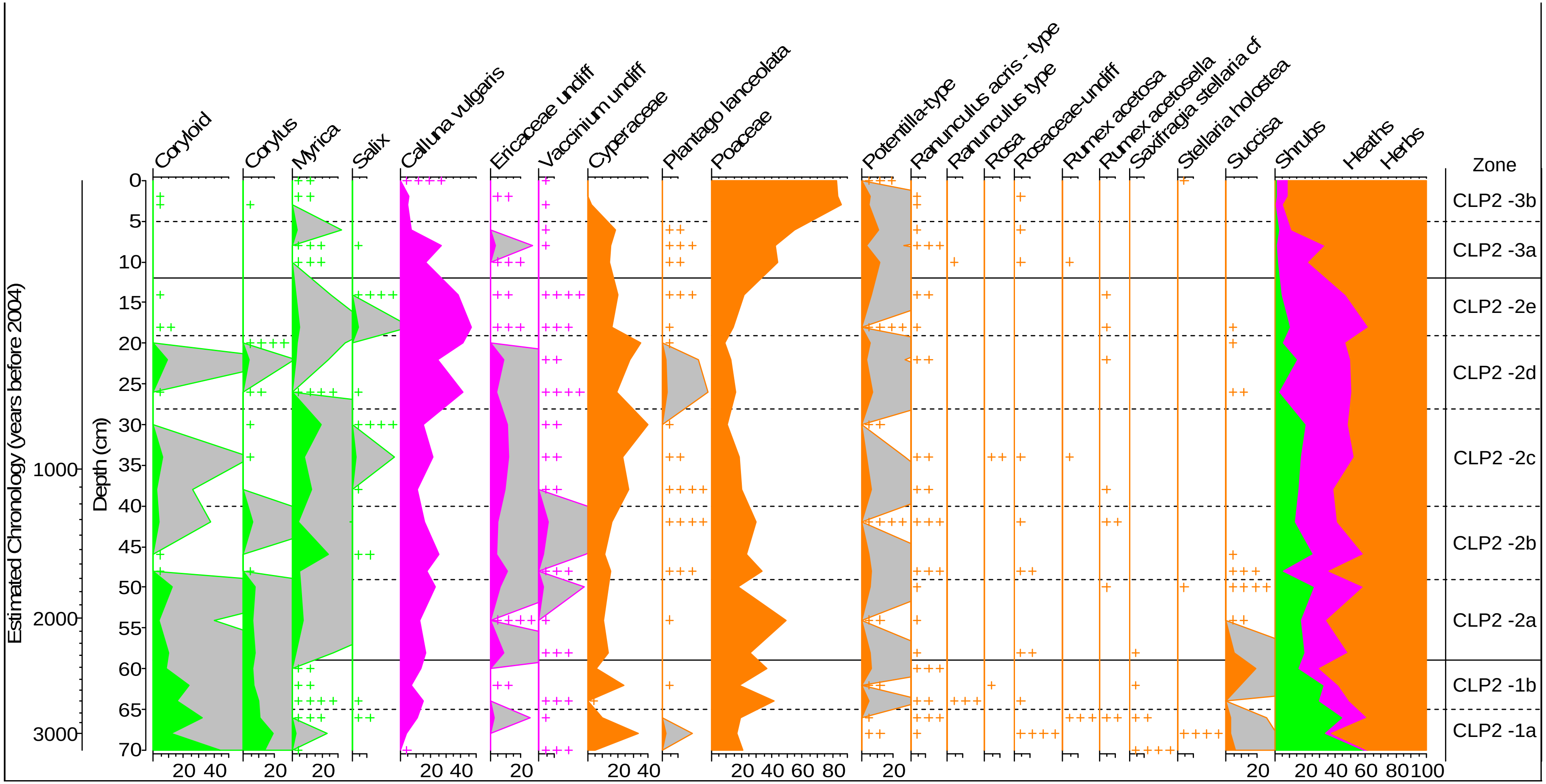

Figure A7.4: CLP2 non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Zonation and chronology as for Figure A7.1

13 Pollen Diagrams CLKH core

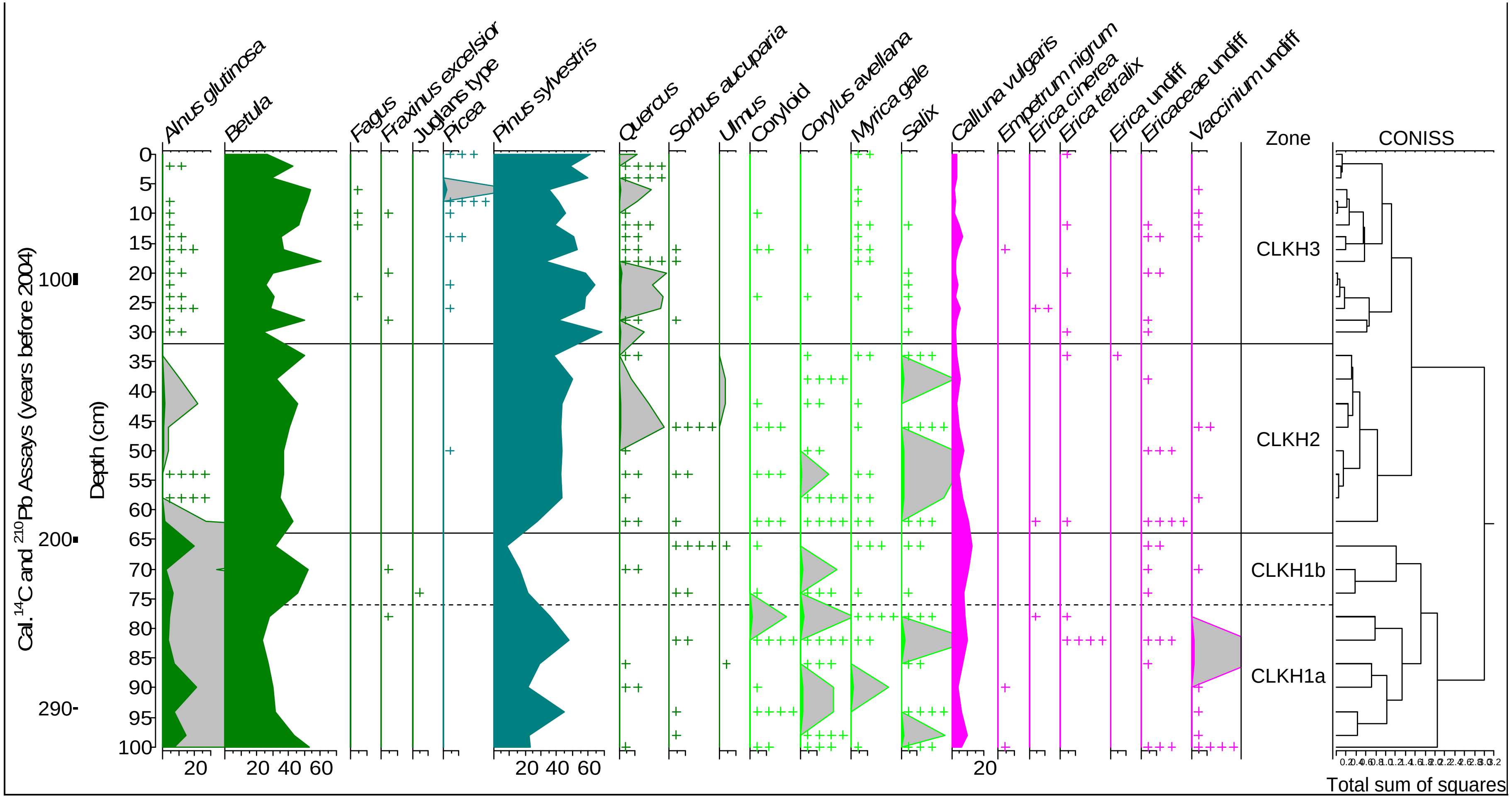

Figure A8.1: CLKH pollen diagram: **a)** Trees shrubs and heaths. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

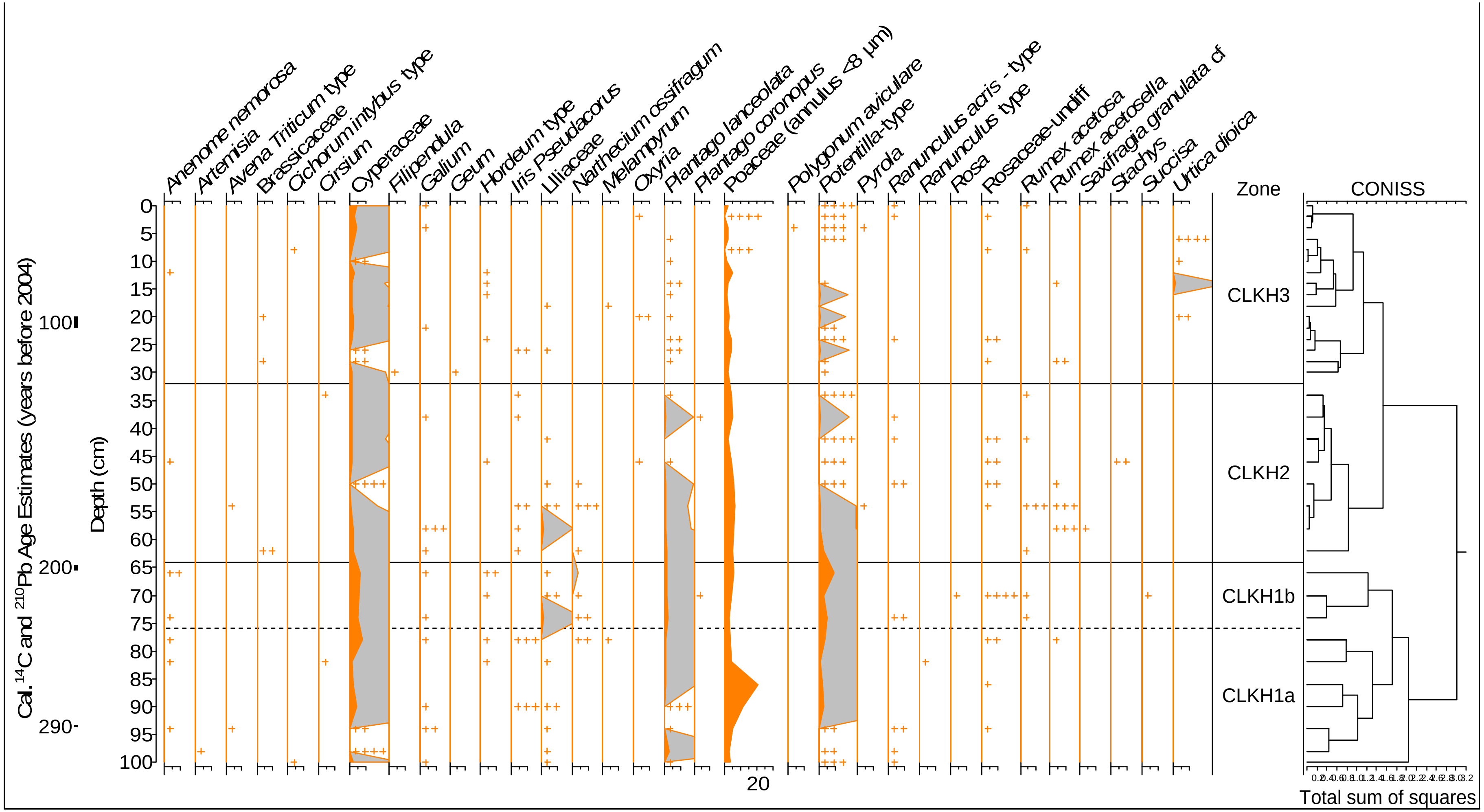

Figure A8.1: CLKH pollen diagram: **b)** Cyperales and herbaceous taxa. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

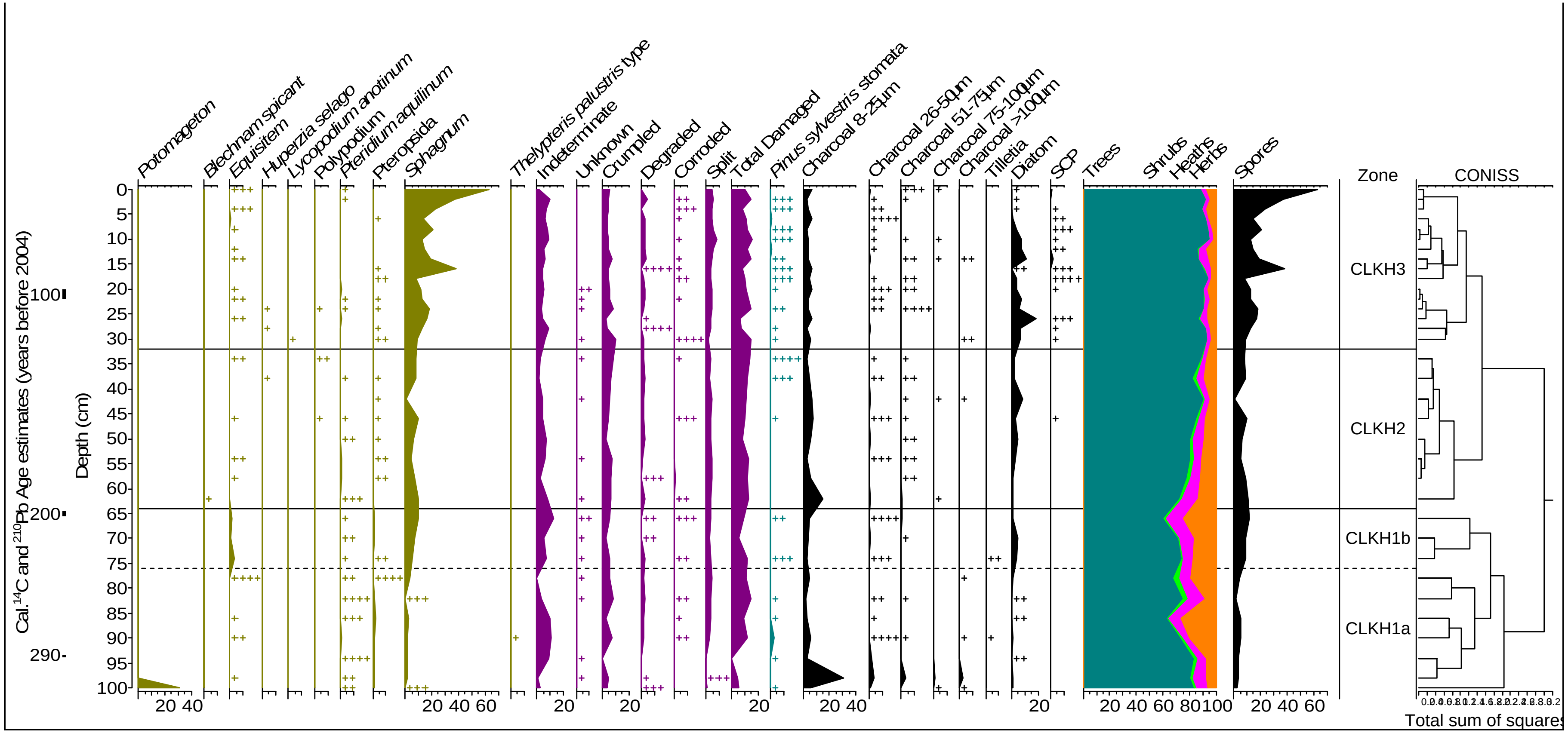

Figure A8.1: CLKH pollen diagram: **c)** Spores, other palynomorphs and group totals. Land pollen is expressed as a percentage of TLP. Spores and other groups of palynomorphs are expressed as a percentage of TLP plus the group. Shaded curves are x 10 exaggerations. Grain counts of taxa <1% are expressed as + symbols. The dendrogram to the right represents a sum of squares analysis implemented by CONISS (Grimm, 1987), used to define vegetation zones. The basal date from the ^{210}Pb Chronology and the midpoint of the calibrated ^{14}C dates are shown to the far left and adjacent to this is the age estimate chronology from the accepted chronological model (Chapter 4).

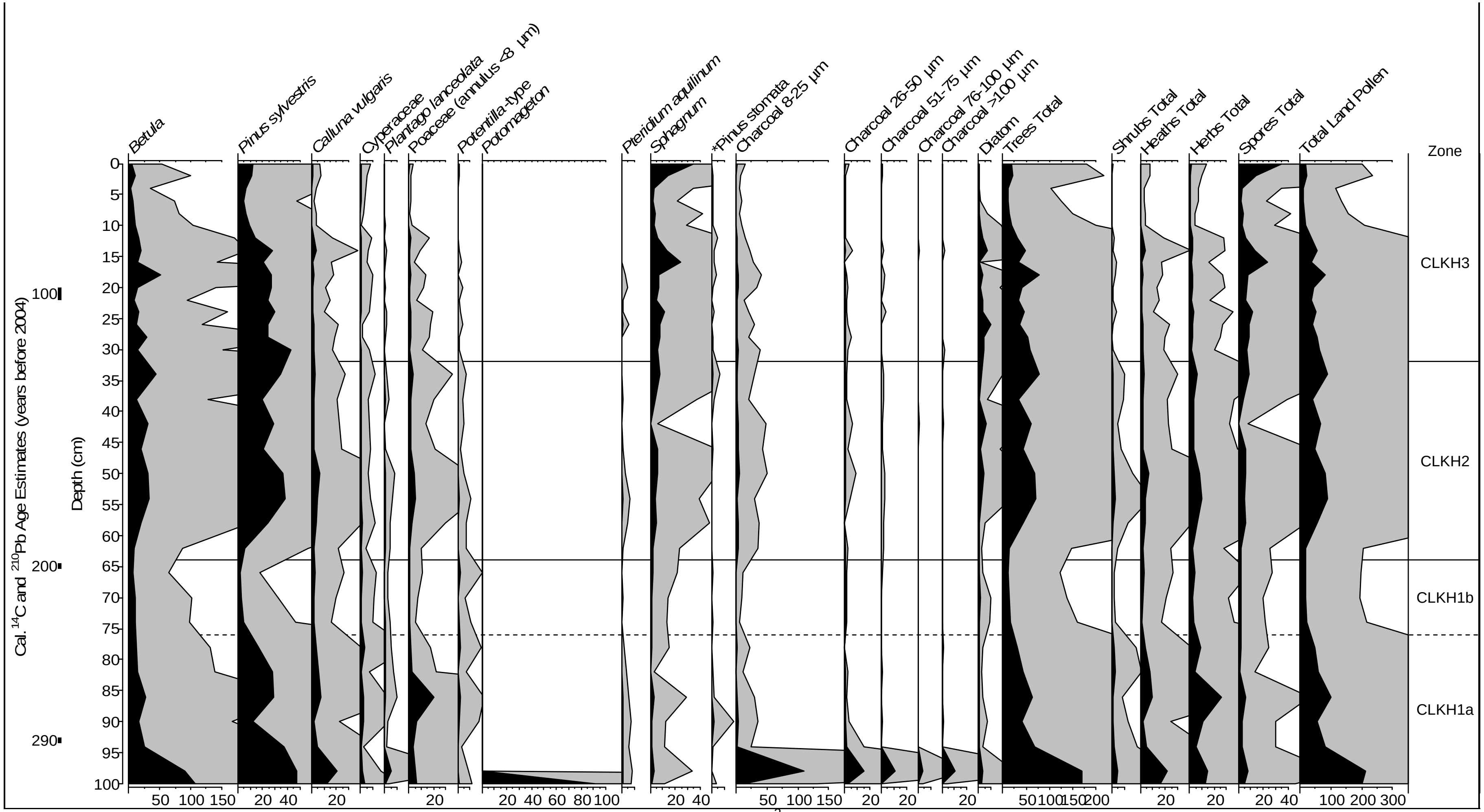

Figure A8.2: CLKH summary pollen diagram. Pollen concentration data in grains per cm^{-3}. (Values displayed as /1000). Exaggeration factor x 10. Zonation and chronology as for Figure A8.1

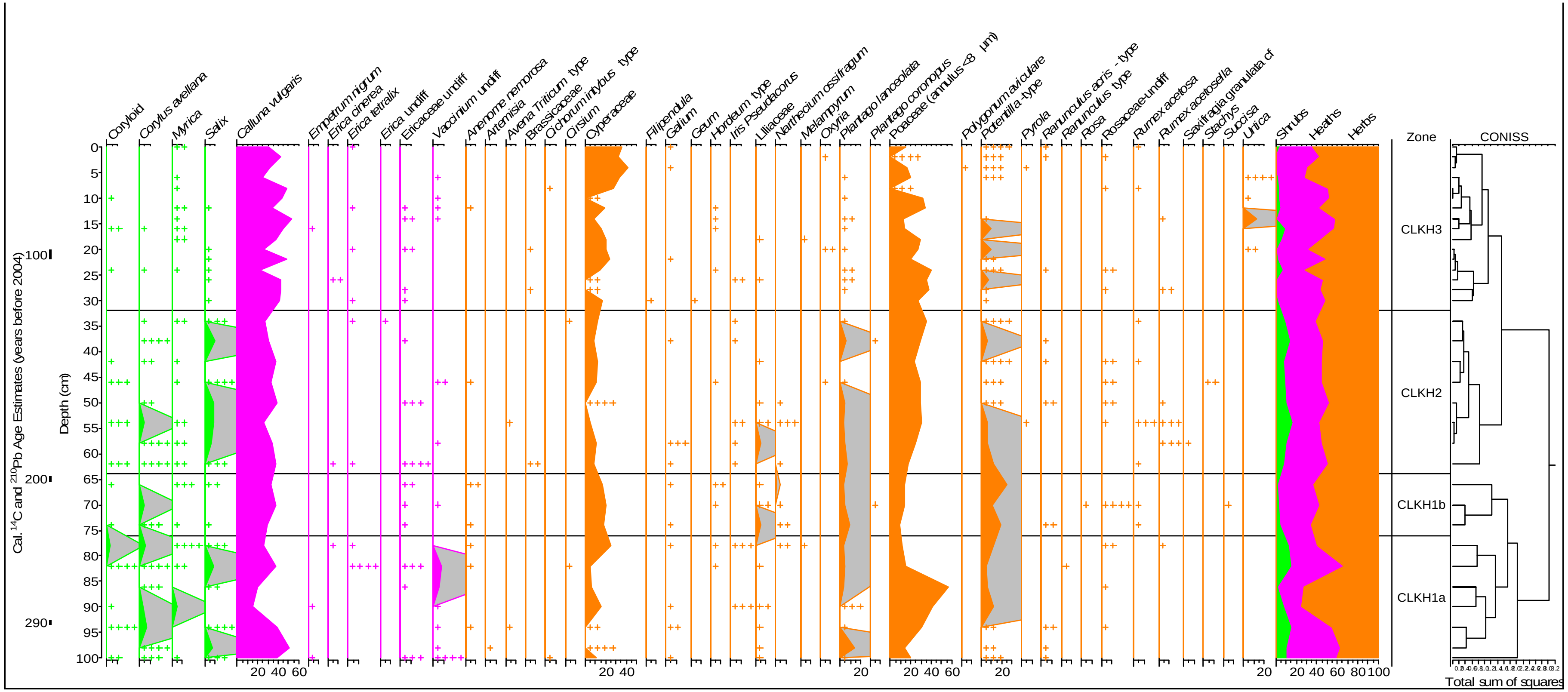

Figure A8.3: CLKH non arboreal summary pollen diagram. Pollen taxa displayed as a percentage of NAP. Zonation and chronology as for Figure A8.1